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The phylogeny of the species of the genus *Agelaia* Lepeletier, 1836, one of the basalmost groups of Epiponini, with notes on male genitalia (Hymenoptera: Vespidae; Polistinae)

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ABSTRACT

A cladistic analysis of the species of the Neotropical social wasp genus *Agelaia* Lepeletier, 1836, was performed employing female morphology and nest architecture data. Analysis resulted in a single cladogram with length 339, consistency index 0.22, and retention index 0.60, supporting *Agelaia* as monophyletic. *Agelaia bequaerti* and *A. anceps* are raised to specific rank. Male genitalia of *A. angulata*, *A. areata*, *A. cajennensis*, *A. centralis*, *A. flavipennis*, *A. fulvofasciata*, *A. multipicta*, *A. ornata*, *A. pallipes*, *A. panamaenis*, *A. testacea*, *A. timida*, *A. vicina*, and *A. yepocapa* are depicted and described, including comparative remarks. A revised identification key is provided.

INTRODUCTION

The genus *Agelaia* Lepeletier, 1836 (= *Stelopolybia* Ducke, 1910), is a representative of the swarming genera of Polistinae, with essentially Neotropical distribution (from Mexico to

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northern Argentina: Richards, 1978; Silveira and Carpenter, 1996; Cooper, 2000, 2001), and it is a conspicuous part of the social wasp fauna in much of tropical America (Jeanne, 1991).

Hitherto, the genus had 31 extant species and one fossil species, *Agelaia electra*, recorded from Dominican amber (Carpenter and Grimaldi, 1997). Species are quite variable in size, features, nest architecture, and in number of individuals as well, with some species reaching colony sizes of millions of adults, e.g., *Agelaia vicina* (Zucchi et al., 1995).

Nests of *Agelaia* are built in cavities, subterranean or arboreal; the pedicels are multiple, fibrous, cell marginal, vertical or horizontal from cavity walls, sometimes with sessile initiation (Wenzel, 1998). The combs grow gradually at margins, may be suspended from each other, fusing, double sided, planar, conical, or spiraling outward (Wenzel, 1998). Cavity nesting species may lack an envelope or sometimes have a reduced envelope restricting access to cavity; exposed arboreal nests may have single or multiple ball-shaped envelopes supported by combs within or by pedicels arising from combs, which are not removed but rather built over as the nest expands in all directions (Wenzel, 1998). The species *A. timida* and *A. baezae* construct a true envelope, while *A. areata* and *A. flavipennis* build an exposed nest of a single spiral comb with the cells on the inside, so that the outermost part of the comb functions as an envelope (Jeanne, 1973; Cooper, 2000).

There is a clear dimorphism between queens and workers (Cooper, 2000). In general, compared with workers, queens of *Agelaia* are usually larger, the dorsal pronotal carina, when developed, is blunter; the valvula shorter and with a narrower, hyaline border and tergum I wider (Richards, 1978; Noll et al., 1997; Cooper, 2000).

The taxonomic history of *Agelaia* has been troublesome. A brief review is given below.

Taxonomic History

Agelaia was proposed by Lepeletier in 1836, however, the taxon was not recognized until recently. De Saussure (1854) placed *Agelaia fuscicornis* (type by monotypy of the genus) in *Polybia* as a species dubiae. Dalla Torre (1894) synonymized *Agelaia* with *Polybia*, thus agreeing with de Saussure, and in 1904, he used the name *Aglaia*, a misspelling of *Agelaia*. On the other hand, in 1944, Bequaert disagreed with DallaTorre (1894) and suggested that *Agelaia* was a *Polistes*.

Ducke (1910) proposed *Stelopolybia*, without indicating the type, for 13 species previously included in *Polybia*, which presented a mesepisternal groove and the stelocyttarus nest, with or without an envelope. Lucas (1912), reviewing works on Hymenoptera, realized that Ducke had not designed a type for *Stelopolybia*. Therefore, he designated *Stelopolybia angulata* (Fabricius 1804) (= *Polistes angulata*) as the type. Ducke (1914), ignoring the designation of Lucas (1912), proposed the genus *Gymnopolybia* for those species of *Stelopolybia* without a nest envelope, and, again, did not designate a type. Richards (1943)[4] designated *Polybia vulgaris* Ducke, 1904 (= *Vespa fulvofasciata* DeGeer, 1773), as the type of *Gymnopolybia* and *Polybia infernalis* Saussure, 1854 (= *Rhopalidia pallens* Lepeletier, 1836), as the type of *Stelopolybia*.

[4] In Araujo (1946: 165) the date of this work is given erroneously as Richards (1938), clearly a typographical error. The correct is Richards (1943).

Richards' (1943) designation of *S. fulvofasciata* as type of *Gymnopolybia* renders it a synonym of *Stelopolybia* Ducke, 1910. Thus, the species of *Stelopolybia* in the sense of Ducke (1914) were unnamed. To complicate this matter further, Bequaert (1944) did not propose a new name for these species. Araujo (1946) then created the genus *Angiopolybia* for the species that were placed in *Stelopolybia* in the sense of Ducke (1914).

Richards (1978) accepted the taxon *Angiopolybia* Araujo and used *Stelopolybia* for those species without an envelope covering their nests. Richards (1978) also described five new species of *Stelopolybia*. Carpenter and Day (1988) studied the problem of the identity of *Agelaia* and concluded that *Agelaia* Lepeletier, 1836, is a senior synonym of *Stelopolybia* Ducke, 1910. Silveira and Carpenter (1996) and Cooper (2000, 2001) described eight more species of *Agelaia*.

Systematic Placement

The phylogenetic position of *Agelaia* has been unstable in published analyses in recent years. Carpenter (1991), who proposed the first phylogenetic analysis of Polistinae based on adult morphology, placed *Agelaia* in a polytomy with *Angiopolybia* and a clade consisting of most of the other genera of Epiponini. The analysis of Wenzel (1993), employing nest characters, placed *Parachartergus* and *Pseudopolybia* in a polytomy together with *Agelaia* and *Angiopolybia* and a clade consisting of most of the other genera of Epiponini. A combined analysis of adult morphology and nest architecture, including also larval characters, resulted in the publication of Wenzel and Carpenter (1994), a work in which most of the Polistinae genera were fully resolved. *Agelaia* was the sister group of *Angiopolybia*, a result that was expected (see taxonomic history above). In contrast, Noll et al. (2004), including morphometric measures of caste differentiation with the matrix of Wenzel and Carpenter (1994), found *Agelaia* as sister group of the nocturnal genus *Apoica*. Arévalo et al. (2004) using both molecular and morphological characters, found a similar result to that of Wenzel and Carpenter (1994), where *Agelaia* was the sister group of *Angiopolybia*. In Pickett and Carpenter (2010), where investigating the origin of sociality was the aim of the work, morphological, behavioral, and molecular data were employed, with the result being *Apoica* as the basalmost genus in the cladogram, followed by *Agelaia* as sister group of the remaining genera of Epiponini. Unfortunately, no species of *Angiopolyia* was included in in their analysis.

More recently, Piekarski et al. (2018) conducted a phylogenomic analysis to investigate the origin of eusociality in Vespidae and recovered *Angiopolybia* as the sister group to all remaining Epiponini, and *Agelaia* and *Apoica* as sister taxa. It was later confirmed by Menezes et al. (2020), who proposed a phylogenomic hypothesis for Epiponini based on Ultra Conserved Element (UCE) data, and by Noll et al. (2020), who used a total evidence analysis. The interpretation of *Angiopolybia* as the sister lineage of all remaining swarm-founding social wasps replaces the original thinking that *Agelaia* is somehow present in the lineage that diverged earlier in Epiponini history and changes the original thinking about some social behavioral features, like caste and nest construction (Noll et al., 2020).

TABLE 1. Character matrix for *Agelaia*. The following symbols are used: "?" = not seen; "*" = all states.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Apoica pallens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Angiopolybia obidensis	0	0	1	1	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	1	0	0	0
Angiopolybia pallens	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0
Angiopolybia paraensis	0	0	1	1	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	1	0	0	0
Angiopolybia zischai	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0
A. acreana	0	1	1	1	0	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	1	1	1
A. anceps	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A. angulata	0	0	0	0	1	0	0	1	1	0	0	0	1	1	1	1	1	0	0	1	0	0	0
A. angulicollis	0	0	0	1	1	0	0	1	1	0	0	0	0	1	1	0	1	0	0	1	0	0	0
A. areata	1	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
A. baezae	1	0	1	0	0	1	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0
A. bequaerti	1	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0
A. brevistigma	0	1	0	1	0	1	0	0	1	1	1	1	1	1	1	0	1	1	1	0	1	0	1
A. cajennensis	0	0	0	0	0	1	0	0	0	0	1	1	1	0	1	0	1	1	0	2	1	0	1
A. centralis	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	2	0	0	0
A. constructor	0	0	0	0	1	0	0	1	1	0	0	0	0	1	1	0	1	0	0	1	0	0	0
A. cornelliana	1	0	0	1	0	1	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0
A. flavipennis	1	0	0	1	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0
A. fulvofasciata	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0
A. hamiltoni	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	1	0	1	0
A. imitatrix	0	0	0	0	0	0	1	0	1	1	1	1	1	0	1	0	0	0	0	2	1	1	1
A. lobipleura	0	0	1	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	0	1
A. melanopyga	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A. multipicta	1	0	0	0	0	1	1	0	1	0	0	0	0	1	1	0	1	0	0	1	0	0	0
A. myrmecophyla	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
A. nebularum	1	0	0	0	0	1	1	0	1	0	0	0	1	1	0	1	1	0	0	0	0	0	0
A. nigrescens	1	0	1	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	1	2	0	1	0
A. ornata	0	0	0	0	1	0	0	1	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0
A. pallidiventris	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0
A. pallipes	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
A. panamaensis	0	0	0	1	1	0	0	1	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0
A. pleuralis	0	0	1	1	0	0	0	0	1	1	1	1	1	0	0	1	0	0	0	2	1	0	1
A. silvatica	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	2	0	0	0
A. testacea	0	0	0	0	1	0	0	1	1	0	0	0	1	1	1	0	1	0	0	1	0	0	0
A. timida	0	0	1	1	0	1	0	0	0	0	1	1	1	0	0	0	1	0	0	2	1	0	1
A. vicina	0	0	1	0	0	1	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0
A. xanthopus	1	0	0	0	0	1	0	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0
A. yepocapa	1	0	1	0	0	1	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0

TABLE 1 *continued*

	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
Apoica pallens	0	0	0	1	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Angiopolybia obidensis	1	1	0	0	1	1	1	0	0	1	0	0	1	0	1	0	1	0	0	1	1	0	0
Angiopolybia pallens	0	1	1	0	1	1	1	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0	0
Angiopolybia paraensis	1	0	1	0	1	1	1	0	0	1	0	0	1	0	1	0	1	0	0	1	1	0	0
Angiopolybia zischai	0	0	1	0	0	1	1	0	0	1	0	0	1	0	1	0	1	0	0	1	1	0	0
A. acreana	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	2	1	0
A. anceps	0	0	0	2	1	0	1	0	0	1	1	0	0	0	0	0	0	2	1	0	0	0	0
A. angulata	1	0	0	2	1	0	0	0	2	0	0	0	0	0	0	0	0	2	1	0	0	0	0
A. angulicollis	1	0	1	1	1	0	0	0	2	0	0	0	0	0	0	0	0	2	1	0	0	0	0
A. areata	0	1	0	1	1	0	0	1	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0
A. baezae	0	0	1	1	1	0	1	0	1	0	0	1	0	1	0	0	0	2	1	0	0	*	1
A. bequaerti	0	0	1	0	1	0	0	0	0	1	1	1	0	0	0	0	0	2	1	0	0	0	0
A. brevistigma	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	1	0
A. cajennensis	0	0	1	1	1	1	1	1	0	1	1	0	0	0	0	1	0	1	1	0	2	1	0
A. centralis	0	0	1	1	1	0	0	1	1	1	1	1	0	0	0	0	0	2	1	0	0	0	0
A. constructor	1	0	1	1	1	0	0	0	2	1	1	0	0	0	0	0	0	2	1	0	0	1	0
A. cornelliana	0	1	1	2	1	0	0	0	1	0	0	1	0	1	0	0	0	2	1	0	0	*	1
A. flavipennis	0	0	0	1	1	0	0	1	1	0	1	1	0	0	0	0	0	2	1	0	0	0	1
A. fulvofasciata	1	1	0	1	1	0	0	0	2	0	1	0	0	0	0	0	0	2	1	0	0	0	0
A. hamiltoni	1	0	0	1	1	0	0	0	2	0	1	0	0	0	0	0	0	2	1	0	0	0	0
A. imitatrix	1	1	1	0	0	1	1	0	0	0	2	0	0	1	0	1	0	1	1	0	2	1	0
A. lobipleura	1	0	0	0	1	1	1	1	0	0	2	0	0	0	0	1	0	1	1	0	1	1	0
A. melanopyga	0	0	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	2	1	0	1	1	0
A. multipicta	1	0	1	2	1	0	0	1	1	1	1	0	0	0	0	0	0	2	1	0	0	0	0
A. myrmecophyla	0	1	0	1	1	0	1	0	1	1	0	1	0	0	0	0	0	2	1	0	0	0	0
A. nebularum	0	0	1	1	1	0	0	0	0	1	1	1	0	0	0	0	0	2	1	0	0	0	1
A. nigrescens	0	0	0	0	1	0	1	1	1	0	2	0	0	0	0	0	0	2	1	0	0	1	0
A. ornata	0	0	0	1	1	0	0	0	2	0	1	0	0	0	0	0	0	2	1	0	0	0	0
A. pallidiventris	1	1	0	2	1	0	0	0	1	1	0	1	0	0	0	0	0	2	1	0	0	0	0
A. pallipes	0	0	1	1	1	0	1	0	1	0	1	1	0	0	0	0	0	2	1	0	0	*	0
A. panamaensis	1	0	0	2	1	0	0	0	2	0	0	0	0	0	0	0	0	2	1	0	0	0	0
A. pleuralis	0	1	0	0	1	1	0	0	0	0	2	0	0	0	0	1	0	1	1	0	2	0	0
A. silvatica	1	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	2	1	0	0	0	1
A. testacea	1	0	0	2	1	0	0	0	2	0	1	0	0	0	0	0	0	2	1	0	0	1	0
A. timida	0	0	1	0	0	1	1	1	0	1	1	0	0	0	0	1	0	1	1	0	0	1	0
A. vicina	1	1	0	2	1	0	0	0	2	0	2	0	0	0	0	0	0	2	1	0	0	*	0
A. xanthopus	1	0	0	2	1	0	0	0	1	0	0	1	0	0	0	0	0	2	1	0	0	0	0
A. yepocapa	0	1	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	2	1	0	1	0	0

TABLE 1 *continued*

	47	48	49	50	51	22	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69
Apoica pallens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Angiopolybia obidensis	0	0	0	0	1	0	1	0	1	0	0	1	1	0	0	0	0	0	0	1	1	0	1
Angiopolybia pallens	0	0	0	0	1	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	1
Angiopolybia paraensis	0	0	0	0	1	0	1	0	1	0	0	1	1	0	0	0	0	0	0	1	1	0	1
Angiopolybia zischai	0	0	0	0	1	0	1	0	1	0	0	1	1	0	0	0	0	0	0	1	1	0	1
A. acreana	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	1	?	?
A. anceps	0	1	0	1	1	1	1	1	1	0	0	0	1	0	0	1	1	1	1	0	0	?	?
A. angulata	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0
A. angulicollis	0	0	0	0	1	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0
A. areata	1	0	0	1	1	0	1	1	1	0	0	1	1	1	0	1	0	1	1	0	1	0	1
A. baezae	0	1	0	1	0	1	1	1	1	0	1	0	1	0	1	1	1	1	1	1	1	1	1
A. bequaerti	0	0	0	1	0	0	0	1	1	0	0	1	1	0	0	1	0	1	1	1	1	1	0
A. brevistigma	1	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1	0	0	1	1	1	?	?
A. cajennensis	1	2	0	1	1	0	0	1	0	1	0	1	0	0	0	1	0	0	0	1	1	1	0
A. centralis	0	0	0	1	0	0	0	1	1	0	0	1	1	0	0	1	1	1	1	0	0	1	0
A. constructor	0	1	1	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	?	?
A. cornelliana	0	1	0	1	0	1	1	1	1	0	1	1	1	1	1	0	1	1	1	0	0	?	?
A. flavipennis	1	2	0	1	1	0	0	1	1	0	0	1	1	0	1	1	0	1	1	1	1	0	1
A. fulvofasciata	0	0	0	1	0	0	1	1	1	0	0	1	1	0	0	1	0	1	0	1	1	1	0
A. hamiltoni	0	1	0	1	0	0	1	1	1	0	0	1	1	0	0	1	0	1	1	1	1	?	?
A. imitatrix	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1	0	0	?	?
A. lobipleura	1	0	0	1	0	1	0	1	0	0	0	1	0	0	0	1	1	1	1	1	1	1	0
A. melanopyga	0	0	0	1	1	1	0	0	1	0	0	1	1	0	0	1	1	1	1	1	1	?	?
A. multipicta	0	1	0	1	0	0	0	1	1	0	0	1	1	0	0	1	1	1	1	0	1	1	0
A. myrmecophyla	0	1	0	1	0	0	0	1	1	0	0	1	1	1	0	1	1	1	1	0	0	?	?
A. nebularum	0	2	0	1	0	0	1	1	1	0	0	0	1	1	1	0	0	1	0	1	1	?	?
A. nigrescens	1	0	0	1	0	0	1	1	1	0	0	1	1	1	0	1	1	1	1	0	0	?	?
A. ornata	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	1	?	?
A. pallidiventris	0	0	0	1	0	0	0	1	1	0	0	1	1	0	0	1	1	1	1	1	1	?	?
A. pallipes	0	0	0	1	0	0	0	1	1	0	0	1	1	0	0	1	1	1	1	0	1	1	0
A. panamaensis	0	1	1	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0
A. pleuralis	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	1	0	1	0	0	?	?
A. silvatica	0	1	0	1	0	0	1	1	1	0	0	0	1	0	1	1	1	0	0	0	0	?	?
A. testacea	0	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	1	0	0	1	0	1	0
A. timida	0	2	0	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	0	1
A. vicina	1	1	0	1	1	0	1	1	1	0	0	0	0	0	0	1	1	0	1	1	1	1	0
A. xanthopus	0	1	0	1	1	0	1	1	1	0	0	0	1	1	1	1	1	1	1	0	1	1	0
A. yepocapa	0	1	0	1	1	0	1	0	1	0	0	1	1	1	1	0	1	1	0	1	1	1	0

MATERIALS AND METHODS

Specimens of *Agelaia* were analyzed at the American Museum of Natural History, University of Vermont, Universidade Estadual de Feira de Santana (UEFS), and Universidade Estadual Paulista (UNESP – São José do Rio Preto). Also, specimens were borrowed from the British Museum of Natural History (BMNH).

