

## TAXA OF THE NEOTROPICAL GRASS-CUTTING ANTS, *ACROMYRMEX (MOELLERIUS)* (HYMENOPTERA: FORMICIDAE: ATTINI)

Harold G. FOWLER\*

---

**ABSTRACT:** *Biological and distributional data are given for the described taxa of Acromyrmex (Moellerius). A. (M.) balzani and A. (M.) fracticornis are restored to species status, while A. (M.) mesopotamicus is synonymized with A. (M.) silvestri. The status of the enigmatic A. (M.) pulverus is discussed. Varietal taxa are synonymized, and subspecific taxa are synonymized with the exceptions of A. (M.) balzani pampanus, while myersi is transferred to subspecific status of landolti. The taxa are examined with respect to their biogeography. A. (M.) landolti is reinterpreted, and a Pleistocene refugia pattern of species distributions is suggested.*

**KEY-WORDS:** Acromyrmex; Moellerius; taxonomy; distribution grass-cutting ants.

---

### INTRODUCTION

The subgenus *Moellerius* of the attine genus *Acromyrmex* is of considerable interest for two major reasons. Firstly, the taxa that comprise this subgenus are of open or shrub rangelands, and are generally harvesters of grasses. Due to this behavior, certain taxa are considered as primary rangeland pests of the Neotropics<sup>24, 25</sup>. Secondly, these same taxa are considered to evidence a morphological transition between taxa of *Acromyrmex (Acromyrmex)* and *Atta*, principally based on the reduction of the medial pronotal spines<sup>8</sup>. If such is indeed the case, our current concepts of the evolution of leaf-cutting ants may be radically altered.

In this contribution, I review the taxa currently known to comprise the subgenus *Moellerius*. It is hoped that this present contribution will help to resolve the taxonomy of this unique group of ants, and to eventually enable future interpretations of attine phylogeny and evolution. Much of this work was completed during the time period 1980 to 1982. Because the late GONÇALVES<sup>29</sup> was at that time revising the genus *Acromyrmex*, I exchanged my views with him, and was anxiously awaiting his complete revision. Unfortunately, his efforts were cut short by his death following a long illness, and I have decided to present the results of my work, dedicating this contribution to the memory of him.

### BIONOMICS

As in all attines, taxa of *Moellerius* are fungus-growers and have an obligate symbiotic relationship with their fungus<sup>55</sup>. As like taxa of the genus *Atta*, taxa of the genus *Acromyrmex*

---

\* Departamento de Ecologia - Instituto de Biociências - UNESP - 13500 - Rfo Claro - SP.

harvest live vegetation as a fungal substrate, and are collectively known as leaf-cutting ants. This behavior separates these two genera from the other attine genera, as these only infrequently use fresh vegetation as a fungal substrate.

Taxa of *Moellerius* are unique in that, as a group, they are found in open habitats. Nests are characteristic of the taxa, and nest architecture and behavior are useful criteria in resolving their relations. Details of nest architecture and behavior can be found in various works<sup>5, 6, 7, 15, 22, 24, 25, 26, 29, 37</sup>.

The interaction of morphology and behavior is marked in the taxa of *Moellerius*. All taxa of the nominate subgenus, and indeed all taxa of *Atta* that harvest dicotyledonous plants characteristically anchor their metathoracic legs at a leaf edge, and then, using their long, scissors-like mandibles, cut out semi-circular sections using the point of attachment of the metathoracic legs as the point of rotation. Taxa of *Moellerius* have specialized, short, compact mandibles, and when compared with broad-leaf harvesters, have relatively shorter metathoracic legs. Due to these morphological characteristics, their behavior when harvesting vegetation is quite different<sup>25</sup>.

Members of *Moellerius* have specialized on plants found in Neotropical rangelands. All taxa generally harvest grasses. However, *A. (M.) versicolor* is known to harvest xeric broad-leaf vegetation<sup>27</sup>, and *A. (M.) striatus* also infrequently harvests dicots<sup>29</sup>. *A. (M.) silvestrii* (= *mesopotamicus*) is reported to cut citrus (?)<sup>26</sup>, while other taxa may infrequently harvest dicot flowers<sup>25</sup>.

## NOMENCLATURAL HISTORY

The genus *Acromyrmex* has experienced a long and varied nomenclatural history, with inclusive taxa having been placed in four distinct genera: *Formica* L., 1758; *Atta* Fabricius, 1804<sup>15</sup>; *Myrmica* Latreille, 1818; and *Oecodoma* Latreille, 1818<sup>34</sup>. *Acromyrmex* was described by MAYR<sup>36</sup>, and interpreted as a subgenus of *Atta*. It included the smaller attines, which corresponded to the Second Division of SMITH<sup>49</sup>. The type species for this taxon is *A. hystrix* (Latreille, 1802)<sup>33</sup>, originally described from a worker from Cayenne, French Guiana, and is now in the Latreille Collection of the Museu d'histoire Naturelle of Paris.

FOREL<sup>17</sup> described *Moellerius* as a subgenus of *Atta* to group the distinctive taxa, *A. landolti* Forel and *A. balzani* Emery. *A. landolti* is the type of *Moellerius*, and was described from a worker collected from an unspecified locality in Colombia. The type is now in the Forel Collection of the Museu d'Histoire Naturelle of Geneva. By describing new taxa and transferring previously described taxa, EMERY<sup>10</sup> broadened the interpretation of the subgenus *Moellerius*. Subsequently, EMERY<sup>12</sup> elevated *Acromyrmex* to the rank of genus, and included *Moellerius* as a subgenus. The revisions of the genus *Acromyrmex* by SANTSCHI<sup>47</sup> and GONÇALVES<sup>29</sup> have followed this placement.

## DIAGNOSIS OF MOELLERIUS

Taxa of this subgenus may be distinguished from those of the nominate subgenus due to their lack of supra-ocular spines; by having short, weakly recurved mandibles, which are not sinuous at the borders; and by behavioral differences in fungal preparation and habitat preference. Taxa of the nominate subgenus have long, strongly recurved mandibles, which are sinuous along the margins, and have prominent supra-ocular spines.

## TERMINOLOGY

I have opted to use a terminology somewhat distinct to that employed by previous students of this group, and have thus homologized the morphological characters of these ants with those of other Hymenoptera<sup>52</sup>. These terms are given in Table 1, and are illustrated in Fig. 1.

