Taxonomy and Distribution of the Argentine Ant, *Linepithema humile* (Hymenoptera: Formicidae)

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ABSTRACT The taxonomy of an invasive pest species, the Argentine ant, is reviewed. *Linepithema humile* (Mayr) 1868 is confirmed as the valid name for the Argentine ant. Morphological variation and species boundaries of *L. humile* are examined, with emphasis on populations from the ant's native range in southern South America. Diagnoses and illustrations are provided for male, queen, and worker castes. Collection records of *L. humile* in South America support the idea of a native distribution closely associated with major waterways in lowland areas of the Paraná River drainage, with recent introductions into parts of Argentina, Brazil, Chile, Colombia, Ecuador, and Peru.

KEY WORDS Argentine ant, *Linepithema humile*, taxonomy, invasive species

THE ARGENTINE ANT, *Linepithema humile* (Mayr) 1868, is among the world's most successful invasive species. This native South American insect has become a cosmopolitan pest, particularly in the Mediterranean climates of North America, Chile, South Africa, Australia, and southern Europe (Suarez et al. 2001). Argentine ants have been implicated in the decline of native arthropod (Cole et al. 1992) and vertebrate faunas (Suarez and Case 2002) and in the alteration of plant community structure (Christian 2001), and they are also agricultural (Haney et al. 1987) and house pests (Gordon et al. 2001).

Several recent studies have been directed at the causes of the Argentine ant's invasive success (Human and Gordon 1996, Orr and Seike 1998, Tsutsui et al. 2000, Giraud et al. 2002). Several of these hypotheses, particularly those of Orr and Seike (1998), Tsutsui et al. (2000), and Giraud et al. (2002) invoke a contrast between some aspect of Argentine ant biology in its native range and Argentine ant biology in its introduced range. Such native/non-native comparisons require sufficient knowledge of the ant in both ranges. Unfortunately, the Argentine ant in its native range is little understood compared with a wealth of knowledge accumulated from introduced populations.

Inadequate taxonomy for *L. humile* is at least partly responsible for hindering our understanding of the Argentine ant in South America. Researchers have displayed an unfortunate tendency to misdiagnose other *Linepithema* species as *L. humile*, probably owing to a combination of the high visibility of *L. humile* in the literature and a perplexing similarity in the worker caste between *Linepithema* species. Examination of major entomological collections reveals worker specimens of multiple *Linepithema* species stored under the *humile* label (personal observations; in LACM, MCSN, MCZC, MHNG, MZSP, NHMB, NHMW, and USNM; see below for explanation of abbreviations).

Taxonomic confusion over *L. humile* extends beyond museum collections. At least one important study, seeking to explain Argentine ant population regulation in the native range through phorid parasitism (Orr and Seike 1998), initially targeted the wrong *Linepithema* species (Orr et al. 2001). Erroneous conclusions from that study were later perpetuated in the invasion biology literature (e.g., Chapin et al. 2000, Feener 2000).

The genus *Linepithema* itself is a well-defined monophyletic group supported by several morphological synapomorphies (Shattuck 1992). Identification of specimens to genus can be accomplished with the keys of Shattuck (1992) and Bolton (1994). However, species limits within *Linepithema* are poorly known, and the only species-level identification key (Santschi 1929) is out of date and unusable. Since Mayr first described *Linepithema fuscum* in 1866, 28 species-level names have been assigned to *Linepithema* (Bolton 1995). There has been no effort to synthesize these isolated descriptions into a coherent taxonomy, and it remains a challenge to identify any *Linepithema* species, including *L. humile.*

The native distribution of the Argentine ant is somewhat better understood. Several lines of evidence point to the Paraná River basin in subtropical South America as being the region of origin. First, Argentine ants from this area have high levels of genetic diversity compared with populations elsewhere, and the genetic diversity of introduced populations seems to be a subset of the Paraná drainage diversity (Tsutsui et al. 2000, Tsutsui and Case 2001). Second, Argentine ants are often found in relatively pristine natural areas within the Paraná drainage coexisting with other ant species (Holway and Suarez 2004; personal observation), even though they also inhabit areas of human disturbance. Finally, subtropical South America holds the highest diversity of *Linepithema* species (Shattuck 1992) and seems to be a region of radiation for this group.

Despite the evidence favoring a native Paraná drainage distribution, reliable records of Argentine ants from this region are sparse. The genetic work of Tsutsui et al. (2000) focused on the southern Paraná drainage, and beyond their collections few museum or literature records have been verified by genetic study or by trained morphologists. Details about the distribution of this ant within the region are not well known, particularly in the northern Paraná drainage, whereas literature records based on dubious identifications of *L. humile* from outside the Paraná drainage cloud our understanding of the true limits of the native distribution.

Here, I clarify the taxonomy and the native distribution of the Argentine ant. Specifically, this study examines the status of the scientific name *L. humile* (Mayr) 1868 as it applies to the Argentine ant, defines the morphological limits of the species, creates a reliable morphological diagnosis, and compiles verified collection records into the most complete data set yet of this species' South American distribution. The goal of this study is to provide researchers with an unambiguous method for identifying Argentine ants and a baseline of knowledge about their native range distribution.

Materials and Methods

Specimens. I examined 6,540 worker, 249 queen, and 366 male *Linepithema* specimens collected across the global distribution of the genus. Particular attention was paid to ants collected in South America, including specimens from the Orr and Seike (1998) study that reported phorid fly parasitism of *L. humile* in Brazil. Specimens were examined during visits to several entomological museums and through institutional and personal loans. Additionally, I observed and collected *Linepithema* in the field in Argentina, Paraguay, Ecuador, Guatemala, the Dominican Republic, Jamaica, Puerto Rico, South Africa, and the western United States on several occasions from 1996 to 2002, in expeditions ranging in length from a few days to several months. These collections consisted mainly of extensive visual searches targeting *Linepithema* nests and foraging ants, sometimes augmented with honey baits, Berlese funnels, malaise traps, and blacklights. Entomological collections cited in this study are abbreviated as follows: ALWC, Alexander L. Wild personal collection, Davis, CA; AVSC, Andrew V. Suarez personal collection, Urbana, IL; BMNH, British Museum of Natural History, London, United Kingdom; IFML, Instituto Fundación Miguel Lillo, Tucumán Argentina; INBP, Museo Nacional de la Historia Natural del Paraguay, San Lorenzo, Paraguay; LACM, Natural History Museum of Los Angeles County, Los Angeles, CA; MACN, Museo Argentina de Ciencias Naturales, Buenos Aires, Argentina; MCSN, Museo Civico de Historia Natural 'Giacomo Doria', Genoa, Italy; MCZC, Museum of Comparative Zoology, Cambridge, MA; MHNG, Muséum d'Histoire Naturelle, Geneva, Switzerland; MZSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; NHMB, Naturhistorisches Museum, Basel, Switzerland; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; PSWC, Philip S. Ward personal collection, Davis, CA; QCAZ, Museo de Zoología de la Pontificia Universidad Católica del Ecuador, Quito, Ecuador; UCDC, R. M. Bohart Museum of Entomology, Davis, CA; USNM, National Museum of Natural History, Washington, DC; and WPMC, William P. MacKay personal collection, El Paso, TX.

