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Monograph of *Nylanderia* (Hymenoptera: Formicidae) of the World: An introduction to the systematics and biology of the genus

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Abstract

This paper serves as an introduction to a world monographic series addressing the species-level taxonomy of the ant genus *Nylanderia*. This series will consist of several regionally based taxonomic revisions. The systematics and biology of *Nylanderia* are discussed in a global context, and a diagnosis of the genus is given. Several morphological features, which are considered putative synapomorphies for the genus, are provided. Morphological descriptions of all three castes (workers, queens, and males) are provided and discussed.

Key words: Formicidae, *Nylanderia*, *Paraparatrechina*, *Paratrechina*, *Prenolepis* genus-group, taxonomy

Introduction

The genus *Nylanderia* (Formicidae: Formicinae) is a large, ecologically important ant genus with a nearly cosmopolitan distribution. It currently is comprised of over 130 extant species and subspecies and two fossil species. Ants from this genus are found in all geographic regions (with the exception of high latitude areas). There are two known fossil species: *N. pygmaea* from Eocene age Baltic amber and *N. vetula* from Miocene age Dominican amber (LaPolla and Dlussky 2010). *Nylanderia* ants are small to medium sized (generally between 1–4 mm in total length) and range in color from pale yellow to black (see Fig.1 for illustration of all three castes). Until recently, most *Nylanderia* species were placed in the genus *Paratrechina*, but molecular phylogenic studies and reassessment of morphological characters prompted resurrection of *Nylanderia* as a valid genus (LaPolla *et al.* 2010a).

Nylanderia species inhabit a wide array of habitats from deserts to rainforests, although they reach their highest species diversity in forested and warmer environments. *Nylanderia* are among the most abundant ant species in many places where the genus occurs. For example, Ward (2000) found that *Nylanderia* (recorded as *Paratrechina*) was the fifth most frequently encountered ant genus in leaf-litter samples from around the world. They are efficient and rapid foragers and often find resources (e.g. baits) first to which they can recruit rapidly, but rarely can defend a resource against other ants that arrive later to baits (J. Longino, pers. comm.). Most are conspicuous, epigaeic generalist species that form large, polydomous nests. Frequent nest movements are known for some species, especially those that nest in leaf litter and rotting wood. For example, *N. bourbonica* can nest opportunistically in temporary sites that are habitable for only a few days or weeks (Hölldobler and Wilson 1990). The small (125–150 individuals) colonies of *N. faisonensis* also inhabit ephemeral locations in the leaf litter or soil of hardwood forests (Lynch *et al.* 1980, identified incorrectly as *Paratrechina melanderi*). A few more morphologically specialized species exist, such as the sand-dwelling *N. arenivaga* and *N. phantasma* from the southeastern United States, several small-eyed species such as *N. microps* from Puerto Rico, and several undescribed species from Australia. There are at least three currently undescribed workerless social parasites known from the eastern United States (Cover, LaPolla, Brady unpublished).

In temperate areas most *Nylanderia* species produce reproductives during the summer, which overwinter in the nest to then emerge early the following spring; *Nylanderia* species are typically among the first ant reproductives to

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fly (Trager 1984; Ichinose 1987) after *Prenolepis*. However, we know little about the reproductive biology of many *Nylanderia* species, especially those inhabiting the tropics. Cases of polygyny have been noted among *Nylanderia* species (Frumhoff and Ward 1992; Arcila *et al.* 2002), but how widespread this condition is within the genus remains unclear. At least one species, *N. flavipes*, is somewhat unusual among ants in having populations that are both monogynous and polydomous (Ichinose 1986).

