

**CONTRIBUTIONS
OF THE
AMERICAN ENTOMOLOGICAL INSTITUTE**

Volume 33, Number 3

ACROPYGA (HYMENOPTERA: FORMICIDAE)
OF THE WORLD

by

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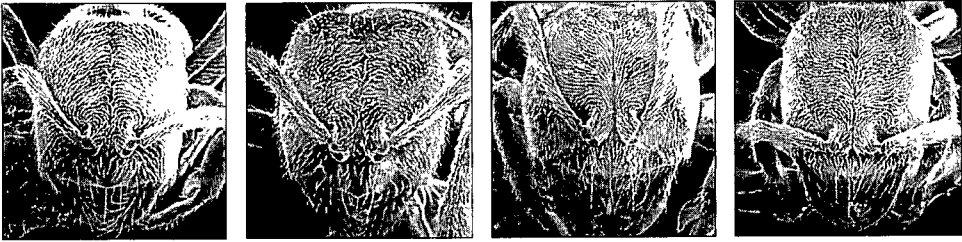
The American Entomological Institute
3005 SW 56th Avenue
Gainesville, FL 32608-5047

2004

ISSN: 0569-4450

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**To Daniel Otte, my mentor and friend,
whose example is an inspiration**



ACROPYGA (HYMENOPTERA: FORMICIDAE) OF THE WORLD

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ABSTRACT: The ant genus *Acropyga* is revised for the first time on a worldwide basis, revealing 37 species. Major taxonomic changes are instituted, including the synonymy of many species. Keys are provided for each caste where they are known, and line drawings and SEM micrographs are provided for workers and males of each species where they are known. Males are documented for the first time for most species and genitalic characters are used along with worker-based characters to construct a provisional species-level phylogeny. This phylogeny suggests that the genus evolved in the Old World, possibly in Africa. The subgenera are synonymized (*Atopodon*, *Malacomyrma*, and *Rhizomyrma*) and replaced with nine informal species-groups. Five species, however, remain unplaced because species-groups to a large extent are based on male genitalic characters. The natural history of the genus is reviewed, and the relationship between *Acropyga* and rhizoecine mealybugs is examined.

The following taxonomic changes are proposed: *ACUTIVENTRIS* SPECIES-GROUP: *acutiventris* Roger 1862 = *acutiventris javana* Karavaiev 1933, *acutiventris carinata* Karavaiev 1933, *crassicornis* Emery 1900, *flava* (Mayr 1862) (synonymy by Forel, 1894), *indosinensis* W.M. Wheeler 1935a, *moluccana* Mayr 1879, *moluccana australis* Forel 1902 (synonymy by Taylor, 1992), *moluccana mysolensis* Forel 1911a, *moluccana occipitalis* Stitz 1912, *moluccana papuana* Mann 1919, *moluccana opaca* Donisthorpe 1948, *undecema* (Donisthorpe 1949); *rubescens* Forel 1894, **NEW STATUS** = *acutiventris rubens* Forel 1911a (synonymy by Emery, 1925), *acutiventris bugnioni* Forel 1911c; *ARNOLDI* SPECIES-GROUP: *arnoldi* Santschi 1926 = *rhodesiana* Santschi 1928b (synonymy by Prins, 1982); *BUTTELI* SPECIES-GROUP: *butteli* Forel 1912c = *termitobia* Forel 1912, *amblyops* Forel 1915a, *meermohri* (Stärcke 1930), *distinguenda* Karavaiev 1933, *baodaensis* Terayama 1985; *inezae* Forel 1912; *nipponensis* Terayama 1985 = *jiangxiensis* Wang and Wu 1992; *DONISTHORPEI* SPECIES-GROUP: *donisthorpei* Weber 1944 = *oko* Weber 1944, *paludis* Weber 1944; *DECEDENS* SPECIES-GROUP: *decedens* (Mayr 1887); *fuhmanni* (Forel 1914) = *berwicki* W.M. Wheeler 1935b; *smithii* Forel 1893 = *kathrynae* Weber 1944, *urichi* Weber 1944; *goeldii* complex: *dubitata* (W.M. Wheeler and Mann 1914); *epedana* Snelling 1973; *exsanguis* (W.M. Wheeler 1909) = *wheeleri* Mann 1922, *bruchii* Santschi 1929, *paramaribensis* Borgmeier 1933, *robae* Donisthorpe 1936; *goeldii* Forel 1893 = *pachycera* (Emery 1906), *goeldii columbica* (Forel 1912b), *goeldii tridentata* (Forel 1912b), *marshalli* (Crawley 1921), *pickeli* Borgmeier 1927, *rutgersi* Bünzli 1935, *borgmeieri* Donisthorpe 1939, *quadriceps* Weber 1944, *trinitatis* Weber 1944; *parvidens* (W.M. Wheeler and Mann 1914) = *mesonotalis* Weber 1944; *MYOPS* SPECIES-GROUP: *ambigua* Emery 1922; *dubia* Karavaiev 1933; *kinomurai* Terayama & Hashimoto 1996; *lauta* Mann 1919; *myops* Forel 1910 = *indistincta* Crawley 1923; *sauteri* Forel 1912a; *PALLIDA* SPECIES-GROUP: *pallida* (Donisthorpe 1938); *PANAMENSIS* SPECIES-GROUP: *panamensis* Weber 1944; *YAEYAMENSIS* SPECIES-GROUP: *yaeyamensis* Terayama and Hashimoto 1996 = *guangxiensis* Terayama, Fellowes, and Zhou 2002, *yunnanensis* Terayama, Fellowes, and Zhou 2002; UNPLACED IN A SPECIES-GROUP: *guianensis* Weber 1944; *oceanica* Emery 1900 = *septemstruma* Terayama, Fellowes, and Zhou 2002; *paleartica* Menozzi 1936; *silvestrii* Emery 1915. *A. emeryi* Forel 1915b is transferred to the genus *Pseudolasius* and thus becomes an unresolved junior secondary homonym of *Pseudolasius emeryi* Forel 1911b. *A. major* Donisthorpe 1949 is considered a *nomen dubium* due to the condition of the type material. Nine new species are described: *DONISTHORPEI* SPECIES-GROUP: *tricuspis*, **NEW SPECIES**; *DECEDENS* SPECIES-GROUP: *goeldii* complex, *hirsutula*, **NEW SPECIES**; *keira*, **NEW SPECIES**; *palaga*, **NEW SPECIES**; *romeo*, **NEW SPECIES**; *MYOPS* SPECIES-GROUP: *gelasis*, **NEW SPECIES**; *hystrix*, **NEW SPECIES**; *PANAMENSIS* SPECIES-GROUP: *ayanganna*, **NEW SPECIES**; UNPLACED IN A SPECIES-GROUP: *stenotes*, **NEW SPECIES**.

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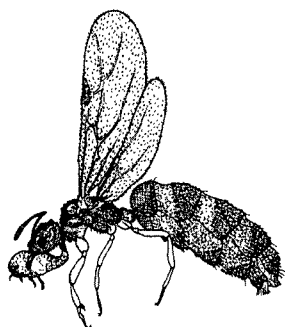
INTRODUCTION

The ant genus *Acropyga* is a fascinating group of formicine ants, found throughout the world in warm temperate and tropical areas. Their biology is especially interesting because of their intimate trophobiotic relationships with mealybugs (Hemiptera: Pseudococcidae) (figs. 1 & 2). In overall appearance, *Acropyga* are small, robust, yellowish ants that appear morphologically rather similar to each other.

The taxonomy of *Acropyga* has for some time been in a state of confusion and uncertainty. The small size of the ants, coupled with the fact that all species possess a thin, collapsible cuticle that can be significantly distorted upon drying has not helped the taxonomic situation. Creighton's (1950) remark about another small-sized, distortion-prone formicine genus, *Brachymyrmex*, as a "miserable little genus" could just as aptly be applied to *Acropyga*. A proliferation of isolated species descriptions has occurred without accompanying comparative work, and this has led to an abundance of synonyms and hindered discovery of new taxa. To make matters even more uncertain, both Agosti (1991) and Bolton (1995) have questioned the monophyly of the genus.

Though *Acropyga* are seldom encountered, either in the field or in research collections, as techniques in leaf litter sampling improve and grow in popularity, these ants will increasingly be collected and catalogued. With published collecting regimens such as the "Ants of the Leaf Litter" (ALL) protocol (Agosti *et al.*, 2001) actively advocating the use of leaf litter sampling techniques for biodiversity assessment purposes, it is hoped that more *Acropyga* specimens will become available for future study. Furthermore this study suggests that many new *Acropyga* species await discovery, especially in the tropics. Thus a worldwide taxonomic synthesis of the genus is much needed.

Taxonomic work on *Acropyga* has been hindered by a general lack of specimens available for study, and it is impossible to know how complete this study has been in terms of the total number of species actually present in the group. For example, my own fieldwork in Guyana, which made extensive use of leaf litter sampling techniques, found three new species from one remote locality (Mt. Ayanganna, Guyana). That study certainly raises the possibility that the genus might be much more diverse than is currently believed.



Figures 1 (left) & 2 (right). 1) Prin's (1982) depiction of an *A. arnoldi* queen carrying the mealybug *Eumyrmococcus scorpiodes* on her mating flight. This behavior has been termed trophophoresy. 2) Scanning electron micrograph of an *A. fuhrmanni* worker carrying a mealybug (*Neochavesia caldasiae*).

This is the first worldwide revision of the genus. Extensive use was made of scanning electron microscopy, since with the small size of most species the added depth of field and magnification of a scanning electron microscope (SEM) allowed for examination of characters not seen by past researchers. SEM micrographs are used to illustrate each species in the genus (workers and males when available for study). Additionally, a preliminary phylogeny of the genus is proposed and informal species-groups are defined (with the consequent synonymy of the subgenera). Morphological characters provided suggest that the genus is in fact monophyletic. A future study by LaPolla *et al.* (in prep) will further demonstrate the monophyly of *Acropyga* both with morphological and molecular data.

Many of the results of this revision of *Acropyga* should be viewed as provisional, since our understanding of many species remains very rudimentary. Longino (2002), in his revision of *Crematogaster* ants from Costa Rica, cited the steps Hillis (1988) considered in the progression of taxonomic knowledge, and those steps seem relevant to this study as well: 1) a typological phase when a number of species are described and the number of valid names increases; 2) a biological species phase when extensive synonymy of polytypic species is proposed and the number of valid names decreases, and 3) a phylogenetic species phase when the polytypic species are resolved into mosaics of closely related forms and the number of valid names increases once again. If this pattern holds true, then the present state of *Acropyga* taxonomy falls squarely within the biological species phase with the completion of this revision. I have proposed a large number of synonyms under variable species, and some of these undoubtedly will be shown by future work to consist of more than one species.

It is apparent that workers and queens of some species display a remarkable range of phenotypic variation in size and shape of various characteristics, both within populations and over large geographical areas. When examined in isolation this variation could be thought to indicate species-level differences (table 1 and fig. 3). This in part has led to the large number of synonyms found in the genus. Even antennal segment number is variable in *Acropyga* both within and between species (table 1). A single specimen may even display differing antennal segment numbers from one antenna to the other (figs. 3b & 3c). An interesting trend was that the highest observed antennal segment number in workers in any given species was always one less segment than the highest antennal segment number observed in conspecific males. Changes in antennal segment number occur at segments 3-5 (numbered with scape as 1st segment), and despite changes in segment number the relative length of the flagellum does not change proportionally to it (table 2). For

example, in *A. goeldii*, reduction from 11 to 10 segments occurs by fusion of segments 3 and 4. Further reduction to 9 segments entails fusion of segments 3, 4, and 5. This pattern appears to hold for all *Acropyga* species where variation in antennal segment number has been observed.

This study makes extensive use of male genitalic characters to define and stabilize species limits, and as more worker-associated males are discovered, some species definitions will need to be reevaluated. Efforts that focus on collecting nest series that include males will greatly contribute to furthering our understanding of *Acropyga* diversity. It is hoped that this study will contribute to efforts to identify *Acropyga* specimens and facilitate the description of new species within a comparative framework.

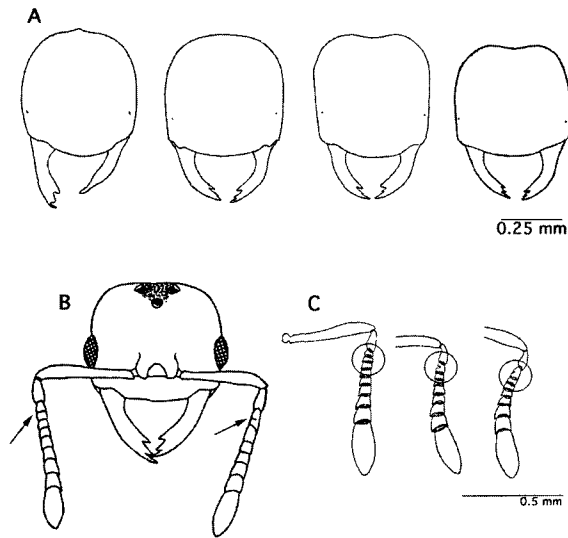


Figure 3. Variation observed within species. A) Bünzli's (1935) drawings of head shape variation observed in *A. exsanguis*. B) An *A. goeldii* queen with differing number of antennal segments on each antennae (modified from Weber, 1944). C) Antennae from three different *A. goeldii* workers depicting range of antennal segments possible in the species (modified from Bünzli, 1935)

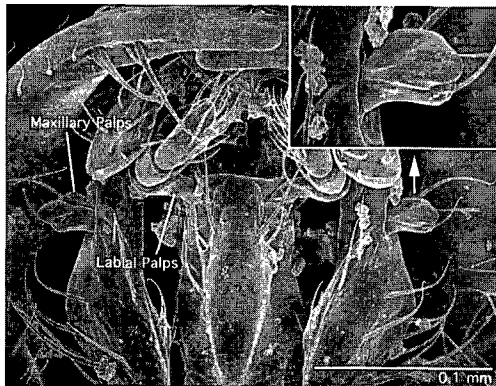


Figure 4. Variation observed in maxillary palp segment number of an *A. exsanguis* worker. Left maxillary palp with two well defined segments, right maxillary palp with second segment partially fused to first segment.

Taxonomic History of the Genus

The genus *Acropyga* was created by Roger (1862) with the description of *Acropyga acutiventris* from Sri Lanka. The two morphological characters that defined the genus at that time were 11-segmented antennae and reduced segmentation of maxillary and labial palps (2:3). Over the next 30 years only a handful of additional species were described in the genus, including *Acropyga decedens*, the first species known from the New World (though originally it was placed in the genus *Brachymyrmex*). In 1893 Forel created the first subgenus, *Rhizomyrma*, to accommodate species that had very low antennal segment counts compared with *A. acutiventris* (down to 7 segments in *A. smithii*). The subgenus *Atopodon* was later created by Forel (1912) to accommodate species that possessed a large, apically truncated basal tooth. Both *Rhizomyrma* and *Atopodon* were raised to genus level at different points, *Rhizomyrma* by Emery in 1906 and *Atopodon* by Forel in 1917. In 1922 Emery proposed the subgenus *Malacomyrma* and placed the newly described *A. silvestrii* in it. In 1925 Emery united the former *Acropyga* subgenera once again, with *Rhizomyrma* and *Atopodon* being returned to the genus. Brown (1973) suggested that the four subgenera of *Acropyga* were probably not valid divisions of the group, though he did not propose synonymy of those names. Agosti (1991), based on several ventral characters, implied that *Malacomyrma* should be raised to genus level, though the paper did not formally change the status of the subgenus. And Bolton (1995) suggested that the genus may in fact not be monophyletic, and therefore in need of division, though no specific recommendations were made.

Most species in the genus were described between 1900-1944, though since they were completed outside the context of any revisionary work on the genus, and largely without comparative study, many of those species are now recognized as synonyms. Of the 74 species and subspecies names proposed, only 28 are here recognized as valid taxa. The largest single work during the 1900-1944 period was that of Weber (1944). Weber made the first attempt to consolidate the growing number of described species of the New World fauna into a single publication. Unfortunately, he did not synonymize any species and himself contributed to a number of synonyms (out of ten species Weber described, all but three are recognized as synonyms in this study). He provided the only available key to the New World *Acropyga* species (and the only key to any part of *Acropyga*), but it proved unworkable as many of the couplets are contradictory. In the New World the only species described after Weber's work was *A. epedana* from southeastern Arizona by Snelling (1973).

In Asia several species continued to be described over the last two decades (Terayama, 1985; Wang and Wu, 1992; Terayama and Hashimoto, 1996; Terayama *et al.* 2002). These studies discovered some interesting species, including the bizarre looking *A. kinomurai* from Japan by Terayama and Hashimoto (1996). Terayama *et al.* (2002) recently revised part of the Oriental/Palaearctic fauna, but the study took a regional approach and artificially divided the fauna by geopolitical boundaries. As a result the 3 newly described species in that study are now considered synonyms, and the study failed to recognize other species in the area as invalid names. Proposed species names need to be applicable across a species range, and therefore faunistic treatments must be careful to avoid an artificially narrow perspective when elucidating species boundaries.

Overview of Natural History

It is the relationship that *Acropyga* have with mealybugs that arguably has elicited the most interest in the genus. All *Acropyga* are thought to be hypogaecic (living entirely underground), surviving primarily, it is believed, by "tending" mealybugs (Hemiptera: Pseudococcidae) on underground roots for their exudate (sometimes referred to as "honeydew") (Weber, 1944; Williams, 1998). This mutually beneficial relationship is called trophobiosis (Hölldobler and Wilson, 1990). Evidence suggests that all *Acropyga* species are obligate coccidophiles, that the ants are dependent

Taxon	workers		males	
	ASC	MTN	ASC	MTN
<i>acutiventris</i> spp. group	11	5	12	3-4
<i>acutiventris</i>	11	5	12	3-4
<i>rubescens</i>	11	5	12	4
<i>arnoldi</i> spp. group	11	6-9	12	5-6
<i>arnoldi</i>	11	6-9	12	5-6
<i>butteli</i> spp. group	11	4-5	12	4
<i>butteli</i>	11	5	12	4
<i>inezae</i>	11	4	12	4
<i>nipponensis</i>	11	5	12	4
<i>decedens</i> spp. group	7-11	3-5	9-12	1-3
<i>decedens</i>	9-11	4-5	12	3
<i>smithii</i>	7-8	4	9	2
<i>fuhrmanni</i>	8	4	9	1
<i>goeldii</i> complex	8-11	3-4	9-12	1-3
<i>dubitata</i>	?	?	11-12	2-3
<i>epedana</i>	10-11	3-4	12	2
<i>exsanguis</i>	8-9	3	9-10	1-2
<i>goeldii</i>	9-11	3-4	12	2-3
<i>hirsutula</i> , new species	11	4-5	12	3
<i>keira</i> , new species	9	3	11	2
<i>palaga</i> , new species	9-10	3	12	3
<i>parvidens</i>	9-11	4	?	?
<i>romeo</i> , new species	8-9	3-4	?	?
<i>donisthorpei</i> spp. group	11	3-5	12	2-3
<i>donisthorpei</i>	11	5	12	3
<i>tricuspis</i> , new species	11	3	12	2

<i>myops</i> spp. group	8-11	3-7	12	3-5
<i>ambigua</i>	9-11	5-6	?	?
<i>dubia</i>	11	6	?	?
<i>gelasis</i> , new species	11	6	?	?
<i>hystrix</i> , new species	11	6-7	12	5
<i>kinomurai</i>	10-11	4	?	?
<i>lauta</i>	8-9	5	?	?
<i>myops</i>	11	5	12	5
<i>sauteri</i>	11	3-4	12	3-4
<i>pallida</i> spp. group	9-11	5-7	12	4-5
<i>pallida</i>	9-11	5-7	12	4-5
<i>panamensis</i> spp. group	8-10	4-5	10-11	2-4
<i>ayanganna</i> , new species	10	5	11	4
<i>panamensis</i>	8	4	10	2
<i>yaeyamensis</i> spp. group	10-11	4	12	2
<i>yaeyamensis</i>	10-11	4	12	2
unplaced in spp. group				
<i>guianensis</i>	10-11	4-5	?	?
<i>oceanica</i>	7-8	4	?	?
<i>paleartica</i>	11	6-8	?	?
<i>silvestrii</i>	10-11	4-7	?	?
<i>stenotes</i> , new species	11	4	?	?

Table 1 (continued from pg. 6). Antennal segment and mandibular teeth number observed in *Acropyga* Species. Note that antennal segment numbers often vary not only among species but also within a species. Queen ASC and MTN are identical with that of the reported worker unless otherwise noted in species descriptions. ASC= antennal segment count; MTN= mandibular teeth number.

Taxon	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	Number Segments	Total Length
<i>palaga</i>	0.365	0.096	0.052	0.044	0.049	0.049	0.053	0.061	0.072	0.204	x	10	0.68
<i>palaga</i>	0.375	0.1	0.082	x	0.044	0.049	0.051	0.056	0.063	0.204	x	9	0.649
<i>palaga</i>	0.371	0.097	0.081	x	0.048	0.052	0.061	0.073	0.077	0.2	x	9	0.689
<i>goeldii</i>	0.467	0.112	0.04	0.041	0.043	0.043	0.045	0.045	0.053	0.094	0.23	11	1.213
<i>goeldii</i>	0.418	0.101	0.072	x	0.039	0.046	0.064	0.064	0.069	0.82	0.213	10	1.906
<i>goeldii</i>	0.428	0.104	0.11	x	x	0.042	0.046	0.054	0.069	0.071	0.205	9	1.129

Table 2. Antennal segment number variation. Antennal measurements for two species of *Acropyga* in which differing number of antennal segments has been observed within the species. Roman numerals represent antennal segment numbers; therefore I= scape through XI= segment 11.

on the mealybugs for survival (see table 3 for listing of *Acropyga* and their associated mealybugs). And though many ant species are known to harvest honeydew from hemipterans, *Acropyga* have taken the relationship further. Queens of eleven species have been observed emerging from their nests prior to their mating flight with a mealybug held in their mandibles (fig. 1) (Bünzli, 1935; Wheeler, 1935b; Brown, 1945; Eberhard, 1978; Prins, 1982; Buschinger *et al.*, 1987; Williams, 1998; Johnson *et al.*, 2001); the mealybug that each queen carries presumably serves as a “seed individual” from which a new generation of mealybugs will be started in the newly founded ant colony (Weber, 1944; Williams, 1998). This behavior has been termed trophophoresy by LaPolla *et al.* (2002), and queens that exhibit this behavior are said to be trophophoretic. Two species (*A. acutiventris*, Taylor, 1992; *A. sauteri*, Terayama, 1988) have been observed with queens that carried gravid female mealybugs on their mating flights, but otherwise nothing is known about the selection process by which a queen chooses an individual mealybug to be taken on her mating flight. Seifert & Heller (1999) reported a possible mistake by a queen (*A. palarctica*), which they observed carrying a worker pupa rather than a mealybug. Trophophoresy has only been observed in one other group of ants, a species in the genus *Tetraponera* (*T. binghami*, identified by Ward, 2001) (subfamily Pseudomyrmecinae) (Klein *et al.*, 1992), which is distinct from *Acropyga* both phylogenetically and ecologically.

The mealybugs utilized by *Acropyga* belong to the subfamily Rhizoecinae, and it is likely that the mealybugs are not able to survive independently of the ants (Williams, 1998). The complexity of the relationship between *Acropyga* and the mealybugs is not well understood, but it appears to be analogous to what has evolved between attine ants and the fungal species that they “farm.” In support of a close relationship between mealybug and ant, Flanders (1957) found that *A. fuhrmanni* stores its own eggs with those laid by the pseudococcids found in the nest. It has also been observed that *A. fuhrmanni* move mealybugs from underground chambers where roots are found to chambers without roots. Flanders (1957) speculated that this was done in order to regulate the amount of honeydew produced in a colony and to protect the roots from overuse by the mealybugs. LaPolla *et al.* (2002) observed that *A. epedana* also keeps mealybugs with brood. Furthermore even when a nest in captivity was starved, workers refused a variety of food items presented to them, suggestive that the ants are completely dependent on the mealybugs as a food source. Fossil evidence suggests that the trophobiotic behavior of *Acropyga* ants is an ancient one. Johnson *et al.* (2001) reported that *Acropyga* queens were discovered in Dominican amber, either holding a mealybug or with a mealybug nearby in the amber matrix. The amber was dated to the Miocene, so the intimate relationship of *Acropyga* and mealybugs is at least 15-20 million years old.

Ant species	Mealybug species	Trophophoresy
<i>A. acutiventris</i>	<i>Xenococcus acropygae</i> [3] <i>X. annandalei</i> [3]	X
<i>A. ambigua</i>	<i>Eumyrmococcus kusiacus</i> [3] <i>E. neoguineensis</i> [3] <i>X. acropygae</i> [3]	X
<i>A. arnoldi</i> #	<i>E. scorpiodes</i> [1]	X
<i>A. ayanganna</i> new species*#	mealybug morpho-1 [6]	
<i>A. decedens</i>	<i>Geococcus coffeae</i> [5] <i>Neochavesia</i> sp. [5] <i>Rhizoecus coffeae</i> [5]	X
<i>A. donisthorpei</i>	<i>Neochavesia weberi</i> [3]	
<i>A. epedana</i> *#	mealybug morpho-2 [6]	X?
<i>A. exsanguis</i>	<i>G. coffeae</i> [5] <i>N. caldasiae</i> [5] <i>Neochavesia</i> sp.(?) [5] <i>Pseudorhizoecus</i> sp. [5] <i>P. proximus</i> [5] <i>R. caladii</i> [5] <i>R. coffeae</i> [5] <i>R. falcifer</i> [5]	X
<i>A. fuhrmanni</i> *#	<i>Neochavesia</i> sp. (<i>eversii</i> ?) [5]	X
<i>A. goeldii</i>	<i>Capinsetella migrans</i> [5] <i>Dysmicoccus radialis</i> [5] <i>Neochavesia</i> sp. [5] <i>R. coffeae</i> [5]	X
<i>A. guianensis</i>	unidentified [5]	
<i>A. kinomurai</i> #	<i>E. kinomurai</i> [4]	
<i>A. lauta</i>	<i>E. kolombangarae</i> [3] <i>E. kusiacus</i> [3]	X
<i>A. nipponensis</i> #	<i>E. nipponensis</i> [2]	
<i>A. paleartica</i>	<i>E. corinthiacus</i> [5]	X
<i>A. panamensis</i> *#	mealybug morpho-3 [6]	
<i>A. parvidens</i> #	unidentified	X
<i>A. oceanica</i>	<i>Eumyrmococcus</i> sp. [3]	
<i>A. sauteri</i> *	<i>E. smithii</i> [3]	X
<i>A. smithii</i>	<i>G. coffea</i> [5] <i>N. eversi</i> [5]	

Table 3. *Acropyga* species known to be associated with mealybugs. If the species has also been observed to display trophophoretic behavior that box is marked with an “X”. *Acropyga* identities that I have confirmed with mealybugs are marked with “*”. *Acropyga* marked with a “#” are species for which voucher material is known to exist for ant and mealybug. Otherwise the identity of the *Acropyga* and the mealybugs must be considered questionable until actual vouchers are made. This table is largely derived from previously published literature with *Acropyga* names updated to follow taxonomic changes in this study. References: [1] Prins (1982); [2] Terayama (1986); [3] Williams (1998); [4] Williams and Terayama (2000); [5] Johnson *et al.* (2002); [6] D.J. Williams, personal communication.

Acropyga can survive in a wide range of habitats, from deserts to rainforests, though they do not seem able to survive in regions where temperatures below freezing persist for several months at a time. Some species, such as *A. pallida* and *A. silvestrii* for example, are found within a very wide range of habitats. Undoubtedly, the *Acropyga* lifestyle of existing below the surface buffers them against extremes of the outside environment. The small eyes, reduced antennae segmentation, lightly pigmented cuticle, and hairs covering the cuticle of *Acropyga* species are suggestive of a completely subterranean existence. Additionally, species display photophobic behavior (Weber, 1944; LaPolla *et al.*, 2002). *Acropyga* nests are found in leaf litter, under stones, in rotten wood (lying on or near the soil surface) and in the soil. Species in which nesting habits are known possess large nests, consisting of at least several thousand individuals, the structure of which is diffuse, with apparently no central nesting location (LaPolla *et al.*, 2002). Tunnels and indistinct chambers stretch out over large areas through the nesting medium. Polygyny has been suggested for several species. The origins of polygyny remains uncertain, but two routes are suggested based on field observations. Bünzli (1935) found both the occurrence of pleometrosis (founding of a colony by multiple queens) and the acquisition of young queens by established colonies in *A. exsanguis*.

MATERIALS AND METHODS

Sources of Material

Specimens were examined from and/or deposited in a number of research collections from around the world, and below follows the list of the institutions and individuals' collections that either contributed directly to this study and/or are depositories for *Acropyga* specimens. Codes for public institutions follow those proposed by Arnett *et al.* (1993), and are used throughout the rest of this work.

- ABPC: A. Buschinger Collection, Institut für Zoologie, Darmstadt, Germany
 AMNH: American Museum of Natural History, New York, USA
 ANIC: Australian National Insect Collection, CSIRO, Canberra, Australia
 BMNH: Natural History Museum, London, UK
 BPBM: Bernice P. Bishop Museum, Honolulu, Hawaii, USA
 CASC: California Academy of Sciences, San Francisco, California, USA
 CFRB: Chinese Academy of Forestry, Beijing, China
 HNHM: Hungarian Natural History Museum, Budapest, Hungary
 ICKH: Kadoorie Farm and Botanic Garden, Hong Kong, China
 IEGG: Istituto di Entomologia "Guido Grandi," Università di Bologna, Bologna, Italy
 INBC: Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica
 ISYC: Southwest Forestry College, Yunnan Prov., Kunming, China
 JSLC: J.S. LaPolla Collection, private collection
 JTLC: J.T. Longino Collection, Evergreen State College, Olympia, Washington, USA
 LACM: Natural History Museum of Los Angeles County, Los Angeles, California, USA
 MCSN: Museo Civico di Storia Naturale "Giamcomo Doria," Genova, Italy
 MCZC: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
 MHNG: Muséum d' Histoire Naturelle, Geneva, Switzerland
 MNHA: Museum of Nature and Human Activities, Hyogo, Japan.
 MZSP: Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil
 NHMB: Naturhistorisches Museum, Basel, Switzerland
 NHMV: Naturhistorisches Museum, Vienna, Austria
 NIAS: National Institute of Agro-Environmental Sciences, Tsukuba, Japan
 PSWC: P.S. Ward Collection, University of California at Davis, California, USA

SAMC: South African Museum, Cape Town, South Africa

SYPC: S. Yamane Collection, Kagoshima University, Kagoshima, Japan

UGBC: Centre for the Study of Biological Diversity, University of Guyana, Georgetown, Guyana

USNM: National Museum of Natural History, Washington DC, USA

Designation of Lectotypes

The International Code of Zoological Nomenclature requires that lectotypes designated after 1999 “contain an express statement of the taxonomic purpose of the designation” (ICZN, 1999). Throughout this revision I have designated lectotypes from syntypic series in order to provide nomenclatural stability. This is especially important in a genus such as *Acropyga*, because in all likelihood there will be taxonomic changes in the future that will change some species definitions from how they are defined here. By providing a lectotype a single specimen is now associated with a published name. Lectotypes are designated for the following species: *A. arnoldi*, *A. decedens*, *A. donisthorpei*, *A. dubitata*, *A. exsanguis*, *A. fuhrmanni*, *A. goeldii*, *A. guianensis*, *A. inezae*, *A. lauta*, *A. myops*, *A. oceanica*, *A. palearctica*, *A. parvidens*, *A. rubescens*, *A. silvestrii*. The specifics of each lectotype designation can be found under the species accounts section.

Analysis of Morphology

Illustrations of species were completed using a scanning electron microscope (Hitachi S-510), which enabled examination of characters not normally seen with traditional light microscopy. Measurements were made at various magnifications using a light microscope (Nikon SMU-Z) and were recorded to the nearest 0.001 mm. All measurements are given in millimeters, unless noted otherwise. Morphological terminology employed throughout follows Bolton (1994), with modifications where noted. Anatomical abbreviations are diagrammed in figs. 5-9 with definitions of a few elaborated here:

HL: Head length: the length of the head proper, excluding the mandibles; measured in full-face view from the midpoint of the anterior clypeal margin to a line drawn across the posterior margin from its highest points (to accommodate species where the posterior margin is concave).

HW: Head Width: the maximum width of the head in full-face view (excluding the portion of the eyes that extend past the lateral sides of the head).

SL: Scape Length: the maximum straight line of the antennal scape excluding the condylar bulb.

ML: Mesosoma Length: the length of the mesosoma (=alitrunk) in lateral view from the anterior mostpoint of the pronotum (including the “neck” of the pronotum) to the posteriormost point of the metapleuron.

GL: Gaster Length: the length of the gaster in lateral view from the anteriormost point of first gastral segment (third abdominal segment) to the posteriormost point of the acidopore.

TL: Total Length: HL+ML+GL.

CI: Cephalic Index: HW x 100/HL

SI: Scape Index: SL x 100/HW

Terminology referring to the inclination of hairs covering the cuticle is as follows: 1) *appressed*: referring to hairs that are flat or nearly flat relative to the surface of the cuticle. 2) *suberect*: referring to hairs that are at an angle from about 45° to 75° relative to the surface from the base through the tip of the hair. 3) *erect*: hairs that are perpendicular or nearly perpendicular to the surface from the base through the tip of the hair. I have dispensed with the terms subdecumbent and decumbent (following Wilson, 1955) because the exact declination of hairs can be difficult to ascertain in *Acropyga* ants and broader terms seem more practical. Subdecumbent hairs are in-

cluded within the term suberect and decumbent hairs within the term appressed.

Mandibular characters are extensively used to diagnose species, but these can be difficult to assess when the mandibles are held close to the head or if dental abrasion has taken place. In such cases, it may be necessary to dissect out the mandibles to examine them properly. Various terms have been employed to describe characteristics of the mandibles. The *number of teeth* on a mandible is given from, and including the apical tooth through, and including, the basal tooth (see fig. 7). Therefore, for example a reference to the 3rd tooth indicates the third tooth from the apical tooth. The *masticatory margin* is defined as the outline from the apical tooth through to the basal tooth. The *inner mandibular margin* is defined as the dorsal outline of the mandible running from the mandibular insertion point to the base of the basal tooth. The short margin from the base of the basal tooth to the apex of the basal tooth is referred to as the *basal tooth margin* when it is distinct from the inner mandibular margin. See fig. 7 for further explanation.

The *metanotal area* (see fig. 6) is defined as the depressed area between the mesonotum and the propodeum. In *Acropyga* species this area is said to be distinct when both the mesonotal and propodeal sulci are present on the dorsum; when one or both of the sulci are not present the area is said to be indistinct. In most species it is typically not very deeply impressed and variation of this character within a species is common.

As previously discussed, the thin cuticle makes *Acropyga* specimens particularly vulnerable to shrinkage upon drying. Though total length and gaster lengths are provided, they should be viewed as potentially imperfect measurements. Every effort has been made to properly measure structures, but in species for which only a few specimens were available for measurement, the gaster and total length figures could be unreliable. If a species matches a description in every aspect except total or gaster lengths, consider that it could be a result of cuticular deformation.

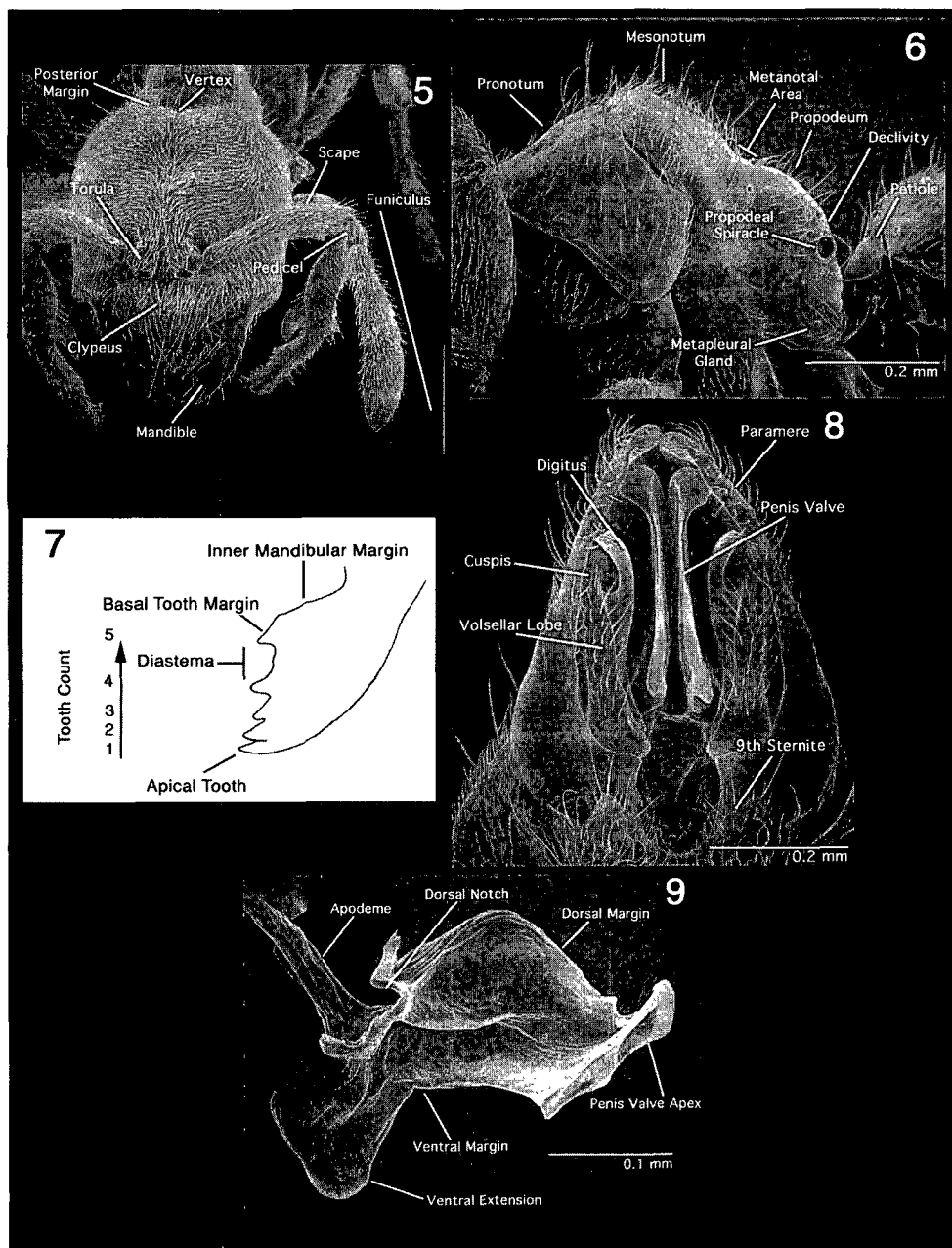
Biogeography

Biogeographic regions follow those outlined in Bolton (1994), who defined 8 regions as follows: Afrotropical (all of sub-Saharan Africa and the southern half of the Arabian Peninsula), Australasian (Australia, New Caledonia, and New Zealand), Indo-Australian (Malay Peninsula, Phillipines, East Malaysia, Indonesia, including New Guinea, and the islands of the Pacific Ocean), Malagasy (Madagascar and surrounding islands), Nearctic, Neotropical, Oriental (Pakistan, Sri Lanka, the Indian subcontinent to the Himalayas, southern China and Taiwan, Myanmar, Thailand, Cambodia, Laos, and Vietnam), and Palaeartic.

Species distribution maps are based on specimens I have examined and occasionally on reliable accounts from the literature. Specimens with imprecise label data are not included on the maps. Distribution maps are intended to provide a general impression of species ranges, but it must be remembered that the exact range of no *Acropyga* species is well understood. For some abundant species, such as *A. acutiventris* and *A. myops*, not every specimen locality is mapped, due to constraints of map scale. Precise locality data for every specimen examined is provided under the material examined section. Maps are based on the Winkel Tripel cartographic projection style.

Inference of Species Boundaries

Species boundaries were inferred on the basis of discrete morphological gaps among specimens. These morphological gaps were considered to indicate the occurrence of reproductive isolation, and in that sense, I have employed a biological species concept in this revision. Male genital characters proved extremely useful in helping refine the boundaries of species when they were available for study, and in groups of species where workers are highly variable, males will probably provide the only morphological criteria to test questions of conspecificity. I have taken a conservative approach in inferring species boundaries. In species that exhibit a high degree of morphological variation, I have made note of the observed variation, but without other forms of



Figures 5-9. Various morphological features of *Acropyga*: 5) head; 6) mesosoma; 7) mandible; 8) genitalia in ventral view; 9) penis valve in lateral view.

evidence suggesting there are different species present (e.g. male genitalic characters), I have “lumped” that variation under a single variable species (for example see *A. goeldii*). It may well be found by future work that some of these “lumped” species are in fact several distinct species. Species should be viewed as working hypotheses (sensu Ward, 2001) that can and should be tested with further morphological data, as well as possibly with molecular, protein, behavioral, ecological, and other forms of data.

Phylogenetic Analysis

Since the genus was in need of reorganization, a phylogenetic analysis was completed to allow for the creation of clade-based species-groups, and to try to ascertain the origins of this widespread genus. Character state designations given below have no significance with respect to polarity. The morphological characters and their alternative states are as follows:

Worker

- 1) Mandibular teeth: (0) 7 and more teeth possible; (1) 7 and/or fewer teeth possible.
- 2) Antennal segment number: (0) 12; (1) 11 only; (2) 11 and fewer.
- 3) Mandibular hairs: (0) more than 15 hairs on dorsal surface; (1) fewer than 15 hairs on dorsal surface.
- 4) Third mandibular tooth: (0) not smaller than neighboring teeth; (1) smaller than neighboring teeth.
- 5) Mandibular form: (0) mandible not at right angle to anterior clypeal margin; (1) mandible at right angle to anterior clypeal margin.
- 6) Mesosomal hairs on pronotum: (0) simple; (1) denticulate.
- 7) Head shape overall: (0) rectangular to subrectangular to square; (1) distinctly rounded.
- 8) Palp formula: (0) not greater than 3:3; (1) greater than 3:3.
- 9) Torulae: (0) open; (1) tubular.
- 10) Propodeal spiracle: (0) not large and round; (1) large and round.
- 11) Eye size: (0) greater than 30 facets; (1) less than 30 facets.

Male

- 12) Antennal segment number: (0) 13; (1) 12; (2) 12 and fewer.
- 13) Mandibular teeth: (0) more than 3; (1) 3 or fewer.
- 14) Body color: (0) light yellow to brownish yellow; (1) dark brown to blackish.
- 15) Paramere shape: (0) rounded; (1) rectangular.
- 16) Digitus apex: (0) not anvil-shaped; (1) anvil-shaped.
- 17) Digitus teeth: (0) peg-like teeth at apex; (1) peg-like teeth laterally placed; (2) no teeth present.
- 18) Digitus orientation: (0) erect; (1) bent toward cuspis.
- 19) Cuspis and digitus: (0) cuspis much shorter than digitus; (1) cuspis and digitus about the same length.
- 20) Volsellar shelf (region from which digiti and cuspi arise caudally): (0) absent; (1) present.
- 21) Penis valve: (0) ventrally with clearly visible teeth; (1) ventrally without clearly visible teeth.
- 22) Penis valve shape: (0) triangular; (1) round; (2) subrectangular; (3) rectangular.
- 23) Penis valve apex: (0) dorsal margin straight at apex; (1) dorsal margin bent downward at apex.
- 24) Penis valve ventral extension: (0) absent; (1) present and ventrally rounded; (2) present and ventrally square-shaped; (3) as in *A. yaeyamensis*.
- 25) Penis valve dorsal notch: (0) absent; (1) present.
- 26) Penis valve dorsal slit: (0) absent; (1) present.
- 27) Penis valve apodeme: (0) not thin; (1) thin.
- 28) Penis valve apex: (0) not laterally expanded and flattened; (1) laterally expanded and flattened.

CHARACTERS	
SPECIES	0000000001111111112222222222 1234567890123456789012345678
<i>Anoplolepis custodiens</i>	01011001000101001010?000000
<i>Prenolepis imparis</i>	0001100100000100200000100000
<i>Acropyga acutiventris</i>	1101000011110000100100000000
<i>A. arnoldi</i>	0101110111110000010010000000
<i>A. ayanganna</i>	1211000011121000100001000010
<i>A. butteli</i>	1100110011110000100010000100
<i>A. decedens</i>	1200000011111000011010000000
<i>A. donisthorpei</i>	1101101011111001001000100000
<i>A. dubitata</i>	???????011121011011013021001
<i>A. epedana</i>	1210000011111011011013010001
<i>A. exsanguis</i>	1210000011121011011013010001
<i>A. fuhrmanni</i>	1210000011121011011012000000
<i>A. goeldii</i>	1210000011111011011013010001
<i>A. hirsutula</i>	???????011111011011013021001
<i>A. hystrix</i>	1101100011110100000000000000
<i>A. inezae</i>	1100110011110000100000000100
<i>A. keira</i>	1210000011121011011013010001
<i>A. myops</i>	1101100011110100100000000000
<i>A. nipponensis</i>	1100110011110000100000000100
<i>A. palaga</i>	1210000011111011011013010001
<i>A. pallida</i>	1200100011110000000000000000
<i>A. panamensis</i>	1210100011121000100001000010
<i>A. rubescens</i>	1101000011110000100100000000
<i>A. sauteri</i>	1100000011110100100000000000
<i>A. smithii</i>	1210000011121001011012000000
<i>A. tricuspis</i>	1100101011111001001000100000
<i>A. yaeyamensis</i>	12000000111110010?1000030000

Table 4. Morphological character matrix. Numbers for characters and character states correspond to those found in the materials and methods section.

Only taxa for which at least males were available for study were included in phylogenetic analyses (see table 4 for list of taxa and character states attributed to them). Cladistic analysis based on maximum parsimony was carried out using heuristic searches in PAUP 4.0b10 (Swofford, 2002). All characters were equally weighted. Pseudoreplicate reweighting was also completed (Kjer *et al.*, 2001), by generating 1000 "fast" bootstrap trees and using those trees to reweight according to RC (rescaled consistency index). After reweighting, a heuristic search was employed. A final analysis was completed by iteratively reweighting each character by its RC until a constant tree length was attained (Farris, 1969). Characters that had multiple states were scaled in all sets of analyses according to their base weight (scaled equal weighting option in PAUP).

All characters were unordered. In each analysis, *Anoplolepis custodiens* and *Prenolepis imparis* were used as outgroups. To assess nodal support, bootstrap analyses were performed for each separate analysis, consisting each time of 100 bootstrap replicates, 10 replicates per bootstrap replicate. A maximum of 1000 trees was set for each bootstrap replicate.

DESCRIPTION OF THE GENUS *ACROPYGA*

Acropyga Roger, 1862: 242. Type species: *Acropyga acutiventris*, by monotypy.

= *Atopodon* Forel, 1912: 771. As subgenus of *Acropyga*. **NEW SYNONYM**. Type species: *Acropyga (Atopodon) inezae*, by subsequent designation of W.M. Wheeler, 1913: 100. *Atopodon* as subgenus of *Rhizomyrma*, Forel, 1917: 249; *Atopodon* raised to genus, W.M. Wheeler, 1922: 695; *Atopodon* subgenus of *Acropyga*, Emery, 1925: 30. *Atopodon* provisional junior synonym of *Acropyga*, Brown, 1973: 173 (unconfirmed).

= *Malacomyrma* Emery, 1922. As subgenus of *Acropyga*. **NEW SYNONYM**. Type species: *Acropyga (Malacomyrma) silvestrii*, by monotypy. *Malacomyrma* provisional junior synonym of *Acropyga*, Brown, 1973: 173 (unconfirmed).

= *Rhizomyrma* Forel, 1893: 347. As subgenus of *Acropyga*. **NEW SYNONYM**. Type species: *Acropyga (Rhizomyrma) goeldii*, by subsequent designation of W.M. Wheeler, 1911: 172. *Rhizomyrma* raised to genus, Emery, 1906: 182; maintained as genus by Forel, 1912b: 89 and Forel, 1917: 249. *Rhizomyrma* as subgenus of *Acropyga*, Emery 1925: 29. *Rhizomyrma* provisional junior synonym of *Acropyga*, Brown, 1973: 173 (unconfirmed).

Characters marked with an (*) are considered synapomorphies for the genus.

WORKER:

- 1) Small, robust, yellow to brownish-yellow (to occasionally slightly reddish-yellow) formicine ants (Total length up to 5 mm as found in *A. rubescens*, typically however most species smaller, around 2 mm in total length).
- 2) Monomorphic.
- 3) Cuticle seemingly always thin, shrinkage and collapsing of cuticle commonly observed in specimens.
- 4) *Antennae incrassate (apical segment always the largest and thickest) with 7-11 segments.
- 5) Surface of scapes and flagellae covered in thick layer of appressed hairs.
- 6) *Torulae tubular and elongated, touching posterior clypeal margin, typically closely set together (only in *A. kinomurai* are torulae very widely separated from each other); small triangular area between torulae.
- 7) *Median portion of anterior clypeal margin always with a single hair; length of hair highly variable, sometimes surpassing apex of closed mandibles.
- 8) Mandibles variable, narrow to broad, with 3-9 teeth possible, though if with more than 6 teeth, some of those teeth are usually quite small (intercalary).
- 9) *Palpal formula always less than 6:4, typically 2:3 or 3:3, though up to 5:4 is known in *A. arnoldi* and *A. palearctica*.
- 10) *Eyes small, typically consisting of fewer than 10 facets, though more than 20 facets observed

in *A. acutiventris* and *A. rubescens*; eyes laterally placed, at the lower 1/4 of the head.

- 11) Head typically covered in a thick layer of short, appressed hairs.
- 12) Maximum width of pronotum wider than that of remainder of mesosoma (in dorsal view).
- 13) Mesosoma and legs robust; legs always with at least a layer of appressed hairs, occasionally with scattered erect hairs as well.
- 14) Metanotal area variable with regards to number of sulci present, though the region is never very deeply impressed.
- 15) *Propodeal spiracle large and round, placed near declivity border.
- 16) Metapleural gland present.
- 17) Petiole always thick and erect, occasionally slightly inclined forward.
- 18) Gaster robust, rounded and larger toward petiole end from where it becomes narrower (to a point) posteriorly; in lateral view tear-drop shaped; gaster sloping toward acidopore dorsally from anterior to posterior; venter more flattened than dorsum.
- 19) Proventriculus asepalous (see Eisner, 1957; Prins, 1980; this study [*A. ayanganna*, **new species**; *A. keira*, **new species** examined]).
- 20) Declivity distinct and steep.
- 21) Mesosomal-petiole muscle insertion point round.
- 22) Ventral mesosomal-petiole articulation point surpasses metacoxal insertions.

QUEEN:

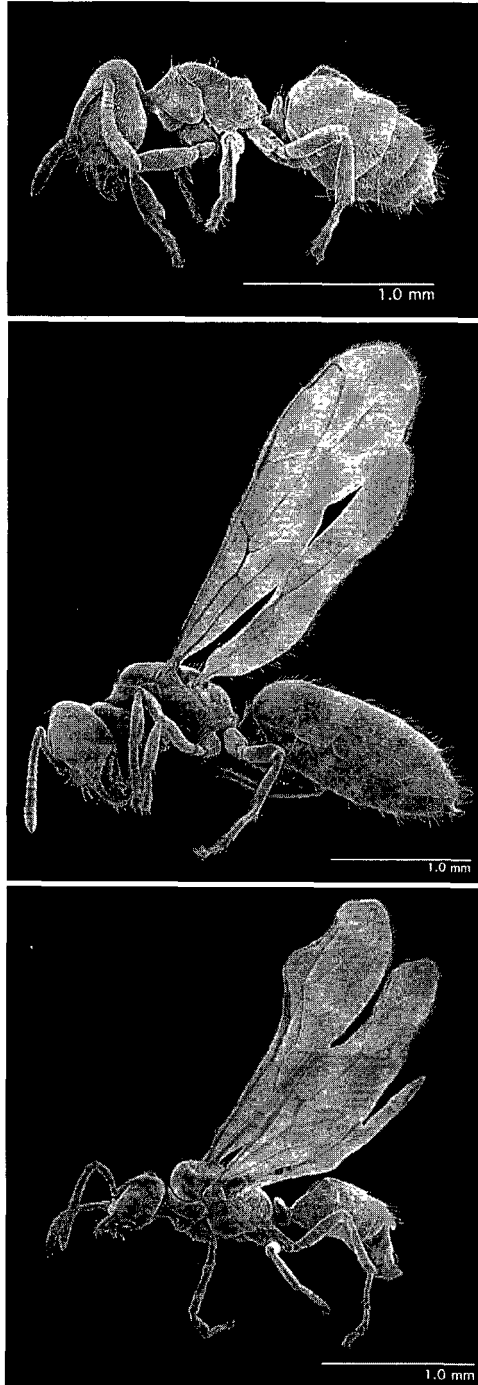
- 23) Yellow to dark brown (almost black) in color.
- 24) Three ocelli present, large and distinct at apex of head.
- 25) Pronotum small and collar-like.
- 26) Mesonotum dorsum flat and wide.
- 27) Propodeum short, and low; declivity typically indistinct from dorsal face of propodeum.
- 28) Similar in overall appearance to workers (though always larger) with modifications expected for caste; antennal segment count and mandibular dentition typically same as found in workers.

MALE:

- 29) Yellow to dark brown (almost black) in color.
- 30) *Antennae with 8-12 segments.
- 31) Three ocelli present, large and distinct at apex of head.
- 32) Eyes large, breaking outline of head in full face view
- 33) Mandibles narrow to broad, with 1 to 6 teeth possible.
- 34) Mesosoma robust, mesonotum large, with flat dorsum.
- 35) Pronotum small and collar-like.
- 36) Propodeum short, and low; declivity typically indistinct from dorsal face of propodeum.
- 37) Genitalia large (proportional to body) and prominent.

LARVAE AND PUPAE:

- 38) Larval body hairs abundant and of three types: simple, denticulate, and branched (Wheeler and Wheeler, 1953).
- 39) Pupae both naked and with cocoons; naked pupae reported for *A. ayanganna*, **new species** and *A. keira*, **new species**; pupae with cocoons reported for *A. acutiventris*.



Figures 10-12. 10) worker of *A. epedana* in lateral view; 11) queen of *A. epedana* in lateral view; 12) male of *A. epedana* in lateral view.

Discussion: *Acropyga* ants belong to the subfamily Formicinae, and Bolton (2003) has recently placed the genus in a redefined Lasiini (see Phylogenetics and Biogeography section for further discussion). See figures 10-12 for general habitus of all three castes; figures 13A & 13B for larvae. Workers of *Acropyga* can be separated from other formicine ants by a combination of possessing 11 or fewer antennal segments; tubular, elongate torulae; small eyes (generally only a few facets) that are laterally placed at lower 1/4 of head; low palp formula (less than 6:4); large, round propodeal spiracles; and heads and gasters covered in a dense layer of short appressed hairs with scattered erect hairs throughout. Queens are very similar in general appearance to workers, though they always possess large, flat mesonota. Males are more difficult to diagnose, though they always have 12 or fewer antennal segments, palp formulae less than 6:4, and large, prominent genitalia. Immature stages of *Acropyga* species are poorly known and a thorough analysis cannot be completed at this time. There may be an interesting trend however in that in the New World pupae have been found to be naked, while in the Old World pupae have cocoons. Given that pupae are known for only 3 species however, it is too early to draw any general conclusions.

As first suggested by Brown (1973) the subgenera of *Acropyga* are here synonymized. The subgenera do little to help understand the diversity found within *Acropyga*, and the largest subgenus, *Rhizomyrma*, was not only ill-defined, but also was not monophyletic. Subgeneric designations are replaced instead by nine informal species-groups. Five species in the genus remain unplaced in a species-group, since to a large extent species-groups are defined by male characters. I have placed some species in species-groups even though their males are unknown only when worker morphology strongly suggests a close relationship. Nonetheless, the species-groups as presented here will undoubtedly change as our understanding of *Acropyga* phylogeny improves, species for which males are currently unknown are discovered and described, and new species are revealed. Species-groups have the advantage of being a means to organize a genus taxonomically, but avoid the potential taxonomic tangles associated with subgenera, since species-groups can be changed without subsequent changes in nomenclature.