Morphological Analysis. Most observations were made at 50× on a Wild stereomicroscope. I conducted morphometric measurements on a subset of male (n = 75), queen (n = 43), and worker specimens (n = 364). A majority of measurements were taken using a dual-axis Nikon stage micrometer with a precision of 0.001 mm, but measurements at IFML and MZSP used an ocular micrometer with a precision of 0.01 mm. I report measurements here to 0.01 mm. I repeated measurements on several specimens by using both optical and stage micrometers to confirm that measurements were consistent between systems.

I used a number of standard morphometric characters. Head measurements are given with the head in full-face view, with the anterior clypeal margin and the posterior border of the head in the same focal plane. I consider ant heads to be prognathous, such that the clypeus is anterior and the frontal area is dorsal.

Head Length (HL). In full-face view, the midline distance from the level of the maximum posterior projection of the posterior margin of the head to the level of the most anterior projection of the anterior clypeal margin. In males, I consider the posterior margin of the head as the vertex between, and not including, the ocelli.

Head Width (HW). In full-face view, the maximum width of the head posterior to the compound eyes.

Minimum Frontal Carinal Width (MFC). In full-face view, the minimum distance between the frontal carinae.

Antennal Scape Length (SL). Measured from the apex of the first antennal segment to the base, exclusive of the radicle.

Profemur Length (FL). In posterior view, measured along the longitudinal axis from the apex to the junction with the trochanter.

Metatibial Length (LHT). In dorsal view, measured along the longitudinal axis from the apex to the level of the lateral condyles, excluding the medial proximal condyle.

Pronotal Width (PW). In dorsal view, the maximum width of the pronotum measured from the lateral margins.

Wing Length (WGL). In males and queens only, the maximum distance between the base of the sclerotized wing veins to the distal margin of the wing.

Weber's Length (WL). In lateral view, the distance between the anterior margin of the pronotum to the posterior margin of the metapleural bulla. For this study, Weber's length was measured only in queens, because in workers the flexible articulation of the pronotum and mesonotum introduces error as an artifact of specimen preservation.

Maximum Mesosomal Length (MML). In males, the distance from the maximum anterior projection of the mesosoma to the maximum posterior projection of the propodeum, with the specimen oriented such that the measurement line of Weber's length (see WL) is held horizontal. In male ants with minimal mesosomal development, MML is equivalent to Weber's length. In male ants with a well developed mesosoma the anterior projection of the mesosoma is often formed by a swollen mesoscutum, and the posterior projection is formed by a rearward projection of the propodeal dorsum above the petiole.

Maximum Mesoscutal Width (MMW). In dorsal view, the maximum transverse width of the mesoscutum.

Eye Length (EL). In full face view, the length of the compound eye along the longitudinal axis.

Eye Width (EW). With eye held in focal plane facing the viewer, the maximum transverse width of the compound eye.

Eye Size (ES). 100*EL*EW.

Scape Index (SI). 100*SL/HL.

Cephalic Index (CI). 100*HW/HL.

In addition to morphometrics, I examined a suite of morphological characters commonly used in ant systematics. These characters include pilosity, pubescence, body color, wing venation, shape of the head, shape of the mesosoma and associated sclerites, shape of the petiole, male genital morphology, and maxillary palp morphology.

Species Delimitation. I follow the view that species are aggregates of interbreeding or potentially interbreeding populations (Mayr 1942). Although resources were not available in the current study to directly examine gene flow, species boundaries can be inferred indirectly through morphological and geographical data. Specifically, character states within biological species are likely to be continuous, while character states may be expected to diverge in the absence of gene flow, leaving a distinct gap. Thus, I delimited the Argentine ant as a biological species through identifying gaps in character states that are concordant between several characters over multiple specimens. Special attention was paid to areas of sympatry and to characters that are potentially related to reproduction (e.g., male morphology).

Geographic Analysis. Maps were drawn in the shareware program Versamap (www.versamap.com) on a Windows PC computer platform by using coordinates provided on specimen labels or inferred from maps and gazetteers for specimens without coordinate data. A number of older specimens did not have sufficiently detailed labels to infer exact coordinates (e.g., "Argentina") and were excluded from the map.

To obtain an estimate of the extent to which *L. humile* records reflect sampling effort versus actual presence/absence, and to more accurately determine the limits of *L. humile* distribution, I mapped sampling points in subtropical South America where *L. humile* was not recorded, in addition to positive records of *L. humile.* These negative sampling points are a combination of museum records of other *Linepithema* species and of sites where I conducted targeted ant collecting on several occasions between 1995 and 2002 without finding *humile.*

In the current study, any collection of *L. humile* in the greater Paraná River drainage was deemed native unless there was an historical record of introduction (e.g., the population at Amingá, Argentina). South American collections were deemed introduced if there was an historical record of introduction, or if they were collected in urban areas outside of the Paraná drainage. A few records were considered ambiguous if they occurred at the periphery of the Paraná watershed strongly disjunct from confirmed native records. These criteria provide a conservative estimate for the designation of introduced populations, as native status may have been inadvertently assigned to some cryptic local introductions within the Paraná drainage. Human commerce undoubtedly moves Argentine ants about within the native range, and it is worth noting that many records of Argentine ants in Argentina and Paraguay are from urban areas.

Nomenclature. To confirm that *L. humile* is the valid species epithet for the pestiferous Argentine ant, I obtained the holotype worker through a loan from NHMW. I also examined syntype males from MCZC and NHMW of *L. fuscum* Mayr 1866, the only species-level taxon in the genus older than *L. humile* and consequently a potential senior synonym. Additionally, I examined type specimens for most of the more recently described species-level taxa in *Linepithema,* including *riograndense* (Borgmeier) 1928, *humile angulatum* (Emery) 1894, *leucomelas* (Emery) 1894, *dispertitum* (Forel) 1885, *dispertitum micans* (Forel) 1908, *humile platense* (Forel) 1912, *iniquum bicolor* (Forel) 1912, *iniquum succinneum* (Forel) 1908, *keiteli* (Forel) 1907, *aspidocoptum* (Kempf) 1969, *iniquum* (Mayr) 1870, *piliferum* (Mayr) 1870, *humile breviscapum* (Santschi) 1929, *humile scotti* (Santschi) 1919, *oblongum* (Santschi) 1929, *melleum* (Wheeler)1908, *melleum dominicense* (Wheeler) 1913, *keiteli subfasciatum* (Wheeler & Mann) 1914, and *keiteli flavescens* (Wheeler & Mann) 1914. Where possible, type specimens were measured and compared with the species boundaries inferred for the Argentine ant. I associated names with the Argentine ant if they fell within the observed range of variation for that species, and I determined the valid name from the associated names using rules of priority (International Commission on Zoological Nomenclature 1999).