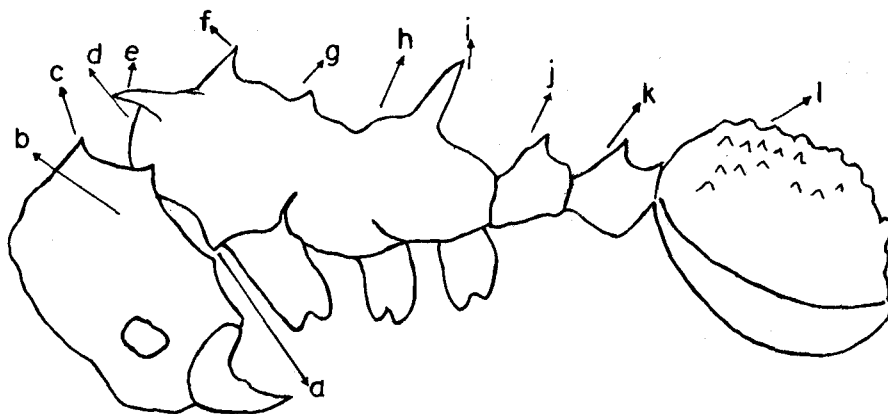


FIG. 1. *Acromyrmex (Moellerius) versicolor*. Letters correspond to characters listed in Table 1. Note that characters b and d are absent, or so vestigial that they do not appear in *A. versicolor*.

**TABLE 1 – TERMINOLOGY EMPLOYED IN THIS PAPER AND ITS CORRESPONDENCE TO TERMINOLOGY ENCOUNTERED IN OTHER TAXONOMIC WORKS ON ACROMYRMEX (MOELLERIUS). CHARACTERS ARE ILLUSTRATED IN FIG. 1.**

Character	Previous Terminology	Terminology Employed Here
a	inferior pronotal spine	inferior pronotal spine
b	supra-ocular spine	supra-ocular spine
c	occipital spine	occipital spine
d	medial pronotal spine	medial pronotal spine
e	lateral pronotal spine	lateral pronotal spine
f	anterior mesonotal spine	anterior mesonotal spine
g	posterior mesonotal spine	posterior mesonotal spine
h	epinotal crest	metanotal crest
i	epinotal spine	propodeal spine
j	petiole	petiole (1st gastral segment)
k	post-petiole	post-petiole (2nd gastral segment)
l	1st segment of gaster	3rd gastral segment

## KEY TO THE MAJOR WORKERS

1 – Antennal scape lobed basally .....	2
– Antennal scape without a basal lobe .....	3
2 – Integument with a vestiment of whitish scales .....	<i>pulverus</i>
– Integument without whitish scales .....	<i>fracticornis</i>
3 – Third gastral segment without tubercles, smooth and striate .....	4
– Third gastral segment tuberculate, never striate .....	5
4 – Frons and vertex of head smooth .....	<i>silvestrii</i>
– Frons and vertex longitudinally striate .....	<i>striatus</i>
5 – Integument with microscopic reticulation .....	6
– Integument devoid of microscopic reticulation .....	7
6 – Propodeal spine length more than 2X basal width, and recurved obliquely posteriorly .....	<i>heyeri</i>
– Propodeal spine length not greater than 2X basal width, and not recurved ..	<i>versicolor</i>
7 – Medial pronotal spine tuberciform; lateral pronotal spine well developed, oriented acutely anteriorly .....	<i>landolti</i>
– Medial pronotal spine tuberciform to prominent; lateral pronotal spine erect or oriented posteriorly .....	<i>balzani</i>

## MATERIAL EXAMINED

All material used for these studies came from the Museum of Comparative Zoology of Harvard University, the American Museum of Natural History, the Museo de Zoologia of the Instituto Miguel Lillo, and the personal collection of H. G. Fowler. More than 6,000 specimens have been examined during this study.

*Acromyrmex (Moellerius) balzani* (Emery)

*Atta (Acromyrmex) balzani* EMERY<sup>9</sup>: 67, ♀; EMERY<sup>10</sup>; FOREL<sup>20</sup>.

*Acromyrmex (Moellerius) balzani*, SANTSCHI<sup>43, 45, 47</sup>; GALLARDO<sup>26</sup>; EMERY<sup>13</sup>; BORGMEIER<sup>2</sup>.

*Atta (Acromyrmex) sp.*, EMERY<sup>10</sup>; GONÇALVES<sup>29</sup>.

*Acromyrmex (Moellerius) var. parens* SANTSCHI<sup>48</sup>; GONÇALVES<sup>29</sup> (syn.)

*Acromyrmex (Moellerius) parens var. parens*, BORGMEIER<sup>2</sup>; GONÇALVES<sup>29</sup> (syn.)

*Acromyrmex (Moellerius) landolti*, FOREL<sup>20</sup>.

*Acromyrmex (Moellerius) landolti*, MANN<sup>35</sup>; SANTSCHI<sup>45, 47, 48</sup>; BORGMEIER<sup>2</sup>.

*Acromyrmex (Moellerius) landolti nivalis* SANTSCHI<sup>45</sup>: 362, ♀; GONÇALVES<sup>29</sup> (syn.)

*Acromyrmex (Moellerius) landolti balzani*, GONÇALVES<sup>29</sup> (syn); FOWLER<sup>23, 24, 25</sup>.

*Sericomyrmex gallardoi* SANTSCHI<sup>44, 45</sup> (syn.)

TYPE LOCALITY: Asunción (?); Paraguay.

*Acromyrmex (Moellerius) balzani pampanus* Weber *Acromyrmex (Moellerius) balzani pampanus* WEBER<sup>54</sup>: 200 ♀, ♀, ♂;

*Acromyrmex (Moellerius) balzani var. multituber* SANTSCHI<sup>45</sup>: 262, ♀; SANTSCHI<sup>48</sup>. (NEW SYNONYM)

TYPE LOCALITY: Rosario on Lake Roãgua, Beni, Bolivia.

MAJOR WORKERS: (Fig. 2)

**Diagnosis:** Eyes small, not salient. Medial pronotal spines tuberciform to prominent, being much more conspicuous than in *landolti*. In *pampanas*, this spine is not developed, and resembles that of *landolti*. Lateral pronotal spines either erect or angled obliquely toward the posterior of the body. Mesonotal crest visible.