The morphological characters were assembled in a data matrix using Winclada version 1.00.08 (Nixon, 2002) (see table 1). A total of 69 characters was studied, 67 of them are characters of adult females and two of nests (see appendix 1). The characters were treated as additive (Farris, 1970), except the multistate characters 20, 34, 44, and 48, which were treated as nonadditive (Fitch, 1971), because nested homology was not observed in the characters state. The characters and their respective state are listed in appendix 1. Outgroup rooting (Nixon and Carpenter, 1993) was implemented with the following taxa: *Apoica pallida* (Olivier), *Angiopolybia obidensis* (Ducke), *Angiopolybia pallens* (Lepeletier), *Angiopolybia zischkai* (Richards), and *Angiopolybia paraensis* (Spinola). An analysis combining the following algorithms was undertaken using TNT (Tree Analysis Using New Technology; Goloboff et al., 2008): Sectorial Search (default), Ratchet (8 up-/4 down-weight percentage and 200 iterations), Tree-Drifting (default), and Tree Fusing (10 rounds), in the search for the most parsimonious tree. All characters had equal weights.

Symetric Resampling Support (Goloboff et al., 2003) was also performed in TNT, employing changing probability 33, number of replications 1000, and collapse groups below 1.

Males of *Agelaia angulata* (Fabricius), *A. areata* (Say), *A. cajennensis* (Fabricius), *A. centralis* (Cameron), *A. flavipennis* (Ducke), *A. fulvofasciata* (DeGeer), *A. multipicta* (Haliday), *A. ornata* (Ducke), *A. pallipes* (Olivier), *A. panamaensis* (Cameron), *A. testacea* (Fabricius), *A timida* Cooper, *A. vicina* (de Saussure), and *A. yepocapa* (Richards) were placed in a humid chamber and male genitalia extracted with forceps. The genital capsule was cleared in lactophenol and examined under glycerin. Drawings (figs. 1–5) were made with a drawing tube and plates with Inkscape 1.0.2.

RESULTS AND DISCUSSION

The analysis resulted in a single cladogram of length 340, consistency index 0.22, and retention index 0.61. *Agelaia* is supported as monophyletic. Five main species clades were found, which we term: the *pleuralis* group, *panamaensis* group, *xanthopus* group, *flavipennis* group, and *bequaerti* group (fig. 6). The support tree presents less resolution and the groups cited were not maintained.

As discussed above, the genus *Agelaia* has been subject to many taxonomic issues. Richards (1978: 235), who still used the name *Stelopolybia* for the taxon, diagnosed it as

> Close to *Angiopolybia* but scutellum with a central longitudinal impressed line (weak in *S. cajennensis*). Anterodorsal plate of mesepisternum much narrower compared to its height. Mesoscutum with a continuous raised lateral margin from just in front to

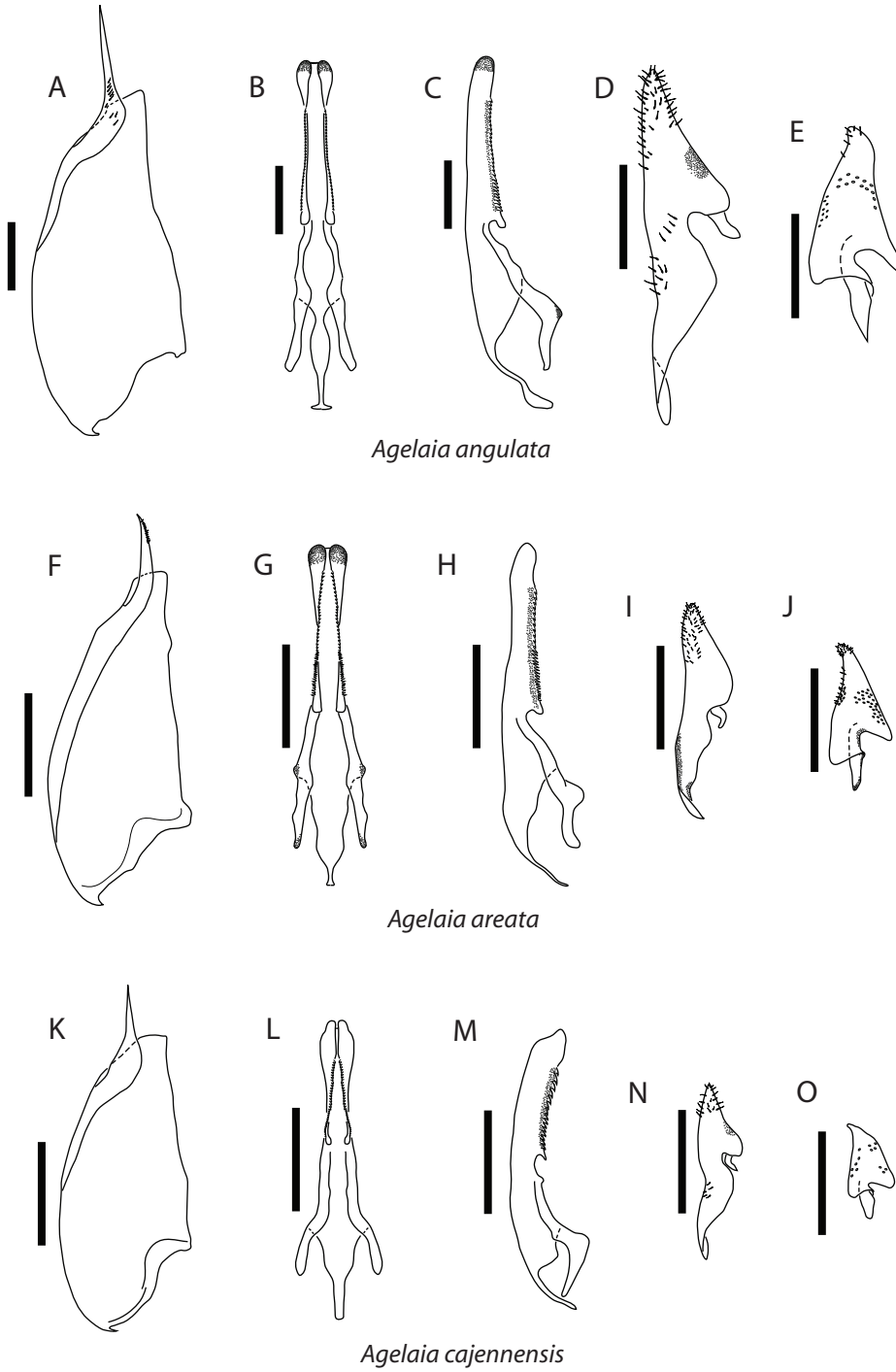


FIGURE 1. Male genitalia, from top to bottom, of *Agelaia angulata*, *Agelaia areata*, and *Agelaia cajennensis*. A, F, and K = paramere, lateral view; B, G, and L = aedeagus, ventral view; C, H, and M = aedeagus, lateral view; D, I, and N = cuspis, lateral view; E, J, and O = digitus, lateral view.

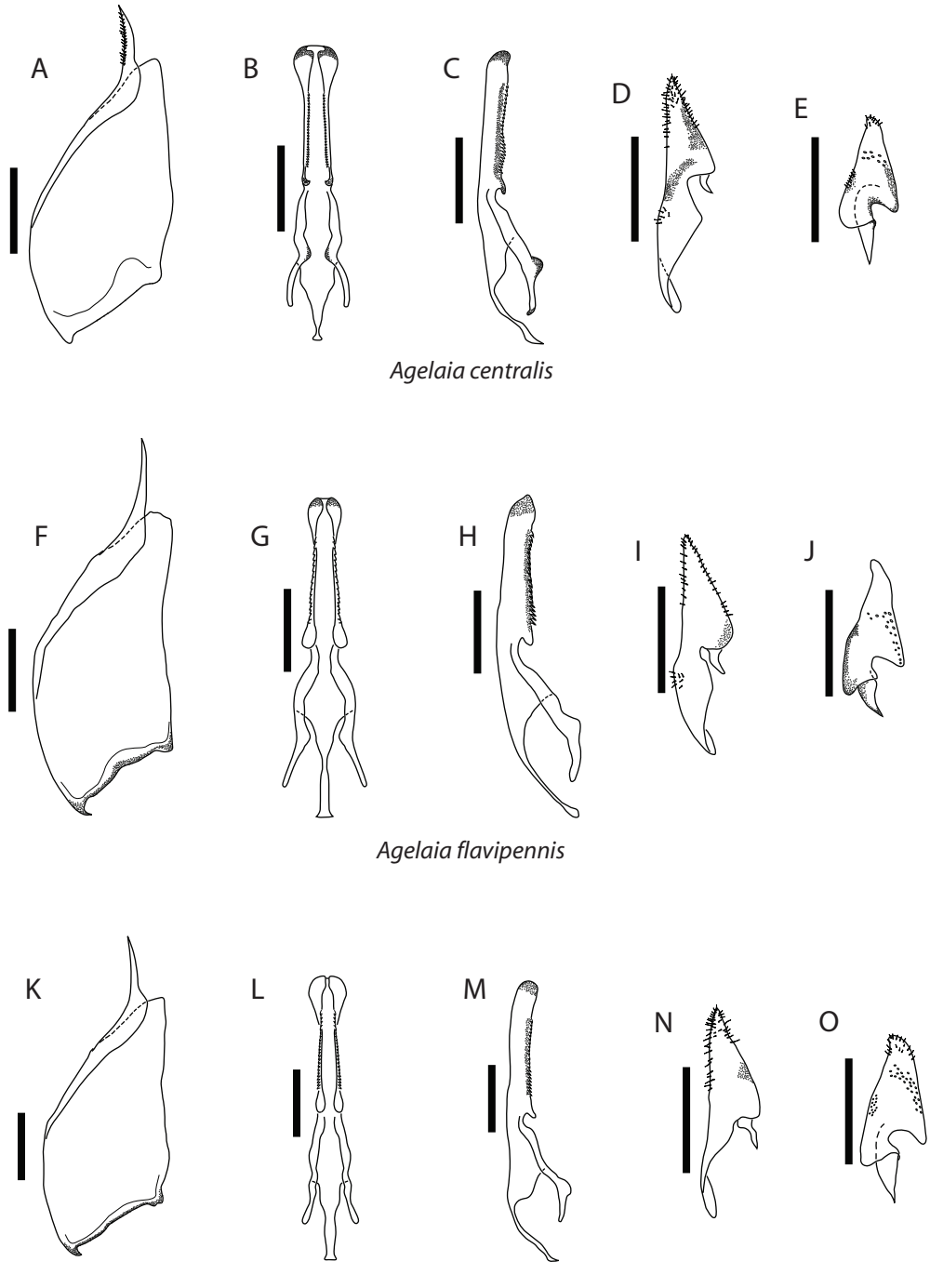


FIGURE 2. Male genitalia, from top to bottom, of *Agelaia centralis*, *Agelaia flavipennis*, and *Agelaia fulvofasciata*. A, F, and K = paramere, lateral view; B, G, and L = aedeagus, ventral view; C, H, and M = aedeagus, lateral view; D, I, and N = cuspis, lateral view; E, J, and O = digitus, lateral view.

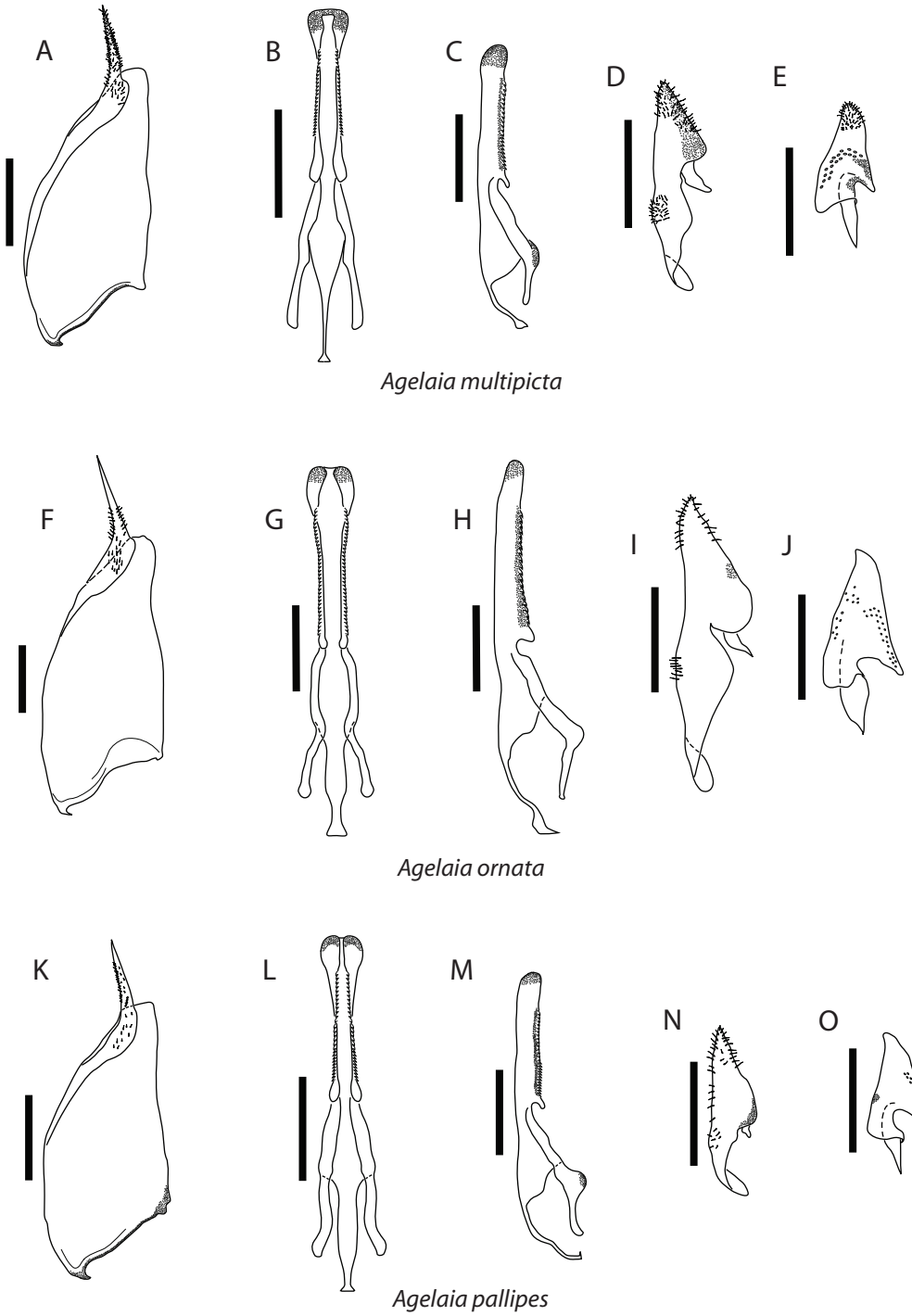


FIGURE 3. Male genitalia, from top to bottom, of *Agelaia multipicta*, *Agelaia ornata*, and *Agelaia pallipes*. A, F, and K = paramere, lateral view; B, G, and L = aedeagus, ventral view; C, H, and M = aedeagus, lateral view; D, I, and N = cuspis, lateral view; E, J, and O = digitus, lateral view.

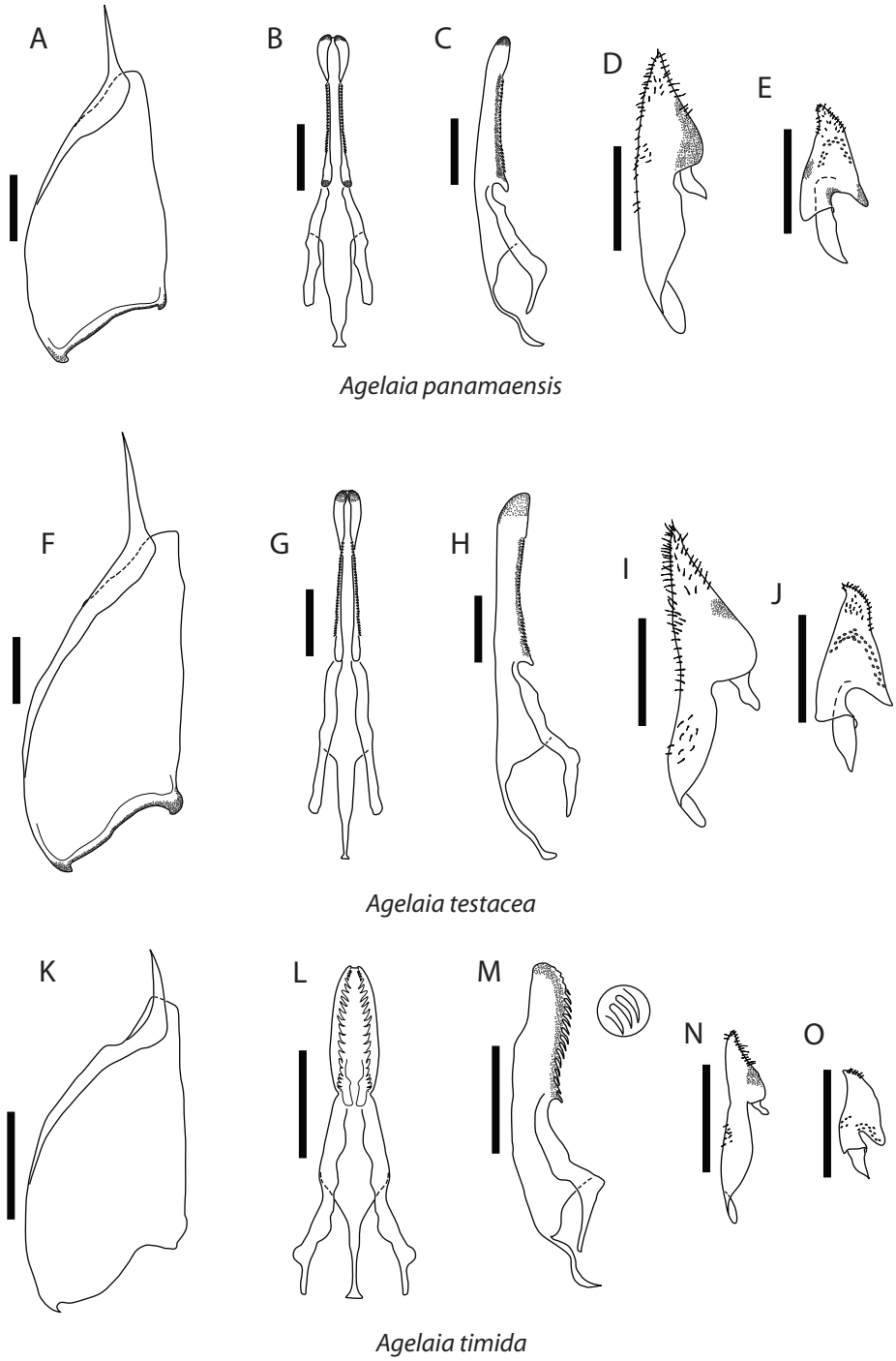


FIGURE 4. Male genitalia, from top to bottom, of *Agelaia panamaensis*, *Agelaia testacea*, and *Agelaia timida*. A, F, and K = paramere, lateral view; B, G, and L = aedeagus, ventral view; C, H, and M = aedeagus, lateral view; D, I, and N = cuspis, lateral view; E, J, and O = digitus, lateral view.

