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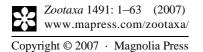
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Table of contents

Abstract	4
Introduction	4
Methods	6
Worker and queen characters	8
Taxonomic synopsis, Costa Rica fauna	8
Key to queens (Costa Rica)	10
Key to workers (Costa Rica)	12
Species accounts	
Azteca alfari Emery 1893	15
Azteca beltii Emery 1893	21
Azteca brevis Forel 1899	22
Azteca chartifex Forel 1896	23
Azteca coeruleipennis Emery 1893	25
Azteca constructor Emery 1896	26
Azteca flavigaster new species	30
Azteca forelii Emery 1893	32
Azteca gnava Forel 1906	34
Azteca instabilis (F. Smith 1862)	35
Azteca longiceps Emery 1893	37
Azteca nigra Forel 1912 new status	38
Azteca nigricans Forel 1899	40
Azteca oecocordia new species	41
Azteca ovaticeps Forel 1904	42
Azteca pittieri Forel 1899	43
Azteca quadraticeps new species	45
Azteca sericeasur new species	46
Azteca tonduzi Forel 1899	49
Azteca velox Forel 1899	
Azteca xanthochroa (Roger 1863)	52
Azteca aurita group	
Key to A. aurita group queens	55
Key to A. aurita group workers	55
Azteca aurita Emery 1893	55
Azteca lallemandi Forel 1899	
Azteca lanuginosa Emery 1893	
Azteca nanogyna new species	
Azteca pilosula Forel 1899	57

Azteca schimperi Emery 1893	58
Azteca jelskii Emery 1893	
Azteca sericea (Mayr 1866)	
Acknowledgments	
Literature cited	

Abstract

The genus Azteca is endemic to the American tropics, where they are abundant arboreal ants. The taxonomy and natural history of the Costa Rican fauna is reviewed, and the A. aurita group is recognized and revised globally. The following synonymies are proposed: A. laticeps Forel under A. chartifex Forel; A. championi Forel, A. eiseni Pergande, A. raptrix Forel, A. ursina Forel, and A. xysticola Forel under A. forelii Emery; A. rossi and A. surubrensis Forel under A. gnava Forel; A. major Forel under A. instabilis (F. Smith); A. prorsa Wheeler under A. longiceps Emery; A. patruelis Forel under A. pittieri Forel; A. nigriventris Forel and A. rectinota Forel under A. velox Forel; A. silvae Forel under A. aurita Emery; A. pruinosa Mann under A. lallemandi Forel; A. lacrymosa Forel under A. pilosula Forel; A. fiebrigi Forel, A. clariceps Santschi, and A. pallida Stitz under A. schimperi Emery; A. columbica Forel under A. jelskii Emery; A. mexicana Emery under A. sericea (Mayr). Azteca velox nigra Forel is raised to species. Azteca aurita pilosula is removed from synonymy and raised to species. The following new species are described: A. sericeasur, A. flavigaster, A. oecocordia, A. nanogyna, and A. quadraticeps.

Key words: Azteca, Azteca aurita group, Costa Rica, Formicidae, key to species

Introduction

The dolichoderine genus Azteca is a strictly neotropical group of arboreal ants (Emery 1893, Forel 1928). They are abundant in lowland habitats from Mexico to Argentina, occurring as both generalized foragers and as specialized inhabitants of myrmecophytic plants. Azteca species exhibit a variety of nesting habits, including the construction of carton nests, the occupation of live and dead plant stems (Forel 1899, Ule 1901, Emery 1913, Davidson 1988, Ayala et al. 1996), and the formation of ant gardens. Ant gardens are arboreal ant nests which sprout epiphytes from carton nest material (Ule 1901, Wheeler 1921, Longino 1986, Davidson 1988, Corbara et al. 1999, Kaufmann & Maschwitz 2006). Striking cases of symbiosis occur between Azteca and highly specialized myrmecophytic plants, the most notable case being the relationship between Azteca and Cecropia (Müller 1876, 1880–1881, Bequaert 1922, Wheeler 1942, Benson 1985, Longino 1991a, b). Also, Azteca ants have developed complex trophic relationships with many species of coccoid Hemiptera (Wheeler 1942, Johnson et al. 2001, Davidson et al. 2003). Azteca workers are often found tending mealy bugs (Pseudococcidae) and soft scales (Coccidae). For Azteca species that nest in live stems, the interior walls of the nest are often encrusted with mealy bugs and scales. Species building carton nests and ant gardens maintain dense populations of mealybugs and scales under the carton of the main nest or under small carton "pavilions" scattered over the vegetation. Very little attention has been paid to the taxonomic diversity of Coccoidea associated with Azteca, and usually only cursory observations of their presence are made during field collections. Because of the richness of the ecological interactions among Azteca, plants, and hemipteran symbionts, Azteca species have been and will continue to be subjects in the study of adaptation and coevolution, and therefore taxonomic work on the genus is particularly important.

The taxonomic bounds of the genus have not changed since its inception (Forel 1878, Shattuck 1992). Members of the genus can be recognized by the combination of (1) a thin, somewhat flexible cuticle, (2) anterolateral margins of clypeus extending anterior to mediolateral regions (with the exception of the *aurita* group, as reported here), (3) mandible with 7–9 teeth, (4) at least larger workers with cordate head shape, with

margin of vertex concave, (5) surface sculpture (other than on mandibles) smooth, micropunctate, microalveolate, or combinations of these, (6) the total absence of coarse surface elements such as spines, tubercles, carinae, rugae, striations, or large puncta, (7) a distinctive petiole which is strongly sloping anteriorly and has a rounded posteroventral lobe, and (8) worker caste polymorphism.

The Asian genus *Philidris* (former *Iridomyrmex cordatus* group) is highly convergent with *Azteca*. In contrast to *Azteca*, the anterolateral margins of the clypeus are posterior to the mediolateral portions, and the mandible has 10–12 teeth. Male characters (Shattuck 1992) and recent molecular evidence (P. S. Ward, pers. com.) ally *Philidris* with other Asian dolichoderines and confirm that the similarity is due to convergence.

The relative clarity of the generic status of *Azteca* is not mirrored in species-level taxonomy. Several factors contribute to taxonomic confusion in *Azteca*, some historical, some biological. The only revision of the genus *Azteca* is that of Emery (1893). Over 140 species-group names were subsequently published by Forel, Wheeler, and others, with no attempts at revision. Many species were described from workers only, with no biological data. Since it is often particularly difficult to separate *Azteca* species with workers only (Longino 1991a, b, 1996), many named *Azteca* species are difficult to circumscribe.

Wheeler and Bequaert (1929) belatedly stated "Apparently the females [i.e., queens] furnish more reliable characters for identification than the workers in the genus Azteca." An analogy can be drawn between the taxonomy of Azteca and the taxonomy of many plants. Botanists typically shun sterile material because it is often more plastic within species and less differentiated between species than reproductive material. Such is the case in Azteca. Workers are polymorphic within colonies, and colonies exhibit prolonged ontogenetic changes in worker morphology (pers. obs.). In contrast, queens are much less variable morphologically and exhibit strong interspecific differences. Within a single locality, species with strongly differentiated queens may have workers that are barely distinguishable.

Correlated with sharp differences in queen morphology are distinctive nesting habits. Nesting habits show great interspecific variation and little intraspecific variation. For example, queens of *Cecropia*-inhabiting species colonize very young *Cecropia* saplings. These queens are often very abundant in the environment, colonizing saplings and apparently competing for domination of saplings (Longino 1989b). I have made extensive collections of neotropical arboreal ants by breaking live and dead branches, searching for carton nests and ant gardens, and dissecting other myrmecophytes such as *Cordia*, *Acacia*, *Triplaris*, *Tococa*, and *Ocotea*. The *Azteca* species which dominate *Cecropia* trees are found only in *Cecropia* trees. In spite of high queen density and competition for saplings, I have never encountered one of these *Azteca* species, either colonies or founding queens, in any plant cavity other than that of a *Cecropia*. Thus, when only workers are available, biological data on nest site can be of critical diagnostic importance.

Because of the unreliability of worker morphology, many names in *Azteca* may remain in nomenclatural limbo indefinitely. Identities of species based solely on a type series of workers, with no data on queen morphology or nesting behavior, will only be resolved by a thorough understanding of the subtle differences between workers of all the species at the type locality. In the mean time, it is important to have species descriptions and a nomenclature for this important genus of neotropical ants.

I have carried out a series of studies on *Azteca* taxonomy and natural history (Longino 1989a, 1991a, 1991b, 1996), with an emphasis on the fauna of Costa Rica. This report reviews the entire *Azteca* fauna of Costa Rica. The report includes a synoptic species list, keys to species based on workers and queens, and individual species accounts. During the study it was discovered that a suite of characters strongly support a monophyletic *A. aurita* species group. It is perhaps the only easily recognized monophyletic group within the genus, and a revision of all known species in the group, including those occurring outside of Costa Rica, is provided in an addendum. The addendum also contains nomenclatural changes to *A. jelskii* and *A. sericea*, species parapatric with the Costa Rican species *A. tonduzi* and *A. sericeasur*, respectively.

Methods

Observations were made at 50x or 63x magnification with a dissecting microscope. Measurements were taken over a long period of time, with varying equipment and precision. Older measurements, including measurements of most types during a visit to European museums in 1990, were taken with an ocular micrometer and are precise to the nearest 0.01mm at best. More recent measurements were made with a micrometer stage with digital output in increments of 0.0001mm. However, variation in specimen orientation, alignment of crosshairs with edges of structures, and interpretation of structure boundaries resulted in measurement precision to the nearest 0.01 to 0.005mm, depending on sharpness of the defined boundary. When measuring workers, larger workers of a series were haphazardly selected. Only one worker from a colony series was measured, and when a species was known from multiple localities, workers were selected from different localities. All measurements are presented in mm. Measurement lists in individual species accounts show the sample size, followed by the median and range (in parentheses) for each metric variable. When sample size for a particular variable differed from the common sample size, it is given following the range, within the parentheses. Except where noted, measurements refer to Costa Rican specimens and may not encompass variation across the entire geographic range.

The following terminology and abbreviations are used:

HLA head length in full face view; perpendicular distance from line tangent to anterolateral clypeus lobes to line tangent to posteriormost extent of vertex lobes (Fig. 1A). This measure is chosen because the anterolateral clypeus lobes are always visible, while the anteriormost extent of the medial lobe may be obscured by the closed mandibles.

HLB medial head length; same as HLA except from anteromedian instead of anterolateral lobe of clypeus (Fig. 1A). This measure is important for the *A. aurita* group, where the lateral lobes are not well defined and the median lobe is strongly protruding. For most *Azteca* HLA and HLB are very similar.

HW head width; in full face view, maximum width of head capsule above eyes (Fig. 1A).

AHW anterior head width; distance across anterior foramen of head, measured across outer edges of mandibular condyles where they insert; measured in anterior, oblique, or dorsal view (Fig. 1B).

SL scape length; length of scape shaft from apex to basal flange, not including basal condyle and neck.

EL eye length, maximum length of eye.

OCW width of median ocellus.

MTSC metatibia seta count; with tibia in anterior view, such that outer (dorsal) margin is in profile, number of erect to suberect setae (distinct from any underlying pubescence) projecting from outer margin.

MNSC Number of erect setae on mesonotum of workers. Very fine, short setae are included in the count, and often these fine setae are only visible at particular angles and proper lighting. Counts are made up to 19 setae, after which specimens are scored as => 20.

CI cephalic index; 100*HW/HL. SI scape index; 100*SL/HL.

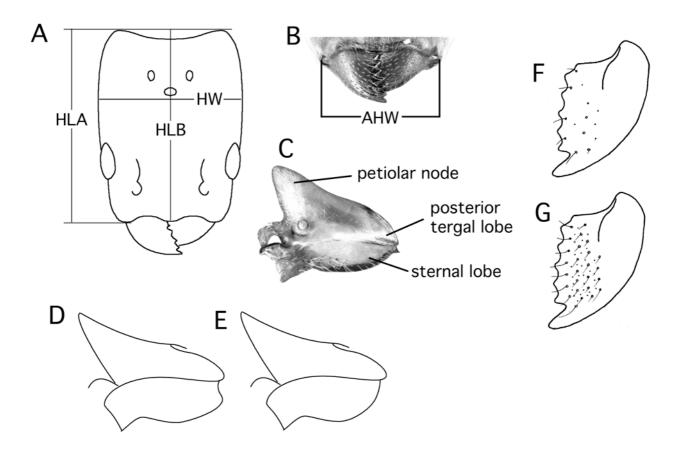


FIGURE 1. Characters for *Azteca* queens and workers. A, B. Head measurements. C. Petiole terminology. D. Petiole on which sternal lobe has concave posterior border (typical of *A. nigra*, *A. gnava*). E. Petiole on which posterior sternal lobe is convex, curving evenly to tergosternal suture (common ground plan). F. Mandible with small, sparse piligerous puncta. G. Mandible with even covering of coarse piligerous puncta.

Collections are referred to by the following acronyms:

AMNH	The American Museum of Natural History, New York, NY, USA.
BMNH	The Natural History Museum, London, U.K.
INBC	Instituto Nacional de Biodiversidad, Costa Rica.
JTLC	John T. Longino, personal collection, Olympia, WA, USA.
LACM	Los Angeles County Museum of Natural History, Los Angeles, CA, USA.
MCSN	Museo Civico de Storia Naturale "Giacomo Doria," Genoa, Italy.
MCZC	Museum of Comparative Zoology, Cambridge, MA, USA.
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland.
MKC	Michael Kaspari collection, University of Oklahoma.
MUCR	Entomology Museum, University of Costa Rica.
NHMB	Naturhistorisches Museum Basel, Switzerland.
NHMW	Naturhistorisches Museum Wien, Austria.
UCDC	University of California, Davis, CA, USA.
USNM	National Museum of Natural History, Washington, DC, USA.
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany.
DEIC	Deutsches Entomologisches Institut, Eberswalde Finow, Germany.

In lists of material examined, all specimens are deposited at JTLC unless otherwise indicated. Specimens in the Longino collection will eventually be distributed to research collections, most likely INBC and LACM. Locality data are from a specimen database in which locality data may be inferred from label data and may not always be faithful renditions of the label (*e.g.*, inferred latitude and longitude; locality name variants, etc.). All new names are nouns in apposition and invariant.

Worker and queen characters

Standard measurements of head width, head length, and scape length are of paramount importance for distinguishing *Azteca* species.

Palpal formula is 6,4, 5,3, or 4,3 (maxillary palp, labial palp).

Surface sculpture: Mandibles are generally shiny at the masticatory margin and microareolate or otherwise sculptured at the base. Sculpture of the intervening region varies interspecifically and can be of diagnostic value. This region may have widely spaced small puncta, or small puncta with a few large puncta concentrated near the masticatory margin, or many large puncta. The interspaces may be shiny, microareolate, or roughened with longitudinal acicular sculpture. A few weak grooves are often visible on a generally shiny surface, but this contrasts with species which have strongly roughened mandibles. Mandibles of the latter appear opaque. The head and mesosoma may be densely micropunctate, imparting a somewhat dull surface, or rarely completely smooth and shiny.

Pilosity and pubescence: *Azteca* generally have a layer of short pubescence throughout, showing interspecific variation in density. The distribution of pilosity, referring to setae that are distinct from the underlying pubescence, is used extensively in this treatment. Important areas for variation in pilosity are the dorsal surface of mandible, lateral and posterior margins of head in full face view, dorsal profile of mesosoma, outer surface of metatibia, ventral margin of petiole, and third and fourth abdominal terga.

Petiole shape: the shape of the sternal lobe and its relation to the posterior tergal lobe (Fig. 1C) vary among species. To see the petiole requires a clear view of the lateral profile. On dried specimens the gaster is often elevated and tightly appressed to the petiole, which obscures the view. The gaster must be pulled away or removed, and the metacoxa pushed forward or removed. The line of fusion between the tergum and sternum is usually visible, and this is oriented horizontally for a standard lateral view.

Taxonomic synopsis, Costa Rica fauna

- A. alfari Emery 1893. Mexico to Argentina.
 - = bicolor Emery 1893
 - = breviscapa Forel 1912
 - = cecropiae Forel 1906
 - = curtiscapa Forel 1912
 - = fumaticeps Forel 1909
 - = langi Wheeler 1942
 - = lucidula Forel 1899
 - = lynchi Brèthes 1914
 - = mixta Forel 1908
 - = virens Forel 1899
- A. beltii Emery 1893. Guatemala to Panama.
 - = laeta Wheeler 1942

- = stolli Forel 1912
- A. brevis Forel 1899. Costa Rica, Guatemala.
- A. chartifex Forel, in Emery 1896b. Costa Rica to Brazil.
 - = *laticeps* Forel 1899. **New synonymy**.
- A. coeruleipennis Emery, 1893. Mexico to Costa Rica.
- A. constructor Emery, 1896b. Guatemala to Venezuela.
 - = emmae Forel 1904
 - = guianae Wheeler 1942
- A. flavigaster. New species. Costa Rica.
- A. forelii Emery 1893. Mexico to Colombia, Trinidad.
 - = championi Forel 1899. New synonymy.
 - = eiseni Pergande 1895. New synonymy.
 - = raptrix Forel 1912. **New synonymy**.
 - = ursina Forel 1899. New synonymy.
 - = xysticola Forel 1899. **New synonymy**.
- A. gnava Forel 1906. Mexico to Costa Rica.
 - = rossi Forel 1909. New synonymy.
 - = surubrensis Forel 1912. New synonymy.
- A. instabilis (F. Smith 1862). Mexico to southern Brazil
 - = major Forel 1899. **New synonymy**.
- A. longiceps Emery 1893. Costa Rica, Guatemala.
 - = prorsa Wheeler 1942. New synonymy.
- A. nanogyna. See Addendum.
- A. nigra Forel 1912. Panama, Costa Rica. New status.
- A. nigricans Forel 1899. Costa Rica, Panama Guatemala.
- A. oecocordia. New species. Costa Rica.
- A. ovaticeps Forel, 1904. Costa Rica to Amazonian Brazil, Bolivia.
 - = aequalis Forel 1906.
 - = aequilata Forel 1904.
 - = tuberosa Forel 1906.
- A. pilosula. See Addendum.
- A. pittieri Forel 1899. Costa Rica.
 - = patruelis Forel 1908. **New synonymy**.
 - = emarginatisquamis Forel, 1920.
- A. quadraticeps. New species. Costa Rica.
- A. schimperi. See Addendum.
- A. sericeasur. New species. Guatemala to Panama.
- A. tonduzi Forel 1899. Costa Rica, Colombia.
- A. velox Forel 1899. Mexico to Colombia.
 - = nigriventris Forel 1899. **New synonymy**.
 - = rectinota Forel 1908. New synonymy.
- A. xanthochroa (Roger 1863). Mexico to Panama.
 - = costaricensis Wheeler 1942.

Addendum

Azteca aurita group

- A. aurita Emery 1893. Panama to Amazonian Brazil
 - = silvae Forel 1899 **New synonymy**.
- A. lallemandi Forel 1899. Panama, Colombia, eastern Brazil
 - = pruinosa Mann 1916 New synonymy.
- A. lanuginosa Emery 1893. Southern Brazil
- A. nanogyna. New species. Costa Rica.
- A. pilosula Forel 1899. Costa Rica, Panama. New status.
 - = *lacrymosa* Forel 1899. **New synonymy**.
- A. schimperi Emery 1893. Mexico to Argentina
 - = A. fiebrigi Forel 1909 New synonymy.
 - = A. clariceps Santschi 1933 New synonymy.
 - = A. pallida Stitz 1937 New synonymy.

Miscellaneous

- A. jelskii Emery 1893
 - = columbica Forel 1912. **New synonymy**.
- A. sericea (Mayr 1866). Mexico.
 - = mexicana Emery 1896a. New synonymy.

Key to queens (Costa Rica)

The queen of A. chartifex is unknown, but it will probably key to A. tonduzi.

1.	Outer margin of hind tibia with abundant erect setae, MTSC usually > 20, if MTSC in the 10–20 range, Cl > 95
-	Outer margin of hind tibia with erect setae reduced to absent, MTSC $<$ 20, if MTSC in the 10–20 range $CI < 80$
2.	Head subrectangular (Fig. 2, coeruleipennis, xanthochroa), CI < 90, obligate Cecropia inhabitant 3
-	Head with sides more rounded (e.g., Fig. 2, <i>constructor</i>), CI > 90, nesting habits various
3.	Color dark brown to black, HW < 1.55mm; head shape as in Fig. 2 (coeruleipennis); palpal formula 6,4
-	Color orange, HW > 1.80mm; head shape as in Fig. 2 (xanthochroa); palpal formula 5,3 xanthochroa
4.	Color solid black throughout; mesosomal dorsum with dense brush of setae over entire surface; many
	setae on margin of vertex as long as distance between lateral ocelli (Fig. 2, constructor); HW 1.4–1.8mm
	(Fig. 4A); palpal formula 5,3; obligate <i>Cecropia</i> inhabitant
-	Color rarely solid black, usually red brown, or black with lighter yellow brown on variable extent of ante-
	rior and lateral face; mesosomal dorsum often with abundant setae but never a dense brush; setae on mar-
	gin of vertex shorter than distance between lateral ocelli; HW various; palpal formula 6,4; not obligate
	Cecropia inhabitants
5.	HW > 2.3mm; face usually uniformly colored light red brown to dark brown
-	HW < 2.2mm; face with variable combination of black to lighter yellow brown (varies from almost
	entirely black with narrow region of lighter color at anterior margin of head capsule, to almost entirely
	yellow brown with patch of infuscation on posteromedian vertex)

о.	Antennae relatively long (SI $>$ 58); ocelli large (OCw $>$ 0.20mm); posterior sternal lobe of petiole snai-
	low and evenly sloping to apex of posterior tergal lobe (Fig. 1E, 5); apex of petiolar node in lateral view
	flattened and scale-like (Fig. 5)
_	Antennae relatively shorter (SI < 55); ocelli small (OCW < 0.15mm); posterior sternal lobe of petiole
	more convex and shorter, meeting posterior tergal lobe before apex (Fig. 1D, 5); apex of petiolar node
	acute but not as strongly flattened, more bluntly rounded (Fig. 5)gnava
7.	HW > 1.9mm (Fig. 4A); face extensively yellow brown with darker brown infuscation on vertex (Fig. 3)
	sericeasur
_	HW < 1.9mm; face coloration as above or more extensively dark brown to black
8.	HW < 1.58mm (Fig. 6A); head almost entirely black, with small band of lighter coloration on anterior
٠.	head capsule (Fig. 3)
-	HW > 1.58mm; head coloration as above or with more extensive yellow coloration extending up sides of
	head and into antennal fossae
9.	Sternal lobe of petiole with posterior margin forming a separate convexity that extends as far posteriorly
	as posterior tergal lobe, with a small notch or concavity between the sternal convexity and the tergal lobe
	(Fig. 1D, 5); head relatively short (Fig. 6A); forms ant gardens
_	Sternal lobe of petiole evenly curved to tergosternal suture, not forming separate convexity or notch, pos-
	terior tergal lobe extending further posteriorly than sternal lobe (Fig. 1E); head relatively longer (Fig. 6A:
	velox, quadraticeps); nests in live or dead stems with variable construction of small carton shelters, but
	not forming large conspicuous ant gardens
10.	Head relatively shorter and more cordate, sides more strongly narrowing anteriorly (Fig. 3, 6A,B) velox
-	Head relatively longer and more quadrate, sides less strongly narrowing anteriorly (Fig. 3, 6A,B)
	quadraticeps
11.	Meso- and metatibial spurs absent; anterior margin of clypeus strongly convex, median lobe extending
	anterad to lateral lobes (HLB/HLA > 1.04); entire body smooth and shiny, highly polished (<i>aurita</i> group)
-	Meso- and metatibia with distinct pectinate spurs; anterior margin of clypeus weakly convex, subparallel
	with lateral lobes (HLB/HLA <1.01); body surface duller, not shiny
12.	Color yellow-orange; posterolateral margins of vertex forming pronounced triangular lobes (Fig. 2); CI >
	85 (Fig. 4A)
-	Color brown; posterolateral margins of vertex not forming pronounced triangular lobes; CI < 80
13.	HW < 0.65mm (Fig. 4A); sides of head relatively more rounded and converging toward posterolateral
10.	lobes of vertex (Fig. 9); outer surface of metatibia with abundant suberect pubescence and numerous, reg-
	ularly spaced, short, erect setae
-	HW > 1.00mm (Fig. 4A); sides of head subparallel, not converging toward posterolateral lobes of vertex
	(Fig. 2); outer surface of metatibia with pubescence relatively short, sparse, appressed, and inconspicu-
	ous; outer surface of metatibia lacking erect setae or with a few, irregularly spaced, short setae near the
	baseschimperi
14.	Head relatively short and broad (CI > 78)
_	Head relatively long and narrow, subrectangular (CI < 78)
	Petiolar node strongly flattened, scale-like (Fig. 5); head short and broad (CI > 100, Fig. 4A)tonduzi
-	Petiolar node not strongly flattened, apex usually bluntly rounded; head relatively longer and thinner (CI
	< 90)
16.	HW > 1.53mm (Fig. 4A); dorsal surface of mandible evenly covered with abundant large piligerous
	puncta (Fig. 1G), setae arising from puncta erect, about as long as width of mandibular teeth; builds car-
	ton galleries on tree trunks, not a Cecropia specialist
_	HW < 1.45; much of dorsal surface of mandible with sparse, small puncta bearing setae that are reduced

	to short remnants, no longer than width of puncta (Fig. 1F), puncta with longer setae restricted to apex and
	near masticatory margin; Cecropia specialists
17.	Fourth abdominal tergum with < 6 erect setae, exclusive of posterior row; dorsal surface of head, when
	viewed in profile, with setae occurring in three clusters separated by distinct gaps, one cluster on and just
	above the clypeus, one around the ocelli (these may be entirely absent), and one on the upper vertex
	scape relatively short (SI 45–49, Fig. 6C); color usually black
-	Fourth abdominal tergum with > 10 erect setae (rarely fewer), exclusive of posterior row; dorsal surface
	of head, when viewed in profile, often with setae bridging the gap between the ocellar region and the
	upper vertex, and often with setae extending up from the clypeus almost to the ocellar region; scape rela-
	tively longer (SI 49–54, Fig. 6C); color black to lighter red brown
18.	Color largely orange; HW > 1.2mm (Fig. 4A)beltii
-	Color largely or entirely black; HW < 1.2mm
19.	Mandible with even covering of coarse, piligerous puncta; mandible surface appearing bristly 20
-	Mandible with row of piligerous puncta along masticatory margin, but large puncta sparse to absent on
	mandible surface proximal to this row, and with at most four puncta bearing setae
20.	Scape relatively short (SI 39–43)
-	Scape longer (SI 50–52)
21.	Head strongly rectangular, with flat sides and posterolateral lobes of vertex relatively angular; head rela-
	tively longer and narrower (SI < 63, Fig. 4B)
-	Head less rectangular, with sides slightly convex, and lateral margin of vertex more broadly rounded
	head relatively shorter and wider (SI > 63, Fig. 4B)
22.	Petiolar node low, anterior face of petiole flat (Fig. 5); metatibia with few erect setae (MTSC < 5); propo-
	deum with sparse short setae concentrated posterior to spiracle; mandible lacking large puncta proximal to
	$masticatory \ margin; \ size \ relatively \ large \ (HW>0.92mm, Fig.\ 4B) \\ oecocordiance \ of \ constant \ of \ constan$
-	Petiolar node higher, anterior face somewhat concave (Fig. 5); metatibia with relatively more setae
	(MTSC 10-20); propodeum with setae sparse or abundant; mandible with about 5 large puncta proximal
	$to\ masticatory\ margin;\ size\ relatively\ smaller\ (HW<0.93mm,\ Fig.\ 4B)longiceps and the state of $

Key to workers (Costa Rica)

Identifying *Azteca* species from the morphological traits of individual workers is difficult. Colonies show strong size variation among workers (Wheeler 1986), and the size of the largest workers increases as colonies mature. The larger a worker is, the more queen-like it is and the more differentiable from other species. The following key is most likely to work when a series from a mature colony is available, so that the largest workers can be selected for examination. When size ranges are given in the key, they refer to these larger workers. The workers of *A. nanogyna* and *A. quadraticeps* are unknown.