**Description:** EMERY<sup>9</sup> and WEBER<sup>53</sup>.

**Variation:** The variation between colonies in any local population is not great. However, between populations, there is a great deal of variation in cephalic tuberculation, ranging from indistinguishable to pronounced. These characters were those employed by SANTSCHI<sup>46, 47</sup> in distinguishing the subspecies *nivalis* and *senex*, as well as slight variations in the thoracic spine lengths. As such, and due to the wide variation exhibited in these characters, I choose not to

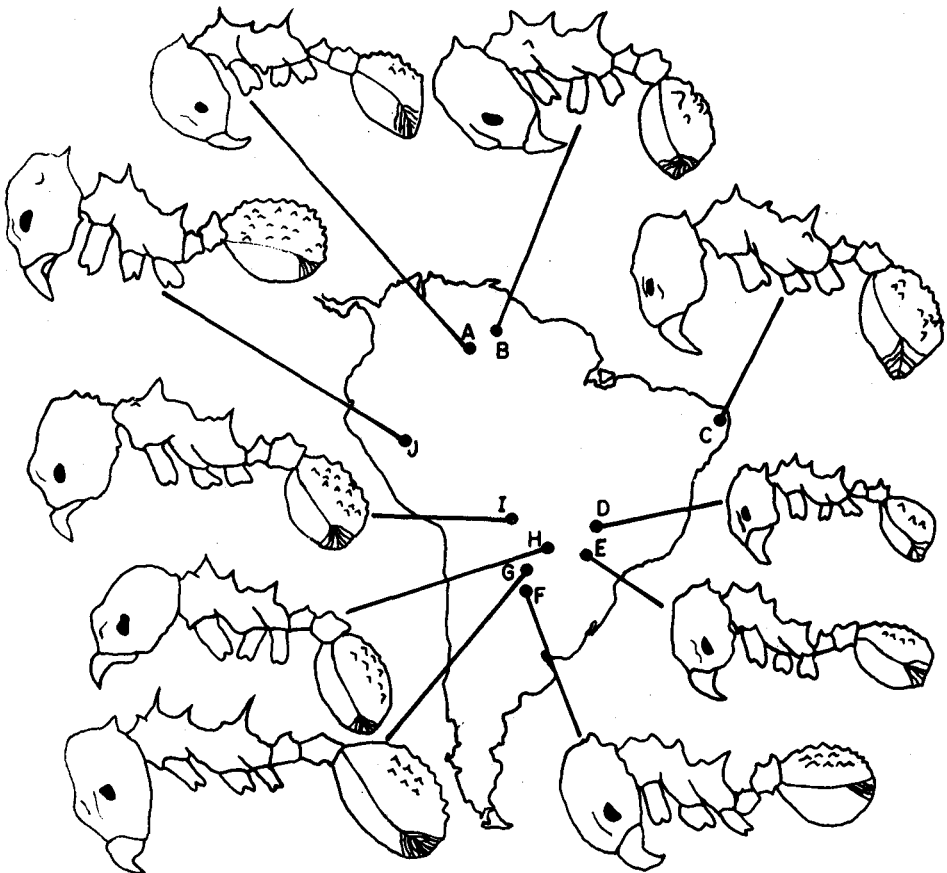


FIG. 2. The distribution and worker variation found in the *landolti* group of species. Letters on the map refer to the following taxa: A = *landolti landolti*; B = *landolti myersi*; C-E = *balzani balzani*; F-G = *fracticornis*; H = *balzani balzani*; I-J = *balzani pampanus*.

recognize these taxa. It should be pointed out that intranidal variation is much more pronounced than internidal variation. Minor workers of *balzani* have a marked reduction of thoracic spination and cephalic and gastral tuberculation. As such, it is impossible to distinguish minor workers of *balzani* from those of *landolti*. Due to this variation in tuberculation, *multituber* must also be synonymized with *pampanus*.

Discussion: It is intriguing how the taxa *balzani* and *landolti* were synonymized, in spite of the (erroneously) recorded sympatry. It is unlikely that the *landolti* group of species (*landolti*, *balzani*, and *fracticornis*) are just these. Rather, this group probably consists of an array of sibling species, especially if the Pleistocene refugia model can be substantiated (see section of Biogeography). Based upon the variation that I have encountered, it would seem that *balzani* is restricted to the south of the Amazon basin, with the western populations probably constituting a distinct, valid species. However, due to the lack of a large series of material from Bolivia and Peru, I have chosen to follow convention and assign these populations to the subgenus *pampanus*.

Distribution: Figs. 2 and 6.

*A. (M.) balzani*, due to worker morphology, nest structure and general behavioral patterns is a member of the *landolti* species group.

*Acromyrmex (Moellerius) fracticornis* (Forel)  
(NEW STATUS)

*Atta (Moellerius) fracticornis*, FOREL<sup>19</sup>: 257, ♀; EMERY<sup>13</sup> (syn.).

*Acromyrmex (Moellerius) fracticornis*, EMERY<sup>13</sup>; SANTSCHI<sup>48</sup>; GONÇALVES<sup>29</sup> (syn.)

*Acromyrmex (Moellerius) fracticornis* var. *joergenseni* FOREL<sup>22</sup>: 236 ♀; GONÇALVES<sup>29</sup> (syn.)

*Acromyrmex (Moellerius) landolti fracticornis*, GONÇALVES<sup>29</sup>; FOWLER<sup>23, 24, 25</sup> (syn.)

TYPE LOCALITY: San Bernadino, Cordillera, Paraguay.

MAJOR WORKERS: (Fig. 2)

Diagnosis: Eyes not salient. Integument devoid of microscopic reticulation. Medial pronotal spines vestigial or absent. Propodeal spines length greater than basal width, and directed posteriorly. Mesonotal spines well developed and erect. In *A. (M.) landolti*, these spines, when present, are directed posteriorly or are poorly developed. Antennal scape with a marked curvature and lobe basally, while other species of the *landolti* species group have scapes of the normal type.

Description: FOREL<sup>19</sup>.

Variation: Internidal variation between workers in any local population is generally low. However, on the northern and southern ridges of its range, *A. (M.) fracticornis* does not show a marked curvature and lobe of the scape, but rather a slight curvature, and an almost indistinct lobe. Due to these gradations, GONÇALVES<sup>29</sup> considered *fracticornis* to be a subspecies of *landolti*. However, I feel that this character is more characteristic. Earlier I<sup>23</sup> described distinct variations in worker morphology, nest types, nest densities, and habitat, which serve to distinguish *balzani* from *fracticornis*.