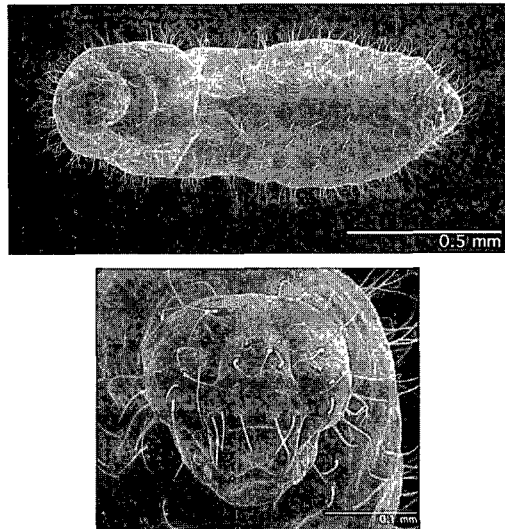


Figure 13. A) *A. fuhrmanni* last instar larva in ventral view. B) *A. fuhrmanni* larva head.

DISTRIBUTION

Acropyga are limited to warm temperate and tropical areas around the world (fig. 14). In the New World, *Acropyga* occur from southern Arizona into northern parts of Argentina, and from the Lesser Antilles and Hispaniola (though curiously they are absent from elsewhere in the Greater Antilles). Two species are currently known from Africa, one in southern Africa, the other in West and East Africa. A single species is restricted to the Palaearctic having been found only in Greece. In the Indo-Australian/Oriental regions, species are known from warmer parts of temperate Japan and China, south through Australia. *Acropyga* have been found as far east as the Solomon Islands, west to India and Sri Lanka. *Acropyga* are present in all regions except the Malagasy. A discussion of biogeographical patterns can be found later in this study.

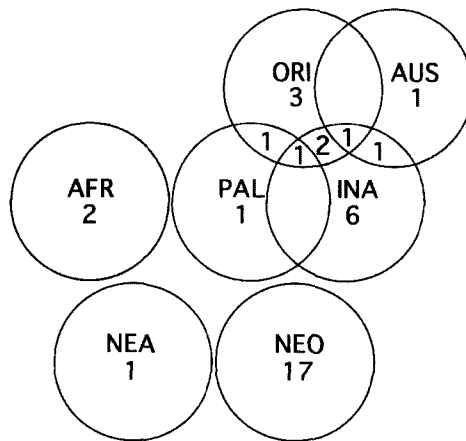


Figure 14. Venn diagram depicting number of *Acropyga* species found in various biogeographical regions around the world. AFR= Afrotropical; AUS= Australasian; INA= Indo-Australian; NEA= Nearctic; NEO= Neotropical; PAL= Palaearctic.

SYNOPSIS OF *ACROPYGA* SPECIES*acutiventris* species-group***acutiventris*** Roger, 1862: 243

- = *acutiventris javana* Karavaiev, 1933: 308, **NEW SYNONYM**
- = *acutiventris carinata* Karavaiev, 1933: 310, **NEW SYNONYM**
- = *crassicornis*, Emery, 1900: 698, **NEW SYNONYM**
- = *flava* (Mayr, 1862: 699) (synonymy by Forel 1894)
- = *indosinensis* W.M. Wheeler, 1935a: 72, **NEW SYNONYM**
- = *moluccana* Mayr, 1879: 658, **NEW SYNONYM**
- = *moluccana australis* Forel, 1902: 477, (synonymy by Taylor 1992)
- = *moluccana mysolensis* Forel, 1911a: 285, **NEW SYNONYM**
- = *moluccana opaca* Stitz, 1911: 370, **NEW SYNONYM**
- = *moluccana occipitalis* Stitz, 1912: 510, **NEW SYNONYM**
- = *moluccana papuana* Mann, 1919: 364, **NEW SYNONYM**
- = *undecema* (Donisthorpe, 1949: 756), **NEW SYNONYM**

rubescens Forel, 1894: 418, **NEW STATUS**

- = *acutiventris rubens* Forel, 1911a: 286. Synonym of *A. rubescens* by Emery (1925)
- = *acutiventris bugnioni* Forel, 1911c: 226, **NEW SYNONYM**

arnoldi species-group

- arnoldi* Santschi, 1926: 245
 = *rhodesiana* Santschi, 1928b: 211 (synonymy by Prins 1982)

butteli species-group

- butteli* Forel, 1912c: 772
 = *termitobia* Forel, 1912c: 773, **NEW SYNONYM**
 = *amblyops* Forel, 1915a: 34, **NEW SYNONYM**
 = *meermohri* (Stärcke, 1930: 375), **NEW SYNONYM**
 = *distinguenda* Karavaiev, 1933: 110, **NEW SYNONYM**
 = *baodaoensis* Terayama, 1985: 284, **NEW SYNONYM**

- inezae* Forel, 1912: 772
nipponensis Terayama, 1985: 287
 = *jiangxiensis* Wang and Wu, 1992: 226, **NEW SYNONYM**

decedens species-group

- decedens* (Mayr, 1887: 521)
fuhrmanni (Forel, 1914: 12)
 = *berwicki* W.M. Wheeler, 1935b: 325, **NEW SYNONYM**

- smithii* Forel, 1893: 349
 = *kathrynae* Weber, 1944: 114, **NEW SYNONYM**
 = *urichi* Weber, 1944: 115, **NEW SYNONYM**

goeldii complex within *decedens* species-group

- dubitata* (W.M. Wheeler, and Mann, 1914: 47)
epedana Snelling, 1973: 7
exsanguis (W.M. Wheeler, 1909: 238)
 = *wheeleri* Mann, 1922: 52, **NEW SYNONYM**
 = *bruchi* Santschi, 1929: 308, **NEW SYNONYM**
 = *paramaribensis* Borgmeier, 1933: 263, **NEW SYNONYM**
 = *robae* Donisthorpe, 1936: 108, **NEW SYNONYM**

- goeldii* Forel, 1893: 348
 = *pachycera* (Emery, 1906: 182), **NEW SYNONYM**
 = *goeldii columbica* (Forel, 1912b: 61), **NEW SYNONYM**
 = *goeldii tridentata* (Forel, 1912b: 61), **NEW SYNONYM**
 = *marshalli* (Crawley, 1921: 93), **NEW SYNONYM**
 = *pickeli* Borgmeier, 1927: 287, **NEW SYNONYM**
 = *rutgersi* Bünzli, 1935: 464, **NEW SYNONYM**
 = *borgmeieri* Donisthorpe, 1939: 153, **NEW SYNONYM**
 = *quadriceps* Weber, 1944: 113, **NEW SYNONYM**
 = *trinitatis* Weber, 1944: 117, **NEW SYNONYM**

hirsutula, **NEW SPECIES***keira*, **NEW SPECIES***palaga*, **NEW SPECIES**

- parvidens* (W.M. Wheeler and Mann, 1914: 46)
 = *mesonotalis* Weber, 1944: 111, **NEW SYNONYM**

romeo, **NEW SPECIES***donisthorpei* species-group

- donisthorpei* Weber, 1944: 118
 = *oko* Weber, 1944: 119, **NEW SYNONYM**
 = *paludis* Weber, 1944: 121, **NEW SYNONYM**

tricuspis, **NEW SPECIES***myops* species-group

- ambigua* Emery, 1922: 107
dubia Karavaiev, 1933: 311
gelasis, **NEW SPECIES**
hystrix, **NEW SPECIES**
kinomurai Terayama & Hashimoto, 1996: 7

lauta Mann, 1919: 365

myops Forel, 1910: 59

= *indistincta* Crawley, 1923: 178, **NEW SYNONYM**

sauteri Forel, 1912a: 72

pallida species-group

pallida (Donisthorpe, 1938: 598)

panamensis species-group

ayanganna, **NEW SPECIES**

panamensis Weber, 1944: 113

yaeyamensis species-group

yaeyamensis Terayama and Hashimoto, 1996: 5

= *guangxiensis* Terayama, Fellowes, and Zhou, 2002: 23, **NEW SYNONYM**

= *yunnanensis* Terayama, Fellowes, and Zhou, 2002: 27, **NEW SYNONYM**

unplaced in a species-group

guianensis Weber, 1944: 120

oceanica Emery, 1900: 333

= *septemstruma* Terayama, Fellowes, and Zhou, 2002: 24, **NEW SYNONYM**

palaearctica Menozzi, 1936: 298

silvestrii Emery, 1915: 21

stenotes, **NEW SPECIES**

NAMES EXCLUDED FROM *ACROPYGA*

Pseudolasius emeryi (Forel)

Rhizomyrma emeryi Forel, 1915b: 347. 2 syntype workers, PAPUA NEW GUINEA: Friedrich-Wilhelmshafen, Biro 901, Montes Hansemann (MHNG) [examined]. *Acropyga emeryi* Emery, 1925: 30, first combination in *Acropyga*; combination in *Pseudolasius*, **NEW COMBINATION**.

This species becomes *Pseudolasius emeryi* (Forel) and thus a junior secondary homonym of *Pseudolasius emeryi* Forel, 1911b: 286. A replacement name is not proposed at this time because any decision without proper analysis of the genus overall could very well only result in yet another synonym being created; *Pseudolasius* is in dire need of taxonomic revision.

The two syntypes described by Forel (1915b) as *Rhizomyrma emeryi*, unequivocally belong in the genus *Pseudolasius*. LaPolla (2002) provided a list of characters useful in separating *Pseudolasius* and *Acropyga* from one another; among those most useful for generic placement of the syntypes examined are: 12 segmented antennae, the lack of a dense layer of appressed hairs on the gaster, and open torulae. An interesting note on the two syntypes- they both bear a label identifying them as *A. oceanica*, probably in reference to *Acropyga oceanica* Emery and presumably Forel's initial identification. The word "TYPE" is written on the *Rhizomyrma emeryi* labels so I have applied that species name to the examined syntypes.

NOMEN DUBIUM

Acropyga major Donisthorpe

Acropyga major Donisthorpe, 1949: 755. 4 syntype males, INDONESIA: Maffin Bay (CASC) [examined 1 male; depository of other males unknown, not in CASC].

Poor condition (specimen broken into pieces and smeared across a card in a pool of glue) of the examined male (I could not locate other specimens of this species and they are presumed lost) prevents proper examination. The published description is also inadequate for identification, thus this name is rendered a *nomen dubium*.

KEY TO WORKERS OF NEW WORLD *ACROPYGA*

A. dubitata is known only from the male and is therefore not included in this key.

- 1a Basal tooth of mandible greatly enlarged, roughly square to rectangular in shape (fig. 30A) 2
- 1b Basal tooth of mandible not enlarged, roughly triangular in shape (fig. 18A) 3
- 2a 8 segmented antennae, with apical segment appearing swollen, twice as wide as other segments and almost as long as all other funicular segments combined; mandible with large, roughly rectangular, apically truncated basal tooth *panamensis* Weber
- 2b 11 segmented antennae, with apical segment not swollen as above; mandible with large, roughly square basal tooth with three distinct cusps, the first two cusps (from apical tooth) are smaller than the third cusp which is offset by a small diastema *tricuspis*, **new species**
- 3a Smaller species (typically, but not always, with TL: < 1.7 mm); head width < 0.401 mm; mandible always with 4 teeth 4
- 3b Larger species (typically, but not always, with TL: > 1.7 mm); head width > 0.401 mm; mandible with 3-5 teeth 6
- 4a Mandible with 3 distinct teeth and a smaller 4th tooth offset from masticatory margin *romeo*, **new species**
- 4b Mandible with 4 distinct, approximately equally sized teeth 5
- 5a Antennae with 7-8 segments; scape length < 0.27 mm *smithii* Forel
- 5b Antennae with 11 segments; scape length > 0.27 mm *stenotes*, **new species**
- 6a Eyes larger (more than 10 facets) than in most species, appearing prominent in full frontal view; antennae with 10 segments; mandible with 5 unequally sized teeth; a gap present between inner mandibular margin and anterior clypeal margin when mandibles fully closed *ayanganna*, **new species**
- 6b Eyes smaller (fewer than 10 facets) than above, not as prominent in full frontal view; antennae with 8-11 segments; mandible with 3-5 teeth 7
- 7a Antennae with 8 segments; mandible with 4 equally sized teeth; a short diastema separates basal tooth from other teeth *fuhrmanni* (Forel)
- 7b Antennae with 8-11 segments; mandible with 3-5 teeth; typically no diastema separates basal tooth from other teeth, but if diastema is present then antennae with at least 9 segments 8
- 8a Dorsal surface of mandibles notably hairy (approximately 20 hairs); in full frontal view, inner mandibular margin typically parallel to anterior clypeal margin when mandibles are fully closed; no gap is present between inner mandibular margin and anterior clypeal margin when mandibles fully closed; mandible always with 4-5 teeth 9
- 8b Dorsal surface of mandibles with less than 20 hairs present; in full frontal view, inner mandibular margin not parallel to anterior clypeal margin when mandibles are fully closed; gap is present between inner mandibular margin and anterior clypeal margin when mandibles fully closed; mandible with 3-5 teeth 10
- 9a In full frontal view, head distinctly rounded in appearance; head and scapes with medium covering of appressed to erect hairs (fig. 24A); mesosoma with many erect hairs throughout; mesonotum lacks appressed hairs; mandible always with 5 teeth *donisthorpei* Weber

- 9b In full frontal view, head rectangular in appearance; head and scapes with dense covering of appressed to erect hairs (fig. 18A); mesosoma with only a few scattered erect hairs throughout; mesonotum with a dense layer of appressed hairs; mandible with 4-5 teeth *decedens* (Mayr)
- 10a Mesonotum with largely appressed hairs, that are short and sparse giving the mesosoma a bare appearance (fig. 22B); antennae with 9 segments; mandible with 3 equally sized teeth *keira*, **new species**
- 10b Mesonotum with erect hairs with appressed hairs underneath (fig. 20B); antennae with 8-11 segments; mandible with 3-5 teeth 11
- 11a Head typically longer than broad; CI of majority of workers from a nest series < 100; mandible with at least 4 teeth; when with 5 teeth, 4th tooth smaller than others 12
- 11b Head typically broader than long; CI of majority of workers from a nest series > 100; mandible with 3-4 teeth; teeth about the same size 13
- 12a Clypeus without a dense covering of hairs; mesosomal dorsum with a dense layer of appressed hairs, particularly on mesonotum with fewer, distinctly longer, erect hairs throughout .
..... *guyanensis* Weber
- 12b Clypeus with a dense covering of hairs; mesosomal dorsum with many erect hairs throughout
..... *hirsutula*, **new species**
- 13a Antennae with 8-9 segments; head width typically (in a nest series) < 0.50 mm; mandible with 3 teeth, never 4 *exsanguis* (Wheeler)
- 13b Antennae with 9-11 segments; head width typically (in a nest series) > 0.50 mm; mandible with 3-4 teeth 14
- 14a Mesonotum much higher than propodeum, appearing as a distinct segment, covered in a layer of long appressed hairs; mandible with 4 distinct teeth; Hispaniola only
..... *parvidens* (Wheeler and Mann)
- 14b Mesonotum not much higher than propodeum, not appearing as a distinct segment; mandible with 3-4 teeth 15
- 15a Mesosomal dorsum with largely appressed to suberect hairs; antennae 10-11 with segments; mandible with 3 distinct teeth, though occasionally a smaller basal tooth is present making mandible 4-toothed; scape length < 0.4 mm *epedana* Snelling
- 15b Mesosomal dorsum with appressed hairs, but also with many erect hairs scattered throughout; antennae with 9-11 segments; mandible with 3-4 teeth; scape length > 0.4 mm
goeldii Forel OR *palaga*, **new species** (males are needed to separate these two species; see discussion under each species for further information)

KEY TO QUEENS OF NEW WORLD *ACROPYGA*

This key must be used with caution because the queen caste is unknown for many species. Additionally only a few specimens were available for study in the vast majority of species in which queens were known, so, the limits of variation remain uncertain for most species. Queens are unknown for the following species and therefore are not included in this key: *dubitata*, *keira*, *palaga*, *romeo* and *stenotes*.

- 1a Basal tooth of mandible greatly enlarged, roughly square to rectangular in shape 2
- 1b Basal tooth of mandible not enlarged, roughly triangular in shape 3

- 2a 8 segmented antennae, with apical segment appearing swollen, twice as wide as other segments and almost as long as all other funicular segments combined; mandible with large, roughly rectangular, apically truncated basal tooth *panamensis* Weber
- 2b 11 segmented antennae, apical segment not swollen; mandible with large, roughly square basal tooth with three distinct cusps, the first two cusps (from apical tooth) are smaller than the third cusp which is offset by a small diastema *tricuspis*, **new species**
- 3a Smaller species (TL: < 2.3); head width < 0.41 mm *smithii* Forel
- 3b Larger species (TL: > 2.3 mm); head width > 0.41 mm 4
- 4a In full frontal view, inner mandibular margin parallel to anterior clypeal margin when mandibles are fully closed; no gap is present between inner mandibular margin and anterior clypeal margin when mandibles fully closed; dorsal surface of mandibles noticeably hairy (approximately 20 hairs) *donisthorpei* Weber
- 4b In full frontal view, inner mandibular margin not parallel to anterior clypeal margin when mandibles are fully closed; gap is present between inner mandibular margin and anterior clypeal margin when mandibles fully closed; dorsal surface of mandibles of variable hairiness, though typically less than 20 hairs present on dorsal surface 5
- 5a Clypeus without a dense covering of hairs (fig. 31A); antennae with 10-11 segments
..... *guianensis* Weber
- 5b Clypeus with a dense covering of hairs (fig. 19A); antennae with 8-11 segments 6
- 6a Antennae with 8 segments; mandible with 4 equally sized teeth *fuhmanni* (Forel)
- 6b Antennae with 8-11 segments, but if with 8 segments then mandible with only 3 equally sized teeth; otherwise mandible with 3-5 teeth 7
- 7a Third mandibular tooth smaller than other teeth *ayanganna*, **new species**
- 7b Third mandibular tooth not smaller than other teeth 8
- 8a Head width < 0.55 mm; mandible with 3 teeth, never 4 *exsanguis* (Wheeler)
- 8b Head width > 0.55 mm; mandible with 3-5 teeth 9
- 9a Mandible with 5 teeth and a short diastema present between 4th tooth and basal tooth
..... *hirsutula*, **new species**
- 9b Mandible with 3-5 teeth; if with 5 teeth then a short diastema is not present between 4th tooth and basal tooth 10
- 10a Dorsal surface of mandibles with at least 10 hairs of about the same length as the mandibular teeth; mandible with 4-5 teeth *decedens* (Mayr)
- 10b Dorsal surface of mandibles with fewer than 10 hairs, and these are shorter in length than the mandibular teeth; mandible with 4 or fewer teeth 11
- 11a Head width > 0.62 mm *goeldii* Forel
- 11b Head width < 0.62 mm 12
- 12a Hispaniola only *parvidens* (Wheeler and Mann)
- 12b Southeastern Arizona (USA) *epedana* Snelling

KEY TO MALES OF NEW WORLD *ACROPYGA*

This key must be used with caution because males are unknown for many species. Additionally, only a few specimens were available for study in the vast majority of species in which males were known, so, the limits of variation remain uncertain for most species. In some cases the most distinctive characteristics of males are found in the terminalia, and examination of these characters

may require dissection. Males are unknown for the following species and therefore are not included in this key: *guianensis*, *parvidens*, *romeo*, *stenotes*.

- 1a In ventral view, digiti much longer than cuspi; digiti with peg-like teeth near, but not at apex; antennae with 10-11 segments 2
- 1b In ventral view, digiti and cuspi of about the same length; digiti with peg-like teeth at apex; antennae with 9-12 segments 3
- 2a Apical segment of antennae wide, about as long as preceding four segments; first funicular segment distinctly swollen in appearance; scape fails to reach posterior margin by about length of first funicular segment; mandible with 2 teeth; basal tooth large and roughly rectangular, apically truncated *panamensis* Weber
- 2b Apical segment not as long as preceding four segments; scape surpasses posterior margin by about length of first funicular segment; mandible with 3 distinct, triangular teeth ...
..... *ayanganna*, **new species**
- 3a Basal tooth roughly square with 3 indistinct cusps; antennae with 12 segments; in dorsal view, dorsal and ventral penis valve margins gently curve toward each other, giving the two penis valves when viewed together a tubular appearance
..... *tricuspis*, **new species**
- 3b Basal tooth roughly triangular, without cusps; antennae with 9-12 segments; in dorsal view, penis valves typically plate-like and parallel to each other 4
- 4a In full frontal view, inner mandibular margin parallel with anterior clypeal margin when mandibles fully closed; penis valve ventral margin with many small teeth; penis valves without distinct laterally expanded tips *donisthorpei* Weber
- 4b In full frontal view, inner mandibular margin not parallel with anterior clypeal margin when mandibles fully closed; penis valve ventral margin without small teeth, appearing smooth; penis valves can possess distinct laterally expanded tips, though if without mandible not as in lug 4a 5
- 5a Parameres in lateral view strongly taper caudally; penis valves without distinctly laterally expanded, flattened tips, though caudally penis valves may bend laterally (fig. 37H) ...
..... 6
- 5b Parameres in lateral view do not taper caudally, entire structure of about the same width along its length; penis valves with distinctive laterally expanded, flattened tips (fig. 38E-H) 8
- 6a In lateral view, paramere coming to a thin point caudally *decedens* (Mayr)
- 6b In lateral view, paramere either rounded or truncated caudally, but not coming to a thin point 7
- 7a Caudal end of paramere rounded *smithii* Forel
- 7b Caudal end of paramere truncated *fuhmanni* (Forel)
- 8a In dorsal view, parameres each with dorsolateral expansions (sometimes no more than a slight bulge in the dorsal outline of the paramere) that often obscures view of the digiti and cuspi; lateral surface of parameres not covered in an extremely dense layer of hairs 9
- 8b In dorsal view, parameres without dorsolateral expansions (dorsal outline of paramere more or less straight with no bulge present), or if with slight dorsolateral expansions then lateral surface of parameres with an extremely dense layer of hairs; otherwise paramere lateral surface not covered in a very dense layer of hairs 10

- 9a Hairs on lateral surface of parameres much shorter near base, becoming longer caudally; antennae with 11 segments; penis valve ventral extension indistinct, small *keira*, **new species**
- 9b Hairs on lateral surface of parameres all of about equal length from base to caudal end; antennae with 9-10 segments; penis valve extension distinct, broadly rounded ventrally *exsanguis* (Wheeler)
- 10a Parameres, in lateral view, nearly square in outline, with only scattered, short hairs on lateral surface; penis valve with dorsal notch; Hispaniola only *dubitata* (Wheeler & Mann)
- 10b Parameres, in lateral view, clearly rectangular in outline, with a thicker layer of long hairs on lateral surface; penis valve without dorsal notch or if with one than lateral surface of parameres covered in a very dense layer of hairs 11
- 11a Parameres with an extremely dense layer of hairs on lateral surface; in dorsal view, penis valves not reaching caudal end of parameres by about half dorsal length of penis valves; penis valve with dorsal notch *hirsutula*, **new species**
- 11b Parameres without an extremely dense layer of hairs on lateral surface; in dorsal view, penis valves nears or reaches caudal end of parameres by distance less than half dorsal length of penis valves; penis valve without dorsal notch 12
- 12a In lateral view parameres ventrally without many long hairs (fig. 39B); penis valve ventral extension anterior margin uneven toward apodeme *epedana* Snelling
- 12b In lateral view parameres ventrally with many long hairs (fig. 40B); penis valve ventral extension anterior margin parallel toward apodeme 13
- 13a Digiti and cuspi not stalk-like; parameres very thin, with caudal ends wider, dorsally coming to a sharp point; in dorsal view parameres more less parallel to each before they bend toward penis valves; penis valves similar to fig. 40D *goeldii* Forel
- 13b Digiti and cuspi stalk-like, with long portion leading to their apexes; parameres not wider caudal ends; in dorsal view parameres bulge outward forming a wide "o" as they bend toward penis valves; penis valves similar to fig. 41H *palaga*, **new species**

KEY TO WORKERS OF OLD WORLD *ACROPYGA*

- 1a Southern Europe or Africa 2
- 1b Australasian, Indo-Australian, and Oriental regions and southern Japan 4
- 2a Head width > 0.55 mm; mandible with 6-9 teeth; southern Africa only ... *arnoldi* Santschi
- 2b Head width < 0.55 mm; mandible with 4-8 teeth; West and East Africa and southern Europe 3
- 3a Basal tooth distinctly offset from masticatory margin; torulae not particularly closely set; southern Europe (Greece) *paleartica* Menozzi
- 3b Basal tooth not distinctly offset from masticatory margin; torulae closely set; West to East Africa *silvestrii* Emery
- 4a Basal mandibular tooth large, rectangular and apically truncated 5
- 4b Basal mandibular tooth roughly triangular, similar in size and shape to other teeth 7
- 5a Mandible with 4 teeth; head width < 0.45 mm *inezae* Forel
- 5b Mandible with 5 teeth; head width > 0.45 mm 6
- 6a Larger species (TL: 2.16-2.52); head width > 0.53 mm *butteli* Forel
- 6b Smaller species (TL: 1.97-2.05); head width < 0.53 mm *nipponensis* Terayama

7a	Mandible with 3-4 teeth; antennae with 7-11 segments	8
7b	Mandible with 5 or more teeth; antennae with 9-11 segments	12
8a	Head width < 0.45 mm	9
8b	Head width > 0.45 mm	10
9a	Antennae with 7-8 segments; torulae very close-set	<i>oceanica</i> Emery
9b	Antennae with 10-11 segments; torulae not very close-set	<i>yaeyamensis</i> Terayama and Hashimoto
10a	Head flat in appearance with posterolateral corners at near right angles; torulae widely separated from each other; sides of head parallel; inner mandibular margin uneven, with slight bulge before masticatory margin	<i>kinomurai</i> Terayama and Hashimoto
10b	Head not flat in appearance, with rounded posterolateral corners; torulae not widely separated; sides of head not parallel; inner mandibular margin even, without bulge before masticatory margin	11
11a	Antennae with 8-9 segments; mandible always with 4 teeth, the basal tooth separated by a short diastema	<i>lauta</i> Mann
11b	Antennae with 11 segments; mandible with 3-4 teeth, the basal tooth not separated by a short diastema	<i>sauteri</i> Forel
12a	Metamesosomal dorsum with distinct erect hairs (fig. 15B); long erect hairs along posterior margin of head	13
12b	Metamesosomal dorsum without distinct erect hairs (fig. 28B); without long erect hairs along posterior margin of head	16
13a	Mandible with 5 teeth and fine striate sculpture running along dorsal surface of mandible; larger species (total length typically > 2.5 mm)	14
13b	Mandible with 6 teeth and no fine striate sculpture along dorsal surface of mandible; smaller species (total length typically < 2.5 mm)	15
14a	Fine mandibular striate sculpture distinct, running from near base of teeth to near mandibular articulation point	<i>acutiventris</i> Roger
14b	Fine mandibular striate sculpture indistinct, running from near base of teeth, but fading or disappearing altogether midway across mandible (midpoint measured from masticatory margin to articulation point)	<i>rubescens</i> Forel
15a	Anterior clypeal margin strongly bulging forward medially, forming a distinct "beak-like" projection; smaller species, HW < 0.5, SL < 0.5; longest erect hairs on mesosomal dorsum about twice as long as shorter erect or appressed hairs	<i>gelasis</i> , new species
15b	Anterior clypeal margin not strongly bulging forward medially, not forming a distinct "beak-like" projection; larger species, HW > 0.54, SL > 0.5; longest erect hairs on mesosomal dorsum about 3 times as long as shorter erect or appressed hairs	<i>hystrix</i> , new species
16a	Larger species, total length > 2.7 mm; head width > 0.6 mm; dorsal surface of mandible with a dense layer of hairs (fig. 28A); Australia only	<i>myops</i> Forel
16b	Smaller species, total length < 2.7 mm; head width < 0.6 mm; dorsal surface of mandible without a dense layer of hairs (fig. 25A); Australia and other regions	17
17a	Basal tooth separated from other teeth by a distinct diastema; basal tooth margin not smoothly continuous with inner mandibular margin; basal tooth apex pointing slightly downward	<i>ambigua</i> Emery

- 17b Basal tooth not separated from other teeth by a distinct diastema; basal tooth margin smoothly continuous with inner mandibular margin; basal tooth apex not pointing downward 18
- 18a Scape length > 0.39, often surpassing posterior margin; pronotum without an anterior shelf; mandible with 6 teeth *dubia* Karavaiev
- 18b Scape length < 0.39, often failing to reach posterior margin; pronotum with an anterior shelf; mandible with 5-7 teeth *pallida* (Donisthorpe)

KEY TO QUEENS OF OLD WORLD *ACROPYGA*

This key must be used with caution because the queen caste is unknown for many species. Additionally only a few specimens were available for study in the vast majority of species in which queens were known, so, the limits of variation remain uncertain for most species. Queens are unknown for the following species and therefore are not included in this key: *gelasis*, *oceanica*, *silvestrii* and *yaeyamensis*.

- 1a Africa or southern Europe 2
- 1b Australasian, Indo-Australian and Oriental regions 3
- 2a Large species (TL: > 4.0 mm); basal tooth not off-set from masticatory margin; gaster darker than head and mesosoma; appressed hairs on head and mesosoma give species a very smooth appearance; southern Africa only *arnoldi* Santschi
- 2b Smaller species (TL: << 4.0 mm); basal tooth off-set from masticatory margin; gaster the same color as head and mesosoma; hairs on head and mesosoma lifted off of surface slightly giving species a spiky appearance; southern Europe *paleartica* Menozzi
- 3a Basal mandibular tooth large, rectangular and apically truncated 4
- 3b Basal mandibular tooth roughly triangular, similar in size and shape to other teeth 6
- 4a Mandible with 4 teeth; head width < 0.55 mm *inezae* Forel
- 4b Mandible with 5 teeth; head width > 0.55 mm 5
- 5a Larger species (TL: > 4.0 mm); scape length > 0.6 mm *butteli* Forel
- 5b Smaller species (TL: < 3.0 mm); head width < 0.6 mm *nipponensis* Terayama
- 6a Mandible with 3-4 teeth 7
- 6b Mandible with 5 or more teeth 9
- 7a Head flat in appearance, posterolateral corners at near right angles; torulae widely separated from each other; sides of head parallel; inner mandibular margin uneven, with slight bulge before masticatory margin *kinomurai* Terayama and Hashimoto
- 7b Head not flat in appearance, with rounded posterolateral corners; torulae not widely separated; sides of head not parallel; inner mandibular margin even, without bulge before masticatory margin 8
- 8a Antennae with 8-9 segments; mandible always with 4 teeth, the basal tooth separated by a short diastema *lauta* Mann
- 8b Antennae with 11 segments; mandible with 3-4 teeth, the basal tooth not separated by a short diastema *sauteri* Forel
- 9a Fine striate sculpture running along dorsal surface of mandible 10
- 9b No fine striate sculpture running along dorsal surface of mandible 11
- 10a Fine mandibular striate sculpture distinct, running from near base of teeth to near dorsal mandibular articulation point *acutiventris* Roger

- 10b Fine mandibular striate sculpture indistinct, running from near base of teeth, but fading or disappearing altogether midway across mandible (midpoint measured from masticatory margin to mandible articulation point) *rubescens* Forel
- 11a Dark brown to almost black in color; head width > 0.8 mm 12
- 11b Yellow to brownish-yellow in color; head width < 0.8 mm 13
- 12a Gaster with dense layer of appressed hairs giving it a dull appearance; Australia only *myops* Forel
- 12b Gaster without a dense layer of appressed hair, giving it a shiny appearance; Indo-Australian and possibly other regions *hystrix*, **new species**
- 13a Head width < 0.55 mm *pallida* (Donisthorpe)
- 13b Head width > 0.55 mm 14
- 14a Mandible with a diastema separating basal tooth from other teeth *ambigua* Emery
- 14b Mandible without a diastema separating basal tooth from other teeth *dubia* Karavaiev

KEY TO MALES OF OLD WORLD *ACROPYGA*

This key must be used with caution because males are unknown for many species. Additionally, only a few specimens were available for study in the vast majority of species in which males were known, so, the limits of variation remain uncertain for most species. In some cases the most distinctive characteristics of males are found in the terminalia, and examination of these characters may require dissection. Males are unknown for the following species and therefore are not included in this key: *ambigua*, *dubia*, *lauta*, *oceanica*, *paleartica* and *silvestrii*.

- 1a Southern Africa; in ventral view digitus strongly bent toward corresponding cuspis; parameres wide and broadly rounded caudally; mandible with 5-6 teeth *arnoldi* Santschi
- 1b Australasian, Indo-Australian and Oriental regions; in ventral view digitus not strongly bent toward cuspis; parameres not wide and broadly rounded caudally; mandible with 5 or fewer teeth 2
- 2a Basal mandibular tooth enlarged and rectangular, apically truncated 3
- 2b Basal mandibular tooth not enlarged and rectangular, apically truncated 5
- 3a Lateral surface of parameres with layer of appressed hairs, becoming shorter and more densely abundant toward base, and longer and sparser caudally; head width > 0.45 mm *butteli* Forel
- 3b Lateral surface of parameres with widely spaced short appressed hairs of even distribution across surface; head width < 0.45 mm 4
- 4a Third mandibular tooth apically truncate as in basal tooth; penis valves similar to fig. 36D *inezae* Forel
- 4b Third mandibular tooth never apically truncate as in basal tooth; penis valves similar to fig. 36H *nipponensis* Terayama
- 5a In dorsal view, parameres with distinct dorsolateral expansions concealing digiti and cuspi from view 6
- 5b In dorsal view, parameres without dorsolateral expansions, digiti and cuspi visible 7
- 6a Base of parameres with sparse layer of short appressed hairs; penis valves similar to fig. 34D; widespread species (Australasian, Indo-Australian and Oriental regions) *acutiventris* Roger

- 6b Base of parameres with dense layer of appressed hairs; penis valves similar to fig. 34H; eastern India and Sri Lanka only *rubescens* Forel
- 7a In ventral view, digiti about 2 times longer than cuspi 8
- 7b In ventral view, digiti about the same size as cuspi 9
- 8a Digiti with small peg-like teeth only found approximately at midlength where cuspi meet; digiti with indentation where they meet cuspi *myops* Forel
- 8b Digiti with small peg-like teeth along medial margin, stretching well beyond midlength to apex; digiti without indentation where cuspi approach digiti *sauteri* Forel
- 9a In lateral view, parameres wide (not losing much width immediately after base of parameres), tapering symmetrically to caudally directed point; in lateral view parameres arrow-shaped; mandible with 6 teeth *hystrix*, **new species**
- 9b In lateral view, parameres either tapering to a point with parameres thin throughout length (losing consider width immediately after base of parameres) or if parameres wide (not losing much width immediately after base of parameres) then tapering asymmetrically to a posterodorsal point; in lateral view parameres roughly rectangular; mandible with 2-5 teeth 10
- 10a Mandible with 4-5 teeth; parameres thin (losing consider width immediately after base of parameres) throughout length *pallida* (Donisthorpe)
- 10b Mandible with 2 teeth; parameres wide (not losing much width immediately after base of parameres), then tapering to posterodorsal point *yaeyamensis* Terayama

SPECIES ACCOUNTS

acutiventris species-group

Acropyga acutiventris Roger

- Acropyga acutiventris* Roger, 1862: 243 (w.q.), type species of genus. Syntype worker(s?) and queen(s?), SRI LANKA: no specific locality provided (depository unknown) [not examined]. Imai *et al.*, 1984: 68, karyotype completed; Terayama *et al.*, 2002: 23, description and key.
- Plagiolepis flava* Mayr, 1862: 699 (q.m.). Syntype queen(s?), syntype male(s?), INDIA: Nicobar Island (depository unknown) [not examined]. Mayr, 1862: 769, first combination in *Acropyga*. Synonymy by Forel, 1894: 418 (here confirmed).
- Acropyga moluccana* Mayr, 1879: 658 (w.). Syntype worker(s?), INDONESIA: Seram Island (depository unknown) [not examined]. **NEW SYNONYM.** Karavaiev, 1933: 310, description of queen and male; G.C. Wheeler & J. Wheeler, 1953: 137, description of larvae.
- Acropyga crassicornis*, Emery 1900: 698 (w.). Holotype worker, NEW GUINEA (country unknown): Sammlung, Kairouan (F. Santschi) (NHMB) [examined]. **NEW SYNONYM.**
- Acropyga moluccana australis* Forel, 1902: 477 (w.). 7 syntype workers, AUSTRALIA: MacKay (Turner) (BMNH) [examined]. Forel, 1911: 286, subspecies of *acutiventris*; Taylor & D.R. Brown, 1985: 108, subspecies of *moluccana*. Synonymy by Taylor, 1992:58 (here confirmed).
- Acropyga moluccana mysolensis* Forel, 1911a: 285 (w.). Holotype worker, INDONESIA: Mysol Island (Bates) (depository unknown) [not examined]. **NEW SYNONYM.**
- Acropyga moluccana opaca* Stitz, 1911: 370 (w.). 5 syntype workers, NEW GUINEA: (no specific locality provided) (depository unknown) [not examined]. **NEW SYNONYM.** Donisthorpe, 1948: 139, description of male.
- Acropyga moluccana occipitalis* Stitz, 1912: 510 (w.). Holotype worker, NEW GUINEA: (no specific locality provided) (depository unknown) [not examined]. **NEW SYNONYM.**
- Acropyga moluccana papuana* Mann, 1919: 364 (w.). 3 syntype workers, SOLOMON ISLANDS: Wai-ai (W.M. Mann) (BMNH) [examined], 7 syntypes workers, SOLOMON ISLANDS: Ugi, 1916 (W.M. Mann) (USNM) [examined]. **NEW SYNONYM.** G.C. Wheeler & J. Wheeler, 1953: 136, description of larvae.
- Acropyga acutiventris javana* Karavaiev, 1933: 308 (w.m.). Syntype workers, syntype male, INDONESIA: Java, Depok, Djungeln (Nr. 2344) and INDONESIA: Java, Buitenzorg, Botanical Gardens (Nr. 2370) (depository unknown) [not examined]. **NEW SYNONYM.**

Acropyga acutiventris carinata Karavaiev, 1933: 310 (w.). Syntype workers, INDONESIA: Sumatra, Payacombo (Nr. 5360) (O. John) (depository unknown) [not examined]. **NEW SYNONYM.**

Acropyga indosinensis W.M. Wheeler, 1935a: 72 (w.). 3 syntype workers, VIETNAM: Coxan (F. Silvestri) (MCZC) [examined]. **NEW SYNONYM.** Replacement name for *A. silvestrii* W.M. Wheeler, 1927: 100.

Pseudolasius undecimus Donisthorpe, 1949: 756 (w.). 2 syntype workers, INDONESIA: Maffin Bay (E.S. Ross) (BMNH) [examined]. **NEW SYNONYM.** Bolton, 1995: 58, first combination in *Acropyga*.

Diagnosis: *Worker:* 11 segmented antennae; mandible with 5 teeth and distinct ridges that run along dorsal surface; many erect hairs on head, mesosoma and gaster giving ant a “spiky appearance”; eyes prominent. *Queen:* As in worker with modifications expected for caste. *Male:* 12 segmented antennae; parameres with dense covering of erect hairs and with dorsolateral expansions medially.

Compare with: *A. rubescens*

Description: *Worker.* Head (fig. 15A): yellow to light brownish-yellow; head about as broad as long; posterior margin concave; covered in a thick layer of appressed hairs, with many scattered erect hairs, especially along posterior margin; eyes relatively large, placed at lower 1/4 of head; 11 segmented, incrassate antennae; scape reaches or surpasses posterior margin by about length of pedicel; clypeus broad, slightly convex medially with many erect hairs, the longest ones along anterior clypeal margin; mandible with 5 uneven teeth; 3rd and 5th tooth (from apical to basal) smaller than others; dorsal surface of mandible with distinct ridges across surface from about base of teeth toward insertion of mandibles; slight gap present between inner mandibular surface and anterior clypeal margin. Mesosoma (fig. 15B): yellow to light brownish-yellow; pronotum in lateral view typically with short shelf before rising sharply toward mesonotum; mesonotum rounded with many erect and appressed hairs at apex; metanotal area distinct; propodeum below level of mesonotum, dorsum flat before steep declivity; propodeum with short erect and appressed hairs. Gaster: yellow to light brownish-yellow to reddish-yellow; petiole thick and erect reaching height of propodeum; yellow to light brownish-yellow; gaster covered in thick layer of appressed hairs with many scattered erect hairs throughout giving a “spiky” appearance.

Queen. As in worker with modifications expected for caste.

Male. Head: yellow to light brownish-yellow, darker around three prominent ocelli; head about as broad as long; covered in layer of appressed hairs with scattered suberect to erect hairs; 12 segmented, slightly incrassate antennae; scape surpasses posterior margin by about length of first two funicular segments; clypeus broad, relatively flat, with scattered short erect hairs; mandible with 3-4 teeth; gap present between inner mandibular margin and anterior clypeal margin. Mesosoma: yellow to light brownish-yellow; pronotum short and collar-like; mesonotum large, rounded anteriorly; mesonotum flat dorsally, with layer of shorter appressed hairs and scattered longer erect hairs throughout; propodeum lower than mesonotum and scutellum; declivity not distinct from propodeum. Gaster: petiole thick and erect; gaster yellow to light brownish-yellow to reddish-yellow, darker dorsally; covered in dense layer of appressed hairs with scattered erect hairs throughout. Genitalia (figs. 34A-D): in lateral view parameres thick, tapering to rounded apices; parameres with medial dorsolateral extensions; cuspi short, bent toward approximately middle of digiti, where cuspi meet digiti with short, peg-like teeth at apices; digiti long and erect; apex rounded; digiti with short-peg-like teeth where cuspi meet; penis valve fig. 34D.

Measurements: *Workers* (n=10): TL: 2.67-3.53; HW: 0.8-0.912; HL: 0.803-0.896; SL: 0.628-0.827; ML: 0.836-1.03; GL: 0.933-1.74; CI: 91.07-104.25; SI: 78.7-97.97. *Queens* (n=3): TL: 4.56-5.09; HW: 1.02-1.06; HL: 0.967-1.01; SL: 0.902-0.971; ML: 1.4-1.63; GL: 2.19-2.63; CI: 102.97-106; SI: 85.09-95.2. *Males* (n=3): TL: 2.89-3.33; HW: 0.604-0.644; HL: 0.588-0.626; SL: 0.529-0.617; ML: 1.03-1.16; GL: 1.27-1.56; CI: 102.72-103.09; SI: 87.58-95.81.

Other material examined: AUSTRALIA: Northern Territory, Howard Springs near Darwin, gallery forest (W.L. Brown); Northern Territory, Baroalba Spring, 12.47S x 132.51E, rainforest (R. W. Taylor); Northern Territory, Baroalba Gorge, 12.50S x 132.52E, rainforest (R. W. Taylor);

Queensland, Iron Range, 143.48 E, 12.43 S (R.W. Taylor & J. Feehan); Queensland, 27 km NNE of Coen, 13° 44' S, 143° 20' E, elev. ca. 530 m (P.S. Ward); Queensland, Claudie River, 12 km WNW Lockhart, 12° 44' S, 143° 14' E, elev. ca. 30 m (P.S. Ward); Queensland, 12.43 S, 143.18 E, 11 km ENE of Mt. Tozer (J.C. Cardale); **INDIA:** Barkuda, Chilka Lake, Ganjam District; Madras Presidency; **INDONESIA:** N. Celebes, SW slope Mt. Klabat, elev. ca. 400-600 m, rainforest (W.L. Brown); E. Borneo, 31 km N. Balikpapan, rainforest (W.L. Brown); Flores Island, Wodeng, 31 km E Maumere, elev. ca. 10-80 (W.L. Brown); Sulawesi, Dumoge-Bone National Park (D.H. Kistner & D.F. Roche); **MALAYSIA:** Selangor, Ulu Gombak Forest Reserve (R. Crozier); Trengganu, Kuala Buka nr. Trengganu, berlease funnel (T. Jaccoud & P. Marcuard); Johar, Kota Tinggi Falls, 1° 50' N, 103° 50' E, elev. ca. 100 m (P.S. Ward); Sabah, Danum Valley; **PAPUA NEW GUINEA:** Sangara (P.M. Room); Orobay (P.M. Room); Wau, Kunai Creek, elev. ca. 1400 m (R.W. Taylor); near Vanimo, rainforest, elev. ca. 50 m (R.W. Taylor); Rihona (R. Vane-Wright); 5-6 km N Brown River, C.P. ca. 80 km, rainforest (W.L. Brown); 24 km N Madang, 5° 01' S, 145° 46' E (P.S. Ward); 5 km SW Mt. Uluman, Karkar Island, 4°41' S, 145° 57' E, elev. ca. 800 m (P.S. Ward); Gulf Prov: Ivimka camp, Lakekamu Basin, 7.73° N, 146.76°, elev. ca. 120 m (R.R. Snelling); **SINGAPORE:** Bukit Timah (D.H. Kistner); **SOLOMON ISLANDS:** Auki, Malaita (W.M. Mann); Star Harbor (W.M. Mann); Ugi (W.M. Mann); Wainoni Bay (W.M. Mann); Western Group, Rendova (E.S. Brown); Guadalcanal, Rese, (E.S. Brown); San Cristoval; **SRI LANKA:** Botanical Garden, Peradeniya (K. Krishna); specific locality unknown (G.B. King); **THAILAND:** Nakhon Ratchasima Prov., Khao Yai National Park, elev. ca. 700 m, rotten wood (W.L. Brown); Khao Yai National Park (Löbl & Burckhardt); Trang Prov: 7.35° N, 99.46° E, Khao Chong Nature Education Center (R.R. Snelling). In: ANIC, LACM, MCZC, USNM.

Distribution and natural history: This species has an extremely large range occupying much of the Australasian, Indo-Australian, and Oriental regions. It is by far the most common and numerous *Acropyga* encountered in research collections. *A. acutiventris* is known to occur in rainforests, with nests found in rotten wood, under stones, and in the leaf litter. It is a known trophophoretic species and as been found associated with at least two species of mealybugs (*Xenococcus acropygae*, and *X. annandalei*).

Discussion: This species is fairly easy to recognize, with the only morphologically similar species being its close relative, *A. rubescens*. A combination of large eyes (more than 20 facets), unique mesosomal shape, and 5-toothed mandibles with distinct striate sculpture on the dorsal surface, enable identification of *A. acutiventris*. Separating workers of this species from *A. rubescens* can be more difficult, though in general it is not as hairy as in *A. rubescens*, is slightly smaller in total length, and the striate sculpture extends approximately across the entire dorsal surface of the mandible. Males of *A. acutiventris* are also less hairy than in *A. rubescens*, but the most reliable means to identify them is by dissecting out the penis valves, which are distinct for each species.

Given the large range and morphological variability of this species, it is not surprising that so many synonyms have been created. In the past, species have been based on variation in color, overall size, head shape differences and antennal segment shape differences. Here, they are all treated as being the same of a wide ranging, variable species. Dissection of males from across the range (penis valve dissections from Australia, India, Papua New Guinea, Singapore, and the Solomon Islands) of *A. acutiventris* revealed no discernable genitalic differences.

Acropyga rubescens Forel, NEW STATUS

Acropyga acutiventris rubescens Forel, 1894: 418, (w.q.m.). 10 syntype workers, 2 syntype queens, 3 syntype males, INDIA: Kanara (Bell) (AMNH) (BMNH) (MCZC) [examined]. The designated lectotype is a worker labeled JSL TYPE # 111 and is deposited at MCZC.

Acropyga acutiventris bugnioni Forel, 1911c: 226 (w.q.). 2 syntype workers, SRI LANKA: no specific locality given (NHMB) [examined]. **NEW SYNONYM.**

Acropyga acutiventris rubens Forel, 1911a: 286 (w.). Holotype worker, no locality provided (depository unknown) [not examined]. Synonym of *A. rubescens* by Emery, 1925 [probably a miss-spelling of *rubescens* (Bolton, 1995)] (here confirmed).

Diagnosis: *Worker:* 11 segmented antennae; mandible with 5 teeth and indistinct ridges that run along dorsal surface fading toward median portion of mandibles; scapes > 0.9 mm; many erect hairs on head, mesosoma and gaster giving ant a “spiky appearance.” *Queen:* As in worker with modifications expected for caste. *Male:* As in *A. acutiventris*, except hairier and penis valve differences (compare figs. 34D and 34H)

Compare with: *A. acutiventris*

Description: *Worker.* Head (fig. 15C): brownish-yellow to reddish-yellow; head about as broad as long; posterior margin concave; covered in a thick layer of appressed hairs, with many scattered, long erect hairs especially along posterior margin; eyes relatively large, placed at lower 1/4 of head; 11 segmented, incrassate antennae; scape nearly reaches or surpasses posterior margin up to length of pedicel; clypeus broad, slightly convex medially with many erect hairs, the longest ones along anterior clypeal margin; mandible with 5 uneven teeth; 3rd and 5th tooth (from apical to basal) smaller than others; dorsal surface of mandible covered in many erect hairs and with indistinct ridges originating near base of teeth and fading entirely toward middle of mandible; slight gap present between inner mandibular surface and anterior clypeal margin. Mesosoma (fig. 15D): brownish-yellow to reddish-yellow; mesosoma covered throughout in dense layer of appressed hairs with scattered erect hairs of varying lengths; pronotum in lateral view typically with short shelf before rising sharply toward mesonotum; mesonotum rounded with many long erect hairs (many times longer than shortest erect hairs); metanotal area distinct; propodeum rounded, below level of mesonotum, propodeal dorsum flat before steep declivity; propodeum with dense layer of erect and appressed hairs. Gaster: brownish-yellow to reddish-yellow, darker than head and mesosoma; petiole thick and erect reaching height of propodeum; yellow to light brownish-yellow; gaster covered in thick layer of appressed hairs with many scattered erect hairs throughout giving a “spiky” appearance.

Queen. As in worker with modifications expected for caste.

Male. Head: brownish-yellow to reddish-yellow, darker around three prominent ocelli; head about as broad as long; covered in layer of appressed hairs with suberect to erect hairs; eyes large, breaking outline of head in full frontal view; 12 segmented, slightly incrassate antennae; scape surpasses posterior margin by about length of first two funicular segments; clypeus broad, relatively flat, with scattered short erect hairs; mandible with 4 teeth; a gap exists between inner mandibular margin and anterior clypeal margin. Mesosoma: light brownish-yellow to reddish-yellow; pronotum short and collar-like; mesonotum large, rounded anteriorly; mesonotum dorsum flat, with layer of shorter appressed hairs and scattered longer erect hairs throughout; propodeum lower than mesonotum and scutellum; declivity not distinct from propodeum. Gaster: petiole thick and erect; gaster brownish-yellow to reddish-yellow, darker dorsally; covered in dense layer of appressed hairs with scattered erect hairs throughout. Genitalia (figs. 34E-H): in lateral view parameres thick, tapering to a rounded apex; parameres with medial dorsolateral extensions; cuspi short, bent toward approximately middle of digiti, where they meet with short, peg-like teeth at apex; digiti long and erect with short peg-like teeth where cuspi meet, apex rounded; penis valve fig. 34H.

Measurements: *Workers* (n=7): TL: 3.39-5.11; HW: 0.891-1.16; HL: 0.915-1.06; SL: 0.914-1.16; ML: 1.07-1.31; GL: 1.35-2.74; CI: 91.53-109.43; SI: 97.39-106.67. *Queens* (n=1): TL: 6.16; HW: 1.36; HL: 1.36; SL: 1.34; ML: 2.23; GL: 2.57; CI: 100; SI: 98.53. *Males* (n=1): TL: 3.52; HW: 0.644; HL: 0.665; SL: 0.611; ML: 1.25; GL: 1.6; CI: 96.84; SI: 94.88.

Other material examined: SRI LANKA: Ratnapura (E.O. Wilson); Kandy, elev. ca. 600-700 m (E.O. Wilson). In: MCZC.

Distribution and natural history: This species is presently known from only 3 localities in Sri Lanka and one locality in India. Nothing is known of its natural history.

Discussion: This species is the largest known *Acropyga* species, and is closely related to *A. acutiventris*. *A. rubescens* has been elevated to species status based on 6 points of distinction from *A. acutiventris*: 1) setation of *A. rubescens* is distinct: a) much denser hairs in general found across body; b) hairs on posterior margin of head often very long, much longer than seen in *A. acutiventris*; c) mesosomal hairs longer and denser; 2) *A. rubescens* larger overall; 3) with longer scapes (higher SI); 4) dorsal mandibular striate sculpture thinner disappearing about mid-way toward mandible articulation point with head; 5) shapes of penis valves differ (compare figs. 34D and 34H); 6) both “forms” are sympatric in India/Sri Lanka region.

arnoldi species-group

Acropyga arnoldi Santschi

Acropyga (*Malacomyrma*) *arnoldi* Santschi, 1926: 245 (w.q.). 7 syntype workers, 1 syntype queen, SOUTH AFRICA: Durban (C.P. Merre) (MCZC) (NHMB) (SAMC) [examined]. The designated lectotype is a worker labeled JSL TYPE # 112 and is deposited at SAMC. The lectotype is one of three specimens flat on a card and is the worker specimen furthest from the queen specimen. Prins, 1982: 245, description of male.

Acropyga (*Malacomyrma*) *rhodesiana* Santschi, 1928b: 211 (w.). 9 syntype workers, ZIMBABWE: Bulawayo, Rifle Kopie (BMNH) (NHMB) (SAMC) [examined]. Synonymy by Prins, 1982: 238 (here confirmed).

Diagnosis: *Worker*: 11 segmented antennae; mandible broad with 6-9 uneven teeth; mesosoma noticeably covered in a thick layer of long appressed hairs. *Queen*: as in worker with modifications expected for caste. *Male*: 12 segmented antennae; mandible broad with 5-6 teeth; parameres broadly rounded at apex.

Compare with: *A. paleartica* and *A. silvestrii*.

Description: *Worker*: Head (fig. 16A): yellow to brownish-yellow; head distinctly longer than broad; covered in a layer of short appressed hairs; posterior margin entire to concave; 11 segmented, incrassate antennae; scape reaches to posterior margin; clypeus convex medially; covered in a layer of appressed to erect hairs; mandible broad, with 6-9 uneven teeth; 3rd tooth and 5th tooth often shorter than other teeth; dorsal surface of mandible with many hairs (approximately 20); anterior clypeal margin and inner mandibular margin nearly parallel. Mesosoma (fig. 16B): yellow to brownish-yellow; in lateral view, pronotum with a short anterior shelf before rising toward mesonotum; pronotum rounded posteriorly; covered in a thick layer of long appressed hairs, with erect hairs often found along posterior border of segment; mesonotum rounded, slightly higher than propodeum, covered in a thick layer of long appressed hairs; metanotal area distinct; propodeum rounded, covered in a thick layer of long appressed hairs; declivity steep. Gaster: petiole erect and broad, with a rounded apex covered in erect hairs; gaster yellow to brownish-yellow; covered in a layer of appressed hairs with suberect to erect hairs scattered throughout, particularly along segmental margins.

Queen. As in worker with modifications expected for caste and with the following differences: mesosomal appressed hairs shorter than in worker; mesoscutellum with several erect hairs.

Male. Head: brownish-yellow to brown toward apex around 3 prominent ocelli; head slightly longer than broad; eyes large taking up most of lateral sides, breaking outline of head in full frontal view; 12 segmented antennae; scape long, surpassing posterior margin by at least the length of the 1st two funicular segments; clypeus slightly convex, rounded medially; with many erect hairs on surface; mandible broad as in worker with 5-6 uneven teeth. Mesosoma: yellow to brownish-yellow; pronotum collar-like, with rounded mesonotum above; covered in a layer of short appressed hairs; mesonotum rounded anteriorly, covered in a thick layer of short appressed hairs; mesonotum and higher than propodeum; declivity steep, with layer of short appressed hairs. Gaster: petiole erect and short, not reaching height of propodeum; petiole apex rounded; gaster yellow to

brownish-yellow; covered in a layer of appressed hairs, with scattered erect hairs along segmental margins. Genitalia (figs. 35A-D): in lateral view, parameres broadly rounded at apices; base of parameres without hairs; dorsally parameres broadly extend laterally, largely concealing digiti and cuspi from view; cuspi short and cylindrical, apically with short, peg-like teeth; digiti long, bent toward cuspi; digiti and cuspi meet apically; apex of digiti truncated, with short, peg-like teeth; penis valve fig. 35D.

Measurements: *Workers* (n=6): TL: 2.13-2.4; HW: 0.517-0.619; HL: 0.634-0.705; SL: 0.466-0.575; ML: 0.686-0.735; GL: 0.81-1.02; CI: 80.99-92.80; SI: 83.77-100.70. *Queens* (n=1): TL: 4.32; HW: 0.826; HL: 0.804; SL: 0.721; ML: 1.07; GL: 2.45; CI: 102.74; SI: 87.29. *Males* (n=1): TL: 3.2; HW: 0.487; HL: 0.487; SL: 0.549; ML: 0.946; GL: 1.77; CI: 100; SI: 112.73.