- 2. Dorsal surface of mandible smooth, not striate; posterolateral margin of vertex evenly rounded (Fig. 3); sternal lobe of petiole with sharp, longitudinal carina......schimperi

3.	Outer surface of hind tibia completely devoid of erect setae, rarely with 1 or 2 short setae on largest workers; palpal formula 5,3
-	Outer surface of hind tibia with 5 or more erect setae (these may be very short, less than a quarter of tibial
	width, and difficult to see); palpal formula 5,3 or 6,4.
4.	Promesonotum strongly produced, bulging, dropping steeply to flat dorsal face of propodeum (Fig. 7) <i>chartifex</i>
-	Promesonotum less strongly produced, posterior mesonotum more shallowly sloping and meeting dorsal
_	face of propodeum at more obtuse angle 5
5.	Dorsal surface of mandible largely smooth with small non-setose puncta, setigerous puncta restricted to masticatory margin (Fig. 1F)
-	Dorsal surface of mandible evenly covered with large setigerous puncta (Fig. 1G)
6.	Dorsum of mesosoma with a relatively "clean" look, with relatively few erect setae, these of relatively
	uniform length (MNSC 2–17, median 8, Fig. 7)
-	Dorsum of mesosoma more "scruffy," with more setae, and these of irregular length (MNSC > 10, median about 20, Fig. 7)
7.	Dorsal face of propodeum with moderately abundant erect setae; SI > 50; HW of larger workers often >
٠.	1.1mm; basal half or more of mandible microalveolate, dull
_	Dorsal face of propodeum devoid of erect setae; SI < 50; HW of larger workers usually < 1.0mm; entire
	mandible generally smooth and shiny on interspaces between puncta
8.	Palpal formula 6,4; color yellow; dorsal face of propodeum and metanotal groove together form a single
	flat "shelf" that abruptly meets rising posterior mesonotum (Fig. 7); obligate <i>Cecropia</i> inhabitant
	coeruleipennis
_	Palpal formula 5,3 or 6,4; color various; dorsal face of propodeum and mesonotum forming two convexi-
	ties that meet at impressed metanotal groove (e.g., Fig. 7, sericeasur worker); nesting habits various 9
9.	Palpal formula 5,3; mostly species (with the exception of A. tonduzi) nesting in myrmecophytes (Cecro-
	pia, Cordia, Triplaris) or narrow-gauge live stems of various plant species, with foraging restricted to the
	hostplant stem interiors or surfaces
-	Palpal formula 6,4; species nesting in large plant cavities or ant gardens, with conspicuous and general-
	ized surface foragers
10.	Head relatively broad, CI > 86 (Fig. 6D); obligate <i>Cecropia</i> inhabitants or nesting in dead stems 11
-	Head relatively narrow, CI < 90 (Fig. 6D); inhabitants of live stems but not obligate <i>Cecropia</i> specialists
11.	Setae on metatibia sparse and short, MTSC 10–20, length of setae one fourth to one third maximum width
	of tibia; HW of larger workers < 0.91mm (Fig. 6D); nests in dead stems often augmented with carton
	nests
-	Setae on metatibia abundant and longer, MTSC > 20, length of setae one half or more maximum width of
	tibia; HW of larger workers > 1.10mm (Fig. 6D); obligate inhabitants of <i>Cecropia</i>
12.	Petiole in profile with node more massive than sternal lobe, perpendicular distance from tergosternal
	suture to apex of node greater than or equal to distance to ventral margin of sternal lobe (Fig. 7); face with
	mottled coloration, light brown to orange with variable extent of medial infuscation (Fig. 3). xanthochroa
-	Petiole in profile with node less massive than sternal lobe, perpendicular distance from tergosternal suture
	to apex of node less than distance to ventral margin of sternal lobe (Fig. 7); face uniformly brown (Fig. 3)
13.	Most of dorsal surface of mandible covered with large piligerous puncta, mandibles appearing bristly
	(Fig. 1G); nesting in live stems of multiple plant species, not obligate inhabitant of <i>Cordia</i> or <i>Triplaris</i>
	nigricans
-	Dorsal surface of mandible with large piligerous puncta, if present, restricted to masticatory margin and

	apex, mandibles not appearing bristly (Fig. 1F); nesting habits various, including obligate inhabitants of Cordia and Triplaris
1/1	Setae on metatibia few and short, MTSC usually about 5, setae about as long as one quarter width of tibia
14.	propodeum with cluster of about 4 setae where dorsal face rounds into posterior face, 0–4 setae anterior of
	this cluster on dorsal face, these setae short, 1–2 times width of propodeal spiracle; largest workers with
	HW > 1.0mm (Fig. 6D)
_	Setae on metatibia more abundant and longer, MTSC 8–17, setae about as long as half width of tibia; dor-
	sal face of propodeum with 4 or more setae, these setae long, > 4 times width of propodeal spiracle; larg-
	est workers with HW < 1.0mm (Fig. 6D)
15	Face of largest workers yellow; dorsal surface of mandible with interspaces between puncta largely
15.	smooth and shining, at most basal third of mandible shagreened; posterior margin of sternal lobe of peti-
	ole with a layer of dense, short, pubescence-like pilosity and 2–4 longer setae; opportunistic inhabitant of
	multiple ant plants and live stems of non-myrmecophytes
_	Face of largest workers brown; dorsal surface of mandible with interspaces between puncta shagreened or
	basal half or more; posterior margin of sternal lobe of petiole with cluster of erect setae of even length
	obligate inhabitant of <i>Cordia alliodora</i> oecocordia
16.	Head relatively broader (CI 78–91, Fig. 6D); obligate inhabitant of <i>Cordia alliodora</i> (or understory Lau-
	raceae, see under A. pittieri) pittieri
_	Head relatively narrower (CI 73–81, Fig. 6D); obligate inhabitant of <i>Triplaris melaenodendron</i>
	longiceps
17.	Mandibles opaque, densely microalveolate/punctate, substriate; posteroventral margin of petiole with
	abundant long coarse setae, shorter pubescence layer much less conspicuous than long setae (Fig. 7)
	majors very large (HW up to 2.2mm); nests in hollow trunks of large, live trees, with nest entrance a fis-
	sure at the base of the tree
-	Mandibles shiny to weakly sculptured; largest workers typically smaller, HW < 1.8mm; nesting habits
	various (the workers of the following species are highly variable and I have not been able to discover
	diagnostic characters that always differentiate them; the following key couplets reflect average differ-
	ences among species, but I have examined many worker series in this complex that I could not place). 18
18.	Gastral dorsum bright yellow, sharply contrasting with dark brown petiole and mesosoma; measurements
	as in Figs. 6E,F
-	Gastral dorsum dark brown, or, if light yellow brown, petiole and mesosoma are lighter brown as well
	gastral color not sharply contrasting with mesosoma color
19.	Head relatively broad (Fig. 3, 6E, CI 101-109); scape relatively short (Fig. 6F, SI 70-85); face usually
	uniformly dark brown (lighter orange brown in one series); setae on posterior margin of vertex usually
	long, subequal in length to eye length; forms ant gardens
-	Head relatively narrower; scape relatively longer; face color various but often a mixture of light and dark
	brown; setae on vertex margin usually shorter than eye length; nesting habits various
20.	Largest workers with HW usually > 1.2mm; general body coloration often light orange brown; head shape
	often strongly cordate (Fig. 3)
-	Largest workers with HW usually < 1.2mm; general coloration often dark brown with light orange brown
	restricted to anterior and lateral portions of head; head shape often less strongly cordate (Fig. 3: velox and
	<i>nigra</i>)
21.	Scape relatively short (Fig. 6F, SI 78–89); nests in plant cavities
-	Scape relatively longer (Fig. 6F, SI 84–105); nests in ant gardens

Species accounts

Azteca alfari Emery 1893

Figures 2,4A,5,6C,7.

Azteca alfari Emery 1893:338. Lectotype worker: Jiménez, Atlantic slope, Costa Rica (Alfaro) [MCSN] (examined). Description of queen: Emery 1896b:4 [as alfaroi].

Azteca bicolor Emery 1893:341. Lectotype queen: Brazil, Matto Grosso (Germain) [MCSN] (examined). Synonymy by Longino 1991b:1575.

Azteca alfaroi race lucidula Forel 1899:113. Lectotype queen: Trinidad (Urich) [MHNG] (examined). Synonymy by Longino 1989a:5.

Azteca virens Forel 1899:115. Syntype workers: Brazil, Amazonas, Pará (Göldi) [MCZC] (examined). Synonymy by Longino 1989a:5.

Azteca alfari subsp. cecropiae Forel 1906:240. Lectotype worker: Brazil, Amazonas, Manaus (Huber) [MHNG] (examined). Description of queen, male: Forel 1908b:387. Synonymy by Longino 1989a:5.

Azteca alfari var. mixta Forel 1908b:386. Lectotype queen: San Bernardino, Paraguay (Fiebrig) [MHNG] (examined). Synonymy by Longino 1989a:6.

Azteca alfaroi var. fumaticeps Forel 1909:250. Syntype workers: Mexico, Buenaventura (Ross) [MHNG] (examined). Description of queen: Wheeler 1942:218. Synonymy by Longino 1989a:7.

Azteca alfari var. curtiscapa Forel 1912:51. Lectotype queen: Panama (Christophersen) [MHNG] (examined). Synonymy by Longino 1989a:7.

Azteca foreli race breviscapa Forel 1912:51 [first available use of Azteca foreli race championi var. breviscapa Forel 1899:112. Syntype workers: Costa Rica (Tonduz) [MCZC, USNM] (examined). Synonymy by Longino 1989a:7.

Azteca alfari var. argentina Forel 1914:287. Syntype workers: Argentina, Misiones, Santa Ana (Bruch) [MHNG] (examined). Description of major worker and queen: Gallardo 1916:115. Synonymy by Longino 1989a:7.

Azteca lynchi Bréthes 1914:93. Syntype worker(s): Bolivia (Arribálzaga). Subspecies of A. alfari: Gallardo 1916:118. Synonymy by Longino 1989a:7.

Azteca alfari var. langi Wheeler 1942:218. Syntype workers, queens, males: Guyana, Kamakusa (Lang) [MCZC] (examined). Synonymy by Longino 1989a:7.

Azteca alfari subsp. lucidula var. zonalis Wheeler 1942:222 (unavailable name). Workers, queens: Panama, Corozal, 21.xi.1911 (Wheeler) [MCZC] (examined). Identification as A. alfari: Longino 1989a:7.

Queen characters. Measurements (n=21): HLA 1.62 (1.51–1.69), HW 1.32 (1.26–1.43), SL 0.76 (0.71–0.85), CI 83 (80–86), SI 47 (45–51).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible largely smooth, with sparse small piligerous puncta, setae in puncta short, larger puncta with long setae near masticatory margin; medial and lateral clypeal lobes at about same level (medial lobe not projecting anteriorly); head weakly quadrate; petiolar node acute, triangular, neither strongly flattened nor bluntly rounded; posteroventral petiolar lobe well-developed, evenly convex; scape and tibia lacking setae, sides of head lacking setae, posterior margin of head with abundant curved setae, pronotum with posterior row of curved setae, mesoscutum with sparse setae, scutellum and propodeum with more abundant setae, petiolar node with cluster of erect setae, third abdominal tergum with abundant erect setae, fourth and fifth abdominal terga with 0–6 erect setae exclusive of posterior row; color light red brown to black.

Worker characters. Measurements (n=13): HLA 0.99 (0.80–1.24), HW 0.88 (0.72–1.07), SL 0.60 (0.53–0.72), CI 91 (86–94), SI 62 (58–69).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible largely smooth, with sparse small piligerous puncta, setae in puncta short, larger puncta with long setae near masticatory margin; medial and lateral clypeal lobes at about same level, medial lobe at most weakly projecting beyond lateral lobes; head with convex sides, strongly cordate posterior margin; mesosoma in lateral profile with promesonotum forming a continuous convexity or mesonotum somewhat elevated above pronotum; posterior mesonotum drops gradually to narrow metanotal groove such that posterior mesonotum, metanotal

groove, and dorsal face of propodeum form a broad, shallow V (dorsal face of propodeum and broad metanotal groove do not form flat, step-like junction with posterior mesonotum); scape and tibia lacking setae, sides of head lacking setae, posterior margin of head with sparse to abundant erect setae, pronotum, mesonotum, and dorsal face of propodeum with conspicuous erect setae, mesonotum usually with about 8 erect setae of relatively uniform length (range 2–17; contrast with *A. ovaticeps*); color brown to yellow.

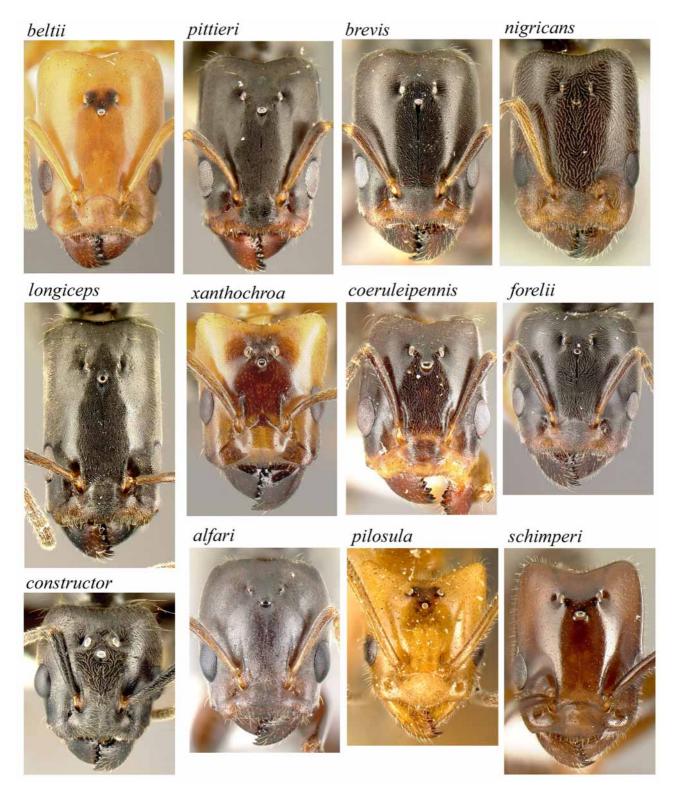


FIGURE 2. Face views of *Azteca* queens, species with relatively long, thin faces, *Cecropia* ants, and *A. aurita* group. Images are not to scale; refer to Fig. 4A,B and individual species accounts for morphometric data.

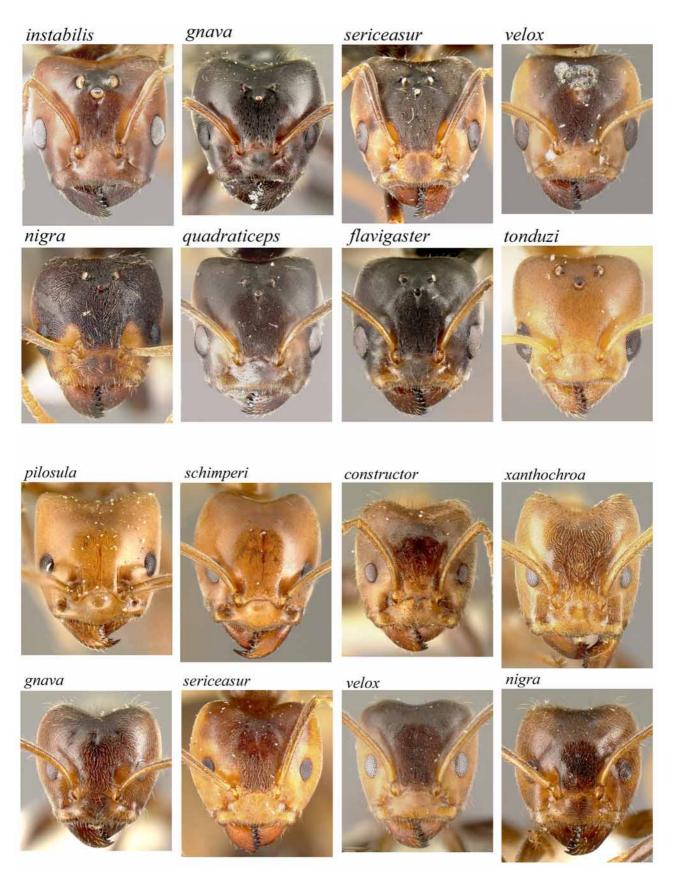


FIGURE 3. Upper two rows: face views of *Azteca* queens, species with relatively short, broad faces. Refer to Fig. 4A and individual species accounts for morphometric data. Lower two rows: face views of representative *Azteca* workers. Images are not to scale.

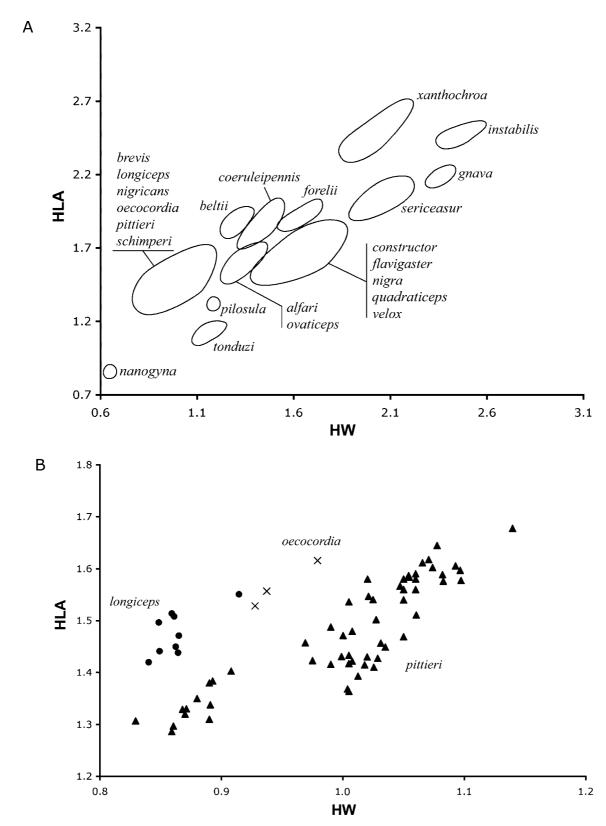


FIGURE 4. A. Morphometric space for subsets of Costa Rican *Azteca* species, based on queen head width and head length. Queens with long thin heads are in upper left part of graph; queens with short broad heads are in lower right. Only Costa Rican data are shown, with the following exceptions: *sericeasur* includes specimens from Panama and Guatemala, *nigra* includes a syntype queen from Panama, *nigricans* includes the holotype queen from Panama, *pilosula* includes a syntype queen from Panama, the three *schimperi* queens are from Colombia, Brazil, and Paraguay, and *velox* includes a syntype queen of *nigriventris* from Colombia. B. Scatterplot of head width by head length, differentiating queens of *A. longiceps*, *A. oecocordia*, and *A. pittieri*. All measurements are in mm.



FIGURE 5. Lateral views of petioles of *Azteca* queens. Images are not to scale.

Similar species. *Azteca alfari* is most similar to *A. ovaticeps* (Longino 1989a). See differentiating characters in key and under *A. ovaticeps*. Workers of *A. alfari* may also be confused with workers of *A. forelii*. Mandibles of *A. alfari* workers are smooth and shiny; mandibles of *A. forelii* workers are roughened and dull.

Range. Central Mexico to northern Argentina.

Biology. The taxonomy and biology of A. alfari are reviewed in Longino (1989a, 1991b).

Azteca alfari is an obligate Cecropia ant. It is the most widespread of the Cecropia ants, extending into the subtropics at both ends of its range. Throughout the range it is the Cecropia ant most likely to be found in open or highly disturbed areas. Founding queens are frequent in Cecropia saplings. As trees grow and form

multiple branches, the nests become polydomous. Workers and brood are dispersed in branch tips, and the bole and inner portions of branches are progressively abandoned (Longino 1991a). Workers vary in aggressiveness geographically and over time. Workers in young colonies are usually aggressive, but in many cases workers in mature colonies are less aggressive, retreating inside of stems on disturbance (Longino 1991a).

Material examined. See Longino (1989a).

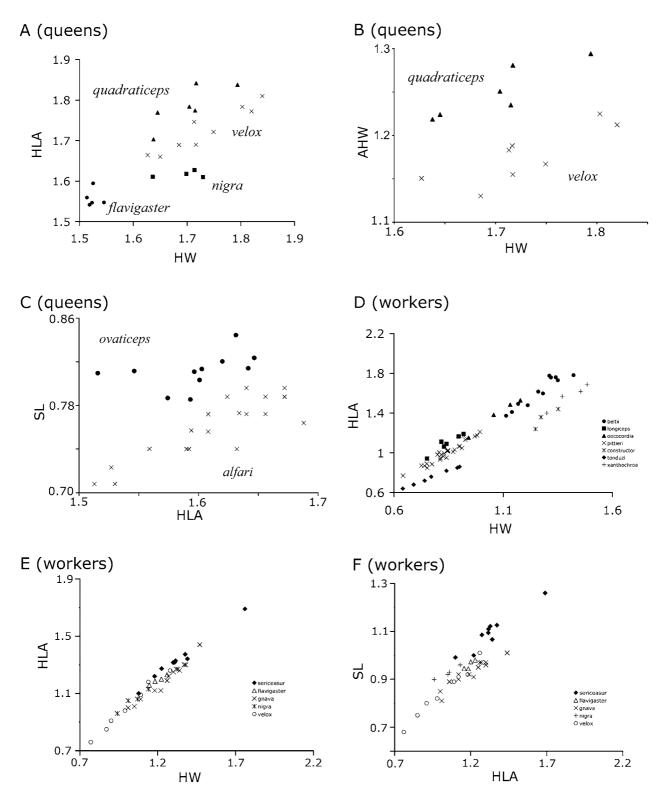


FIGURE 6. Morphometric scatterplots. A. Queens of *A. velox* and relatives. B. Queens of *A. quadraticeps* and *A. velox*. C. Queens of *A. alfari* and *A. ovaticeps*. D–F. Workers of subsets of Costa Rican *Azteca* species.

Azteca beltii Emery 1893

Figures 2,4A,5,6D.

Azteca bicolor race beltii Emery 1893:142. Holotype worker, Costa Rica (Alfaro) [MCSN] (examined). Raised to species: Longino 1996:136.

Azteca fasciata subsp. laeta Wheeler 1942:227. Holotype queen: Panama, Canal Zone, Barro Colorado Island, 9 July 1924 (Wheeler #637), from a domatium of *Cordia alliodora* [MCZC] (examined). Synonymy by Longino 1996:136. Azteca stolli Forel 1912:54. Syntype workers: Guatemala, Retaluleu (Stoll) [MHNG] (examined). Synonymy by Longino 1996:136.