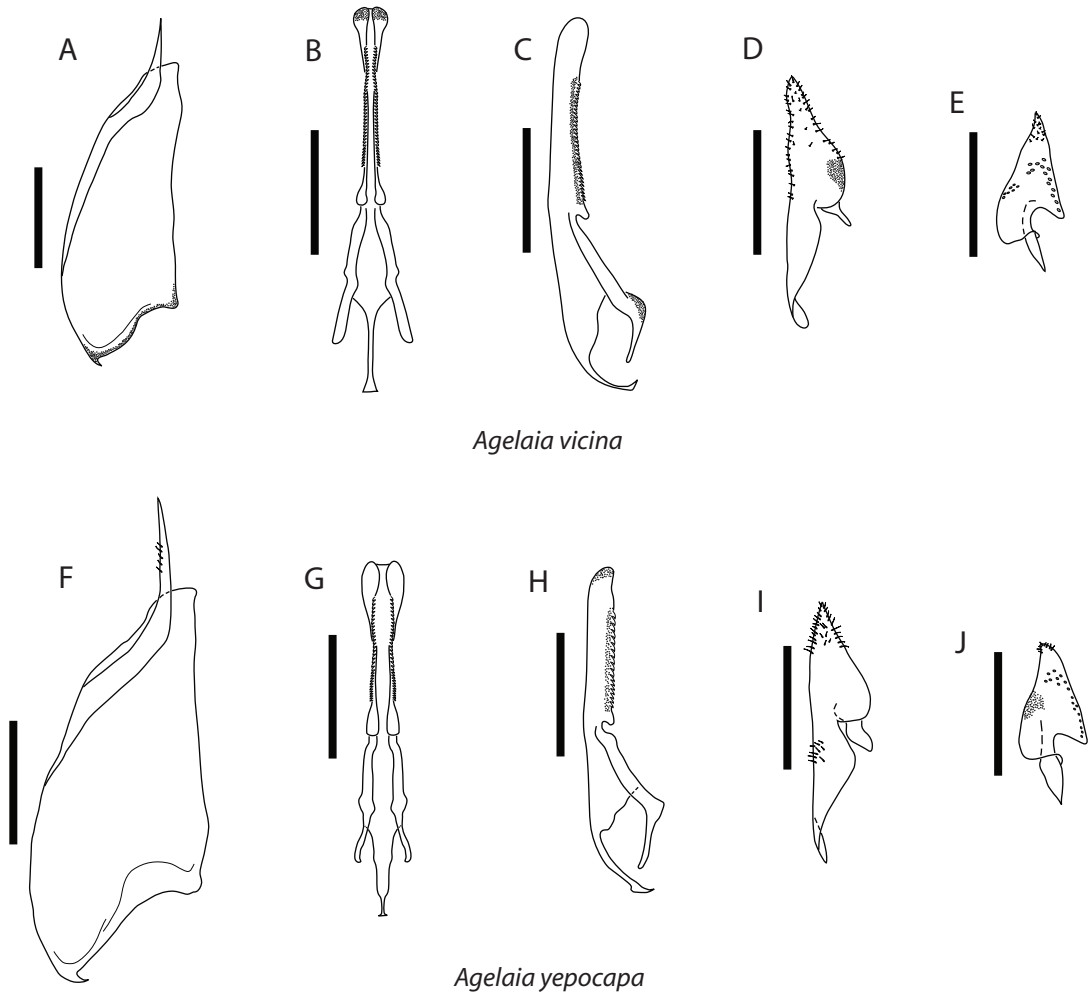


FIGURE 5. Male genitalia, from top to bottom, of *Agelaia vicina* and *Agelaia yepocapa*. A and F = paramere, lateral view; B and G = aedeagus, ventral view; C and H = aedeagus, lateral view; D and I = cuspis, lateral view; E and J = digitus, lateral view.

just behind the tegula. Metapleural basalar area with a keel marking off a narrow dorsal area, keel sometimes rather weak but the whole area narrower than in *Angiopolybia* and more distinct from the metapleuron.

Ducke (1910) diagnosed *Agelaia* (=*Stelopolybia*) with a mesepisternal groove and the stelocyttarus nest, with or without envelope, however some species are, at present, included in *Angiopolybia*. Richards considered the nests of *Stelopolybia* (= *Agelaia*) as typical, built in cavities and without envelopes (Richards, 1978: 237). Araujo (1946) argued that just the feature "nest with envelope" was sufficient to separate the species in his new genus, *Angiopolybia*, from those without an envelope (now *Agelaia*). Carpenter (1991) coded *Agelaia* as having a nest envelope in his matrix, with the character as a synapomorphy for his *Agelaia-Polybia* compo-

nent. As shown in our phylogeny and pointed out by Cooper (2000), some species of *Agelaia* have nests with an envelope, however, nests built in cavities (char. 68: 1) is a synapormorphy for the genus. The nest envelope (char. 69:1) is shared by all species of *Angiopolybia* and *Agelaia flavipennis* and *A. areata*, *A. timida*, and *A. baezae* (Cooper, 2000), which indicates multiple origins of the envelope. Unfortunately, some species of *Agelaia* have not had their nests described yet, which renders this character ambiguous on our tree (see appendix 1 and fig. 6).

Other synapomorphies that support *Agelaia* as monophyletic are: (1) the medial scutellar line not forming two distinct lateral lobes (char. 41:1).—The impressed line is a feature cited by Richards (1978) and Ducke (1910) for the genus (see above), but, we observed two states for *Agelaia*, forming two lateral lobes with the medial line strong or, when not forming two lateral lobes, the medial line is weaker; (2) the metanotum compressed (char. 42:1), a feature that is shared with others species of Epiponini; and (3) the forecoxae without bristles (except component A, which has bristles, sharing this state with the outgroup). The spiracles of tergum I positioned on anterior third (char. 62:1) and the tergum I not concave (char. 63:1) are homoplastic in *Agelaia*.

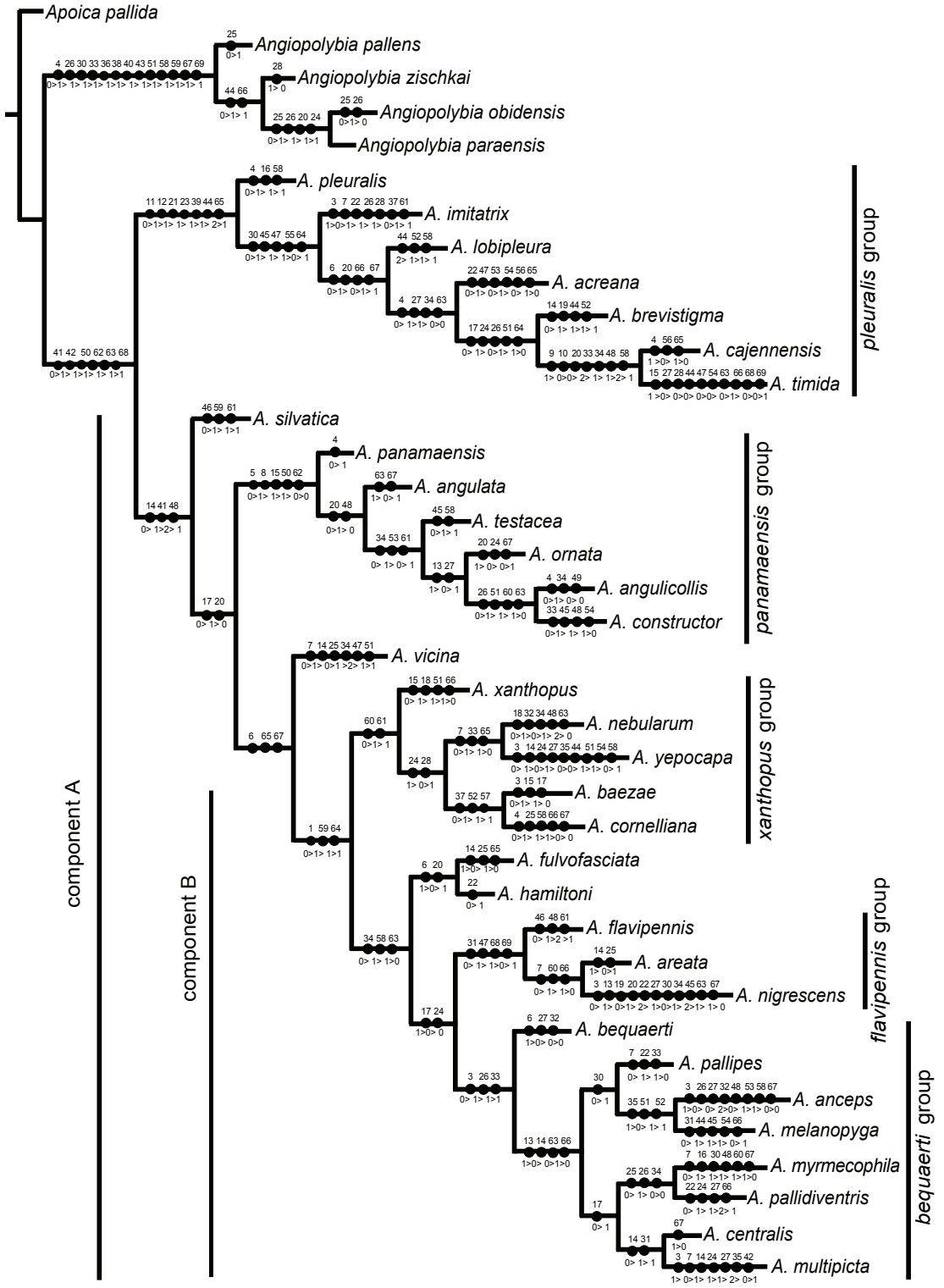
The *pleuralis* Group

Silveira and Carpenter (1996) suggested that *A. lobipleura*, *A. cajennensis*, *A. acreana*, and *A. brevistigma*, based on morphological evidence, would form a monophyletic group supported by the presence of a concave shining area in the malar space (char. 11:1) and an elongate prestigma (char. 55:1). Later, Cooper (2000; 2001) described seven new species, three of which (*A. timida*, *A. pleuralis*, and *A. imitatrix*) also share these features, except *A. pleurais*, which has the prestigma short as found in most species of *Agelaia*, with the tip truncate or pointed (Silveira and Carpenter, 1996: 71), however, variation on the size of prestigma was reported by Richards (1978) and Silveira and Carpenter (1996). Cooper (2000: 233) in his description of *A. imitatrix* pointed out that the grouping of *A. lobipleura*, *A. pleuralis*, and *A. imitatrix* is supported by the lamellate anterior margin of pronotum very wide below the level of the pronotal fovea.

These species, together with *A. pleuralis* forms a monophyletic group (here called of *pleuralis* group; see fig. 6), which is supported by not only the characters cited by Silveira and Carpenter (1996), but also by the interocellar space distinctly prominent (char. 21:1); the occipital carina emarginate on the medial region (char. 23:1); the scutum convex and projected anteriorly (char. 39:1); and the propodeal carina extending longitudinally (char. 44:2).

Concerning the tip of prestigma, it seems that the state "rounded" had independent origins for *A. acreana* and *A. cajennensis*, but, as with the prestigma, this structure also has intraspecific variations. This is the same case for *Angiopolybia pallens*, which apparently has the prestigma longer than wide, and the tip rounded, while *An. paraensis* and *An. obidensis* have the prestigma as long as wide (Silveira and Carpenter, 1996). Andena et al. (2007a), in their phylogeny of *Angiopolybia* species, coded the prestigma "as long as wide" for all species of that genus.

Silveira and Carpenter (1996) proposed that a very weak dorsal pronotal carina for *A. lobipleura* and *A. acreana* might be considered a transitional state toward its complete absence in *A. cajennesis* and *A. brevistigma*, and then this provides additional support for the mono-


Apoica pallida
Angiopolybia pallens
Angiopolybia zischkai
Angiopolybia obidensis
Angiopolybia paraensis
A. pleuralis
A. imitatrix
A. lobipleura
A. acreana
A. brevistigma
A. cajennensis
A. timida
pleuralis group
A. silvatica
A. panamaensis
A. angulata
A. testacea
A. ornata
A. angulicollis
A. constructor
panamaensis group
A. vicina
A. xanthopus
A. nebularum
A. yepocapa
A. baezae
A. cornelliana
xanthopus group
A. fulvofasciata
A. hamiltoni
A. flavipennis
A. areata
A. nigrescens
flavipennis group
A. bequaerti
A. pallipes
A. anceps
A. melanopyga
A. myrmecophila
A. pallidiventris
A. centralis
A. multipicta
bequaerti group
component A
component B

phyly of a group comprising these four species. Our phylogeny supports the point of view of Silveira and Carpenter (1996), including *A. timida*, *A. imitatrix*, and *A. pleurais* described by Cooper (2000, 2001) later, which share the same features. The optimization of character 29 (dorsal pronotal carina) is ambiguous for the species of *Agelaia* as a whole but shows a clear separation from the *pleuralis* group, which has the dorsal pronotal carina weak or absent (state 0) while component A, with species sharing the dorsal ponotal carina marked (state 1).

As stated above by Silveira and Carpenter (1996), *A. lobipleura, A. acreana, A. cajennesis* and *A. brevistigma*, form a monophyletic group (even though a phylogenetic analysis was not performed), with *Agelaia acreana* and *A. lobipleura* as sister taxa and these species as sister of *A. cajennensis* + *A. brevistiga* would group together, Silveira and Carpenter (1996) followed the grouping proposed by Richards (1978: 241), who cited the similarities between *A. brevistigma* and *A. cajennensis.* The proposed grouping of Silveira and Carpenter (1996) would be correct, although the new species described by Cooper (2000) changed the position of those species. Cooper (2000: 184–185) in his description of *A. timida* stated that he previously identified two nests of this species as *A. cajennensis.* Actually, both species are very similar and the clade *A. cajennensis* + *A. timida* share, in figure 6, the following characters: distance between the tentorial furrow and internal margin of the eyes less than subantennal suture (char. 9:0); subantennal suture marked (char. 10:1); ocelli anterior to declivity of vertex (char. 20:2); carina of pronotal tubercle not covering the entire tubercle (char. 22:1) and positioned on medial region margin (char. 34:1); tip of propodeal valvula subtriangular (char. 48:2) and the tegula with a discal area hyaline (char. 58:1).

Component A

The medial scutellar line strongly marked, forming two distinct lobes (char. 41:2; see above), supports the component A, which has *A. silvatica* as the basalmost species. Richards (1978), as already cited above, used this feature to separate *Angiopolybia* from *Agelaia*. Richards (1978) also stated that it is weaker in *A. cajennensis.* In all species of *Angiopolybia* the medial line is absent or sometimes visible in *An. pallens* though transparent (Richards, 1978). Andena et al. (2007a) considered the line absent for species of *Angiopolybia* and present for *Agelaia* and *Apoica* species (these last two were considered outgroups). The absence vs. presence of medial line on the scutellum is one of those characters cited by Andena et al. (2007a) that supports *Angiopolybia* and *Agelaia* as monophyletic groups. Here we considered three states: evanescent (0) for *Apoica* and all species of *Angiopolybia*; marked, not forming two distinct lobes (1), supporting the *cajennensis* group; and marked, forming two distinct lobes (2), supporting the remaining species of *Agelaia* (component A). Except *A. silvatica*, the remaining species share the upper region of the gena equal to or very slightly narrower than the medial region (char.

FIGURE 6. The cladogram for the species of *Agelaia*, with length 340, consistency index 0.22, and retention index 0.61, based on the data matrix from table 1. Characters numbers are placed above circles with state number below; filled circles denote an uncontroverted step, while open circles indicate reversals and convergences.

17:1) and the ocelli at the same declivity of the vertex (char. 20:0). The subantennal suture marked (char. 10:1) is found in all species of component A and the clade (*A. cajennesis* + *A. timida*), within the *cajennensis* group. On the other hand, a subantennal suture weak (state 0) is present in all species of the *cajennensis* group, except the clade cited above. The optimization of this character is ambiguous and certainly had independent origins within Epiponini.

The *panamaensis* Group

The *panamaensis* group is supported by two synapomorphies. The clypeus of these species is completely convex (char. 5:0); the remaining species have the clypeus compressed at the base (state 1). This character had not yet been described until now, but it clearly differentiates the group from the remaining species of *Agelaia*; moreover, the pubescence within this group of species is absent (char. 8:1) and punctation is present all over (char. 6:0). When present, the pubescence may be found with different patterns within Epiponini. We have seen it long and dense, as well short and scattered, however, such features may vary within species. Thus, we coded for only two states, present and absent The forecoxae without bristles (char. 50:1) is also shared by all species of this clade and the species of *Angiopolybia*, which are homoplastic in our phylogeny. The strongly produced humeri present another feature (char. 32:2) easily seen in species of this clade, as do the spiracles of tergum I positioned after the first third (char. 62:0). *Agelaia panamaensis* is the only species of this clade with humeri less projected.