Other material examined: **NAMIBIA:** Brandburg, Wasserfallflache, elev. 1960 m, 21° 10' S, 14° 32' E (S. van Noort); **SOUTH AFRICA:** Cape Prov., Cape Town; Signal Hill (B.L. Fisher); Jacobsbaai, 32° 58' S, 17° 54' E (A.J. Prins); Paternoster, 32° 49' S, 17° 54' E; vic. Signal Hill; Grahamstown (L. Weatherill and W.L. Brown); Western Cape, Koeberg Nature Reserve (northern part), 33° 37' S, 18° 24' E (H.G. Robertson). In: BMNH, SAMC.

Distribution and natural history: This species range is throughout southern Africa (roughly defined as the area south of the Zambezi River). The exact northern limit of *A. arnoldi* is unclear, however, it does not appear to overlap with the other described African species *A. silvestrii*, which is known to extend at least into northern Tanzania.

This species is known to tend the mealybug *Eumyrmococcus scorpiodes* (see De Lotto, 1977 for more details) and has trophophoretic queens (Prins, 1982). Alates have been collected from March to July. Prins (1982) discovered trophophoretic queens in July. *A. arnoldi* has been found in a variety of habitats throughout southern Africa from deserts to woodlands.

Discussion: This species is easy to recognize from other *Acropyga* by its broad, many-toothed mandible (at least 6 teeth and up to 9) and by the 5 to 4 segmented maxillary palps. It is the only *Acropyga* known from southern Africa. The combination of high number of mandibular teeth and high number of maxillary palpal segments suggests that this species is primitive.

The other African species, *A. silvestrii* has up to 7 teeth, but its palp formula is never greater than 3:3, and it is known to have antennal segment counts as low as 10 (possibly indicative of belonging to a more derived group). *A. palearctica* has been observed with up to 8 mandibular teeth, and possesses a 5:3 palp formula. The relationship of *A. arnoldi* to *A. palearctica* and *A. silvestrii* is unclear since those two species await discovery of males. Interestingly, the mealybug utilized by *A. palearctica* (*Eumyrmococcus corinthiacus*) is thought to be closely related to the mealybug species utilized by *A. arnoldi* (Williams, 1998).

butteli species-group

Acropyga butteli Forel

Acropyga (Atopodon) butteli Forel, 1912c: 772 (q.). Holotype queen, MALAYSIA: Selangor (von Buttel-Reepen) (not in MNNG) [not examined].

Acropyga (Atopodon) termitobia Forel, 1912c: 773 (q.). Holotype queen, MALAYSIA: Selangor (von Buttel-Reepen) (not in MNNG) [not examined]. **NEW SYNONYM.**

Acropyga (Atopodon) amblyops Forel, 1915a: 34 (w.). 2 syntype workers, INDONESIA: Sumatra, Sinabang Simalur [?], (E. Jacobson) (MHNG) [examined]. **NEW SYNONYM.**

Atopodon meermohri Stärcke, 1930: 375 (w.). Syntype worker(s?), INDONESIA: Palau Island (depository unknown) [not examined]. **NEW SYNONYM.** Bolton, 1995: 57, first combination in *Acropyga*.

Acropyga (Atopodon) distinguenda Karavaiev, 1935: 110 (w.q.m.). Syntype worker(s?), syntype queen(s?), syntype male(s?), VIETNAM (depository unknown) [not examined]. **NEW SYNONYM.**

Acropyga (Atopodon) baodaensis Terayama, 1985: 284 (w.q.m.). Holotype worker, TAIWAN: Nanshanchi, Nanfen Cun, Ren'ai Xiang, Nantou Hsien (M. Terayama) (NIAS) [not examined]; 5 paratype workers, 1 paratype queen, locality the same as holotype (BMNH) (BPBM) [examined]. **NEW SYNONYM.** Terayama *et al.*, 2002: 28, description and key

Diagnosis: *Worker*: 11 segmented antennae; mandible broad, with 5 teeth, basal tooth enlarged and rectangular, apically truncated; head width > 0.53mm. *Queen*: As in worker with modifications expected for caste. *Male*: 12 segmented antennae; mandible broad with 4 teeth; 3rd and basal tooth enlarged and rectangular, apically truncated, as in worker caste; digiti with rounded apices.

Compare with: *A. inezae* and *A. nipponensis*

Description: *Worker*: Head (fig. 16C): yellow; covered in a thick layer of short appressed hairs; head distinctly longer than broad, often becoming narrower anteriorly; posterior margin slightly concave medially, sometimes with several short erect hairs; 11 segmented, slightly incrassate antennae; scape fails to reach posterior margin by about length of first two funicular segments, occasionally scape longer, failing posterior margin by about 1/2 length of pedicel; clypeus broad, convex medially, with many erect hairs; median portion of clypeal anterior margin slightly pointed giving clypeus a slight "beak-like" appearance; mandible broad, with 5 teeth; basal tooth enlarged and rectangular, apically truncated; anterior clypeal margin and inner mandibular margin nearly parallel. Mesosoma (fig. 16D): yellow; in lateral view, pronotum rises steeply toward mesonotum; covered in layer of appressed hairs, long, erect hairs posteriorly placed; mesonotum nearly flat, about same height as propodeum; covered dorsally in a layer of appressed hairs, often with several short, erect to suberect hairs scattered throughout; metanotal area often distinct; propodeum dorsum with appressed hairs; declivity steep, without hairs present. Gaster: yellow; covered in layer of appressed hairs with scattered erect to suberect hairs throughout.

Queen. As in worker with modification expected for caste and the following differences: head and mesonotum with more erect hairs than in worker.

Male. Head: brownish-yellow, darker toward apex around three prominent ocelli; head oval-shaped, longer than broad, becoming narrower toward apex; eyes large, breaking outline of head in full frontal view; 12 segmented antennae; scapes surpass posterior margin by about length of first 2 funicular segments; clypeus broad, slightly convex medially, with erect hairs scattered throughout; shape of anterior clypeal margin similar to that of worker, but median point less defined; mandible broad with 4 teeth; basal tooth enlarged and rectangular, apically truncated, as in worker. Mesosoma: yellow; pronotum short and collar-like, overarched by mesonotum; mesonotum rounded anteriorly; dorsum flat with erect hairs scattered throughout, especially on scutellum; propodeum and declivity difficult to distinguish from each other. Gaster: yellow; covered in a layer of appressed hairs, with scattered erect hairs throughout. Genitalia (figs. 35E-H): in lateral view, parameres thin, tapering to rounded apices; lateral surface covered in layer of appressed hairs that are shorter and thicker toward base, becoming longer and sparser toward tip; in dorsal view parameres give genitalia a roughly triangular appearance; cuspi short, sharply bent toward digiti, with peg-like teeth at apex; digiti longer than cuspi and straight with rounded apex; peg-like teeth at about mid-length of digiti where cuspi meet; penis valve fig. 35H.

Measurements: *Workers* (n=9): TL: 2.16-3.00; HW: 0.549-0.787; HL: 0.607-0.882; SL: 0.442-0.522; ML: 0.555-0.643; GL: 0.965-1.49; CI: 81.46-90.44; SI: 66.33-83.16. *Queens* (n=1): TL: 4.02; HW: 0.733; HL: 0.806; SL: 0.653; ML: 1.21; GL: 2.00; CI: 90.94; SI: 89.09. *Males* (n=2): TL: 2.5-2.73; HW: 0.477-0.503; HW: 0.506-0.507; SL: 0.44-0.449; ML: 0.843-0.898; GL: 1.15-1.33; CI: 94.08-99.41; SI: 87.48-94.13.

Other material examined: **BRUNEI:** Sungai Liung Rec. Park (D.H. and A.C. Kistner); **INDONESIA:** Sulawesi, Utara, Dumoga-Bone National Park (R.H.L. Disney); **MALAYSIA:** Sarawak, 4th Div., G. Mulu National Park, R.G.S. Expedition, Long Pala, lowland rainforest, in root mat (B. Bolton); Sarawak, 4th Div., G. Mulu National Park, soil core, mixed dipterocarp forest (M. Collins); Sarawak, Miri, Lambir National Park, Tower Region (S. Yamane). In: BMNH, SYPC.

Distribution and natural history: This species ranges from Taiwan south to Indonesia. It has been collected in rainforests from root mats, soil cores, and in rotten wood. Terayama *et al.*

(2002) listed this species as occurring with the mealybug *Eumyrmococcus nipponensis*, but this record may be an error, as that mealybug was known previously only to be associated with *A. nipponensis*, and its listing by Terayama *et al.* (2002) was not considered a new record.

Discussion: This species is fairly easy to recognize with its five teeth, rectangular, apically truncated basal tooth and large size (TL > 2.0mm). The types of *A. amblyops* (a synonym of *A. butteli*) are larger than other examined specimens placed in *A. butteli* and this may be indicative of a "composite species" as it is defined here. However I conclude splitting is unnecessary since the size variation observed in head and scape characteristics appears to represent a continuum rather than discrete morphological discontinuities (figs. 48D and 49F), and that if more specimens were measured the "gap" observed between the *A. amblyops* types and the other specimens would close. The synonymized species are only distinguishable by differences in size. Until male specimens associated with different sized workers indicate they are not conspecific, I consider *A. butteli* a single, variable species.

Acropyga inezae Forel

Acropyga(*Atopodon*) *inezae* Forel, 1912c: 772 (w.). Syntype worker(s?), INDONESIA: Sumatra (NHMB) [examined].
Lectotype is a worker labeled JSL TYPE # 113 is deposited at NHMB. Karavaiev, 1933: 314, description of queen and male.

Diagnosis: *Worker:* 11 segmented antennae; mandible with 4 teeth, basal tooth enlarged and rectangular, apically truncated. *Queen:* As in worker with modifications expected for caste. *Male:* 12 segmented antennae; 4 mandibular teeth; parameres thin; digiti with truncated apices; cuspi meet digiti about half way along length of digiti.

Compare with: *A. butteli* and *A. nipponensis*

Description: *Worker:* Head (fig. 17A): yellow; covered in layer of appressed hairs; head longer than broad; posterior margin entire; 11 segmented, incassate antennae; scapes fail to reach posterior margin by about length of 1st three funicular segments; clypeus broad, convex medially; median portion clypeal anterior margin with rounded bulge giving clypeus a beak-like appearance; mandible broad with 4 teeth; basal tooth enlarged and rectangular, apically truncated; 3rd tooth without well-defined cusp and larger than 1st and 2nd teeth, occasionally forming a truncated tooth similar to basal tooth; basal tooth offset from other teeth; anterior clypeal margin and inner mandibular margin nearly parallel. Mesosoma (fig. 17B): yellow; pronotum covered with appressed hairs, long, erect hairs placed posteriorly; mesonotum flat, at about same height as propodeum; dorsum covered in appressed hairs; metanotal area indistinct; propodeum flat rounded into steep declivity. Gaster: yellow, covered in a thick layer of appressed hairs with scattered erect hairs throughout.

Queen. As in worker caste with modifications expected for caste and with the following differences: scape slightly longer in queens, occasionally reaching posterior margin to slightly failing to reach posterior margin; color yellow to brownish-yellow.

Male. Head: brownish-yellow, darker toward apex around three prominent ocelli; head slightly longer than broad; eyes large, breaking outline of head in full frontal view; 12 segmented antennae; scapes fail to reach posterior margin by about length of pedicel; clypeus broad, slightly convex medially, with erect hairs scattered throughout; shape of anterior clypeal margin similar to that of worker caste, but median tooth less defined; mandible broad with 4 teeth, basal tooth enlarged and rectangular, apically truncated as in worker caste. Mesosoma: yellow; pronotum short and collar-like, overarched by mesonotum; mesonotum rounded anteriorly; dorsum flat with erect hairs scattered throughout, especially on scutellum; propodeum short; declivity steep. Gaster: yellow; covered in a layer of appressed hairs, with scattered erect hairs throughout. Genitalia (figs. 36A-D): in lateral view, parameres thin, taper to rounded apices; hairs evenly distributed across dorsal surface of parameres; in dorsal view parameres give genitalia a roughly triangular appearance; cuspi short,

bent toward digiti, with peg-like teeth at apex; digiti longer than cuspi and bent toward cuspi with truncated apex; peg-like teeth found at about mid-length of digiti where cuspi meet; penis valve fig. 36D. .

Measurements: *Workers* (n=6): TL: 1.48-1.7; HW: 0.403-0.432; HL: 0.485-0.522; SL: 0.313-0.341; ML: 0.31-0.449; GL: 0.612-0.811; CI: 79.01-86.21; SI: 73.30-81.38. *Queens* (n=2): TL: 2.74-2.92; HW: 0.52-0.526; HL: 0.571-0.583; SL: 0.412-0.439; ML: 0.819-0.848; GL: 1.34-1.5; CI: 89.19-92.12; SI: 60.22-72.78. *Males* (n=2): TL: 1.66-1.78; HW: 0.316-0.362; HL: 0.364-0.38; SL: 0.218-0.23; ML: 0.464-0.557; GL: 0.831-0.844; CI: 86.81-95.26; SI: 60.22-72.78.

Other material examined: **BRUNEI:** Tasek Merimbun, Tutong (K. Eguchi); **INDONESIA:** SE Borneo, 17-46 km W of Batulitjin, lowland rainforest (W.L. Brown); Sangkima, Kutai National Park (S. Yamane). In: BMNH, SYPC.

Distribution and natural history: This species is known only from Sumatra and Borneo. Nothing is known of its natural history.

Discussion: This species can be recognized from other species in the *butteli* species-group since it only has 4 mandibular teeth as opposed to 5. The 3rd tooth from apical has a distinctive appearance that can be diagnostic; this tooth in some specimens examined looks similar in appearance to the truncated basal tooth. It seems likely that the unique shape of the 3rd tooth resulted from the fusion of 2 formerly separate teeth, but what is not clear is if *A. inezae* ever has 5 teeth, with the 3rd tooth being separated into 2 distinct teeth. The specimen sample available for study was small, so it cannot be completely discounted that 5 teeth may be possible. Future analysis of the *butteli* species-group should take the possibility of variation in teeth number into account for this species.

Acropyga nipponensis Terayama

Acropyga nipponensis Terayama, 1985: 287 (w.). 1 holotype worker, JAPAN: Noboritachi, Mikura-jima Is., Tokyo (K. Masuko) (NIAS) [not examined]. Terayama *et al.*, 2002: 30, description and key.

Acropyga jiangxiensis Wang and Wu, 1992: 226 (w.m.). 1 holotype worker, CHINA: Jiangxi Provin., Fenyi Co., Dagang Mt. (C. Wang) (CFRB) [not examined]; 1 worker paratype, 1 male paratype, same locality as holotype (CFRB) [examined]. **NEW SYNONYM.** Terayama *et al.*, 2002: 29, description and key.

Diagnosis: *Worker:* 11 segmented antennae; mandible broad, with 5 teeth, basal tooth enlarged and rectangular, apically truncated; HW: < 0.5 mm. *Queen:* As in worker with modifications expected for caste. *Male:* 12 segmented antennae; parameres extremely thin and long; mandible with 4 teeth; basal tooth as in worker though less pronounced.

Compare with: *A. butteli* and *A. inezae*.

Description: *Worker.* Head (fig. 17C): light brownish-yellow; covered in a dense layer of short, appressed hairs; head longer than broad; posterior margin entire to slightly concave medially; 11 segmented, incrassate antennae; scape fails to reach posterior margin by about half the length of pedicel; clypeus broad, with appressed to erect hairs on surface; anterior clypeal margin uneven coming to three points, a medial and 2 lateral points; mandible broad, with 5 teeth; basal tooth enlarged and rectangular, apically truncated; anterior clypeal margin and inner mandibular margin nearly parallel. Mesosoma (fig. 17D): light brownish-yellow; in lateral view, with short shelf before rising sharply toward mesonotum; pronotum with appressed hairs, long erect hairs posteriorly; mesonotum slightly higher than propodeum, covered in a layer of appressed to erect hairs; metanotal area distinct; propodeum gently rounded, with appressed hairs dorsally; declivity steep. Gaster: petiole thick and erect, reaching height of anterior portion of propodeal spiracle; gaster light brownish-yellow with dense layer of appressed hairs, with scattered erect hairs throughout.

Queen. As in worker with modifications expected for caste.

Male. Head: brownish-yellow, darker toward apex around 3 prominent ocelli; head longer than broad; covered in a thick layer of appressed hairs; eyes large, breaking outline of head in full

frontal view; 12 segmented, incrassate antennae; scape surpasses posterior margin by about length of the pedicel; clypeus broad, slightly convex medially, with scattered erect hairs; mandible with 4 teeth, the basal as in worker, though less distinct; inner mandibular margin and anterior clypeal margin nearly parallel. Mesosoma: unfortunately the mesosoma of the single examined male specimen was too badly distorted to be described properly. Gaster: brownish-yellow; covered in a thick layer of appressed hairs with scattered erect hairs throughout. Genitalia (figs. 36E-H): in lateral view, parameres long and very thin, each tapering to a pointed apex; cuspi bent slightly toward digiti; cuspi apices with short, peg-like teeth; digiti straight and long, about 2 times as long as cuspi; digiti with apices rounded, each with short peg-like teeth midlength where cuspi bends toward them; penis valve fig. 36H.

Measurements: *Workers* (n=5): TL: 1.97-2.05; HW: 0.457-0.487; HL: 0.576-0.597; SL: 0.391-0.417; ML: 0.436-0.532; GL: 0.878-0.944; CI: 76.55-83.97; SI: 80.29-89.72. *Queens* (n=1): TL: 2.85; HW: 0.604; HL: 0.688; SL: 0.528; ML: 0.882; GL: 1.3; CI: 90.42; SI: 87.42. *Males*: not completed as specimen was too badly distorted to be measured properly.

Other material examined: INDONESIA: Teluk, Kabah Kutai National Park, E. Kalimantan (S. Yamane); **MALAYSIA:** Sabah: Tunku Abdul Rahman National Park, rainforest (B.B. Lowery); **PHILIPPINES:** Palawan, 60 m. Iwahig Penal Col., c. Puerto Princesa, 9.44 N, 118.44 E, rainforest along creek beds (B.B. Lowery). In: ANIC, SYPC.

Distribution and natural history: This species has been recorded as far north as temperate regions of Japan, south and west to China and Indonesia. *A. nipponensis* can survive in a wide range of habitats, occurring in both rainforests and temperate forests. It has been collected along creek beds and under stones. This species has been found in trophobiotic association with the mealybug *Eumyrmococcus nipponensis* in Japan.

Discussion: The primary means of separating workers of *A. nipponensis* from *A. butteli* is by differences in head width (< 0.5 mm in the former, > 0.5 mm in the latter). Examination of figure 48D reveals distinct morphometric differences between the two species. Queen morphology also suggests that the two species are not conspecific. An *A. nipponensis* queen measured had a total length of 2.85 mm versus an *A. butteli* queen with a total length of 4.02 mm. The male described in this study as *A. nipponensis* is associated with workers of the species originally described as *A. jiangxiensis*, a species now treated as a junior synonym. This male is clearly different from *A. butteli* and *A. inezae* males (compare figs. 35E-H and 36A-H). The paratype worker of *A. jiangxiensis* examined cannot be separated from workers of *A. nipponensis* and they are therefore considered to be conspecific. The two characters cited by Terayama *et al.* (2002) as separating *A. nipponensis* and *A. jiangxiensis* are suspect, for both are difficult to interpret with such a small sample size. Slight shape changes in the posterior margin and the dorsum of the propodeum were used to warrant recognition of two species, but here I treat those morphological differences as simply intraspecific variation. As male specimens are collected from across the range of *A. nipponensis* the status of this species should be reexamined.

decedens species-group

Acropyga decedens (Mayr)

Brachymyrmex decedens Mayr, 1887: 521 (w.q.m.). 6 syntype workers, 3 syntype queens, 1 syntype male, BRAZIL: St. Catharina (G. Mayr) (NHMV) [examined]. The designated lectotype is a worker labeled JSL TYPE # 115 and is deposited at NHMV. Emery, 1906: 184, first combination in *Rhizomyrma*; Emery, 1925: 29, first combination in *Acropyga*.

Diagnosis: *Worker:* 9-11 segmented antennae; mandible broad with 4-5 teeth, nearly at right with inner mandibular margin; apical tooth distinctly longer than other teeth; head broader than long. *Queen:* as in worker with modifications expected for caste. *Male:* 12 segmented antennae; parameres taper to a point; cuspi bend toward and meet digiti.

Compare with: *A. donistorpei*, *A. goeldii* and *A. guianensis*

Description: *Worker.* Head (fig. 18A): yellow; typically broader than long; covered in a thick layer of appressed hairs, with shorter erect hairs toward posterior margin; posterior margin entire to slightly concave; 9-11 segmented, incrassate antennae; scape reaches to posterior margin; mandible with 4-5 teeth; 3rd tooth smaller than others when 5 teeth present; apical tooth often distinctly longer than other teeth; inner mandibular margin and anterior clypeal margin at slight less than right angles to each other. Mesosoma: yellow; covered in thick layer of appressed to erect hairs; pronotum in lateral view rises toward rounded mesonotum; mesonotum slightly higher than propodeum, dorsally with longer erect hairs and thick layer of appressed hairs; metanotal area distinct; propodeum with short erect hairs; declivity steep. Gaster: petiole thick and erect, slightly thinner toward apex, reaching height of propodeal spiracle; gaster yellow; covered in a thick layer of appressed hairs with many erect hairs throughout.

Queen. As in worker with modifications expected for caste and the following differences: brownish-yellow; eyes black; head much broader than long; apical tooth very long, almost 2x length of 2nd tooth.

Male. Head: brownish-yellow, brown toward apex around 3 prominent ocelli; head longer than broad; eyes large, filling nearly all of lower lateral sides of head; covered in a layer of appressed to short erect hairs; 12 segmented antennae; scapes surpass posterior margin by about half the length of pedicel; clypeus broad, slightly convex, with erect hairs; mandible with 3 distinct teeth, the 2nd tooth smaller than others; a diastema present between apical and 2nd teeth; gap present between inner mandibular margin and anterior clypeal margin. Mesosoma: pronotum collar-like, overarched by mesonotum; mesonotum flat, covered in appressed to short erect hairs; propodeum flat with short erect hairs; declivity steep. Gaster: petiole erect, slightly convex at apex; gaster brownish-yellow, lighter than head and mesosoma; covered in appressed hairs, with scattered suberect to erect hairs throughout. Genitalia (figs. 37A-D): parameres taper to a point; parameres with many long erect hairs across surface; cuspi bent toward digiti, and meet digiti dorsally; both structures with short, peg-like teeth at apex; digiti thick, rounded apically; penis valve fig. 37D.

Measurements: *Workers* (n=4): TL: 2.02-2.59; HW: 0.507-0.584; HL: 0.505-0.602; SL: 0.36-0.459; ML: 0.603-0.71; GL: 0.818-1.28; CI: 96.68-106.53; SI: 69.70-78.87. *Queens* (n=2): TL: 3.07-3.11; HW: 0.698-0.736; HL: 0.597-0.615; SL: 0.508-0.515; ML: 1.08-1.1; GL: 1.37-1.41; CI: 116.92-119.67; SI: 69.02-73.78. *Males* (n=1): TL: -; HW: 0.381; HL: 0.402; SL: 0.304; ML: 0.687; GL: -; CI: 94.78; SI: 79.79.

Other material examined: ECUADOR: Jatun Sacha, 7 km ESE Pto. Misahualli, 1° 04' S, 37° 37' W, elev. 400 m (P.S. Ward). In: MCZC.

Distribution and natural history: I have only seen specimens of this species from one locality in Brazil (type locality) and one in Ecuador, though it has been reported from a number of localities throughout South America. It has been reported as being trophophoretic, and associated with at least 3 mealybug species: *Geococcus coffeae*, *Neochavesia* sp., *Rhizoecus coffeae*. Though it should be noted that in the literature *A. goeldii* has often been misidentified as *A. decedens* so the mealybug records must be considered suspect.

Discussion: This species can be distinguished from *A. donistorpei* by having an inner mandibular margin that is not at a distinct right angle with the anterior clypeal margin. *A. decedens* can be distinguished from *A. guianensis* because that species always possesses a head that is distinctly longer than broad. In the case of *A. goeldii* diagnosis can be difficult if the specimen possesses a 4-toothed mandible. The mandible is always broader in *A. decedens* than it is in *A. goeldii*, however the difference can be hard to distinguish if you haven't looked at a lot of *Acropyga* specimens. It is therefore not surprising given the similarity of *A. decedens* and *A. goeldii* workers that the latter species was considered a junior synonym of the former by Costa Lima (1931). The best way of separating the two species is with associated male specimens, for males of the two species are

relatively easy to distinguish from one another, and in fact indicate they are not closely related to one another despite the similarity in the worker caste.

Acropyga fuhrmanni (Forel)

Rhizomyrma fuhrmanni, Forel, 1914: 12 (w.q.). 3 syntype workers, 1 syntype queen, COLOMBIA: Puerto de los Pobres, Cauca border, Dep. Antioquia, elev. 720 m (MHNG) [examined]. The designated lectotype is a worker labeled JSL TYPE # 116 and is deposited at MHNG. Emery, 1925: 29, first combination in *Acropyga*; Weber, 1944: 97, description and key and description of larvae and male.

Acropyga (Rhizomyrma) berwicki, W.M. Wheeler, 1935b: 325 (w.). 18 syntype workers, TRINIDAD: San Raphael, B.W.I. (E.J.H. Berwick) (MCZC) [examined]. **NEW SYNONYM.**

Diagnosis: *Worker*: 8 segmented antennae; head usually broader than long; mandible with four distinct teeth, a short diastema separating basal tooth from other teeth. *Queen*: as in worker with modifications expected for caste. *Male*: 9 segmented antennae; eyes close to anterior margin of head; parameres long and rectangular, though they taper toward apex; digiti distinctly long, in dorsal view appearing nearly as long as penis valves.

Compare with: *A. ayanganna* and *A. smithii*

Description: *Worker*. Head (fig. 18B): yellow to brownish-yellow; head typically broader than long; covered in a layer of appressed to suberect hairs, with erect hairs on posterior margin; posterior margin entire; eyes often appearing (relatively) large and prominent, close to anterior margin; 8 segmented, incrassate antennae; scape fails posterior margin by about the length of pedicel; clypeus with abundant erect hairs; mandible with 4 distinct teeth; only a slight gap between clypeal margin and the inner mandibular margin. Mesosoma (fig. 18C): in lateral view anterior portion of pronotum with a short, shelf-like extension before rising steeply toward mesonotum; mesonotum and posterior pronotum bearing numerous erect hairs; a thick layer of appressed and suberect hairs on mesonotum underneath several erect hairs; mesonotum slightly higher than propodeum; metanotal area distinct; propodeum bearing numerous erect and suberect hairs; declivity steep. Gaster: brownish-yellow; petiole thick and erect; gaster yellow; covered in a layer of thick appressed hairs, with erect hairs scattered throughout.

Queen. As in worker with modifications expected for caste and with the following differences: anterior portion of mesonotum slightly overhangs pronotum; dorsum covered with a thick layer of appressed hairs and scattered erect hairs; scutellum of variable pilosity.

Male. Unfortunately the single known male specimen was in such poor condition (shriveled) as to prevent description of the mesosoma; therefore only a description of the head, gaster and genitalia follows. Head: brownish-yellow, darker toward apex around 3 prominent ocelli; head longer than broad, oval in appearance; covered in a layer of appressed hairs; eyes large, breaking outline of head in full frontal view; eyes very close to anterior margin of head as in other castes; 9 segmented, incrassate antennae; apical segment about as long as proceeding 3 segments; scape reaches to posterior margin; clypeus narrow, with a few erect hairs; mandible with long apical tooth and a sharp basal angle not fully developed into a distinct tooth; gap exist between inner mandibular margin and anterior clypeal margin. Gaster: brownish-yellow; covered in layer of appressed hairs, with scattered erect hairs throughout. Genitalia (figs. 37E-H): parameres in lateral view, long and rectangular, though tapering toward apex and covered in numerous erect hairs; in dorsal view, parameres with slight lateral expansions; cuspi tubular in shape, tapering toward apices which bear several short, peg-like teeth where they meet with digiti; digiti long, in dorsal view appearing almost as long as penis valves; tip of digiti slightly anvil-shaped, bearing short, peg-like teeth toward dorsal surface; penis valve fig. 37H.

Measurements: *Workers* (n=34): TL: 1.39-2.56; HW: 0.434-0.642; HL: 0.43-0.612; SL: 0.272-0.484; ML: 0.446-0.698; GL: 0.496-1.19; CI: 93.23-111.94; SI: 58.62-79.08. *Queens* (n=5): TL: 2.55-2.88; HW: 0.516-0.714; HL: 0.488-0.626; SL: 0.306-0.518; ML: 0.798-1.2; GL: 1.23-1.5; CI: 99.61-114.06; SI: 56.46-75.58.

Other material examined: **BOLIVIA:** Cachuela Esperanza (W.M. Mann); Isiamas (W.M. Mann); Ixiamas; **BRAZIL:** Para (D.F. Darlington); Para; Utinga tract, nr Belem. B (W.L. Brown); Amazonas, Manaus to Itacoatiara Rd.; km 49 (W.L. Brown); Para, Pirelli Plantation (Iriboca) nr Belem (P.F. Darlington); Mt. Mpio, Chapada dos Quimardes. Veu de Noiva, trail to waterfall (J.C. Trager); Ilheus, CEPAC (J. Delabie); Ilheus, CEPAC (J.R.M. Sambos); **COLOMBIA:** Chinchina (Valenzuela); Cundinamarca; Bogota-Villavicencio Hwy., km 79 (W.L. Brown & I. de Polanta); Putumayo, villa Garzon (D. Jackson); Venecia (S. Flanders); **COSTA RICA:** Alajuela, 6.5 km East of Monteverde, elev. 950 m, 10° 18' N, 84° 45' W (J. Longino); Rio Penas Blancas, elev. 800 m, 10° 19' N, 84° 43' W, 27 (J. Longino); Heredia, 17 km south of Pto. Viejo, elev. 550 m, 10° 18' N, 84° 2' W (J. Longino); 8 km southwest of Pto. Viejo, elev. 150 m, 10° 24' N, 84° 3' W (J. Longino); Est. Biol. La Selva, elev. 50 m, 10° 26' N, 84° 0' W (J. Longino); same locality, elev. 50-150 m, 10° 26' N, 84° 1' W; same locality, elev. 50-150 m, 10° 26' N, 84° 1' W (C.W. Thompson); same locality, elev. 50-150 m, 10° 26' N, 84° 1' W (C.W. Thompson); same locality, 10° 26' N, 84° 1' W; Limon, Res. Biol. Hitoy-Cerere, elev. 500 m, 9°40' N, 83° 2' W (J. Longino); Navarro Farm, elev. 1100 m, 9° 49' N, 83° 53' W [approximate coordinates provided by J.T. Longino, pers. comm.] (W.M. Mann); **ECUADOR:** Canar, 2-6 km above Cochancay on Guayaquil-Tambo Highway, elev. 500-700 m (W.L. Brown); **GUYANA:** Kartabo (W.M. Wheeler); **TRINIDAD:** San Raphael (E.J.H. Berwick). In: BMNH, JSLC, JTLC, MCZC, MZSP, USNM.

Distribution and natural history: This species has a wide range from Central America (recorded as far north as Costa Rica) south throughout tropical South America. *A. fuhrmanni* has been found in litter, and in a variety of habitats from grassy, open areas to rainforests. It has been recorded occurring up to an elevation of 950 m. Wheeler (1935) stated that this species was also found in cacao plantations. Queens are trophophoretic, having been recorded with at least one mealybug species belonging to the genus *Neochavesia*. Wheeler (1935) noted that workers and queens (he unfortunately did not indicate if the queens were alate or dealate however) carried mealybugs when a nest was disturbed.

Discussion: This species is fairly easy to recognize with its 8-segmented antennae and relatively large eyes, set close to head's anterior margin. Some specimens have been examined where the gaster is darker than the rest of the body giving them an almost bi-colored appearance. However, all other characters suggest these specimens are conspecific with specimens that are yellow colored throughout. Additionally, size of the worker is variable with a series of specimens from Costa Rica being the largest (TL: 2.3-2.6), while most *A. fuhrmanni* are around 1.6 mm in total length. Unfortunately despite being one of the more common species in collections, only one male specimen is known, and it was in very poor condition. Therefore, as males are collected across the range of this species, they should be examined to address any questions of conspecificity.

A. fuhrmanni is a member of the *decedens* species-group and is the sister species to the *goeldii* complex of species. Its penis valves are elongated as in *A. smithii*, though they are not as wide.

Acropyga smithii Forel

Acropyga (Rhizomyrma) smithii Forel, 1893: 349 (q.). Holotype queen, ST. VINCENT AND THE GRENADINES: St. Vincent, elev. 457.2 m, (H.H. Smith) (BMNH) [examined]. The holotype queen is labeled JSL TYPE #101.

Acropyga (Rhizomyrma) kathrynae Weber, 1944: 114 (w.). 4 syntype workers, TRINIDAD: Maracas Valley. B.W.I. (N.A. Weber) (MCZC) [examined]. **NEW SYNONYM.**

Acropyga (Rhizomyrma) urichi Weber, 1944: 115 (w.q.m.). 2 syntype workers, 1 syntype queen, 1 syntype male, TRINIDAD: Maracas Valley. B.W.I. (N.A. Weber) (MCZC) [examined]. **NEW SYNONYM.**

Diagnosis: *Worker:* 7-8 segmented antennae; mandibles broad with 4 distinct teeth; mesosomal dorsum relatively flat (pronotum and mesonotum at about same height); an especially small species (total length < 1.7 mm). *Queen:* as in worker with modifications expected for caste. *Male:* 9 segmented antennae; head longer than broad; in lateral view, parameres slightly tapering to a rounded apex; cuspi short meeting digiti dorsally.

Compare with: *A. exsanguis*, *A. fuhrmanni*, and *A. stenotes*

Description: *Worker.* Head (fig. 19A): yellow; covered in a layer of thick layer of appressed hairs; head distinctly longer than broad; posterior margin entire; 7-8 segmented, distinctly incrassate antennae; scape fails to reach posterior margin by about the length of the first two funicular segments; clypeus with abundant erect to suberect hairs; mandibles narrow with 4 distinct teeth; gap exists between inner mandibular margin and anterior clypeal margin. Mesosoma (fig. 19B): pronotum rises gently from margin toward mesonotum; mesosomal dorsum flat; mesonotum and propodeum at about the same level; abundant suberect to erect hairs on mesonotum; metanotal area distinct; propodeum distinct; declivity steep. Gaster: petiole thick and erect, well below level of propodeum; gaster yellow; covered in a thick layer of appressed hairs, with scattered erect hairs throughout.

Queen. As in worker with modifications expected for caste.

Male. Head: brownish-yellow, darker around 3 prominent ocelli; head longer than broad; covered in layer of short appressed hairs with scattered, longer hairs, especially along sides; 9 segmented, slightly incrassate antennae, with apical segment about as long as three preceding segments; scape fails posterior margin by about length of pedicel; posterior margin entire; clypeus medially convex with many long erect hairs on surface; mandible narrow with 2 teeth, a small tooth at basal angle and a long apical tooth; apical tooth separated from basal tooth by a wide, smooth diastema; a slight gap exists between inner mandibular margin and outer clypeal margin. Mesosoma: light yellow; pronotum narrow and collar-like with only a few erect; pronotum overarched by mesonotum; mesonotum rounded anteriorly and covered in a layer of appressed hairs, occasionally with a few erect hairs; propodeum rounded; declivity steep. Gaster: petiole thick and erect; gaster yellow; covered in a layer of appressed hairs with scattered erect hairs throughout. Genitalia (figs. 38A-D): in lateral view, parameres taper to rounded apices; posterior portion of parameres with many long erect hairs; cuspi short, round and each tapering to an apical point; digiti flat and anvil-shaped apically; cuspi meet digiti dorsally; penis valve fig. 38D.

Measurements: *Workers* (n=13): TL: 1.23-1.62; HW: 0.316-0.364; HL: 0.36-0.408; SL: 0.192-0.251; ML: 0.354-0.449; GL: 0.492-0.764; CI: 81.86-97.2; SI: 58.02-69.76. *Queens* (n=2): TL: 2.07-2.24; HW: 0.395-0.408; HL: 0.427-0.449; SL: 0.256-0.281; ML: 0.627-0.634; GL: 1.02-1.16; CI: 90.87-92.51; SI: 64.81-68.87. *Males* (n=2): TL: 1.5; HW: 0.275-0.287; HL: 0.313-0.324; SL: 0.208-0.21; ML: 0.474-0.51; GL: 0.65; CI: 87.86-88.58; SI: 73.17-75.64

Other material examined: **BELIZE:** From soil sample from Belize (British Honduras) intercepted at Mobile, Alabama, USA, 25 April 1927; **COLOMBIA:** Magdalena; 4 km N. San Pedro, elev. 550 m, 10° 57' N, 74° 3' W (J. Longino); Rio Porce, elev. 1020 m (N.A. Weber); Ant., Providencia; Estacion Biol.; Quebrada La Tirana, elev. 520 m (C. Kugler); **HONDURAS:** Depto Cortes, Lago Yojoa, E. side island-hill; Island at Agua Azul Hotel, elev. 700 m (W.L. Brown); **PANAMA:** Barro Colorado Island; Canal Zone (N.A. Weber); **PERU:** Madre de Dios, Cocha Cashu, 90° 19' S, 36° 71' W (D.W. Davidson); Cuzco Amazonico; 15km NE of Puerto Maldonado (S.P. Cover & J.E. Topin); **TRINIDAD:** (C. Callen & Strickland); Maracas Valley; B.W.I. (N.A. Weber); Maracas Vallley; B.W.I. (N.A. Weber); Mason's Estate; near Arima (N.A. Weber); St. Augustine; Tuacarigua River; B.W.I. (N.A. Weber). In: JTLC, LACM, MCZC, USNM.

Distribution and natural history: The species has a large range from Central America (to Belize) southward, probably throughout tropical South America. It has also been found in the Lesser Antilles. This species is also the first recorded *Acropyga* species being transported by man (from Belize to Alabama presumably by ship: information from label data). Given that many *Acropyga* inhabit coffee and cacao plantations, the potential for transport by humans is real and warrants further investigation.

A. smithii is known to inhabit rainforests and cacao plantations. It occurs in the soil and litter; Weber (1944) reported nests from red clay soils down to a depth of 7.5 cm. Queens have been

recorded from under the bark of a rotten log. Weber (1944) reported that at least two queens were found in one nest, indicating that this species may be polygynous. Winged reproductives have been collected from January-May. Two mealybug species have been recorded with this species, *Neochavesia eversi*, and *Geococcus coffeae*.

Discussion: This is among the smallest New World species (TL: 1.2-1.6); *A. panamensis* is around the same size, though it is quite different morphologically from *A. smithii*. *A. smithii* workers can possess antennal segment counts as low as 7 segments, the lowest number observed in a New World *Acropyga* (the only other species to have antennal segment counts this low is *A. oceanica* from Southeastern Asia). *A. smithii* could be confused with *A. stenotes* because they both are small species that have distinctly longer than broad heads, but *A. stenotes* has 11-segmented antennae.

A. smithii is the only member of the *decedens* species-group known to possess broadly rounded paramere apices in the male. It shares several characteristics with *A. fuhrmanni* such as elongated penis valves, antennal segment counts in the worker not greater than 8 segments and similarly shaped mandibles.

goeldii complex within the *decedens* species-group

Acropyga dubitata (W.M. Wheeler and Mann)

Rhizomyrma dubitata W.M. Wheeler and Mann, 1914: 47 (m.). 17 syntype males, DOMINICAN REPUBLIC: St. Domingo; San Francisco Mountains, 14 September 1905 (A. Busck) (LACM) (MCZC) (USNM) [examined]. The designated lectotype is a male labeled JSL TYPE # 117 and is deposited at MCZC. Emery, 1925: 29, first combination in *Acropyga*.

Diagnosis: *Worker:* unknown. *Queen:* unknown. *Male:* 11-12 segmented antennae; parameres short and rectangular in shape; apex of paramere with a dorsocaudal point.

Compare with: *A. hirsutula* and *A. keira*

Description: *Worker:* Unknown.

Queen. Unknown.

Male. Head: brownish-yellow, darker toward apex near 3 prominent ocelli; head broader than longer, broadest toward apex; eyes large, breaking outline of head in frontal view; 11-12 segmented, slightly incrassate antennae; scape reaches or surpasses posterior margin by about length of pedicel; clypeus slightly convex, covered in dense layer of appressed hairs, with erect hairs medially placed along anterior margin; mandible with 2-3 teeth, though basal tooth can be thickened into the mandible (creating a small notch rather than a proper tooth), so that mandible effectively only has an apical tooth; a gap exists between anterior clypeal margin and inner mandibular margin. Mesosoma: yellow; pronotum short and collar-like around mesonotum, which is broadly rounded anteriorly and laterally; mesonotum flat, covered in a layer of mostly appressed hairs; propodeum low, broadly rounded into indistinct declivity. Gaster: petiole thick and erect, roughly rectangular in lateral view; gaster yellow; covered with appressed hairs, with scattered erect hairs placed posteriorly near genitalia. Genitalia (figs. 38E-H): parameres short, rectangular, covered with scattered hairs; dorsal apices of parameres with a dorsocaudal point; cuspi short and cylindrical, with short, peg-like teeth at apices; digiti anvil-shaped apically, bent toward cuspi, apices with short, peg-like teeth; penis valve fig. 38H.

Measurements: *Males* (n=7): TL: 1.67-2.35; HW: 0.403-0.482; HL: 0.404-0.487; SL: 0.33-0.43; ML: 0.716-0.912; GL: 0.546-0.962; CI: 91.3-101.69; SI: 81.89-92.0.

Distribution and natural history: This species has only been collected once from the San Francisco Mountains (Dominican Republic), and it appears to be endemic to Hispaniola. Nothing is known about the natural history of this enigmatic *Acropyga* species.

Discussion: Only males of *A. dubitata* are known, and it appears the species is endemic to Hispaniola. It is possible that *A. parvidens* (in which males are not known) is really *A. dubitata*

(the older available name). *A. dubitata* males have up to 12 antennal segments suggesting that the workers would have up to 11 as seen in *A. parvidens*. It is interesting to note that no other *Acropyga* are known to occur in the Greater Antilles other than on Hispaniola. Whether this is an artifact of collecting or of some biological interest is unknown as this time.

Based on the dorsal notch on the penis valve (figs. 38H and 40H), the closest relative to *A. dubitata* is *A. hirsutula*. Additionally, each of these species have highly contoured penis valves with square ventral extensions. The fossil *Acropyga* species from Dominican amber is not closely related to members of the *decedens* species-group (LaPolla, in prep).

Acropyga epedana Snelling

Acropyga epedana Snelling, 1973: 7 (w.). 1 holotype worker, USA: Arizona: Cochise Co.; 3.1 miles west of Montezuma's Pass; elev. ca. 1676 m (R.R. Snelling) (LACM) [not examined]; 3 paratype workers, same locality as holotype (LACM) [examined]. LaPolla *et al.*, 2002: 367, description of queen and male.

Diagnosis: *Worker:* antennae 10-11 segmented; scape reaches posterolateral corners; mandible with three distinct teeth, occasionally a smaller fourth tooth found along inner mandibular margin; mesosoma with abundant, generally appressed hairs. *Queen:* as in worker with modification expected for caste. *Male:* antennae 12 segmented; mandibles with two distinct teeth, occasionally a smaller tooth is present at basal angle; rectangular shaped parameres; cuspi and digiti meet apically forming an oval-shaped space between them in ventral view.

Compare with: species of the *goeldii* complex.

Description: *Worker.* Head (fig. 19C): yellow to brownish-yellow; head typically about as broad as long, occasionally is slightly longer than broad; posterior margin entire; surface covered in a thick layer of short appressed hairs; 10-11 segmented, incrassate antennae; scapes reach to posterior margin; clypeus with many erect hairs; mandibles with 3 distinct teeth; occasionally a smaller 4th tooth found near inner mandibular margin; gap exists between anterior clypeal margin and inner mandibular margin. Mesosoma (fig. 19D): yellow to brownish-yellow; in lateral view pronotum rises steeply toward mesonotum; mesonotum with a thick layer of abundant, largely appressed hairs; mesonotum distinctly higher than propodeum; metanotal area distinct; propodeum rounded with abundant appressed hairs on dorsum; declivity steep. Gaster: petiole erect to slightly inclined forward; petiole rounded at apex with several erect hairs; gaster yellow; covered in a thick layer of appressed hairs, with scattered erect hairs throughout.

Queen. As in worker with modification expected for caste and the following differences: scutellum distinct, roughly oval, slightly paler than mesonotum, with fewer suberect hairs covering dorsum; propodeum with fewer short, suberect hairs than other parts of the mesosoma

Male. Head: brownish-yellow, darker at apex around 3 prominent ocelli; covered in a thin layer of appressed hairs; 12 segmented antennae; scapes surpass posterior margin by about the length of the first two funicular segments; clypeus with several long hairs on anterior margin, though generally less pilose than the rest of the head; mandibles with 2 distinct teeth, a smaller tooth occasionally present at basal angle; large gap exists between anterior clypeal margin and inner mandibular margin. Mesosoma: yellow to brownish-yellow; pronotum short and collar-like; anterior of mesonotum rounded, dorsum flat, covered in short, suberect hairs; propodeum with fewer short, suberect hairs than other parts of the mesosoma; declivity short, but steep. Gaster: petiole erect but short; gaster brownish-yellow with more brown dorsally; covered in a thin layer of appressed hairs, with a few scattered suberect hairs present. Genitalia (figs. 39A-D): parameres long, and rectangular; anteriorly parameres without hairs, the posterior ends with scattered erect hairs; cuspi cylindrical, with short, peg-like teeth at apices; digiti elongate with apices roughly anvil-shaped; dorsal tip of digiti with short, peg-like teeth where they meet the cuspi; penis valve fig. 39D.

Measurements: *Workers* (n=10): TL: 1.83-2.28; HW: 0.481-0.539; HL: 0.482-0.534; SL: 0.343-0.394; ML: 0.592-0.612; GL: 0.731-1.12; CI: 94.01-106.1; SI: 66.04-77.05. *Queens* (n=6):

TL: 3.03-3.17; HW: 0.592-0.612; HL: 0.571-0.602; SL: 0.443-0.485; ML: 0.854-0.956; GL: 1.51-1.71; CI: 100.3-111.0; SI: 74.5-80.7. *Males* (n=3): TL: 2.00-2.13; HW: 0.419-0.425; HL: 0.410-0.424; SL: 0.330-0.374; ML: 0.726-0.775; GL: 2.00-2.13; CI: 100.5-102.4; SI: 78.8-88.0

Other material examined: USA: Arizona: Santa Cruz Co.; Pajarito Mtns; 8 miles W. jct. I-19 on Rt. 289 at FSR 221 (Walker Canyon); elev. ca. 1052 m (S.P. Cover); Arizona: Cochise Co.; 13.8 mi NW jct, Rt. 80 on FSR 74; elev. ca. 1757 m (S.P. Cover); Arizona: Cochise Co.; ca. 5 miles west of Portal, near Southwestern Research Station (31°53.32' N, 109°12.48' W; 1676 m elevation) (J.S. LaPolla and U.G. Mueller); Arizona: Cochise Co.; 0.4 mi. NW Southwestern Research Station (31°53.20' N, 109°12.24' W; elev. ca. 1737 m) (S.P. Cover). In: JSLC, LACM, MCZC.

Distribution and natural history: *A. epedana* is presently known from 5 sites in southeastern Arizona, though it probably ranges south into Mexico through the Sierra Madre Occidental. *A. epedana* appears to occur only at higher elevations (where annual rainfall is greater) between 1052 m - 1676 m, in open oak/juniper woodland habitat.

The natural history and behavior of *A. epedana* has been extensively documented by LaPolla *et al.* (2002). Alates have been collected from nests in August, and there is evidence that nest founding takes place at this time of year (probably corresponding to the monsoonal rains). LaPolla *et al.* (2002) discovered an apparently founding queen in a small chamber with eggs in mid-August. A *Rhizoecus* mealybug species is known to be associated with *A. epedana* (Williams, pers. comm.).

Discussion: A member of the *decedens* species-group, this species is very similar in general appearance to *A. goeldii* and *A. palaga*. It may represent a northern population of *A. goeldii* and thus may be over-split as recognized here (see discussions of *A. goeldii* and *A. palaga* for further analysis of problems with some species of *goeldii* complex). However, differences in the penis valves of the three species suggest they are distinct species (figs. 39D, 40D, and 41H). The main difference is in the ventral extension of the penis valve. In *A. epedana* the ventral extension is much narrower at the base and comes more to a point than in the broadly rounded base of *A. goeldii*, and lacks distinct ventral curve from the caudal end of the penis valve through the ventral extension found in *A. palaga*. The head of *A. epedana* workers are generally not as wide or long as is found in the other two species. Finally, *A. epedana* workers do not possess very many erect hairs on the mesosomal dorsum, unlike *A. goeldii* and *A. palaga*. Instead the dorsum is largely covered in a dense layer of appressed hairs.

Acropyga exsanguis (W.M. Wheeler)

Rhizomyrma exsanguis W.M. Wheeler, 1909: 238 (w.). 3 syntype workers, MEXICO: Jalapa (F. Silvestri) (MCZC) [examined]. The designated lectotype is a worker labeled JSL TYPE # 118 and is deposited at MCZC. Lectotype is 1 of 3 specimens on the same card. The lectotype is the specimen to the right of the middle specimen if the card is oriented away from an examiner. The worker is raised up slightly off the card and the head is not glued down to the surface. Mann 1922: 53, first combination in *Acropyga*.

Acropyga (Rhizomyrma) wheeleri Mann, 1922: 52 (w.q.). 8 syntype workers, HONDURAS: Lombardia (Hugrich) (MCZC) (USNM) [examined]. **NEW SYNONYM.**

Acropyga (Rhizomyrma) bruchi Santschi, 1929: 308 (w.). 3 syntype workers, ARGENTINA: Santa Fe, Rosario (NHMB) [examined]. **NEW SYNONYM.**

Acropyga (Rhizomyrma) paramaribensis Borgmeier, 1933: 263 (w.q.). Syntype workers, syntype queens, SURINAM: Paramaribo (depository unknown) [not examined]. **NEW SYNONYM.** Borgmeier 1934: 109, description of male; Bünzli 1935: 519, description of larva; Kempf 1972: 17, first combination in (*Rhizomyrma*).

Acropyga (Rhizomyrma) robae Donisthorpe, 1936: 108 (w.q.m.). Holotype worker, COLOMBIA: La Esperanza (R. Roba) (BMNH) [examined]; 7 paratype workers, 5 paratype queens, 1 paratype male, same locality as holotype (BMNH) (MCZC) [examined]. **NEW SYNONYM.**

Diagnosis: *Worker:* 8-9 segmented antennae; scape typically slightly fails posterior margin; head about as broad as long; head width < than 0.52 mm; mandible with 3 distinct teeth; mesonotum dorsum with a thick layer of hairs, with scattered erect hairs. *Queen:* as in worker with modifica-

tions expected for caste. *Male*: 9-10 segmented antennae; parameres long and rectangular with many long erect hairs covering lateral surface; parameres often with distinct dorsolateral expansions.

Compare with: *A. keira* and *A. romeo*

Description: *Worker*. Head (fig. 20A): yellow; head about as broad as long; covered in a dense layer of appressed hairs, with scattered erect hairs toward posterior margin; posterior margin slightly concave medially; 8-9 segmented, incrassate antennae; apical segment about as long as preceding 4 segments; scape reaches or slightly fails posterior margin; clypeus with dense layer of erect hairs of varying lengths; mandible with 3 distinct teeth; gap exists between inner mandibular margin and anterior clypeal margin. Mesosoma (fig. 20B): yellow; in lateral view, pronotum rises steeply toward mesonotum; pronotum with appressed hairs, erect hairs more posteriorly placed; mesonotum usually high and dorsally rounded, covered in dense layer of appressed hairs, with erect hairs scattered throughout; metanotal area distinct; propodeum below level of mesonotum, rounded with appressed and erect hairs; declivity steep. Gaster: petiole thick and erect; petiole reaches about midline of propodeal spiracle; gaster yellow; covered in a dense layer of appressed hairs, with scattered erect hairs throughout.

Queen. As in worker, with modifications expected for caste and the following differences: scutellum with appressed and erect hairs; two longest hairs (almost as long as scutellum) anterolaterally placed opposite each other.

Male. Head: brownish-yellow anteriorly becoming dark brown around 3 prominent ocelli; head about as broad as long; 9-10 segmented, incrassate antennae; apical segment about as long as preceding 3 segments; scape reaches or slightly surpasses posterior margin; clypeus with dense layer of appressed and erect hairs; mandible with 1-2 teeth; basal tooth, when present, small and indistinct, separated from apical tooth by wide diastema; gap exists between inner mandibular margin and anterior clypeal margin. Mesosoma: pronotum short and collar-like, overarched by mesonotum; anterior mesonotum broadly rounded; mesonotum dorsum flat, covered in a layer of largely short appressed hairs, with scattered longer appressed to erect hairs throughout; propodeum slightly rounded, with appressed hairs; declivity very short, but steep. Gaster: petiole thick and erect; gaster brownish-yellow, dorsum darker. Genitalia (figs. 39E-H): in lateral view, parameres elongate and rectangular, covered in scattered suberect to erect hairs; parameres with dorsolateral expansions apically, varying from completely covering to only slightly covering *digiti* and *cuspi* in dorsal view; *cuspi* cylindrical, curved apically toward *digiti*; apices of *cuspi* with short, peg-like teeth; *digiti* anvil-shaped apically, meeting *cuspi* on dorsal surface, where short, peg-like teeth are present; penis valve fig. 39H.

Measurements: *Workers* (n=22): TL: 1.72-2.38; HW: 0.462-0.511; HL: 0.451-0.522; SL: 0.318-0.380; ML: 0.427-0.592; GL: 0.710-1.32; CI: 94.64-104.7; SI: 67.37-76.14. *Queens* (n=5): TL: 2.17-3.48; HW: 0.52-0.547; HL: 0.508-0.547; SL: 0.367-0.443; ML: 0.828-0.963; GL: 1.14-1.97; CI: 100-107.28; SI: 67.34-82.96. *Males* (n=6): TL: 1.87-2.41; HW: 0.346-0.412; HL: 0.388-0.410; SL: 0.267-0.311; ML: 0.67-0.785; GL: 0.79-1.28; CI: 89.18-105.93; SI: 67.65-75.49.

Other material examined: **BELIZE:** Chiquibul Forest Reserve, La Cuevas (J. Beard and L. Tarel); **COLOMBIA:** Chinchina; La Esperanza; Cundinamara, elev. 1250 m (R.P. Roba); **COSTA RICA:** Guanacaste, Santa Rosa National Park, 10° 51' N, 85° 37' W; elev. 300 m (J. Longino); Heredia, La Selva (Talbot and VanDevender); Heredia, La Selva, elev. 1000 m (J. Longino); Heredia, 16 km SSE La Virgen, 10° 16' N, 84° 05' W, elev. 1150 m (J. Longino); Puntarenas, Monteverde, 10° 18' N, 84° 49' W, elev. 1100 m (J. Longino); Turrialba (N.A. Weber); **GUATEMALA:** Retalhuleu (F.J. Hambleton); **GUYANA:** Oko River, tributary of Cuyuni River (N.A. Weber); **MEXICO:** Chiapas, 12.5 km NW Ocosingo, elev. 1400 m (R.S. Anderson); **PANAMA:** Barro Colorado Is-

land, Canal Zone (W.L. Brown and E.S. McCluskey); **SURINAM**: Paramaribo (G. Bünzli); Jagtlast (G. Bünzli). In: BMNH, JTLC, MCZC, USNM.

Distribution and natural history: This species has a wide distribution, ranging from central Mexico to northern Argentina. A number of mealybugs have been recorded living with this species: *Neochavesia* sp., *Geococcus coffeae*, *Rhizoecus coffeae*, *Pseudorhizoecus proximus*, *Rhizoecus caladii*, and *Rhizoecus falcifer*. Trophophoretic behavior by queens has been observed on at least three separate occasions: queens carrying *Rhizoecus coffeae* by Bünzli (1935) and Roba (1936) and *Pseudorhizoecus* sp. by Weber (1957).