Queen characters. Measurements (n=9): HLA 1.90 (1.83–1.93), HW 1.30 (1.27–1.36), SL 0.84 (0.83–0.86, n=8), CI 70 (69–73), SI 45 (44–46, n=8).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible largely smooth, with sparse piligerous puncta, setae in puncta short, little longer than width of puncta, larger puncta with long setae near masticatory margin; medial and lateral clypeal lobes at about same level; head rectangular, posterior margin distinctly excised medially; petiolar node short, bluntly rounded; posteroventral petiolar lobe shallow, evenly convex from front to back; scape with sparse erect setae, inconspicuous and only visible at certain angles, about as long as one quarter maximum width of scape; middle and hind tibia with sparse erect setae, fine, inconspicuous, longest about as long as one fifth maximum width of tibia (MTSC 5-10), side of head with 0–2 short erect setae near mandibular insertion, lacking setae elsewhere, posterior margin of head with sparse short setae; pronotum with posterior row of erect setae, mesoscutum, scutellum and propodeum with sparse erect setae, petiolar node with rim of erect pubescence, in profile with 0–4 erect setae projecting above apex, posteroventral lobe with layer of dense, whitish, erect, pubescence; gastral terga with sparse erect setae; general body color yellow orange, gastral terga with prominent medial dark brown bands, mandibles red brown, middle and hind femur and tibia variably infuscated.

Worker characters. Measurements (n=9): HLA 1.62 (1.37–1.78), HW 1.28 (1.11–1.42), SL 0.77 (0.75–0.81), CI 81 (76–83), SI 48 (45–56).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible smooth and shining, with moderately abundant piligerous puncta; medial and lateral clypeal lobes at about same level; head elongate with weakly convex sides, strongly excavate posterior margin; in lateral profile pronotum shallowly convex, mesonotum more strongly convex and forming separate convexity that protrudes above pronotum; scape with sparse, inconspicuous erect setae, length of setae about one quarter maximum width of scape; mid and hind tibia with moderately abundant erect setae, setae inconspicuous, longest about one quarter maximum width of tibia; side of head with 1–2 short erect setae near mandibular insertion, absent elsewhere along side; posterior margin of head with sparse short erect setae; pronotum, mesonotum, and dorsal face of propodeum with sparse, short, erect setae; color of smaller workers brown, approaching coloration of queen on larger workers.

Similar species. The yellow color and large size distinguishes queens of *A. beltii* from all other species with elongate rectangular heads. The workers of *A. beltii* are most similar to workers of *A. oecocordia*. The largest workers of the former have yellow faces, while workers of the latter always have brown faces.

Range. Mexico to Costa Rica.

Biology. The taxonomy and biology of *A. beltii* is reviewed in Longino (1996).

Azteca beltii is most abundant in moist and dry forest habitats, although it occurs as a low density element in wet forests. At La Selva Biological station in the Atlantic lowlands of Costa Rica, workers have been collected in a *Ficus* tree in the lab clearing and from one tree (of about 50) sampled by canopy fogging. It is likely that in wet forests it is found in highly insolated environments like the uppermost portion of the canopy and perhaps relict trees in clearings. In dry forest habitats it is known to nest in live stems in a wide variety of plant species. Very often it nests in myrmecophytes such as *Cecropia*, *Cordia alliodora*, and *Triplaris melaen*-

odendron, but it has also been found nesting in non-myrmecophytes *Piper tuberculatum* (Piperaceae), *Cochlospermum* (Cochlospermaceae), and *Pithecellobium saman* (Fabaceae). Colonies are large and polydomous, nesting in the live shoot tips over large portions of the crowns of trees. But the workers are timid and appear to spend most of their time inside the stems, so they are not conspicuous ants on the surface. The nest chambers in the live stems usually have very high densities of coccoid Hemiptera. A tree with a large colony of *A. beltii* can appear herbivore-free on the surface, yet harbor a very large population of Hemiptera that is hidden from view inside of the stems.

Comments. The species as currently delimited occurs from Mexico to Panama, but very similar or possibly conspecific forms occur throughout South America. *Azteca fasciata* and *A. mayrii* are two South American taxa that are closely related to or conspecific with *A. beltii*.

Material examined. COSTA RICA: Guanacaste: Headquarters, Santa Rosa Nat. Park, 10°50'N, 85°37'W, 300m, 16 Jul 1989 (D. H. Janzen) — worker; Bosque Humedo, Santa Rosa Nat. Park, 10°51'N, 85°37'W, 300m, 12 Jul 1985 (J. Longino) — worker, queen; oak forest, Santa Rosa Nat. Park, 10°52'N, 85°36'W, 300m, 15 Jul 1985 (J. Longino) — queen; S end Playa Narano, Santa Rosa Nat. Park, 10°47'N, 85°40'W, 5m, 7 Apr 1990 (J. Longino) — worker; Palo Verde Biological Station, 10°21'N, 85°21'W, 10m, 5 Feb 1989 (J. Longino) — workers; *Heredia*: La Selva Biological Station, 10°26'N, 84°01'W, 50m, 13 Dec 1997 (J. Longino) — worker; same locality, 13 Jan 1996 (ALAS) — worker; 11km SE La Virgen, 10°20'N, 84°04'W, 500m, 17 Apr 2003 (D. Brenes) — worker; *Puntarenas*: Curu Wildlife Refuge, 9°47'N, 84°55'W, 5m, 28 Mar 1993 (J. Longino) — queen, workers; Guacimal, rd to Monteverde, 10°13'N, 84°51'W, 400m, 5 Jul 1991 (J. Longino) — queen, workers; Guaria, rd to Monteverde, 10°14'N, 84°51'W, 700m, 25 Jul 1984 (J. Longino) — queen; Guaria, rd to Monteverde, 10°15'N, 84°50'W, 700m, 27 Jul 1984 and 5 Jul 1991 (J. Longino) — queen, workers; Ojo de Agua, rd to Monteverde, 10°16'N, 84°50'W, 800m, 28 Jul 1984 and 5 Jul 1991 (J. Longino) — worker; Rio Lagartos & PanAmerican Highway, 10°10'N, 84°55'W, 100m, 23 Jan 1993 (J. Longino) — males, workers; 7km S Santa Elena, 10°16'N, 84°50'W, 750m, 7 Sep 1985 (J. Longino) — alate queens; HONDURAS: Comayagua: 1mi W. Taulabe, 1990 (C. Catton) — alate queen, worker; MEXICO: Veracruz: Tempoal, 3 Jul 1964 — alate queen [LACM].

Azteca brevis Forel 1899

Figures 2,4A,5.

Azteca brevis Forel, 1899:121. Syntype workers: Costa Rica (Tonduz) [MCZC] (examined). *Azteca* JTL-001: morphospecies code used in Longino 1996:141.

Queen characters. Measurements (n=9): HLA 1.57 (1.49–1.59), HW 1.11 (1.10–1.16), SL 0.62 (0.60–0.64), CI 74 (72–76), SI 41 (40–42).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible coarsely punctate, puncta bearing stiff erect setae, mandible appearing bristly; medial and lateral clypeal lobes at about same level; head subrectangular, posterior margin weakly excised medially; petiolar node short, broadly triangular; posteroventral petiolar lobe strongly convex from front to back, laterally compressed and tectiform; scape with sparse and inconspicuous erect setae, about as long as one third maximum width of scape; hind tibia devoid of erect setae or with at most 1 or 2, side of head with 0–2 short setae near mandibular insertion, setae lacking elsewhere, posterior margin of head with moderately abundant erect setae; pronotum with posterior row of erect setae and occasionally setae on medial area; mesoscutum, scutellum and propodeum with moderately abundant erect setae; petiolar node lacking rim of whitish erect pubescence, in profile with 2 erect setae projecting above apex, posteroventral lobe with abundant long setae; gastral terga with sparse erect setae; general body color dark brown.

Worker characters. Measurements (n=3): HLA 1.07 (0.99–1.09), HW 0.96 (0.89–1.00), SL 0.51 (0.48–0.51), CI 93 (92–94), SI 49 (48–50).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible with abundant piligerous puncta, surface between puncta smooth and shining, variable extent of base faintly microareolate; medial and lateral clypeal lobes at about same level; head subquadrate with weakly convex sides, moderately excavate posterior margin; in lateral profile mesosoma compact, pronotum and mesonotum nearly forming a single convexity, with promesonotal suture very weakly impressed; scape with sparse, inconspicuous erect setae, length of setae about one half maximum width of scape; hind tibia lacking erect setae; side of head lacking erect setae; posterior margin of head with sparse erect setae; pronotum and mesonotum with abundant erect setae, dorsal face of propodeum lacking erect setae; color red brown.

Similar species. The bristly mandibles ally this species with *A. forelii* and *A. nigricans*. Queens of *A. brevis* are smaller than queens of *A. forelii* (Fig. 4A). Queens of *A. brevis* have shorter scapes than queens of *A. nigricans* (SI 39–43 versus 50–52, respectively). Workers of *A. brevis* are distinguished from workers of *A. nigricans* by the reduced number of setae on the hind tibia, 0–2 on *A. brevis* versus > 5 on *A. nigricans*.

Range. Costa Rica.

Biology. In Costa Rica *A. brevis* is known only from the Pacific side, and mostly from the wet forests of the southern Pacific lowlands. Nests are in live stems of trees. Stems occupied by ants are covered with runways of characteristic crusty black carton, with the carton full of small round holes from which workers emerge. Colonies are polydomous, with workers and brood distributed in multiple branch tips. Colonies maintain large populations of coccoid Hemiptera inside the stems. Nests have been found in *Licania* (Chrysobalanaceae), *Grias* (Lecythidaceae), *Myriocarpa* (Urticaceae), *Tetrathylacium costaricensis* (Flacourtiaceae), *Ocotea nicaraguensis* (Lauraceae), and an unidentified tree in the Moraceae. Leanne Tennant, studying the incipient ant plant *Tetrathylacium costaricensis*, found *A. brevis* to be one of the most common inhabitants.

Comments. This species was discussed in Longino (1996) as an unnamed morphospecies (JTL-001) similar to *A. nigricans*. Examination of the types of *A. brevis* revealed that it was conspecific with this morphospecies.

Additional material examined. COSTA RICA: *Guanacaste*: Cerro El Hacha, Guanacaste Conservation Area, 10°59'N, 85°33'W, 300m, 1 Jan 1988 — alate queen [MUCR]; *Puntarenas*: Sirena, Corcovado National Park, 8°29'N, 83°36'W, 5m, Feb-Apr 2000 (M. Schmidt) — alate queen, worker; same locality, numerous collections and dates (J. Longino) — worker, queens, males; same locality, numerous collections and dates (L. Tennant) — workers, queens; 19km S Ciudad Neily, 8°29'N, 82°58'W, 20m, 25 Mar 1990 (J. Longino) — males, alate queens; Golfito, 8°39'N, 83°09'W, 50m, 6 Aug 1957 (A. Menke) — alate queen [LACM].

Azteca chartifex Forel 1896

Figure 7.

Azteca chartifex Forel, in: Emery 1896b:4. Syntype workers: Trinidad (Urich) [MHNG, MCZC] (examined).

Azteca chartifex race laticeps Forel 1899:117. Syntype workers: Costa Rica (Tonduz); and Panamá, Bugaba, Volcan de Chiriquí (Champion) [MHNG] (examined). Further description of workers: Forel 1906:236. NEW SYNONYMY

Worker characters.Measurements (n=5 workers from Costa Rica to Brazil): HLA 0.88 (0.84–0.96), HW 0.97 (0.87–1.05), SL 0.78 (0.64–0.85), CI 108 (100–110), SI 87 (74–89).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible smooth and shining, with moderately abundant small piligerous puncta; medial and lateral clypeal lobes at about same level; head with strongly convex sides, strongly cordate posterior margin; in lateral profile promesonotum forming single strongly protruding convexity, posterior mesonotum dropping abruptly to much lower metanotal groove and dorsal face of propodeum; scape and tibia lacking erect setae; sides and posterior margin of head lacking erect setae; posterior pronotum with conspicuous cluster of 6 or more long erect setae, mesonotum with 0–4 shorter erect setae, dorsal face of propodeum with 4–6 erect setae at variable angles to

surface; color red brown.

Range. Costa Rica to southern Brazil.

Biology. Azteca chartifex occurs in wet forest habitats. Colonies are polydomous, occurring in clusters of large, pendant carton nests. The carton is dry and paper-like. The nests are never penetrated by epiphytes or other plant roots, and in this regard are very different from the ant gardens of A. gnava and A. nigra. They can occur in very exposed and highly insolated environments, and seem more abundant in seasonal moist to dry habitats than in weakly seasonal wet forest.

I have observed two colonies in Costa Rica, both in the lowland forest of the Osa Peninsula. Both colonies were in regenerating second growth forest. One colony was on a large *Inga* (Fabaceae) tree and several adjacent *Psidium* (Myrtaceae) trees. There were about eight large nests within a 10m radius. Individual nests were up to 2m long and tapering. I cut into several nests and dissected one nest thoroughly, finding only workers and larger brood. This particular colony was relatively long-lived: I first observed it in 1990, and when I walked by the same site six years later the colony was still there and looked relatively unchanged. The second colony I observed was a single large nest on a palm trunk, about 10m high. It was in an area of dense vegetation and it is likely there were other nests in the vicinity. Forel's subspecies *laticeps* was collected from a carton nest on *Psidium* (the Champion series from Chiriquí, Panamá).

Comments. The production of large pendant carton nests by *Azteca* is a common phenomenon in moist to wet forests from Panama southward through tropical South America. Some of them are made by the *A. aurita* group (see Addendum), but the majority are made by the *A. trigona* group. The workers of the *A. trigona* group exhibit a strongly hump-shaped promesonotum (Fig. 7: *chartifex*) which drops steeply and abruptly to the much lower dorsal face of the propodeum. Other characters exhibited by but not unique to the group are 5,3 palpal formula, prominent meso and metatibial spurs, broad heads (CI > 99), and few to no metatibial setae which, if present, are very short and inconspicuous. The queens have very broad, strongly cordate heads (CI 109–135). The only other *Azteca* queens with heads that proportionately broad are *A. gnava*, which have strongly setose tibia and a 6,4 palpal formula. The species group as a whole has a sharp geographic boundary: it is common in central Panama, but Costa Rica is the far northern limit of the group, with a single rare species in the southern Pacific lowlands.

The species-group taxa associated with this group are *A. trigona* and its synonyms and infraspecific forms *festai*, *gaigei*, *mathildae*, *mediops*, *subdentata*; *A. chartifex* and its infraspecific forms *cearensis*, *decipiens*, *lanians*, *laticeps*, *multinida*, *spiriti*, *stalactitica*; *A. barbifex*; and *A. severeni*. Queens are known for only two of these: *A. trigona* and *A. barbifex*. I have examined the types of most of the taxa and made measurements of HLA, HW, and SL. When the data for workers are all plotted together, they form one continuous cloud of points along one line of allometry. However, when I examine just series from Panama and Costa Rica, two groups emerge. One group has the largest workers (selecting one of the larger workers of each series) with HW 1.21–1.36mm, CI > 111, and the posterior margin of the head with a very deep, V-shaped medial impression. Another group has the largest workers with HW 0.93–1.06mm, CI < 111, and the posterior margin of the head with a shallower, less strongly V-shaped medial impression. The former I identify as *A. trigona*; the latter as *A. chartifex*. The various subspecies of *A. trigona* and *A. chartifex* fall within these respective size ranges, with the exceptions of *A. trigona gaigei*, with HW 1.06mm, and *A. chartifex lanians*, with HW 1.22mm. *Azteca severeni*, with HW 1.11mm, is intermediate.

Queens are remarkably rare in this group. I have been able to examine and measure eight queens, including the holotype queen of *A. trigona* and the syntype queen of *A. barbifex*. Six of the queens, which I identify as *A. trigona*, form a cluster with HW 1.64–1.82mm. A queen from Bolivia has a very broad head, with HW 2.07mm, and the queen of *A. barbifex* is distinctly smaller, with HW 1.20mm. *Azteca barbifex* workers are similar in size and shape to *A. chartifex* workers. Thus it is possible that there are two main lineages, *A. trigona* having large queens and workers, and *A. chartifex* having small queens and workers. *Azteca barbifex* workers fall well within the cloud of points formed by *A. chartifex* and its subspecies.

The very broad heads and short, small mandibles suggest very powerful cutting ability, like bolt cutters. Perhaps *Azteca trigona* group queens found their nests in hard dead wood, and this head structure is an adaptation for quickly excavating a chamber in hard wood.

Additional material examined. COSTA RICA: *Puntarenas*: Sirena, Corcovado National Park, 8°29'N, 83°36'W, 5m, 16 Dec 1990 (J. Longino) — workers; Cedral, Corcovado National Park, 8°33'N, 83°33'W, 5m, 12 Feb 1996 (J. Longino) — workers; **PANAMA**: *Canal Zone*: Pipeline Road, 9°07'N, 79°44'W, 50m, 10 Sep 1990 (D. M. Olson) — worker.

Azteca coeruleipennis Emery 1893

Figures 2,4A,5,7.

Azteca coeruleipennis Emery 1893:130. Lectotype queen: Costa Rica, western slope (Alfaro) [label: "Alajuela, Cecropia, III 90"] [MCSN] (examined).

Queen characters. Measurements (n=5): HLA 1.93 (1.74–1.98), HW 1.48 (1.35–1.53,8), SL 0.98 (0.90–1.03,8), CI 77 (75–78), SI 51 (50–53).

Palpal formula 6,4; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible faintly microareolate, dull, with sparse small piligerous puncta, setae in puncta short, larger puncta with long setae near masticatory margin; medial and lateral clypeal lobes at about same level (medial lobe not projecting anteriorly); head quadrate, with sides slightly converging posteriorly; petiolar node low, bluntly rounded; posteroventral petiolar lobe evenly convex, shallow, not strongly developed; scape with abundant fine erect setae, about as long as one half maximum width of scape; middle and hind tibia with abundant erect setae, longest of these about as long as maximum width of tibia (MTSC 20–30); sides of head below level of eyes with 1–2 erect setae, sides of head posterior to eyes with 0–2 short erect setae; posterior margin of head with abundant long curved setae; pronotum with abundant long setae on posterior third; mesoscutum, scutellum, and propodeum with abundant setae, those on scutellum and propodeum longer than those on mesoscutum; petiolar node with variable number of long setae on apex, abundant long setae on posteroventral lobe; all gastral terga with abundant erect setae; color dark brown to black.

Worker characters. Measurements (n=3): HLA 1.00 (0.97–1.08), HW 0.93 (0.91–0.99), SL 0.71 (0.70–0.72), CI 94 (91–94), SI 72 (66–72).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible largely smooth and shining, grading to dull, microareolate sculpture at base, with sparse small piligerous puncta, setae in puncta short, larger puncta with long setae near masticatory margin; medial and lateral clypeal lobes at about same level, medial lobe at most weakly projecting beyond lateral lobes; head with convex sides, strongly cordate posterior margin; mesosoma in lateral profile with promesonotum forming a continuous convexity or mesonotum somewhat elevated above pronotum; posterior mesonotum drops abruptly to metanotal groove, dorsal face of propodeum and broad metanotal groove form a flat, step-like junction with posterior mesonotum; scape and tibia with abundant erect setae, length of setae about one half maximum width of scape or tibia, respectively; sides of head with abundant erect setae from mandibular insertions to level of eye, extending variable distance posterior to eye, often leaving posterior portion devoid of setae; posterior margin of head with abundant erect setae; promesonotum with abundant long erect setae; dorsal face of propodeum with no erect setae or with sparse setae that are much shorter than those of promesonotum; color yellow orange.

Similar species. Among the *Cecropia* ants, *A. coeruleipennis* is most easily confused with *A. alfari* and *A. ovaticeps*. The presence of tibial setae, the distinctive shape of the mesonotum, and the 6,4 palpal formula will separate *A. coeruleipennis* from *A. alfari* and *A. ovaticeps*.

Range. Mexico to Costa Rica.

Biology. The taxonomy and biology of *A. coeruleipennis* is reviewed in Longino (1989b, 1991a, b). The species is an obligate *Cecropia* ant. It occurs in highly seasonal habitats. Nests are dispersed in both the tree bole and outer branches, with brood dispersed throughout the nesting space.

Comments. Prior to this report I had never investigated palpal formula in *Azteca*. It was surprising to discover that *A. coeruleipennis* had a palpal formula of 6,4, while all other *Cecropia* ants have 5,3. A palpal formula of 6,4 is probably plesiomorphic in the genus, which implies that *A. coeruleipennis* might be a very old *Cecropia* ant and sister to all the other *Cecropia* ants. Perhaps this species has survived the arrival of newer *Cecropia* ants by being a dry-forest specialist, a habitat that is marginal for *Cecropia* trees.

Material examined. See Longino (1991b).

Azteca constructor Emery 1896

Figures 2,3,4A,5,6D,7.

Azteca constructor Emery 1896:2. Syntype workers, queens, males: Costa Rica, Atlantic and Pacific slopes (Alfaro) [label: Jimenez, C. R. v.95] [MCSN] (examined).

Azteca emmae Forel 1904b:702. Syntype workers, females, males: Costa Rica, Chañas Gudas [Prov. Puntarenas: Cañas Gordas?] (Pittier) [MHNG, MCZC] (examined). Synonymy by Longino 1991b:1585.

Azteca constructor var. guianae Wheeler 1942:226. Syntype workers, queen: Guyana, Kartabo (Wheeler) [MCZC] (examined). Synonymy by Longino 1991b:1585.

Queen characters. Measurements (n=12): HLA 1.75 (1.56–1.79,6), HW 1.61 (1.45–1.73), SL 0.87 (0.79–0.94), CI 94 (91–98,6), SI 51 (49–53,6).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible roughened, dull, with sparse small piligerous puncta, setae in puncta short, larger puncta with long setae near masticatory margin; medial and lateral clypeal lobes at about same level (medial lobe not projecting anteriorly); head quadrate, with sides somewhat convex, weakly cordate posteriorly; petiolar node low, triangular, acute, but apex rounded, not sharp; posteroventral petiolar lobe evenly convex, shallow, not strongly developed, ending before posterior margin of sternite, leaving small rim formed by posteriormost portion of sternite; scape with abundant erect setae, about as long as one half to two thirds maximum width of scape; middle and hind tibia with abundant erect setae, longest of these about as long as maximum width of tibia (MTSC 20–35); sides of head with erect setae variably abundant, from nearly absent to moderately abundant; posterior margin of head with abundant very long setae; pronotum with abundant long setae on posterior third; mesoscutum, scutellum, and propodeum with dense brush of abundant setae; petiolar node with variable number of long setae on apex, abundant long setae on posteroventral lobe; all gastral terga with abundant erect setae; color black.

Worker characters. Measurements (n=10): HLA 1.36 (1.24–1.44,3), HW 1.01 (0.68–1.35), SL 0.76 (0.53–0.89), CI 94 (94–101,3), SI 64 (60–69,3).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible faintly roughened, not smooth and shining, with sparse small piligerous puncta, setae in puncta short to long, larger puncta with long setae near masticatory margin; medial and lateral clypeal lobes at about same level, medial lobe at most weakly projecting beyond lateral lobes; head with convex sides, strongly cordate posterior margin; mesosoma in lateral profile with promesonotum forming a broad convexity, promesonotal suture weakly impressed, such that pronotum and mesonotum tend toward being separate convexities, mesonotum more strongly convex than pronotum; metanotal groove broad; petiole in profile with node less massive than sternal lobe, perpendicular distance from tergosternal suture to apex of node less than distance to ventral margin of sternal lobe (in contrast to *A. xanthochroa*, on which the petiolar node is larger relative to sternal lobe); scape with abundant erect setae, length of setae about one half maximum width of scape; mid and hind tibia with abundant erect setae, longest setae about one half maximum width of tibia; sides of head with abundant

short erect setae from mandibular insertions to level of eye, becoming sparse to absent posterior to eye; posterior margin of head with abundant long curved setae; mesosomal dorsum with abundant erect setae, those on pronotum long, on mesonotum shorter, on dorsal face of propodeum very short, grading into pubescence; color brown.

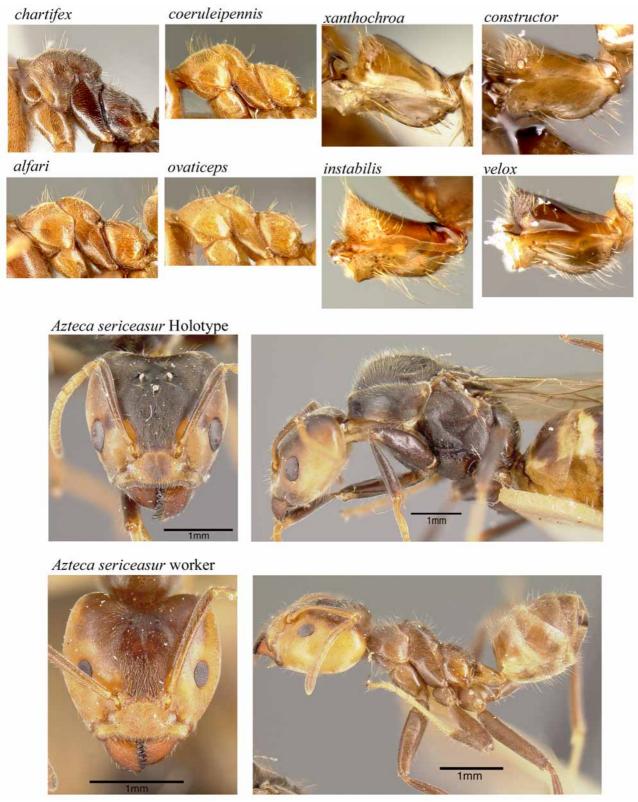
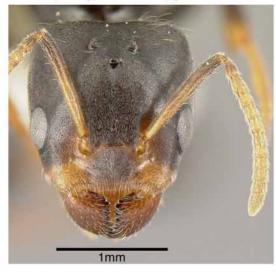


FIGURE 7. Upper left: lateral views of *Azteca* worker mesosoma. Images are not to scale. Upper right: lateral views of *Azteca* worker petioles. Images are not to scale. Lower figures: holotype queen and paratype worker of *A. sericeasur*.