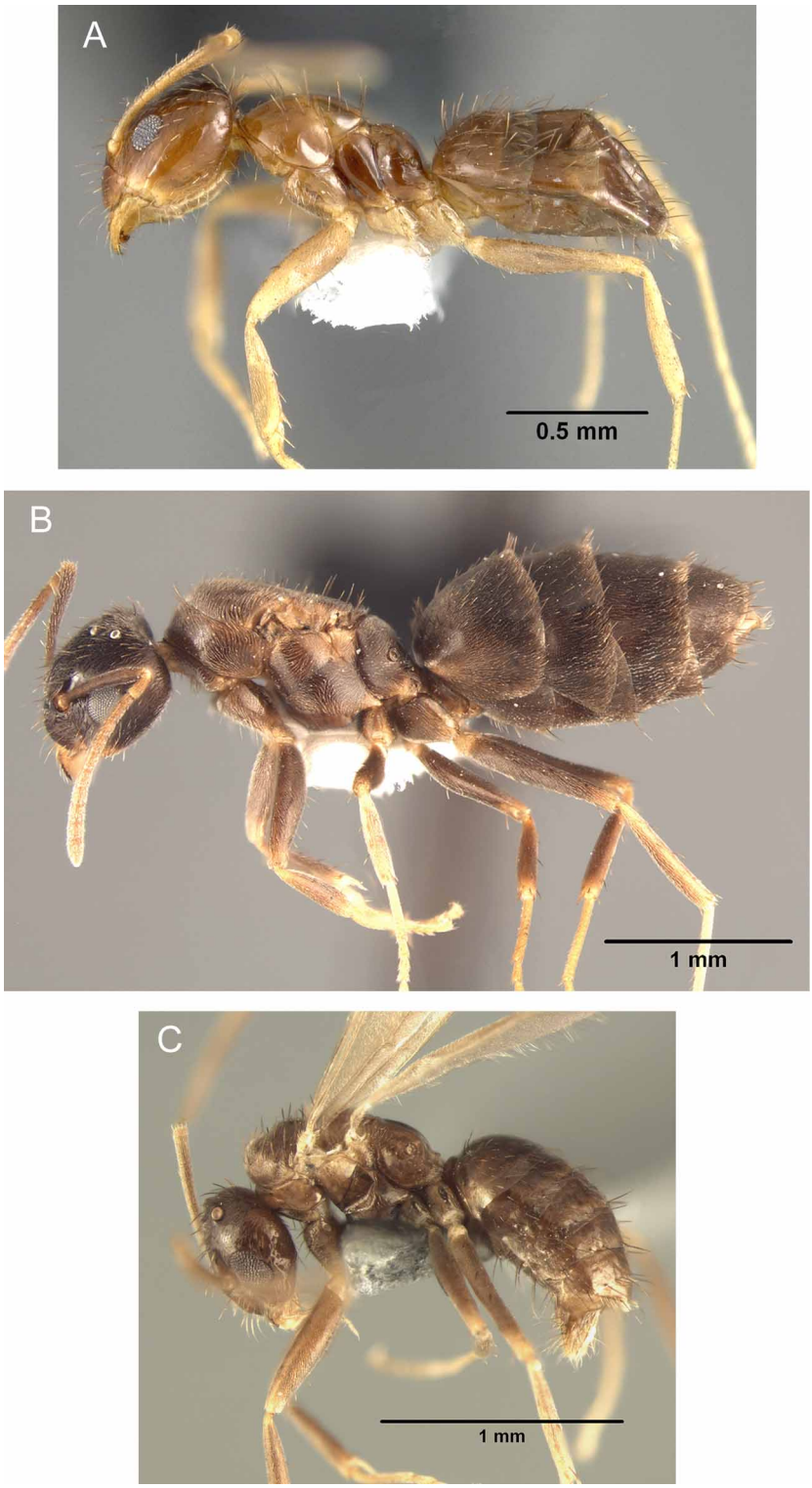

FIGURE 1. Three castes typically observed in *Nylanderia*; all three castes depicted are of *N. vividula*: A) worker; B) queen (dealate); C) male.

Several *Nylanderia* species have been reported as being tramps. For example, *N. bourbonica* and *N. vaga* are commonly encounteredin the tropics and subtropics and have spread across large areas (Klotz *et al.* 1995; Wilson and Taylor 1967; Wetterer 1998). Infestations can involve smaller areas, although population sizes can be very large, as with *N. pubens* in the Caribbean (Wetterer and Keularts 2008). An unknown Nylanderia species has invaded Texas and several other states in the American southeast in a sudden, explosive outbreak (Gotzek, Brady, Kallal, LaPolla, in prep). Several other species in the genus have also been reported as introduced outside their native range, including *N. clandestina*, *N. flavipes*, *N. fulva*, *N. guatemalensis*, and *N. vividula* (McGlynn 1999). However, it is important to note that species identifications within *Nylanderia* are often suspect given the taxonomic uncertainties that have befuddled so many who have worked on the genus. Additionally, the identities of some reportedly invasive species, such as *N. bourbonica* and *P. vaga*, have never been clarified, leaving accurate identifications difficult or impossible. Preliminary results suggest that while several *Nylanderia* have spread through human activity, the names used for these taxa may be in error. Because of this situation, even creating an accurate list of invasive species within the genus is currently impossible and will only be achievable when a comprehensive revision of the group has been completed. But even without reliable identifications, it would appear that "invasiveness" has originated multiple times within *Nylanderia*. The broad-scale phylogeny of LaPolla *et al.* (2010a) suggests at least four separate origins of invasive species, but denser taxon sampling and refinement of taxonomy will be necessary for a more accurate total.