For all the Epiponini the punctation on the clypeus has been a challenging character because it is difficult sometimes to find a pattern. In the case of *Agelaia* it appears only on the first third in most species, while the size, distribution, and depth of the punctations shows variation. Apart from *A. pleuralis*, *A. imitatrix*, *A. silvatica*, *A. fulvofasciata*, *A. hamiltoni*, *A. bequaerti*, and the *panamaensis* group, all other species of the genus have punctation only on the first third. In the excepted species cited, punctation is predominant only on the first third, although it continues on the remaining two-thirds, becoming sparser and shallower.

Agelaia angulata was subdivided by Richards (1978: 244) into two subspecies, *A. angulata angulata* and *A. angulata bertonii*, based on differences in the pronotal carina. Gacete-Barrett (1999) raised to specific rank the subspecies *bertonii*, an action that was criticized by Cooper (2000), who, based on series of specimens deposited in the BMNH, synonymized *A. bertonii* with *A. angulata*. We follow Cooper's course and consider *A. bertonii* as a synonym of *A. angulata*. *Agelaia testacea* has the pronotal carina projecting as in *A. angulata*, however, the pronotal prominence is shorter and blunter (= carina of pronotal tubercle on medial region: char. 34:0) and the propodeal valvula narrower (Richards, 1978: 245). Also, other characters separated these species: *A. testacea* with inferior region of gena less dilated (char. 16:0); propodeal furrow absent (char. 45:1); propodeal valvula with carina present (char. 49:1) and narrow, as described by Richards (1978); forecoxae convex (char. 53:0); tegula with a hyaline area (char. 58:1); spiracles of tergum I projected (char. 61:1); posterior region of tergum I more flat (char. 63:1); and tergum II rounded (char. 67:0).

Agelaia ornata + (*A. angulicollis* + *A. constructor*) is supported by the malar space narrow (char. 13:0) and the margin of the pronotal fovea positioned anteriorly (char. 27:1). Richards

(1978: 245–246) stated that despite the similarities of *A. ornata* and *A. angulicollis*, they can be separated by the propodeal valvula, which is sharper in *A. ornata*; however, it is important to note that in both species the propodeal valvula is narrow with the tip rounded, which differs from *A. constructor*, in which the tip is truncate and not sharp.

Component B

Except *A. vicina*, the remaining species of the clade, here named Component B group, are supported by the eyes bare (char. 1:1), a feature that is also variable within species, with some specimens having few short, scattered hairs on the eyes. Despite the insertion of the ligament on tergum I prominent and carinate (char. 59:1) and the tergum I convex in profile (char. 64:1) are shared with other species, they are typical features of this group.

The *xanthopus* Group

The *xanthopus* group has tergum I subparallel after the spiracles (char. 60:1), which are projected (char. 61:1). The basalmost *A. xanthopus* is easily recognized by the pronotum with a fovea lying in a deep hollow, bounded anteriorly by the strongly raised and curved prominence (Richards, 1978: 249). Richards (1978) subdivided this species into two subspecies: *A. xanthopus xanthopus*, which has yellow markings, and *A. xanthopus melonotica*, which is blackish brown with only the legs partly yellow (Cooper, 2000). The pronotal fovea of the clade (*A. nebularum* + *A. yepocapa*) + (*A. baezae* + *A. cornelliana*) is in a shallow concavity (char. 26:1), and the posterior margin of the head in dorsal view is at the same level as the eyes (char. 24:1).

The grouping of *A. cornelliana* + *A. baezae* was expected. Richards (1943) had divided the *A. cornelliana* into three subspecies: *A. cornelliana cornelliana*, *A. cornelliana subterranea*, and *A. cornelliana baezae.* In 1978, Richards (p. 242) raised the subspecies *baezae* to species rank, stating that "this species differs from *S. cornelliana* in its stronger pronotal keel, broader less acutely pointed tegula." Cooper (2000: 193) identified variation in the pronotal carina and tegula in the species of *A. baezae.* He stated: "I would be disposed, therefore, to consider *A. conrelliana* and *A. baezae* as a single species showing latitudinal variation. On the other hand, the specimens from the Pastaza Valley indicate that there could be more than one species occupying different altitudes in the Andes." The specimens of *A. cornelliana* and *A. baezae* we saw in this work match the variations cited by Cooper (2000), however, we had in hand only one specimen of *A. baezae* from Pastaza Valley, which makes a more detailed comparative analysis difficult. We follow the suggestion of Cooper (2000) and do not synonymize the species. The clade *A. cornelliana* + *A. baezae* is supported by the tegula projected anteriorly (char. 57:1).

Cooper (2000) pointed out that *A. nebularum* is closest to *A. cornelliana*, *A. baezae*, and *A. xanthopus*, which are also montane species with tergum subrectangular behind the spiracles and with ground color black or blackish brown. In figure 6 all the *xanthopus* group has tergum I subrectangular (= subparallel) (char. 60:1). Although the species is black or blackish brown, Cooper (2000) cited a variant of *A. yepocapa* from Mexico, which has the anterior half of the

mesepisternum paler and a specimen from Jalapa that has only the mesepisternal sulci black. *Agelaia nebularum* + *A. yepocapa* and *A. fulvofasciata* are the only three species in component A, which have bristles on tergum I long and dense (char. 65:0).

The Clade (*Agelaia fulvofasciata* + *A. hamiltoni*) + (*flavipennis* Group + bequaerti Group)

The homoplastic characters carina on pronotal tubercle on the middle region (char. 34:1); tegula with a hyaline area (char. 58:1) and tergum I slightly concave (char. 63:0) are shared by this clade.

The Clade *A. fulvofasciata* + *A. hamiltoni*

Agelaia fulvofasciata and *A. hamiltoni* are species from east of the Andes and Cooper (2000: 181), in his identification key, keyed them out with the dorsal pronotal carina raised forming a blunt shoulder at the sides, terga brown or blackish brown, with yellow strips and the eyes with short hairs. The pronotal carina is a very variable feature within *Agelaia* and has been frequently described as "slightly projected at sides or less projecting at sides" for *A. fulvofasciata* and *A. hamiltoni* respectively (Cooper, 2000). In order to avoid such lack of precision in the description, here we coded only two states: as character 29:0, shared by all species of the component A (as cited above), and as absent or evanescent (char. 29:1). The humeri strongly produced (char. 32:2) is also shared by this clade.

The *flavipennis* Group

The features shared by this clade are the absence of bristles on pronotum (char. 31:1) and propodeum (char. 47:1), the nest arboreal (shared with *A. timida*) (char. 68:0) and with an envelope (char. 69:1) (shared with *A. timida* and *A. baezae*).

Richards (1978: 253) proposed that *Agelaia flavipennis* was very close to *A. multipicta*, but distinguished by the shape and color of the propodeal valvula and, in nearly all specimens, by the shape of the first metasomal tergum. The medial carina of the propodeal valvula is absent in both species (char. 49:0), a feature shared by most species of the *angulata* group. Probably Richards (1978), when he referred to medial carina of propodeal valve, meant the tip of propodeal valvula, which is subtriangular (char. 48:2) in *A. flavipennis* and truncate in *A. multipicta* (char. 48:1). Again, Richards (1978) was not clear about the metasomal tergum. Here, the differences concerning this feature are tergum I slightly concave from medial to posterior region (char. 63:0), and bristles present and long (char. 65:0) in *A. flavipennis* vs. tergum I almost flat (char. 63:1) and bristle absent (char. 65:1) in *A. multipicta.* Also, tergum I widens gradually after spiracles in both species (char. 60:0), a feature that separates *A. flavipennis* from *A. areata* + *A. nigrescens*, which are subparallel (char. 60:1).

Cooper (2000: 192) reported that species of *A. flavipennis* from Villa Tunari, Bolivia, may or may not have the tegula produced in front, while *A. areata* from western Ecuador have the

tegula pointed in front. In this work we abandon this feature, because it is highly variable within *Agelaia*, as also shown by Cooper (2000): "Richards (1978) gives much weight as to whether the tegula is produced into a point or process in front. This is certainly a useful character, but it is variable in the species where it occurs."

Cooper (2001) described *A. nigrescens* near *A. myrmecophila* but separated from the latter by its bare eyes, gena more tapered above, and body with darker coloration. In our phylogeny we coded only two states for the hair on the eyes: hairs long (char. 1:0), which supports the *cajennensis* group plus *A. sylvatica*, and absent or short, scattered (char. 1:1), shared for the remaining species. Thus, despite *A. nicrescens* having bare eyes and *A. myrmecophila* has short and scattered, they were coded as only one state.

The *bequaerti* Group

The species of this clade have been subject to taxonomic issues, however, despite their sharing these features with other species of *Agelaia*, the clade is supported by lateral margin of clypeus sinuous (char. 3:1), pronotal fovea in a shallow concavity (char. 26:1), and carina of the pronotal tubercle not covering the length of the entire tubercle (char. 33:1).

Richards (1978: 253) stated:

> the species allied to *S. multipicta* and *S. pallipes* are very difficult to classify. The allies of the first tend to have gastral tergite I wider and more angled at the sides, and the gaster is always more or less distinctly banded with yellow. The allies of the second species tend to have gastral tergite I narrower with the sides more diverging in a straight line from base to apex and the gaster is not banded but with the sides more diverging in a straight line from base to apex and gaster is not banded but with whole segments black, brown or yellowish.

In our cladogram (fig. 6) the *multipicta* group was separated into two groups, *A. pallipes* and allies and *A. multipicta* and its allies, similar to what Richards (1978: 253) proposed, however, the features cited by Richards do not support his groups. All the characters related to tergum I are shared by both groups: tergum flat from medial to posterior region (char. 63:1) and tergum I after spiracles rounded (char. 64:1). The *pallipes* clade shares with *A. myrmecophila* the lateral margin of the pronotum rounded (char. 30:1), while the *multipicta* clade is supported by the top of the gena slightly narrower than the medial region (char. 17:1). Here we have also to consider that *A. bequaerti* as well as *A. anceps* were considered varieties of *A. multipicta multipicta* respectively (see below) by Richards (1978). In figure 6, *A. bequaerti* is the basalmost species not included in either group cited above, although *A. anceps* is within the *pallipes* group. Both species differ from *A. multipicta* in having pubescence on gena present (char. 15:0) and bristles on pronotum long and dense (char. 31:0). *Agelaia anceps* differs from *A. multipicta* and *A. bequaerti* in characters related with forecoxae (chars. 51 and 52; see also below).

Agelaia bequaerti was a variety of *A. pallipes* (Richards and Richards, 1951), which was later synonymized with *A. multipicta* (Richards, 1978: 254). In 1978, Richards, divided *A. mul-*

tipicta into two subspecies, one of which, *A. multipicta fulvanceps*, was synonymized with *A. centralis* by Carpenter (1999). Garcete-Barrett (1999) raised *A. bequaerti* to specific rank. Cooper (2000: 195) disagreed with Garcete-Barrett (1999) and synonymized *A. bequaerti* with *A. centralis*, citing differences in color, but "in structure typical *A. centralis* is like *A. bequaerti.*"

Based on specimens we have seen, we raise, again, *A. bequaerti* to specific rank based on the following features: punctation on clypeus all over (char. 6:0), malar space wide (char. 13:1), width of gena more than medial region of the eyes (char. 14:1), pubescence on bottom of gena present (char. 15:0), upper region of gena narrower than medial region (char. 17:0), ocelli at the same declivity of vertex (char. 20:0), bristles on pronotum long and dense (char. 31:0), humeri less projected (char. 32:0), tergum I concave (char. 63:0), tergum II diverging abruptly posteriorly (char. 66:1), and tergum II subparallel (char. 67:1) for *A. bequaerti* vs. punctation on clypeus only on first third (char. 6:1), malar space narrow (char. 13:0), width of gena less than medial region of the eyes (char. 14:0), pubescence on bottom of gena absent (char. 15:1), upper region of gena equal to medial region (char. 17:1), ocelli anterior to the declivity of vertex (char. 20:2), bristles on pronotum short and scattered (char. 31:1), humeri more projected (char. 32:1), tergum I almost flat (char. 63:1), tergum II diverging gradually posteriorly (char. 66:0), and tergum II more rounded (char. 67:1) in *A. centralis.*

Most of the features shared by *Agelaia pallidiventris* + *A. myrmecophila* are related to the pronotum, in which the pronotal fovea is circular (char. 25:1) in a wide concavity (char. 26:0) and the carina of the pronotal tubercle anterior (char. 34:0). Cooper (2000: 195) also pointed out that the nest of *A. pallidiventris* is like that of *A. myrmecophila*, within the carton nest of an ant.

Finally, *A. melanopyga* + *A. anceps* share the carina of the pronotal tubercle straight (char. 35:0), the external margin of forecoxae rounded (char. 51:1), and anteromedial region slightly projecting (char. 52:1). As pointed out by Cooper (2000) *A. melanopyga* shares the same distinctive livery with *A. pallipes*, but their distributions do not overlap.

Richards (1978: 235) saw the holotype of *obscura* Araujo, as well as specimens collected in Rio de Janeiro, Brazil, which he placed as a small, dark form of *Stelopolybia multipicta.* The species shows ground color black with not very extensive yellow markings on the head and thorax (= mesosoma), a yellow-banded gaster and legs, which are mainly yellowish brown to darker (Richards, 1978: 235). As also pointed out by Richards (1978) the "morph" *anceps* has much more conspicuous bands on the sternites than on the tergites. Cooper (2000) also cited variation on the color of the form of *anceps*, with some species intermediate with the typical form. Besides coloration, other features might be considered polymorphic in relation to *A. multipicta*, such as: bristles on the first third on clypeus absent (char. 7:0), gena less than medial region (char. 14:0), pubescence on inferior region of gena absent (char. 15:0), upper region of gena narrower than media region (char. 17:0), lateral margin of pronotum subparallel (char. 30:1), bristles on pronotum long (char. 31:0), humeri rounded (char. 32:0), external margin of forecoxae nearly straight (char. 51:1), anterolateral region of forecoxae projected (char. 52:1), forecoxae compressed in lateral view (char. 53:1), and tergum II subparallel (char. 67:0). Based on these characters we also raise *A. anceps* as species.

Most clades in this work are supported by homoplasies, but on the other hand, analysis of the data matrix resulted in a single tree. We must consider that most males and nests are unknown for this genus and might improve the optimization of some characters. Even lacking these unknown data our phylogeny shows a clear resolution of all species of *Agelaia* and certainly will contribute to knowledge of the Epiponini tribe.

Descriptions and Remarks on Male Genitalia

Agelaia angulata Fabricius, 1804

Brazil: cerrado, Mato Grosso State, 1 male (BMNH)

Description: (1) paramere about 2.2× longer than wide; spine with short, scattered hairs on base; apical angle truncate (fig. 1A); (2) aedeagus long; lobe broad on apical region only; row of teeth extending ventrolaterally, basal teeth stronger than those on apical region; ventral process little projected and rounded (fig. 1B, C); (3) cuspis long and wider apically, with short spaced hairs (fig. 1D); (4) digitus wide apically, rounded, with evanescent hairs; mesal surface with evenly and spaced punctures (fig. 1E).

Agelaia areata Say, 1873

Panama: Changuinola Dist. Boca Toro, 1 male (AMNH)]

Description: (1) paramere about 2.4× longer than wide; spine long with evanescent hair on apical portion; apical angle truncate (fig. 1F); (2) aedeagus long; lobe broad apically, extending to medial region; row of teeth extending ventrolaterally, basal teeth stronger than those on apical region; ventral process little projected and rounded (fig. 1G, H); (3) cuspis long and wider apically, with very short, scattered hairs (fig. 1I); (4) digitus acute apically, pointed, with short hairs extending to medial region; mesal surface with punctures extending to basal region (fig. 1J).

Agelaia cajennensis Fabricius, 1798

Colombia: Nariños, Barbacoas, 1 male (BMNH)

Description: (1) paramere ~2× longer than wide; spine without hairs; apical angle truncate (fig. 1K); (2) aedeagus long, lobe broad, becoming more constricted on distal end, extending to medial region; row of teeth extending ventrolaterally with stronger teeth on apical region than those on basal region; ventral process little projected ad pointed (fig. 1L and M); (3) cuspis long and acute apically, with short, spaced hairs (fig. 1N); (4) digitus acute apically, pointed, without hairs; mesal surface with sparse punctures (fig. 1O).

Agelaia centralis Cameron, 1907

Panama: Canal Zone, Barro Colorado, 1 male (AMNH)

Description: (1) paramere about 1.7× longer than wide, spine with hairs on margin only; apical angle truncate (fig. 2A); (2) aedeagus long; lobe broad on apical region only; row of teeth extending ventrolaterally, basal teeth stronger than those on apical region; ventral process little projected, curved and rounded (fig. 2B, C); (3) cuspis long and acute apically, with short and sparsed hair (fig. 2D); (4) digitus wide apically, rounded, with scattered short hairs, mesal surface with evenly spaced punctures (fig. 2E).

Agelaia flavipennis Ducke, 1905

Brazil: Cristalandia, Goias State, 1 male (BMNH)

Description: (1) paramere about 1.9× longer than wide; spine without hairs; apical angle truncate (fig. 2F); (2) aedeagus long, lobe broad on apical region only, slightly pointed at distal end; row of teeth extending ventrolaterally, basal teeth stronger than those on apical region; ventral process little projected, rounded (fig. 2G, H); (3) cuspis long and acute apically, with very short and well-spaced hairs (fig. 2I); (4) digitus acute apically, pointed, without hairs; mesal surface with evenly spaced punctures (fig. 2J).

Agelaia fulvofasciata DeGeer, 1773

[Surinam]: Paramaribo, 1 male (AMNH).