Azteca flavigaster Holotype





Azteca flavigaster worker





Azteca quadraticeps Holotype





FIGURE 8. Holotype queen and paratype worker of *A. flavigaster*; holotype queen of *A. quadraticeps*.

Similar species. The queens of *A. constructor* are very distinctive and not easily confused with any other species. Workers of *A. constructor* and *A. xanthochroa* are very similar. Large workers of *A. constructor* retain a chocolate brown color, while large workers of *A. xanthochroa* become more mottled orange. The petiolar

node of *A. constructor* workers is relatively low, while the posteroventral lobe is relatively deep and strongly convex. Workers of *A. xanthochroa* are the reverse, with relatively taller node and shallower ventral lobe.



FIGURE 9. Holotype queen and paratype worker of A. oecocordia; holotype queen of A. nanogyna.

Range. Guatemala south through Central America to north coastal Colombia, Venezuela, and Guyana. **Biology.** The taxonomy and biology of *A. constructor* are reviewed in Longino (1989b, 1991a, b). The species is an obligate *Cecropia* ant. It inhabits a broad range of habitats and elevations. It is often associated with forest gaps or edges where there are relatively larger and older *Cecropia* trees. Mature colonies occupy a

single carton nest in the bole of the tree. The nest is spindle-shaped and causes a deformation of the trunk. All larvae and alate sexuals are concentrated in this single nest. Branch tips, which all communicate internally with the carton nest, contain only workers and Hemiptera. Workers of this species are extremely aggressive, and respond to any disturbance by pouring out of large fissures near the carton nest and blackening the trunk surface (Longino 1991a).

Alate queens of this species and another common *Cecropia* ant, *A. xanthochroa*, are relatively common in Malaise trap samples from the Atlantic slope rainforests of Costa Rica. No other *Azteca* species are common in Malaise traps, even though they are common in the environment. Even the other common *Cecropia* ants, *A. alfari* and *A. ovaticeps*, are not common in Malaise samples. This implies that there is something distinctive about the behavior of queens of these two species that makes them more susceptible to capture.

Material examined. See Longino (1991b).

Azteca flavigaster new species

Figures 3,4A,5,6A,6E,6F,8.

Holotype alate queen: Costa Rica, Prov. Puntarenas, Punta Quepos, 9°24'N, 84°10'W, 5m, 4 Jun 1989 (J. Longino) [INBC, specimen (pin) code JTLC000005689].

Paratypes: same data as holotype; 4 workers, 3 alate queens [JTLC000005689, INBC; JTLC000005687, USNM; JTLC000005688, MCZC; INBIOCRI001281548, LACM].

Measurements of holotype. HLA 1.62, HLB 1.59, HW 1.53, HW 1.53, SL 1.03, EL 0.44, OC 0.10, MTSC 30.

Diagnosis. Among the species with 6,4 palpal formula, *A. flavigaster* has the smallest queen head size. The most similar species are *A. quadraticeps*, *A. velox*, and *A. nigra*, all of which have larger queen head size. The workers have a unique coloration, with bright yellow gastral dorsum and contrastingly dark brown mesosoma.

Queen characters. Measurements (n=5): HLA 1.55 (1.54–1.60), HW 1.52 (1.51–1.55), SL 1.04 (1.01–1.04), CI 98 (96–100), SI 67 (65–67).

Palpal formula 6,4; ocelli small; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible with small piligerous puncta, setae in puncta short, subdecumbent, interspaces between puncta smooth and shiny on apical half of mandible, gradually becoming faintly microareolate at base; medial and lateral clypeal lobes at about same level; head subquadrate, posterior margin not strongly cordate, very shallowly excavate; petiolar node tall, strongly compressed into thin scale at apex; posteroventral petiolar lobe evenly convex from front to back; scape with abundant erect setae, about as long as one half maximum width of scape; middle and hind tibia with abundant erect setae, longest of these about as long as one half maximum width of tibia (MTSC 20–35); sides of head without erect setae; posterior margin of head with erect setae; pronotum with erect setae on posterior margin; mesoscutum, scutellum, and propodeum with abundant erect setae; petiolar node with irregular pubescence and sparse short erect setae, 0–2 pairs of erect setae extending above apex in profile, posterior border of sternal lobe of petiole with uniform layer of short erect setae; gastral terga with sparse long erect setae; most of head dark brown, with lighter orange coloration restricted to anterior malar area near mandibular insertions.

Worker characters. Measurements (n=4): HLA 1.19 (1.16–1.23), HW 1.20 (1.15–1.26), SL 0.96 (0.94–0.98), CI 101 (99–102), SI 81 (80–82).

Palpal formula 6,4; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible smooth and shining, with moderately abundant small piligerous puncta, setae in puncta short, erect, larger puncta with long setae near masticatory margin; medial and lateral clypeal lobes at about same level; head with convex sides, strongly cordate posterior margin; in lateral profile promesonotum forming single convex-

ity; scape with abundant erect setae, length of setae about one half maximum width of scape; mid and hind tibia with abundant erect setae, longest setae about one half maximum width of tibia; side of head with 1–5 erect setae on malar area, otherwise lacking setae; posterior margin of head with abundant erect setae; pronotum, mesonotum, and dorsal face of propodeum with abundant long erect setae; anterior and anterolateral portions of head light yellow brown, variable extent of darker brown on medial vertex and posteriorly, mesosoma variably light to dark brown, gastral dorsum bright yellow, contrasting with darker mesosoma.

Etymology. The name refers to the bright yellow gaster of the worker.

Range. Costa Rica, Panama, Ecuador.

Biology. Most observations of A. flavigaster have been made in the southern Pacific lowlands of Costa Rica, in moderately seasonal evergreen forest. Azteca flavigaster is a generalist cavity nester with conspicuous surface-foraging workers. In a degraded patch of forest near Quepos, at a pasture edge, I observed abundant workers on the trunk of a live, 40cm diameter tree, emerging from a long narrow fissure at the base. Abundant workers were also on the base of another small tree in the same forest patch. This tree had a dead branch at ground level with workers, brood, and scattered alate females in two parallel cavities, each with horizontal carton partitions. Large columns of workers went up the trunk to a larger dead branch further up. In a patch of mature forest near Ciudad Neily an aggregation of workers were in cavities in the main stem of a sapling of Grias (Lecythidaceae). At Sirena in Corcovado National Park I made several observations of this species. I observed a column of foraging workers on the ground surface, flowing in and out of a 4cm diameter hole extending horizontally into the ground. I observed workers 18m high in the canopy of a *Perebea trophophylla* (Moraceae) tree, with an aggregation of workers in a small knot. I observed an incipient colony in an Acacia alleni tree, the common myrmecophytic acacia in Corcovado. The tree was in poor shape, without a dominant Pseudomymex colony. The Azteca occupied several of the thorns, one of which contained a physogastric queen and small brood. Finally, I observed two founding queens in a dead and tattered Costus (Costaceae) inflorescence. The inflorescence was filled with many old chambers containing dead Azteca queen remains. The two living queens were in adjacent chambers, but not in contact. Each had brood, and one had nanitic workers. When I put the queens together in the same vial, they immediately locked mandibles in combat. Other researchers at Sirena have collected founding queens in chambers of Tetrathylacium costaricensis and T. macrophyllum.

Workers with the same coloration and habitus of *Azteca flavigaster* occur in the Atlantic lowlands of Costa Rica, but are rare. At La Selva Biological Station these workers have been collected twice. A worker was collected in a Berlese sample of canopy soil and epiphytes, and a nest or nest fragment was found in a live branch of *Coussapoa* (Cecropiaceae). The nest also contained workers of *Camponotus atriceps*, in a parabiotic association.

Comments. Although workers matching *A. flavigaster* have been found on the Atlantic side of Costa Rica and in other countries, no queens have been collected to confirm these identifications. However, the new species *A. quadraticeps* is known only from queens from the Atlantic lowlands. It is possible that *A. quadraticeps* and *A. flavigaster* are allopatric or parapatric sister taxa with similar workers, and that the Atlantic slope workers with yellow gasters are actually the workers of *A. quadraticeps*.

Additional material examined. COSTA RICA: *Heredia*: La Selva Biological Station, 10°26′N, 84°01′W, 50m, 8 Nov 1993 (ALAS) — worker [INBC]; same locality, 20 Apr 2004 (A. Fitch) — worker; *Puntarenas*: Sirena, Corcovado National Park, 8°29′N, 83°36′W, Feb-Apr 2000 (M. Schmidt) — dealate queen; same locality, multiple collections (J. Longino) — workers, queens; same locality, 22 Jul 1987 (L. Tennant) — dealate queen; 19km S Ciudad Neily, 8°29′N, 82°58′W, 20m, 26 Mar 1990 (J. Longino) — workers; same locality, 25 Mar 1990 (P. S. Ward) — worker; ECUADOR: *Los Rios*: Jauneche, 19km WSW Mocache, 1°14′S, 79°40′W, 60m, 11 Aug 1991 (P. S. Ward) — workers; PANAMA: *Canal Zone*: Pipeline Road, 9°07′N, 79°44′W, 50m, 10 Sep 1990 (D. M. Olson) — worker.

Azteca forelii Emery 1893

Figures 2,4A,5.

Azteca forelii Emery 1893:337. Syntype worker(s): Costa Rica, western slope, Bagaces (Alfaro) [MCSN] (examined). Azteca eiseni Pergande 1896:868. Syntype workers: Mexico, Santiago Iscuintla (Eisen) [USNM, MHNG] (examined). NEW SYNONYMY

Azteca foreli var. eiseni Pergande: Forel 1899:111.

Azteca foreli race championi Forel 1899:112. Syntype workers: Colombia, Sierra Nevada de Santa Marta, Dibulla (Forel, Lallemand) [MHNG] (examined). NEW SYNONYMY

Azteca foreli race ursina Forel 1899:112. Syntype workers, males: Trinidad (Urich) [MHNG] (examined). NEW SYN-ONYMY

Azteca foreli var. xysticola Forel 1899:111. Syntype workers: Colombia, Bonda (Forel); and Santa Marta (Forel) (Santa Marta workers later described as *raptrix* Forel) [MHNG] (examined). NEW SYNONYMY

Azteca foreli var. raptrix Forel 1912:50. Syntype workers: Colombia, Santa Marta (Forel) [MHNG] (examined). NEW SYNONYMY

Queen characters. Measurements (n=5): HLA 1.94 (1.86–1.98), HW 1.59(1.55–1.70), SL 0.96 (0.89–0.98), CI 85 (79–87), SI 49 (48–50).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible coarsely punctate, puncta bearing stiff erect setae, mandible appearing bristly; medial and lateral clypeal lobes at about same level; head subrectangular, posterior margin moderately excised medially; petiolar node short, triangular; posteroventral petiolar lobe strongly convex from front to back, laterally compressed and tectiform; scape with sparse and inconspicuous erect setae, about as long as one third maximum width of scape; hind tibia devoid of erect setae or with at most 1 or 2, side of head with 0–5 very short, inconspicuous subdecumbent to suberect setae, posterior margin of head with sparse, long, erect setae; pronotum with posterior row of erect setae; mesoscutum, scutellum and propodeum with moderately abundant erect setae; petiolar node in profile with rim of whitish erect pubescence, no erect setae projecting above apex, posteroventral lobe with abundant setae; gastral terga with sparse erect setae; general body color dark brown, the following lighter yellow brown: thin strip of anterior clypeus and area near mandibular insertions, thin anterior and posterior bands on gastral terga, gastral sterna.

Worker characters. Measurements (n=9): HLA 1.46 (0.90–1.74), HW 1.38 (0.94–1.69), SL 0.80 (0.61–0.92), CI 95 (94–104), SI 58 (53–68).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible with abundant small piligerous puncta, setae in puncta conspicuous, erect, mandible appearing bristly, surface between puncta microareolate, dull; medial and lateral clypeal lobes at about same level; head subquadrate with weakly convex sides, moderately excavate posterior margin; in lateral profile pronotum shallowly convex, mesonotum strongly convex and forming separate convexity that strongly protrudes above level of pronotum; scape with sparse, inconspicuous erect setae, length of setae about one half maximum width of scape; hind tibia lacking erect setae; side of head with 1–2 short erect setae near mandibular insertion, absent elsewhere; posterior margin of head with sparse erect setae; pronotum, mesonotum, and propodeum with abundant erect setae; color red brown.

Similar species. The bristly mandibles ally this species with *A. brevis* and *A. nigricans*. Queens of *A. forelii* are much larger than either *A. brevis* or *A. nigricans*. Workers of *A. forelii* are superficially similar to workers of *A. alfari*, but can be differentiated by the setae and dull surface sculpture of the mandibles.

Range. Southern Mexico to Ecuador and west to the Santa Marta region of Colombia.

Biology. *Azteca forelii* favors tropical dry forest or seasonal wet forest. In Costa Rica it occurs at low density throughout the Pacific slope but is not known from the wet Atlantic slope. It needs large trees in which to nest, and thus mature forests are favored, but large trees along roadsides or pasture edges will suffice.

This species has been collected from ramifying systems of carton galleries on the surfaces of trees. Forel (1899) reported var. *xysticola* with carton galleries on granitic rocks or on tree trunks. The galleries were

reported to be indistinguishable from those of *Crematogaster stollii*. He later described var. *raptrix* and concluded that the *Azteca* had actually invaded and taken over the carton galleries of a *Crematogaster stollii* nest (Forel 1912).

I have observed colonies of this species three times. One was in Corcovado National Park, Costa Rica, in a canopy *Ficus* (Moraceae). Fresh carton galleries occurred on nearly every branch and multiple galleries extended down the bole. Another was at Ciudad Neily, also in Costa Rica's southern Pacific lowlands. A similar set of galleries covered the branches of a canopy *Sapium* (Euphorbiaceae). In this case I discovered that the carton galleries covered the entrances to numerous small cavities in the live branch tips. These cavities were filled with ant brood and coccoid Hemiptera, and occasionally there were alate queens. A third colony was near Santa Marta, Colombia, in Tayrona National Park. A system of carton galleries covered a small road-side *Inga* (Mimosaceae) tree. A part of the colony occupied the dead core of a live branch. In each case, a few galleries extended all the way down the trunk and into the soil at the base of the tree. No foragers were ever observed outside of the galleries unless the galleries were broken open. Although I found the occasional hemipteran under the surface galleries, I never found ant brood there. All brood and the vast majority of the hemipterans occur in plant cavities to which the galleries lead.

These ants can be difficult to locate in a tropical forest because workers are never exposed on the surface and the galleries are superficially similar to those of the ubiquitous nasutiform termites. However, on close inspection the carton is quite different from termite carton. It is a light-colored coarse thatch instead of the dark mud-like material of termite galleries. The thatch-like galleries are unique in the genus and do not resemble the more papery carton typical of other *Azteca* (e.g. *A. aurita* and *A. chartifex* groups) or the very friable carton of ant garden species. What is remarkable, and this was also observed by Forel, is how similar the carton material and gallery systems are to those of *Crematogaster stollii*. *Crematogaster stollii* is broadly sympatric with *A. forelii*, occurring in about the same densities in the same kinds of habitats. Forel thought that *A. forelii* might usurp *C. stollii* nests, and there is also the possibility that *C. stollii* usurps *A. forelii* nests, but I have seen no evidence of this. In all the colonies I have seen of both *A. forelii* and *C. stollii*, the extensive system of carton galleries was fully occupied and there were areas of fresh carton construction.

Queens were unknown prior to this study. The Ciudad Neily collection is the only one for which workers and queens were associated. A few alate queens have been collected at scattered localities, all of them from blacklights.

Comments. Workers of this infrequently collected species can be recognized by 1) densely punctate/striate mandibles which are opaque nearly to the masticatory margin, and 2) reduced pilosity on the appendages. There are five infraspecific taxa: *eiseni* (Mexico), *championi*, *raptrix*, *xysticola* (all from Santa Marta area, Colombia), and *ursina* (Trinidad). The differences among them are minor color differences and I see no evidence of multiple species.

Additional material examined. COLOMBIA: *Magdalena*: Tayrona National Park, Cañaveral, 11°19'N, 73°56'W, 50m, 12 Aug 1985 (J. Longino) — worker; COSTA RICA: *Guanacaste*: Santa Rosa Nat. Park, Playa Naranjo area, 10°48'N, 85°41'W, 10m, 1–28 Feb 1991 (E. Alcazar) — alate queen [INBC]; Estacion Pitilla, Guanacaste Cons. Area, 10°59'N, 85°26'W, 700m, 1–30 Apr 1991 (P. Rios) — alate queen [INBC]; R. Gongora, 6 km NE de Queb. Grande de Liberia, 10°53'N, 84°32'W, 700m, 1–28 Feb 1992 (III Curso Parataxonomo) — alate queen [INBC]; *Puntarenas*: Sirena, Corcovado National Park, 8°29'N, 83°36'W, 5m, 12 May 1981 and 8 Aug 1982 (J. Longino) — workers; Llorona, Corcovado National Park, 8°35'N, 83°42'W, 5m, 16 Jun 1980 (J. Longino) — worker; 19km S Ciudad Neily, 8°29'N, 82°58'W, 20m, 25 Mar 1990 (J. Longino) — alate queens, workers; ECUADOR: *Guayas*: Cerro Blanco, 15km W Guayaquil, 2°10'S, 80°02'W, 100m, 13 Aug 1991 (P. S. Ward) — workers [UCDC]; *Napo*: Lago Agrio, 16 Aug 1975 (A. Langley) — alate queen [USNM]; GUATEMALA: *Escuintla*: Finca Caobanal, 14°06'N, 90°40'W, Feb 1993 (J. Gilardi) — workers; MEXICO: *Jalisco*: Chamela Biological Station, 19°30'N, 105°02'W, 100m, 17 Dec 1987 (P. S. Ward) — alate queen [UCDC]; PANAMA: *Canal Zone*: Barro Colorado Island, 9°09'N, 79°51'W, 100m, 3 Jul 1997 (J. Longino) — worker; *Darien*: Cana, 7°43'N, 77°42'W, 700m, Aug 1987 (D. M. Olson) — alate queen.

Azteca gnava Forel 1906

Figures 3,4A,5,6E,6F.

Azteca paraensis subsp. gnava Forel 1906:241. Syntype workers: Costa Rica (Biolley) (in an abandoned termite nest); and "Surubrés, touffe d'orchidée, dans un nid de termites"; and "San Mateo, racines de goyavier (le meme)" [MHNG] (examined, one Costa Rica (Biolley) worker here designated LECTOTYPE).

Azteca paraensis subsp. gnava var. surubrensis Forel 1908a:62 (unavailable name). Syntype workers: Costa Rica, Surubres and El Hiquito near San Mateo (Biolley), dans des racines de goyaviers [MHNG] (examined).

Azteca gnava Forel; Forel 1912:49.

Azteca gnava surubrensis Forel 1912:49 (first available use of surubrensis Forel 1908) [MHNG] (examined). NEW SYNONYMY

Azteca ulei subsp. rossi Forel 1909:251. Syntype workers: Mexico, amongst orchids in antgarden (Ross) [MHNG] (examined). NEW SYNONYMY

Queen characters. Measurements (n=5): HLA 2.19 (2.18–2.20), HW 2.37 (2.33–2.47), SL 1.14 (1.11–1.20), CI 108 (107–113), SI 52 (50–55).

Palpal formula 6,4; ocelli small; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible with abundant piligerous puncta, setae in puncta a combination of longer erect setae and shorter subdecumbent setae, interspaces between puncta faintly microareolate with varying development of roughened, acicular sculpture; medial and lateral clypeal lobes at about same level; head with convex sides, posterior margin strongly cordate; petiolar node in lateral view varying from triangular to flattened and scale-like at apex; posteroventral lobe of petiole deep, with posterior margin forming a concave or vertical surface, meeting tergum anterior to posterior limit of posterior tergal lobe (Fig. 1D, 5); scape with abundant erect setae, about as long as one half to two thirds maximum width of scape; middle and hind tibia with abundant erect setae, longest of these about as long as one half maximum width of tibia (MTSC 20-40); side of head with 0-1 erect setae near mandibular insertion, lacking elsewhere; posterior margin of head with abundant long erect setae; pronotum with erect setae on anterior margin and posterior margin, leaving bare space medially; mesoscutum, scutellum, and propodeum with abundant erect setae; petiolar node rimmed with erect pubescence and irregular longer erect setae, 2–3 pairs of erect setae usually extending above apex in profile, posterior border of sternal lobe of petiole with dense layer of erect setae of irregular lengths; gastral terga with moderately abundant long erect setae; almost entire body uniform dark red brown, lighter orange brown around antennal fossa.

Worker characters. Measurements (n=14): HLA 1.24 (1.00–1.44), HW 1.29 (1.01–1.47), SL 0.94 (0.81–1.01), CI 105 (101–109), SI 77 (70–85).

Palpal formula 6,4; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible smooth and shining near masticatory margin, grading to microareolate and dull at base, with moderately abundant small piligerous puncta, setae in puncta short, erect, larger puncta with long setae near masticatory margin; medial and lateral clypeal lobes at about same level; head with strongly convex sides, strongly cordate posterior margin; in lateral profile pronotum evenly sloping, slightly convex, mesonotum more strongly convex, forming separate convexity; posteroventral lobe of petiole well developed, deep; scape with abundant erect setae, length of setae about one half to equal to maximum width of scape; mid and hind tibia with abundant erect setae, longest setae about one half to two thirds maximum width of tibia; side of head with 2–5 erect setae irregularly distributed along side; posterior margin of head with abundant long erect setae; pronotum, mesonotum, and dorsal face of propodeum with abundant long setae, those on dorsal face of propodeum sometimes shorter, sparser, less erect than those on pronotum and mesonotum; most of body light to dark brown.

Similar species. The queens of *A. gnava* are most similar in size and shape to queens of *A. instabilis* and *A. sericeasur*. They differ from *A. instabilis* by the small ocelli (OCW < 0.15 for *A. gnava*, > 0.20 for *A. instabilis*), and from *A. sericeasur* by the uniformly brown face (with extensive yellow coloration on *A. sericeasur*). *Azteca gnava* differs from both species in the deep posteroventral petiolar lobe, with vertical to

concave posterior face. Workers of *A. gnava* are difficult to distinguish from *A. velox* and *A. nigra*. They tend to be somewhat larger than both. The ventral petiolar lobe is more strongly developed than *A. velox*, and the scapes tend to be relatively shorter than *A. nigra* (Fig. 6F).

Range. Southern Mexico to Panama.

Biology. Azteca gnava occurs in the canopy of wet to moist forest habitats, where it forms ant gardens. Ant gardens are moderately abundant in Costa Rica, usually in the canopy of wet to moist forest, and often in trees overhanging streams or river margins. Costa Rican ant gardens are formed by a number of species, including *Odontomachus panamensis* (in parabiotic association with *Crematogaster carinata*), *C. jardinero*, *C. longispina*, *Pheidole violacea*, *Azteca gnava*, and *A. nigra*.

Azteca gnava ant gardens are large and their associated epiphytes usually appear dense and well established (e.g. robust Aechmea (Bromeliaceae) plants, dense mats of Peperomia (Piperaceae), hemiepiphytic Coussapoa). In Corcovado National Park, Costa Rica, A. gnava ant gardens often have abundant growth of Peperomia macrostachya and Aechmea tillandsioides var. kienastii. Colonies usually occur as one or more large central nests and numerous smaller satellite nests, forming an "archipelago" of ant gardens. Larger nests may be over 50cm diameter. Invariably, large populations of coccoid Hemiptera are sheltered beneath the ant gardens, attached to the supporting branch of the host tree and sometimes on the epiphytes on the nest. Ant brood can be found dispersed throughout the gardens.

Queens were unknown prior to this study and they are very rarely encountered. In the one case in which I observed a colony queen, it inhabited the central and largest ant garden. Very occasionally alate queens are taken in Malaise traps. On Barro Colorado Island, Panama, I collected an alate queen flying in the forest at 1700hrs.

Comments. *Azteca gnava* may be close to or the same as *A. ulei*, the ants from Ule's classic studies of Amazonian ant gardens (Ule 1901).