Bünzli (1935) extensively documented the natural history of *A. exsanguis* (under the synonym *A. paramaribensis*). This species is highly polygynous. Bünzli (1935) found both pleometrosis (founding of a colony by multiple queens), and the acquisition of young queens by established colonies in *A. exsanguis*, suggesting multiple possible origins of polygyny. Bünzli (1935) found that *A. exsanguis* possesses large, diffuse nests in the soil (similar to those described by LaPolla *et al.* (2002) for *A. epedana*). The species is known to make vertical nest movements in the soil depending on soil conditions. For instance, as the upper layers of soil dry, Bünzli (1935) found the ants moved deeper into the ground.

Discussion: Workers are distinguishable from other species in the *decedens* species-group by the 8-9 antennal segments and the small head width (< 0.52 mm). Worker mandibular dentition seems to be stable at 3 distinct teeth. However Bünzli (1935) reported observing 4 teeth and 7 antennal segments in *A. paramaribensis* (a junior synonym). Fortunately a large sample of this species was available for study, and I never observed a 4th mandibular tooth or 7 antennal segments among any specimens. Therefore, I suspect that Bünzli was in error or that the latter conditions are extremely rare aberrations. He may have confused *A. exsanguis* with *A. smithii*, which does have 4 mandibular teeth and can possess as few as 7 antennal segments. This species could be confused with *A. romeo*, but can be separated from it based on the presence of a 4th smaller basal tooth.

Males of this species are distinct, with dorsolateral expansions of varying degrees found in the parameres (from slight lateral expansions to expansions that completely cover the digiti and cuspi in dorsal view). Variation in the dorsolateral expansion of the parameres at first led me to believe that there were several species present, but after examining multiple male specimens it is clear that the variation is a continuum and the specimens were indeed conspecific. Examination of the penis valves revealed that they are the same structural type regardless of the extent of the dorsolateral expansion.

Acropyga goeldii Forel

Acropyga (Rhizomyrma) goeldii Forel, 1893: 348 (w.). 3 syntype workers, BRAZIL: Parahyba, Prov. Rio de Janeiro (Goeldi) (MHNG) (AMNH) [examined]. The designated lectotype is a worker specimen labeled JSL TYPE # 108 and is deposited at MHNG. Forel 1912b: 60, first combination in *Rhizomyrma*; Emery, 1925: 29, first combination in *Acropyga*; Costa Lima 1931: 7, junior synonym of *A. decedens*; W.M. Wheeler, 1935b: 322, revived from synonymy; Weber 1944: 93, description and key.

Rhizomyrma pachycera Emery, 1906: 182 (w.q.). Syntype worker, syntype queen. PARAGUAY: Tacuru Pucu (MCSN) [examined]. Emery, 1925: 29, first combination in *Acropyga*; Weber, 1944: 95, description and key. **NEW SYNONYM.**

Rhizomyrma goeldii columbica Forel, 1912b: 61 (w.). Holotype worker, COLOMBIA (no specific locality given) (MHNG) [examined]. **NEW SYNONYM.** Emery, 1925: 29, first combination in *Acropyga*; Weber, 1944: 94, description and key.

Rhizomyrma goeldii tridentata Forel, 1912b: 61 (q.m.). 3 syntype males, 3 syntype queens, PANAMA (no specific locality given) (Christopherson) (MHNG) [examined]. Emery, 1925: 29, first combination in *Acropyga*; Weber, 1944: 94, description and key. **NEW SYNONYM.**

Rhizomyrma marshalli Crawley, 1921: 93 (w.). Holotype worker, BARBADOS: B.W.I. (J.R. Bovell) (BMNH) [examined]. **NEW SYNONYM.** Emery, 1925: 30, first combination in *Acropyga*; Weber, 1944: 101, description and key.

Acropyga (Rhizomyrma) pickeli Borgmeier, 1927: 287 (w.q.). Syntype workers, 2 syntype queens, BRAZIL: Parahyba do Norte (MCZC, queens only; depository for workers unknown) [examined queens only]. **NEW SYNONYM.** Costa Lima, 1931: 7, junior synonym of *A. decedens*; Borgmeier, 1932: 238, revived from synonymy; W.M. Wheeler, 1935b: 322, listed; Weber, 1944: 102, description and key.

Acropyga (Rhizomyrma) rutgersi Bünzli 1935: 464 (w.q.m.). Syntype workers, syntype queens, syntype males, SURINAM: Paramaribo (depository unknown) [not examined]. **NEW SYNONYM.** Weber, 1944: 104, description and key.

Acropyga (Rhizomyrma) borgmeieri Donisthorpe, 1939: 153 (m.). Holotype male, GUYANA: Forest Settlement, Mazaruni River (BMNH) [examined]. **NEW SYNONYM.** Weber, 1944: 111, description and key.

Acropyga (Rhizomyrma) quadriceps Weber, 1944: 113 (w.). 4 syntype workers, TRINIDAD: Maracas Valley, B.W.I. (N.A. Weber) (MCZC) [examined]. **NEW SYNONYM.**

Acropyga (Rhizomyrma) trinitatis Weber, 1944: 117 (w.q.). 4 syntype workers, 1 syntype queen, TRINIDAD: between 10-12th mile of Arima-Blanchisseuse Road (N.A. Weber) (MCZC) [examined]. **NEW SYNONYM.**

Diagnosis: *Worker:* 9-11 segmented antennae; scape reaches or surpasses posterior margin; 3-4 teeth on mandible; head as broad or broader than long; clypeus with abundant erect hairs. *Queen:* as in worker with modifications expected for caste. *Male:* 12 segmented antennae; parameres rectangular and thin with apex wider reaching a sharp dorsocaudal point.

Compare with: *A. palaga* and other members of the *goeldii* complex, *A. decedens*, and *A. guianensis*

Description: *Worker:* Head (fig. 20C): yellow; head about as broad as long; posterior margin slightly concave to entire; covered in a layer of appressed hairs, with several erect hairs usually along posterior margin; 9-11 segmented, incrassate antennae; scapes reaches or slightly surpasses (less than half length of pedicel) posterior margin; clypeus narrow, convex, covered in abundant erect hairs; mandible with variable numbers of teeth; with 4 distinct teeth, 3 distinct teeth and a minute basal tooth, or only 3 distinct teeth with no evidence of a 4th tooth; gap exists between anterior clypeal margin and inner mandibular margin. Mesosoma (fig. 20D): yellow; in lateral view pronotum with a short anterior shelf before rising sharply toward mesonotum; posteriorly pronotum with many erect hairs; mesonotum covered in a thick layer of appressed hairs, with many scattered erect hairs; mesonotum higher than propodeum; metanotal area often distinct, with one or two sulci present; propodeum rounded with thick layer of appressed hairs, and scattered erect hairs; declivity steep. Gaster: petiole thick and erect; petiole does not reach level of propodeum; gaster yellow; covered in a layer of appressed hairs, with scattered erect hairs throughout.

Queen. As in worker with modifications expected for caste and the following differences: mesosoma with many short, erect hairs.

Male. Head: brown to yellowish-brown, darker at apex around 3 prominent ocelli; head broader than long, though anteriorly, narrowing giving head a roughly triangular appearance; covered in a layer of appressed to erect hairs; eyes large, breaking outline of head in full frontal view; 12 segmented, slightly incrassate antennae, the apical segment about as long as preceding 2-3 segments; scape surpasses posterior margin by about length of pedicel; clypeus convex medially, covered in thick layer of erect hairs; mandible with 2-3 distinct teeth; when with 2 teeth a wide diastema separates apical and basal tooth; gap exists between anterior clypeal margin and inner mandibular margin. Mesosoma: brownish-yellow; pronotum short and collar-like; mesonotum anteriorly rounded, dorsally flat, covered in a layer of short appressed to erect hairs; scutellum roughly oval-shaped, covered in longer erect hairs; propodeum rounded into short, steep declivity. Gaster: petiole thick and erect; gaster brownish-yellow, covered in layer of appressed hairs, with scattered erect hairs throughout. Genitalia (figs. 40A-D): in lateral view, parameres long, rectangular, with scattered erect to suberect hairs; shape of parameres variable from thin but expanded at apex to a sharp dorsal point and slightly wider ventral aspect, to thick throughout length and square at apex; cuspis cylindrical; digitus with apices anvil-shaped; digitus meets cuspis dorsally, where both have structures have a series of short, peg-like teeth; penis valve fig. 40D.

Measurements: *Workers* (n=12): TL: 2.03-2.57; HW: 0.524-0.623; HL: 0.503-0.616; SL: 0.398-0.473; ML: 0.554-0.714; GL: 0.723-1.32; CI: 94.78-110.81; SI: 64.91-78.63. *Queens* (n=2): TL: 3.19-3.21; HW: 0.652-0.669; HL: 0.568-0.613; SL: 0.475-0.529; ML: 1.02-1.05; GL: 1.55-1.6; CI: 109.14-114.79; SI: 72.85-79.07. *Males* (n=5): TL: 2.38-2.51; HW: 0.448-0.461; HL: 0.439-0.453; SL: 0.346-0.403; ML: 0.833-0.986; GL: 0.98-1.18; CI: 100-102.9; SI: 76.89-87.42.

Other material examined: **BARBADOS** (R.W.E. Tucker); **COLOMBIA:** Valla, Cali, elev. 1000 m (W. Eberhard); **GUYANA:** Mazaruni River (N.A. Weber); **SURINAM:** (G. Bünzli); **TRINIDAD:** St. Augustine, B.W.I. (N.A. Weber); Woodford Est., B.W.I. (R.G. Fennah); **VENEZUELA:** Macuto (N.A. Weber); Rancho Grande to Ocumare, Aragua, elev. 420 m (W.L. & D.E. Brown). In: BMNH, MCZC, USNM.

Distribution and natural history: This species has a wide range across tropical South America, and has been recorded occurring as far north as Barbados and Costa Rica. It is a known trophophoretic species and is associated with at least 4 mealybug species: *Capitisetella migrans*, *Dysmicoccus radialis*, *Neochavesia* sp., and *R. coffeae*.

Weber (1944) reported this species was found “tending the common Trinidad type of coccids on rootlets of small plants which were interwoven into the husk of a brazil nut fruit lying on the ground. Under the husk was yellow sandy clay soil in which the ants had tunnels.” He also reported trying to feed a small nest series he placed in a glass container to observe them while they were alive and found they did not eat pieces of fruit offered to them. As in *A. epedana* (LaPolla *et al.*, 2002) this species apparently only fed on honeydew produced by the mealybugs, and the nest died within a month (mealybugs were present, but they had no roots to feed on). He did not report if any of the mealybugs had been eaten by the ants, and interestingly carnivory in “starving” nests has not been reported.

This is most likely the species Eberhard (1978) reported as being trophophoretic (identified from specimens deposited at MCZC). He observed several mating swarms of males and females, each consisting of several dozen individuals. The swarms seemed to be either predominantly male or predominantly female. Eberhard (1978) observed that the emergence of reproductives occurs in the day after a recent rainfall and that they come out of the nest through small holes (in this case in a grass lawn). Around the holes several workers were observed on the surface, and this is perhaps the only time that *Acropyga* workers emerge from their nests to the surface. Predation of alate queens that had recently emerged from nests by the ponerine ant, *Ectatoma ruidum* was also observed.

Discussion: The species boundary of *A. goeldii* was difficult to ascertain, and there is still some degree of uncertainty surrounding this species and its immediate relatives. The difficulty arises from the fact that workers within the *goeldii* complex are very difficult to distinguish from each other. *A. goeldii* workers are virtually indistinguishable from *A. palaga* (see *A. palaga* for further discussion), but additionally, *A. epedana*, *A. keira*, and *A. exsanguis* all present difficulties in identification from one another. Listed are characters that can provide some diagnostic help in identifying this species; comments in parentheses are for *A. goeldii*. From: *A. exsanguis* (usually wider head, more antennal segments and larger in total length), *A. keira* (many more erect hairs on mesosoma), *A. epedana* (more erect hairs on mesosoma and longer, wider head).

Since *A. goeldii* is such a variable species, the worker caste is unreliable for diagnostic purposes. Worker specimens have been observed, for instance, with a range of mandibular teeth from 3 well-defined teeth, 3 well defined teeth and a smaller more offset basal tooth, to 4 well defined teeth. Additionally, the mesonotal dorsum has been observed to be at the same height as the propodeum in some specimens, but in other specimens the mesonotum rises well above the level of the propodeum. The shape of the worker head is variable as first observed by Bünzli (1935). At this time however I do not believe that the variation observed warrants separate species recognition (see below).

The taxonomy as presented of the *decedens* species-group relies heavily on male morphology, but males are scarce in collections, thereby making assessment of male variation among and between species difficult. Hence, I have been hesitant to "split" some of the variation observed in workers of this species as separate species. Males have proven exceedingly useful in the ascertaining of most species boundaries in the *decedens* species-group. However, even males for *A. goeldii* are, like the workers, morphologically variable. The defining characteristics are found in the penis valve structures. In *A. goeldii* penis valves possess a rounded ventral extension and the dorsal margin of the penis valves bulge out slightly toward the apodeme (see fig. 40D). The ventral aspect of the penis valves are also unique to the species. In contrast, the parameres vary considerably and look similar to *A. palaga* (see fig. 41F), in that the width of the parameres does not vary much across its length, or they can become narrower caudally from the base and become wide again near the caudal ends. Specimens in which parameres resembled *A. palaga* but the penis valves fit the *A. goeldii* type for now are regarded as *A. goeldii*. Nonetheless, as more worker-associated male specimens of this species become available its status should be reevaluated, because it would not be surprising if there are several species (some of which may or may not be closely related) "hidden" under what is presently known as *A. goeldii*. For instance, the workers of *A. decedens* are difficult to distinguish from *A. goeldii*, and the latter was even synonymized with *A. decedens* by Costa Lima (1931). However, despite the morphological similarity of workers, *A. decedens* and *A. goeldii* are clearly not closely related once male morphology is compared.

Acropyga hirsutula, NEW SPECIES

Holotype queen, PERU: Tingo Maria and vicinity (W.L. Brown and W. Sherbrooke) (MCZC); 1 paratype queen, 5 paratype males, same locality as holotype (MCZC); 4 paratype workers, 4 paratype males, ECUADOR: Napo: Carlos J. Arosemena Tola, 500 m, 01° 09' S, 077° 53' W (A.L. Wild) (#AW2298) (JSLC) (MCZC). The holotype is labeled JSL TYPE # 104.

Diagnosis: *Worker*: 11 segmented antennae; head longer than broad; mandible with at least 4 teeth; when with 4 teeth a short diastema separates basal tooth from others; when with 5 teeth, 4th tooth smaller than others; clypeus with a dense covering of hairs. *Queen*: as in worker. *Male*: 12 segmented; parameres rectangular shaped covered in a thick layer of erect hairs; penis valve with prominent, roughly square, ventral extension, forming a long curve from tip.

Compare with: *A. decedens* and *A. dubitata*

Description: *Worker*. Head (fig. 21A): yellow; posterior margin slightly concave; covered in a thick layer of appressed hairs, with scattered suberect to erect hairs; 11 segmented, incrassate antennae; scape surpasses posterior margin by about the length of the pedicel; clypeus broad, convex medially, covered in a thick layer of appressed to erect hairs; mandible with 4-5 teeth; basal tooth offset by a diastema when with only 4 teeth, or with a smaller tooth present when with 5 teeth; gap exists between anterior clypeal margin and inner mandibular margin. Mesosoma (fig. 21B): yellow, in lateral view pronotum rises steeply toward mesonotum; posteriorly pronotum with many erect hairs; mesonotum covered in a thick layer of appressed hairs, with many scattered erect hairs; mesonotum higher than propodeum; metanotal area distinct, with one or two sulci present; propodeum rounded with thick layer of appressed hairs, and scattered erect hairs; declivity steep. Gaster: petiole thick and erect; gaster yellow; covered in a thick layer of appressed hairs, with many erect hairs throughout.

Queen. As in worker with modifications expected for caste.

Male. Head: brown, slightly paler on clypeus, mandible and antennae, darker at apex around 3 prominent ocelli; head longer than broad; covered in layer of thick appressed hairs, becoming suberect to erect along posterior margin; posterior margin entire; eyes large, breaking outline of head when in full frontal view; 12 segmented, slightly incrassate antennae; apical segment about as long as preceding 2 segments; scape surpasses posterior margin by about the length of the first 2

funicular segments; clypeus narrow, convex medially, covered in a thick layer of appressed to erect hairs; mandible with 3 indistinct teeth, the basal tooth slightly offset from masticatory margin. Mesosoma: brownish-yellow; pronotum short and collar-like, overarched by rounded mesonotum; pronotum covered in thick layer of appressed to erect hairs; mesonotum broad and flat, covered in thick layer of appressed to erect hairs; propodeum gently rounded; declivity not distinct from propodeum. Gaster: petiole thick and erect; gaster brownish-yellow; covered in thick layer of appressed hairs, with scattered erect hairs throughout. Genitalia (figs. 40E-H): in lateral view parameres roughly rectangular, covered in thick layer of erect hairs; cuspi cylindrical, with short, peg-like teeth at apices; digiti roughly anvil-shaped apically, with ventral portion elongated to a sharp point; cuspi and digiti meet dorsally, forming a roughly oval-shaped space between them; penis valves in dorsal view not reaching caudal ends of parameres; in ventral view, penis valve ventral extension prominent; penis valve fig. 40H.

Etymology: The specific epithet *hirsutula* is Latin for hairy or bristly, in reference to the abundant pilosity of this species, especially on the clypeus and gaster.

Measurements: *Workers* (n=2): TL: 2.04-2.07; HW: 0.477-0.482; HL: 0.523-0.543; SL: 0.381-0.41; ML: 0.553-0.568; CI: 88.77-91.20; SI: 79.05-85.95. *Queens* (n=2): TL: 2.89-2.96; HW: 0.609-0.629; HL: 0.653-0.655; SL: 0.588-0.591; ML: 0.929-1.21; CI: 93-96.3; SI: 94-98.1. *Males* (n=2): TL: 2.08-2.16; HW: 0.414-0.456; HL: 0.45-0.487; SL: 0.406-0.412; ML: 0.714-0.779; GL: 0.816-1; CI: 92-93.93; SI: 90.4-98.1.

Distribution and natural history: *A. hirsutula* is known from two localities: one in Ecuador and one in Peru. The specimens from Peru are alates (males and queens) marked as being collected at lights. A nest in Ecuador was discovered under a rock along the bank of a river. The nest was large, with many tunnels and indistinct chambers, and was found to contain multiple dealate queens (Alex Wild, pers. comm.).

Discussion: The queens of this species are quite distinctive, with an extremely hairy clypeus and gaster. The males are also of great interest since their penis valves have a dorsal notch (see fig. 40H), only observed in one other species, *A. dubitata*, from Hispaniola. The elongated, square-shaped ventral extension and heavy contours of the surface of the penis valves also suggest a close relationship with *A. dubitata*.

Acropyga keira, NEW SPECIES

Holotype worker, COSTA RICA: Heredia, La Selva Biological Station, elev. 50-150 m, 10° 26' N, 84° 1' W (J. Longino) (INBC); 1 paratype worker, 1 paratype male, same locality as holotype (MCZC). The holotype is labeled JSL TYPE # 102.

Diagnosis: *Worker:* 9 segmented antennae (but see description); mesosoma with short, appressed hairs, giving it a bare appearance; mandible with 3 teeth. *Queen:* unknown. *Male:* 11 segmented antennae; parameres roughly rectangular, covered in hairs of varying lengths, with thickest concentration toward the middle.

Compare with: *A. exsanguis* and *A. romeo*

Description: *Worker.* Head (fig. 22A): yellow; head longer than broad; covered in layer of short appressed hairs; posterior margin slightly concave; 9 segmented, incrassate antennae (note that males have 11 segments suggesting workers could have up to 10 segments); scape reaches or fails to reach posterior margin by about half length of pedicel; clypeus narrow, convex and covered in thick layer of suberect to erect hairs of varying lengths; mandible with 3 teeth; gap exists between anterior clypeal margin and inner mandibular margin. Mesosoma (fig. 22B): yellow; pronotum in lateral view rises steeply toward mesonotum; covered in thin layer of short appressed hairs, except along posterior end where several erect hairs are present; mesonotum nearly at level of propodeum, covered in layer of short appressed hairs; metanotal area distinct; propodeum with layer of short appressed hairs; declivity steep. Gaster: petiole thick and erect; gaster yellow; cov-

ered in appressed hairs, with scattered erect hairs throughout, especially along posterior segmental margins.

Queen. Unknown.

Male. Head: brownish-yellow, darker toward apex around 3 prominent ocelli; head about as broad as long; posterior margin broadly rounded, with rounded posterolateral corners; eyes large, breaking outline of head in full frontal view; 11 segmented antennae; scape surpasses posterior margin by about half length of pedicel; clypeus slightly convex, covered in a dense layer of suberect to erect hairs; mandible typically with 2 teeth separated by a diastema; occasionally a small tooth develops near apical tooth, making mandible 3-toothed; a gap exists between anterior clypeal margin and inner mandibular margin. Mesosoma: yellow; pronotum collar-like, overarched by mesonotum, which is rounded anteriorly; mesonotum flat covered with layer of short appressed hairs; propodeum broadly rounded into an indistinct declivity. Gaster: petiole thick and erect; gaster yellow; covered in layer of short appressed hairs. Genitalia (figs. 41A-D): parameres rectangular, coming to a point dorsocaudally; parameres mostly covered in layer of hairs of varying lengths, longest near middle of parameres, and then parameres bare toward base; cuspi cylindrical, bending toward apices with a number of short, peg-like teeth; digiti anvil-shaped, bent toward cuspi, meeting them dorsally, where there are a series of short peg-like teeth; penis valve fig. 41D.

Etymology: The specific epithet *keira* is Greek for cut short, in reference to the distinctly short hairs that are found on the head and mesosoma.

Measurements: *Workers* (n=4): TL: 2.14-2.23; HW: 0.491-0.513; HL: 0.532-0.543; SL: 0.39-0.413; ML: 0.588-0.609; GL: 1.02-1.1; CI: 90.9-95.5; SI: 76.8-82.1. *Males* (n=2): TL: 1.93-2.09; HW: 0.369-0.378; HL: 0.406-0.407; SL: 0.35-0.354; ML: 0.624-0.741; GL: 0.901-0.947; CI: 90.9-93.0; SI: 92.6-95.9

Distribution and natural history: This species is known only from its type locality in Costa Rica. Workers and males were collected from a nest in July, but otherwise nothing is known of its natural history.

Discussion: The short appressed hairs that cover *A. keira* are the main distinguishing characteristic of the worker. Nonetheless, *A. keira* workers can be difficult to distinguish from other members of the *goeldii* complex, especially from *A. exsanguis* workers. *A. keira* has very few erect to suberect hairs on the mesosoma, and when present they are only found on the posterior region of the pronotum, whereas *A. exsanguis* always has abundant erect to suberect hairs on the mesosoma. The head of *A. keira* is also typically longer than broad, while in *A. exsanguis* the head is typically broader or at least as broad as long.

The best way to confirm *A. keira* is with male specimens, which are very distinct from *A. exsanguis* and other closely related species. The penis valve of *A. keira* is unique in that it is shorter (as measured from apodeme to caudal tip) than other *goeldii* complex members, and the laterally expanded, flattened tips are distinctly large relative to the whole structure (see fig. 41H).

Acropyga palaga, NEW SPECIES

Holotype worker, COSTA RICA: Estrella Valley (W.M. Mann) (USNM); 3 paratype workers, 6 paratype males, same locality as holotype (USNM) (MCZC). The holotype is labeled JSL TYPE # 105.

Diagnosis: *Worker:* 9-10 segmented antennae (but see description); metanotal area distinct; mandibles with 3 distinct teeth; otherwise as in *A. goeldii*. *Queen:* unknown. *Male:* 12 segmented antennae; parameres rectangular, about the same width throughout length; penis valves sharply curved ventrally from tip of penis to ventral extension.

Compare with: *A. goeldii* and other members of the *goeldii* complex.

Description: *Worker:* Head (fig. 22C): yellow; head about as broad as long; posterior margin slightly concave; covered in a layer of short appressed hairs, with several erect hairs usually along posterior margin; 9-10 segmented, incrassate antennae (males have 12 segments, so it is likely this

species can have workers with up to 11 segments); scape fails to reach posterior margin by less than half length of pedicel; clypeus convex and narrow, covered with abundant erect hairs; mandible with 3 distinct teeth; gap exists between anterior clypeal margin and inner mandibular margin. Mesosoma (fig. 22D): yellow; in lateral view pronotum with a short anterior shelf before rising sharply toward mesonotum; posterior pronotum with many erect hairs; mesonotum covered in a thick layer of appressed hairs, with scattered erect hairs; mesonotum higher than propodeum; metanotal area distinct; propodeum rounded with a thick layer of appressed hairs; declivity steep. Gaster: petiole thick and erect; petiole does not reach level of propodeum; gaster yellow; covered in a layer of appressed hairs, with scattered erect hairs throughout.

Queen. Unknown.

Male. Head: brownish-yellow to brown, darkest at apex around 3 prominent ocelli; head longer than broad, becoming broader toward apex; covered in a layer of short appressed hairs; 12 segmented, slightly incrassate antennae, apical segment about as long as preceding 2 segments; scape surpasses posterior margin by about length of pedicel; clypeus narrow, convex medially, covered in thick layer of erect hairs; mandible with 3 distinct teeth; a gap exists between anterior clypeal margin and inner mandibular margin. Mesosoma: brownish-yellow; pronotum short and collar-like; mesonotum anteriorly rounded, dorsally flat, covered in layer of short appressed hairs, with widely scattered erect hairs; propodeum low, with indistinct declivity. Gaster: petiole thick and erect; gaster brownish-yellow, covered in layer of appressed hairs, with scattered erect hairs throughout. Genitalia (figs. 41E-H): in lateral view, parameres long, rectangular, with scattered erect to suberect hairs; cuspi long, cylindrical; digiti with long, stalk-like posterior portion, apices anvil-shaped; digiti meet cuspi dorsally, where both have structures have a series of short, peg-like teeth; penis valve fig. 41H.

Etymology: The specific epithet *palaga* is Latin for an ingot of gold, in reference to the yellowish color of the workers.

Measurements: *Worker* (n=8): TL: 1.97-2.5; HW: 0.52-0.608; HL: 0.504-0.6; SL: 0.344-0.472; ML: 0.573-0.706; GL: 0.869-1.18; CI: 99.62-104.65; SI: 66.15-77.76. *Male* (n=8): TL: 2.23-2.46; HW: 0.425-0.473; HL: 0.424-0.494; SL: 0.398-0.426; ML: 0.794-0.854; GL: 0.91-1.24; CI: 86.03-101.5; SI: 89.03-103.29.

Other material examined: COSTA RICA: Alajuela (F.L. Wellman). In: USNM.

Distribution and natural history: This species has only been collected from two localities in Costa Rica. According to label data it has been collected at coffee roots. Males were collected in both April and August, apparently from nests.

Discussion: Based on samples I have examined, workers of *A. palaga* are virtually indistinguishable from *A. goeldii*. One possible way to distinguish workers is by the shape of the clypeus. In *A. goeldii* the posterior clypeal margin rises slightly toward the torulae and is wider, whereas in *A. palaga* the posterior clypeal margin is strictly transverse toward the torulae and is narrower. However, the extent to which both species vary is not possible to assess at this time due to the low number of specimens available for study. Another worker character that appears to be stable for *A. palaga* is that of the distinct metanotal area (with two sulci present), but *A. goeldii* may sometimes possess a distinct metanotal area. *A. palaga* appears to possess fewer hairs on the mesosoma than *A. goeldii*, but given the variation observed in *A. goeldii* the utility of this character remains unclear.

Despite similarities in workers, examination of males suggests at least two species are present (see *A. goeldii* discussion for more detail). *A. palaga* males possess rectangular parameres in which width does not change much across their length. This in contrast to *A. goeldii* males in which the parameres typically decrease in width toward the apex. Once dissected the penis valves are distinct from *A. goeldii*, with a curved ventral aspect from the penis valve tip through the ventral extension (see fig. 41H). The dorsal margins of *A. palaga* penis valves are nearly straight,

whereas *A. goeldii* possesses a humped dorsal margin. Additionally, the penis valves also exhibit a straight margin toward the apodeme from the ventral portion of the ventral extension. Finally, *A. palaga* possesses a ventral extension that narrows significantly toward the base, unlike *A. goeldii*.

I did notice some variation in paramere width between the two populations of *A. palaga* examined. Specimens from Alajuela, Costa Rica had wider parameres than those from Estrella Valley, Costa Rica. The penis valves from the Alajuela specimens were not quite as curved at the penis valve caudal ends as the Estrella specimens. Despite those differences both populations had males with a more or less parallel dorsal margins and narrow, curved ventral extensions. The agreement of those characters with each population has led me to consider them the same species. But as more specimens become available for study, variation can be more accurately addressed and changes may be necessary in the taxonomy.

Acropyga parvidens (W.M. Wheeler and Mann)

Rhizomyrma parvidens W.M. Wheeler and Mann, 1914: 46 (w.). 2 syntype workers, HAITI: Petionville (W.M. Mann) (MCZC) [examined]. The designated lectotype is a worker labeled JSL TYPE # 121 and is deposited at MCZC.

Emery, 1925: 30, first combination in *Acropyga*; Weber, 1944: 100, description and key.

Acropyga (Rhizomyrma) mesonotalis Weber, 1944: 111 (w.q.). 4 syntype workers, 1 syntype queen, HAITI: Petionville (N.A. Weber) (MCZC) [examined]. **NEW SYNONYM.**

Diagnosis: *Worker:* 9-11 segmented antennae; mandible with 4 prominent teeth; mesonotum much higher than propodeum, with a layer of appressed hairs at apex. *Queen:* As in worker with modification expected for caste. *Male:* unknown.

Compare with: species of the *goeldii* complex

Description: *Worker:* Head (fig. 23A): yellow; head about as broad as long; posterior margin concave; covered in a layer of appressed hairs, with a few erect hairs along posterior margin; 9-11 segmented, incrassate antennae; scape reaches to posterior margin; clypeus medially convex, with erect hairs; mandible with 4 prominent teeth; basal tooth smaller than other teeth; gap exists between anterior clypeal margin and inner mandibular margin. Mesosoma (fig. 23B): yellow; pronotum with a slight anterior shelf; pronotum in lateral view rises steeply toward a high mesonotum; pronotum with scattered appressed hairs except along posterior end where several erect hairs are present; mesonotum distinct, much higher than propodeum; mesonotum with many appressed hairs; metanotal area distinct; propodeum with a few scattered appressed to erect hairs; declivity steep (pictured specimen is slightly distorted causing the propodeum to appear less steep). Gaster: petiole thick and erect; gaster yellow; covered in thick layer of appressed hairs, with scattered erect hairs throughout, especially along posterior segmental margins.

Queen. As in worker with modification expected for caste and with the following differences: mesosomal dorsum covered in thick layer of appressed hairs, with scattered erect hairs; longest mesosomal hairs typically on scutellum.

Male. Unknown.

Measurements: *Workers* (n=4): TL: 1.99-2.19; HW: 0.496-0.551; HL: 0.489-0.54; SL: 0.339-0.408; ML: 0.527-0.589; GL: 0.941-1.09; CI: 98.61-104.7; SI: 66.21-74.05. *Queens* (n=3): TL: 2.83-2.87; HW: 0.576-0.597; HL: 0.55-0.591; SL: 0.431-0.495; ML: 0.841-0.915; GL: 1.34-1.48; CI: 100.85-104.73; SI: 74.83-82.91.

Other material examined: DOMINICAN REPUBLIC: Hato Mayor, P.N. Los Haitises, west of Sabana (M.A. Ivie); Villa Altigracia, 18° 42'N, 70° 11'W, 200 m. (M.A. Ivie). In: PSWC.

Distribution and natural history: *A. parvidens* appears to be endemic to Hispaniola, having been found in leaf litter in both Haiti and the Dominican Republic. Weber (1944) reported *A. parvidens* was found associated with mealybugs (though they were not identified), and in fact a delate queen specimen (PSWC) was examined that clutched a mealybug between her mandibles. Unfortunately, the mealybug is too badly distorted for identification.

Discussion: Without discovery of the male of this species, its status as a valid species remains dubious. It is also tentatively placed in the *decedens* species-group, pending the discovery of males. It is certainly possible that *A. parvidens* is *A. dubitata*, the other known species from Hispaniola, which is known only from males. The fact that *A. parvidens* workers have 9-11 antennal segments and *A. dubitata* males 11-12 segments, is consistent with their being the same species. Additionally, *A. dubitata*'s sister species, *A. hirsutula* possesses workers that very much resemble *A. parvidens*, which may be another indication *A. dubitata* and *A. parvidens* are conspecific. The discovery of worker-associated males will be needed to finally answer questions of conspecificity.

A. parvidens closely resembles *A. goeldii*, but they are effectively separated by the clypeus: *A. parvidens* possesses far fewer hairs on the clypeal surface than *A. goeldii*. The synonymy of *A. mesonotalis* presented here is based on the character Weber (1944) used to define this species, which were the small teeth of the specimens he examined. Unfortunately, he did not consider that the smaller teeth could be the result of dental abrasion, a common artifact in many *Acropyga* specimens. Examination of the *A. mesonotalis* syntypes revealed that the smaller teeth are simply an artifact of dental abrasion and not indicative of separate species.

Acropyga romeo, NEW SPECIES

Holotype worker, GUYANA: Camp on Potaro River at base of Mt. Ayanganna, N 05° 18.08, W 059° 54.67, elev. 695 m +/- 13 m (J.S. LaPolla *et al.*) (UGBC); 3 paratype workers, same locality as holotype (USNM) (MCZC). The holotype is labeled JSL TYPE # 106.

Diagnosis: *Worker:* 9 segmented antennae; mandible with 4 teeth; 4th tooth very small and offset from masticatory margin; head longer than broad, becoming narrower toward anterior end; small species (total length: < 1.5 mm). *Queen:* unknown. *Male:* unknown.

Compare with: *A. exsanguis*, *A. keira* and *A. smithii*

Description: *Worker:* Head (fig. 23C): yellow; covered in a layer of short appressed hairs; head longer than broad, becoming narrower toward anterior end; posterior margin entire; 8-9 segmented, incrassate antennae; scape fails to reach posterior margin by about length of first 2 funicular segments; clypeus narrow, medially convex, covered in a dense layer of hairs; mandible narrow, with 4 teeth; apical tooth often much longer than other teeth; basal tooth very small, offset from masticatory margin; gap exists between anterior clypeal margin and inner mandibular margin. Mesosoma (fig. 23D): yellow; in lateral view, pronotum rises steeply toward mesonotum; pronotum with a layer of appressed hairs and scattered erect hairs posteriorly; mesonotum at about same height as propodeum; mesonotum with layer of appressed to erect hairs; metanotal area distinct; propodeum short and flat, with appressed to erect hairs; declivity steep. Gaster: petiole thick and erect, slightly surpassing height of propodeal spiracle; gaster yellow; covered in dense layer of appressed hairs, with scattered erect hairs throughout.

Queen. Unknown.

Male. Unknown.

Etymology: Named in honor of Romeo Williams with admiration and thanks. Romeo is a Guyanese field guide and naturalist who made my 3 month expedition to Guyana in the autumn of 2002 in search of *Acropyga* and other ants possible. The name is treated as a noun in apposition.

Measurements: *Workers* (n=4): TL: 1.41-1.44; HW: 0.334-0.351; HL: 0.384-0.402; SL: 0.242-0.266; ML: 0.371-0.402; GL: 0.621-0.67; CI: 85.32-90.23; SI: 70.20-79.64.

Distribution and natural history: This species is known only from its type locality at the base of Mt. Ayanganna in western Guyana. *A. romeo* was collected from leaf litter samples in *Dicymbe* dominated forest that also contained *A. stenotes*, but otherwise nothing is known of its natural history.

Discussion: This species can be confused with *A. exsanguis* and *A. keira*. In all specimens of *A. exsanguis* examined in this study, the species always has had only 3 teeth on the mandible, with no sign of a smaller offset basal tooth as seen in *A. romeo*. *A. keira* also has only been observed to possess 3 teeth on its mandibles, and it has very short appressed hairs on its mesosoma, as opposed to the longer hairs observed in *A. romeo*. Finally both *A. exsanguis* and *A. keira* are larger species.

This species appears to belong to the *decedens* species-group, though until males are associated with workers its phylogenetic placement in the genus remains problematic. The combination of a narrow, 4-toothed mandible and a narrow, hairy clypeus suggests placement in the species group. This is among the smallest of the New World *Acropyga* species, around the same size as *A. smithii* and *A. panamensis*.

donisthorpei species-group

Acropyga donisthorpei Weber

Acropyga (Rhizomyrma) donisthorpei Weber, 1944: 118 (w.). 2 syntype workers, GUYANA: Kartabu Point (N.A. Weber) (MCZC) [examined]. The designated lectotype is a worker labeled JSL TYPE # 114.

Acropyga (Rhizomyrma) oko Weber, 1944: 119 (w.). 2 syntype workers, GUYANA: Oko River, Cuyuni tributary (N.A. Weber) (MCZC) [examined]. **NEW SYNONYM.**

Acropyga (Rhizomyrma) paludis Weber, 1944: 121 (w.m.). 1 syntype worker, 1 syntype male, GUYANA: HMPS, Mazaruni River (N.A. Weber) (MCZC) [examined]. **NEW SYNONYM.**

Diagnosis: *Worker:* 11 segmented antennae; dorsal surface of mandible with many erect hairs; inner mandibular margin roughly parallel to clypeal margin; mandible with 5 teeth, the 3rd tooth (from apical) being much smaller than others. *Queen:* as in worker with modifications expected for caste. *Male:* 12 segmented antennae; mandible similar to worker, but with only 3 teeth; digiti plate-like, pointing ventrally.

Compare with: *A. decedens*

Description: *Worker.* Head (fig. 24A): brownish-yellow; head longer than broad, covered in layer of appressed hairs, with a few erect hairs along posterior margin; posterior margin entire to slightly concave medially; 11 segmented, incrassate antennae; scape fails to reach posterior margin by about half the length of the pedicel; scape covered in short, suberect to erect hairs; clypeus convex with erect hairs; mandible with 5 teeth; the 3rd tooth is typically much smaller than others; a short diastema exists between 4th and basal tooth; dorsal surface of mandible with many short (approximately 20 hairs) erect hairs, giving it a hairy appearance in full frontal view; inner mandibular margin parallel to clypeal margin. Mesosoma (fig. 24B): brownish-yellow; pronotum in lateral view with a distinct shelf-like extension before rising steeply toward mesonotum; posterior portion of pronotum with erect hairs of varying lengths; mesonotum with many erect hairs; metanotal area distinct; propodeum rounded, with many erect hairs; declivity steep. Gaster: petiole erect, slightly concave at apex; gaster brownish-yellow; covered in appressed hairs, with scattered erect hairs throughout, especially along posterior segmental margins.

Queen. As in worker with modifications expected for caste.

Male. Head: brownish-yellow, brown toward apex around 3 prominent ocelli; head broader than long, covered in layer of appressed hairs; posterior margin rounded toward apex, giving head a slight triangular appearance in full frontal view; 12 segmented antennae; scape surpasses posterior margin by about half the length of pedicel; clypeus slightly convex, with erect hairs; mandible with 3 distinct teeth; diastema present between apical and 2nd tooth; inner mandibular margin, as in worker, roughly parallel to the clypeal margin. Mesosoma: pronotum collar-like, overarched by mesonotum; mesonotum flat, covered in appressed hairs; scutellum with scattered erect hairs; propodeum nearly flat with indistinct declivity. Gaster: petiole erect, slightly convex at apex; gaster brownish-yellow, lighter than head and mesosoma; covered in appressed hairs, with scattered suberect to erect hairs throughout. Genitalia (figs. 42A-D): parameres taper to rounded points

apically, with many erect hairs at apices; cuspi meet digiti apically; digiti plate-like, apically becoming sickle-shaped, pointing ventrally; penis valve fig. 42D.

Measurements: *Workers* (n=6): TL: 1.86-2.23; HW: 0.479-0.537; HL: 0.553-0.602; SL: 0.381-0.43; ML: 0.525-0.602; GL: 0.715-1.08; CI: 86.62-89.2; SI: 73.7-80.72. *Queens* (n=1): TL: 3.89; HW: 0.612; HL: 0.641; SL: 0.531; ML: 1.02; GL: 2.23; CI: 95.48; SI: 86.76. *Males* (n=1): TL: 2.55; HW: 0.475; HL: 0.454; SL: 0.427; ML: 0.825; GL: 1.27; CI: 104.63; SI: 89.89.

Other material examined: **BOLIVIA:** Cachuela Esperanza (W.M. Mann); Santa Cruz: Aserradero Moira, 14° 34' S, 61° 12' W (P.S. Ward); **GUYANA:** HMPS, Mazaruni (N.A. Weber); Kartabu Point (N.A. Weber); Oko River, Cuyuni Trib. (N.A. Weber); **PERU:** Madre de Dios, Cuzco Amazonico: 15km NE of Puerto Maldonado (S.P. Cover and J.E. Tobin); Loreto: 15 km WSW Yurimaguas; 5° 59' S, 76° 13' W, 200 m (P.S. Ward). In: MCZC, PSWC, USNM.

Distribution and natural history: This species has a wide range, stretching north from Bolivia northwest to Peru then east to Guyana, probably occupying much of tropical South America. Weber (1944) reported this species from rainforests, nesting in the leaf litter and rotten wood. It has been reported with one mealybug species belonging to the genus *Neochavesia*.

Discussion: Workers of this species can be separated from *A. decedens* by the rounded posterolateral corners giving the head an overall oval appearance in full frontal view. The dorsal surface of the mandible is also distinctly hairy. The inner mandibular margin and anterior clypeal margin form roughly right angles to each other, a characteristic observed only in one other New World species, *A. tricuspis*, which is easy to diagnose because of its enlarged, square basal tooth.

A. donisthorpei is a close relative of *A. tricuspis*, sharing with it in males a downward bend in the dorsal margin of the penis valves, similarly shaped parameres, and in workers the oval shaped heads and similar mandibular structures.

Acropyga tricuspis, NEW SPECIES

Holotype worker, BRAZIL: Amazonas, Ponta Negra; N. of Manaus; M-163 (W.L. Brown) (MCZC); 2 paratype workers, 2 paratype queens, 1 paratype male (MCZC). The holotype is labeled JSL TYPE # 103.

Diagnosis: *Worker:* 11 segmented antennae; mandible with an enlarged, square-shaped basal tooth with three distinct cusps. *Queen:* as in worker except for modifications expected for caste. *Male:* 12 segmented antennae; basal tooth as in worker, though less distinct.

Compare with: This species is unique in its appearance.

Description: *Worker.* Head (fig. 24C): brownish-yellow; head oval, rounded at posterolateral corners; head longer than broad; covered in a layer of short appressed hairs; posterior margin slightly concave; 11 segmented, incrassate antennae, with apical segment about as long as the four preceding segments; scape fails to reach posterior margin by about the length of the first two funicular segments; clypeus medially convex with longer erect hairs on surface; mandibles short and thick with 3 teeth; basal tooth enlarged and roughly square with 3 distinct cusps, first and second cusps comparatively smaller than the third cusp which is offset by a short diastema; inner mandibular margin and anterior clypeal margin nearly parallel. Mesosoma (fig. 24D): brownish-yellow; pronotum in lateral view with a short anterior shelf that rises steeply toward mesonotum; posterior portion of pronotum with several long, erect hairs; mesonotum slightly elevated above level of propodeum, covered with layer of appressed hairs and suberect to erect hairs; metanotal area distinct; propodeum with steep declivity. Gaster: petiole thick and erect; gaster brownish-yellow, covered in thick layer of appressed hairs with scattered suberect hairs.

Queen. As in worker except for modifications expected for caste.

Male. Head: brownish-yellow, darker toward apex around 3 prominent ocelli; head narrows toward apex; entire head covered in a fine layer of appressed hairs; 12 segmented antennae; scape reaches to posterior margin; clypeus slightly convex with several long erect hairs on surface; mandible short and thick with two teeth, the basal tooth as in workers and queens, except cusps are less

well-defined. Mesosoma: brownish-yellow; pronotum small and collar-like, overarched by mesonotum; mesonotum rounded anteriorly, dorsum flat and covered in a thick layer of appressed hairs; propodeum flat, sloping gently toward declivity; declivity very short and indistinct. Gaster: petiole thick and erect; gaster brownish-yellow; covered in thick layer of appressed hairs with scattered suberect to erect hairs. Genitalia (figs. 42E-H): parameres taper to rounded apices; parameres with numerous long hairs, becoming more numerous toward apices; cuspi taper to pointed apices, giving them a tubular appearance in ventral view; cuspi meets digiti dorsally; digiti anvil-shaped and flat; penis valve fig. 42H.

Etymology: The specific epithet *tricuspis* is Latin for three points, in reference to the three cusps found on the enlarged basal tooth.

Measurements: *Workers* (n=4): TL: 1.82-1.96; HW: 0.476-0.48; HL: 0.516-0.562; SL: 0.302-0.334; ML: 0.503-0.522; GL: 0.752-0.933; CI: 83.63-93.02; SI: 64.25-70.17. *Queens* (n=3): TL: 2.8-2.91; HW: 0.538-0.59; HL: 0.587-0.62; SL: 0.438-0.474; ML: 0.886-0.906; GL: 1.28-1.43; CI: 91.65-96.41; SI: 77.97-82.87. *Males* (n=2): TL: 1.89-1.90; HW: 0.382-0.392; HL: 0.42-0.448; SL: 0.342-0.346; ML: 0.704-0.728; GL: 0.72-0.762; CI: 87.5-90.95; SI: 87.24-90.58.

Other material examined: BRAZIL: Amazonas, Faz. Entelo, 80 km NNE, Manaus, elev. 80 m, 2° 25' S, 59° 46' W (P.S. Ward). In: PSWC.

Distribution and natural history: This species is only known from two localities in Brazil. It has been collected in rainforest from leaf litter and rotten wood, but otherwise nothing is known of its natural history.

Discussion: This species is easy to recognize with its distinctively enlarged, roughly square basal tooth with 3 discernable cusps. The enlarged basal tooth of *A. tricuspis* is interesting because unlike species of the Old World *butteli* species-group and the New World *A. panamensis*, the enlarged basal tooth is square in shape rather than rectangular. An enlarged basal tooth has evolved independently at least 3 times within the genus, and in the New World the two species recorded with an enlarged basal tooth are not closely related to each other. *A. tricuspis* is most closely related to *A. donisthorpei* (see there for further discussion).

myops species-group

Acropyga ambigua Emery

Acropyga (Atopodon) ambigua Emery, 1922: 107 (w.q.). 2 syntype workers, 1 syntype queen, PAPUA NEW GUINEA: N.E.: Friedrich-Wilhelmshafen (L. Birö) (probably in HNHM) [not examined].

Diagnosis: *Worker:* 9-11 segmented antennae; basal tooth separated from other teeth by a distinct diastema; basal tooth margin distinct and not smoothly continuous with inner mandibular margin, slightly below inner mandibular margin. *Queen:* as in worker with modifications expected for caste. *Male:* unknown.

Compare species: *A. pallida*

Description: *Worker.* Head (fig. 25A): yellow; head covered in layer of appressed hairs, with occasional scattered suberect to erect hairs, especially along posterior margin; head longer than broad, though occasionally as long as broad; posterior margin entire; 9-11 segmented, incrassate antennae; scape reaches or slightly fails (approximately less than half length of pedicel) to reach posterior margin; clypeus broad, slightly convex medially; clypeus with appressed to erect hairs; mandible broad, with 5-6 teeth; basal tooth separated from other teeth by a distinct diastema in which a small tooth occasionally develops (making mandible 6-toothed); 4th tooth (from apical) often separated from 3rd tooth by a short diastema, in which a small tooth occasionally develops (making mandible 6 toothed); basal tooth margin not smoothly continuous with inner mandibular margin; anterior clypeal margin and inner mandibular margin nearly parallel. Mesosoma (fig. 25B): yellow; in lateral view, pronotum rises steeply toward mesonotum; pronotum with short appressed to suberect hairs throughout, longer erect hairs on posteriorly; mesonotum often rounded,

slightly higher than propodeum; dorsum covered in layer of short appressed hairs with suberect to erect hairs throughout and of variable lengths; metanotal area distinct; propodeal dorsum with short appressed to suberect hairs; declivity steep. Gaster: petiole thick and erect, apex reaches height of propodeal sprig; gaster yellow; covered in thick layer of appressed hairs with scattered erect hairs throughout.

Queen. As in worker with modifications expected for caste and the following differences: color dark brown throughout; head broader than long.

Male. Unknown.

Measurements: *Workers* (n=17): TL: 1.52-1.96; HW: 0.402-0.518; HL: 0.395-0.571; SL: 0.281-0.413; ML: 0.402-0.516; GL: 0.656-0.93; CI: 88.71-101.07; SI: 68.37-84.63. *Queens* (n=1): TL: 3.13; HW: 0.668; HL: 0.651; SL: 0.489; ML: 0.912; GL: 0.912; CI: 102.61; SI: 73.2.

Other material examined: **INDONESIA:** Irian Jaya, Pt. Freeport Concession, Siewa Camp, 03.04° S, 136.38° E, elev. 200 ft. (R.R. Snelling); **MALAYSIA:** Sarawak, 4th Division, Gn. Mulu National Park, elev. 130 m, soil core (N.M. Collins); **PAPUA NEW GUINEA:** near Popondetta, elev. <50 m (R.W. Taylor); "Timber Track" ca. 16 km NW of Lae, elev. ca. 220 m (R.W. Taylor); near Kokoda (R.W. Taylor); Yawastora near Wewak, elev. 50 m (R.W. Taylor); Bewani Road near Vanimo ca. 10 km, elev. 380 m (W.L. Brown); Gulf Prov., Ivimka camp, Lakemu Basin, 7.7° S, 146.8° E, elev. 120 m (R.R. Snelling). In: ANIC, BMNH, LACM, MCZC.

Distribution and natural history: This species has been found in Indonesia, Malaysia and Papua New Guinea, according to label data in rainforests from leaf litter and soil cores. It has been reported as being trophophoretic and been associated with 3 mealybug species: *Eumyrmococcus kusiacus*, *E. neoguineensis*, *Xenococcus acropygae* (Williams, 1998).

Discussion: Workers of this species can be difficult to distinguish from *A. pallida*, especially if a specimen is on the lower end for head width measurements. Examination of figure 49A reveals morphometric differences between the two species. Typically *A. ambigua* head width is greater than 0.45 mm, while *A. pallida* is less than 0.45 mm, although exceptions occur. Smaller individuals of *A. ambigua* are difficult to distinguish because the mandible, which is distinct in larger individuals can become similar to the *A. pallida* mandible type, that is in lacking a distinct diastema associated with the basal tooth. Another problem arises in that *A. pallida* specimens can form diastemas between the 4th and basal tooth as a result of dental abrasion. When this occurs and the head width is below 0.45 mm the specimens are nearly impossible to separate between the two species, though plotting head width against head length as in fig. 49A can be helpful.

I have examined a single queen which looks like *A. ambigua*, except for the fact that her head width is very low (0.468 mm) (the specimen is from Papua New Guinea and is deposited at LACM). Although, I provisionally have identified this specimen as *A. ambigua*, it should be reexamined as more material becomes available, since it may be indicative of a separate but phenotypically similar species. There is a single worker-associated with the queen, and it matches the description of *A. ambigua*.

A. ambigua is provisionally placed in the *myops* species-group because of similarly shaped mandibles and mesosoma to *A. myops*. However, until males for this species are discovered, its species-group placement remains questionable.

Acropyga dubia Karavaiev

Acropyga dubia Karavaiev, 1933: 311 (w.m.). 3 syntype workers, 1 syntype male, INDONESIA: Sumatra (O. John) (depository unknown) [not examined]. The syntypes of this species could not be located for examination. The original description includes description of a male, but because the syntypes could not be located and no other male specimens have been found in collections, the male unfortunately can not be described at this time.

Diagnosis: *Worker:* 11 segmented antennae; mandible with 6 teeth; head slightly longer than broad; dorsum with dense layer of appressed hairs, with occasional scattered erect hairs. *Queen:* as in worker with modifications expected for caste. *Male:* unknown.

Compare with: *A. myops*

Description: *Worker.* Head (fig. 25C): yellow; head slightly longer than broad; posterior margin entire to slightly concave medially; 11 segmented, incrassate antennae; scape reaches or nearly reaches (approximately 1/3 length of pedicel) posterior margin; clypeus convex medially, with appressed to erect hairs on surface; mandible broad with 6 teeth; 3rd tooth from apical smaller than others; basal tooth sometimes smaller than others and set back further than other teeth on masticatory margin; dorsal surface of mandible covered in a thick layer of short erect hairs (approximately 25 hairs); inner mandibular margin and anterior clypeal margin nearly parallel with each other. Mesosoma (fig. 25D): yellow; in lateral view pronotum rises steeply toward mesonotum; pronotum covered in layer of appressed hairs, with scattered erect hairs posteriorly; mesonotum rounded, covered in layer of appressed hairs; scattered erect hairs throughout; metanotal area distinct; propodeum rounded, covered in layer of appressed hairs; declivity steep. Gaster: petiole thick and erect, reaching height of upper portion of propodeal spiracle; gaster yellow; covered in a thick layer of appressed hairs, with scattered erect hairs throughout.

Queen. As in worker with modifications expected for caste and with the following differences: overall color brownish-yellow, darker toward apex of head and on gaster dorsum.

Male. Unknown, but see below.

Measurements: *Workers* (n=8): TL: 1.79-2.15; HW: 0.485-0.55; HL: 0.499-0.585; SL: 0.399-0.447; ML: 0.538-0.611; GL: 0.623-0.957; CI: 89.91-97.21; SI: 79.89-81.81. *Queens* (n=1): TL: 3.06; HW: 0.663; HL: 0.6; SL: 0.606; ML: 1.1; GL: 1.36; CI: 110.5; SI: 91.40.

Other material examined: MALAYSIA: Sarawak, 4th Division, Gn. Mulu National Park, soil core (N.M. Collins) (ANIC); Sabah, Gn. Silam, elev. 880 m (R. Leakey); Borneo, Sabah, Mt. Kinabalu near park headquarters (S. Yamane) (SYPC).

Distribution and natural history: I have only examined specimens of this species from Malaysian Borneo, though the original description reports the syntypes as being from Sumatra.

Discussion: This species has workers that are morphologically similar to *A. myops*, but differ primarily in possessing a narrower head (< 0.6 mm in *A. dubia* versus > 0.6 mm in *A. myops*), and in geographical distribution (*A. dubia* has not been found in Australia, the only known location for *A. myops*).

This species has been provisionally placed in the *myops* species-group, based on its similarities to *A. myops*. Once males are discovered for this species, however, its placement should be reevaluated.

***Acropyga gelasis*, NEW SPECIES**

Holotype worker, INDONESIA: Banggai Arch., Potil Kecil, 1 28°S, 123 34' E (M.J.D. Brendell) (BMNH); 14 paratype workers (BMNH) (MCZC). The holotype is labeled JSL TYPE #109.

Diagnosis: *Worker.* 11 segmented antennae; head and mesosoma brownish-yellow, gaster darker; clypeus broad, with distinct beak-like tip medially; median portion of head and posterior margin with many erect hairs; appressed hairs on head sparse, none on mesosomal dorsum. *Queen:* unknown. *Male:* unknown.

Compare with: *A. hystrix*

Description: *Worker.* Head (fig. 26A): brownish-yellow, darker toward apex; head longer than broad; posterior margin concave medially; short erect hairs scattered from median portion of head and along posterior margin; 11 segmented, incrassate antennae; scape reaches to nearly reaches (approximately 1/3 length of pedicel) to posterior margin; scape with short erect hairs toward apical end; clypeus broad, convex medially; median portion of anterior clypeal margin projects forward, giving it distinct "beak-like" appearance in full frontal view; mandible with 6 teeth; 3rd tooth from apical often smaller than others; inner mandibular margin uneven. Mesosoma (fig. 26B): brownish-yellow; in lateral view, pronotum rises steeply toward mesonotum; pronotum with

short erect hairs anteriorly and longer erect hairs posteriorly; mesonotum rounded, with many short and longer erect hairs dorsally; mesonotum slightly higher than propodeum; metanotal area distinct; propodeal dorsum flat, rounding into steep declivity. Gaster: petiole thick and erect, reaching height of upper portion of propodeal spiracle; gaster dark brownish-yellow; with a layer of appressed hairs, scattered longer, erect hairs throughout.

Queen. Unknown.

Male. Unknown.

Etymology: The specific epithet *gelasis* is Greek for to laugh, alluding to the odd looking medial point of the anterior clypeal margin.