Description: (1) paramere about 1.8× longer than wide; spine without hairs; apical angle truncate (fig. 2K); (2) aedeagus long, lobe broad on apical region only, row of teeth extending ventrolaterally, basal teeth stronger than those on apical region; ventral process little projected, pointed (fig. 2L, M); (3) cuspis long and acute apically, with short, evenly spaced hairs (fig. 2N); (4) digitus wide apically, rounded, with scattered hairs; mesal surface with slightly spaced punctures (fig. 2O).

Agelaia multipicta Haliday, 1836

Mexico: Fortin Flores, 1 male (AMNH)

Description: (1) paramere about 1.7× longer than wide; spine with short, dense hairs all over, apical angle truncate (fig. 3A); (2) aedeagus long, lobe broad on apical region only, row of teeth extending dorsoventrally; the teeth have the same size, from top to bottom, however, those close to basal region are less spaced than those of apical region; ventral process little projected, pointed (fig. 3B, C); (3) cuspis wider apically, pointed, with dense, short hairs (fig. 3D); (4) digitus wide apically, rounded, with dense hairs; mesal surface with evenly spaced punctures (fig. 3E).

Agelaia ornata Ducke, 1905

Colombia: Meta, La Macarena, 1 male (BMNH)

Description: (1) paramere about 1.8× long than wide; spine with short and space hairs on first half, apical angle rounded (fig. 3F); (2) aedeagus long, lobe broad on apical region only, becoming pointed on distal end; row of teeth extending dorsoventrally; the teeth have the same size, from top to bottom; ventral process little projected, rounded (fig. 3G, H); (3) cuspis wider apically, pointed, with slightly spaced and very short hairs (fig. 3I); (4) digitus wide apically, rounded, without hairs; mesal surface with evenly spaced punctures (fig. 3J).

Agelaia pallipes Olivier, 1792

Peru: Valle Chanchamayo, 1 male (AMNH)

Description: (1) paramere about 1.9× longer than wide; spine with short and closely spaced hairs all over, apical angle truncate (fig. 3K); (2) aedeagus long, lobe broad apically, extending medial region; row of teeth extending dorsoventrally; the teeth have the same size, from top to bottom, however, those close to basal region are less spaced than those of apical region; ventral process little projected, rounded (fig. 3L, M); (3) cuspis wider apically, pointed, with spaced and short hairs (fig. 3N); (4) digitus wider apically, rounded, without hairs; mesal surface with few and evenlyspaced punctures (fig. 3O).

Agelaia panamaensis Cameron, 1906

country not specified Moca, Guantalon, 1 male (AMNH)

Description: (1) paramere about 1.7× longer than wide; spine without hairs, apical angle rounded (fig. 4A); (2) aedeagus long, lobe broad apically only; row of teeth extending dorsoventrally; teeth have the same size, from top to bottom; ventral process little projected, rounded (fig. 4B, C); (3) cuspis wider apically, pointed, with spaced and short hairs (fig. 4D); (4) digitus wide apically, pointed, with short and evenly spaced hairs; mesal surface with evenly spaced punctures (fig. 4E).

Agelaia testacea Fabricius, 1804

Ecuador: Pompeya, 1 male (AMNH)

Description: (1) paramere about 1.8× longer than wide; spine without hairs, apical angle truncate (fig. 4F); (2) aedeagus long, lobe broad apically only; row of teeth extending dorsoventrally; teeth have the same size, from top to bottom; ventral process little projected, acute (fig. 4G, H); (3) cuspis long and acute apically, with short and evenly spaced hairs (fig. 4I); (4) digitus wide apically, rounded, with short and evenly spaced hairs; mesal surface with evenly spaced punctures (fig. 4J).

Agelaia timida Cooper, 2000

Colombia: Vaupes, Mitu, 1 male (BMNH)

Description: (1) paramere about 1.6× longer than wide; spine without hairs, apical angle truncate (fig. 4K); (2) aedeagus short, wide lobe, broad apically; row of teeth extending dorsoventrally; the teeth are very long, stronger apically than basally; ventral process little projected, acute (fig. 4L, M); (3) cuspis long and acute apically, with very short, scattered hairs (fig. 4N); (4) digitus acute apically, pointed, with scattered short hairs; mesal surface with evenly spaced punctures, extending to basal region (fig. 4).

Agelaia vicina de Saussure, 1854

Brazil: Poa [= Porto Alegre], Rio Grande do Sul State, 1 male (AMNH)]

Description: (1) paramere about 2.2× long than wide; spine without hairs, apical angle truncate (fig. 5A); (2) aedeagus very long and thin, lobe broad apically only; row of small teeth extending dorsoventrally; teeth have same size, from top to bottom; ventral process little projected, rounded (fig. 5B, C); (3) cuspis wider apically, pointed, with evenly spaced, short hairs (fig. 5D); (4) digitus pointed apically, rounded, with short, evenly spaced hairs; mesal surface with evenly spaced punctures (fig. 5E).

Agelaia yepocapa Richards, 1978

[Mexico]: Omilteme, 1 male (BMNH) – country not specified in the label

Description: (1) paramere ~2× longer than wide; spine with short and closely spaced hairs on first half, apical angle truncate (fig. 5F); (2) aedeagus long, lobe broad on apical region only; row of teeth extending dorsoventrally; teeth have the same size, from top to bottom; ventral process little projected, rounded (fig. 5G, H); (3) cuspis wider apically, acute, with evenly spaced, short hairs (fig. 5I); (4) digitus wider apically, rounded, with short, scattered hair on top; mesal surface with evenly spaced punctures (fig. 5J).

REMARKS

Data on male genitalia are still rare in Epiponini, however, they have been useful in phylogenetic analysis (Andena et al., 2007b). Unfortunately, most males of the species of *Agelaia* remain unknown. Richards (1978) described only external aspects of *A. cajennensis* (p. 240), *A. vicina* (p. 246), *A. fulvofasciata* (p. 250), *A. areata* (p. 256), *A. myrmecophila* (p. 257), *A. pallipes pallipes* (p. 258), and *A. pallipes cuzcoensis* (p. 259). Cooper (2000) described the male genitalia of *A. timida*. The comments below are based on the redescription of the male genitalia in this work and data available in literature.

Although the relation of height to width of the paramere is variable within *Agelaia*, it is more than 2× longer than wide or less. Most species of *Agelaia* have the paramere with a height

less than 2× the width, however the parameres of *A. cajennensis*, *A. angulata*, *A. vicina*, *A. yepocapa*, and *A. areata* are greater than 2×. The spine of the paramere may or may not present bristles. For those species in which the bristles are present, they may not present much variation in size, although their position is quite variable. *Agelaia angulata* present only a few scattered bristles on the base, whereas *A. multipicta* and *A. pallipes* present bristles all over, and are denser in *A. multipicta.* Interestingly, some species present only a few bristles on the margin, as in *A. areata*, *A. centralis*, and *A. yepocapa.* The apical angle of paramere is truncate for the most species, except *A. ornata* and *A. panamaensis*, in which it is rounded.

The aedeagus does not present much variation, being long and broad apically. In *Agelaia areata* and *A. cajennensis* the apical lobe is smaller, extending to the medial region (see fig. 1B, G). The teeth of the aedeagus deserve attention, although sometimes they are difficult to see in detail. In all species seen, the teeth extend ventrolaterally; three patterns of teeth distribution were found: (1) teeth stronger basally than apically (*A. angulata*, *A. areata*, *A. centralis*, *A. flavipennis*, *A. fulvofasciata*); (2) teeth stronger apically than basally (*A. cajennensis*); (3) teeth have the same size, from top to bottom (*A. multipicta*, *A. ornate*, *A. pallipes*, *A. panamaensis*, *A. testacea*, *A. vicina*, *A. yepocapa*). *Agelaia timida* has an aberrant aedeagus, which is very thick and with longer teeth, showing pattern 2 (stronger apically), however, Cooper (2000: 178: figs. 1–4) depicted two different aedeagus tips for *A. timida*, one from Mitu and other from Cutucu. We dissected the male genitalia of one specimen also from Mitu that seems very similar to that depicted by Cooper (2000), but the size of the teeth in his drawings is more even compared with ours. On the other hand, the aedeagus of the specimen from Cutucu is very different, compared with that found in Mitu. We did not have Cooper's specimens from Cutucu in hand, but the differences seen may suggest a new species allied to *A. timida*.

The cuspis and the digitus of the species of *Agelaia* do not present many differences, except in relation to the apical region, which may be wider or more acute, and in the distribution and density of bristles.

At the moment, it is difficult to present any general discussion about the male genitalia of *Agelaia*; however, based on the tree, it seems to show homoplasy, with states having multiple origins within the genus.

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APPENDIX 1

List of Characters of the Genus *Agelaia*

1. Hairs on eyes: **0,** long, dense; **1,** short, scattered, or absent.
2. Clypeus: **0,** touching the eyes; **1,** not touching the eyes.
3. Lateral margin of clypeus: **0,** straight; **1,** sinuous.
4. Apex of clypeus: **0,** rounded/truncate; **1,** acute.
5. Clypeus in profile: **0,** compressed; **1,** convex.
6. Punctation on clypeus: **0,** all over; **1,** present only on first ventral third.
7. Bristles on first ventral third of clypeus: **0,** absent; **1,** present.
8. Pubescence of first ventral third of clypeus: **0,** present; **1,** absent.
9. Distance between the tentorial furrow and internal margin of the eyes: **0,** less than subantennal suture; **1,** equal to or more than subantennal suture.
10. Subantennal suture: **0,** marked; **1,** weak.
11. Malar space: **0,** with a reticulate-coriaceous area; **1,** with a wholly dull to finely sculptured area.
12. Color of the malar space: **0,** dull; **1,** shinning.
13. Width of malar space: **0,** narrow; **1,** wide.
14. Gena: **0,** less than medial region of eyes; **1,** equal to or more than the medial region of eyes.
15. Pubescence of lower region of gena: **0,** present; **1,** absent.
16. Lower margin of gena: **0,** not dilated; **1,** dilated.
17. Upper region of gena: **0,** narrower than medial region; **1,** equal to or wider than medial region.
18. Palpal formula: **0,** 6:4; **1,** 6:3.
19. Bristles of frons and vertex: **0,** present, long; **1,** absent or very short, scattered.
20. Ocelli: **0,** in the same level at declivity of vertex; **1,** in a flattened area of vertex; **2,** anterior to declivity of vertex.
21. Interocellar space: **0,** not or slightly prominent; **1,** distinctly prominent.
22. Interocellar space: **0,** less than a diameter of the posterior ocelli; **1,** equal to or more than a diameter of the posterior ocelli.
23. Occipital carina: **0,** not emarginated on medial region; **1,** emarginated on medial region.
24. Posterior margin of head, dorsal view: **0,** same level of the eyes; **1,** above the eyes.
25. Pronotal fovea: **0,** oval; **1,** circular.
26. Pronotal fovea: **0,** in a wide concavity; **1,** in a shallow concavity.
27. Anterior margin of pronotal fovea: **0,** not prominent; **1,** prominent, not forming a carina**;** **2,** prominent, forming a carina.
28. Inferior margin of pronotal fovea: **0,** prominent; **1,** not prominent.
29. Pronotal carina: **0,** marked, evident; **1,** absent or evanescent.
30. Lateral margin of pronotum, dorsal view: **0,** subparallel; **1,** rounded.
31. Bristles on pronotum: **0,** present, long and dense; **1,** absent or short, scattered.
32. Humeri: **0,** rounded; **1,** slightly produced; **2,** moderately to strongly produced.
33. Carina of pronotal tubercle: **0,** along the entire tubercle, exceeding its lower end; **1,** not covering the length of the entire tubercle.
34. Carina of pronotal tubercle: **0,** on the anterior region; **1,** on the middle region; **2,** on the posterior region.

APPENDIX 1 *continued*

35. Carina of pronotal tubercle: **0,** nearly straight; **1,** angled.
36. Lateral carina of propleuron: **0,** along the entire margin; **1,** only on inferior region.
37. Inferior region of the lateral carina of propleuron: **0,** forming a projected lamella anteriorly; **1,** not forming a projected lamella anteriorly.
38. Dorsal mesepisternal plate: **0,** more than 1.5× longer than wide; **1,** equal to or less than 1.5× longer than wide.
39. Scutum, lateral view: **0,** slightly convex, projected medially to posteriorly; **1,** evidently convex, projected anteriorly.
40. Mesonotal lateral view: **0,** continuous; **1,** interrupted.
41. Medial scutellar line: **0,** evanescent; **1,** marked, not forming two lateral lobes; **2,** marked, forming two lateral lobes.
42. Metanotum: **0,** convex; **1,** compressed.
43. Carina on metapleural basal area: **0,** present; **1,** absent.
44. Carina of propodeum: **0,** absent; **1,** present, only on inferior region; **2,** present, extending longitudinally.
45. Longitudinal furrow on propodeum: **0,** present, weak; **1,** absent.
46. Propodeum, medial region: **0,** with a concavity; **1,** without a concavity.
47. Bristles on propodeum:**0,** present, long; **1,** absent or very short, scattered.
48. Tip of propodeal valvula: **0,** rounded; **1,** truncate; **2,** subtriangular.
49. Medial carina on propodeal valvula: **0,** absent; **1,** present.
50. Forecoxae: **0,** with bristles; **1,** bare.
51. External margin of forecoxae, frontal view: **0,** nearly straight; **1,** rounded.
52. Anterolateral region of forecoxae, frontal view: **0,** not projected; **1,** projected.
53- Forecoxae, lateral view: **0,** convex; **1,** compressed.
54. Wings, posterior vein of the third submarginal cell: **0,** straight; **1,** curved posteriorly.
55. Prestigma: **0,** longer than wide; **1,** as long as wide.
56. Apex of prestigma: **0,** truncate; **1,** rounded.
57. Tegula: **0,** not projected anteriorly; **1,** projected anteriorly.
58. Tegula: **0,** without a hyaline area; **1,** with a hyaline area.
59. Insertion of the ligament on tergum I: **0,** not prominent; **1,** prominent, carinate.
60. Tergum I, after spiracles: **0,** widelly gradually; **1,** subparallels.
61. Spiracles of tergum I: **0,** not projected; **1,** projected.
62. Position of the spiracles of tergum I: **0,** after anterior third; **1,** in anterior third.
63. Tergum I, medial to posterior region, dorsal view: **0,** slightly concave; **1,** straight.
64. Tergum I, after spiracles, lateral view: **0,** convex; **1,** rounded.
65. Bristles on tergum I: **0,** present, long; **1,** absent or very short.
66. Tergum II, posterior part, dorsal view: **0,** diverging gradually; **1,** diverging abruptly.
67. Tergum II, dorsal view: **0,** rounded; **1,** subparallels.
68. Nest: **0,** arboreal; **1,** in cavities.
69. Nest envelope: **0,** absent; **1,** present.

APPENDIX 2

Key to the Species of *Agelaia* Lepeletier

Modified from Cooper (2000, 2001) and Garcete-Barrett (personal commun.).

This key does not identify subspecies, for which see Richards (1978).

1. Dorsal pronotal carina obsolete or very weak (fig. 7A, B); pterostigma about 1.5–2× as long as wide (fig. 7E). Malar space of female with slightly concave, hairless, reticulate-coriarious area (fig. 8A). Male with aedeagus broader, pointed and not widened at apex and clypeus with inconspicuous pubescence. Terga without a posterior, yellowish band 2
– Dorsal pronotal carina developed (fig. 7C–7D); pterostigma about as long as wide (fig. 7F). Malar space of female without a concave area, wholly dull due to fine sculpturation and with scattered hairs (fig. 8B). Male with aedeagus narrower and widened at apex; clypeal pubescence more conspicuous. Terga with or without a posterior band 8
2. Lamellate anterior margin of pronotum very wide; tip of pterostigma obliquely truncate (fig. 7E). Dorsal pronotal carina very weak, visible (fig. 7B) 3
– Lamellate anterior margin of pronotum not very wide; tip of pterostigma usually more rounded (fig. 7F). Dorsal pronotal carina very weak, scarcely visible 5
3. Anterior margin of pronotum markedly sinuate below fovea (fig. 8C). Malar space of female about as long as height of antennal socket (fig. 8D). Forewind length 9.5–10.5 mm, mean 8.9
Amazon Basin of Ecuador and Peru, Brazil (Mato Grosso) . . . . . *A. lobipleura* (Richards)
– Anterior margin of pronotum feebly sinuate below fovea. Malar space of female about as long as two-thirds height of antennal socket 4
4. Forewing length 10.5–11.55 mm, mean 11.22. Proepisternum with hind end projecting in profile. Malar space of female about as long as height of antennal socket. Head black.
E. Andes of Bolivia . . . . . *A. imitatrix* Cooper
– Forewing length 8.75–9.8 mm, mean 8.96. Proepisternum with hind end not projecting in profile. Malar space of female about as two-thirds height of antennal socket. Head yellow with black markings.
Costa Rica, Pacific Coast of Colombia and Ecuador . . . . . *A. pleuralis* Cooper
5. Dorsal pronotal carina very weak; almost entirely yellow (fig. 8E), mesoscutum without distinct dark stripes (fig. 8F), terga largely brown (fig. 9A); forewing length ca. 11 mm; female with eye separated from clypeus.
Amazon Basin of Ecuador and Brazil, Guyane . . . . . *A. acreana* Silveira and Carpenter
– Dorsal pronotal carina obsolete; mesoscutum yellow with three distinct, dark stripes or brown with two narrow, yellow, discal stripes; terga from pale yellow to light brown, with sometimes marked yellow bands; forewingFW length 8.2–10.5 mm. Female with eye in contact with the clypeus 6
6. Labial palpi with four segments. Pronotum with longer hairs (fig. 9C); mesoscutum reticulate-coriarious and a little shining (fig. 9B); T1L/AW 1.65–2, mean 1.82. Nest a comb under a leaf covered by an envelope.
Amazon Basin of Colombia, Ecuador and Brazil, Guyane . . . . . *A. timida*. Cooper
– Labial palpi with three segments. Pronotum with short hairs, even pubescence only (fig. 9D); mesoscutum finely granulate and dull; T1L/AW 1.4–1.75, mean 1.55 7