Intranidal variation is pronounced due to allomorphic scaling patterns related with worker polymorphism. In the smaller workers, all spines are reduced, but the scape retains its characteristic form. Males are characteristic (Fig. 3).

The male genitalia is distinct from that of *landolti* and *striatus* (Fig. 5). The basic difference lies in the strongly lobed gonostyle (Fig. 5), which is much reduced in the other taxa.

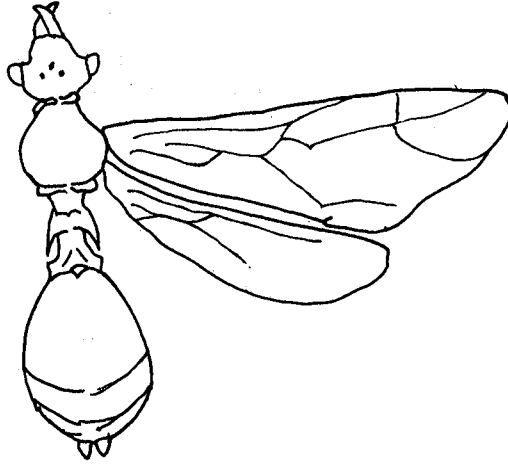


FIG. 3. Habitus of male *Acromyrmex fracticornis* from Asunción, Paraguay.

*Acromyrmex (Moellerius) heyeri* (Forel)

*Atta (Moellerius) heyeri* FOREL<sup>17</sup>: 31, ♀; EMERY<sup>10</sup>: 111, ♀, ♀; FOREL<sup>21</sup>; BRUCH<sup>4</sup> (syn.) FOREL<sup>18</sup>.

*Acromyrmex (Moellerius) heyeri*, BRUCH<sup>4</sup>; SANTSCHI<sup>43, 48</sup>; GALLARDO<sup>26</sup>; EMERY<sup>13</sup>; BORGMEIER<sup>2</sup>; GOMES COSTA<sup>28</sup>; GONÇALVES<sup>29</sup>; FOWLER<sup>23, 24, 25</sup>.

*Atta (Acromyrmex) lundj*, ROGER<sup>41</sup>: 200, ♀; EMERY<sup>9</sup>; IHERING<sup>31</sup>; GONÇALVES<sup>29</sup> (syn.)

*Atta hystrix*, BERG<sup>1</sup>; GONÇALVES<sup>29</sup> (syn.)

*Acromyrmex (Moellerius) heyeri* var. *gaudens* SANTSCHI<sup>47</sup>: 164, ♀; SANTSCHI<sup>48</sup> (NEW SYNONYM).

*Acromyrmex (Moellerius) heyeri* var. *lillensis* SANTSCHI<sup>47</sup>: 165, ♀; SANTSCHI<sup>48</sup> (NEW SYNONYM).

TYPE LOCALITY: São Leopoldo, Rio Grande do Sul, BRAZIL.

MAJOR WORKERS: (Figs. 2 and 4)

Diagnosis: Eyes small, salient. Integument with microscopic reticulation. Anterior mesonotal spines and lateral pronotal spines well developed. Median pronotal spines vestigial or absent. Propodeal spines much longer than basal width, and directed posteriorly at an obtuse angle.

Description: FOREL<sup>17</sup>.

Variation: Variation among workers in a local population is slight with respect to spination. On a larger scale (Fig. 4) demonstrate considerable variation in the shape and orientation of the pronotal spines, as well as in coloration. The more eastern populations are characterized by a darker gaster, and are more bicolored than western populations. Within a nest, worker variation is strong, with minor workers generally showing weakly developed spination, although the epinotal spines are quite well developed and are characteristic.

Due to lack of evidence that the varieties *lillensis* and *gaudens* are allopatric and distinct enough to recognize varieties, these forms are synonymized. Based on their known

distributions, these varieties are in fact sympatric, and nothing suggests that there is a break in morphological variation associated with any obvious geographic feature to warrant subspecific status. SANTSCHI<sup>47</sup> based the variety descriptions on cephalic sculpture and coloration, but these differences are so slight and variable that they can be found within a single nest.

Distribution: (Fig. 6).

*Acromyrmex (Moellerius) landolti* (Forel)

*Atta (Acromyrmex) landolti* FOREL<sup>17</sup>: 357, ♀; EMERY<sup>9</sup>.

*Atta (Moellerius) landolti*, EMERY<sup>10</sup>.

*Acromyrmex (Moellerius) landolti* EMERY<sup>13</sup>; SANTSCHI<sup>47</sup>; WHEELER<sup>57</sup>.

*Acromyrmex (Moellerius) landolti cloosae* FOREL<sup>21</sup>: 179, ♀ (NEW SYNONYM).

*Acromyrmex (Moellerius) balzani planorum* WEBER<sup>53</sup>: 409, ♀ (NEW SYNONYM).

TYPE LOCALITY: Unspecified, Colombia.

*Acromyrmex (Moellerius) landolti myersi* (Weber)  
(NEW SYNONYM)

*Acromyrmex (Moellerius) balzani myersi* WEBER<sup>53</sup>: 408, ♀.

TYPE LOCALITY: Rupununi savanna, Guiana.

MAJOR WORKERS: (Fig. 2)

Diagnosis: Eyes small, not salient. Medial pronotal spines reduced, crest like, much less than observed in either *balzani* or *fracticornis*. Lateral pronotal spines with broad base and slightly acute (*landolti landolti*) or at an acute angle and oriented anteriorly (*landolti myersi*). Anterior mesonotal spine mucronated, well developed, especially in *landolti myersi*. Posterior mesonotal spine absent.

Description: FOREL<sup>17</sup>.

Variation: Between geographic populations, variation in cephalic tuberculation is readily apparent, but this variation follows no clinal pattern. This character was the major one used to separate *balzani* and *landolti*, but is too variable to be used with confidence. Within a nest the smaller workers are characterized by a marked reduction of gastral tuberculation and thoracic spination.

The male genital capsule (Fig. 5) differs from that of *fracticornis* by its lack of lobed gonostyles, and from that of *A. striatus* which has a more open gonostyle, which is strongly angled, unlike that of *landolti*.