Measurements: *Workers* (n=5): TL: 2.09-2.31; HW: 0.528-0.538; HL: 0.557-0.599; SL: 0.406-0.432; ML: 0.59-0.687; GL: 0.921-1.09; CI: 88.31-96.59; SI: 76.75-81.05.

Distribution and natural history: This species is known only from its type locality in Indonesia. Nothing is known of its natural history.

Discussion: With a unique “beak-like” medial portion of the anterior clypeal margin, *A. gelasis* is fairly easy to separate from other species. The structure of the anterior clypeal margin, “the beak”, is similar to that of the *butteli* species-group, though it seems to be a result of convergence rather than indicative of a close relationship. Overall, this species, along with *A. hystrix*, is darker (brownish-yellow) and with less pilosity than other *Acropyga* species.

The species' placement within the *myops* species-group is based on the fact that *A. gelasis* possesses widely separated torulae and mandibles that appear similar to *A. myops*. Worker morphology suggests *A. gelasis* is closely related to *A. hystrix*.

Acropyga hystrix, NEW SPECIES

Holotype worker, MALAYSIA: Sarawak, 4th Div., G. Mulu National Park, RGS Expedition, Long Pala, lowland rainforest under a log (B. Bolton) (BMNH); 14 paratype workers, 2 paratype queens, 2 paratype males (BMNH) (MCZC). The holotype is labeled JSL TYPE # 110.

Diagnosis: *Worker:* 11 segmented antennae; mandible with 6-7 teeth; pronotal and mesonotal dorsa with long erect hairs and a thinner layer of short erect hairs. *Queen:* As in worker with modifications expected for caste. *Male:* 12 segmented antennae; parameres broad, tapered to a sharp medial point, with many scattered erect hairs; mandible with 6 teeth.

Compare with: *A. acutiventris* and *A. gelasis*

Description: *Worker.* Head (fig. 26C): brownish-yellow; darker brownish-yellow toward apex; head slightly longer than broad; posterior margin entire, with distinct long erect hairs scattered throughout; 11 segmented, incrassate antennae; scape reach or surpasses posterior margin by approximately length of pedicel; scape with erect hairs scattered throughout length; clypeus broad and wide, convex medially, with scattered erect hairs throughout; mandible broad, with 6-7 teeth; 3rd tooth from apical usually smaller than others; if with 7 teeth, 7th tooth at meeting of inner mandibular margin and masticatory margin, often smaller than other teeth. Mesosoma (fig. 26D): brownish-yellow; in lateral view, pronotum rises steeply toward mesonotum; mesonotum with sparse covering of appressed hairs, long erect hairs posteriorly; mesonotum rounded, slightly higher than level of propodeum, with distinct long, erect hairs on dorsum; metanotal area distinct; propodeal dorsum flat, with sparse short appressed to erect hairs; declivity steep. Gaster: petiole thick and erect, reaching height of propodeal spiracle; gaster brownish-yellow; gaster dorsum slightly darker than venter; covered in layer of short, appressed hairs, though shinier than most other species; scattered erect hairs throughout.

Queen. As in worker with modifications expected for caste and the following differences: color much darker than observed in worker, becoming almost black.

Male. Head: brownish-yellow; darker toward apex around 3 prominent ocelli; covered in layer of appressed hairs; longer, erect hairs along posterior margin; head about as broad as long; posterolat-

eral corners rounded, giving head an overall round appearance; 12 segmented, slightly incrassate antennae; scapes surpass posterior margin by about length of first 3 funicular segments; clypeus broad, convex medially; mandible broad with 6 teeth; inner mandibular margin parallel with anterior clypeal margin. Mesosoma: brownish-yellow; pronotum small and collar-like, overarched by mesonotum; mesosomal dorsum with appressed hairs and scattered erect hairs; propodeum wide, sloping with an indistinct declivity. Gaster: petiole thick and erect; gaster brownish-yellow, covered in layer of appressed hairs with scattered erect hairs throughout. Genitalia (see figs. 43A-D): in lateral view, parameres broad, tapered to short medial points at midheight, with many scattered erect hairs; cuspi taper toward apices with peg-like teeth; cuspi slightly bent toward digiti; digiti erect, thick and apically truncated, with short, peg-like teeth on apices where they meet with cuspi; penis valve fig. 43D

Etymology: The specific epithet *hystrix* is Greek for porcupine in reference to the long, stout erect hairs on the mesosoma.

Measurements: *Workers* (n=6): 2.24-2.69; HW: 0.543-0.647; HL: 0.607-0.665; SL: 0.511-0.549; ML: 0.596-0.7; GL: 0.964-1.33; CI: 89.46-96.68; SI: 82.53-90.98. *Queens* (n=2): TL: 3.99-4.00; HW: 0.803-0.813; HL: 0.782-0.799; SL: 0.743; ML: 1.22-1.27; GL: 1.95-1.97; CI: 101.75-102.69; SI: 91.39-92.53. *Males* (n=1): TL: 2.68; HW: 0.504; HL: 0.514; SL: 0.415; ML: 0.978; GL: 1.19; CI: 98.05; SI: 82.34.

Other material examined: MALAYSIA: Sarawak, 4th Div., G. Mulu National Park (P.M. Hammond & J.E. Marshall). In: BMNH.

Distribution and natural history: This species is known only from Sarawak on Borneo. A nest was found in the soil under a log, but otherwise nothing is known of this species' natural history.

Discussion: This species can be distinguished from *A. acutiventris* by the lack of ridges on the surface of the mandible, and from *A. gelasis* by not possessing a prominent "beak-like" median portion of the clypeus. Additionally, the erect mesosomal hairs of *A. hystrix* are longer than those of *A. gelasis*. Overall, this species, along with *A. gelasis*, is darker and with less pilosity than most other *Acropyga* species.

The species' placement within the *myops* species-group is based on the fact that *A. hystrix* workers possess widely separated torulae, and by the fact that the reproductives are very dark (dark brown to black), as are the reproductives of *A. myops*. The mandibles of this species are similar to *A. myops*.

Acropyga kinomurai Terayama & Hashimoto

Acropyga (Rhizomyrma) kinomurai Terayama & Hashimoto, 1996: 7. Holotype worker, JAPAN: Yoshino, Ishigaki-jima, Yaeyama Is., Okinawa Pref. (K. Kinomura) (MNHA) [not examined]. Specimens (worker and queen) examined for this study were from the type locality and had the same date and collector as listed in Terayama & Hashimoto (1996) for the holotype and subsequent paratypes, though the examined specimens were not labeled with any type designation. Terayama *et al.*, 2002: 25, description and key.

Diagnosis: *Worker:* 10-11 segmented antennae; flattish head distinctly square to rectangular in shape with prominent posterolateral corners and parallel sides; torulae widely separated; mandibles with 4 teeth, dorsum densely covered in hairs. *Queen:* as in worker with modifications expected for caste. *Male:* unknown.

Compare with: This species is unique in its appearance.

Description: *Worker.* Head (fig. 27A): yellow; covered in a thick layer of appressed to suberect hairs; head broader than long, distinctly square to rectangular in appearance; posterolateral corners distinct; posterior margin entire to slightly concave medially, with short erect hairs; 10-11 segmented, incrassate antennae; scape reaches to posterior margin; clypeus narrow and flat, with many long hairs (reaching toward apical teeth of closed mandibles) along anterior clypeal margin; toru-

lae widely separated from each other; mandible with 4 teeth; dorsal surface of mandible with dense covering of hairs; gap exists between inner mandibular margin and anterior clypeal margin. Mesosoma (fig. 27B): yellow; in lateral view pronotum rises steeply toward mesonotum; pronotum covered in dense layer of appressed to erect hairs; dorsum nearly flat, with propodeum slightly lower than mesonotum; mesonotum flat, covered in a dense layer of appressed to erect hairs; metanotal area indistinct; propodeum flat, covered in a dense layer of appressed to erect hairs; declivity gently sloping. Gaster: petiole thick and erect, with many short erect hairs on surface, reaching height of propodeum; gaster yellow; covered in layer of appressed hairs with scattered erect hairs throughout.

Queen. As in worker with modifications expected for caste and the following differences: color darker than worker, being brownish-yellow; pronotum very narrow.

Male. Unknown.

Measurements: *Workers* (n=1): TL: 2.09; HW: 0.5; HL: 0.438; SL: 0.357; ML: 0.547; GL: 1.1; CI: 114.16; SI: 71.4. *Queens* (n=1): TL: 3.0; HW: 0.603; HL: 0.525; SL: 0.514; ML: 0.924; GL: 1.55; CI: 114.86; SI: 85.24.

Other material examined: JAPAN: Yoshino, Ishigaki-jima, Yaeyama Is., Okinawa Pref. (K. Kinomura). In: BMNH.

Distribution and natural history: This species is known only from its type locality. A dealate queen was found in August. An *A. kinomurai* nest was taken under a stone. The mealybug *Eumyrmococcus kinomurai* has been found in the nests of *A. kinomurai* (Williams and Terayama, 2000).

Discussion: This is a bizarre looking and easy to recognize species with its uniquely square head and very widely set torulae. The placement of the torulae is particularly interesting because the great distance between the structures is unique among *Acropyga*. Based on the widely set torulae, *A. kinomurai* is provisionally placed in the *myops* species-group, pending discovery of worker-associated male specimens. This species also shares a very similar mesosomal structure (flat dorsum and short pronotum) with *A. lauta* and *A. sauteri*, other species in the *myops* species-group. The outer surface of the worker mandibles are similar to *A. lauta* in being covered in a dense layer of hairs suggesting a possible relationship between the two species. Unfortunately, *A. lauta* also is without known male specimens, and it has torulae that are close together, possibly indicating it is not a close relative of *A. kinomurai*.

Acropyga lauta Mann

Acropyga (Rhizomyrma) lauta Mann, 1919: 365 (w.q.). 7 syntype workers, 1 syntype queen, SOLOMON ISLANDS: Auki, Malaita (W.M. Mann) (MCZC) [examined]; 12 syntype workers, 4 syntype queens, SOLOMON ISLANDS: Pamua (W.M. Mann) (USNM) [examined]. The designated lectotype is a worker labeled JSL TYPE # 127 and is deposited at MCZC.

Diagnosis: *Worker:* 8-9 segmented antennae; mandible with 4 teeth, basal tooth separated by a short diastema. *Queen:* as in worker with modifications expected for caste. *Male:* unknown.

Compare with: *A. sauteri*

Description: *Worker.* Head (fig. 27C): yellow; head covered in thick layer of appressed hairs; head longer than broad; posterior margin entire; 8-9 segmented, incrassate antennae; scape fails to reach posterior margin by about length of pedicel; clypeus narrow, with many suberect to erect hairs on surface; clypeus convex medially; mandible typically with 4 distinct teeth, the 4th tooth from apical separated by a short diastema; smaller 5th tooth can sometimes form in the diastema region; inner mandibular margin nearly parallel to anterior clypeal margin; dorsal surface of mandible very hairy (< 20 hairs). Mesosoma (fig. 27D): yellow; in lateral view pronotum with short anterior shelf before rising steeply toward mesonotum; mesonotum covered in a dense layer of short suberect to erect hairs; longer hairs occasionally found posteriorly; mesonotum at same height

as pronotum and propodeum; mesonotum dorsum flat, covered in a dense layer of short suberect to erect hairs; metanotal area distinctly pinched in laterally from mesonotum and propodeum giving it an "hour glass" appearance in dorsal view; propodeum dorsum flat, covered in a dense layer of short suberect to erect hairs; declivity steep. Gaster: petiole thick and erect, narrowing slightly toward apex, reaching height of bottom portion of propodeal spiracle; gaster yellow; covered in a dense layer of appressed hairs with scattered erect hairs throughout.

Queen. As in worker with modifications expected for caste, and with the following differences: darker than worker (brownish-yellow in color).

Male. Unknown.

Measurements: *Workers* (n=8): TL: 1.94-2.34; HW: 0.51-0.579; HL: 0.49-0.556; SL: 0.356-0.427; ML: 0.541-0.647; GL: 0.89-1.14; CI: 99.03-108.17; SI: 68.07-78.24. *Queens* (n=2): TL: 2.82-3.36; HW: 0.547-0.56; HL: 0.528-0.54; SL: 0.422-0.44; ML: 0.946-0.988; GL: 1.31-1.87; CI: 101.3; SI: 75.36.

Other material examined: SOLOMON ISLANDS: San Cristobal, Huni R., est. N.E. Wainoni; San Cristobal, 4 mi. up Warahito from R. Pagato; Santa Ysabel, Tatamba; San Cristobal, c. 6 mi. SE of Waimoni, elev. 2325 ft. In: ANIC.

Distribution and natural history: This species has only been recorded from the Solomon Islands. Johnson *et al.* (2001) recorded this species as trophophoretic. It has been associated with the mealybugs *Eumyrmoccus kolobangarae* and *E. kusiacus*.

Discussion: The worker of this species is easily separated from *A. sauteri* by the presence of 8-9 segmented antennae and the basal teeth offset by a diastema separating them from the other teeth. The large size of the species and four teeth on the mandible, coupled with the fact it possesses darker queens, has led to its provisional placement within the *myops* species-group. *A. lauta* has a similar mesosomal structure to *A. kinomurai* and *A. sauteri*. Like *A. kinomurai* and *A. sauteri*, *A. lauta* also displays reduced mandibular dentition. Based on the dense covering of hairs on the mandibles, this species may be most closely related to *A. kinomurai*. However, *A. lauta* torulae are closely set, unlike other members of the *myops* species-group. Therefore, the exact placement of *A. lauta* awaits discovery of worker-associated males.

Acropyga myops Forel

Acropyga myops Forel, 1910: 59 (w.m.). Syntype workers, syntype male, AUSTRALIA: Bombala, New South Wales, 213 (Fr) (AMNH, workers only; male depository unknown) [examined workers only]. The designated lectotype is a worker deposited at AMNH. Emery, 1925: 30, first combination in *Rhizomyrma*.

Acropyga indistincta Crawley, 1923: 178 (w.). Holotype worker, AUSTRALIA: Mundaring, W. Australia (J. Clark) (MCZC) [examined]. **NEW SYNONYM.**

Diagnosis: *Worker:* 11 segmented antennae; mesosomal dorsum with short appressed hairs, giving it a bare appearance; mesonotum broadly rounded, higher than propodeum; head width > 0.6 mm. *Queen:* As in worker, with modifications expected for caste. *Male:* 12 segmented antennae; parameres taper toward apices where many shorter hairs bend toward penis valves; in dorsal view parameres form "v" shape from apex to the base.

Compare with: *A. acutiventris* and *A. dubia*

Description: *Worker.* Head (fig. 28A): yellow; head covered in a layer of dense appressed hairs; head about as long as broad to slightly longer than broad; posterior margin entire to slightly concave; 11 segmented, incrassate antennae; scape reaches or slightly surpasses (less than half length of pedicel) posterior margin; clypeus broad, medially convex, with longer, erect hairs; mandible broad with 5-6 teeth; small, indistinct tooth often at basal angle; 3rd tooth from apical smaller than others; a short diastema between 4th and 5th tooth (numbered from apical); dorsal surface of mandible covered in many erect hairs (≥ 20 hairs); hairs close to masticatory margin often extend passed length of teeth; inner mandibular margin parallel with anterior clypeal margin. Mesosoma

(fig. 28B): yellow; in lateral view, pronotum rises steeply toward mesonotum; pronotum covered in dense layer of short appressed to suberect hairs; mesonotum dorsum broadly rounded toward metanotal area; mesonotum covered in dense layer of short appressed to suberect hairs; mesonotum higher than propodeum; metanotal area distinct; propodeum covered in dense layer of short appressed hairs, gently rounded toward steep declivity. Gaster: petiole short, but thick and erect, rounded apically; reaches at most lower portion of propodeal spiracle; gaster yellow; covered in layer of very short appressed hairs, with sparsely scattered erect hairs throughout.

Queen. As in worker, with modifications expected for caste and the following differences: can vary in color from a brownish-yellow to a dark brown (almost black); head broader than long.

Male. Head: brownish-yellow to dark brown; head covered in a dense layer of appressed hairs, with scattered short erect hairs near vertex; head broader than long, though becoming narrower around 3 prominent ocelli; 12 segmented, incrassate antennae; scape surpasses posterior margin by about half length of pedicel; clypeus broad, slightly medially convex, with scattered erect hairs throughout; mandibles broad with 5 distinct teeth; 2nd and 3rd teeth from apical smaller than others; a short diastema often found between 4th and 5th teeth; dorsal surface of mandible hairy (approximately 15 hairs); hairs toward masticatory margin often surpass length of teeth. Mesosoma: brownish-yellow to dark brown; pronotum narrow and collar-like, overarched by broadly rounded mesonotum; mesonotum with dense layer of appressed hairs to short erect hairs; longest and most erect hairs found on scutellum; propodeum rounded, with layer of appressed hairs to erect hairs; declivity not distinct from propodeum. Gaster: petiole thick and erect, rounded apically; petiole can reach height of propodeum; gaster brownish-yellow to dark brown; covered in a dense layer of appressed hairs, with scattered suberect to erect hairs throughout. Genitalia (figs. 43E-H): in lateral view, parameres long, taper to rounded apices; parameres with erect hairs throughout, shorter and more abundant erect hairs at apices; cuspi short and rounded, reaching only approximately 1/4 length of digiti; cuspi with peg-like teeth at apices; digiti long and broad, plate-like with broadly rounded apices, with peg-like teeth where cuspi meet; penis valve fig. 43H.

Measurements: *Workers* (n=7): TL: 2.8-3.43; HW: 0.624-0.731; HL: 0.667-0.773; SL: 0.527-0.631; ML: 0.669-0.875; GL: 1.33-1.86; CI: 93.55-100.42; SI: 80.83-87.96. *Queens* (n=2): TL: 1.98-2; HW: 0.872-0.928; HL: 0.812-0.874; SL: 0.716-0.792; ML: 1.27-1.53; GL: 1.14-.713; CI: 106.18-107.39; SI: 82.11-85.34. *Males* (n=2): TL: 2.48-2.64; HW: 0.525-0.563; SL: 0.48-0.453; ML: 0.971-1.2; GL: 0.713-1.14; CI: 100-109.77; SI: 73.3-91.43.

Other material examined: AUSTRALIA: Katoomba, New South Wales; Black Mountain, ACT, elev. 2000 ft. (T. Greaves and W.L. Brown); Queensland, Brisbane, Ithica Creek, med. sclerophyll (B.B. Lowery); New South Wales, Gerroa, Seven Mile Beach, coastal scrub (B.B. Lowery); New South Wales, Hills to W. of Mudgee, elev. ca. 2000 ft., dry sclerophyll (B.B. Lowery); New South Wales, 1 mi. N of Eungella, elev. 700 ft., dry sclerophyll (B.B. Lowery); New South Wales, Trial Bay, South West Rocks, dry sclerophyll (B.B. Lowery); South Australia, Flinders Range, Oraparinna (P.J.M. Greenslade); South Australia, Flinders Range, Alligator Creek (P.J.M. Greenslade); Queensland, Dawes, 20 mi SE of Biloela, dry sclerophyll (B.B. Lowery); Brindabe 11a Ra., ACT, 26 Euc. For. (W.L. Brown); Northern Territory, Sawcut Gorge, 12.55S x 132.56E (R.W. Taylor); Queensland, Cunningham's Gap (P.J.M. Greenslade); South Australia, Flinders Range, Mambray Creek (P.J.M. Greenslade); Queensland, Mareeba, 3 km along Davies Creek, dry sclerophyll (B.B. Lowery); Queensland, 5 mi W of Mt. Garnet, dry sclerophyll (B.B. Lowery); Queensland, Ravenshoe Millstream Nat. Park, dry sclerophyll (B.B. Lowery); Queensland, 18 km S of Banana, brigalow scrub (B.B. Lowery); Queensland, on bank of Daintree River near Daintree, rainforest (B.B. Lowery); New South Wales, Barton Highway near the A.C.T. (B.B. Lowery); Queensland, near Gordonvale, dry sclerophyll (B.B. Lowery); Queensland, The Boulders National Park near Babinda, rainforest (B.B. Lowery); Queensland, "St. Renams," 20 km H Junction, Kennedy Highways Mt., Surprise Road, dry sclerophyll (B.B. Lowery); New South Wales, 55 S of Grafton

(P.J.M. Greenslade); New South Wales, Dharug Nat. Park, Bedlam Creek, wet sclerophyll (B.B. Lowery); Queensland, 18 km SW of Walkerston, dry sclerophyll (B.B. Lowery); New South Wales, 15 km S of Dubbo, dry sclerophyll (B.B. Lowery); Sea Lake, Victoria (coll. J.C. Goudie); New South Wales, R. Nat. Park (W.L. Brown); Queensland, Cooloola, Noosa River (P.J.M. Greenslade); New South Wales, Karuah, swampy sclerophyll (B.B. Lowery); New South Wales, Bulahdelah Mt., 8 km W of Bulahdelah, wet sclerophyll (B.B. Lowery); New South Wales, Grose Valley, Blue Gum Forest, wet sclerophyll (B.B. Lowery); New South Wales, Burrinjuck Dam Sanctuary, dry sclerophyll (B.B. Lowery); New South Wales, Newlands Creek, 10 km W of Merrimbula, dry sclerophyll (B.B. Lowery); New South Wales, Jindalee S.F., dry sclerophyll (B.B. Lowery); New South Wales, Bateman's Bay, Long Beach area, wet sclerophyll (B.B. Lowery); New South Wales, 10 km N of Borrowa, dry sclerophyll (B.B. Lowery); Queensland, Girraween Nat. Park, 28° 50' S, 151° 56' E, elev. 850 m (P.S. Ward); ACT, 5 km S Cotter Reserve, elev. ca. 600 m, 35.35° S, 148.95° E, Brindabella Range (R.R. Snelling and R.W. Taylor). In: ANIC, LACM, MCZC.

Distribution and natural history: This appears to be the only *Acropyga* endemic to Australia. It occurs in a wide range of habitats from savannas to rainforests but is absent (like all Australian *Acropyga*) from the arid interior of the continent.

Discussion: This species is among the largest (head width > 0.6 mm; total length: 2.8-3.43 mm). It is distinguished from *A. acutiventris* by not having fine mandibular striate sculpture on the dorsal surface, and from *A. dubia* by its larger head width.

Both queens and males of *A. myops* are very dark brown to almost black in color, a characteristic shared only with *A. hystrix*. The digiti and cuspi of *A. myops* are similar to *A. sauteri*, an indication that the two species are closely related.

Acropyga sauteri Forel

Acropyga (Rhizomyrma) sauteri Forel, 1912a: 72 (w.). Syntype workers, TAIWAN: (no specific locality provided) (depository unknown) [not examined]. Wheeler, W.M., 1928: 31, description of queen; Santschi, 1928a: 36, description of queen and male; Terayama *et al.*, 2002: 25, description and key.

Diagnosis: *Worker:* 11 segmented antennae; mesosomal dorsum flat with many short erect hairs; pronotum short, rises very steeply toward mesonotum; mandible with 3-4 teeth. *Queen:* As in worker with modifications expected for caste. *Male:* 12 segmented antennae; digiti 2.5 times longer than cuspi, with peg-like teeth along sides.

Compare with: *A. lauta*

Description: *Worker.* Head (fig. 28C): yellow; head covered in layer of short appressed hairs; head about as broad as long; posterior margin slightly concave medially; short erect hairs along posterior margin; 11 segmented, incrassate antennae; scape reaches or slightly surpasses posterior margin; clypeus broad, slightly convex, with many erect hairs on dorsal surface; mandible with 3-4 teeth; apical tooth often much longer than others; when present, 4th tooth smaller and offset from masticatory margin; when with 3 teeth, a small hump present along inner mandibular margin where a 4th tooth would be; gap exists between inner mandibular margin and anterior clypeal margin. Mesosoma (fig. 28D): yellow; in lateral view, pronotum with short shelf rising sharply toward mesonotum; pronotum covered with short erect hairs; mesosomal dorsum flat; mesonotum and propodeum at same height; mesonotum and propodeum covered in layer of short erect hairs; metanotal area indistinct; declivity steep. Gaster: petiole thick and erect reaching height of bottom portion of propodeal spiracle; gaster yellow, with thick covering of appressed hairs with scattered erect hairs throughout.

Queen. As in worker with modifications expected for caste and the following differences: color a brownish-yellow, darker on apex of head, mesosomal and gaster dorsa.

Male. Head: yellow to dark brownish-yellow toward apex around 3 prominent ocelli; head covered in a layer of short erect hairs; head broader than long; 12 segmented, slightly incrassate antennae;

scape surpasses posterior margin by about 1/2 length of pedicel; clypeus broad, convex medially; mandible with 3-4 teeth; mandibular shape as in worker. Mesosoma: brownish-yellow; pronotum small and collar-like, overarched by mesonotum; dorsum flat with dense layer of short erect hairs; scutellum with longer erect hairs; propodeum long, slightly below level of mesonotum; declivity short and steep. Gaster: petiole thick and erect; gaster brownish-yellow, covered in a layer of appressed hairs. Genitalia (figs. 44A-D): in lateral view, parameres long and thin, tapering to rounded apices; cuspi short, nearly straight, with short peg-like teeth at rounded apices; digiti straight, much longer than cuspi (ca. 2.5 times), with short, peg-like teeth along sides toward truncated apices; penis valve fig. 44D.

Measurements: *Workers* (n=2): TL: 2.16-2.59; HW: 0.527-0.568; HL: 0.561-0.596; SL: 0.413-0.418; ML: 0.681-0.687; GL: 0.909-1.31; CI: 101.25-105.2; SI: 66.67-72.71. *Queens* (n=1): TL: 3.39; HW: 0.732; HL: 0.619; SL: 0.495; ML: 1.19; GL: 1.58; CI: 118.26; SI: 67.62. *Males* (n=1): TL: 2.21; HW: 0.5; HL: 0.452; SL: 0.371; ML: 0.819; GL: 0.941; CI: 110.62; SI: 74.2.

Other material examined: **JAPAN:** Yasaka (T. Uye); Suwanose-jima, Kagoshima (H. Watanabe); **TAIWAN:** Shinta (M. Yanagihara); **MACAO:** (specific locality not provided) (F. Silvestri). In: MCZC, SYPC.

Distribution and natural history: This species has one of the most northerly distributions in the genus, ranging from Japan south to Macao in southern China. It has been found in grasslands and forests, under stones as well as in leaf litter and soil. It is a trophophoretic species, associated with the mealybug *Eumyrmococcus smithii*. Terayama (1988) reported that queens carried gravid mealybugs on their mating flights.

Discussion: The worker of this species is fairly easily recognized, with 3-4 teeth and no diastema separating the basal teeth from the other teeth. *A. sauteri* is currently placed in the *myops* species-group. The long digiti, similar shaped parameres and dark color of the male suggest a close relationship with *A. myops*.

pallida species-group

Acropyga pallida (Donisthorpe)

Bothriomyrmex pallidus Donisthorpe, 1938: 598 (w.). Holotype worker, INDONESIA: Cyclops Mountains, Mt. Lina, elev. 3,500 ft. (L.E. Chessman) (BMNH) [examined]. Shattuck, 1992: 60, first combination in *Acropyga*.

Diagnosis: *Worker:* 9-11 segmented antennae; 5-7 mandibular teeth; inner mandibular margin and basal tooth margin are even with each other; no diastema between the 4th tooth and the basal tooth. *Queen:* as in worker with modifications expected for caste. *Male:* in lateral view, parameres become thinner tapering to pointed tips; digiti truncated, slightly longer than cuspi; digiti meet cuspi at apices.

Compare with: *A. ambigua*

Description: *Worker:* Head (fig. 29A): yellow; covered in layer of appressed hairs; distinctly longer than broad; posterior margin entire to slightly concave medially; 9-11 segmented, incrassate antennae; scape fails to reach posterior margin by about length of first two funicular segments; clypeus narrow, convex medially, with many erect hairs; mandible broad, tooth number variable with 5-7 approximately equally sized teeth; when 7 teeth present, additional (6th and 7th) teeth along inner mandibular margin usually smaller and found along inner mandibular margin; inner mandibular margin and clypeal margin nearly parallel. Mesosoma (fig. 29B): yellow; in lateral view, pronotum with short anterior shelf, then rising toward mesonotum; erect hairs along posterior portion of pronotum; mesonotum variable from flat (at about level of propodeum) to rising above level of propodeum; mesonotum covered in layer of appressed hairs, with scattered erect hairs; metanotal area often distinct; propodeum flat, with layer of appressed hairs; declivity steep. Gaster: petiole thick and erect, reaching level of anterior portion of propodeal spiracle; gaster yellow; covered in

dense layer of appressed hairs, with scattered erect hairs throughout.

Queen. As in worker with modifications expected for caste.

Male. Head: brownish-yellow, darker toward apex around 3 prominent ocelli; covered in layer of appressed hairs; head about as broad as long, becoming narrower toward apex; eyes large, breaking outline of head in full frontal view; 12 segmented, incrassate antennae; scape reaches posterior margin; clypeus narrow, convex medially; mandible broad with 4-5 teeth. Mesosoma: brownish-yellow; pronotum short and collar-like, overarched by mesonotum; mesonotum rounded anteriorly; dorsum flat with appressed hairs; propodeum short and low; declivity short and indistinct. Gaster: petiole thick and erect reaching height of propodeum; gaster brownish-yellow; covered in a layer of appressed hairs with scattered erect hairs throughout. Genitalia (figs. 44E-H): in lateral view parameres taper to caudal points; digiti slightly longer than cuspi, with truncated apices; short peg-like teeth at apex of digiti; cuspi meet digiti at apices; cuspi with short peg-like teeth at apices; penis valves fig. 44H.

Measurements: *Workers* (n=17): TL: 1.4-2.06; HW: 0.352-0.447; HL: 0.372-0.519; SL: 0.228-0.363; ML: 0.365-0.495; GL: 0.62-1.06; CI: 82.88-94.89; SI: 64.59-84.92. *Queens* (n=3): TL: 2.55-2.91; HW: 0.504-0.543; HL: 0.519-0.580; SL: 0.412-0.452; ML: 0.831-0.998; GL: 1.2-1.44; CI: 91.49-93.11; SI: 81.75-85.77. *Males* (n=1): TL: 1.75; HW: 0.352; HL: 0.361; SL: 0.304; ML: 0.633; GL: 0.754; CI: 97.51; SI: 86.36.

Other material examined: AUSTRALIA: New South Wales, 3 miles east of Berry, elev. 150 ft., relict rainforest (B.B. Lowery); New South Wales, Mt. Nullum, Murwillumbah, elev. 300 ft., dry sclerophyll (B.B. Lowery); New South Wales, Gerroa, 10 mi south of Kiama, beach scrub (B.B. Lowery) (ANIC); New South Wales, Faunal Reserve, Brunswick Head, rainforest (B.B. Lowery); New South Wales, Royal National Park, 34° 09'S, 151° 01'E, elev. 50 m (P.S. Ward); Northern Territory, Baroalba Spring, 12.47 S x 132.51 E, rainforest (R.W. Taylor); Northern Territory, Baroalba Spring, 12° 47' S, 132° 51' E, Euc. savanna (R.W. Taylor & J.E. Feehan); Northern Territory, 46 km SSW of Borrooloola, 16° 28' S, 136° 09' E (J.E. Feehan); Queensland, Coolooa, rainforest (P.J.M. Greenslade); Queensland, Coolooa, rainforest (P.J.M. Greenslade); Queensland, Miriani near MacKay, dry sclerophyll (B.B. Lowery); Queensland, Stony Creek near Shiptons Flat, 15° 50' S, 145° 13' E (J.E. Feehan); WA: Tunnel Creek National Park, 17° 36' S, 125° 09' E, elev. 150 m (P.S. Ward); INDONESIA: Sulawesi Utara, Dumoga-Bone National Park, lowland forest, elev. 200-400 m, leaf litter sample; MALAYSIA: Borneo, Sabah, Sayap Kinabalu, elev. ca. 1000 m (K. Eguchi); PAPUA NEW GUINEA: Cyclops Mountains, Mt. Lina, elev. 3,500 ft. (L.E. Chessman); Timber Track, ca. 16 km NW Lae, elev. ca. 220 m, rotten wood (R.W. Taylor); 5 km SW of Mt. Uluman, Karkar Island, 4° 41' S, 145° 57' E, elev. 800 m (P.S. Ward); PHILIPPINES: Luzon, Mt. Makiling, Lagunas, rainforest litter near summit (R.A. Morse); Luzon, 16 km S of Real, 14° 40' N, 121° 36' E, relict rainforest on steep slopes (B.B. Lowery). In: ANIC, BMNH, MCZC, SYPC.

Distribution and natural history: This species ranges from Australia, north to the Philippines, and west to Borneo. *A. pallida* has been found in a wide range of habitats from savanna to rainforests, nesting in litter and rotten wood.

Discussion: This species can be difficult to distinguish from *A. ambigua*, see discussion there for diagnostic characters. As defined here this species displays considerable variation in mandibular tooth number and mandibular shape, causing some difficulty in determining the boundary of this species. The two most important diagnostic characters are from the mandible: the inner margin and basal tooth margin are even with each other, and there is no diastema between the 4th tooth and the basal tooth (as in *A. ambigua*). When 6 or 7 teeth are present these additional teeth are found along the inner mandibular margin and smooth out the masticatory margin, making it less square in appearance in full frontal view.

While outside of Australia only 5-toothed specimens were examined, within Australia the full range of possible teeth known to occur in this species was observed (5-7 teeth). Whether this is an artifact of collecting (most specimens examined were from Australia), indicative of a latitudinal

gradient, or means there is more than one species present remains unclear and the observation warrants further investigation. Since males are known only from Australia, collections in other portions of this species' range will be helpful in clarifying questions about conspecificity.

panamensis species-group

***Acropyga ayanganna*, NEW SPECIES**

Holotype worker, GUYANA: Mt. Ayanganna; Falls Camp; 5° 22.332' N, 59° 57.563' W; elev. ca. 1134 m, (J.S. LaPolla et al.) (#JSL 021012-10) (UGBC); 9 paratype workers, 1 paratype queen, 5 paratype males (MCZC) (USNM). The holotype is labeled JSL TYPE # 120.

Diagnosis: *Worker*: 10 segmented antennae; eyes relatively large; mandible with 4 distinct teeth, and a smaller tooth between 2nd and 3rd teeth; scape surpasses posterior margin by about length of pedicel. *Queen*: As in worker with modifications expected for caste. *Male*: 11 segmented antennae; caudally parameres taper to a point; cuspi much shorter than digiti; mandible with 3 distinct teeth and occasionally smaller teeth between apical and 2nd or between 2nd and 3rd teeth.

Compare with: *A. fuhrmanni* and *A. guianensis*

Description: *Worker*: Head (fig. 29C): yellow; covered in a dense layer of appressed hairs; head about as long as broad; posterior margin slightly concave; several erect hairs found at post-rolateral corners; eyes relatively large, placed at lower 1/4 side of head; 10 segmented, incrassate antennae; scape surpasses posterior margin by about length of pedicel; scape with many erect hairs scattered throughout; clypeus covered in dense layer of erect hairs; medially clypeus strongly convex; mandible with 4 distinct teeth; a smaller tooth often present between the 2nd and 3rd larger teeth (from apical) making mandible 5-toothed; a short diastema present between 3rd and 4th larger teeth; a gap exist between inner mandibular margin and anterior clypeal margin. Mesosoma (fig. 29D): yellow; in lateral view pronotum rises steeply toward mesonotum; covered in layer of appressed hairs, some of them long; pronotum with several, long erect hairs posteriorly; mesonotum with a layer of appressed hairs, several longer erect hairs throughout; mesonotum much higher than propodeum; metanotal area distinct; propodeum with appressed hairs; declivity steep. Gaster: petiole thick and erect reaching base of propodeal spiracle; gaster yellow; covered in thick layer of appressed hairs, with scattered erect hairs throughout.

Queen. As in worker with modifications expected for caste.

Male. Head: yellowish-brown, darker toward apex around 3 prominent ocelli; head broader than long, becoming narrower toward apex; covered in layer of appressed hairs; posterior margin with several erect hairs; 11 segmented, slightly incrassate antennae; apical segment about as long as proceeding 3 segments; scape surpasses posterior margin by about length of first two funicular segments; clypeus narrow, covered in layer of erect hairs; clypeus slightly convex medially; mandible with 3 distinct teeth; a smaller tooth can sometimes be found between the larger apical and 2nd and/or between 2nd and 3rd teeth, effectively making mandible 4-toothed; a gap exist between inner mandibular margin and anterior clypeal margin. Mesosoma: brownish-yellow; pronotum short and collar-like, overarched by mesonotum; anterior mesonotum broadly rounded; dorsum of mesonotum flat, covered in layer of largely short appressed hairs, with scattered longer appressed to erect hairs throughout; propodeum slightly rounded, with appressed hairs; declivity steep. Gaster: petiole, thick and erect; gaster brownish-yellow, dorsum darker. Genitalia (figs. 45A-D): in lateral view parameres taper to a point at apices; covered with many erect hairs, with many longer hairs posteriorly; volsellar lobes with many short, erect hairs; cuspi short and rounded, with peg-like teeth at apex, not reaching digiti; digiti large, rounded at apices; peg-like teeth on side facing cuspi; digiti much longer than cuspi; penis valve fig. 45D.

Etymology: The specific epithet *ayanganna* refers to Mount Ayanganna, a remote peak in the Pakaraima Mountains in western Guyana, and is the locality where this species was discovered.

Measurements: *Workers* (n=4): TL: 2.28-2.57; HW: 0.598-0.649; HL: 0.591-0.648; SL: 0.483-0.566; ML: 0.665-0.726; GL: 1.02-1.22; CI: 100.15-103.32; SI: 77.53-89.27. *Queens* (n=1): TL: 3.88; HW: 0.864; HL: 0.830; SL: 0.762; ML: 1.31; GL: 1.74; CI: 88.19; SI: 104.09. *Males* (n=2): TL: 2.47-2.56; HW: 0.505-0.528; HL: 0.46-0.485; SL: 0.452-0.462; ML: 0.921-0.96; GL: 1.09-1.11; CI: 108.87-109.78; SI: 85.61-91.49.

Distribution and natural history: This species is known only from Mount Ayanganna in Guyana. *A. ayanganna* forms large nests, with many thousands of workers. Some nests were found along a stream bank in sandy soil, under rocks and root mats. Other nests were found in the surrounding forest under stones and in rotten logs. This species was very abundant at the type locality. Many nests were located and it was often difficult to distinguish where one colony ended, and another began. Several dealate queens were collected along with workers, which suggests the species is polygynous.

The physical structure of the nests was diffuse (no obvious central nesting area), like many other *Acropyga* species in which nesting habits are known, with many tunnels and chambers where brood and mealybugs were kept. The distinctness of the chambers however stands in contrast to observations of several other *Acropyga* species, which construct chambers that appear to be little more than slight expansions of tunnels (LaPolla *et. al*, 2002). When a number of *A. ayanganna* workers, brood and mealybugs were collected and placed in a petri dish overnight, the ants gathered their brood and mealybugs and placed them into a distinct chamber they constructed from loose dirt in the petri dish, supporting the observation that this species constructs well-defined chambers. Furthermore, mealybugs and brood were kept together in a mixed pile.

Discussion: The worker caste of *A. ayanganna* closely resembles *A. fuhrmanni* in overall appearance. Several key features separate workers of the two species, however. Among those characters are the 10 segmented antennae and 5 mandibular teeth of *A. ayanganna*. *A. fuhrmanni* is known only from specimens with 8 segmented antennae and 4 mandibular teeth. The greatest similarity is in the head, where both species possess relatively large eyes that are close to the anterior margin of the head. Despite the similarity of the worker caste between *A. ayaganna* and *A. fuhrmanni*, they are not closely related. The sister species to *A. ayanganna* is *A. panamensis*. This is interesting because based solely on overall worker morphology, they appear very distantly related to each other. However, the males of these two species reveal their close relationship by the presence of similar cuspi and digiti, parameres and penis valves, all of which serve as synapomorphies. The differences observed in the worker morphology between *A. ayanganna* and *A. panamensis* underscores the importance of examining males to determine phylogenetic relationships, and not relying strictly upon worker morphology.

Acropyga panamensis Weber

Acropyga (Rhizomyrma) panamensis Weber, 1944: 113. Neotype worker, PANAMA: Barro Colorado Island; Canal Zone; B41 (W.L. Brown and E.S. McCluskey) (MCZC). This species was described by Weber (1944) from a single worker specimen, which has subsequently been lost (though the pin remains the specimen does not). In the interest of nomenclatural stability a neotype is designated. The neotype is from the original type locality. The neotype is labeled JSL TYPE # 123.

Diagnosis: *Worker:* 8 segmented antennae; scape fails to reach posterior margin by about the length of first three funicular segments; mandible with an enlarged, rectangular, apically truncated basal tooth; apical segment is much wider than preceding funicular segments giving it a swollen appearance. *Queen:* As in worker except for modifications expected for caste; scape is slightly longer than in worker. *Male:* 10 segmented antennae; basal tooth, as in other castes, though not as prominent; antennal shape also as in other castes; digiti long, thick and with rounded apices; cuspi significantly shorter, bending toward digiti at about half of digiti length.

Compare with: This species is unique in its appearance.

Description: *Worker.* Head (fig. 30A): brownish-yellow; head distinctly longer than broad; covered in thick layer of short appressed hairs; posterior margin entire; 8 segmented, extremely incrassate antennae; apical segment more than twice as wide as pedicel and about as long as all other funicular segments combined, giving it a swollen appearance; scape short, fails to reach posterior margin by about the length of the first three funicular segments; clypeus convex medially, with several long erect hairs on surface; mandible broad with 4 teeth; the basal tooth enlarged, rectangular, and apically truncated; inner mandibular margin and anterior clypeal margin parallel. Mesosoma (fig. 30B): brownish-yellow; in lateral view entire mesosoma appears roughly rectangular; pronotum in lateral view, with short anterior shelf then rising steeply toward mesonotum; pronotum covered in a dense layer of short hairs; pronotum distinctly rounded posteriorly; entire dorsum nearly flat; mesonotum covered in thick layer of short appressed hairs; propodeum not much lower than mesonotum, with a thick layer of short appressed hairs; propodeum strongly rounded posteriorly with steep declivity. Gaster: petiole thick and erect, roughly triangular in lateral view; gaster brownish-yellow; covered in a layer of short appressed hairs, with scattered suberect to erect hairs throughout.

Queen. As in worker with differences associated with caste and with the following differences: scape slightly longer than in worker, only fails to reach posterior margin by about length of pedicel; mesonotum higher than propodeum which is nearly flat.

Male. Head: brownish-yellow, becoming dark brown around 3 prominent ocelli; covered in short suberect to erect hairs; eyes prominent; 10 segmented, incrassate antennae; apical segment wide, about as long as preceding four segments; scape fails to reach posterior margin by about length of pedicel; clypeus slightly convex medially, with numerous erect hairs on surface; mandible with 2 teeth, the basal tooth as in worker, though not as long and less distinct. Mesosoma: brownish-yellow to brown; pronotum small and collar-like, overarched by mesonotum; mesonotum flat and covered in short hairs; scutellum with longest erect hairs; propodeum small and rounded with short, but distinct declivity. Gaster: petiole thick and erect, short and wide; gaster largely dark brown, covered in a thick layer of appressed hairs, with scattered suberect to erect hairs throughout. Genitalia (figs. 45E-H): parameres taper to points caudally; posterior end (last 1/3 of length) with many long hairs; cuspi short, nearing lower half of digiti, with prominent teeth at apices; digiti much longer than cuspi, thick and rounded apically; near cuspi, digiti with prominent teeth, the last few as high as cuspi teeth; penis valve fig. 45H.

Measurements: *Workers* (n=5): TL: 1.39-1.58; HW: 0.315-0.393; HL: 0.41-0.457; SL: 0.21-0.266; ML: 0.39-0.45; GL: 0.546-0.718; CI: 76.83-86.0; SI: 63.35-74.51. *Queens* (n=4): TL: 1.97-2.54; HW: 0.391-0.42; HL: 0.474-0.508; SL: 0.313-0.326; ML: 0.566-0.732; GL: 0.899-1.35; CI: 79.8-83.54; SI: 77.62-80.05. *Males* (n=2): TL: 1.65-1.8; HW: 0.297-0.312; HL: 0.345-0.354; SL: 0.191-0.197; ML: 0.561-0.605; GL: 0.739-0.849; CI: 83.89-94.43; SI: 61.22-66.33

Other material examined: **COSTA RICA:** Guanacaste, Santa Rosa National Park, elev. 300 m, 10° 51' N, 85° 37' W (J. Longino); Puntarenas, Par. Nac. Corcovado, elev. 100 m, 8° 29' N, 83° 36' W (J. Longino); **GUYANA:** Iwokrama Forest Reserve, Whitewater Camp, N 04° 43.890, W 058° 50.992, virgin rainforest JSL #021107-9a-c (J.S. LaPolla); **PANAMA:** Barro Colorado Island; Canal Zone; B41 (W.L. Brown and E.S. McCluskey). In: JTLC, JSLC, MCZC, USNM.

Distribution and natural history: This species has been found primarily in Costa Rica and Panama, but its recent collection in Guyana suggests it has a much larger range than is presently known. *A. panamensis* has been collected from leaf litter samples, in rotten logs and under stones from both wet and dry forests. Current collections have all been from 300 meters or below in elevation. Alates (both males and queens) were collected in January from Panama.

Discussion: *A. panamensis* is easy to recognize with its distinctively large apical antennal segments, short scapes, and enlarged, rectangular, truncated basal teeth. The basal tooth of *A.*

panamensis is not unique among species in the genus. In the New World, *A. tricuspis* possesses a large basal tooth similar to *A. panamensis*, though the former species has 3 distinct cusps on the basal tooth and it is more square in shape than rectangular. Species belonging to the *butteli* species-group all possess enlarged, rectangular, truncated basal teeth similar to *A. panamensis* as well, but they do not appear to be closely related. The closest relative to *A. panamensis* is *A. ayanganna* (see discussion for *A. ayanganna* for further discussion), a species whose basal tooth is of a more "typical" form. What this suggests is that enlarged basal teeth have evolved at least 3 independent times in the genus (see fig. 51). Outside of *Acropyga* I have also observed a similarly shaped basal teeth in an Afrotropical *Pseudolasius* species. Why this tooth structure has evolved multiple times in the genus is unclear, and unfortunately our present knowledge of all *Acropyga* with enlarged basal teeth is very limited.

yaeyamensis species-group

Acropyga yaeyamensis Terayama and Hashimoto

Acropyga (Rhizomyrma) yaeyamensis Terayama and Hashimoto, 1996: 5 (w.). Holotype worker, JAPAN: Urauchi, Iriomote-jima, Yaeyama Is., Okinawa Pref. (M. Terayama) (MNHA) [examined]. Terayama *et al.*, 2002: 26, description and key.

Acropyga (Rhizomyrma) guangxiensis Terayama, Fellowes, and Zhou, 2002: 23 (w.). Holotype worker, CHINA: Guanxi, Huaping (J.R. Fellowes) (ICKH) [not examined]. **NEW SYNONYM.**

Acropyga (Rhizomyrma) yunnanensis Terayama, Fellowes, and Zhou, 2002: 27 (m.). Holotype male, CHINA: Yunnan, Xishuangbanna, Nangong-shan (Z. Xu) (ISYC) [not examined]. **NEW SYNONYM.**

Diagnosis: *Worker:* 10-11 segmented antennae; mandible with 4 teeth; HW: < 0.425 mm. *Queen:* unknown. *Male:* 12 segmented antennae; parameres short, and roughly rectangular, coming to a dorsocaudal point.

Compare with: *A. oceanica*

Description: *Worker.* Head (fig. 30C): yellow; head longer than broad; posterior margin entire to slightly concave medially; covered in a thick layer of appressed hairs; 10-11 segmented, incrassate antennae; scape fails to reach posterior margin by about length of pedicel; clypeus narrow, with scattered erect hairs; mandible with 4 approximately similarly sized teeth; 4th tooth sometimes separated from others by a short diastema; slight gap between inner mandibular margin and anterior clypeal margin. Mesosoma (fig. 30D): yellow; in lateral view, pronotum with short anterior shelf before rising toward mesonotum; with sparse covering of appressed to erect hairs; mesonotum rounded dorsally, with dense layer of appressed hairs to scattered erect hairs; mesonotum often higher than propodeum; metanotal area often distinct; propodeum rounded dorsally, with layer of appressed hairs; declivity steep. Gaster: petiole thick and erect reaching height propodeal spiracle; gaster yellow, covered in thick layer of appressed hairs, with scattered erect hairs throughout.

Queen. Unknown.

Male. Head: brownish-yellow, darker toward apex around 3 prominent ocelli; head longer than broad; covered in a thick layer of appressed hairs; 12 segmented, incrassate antennae; scape fails to reach posterior margin by about half length of the pedicel; clypeus narrow, slightly convex medially, with scattered erect hairs; mandible with 2 teeth, widely separated by a diastema; a slight gap between inner mandibular margin and anterior clypeal margin. Mesosoma: unfortunately the mesosoma of the single known male specimen was too badly distorted to be described properly. Gaster: brownish-yellow; covered in a thick layer of appressed hairs with scattered erect hairs throughout. Genitalia (figs. 46A-D): in lateral view parameres short, roughly rectangular, dorsocaudally coming to a point; cuspi bent toward digiti, with short, peg-like teeth at apices; digiti about as long as cuspi, apically anvil-shaped; digiti with short, peg-like teeth where they meet cuspi; penis valve fig. 46D.

Measurements: *Workers* (n=3): TL: 1.28-1.38; HW: 0.378-0.419; HL: 0.43-0.454; SL: 0.244-0.294; ML: 0.344-0.41; GL: 0.498-0.535; CI: 87.91-92.76; SI: 64.55-71.71.

Other material examined: CHINA: Szechuan, above Chu Lao Tung, Mt. Ormei (W.L. Brown); NEPAL: Godavari (C. Baroni-Urbani). In: MCZC, NHMB.

Distribution and natural history: This species has a wide range from Okinawa Island west to Nepal. It has been found in leaf litter and at fairly high elevations (up to 1380 m), but otherwise nothing is known of its natural history.

Discussion: This species most closely resembles *A. oceanica* in its small size and 4 toothed mandible. It can be easily separated from *A. oceanica* based on a higher antennal segment count (10-11 segments versus 7-8 segments), and by the fact that the torulae of *A. oceanica* are extremely closely set together, whereas *A. yaeyamensis* has torulae positions that are more typical for the genus.

The synonyms, *A. guangxiensis* and *A. yunnanensis*, based on worker morphology are indistinguishable from each other and *A. yaeyamensis*. Terayama *et al.* (2002) discussed differences in mesosomal characters and number of ommatidia to separate the supposed species, but those characters are unreliable. The differences in mesosomal structure, the metanotal area being either distinct or indistinct, could easily be intraspecific variation, as is seen in many other *Acropyga* species. Terayama *et al.* (2002) state differences from 1 ommatidium to 4 ommatidia to separate *A. guangxiensis* and *A. yunnanensis* respectively, but such small differences in ommatidia number to separate species is unreliable since the extent of variation in that character remains unknown. Nonetheless, it is important to note that the male described in this study as *A. yaeyamensis* is geographically distant (Nepal) from the type locality. As males of this species are collected from across its range they should be examined with associated worker specimens to make certain there is not in reality more than one species present in a group of morphologically very similar workers. Although I have not examined the male described for *A. yunnanensis*, the figure provided matches the specimen used in this study for *A. yaeyamensis* very closely. Until males can be associated with workers and used to distinguish separate species I feel it unwarranted at this time to recognize more than one species.

Unplaced Species

Acropyga guianensis Weber

Acropyga (Rhizomyrma) guianensis Weber, 1944: 120 (w.). 3 syntype workers, GUYANA: HMPS, Mazaruni River (N.A. Weber) (MCZC) [examined]. The designated lectotype is a worker on the same point as one of the paralectotypes; the lectotype is the specimen raised up slightly off of the point, and is labeled JSL TYPE # 124. The second paralectotype, on another point, has another *Acropyga* specimen next to it that is clearly not *A. guianensis* (probably *A. smithii*), so it is not a paralectotype of this species.

Diagnosis: *Worker:* 10-11 segmented antennae; head distinctly longer than broad; mandible with 4-5 teeth, a distinct diastema between 3rd and 4th tooth; dorsum of mesosoma rounded in lateral view, with a layer of appressed hairs underneath several prominent erect hairs. *Queen:* as in worker with modifications expected for caste. *Male:* unknown.

Compare with: larger species of the *goeldii* complex, *A. ayanganna*, and *A. decedens*

Description: *Worker:* Head (fig. 31A): brownish-yellow; head distinctly longer than broad; covered in appressed hairs; posterior margin entire to slightly concave; suberect to erect hairs often at posterolateral corners; 10-11 segmented, incassate antennae; scape typically surpasses posterior margin by about the length of the pedicel; clypeus convex medially, surface with numerous long erect hairs; mandible usually with 4 teeth; 4th tooth separated by a short diastema; a smaller tooth can sometimes be found in the diastema region separating the 4th and basal teeth, making the mandible effectively 5-toothed. Mesosoma (fig. 31B): brownish-yellow; in lateral view, pronotum rises steeply toward mesonotum; posteriorly pronotum with many long erect hairs; mesonotum

with many longer erect hairs and thick layer of appressed hairs underneath; propodeum slightly below layer of mesonotum; mesosomal dorsum rounded from posterior portion of pronotum through the propodeum; declivity steep. Gaster: petiole thick and erect; gaster brownish-yellow; covered with a thick layer of appressed hairs, with many scattered erect hairs throughout, giving gaster a spiky appearance, especially toward posterior end.

Queen. As in worker except for modifications expected with caste, and with the following differences: overall much darker than worker, becoming brown dorsally in many specimens; mesonotum flat, with abundant suberect to erect hairs and a dense layer of appressed hairs; scutellum with many erect hairs; propodeum low.

Male. Unknown.

Measurements: *Workers* (n=10): TL: 1.83- 2.4; HW: 0.472- 0.532; HL: 0.508- 0.609; SL: 0.408-0.5; ML: 0.488- 0.682; GL: 0.693- 1.09; CI: 84.24- 95.36; SI: 84.50- 96.08. *Queens* (n=3): TL: 3.48-3.65; HW: 0.631-0.64; HL: 0.696-0.7; SL: 0.612-0.636; ML: 1.07-1.18; GL: 1.87-1.77; CI: 90.29-91.82; SI: 96.84-100.79.

Other material examined: **BOLIVIA:** Caranavi, nr radio, elev. 800 m (Kugler and Lambert); Covendo (W.M. Mann); S. Helena (W.M. Mann); Santa Cruz: Aserradero Moira, 14° 34' S, 61° 12' W (P.S. Ward); Tumpupasa; **BRAZIL:** Mt. Chapada dos Quimaraes; Cachoeira Pedra Furada (J.C. Trager); Utiariti, Mt. Rio Papagio (Lenko and Pereira); **COLOMBIA:** Magdalena, 3 km SE of Minca, elev. 1050 m, 11° 8' N, 74° 6' W (J. Longino); **ECUADOR:** Manabf, 78 km NE of Chone, elev. 450 m (S. and J. Peck); Napo, 20 km S of Tena, elev. 600 m (S. and J. Peck). In: BMNH, LACM, MCZC, MZSP.

Distribution and natural history: This species has a large range, having been collected from northern South America south into Bolivia. It has been collected from leaf litter in rainforest, but otherwise nothing is known of its natural history.

Discussion: At first examination it is possible to confuse the worker of *A. guianensis* with some members of the *goeldii* complex of species. Upon closer inspection, however, it is fairly easy to distinguish this species with its head longer than broad and a distinctive mandibular dentition: 4 teeth with basal tooth separated by a diastema, or 5 teeth with a small tooth in the diastema region. The mesosoma is useful for identification as well, with mesosomal shape and the placement of dorsal hairs being diagnostic (see fig. 31B). Additionally, the clypeus is broad and lacks a dense covering of erect hairs, which are commonly observed many *goeldii* complex species.

The lack of a worker-associated male specimen for this species makes its placement within the genus problematic and it therefore remains unplaced in a species-group. Despite its initial appearance to the contrary, I do not think this species belongs in the *decedens* species-group, for its mandibles, clypeus and mesosomal characters (see above for contrasts) do not suggest placement in that group. The narrow-headed *A. stenotes* is possibly closely related to *A. guianensis* based on similar mesosomal characteristics (see *A. stenotes* discussion section for more details). Once males are discovered for this species a more precise phylogenetic placement will be possible.