LaPolla *et al.* (2010a) recently reviewed the taxonomic history and status of this genus. Despite the importance of *Nylanderia* among the world's ant faunas, with the exception of Trager's (1984) treatment of the species in the United States and the faunistic study of the Japanese species by Terayama (1999), there have been no taxonomic revisions of the genus. The lack of a modern taxonomic synthesis has greatly hindered biological research on *Nylanderia*. This situation has also significantly hampered the identification and study of invasive *Nylanderia* species around the world, which may threaten biodiversity conservation efforts. The species-level taxonomy of *Nylanderia* has by and large become a hopeless tangle of names that cannot be easily applied to specimens. Species have been described outside of a comparative framework and this has led to an abundance of synonyms and poorly defined species. The lack of a global synthesis has resulted in most recent publications either simply listing *Nylanderia* as morphospecies, as names that cannot be reliably applied to any particular set of specimens, or by using one of the more commonly "known" species regardless of the appropriateness of the usage and seldom with justification.

In a recent paper examining the phylogenetic relationships of *Nylanderia* and related genera, LaPolla *et al.* (2010a) placed the genus within a well-defined *Prenolepis*-genus group containing *Euprenolepis*, *Nylanderia*, *Paratrechina* (*sensu stricto*) *Paraparatrechina*, *Prenolepis*, and *Pseudolasius* (see also Brady *et al.* 2006). LaPolla *et al.* (2010a) found that *Paratrechina* (*sensu lato*) (Fig. 2) was polyphyletic and segregated into three distinct, robust clades: *Paratrechina* (*sensu stricto*), *Paraparatrechina*, and *Nylanderia*. The sister taxon to *Nylanderia* was found to be a clade containing three genera: (*Pseudolasius* + (*Euprenolepis* + *Paratrechina*)) (Fig. 2). The finding of a polyphyletic *Paratrechina* (*sensu lato*) was not particularly surprising because the genus had never before been the subject of rigorous phylogenetic analysis and several related genus-group names had been variously treated as separate genera, subgenera or synonyms of *Paratrechina* (*sensu lato*) over the past 120 years (see Fig. 1 in LaPolla *et al.*, 2010a). The main morphological character used to define the genus was the presence of erect macrosetae on the mesosoma and scapes. However, it is now known that within the *Prenolepis* genus-group this seemingly simple character is in reality a complex of different characters involving not just the presence or absence of macrosetae, but also their position, number, whether they are paired or unpaired, etc. Thus what was previously considered to be a single character with two states (macrosetae present or absent) is in fact a series of characters with numerous states. To clarify the generic limits within this set of genera, LaPolla *et al.* (2010a) suggested a number of morphological characters that might be potential synapomorphies for *Nylanderia* and thus support its treatment as separate from *Paratrechina*. These characters were the presence of six mandibular teeth (rarely 7) and the pairing of macrosetae on the pronotum and mesonotum with no erect macrosetae found on the propodeum (with one known exception); a more complete list of morphological characters defining *Nylanderia* is provided below.

To overcome the taxonomic impediments outlined above and place the genus on a firm footing, we are undertaking this "*Nylanderia* of the World" monograph series to revise the genus on a global basis. This will take place over a series of regionally based taxonomic revisions and conclude with a synthesis of what has been learned about this ecologically important and taxonomically challenging genus. Following this paper is Part 1 of the monographic

series, a revision of the Afrotropical *Nylanderia* species. We hope by the end of this series that *Nylanderia* will be much better understood taxonomically and that the ability to identify species will lead to further refinements to our species-level understanding of these ants and to increased study of their biology.