The descriptions of nest structure<sup>14,37</sup>, indicate striking differences from the nests of *balzani* and *fracticornis*, as previously discussed<sup>23</sup>. Chief differences include multiple nest openings which are distant. The nests of *balzani* generally have one nest entrance, while *fracticornis* may have various, but these are on a nest mound. This behavioral difference adds further support to the species status which returns to these taxa.

Distribution: (Fig.6).



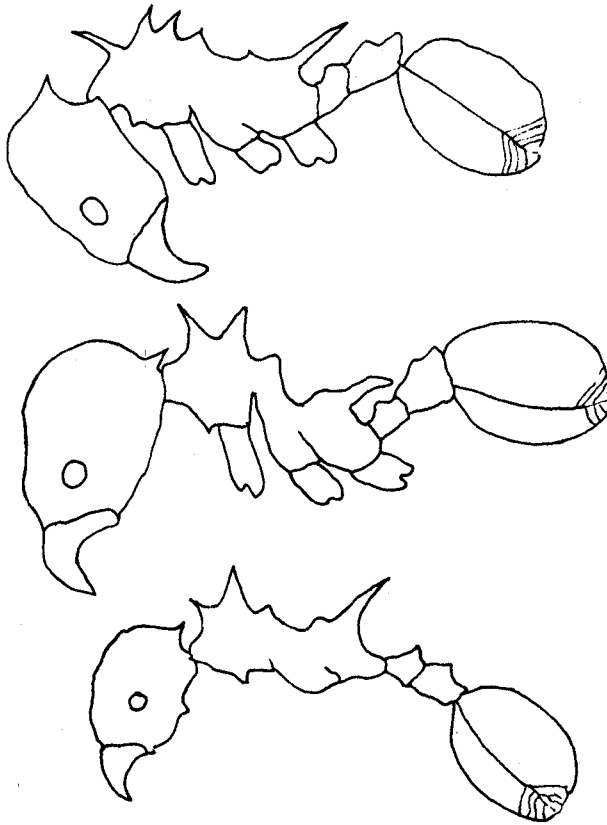


FIG. 4. Worker variation in *Acromyrmex heyeri*. Northernmost populations at top, southernmost population at the bottom.

*Acromyrmex (Moellerius) pulvereus* Santschi  
(*Nomina dubia*)

*Acromyrmex (moellerius) pulvereus* SANTSCHI<sup>44</sup>:52, ♀; SANTSCHI<sup>47</sup>.  
TYPE LOCALITY: Unquillo, Cordoba, Argentina.

MAJOR WORKER:

Diagnosis: According to SANTSCHI<sup>44</sup> this species differs from the typical *fracticornis* by having whitish scales on the body.

Discussion: The description provided by SANTSCHI should be interpreted with caution. The presence of whitish scales on workers would indeed be unique for attini. It is more probable, however, that this is really a *fracticornis* which either obtained the "whitish scales" from a collecting fluid, or possessed a fungal disease. It is interesting that, in spite of the seeming uniqueness of this "taxon", it was not highlighted in the generic revision by SANTSCHI<sup>47</sup>.

Moreover, the type locality abutts with the geographic range of *fracticornis* (Fig. 6), and is only know form its type. I have not seen the type, and must retain this taxon with much reservation.

*Acromymex (Moellerius) silvestrii* (Emery)

*Atta (Moellerius) silvestrii* EMERY<sup>10</sup>: 108, ♀; EMERY<sup>11</sup>; FOREL<sup>20</sup>.

*Acromymex (Moellerius) silvestrii*, SANTSCHI<sup>47</sup>.

*Acromymex (Moellerius) mesopotamicus* GALLARDO<sup>26</sup>: 337, ♀; SANTSCHI<sup>47</sup>. (NEW SYNONYM)

TYPE LOCALITY: La Carlota, Cordoba, Argentina.

MAJOR WORKER:

Diagnosis: Thoracic spines variable, ranging from poorly developed (ex. *mesopotamicus*) to well-developed. Medial pronotal spines vestigial or absent. Carinae and frons heavily striated, which is not the case in *striatus*.

Description: EMERY<sup>10</sup>.

Variation: This taxon is highly variable with respect to thoracic spination. Generally, more northern populations have longer spines, but a large degree of inter and intranidal variation in this character obviates its taxonomic usefulness. SANTSCHI<sup>47</sup> commented upon the apparent hybridization of *mesopotamicus* with *silvestrii*, in that phena classifiable to both could be found in the same nest, as well as intermediate forms. After examining many specimens from Argentina, I have found that this is indeed true, and prudence calls for the taxon of *mesopotamicus* to be synonymized with *silvestrii*.

Distribution: (Fig. 6).

*Acromymex (Moellerius) striatus* (Roger)

*Atta striata* ROGER<sup>41</sup>: 202-203, ♀, ♀, ♂.

*Atta (Acromymex) striata*, IHERING<sup>31</sup>.

*Atta (Moellerius) striata*, EMERY<sup>10, 11</sup>; FOREL<sup>21</sup>; SANTSCHI<sup>42</sup>.

*Acromymex (Moellerius) striatus*, BRUCH<sup>4</sup>; GALLARDO<sup>26</sup>; SANTSCHI<sup>43</sup>; BORGMEIER<sup>2</sup>; WHEELER<sup>57</sup>; CARBONELL<sup>7</sup>; FERREIRA LIMA<sup>16</sup>; KUSNEZOV<sup>32</sup>; GOMES COSTA<sup>28</sup>; GONÇALVES<sup>29</sup>; FOWLER<sup>24, 25</sup>.

*Acromymex (Moellerius) striatus* var. *laeviventris* SANTSCHI<sup>44</sup>: 320, ♀ (NEW SINONYM).

TYPE LOCALITY: Montevideo, Uruguay.

MAJOR WORKER:

Diagnosis: Gena with longitudinal striations. Medial pronotal spines absent or vestigial. Lateral pronotal spines and anterior mesonotal spines well developed. 3rd gastral segment smooth and shiny, without tubercules.

Description: ROGER<sup>41</sup>.

Variation: This species is the least variable of all taxa of this subgenus. The variety *laeviventris* was based solely upon the coloration of the gaster, and not be further recognized. This taxon can be grouped with *silvestrii* and *heyeri* based upon worker morphology and

geographical range. Due to the constancy of taxonomic markers, this taxon does not present any serious problem. As in all taxa of *Acromyrmex*, the trend for reduced thoracic spination in minor workers is present, although the genal striations remain present.