Additional material examined. COSTA RICA: Alajuela: Atenas, Nov 1977 (L. D. Gómez P.) — workers [USNM]; Heredia: 11km ESE La Virgen, 10°21'N, 84°03'W, 300m, Feb-Apr 2004 (ALAS) — alate queen; Limon: Hamburg Farm, 10°15'N, 83°27'W, 50m, 28 Nov 1925 (F. Nevermann) — workers [USNM]; Tortuguero, 10°32'N, 83°31'W, 5m, 5 Jul 1985 (J. Longino) — workers, dealate queen; 10km ESE Moravia, 9°48'N, 83°22'W, 500m, 28 Aug 1985 (J. Longino) — workers; Hitoy Cerere Biol. Reserve, 9°40'N, 83°02'W, 100m, 1 Sep 1985 (J. Longino) — workers; *Puntarenas*: Sirena, Corcovado National Park, 8°29'N, 83°36'W, 5m, multiple collections and dates (J. Longino) — workers; same locality, 1–30 Apr 1992 (G. Rodriguez) alate queen [INBC]; Llorona, Corcovado National Park, 8°35'N, 83°42'W, 5m, 8 Jun 1982 (J. Longino) workers; Rio Niño, Corcovado National Park, 8°33'N, 83°29'W, 300m, 11 Feb 1996 (J. Longino) — workers, males; 5km SW Las Alturas, 8°55'N, 82°52'W, 1240m, 24 Mar 1990 (J. Longino) — worker (tentative determination); 19km S Ciudad Neily, 8°29'N, 82°58'W, 20m, 25 Mar 1990 (J. Longino) — workers, male; Rancho Quemado, Osa Peninsula, 8°42'N, 83°33'W, 200m, 1–30 Nov 1991 (F. Quesada) — alate queen [INBC]; same locality, 1–30 Apr 1992 (K. F. Flores) — alate queen [INBC]; **GUATEMALA**: *Izabal*: Livingston, 15°50'N, 88°45'W (Schwarz & Barber) — alate queen [USNM]; **HONDURAS**: *Comayagua*: 1mi W. Taulabe, 1990 (C. Catton) — worker; **PANAMA**: Canal Zone: Barro Colorado Island, 9°09'N, 79°51'W, 100m, 4 Jul 1997 (J. Longino) — alate queen.

Azteca instabilis (F. Smith 1862)

Figures 3,4A,5,7.

Tapinoma instabilis F. Smith 1862:31. Syntype workers: Panama [BMNH] (examined).

Liometopum instabile (F. Smith) (part): Mayr 1878:870.

Azteca instabilis (F. Smith): Emery 1893:135. Description of queen: Emery 1896a:2.

Azteca instabilis var. major Forel 1899:107. Syntype workers: Panama, Bugaba, Caldera (Champion) [MHNG] (examined). NEW SYNONYMY

Queen characters. Measurements (n=5): HLA 2.49 (2.42–2.52), HW 2.47 (2.39–2.55), SL 1.50 (1.42–1.50), CI 100 (98–101), SI 60 (58–62).

Palpal formula 6,4; ocelli large (OCW > 0.20mm); middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible smooth, very faintly microareolate, with moderately abundant small piligerous puncta, setae in puncta short, suberect, larger puncta with long setae near masticatory margin; medial and lateral clypeal lobes at about same level (medial lobe not projecting anteriorly); head quadrate, with sides somewhat convex, cordate posteriorly; petiolar node tall, strongly compressed into thin scale at apex; posteroventral petiolar lobe evenly convex from front to back, broad and flat laterally, ending before posterior margin of sternite, leaving small rim formed by posteriormost portion of sternite; scape with abundant erect setae, about as long as one half maximum width of scape; middle and hind tibia with abundant erect setae, longest of these about as long as one half maximum width of tibia (MTSC 30–35); sides of head without erect setae; posterior margin of head with abundant erect setae; pronotum with erect setae on anterior and posterior margins, absent from medial area; mesoscutum, scutellum, and propodeum with abundant erect setae; petiolar node with variable number of long setae on apex, abundant long setae on posteroventral lobe; all gastral terga with abundant erect setae; color red brown.

Worker characters. Measurements (n=4): HLA 1.88 (1.76–2.10), HW 1.85 (1.80–2.13), SL 1.39 (1.34–1.41), CI 101 (95–102), SI 74 (67–76).

Palpal formula 6,4; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible strongly microareolate, dull, with moderately abundant small piligerous puncta, setae in puncta short, erect, larger puncta with long setae near masticatory margin; medial and lateral clypeal lobes at about same level; head with convex sides, strongly cordate posterior margin; mesosoma in lateral profile with sloping pronotum, mesonotum forming separate convexity, posterior mesonotum and dorsal face of propodeum together forming single shallow concavity, with no notch marking metanotal groove; scape with abundant erect setae, length of setae about one half maximum width of scape; mid and hind tibia with abundant erect setae, longest setae about one half maximum width of tibia; sides of head without erect setae; posterior margin of head with abundant erect setae; pronotum, mesonotum, and dorsal face of propodeum with abundant long erect setae; color dark brown to light orange brown, if somewhat bicolored gaster is darker then mesosoma.

Similar species. Azteca instabilis queens are readily identified by the large size and large ocelli. Azteca gnava and A. sericeasur are similarly large but have much smaller ocelli (OCW < 0.15mm). Larger workers of A. instabilis are identified by the dull dorsal surface of the mandibles, large size, and densely setose tibiae.

Range. Kempf (1972) lists *A. instabilis* from scattered localities in Brazil, the Guianas, Peru, Colombia, Panama, Costa Rica, Honduras, Guatemala, Belize, and Mexico. I have examined material from Mexico, Honduras, Nicaragua, Costa Rica, Panama, and Bolivia.

Biology. *Azteca instabilis* is the largest species in the genus. It occurs in wet to dry forest habitats, usually below 500m elevation.

Azteca *instabilis* makes its nest in the hollow trunks of trees which have a large crevice or fissure at the base. When I encounter them, workers are issuing from the fissure in large numbers, usually ascending the tree and often blanketing the surrounding forest floor. In one case I was able to peer up into such a fissure, and I observed a very large carton nest filling the trunk cavity. Colonies can be long-lived. During extended field work at Sirena in Corcovado National Park, I frequently passed a large tree with a very active *A. instabilis* colony in the trunk, with workers flowing in and out of a large fissure at the base. I returned to the site 16 years later to find the same fissure with *A. instabilis* workers still active.

When examining *Azteca* queens in museum collections, *A. instabilis* is usually the most abundant species because the large queens frequently come to lights at night. This is in sharp contrast to most other *Azteca*, whose alate queens are usually encountered as diurnal strays, occasional specimens in Malaise traps, or parts of nest collections. This correlates with the fact that *A. instabilis* queen ocelli are absolutely and relatively far

larger than ocelli on any other *Azteca* queen I have examined. The enlarged ocelli are not the result of an allometric relationship with head size, since *A. sericea* and *A. sericeasur*, with queens nearly as large, have tiny ocelli typical of smaller queens. Ocelli concentrate light and detect light of low intensity (Chapman 1982), suggesting a functional relationship between large ocelli and nocturnal habits.

Workers frequently forage on the surface, both day and night. They visit extrafloral nectaries, and may tend coccoid Hemiptera under small carton shelters.

Additional material examined. COSTA RICA: Alajuela: Upala, Colonia Libertad, 10°54'N, 85°02'W, 550m, 10 Nov 1987 (Lezama) — alate queen [MUCR]; Upala, Pilon de Bijagua, 10°54'N, 85°02'W, 750m, 18 Nov 1993 (Lezama) — alate queen [MUCR]; Upala, Colonia Libertad, 10°54'N, 85°02'W, 450m, 9 May 1988 (L. Gonzalez & J. Sot) — alate queen [MUCR]; Upala, Guatuso, Asent. La Garroba, 10°54'N, 85°02'W, 90m, 10 Nov 1987 (Lezama) — alate queen [MUCR]; Casa Eladio, Rio Penas Blancas, 10°19'N, 84°43'W, 800m, 22 May 1987 (J. Longino) — alate queen; Guanacaste: Headquarters, Santa Rosa Nat. Park, 10°50'N, 85°37'W, 300m, 13 Jul 1985 (J. Longino) — worker; *Heredia*: 10km SE La Virgen, 10°20'N, 84°05'W, 500m, 16 Feb 2003 (J. Longino) — alate queen; La Selva Biological Station, 10°26'N, 84°01'W, 50m, numerous collections and dates (ALAS, G. Gentry, J. Longino, R. Vargas C.) — workers, alate queens [INBC]; 11km ESE La Virgen, 10°21'N, 84°03'W, 300m, numerous collections and dates (ALAS, D. Brenes) — workers [INBC]; 16km SSE La Virgen, 10°16'N, 84°05'W, 1100m, multiple dates and collections (ALAS, D. Brenes, R. Vargas. C) — workers [INBC]; Puntarenas: Curu Wildlife Refuge, 9°47'N, 84°55'W, 5m, 28–29 Mar 1993 (J. Longino) — workers, alate queen; Sirena, Corcovado National Park, 8°29'N, 83°36'W, 5m, multiple dates and collections (J. Longino) — workers, alate queens; Llorona, Corcovado National Park, 8°35'N, 83°42'W, 5m, 22 Mar 1981 (J. Longino) — workers; **MEXICO**: *Chiapas*: Ruinas Yaxchilan, 16°54'N, 90°50'W, 100m, 17 Dec 1991 (P. S. Ward) — workers; Ruinas Bonampak, 16°42'N, 91°04'W, 300m, 18 Dec 1991 (P. S. Ward) workers; Veracruz: 10km N Cárdenas, 10m, 28 May 1988 (W. P. Mackay) — workers; PANAMA: Colon: Est. Biol. Galeta, 9°24'N, 79°52'W, 10m, multiple collections and dates (J. Dunn) — workers; *Darién*: no specific locality (Festa) — alate queen, workers [MCSN].

Azteca longiceps Emery 1893

Figures 2,4A,4B,5,6D.

Azteca longiceps Emery 1893:344. Holotype queen: Costa Rica, Alajuela (Alfaro) [MCSN] (examined). Azteca prorsa Wheeler, 1942:238. Syntype workers: Guatemala, Escuintla, December 1911 (Wheeler), in hollow twigs of *Triplaris auriculata* [LACM] (examined). NEW SYNONYMY

Queen characters. Measurements (n=9): HLA 1.47 (1.42–1.55), HW 0.86(0.84–0.91), SL 0.58 (0.56–0.61), CI 59 (57–60), SI 40 (38–41).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible with row of large puncta at masticatory margin, these bearing long setae, about 4 large puncta posterior to this row, lacking setae, otherwise puncta small, surface microareolate, dull; medial and lateral clypeal lobes at about same level; head rectangular, posterior margin distinctly excised medially; petiolar node short, bluntly rounded; posteroventral petiolar lobe deep, strongly convex from front to back; scape with moderately abundant erect setae, about as long as one third maximum width of scape; middle and hind tibia with moderately abundant erect setae, longest about as long as one third to one half maximum width of tibia (MTSC 10–20), side of head with 0–4 short, inconspicuous erect setae, posterior margin of head with abundant long erect setae; pronotum with posterior row of erect setae, occasionally a pair of setae on the medial area; mesoscutum, scutellum and propodeum with moderately abundant erect setae; petiolar node in profile with 2–4 pairs erect setae projecting above apex, posteroventral lobe with abundant short erect setae; gastral terga with very sparse erect setae; general body color uniformly dark brown.

Worker characters. Measurements (n=6): HLA 1.10 (0.94–1.19), HW 0.84 (0.75–0.92), SL 0.54 (0.50–0.58), CI 77 (74–80), SI 50 (49–54).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible smooth and shiny on apical half or more, becoming microareolate and dull near base, with sparse puncta, row of puncta along masticatory margin with setae, others lacking setae; medial and lateral clypeal lobes at about same level; head elongate with weakly convex sides, strongly excavate posterior margin; in lateral profile pronotum shallowly convex, mesonotum more strongly convex and forming separate convexity that weakly protrudes above pronotum; scape with moderately abundant erect setae, length of setae about one half maximum width of scape; mid and hind tibia with abundant erect setae, longest about one half maximum width of tibia; side of head with 5–10 short erect setae; posterior margin of head with abundant short erect setae; pronotum, mesonotum, and propodeum with abundant erect setae; color brown.

Similar species. The 5,3 palpal formula, the presence of tibial spurs, and the elongate rectangular head places *A. longiceps* among the species treated in Longino (1996). The lack of conspicuous erect setae on the mandibles differentiates it from *A. brevis* and *A. nigricans*. The remaining similar species are *A. beltii*, *A. oecocordia*, and *A. pittieri*. Queens of *A. longiceps* differ from queens of *A. beltii* in the smaller size and brown color. They differ from *A. pittieri* in the relatively longer, more rectangular head (Fig. 4B). They differ from *A. oecocordia* in the less triangular petiolar node, more setose hind tibia, larger puncta on the mandible, and smaller size.

Range. Costa Rica, Guatemala.

Biology. The taxonomy and biology of *A. longiceps* was reviewed in Longino (1996). *Azteca longiceps* is an obligate inhabitant of myrmecophytic *Triplaris* trees.

Additional material examined. COSTA RICA: *Limón*: Fca. de E. Rojas, Sector Cerro Cocorí, 10°36'N, 83°43'W, 150m, 1–30 Apr 1994 (E. Rojas) — queen [INBC]; *Puntarenas*: Guaria, rd to Monteverde, 10°15'N, 84°50'W, 700m, 5 Jul 1991 (J. Longino) — queens, workers; Ojo de Agua, rd to Monteverde, 10°16'N, 84°50'W, 800m (J. Longino) — males, queens, workers; Lindora, 2.5km SW Monteverde, 10°18'N, 84°50'W, 840m, 26 May 1991 (J. Longino) — queens, workers; same locality, 8 Jul 1991 (J. Longino) — queens, workers; Sector Laguna Meandrica, R. B. Carara, 9°47'N, 83°25'W, 100m, 1–30 Jun 1990 (R. Zuñiga) — queen [INBC].

Azteca nanogyna

See Addendum: A. aurita group.

Azteca nigra Forel 1912 new status

Figures 3,4A,5,6A,6E,6F.

Azteca velox race nigra Forel 1912:48. Syntype workers, queen, males: Panama (Christophersen) [MHNG] (examined).

Queen characters. Measurements (n=4): HLA 1.61 (1.61–1.63), HW 1.71 (1.64–1.73), SL 1.05 (1.02–1.08), CI 105 (102–107), SI 65 (63–67).

Palpal formula 6,4; ocelli small; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible with small piligerous puncta, setae in puncta short, subdecumbent, interspaces between puncta shiny, becoming faintly microareolate at base; medial and lateral clypeal lobes at about same level; head with convex sides, posterior margin weakly cordate, shallowly excavate; petiolar node tall, strongly compressed into thin scale at apex; posteroventral lobe of petiole deep, with posterior margin forming a separate convexity

that extends as far posteriorly as posterior tergal lobe, with a small notch or concavity between the sternal convexity and the tergal lobe (Fig. 1D, 5); scape with moderately abundant erect setae, about as long as one half maximum width of scape; middle and hind tibia with abundant erect setae, longest of these about as long as one half maximum width of tibia (MTSC 25–30); side of head with 2–4 short erect setae near mandibular insertions, bare elsewhere; posterior margin of head with abundant erect setae; pronotum with erect setae on posterior margin; mesoscutum, scutellum, and propodeum with abundant erect setae; petiolar node rimmed with erect pubescence and sparse longer erect setae, 0–2 pairs of erect setae extending above apex in profile, posterior border of sternal lobe of petiole with dense layer of erect setae of irregular lengths; gastral terga with sparse long erect setae; light orange brown coloration on clypeus, malar area, antennal fossa, and side of head, variable extent of infuscation on medial and posterior vertex.

Worker characters. Measurements (n=4): HLA 1.06 (0.96–1.13), HW 1.04 (0.94–1.14), SL 0.93 (0.90–0.96), CI 100 (96–101), SI 88 (85–94).

Palpal formula 6,4; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible smooth and shining, with moderately abundant small piligerous puncta, setae in puncta short, erect, larger puncta with long setae near masticatory margin; medial and lateral clypeal lobes at about same level; head with moderately to weakly convex sides, moderately cordate posterior margin; in lateral profile promesonotum forming single convexity; posteroventral lobe of petiole with small posterior notch, similar to queen, but small and barely discernable; scape with abundant erect setae, length of setae about one half maximum width of scape; mid and hind tibia with abundant erect setae, longest setae about one half maximum width of tibia; side of head with about 5 erect setae on malar area, short erect setae variably present along entire side of head; posterior margin of head with abundant erect setae; pronotum, mesonotum, and dorsal face of propodeum with abundant long erect setae; anterior and anterolateral portions of head light yellow brown, variable extent of darker brown on medial vertex and posteriorly, mesosoma and gaster brown.

Similar species. Queens of *A. velox*, *A. quadraticeps*, and *A. flavigaster* are all very similar to *A. nigra* but differ in head size (Fig. 6A) and the lack of a posterior notch on the posteroventral petiolar lobe (Fig. 1E versus 1D). Workers of *A. flavigaster*, *A. nigra*, and *A. velox* are all very similar in terms of size and shape (workers of *A. quadraticeps* are unknown but are expected to be in this group as well). Workers of *A. flavigaster* are distinguished from *A. nigra* by the bright yellow gastral dorsum. Workers of *A. velox* are most similar to *A. nigra* in terms of general size and coloration. *Azteca velox* workers tend to have relatively shorter scapes (Fig. 6F). On the largest workers of *A. nigra* the presence of a small posterior notch on the posteroventral petiolar lobe may distinguish them from both *A. flavigaster* and *A. velox*.

Range. Costa Rica, Panama.

Biology. Azteca nigra occurs in lowland wet forest, where it forms ant gardens in the understory. I have observed two colonies, both in the Atlantic lowlands of Costa Rica. One was in Tortuguero National Park and the other at La Selva Biological Station. The Tortuguero collection was a cluster of small ant gardens in low vegetation. One nest was adjacent to a group of rotten sticks, inside of which were males and winged queens. Inside another stick was an aggregation of Camponotus atriceps workers, living parabiotically with the Azteca. The La Selva collection was also a series of small carton nests sprouting a few epiphytes. The nests were scattered on stems and leaves of a cluster of low melastomes. The nests covered coccoid Hemiptera and contained ant brood. A few higher nests on individual melastome leaves contained alate queens. One basal, central nest was built around a 50cm long dead branch. Camponotus atriceps were parabiotic in the central nest and some of the satellite nests. The Camponotus and Azteca occupied separate chambers, but the chambers were connected and the two species moved freely among each other as the nests were being disturbed. In the central nest, which was a combination of carton chambers and chambers in the dead branch, the Azteca were clearly associated with the carton areas. It appeared that the Camponotus were living parabiotically in the nest of the Azteca, with the Azteca being the primary architects and owners of the nests.

Additional material examined. COSTA RICA: *Heredia*: La Selva Biological Station, 10°26′N, 84°01′W, 50m, 28 Jan 1989 (J. Longino) — alate queens and workers; 11km ESE La Virgen, 10°21′N, 84°03′W, 300m, 19 Feb and 20 Mar 2004 (D. Brenes) — worker; *Limón*: Tortuguero, 10°32′N, 83°31′W, 5m, 1 Jul 1985 (J. Longino) — workers; same locality, 5 Jul 1985 (J. Longino) — workers, alate queens, males.

Azteca nigricans Forel 1899

Figures 2,4A,5.

Azteca fasciata var. nigricans Forel, 1899:122. Unique syntype queen: Panama, Bugaba, Volcan de Chiriqui (Champion) [MHNG] (examined). Raised to species: Longino 1996:141.

Azteca JTL-002: morphospecies code used in Longino 1996:141.

Queen characters. Measurements (n=5): HLA 1.55 (1.48–1.64), HW 1.09 (1.05–1.17), SL 0.76 (0.74–0.79), CI 71 (70–73), SI 50 (48–51).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible coarsely punctate, puncta bearing stiff erect setae, mandible appearing bristly; medial and lateral clypeal lobes at about same level; head subrectangular, posterior margin weakly excised medially; petiolar node short, broadly triangular; posteroventral petiolar lobe strongly convex from front to back; scape with sparse and inconspicuous erect setae, about as long as one third maximum width of scape; hind tibia with short inconspicuous suberect setae, longest of these about as long as one sixth maximum width of tibia (MTSC 5–10); side of head with 0–2 short setae near mandibular insertion, setae lacking elsewhere, posterior margin of head with sparse erect setae; pronotum with posterior row of erect setae; mesoscutum and scutellum with very sparse erect setae; propodeum with a few erect setae on sides, none on dorsomedial area; petiolar node with rim of whitish erect pubescence, a few longer erect setae on lower sides but in profile with none projecting above apex, posteroventral lobe with abundant long setae; gastral terga with very sparse erect setae; general body color dark brown, the following lighter yellow brown: thin strip of anterior clypeus and area near mandibular insertions, thin anterior and posterior bands on gastral terga, gastral sterna.

Worker characters. Measurements (n=4): HLA 1.31 (1.04–1.42), HW 1.09 (0.92–1.20), SL 0.73 (0.67–0.77), CI 84 (83–88), SI 56 (54–64).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible with abundant piligerous puncta, surface between puncta smooth and shining, variable extent of base faintly microareolate; medial and lateral clypeal lobes at about same level; head subquadrate with weakly convex sides, moderately excavate posterior margin; in lateral profile mesosoma compact, pronotum and mesonotum nearly forming a single convexity, with promesonotal suture very weakly impressed; scape with sparse, inconspicuous erect setae, length of setae about one half maximum width of scape; outer surface of hind tibia with a row of about 5 very short, inconspicuous, suberect setae; side of head lacking erect setae or with 1–2 near mandibular insertion; posterior margin of head with sparse erect setae; pronotum and mesonotum with sparse erect setae, dorsal face of propodeum lacking erect setae; color red brown.

Similar species. The bristly mandibles ally this species with *A. forelii* and *A. brevis*. Queens of *A. nigricans* are smaller than queens of *A. forelii* (Fig. 4A). Queens of *A. brevis* have shorter scapes than queens of *A. nigricans* (SI 39–43 versus 50–52, respectively). Workers of *A. brevis* are distinguished from workers of *A. nigricans* by the reduced number of setae on the hind tibia, 0–2 on *A. brevis* versus > 5 on *A. nigricans*.

Range. Panama, Costa Rica, Guatemala.

Biology. Longino (1996) reviewed the taxonomy and biology of this species. It is found in wet forest habitats, where it nests in live stems of a wide variety of trees, including *Cecropia insignis*, *Inga*, *Pentaclethra macroloba*, *Erythrina poeppigiana* (Fabaceae), *Tetrathylacium costaricensis*, *Licania*, *Phoebe chavarriana* (Lauraceae), and *Dendropanax arboreus* (Araliaceae). The workers make small holes in shoot tips of live

trees, leading to irregular cavities containing brood. The walls of the cavities are lined with abundant coccoid Hemiptera. As flushes of new growth occur, the ants move into the new shoots and progressively abandon older chambers lower in the branch. Colonies are polydomous, with brood distributed in multiple nests. Colonies can be large, occurring in large portions of large canopy trees. In contrast to the similar species *A. brevis*, workers do not use carton construction and often have exposed foragers on stems. Although new alate queens are often dispersed in the nests of a colony, I have never found a physogastric colony queen. This suggests that colonies are monogynous, with the colony queen hidden in one of the many nests that occur in tree crowns. Brood must be transported externally to new nests.

Comments. In Longino (1996), two morphospecies, JTL-001 and JTL-002, were considered close to or conspecific with *A. nigicans*. The former was discovered to be *A. brevis*, and the measurements of the latter cluster with the holotype queen of *A. nigricans*. The separateness of *A. brevis* and *A. nigricans* was further supported when the two species were found to be sympatric in Corcovado National Park. I found both species nesting in the canopy of a large *Licania* tree in Corcovado National Park. At the time I did not understand the species boundaries, but in the field I observed behavioral differences. In my field notes I commented that *Azteca* high in the crown produced a black crusty carton on the stem surfaces and were rarely seen exposed on the surface, while another group of *Azteca* lower in the crown looked similar but did not make carton and were active and exposed on the surface of the live stems in which they nested. The former were *A. brevis* and the latter *A. nigricans*.

Additional material examined. COSTA RICA: *Heredia*: La Selva Biological Station, 10°26'N, 84°01'W, 50m, numerous collections and dates (ALAS, Longino, Wetterer) — workers, queens [INBC]; 11km ESE La Virgen, 10°21'N, 84°03'W, 300m, 21 Mar–6 Apr 2004 (ALAS) — worker [INBC]; 11km SE La Virgen, 10°20'N, 84°04'W, 500m, numerous collections and dates (ALAS) — workers [INBC]; *Limón*: Parismina, 10°12'N, 83°38'W, 5m, 18 Oct 1926 (F. Nevermann) — worker, alate queen [USNM]; *Puntarenas*: Sirena, Corcovado National Park, 8°29'N, 83°36'W, 5m, 7 Sep 1982 (J. Longino) — workers; same locality, 3 Jul 1987 (L. Tennant) — worker; **GUATEMALA**: *Escuintla*: Finca Caobanal, 14°06'N, 90°40'W, Feb 1993 (J. Gilardi) — workers.

Azteca oecocordia new species

Figures 2,4A,4B,5,6D,9.

Azteca JTL-003: morphospecies code used in Longino 1996:138.

Holotype queen: Costa Rica, Prov. Puntarenas, Guacimal, rd to Monteverde, 10°14'N, 84°51'W, 5 Jul 1991, 500m (J. Longino#2988) [INBC, specimen code INBIOCRI001279956].