7. Parastigma about 1.5× as long as wide (fig. 9E); female with eye narrowly separated from clypeus (fig. 10A). Extensively brown merging into yellow; mesoscutum brown or blackish brown with two narrow, yellow, discal stripes (fig. 10C).
   Amazon basin of Colombia and Ecuador ..... *A. brevistigma* (Richards)
– Parastigma about 1.75–2× as long as wide (fig. 9F); female with eye usually touching clypeus (fig. 10B). Yellow with brown to black maculation; mesoscutum yellow with three distinct black stripes.
   Mexico to Panama, Pacific Coast of Colombia and Ecuador, Amazon Basin of Colombia, Ecuador, Peru, Bolivia and Brazil, Trinidad, Guyanas, central and S.E. Brazil .... *A. cajennensis* (Fabricius)
8. Transverse carina beneath forewing projecting forwards beyond base of costa as a small point. Black (fig. 10D); with or without yellow maculation; forewing length 9–10.5 mm
   S.E. Brazil, Paraguay, N. Argentina ..... *A. vicina* (de Saussure)
– Transverse carina at base of forewing not projecting beyond costa 9
9. Dorsal pronotal carina lobate at sides (fig. 10E). Sides of tergum I divergent after spiracles (fig. 10F); female clypeus with coarse, scattered (fig. 11A) punctures on dorsal half; at least terga III–VI and sterna IV–VI entirely black (fig. 11B); forewing length 12–18 mm 10
– Dorsal pronotal carina not lobate at sides (fig. 7C and D), or if slightly lobate then terga brown and often with a yellow band (fig. 11C). Female clypeus smooth, without coarse punctures. If terga III–VI and sterna IV–VI entirely black then either; forewing length less than 12 mm or tergum I subrectangular after spiracles 15
10. Ground color of head and thorax, base of tergum II widely, whitish, yellow, or testaceous (fig.11E) 11
– Head and thorax black, with or without yellow maculation (fig. 11F); metasoma entirely black, sometimes with apex of tergum I and base of tergum II narrowly yellow 12
11. Workers with T1L/AW 2.2–2.4 and lateral margin of clypeus weakly sinuate (fig. 11A). Ground color of head and thorax whitish to pale yellow (fig. 12A). Forewing length 13.5–15.5 mm
   Guianas, lower Amazon basin ..... *A. constructor* (de Saussure)
– Workers with T1L/AW 1.6–1.7 and lateral margin of clypeus moderately sinuate (fig. 12B). Ground color of head and thorax yellow to testaceous (fig. 12C). Forewing length.16.5–18 mm
   entire Amazon basin ..... *A. testacea* (Fabricius)
12. Tibiae and tarsi entirely yellow (fig. 12D) 13
– Tibiae and tarsi black or blackish brown (fig. 12E), foretibia sometimes with a yellowish stripe 14
13. Scutellum and metanotum wholly or partly, two propodeal stripes yellow. Forewing length 13–16 mm
   Amazon basin of Colombia, Ecuador, Peru, Bolivia, Brazil, Guyana .....*A. ornata* (Ducke)
– Thorax entirely black .(fig. 12F). Forewing length 14–16 mm
   Colombia and Ecuador west of Andes, Brazil (Pará, Mato Grosso) .... *A. angulicollis* (Spinola)
14. Dorsal pronotal carina more lobate at sides; anterior pronotal carina usually very sharp in front of fovea (fig. 13A); T1L/AW of workers 1.7–2, mean 1.89. Forewing length 15–17 mm
   Widely distributed east of Andes from Venezuela to Paraguay and N. Argentina .... *A. angulata* (Fabricius)
– Dorsal pronotal carina less lobate at sides; anterior pronotal carina less sharp in front of fovea; T1L/AW of workers 1.68–1.88, mean 1.75. Forewing length 15–17 mm
   Mexico to Panama, N. and N.E. Colombia ..... *A. panamaensis* (Cameron)
15. Tergum I subsessile; in dorsal view conical or bulbous .....queens (part), 16

– Tergum I petiolate (fig. 11D) ..... queens (part), workers and males, 18

16. Tergum I conical. Forewing length ca. 9 mm. Nest associated with ants.
Amazon Basin of Colombia, Ecuador, Peru, Bolivia, central and southeastern Brazil, Guyana ... . *A. myrmecophila* (Ducke)

– Tergum I bulbous. Nest an exposed spiral comb 17

17. Lateral margin of clypeus sinuate; dorsal pronotal carina almost effaced in middle; mesepisternum with a large, ventral mark; forewing length ca. 10 mm
Mexico to W. Ecuador, Venezuela, premontane zone E. Andes of Colombia .... *A. areata* (Say)

– Lateral margin of clypeus little sinuate; dorsal pronotal carina well developed for entire length; mesepisternum without a ventral mark; forewing length ca. 11.5 mm
Venezuela, entire Amazon basin, Brazil (Mato Grosso, Goias) ..... *A. flavipennis* (Ducke)

18. Valvula with hyaline border narrow (fig. 13B). Margin of dorsal pronotal carina narrowly hyaline for most of length (fig. 7D); tegula sometimes produced in front (fig. 13C); tergum I subquadrate behind spiracles; ground color bright yellow (fig. 11D), head and thorax with sharply defined black maculation, but mesepisternum without a ventral mark, terga brown or blackish brown with a broad, posterior yellow band (fig. 13D); forewing length 10–11 mm (see couplet 17 ..... workers and males of *A. flavipennis* (Ducke)

– Valvula with hyaline border much wider (fig. 13E) 19

19. Anterior pronotal carina very strongly raised in front of fovea, so that fovea is at the bottom of a deep hollow. Tergum I subrectangular behind spiracles; blackish brown, with or without yellow maculation; forewing length 10.15–12.5 mm
Mexico to Costa Rica ..... *A. xanthopus* (de Saussure)

– Anterior pronotal carina not very strongly raised in front of fovea (fig. 13F) 20

20. Tegula produced into a point or process in front. Tergum I subrectangular behind spiracles; black or blackish brown, with or without yellow maculation and posterior half of mesepisternum below scrobal furrow with at most one or two yellow spots; forewing length 9.5–12 mm
E. Andes from Colombia to Bolivia 21

– Tegula not produced in front or if somewhat pointed, then yellow with extensive black maculation, posterior half of mesepisternum below scrobal furrow yellow and from west of Andes ..22

21 Lateral margin of clypeus more sinuous; apex of clypeus without an acute projection; punctation on clypeus all over; shape of pronotal fovea oval; anterior margin of pronotal fovea not forming a carina (Panama, Colombia, Ecuador..... *A. baezae* Richards
Lateral margin of clypeus straight; apex of clypeus with a small and acute projection; punctation on clypeus on first third; shape of pronotal fovea; anterior margin of pronotal carina forming a carina (Ecuador, Peru, Bolivia..... *A. cornelliana* (Richards)

22. Propodeal furrow with a fine, weak longitudinal carina; tergum I behind spiracles subrectangular; T1L/AW of workers 2.1–2.2. Black to blackish brown; terga 2–5 and sterna 2–4 with a posterior, sulphur-yellow band; forewing length 12–12.5 mm
E. Andes of Bolivia ..... *A. nebularum* Cooper

– Propodeal furrow ecarinate; sides of tergum I sometimes divergent after spiracles (fig. 14B); T1L/AW less than 2 23

23. Dorsal pronotal carina more raised, forming a distinct and usually blunt shoulder at sides (fig. 14C). Terga brown, sometimes blackish brown, often with a conspicuous, posterior, yellow band. Eyes with short hairs (fig. 14E); forewing length 10.5–14 mm
east of Andes 24

– Dorsal pronotal carina less raised, not forming a distinct shoulder at sides (fig. 14F). Eyes bare if terga brown and with a conspicuous band then from N. Colombia 25

24. Dorsal pronotal carina slightly lobate at sides. Workers and males: pronotum with outstanding hairs (fig. 14D); tergum I behind spiracles usually distinctly longer than apical width and with sides more divergent (fig. 14B); T1L/AW of workers 1.52–1–87, mean 1.7; of males 1.71–1.82; queen: T1L/AW 1.29–1.52, mean 1.45.
entire Amazon basin, Guianas, Brazil (Mato Grosso) ..... *A. fulvofasciata* (DeGeer)

– Dorsal pronotal carina less projecting at sides. Workers and males: pronotum without outstanding hairs (fig. 13F); length of tergum I behind spiracles about equal to apical width and sides little divergent (fig. 15A); T1L/AW of workers 1.5–1.68, mean 1 .55; of males 1.4–1.6; T1L/AW of putative queen 1.48. Nest assosciated with ants.
Amazon basin of Colombia, Ecuador, Peru, Brazil, Venezuela, Guianas ..... *A. hamiltoni* (Richards)

25. Metasomal segments IV–VI entirely black (fig. 15B); if ground color black then from Upper Amazon Basin 26

– Metasomal segments IV–VI not entirely black, at least sternum IV with some yellow maculation (fig. 15C); if ground color black then from S.E. Brazil 28

26. Eyes with short hairs; tegula usually pointed in front; all terga black, I–III with a yellow band; forewing length 9.8–11 mm
Mexico to Panama ..... *A. yepocapa* (Richards) (part)

– Eyes essentially bare with a few very short hairs (fig. 15D); tegula rounded in front (fig. 14A); if from Central America then terga I–III brown 27

27. TI L/AW of workers and males ca. 1.7. Coloration variable: metasoma entirely black (ssp. *cuzcoensis* (Schrottky) from Upper Amazon Basin) or terga I–II testaceous to brown and sometimes with a yellow band on terga II–III (ssp. *pallipes*
(Olivier) (fig. 15E); forewing length 9.8 – 11 mm
entire Amazon basin, Venezuela, Guianas, central and S.E. Brazil, Paraguay, N. Argentina .... *A. pallipes* (Olivier)

– T1L/AW of workers and males 1.4–1.6; terga I–III brown, II–III with a yellow band (fig. 15B); forewing length 7.35–9.3 mm
Costa Rica, Panama, Pacific coast of Colombia, Amazon basin of Colombia and Ecuador ... *A. melanopyga* Cooper

28. All terga brown (posterior terga sometimes with a blackish suffusion); with or without a yellow band (fig. 15F) 29

– Terga black or blackish (terga I–II sometimes brown); at least terga II–III with a yellow band (fig. 15C) 31

29. Eye essentially bare with a few very short hairs (fig. 16A). Terga sometimes with a complete, yellow band. forewing length 10–12.25 mm (see couplet 32)
Mexico to Panama, N. and W. Colombia, W. Ecuador ..... *A. centralis* (Cameron) (part)

– Eye with short hairs (fig. 16B). If some terga with a yellow band then this very narrow and usually interrupted.
east of Andes 30

30. Anterior pronotal carina in front of fovea more acute and with edge narrowly hyaline for a short distance (fig. 16C). Workers with clypeus brown or blackish (fig. 16B). forewing length 8.5–11 mm
Amazon basin of Colombia, Ecuador, and Peru ..... *A. pallidiventris* (Richards)

– Anterior pronotal carina, less acute in front of fovea, without a hyaline edge (fig. 16D). Workers with clypeus yellow (fig. 16E). Males with aedeagus abruptly dilated at apex. Forewing length 8.4–10.15 mm (see couplet 16) .....workers and males of *A. myrmecophila* (Ducke)

31. Eye essentially bare with a few very short hairs (fig. 17A). Length of tergum I behind spiracles distinctly more than apical width. forewing length 9–12.25 mm
Venezuela and east of Andes 32
– Eye with short hairs. West of Andes or if from Venezuela and E. Colombia then tergum I subquadrate behind spiracles 35

32. Anterior pronotal carina more acute in front of fovea; tergum I with spiracular tubercle less prominent and sides behind spiracles more evenly divergent. Mesepisternum below dorsal groove maculate, sometimes almost entirely black; terga black, at least terga 2–3 with a yellow band. Female clypeus black marked, sometimes almost entirely black (fig. 17A).
central and S.E. Brazil, Paraguay, N. Argentina 33
– Anterior pronotal carina less acute in front of fovea; tergum I with spiracular tubercle more prominent and sides usually less divergent before apex of tergum. Mesepisternum below dorsal groove entirely yellow. Terga 1–2 mainly brown or blackish, other terga black and all terga with a conspicuous yellow band. Female clypeus entirely yellow (see couplet 29)
E. Colombia, Venezuela, Trinidad, Guyana, Suriname, Paraguay ..... (part) 34

33. Bristles on first third of clypeus absent; gena less than eyes in profile, narrowing to top; ocelli at the same declivity of vertex; posterior margin of head at same level of eyes; humeri rounded.....
..... *A. anceps* (de Saussure)
– Bristles on first third of clypeus present (fig. 17A); gena more than eyes in profile, not narrowing to top (fig. 17B); ocelli in a flattened area at declivity of vertex; posterior margin of head above the eyes; humeri slightly produced ..... *A. multipicta* (Haliday)

34. Punctation on clypeus all over; width of gena more than eyes in profile, narrowing to top; ocelli at the same declivity of vertex; humeri less projected; tergum I concave; tergum II diverging abruptly posteriorly, subparallel ..... *A. bequaerti* (Richards)
– Punctation on clypeus only on first third (fig. 16A); width of gena less than half eyes in profile, not narrowing to top; ocelli anterior to the declivity of vertex; humeri more projected; tergum I almost flat; tergum II diverging gradually posteriorly, more rounded ..... *A. centralis* (Cameron)
– Smaller: forewing length 8.6–9.6 mm, mean 8.06; T1L/AW 1.5–1.6, mean 1.55. Mesepisternum below dorsal groove entirely yellow.
Colombia, Ecuador, Peru ..... *A. nigrescens* Cooper

35. Frontal line not more strongly impressed above interantennal prominence than on prominence itself; tegula rounded in front. Mesepisternum. below dorsal groove entirely yellow. Forewing length 9.6–10.15 mm
foothills W. Andes of Ecuador ..... *A. silvatica* Cooper
– Frontal line not more strongly. impressed above interantennal prominence than on prominence itself; tegula sometimes pointed in front. Mesepisternum below dorsal groove usually maculate. 36

36. Dorsal pronotal carina more raised at sides; valvula shorter with a narrower hyaline border; tergum I subquadrate behind spiracles. Males with lateral margin of clypeus less sinuate. Tergal bands broader. Forewing length 8.5–9.5 mm (see couplet 17) .....workers and males of *A. areata* (Say)
– Dorsal pronotal carina less raised at sides; valvula longer with. a broader hyaline border; tergum I longer, subrectangular or with sides divergent after spiracles. Males with lateral margin of clypeus more sinuate. Tergal bands narrower. Forewing length 9.8–11 mm (see couplet 26) .....
..... *A. yepocapa* (Richards) (part)

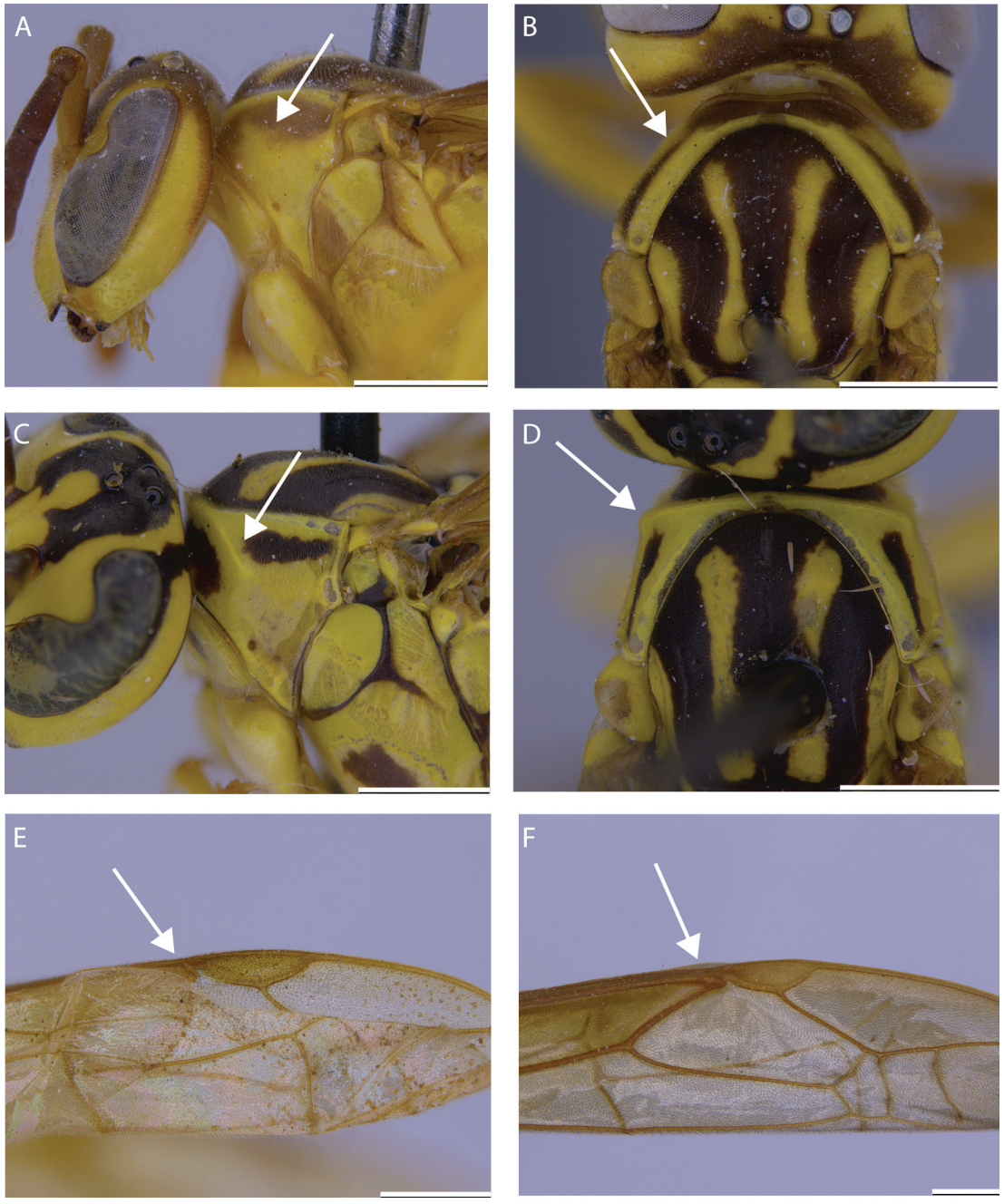

FIGURE 7. **A.** Dorsal pronotal carina obselete in *Agelaia cajennensis*; **B.** lateral view, pronotal carina obselete in *Agelaia cajennensis*; **C.** dorsal pronotal carina developed in *Agelaia. flavipennis*; **D.** lateral view pronotal carina developed in *Agelaia. flavipennis*; **E.** pterostigma about 1.5–2× as long as wide in *Agelaia lobipleura*; **F.** pterostigma about as long as wide in *Agelaia angulata*. Scale bars = 1 mm.