Acropyga oceanica Emery

Acropyga (Rhizomyrma) oceanica Emery, 1900: 333 (w.q.m.). 2 syntype workers, PAPUA NEW GUINEA: N.E.: Friedrich-Wilhelmshafen (L. Birö) (MCSN) [examined]. The designated lectotype is a worker labeled JSL TYPE # 128 and is deposited at MCSN. The lectotype is the worker specimen whose head is off of the card; the worker whose head is glued to the card is *A. ambigua*. Though the queen and male were briefly described in the original description they were not part of the collection at MCSN, and were not able to be located in other collections known to contain a large number of Emery type material.

Acropyga (Rhizomyrma) septemstruma Terayama, Fellowes, and Zhou, 2002: 24 (w.). Holotype worker, CHINA: Hong Kong, Northeast New Territories, Sha Lo Tung (J.R. Fellowes) (ICKH) [not examined]. **NEW SYNONYM.**

Diagnosis: *Worker:* 7-8 segmented antennae; small species (TL: 1.16-1.43); 4 distinct teeth on mandible; torulae very closely set together; antennal apical segment long, about as long as preceding 4 segments combined. *Queen:* unknown. *Male:* unknown.

Compare with: *A. yaeyamensis*.

Description: *Worker.* Head (fig. 31C): yellow; head longer than broad; posterior margin entire; 7-8 segmented, incrassate antennae; apical antennal segment about as long as preceding 4 segments combined; scape fails to reach posterior margin by about length of pedicel; torulae very closely set together, so that little space exists between them; clypeus narrow, slightly convex medially, with erect hairs on surface; mandible narrow with 4 distinct, nearly even teeth; dorsal surface of mandibles with dense cluster of hairs near masticatory margin (only easily seen with SEM examination); gap exists between inner mandibular margin and anterior clypeal margin. Mesosoma (fig. 31D): yellow; in lateral view pronotum with short anterior shelf; pronotum rises steeply toward mesonotum; pronotum without hairs except for a few erect hairs posteriorly; mesosomal dorsum flat; mesonotum with a dense layer of appressed to erect hairs; propodeum with erect hairs; declivity steep. Gaster: petiole thick and erect; gaster yellow, covered in a thick layer of appressed hairs, with scattered erect hairs throughout.

Queen. Unknown, but see below.

Male. Unknown, but see below.

Measurements: *Workers* (n=5): TL: 1.16-1.43; HW: 0.329-0.351; HL: 0.345-0.396; SL: 0.22-0.264; ML: 0.34-0.415; GL: 0.437-0.653; CI: 87.83-95.36; SI: 66.87-79.52.

Other material examined: **INDONESIA:** Sulawesi, Dumoge-Bone National Park (D.H. Kistner & D. F. Roche); **MALAYSIA:** Borneo, Sabah, Tawau Hills National Park (S. Yamane); **PAPUA NEW GUINEA:** N. Dist., Popondetia (P.M. Room); Gulf Prov., Ivimka Camp, Lakekamu Basin, 07.73 N, 146.76 E, elev. 120 m (R.R. Snelling); **SINGAPORE:** Bukit Timah National Reserve, degraded coastal hill forest on granite (D.H. Murphy). In: ANIC, LACM, SYPC.

Distribution and natural history: This species ranges throughout the Indo-Australian region, reaching as far north as southern China. It has been recorded from leaf litter, and been collected in bamboo forest from a pitfall trap. An *Eumyrmoccus* sp. mealybug was recorded with this species by Williams (1998), but the record must be considered questionable given the difficulty in the past in identifying this *Acropyga* species.

Discussion: This is the smallest known *Acropyga* and the antennal segment count is the lowest of any known Old World species. Its torulae are also extremely closely set together with virtually no space between them. It can relatively easily be separated from other small *Acropyga* species by its low antennal segment count (7-8) and the presence of 4 distinct teeth on the mandible. Morphologically the worker of this species resembles *A. smithii* of the New World. Both of those species have as few as 7 antennal segments, 4 distinct mandibular teeth and similar mesosomal structures. This similarity however is probably the result of convergence.

The lack of worker-associated males for this species is frustrating since Old World males have not been recorded with antennal segment counts below 12 segments. With the worker of this species only possessing up to 8 segments, males would be expected with as few as 9 antennal segments. This could be phylogenetically very interesting, but will have to await future discovery of the males.

Emery recorded the worker as having up to 9 segments, but that is erroneous, because one of the specimens he determined as this species was in actuality an *A. ambigua* specimen with 9 segments. Nine segmented antennae have not been recorded in the worker of this species.

Acropyga palearctica Menozzi

Acropyga palearctica Menozzi, 1936: 298 (w.). 4 syntype workers, GREECE: T. Mili; Scarpauto (C. Menozzi) (IEGG) [examined]. The designated lectotype is a worker labeled JSL # 126 and is deposited at IEGG.

Diagnosis: *Worker:* Antennae 11 segmented; 6-8 uneven mandibular teeth; basal tooth offset from masticatory margin. *Queen:* As in worker with modifications expected for caste. *Male:* unknown.

Compare with: *A. arnoldi* and *A. silvestrii*.

Description: *Worker:* Head (fig. 32A): yellow; covered by a layer of short appressed hairs; head distinctly longer than broad; posterior margin entire; 11 segmented, incrassate antennae; apical segment about as long as preceding four segments; scape reaches posterior margin to slightly failing to reach posterior margin; clypeus medially convex, with longer erect hairs on surface; mandible with 6-8 uneven teeth; basal tooth typically offset from masticatory margin; inner mandibular margin nearly parallel with anterior clypeal margin. Mesosoma (fig. 32B): yellow; entire mesosoma covered in layer of short appressed hairs; in lateral view, pronotum rounded broadly toward mesonotum; mesonotum flat, at about same level as propodeum; metanotal area often distinct; propodeum dorsum flat; declivity steep. Gaster: yellow; covered in a layer of short appressed hairs, with scattered, longer erect hairs throughout.

Queen. As in worker with modifications expected for caste.

Male. Unknown, but see below.

Measurements: Workers (n=4): TL: - ; HW: 0.462-0.496; HL: 0.549-0.574; SL: 0.441-0.556; ML: 0.47-0.532; GL: - ; CI: 81.18-87.48; SI: 88.91-119.31. Queen (n=1): TL: 2.77; HW: 0.577; HL: 0.591; SL: 0.515; ML: 0.952; GL: 1.23; CI: 97.63; SI: 89.25.

Other material examined: GREECE: Perachora. In: ABPC.

Distribution and natural history: This species is the only *Acropyga* known to occur in the Mediterranean area. It also has one of the most northerly distributions of any *Acropyga* species. It has been found in pine forests. This species has been observed in mating swarms in the afternoon, though actual mating was observed by Buschinger *et al.* (1987) to take place on the tops of rocks, on which both queens and males crawled. Queens were observed to crawl into the soil after dealation. It is a known trophophoretic species associated with *E. corinthiacus*.

Discussion: This species in many ways resembles *A. arnoldi*, with a high number of mandibular teeth, high number of maxillary palpal segments (up to 5) and a similarly shaped pronotum. The known distributions of the two species are quite different: *A. arnoldi* is known only from southern Africa. Additionally, *A. arnoldi* is larger species with head width greater than 0.55 mm, while *A. palearctica* is known from specimens with head widths less than 0.5 m. *A. silvestrii* is smaller than *A. palearctica* with regards to head width, possesses torulae that are much more closely set together (compare figs. 32B and 32C).

Unfortunately, I could not locate males for this study despite the fact that they have been collected in the past (Buschinger *et al.*, 1987), and they therefore remain undescribed. Without males I have chosen not to place *A. palearctica* in a species-group. With a high number of mandibular teeth (up to 8) and a 5-segmented maxillary palp, I suspect that *A. palearctica* is a primitive species within the genus, perhaps even being closely related *A. arnoldi*. It is interesting to note that the mealybugs utilized by *A. palearctica* and *A. arnoldi* are thought to be closely related to each other (Williams, 1998; see under *A. arnoldi* for more details).

Acropyga silvestrii Emery

Acropyga silvestrii Emery, 1915: 21. 5 syntype workers, ERITREA: Ghinda (MNHG) [1 worker examined]. The designated lectotype is a worker labeled JSL TYPE # 125 and is deposited at MHNG. Emery, 1922: 109, combination in subgenus *Malacomyrma*.

Diagnosis: *Worker:* Antennae 11-10 segmented; head distinctly longer than broad; head width not greater than 0.5 mm; in lateral view pronotum with short shelf; mesosomal dorsum flat, with appressed hairs. *Queen:* unknown. *Male:* unknown.

Compare with: *A. arnoldi* and *A. palearctica*

Description: *Worker.* Head (fig. 32C): yellow to slightly brownish yellow; covered in dense layer of appressed hairs; head distinctly longer than broad; posterior margin entire; 11-10 segmented, incrassate antennae; apical segment about as long as proceeding 3 segments; scape fails to

reach posterior margin by about length of pedicel; clypeus medially slightly convex, with several erect hairs; mandible with 4-7 uneven teeth; inner mandibular margin nearly parallel with anterior clypeal margin. Mesosoma (fig. 32D): yellow; pronotum in lateral with a short shelf, then rising steeply toward mesonotum; mesonotum flat, covered in layer of appressed to suberect hairs; metanotal area often distinct; propodeum at about same height as mesonotum, rounded toward a steep declivity. Gaster: petiole thick and erect, rounded at apex; gaster yellow; covered in a thick layer of appressed hairs, with suberect to erect hairs scattered throughout.

Queen. Unknown.

Male. Unknown.

Measurements: *Worker* (n=10): TL: 1.16-2.15; HW: 0.383-0.454; HL: 0.429-0.506; SL: 0.297-0.349; ML: 0.425-0.567; GL: 0.64-1.16; CI: 84.0-95.18; SI: 72.12-82.2.

Other material examined: CAMEROON: Mbalmayo (N. Stork); Ottotome (A. Dejean); GHANA: Ashanti; Effiduase (R. Belshaw); Eastern Bunso near Tafo; RWANDA: Rangiro (P. Werner); TANZANIA: Mkomazi Game Reserve; Maji Kununua; elevation 1600 m; 3° 53' S, 37° 49' E (H.G. Robertson); TOGO: Paliume; Kpime Forest. In: BMNH, SAMC.

Distribution and natural history: The distribution of *A. silvestrii* stretches from western Africa as far south and east as northern Tanzania. Interestingly, even though the species is found in savanna type habitat in many places across its range, *A. silvestrii* apparently does not overlap with *A. arnoldi*, which is found exclusively in southern Africa. The species is found in a variety of habitats from tropical savannas to rainforests; it has also been collected from cacao plantations. It has been recorded from elevations up to 1600 m.

Discussion: This species can be easily separated from *A. arnoldi* by its size (*A. silvestrii* TL: 1.6-2.1; HW: 0.383-0.454 versus *A. arnoldi* TL: 2.1-2.4; HW: 0.517-0.619). Differentiation from *A. paleartica* can be slightly more difficult, though the torulae of *A. silvestrii* are very closely set together (almost touching medially) and their mandibles do not have offset basal teeth.

The relationship of this species to *A. arnoldi* is unclear since males remain unknown. *A. silvestrii* is observed with up to 7 teeth, but has not been observed with at least a 4-segmented maxillary palp as in *A. arnoldi* and *A. paleartica*. This is the only *Acropyga* known from the rainforests of Africa, which is interesting because in other areas where rainforests are found the diversity of *Acropyga* is substantially higher. The low species diversity found in Africa may be an artifact of collecting since there are few collections from Africa (particularly West Africa) available for study, or may indicate something of biological interest.

Acropyga stenotes, NEW SPECIES

Holotype worker, GUYANA: Camp on Potaro River at base of Mt. Ayanganna, N 05° 18.08, W 059° 54.67, elev. 695 m +/- 13 m, *Dicymbe* forest (J.S. LaPolla et al.) (UGBC); 9 paratype workers (MCZC) (USNM). The holotype is labeled JSL # 107.

Diagnosis: *Worker*: 11 segmented antennae; head distinctly longer than broad, with head especially narrow-headed; mesosomal dorsum rounded in lateral view; mandible with 4 distinct teeth. *Queen*: unknown. *Male*: unknown.

Compare with: *A. smithii*

Description: *Worker*. Head (fig. 33A): yellow; head covered in a layer of short appressed hairs; head distinctly longer than broad, especially narrow-headed in full frontal view; posterior margin entire; posterolateral corners rounded; 11 segmented, incassate antennae; scape fails to reach posterior margin by about length of first 2 funicular segments; clypeus narrow, slightly convex medially; clypeus with scattered erect hairs, longest ones along anterior clypeal margin; mandible narrow, with 4 distinct approximately similarly sized teeth; gap exists between anterior clypeal margin and inner mandibular margin. Mesosoma (fig. 33B): yellow; in lateral view, pronotum with short shelf before rising sharply toward mesonotum; posteriorly pronotum with appressed to

short erect hairs; mesosomal dorsum gently rounded from posterior pronotum through declivity; mesonotum flat with layer of appressed hairs; metanotal area indistinct; propodeum flat, slightly lower than mesonotum; declivity steep. Gaster: petiole thick and erect, reaching height of anterior portion of propodeal spiracle; gaster yellow; covered in a thick layer of appressed hairs, with scattered erect hairs throughout.

Queen. Unknown.

Male. Unknown.

Etymology: The specific epithet *stenotes* is Greek for narrowness, in reference to the narrow head of this species.

Measurements: *Workers* (n=2): TL: 1.53; HW: 0.353-0.363; HL: 0.422-0.459; SL: 0.293-0.31; ML: 0.414-0.436; GL: 0.635; CI: 76.91-86.02; SI: 80.72-87.82.

Distribution and natural history: This species is known only from its type locality at the base of Mt. Ayanganna in western Guyana. It was collected from leaf litter samples in *Dicymbe* dominated forest along with *A. romeo*, but otherwise nothing is known of its natural history.

Discussion: This species is fairly easy to recognize with its small size and distinctly narrow head. Its small size may initially make it difficult to distinguish from *A. smithii*, but *A. smithii* possesses no more than 8 antennal segments, versus *A. stenotes* which has 11 segments. *A. stenotes* was among 3 new species of *Acropyga* discovered on an ant bioinventory of Mt. Ayanganna in western Guyana in the autumn of 2002. The rounded aspect of the mesosomal dorsum and long head suggests that this species is related to *A. guianensis*. However, males of neither *A. stenotes* or *A. guianensis* are known, and therefore their relationship to each other remains unclear. Given the uncertain relationship of this species to other members of the genus it is unplaced in a species-group pending discovery of worker-associated males.

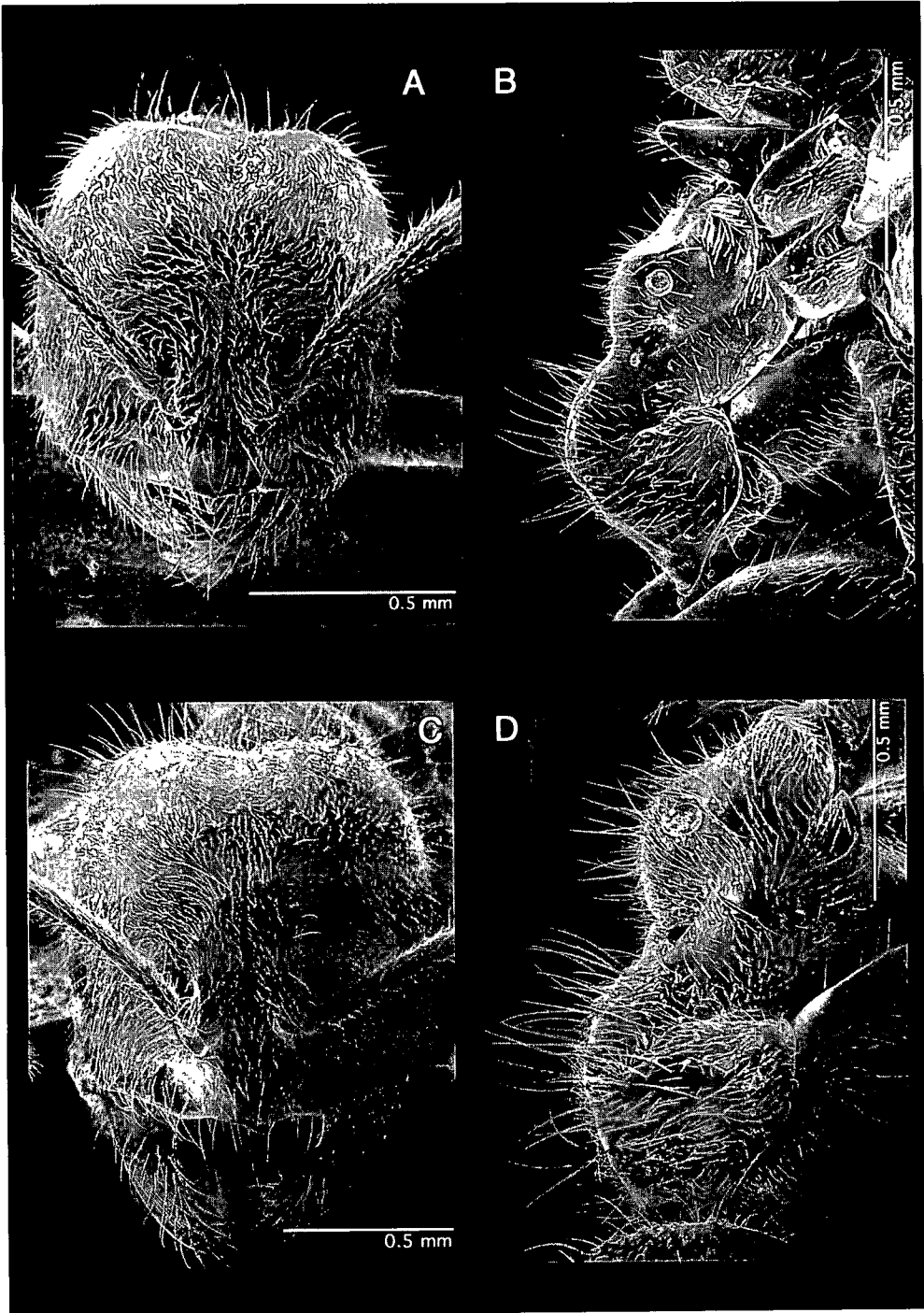


Figure 15. *A. acutiventris* worker: A) head in full frontal view; B) mesosoma in lateral view. *A. rubescens* worker: C) head in full frontal view; D) mesosoma in lateral view.

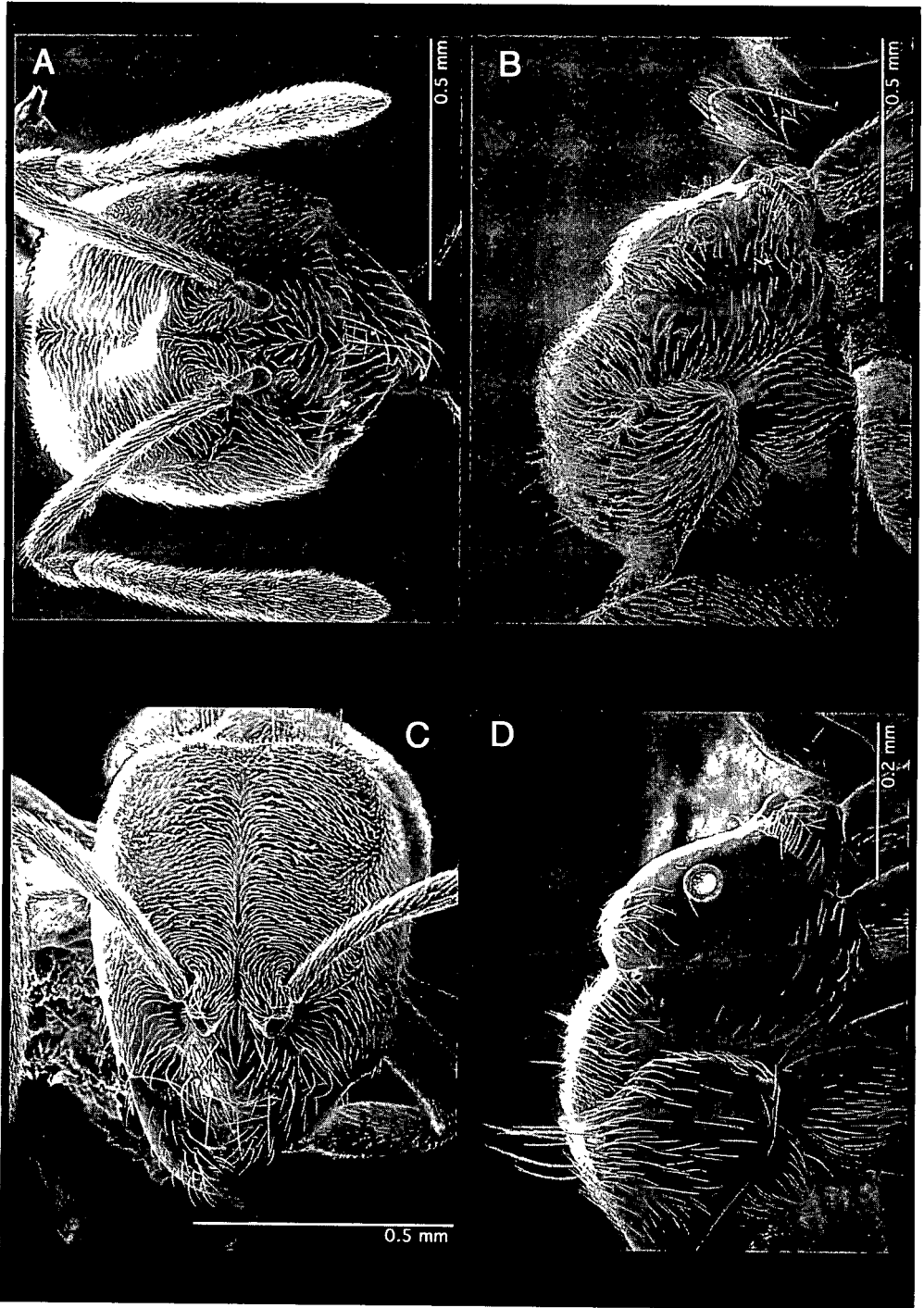


Figure 16. *A. arnoldi* worker: A) head in full frontal view; B) mesosoma in lateral view. *A. butteli* worker: C) head in full frontal view; D) mesosoma in lateral view.

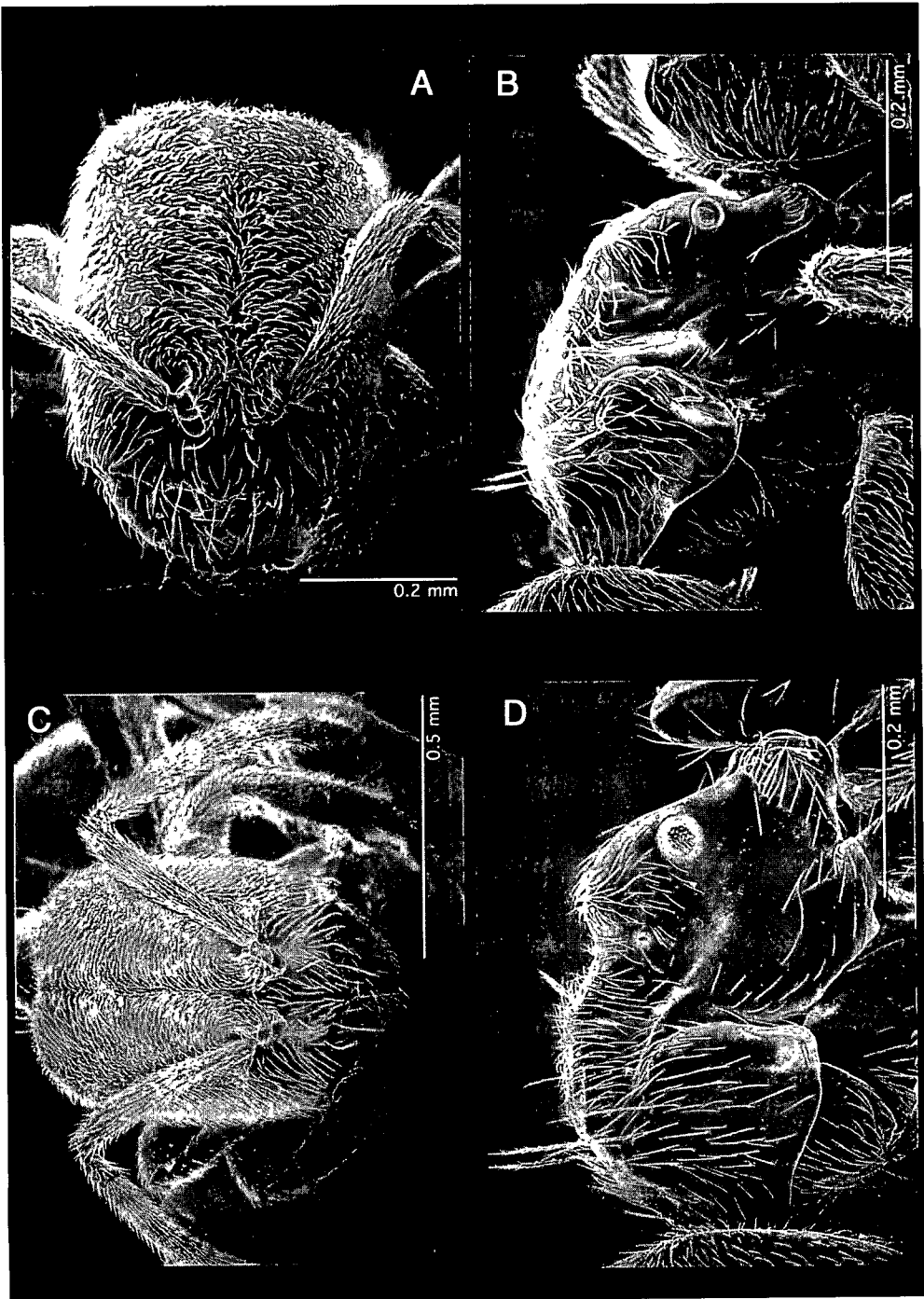


Figure 17. *A. inezae* worker: A) head in full frontal view; B) mesosoma in lateral view. *A. nipponensis* worker: C) head in full frontal view; D) mesosoma in lateral view.

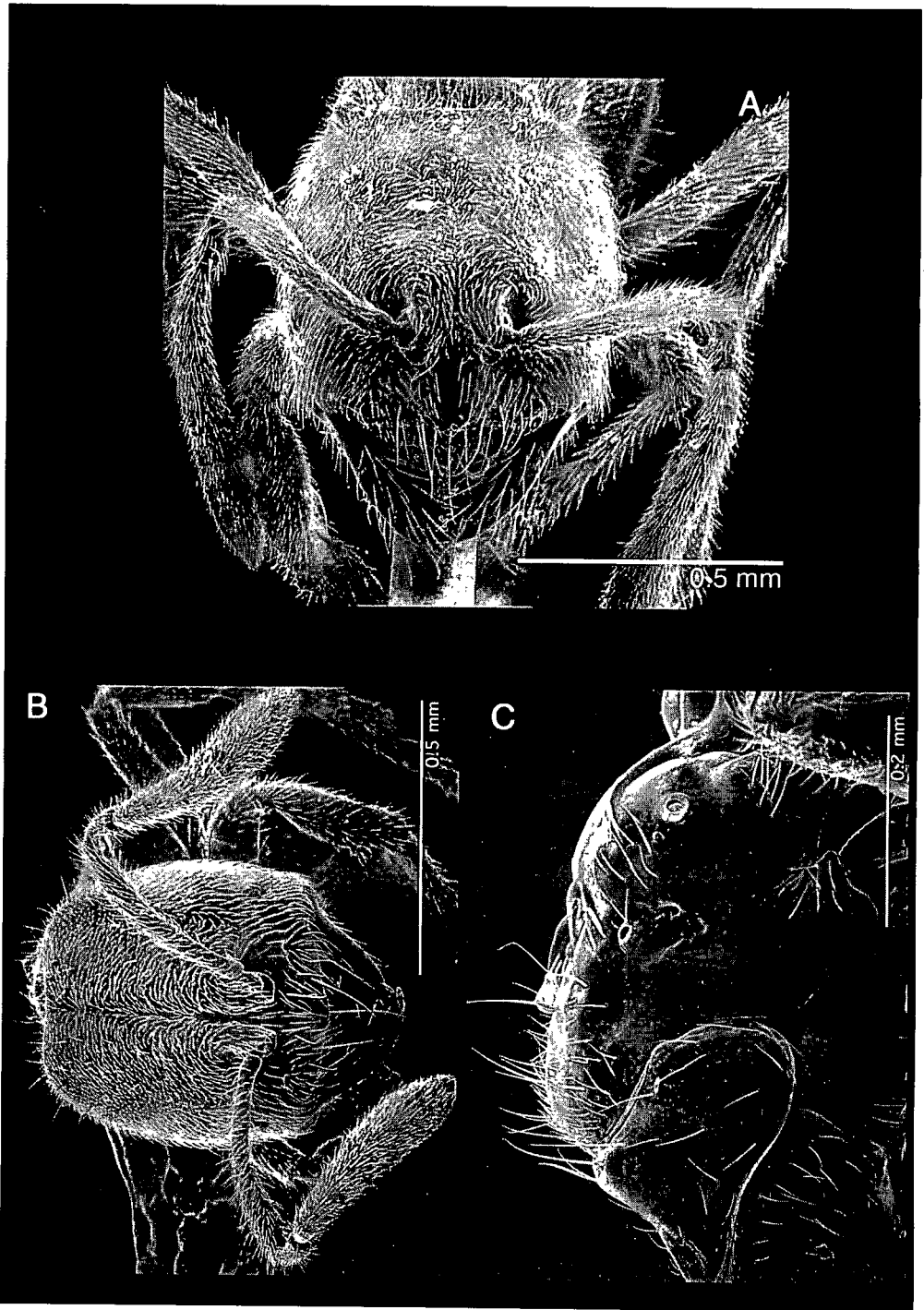


Figure 18. *A. decedens* worker: A) head in full frontal view. *A. fuhrmanni* worker: B) head in full frontal view; C) mesosoma in lateral view.

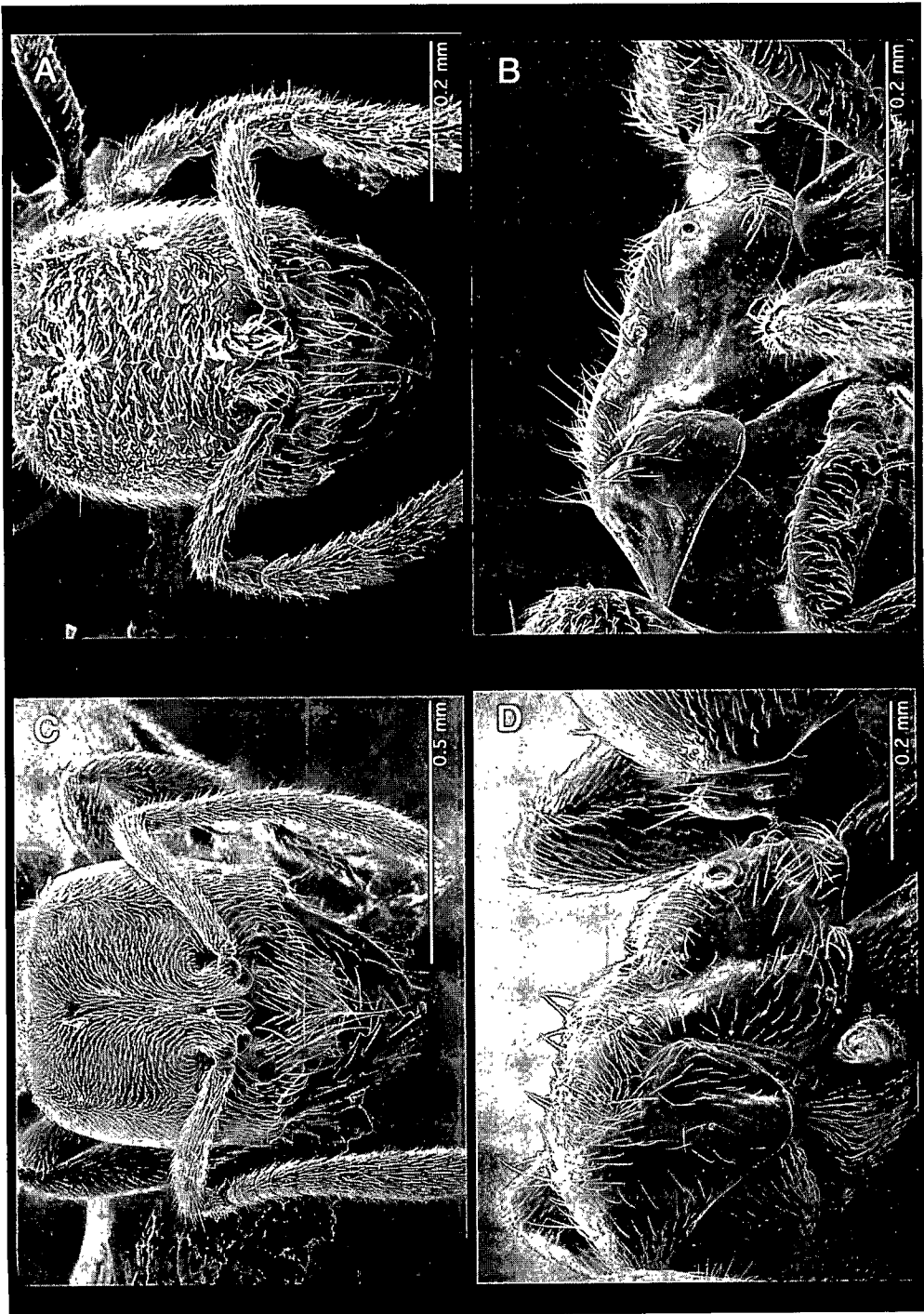


Figure 19. *A. smithii* worker: A) head in full frontal view; B) mesosoma in lateral view. *A. epedana* worker: C) head in full frontal view; D) mesosoma in lateral view.

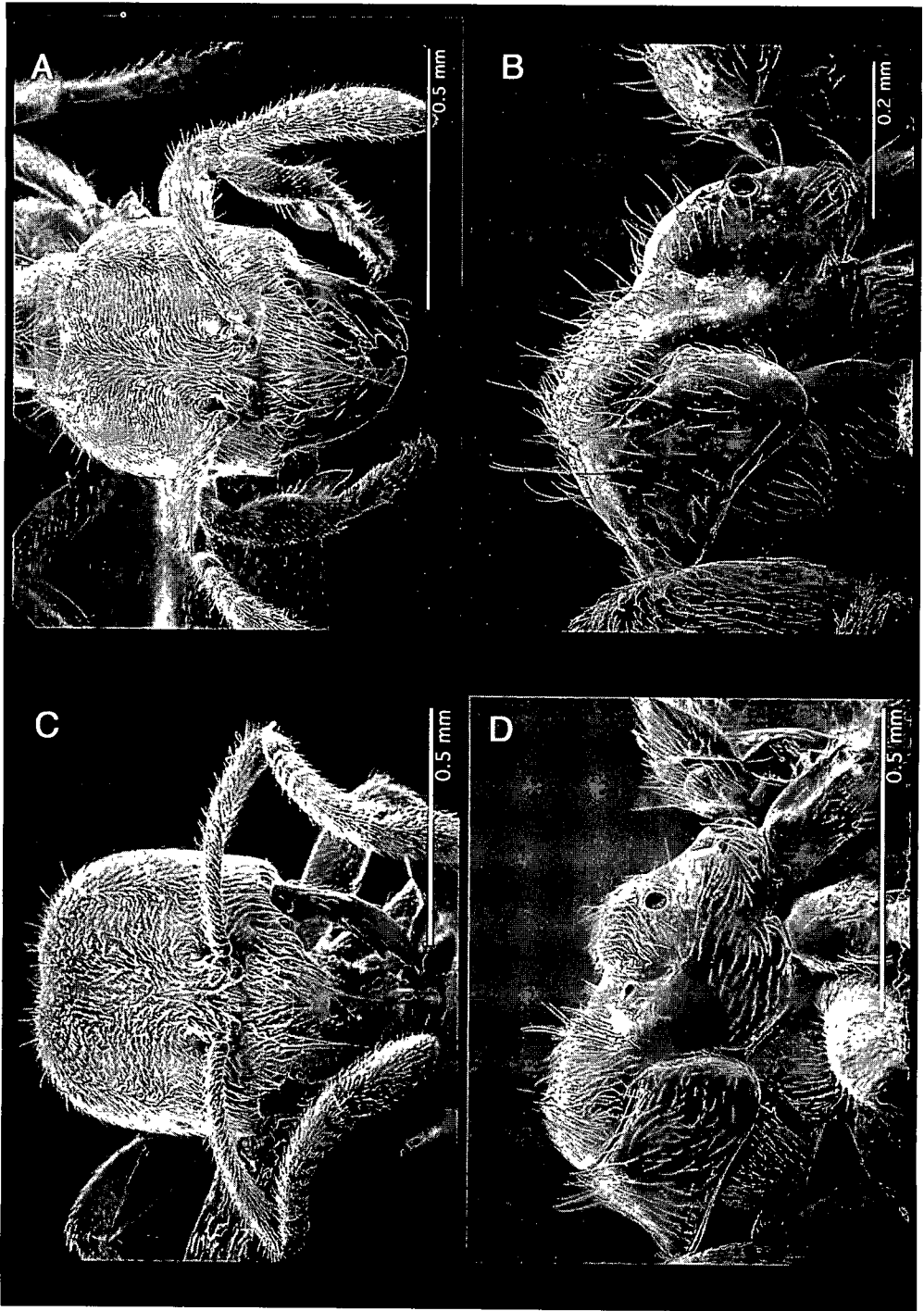


Figure 20. *A. exsanguis* worker: A) head in full frontal view; B) mesosoma in lateral view. *A. goeldii* worker: C) head in full frontal view; D) mesosoma in lateral view.



Figure 21. *A. hirsutula* worker: A) head in full frontal view; B) mesosoma in lateral view.

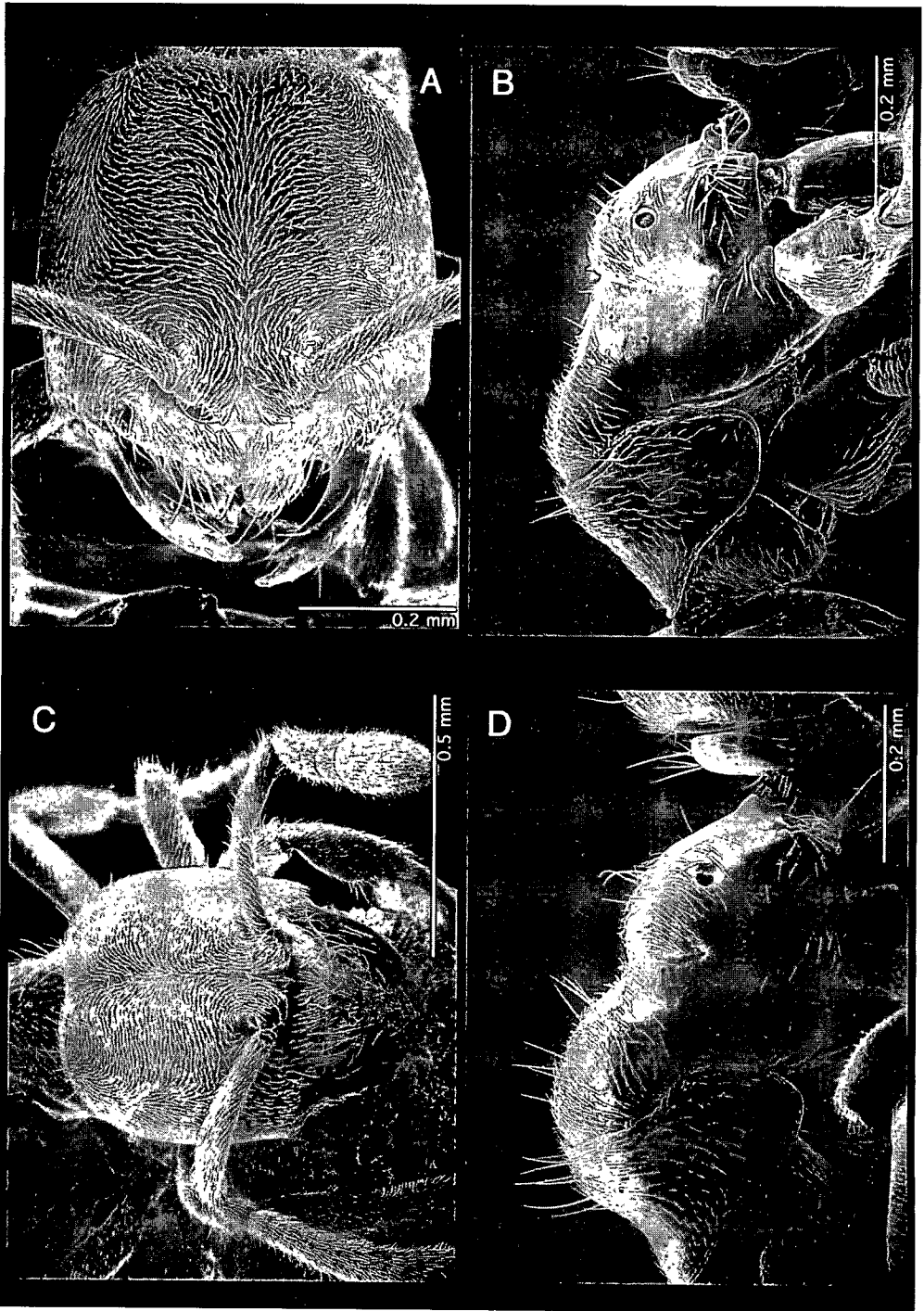


Figure 22. *A. keira* worker: A) head in full frontal view; B) mesosoma in lateral view. *A. palaga* worker: C) head in full frontal view; D) mesosoma in lateral view.

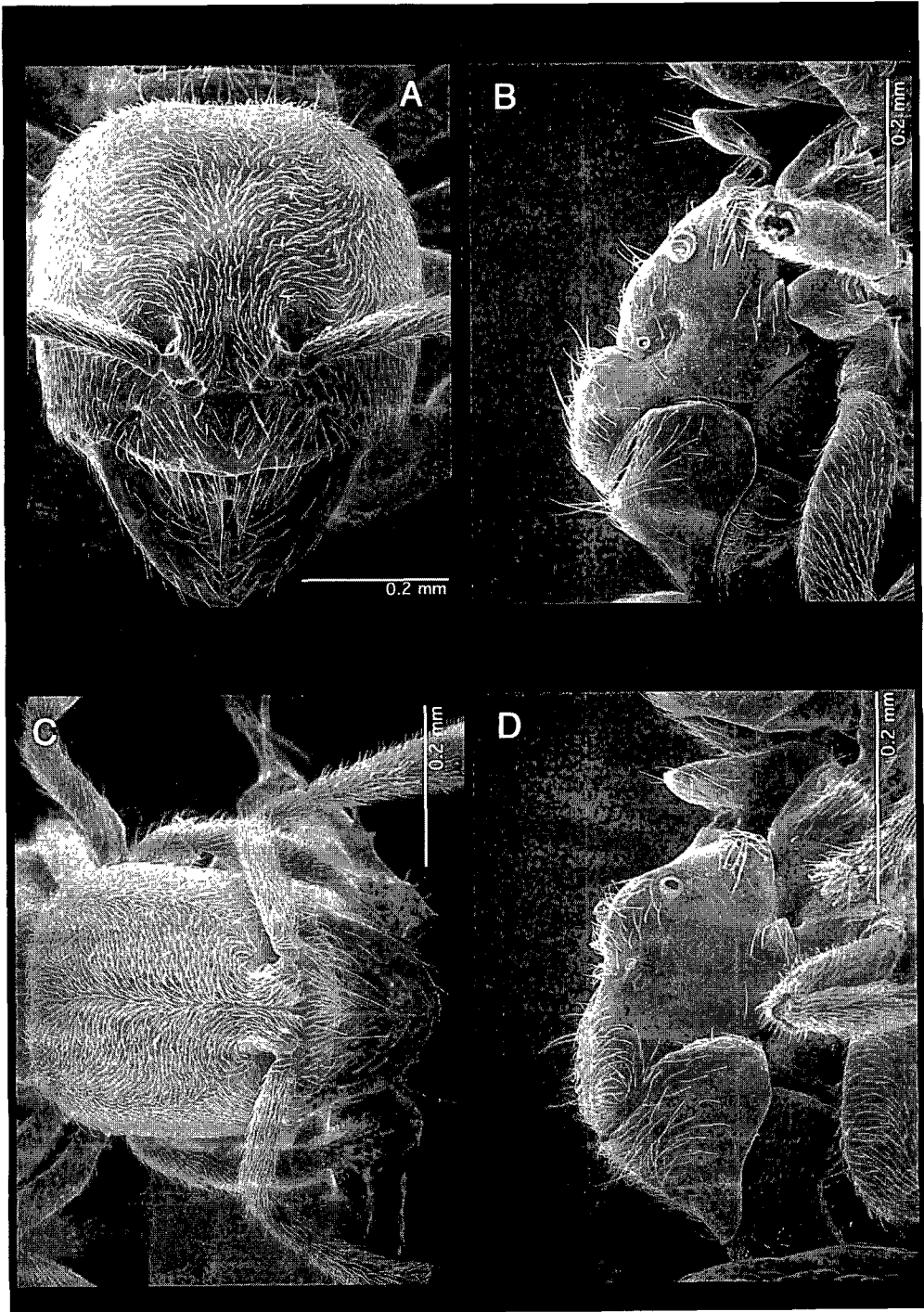


Figure 23. *A. parvidens* worker: A) head in full frontal view; B) mesosoma in lateral view. *A. romeo* worker: C) head in full frontal view; D) mesosoma in lateral view.

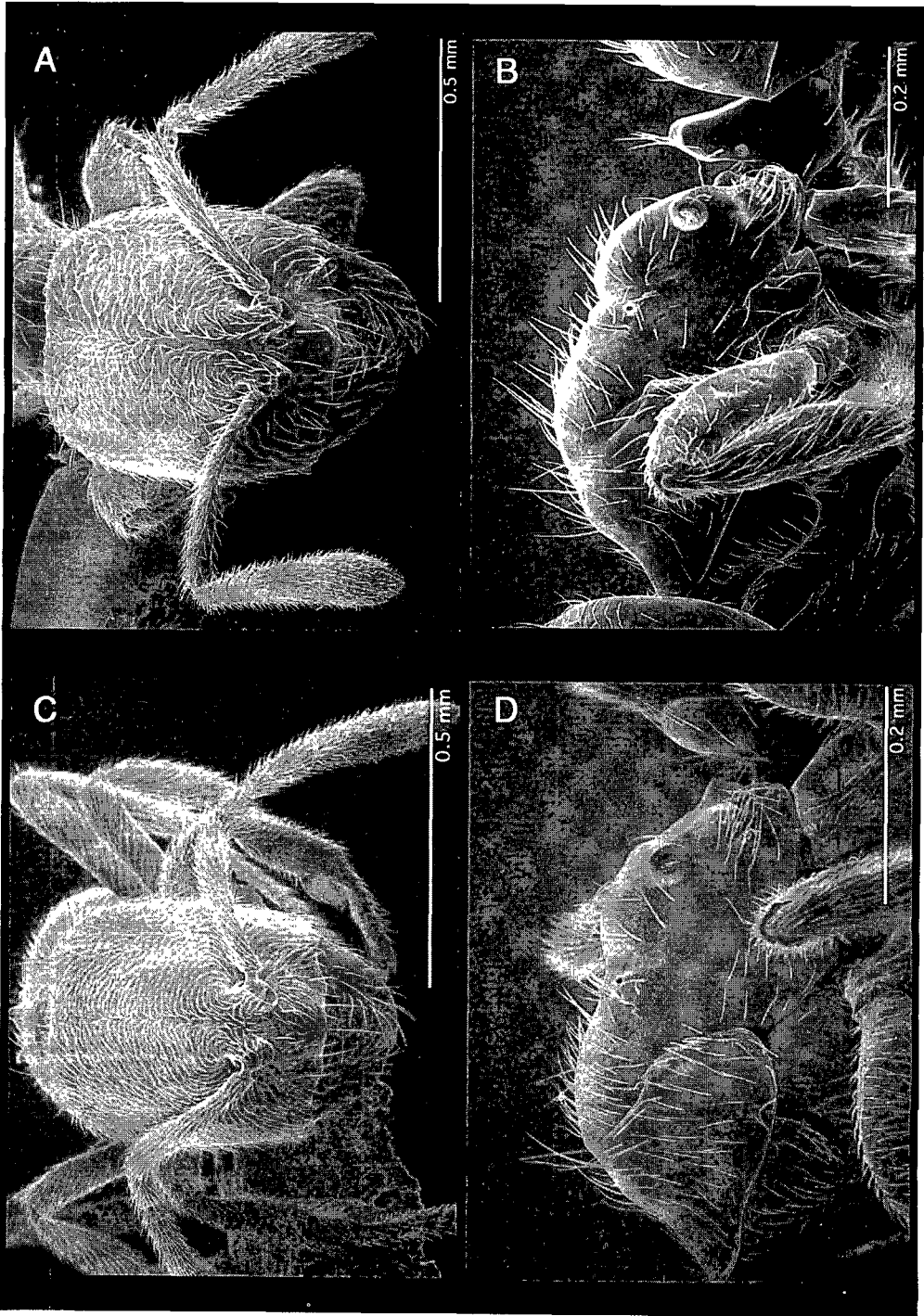


Figure 24. *A. donisthorpei* worker: A) head in full frontal view; B) mesosoma in lateral view. *A. tricuspis* worker: C) head in full frontal view; D) mesosoma in lateral view.

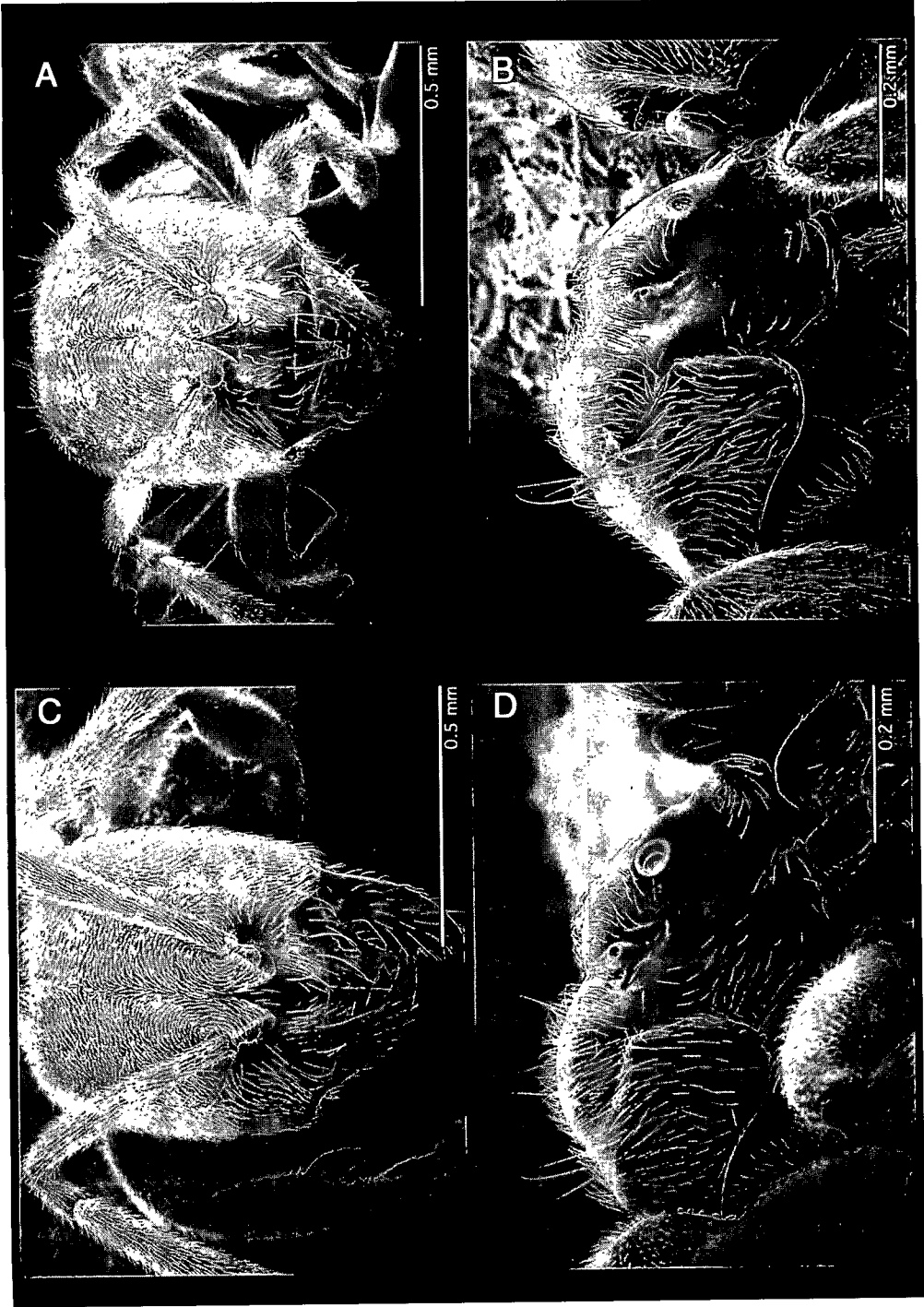


Figure 25. *A. ambigua* worker: A) head in full frontal view; B) mesosoma in lateral view. *A. dubia* worker: C) head in full frontal view; D) mesosoma in lateral view.

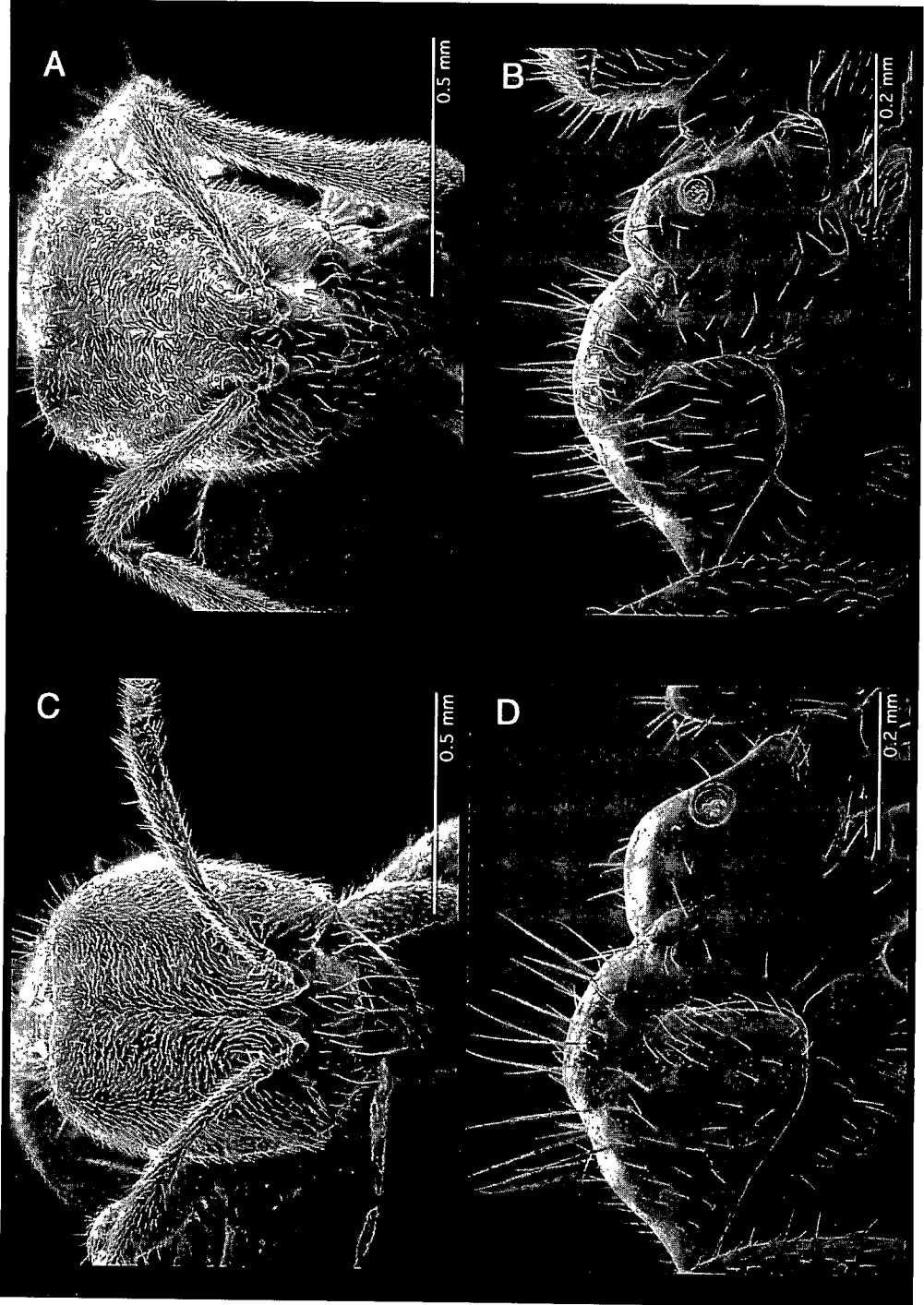


Figure 26. *A. gelasis* worker: A) head in full frontal view; B) mesosoma in lateral view. *A. hystrix* worker: C) head in full frontal view; D) mesosoma in lateral view.