Paratypes: same locality and date as holotype but (J. Longino#2977-s), 1 queen [INBIOCRI001279936, MCZC]; (J. Longino#2982), 2 workers [INBIOCRI001279943, INBC]; (J. Longino#2976), 2 workers [INBIOCRI001279934, USNM]; (J. Longino#2973), 3 workers [INBIOCRI001279932, LACM]; Guacimal, rd to Monteverde, 10°13'N, 84°51'W, 400m, 5 Jul 1991 (J. Longino#3001), 2w [INBIOCRI001279971, MCZC]; same locality as holotype, Feb 1999 (J. Dunn), 1 queen, 1 worker [INBIOCRI002281961, USNM].

Measurements of holotype. HLA 1.62, HLB 1.58, HW 0.98, SL 0.67, EL 0.34, OC 0.07, MTSC 3.

Diagnosis. The 5,3 palpal formula, the presence of tibial spurs, and the elongate rectangular head places *A. oecocordia* among the species treated in Longino (1996). The lack of conspicuous erect setae on the mandibles differentiates it from *A. brevis* and *A. nigricans*. The remaining similar species are *A. beltii*, *A. longiceps*, and *A. pittieri*. Queens of *A. oecocordia* differ from queens of *A. beltii* in the smaller size and brown color. They differ from *A. pittieri* in the relatively longer, more rectangular head (Fig. 4B). They differ from *A. longiceps* in the more triangular petiolar node, less setose hind tibia, smaller puncta on the mandible, and larger size.

Queen characters. Measurements (n=3): HLA 1.56 (1.53–1.62), HW 0.94 (0.93–0.98), SL 0.67 (0.65–0.67), CI 61 (60–61), SI 42 (42–44).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible (excluding masticatory margin and apex) with small piligerous puncta, setae in puncta short, subdecumbent, interspaces between puncta smooth and shiny on apical third of mandible, becoming faintly microareolate on basal two thirds; medial and lateral clypeal lobes at about same level; head rectangular, posterior margin distinctly excised medially; petiolar node short, broadly triangular, blunt; posteroventral petiolar lobe shallow, evenly convex from front to back; scape with sparse erect setae, inconspicuous and only visible at certain angles, about as long as one quarter maximum width of scape; middle and hind tibia with very sparse erect setae, fine, inconspicuous, longest about as long as one fifth maximum width of tibia (MTSC 0–5), side of head with 0–1 short erect setae near mandibular insertion, lacking setae elsewhere, posterior margin of head with sparse short setae; pronotum with posterior row of erect setae, mesoscutum, scutellum and propodeum with sparse erect setae, petiolar node in profile with 2 pairs erect setae projecting above apex, posteroventral lobe with abundant short erect setae; gastral terga with very sparse erect setae; general body color uniformly brown.

Worker characters. Measurements (n=4): HLA 1.43 (1.15–1.53), HW 1.10 (0.94–1.18), SL 0.68 (0.61–0.70), CI 77 (76–82), SI 47 (46–53).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible smooth and shiny on apical third, becoming microareolate and dull on basal two thirds, with abundant small puncta, row of puncta along masticatory margin with setae, others lacking setae; medial and lateral clypeal lobes at about same level; head elongate with weakly convex sides, strongly excavate posterior margin; in lateral profile pronotum shallowly convex, mesonotum more strongly convex and forming separate convexity that protrudes above pronotum; scape with sparse, inconspicuous erect setae, length of setae about one quarter maximum width of scape; mid and hind tibia with 1–5 erect setae, setae inconspicuous, longest about one quarter maximum width of tibia; side of head lacking erect setae; posterior margin of head with sparse short erect setae; pronotum and mesonotum with moderately abundant erect setae, propodeum with 2–3 setae at juncture of dorsal and posterior faces; color brown.

Etymology. The name refers to this species' habit of making its home in *Cordia*.

Range. Costa Rica.

Biology. This species is only known from one small area in the Monteverde region of Costa Rica, and all collections are from *Cordia alliodora*. It appears to be a *Cordia* specialist, like *A. pittieri*. Its behavior appears similar to *A. pittieri* in all respects. Founding queens are found in *Cordia* nodes. Mature colonies dominate most nodes of a tree, but may coexist with *Cephalotes setulifer* on the same tree. Individual nodes usually contain coccoid Hemiptera on the interior walls, and the ants build small carton partitions inside the nodes.

Azteca ovaticeps Forel 1904

Figures 4A,6C,7.

Azteca alfaroi var. ovaticeps Forel 1904a:44. Syntype queens, workers: Brazil, Pará (Göldi) [MHNG, MCZC] (examined). Raised to species: Longino 1989a:8.

Azteca alfari var. aequilata Forel 1904b:691. Lectotype worker: Brazil, Amazonas, Cachveira Juruá (ex *Cecropia* No. 5587) [MHNG] (examined). Synonymy by Longino 1989a:8.

Azteca alfari var. aequalis Forel 1906:239. Lectotype worker: Brazil, Mexiana Island, Amazon delta (Hagmann) [MHNG] (examined). Description of queen, male: Forel 1908b:387. Synonymy by Longino 1989a:8.

Azteca alfari subsp. tuberosa Forel 1906:240. Syntype workers, queen: Brazil, Ceará (Diaz da Rocha) [MHNG, MCZC] (examined). Synonymy by Longino 1989a:8.

Queen characters. Measurements (n=11): HLA 1.60 (1.52–1.65), HW 1.34 (1.27–1.37), SL 0.81 (0.79–0.84), CI 83 (82–85), SI 51 (49–53).

Similar to *A. alfari* in almost all respects; differing as follows: fourth abdominal tergum with > 10 erect setae (rarely fewer), exclusive of posterior row (< 6 in *A. alfari*); dorsal surface of head, when viewed in profile, often with setae bridging the gap between the ocellar region and the upper vertex, and often with setae extending up from the clypeus almost to the ocellar region (these areas devoid of setae in *A. alfari*); scape relatively long (SI 49–54 versus 45–49 in *A. alfari*, Fig. 6C); color usually light red brown, *A. alfari* usually black.

Worker characters. Measurements (n=5): HLA 1.16 (0.93–1.31), HW 1.02 (0.87–1.19), SL 0.71 (0.59–0.78), CI 92 (88–94), SI 61 (60–67).

Similar to *A. alfari* in almost all respects and not always distinguishable. In general *A. ovaticeps* is more setose, with a "scruffy" appearance on the mesosomal dorsum. There are always > 10 setae on the mesonotum, with median number about 20, and they are of irregular length. In contrast, *A. alfari* has a cleaner look, with fewer dorsal setae. There are 2–17 setae on the mesonotum, with median number 8, and they are of relatively more even length.

Similar species. Azteca ovaticeps is distinguished from A. alfari as described above. Workers of A. ovaticeps may also be confused with workers of A. forelii. Mandibles of A. ovaticeps workers are smooth and shiny; mandibles of A. forelii workers are roughened and dull.

Range. Costa Rica to Amazonian Brazil and Bolivia.

Biology. The taxonomy and biology of A. ovaticeps is reviewed in Longino (1989a, 1991b).

Azteca ovaticeps is an obligate Cecropia ant. Its biology is very similar to A. alfari, with which it is often locally sympatric. Azteca ovaticeps tends to be more abundant in mature forest areas, older second growth forest, and river banks in mature forest, while A. alfari becomes dominant in open and highly disturbed habitats, such as roadsides and agricultural areas. Azteca ovaticeps is more geographically variable than A. alfari and may be paraphyletic with respect to A. alfari (Longino 1989a, Ayala et al. 1996).

Material examined. See Longino (1989a).

Azteca pilosula Forel 1899

See Addendum: A. aurita group.

Azteca pittieri Forel 1899

Figures 2,4A,4B,5,6D.

Azteca pittieri Forel, 1899:120. Syntype workers: Costa Rica, Buenos Aires (Pittier) [MHNG] (examined).

Azteca longiceps subsp. patruelis Forel, 1908b:392. Syntype workers, queen: Mexico, near Colima (Townsend), in Cordia alliodora [MHNG] (examined). NEW SYNONYMY

Azteca patruelis Forel: Longino 1996:142, Ayala et al. 1996 (misidentifications).

Azteca pittieri var. emarginatisquamis Forel, 1920:204. Syntype workers: Costa Rica (Pittier, n.6701), found by Chodat in cauline swellings of *Cordia gerascanthus* [MHNG] (examined). Synonymy by Longino 1996:144.

Azteca JTL-007: morphospecies code used in Longino 1996.

Queen characters. Measurements (n=64): HLA 1.48 (1.29–1.68, 62), HW 1.02 (0.83–1.14), SL 0.65 (0.59–0.72, 13), CI 68 (63–74, 62), SI 44 (42–45, 13).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible with row of large puncta at masticatory margin, these bearing long setae, otherwise puncta small and lacking setae, surface smooth and shiny over variable extent of surface, becoming faintly microareolate and dull toward base; medial and lateral clypeal lobes at about same level; head rectangular, posterior margin distinctly excised medially; petiolar node short, bluntly rounded; posteroventral petiolar lobe moderately convex from

front to back; scape with moderately abundant erect setae, about as long as one half maximum width of scape; middle and hind tibia with moderately abundant erect setae, longest about as long as one third maximum width of tibia (MTSC 5–15), side of head with 0–5 short erect setae near mandibular insertion, lacking setae elsewhere, posterior margin of head with abundant short setae; pronotum with posterior row of erect setae, mesoscutum and propodeum with sparse to abundant erect setae, scutellum with abundant erect setae, petiolar node in profile with 4–8 pairs erect setae projecting above apex, posteroventral lobe with abundant short erect setae; gastral terga with sparse erect setae; general body color uniformly dark brown.

Worker characters. Measurements (n=28): HLA 1.01 (0.77–1.21), HW 0.84 (0.64–0.99), SL 0.53 (0.44–0.60), CI 0.83 (0.78–0.89), SI 0.54 (0.49–0.60).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible smooth and shiny, row of large puncta along masticatory margin with setae, others small and lacking setae; medial and lateral clypeal lobes at about same level; head elongate with weakly convex sides, strongly excavate posterior margin; in lateral profile pronotum shallowly convex, mesonotum slightly more convex and forming slightly separate convexity; scape with moderately abundant, inconspicuous erect setae, length of setae about one half maximum width of scape; mid and hind tibia with moderately abundant erect setae, longest about one half maximum width of tibia; side of head with 2–5 short erect setae anterior to eye, lacking setae elsewhere; posterior margin of head with abundant short erect setae; pronotum, mesonotum, and dorsal face of propodeum with abundant erect setae; color brown.

Range. Mexico to Panama.

Biology. The taxonomy and biology of this species is reviewed in Longino (1996). More recent studies of the relationship between *Cordia alliodora* and *Azteca pittieri* are Tillberg (2004), and Trager & Bruna (2006). This species is the dominant inhabitant of the ant plant *Cordia alliodora*. Most *Cordia alliodora* plants in Costa Rica harbor colonies of *A. pittieri*. Founding queens can be found alone in *Cordia* nodes, and never seem to found pleometrotically. Colonies are apparently monogynous, with workers, brood, and coccoid Hemiptera dispersed in nodes throughout the tree. Workers are aggressive and forage on the surface of the host tree, but do not generally forage off the host tree.

A set of collections of *A. pittieri* have been made from understory Lauraceae. I collected workers from small trees (either *Ocotea* or *Licaria*) at Tortuguero, and workers and alate queens from *Ocotea nicaraguensis* at Carara Biological Reserve. These were dispersed in live branch tips, with general colony structure and behavior much like the colonies in *Cordia*. INBio Parataxonomists collected isolated queens at Rancho Quemado on the Osa Peninsula.

Comments. The collections from Lauraceae are probably a distinct species, and I use the morphospecies code JTL-007 for them, but I cannot identify any morphological characters that distinguish them from the *Cordia*-inhabiting *A. pittieri*. The mandibles tend to be somewhat more setose, with larger and more abundant piligerous puncta compared to the specimens from *Cordia*. On some workers there are a few short setae on the side of the head posterior to eye, and the general surface pubescence is more abundant and longer. All other characters fall well within the range of variation for the *Cordia* specimens.

In Costa Rica, the queens of the *Cordia*-inhabiting *A. pittieri* cluster into two size classes (Fig. 4B). Smaller queens are from the Pacific lowlands, up to about 500m elevation. Larger queens occur at higher elevations on the Pacific slope, throughout the Atlantic lowlands of Costa Rica, and the scattered collections from further north in Central America and southern Mexico, including the type of *A. patruelis*. Given that the two forms are parapatric and appear to have identical natural history, I am reluctant to consider them distinct species until additional collections and characters are examined.

The types of *A. patruelis* were sent to Forel by Wheeler, and Wheeler (1942:15) provided additional notes on the specimens. They were sent to Wheeler by C. H. Tyler Townsend, who collected them near Cualata, on the slopes of Volcán de Colima, Mexico, in *Cordia alliodora*. The ants kept large red lecanoid coccids in the nest.

Material examined. COSTA RICA: Guanacaste: Estacion Maritza, Guanacaste Conservation Area, 10°58'N, 85°30'W, 600m, 22-23 Feb 1996 (J. Longino) — workers, queens; Bosque Humedo, Santa Rosa Nat. Park, 10°51'N, 85°37'W, 300m, 12 Jul 1985 (J. Longino) — queens; oak forest, Santa Rosa Nat. Park, 10°52'N, 85°36'W, 300m, 15 Jul 1985 (J. Longino) — queens; Nuevo Arenal, 10°32'N, 84°54'W, 600m, 3 Jul 1991 (J. Longino) — workers, males, queens; Taboga Hill, 10°20'N, 85°12'W, 1 Aug 1971 (C. R. Carroll) workers, alate queens [LACM]; Santa Rosa National Park, 0-300m, Feb 1982 (C. Pringle) — worker [UCDC]; Heredia: Chilamate, 10°27'N, 84°04'W, 70m, 1 Sep 1989 (P. Hanson) — alate queen [MUCR]; La Selva Biological Station, 10°26'N, 84°01'W, 50m, multiple collections and dates (ALAS, Kojima, J. Longino) — workers, queens, males [INBC]; Limón: 6km WNW Pto. Viejo, 9°40'N, 82°49'W, 50m, 3 Sep 1985 (J. Longino) — queens; *Puntarenas*: Corcovado National Park, 8°29'N, 83°36'W, 13 Jan 1987 (D. W. Davidson) — worker [LACM]; Guacimal, rd to Monteverde, 10°13'N, 84°51'W, 300m, 20 Jul 1984 (J. Longino) queen; Guacimal, rd to Monteverde, 10°13'N, 84°51'W, 400m, 5 Jul 1991 (J. Longino) — queens, males, workers; Guacimal, rd to Monteverde, 10°14'N, 84°51'W, 500m, 25 Jul 1984 and 5 Jul 1991 (J. Longino) queens, males, workers; Guaria, rd to Monteverde, 10°14'N, 84°51'W, 700m, 25 Jul 1984 (J. Longino) queens; Guaria, rd to Monteverde, 10°15′N, 84°50′W, 700m, 27 Jul 1984 (J. Longino) — queen; Ojo de Agua, rd to Monteverde, 10°16'N, 84°50'W, 800m, 28 Jul 1984 (J. Longino) — queens, males, workers; Lindora, 2.5km SW Monteverde, 10°18'N, 84°50'W, 840m, 8 Jul 1991 (J. Longino) — queen; 4km E Palmar Norte, 8°58'N, 83°25'W, 40m, 26 Mar 1990 (J. Longino) — queens, workers; 5km SSW Monteverde, 10°16'N, 84°50'W, 750m, 4 Jun 1990 (J. Longino) — alate queens; Puerto Jimenez, 8°32'N, 83°19'W, 10m, Dec 1991 (P. Hanson & Godoy) — dealate queen; San José: 3.5km NE Santiago de Puriscal, 9°52'N, 84°18'W (D. H. Janzen) — alate queen [USNM]; EL SALVADOR: San Salvador, 13°42'N, 89°12'W, Oct 1959 (N. L. H. Krauss) — dealate queens [USNM]; GUATEMALA: Finca El Chilero, 30 Mar 1977 (J. W. Stead) — workers [LACM]; Alta Vera Paz: Cacao, Trece Aguas, 15°24'N, 89°45'W (Barber & Schwarz) — dealate queen [USNM]; **HONDURAS**: Choluteca: Tres Piedras, 5 Apr 1977 (J. W. Stead) — workers [LACM]; **MEXICO**: Chiapas: 8km ENE Guadaloupe Victoria (D. W. Davidson) — worker [LACM]; Jalisco: Chamela Biological Station, 19°31'N, 105°02'W, 15 Jul 1984 (D. H. Feener) — workers [LACM]; Chamela Biological Station, 19°30'N, 105°02'W, 100m, 18 Dec 1987 (P. S. Ward) — queen, worker [UCDC]; Veracruz: Los Tuxtlas Biological Station, 18°35'N, 95°05'W, 22 Sep 1984 (G. Ibarra) — worker [LACM]; NICARAGUA: Estelí: 8km S Estelí, 23 Mar 1977 (J. W. Stead) — workers [LACM]; PANAMA: Canal Zone: Ancon, 8°57'N, 79°33'W, 6 Jul 1924 (G. C. Wheeler) — dealate queen.

Morphospecies JTL-007: **COSTA RICA**: *Limón*: Casa Verde, Tortuguero, 10°35'N, 83°31'W, 5m, 23 Jun 1988 (J. Longino) — males, workers; *Puntarenas*: Carara Biological Reserve, Estación Quebrada Bonita, 9°47'N, 84°36'W, 30m, 13 Feb 1989 (J. Longino) — queens, males workers; Rancho Quemado, Osa Peninsula, 8°42'N, 83°33'W, 200m, 21 Mar–7 Apr 1992 (F. Quesada) — queen [INBC]; same locality, 12–24 May 1993 (A. Gutierrez) — queen [INBC].

Azteca quadraticeps new species

Figures 3,4A,5,6A,6B,8.

Holotype alate queen: Costa Rica, Prov. Limón, Tortuguero, 10°32'N, 83°31'W, 5m, 1 Jul 1985 (J. Longino#0389-s) [INBC, specimen code JTLC000005714].

Paratypes: same data as holotype; 1 alate queen [JTLC000005715, MCZC], 1 alate queen [JTLC000009450, USNM].

Measurements of holotype. HLA 1.84, HLB 1.81, HW 1.72, AHW 1.28, SL 1.19, EL 0.46, OC 0.09, MTSC 33.

Diagnosis. Queen with the same characters as *A. flavigaster*, differing only in the larger size. It differs from *A. velox* in the more quadrate head shape, less narrowed anteriorly (Fig. 6B) and with less rounded sides (Fig. 3).

Queen characters. Measurements (n=6): HLA 1.78 (1.70–1.84), HW 1.71 (1.62–1.79), SL 1.16 (1.11–1.19), CI 96 (93–98), SI 65 (64–66).

Palpal formula 6,4; ocelli small; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible with small piligerous puncta, setae in puncta short, subdecumbent, interspaces between puncta smooth and shiny on apical half of mandible, gradually becoming faintly microareolate at base; medial and lateral clypeal lobes at about same level; head subquadrate, posterior margin not strongly cordate, very shallowly excavate; petiolar node tall, strongly compressed into thin scale at apex; posteroventral petiolar lobe evenly convex from front to back; scape with abundant erect setae, about as long as one half maximum width of scape; middle and hind tibia with abundant erect setae, longest of these about as long as one third maximum width of tibia (MTSC 25–35); sides of head without erect setae; posterior margin of head with erect setae; pronotum with erect setae on posterior margin; mesoscutum, scutellum, and propodeum with abundant erect setae; petiolar node with rim of erect pubescence and sparse longer erect setae, 1–2 pairs of erect setae extending above apex in profile, posterior border of sternal lobe of petiole with uniform layer of short erect setae; gastral terga with sparse long erect setae; most of face dark brown, with lighter orange coloration restricted to anterior malar area near mandibular insertions and antennal fossa.

Etymology. The name refers to the somewhat quadrate shape of the head. Its close relative, *A. velox*, has more rounded sides of the head.

Range. Costa Rica.

Biology. This species is known only from queens. They have been collected in lowland to mid-elevation (700m) rainforest in the Atlantic lowlands of Costa Rica.

Comments. Azteca quadraticeps is in a cluster of species that are difficult to distinguish: A. flavigaster, A. nigra, A. sericeasur, and A. velox. It is likely that the workers of A. quadraticeps have been collected and either left unidentified or misidentified. One possibility is that A. quadraticeps is an Atlantic slope version of A. flavigaster, and Atlantic slope worker collections identified as A. flavigaster are A. quadraticeps. Other possibilities are that A. quadraticeps workers masquerade as A. velox, A. nigra, or smaller workers of A. sericeasur.

Additional material examined. COSTA RICA: *Guanacaste*: Estacion Pitilla, Guanacaste Cons. Area, 10°59'N, 85°26'W, 700m, 1–30 Jan 1989 (coll. GNP Biodiversity Survey) — queen [INBC]; Fca. Pasmompa, 5Km SW Santa Cecilia, 11°01'N, 84°34'W, 400m, 1–30 Mar 1989 (coll. GNP Biodiversity Survey) — queen [INBC]; same locality, Mar 1989 (coll. PNG Inventario de Biodiversidad) — queens [INBC]; *Heredia*: 11km ESE La Virgen, 10°21'N, 84°03'W, 300m, 12 Feb–18 Apr 2004 (ALAS) — queens [INBC].

Azteca schimperi Emery 1893

See Addendum: A. aurita group.

Azteca sericeasur new species

Figures 3,4A,5,6E,6F,7.

Holotype alate queen: Costa Rica, Prov. Limón, Hamburg Farm [10°15'N, 83°27'W], 50m, 11 Jul 1925 (F. Nevermann) [USNM, specimen (pin) code JTLC000005642].

Paratypes: same data as holotype; 2 workers [JTLC000005642, USNM]; alate queen, worker, male [JTLC000005643, MCZC]; alate queen, 2 workers [JTLC000009416, INBC]; 2 workers, 1 male [JTLC000009415, LACM]; 8 workers [JTLC000009412, JTLC000009413, JTLC000009414, USNM]; 3 workers [JTLC000009405, JTLC].

Measurements of holotype. HLA 2.14, HW 2.13, SL 1.335, EL 0.518, OC 0.102, MTSC 30.

Diagnosis. The shape and size of the queen head distinguishes this species from all others except *A. sericea*. It differs from *A. sericea* in the presence of erect setae on the posterior margin of the head. It is very similar to *A. velox*, differing only in the larger size. *Azteca gnava* and *A. instabilis* are similar but larger. *Azteca gnava* has the head solid dark brown; *A. sericeasur* has much of the anterior and lateral head light orange brown. *Azteca instabilis* has large ocelli (OCW > 0.20mm); *A. sericeasur* has small ocelli (OCW about 0.10mm).

Queen characters. Measurements (n=10): HLA 2.00 (1.94–2.14), HW 2.00 (1.94–2.17), SL 1.31 (1.28–1.39), CI 100 (99–104), SI 66 (62–67).

Palpal formula 6,4; ocelli small; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible with small piligerous puncta, setae in puncta short, subdecumbent, interspaces between puncta smooth and shiny on apical half of mandible, gradually becoming faintly microareolate at base; medial and lateral clypeal lobes at about same level; head broadly cordate with rounded sides; petiolar node tall, strongly compressed into thin scale at apex; posteroventral petiolar lobe evenly convex from front to back; scape with abundant erect setae, about as long as one half maximum width of scape; middle and hind tibia with abundant erect setae, longest of these about as long as one third to one half maximum width of tibia (MTSC 20–30); sides of head without erect setae; posterior margin of head with abundant erect setae; pronotum with erect setae on posterior margin; mesoscutum, scutellum, and propodeum with abundant erect setae; petiolar node with rim of dense erect whitish pubescence, sparse longer setae, one pair extending above apex in profile, posterior border of sternal lobe of petiole with dense layer of long erect pubescence and several erect setae that are about twice as long as pubescence; gastral terga with sparse long erect setae; light orange brown coloration on clypeus, malar area, antennal fossa, and side of head, variable extent of infuscation on medial and posterior vertex.

Worker characters. Measurements (n=9): HLA 1.32 (1.10–1.69), HW 1.31 (1.08–1.76), SL 1.09 (0.99–1.26), CI 99 (96–104), SI 83 (75–90).

Palpal formula 6,4; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible smooth and shining, with moderately abundant small piligerous puncta, setae in puncta short, erect, larger puncta with long setae near masticatory margin; medial and lateral clypeal lobes at about same level; head with convex sides, strongly cordate posterior margin; in lateral profile promesonotum forming single convexity; scape with abundant erect setae, length of setae about one half maximum width of scape; mid and hind tibia with abundant erect setae, longest setae about one half maximum width of tibia; sides of head without erect setae; posterior margin of head with erect setae; pronotum and mesonotum with abundant long erect setae, somewhat sparser erect setae on dorsal face of propodeum; color light to dark brown, if somewhat bicolored gaster is darker then mesosoma.

Etymology. The name refers to this species being a southern version of the Mexican species *A. sericea*. **Range.** Guatemala, Costa Rica, Panama.

Biology. Azteca sericeasur occurs in moist to wet forest habitats. Queens establish in live stems of understory trees, near the base. Mature colonies are polydomous and dispersed. Foraging columns extend across low vegetation and on the forest floor, connecting multiple small pavilions made of carton (paper-like material constructed by the ants from masticated plant fibers). Clusters of workers and brood occur in the pavilions, and the pavilions may cover membracids and pink scale insects, which the ants tend. Thus the queen is located in a permanent and well-protected site, while the colony is widely spread in a large number of small ephemeral nests.