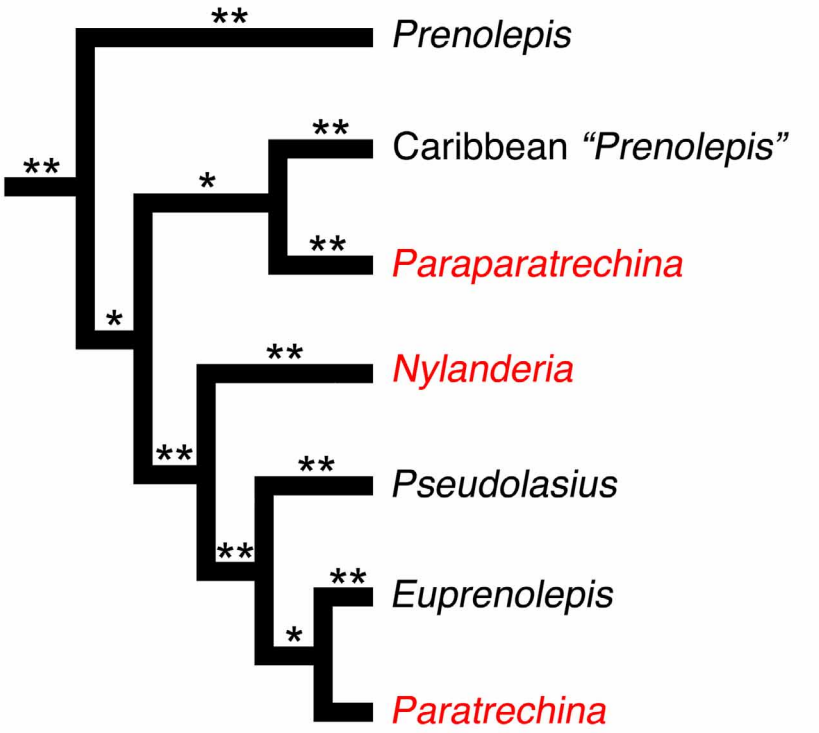

FIGURE 2. Cladogram (i.e., branch lengths have no meaning) of *Prenolepis* genus-group taxa based on the molecular work of LaPolla *et al.* (2010a) and LaPolla *et al.* (unpublished). Branches with a single asterisk were strongly supported by very high Bayesian posterior probabilities (0.99–1.0) in one or both studies, but had bootstrap proportions under 98. Branches with two asterisks were additionally strongly supported by very high bootstrap proportions (98–100) under both maximum likelihood and maximum parsimony criteria. Genera in red represent *Paratrechina* in the broad sense (demonstrating its polyphyly) as defined before the LaPolla *et al.* (2010a) study. Support values for *Paratrechina* are not indicated because this genus presently contains a single species. The Caribbean "*Prenolepis*" are being described as a new genus (LaPolla *et al.*, unpublished).

Description of *Nylanderia*

The following genus description is modified from Trager (1984). Habitus views of all three castes are provided in Fig. 1. Workers are generally monomorphic although some species are variable in size, with a possible example of worker polymorphism observed in *N. amblyops* from Madagascar.

Workers:
— Small to medium sized (generally between 1.0–4.0 mm in total length [defined as: head length + Weber length + gaster length]) formicine ants ranging in color from pale yellow to black; cuticle usually smooth and shining, but sculpturing present in several African species.
— Mandibles typically with 6 or, rarely, 7 teeth present; palp formula 6:4 except in *N. dodo* which is 5:3. For an example of a typical *Nylanderia* mandible, labium, and maxillae see Fig. 3.
— Clypeus subrectangular, medially convex, with scattered erect setae.
— Antennae 12-segmented; scapes surpass posterior margin of head; scapes with erect macrosetae and a layer of pubescence.
— Eyes usually well developed (although small-eyed species are known), placed midlength or anterior and laterally on head; ocelli often absent, but when present, indistinct.
— Sides of head parallel or gently convex, merging into broadly rounded posterior corners.
— Posterior margin straight or medially convex.