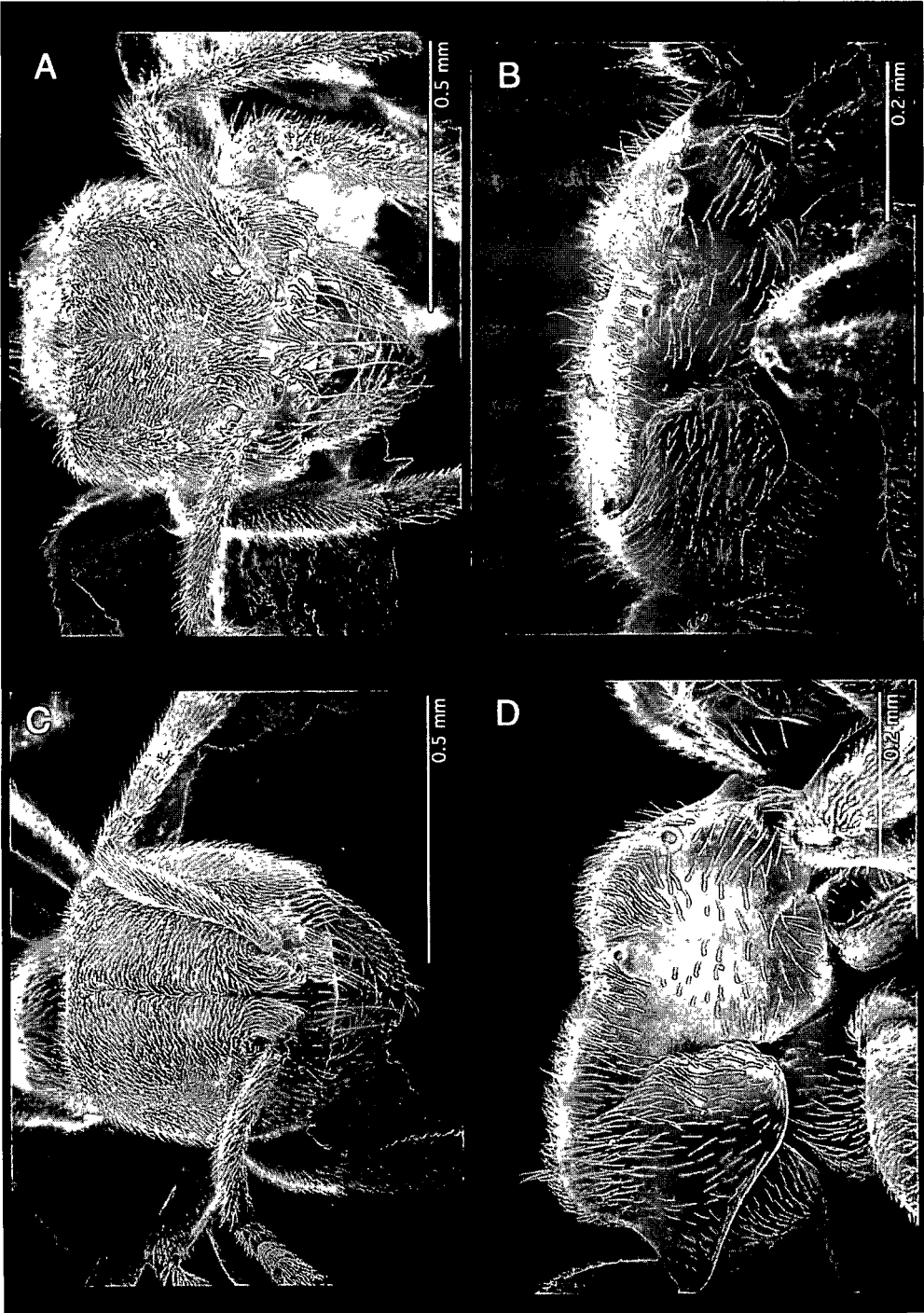


Figure 27. *A. kinomurai* worker: A) head in full frontal view; B) mesosoma in lateral view. *A. lauta* worker: C) head in full frontal view; D) mesosoma in lateral view.

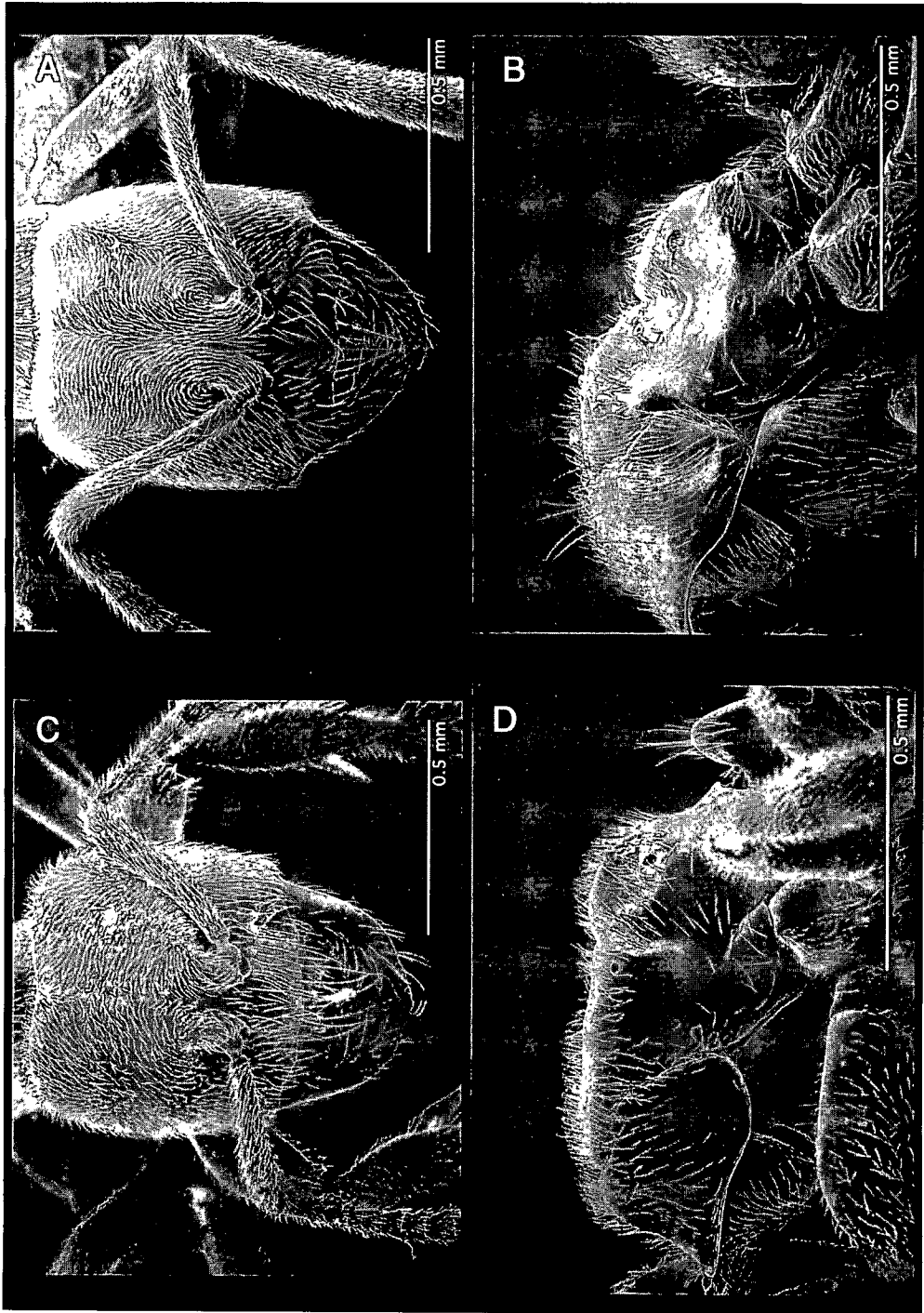


Figure 28. *A. myops* worker: A) head in full frontal view; B) mesosoma in lateral view. *A. sauteri* worker: C) head in full frontal view; D) mesosoma in lateral view.

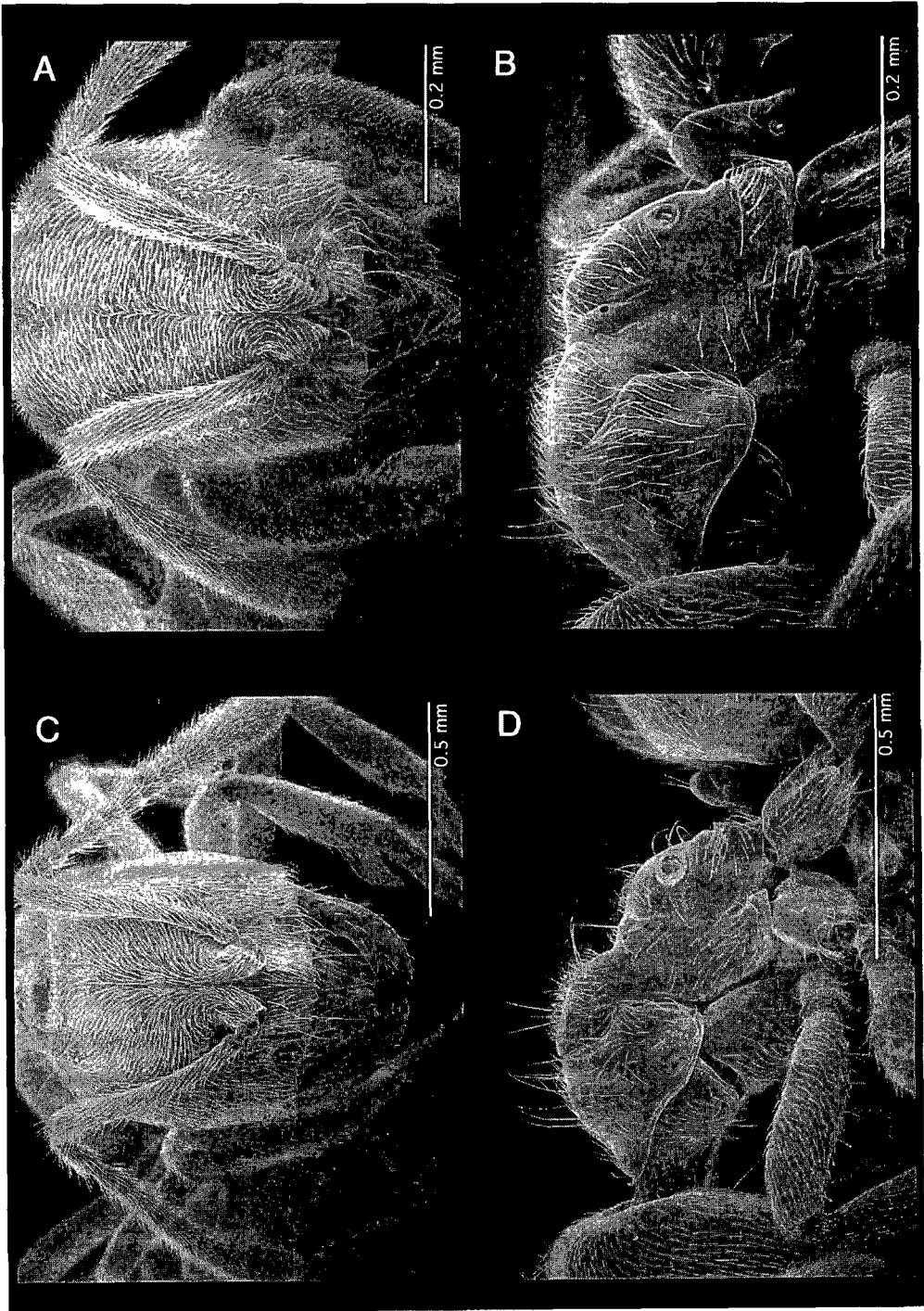


Figure 29. *A. pallida* worker: A) head in full frontal view; B) mesosoma in lateral view. *A. ayanganna* worker: C) head in full frontal view; D) mesosoma in lateral view.

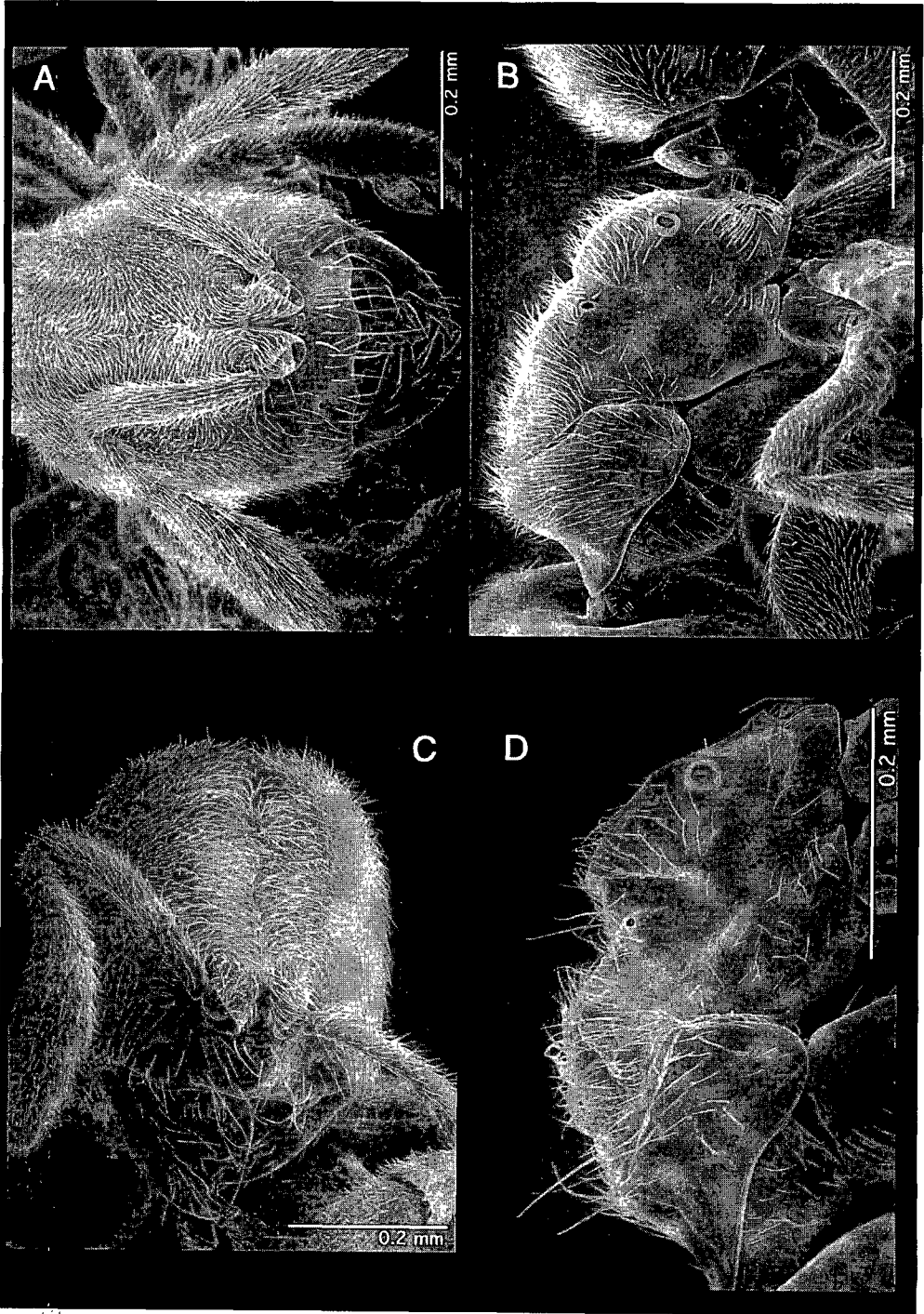


Figure 30. *A. panamensis* worker: A) head in full frontal view; B) mesosoma in lateral view. *A. yaeyamensis* worker: C) head in full frontal view; D) mesosoma in lateral view.

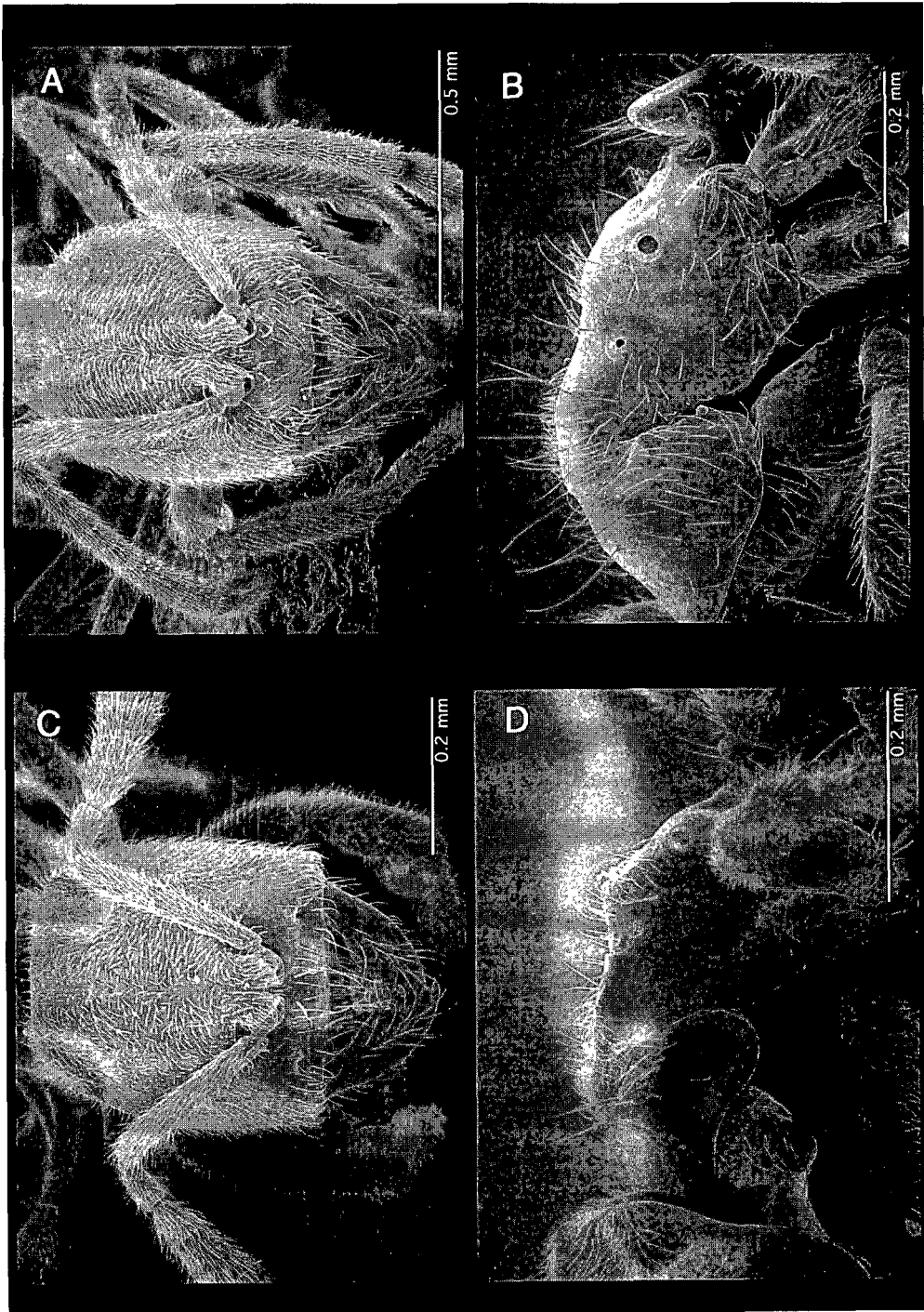


Figure 31. *A. guianensis* worker: A) head in full frontal view; B) mesosoma in lateral view. *A. oceanica* worker: C) head in full frontal view; D) mesosoma in lateral view.

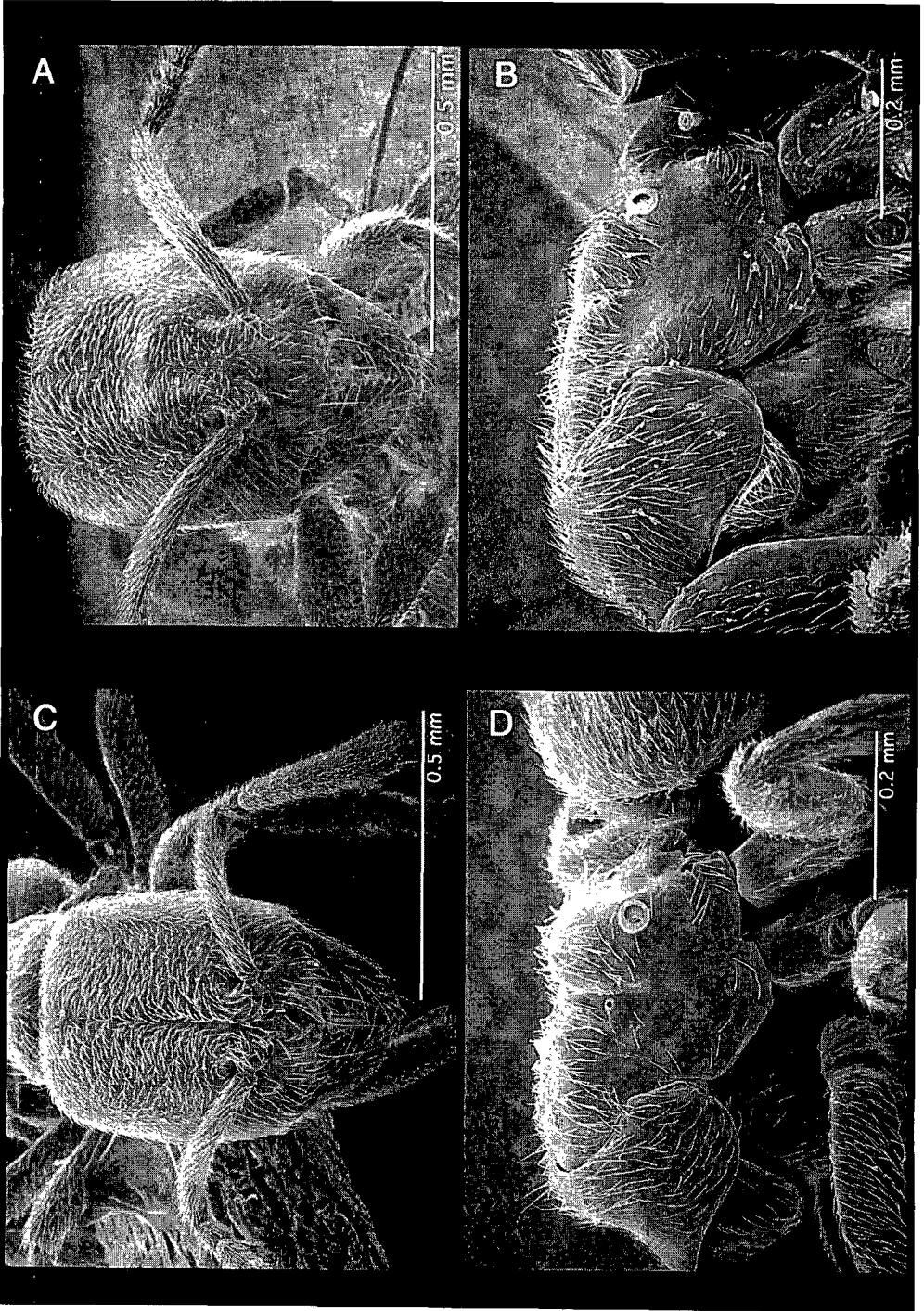


Figure 32. *A. paleartica* worker: A) head in full frontal view; B) mesosoma in lateral view. *A. silvestrii* worker: C) head in full frontal view; D) mesosoma in lateral view.

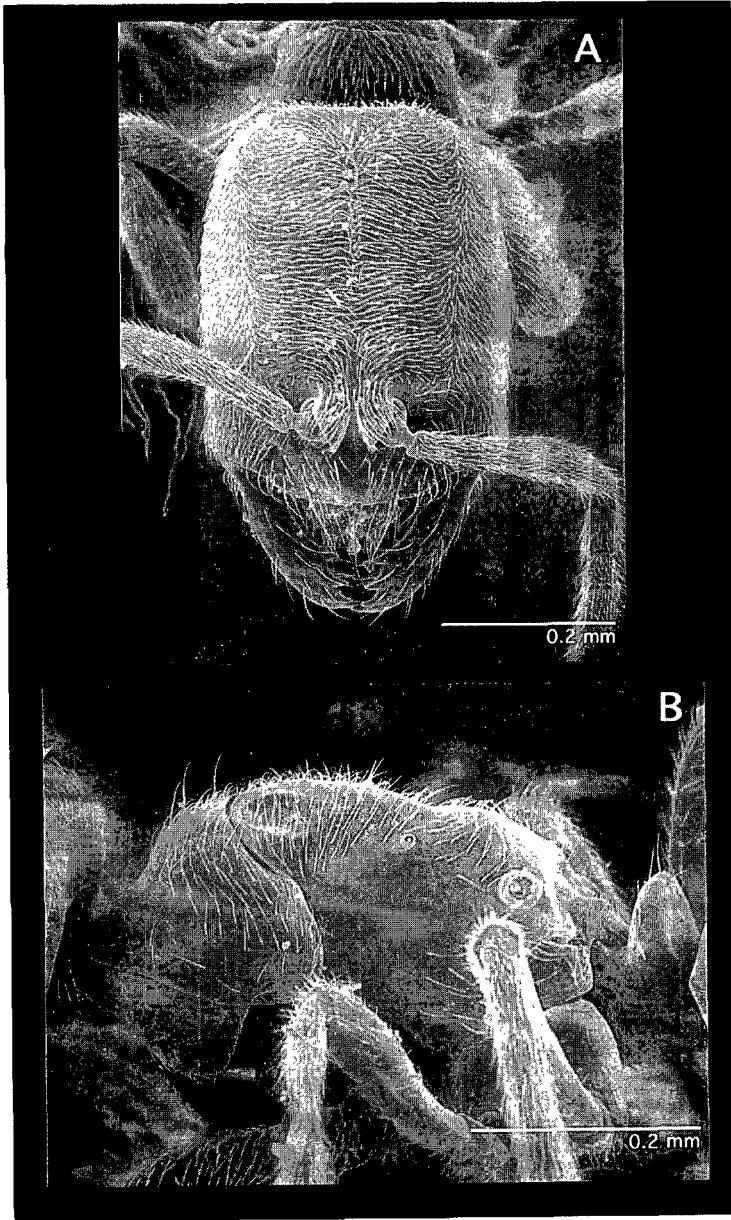


Figure 33. *A. stenotes* worker: A) head in full frontal view; B) mesosoma in lateral view.

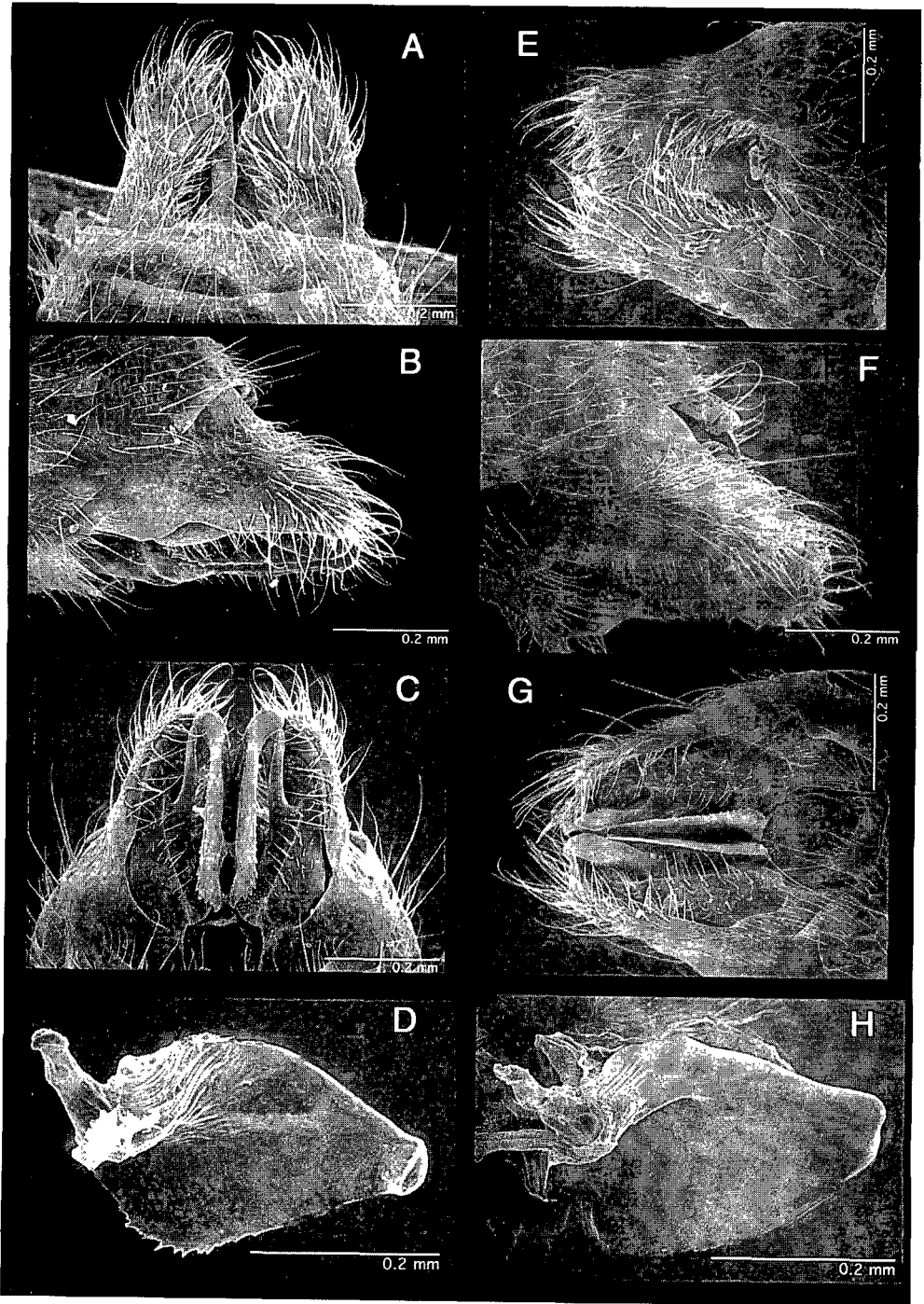


Figure 34. *A. acutiventris* genitalia (A-D). A) dorsal view; B) lateral view; C) ventral view; D) penis valve. *A. rubescens* genitalia (E-H). E) dorsal view; F) lateral view; G) ventral view; H) penis valve.

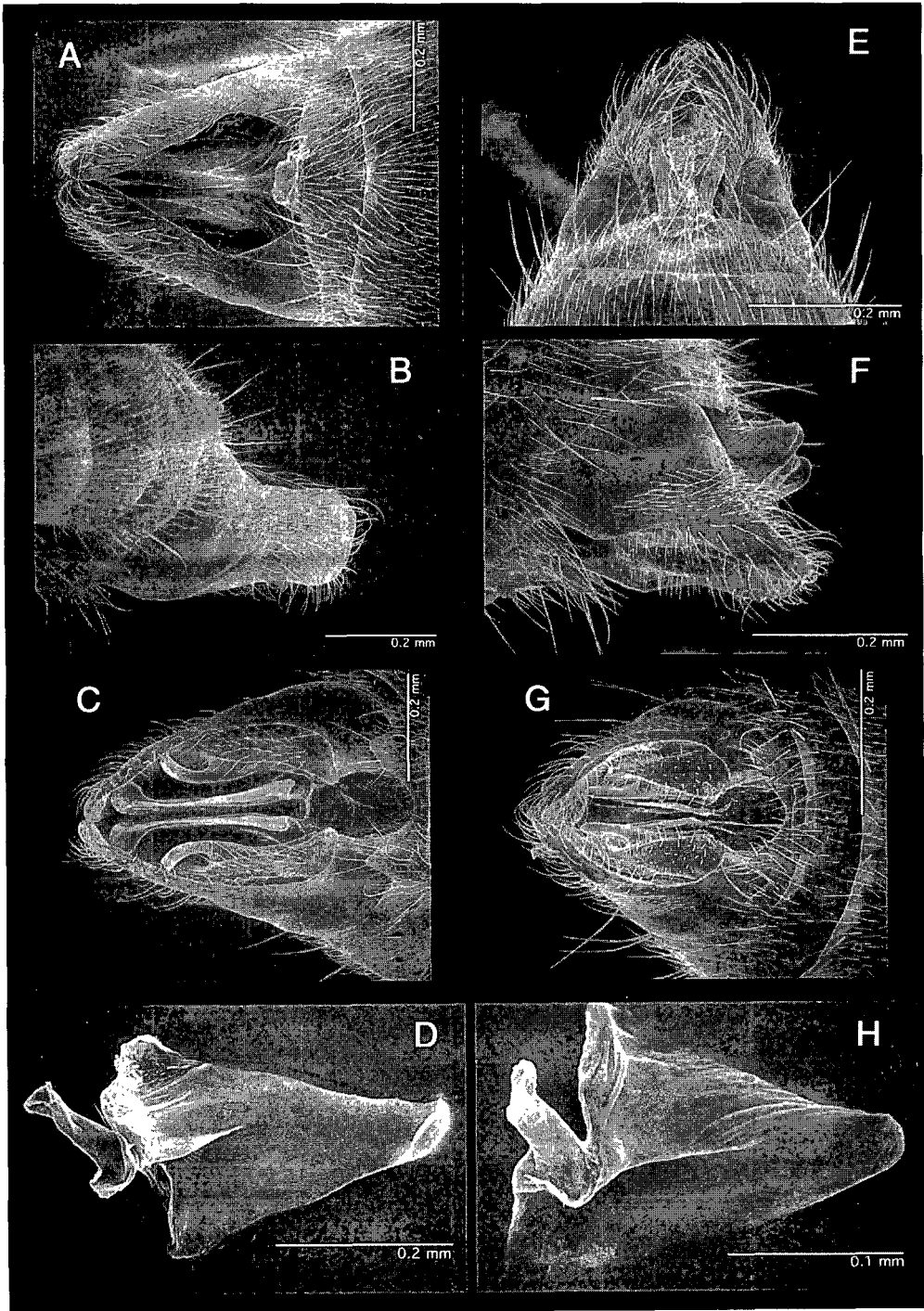


Figure 35. *A. arnoldi* genitalia (A-D). A) dorsal view; B) lateral view; C) ventral view; D) penis valve. *A. butteli* genitalia (E-H). E) dorsal view; F) lateral view; G) ventral view; H) penis valve.

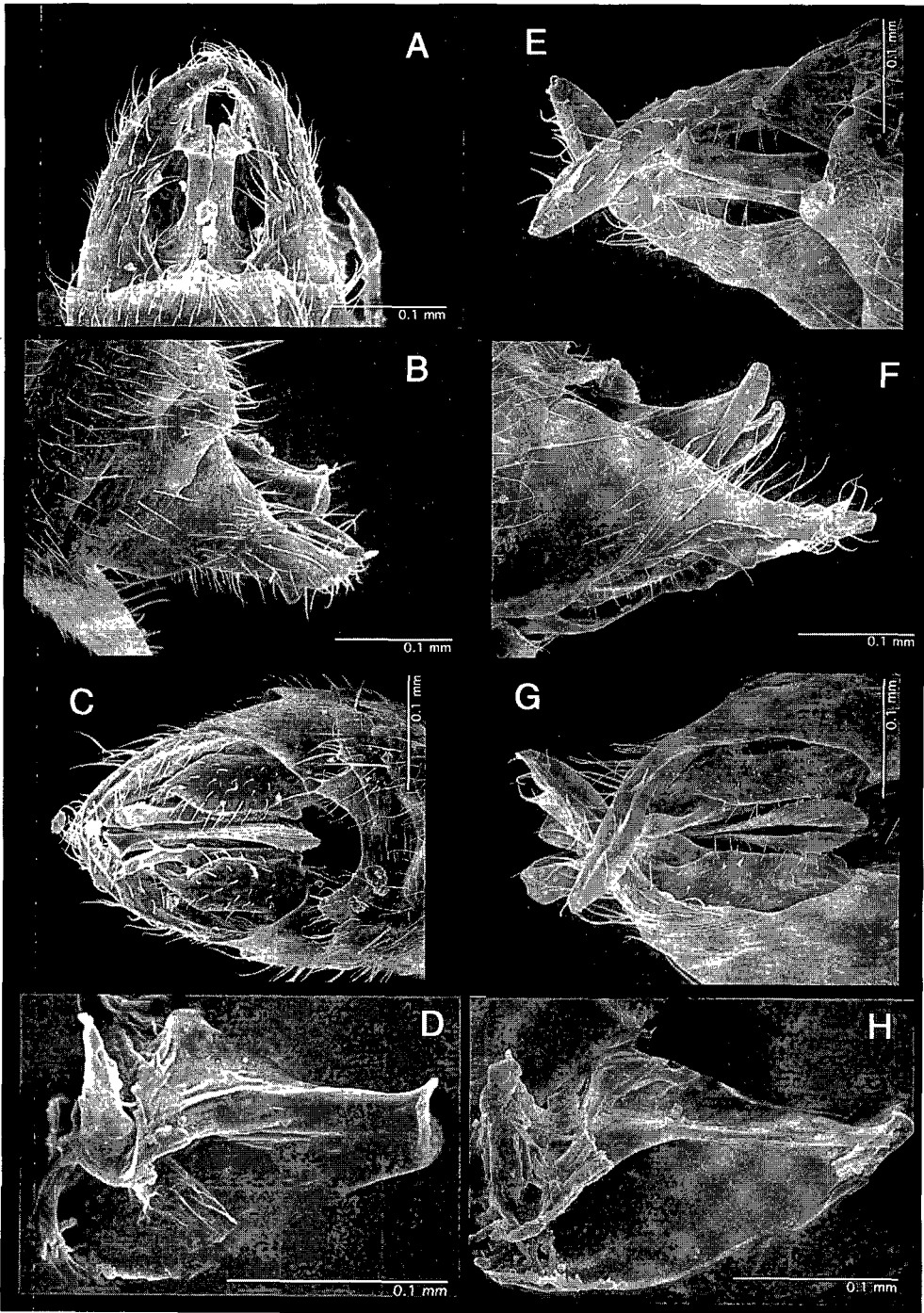


Figure 36. *A. inezae* genitalia (A-D). A) dorsal view; B) lateral view; C) ventral view; D) penis valve. *A. nipponensis* genitalia (E-H). E) dorsal view; F) lateral view; G) ventral view; H) penis valve.

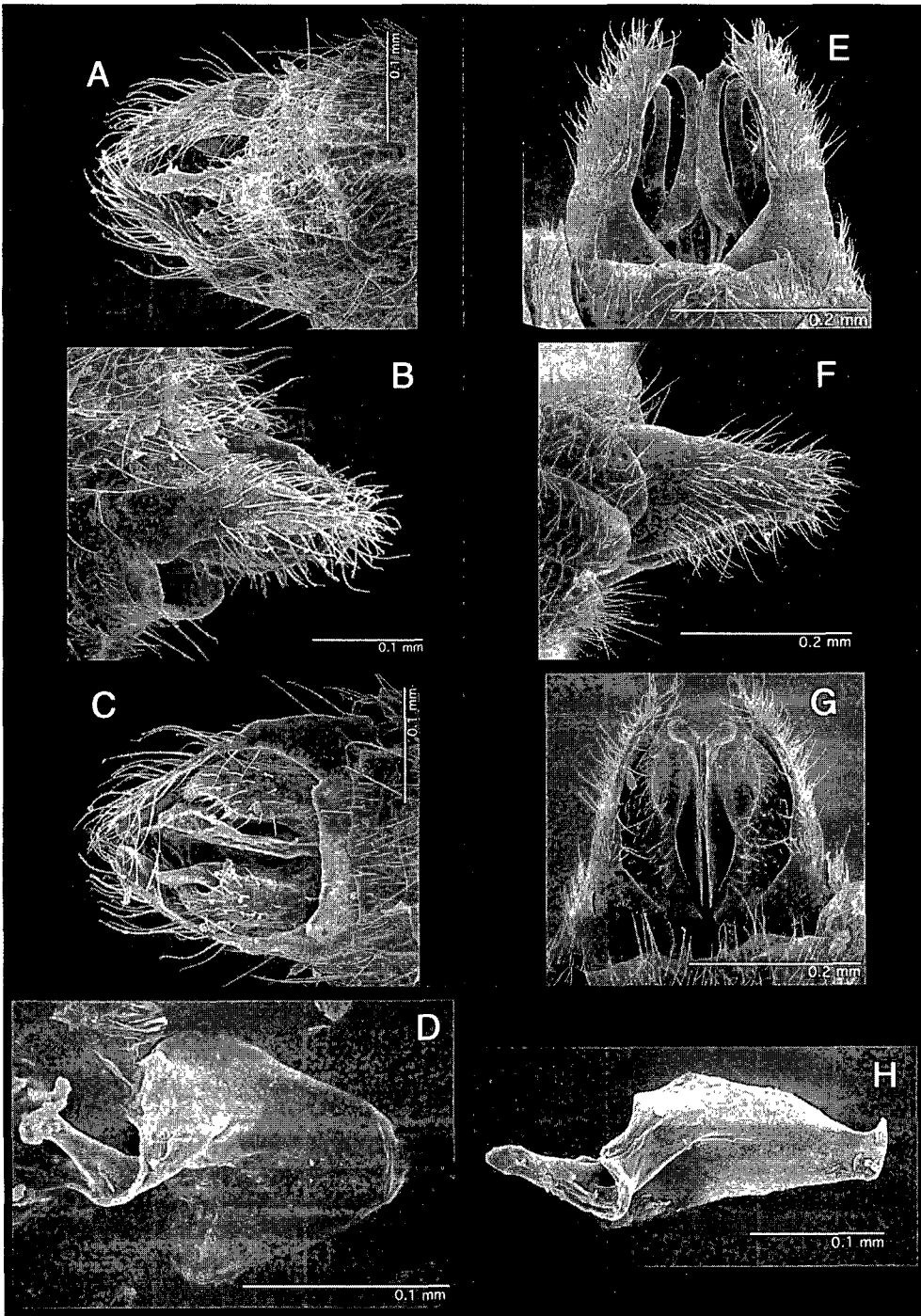


Figure 37. *A. decedens* genitalia (A-D). A) dorsal view; B) lateral view; C) ventral view; D) penis valve. *A. fuhrmanni* genitalia (E-H). E) dorsal view; F) lateral view; G) ventral view; H) penis valve.

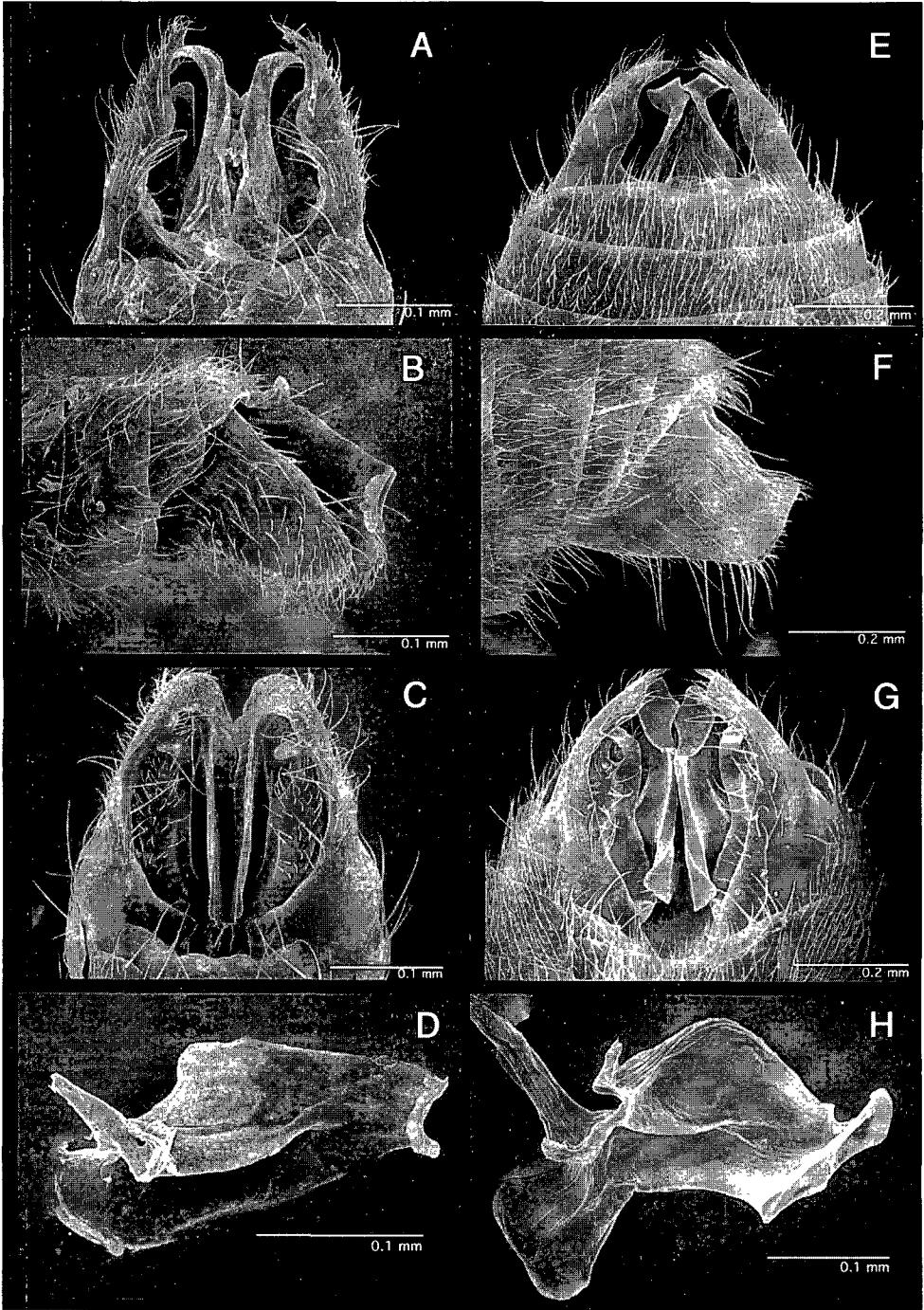


Figure 38. *A. smithii* genitalia (A-D). A) dorsal view; B) lateral view; C) ventral view; D) penis valve. *A. dubitata* genitalia (E-H). E) dorsal view; F) lateral view; G) ventral view; H) penis valve.

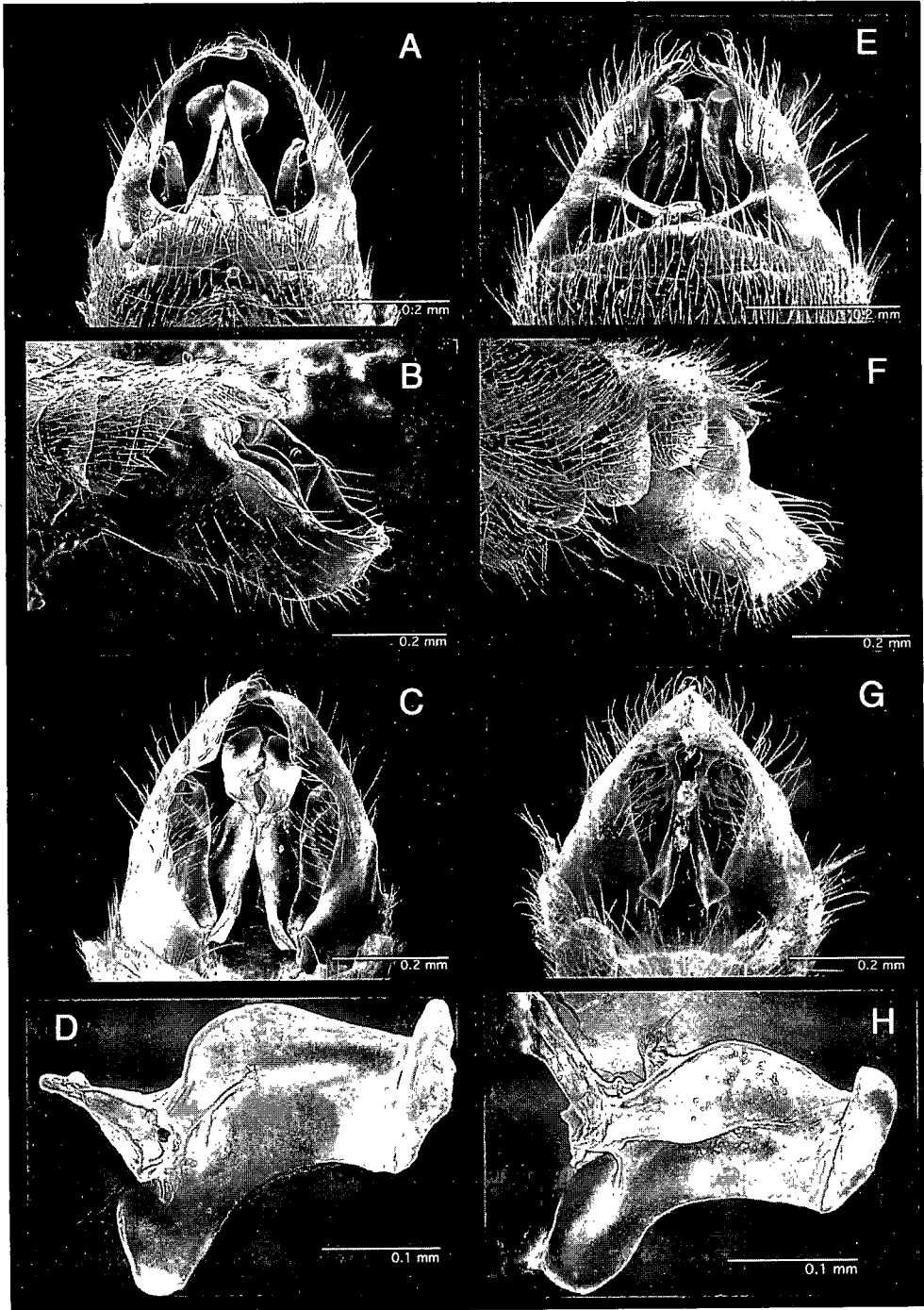


Figure 39. *A. epedana* genitalia (A-D). A) dorsal view; B) lateral view; C) ventral view; D) penis valve. *A. exsanguis* genitalia (E-H). E) dorsal view; F) lateral view; G) ventral view; H) penis valve.

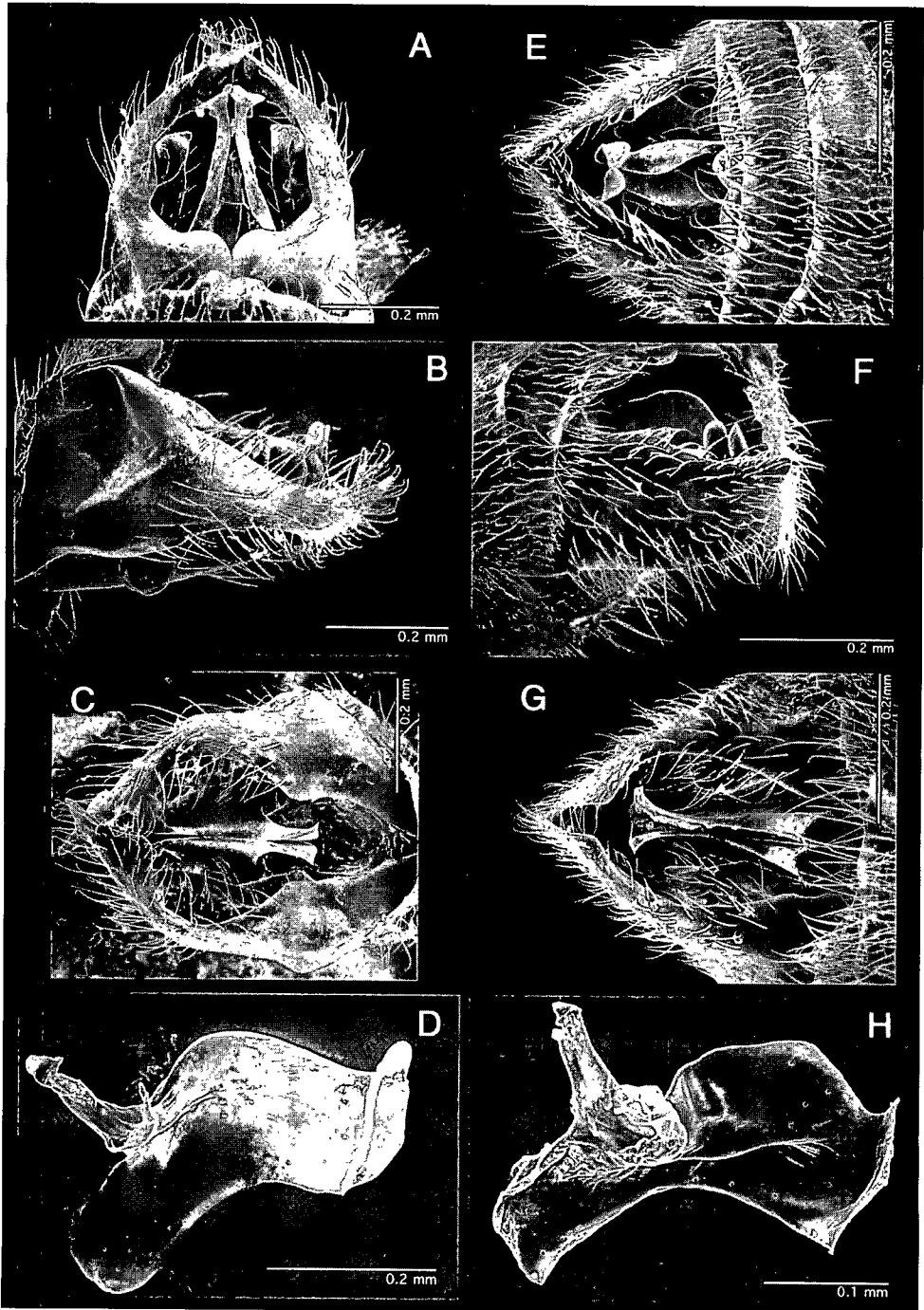


Figure 40. *A. goeldii* genitalia (A-D). A) dorsal view; B) lateral view; C) ventral view; D) penis valve. *A. hirsutula* genitalia (E-H). E) dorsal view; F) lateral view; G) ventral view; H) penis valve.