Taxonomy

Linepithema humile **(Mayr)**
(Worker, Figs. 1 and 5; queen, Figs. 8, 9, and 10; male, Figs. 11, 12, and 13)

Hypoclinea humilis Mayr 1868: 164. Worker description.
Iridomyrmex humilis (Mayr); Emery 1888: 386–388. First combination in *Iridomyrmex*.
Iridomyrmex humilis (Mayr); Wheeler 1913: 27–29. Male and queen description, worker redescription.
Iridomyrmex humilis (Mayr); Newell and Barber 1913: 38–39 (egg), 40–41 (larva), 42–45 (worker, male, queen pupae).
Iridomyrmex humilis variety *arrogans* Chopard 1921: 241–245. Syn. Nov. Junior synonym of *I. humilis* by Bernard 1967: 251. Restored to subspecies of *L. humile* by Shattuck 1992: 16.
Iridomyrmex riograndensis Borgmeier 1928: 64. Syn. Nov.
Iridomyrmex humilis (Mayr); Wheeler and Wheeler 1951: 186–189. Summary of larval biology.
Linepithema riograndense (Borgmeier); Shattuck 1992: 16.
Linepithema humile (Mayr); Shattuck 1992: 16. First combination in *Linepithema*.

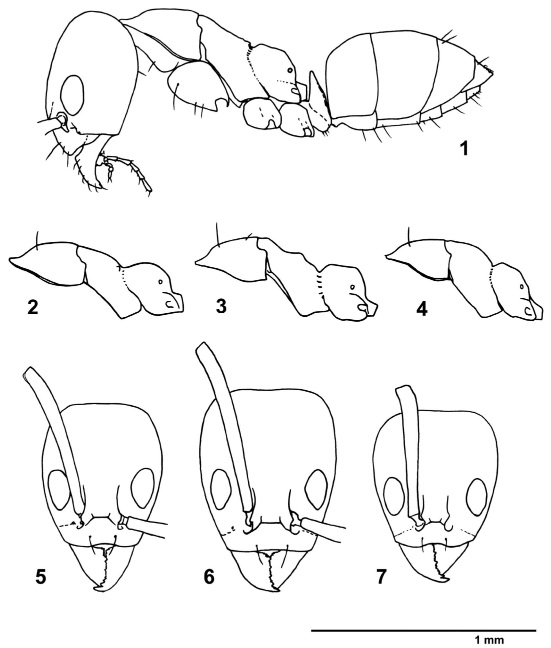
Type Material Examined

Hypoclinea humilis Mayr 1868. one worker HOLOTYPE. Argentina, Buenos Aires (1866, Stroebel coll.) [NHMW].
Iridomyrmex riograndensis Borgmeier 1928. Eight worker SYNTYPES. Brazil, Rio Grande do Sul, s.loc. (19.I.1918) [MZSP].

Additional Material Examined

South American material examined given in Table 1. Specimens collected outside of South America are listed below. Given the large quantity of Argentine ants collected in California, I only list here a representative subsample of California specimens that were given a relatively thorough examination under the microscope (e.g., setal counts and measurements).

AUSTRALIA. Sydney [MZSP]; Victoria (s. loc.) [BMNH]. BELGIUM. Bruxelles Capitale: Brussels [BMNH, NHMB], Brussels Botanical Garden [MHNG]. BERMUDA. Bermuda (s. loc.) [BMNH]. CAMEROON. Centre-Sud: Nkoemvom [BMNH]. FRANCE. Provence-Alpes-Côte d'Azur: Cannes [MCZC, NHMB], Castellane [BMNH], Hyeres [BMNH], Ste. Maxime [NHMB]; Midi-Pyrénées: Toulouse [IFML]. GERMANY. Berlin: Botanical Garden [MHNG]. ITALY. Campania: nr. Naples [BMNH]; Liguria: San Remo [NHMB]; Sicilia: Palermo [BMNH]; Toscana: Monte Argentario Giannella [BMNH], Orbetello [BMNH]; Varazze (Savona) [MZSP]. LESOTHO. Maseru: Maseru [BMNH]. MOROCCO. Tanger, Tangier [USNM]. MEXICO. Baja California: Ensenada, Cortera FR [AVSC]; Baja California Sur: Guerrero Negro [AVSC]; Distrito Federal: Mexico City [BMNH], Distrito Federal (s.loc.) [WPMC]. NAMIBIA. Erongo: Swakopmund [BMNH]. POLAND. Dolnoslaskie: Breslau [NMHB]. PORTUGAL. Faro: Algarve, Luz nr. Lagos [BMNH]; Lisboa: Cascais [USNM], Estoril [USNM], Lisbona [MCZC, NHMB], Mafra [USNM], Praia das Macas [USNM]; Madeira: Funchal [MCZC, NHMB], Porto Moniz [BMNH], Ribeira Brava [BMNH], Ilheu Chão [BMNH], Porto Santo [BMNH], São Vicente [BMNH], Vale de Paraiso [BMNH], Praia Formosa [BMNH], Porto da Cruz [BMNH], Feiteiras [BMNH], Caramujo [BMNH], Lower Levada [BMNH], Madeira Is. (s. loc.) [BMNH, MHNG, NHMB]; Porto: Leça [BMNH], Oporto [BMNH]. SOUTH AFRICA. Eastern Cape: Queenstown [BMNH], Somerset East [BMNH]; Mpumalanga: Nelspruit [BMNH]; Northern Cape: Colesberg [ALWC]; Western Cape: Capetown [BMNH], Table Mt. [BMNH], nr. George [BMNH]. SPAIN. Andalucia: Malaga [USNM]; Canarias: Arenara [BMNH], Cruz de Tejeda [BMNH], Gran Canaria, Las Palmas, Telde [BMNH, MCZC, USNM], Orotava [BMNH], Santa Brigida [BMNH], Tenerife, Agua Mansa [NHMB], Tenerife, Ladera de Guimar [BMNH], Tenerife, Volcan de Guimar [NHMB], Tenerife (s. loc.) [BMNH]; Cataluña: Playa de Aro [NHMB]; Galicia: Mte. Ferro b. Bayona [BMNH]; Islas Baleares: Minorca, Cala Forçat [BMNH]. UNITED KINGDOM. Edinburgh: Edinburgh [BMNH]; Sussex: Lewes [BMNH]; Eastborne [BMNH]; Exeter [BMNH]; Windsor [BMNH]; Glasgow [BMNH]; W. Maidstone, Kent [BMNH]; Chillingham [BMNH]; Farnham House Lab, Imperial Bureau of Entomology [BMNH]. UNITED STATES. Alabama: Lowdnes Co., Ft. Deposit [USNM]; California: Alameda Co., Berkeley [UCDC, USNM]; Humboldt Co., Redway [ALWC]; Los Angeles Co., Pasadena [MZSP, USNM], Monterrey Co., Big Sur [ALWC]; Orange Co., Bolsa Chica Marsh [MZSP]; Riverside Co., Lake Skinner Camp [AVSC]; Sacramento Co., Sacramento [UCDC]; San Diego Co., UC Elliot Reserve [AVSC]; San Diego Co., San Diego [UCDC]; San Diego Co., E. San Diego [UCDC]; San Diego Co., Pacific Beach [UCDC]; San Diego Co., Mission Hills [UCDC]; San Diego Co., Kate Sessions Park [UCDC]; San Diego Co., Balboa Park [UCDC]; San Diego Co., Point Loma [UCDC]; San Joachin Co., Caswell State Park [PSWC]; San Luis Obispo Co., Oso Flaco Lake [LACM]; San Mateo Co., Colma [USNM]; San Mateo Co., San Bruno Mt. [PSWC]; Santa Clara Co., South Coyote [PSWC]; Sonoma Co., Russian R. 6k E. Healdsburg [UCDC]; Yolo Co., 6kW Capay [PSWC]; Yolo Co., Davis [PSWC, UCDC]; Yolo Co., Grasslands Regional Park, 8k SW Davis [PSWC, UCDC]; Florida: Escambia Co., Gonzalez [MCZC]; Louisiana: Plaquemines Co., Happy Jack [BMNH], Orleans Co., New Orleans [BMNH], Lousiana (s. loc.) [BMNH]; Mississippi: Coahoma Co., Clarkesdale [USNM], Copiah Co., Hazelhurst [MCZC], Oktibbeha Co., Starkville [BMNH]; South Carolina: York Co., York [BMNH].