— Pronotum typically broadly convex (Fig. 4); in lateral view, pronotal margin convex and then leveling off towards the mesonotal margin; in a few species pronotal margin nearly flat in lateral view (Fig. 4E); macrosetae on pronotum variable, although often with two pairs of long erect macrosetae and scattered shorter erect setae.
— Mesonotum typically flat to slightly convex; mesonotum with scattered erect macrosetae (often with two pairs of long erect macrosetae and scattered shorter erect setae).
— Propodeum shape variable (Fig. 4); dorsal face can be slightly convex but fairly short (Fig. 4A), short and angular (Fig. 4B), or strongly convex and dome-like (Fig. 4C); propodeum always lacking erect macrosetae, although a fringe of pubescence often present on anterior of propodeum (one known exception, an undescribed species from Papua New Guinea, Fig. 4D).
— Legs with abundant, scattered macrosetae.
— Petiole wedge-shaped (cuneate), never surpassing the height of the propodeum in lateral view, although in some species it approaches height of propodeum.
— Gaster large and oval shaped, becoming pointed distally towards acidopore; usually with abundant, scattered erect macrosetae and often a layer of pubescence.
— Petiolar foramen long, extending beyond the anteriormost points of the metacoxal cavities.

Queens:
— Generally as in worker with modifications expected for caste.
— Eyes large and conspicuous, with three well developed ocelli.
— Mandibles with 6 or, rarely, 7 teeth present.
— Scapes generally shorter relative to head length than observed in conspecific workers.
— Typically most of cuticle covered in a dense layer of pubescence; scattered macrosetae found on scapes, head, pronotum, mesonotum, legs and gaster; general body color often darker than workers.
— Mesosoma large, with collar-like pronotum and overarching mesonotum.
— Mesonotum large and flat, typically with scattered macrosetae.
— Propodeum typically with short, subangular dorsal face, even in species with a long dorsal face in the worker.
— Gaster very large, with scattered macrosetae.

Males:
— Sculpture and color pattern of males generally approaching those of workers.
— Mandibles well developed with a prominent apical tooth and often a small, basal tooth (or just a pronounced basal angle), with smaller denticles present along masticatory margin in some species.
— Scapes long, surpassing posterior margin of head; antennae 13-segmented.
— Eyes large and conspicuous, with three well developed ocelli.
— Mesosoma large, with collar-like pronotum and overarching mesonotum.
— Mesonotum large and flat, typically with scattered macrosetae.
— Propodeum inconspicuous, with very short dorsal face.
— Genitalia prominent; parameres often subtriangular in appearance; digiti and cuspi highly variable; 9th sternite often obscured by 8th sternite in which case it is only visible with dissection.

Note on the use of the term macroseta

Macroseta is here defined as any large, erect or suberect seta; this term is synonymous with macrochaeta, which was used by Trager (1984). These setae are typically barbulate, but this feature is often only visible under very high magnification with proper lighting. The reason for the change from macrochaetae to macrosetae is that the term chaetae can be applied either to a true seta (an articulated, thin outgrowth of the cuticle) or a spine (non-articulated) (Torre-Bueno 1989). Therefore, the term macroseta seems more appropriate for *Nylanderia* species since the structures in question are true setae. These setae can usually be easily distinguished from thinner, shorter and typically appressed pubescence that is found on most species. Occasionally, especially on the scapes, distinguishing between decumbent pubescence and true macrosetae can be difficult. This will be noted for species where this distinction is difficult. The term macrosetae will be used throughout the *Nylanderia* of the World monograph series.