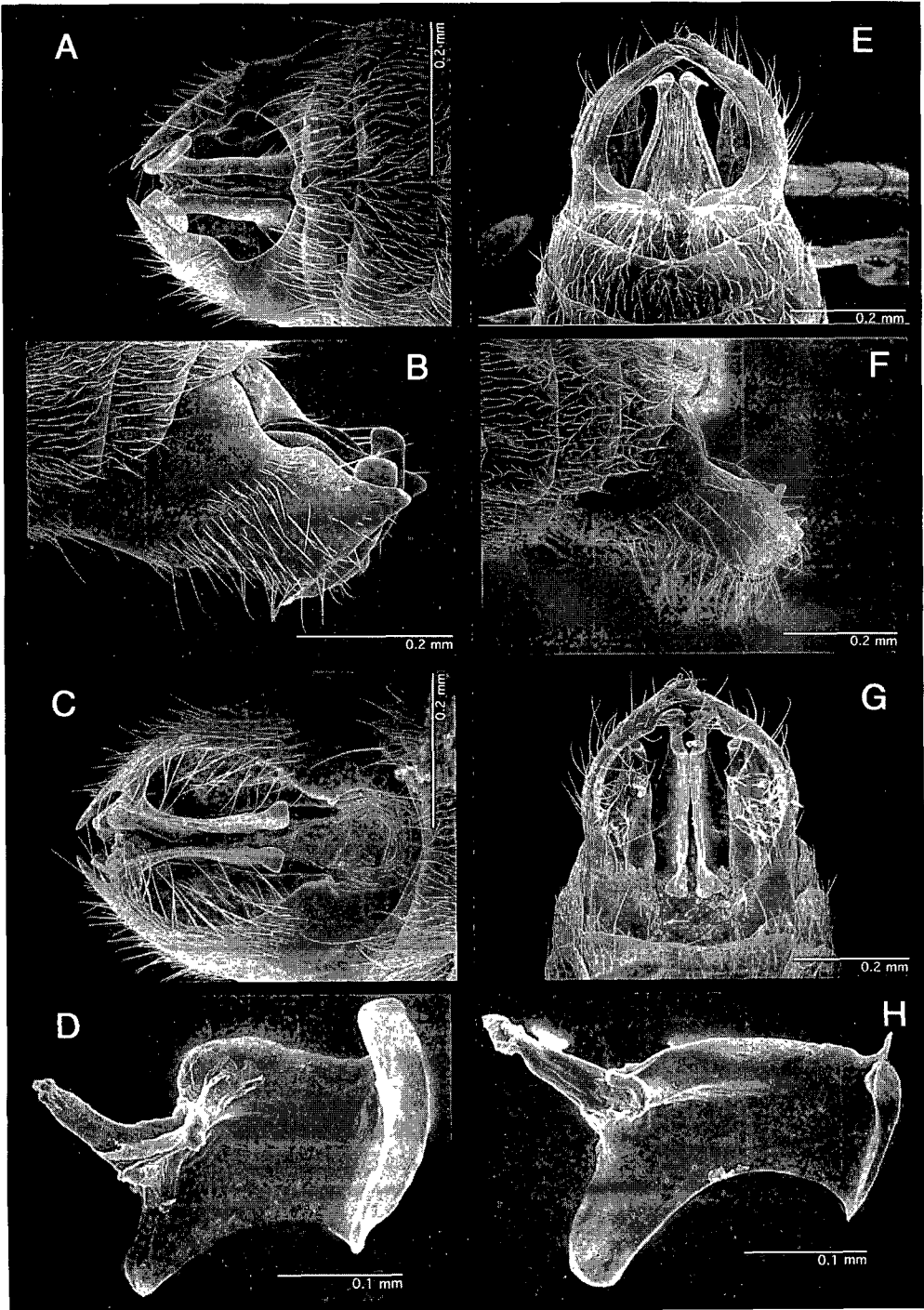


Figure 41. *A. keira* genitalia (A-D). A) dorsal view; B) lateral view; C) ventral view; D) penis valve. *A. palaga* genitalia (E-H). E) dorsal view; F) lateral view; G) ventral view; H) penis valve.

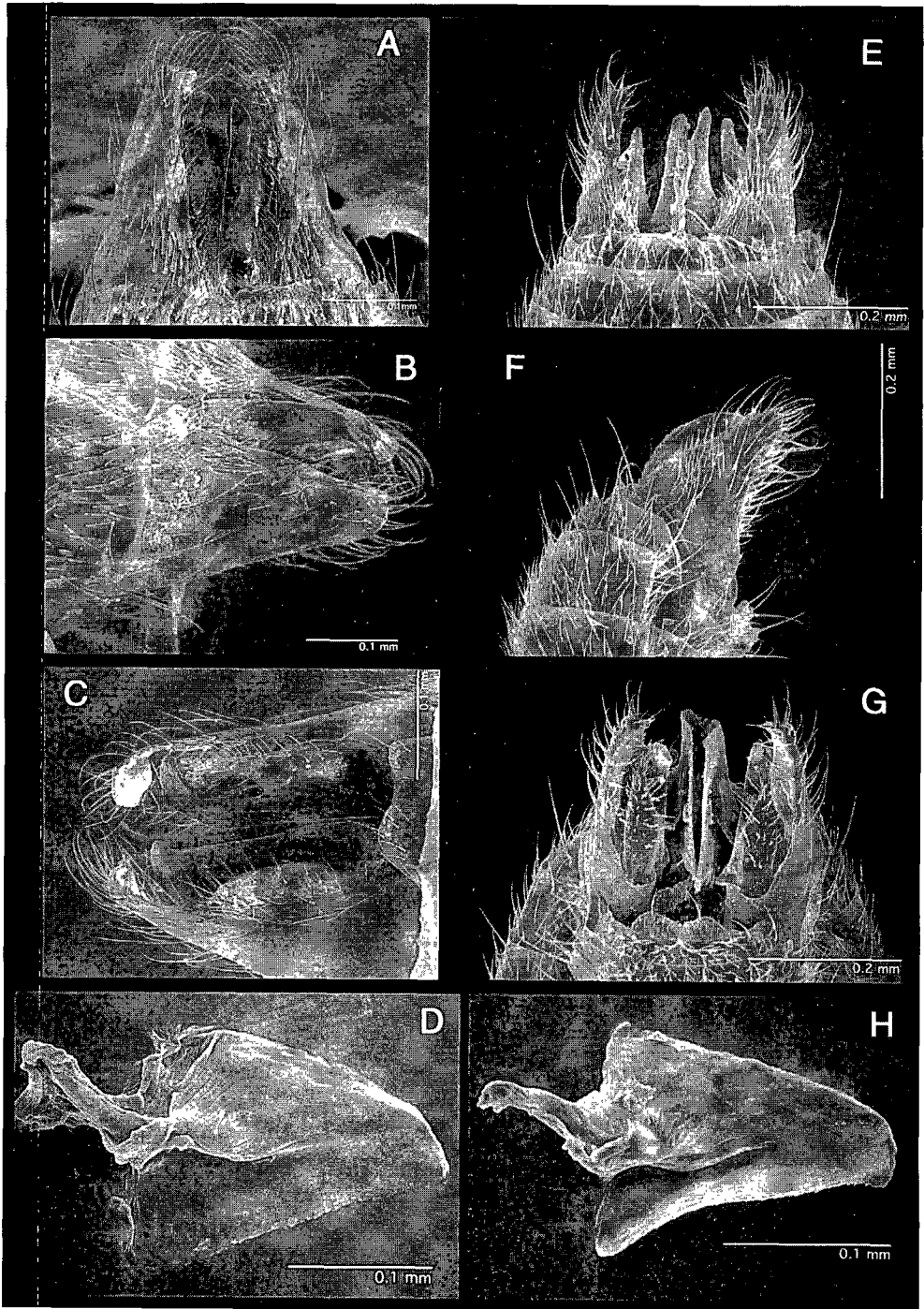


Figure 42. *A. donisthorpei* genitalia (A-D). A) dorsal view; B) lateral view; C) ventral view; D) penis valve. *A. tricuspis* genitalia (E-H). E) dorsal view; F) lateral view; G) ventral view; H) penis valve.

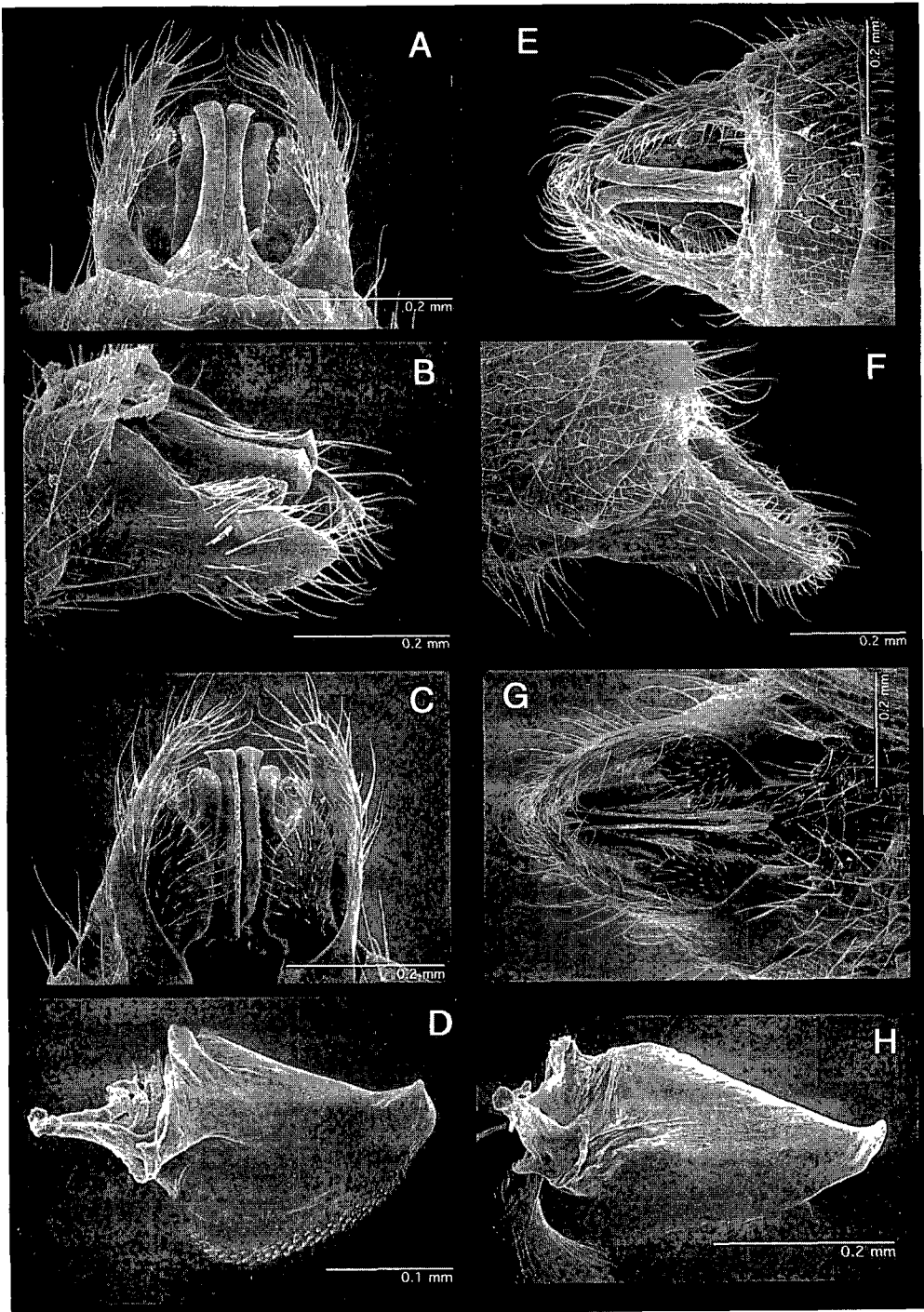


Figure 43. *A. hystrix* genitalia (A-D). A) dorsal view; B) lateral view; C) ventral view; D) penis valve. *A. myops* genitalia (E-H). E) dorsal view; F) lateral view; G) ventral view; H) penis valve.

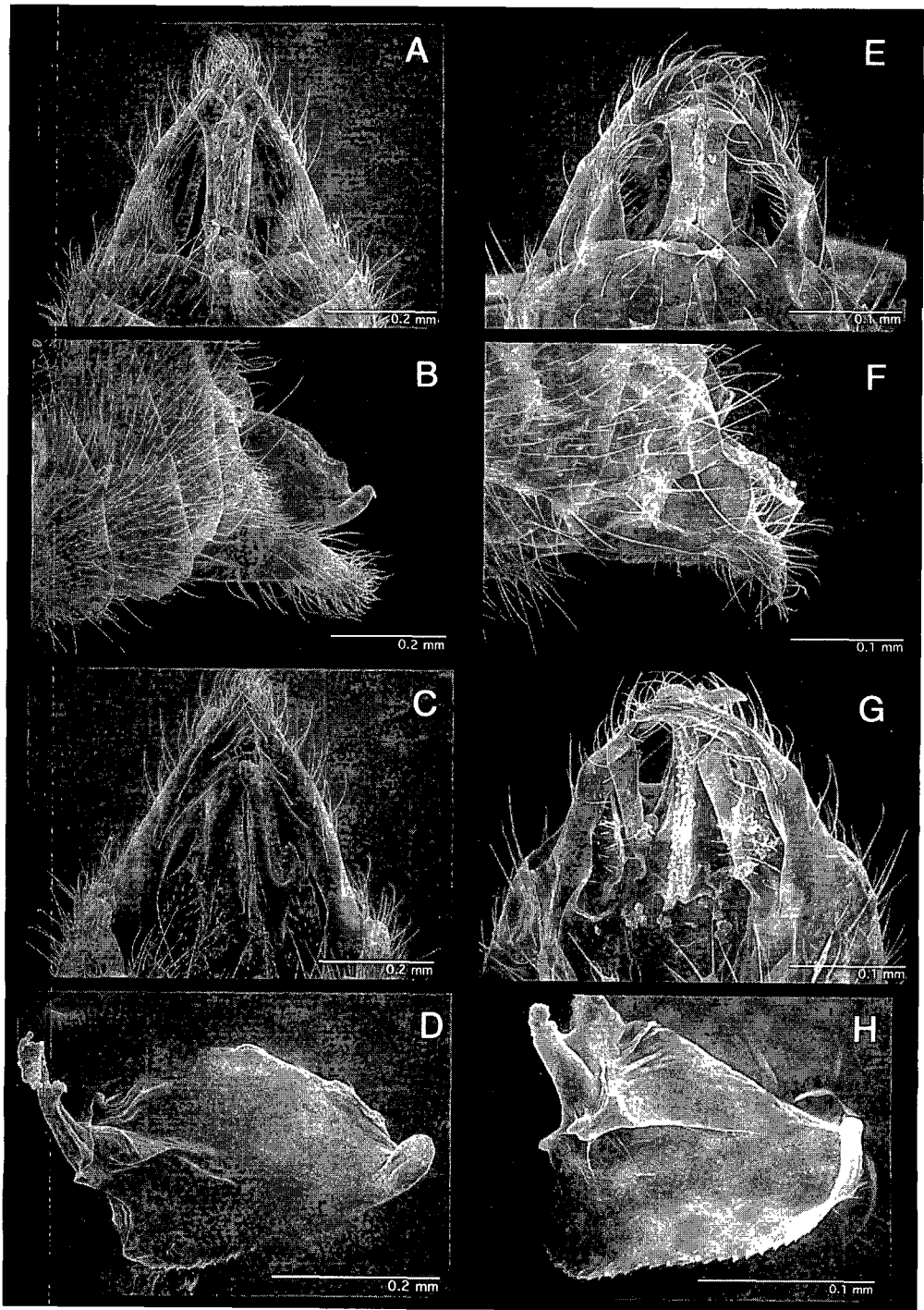


Figure 44. *A. sauteri* genitalia (A-D). A) dorsal view; B) lateral view; C) ventral view; D) penis valve. *A. pallida* genitalia (E-H). E) dorsal view; F) lateral view; G) ventral view; H) penis valve.

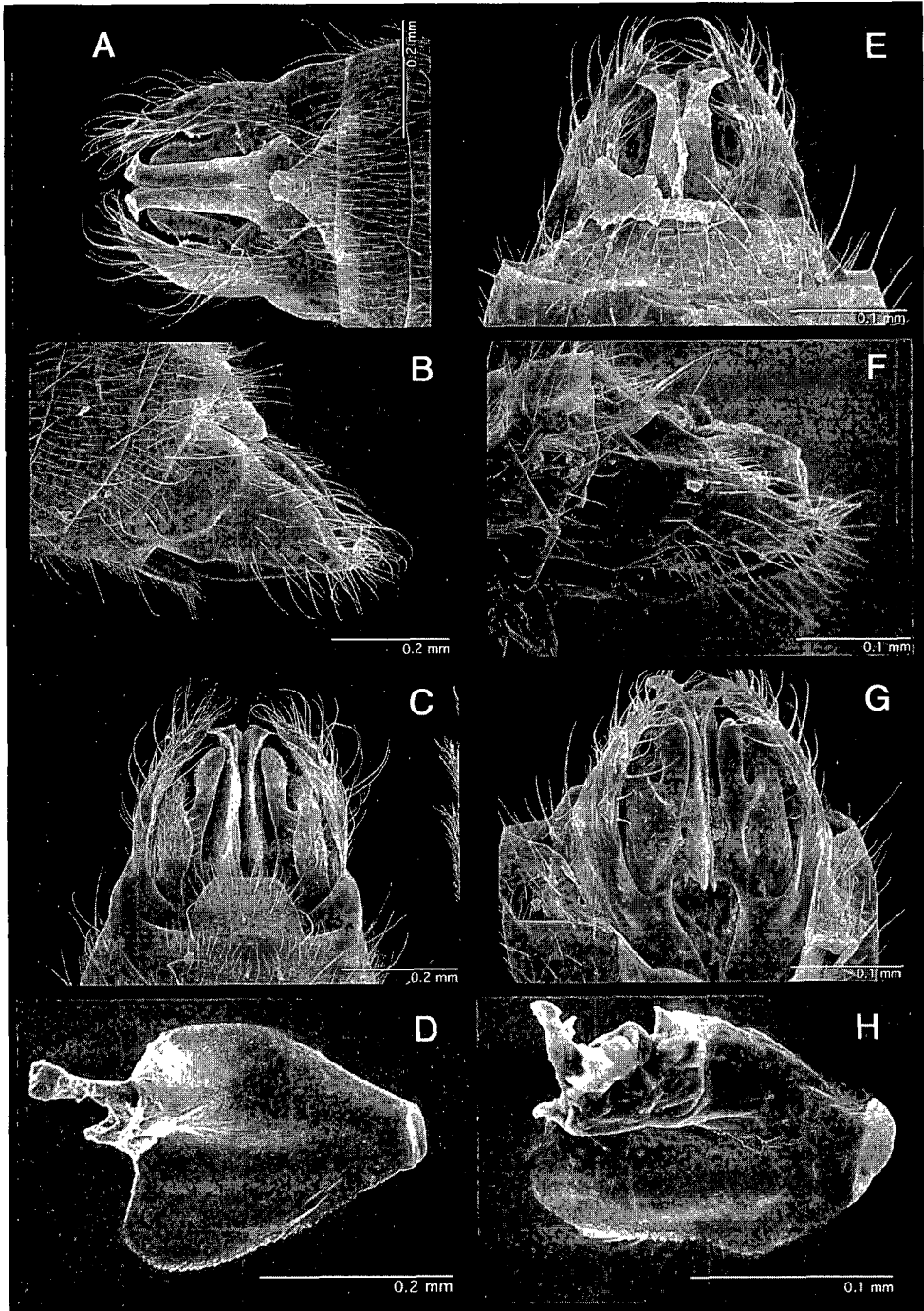


Figure 45. *A. ayanganna* genitalia (A-D). A) dorsal view; B) lateral view; C) ventral view; D) penis valve. *A. panamensis* genitalia (E-H). E) dorsal view; F) lateral view; G) ventral view; H) penis valve.

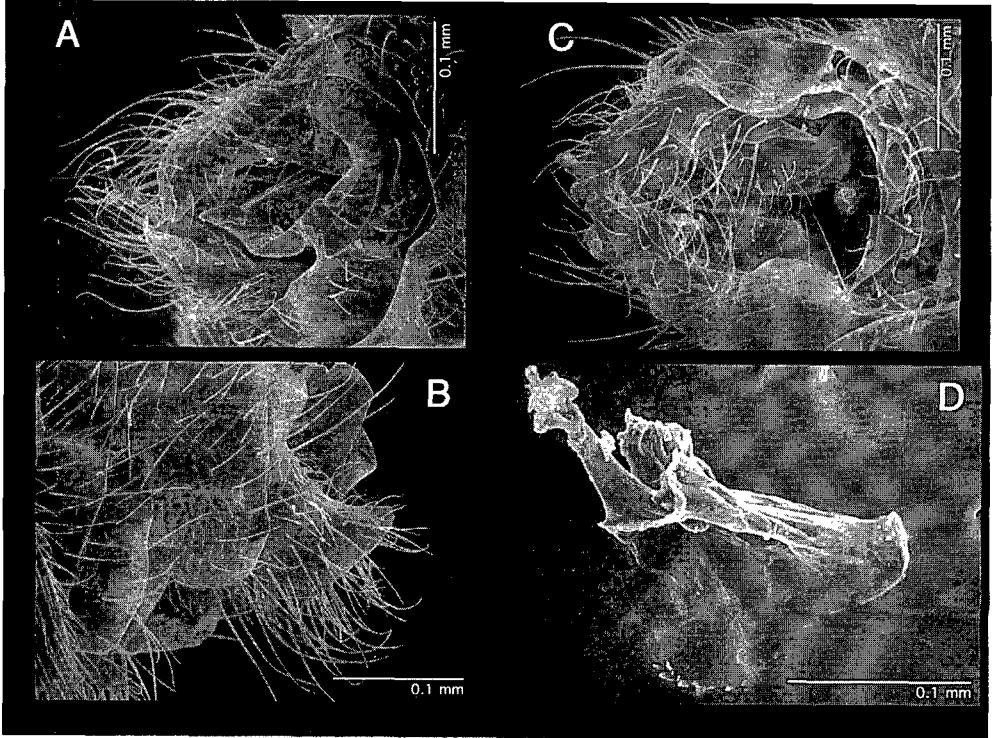
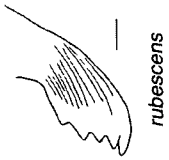


Figure 46. *A. yaeyamensis* genitalia (A-D). A) dorsal view; B) lateral view; C) ventral view; D) penis valve.

acutiventris species-group

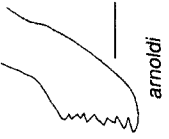


acutiventris



rubescens

arnoldi species-group

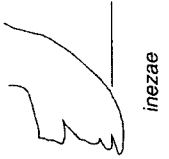


arnoldi

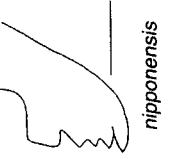
butteli species-group



butteli



inezae



nipponensis

decedens species-group



decedens



fuhrmanni



smithii



epedana



exsanguis



goeldii



hirsutula

donisthorpei species-group

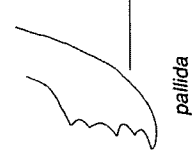


donisthorpei



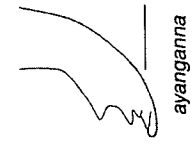
tricuspis

pallida species-group



pallida

panamensis species-group



ayanganna



panamensis

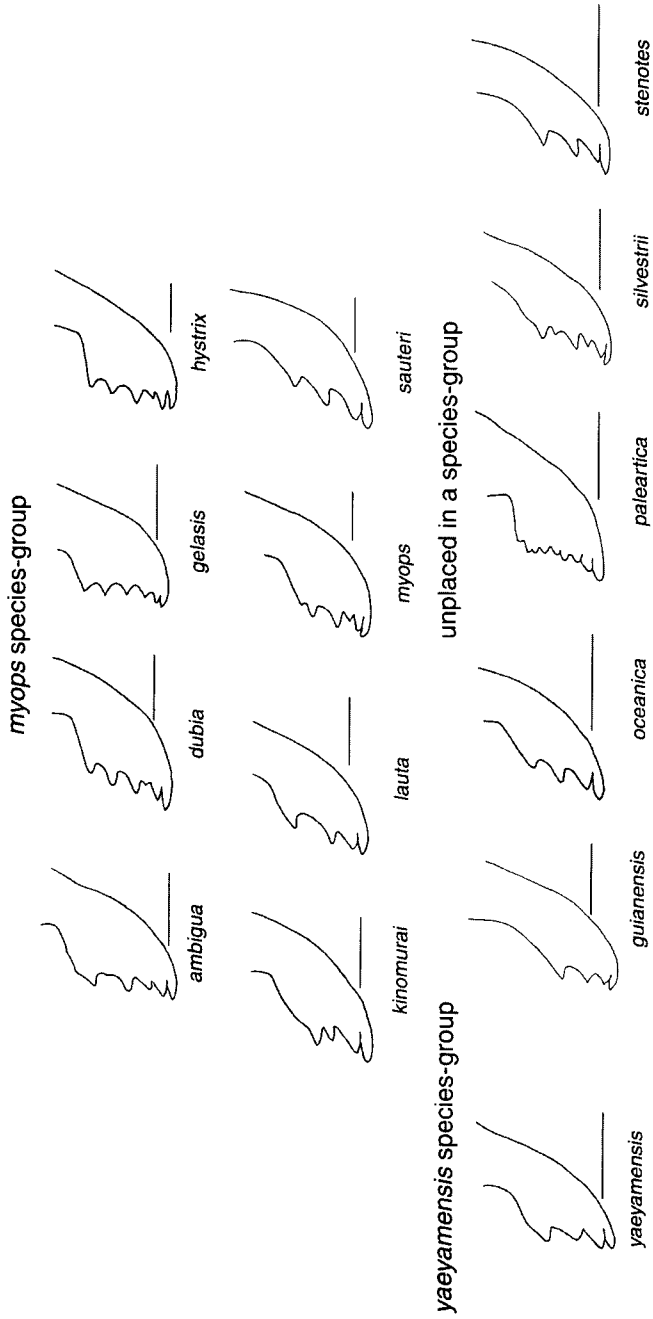


Figure 47 (continued from pg. 116). Worker mandibles in full frontal view; hairs not shown. Scale bar = 0.1 mm. *A. hirsutula* mandible based on queen.

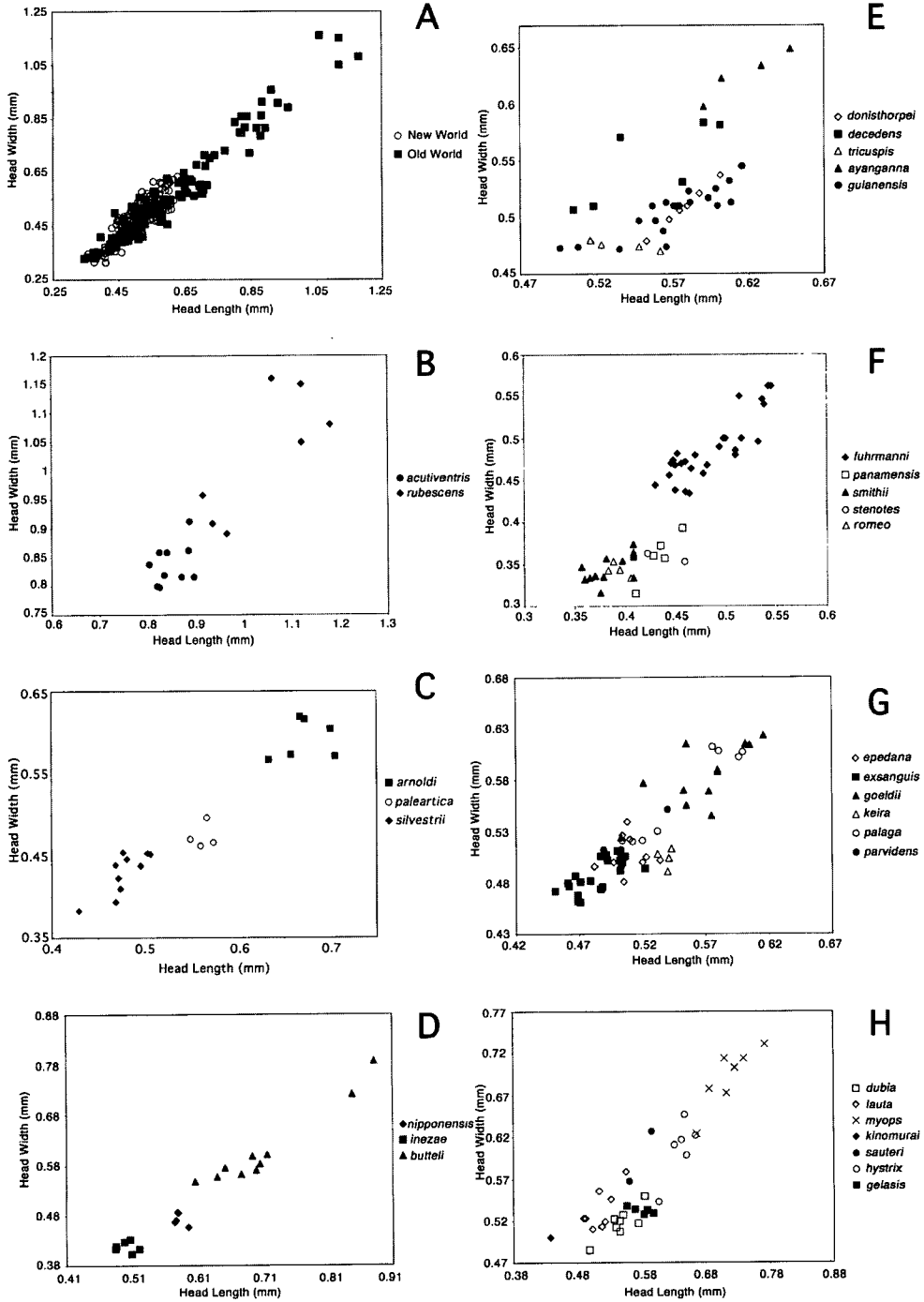


Figure 48. Bivariate plots of head width versus head length of *Acropyga* workers (A-H).

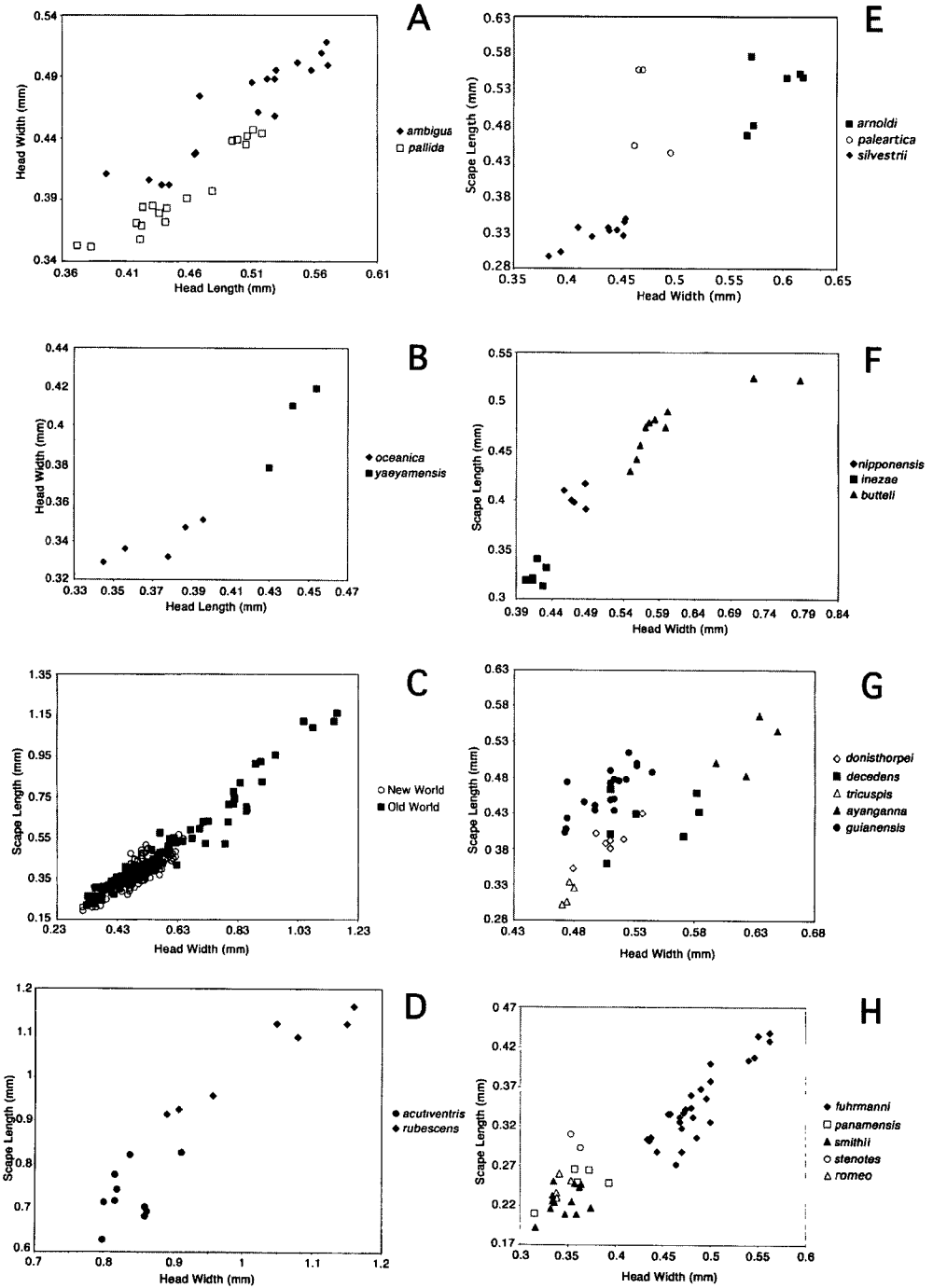


Figure 49. Bivariate plots of head width versus head length of *Acropyga* workers (A-B); bivariate plots of scape length versus head width of *Acropyga* workers.

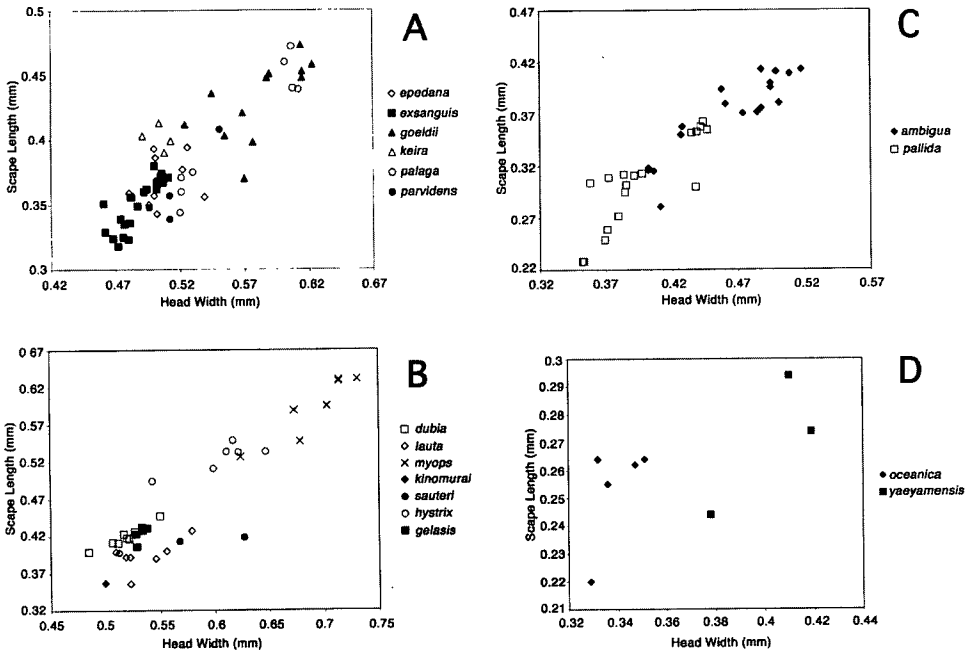


Figure 50. Bivariate plots of scape length versus head width of *Acropyga* workers (A-D).

PHYLOGENETICS AND BIOGEOGRAPHY

"Science and its demanding methodology has moved the story of the creation of species from myths, legends, and just-so stories, to a narrative based on evolution." R.J. Blahnik (1998)

The evolution and subsequent dispersal of *Acropyga* is of considerable interest because the group's history has profound implications for the evolution of complex behavior, including symbiosis in general, and, more specifically obligatory trophobiosis and trophophoresy. Despite suggestions to the contrary (Agosti, 1991; Bolton, 1995), the genus is monophyletic (see description of genus for a list of morphological synapomorphies for the genus). Agosti (1991) relied on mesosomal and gastral ventral characters to separate *Malacomyrma* from the rest of *Acropyga*, into the *Pseudolasius* genus-group and *Lasius* genus-group respectively. However, those characters were not examined cladistically. For example, Agosti (1991) states that the *Lasius* genus-group possesses a tergite and sternite that are not fused anteriorly, while the *Pseudolasius* genus-group consists of genera in which the tergite and sternite are often fused anteriorly. In the case of *Malacomyrma* species (*A. arnoldi* and *A. silvestrii*), the tergite and sternite are not fused anteriorly, thus rendering their placement by Agosti in the *Pseudolasius* genus-group suspect with respect to that character. The differences in the helcium between *Malacomyrma* and other *Acropyga* listed in Agosti (1991) were not observed in the present study. Agosti split some groups of genera that have long been thought to be closely related, such *Prenolepis* and *Paratrechina* (Trager, 1984). Ventral characters, however, are of value in recovering the phylogenetic history of the subfamily Formicinae and will be more completely examined elsewhere (LaPolla *et al.*, in prep). Finally, molecular data from the D2 region of the 28S rRNA and Efl-alpha genes also suggest that *Acropyga* is monophyletic (LaPolla *et al.*, in prep). Thus, both morphological and molecular characters support the monophyly of the genus.

Bolton (2003) has recently placed *Acropyga* as a redefined Lasiini, removing it from the Plagiolepidini. The placement of *Acropyga* within the Lasiini seems a reasonable estimate of its phylogenetic position, but the subfamily still awaits a cladistic analysis (see above). Bolton (2003) further suggests that *Acropyga* may be most closely related to five genera within the Lasiini: *Acanthomyops*, *Anoplolepis*, *Cladomyrma*, *Lasius* and *Mymecocystus*. This is based on the absence of a transverse sulcus across abdominal sternite III (first gastral segment) posterior to the helcium sternite. Among those genera, two immediately seem possible candidates as *Acropyga*'s sister taxon: *Anoplolepis* and *Cladomyrma*. *Anoplolepis* was formerly placed in the Plagiolepidini (its former subgenus *Tapinolepis* still remains in the tribe as a separate genus) and its reduced antennal segmentation may link it with *Acropyga*. Agosti (1991) suggested *Acropyga* may be most closely related to *Cladomyrma* based on overall mesosomal shape. Additionally, *Cladomyrma* also possesses reduced antennal segmentation.

With the monophyly of the genus established, some interesting questions about its current distribution can be addressed. *Acropyga* is nearly worldwide in distribution (fig. 14), though it does not inhabit areas where freezing temperatures persist for several months. Therefore, the northern limits of the genus are around 40° N, the southern limits around 40° S. Its known diversity is greatest in the Neotropical region with 17 species, and in the Indo-Australasian region with 11 species. Some species are extremely wide-ranging. For example, *A. acutiventris* is found in a wide variety of habitats in the Oriental, Australasian and Indo-Australian regions. *Acropyga* attains its highest diversity in rainforests, and it is in these areas where many more *Acropyga* undoubtedly await future discovery. Few formicine genera have such a large distribution. In fact, only *Camponotus* is truly worldwide, whereas most genera in the subfamily have much more limited distributions. For example, *Myrmelachista* is found strictly in the New World tropics, and *Pseudolasius* is found strictly in the Old World tropics. *Acropyga*'s distribution pattern is unique

within the subfamily. How did *Acropyga* achieve its current distribution?

A phylogeny of the genus was constructed using morphological characters derived from both workers and males (see Material and Methods for a list of characters). The results of this phylogenetic analysis must be considered provisional since males, a source of essential character data, remain unknown in many species. Additionally, the males of most *Acropyga* species are known imperfectly because the small available samples make variation difficult to assess. Even so, a preliminary phylogenetic analysis provides an improved framework for study, including the consideration of biogeographical patterns.

Three kinds of analysis were completed, all of which employed a base weight of 1 scaled for characters with greater than 2 character states. Equally weighted parsimony analysis (EWP) found 4 equally parsimonous trees. A strict consensus of those trees is presented in figure 51. Successive approximations weighting analysis (SAW) and pseudoreplicate reweighting analysis (PRA), found the same number of trees and topology as the equally weighted parsimony analysis. Most branches of the EWP tree are not well supported by bootstrap analysis (fig. 51). Confidence in the proposed phylogeny is bolstered, however, by the fact that the two alternative analyses recovered a tree topology that was the same as the tree topology recovered by EWP.

The EWP phylogeny suggests that *A. arnoldi* is the sister species to all the remaining *Acropyga* species. *A. arnoldi* is a large species that possesses a high number of maxillary palp segments (up to 5) and the highest number of mandibular teeth (up to 9) found in the genus. Only one other species comes close to this character combination, *A. palearctica* (possessing up to 5 maxillary palp segments and 8 mandibular teeth), the phylogenetic placement of which remains unresolved pending the discovery and analysis of males. The phylogenetic position of *A. arnoldi* suggests that *Acropyga* is of African origin, though with no bootstrap support and only two synapomorphies for that node, doubt remains. An African origin is interesting because only 2 species are currently known from Africa. Unfortunately, *A. silvestrii* remains unplaced in the genus awaiting the discovery of males. Worker morphology, however, suggest the species is closely related to *A. arnoldi*. An African origin for the genus conflicts with the hypothesis of Johnson *et al.* (2001), who concluded that *Acropyga* had evolved in the New World during the Oligocene and only later dispersed into the Old World. A New World origin for *Acropyga* is highly unlikely based on the present analysis.

Acropyga may be of Gondwanan origin. The phylogenetic position of *A. myops*, a species wholly restricted to Australia, near the base of the tree suggests that the genus maybe quite old, as Australia and Africa were lasted connected, along with South America and Antarctica in the Cretaceous. Unfortunately, the proposed phylogeny fails to resolve the relationships among species in the *myops* species-group, and thus *A. myops* may well be derived from Asian species rather than from African ones. If this is the case, the migration from Africa to Asia could have occurred as late as the Eocene, which could indicate that the genus came into existence well after the Cretaceous. The separation of India from Africa in the late Cretaceous, and its subsequent collision with Asia in the Eocene (Hall, 1998), could have delivered *Acropyga* to that region as well, but this scenario would require that the genus dispersed from Asia into Australia only recently, rather than at the break-up of Gondwana. Further investigation of species in the Old World, particular those at the base of the tree, will need to be completed for a more thorough understanding of the phylogeography of the genus.

The discovery of a formicine ant from New Jersey amber by Grimaldi and Agosti (2001) demonstrates that the subfamily existed at least as far back as 92 mya, thus a Cretaceous origin for *Acropyga* is certainly not impossible. If, however, the genus extends so far back into early ant evolution, the absence of *Acropyga* from Madagascar is curious. Despite extensive leaf-litter sampling by Brian Fisher and others on the island, no *Acropyga* have been discovered to date (Fisher, personal communication); therefore the lack of specimens from Madagascar does not seem to be due to collecting bias. The genus is also unknown from Baltic amber, which dates to the Eocene

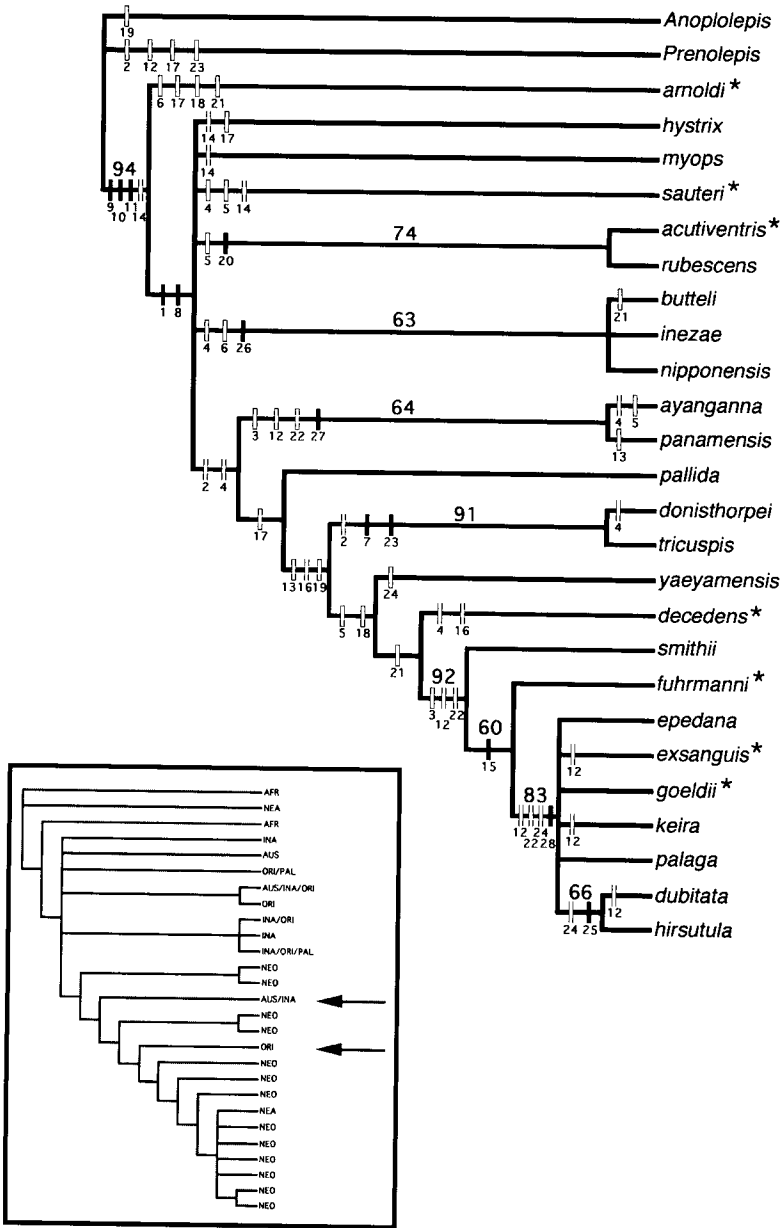


Figure 51. Cladogram of strict consensus tree summarizing four shortest trees using “scaled,” equally weighted characters (see text) to estimate relationships among *Acropyga* species (treelength= 51.5 steps). Character changes are shown as vertical bars with character number under each bar. Vertical bars are as follows: filled, no homoplasy; unfilled closed, parallel homoplasy elsewhere on tree; open, multiple changes within a clade. Numbers above branches represent bootstrap values. Asterisks indicate species in which queens are known to be trophophoretic. INSERT: biogeographic regions in which various species are found. AFR= Afrotropical; AUS= Australasian; INA= Indo-Australian; NEA= Nearctic; NEO= Neotropical; PAL= Palearctic. Arrows pointing out that with this phylogeny the New World fauna is not monophyletic. See text for discussion. Outgroup species are listed for the biogeographic region in which the specific species used for analysis are found.

(45 mya), but this could be an artifact of what groups amber tends to represent. With their hypogaecic habits, individual *Acropyga* would not be expected to become trapped in plant resins very often, except for the reproductives as they fly about for brief mating flights (DuBois and LaPolla, 1999).

The New World fauna includes all of the most derived species in the genus. However, the placement of *A. pallida* and *A. yaeyamensis*, remains problematic. If the current placement in the phylogeny is correct it suggests two possible scenarios: 1) that the New World was invaded 3 times- once leading to the evolution of the *panamensis* species-groups, again leading to the *donisthorpei* species-group, and then again leading to the evolution of the *decedens* species-group or 2) that the Old World was re-invaded by a New World lineage leading to the evolution of *A. yaeyamensis* and *A. pallida*. The second scenario may indicate that the New World fauna is derived from a more ancient time (the break-up of Gondwana?) and that the New World clade evolved in situ, with no "invasion" of the region ever in fact occurring. There is no evidence favoring either hypothesis, and an explanation of the placement of both *A. yaeyamensis* and *A. pallida* is needed. Unfortunately, only a single male specimen of *A. yaeyamensis* was available for study and it was not in particularly good condition (the specimen was very shriveled and badly distorted). Nonetheless, the character data suggest a close relationship of this species with the New World fauna. Homoplasy in the data matrix may be responsible for the current position of *A. yaeyamensis* and *A. pallida* within the New World clade, and as more males become available for study, the data will need to be reanalyzed.

If the New World *Acropyga* species are of recent origin (at least the *decedens* species-group), then it seems likely that *Acropyga* migrated to the region via Beringia in the mid to late Oligocene, a time when conditions were generally warmer (Cox and Moore, 2000). By the Miocene conditions in Beringia deteriorated, becoming cooler, as evidenced by the presence of cool-weather adapted mammals, and the climate continued to become colder through the Pleistocene (Cox and Moore, 2000). The final break between Asia and North America occurred 13,000-14,000 years ago (Cox and Moore, 2000).

Further evidence that *Acropyga* had reached the New World no later than the Oligocene is the presence of an extinct species in Dominican amber (LaPolla, in prep). It was in the Oligocene that the protoisthmus that what would later become the Greater Antilles was already in place between North and South America. The fossil *Acropyga* species from Dominican amber proves that by the Miocene at least the genus was definitely present in the New World. The Dominican amber fossils are unlike any extant species in the New World (LaPolla, in prep), and placement within any extant species-group is not possible. The fossil species possesses a high number of mandibular teeth (up to 8), which may indicate a relationship with species such as the African *A. arnoldi*. Male morphology, suggest the species may be related to the extant *decedens* species-group or to *A. yaeyamensis*, but without being able to dissect out male genitalia its placement remains problematic. Interestingly the extant *Acropyga* fauna of Hispaniola belongs to the *decedens* species-group. The sister taxon to *A. dubitata* (a Hispaniolan endemic) is *A. hirsutula*, which is found in South America (Peru and Ecuador). It has been estimated that limited faunal exchanges between North and South America began around 15 mya, and a full faunal exchange between the two continents occurred between 3-5 mya. By the end of the Pliocene (ca. 1.8 mya), the Ice Ages began and this event probably pushed *Acropyga* into the current distribution pattern around the world.

Some interesting morphological trends are suggested by the *Acropyga* phylogeny. The most obvious is that reduction in meristic characters is much more common among the New World fauna. The number of antennal segments, for instance, remains almost uniformly at 11 segments for the vast majority of Old World species (table 1). In the New World, the reduction of antennal segments from 11 all the way down to 7 is common, and even closely related species display a wide degree of variation (table 1). For instance, the range in antennal segment number in the *decedens* species-group is from 7-11 segments. Mandibular tooth number is also reduced in the New World

fauna, with no species possessing more than 5 teeth, and mandibular-shape changes among the most derived species have led to thinner, scapulate mandibles. In general, New World species are also smaller in size than Old World species (48A & 49C). These morphological trends seem consistent with the present phylogeny, with the smallest number of reductions occurring among the more primitive Old World species and the greatest number of reductions occurring in the more derived New World species. These morphological changes probably are indicative of a group that has become progressively more hypogaecic and more modified for life with mealybugs over time.

Relationship with mealybugs

Unfortunately, because no phylogeny of mealybugs is available, it is not possible to determine whether or not, and to what extent, *Acropyga* and their mealybug symbionts have coevolved. *Acropyga*-associated mealybugs all belong to the subfamily Rhizoecinae. But because many *Acropyga* have been found with more than one species of mealybugs, it seems unlikely that the evolution of mealybugs and ants conform to the classic pattern of tight, species-to-species coevolution. Instead, the *Acropyga*-mealybug system appears to consist of two clades that have become mutually dependent, but the degree of species specificity remains uncertain. Evidence for considerable flexibility in relationships is exemplified by relationship of *Acropyga* species with the mealybug *Geococcus coffeae*, which is attended by at least 2 *Acropyga* species in South America, even though the species was introduced into the New World by man within the past 200 years (Williams, 1998).

Extant *Acropyga* are currently known to utilize 8 genera of mealybugs (table 3), but the relationships of the mealybug genera remains largely uncertain, and the status of many Rhizoecine genera remains unclear (Williams, 1998); the group clearly awaits a thorough phylogenetic analysis. Williams (1998) suggested that the Old World mealybug genera, and the only ones utilized by Old World *Acropyga*, *Eumyrmococcus* and *Xenococcus*, are closely related to the New World *Neochavesia*, a mealybug genus utilized by *Acropyga* in the New World (collectively known as the *Eumyrmococcus* group). The other genera utilized by *Acropyga*, *Capitisetella*, *Dysmicoccus*, *Pseudorhizoecus*, and *Rhizoecus*, are all thought to be closely related (collectively known as the *Rhizoecus* group). Interestingly, their worldwide distribution, *Rhizoecus* and *Dysmicoccus* are only utilized by *Acropyga* species of the *decedens* species-group, which is found exclusively in the New World, and which is the most derived group within the genus. Johnson *et al.* (2001) suggested that *Electromyrmococcus*, known only from Dominican amber with the fossil *Acropyga*, may link the *Eumyrmococcus* group and the *Rhizoecus* group.

Rhizoecine mealybugs appear to be much more diverse than *Acropyga*. For instance, in the mealybug genus *Rhizoecus*, there are around 65 species in the New World (Williams and Granara de Willink, 1992), whereas only 18 species of *Acropyga* are known from the same region. Assuming there is some link between number of ant species and number of mealybug species, this may be another indication that many *Acropyga* species await discovery, or that *Acropyga* utilize a larger number of mealybug species than is presently known, or that only a few *Rhizoecus* species enter into trophobiotic relationships with *Acropyga*. It is clear that outside of the New World, *Rhizoecus* species do not appear to be obligate myrmecophiles with *Acropyga*. Another example is *Eumyrmococcus*, which numbers 17 species in the Indo-Australasian and Oriental regions, where *Acropyga* numbers only 13 known species.

Honeydew produced by scale insects was readily available in the Cretaceous, with scale insects making up nearly 10% of all insect samples from New Jersey and Canadian amber (Grimaldi and Agosti, 2001; Johnson *et al.*, 2001). Thus, *Acropyga* could have entered into their trophobiotic relationships very early in the course of ant evolution. If this is the case, *Acropyga* may have very well been the first ants to enter into an obligatory symbiotic relationship of any sort. For example,

the obligatory relationships of attine ants did not evolved until at earliest the end of the Cretaceous, with the possibility of the behavior not evolving until the Eocene (Mueller *et al.*, 1998; Mueller *et al.*, 2001). Quaintly put, this could mean that ants were ranchers before they were farmers. The relationship between mealybugs and *Acropyga* ants is fascinating and much remains to be learned. What can be said at this time is that trophophoresy in *Acropyga* is almost certainly an ancient behavior that may extend back to the close of the Cretaceous 65 mya. The behavior has only evolved once in the subfamily (the report of trophophoretic behavior in *Cladomyrma* queens turns out to have been a misidentification of an *Acropyga* queen [Agosti *et al.*, 1999]) and twice in the ants overall, though the evolution of trophophoresy in *Tetraponera* is certainly much more recent. *Acropyga* may very well represent the first group of ants to enter into an obligatory trophobiotic relationship with Sternorrhyncha, and the phylogeny and biogeography of *Acropyga* suggest that soon after formicines evolved they rapidly entered into complex trophobiotic relationships.

ACKNOWLEDGEMENTS

I am extremely grateful to my dissertation committee consisting of: Mike May and Karl Kjer (Rutgers Univ.), Ted Schultz (USNM) and Daniel Otte (ANSP), for all their forms of constant support and faith in me that made this study possible. I thank the following people for helpful advice and assistance: Donald Azuma, Jon Gelhaus and Jason Weintraub (ANSP), and Dana Price (Rutgers Univ.). I am grateful to the following people who provided me with specimens: Barry Bolton (BMNH), Carlos Brandão (MZSP), Daniel Burckhardt (NHMB), James Carpenter and David Grimaldi (AMNH), Stefan Cover (MCZC), Brian Fisher (CASC), Yoshiaki Hashimoto (MNHA), Jack Longino (JTL), Stefano Maini and Fabrizio Santi (IEGG), Bernhard Merz (MHNG), Gordon Nishida (BPBM), Roberto Poggi (MCSN), Valter Raineri (MCSN), Hamish Robertson (SAMC), Steve Shattuck (ANIC), Stefan Schödl (NHMV), Ted Schultz (USNM), Roy Snelling (LACM), Phil Ward (PSWC), Seiki Yamane (SYPC), and Zhang Zhen (CFRB). Useful samples of *Acropyga* and other formicines were also provided by: Alfred Buschinger, Ross Crozier, Jacques Delabie, Ulrich Maschwitz, and Achim Moog. Changlu Wang (Ohio State University) provided information regarding the types at CFRB. I thank Vicki Funk and Carol Kelloff (USNM) for providing me with the funds and opportunity to travel to Guyana for 3 months. I am indebted to Romeo Williams for guiding me through the jungles of Guyana. I thank Doug Williams (BMNH) for providing identifications for many mealybug species. I am indebted to Barry Bolton, Mike May, Dan Otte, Ted Schultz and Phil Ward for their advice, comments and corrections on the manuscript. I am of course solely responsible for any errors that inevitably remain. Finally, I thank Lauren Spearman for her endless support, understanding, and love through it all. Funds for parts of this study were provided by the Ernst Mayr Grant Committee (Museum of Comparative Zoology), Cook College (Rutgers University), and the Biological Diversity of the Guianas Program (Smithsonian Institution). This is NJAES Publication D-08-08190-03-04, supported by State and U.S. Hatch Act funds.

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ACROPYGA DISTRIBUTION MAPS