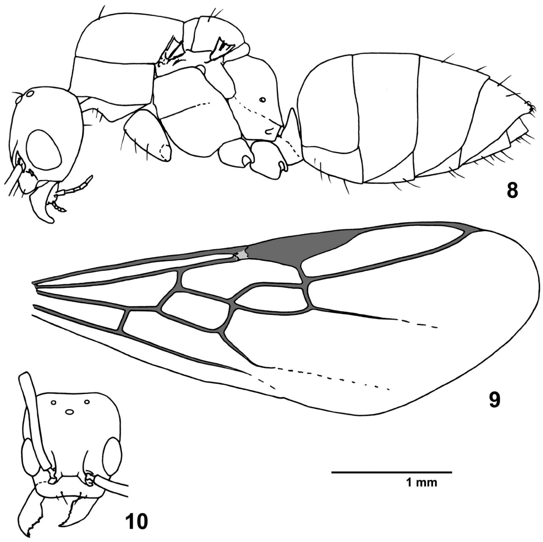
Figs. 1–7. *Linepithema* workers. 1. *L. humile*, lateral view. Specimen from Ñeembucú, Paraguay. 2. Undescribed *Linepithema* species, mesosoma, lateral view. Specimen from Parque Nacional El Palmar, Entre Rios, Argentina. 3. *L. iniquum*, mesosoma, lateral view. Specimen from the Reserva Natural del Bosque Mbaracayú, Paraguay. 4. Undescribed *Linepithema* species, mesosoma, lateral view. Specimen from the Reserva Natural del Bosque Mbaracayú, Canindeyú, Paraguay. 5. *L. humile*, head, full face view, same specimen as 1. 6. *L. oblongum*, head, full face view. Specimen from Infiernillos, Tucumán, Argentina. 7. Undescribed *Linepithema* species, head, full face view. Same specimen as in Fig. 2.

Worker Measurements. HOLOTYPE: HL 0.74, HW 0.66, MFC 0.16, SL 0.76, FL 0.65, LHT 0.68, PW 0.45, ES 2.93, SI 115, CI 89.

Others (n = 81): HL 0.62–0.78, HW 0.53–0.72, MFC 0.14–0.18, SL 0.62–0.80, FL 0.52–0.68, LHT 0.57–0.76, PW 0.35–0.47, ES 1.98–3.82, SI 108–126, CI 84–93.

Worker Diagnosis. A large (HL ≥ 0.62 mm) slender *Linepithema.* Head in full-face view longer than broad (CI 84–93), narrowed anteriorly and reaching its widest point just posterior to the compound eyes. Lateral margins broadly convex, grading smoothly into posterior margin. Posterior margin of head straight in smaller workers to weakly concave in larger workers. Compound eyes large (ES 1.98–3.82), comprising 82–110 ommatidia (normally around 100). Antennal scapes long (SI 108–126), as long or slightly longer than HL and easily surpassing posterior margin of the head in full-face view. Maxillary palpi relatively short, segments 4 and 5 both noticeably shorter than segment 2.

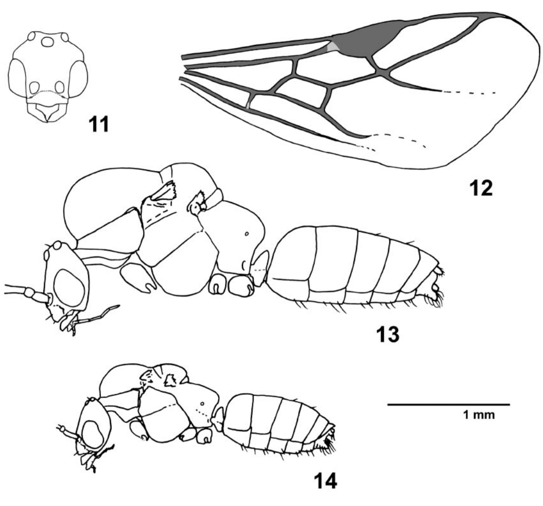
Pronotum and mesonotum forming a continuous convexity in lateral view, mesonotal dorsum nearly straight, not angular or strongly impressed, although sometimes with a slight impression in the anterior half.



Figs. 8–10. *L. humile*, queen. Specimen from Victoria, Entre Rios, Argentina. 8. Lateral view. 9. Right forewing, dorsal view. 10. Head, full face view.

Metanotal groove moderately impressed. Propodeum in lateral view inclined anteriad. In lateral view, dorsal propodeal face meeting declivity in a distinct though obtuse angle, from which the declivity descends in a straight line to the level of the propodeal spiracle.

Dorsum of head, mesosoma, petiole, and abdominal tergites 3 and 4 (=gastric tergites 1 and 2) devoid of erect setae (very rarely with a pair of small setae on abdominal tergite 4). Clypeus bearing a pair of long, forward-projecting setae. Abdominal tergites 5 and 6 each bearing a pair of long, erect setae. Ventrum of



Figs. 11–14. *Linepithema* males. 11. *L. humile*, head, full face view. 12. *L. humile* right forewing, dorsal view. 13. *L. humile*, lateral view. 11–13. Single specimen from Victoria, Entre Rios, Argentina. 14. Undescribed *Linepithema* species in the *humile*-group, male, lateral view. Specimen from Tafí del Valle, Tucumán, Argentina.