FIGURE 8. **A.** Malar space with slightly concave and reticulate-coriarious area in *Agelaia cajennensis*; **B.** malar space without a concave area, wholly dull due to fine sculpturation in *Agelaia angulata*; **C.** anterior margin of pronotum markedly sinuate below fovea in *Agelaia lobipleura*; **D.** malar space about as long as height of antennal socket in *Agelaia lobipleura*; **E.** dorsal pronotal carina, very weak; almost entirely yellow in *Agelaia acreana*; **F.** mesoscutum without distinct dark stripes in *Agelaia acreana.* Scale bars = 1 mm.

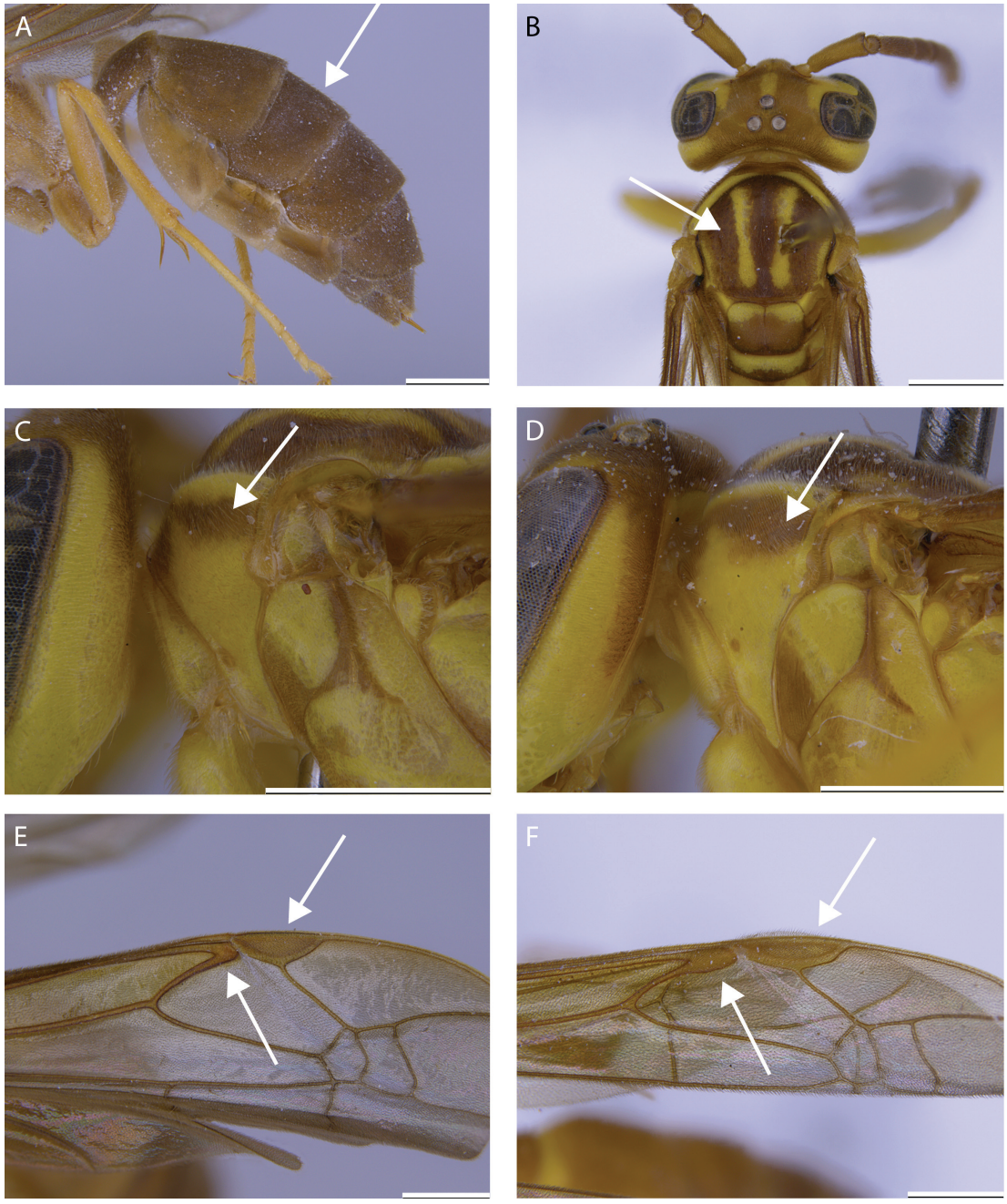

FIGURE 9. **A.** Terga largely brown in *Agelaia acreana*; **B.** mesoscutum reticulate-coriarious and a little shining brown with two narrow, yellow, discal stripes in *Agelaia timida*; **C.** pronotum with longer hairs in *Agelaia timida*; **D.** pronotum with short, even pubescence only in *Agelaia cajennensis*; **E.** parastigma about 1.5× as long as wide in *Agelaia brevistigma*; **F.** parastigma about 1.75–2× as long as wide in *Agelaia cajennensis*. Scale bars = 1 mm.

FIGURE 10. **A.** Eye narrowly separated from clypeus in *Agelaia brevistigma*; **B.** eye touching clypeus in *Agelaia cajennensis*; **C.** mesoscutum brown or blackish brown with two narrow, yellow, discal stripes in *Agelaia brevistigma*; **D.** metasoma entirely black in *Agelaia vicina*; **E.** dorsal pronotal carina lobate at sides in *Agelaia constructor*; **F.** sides of tergum I divergent after spiracles in *Agelaia constructor*. Scale bars = 1 mm.

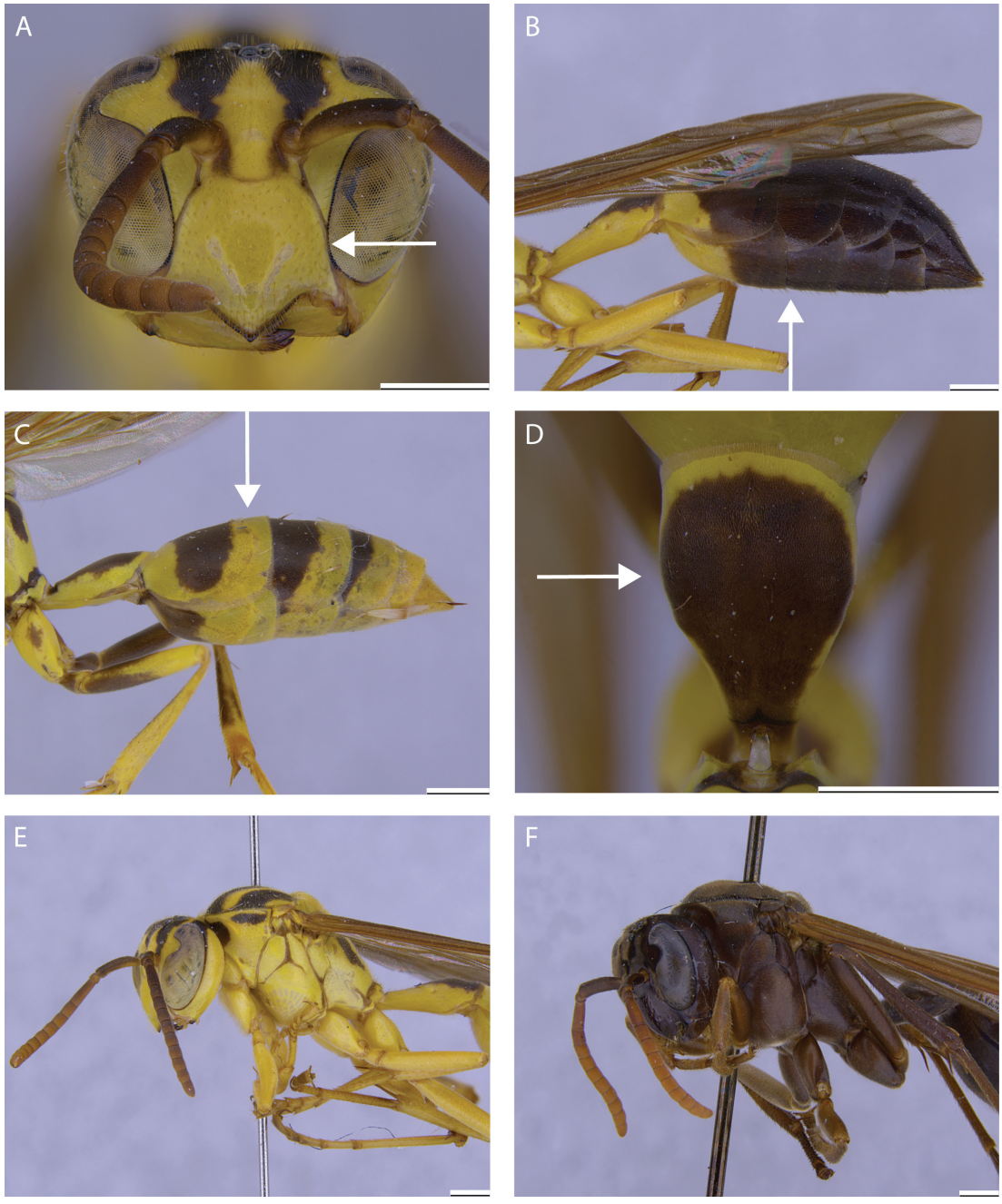

FIGURE 11. **A.** Clypeus with coarse, scattered and lateral margin weakly sinuate in *Agelaia constructor*; **B.** Terga III–VI and sterna IV–VI entirely black sinuate in *Agelaia constructor*; **C.** terga brown and often with a yellow band in *Agelaia. flavipennis*; **D.** tergum I petiolate in *Agelaia. flavipennis*; **E.** ground color of head and thorax, base of tergum II widely, whitish, yellow in *Agelaia constructor*; **F.** head and thorax black, with or without yellow maculation in *Agelaia angulata.* Scale bars = 1 mm.

FIGURE 12. **A.** Ground color thorax whitish to pale yellow in *Agelaia constructor*; **B.** lateral margin of clypeus moderately sinuate in *Agelaia testacea*; **C.** Ground Color of head and thorax yellow to testaceous in *Agelaia testacea*; **D.** tibiae and tarsi entirely yellow in *Agelaia angulicollis*; **E.** tibiae and tarsi black or blackish brown in *Agelaia angulata*; **F.** thorax entirely black in *Agelaia angulicollis.* Scale bars = 1 mm.

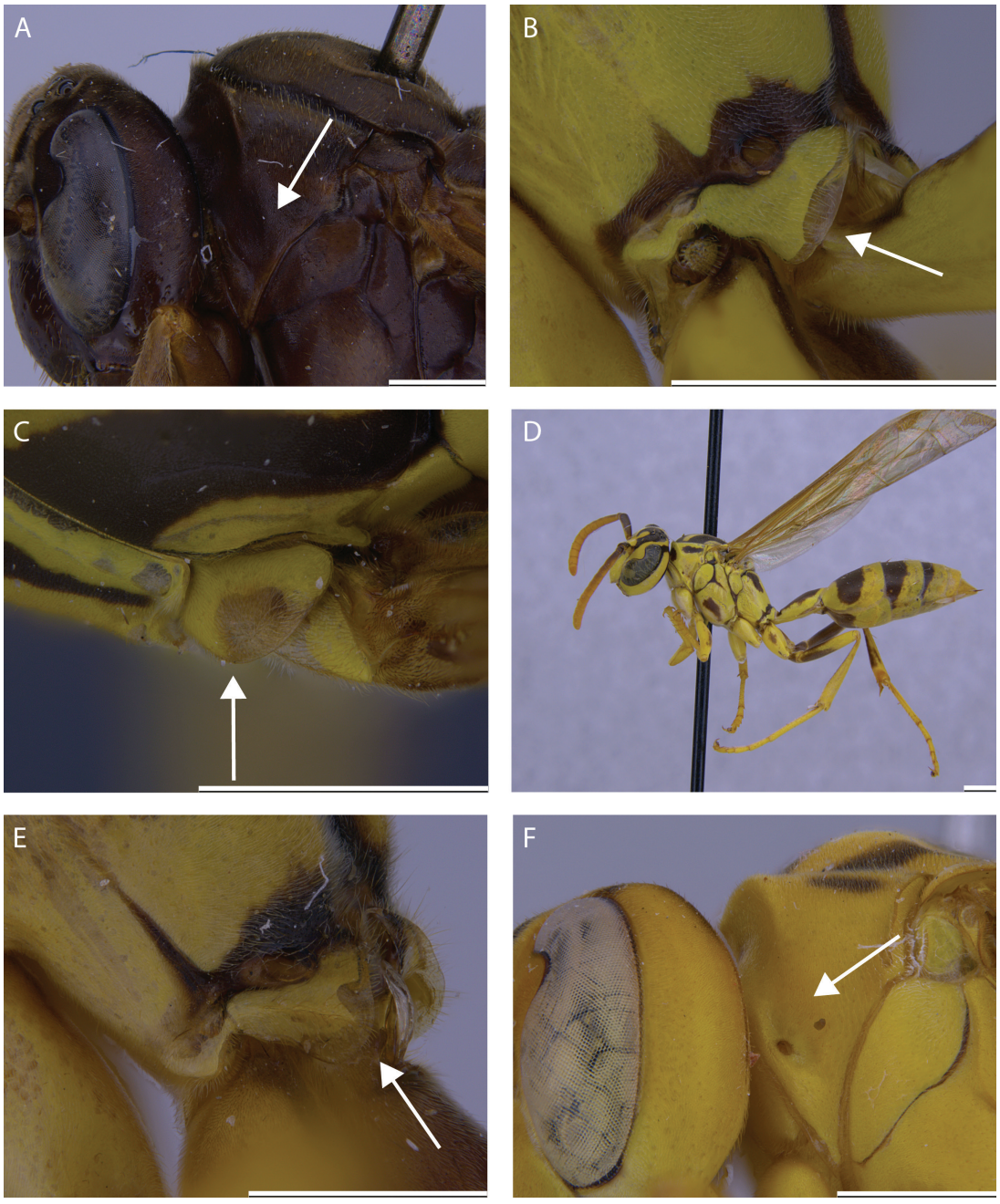

FIGURE 13. **A.** Pronotal carina less sharp in front of fovea in *Agelaia angulata*; **B.** valvula with hyaline border narrow in *Agelaia. flavipennis*; **C.** tegula produced in front in *Agelaia. flavipennis*; **D.** head and thorax with sharply defined black maculation but mesepisternum without a ventral mark in *Agelaia. flavipennis*; **E.** valvula with hyaline border much wider in *Agelaia fulvofasciata*; **F.** anterior pronotal carina not very strongly raised in front of fovea in *Agelaia hamiltoni*. Scale bars = 1 mm.

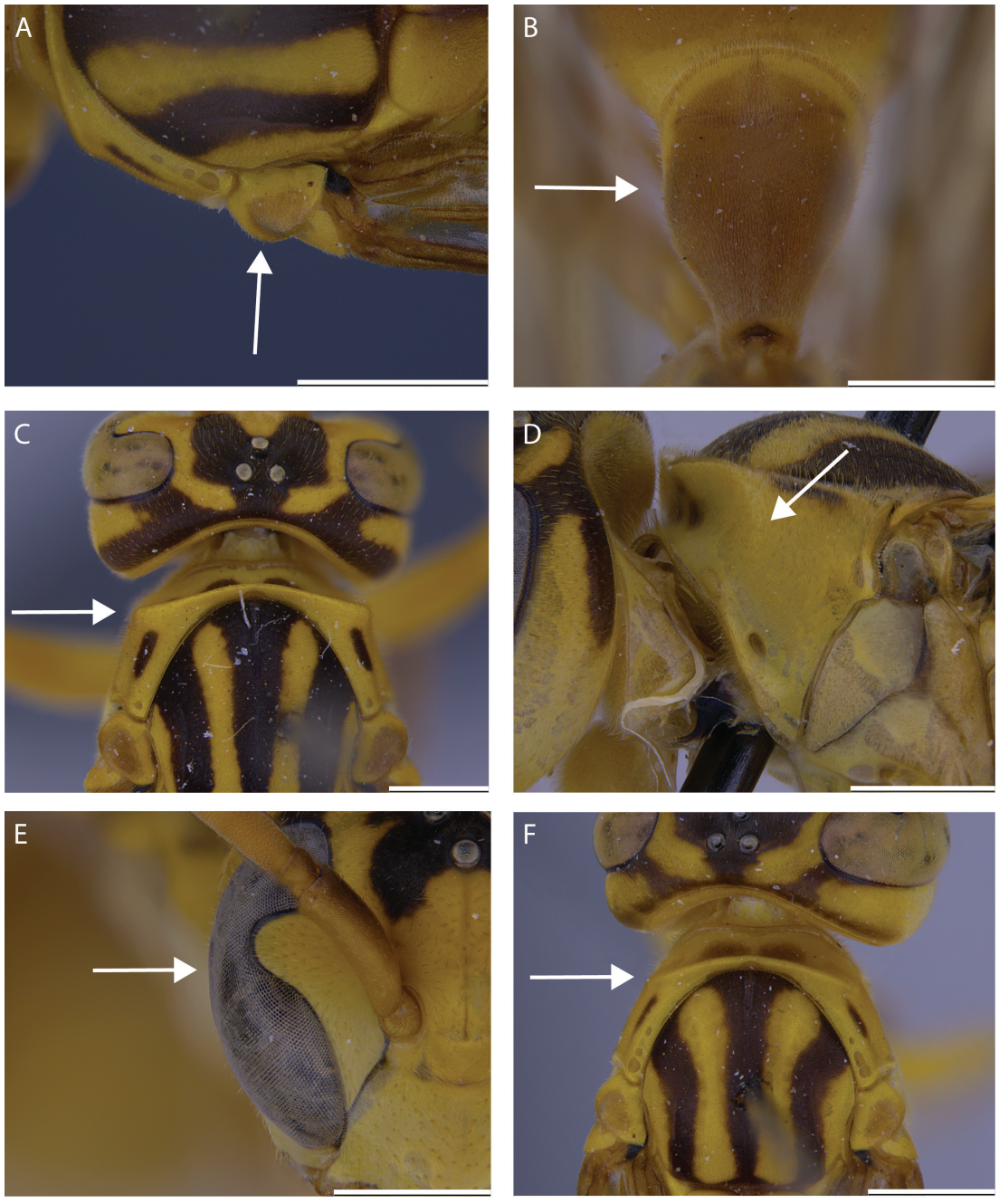

FIGURE 14. **A.** Tegula not produced in front or if somewhat pointed in *Agelaia pallipes*; **B.** tergum I divergent after spiracles in *Agelaia fulvofasciata*; **C.** dorsal pronotal carina forming a distinct and usually blunt shoulder at sides in *Agelaia fulvofasciata*; **D.** pronotum with outstanding hairs in *Agelaia fulvofasciata*; **E.** eyes with short hairs in *Agelaia fulvofasciata*; **F.** dorsal pronotal carina less raised, not forming a distinct shoulder at sides in *Agelaia pallipes*. Scale bars = 1 mm.

