

HISTORICAL RESUME

The seed-harvester ant genus *Pogonomyrmex* consists of 75 described species and subspecies that occur as three biogeographic faunas, one in North America (32 species) (Bolton, 2011; Johnson & Overson, 2012), one in South America (34 species plus six subspecies) (Bolton, 2011), and one on the Caribbean Island of Hispaniola (3 species) (Johnson & Cover, 2012); no species are common to any two faunal areas. The genus has a long history in both North and South America, but taxonomic progress on the South American fauna has lagged because of the paucity of South American taxonomists and ecologists.

The history of the genus *Pogonomyrmex* began with the description of two species that were initially placed in other genera, *Formica badia* (Latreille, 1802) from Carolina, United States, and *Atta bispinosus* from Chile (Spinola, 1851). It was not until 1868 that Gustav Mayr (Mayr, 1868) erected the genus *Pogonomyrmex* wherein he described three new species from Argentina (*P. coarctatus*, *P. rastratus*, and *P. carbonarius*); the latter two species would remain a taxonomic problem and their identity would remain in confusion for the next 140 years. Mayr published two additional papers on South American *Pogonomyrmex* (Mayr, 1870, 1887); the first paper described *P. angustus*, transferred *Atta bispinosus* (Spinola, 1851), *Formica badia*, and *Myrmica crudelis* (= *Atta crudelis*) to *Pogonomyrmex*, and he described two additional forms from North America (*P. opaciceps* [= *P. occidentalis*] and *P. subdentatus*), thus establishing *Pogonomyrmex* as a New World genus that occurred in both North and South America. The second paper described two additional species (*P. uruguayensis* and *P. cunicularius*) and (erroneously) placed *P. carbonarius* as a junior synonym of *P. rastratus*. Overall, Mayr defined the early history of *Pogonomyrmex* and he described a total of six species from South America. Only three additional species were described prior to 1900 (*P. mayri*, *P. theresiae* [described twice] and *P. naegelii*) (Forel, 1886, 1899a, 1899b, 1899c), though Emery (1878) had previously made

the name *P. naegelii* available. The only other substantive paper during this era was a catalogue for Hymenoptera of the world (Dalle Torre, 1893).

The next era for descriptions of South American *Pogonomyrmex* was dominated by three European entomologists, Auguste Forel, Carlos Emery, and Felix Santschi (Swiss, Italian, and Swiss, respectively). This era began with the description of several species by Emery (1906) and ended in 1936, just prior to the death of Felix Santschi. These three individuals collectively described 40 of the 59 forms of South American *Pogonomyrmex* known prior to this revision (Figure 1), as well as several thousand other ant species. These three authors also described numerous North American ant species, but relatively few of these species/subspecies were *Pogonomyrmex* (six of 56; four by Emery, two by Forel). There was a lull in species descriptions following the deaths of these three taxonomists with South America suffering most because of the lack of native ant taxonomists. Throughout this period, none of these authors saw any of these species in the field, but rather specimens were collected by South American naturalists (mostly Strobel, Dr. Charles Bruch, Dr. Carrete, Dr. Weiser, C. Berg), who sent the specimens to Europe for identification and/or description.

From the mid 1930's to the mid 1940's, several additional forms were described by other individuals: *P. ater* from Argentina (Donisthorpe, 1933), *P. bispinosus* var. *intermedia* from Chile (Mennozi, 1935), and *P. venezuelensis* and *P. venezuelensis* ssp. *rupununi* from Venezuela (Weber, 1943). However, Angel Gallardo was the first native taxonomist (from Argentina) to describe a South American species of *Pogonomyrmex* (*P. catanlilensis* and *P. longibarbis* from Argentina) (Gallardo, 1931). Problematically, the piecemeal one-species-at-a-time approach used by these authors resulted in most of these names later being placed as junior synonyms of previously described species. Gallardo also wrote a review of the *Pogonomyrmex* of Argentina, which was a significant advance because it

collated information on this genus into one paper. It also translated all previous descriptions into one (Spanish) language (Gallardo, 1932), with the exception of several species that had been described in Latin (*P. coarctatus*, *P. carbonarius*, *P. rastratus*).