Distribution: Fig. 6.

*Acromyrmex (Moellerius) versicolor* (Pergande)

*Atta versicolor* PERGANDE<sup>38</sup>: 31, ♀.

*Atta (Moellerius) versicolor*, EMERY<sup>10</sup>; WHEELER<sup>56</sup>; SMITH<sup>50</sup>.

*Acromyrmex (Moellerius) versicolor*, EMERY<sup>13</sup>; CREIGHTON<sup>8</sup>.

TYPE LOCALITY: Calamujit, Baja California, Mexico.

*Acromyrmex (Moellerius) versicolor chisosensis* (Wheeler)

*Atta (Moellerius) versicolor chisosensis* WHEELER<sup>56</sup>: 705, ♀.

*Acromyrmex (Moellerius) versicolor chisosensis*, EMERY<sup>14</sup>; CREIGHTON<sup>8</sup>.

TYPE LOCALITY: Chisos Mountains, Texas, United States of America.

MAJOR WORKER: (FIG. 1).

Diagnosis: Medial pronotal spine well developed and with an acute inclination, oriented anteriorly. Eyes small, convex and salient. Propodeal spine much longer than its basal width.

According to WHEELER<sup>56</sup>, *chisosensis* can be distinguished from the nominate subspecies by being a lighter color, and by being markedly shinier, due to a reduction of cephalic sculpture.

Description: PERGANDE<sup>38</sup> and WHEELER<sup>56</sup>.

Variation: The workers I examined were quite uniform with respect to thoracic spination, irrespective of size. In smaller workers, there is a tendency toward a reduction of the tuberculation of the 3rd gastric segment, and the two subspecies are not distinguishable if small workers are used. The propodeal spines are well developed in workers of all sizes, but the thoracic spines tend to reduce in smaller workers.

This taxon is probably the most xeric adapted of the subgenus. It is apparently unique in that it heavily cuts xeric dicotyledonous plants<sup>27</sup>, although the mechanics of cutting are typical of the subgenus. This taxon is comprised of two disjunct subspecies, and is disjunct from other taxa of *Moellerius*.

Distribution: Fig. 6.

## BIOGEOGRAPHY

The concentration of taxa of *Acromyrmex (Moellerius)* south of the tropics of South America, as well as the disjunct, amphitropical distribution of *Acromyrmex (Moellerius)* as a whole, with the exception of *A. (M.) landolti (sensu lato)*, is reminiscent of the similarities of the disjunct flora of the arid and semi-arid regions of North and South America<sup>39</sup>. The high degree of biogeographic congruence between the taxa of *Prosopis* (Leguminosae) and *Acromyrmex (Moellerius)* suggests that they have experienced a common evolutionary history. This argument, however, runs contrary to other studies of the fauna north and south of the New

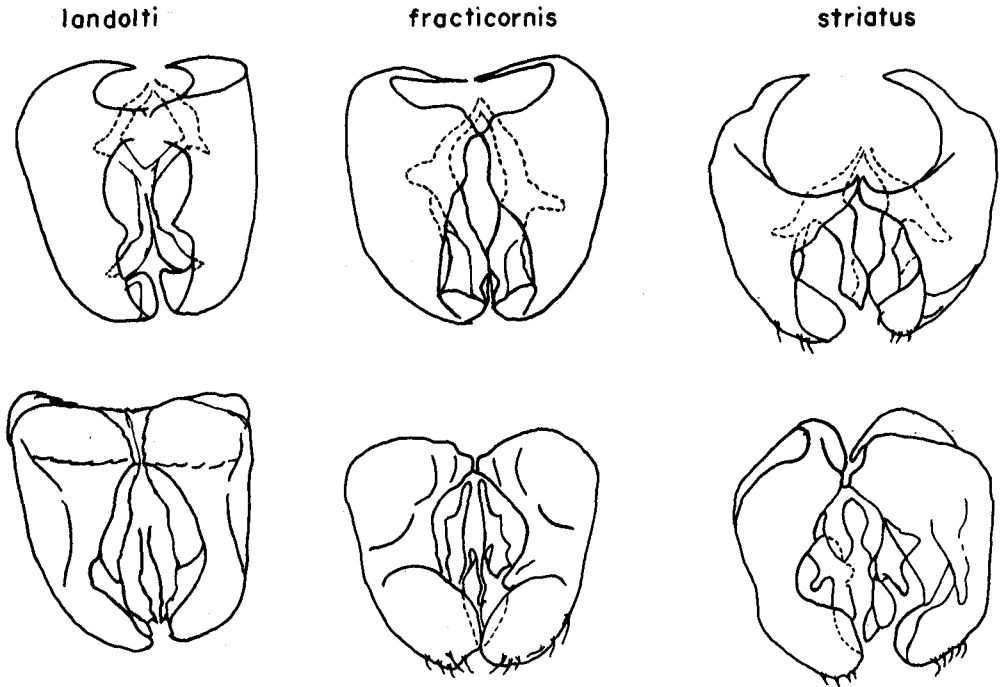


FIG. 5. Male genital capsules of three species of *Acromyrmex* (*Moellerius*), *A. landolti*, *A. fracticornis* and *A. striatus*.

World tropics, which have failed to document faunal similarity, and which support the theory of long-distance dispersal of the flora, notably of the genera *Prosopis* and *Larrea*, but not of the fauna<sup>30, 40, 51</sup>.

It is dubious that the taxa of *Acromyrmex* (*Moellerius*) are dependent upon the plant genera *Prosopis* and *Larrea*, due to their harvesting behavior, the nature of their fungus gardens, and general tendency to harvest grasses. Even though *A. (M.) versicolor* relies heavily upon these plant genera<sup>27</sup>, this behavior was probably derived. A common paleoecologic origin of the plant and ant taxa is a more likely explanation for contemporary biogeographic patterns. Indeed, zones of late Pleistocene caatinga in South America<sup>3</sup> are congruent with the contemporary distribution of the taxa of *Acromyrmex* (*Moellerius*) (Fig. 6).