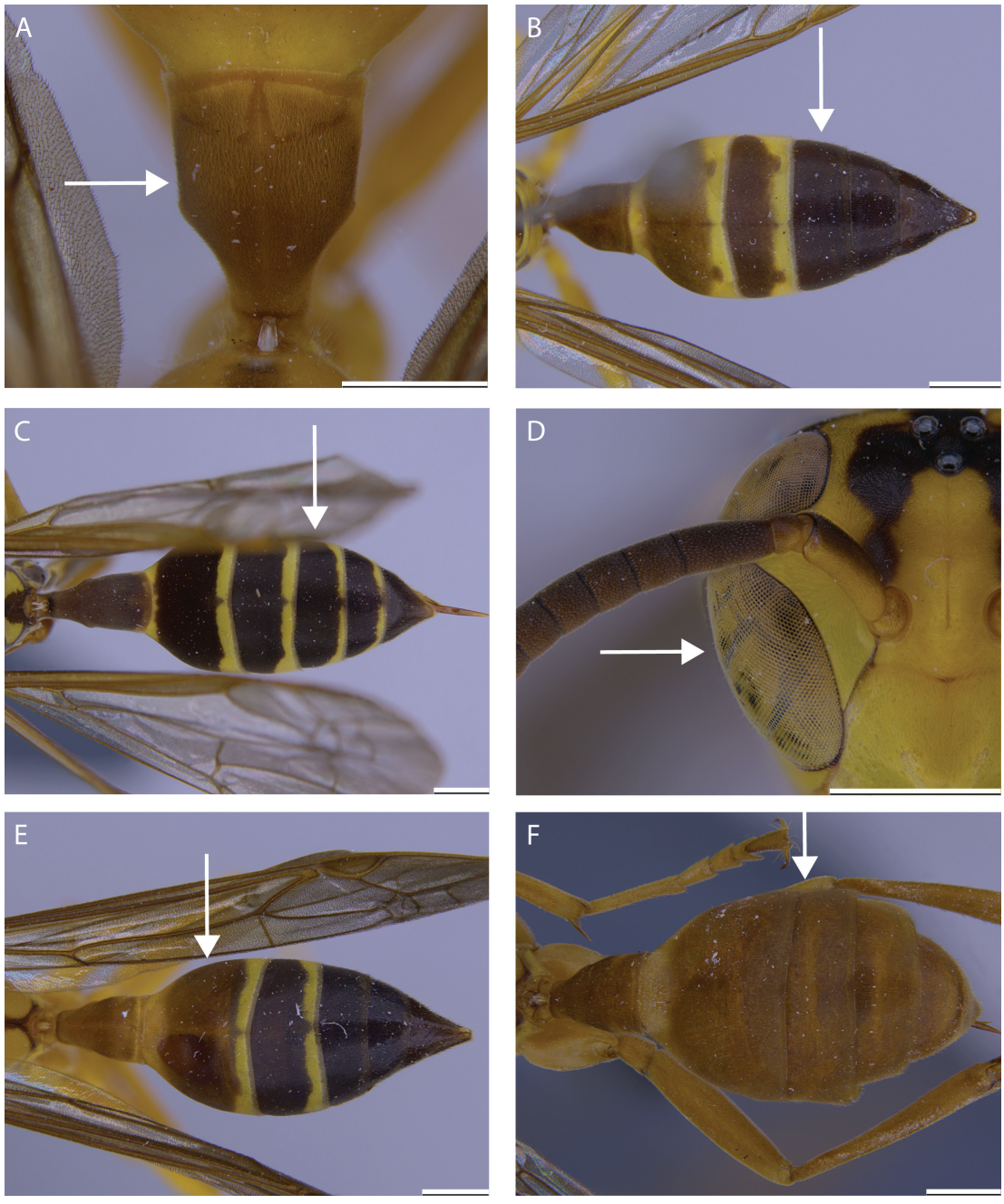

FIGURE 15. **A.** Tergum I behind spiracles about equal to apical width and sides little divergent in *Agelaia hamiltoni*; **B.** metasomal segments IV–VI entirely black in *Agelaia melanopyga*; **C.** metasomal segments IV–VI not entirely black, at least sternum IV with some yellow maculation in *Agelaia multipicta*; **D.** eyes essentially bare with a few very short hairs in *Agelaia pallipes*; **E.** terga I–II testaceous to brown and with a yellow band on terga II–III in *Agelaia pallipes*; **F.** all terga brown in *Agelaia centralis.* Scale bars = 1 mm.

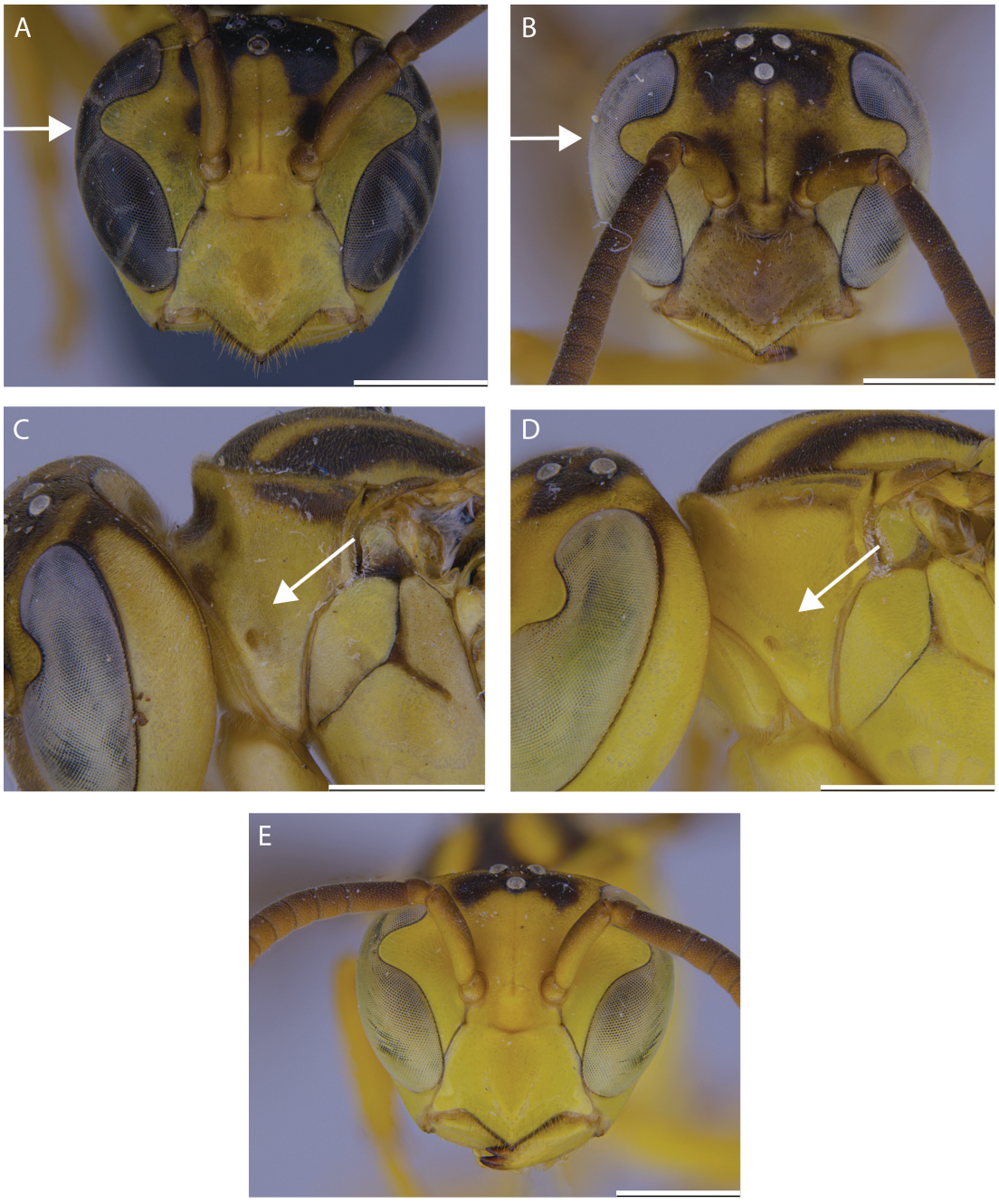

FIGURE 16. **A.** Eye essentially bare with a few very short hairs in *Agelaia centralis*; **B.** eye with short hairs and clypeus brown or blackish in *Agelaia pallidiventris*; **C.** pronotal carina in front of fovea more acute and with edge narrowly hyaline for a short distance in *Agelaia pallidiventris*; **D.** pronotal carina less acute in front of fovea, without a hyaline edge in *Agelaia myrmecophila*; **E.** clypeus with coloration yellow in *Agelaia myrmecophila.* Scale bars = 1 mm.

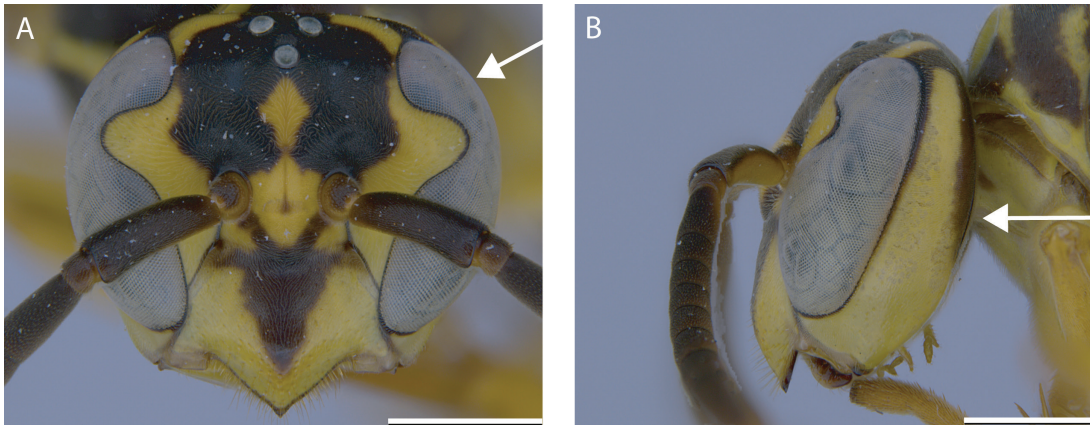

FIGURE 17. **A.** Eye essentially bare with a few very short hairs and clypeus black marked with bristles on first third in *Agelaia multipicta*; **B.** Gena more than eyes in profile, not narrowing to top in *Agelaia multipicta*. Scale bars = 1 mm.

APPENDIX 3

List of Species of *Agelaia* Examined

Agelaia angulata angulata: **Brazil**: cerrado, Mato Grosso State, 1 male* (BMNH); Porto Velho, Rondonia State, 6 female (DZSJRP-Hymenoptera); **Peru:** Previsto, 1 female (BMNH); Madre de Dios, 1 female (AMNH).

Agelaia angulata bertoni: **Argentina:** Missiones, Cataratas del Iguazu, 1 female [paratype] (BMNH).

Agelaia angulicollis: **Colombia**: Valle del Cauca, Anchicaya, 1female (BMNH).

Agelaia areata: **Ecuador:** Tungurahua, Yanayaca, 1 female (BMNH); **Guatemala**: S. Geronimo, 1 female (BMNH); **Panama:** Changuinola Dist. Boca Toro, 6 females and 1 male* (AMNH); **Venezuela:** Aragua, Rancho Grande, 1 female (AMNH).

Agelaia acreana: **Brazil:** Rio Branco, Acre State, 1 female [paratype] (AMNH).

Agelaia baezae: **Ecuador:**Napo Pastaza, Reventador, 1female (BMNH).

Agelaia brevistigma: **Colombia:** Huila, Las Cuervas de los Guacharos, 1 female (BMNH); Amazonas, Leticia, 1 female [paratype] (BMNH).

Agelaia cajennensis: **Brazil**: Base camp, Mato Grosso, 1 female (BMNH); [locality not specified], Mato Grosso, 1 female (BMNH); **Colombia:** Nariño, Barbacoa, 1 male* (BMNH).

Agelaia centralis: **Panama:** Vila de Chriqui, 1 female (BMNH); **British Guiana:** Mazaruni, 1 male* (BMNH); **Panama:** Canal Zone, Barro Colorado, 1 male* (AMNH).

Agelaia cornelliana cornelliana: **Peru:** Huaca pucllana, Rio Tarma, 1 female [paratype] (BMNH).

Agelaia cornelliana subterranean: **Bolivia**: La Paz, Chulumani, 1 female (BMNH); **Peru:** Cusco, Machu Picchu, 1 female (BMNH).

Agelaia centralis: **Panama:** Vila de Chriqui, 1 female (BMNH); Canal Zone, Barro Colorado, 1 male* (AMNH); **British Guiana:** Mazaruni, 1 male* (BMNH).

Agelaia constructor: **British Guiana:** Essequibo, 1 female (BMNH).

Agelaia flavipennis: **Brazil:** Gurupi, Goias State [presentely Tocantins State], 1 female (BMNH); Cristalandia, Goias State [presentely Tocantins State], 1 male* (BMNH).

Agelaia fulvofasciata: **Brazil**: locality not specified, Para State, 1 female (BMNH); Porto Velho, Rondonia State, 1 female (DZSJRP-Hymenoptera)]; **Suriname:** Marowijne River, 1 female (BMNH); **Surinam:** Paramaribo, 1 male* (AMNH).

Agelaia hamiltoni: **Brazil:** [locality not specified], Mato Grosso State, 1 female (BMNH); Manaus, Reserva Ducke, Amazonas State, 1 female [paratype] (BMNH)].

Agelaia humeralis: **Ecuador:** Tungarahua, 1 female (BMNH).

Agelaia imitatrix: **Bolivia:** La Paz, Coroico, 1 female [paratype] (BMNH).

Agelaia lobipleura lobipleura: **Brazil:** [locality not specified], Mato Grosso State, 2 females (BMNH).

Agelaia melanopyga: **Panama:** El cermeno, 1 female [paratype] (BMNH).

Agelaia multipicta: **Brazil:** Ribeirão Preto, Sao Paulo State, 1 female (BMNH); **Mexico:** Fortin Flores, 1 male* (AMNH).

Agelaia multipicta fulvanceps: **Colombia:** N. Sierra Nevada de S. Marta, 1 female (BMNH).

Agelaia myrmecophila: **Brazil:** Manaus, Amazonas State, 1 female (BMNH).
Agelaia nebularum: **Bolivia:** La Paz, Chulomani, 1 female [paratype] (BMNH).
Agelaia nigrescens: **Peru:** Junín, Quebrada, Mala Noche, 1 female [paratype] (BMNH).
Agelaia ornata: **Peru:** Cord. Azul, Previsto, 1 female (BMNH); **Colombia:** Meta, La Macarena, 1 male* (BMNH).
Agelaia panamaensis: **Guatemala:** Guatemala City, 1 female (BMNH); **Costa Rica:** San Jose, San Antonio de Escazú, 1 female (BMNH); [country not specified]: Moca, Guantalon, 1 male* (AMNH).
Agelaia pallidiventris: **Brazil:** Manaus, Amazonas State, 1 female (BMNH).
Agelaia pallipes pallipes: **Brazil:** Manaus, Amazonas State, 1 female (DZSJRP-Hymenoptera); Bebedouro, Sao Paulo State, 1 female (DZSJRP-Hymenoptera); **Peru:** Huanuco, Yanayacu, Rio Pachitea, 1 female (BMNH); **Argentina:** Missiones, Iguazu Nat. Park. 1 female (BMNH).
Agelaia pallipes cuzcoensis: **Peru:** Cord. Azul, Divisoria, 1 female (BMNH); Vale Chanchamayo, 1 male* (AMNH); **Bolivia:** La Paz, Chulumani, 1 female (BMNH).
Agelaia pallipes centralis: **Colombia:** Barbacoas, 1 female (BMNH).
Agelaia pleuralis: **Costa Rica:** Heredia, 1 female [paratype] (BMNH); **Brazil:** Campo, Mato Grosso State, 1 female (BMNH).
Agelaia silvatica: **Ecuador:** Pichincha, Nambillo, 1 female [paratype] (BMNH).
Agelaia testacea: **British Guiana:** [locality not specified], 1 female (BMNH); **Brazil:** Faz. Suia Missu, Serra Roncador, Mato Grosso State, 3 female (BMNH); **Ecuador:** Pompeya, 1 male*(AMNH).
Agelaia timida: **Ecuador:** Prov, Napo, 1 female [paratype] (BMNH); **Colombia:** Vaupes, Mitu, 1 male* (BMNH).
Agelaia vicina: **Argentina:** Missiones, P. N. Iguazu, 1 female (BMNH); **Brazil:** Itatiaia, Rio de Janeiro State, 1 female (BMNH); Poa [= Porto Alegre], Rio Grande do Sul State, 1 male* (AMNH).
Agelaia xanthopus melanotica: **[Costa Rica]:** Irazu, 1 female [paratype] (BMNH).
Agelaia xanthopus: note – M. de Buysson – 1903-333, 1 female (BMNH)
Agelaia yepocapa: **Mexico:** Cerro Zunil, 1 female (BMNH); [**Mexico]:** Omilteme, 1 male* (BMNH).

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