Table 1. Collection records of *L. humile* in South America

Country	Admin.	Locality	Status	Latitude	Longitude	Collection
Argentina	Buenos Aires	Boca		34° 38′ S	58° 21′ W	ALWC
Argentina	Buenos Aires	Buenos Aires		34° 36′ S	58° 28′ W	BMNH, MHNG, NHMB, NHMW, UCDC
Argentina	Buenos Aires	Campana		34° 12′ S	58° 56′ W	ALWC
Argentina	Buenos Aires	Reserva Costanera Sur		34° 07′ S	58° 21′ W	AVSC
Argentina	Buenos Aires	Isla Martin Garcia		34° 21′ S	58° 16′ W	MACN, NHMB
Argentina	Buenos Aires	La Plata		34° 56′ S	57° 57′ W	NHMB
Argentina	Buenos Aires	Lima-Zárete		34° 03′ S	59° 12′ W	IFML
Argentina	Buenos Aires	Olivos		34° 31′ S	58° 30′ W	MACN
Argentina	Buenos Aires	Reserva Otamendi		34° 14′ S	58° 54′ W	ALWC, AVSC, IFML
Argentina	Buenos Aires	Rosas- F.C.Sud		35° 58′ S	58° 56′ W	MACN
Argentina	Buenos Aires	Santa Coloma		34° 26′ S	59° 02′ W	ALWC
Argentina	Chubut	Rawson	*	43° 18′ S	65° 06′ W	PSWC
Argentina	Corrientes	Ayo. Cuay Grande		28° 47′ S	56° 17′ W	ALWC
Argentina	Corrientes	Corrientes		27° 28′ S	58° 50′ W	MACN
Argentina	Corrientes	Ita Ibate		27° 25′ S	57° 10′ W	AVSC
Argentina	Corrientes	Port Alvear		29° 07′ S	56° 33′ W	AVSC
Argentina	Corrientes	Sto. Tomé		28° 33′ S	56° 03′ W	IFML
Argentina	Entre Rios	10k S Medanos		33° 29′ S	58° 52′ W	ALWC
Argentina	Entre Rios	Colon		32° 15′ S	58° 07′ W	AVSC
Argentina	Entre Rios	Diamante		32° 01′ S	60° 39′ W	ALWC
Argentina	Entre Rios	Est. Sosa		31° 44′ S	59° 55′ W	MACN, MHNG, NHMB
Argentina	Entre Rios	Parque Nacional El Palmar		31° 53′ S	58° 13′ W	AVSC
Argentina	Entre Rios	Parque Nacional Pre Delta		32° 7′ S	60° 38′ W	AVSC
Argentina	Entre Rios	Port Ibicuy		33° 48′ S	59° 10′ W	AVSC
Argentina	Entre Rios	Victoria		32° 38′ S	60° 10′ W	ALWC
Argentina	Entre Rios	Villaguay		31° 51′ S	59° 01′ W	NHMB
Argentina	Formosa	Clorinda		25° 17′ S	57° 43′ W	IFML
Argentina	Formosa	Formosa		26° 11′ S	58° 11′ W	MACN, NHMB
Argentina	Formosa	Mojon de Fierro		26° 03′ S	58° 03′ W	IFML
Argentina	La Rioja	Amingá	*	28° 50′ S	66° 54′ W	ALWC, IFML
Argentina	La Rioja	Chuquis	*	28° 54′ S	66° 58′ W	ALWC
Argentina	Misiones	Parque Nacional Iguazú		25° 42′ S	54° 26′ W	IFML
Argentina	Misiones	Posadas		27° 23′ S	55° 53′ W	MZSP
Argentina	Santa Fe	10k E Santa Fe, Ruta 168		31° 41′ S	60° 34′ W	ALWC
Argentina	Santa Fe	Fives Lille		30° 09′ S	60° 21′ W	NHMB
Argentina	Santa Fe	Port Ocampo		28° 30′ S	59° 16′ W	AVSC
Argentina	Santa Fe	Rosario		32° 57′ S	60° 40′ W	MACN
Argentina	Tucumán	Tichuco	?	26° 31′ S	65° 15′ W	ALWC
Brazil	Amazonas	Manaus	*	03° 07′ S	60° 02′ W	MZSP
Brazil	Goiás	Anapolis	*	16° 20′ S	48° 58′ W	MZSP
Brazil	Mato Grosso do Sul	Corumbá. Faz. Sta. Blanca		19° 01′ S	57° 39′ W	MZSP
Brazil	Mato Grosso do Sul	Corumbá. Pto. Esperança		19° 37′ S	57° 27′ W	MZSP
Brazil	Mato Grosso do Sul	Passo do Lontra		19° 34′ S	57° 01′ W	PSWC, UCDC
Brazil	Mato Grosso do Sul	Pto. Murtinho		21° 42′ S	57° 52′ W	MZSP
Brazil	Rio de Janeiro	Rio de Janeiro	*	22° 54′ S	43° 14′ W	MCSN, MCZC, MHNG
Brazil	Rio Grande do Sul	N. Würtemberg		28° 18′ S	53° 30′ W	MZSP
Brazil	Rio Grande do Sul	Pelotas	?	31° 46′ S	52° 20′ W	BMNH
Chile	La Araucania	Temuco	*	38° 44′ S	72° 36′ W	MZSP
Chile	Santiago	Santiago, Metropolitan area	*	33° 27′ S	70° 40′ W	AVSC
Chile	Valparaiso	10k E Viña del Mar	*	33° 00′ S	71° 31′ W	AVSC
Colombia	Quindió	Armenia	*	4° 30′ S	75° 42′ W	WPMC
Ecuador	Pichincha	Carapungo	*	0° 05′ S	78° 30′ W	ALWC
Ecuador	Pichincha	Mitad del Mundo	*	0° 00′ S	78° 27′ W	ALWC
Ecuador	Pichincha	Quito	*	0° 11′ S	78° 30′ W	QCAZ
Paraguay	Alto Paraguay	Pto. 14 de Mayo		20° 23′ S	58° 08′ W	MCSN
Paraguay	Asunción	Asuncion		25° 16′ S	57° 40′ W	IFML, MACN, NHMB, USNM
Paraguay	Boquerón	P.N. Defensores del Chaco, Cerro Leon		20° 25′ S	60° 20′ W	ALWC
Paraguay	Central	San Lorenzo		25° 20′ S	57° 31′ W	ALWC
Paraguay	Cordillera	San Bernadino		25° 16′ S	57° 19′ W	MHNG
Paraguay	Ñeembucú	Pilar		26° 52′ S	58° 18′ W	ALWC
Paraguay	Ñeembucú			26° 52′ S	57° 47′ W	ALWC
Paraguay	Pte. Hayes	Benjamin Aceval		24° 58′ S	57° 34′ W	USNM
Paraguay	Pte. Hayes	Rio Confuso, Ruta Trans-Chaco		25° 06′ S	57° 33′ W	ALWC, IBNP
Paraguay	Pte. Hayes	Villa Hayes		25° 06′ S	57° 34′ W	ALWC, IBNP
Paraguay	Pte. Hayes	5k SE Pozo Colorado		23° 33′ S	58° 46′ W	ALWC
Paraguay	Pte. Hayes	Rt. 5 3k SE Concepción		23° 27′ S	57° 27′ W	ALWC
Paraguay	San Pedro	Pto. Rosario		24° 30′ S	57° 00′ W	ALWC
Peru	Lima	Los Condores	*	12° 03′ S	77° 03′ W	MZSP
Uruguay	Colonia	Carmelo		33° 59′ S	58° 17′ W	MACN, NHMB
Uruguay	Colonia	Colonia de Sacramento		34° 28′ S	57° 51′ W	AVSC
Uruguay	Montevideo	Montevideo		34° 51′ S	56° 10′ W	MACN, NHMB, NHMW