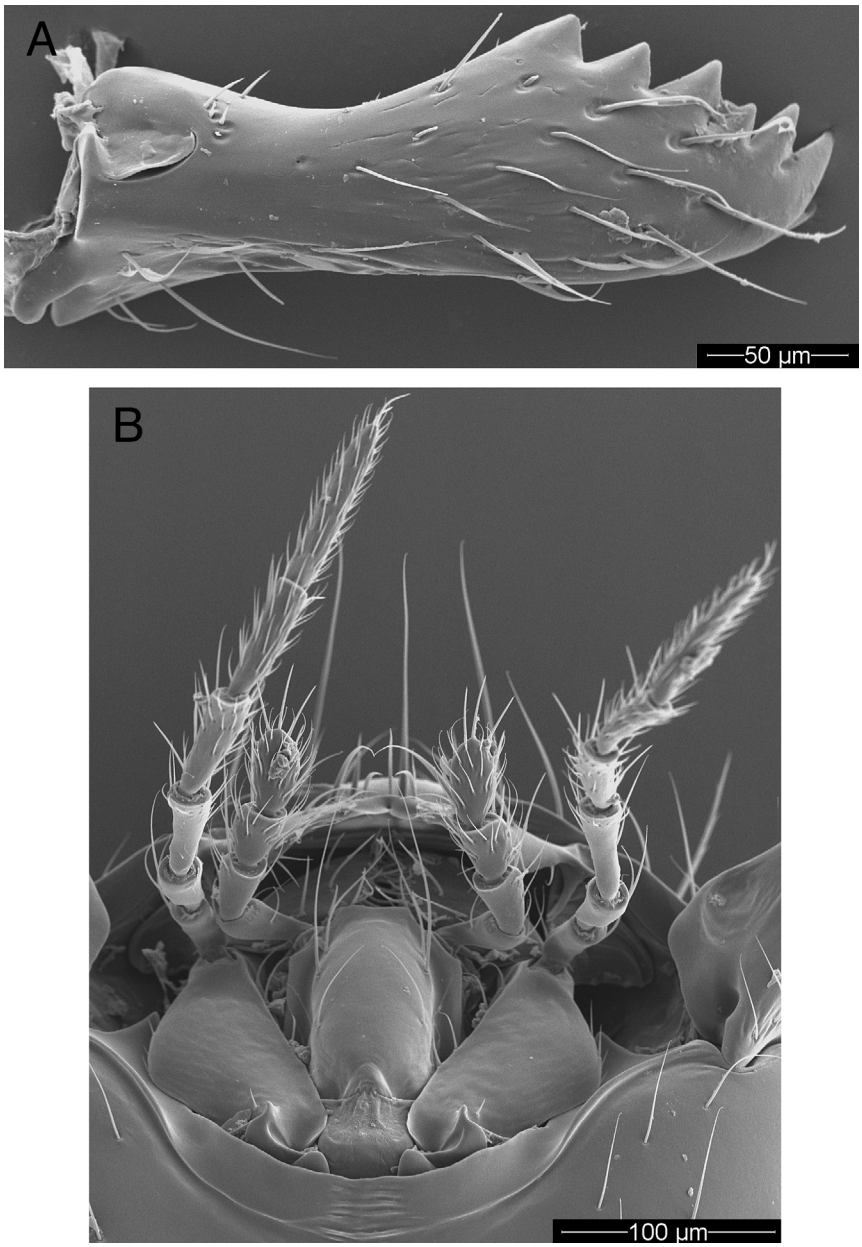

FIGURE 3. *Nylanderia flavipes* mouthparts: A) mandible; B) ectal view of maxillae and labium.

Discussion

Nylanderia workers can generally be easily distinguished from other formicines based on the presence of 6 mandibular teeth, erect macrosetae on the scapes and legs, and paired erect macrosetae on the pronotum and mesonotum. These morphological features are considered synapomorphies for the genus, and will effectively separate this genus from other genera. Overall, the body shape for most *Nylanderia* workers is compact and robust (Fig. 1) in that the mesosomal regions are generally short (as measured against the long axis of the body) and relatively high when compared to a species such as *Paratrechina longicornis*. There are, however, several species where the mesosoma is more elongated (Fig. 4E), superficially resembling *Paratrechina longicornis*. Long erect macrosetae are almost never found on the dorsal face of the propodeum, with one known exception (Fig. 4D). However, species with an elongated mesosoma or short propodeal macrosetae do possess 6 mandibular teeth, erect macrosetae on the scapes and legs, and paired erect macrosetae on the pronotum and mesonotum which support their placement within *Nylanderia* based on the definition of the genus proposed above. Additionally, when macrosetae are present on the propodeum they show a pattern generally similar to that found on the pronotum and mesonotum of *Nylande-*