The lack of native South American ant taxonomists began to change by the late 1940's with the arrival of Walter Kempf and Nicholas Kusnezov. Kempf contributed little to our understanding of *Pogonomyrmex* because he worked in Brazil, where there are few species of *Pogonomyrmex*. In contrast, Kusnezov worked in Argentina, where he spent extensive time in the field collecting and observing species of *Pogonomyrmex*. Kusnezov also described seven forms of *Pogonomyrmex* (six from Argentina, one from Bolivia) (Kusnezov, 1949, 1951, 1953, 1954), and wrote the first taxonomic revision (in Spanish) for species of *Pogonomyrmex* in Argentina (Kusnezov, 1949, 1951). More importantly Kusnezov was the first author to link the ecology and evolutionary history for species in North and South America. Kusnezov (1978) later updated his key to *Pogonomyrmex* of Argentina, which was updated by other authors (Cuezzo & Claver, 2009; Taber, 1998). However, these keys are difficult to use and/or generally unsatisfactory for obtaining a correct species identification.

The only subsequent revisionary work was a treatment of the ants of Chile (Snelling & Hunt, 1975), which included a taxonomic update, distribution maps, and a key to the five species of *Pogonomyrmex* known to occur in Chile (*P. angustus*, *P. bispinosus*, *P. laevigatus*, *P. odoratus* and *P. vermiculatus*). The true identity of the latter species, *P. vermiculatus*, has also been in a state of confusion since its description (Snelling & Hunt, 1975). There was a subsequent lag of work on South American *Pogonomyrmex* until 1990 (despite a sharp upturn of research on the genus in North America beginning in the late 1960's). Since that time, five species have been described by South American taxonomists, two from Venezuela (*P. sylvestris*,

P. stefani) (Lattke, 1990, 2006), one from Columbia (*P. striatinodis*) (Fernández & Palacio, 1997), and two from Argentina (*P. kusnezovi* and *P. mendozanus*) (Cuezzo & Claver, 2009). In total, only 13 of the 59 forms of South American *Pogonomyrmex* have been described by native taxonomists.

Throughout this time and to this date, several problems have resulted in a poor understanding of the identity of many species. The diverse group of authors created interpretive difficulties because species were described in six languages (Latin, German, Italian, Spanish, French, and English). Additionally, syntypes were scattered across museums in Europe and South America, with those from Europe being mostly unavailable to South American taxonomists. These problems were compounded by the brief descriptions and a lack of voucher material, which resulted in misidentification of species in later studies.

Over this entire time, few studies examined the natural history and ecology of *Pogonomyrmex* in South America. Carlos Bruch was the first investigator to contribute information on the natural history of *Pogonomyrmex* (Bruch, 1916, 1917) by describing the nest structure of several species. Later investigators included studies by Marcus on internal anatomy (Marcus, 1953; Marcus & Marcus, 1951) and studies by Kusnezov on distribution and habitat affiliations (Kusnezov, 1949, 1951). A number of studies on *Pogonomyrmex* have also been conducted in Chile that mostly examined distribution, abundance, habitat use, foraging behavior, and activity patterns and orientation (Torres-Contreras, 2001; Torres-Contreras & Olivares-Donoso, 2007).

Beginning in the early 2000's, a research group from Buenos Aires, Argentina, under the direction of Javier Lopez de Casanave, began studies on the ecology of seed predation by *Pogonomyrmex* in the Monte Desert (Mendoza Province). However, there were taxonomic problems with these studies as two of the three species studied by this group were misidentified (*P. neuquensis*

as *P. rastratus*; *P. mendozanus* as *P. pronotalis*) (e.g., Pirk & Lopez de Casenave, 2006; Pirk, Lopez de Casenave, & Pol, 2004; Pol & Lopez de Casenave, 2004; Pol, Lopez de Casenave, Feldhaar, Milesi, & Gadau, 2008). Other recent studies include seed predation by *P. cunicularius pencosensis* in the Monte Desert (Aranda-Rickert & Fracchia, 2011), colony founding by *P. cunicularius cunicularius* and *P. cunicularius pencosensis* (Johnson, 2010), and queen morphology of *P. laticeps* (Peeters, Johnson, & Keller, 2011). Taber (1998) also provided a phylogeny based on morphological characters, distribution maps, and a key to the *Pogonomyrmex* of North America, South America, and Hispaniola.