Unplaceable records: Argentina, "Mercedes" [MACN]; Argentina, "á de Julio. Osc. Orbeal" [MACN]; Argentina, "Est. Gilbert" [MACN]; Argentina, Entre Rios (s.loc) [MACN]; Argentina, Buenos Aires (s.loc) [MACN]; Argentina, Santa Fe (s.loc) [NHMB], Argentina (s.loc) [NHMW]; Brazil, Rio Grande do Sul (s.loc) [MZSP], Paraguay, "Chaco" [NHMW]; Paraguay, "Paraná R." [MCZC]; Uruguay (s.loc) [MHNG].

*, introduced population; ?, population origin ambiguous; possibly introduced.

metasoma with scattered erect setae. Gula with a pair of short setae. Body and appendages, including gula, the entire mesopleuron, and abdominal tergites, covered in dense pubescence.

Body and appendages concolorous, most commonly a medium reddish or yellowish brown but ranging in some populations from testaceous to dark brown, never yellow or piceous. Integument shagreened and lightly shining.

Worker Geographic Variation. Specimens from introduced populations outside of South America tend to fall toward the upper range of size variation in nearly all measurements, although there is considerable variation both in the native and the introduced ranges. The holotype worker from Buenos Aires is among the largest ants from either range. Some Paraguayan populations, particularly those farther than 10 km from the Paraguay River, have a slightly smaller eye size (<95 ommatidia) and tend to be smaller than ants in the southern Paraná drainage and along the major riverways. In general, Paraguayan specimens vary more in color than specimens from elsewhere, from testaceous to dark brown. The diagnostically sparse pilosity is generally consistent across all specimens, but several workers from Campana, Buenos Aires, have small erect setae on abdominal tergite 4 (=gastric tergite 2). These Campana workers otherwise fall within the range of variation for *L. humile,* and males from the same series clearly belong to *L. humile.*

Queen Measurements. (n = 13) HL 0.83–0.92, HW 0.83–0.93, SL 0.81–0.89, WGL 4.42–4.51, WL 1.67–2.09, FL 0.78–0.90, LHT 0.88–0.97, ES 7.3–9.4, SI 96–102, CI 93–101.

Queen Diagnosis. A robust species, difficult to distinguish from queens of related *Linepithema,* with long antennal scapes and large eyes. Head in full face view normally somewhat longer than broad (CI 93–101), lateral margins convex and broadly curved into the posterior margin. Posterior margin of head straight to slightly concave, never deeply or conspicuously concave. Eyes large (ES 7.3–9.4). Antennal scapes long (SI 96–102) and nearly equal to head length.

Entire body covered in a dense pubescence, a bit thicker and longer than that of the worker. Pilosity is also more developed than in the worker, with 2–11 (mean = 6) erect setae on the mesoscutum, 1–7 (mean = 4) erect setae on the scutellum, and 1–10 (mean = 3) erect setae on abdominal tergite 3, including the posterior row. Color as for the worker.

Queen Geographic Variation. Alate queens are much more common in collections from the native range than in collections from outside of South America. This observation is unlikely to be a sampling artifact given how heavily the introduced populations are represented in collections.

Male Measurements. (n = 25) HL 0.56–0.71, HW 0.56–0.74, SL 0.13–0.16, MML 1.40–1.96, MMW 0.76–1.12, WGL 2.55–3.26, FL 0.60–0.77, LHT 0.51–0.66, SI 12.8–15.4, CI 98.2–106.0.

Male Diagnosis. A robust ant, larger than the worker, with an exceptionally well-developed mesosoma. Head about as broad as long in full face view (CI 98.2–106.0) and somewhat dorso-ventrally compressed in lateral view. Eyes large, occupying much of antero-lateral surface of head and forming the anterior margin of the head lateral to the clypeus and the lateral margin of the head anterior to midpoint. Ocelli large and in full frontal view set above the adjoining postero-lateral margins. Anterior clypeal margin straight to broadly convex. Mandibles small, having a single apical tooth and four to eight denticles along the masticatory margin and rounding into the inner margin. Masticatory margin relatively short, about the same length as the inner margin. Inner margin roughly parallel to, or even converging distally with, the exterior lateral margin.

Mesosoma well-developed, considerably wider than head width, and larger in bulk and in length than metasoma. Mesoscutum greatly enlarged, projecting forward in a convexity overhanging the pronotum. Scutellum large, convex, nearly as tall as mesoscutum and projecting well above the level of the propodeum. Propodeum overhanging petiolar node, and declivitous face strongly concave.

Wings short relative to mesosomal length (Fig. 17) and bearing a single submarginal cell. Wing color whitish or yellowish, with dark brown veins and stigma. Petiolar scale with a broad crest and taller than the length of the node. Ventral process well developed. Gaster oval in dorsal view, nearly twice as long as broad. Parameres terminating as rounded pilose lobes. Digitus short, with a sharp, downturned terminal filament.

Dorsal surfaces of body largely devoid of erect setae, occasionally with a few fine, short setae scattered on mesoscutum, scutellum, and posterior abdominal tergites. Venter of gaster with scattered setae. Pubescence dense on body and appendages, becoming sparse only on the medial propodeal dorsum. Color as for the worker.

Male Geographic Variation. As in workers, specimens from introduced populations outside of South America tend to fall in the upper range of size variation.

Discussion

Taxonomy. These taxonomic results support current nomenclatural use. The holotype worker of Mayr's *Hypoclinea humilis* falls neatly within the range of variation present in the Argentine ant both in South America and in locations around the world where the ant is invasive (Figs. 15 and 16). The only older species-level name in the genus, *Linepithema fuscum* Mayr 1866, pertains to a male ant whose slender build, elongate genitalia, and distinct queen-like wing venation indicate only a distant relation to *L. humile.* Borgmeier's species *riograndense,* described from Rio Grande do Sul, Brazil, is clearly conspecific with *L. humile* and is synonymized here. Borgmeier's specimen identifications in MZSP reveal that he considered the name *humile* to apply to a common, probably undescribed southern Brazilian *Linepithema* with

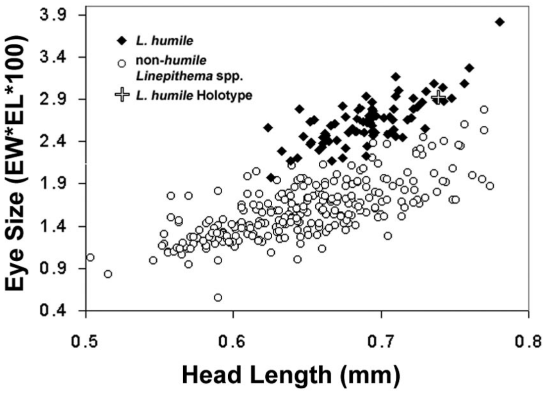


Fig. 15. Bivariate plot of eye size and head length in worker *Linepithema* ants sampled from across the global distribution of the genus. *L. humile* has larger eyes relative to head length than other *Linepithema* species.