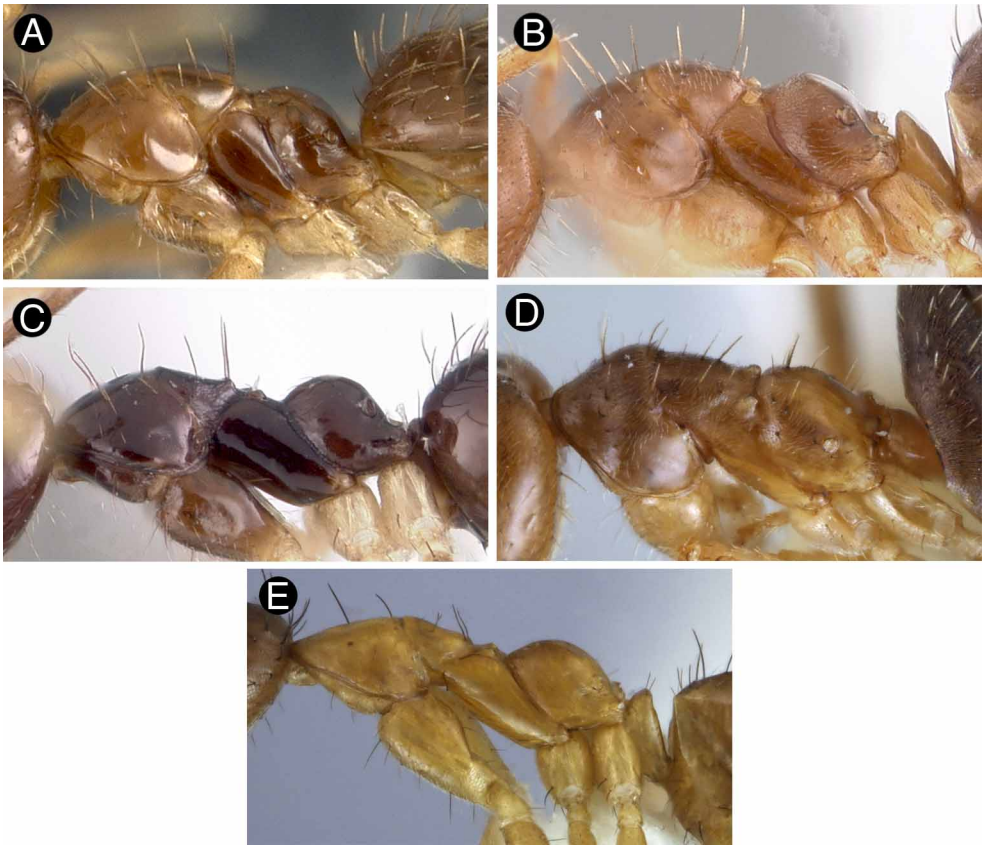

FIGURE 4. Mesosoma of various *Nylanderia* species in lateral view: A) *vividula*; B) *weissi*; C) *lepida*; D) undescribed Papua New Guinean species; E) elongate undescribed species from Sumatra, Indonesia.