For much of its history, *Pogonomyrmex* has been divided into several subgenera. Forel's description of *P. mayri* (Forel, 1899a) was significant because he placed this species into a new subgenus (*Janetia*) based on its unique morphology. This subgenus was later transferred to *Forelomyrmex* because *Janetia* was an occupied name (Wheeler, 1913). At about this same time, William Morton Wheeler arrived on the scene in North America, but he influenced the taxonomy of South American species by describing *P. imberbicus* from the United States; he placed *P. imberbicus* and *P. naegelii* in his new subgenus *Ephebomyrmex* (Wheeler, 1902). About 10 years later, Forel (1912) described *Hylomyrma* as a fourth subgenus from South America. *Hylomyrma* was subsequently elevated to generic status (Wheeler 1922). At present, *Hylomyrma* maintains a generic status (Bolton, 2011), and it appears to be the sister genus to *Pogonomyrmex* (Jansen & Savolainen, 2010, Moreau, et al. unpublished data). The other two subgenera (*Ephebomyrmex*, *Forelomyrmex*) remained valid for the next several decades. *Forelomyrmex* was later provisionally synonymized under *Pogonomyrmex* (Brown, 1973) without discussion, and Snelling finalized the synonymy (Snelling, 1981), again without discussion; *Ephebomyrmex* was elevated to generic status and later placed as a subgenus several times during that period (Bolton, 2011).

Significantly, several recently described species from northern South America resulted in substantial morphological data to justify changing the status of these subgenera. The first of these species, *P. sylvestris*, was collected in humid tropical forest habitat in Venezuela, and it shared characters with all three subgenera, resulting in *Forelomyrmex* and *Ephebomyrmex* being placed as synonyms of *Pogonomyrmex* (Bolton, 2011; Lattke, 1990). Two additional species were subsequently described from forest habitats of northern South America (*P. striatinodis*, *P. stefani*); both species showed a similar morphological intermediacy across the three subgenera that further supported subsuming *Ephebomyrmex* and *Forelomyrmex* under *Pogonomyrmex*. These three species were also considered to be morphologically primitive for the genus, which was used to suggest that the genus evolved in humid tropical habitats of South America (Fernández & Palacio, 1997; Lattke, 2006).

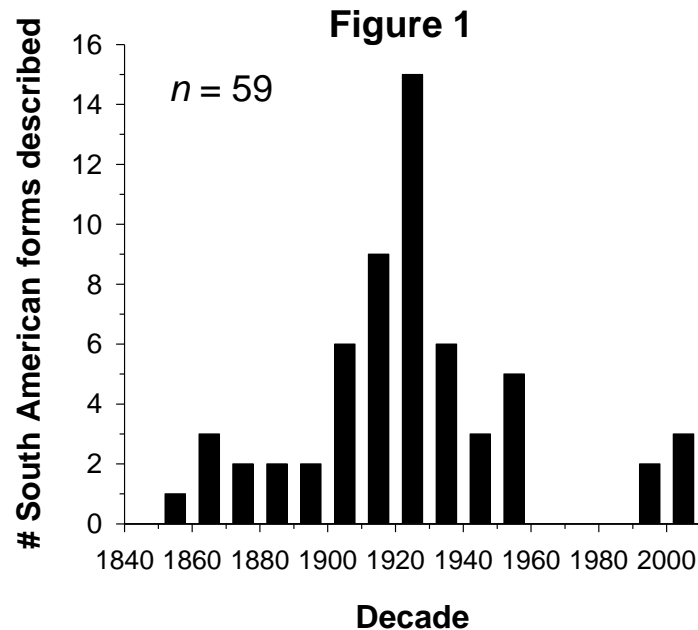


Figure 1. Number of South American forms of *Pogonomyrmex* described by decade.

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