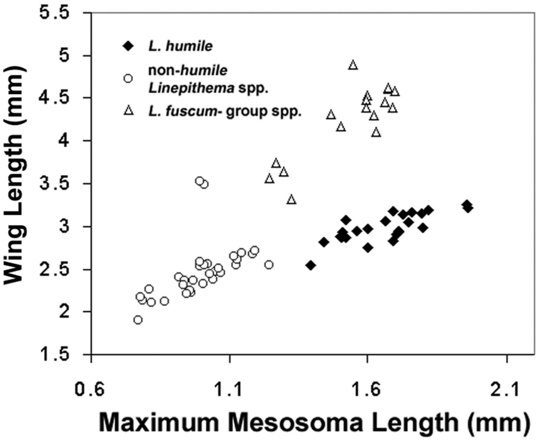


Fig. 17. Bivariate plot of wing length and maximum mesosomal length in male *Linepithema* ants sampled from across the global distribution of the genus.

short antennal scapes and more extensive pilosity. The aptly named subspecies *L. humile arrogans* Chopard, described from introduced *L. humile* populations in southern France, was probably inadvertently resurrected by Shattuck (1992) from an earlier synonymy. Here, I return *arrogans* to synonymy because there is no reason to view introduced Argentine ant populations as being heterospecific.

Diagnosis. *L. humile* diagnosis is straightforward in the male caste. The distinctive bulky males of *humile* are not easily confused with males of any other species. Males of closely related forms share structural similarities with *L. humile* (e.g., the undescribed species in Fig. 14) but are considerably smaller (Fig. 17) with a much less developed mesosoma. The lack of known intergrades strongly supports the specific status of *L. humile.* The only other congeneric males that share the size of *humile* are montane Andean and Caribbean forms associated with *L. fuscum,* but these are unlikely to be confused with *L. humile. Linepithema fuscum*-group males are structurally divergent (Shattuck 1992), with an unusually elongate habitus, a propodeum with a convex posterior face in lateral view, two submarginal cells in the forewing, and considerably longer wings relative to maximum mesosomal length (Fig. 17).

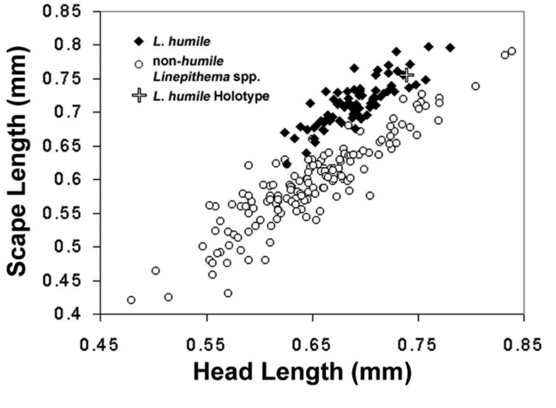


Fig. 16. Bivariate plot of antennal scape length and head length in worker *Linepithema* ants sampled from across the global distribution of the genus. Several species with long antennal scapes, *L. oblongum*, *L. leucomelas*, and *L. iniquum*-complex ants, were excluded.

Diagnosis is somewhat more problematic in workers, as no single character serves to separate *L. humile* from congeneric species. Table 2 provides a summary of the minimum combination of three character states that can diagnose nearly all *L. humile* worker specimens over the full geographic distribution of *Linepithema.* Figure 15 shows a consistent though not absolutely diagnostic difference in eye size versus head length between the large-eyed *L. humile* and all other non-*humile* specimens. Figure 16 plots antennal scape length versus head length in *L. humile* versus several other species, excluding the distinct long-scaped species *L. oblongum, L. leucomelas,* and ants of the *L. iniquum*-complex. These species are readily recognizable with other characters. Specifically, *iniquum*-complex ants have a strongly impressed mesonotal dorsum (Fig. 3), pronotal setae, and smaller eyes (ES < 2.0). *L. leucomelas* has a distinct white/brown bicoloration reminiscent of the ant *Tapinoma melanocephalum* (F.) 1793, standing setae on gastric tergites 1 and 2, and smaller eyes (ES < 2.0).

L. oblongum (Fig. 6) is the species most similar to *L. humile.* This poorly known ant seems to be confined to the high Andes in northern Argentina and Bolivia. Workers share the sparse pilosity and a similar mesosomal profile with *L. humile,* but they are somewhat more elongate (CI 81–88, mean = 84 in *L. oblongum;* CI 84–93, mean = 90 in *L. humile*) and have relatively smaller eyes (Fig. 18). *Linepithema oblongum* workers also have a noticeably smoother and shinier integument on the gastric dorsum than *L. humile,* and most workers have only sparse pubescence on gastric tergites 2 and 3, although some of the larger specimens

Table 2. Minimally diagnostic characters for *L. humile* workers

Character	*L. humile*	Other *Linepithema* species
Pilosity	Dorsum of head, mesosoma, and first two segments of the gaster devoid of erect setae (second gastric tergite very rarely with small setae)	Variable, usually with pronotal setae. In the lowland Paraná River drainage, nearly all non-*humile* specimens have erect setae on the pronotum and all gastric tergites. Elsewhere, specimens that lack erect setae on the pronotum and first two tergites have a smaller eye size and/or a shorter relative scape length than in *L. humile*
Length of first antennal segment	Relatively long (SL > 0.60, SI > 108)	Variable, SI usually < 106. Specimens with long first antennal segments either have a very strongly impressed mesonotal profile (*L. iniquum*-complex), are bicolored (*L. leucomelas*), or have smaller relative eye size and a more sparse pubescence (*L. oblongum*)
Eye size	Relatively large (ES > 2.0)	Variable, but ES usually smaller than 2.0

No other *Linepithema* species possess these character states in this combination, although a few species may show one or rarely two of them together.

within a series may retain a dense pubescence. Males of *L. oblongum* are much smaller than those of *L. humile* (MML < 1.1), and they lack the extraordinary mesosomal development of *L. humile* males. This species may be the sister taxon of the Argentine ant, a possibility that is currently being pursued with molecular genetic data (unpublished data).