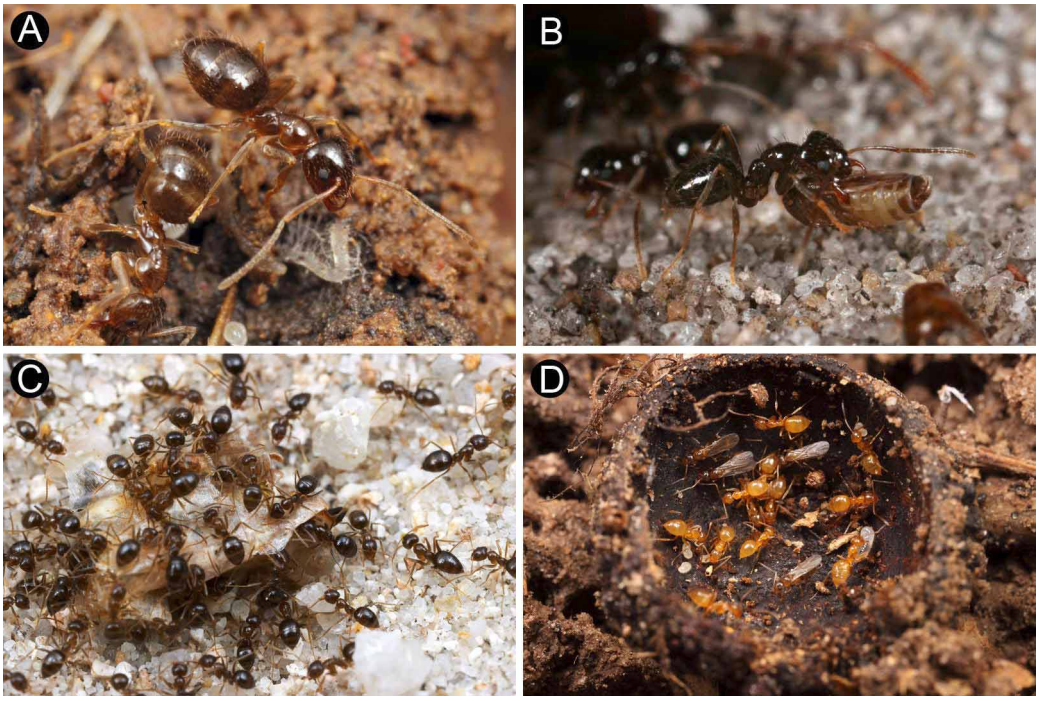

FIGURE 5. A) Australian *Nylanderia* workers active on the surface above their nest (New South Wales, Australia, S. Shattuck); B) a worker returns an arthropod prey item to its colony (New South Wales, Australia, S. Shattuck); C) a large number of workers recruited to an insect carcass (Cape York Peninsula, Queensland, A. Wild); D) a *Nylanderia* nest in the leaf litter, hidden away in a rotting acorn (Dixon Springs, Illinois, A. Wild).

ria, with the macrosetae being numerous and of varying lengths. This is in contrast to related genera, for example Paraparatrechina, where the macrosetae are limited to a single, distinct pair. Given the differences in the patterns of these macrosetae among these genera, and when considering additional characters as outlined above, we interpret the presence of macrosetae on the propodeum within *Nylanderia* as having arisen independently from those observed in other closely related genera.

The main features used to distinguish *Nylanderia* queens from other *Prenolepis* genus-group genera come primarily from the mandibles and scapes. Like workers, *Nylanderia* queens have erect macrosetae on their scapes. However, the macrosetae are often not as distinct as in workers because the macrosetae are often shorter and usually surrounded by a thick layer of decumbent pubescence. When considering genera such as *Euprenolepis* and *Pseudolasius* in which queens also possess macrosetae on the scapes, differences in mandibular tooth count will distinguish *Nylanderia* queens. There are 5 teeth present in *Euprenolepis* queens and 5 or fewer in *Pseudolasius* (LaPolla 2009; LaPolla *et al.* 2010a) while *Nylanderia* possesses 6 (or rarely 7) teeth. In other genera such as *Paratrechina* (LaPolla *et al.* 2010a) and *Paraparatrechina* (LaPolla *et al.* 2010b) the queens have no erect macrosetae on their scapes. For *Prenolepis*, if erect macrosetae are present on the scapes, the more posterior placement of the eyes will distinguish them from *Nylanderia*.

Male *Nylanderia* can be more difficult to distinguish from other *Prenolepis* genus-group genera because there is considerable variation in the genitalic structures at the species-level for all genera, and features such as mandibular dentition are not useful since dentition is always reduced in males from that observed in workers and queens (usually to 1 or 2 teeth). The scapes can be useful in separating male *Nylanderia* from some *Prenolepis* genus-group genera since they possess macrosetae similar to those found in workers and queens, but at reduced numbers. *Paratrechina* and *Paraparatrechina* males, like workers and queens of these genera, never have macrosetae on their scapes. In general *Nylanderia* males have subtriangular parameres, but similar shaped parameres are also seen in some species of *Euprenolepis*, *Prenolepis*, and *Pseudolasius*. Both *Euprenolepis* and *Pseudolasius* (LaPolla 2009) have reduced labial and maxillary palp numbers from the more typical 6 maxillary and 4 labial palps observed in other *Prenolepis* genus-group genera. For *Prenolepis* the separation of males from *Nylanderia* is unclear, largely because for the vast majority of *Prenolepis* species the males are unknown. The Caribbean *Prenolepis* are presently being revised by two of the authors (JSL and SGB) and these will soon be placed in their own genus (LaPolla *et al.* in press). For this group of species, the parameres are distinct from *Nylanderia* in that they are extremely long and thin. Separation of the widespread North American *Prenolepis imparis* from *Nylanderia* is based on the extremely short scapes (not much longer than the head) that lack macrosetae.

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