Along the Río San Luis near Monteverde, I found workers coming and going from a fissure at the base of a live Xanthoxylem (Rutaceae) at a pasture edge. A colony of Camponotus novogranadensis was using the same entrance, in an apparent case of parabiosis. I have several observations of colonies from the Osa Peninsula. One colony was spread over an area of several square meters, in the dead, hollow core of a live Chimarrhis parviflora (Rubiaceae), in nearby dead sticks, and filling hollow stems of an adjacent Tetrathylacium costaricensis plant (Flacourtiaceae). The Tetrathylacium contained workers, small brood, and mealybugs, but no sexuals or large brood. Small carton nests covered some of the stems and nest entrances. The dead core of the Chimarrhis contained a small pocket of carton, in which I found the grossly distended colony queen and abundant small brood. In another case I found workers streaming through low vegetation. A nest was in a small sapling; the lowest part of the nest was 4m above the ground. There were numerous small cavities and knotholes in the trunk; these were all filled with workers and brood. The lowermost knothole was covered with a carton nest, and the bulk of the workers were in the carton portion. I looked in the carton and in all the knotholes, but I never found a queen. Leanne Tennant, in her study of Tetrathylacium costaricensis in Corcovado, found at least two of her study plants inhabited by A. sericeasur. Males may be produced in large numbers in the small satellite nests. In August, 1982, I observed a series of carton shelters on vine stems at the base of a buttressed tree, and they were packed with hundreds of adult males. Alate queens are few in collections; two were collected in October and one in July. Nest series with alate queens have been taken twice, both in July. I collected a founding queen in the internode of a Cecropia sapling at Estacion Pitilla in the Guanacaste Conservation Area, and Joel Dunn found an incipient colony in a *Cordia bicolor* plant near Monteverde.

The queens are generally setose ants, with abundant fine flexuous setae on most body parts. An exception was the queen from the *Chimarrhis* plant described above. This queen was almost completely devoid of erect setae anywhere on the body, including the tibiae, and the pubescence was sparse and patchy. When collecting from this colony, it took me more than an hour to locate the colony center, chop into the *Chimarrhis* tree, and extract the physogastric queen. This is probably the oldest queen I have examined, the others being alates or foundresses in incipient colonies (and thus more easy to locate and collect). It may be that once queens establish and become sedentary in the middle of a large colony, they gradually become depilated, perhaps through constant grooming by workers.

Comments. This species is very similar to *A. sericea*, differing in the presence of erect setae on the posterior margin of the head. *Azteca sericea* is known from Mexico and Guatemala, where it is associated with myrmecophytic orchids. See further discussion of *A. sericea* in the Addendum.

Additional material examined. COSTA RICA: Alajuela: 11mi N Florencia, 10°31'N, 84°29'W, 6 Jul 1963 (D. H. Janzen) — workers [USNM]; Guanacaste: Cerro El Hacha, Guanacaste Conservation Area, 10°59'N, 85°33'W, 300m, 1988 (unknown) — alate queen [MUCR]; Estacion Pitilla, Guanacaste Cons. Area, 10°59'N, 85°26'W, 700m, 24 Jan 1991 (J. Longino) — dealate queen; *Heredia*: 11km SE La Virgen, 10°20'N, 84°04'W, 500m, 17 Apr 2003 (ALAS) — alate queen; *Limon*: Hamburg Farm, 10°15'N, 83°27'W, 50m, 11 Jul 1925 (F. Nevermann) — workers, alate queens, males; *Puntarenas*: Sirena, Corcovado National Park, 8°29'N, 83°36'W, 5m, numerous collections and dates (J. Longino) — workers, males; same locality, Oct 1990 (Saborio) — alate queen [INBC]; Los Planes, Corcovado National Park, 8°38'N, 83°40'W, 100m, 4 Dec 1981 (J. Longino) — workers; San Pedrillo, Corcovado National Park, 8°37'N, 83°44'W, 5m, 22 Mar 1981 (J. Longino) — workers; Llorona, Corcovado National Park, 8°35'N, 83°42'W, 5m, 2 Jan 1982 (J. Longino) — workers; Rio San Luis, 10°17'N, 84°48'W, 850m, 4 Jun 1990 (J. Longino) — workers; Wilson Botanical Garden, 4km S San Vito, 8°47'N, 82°58'W, 1200m, 23 Mar 1990 (J. Longino) — workers; Rancho Quemado, Osa Peninsula, 8°42'N, 83°33'W, 200m, 1 Oct-30 Nov 1990 (B. Apu) — alate queen [INBC]; same data, 15 Dec 1990 (J. Longino) — queen and workers; Golfito, 8°39'N, 83°09'W, 50m, 23 Jul 1957 (Truxal & Menke) — alate queen [LACM]; Monteverde, 10°18'N, 84°48'W, 1400m, 7 Feb 1999 (J. Dunn) — queen and workers. GUA-**TEMALA**: no specific locality — dealate queen [USNM]. **PANAMA**: Canal Zone: Las Cascadas, cacao plantation, 12 Jul 1924 (G. C. Wheeler) — alate queen, workers.

Figures 3,4A,5,6D.

Azteca tonduzi Forel 1899:114. Syntype workers, males: Costa Rica (Tonduz) [MHNG, MCZC] (examined).

Queen characters. Measurements (n=5): HLA 1.16 (1.10–1.16), HW 1.19 (1.13–1.22), SL 0.76 (0.74–0.77), CI 103 (103–105), SI 66 (64–67).

Palpal formula 5,3; ocelli small; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible with abundant piligerous puncta, setae in puncta fine, subdecumbent, interspaces between puncta smooth and shiny; medial and lateral clypeal lobes at about same level; head subquadrate, posterior margin nearly flat; petiolar node strongly compressed into thin scale at apex; posteroventral petiolar lobe shallow, evenly convex from front to back; scape with sparse erect setae, inconspicuous and only visible at certain angles, about as long as one quarter maximum width of scape; middle and hind tibia with moderately abundant erect setae, fine, inconspicuous, longest about as long as one fifth maximum width of tibia (MTSC 5–10); side of head with 0–5 short erect setae; posterior margin of head with moderately abundant short erect setae; pronotum with erect setae on posterior margin; mesoscutum and scutellum with sparse, short, erect setae, propodeum with similar covering of erect setae or with only a few erect setae concentrated at anterior margin; petiolar node rimmed with erect pubescence and 2–4 longer erect setae, posterior border of sternal lobe of petiole with tuft of short whitish setae; gastral terga with sparse erect setae; entire body light yellow brown to brown.

Worker characters. Measurements (n=7): HLA 0.76 (0.64–0.86), HW 0.77 (0.64–0.90), SL 0.58(0.49–0.62), CI 102 (100–105), SI 76 (72–79).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible smooth and shining, with moderately abundant small piligerous puncta; medial and lateral clypeal lobes at about same level; head with moderately convex sides, strongly cordate posterior margin; in lateral profile promesonotum forming single low convexity; scape with sparse, inconspicuous erect setae, length of setae about one quarter maximum width of scape; mid and hind tibia with moderately abundant erect setae, setae inconspicuous, longest about one quarter to one third maximum width of tibia; side of head with 5 or more fine, short erect setae distributed more or less evenly along side; posterior margin of head with abundant short erect setae; pronotum and mesonotum with abundant erect setae, those on dorsal face of propodeum fewer, shorter, and less erect; color light yellow brown to brown.

Similar species. The queen is distinguishable from other species by its small size. Workers are superficially similar to small workers of *A. velox*, *A. nigra*, *A. flavigaster*, *A. gnava*, and *A. sericeasur*, but differ in the palpal formula being 5,3 instead of 6,4.

Range. Costa Rica.

Biology. Azteca tonduzi is an inconspicuous species which nests in hollow dead stems and sometimes forms carton nests among epiphytes. The types were collected in orchid pseudobulbs (Forel 1899). In Costa Rica I have collected this species multiple times. A dealate queen was in a dead branch of Ficus werckleana, a colony inhabited dead branches of Terminalia catappa along a beach edge, a colony inhabited dead culms of Uniola (sea oats) at the edge of a mangrove swamp, and workers were in small carton nests over coccoid Hemiptera on a branch of Licania. The largest colony I have observed was in a mangrove swamp near the mouth of the Rio Llorona in Corcovado National Park. Workers were very abundant, nesting in bases of several species of bromeliads. On the mangrove branches and trunks there were carton shelters containing brood and coccoid Hemiptera. The colony spread across multiple trees of Avicennia and Laguncularia. Alate queens have been encountered flying during the day and occasionally at blacklights.

Comments. Azteca tonduzi is very similar to the South American A. jelskii (see Addendum).

Additional material examined. COSTA RICA: Heredia: Est. Magsasay, 10°24'N, 83°57'W, 200m, 1–30

Apr 1991 (M. A. Zumbado) — queen [INBC]; La Selva Biological Station, 10°26'N, 84°01'W, 50m, multiple dates and collections (ALAS, J. Longino, R. Vargas C.) — workers, queens [INBC]; 11km ESE La Virgen, 10°21'N, 84°03'W, 300m, multiple dates in 2004 (ALAS) — workers [INBC]; *Limón*: Hitoy Cerere Biol. Reserve, 9°40'N, 83°02'W, 200m, Dec 1990 (G. Carballo) — alate queen [INBC]; *Puntarenas*: Llorona, Corcovado National Park, 8°35'N, 83°42'W, 5m, 16 Jun 1980 and 10 Aug 1982 (J. Longino) — workers; Manuel Antonio Nat. Park, 9°23'N, 84°09'W, 20m, 27 Jul 1985 (J. Longino, P. S. Ward) — queens, males, workers [UCDC]; same locality, 1–30 Jan 1992 and 1–30 Mar 1993 (G. Varela) — queens [INBC]; Carara Biological Reserve, Estación Quebrada Bonita, 9°47'N, 84°36'W, 30m, 24 Jul 1985 (J. Longino) — dealate queen; same locality, 1–30 May 1990 (R. Zuñiga) — queen [INBC]; same locality, 1–30 Jun 1990 (E. Bello) — queen [INBC]; same locality, 25 Jul 1985 (P. S. Ward) — worker [UCDC]; Esterillos Este, 9°31'N, 84°27'W, 0m, 29 Jul 1985 (J. Longino) — worker; Punta Quepos, 9°24'N, 84°10'W, 5m, 4 Jun 1989 (J. Longino) — alate queen; 1.8mi W Rincon, 8°42'N, 83°29'W, 4 Feb 1971 (Donahue & Hogue) — alate queen [LACM]; Curu Wildlife Refuge, 9°47'N, 84°55'W, 5m, 29 Mar 1993 (J. Longino) — workers; Tivives, 9°52'N, 84°41'W, 10m, 10 Mar 1991 (D. M. Olson) — worker.

Azteca velox Forel 1899

Figures 3,4A,5,6A,6B,7,6E,6F.

Azteca velox Forel 1899:108 [new name for Azteca coeruleipennis var. fasciata Pergande 1895, not Emery 1893]. Syntype workers: Mexico, Santiago Iscuintla (Eisen and Vaslit) [NHMW, USNM] (examined). Description of queen, male: Forel 1899:108.

Azteca velox var. nigriventris Forel 1899:109. Syntype workers, queens: Colombia, pied de la Sierra Nevada de Santa Marta, and San Antonio 1000 meters (Forel) [MHNG] (examined). Forel 1906:241. NEW SYNONYMY

Azteca velox var. rectinota Forel 1908a:61. Syntype workers: Costa Rica, Puntarenas (Biolley) [MHNG] (examined). NEW SYNONYMY

Queen characters. Measurements (n=11): HLA 1.72 (1.66–1.81), HW 1.72 (1.63–1.84), SL 1.06 (1.03–1.14, 10), CI 100 (98–103), SI 63 (60–65).

Palpal formula 6,4; ocelli small; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible with small piligerous puncta, setae in puncta short, subdecumbent, interspaces between puncta shiny but faintly microareolate at base to weakly roughened near masticatory margin; medial and lateral clypeal lobes at about same level; head with convex sides, posterior margin not strongly cordate, very shallowly excavate; petiolar node tall, strongly compressed into thin scale at apex; posteroventral petiolar lobe evenly convex from front to back; scape with abundant erect setae, about as long as one half maximum width of scape; middle and hind tibia with abundant erect setae, longest of these about as long as one third maximum width of tibia (MTSC 15–30); sides of head without erect setae; posterior margin of head with erect setae; pronotum with erect setae on posterior margin; mesoscutum, scutellum, and propodeum with abundant erect setae; petiolar node rimmed with erect pubescence and sparse longer erect setae, 1–2 pairs of erect setae extending above apex in profile, posterior border of sternal lobe of petiole with dense layer of erect setae of irregular lengths; gastral terga with sparse long erect setae; light orange brown coloration on clypeus, malar area, antennal fossa, and side of head, variable extent of infuscation on medial and posterior vertex.

Worker characters. Measurements (n=7): HLA 0.98 (0.76–1.26), HW 0.99 (0.77–1.28), SL 0.82 (0.68–1.01), CI 101 (97–102), SI 84 (78–89).

Palpal formula 6,4; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible smooth and shining, with moderately abundant small piligerous puncta, setae in puncta short, erect, larger puncta with long setae near masticatory margin; medial and lateral clypeal lobes at about same level; head with convex sides, strongly cordate posterior margin; in lateral profile promesonotum forming single convexity; scape with abundant erect setae, length of setae about one half maximum width of scape; mid and hind

tibia with abundant erect setae, longest setae about one half maximum width of tibia; side of head with about 5 erect setae on malar area, short erect setae variably present along entire side of head; posterior margin of head with abundant erect setae; pronotum, mesonotum, and dorsal face of propodeum with abundant long erect setae; anterior and anterolateral portions of head light yellow brown, variable extent of darker brown on medial vertex and posteriorly, mesosoma and gaster brown.

Similar species. Queens of *A. quadricephala* have a more quadrate head shape and are less narrowed anteriorly (Fig. 6B). Queens of *A. nigra* have a somewhat shorter head and the ventral petiolar lobe is deeper and ends before the posterior tergal lobe. Queens of *A. flavigaster* have smaller heads (Fig. 6A).

Range. Mexico to Colombia and Venezuela.

Biology. Azteca velox is a common species in a wide variety of habitats. It occurs most abundantly in seasonally dry areas, synanthropic habitats, and beach margins. Workers are common diurnal surface foragers. They are generalized scavengers and frequently visit extrafloral nectaries. The nests are polydomous, dispersed in multiple plant cavities. The cavities can be in live or dead stems. Colonies have also been associated with myrmecophytic orchids: *Epidendrum bicornutum* in Costa Rica (Forel 1906) and *Caularthron bilamellatum* in Panama (Fisher 1992). Colonies also develop, to variable extent, carton nests as extensions of nests in plant cavities.

In Santa Rosa National Park, Costa Rica, I observed several colonies. An incipient colony was in the hollow live stems of an understory shrub, *Cassia hayesiana* (Fabaceae). The total stem length of the occupied space was about 1m, with inner cavity diameter of 0.5–1.0cm. There was one physogastric queen and no other reproductives. At two entrance sites they had built small globular carton dwellings, 2cm across and packed with workers and brood. The section of hollow stem near the queen was entirely plugged with a mass of eggs and young brood. The nest also contained a *Microdon* (Syrphidae) puparium.

A second incipient colony was in a shaded *Cordia alliodora* tree, a myrmecophyte usually occupied by *Azteca pittieri*. A lone physogastric queen was in one of the internodes, and workers and brood were dispersed in other nodes of the tree. Some of the *Cordia* nodes had small carton nests built on the surface.

In the forest at Santa Rosa I also observed a parabiotic association between *Azteca velox* and *Camponotus atriceps*. Workers of *Azteca* and *Camponotus* were running in and out of the same fissure in a tree trunk, showing no aggressiveness toward each other.

I observed a colony near Punta Quepos, at the edge of a small patch of degraded forest surrounded by pasture. About 4m of trailside had 10–20cm long carton nests scattered in the vegetation, on larger stems. I scraped one nest into a plastic bag—it contained a very high density of workers but no brood. A dead branch, in contrast, was packed with brood, males, and alate females. The dead branch was 3cm diameter with a 1–1.5cm diameter continuous internal cavity. The ants had constructed rather regular perforated platforms inside the branch, every 1–1.5cm, making the inside look much like a *Cecropia* branch interior.

Comments. Neither the morphological definition of this species nor the use of the name A. velox are very well supported. The differences among A. sericeasur, A. velox, A. nigra, A. quadraticeps, and A. flavigaster are subtle. I base the differences among the species mainly on the queens. The Azeca velox queen is smaller than A. sericeasur, larger than A. flavigaster, with more rounded head than A. quadraticeps, and longer head than A. nigra. These conclusions are based on very small sample sizes of available queens. Workers of A. flavigaster have a distinctive color pattern (contrasting yellow gaster and brown mesosoma), and the workers of A. quadraticeps are unknown. The workers of A. sericeasur, A. velox, and A. nigra are very similar. The largest workers of A. velox and A. nigra are always relatively small. In the field even large populous colonies are entirely composed of small workers. In contrast, populous colonies of A. sericeasur (and A. instabilis, which is hard to distinguish from this group in the field) have much larger workers in amongst the small workers. Azteca velox and A. nigra workers differ slightly in scape length, with A. velox having proportionately shorter scapes. Azteca nigra appears to be a wet forest version of A. velox, having similar nesting behavior of using a combination of dead sticks and carton nests, but with much greater development of the carton nests into ant gardens.

The types of *A. velox* are a few small workers from Mexico, collected in the late 1800's. They have erect setae on the posterior margin of the vertex, distinguishing them from *A. sericea*, the size is small, separating them from *A. sericeasur*, and the scapes are relatively short, separating them from *A. nigra*. The fact that the species I am calling *A. velox* is common in the open, seasonally dry habitats of Santa Rosa National Park, and Santa Rosa has many ant species that are widespread in similar habitats from there to southern Mexico, further strengthens the identity.

Forel (1899) discovered the Pergande homonym *fasciata* and proposed the replacement name *velox*. At the same time he described the queen and male, based on additional material from Costa Rica (Tonduz); Panama, Bugaba (Champion); and Colombia, pied de la Sierra Nevada de Santa Marta (Forel). It was not clear from which specimens he described the various castes. He noted that the species lived in hollow trunks, including fallen dead trees, and that it was uncertain whether carton construction was used for the nest. Some of this non-Pergande material has been incorrectly labeled as types and distributed to museums (MCZC, AMNH). The USNM, however, has true syntypes from Pergande's original collection (type #4481), in the type collection.

In the same paper Forel described the subspecies *nigriventris*, based on his material from the Santa Marta region of Colombia. The syntypes included queens. I examined this material and it matched my concept of *A. velox*. Forel (1906:241) later identified additional Costa Rican material as *nigriventris*. This material was collected by Biolley in Esparza, from pseudobulbs of *Epidendrum bicornutum*, with the note "in constant symbiosis." I examined this material and it matches my concept of *A. velox*.

Additional material examined. COSTA RICA: Alajuela: R. N. V. S. Caño Negro, 10°53'N, 83°12'W, 20m, 5–28 Feb 1995 (K. F. Flores) — adult queen [INBC]; Guanacaste: Headquarters, Santa Rosa Nat. Park, 10°50'N, 85°37'W, 300m, 13 Jul 1985 (J. Longino) — workers; Bosque Humedo, Santa Rosa Nat. Park, 10°51'N, 85°37'W, 300m, 12 Jul 1985 (J. Longino) — dealate queen, workers; oak forest, Santa Rosa Nat. Park, 10°52'N, 85°36'W, 300m, 15 Jul 1985 (J. Longino) — dealate queen, workers; Guacimo, Tempisque, 20 Jan 1937 (A. Alfaro) — worker [USNM]; Playa Ostional, 9°59'N, 84°18'W, 5m, 13–16 Jun 2004 (B. Gamboa, D. Briceño, M. Moraga, Y. Cárdenas) — queen [INBC]; Limón: Pto Viejo de Limon, 9°40'N, 82°45'W, 5m, 21 Mar 1987 (J. Longino) — worker; *Puntarenas*: Sirena, Corcovado National Park, 8°29'N, 83°36'W, 5m, multiple dates and collections (J. Longino) — workers, males; Llorona, Corcovado National Park, 8°35'N, 83°42'W, 5m, 2 Jan 1982 and 21 Mar 1981 (J. Longino) — workers; Manuel Antonio Nat. Park, 9°23'N, 84°09'W, 20m, 27–28 Jul 1985 (J. Longino) — queen, worker; Punta Quepos, 9°24'N, 84°10'W, 5m, 4 Jun 1989 (J. Longino) — queens, males, workers; Rancho Quemado, Osa Peninsula, 8°42'N, 83°33'W, 200m, 15 Dec 1990 (J. Longino) — workers; Golfito, 8°39'N, 83°09'W, 50m, 15 Aug 1957 (A. Menke) — dealate queen [LACM]; same locality, Jan 1999 (P. Hanson) — worker; Esparza, Feb 1905 (Biolley) — alate queens, workers [MHNG]; Curu Wildlife Refuge, 9°47'N, 84°55'W, 5m, 28 Mar 1993 (J. Longino) — worker; PAN-AMA: Canal Zone: Barro Colorado Island, 9°09'N, 79°51'W, 100m, 5 Apr 1987 (B. Fisher) — queen, male, worker [LACM]; VENEZUELA: Aragua: Rancho Grande, 10°21'N, 67°41'W, 1100m, 1945 (W. Beebe) dealate queen [LACM].

Azteca xanthochroa (Roger 1863)

Figures 2,3,4A,5,6D,7.

Liometopum (?) xanthochroum Roger 1863:167. Holotype queen: Mexico.

Iridomyrmex xanthochrous (Roger); Mayr 1866:497 (part) [Mexican workers described; later found to be a different species].

Liometopum instabile; Mayr (not Smith) 1877:870 (part) [incorrectly synonymized under instabile].

Azteca instabilis var. xanthochroa (Roger); Emery 1893:137 (part) [reinstated].

Azteca xanthochroa (Roger); Emery 1896b:2 [description of Costa Rican workers; exclusion of Mexican workers

described in Mayr 1866]; Wheeler 1942:248 [description of workers from Guatemala].

Azteca xanthochroa var. costaricensis Wheeler 1942:248 [n.nov. for Costa Rican workers described by Emery 1896b:2 as xanthochroa]. Lectotype worker: Costa Rica, Limón province, Jimenez (Alfaro) [label: "Jimenez, C.R. v.95"] [NHMW] (examined). Synonymy by Longino 1991b:1594.

Queen characters. Measurements (n=10): HLA 2.42 (2.37–2.65), HW 1.97 (1.90–2.17), SL 1.32 (1.25–1.37), CI 82 (79–83), SI 54 (51–56).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible smooth and shining or very faintly sculptured, with sparse small piligerous puncta, setae in puncta very short, appressed and little larger than width of puncta, larger puncta with long setae near masticatory margin; medial and lateral clypeal lobes at about same level (medial lobe not projecting anteriorly); head quadrate, sides subparallel to slightly diverging, strongly cordate posteriorly, with angulate posterolateral margins; petiolar node tall, triangular, acute; posteroventral petiolar lobe evenly convex, shallow, not strongly developed; scape with abundant erect setae, about as long as one half maximum width of scape; middle and hind tibia with abundant erect setae, longest of these one half to two thirds maximum width of tibia (MTSC 25–35); sides of head with 1–2 erect setae near mandibular insertions, absent elsewhere; posterior margin of head with abundant short erect setae; pronotum with abundant long setae on posterior third; mesoscutum with anterior one half to one third usually devoid of erect setae, posterior two thirds to one half with abundant setae, occasionally erect setae sparse to nearly absent throughout; scutellum with abundant long setae; propodeum with sparse erect setae, occasionally bare; petiolar node with 0–6 erect setae, 0–4 long setae and more abundant short, fine setae on posteroventral lobe; all gastral terga with abundant erect setae; color orange.

Worker characters. Measurements (n=4): HLA 1.59 (1.40–1.69), HW 1.41 (1.30–1.49), SL 1.05 (0.95–1.08), CI 89 (87–93), SI 67 (62–68).

Palpal formula 5,3; middle and hind tibia with prominent pectinate apical spur; dorsal surface of mandible smooth and shining, with sparse small piligerous puncta, setae in puncta very short, appressed and little larger than width of puncta, larger puncta with long setae near masticatory margin; medial and lateral clypeal lobes at about same level; head with convex sides, strongly cordate posterior margin; mesosoma in lateral profile with promesonotum forming a single broad convexity, or mesonotum forming a distinct, somewhat more strongly produced convexity; metanotal groove broad; petiole in profile with node larger than sternal lobe, perpendicular distance from tergosternal suture to apex of node greater than distance to ventral margin of sternal lobe (in contrast to *A. constructor*, on which the petiolar node is smaller relative to sternal lobe); scape with abundant erect setae, length of setae about one half maximum width of scape; mid and hind tibia with abundant erect setae, longest setae about one half maximum width of tibia; sides of head with erect setae short, sparse to absent; posterior margin of head with abundant short erect setae; pronotum with abundant long erect setae; mesonotum with setae absent on anterior half, grading to longer setae on posterior half; dorsal face of propodeum with very short setae, grading into pubescence; color brown to mottled orange brown.