Difficulties arise in explaining the disjunct distribution of *A. (M.) versicolor* from the other taxa. The absence of any related taxa in Central America and most of Mexico suggests that, if dispersal occurred via islands of suitable caatinga vegetation during the Pleistocene, then the subsequent reduction of these enclaves occurred in such a manner that endemism could not be supported, and these hypothetical taxa of intermediate taxonomic status became extinct. It could also be argued that the presence of *A. (M.) versicolor* in Northern Mexico and the southwestern United States resulted from an exceptionally long-distance dispersal, which seems highly improbable. It is possible that uncollected taxa occur in Central America, but due to the conspicuousness of these ants, as well as the absence of large areas of appropriate habitat, this possibility also seems improbable. Further biogeographic and systematic work is obviously needed to explain this most interesting distributional pattern.



FIG. 6. The geographic distribution of taxa of *Acromyrmex* (*Moellerius*).

Examining the contemporary distribution of the taxa of *Acromyrmex* (*Moellerius*) (Fig. 6), the Pleistocene caatinga refuge model is strongly supported, as all existant taxa are found in areas that were within the natural domains of the caatinga 13,000 to 18,000 B.P.<sup>3</sup> As these expansive enclaves of caatinga shrunk, the stage was then set for classical allopatric speciation. The marked congruence of the Neotropical taxa with Pleistocene caatinga suggest the pattern, and additional collections from northeastern Argentina, eastern Paraguay, southeastern Bolivia, and the states of Mato Grosso, Pará, and other savanna areas from the Amazon could provide definitive proof of the refuge model, or suggest alternative explanations. By considering the potential geographic barriers, notably the Andes and the Amazon rain forest, it seems highly unlikely that populations freely interbreed, and that the taxa recognized here are valid.

FWLER, H.G. – Taxa das formigas cortadeiras de grama neotropicais, *Acromyrmex* (Moellerius) (Hymenoptera: Formicidae). *Científica*, São Paulo, 16(2): 281-296, 1988.

**RESUMO:** Dados biológicos e de distribuições das espécies descritas de *Acromyrmex* (Moellerius) são usados para clarificar a taxonomia do grupo. *A.(M.) fracticornis* e *A.(M.) balzani* são elevadas ao nível de espécie, e *A.(M.) mesopotamicus* se considera como sinônimo de *A.(M.) silvestrii*. É discutida a espécie enigmática *A.(M.) pulvereus*. As variedades são sinonimizadas, como muitas subespécies. *A.(M.) balzani pampanus* se mantém, mas *myeresi* é transferida para *landolti*. Neste trabalho é discutida a biogeografia das espécies. *A.(M.) landolti* tem uma interpretação nova, e um modelo de refúgio pleistocênico se propõe para explicar os padrões de distribuição das espécies.

**UNITERMOS:** *Acromyrmex*; Moellerius; taxonomia; distribuição; formigas cortadeiras.

## REFERENCES

1. BERG, C. – Enumeración sistemática de los formicideos argentinos, chilenos y uruguayos. *An. Soc. Cient. Argent.*, 29: 5-43, 1980.
2. BORGMEIER, T. – Catálogo sistemático e sinonímico das formigas do Brasil. Parte II. *Arch. Mus. Nac.*, 29: 67-164, 1927.
3. BROWN, K. S., JR. & AB'SABER, A. N. – Ice-age forest refuges and evolution in the Neotropics: correlation of paleoclimatological, geomorphological and pedological data with modern biological endemism. *Paleoclimas*, 5: 1-30, 1979.
4. BRUCH, C. – Catálogo sistemático de los formicideos argentinos. *Rev. Mus. La Plata*, 19: 154-169, 1914.
5. BRUCH, C. – Costumbres y nidos de hormigas. *Physis*, 4: 539-541, 1919.
6. BRUCH, C. – Costumbres y nidos de hormigas. 2ª Parte. *An. Soc. Cient. Argent.*, 84: 144-168, 1919.
7. CARBONELL, C. S. – Las hormigas cortadoras del Uruguay. *Rev. Assoc. Ing. Agron.*, 3: 1-12, 1943.
8. CREIGHTIN, W. S. – The ants of North America. *Bull. Mus. Comp. Zool.*, 104: 1-585, 1950.
9. EMERY, C. – Voyage de M. E. Simon au Venezuela. Formicidae. *Ann. Soc. Entomol.*, 10: 55-76, 1890.
10. EMERY, C. – Revisions delle species del genere *Atta* appartenenti ai sottogeneri *Moellerius* e *Acromyrmex*. *Mem. Acad. Sci. Inst.*, 6: 107-122, 1905.
11. EMERY, C. – Studi sulle formiche della fauna neotropica. XXVI. *Bul. Soc. Entomol. Ital.* 37: 107-194, 1905.
12. EMERY, C. – Etudes sur les Myrmicinae. V-VII. *Ann. Soc. Entomol. Belg.* 57: 250-262, 1913.
13. EMERY, C. – Fam. Formicidae, Subfam. Myrmicinae. In: WYTSMAN, ed. *Genera Insectorum*. s.1., s. ed. 1922.
14. ESPINA, E. R. & TIMAURE, A. – Características de los nidos de *Acromyrmex landolti* (Forel) en el oeste de Venezuela. *Rev. Agron. Zulia*, 4: 53-62, 1977.
15. FABRICIUS, J. C. – *Systema Piezatorum*. Brunsvigae, s. ed., 1804.
16. FERREIRA LIMA, A.D. – Insetos fitofagos de Santa Catarina. *Bol. Fitossanit.*, 2: 233-251, 1945.
17. FOREL, A. – Formicidae. *Biol. Centr. Amer., Hymenoptera*, 3: 1-169, 1899.
18. FOREL, A. – Ameisen aus São Paulo (Brasiline), Paraguay, etc. *Verh. Z. B. Ges. Wein.*, 58: 340-418, 1908.
19. FOREL, A. – Ameisen aus Guatemala unsw. Paraguay und Argentinien. *Dtsch. Ent. Zeitschr.*: 239-269, 1909.