The problem of *L. humile* worker diagnosis is simplified within the native range. No other lowland *Linepithema* in the Paraná River drainage lacks erect setae on the mesosoma and first two gastric tergites. Care should be taken when considering setal characters in damaged or roughened specimens, because setae are often lost.

This setal character was noted by Orr et al. (2001) in separating ants that were attacked by parasitic *Pseudacteon* flies (Diptera: Phoridae) from those that were not attacked. In examining Orr's specimens I confirmed that the relatively hairless forms that Orr et al. (2001) found not to be attacked by *Pseudacteon* are *L. humile.* Conversely, the more setose ants attacked

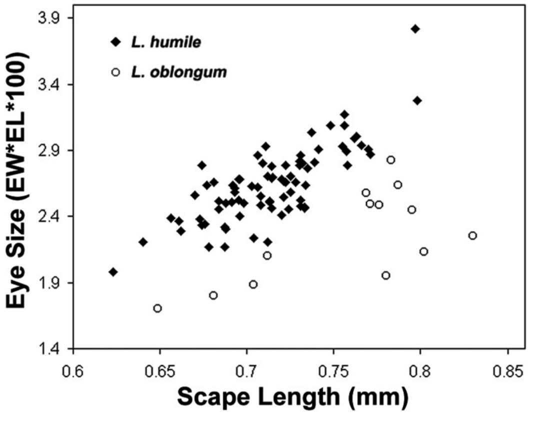


Fig. 18. Bivariate plot of eye size and antennal scape length in the morphologically similar species *L. humile* and *L. oblongum. L. oblongum* consistently has smaller eyes for a given scape length than does the Argentine ant *L. humile.*

by *Pseudacteon* were several other *Linepithema* species. We remain without positive evidence then that Argentine ants are attacked by phorid parasitoids.

Distribution. The Argentine ant's native distribution seems to be limited to the Paraná River drainage (Fig. 19), confirming the conclusion of Tsutsui et al. (2001). South American records of *L. humile* outside the Paraná drainage are invariably from urban areas, an observation that strongly supports the notion of recent introduction by human commerce. Paraná drainage records are also more abundant than non-Paraná records (49 versus 8). Furthermore, most records fall within a few kilometers of the largest rivers: the Paraná, the Paraguay, and the Uruguay. This is unlikely to be a sampling artifact, as evidenced from numerous records of other, non-*humile* species distant from major rivers (Fig. 20).

Records of *L. humile* in South America show the following pattern: patchy local abundance in low areas of the Paraná River drainage; common along major rivers (perhaps aided through frequent natural dispersal along the river); and very recent dispersal out of the Paraná drainage with human activity. Interestingly, some of the more morphologically divergent *L. humile,* including those with color variations and smaller compound eyes, are found >10 kilometers away from large rivers in the northern part of the native range. It is unlikely that this variation reflects the existence of cryptic species, given that much of the variation is allopatric and that *L. humile* males show remarkable consistency in diagnostic traits across populations. Specimens from the southern native range tend to look more like the common pest *L. humile,* although there is still a fair amount of variation. Overall this pattern raises the hypothesis of a northern origin for the species with later dispersal along the rivers. This hypothesis could be tested with genetic data in a phylogeographic framework (Avise 2000).

The history and biology of the Argentine ant in its native range is liable to be complex. Argentine ants likely move along river channels during periods of natural disturbance, and some of the native range

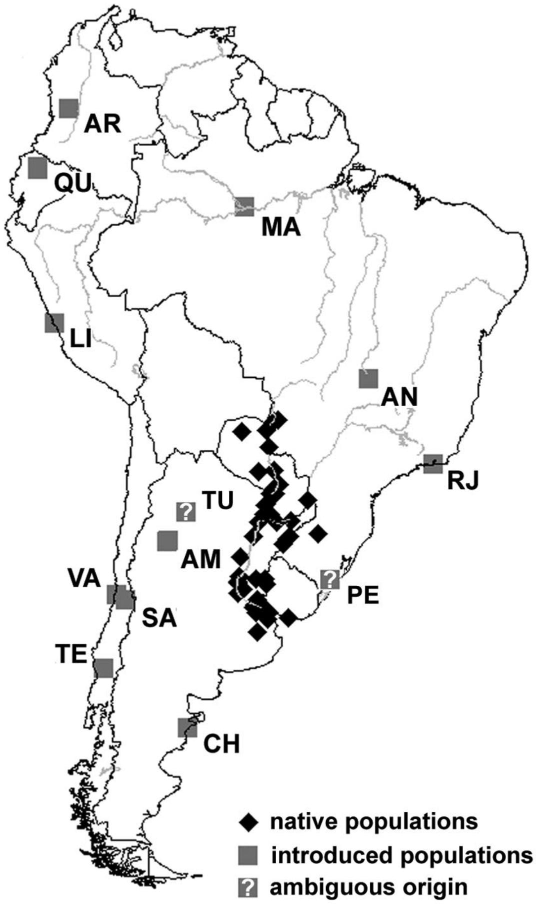


Fig. 19. Distribution of *L. humile* in South America based on collection records. AM, Amingá and Chuquis, Argentina; AN, Anápolis, Brazil; AR, Armenia, Colombia; LI, Lima, Peru; MA, Manaus, Brazil; PE, Pelotas, Brazil; QU, Quito, Carapungo, and Mitad del Mundo, Ecuador; RA, Rawson, Argentina; RJ, Rio de Janeiro, Brazil; SA, Santiago, Chile; TE, Temuco, Chile; TU, Tichuco, Tucumán, Argentina; VA, Valparaiso, Chile.

records probably correspond to recent local introductions through human commerce. It bears noting that *L. humile* is present in many urban areas along the Paraná and Paraguay rivers. The preponderance of Argentine ant records from flat, expansive flood plains suggests that records from fast-running, deeply channelized stretches of the Upper Paraná such as Argentina's Foz do Iguaçu also may not represent native populations.

The morphological diversity in native-range *L. humile* raises the issue of intraspecific diversity in other aspects of Argentine ant biology. Tsutsui and Case (2001) note variation in colony structure in the native range, and there also may be variation in mating systems and in colony life history. Studies that make use of contrasts between Argentine ant biology between native and introduced ranges would do well not to treat native range *L. humile* as a monolithic entity.

Fig. 20. Distribution of *L. humile* in southern South America, the Argentine ant's native range. Argentine ants are concentrated along the major waterways of the Paraná, Paraguay, and Uruguay rivers.

Rather, care should be taken to chose *L. humile* populations that are most likely to be close relatives of the introduced populations under study. Genetic work of Tsutsui et al. (2001) indicates that a southern Paraná population represents the source population for California *L. humile.* It also remains a possibility that some biological changes that contribute to the Argentine ants' invasive success occurred within the native range before introduction. Detailed studies of Argentine ant biology mapped onto a population-level phylogeny over the whole of the native range could determine if this were the case, as well as shed light on the sequence of evolutionary events leading to invasiveness in Argentine ants.

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