20. FOREL, A. – Ameisen der Herrn Prof. v. Ihering aus Brasilien (São Paulo usw.) nebst einigen anderen aus Sudamerika und Afrika. *Dtsch. Ent. Zeitschr.*: 285-312, 1911.
21. FOREL, A. – Formicides neotropiques. Part II. *Mem. Soc. Ent. Belg.*, 19: 179-209, 1912.
22. FOREL, A. – Fourmis d'Argentine, du Bresil, du Guatemala et de Cuba. *Bull. Soc. Vaud. Sci. Nat.*, 49: 203-250, 1913.
23. FOWLER, H. G. – *Acromyrmex (Moellerius) landolti* Forel en el Paraguay: las subespecies *balzani* (Emery) y *fracticomis* (Forel) (Insecta: Hymenoptera). *Neotropica*, 23: 39-44, 1977.
24. FOWLER, H. G. – Las hormigas cortadoras del Paraguay de los generos *Atta* Fabricius y *Acromyrmex* Mayr. *Informes Cientificos, Univ. Nac. Asunción*, 2: 30-70, 1979.
25. FOWLER, H. G. – Leaf-cutting ants of the genera *Atta* and *Acromyrmex* of Paraguay (Hymenoptera: Formicidae). *Dtsch. Ent. Zeitschr.*, N.F., 32: 19-34, 1985.
26. GALLARDO, A. – Notes systematiques et ethologiques sur les fourmis Attines de la Rep. Argentine. *An. Mus. Nac. Hist. Nat.*, 28: 317-344, 1916.
27. GAMBOA, G. J. – Foraging and leaf-cutting of the desert gardening ant. *Acromyrmex versicolor* (Pergande) (Hymenoptera: Formicidae). *Ocoecologia*, 20: 102-110, 1975.
28. GOMES COSTA, R. – *As formigas cortadeiras de Rio Grande do Sul*. Porto Alegre, Universidade Federal, 1954. (Tese-Doutoramento).
29. GONÇALVES, C. R. – O gênero *Acromyrmex* no Brasil (Hym. Formicidae). *Studia Ent.*, 4: 113-180, 1961.
30. HURD JR, P. D. & LINSLEY, E.G. – The principle *Larrea* bees of the southwestern United States (Hymenoptera: Apoidea). *Smiths. Contr. Zool.*, 193: 1-74, 1975.
31. IHERING, H. von. – Die Ameisen von Rio Grande do Sul. *Berlin Ent. Z.*, 39: 321-446, 1894.
32. KUSNEZOV, N. – La fauna mirmecologica de Bolivia. *Fol. Univ. Cochabamba*, 6: 129-147, 1953.
33. LATREILLE, P. A. – *Historie naturelle des fourmis*. Paris, 1802. 445p.
34. LATREILLE, P. A. In: DETERVILLE, P. – *Nouv. Dict. Hist. Nat.* s.1., s. ed., 1818. v.23, p.50.
35. MANN, W. M. – The ants of Brazil. *Bull. Mus. Comp. Zool.*, 60: 399-490, 1916.
36. MAYR, G. L. – Die Formiciden der Reise der osterreichischen Fragatta "Novara" um die Erde in den Jahren 1857-1859. *Zoolog.*, 1: 1-119, 1865.
37. NAVARRO, J.G., & JAFFE, K. – On the adaptive value of nest features in the grass-cutting ant, *Acromyrmex landolti*. *Biotropica*, 17: 347-348, 1985.
38. PERGANDE, T. – On a collection of Formicidae from Lower California and Sonora, Mexico. *Proc. Cal. Acad. Sci.*, 4: 26-36, 1893.
39. RAVEN, P.H. – Amphitropical relations in the flora of North and South America. *Quart. Rev. Biol.*, 29: 151-177, 1963.
40. RAVEN, P. H., & AXELROD, D. I. – Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.*, 61: 539-673, 1974.
41. ROGER, J. – Die neu aufgefueherten Gattungen und Arten meines Formiciden Verzeichnisses. *Berlin Ent. Z.*, 7: 131-214, 1863.
42. SANTSCHI, F. – Quelques fourmis de l'Amerique australe. *Rev. Suisse Zool.*, 10: 519-534, 1912.
43. SANTSCHI, F. – Formicides sudamericains nouveaux ou peu connus. *Physis*, 2: 365-399. 1916.
44. SANTSCHI, F. – Nouveaux formicides de la Rep. Argentine. *An. Soc. Cient. Argent.*, 87: 37-57, 1919.
45. SANTSCHI, F. – Myrmicines, dolichoderines et autres formicides neotropiques. *Bull. Soc. Vaud. Sci. Nat.*, 54: 345-378, 1922.
46. SANTSCHI, F. – Nouvelles fourmis brasilennes. *Ann. Soc. Ent. Belg.*, 64: 5-20, 1924.
47. SANTSCHI, F. – Revision du genre *Acromyrmex* Mayr. *Rev. Suisse Zool.*, 31: 355-398, 1925.
48. SANTSCHI, F. – Nouveaux formicides brasiiliens et autres. *Bull. Ann. Soc. Ent. Belg.*, 65: 221-247, 1925.

49. SMITH, F. – Catalogue of hymenopterous insects in the collection of the British Museum. Part VI. Formicidae. London, Br. Mus. Nat. Hist., 1958.
50. SMITH, M. R. – A generic and subgeneric synopsis of the United States ants based on the workers. *Amer. Midl. Nat.*, 37: 521-647, 1947.
51. SOLBRIG, O. T.; BLAIR, W. F.; ENDERS, F. A.; HULSE, A. C.; HUNT, J. H.; MARIES, M. A.; NEFF, J.; OTTE, D.; SIMPSON, B. B. & TOMOFF, C. S. – The biota: the dependent variable. In: ORIANS, G. H. & SOLBRIG, O. T., eds. – *Convergent evolution in warm deserts*. Dowden, Hutchinson & Ross, 1977. p. 50-66. (US/IBP Synthesis Series 3.)
52. TULLOCK, G. S. – Morphological studies of the thorax of the ant. *Ent. Amer.*, 15: 93-130, 1935.
53. WEBER, N.A. – The biology of the fungus-growing ants. Part I. New forms. *Rev. Ent.*, 7: 378-409, 1937.
54. WEBER, N.A. – The biology of the fungus-growing ants. Part IV. Additional new forms. Part V. The attines of Bolivia. *Rev. Ent.*, 9: 154-206, 1938.
55. WEBER, N.A. – Gardening ants – the attines. *Mem. Am. Philos. Soc.*, 92: 1-146, 1972.
56. WHEELER, W.M. – The fungus-growing ants of North America. *Bull. Am. Mus. Nat. Hist.*, 23: 669-807, 1907.
57. WHEELER, W.M. – *Mosaics and other anomalies among ants*. Cambridge, Harvard Univ. Press., 1937. 179 p.

Recebido em 23.03.87.