Similar species. The queens of *A. xanthochroa* are very distinctive and not easily confused with any other species. Workers of *A. constructor* and *A. xanthochroa* are very similar. Large workers of *A. constructor* retain a chocolate brown color, while large workers of *A. xanthochroa* become more mottled orange. The petiolar node of *A. constructor* workers is relatively low, while the posteroventral lobe is relatively deep and strongly convex. Workers of *A. xanthochroa* are the reverse, with relatively taller node and shallower ventral lobe.

Range. Mexico to Costa Rica.

Biology. The taxonomy and biology of *A. xanthochroa* is reviewed in Longino (1989b, 1991a, b). The species is an obligate *Cecropia* ant. It is one of the most common *Cecropia* ants in Costa Rica, occurring in wet to moist forest habitats and extending to relatively high elevations (up to 1400m). Mature colonies occupy a single carton nest in the bole of the tree. All larvae and alate sexuals are concentrated in this single nest. Branch tips, which all communicate internally with the carton nest, contain only workers and Hemiptera. Workers of this species are very aggressive, and respond to any disturbance by pouring out of branch tips. A

distinctive feature of this species is that workers maintain a vertical fissure near the base of the tree, far below the carton nest. Workers can move freely inside the trunk from the nest to this fissure. Thus, when the tree is disturbed at the base, workers suddenly appear on the trunk at ground level (Longino 1991a).

Material examined. See Longino (1991b).

Addendum

Azteca aurita group

Diagnosis. Queen and worker: Palpal formula 4,3; middle and hind tibia lacking apical spur; anteromedial border of clypeus strongly convex and extending well beyond anterolateral clypeal lobes, HLB/HLA > 1.04. Queen: general body size small, similar in size to major workers; integument extremely smooth and shining, glass-like, with appressed pubescence extremely dilute; pilosity, when present, a stubble of short, stiff, fully erect setae; petiole bluntly subpyramidal to bilobed, never flat and scale-like.

Worker: Head always cordate, with variable tendency for posterolateral portions of occipital border to be drawn out into angular projections; scape, tibiae, lateral and posterior margins of head, and mesosomal dorsum devoid of setae; mandibles either of two forms, both unique to the species group: (1) dorsal surface strongly flattened, densely and finely striate, mat, or (2) dorsal surface convex and shiny, masticatory margin strongly sinuous, with large, projecting apical tooth; petiole as in queen.

Biology. Members of the *A. aurita* species group are widespread but rare. They construct carton nests on the branches of trees, nests which are always bare of epiphytes (they do not form ant gardens).

The diminutive and highly derived queens of the group suggest a social parasitism syndrome (Forel 1928, Hölldobler and Wilson 1990). Species in the *A. aurita* group have queens that are about the same size as workers, and the gaster is very small in proportion to the rest of the body. This contrasts with more typical *Azteca* species, which have queens much larger than workers and with large gasters, presumably full of resources for founding new colonies on their own. It is difficult to imagine the small *aurita*-group queens doing so, and a more likely scenario is for *aurita*-group queens to insinuate themselves into established colonies of other species, killing the host queen and having the host workers rear the parasites' offspring. It is not even clear how they function once established; *aurita*-group colonies are enormous, and it seems paradoxical that such small queens could generate sufficient eggs to populate them. The morphology of *A. nanogyna* carries this paradox to an extreme, and a possibility in this case is that *A. nanogyna* is a workerless social parasite.

The *A. aurita* group is perhaps the most circumscribable set of species in the genus, with a distinctive suite of characters. The reduced palpal segmentation and the lack of tibial spurs are both unique to the group and, being losses, are likely apomorphic traits that support the monophyly of the group. The group is most similar to *A. trigona* and *A. chartifex*. Shared worker traits include reduced pilosity, cordate head shape, and the construction of large, pendant, epiphyte-free carton nests. Although many worker series of *A. trigona* have shiny mandibles, a few have faint aciculate sculpture. Also, the mandibles are somewhat flattened, approaching the condition in the *A. aurita* group. *Azteca trigona* workers retain at least a few erect setae on the mesosoma, and often a few setae occur on the tibiae. The queens of the two groups could not be more different. Queens of *A. trigona* are much larger than workers, have broadly cordate heads much wider than long, a mat to sublucid integument, a strongly flattened and scale-like petiole, and no stubbly pilosity.

Knowledge of the taxonomy and natural history of this group is in its incipient stages, but what we do know suggests that additional study would be highly rewarding.

Key to A. aurita group queens

1.	Color uniform orange; CI > 80
-	Color uniform brown; CI < 80
2.	Pilosity absent on posterior and posterolateral borders of head, dorsum of mesosoma, petiole, and gaster
	(tibiae, scape, and all of face and mandibles below level of lower margin of eyes with dense, short, white
	erect pilosity); HW < 1.15mmaurita
-	Short erect pilosity present on all margins of head and on dorsum of mesosoma, petiole, and gaster; HW >
	1.15mm
3.	Dense, short, erect pilosity on scape and tibiae; head relatively narrower (CI < 92) pilosula
-	Scape and tibiae lacking erect pilosity; head relatively broader (CI > 92)lallemandi
4.	Gastral dorsum lacking erect setae; HLA > 1.35mmschimperi
-	Gastral dorsum with erect setae; HLA < 1.35mm
5.	HLA about 1.3mm
-	HLA about 0.86mm

Key to A. aurita group workers (the worker of A. nanogyna is unknown)

Azteca aurita Emery 1893

Azteca aurita Emery 1893:346. Holotype queen: Brazil, Pará, Braganza (Oberthür) [MCSN] (examined).

Azteca lacrymosa Forel 1899:116 (part). Syntype workers: Costa Rica (Tonduz); and Colombia, Sierra Nevada de Santa Marta, Hac. la Esperanza (Lallemand, Forel) [MHNG, MCZC] (examined; Costa Rican series is *A. pilosula*, Colombian series is *A. aurita*). Incorrect synonymy under *A. aurita* Emery: Forel 1906:237.

Azteca lacrymosa race silvae Forel 1899:116. Syntype workers: Brazil, Amazonas, Pará (Göldi) [MHNG, MCZC] (examined). NEW SYNONYMY

Azteca aurita r. silvae Forel: Forel 1906:237.

Queen characters. Measurements (n=2): HLA 1.28 (1.25–1.30), HW 1.11 (1.10–1.11), SL 1.21 (1.18–1.24), CI 87 (85–88), SI 95 (94–95).

Palpal formula 4,3; middle and hind tibia lacking apical spur; mandible strongly flattened, apical tooth much longer than penultimate tooth; medial clypeal lobe strongly convex and protruding, extending well beyond lateral clypeal lobes; head quadrate, sides flat and diverging posteriorly, posterior margin strongly angulate laterally, deeply excavate medially; petiolar node short, broadly triangular; scape, mandible, lateral margin of head anterior to compound eye, and legs covered with uniform vestiture of short, dense, white pilosity; lateral margin of head posterior to eye, posterior margin of head, mesosomal dorsum, petiolar dorsum, and gaster lacking erect setae; entire body orange, with smooth, highly polished and reflective surface.

Worker characters. Measurements (n=2): HLA 1.22 (1.11–1.32), HW 1.21 (1.11–1.30), SL 1.11 (1.03–1.19), CI 99 (98–100), SI 92 (90–93).

Currently indistinguishable from A. pilosula.

Range. Brazil, Colombia.

Additional material examined. BRAZIL: *Pará*: Santarem — worker [MHNG]; Pará (W. M. Mann) [LACM]; **COLOMBIA**: no specific locality (Santschi coll.) — queen [NHMB]; *Magdalena*: Esperanza (Forel) — workers, headless queen [MHNG] [*A. lacrymosa* syntypes].

Azteca lallemandi Forel 1899

Azteca lallemandi Forel 1899:119. Syntype workers: Colombia, Sierra Nevada de Santa Marta, Naranjo (Forel) [MHNG, MCZC] (examined).

Azteca lanuginosa subsp. pruinosa Mann 1916:472. Syntype workers: Brazil, Rondonia, Rio Madeira, Abuna (Mann & Baker) [MHNG] (examined) NEW SYNONYMY.

Queen characters. Measurements (n=4): HLA 1.27 (1.22–1.32), HW 1.22 (1.21–1.30), SL 1.18 (1.13–1.27), CI 99 (95–99), SI 94 (90–96).

Palpal formula 4,3; middle and hind tibia lacking apical spur; mandible strongly flattened, apical tooth much longer than penultimate tooth, dorsal surface smooth and shiny, pubescent; medial clypeal lobe strongly convex and protruding, extending well beyond lateral clypeal lobes; head quadrate, sides flat and diverging posteriorly, posterior margin strongly angulate laterally, deeply excavate medially; petiolar node short, bluntly triangular; posteroventral petiolar lobe deep, strongly convex from front to back, laterally compressed and tectiform; lateral and posterior margins of head, mesosomal dorsum, dorsal and ventral margins of petiole, and gaster covered with uniform vestiture of short, dense, white pilosity; scape and legs lacking erect setae; entire body orange, with smooth, highly polished and reflective surface.

Worker characters. Measurements (n=2): HLA 1.22 (1.11–1.32), HW 1.21 (1.11–1.30), SL 1.11 (1.03–1.19), CI 99 (98–100), SI 92 (90–93).

Compared to *A. pilosula* and *A. aurita*, head relatively broader (CI > 105 versus < 106), posterolateral margins of vertex more rounded and cordate, not as angulate. Compared to *A. pilosula*, *A. lallemandi* has a deeper, more convex posteroventral petiolar lobe.

Range. Brazil (Rondonia), Colombia, Panama.

Biology. The type specimens were collected in a carton nest on a *Cecropia* trunk.

Additional material examined. COLOMBIA: *Magdalena*: Rio Frio, 28 Sep 1926 (G. Salt) — dealate queen [MCZC]; same locality, 1 Sep 1927 (G. Salt) — adult workers [MCZC]; **PANAMA**: *Canal Zone*: Barro Colorado Island, 9°09'N, 79°51'W, 100m, Jan 1960 (W. L. Brown & E. S. McCluskey) — queens [MCZC]; same locality, 4 Jun 1978 (Silberglied & Aiello) — queen [USNM]; same locality, Jan 1992 (M. Kaspari) — queen [MKC]; *Colon*: Est. Biol. Galeta, 9°24'N, 79°52'W, 10m, 23 Sep 1999 (J. Dunn) — worker.

Azteca lanuginosa Emery 1893

Azteca lanuginosa Emery 1893:341. Holotype worker: Brazil, S. Catharina (Schmalz) [MCSN] (examined). Description of queen, male: Forel 1908b:389.

Queen characters. Measurements (n=1): HLA 1.30, HW 0.96, SL 0.90, CI 74, SI 69.

Similar to the queen of *A. schimperi*, but smaller and much more pilose throughout; setae more dense on legs and scapes, abundant on mesosomal dorsum, petiolar node, and gaster.

Worker characters. Measurements (n=2): HLA 1.25 (1.15–1.35), HW 1.24 (1.14–1.34), SL 0.89 (0.82–0.95), CI 99 (99–99), SI 71 (70–71).

Head shape, mandible shape and sculpture, and pilosity very like *A. schimperi*, but pubescence thicker, woolier; color uniformly brown.

Range. Southern Brazil.

Biology. The Ehrhardt series described by Forel (1908b) was from a carton nest on a *Cecropia* tree.

Additional material examined. BRAZIL: *Santa Catarina*: dist. Jaraguá, Itapocú river basin, 11 Dec 1907 (Ehrhardt) — queens, males, workers [MHNG]; *Sao Paulo*: Ypiranga, E. S. Paulo, "Museu 1906, N. 2394" — worker [MHNG]; "S. Paulo" (von Ihering) — workers [MHNG].

Azteca nanogyna new species

Figures 4A,9.

Holotype queen: Costa Rica, Prov. Guanacaste, Estacion Maritza, Guanacaste Conservation Area, 10°58'N, 85°30'W, 600m, 23 Feb 2003 (J. S. Noyes) [INBC, specimen code JTLC000004288]

Measurements of holotype. HLA 0.86, HLB 0.91, HW 0.64, SL 0.58, EL 0.22, OC 0.04, MTSC 6 (very fine, short).

Diagnosis. *Azteca nanogyna* is a member of the *A. aurita* group and has the smallest queen of any known species in the genus.

Queen characters. Palpal formula 4,3; middle and hind tibia lacking apical spur; dorsal surface of mandible smooth and shiny, pubescent; medial clypeal lobe strongly convex and protruding, extending well beyond lateral clypeal lobes; head subrectangular, somewhat swollen between ocellar region and compound eye, posterior margin a smoothly rounded excavation; petiolar node bluntly triangular; posteroventral petiolar lobe very low, very shallowly convex, ending posteriorly in a somewhat abrupt shelf, rising steeply to tergosternal suture, leaving small posterior rim on sternite; entire body covered with uniform vestiture of sparse, white, suberect pubescence; scape, all margins of head, legs, petiole, and first gastral tergum with evenly distributed short, white, erect setae emerging above pubescence, similar but sparser setae on mesosomal dorsum; body dark brown becoming lighter brown on mandibles, legs; body with smooth, highly polished and reflective surface.

Etymology. The name refers to the small size of the queen.

Range. Costa Rica.

Biology. The single specimen was collected in tropical moist forest. John Noyes collected the specimen using a screened sweep net.

Comments. This is by far the smallest queen known in the genus *Azteca*. The color and narrow head clearly ally it with *A. lanuginosa* and *A. schimperi*.

Azteca pilosula Forel 1899 new status

Figures 2,3,4A.

Azteca aurita race pilosula Forel 1899:115. Syntype queens: Costa Rica (Tonduz); and Panama, Bugaba (Champion) [MHNG, MCZC] (examined, 1 MHNG Costa Rican queen here designated LECTOTYPE). Incorrect synonymy under A. aurita Emery: Forel 1912:54.

Azteca lacrymosa Forel 1899:116 (part). Syntype workers: Costa Rica (Tonduz); and Colombia, Sierra Nevada de Santa Marta, Hac. la Esperanza (Lallemand, Forel) [MHNG, MCZC] (examined; MHNG Costa Rican worker here designated LECTOTYPE). Incorrect synonymy under A. aurita Emery: Forel 1906:237. NEW SYNONYMY

Queen characters. Measurements (n=2): HLA 1.32 (1.31–1.34), HW 1.19 (1.18–1.19), SL 1.27 (1.24–1.30), CI 90 (89–90), SI 96 (92–99).

Palpal formula 4,3; middle and hind tibia lacking apical spur; mandible strongly flattened, apical tooth much longer than penultimate tooth, dorsal surface shiny, smooth basally, with elongate puncta and grooves near masticatory margin, densely covered with suberect setae; medial clypeal lobe strongly convex and protruding, extending well beyond lateral clypeal lobes; head quadrate, sides flat and diverging posteriorly, posterior margin strongly angulate laterally, deeply excavate medially; petiolar node short, broadly triangular; posteroventral petiolar lobe very low, hardly developed; almost entire body —scape, flagellum, mandible, margins and dorsum of head, mesosoma, legs, petiole, and gaster—covered with uniform vestiture of short, dense, white pilosity, somewhat sparser on gastral terga; entire body orange, with smooth, highly polished and reflective surface.

Worker characters. Measurements (n=2): HLA 1.35 (1.26–1.45), HW 1.39 (1.26–1.52), SL 1.07 (0.92–1.22), CI 103 (100–105), SI 79 (73–84).

Palpal formula 4,3; middle and hind tibia lacking apical spur; mandible strongly flattened, apical tooth much longer than penultimate tooth, dorsal surface with longitudinal, finely acicular sculpture, dull; medial clypeal lobe strongly convex and protruding, extending well beyond lateral clypeal lobes; head with moderately convex sides, subangulate posterolateral margins, posterior margin in the form of a shallow "V;" in lateral profile pronotum gently sloping and weakly convex, mesonotum more strongly convex and with profile asymmetrical, with highest point shifted forward, long sloping posterior face dropping to depressed basal face of propodeum; scape, tibiae, and mesosoma with dense white pubescence but no erect setae; side of head with no erect setae, posterior margin with sparse, very short erect setae grading into white pubescence; petiolar node with rim of white pubescence, about 6 longer erect setae on anterior face and apex, posteroventral margin with dense erect pubescence; head clear orange brown, mesosoma, legs, and gaster darker red brown.

Range. Costa Rica, Panama, Colombia.

Biology. *Azteca pilosula* nests in large exposed carton nests. The Tonduz collection from Costa Rican was an "arboreal nest," and Forel's Colombian collection was from a large carton nest. In Corcovado National Park in Costa Rica I found a large carton nest on a horizontal log over a trail. Workers from this nest were tending scale insects on the spathe of a nearby aroid.

Comments. Tonduz's Costa Rican collection was most likely a single nest series, the queens of which were described as *A. pilosula* and the workers as *A. lacrymosa*. Forel later synonymized both under *A. aurita*. However, *A. pilosula* and *A. aurita* are distinct. The queen of *A. pilosula* has short, white, dense setae on all head margins, appendages, and dorsa of mesosoma, petiole, and gaster. *Azteca aurita* has similar short dense pilosity on the appendages and anterior head, but lacks it on the posterior and posterolateral margins of head and the dorsa of mesosoma, petiole, and gaster.

Additional material examined. COSTA RICA: *Puntarenas*: Sirena, Corcovado National Park, 8°29'N, 83°36'W, 5m, 28 Jun 1980 (J. Longino) — workers; **PANAMA**: *Canal Zone*: Monte Lirio [9°14'N, 79°15'W], 18 Nov 1911 (W. M. Wheeler) — workers [MCZC].

Azteca schimperi Emery 1893

Figures 2,3,4A,5.

Azteca schimperi Emery 1893:340. Syntype workers: Costa Rica, Alajuela [10°01'N, 84°13'W, 1100m] (Alfaro) [MCSN, MCZC, MHNG] (examined). Description of male, queen: Forel 1908b:387.

Azteca fiebrigi Forel 1909:261. Syntype workers, queens, males: Paraguay, San Bernardino (Fiebrig), in carton nest [MHNG] (examined). NEW SYNONYMY

Azteca lanuginosa var. clariceps Santschi 1933:121. Syntype workers: Argentina, Pilcomayo, Tacaaglé (R. José Zurflüh), no. 1954 [NHMB] (examined). NEW SYNONYMY

Azteca muelleri var. pallida Stitz 1937:135. Syntype workers: Mexico, Veracruz, Misantha [Misantla?] (Gugelmann) [ZMHB] (examined). NEW SYNONYMY

Queen characters. Measurements (n=3 queens from Colombia, Brazil, and Paraguay): HLA 1.44 (1.40–1.47), HW 1.05 (1.04–1.06), SL 0.97 (0.94–1.01), CI 72 (71–76), SI 69 (65–69).

Palpal formula 4,3; middle and hind tibia lacking apical spur; apical tooth of mandible about twice as long as penultimate tooth, dorsal surface shiny, smooth, with sparse piligerous puncta; medial clypeal lobe strongly convex and protruding, extending well beyond lateral clypeal lobes; head rectangular, sides parallel and flat, posterolateral margins subangular but rounded, posterior margin a moderately developed V-shaped impression; petiolar node triangular; posteroventral petiolar lobe developed, moderately convex from front to back, laterally compressed and tectiform; scape, sides and posterior margin of head with dense vestiture of short, erect setae; femora with similar setae but erect setae nearly absent from outer margins of middle and hind tibia; pronotum and mesoscutum with these short setae very sparse, more abundant on scutellum and propodeum; petiolar node and ventral margin of petiole with abundant short setae; gaster devoid of erect setae; entire body red brown, with smooth, highly polished and reflective surface.

Worker characters. Measurements (n=4): HLA 1.42 (1.16–1.51), HW 1.41 (1.18–1.45), SL 0.94 (0.85–1.01), CI 99 (96–102), SI 68 (64–73).

Palpal formula 4,3; middle and hind tibia lacking apical spur; mandible of typical thickness at base, with microareolate sculpture, dull, becoming smooth and shiny, somewhat flattened toward masticatory margin; masticatory margin concave, curving toward enlarged apical tooth, apical tooth much larger than penultimate tooth; medial clypeal lobe strongly convex and protruding, extending well beyond lateral clypeal lobes; head with convex sides, strongly cordate posterior margin; in lateral profile promesonotum forming single convexity, evenly convex to middle of mesonotum, posterior mesonotum drops steeply to depressed basal face of propodeum; petiolar node somewhat pillow-shaped, blunt and weakly bilobed apically, posteroventral lobe shallow, weakly convex from front to back, ending posteriorly in a somewhat abrupt shelf, rising steeply to tergosternal suture, leaving distinct posterior rim on sternite, laterally very strongly compressed, forming sharp median carina (this character less developed on South American material); scape, entire head capsule, mesosoma, legs, petiolar node, and gastral dorsum with appressed pubescence but completely lacking erect setae; color clear yellow orange to red brown, face shining.

Range. Mexico to Argentina.

Biology. This species makes large external carton nests. I have observed four nests, three in Costa Rica and one in Panama, and all have been in *Cecropia* trees (*C. peltata*, *C. obtusifolia*, and *C. longipes*). Benson (1985) also observed *A. schimperi* in *Cecropia* trees. However Forel (1908b), describing the queen and male from a collection from Bahia, Brazil, explicitly stated that the carton nest was perched on the branches of a tree that was not *Cecropia*.

The three nests I have seen in Costa Rica were all at the edges of roads in highly human altered landscapes (pasture edges, coffee farms) in seasonally dry areas. The globular carton nests are very conspicuous on the highly visible branches of *Cecropia* trees, and in my studies of *Cecropia* in Costa Rica I always looked for them. Yet I have only seen these three over many years of work in Costa Rica. I have never been able to examine a nest closely, but I have been able to observe the base of the trees in which they occurred. In one case workers were foraging not only on the base of the tree but also on surrounding low vegetation. In another case, on a tree with stump sprouts at the base, workers were swarming over the sprouts but not actually entering the internodes. These observations contrast with typical *Cecropia* ants, which never forage off the host plant and usually enter and occupy any sprouts at the base of the tree. Thus *A. schimperi* seems to occupy *Cecropia* trees more "lightly" than the dominant obligate *Cecropia* ants.

As suggested in the introduction to the species group, A. schimperi could be a temporary social parasite of *Cecropia* ants, usurping an existing *Azteca* colony as a means of establishing its own. Such a scenario might

explain the somewhat less specialized use of *Cecropia* by *A. schimperi*; it may be a specialist on *Cecropia* ants rather than *Cecropia* trees.

Comments. Azteca schimperi has a very broad range, vying with A. alfari for the Azteca species with the largest range. It is a relatively distinctive species with little discernable variation over the range; specimens from Argentina and Paraguay look very like specimens from Central America and Mexico.

Additional material examined. BELIZE: Manatee (J. D. Johnson) — workers; BRAZIL: Amazonas: Manaus, 3°07'S, 60°02'W, 14 Apr 1982 (INPA) — alate queen, male, worker; same data (Bequaert) — worker [LACM]; Bahia: "Bahia" — worker, male [MCSN, MHNG]; Federal District: Brasilia, 15°47'S, 47°55'W (H. C. Morais) — worker; COLOMBIA: Magdalena: El Campano, 11°07'N, 74°06'W, 1300m, 13 Aug 1985 (J. Longino, P. S. Ward) — alate queens [UCDC]; COSTA RICA: Alajuela: 3km S Naranjo, 10°04'N, 84°23'W, 1000m, 12 Jul 1991 (J. Longino) — workers; Guanacaste: PanAm Hwy, 5km S La Cruz, 11°02'N, 85°38'W, 200m, 11 Jul 1991 (J. Longino) — workers; same locality, 17 Jan 1991 (F. Joyce) — workers; Puntarenas: Guaria, rd to Monteverde, 10°14'N, 84°51'W, 700m, 23 Jun 1992 (J. Longino) — workers; GUATEMALA: Patulul, 2 Jan 1912 (W. M. Wheeler) — worker; Escuintla: Escuintla [14°18'N, 90°47'W], 28–30 Dec 1911 (W. M. Wheeler) — workers; GUYANA: no specific locality — workers [MHNG]; PANAMA: Canal Zone: Barro Colorado Island, 9°09'N, 79°51'W, 100m, 3 Jul 1997 (J. Longino) — workers; PARAGUAY: Parana R. (Fiebrig) — workers, queens [LACM].

Undetermined A. aurita group workers

Azteca trigona; Emery 1896a:3 (not Emery 1893). Workers: Panama, Golfo de Darién (Festa) [MHNG] (examined) (description of workers misidentified as A. trigona; identified as A. aurita by Forel 1906:237).

I examined these specimens but did not measure them. My original notes say that the specimens were very similar to my collection of *A. pilosula* from Corcovado National Park.

Azteca jelskii Emery 1893

Azteca jelskii Emery 1893:338. Syntype workers: French Guiana, Cayenne (Jelski) [MCSN] (examined). Azteca tonduzi var. columbica Forel 1912:51. Syntype workers: Colombia, Ouriheka [=Orihueca] near Rio Frio (Forel) [MHNG] (examined). NEW SYNONYMY

Range. Northern South America to Peru, Bolivia.

Biology. The types of *columbica* were collected on a live tree that also contained a nest of *Dolichoderus decollatus* (Forel 1912). Doug Yu's Manu collection was from a carton nest on *Inga stipulacea*. In Venezuela I collected a nest in a dead vine stem, and a polygynous nest with many dealate queens in a dead *Cecropia* branch.

Comments. *Azteca jelskii* is a South American version of *A. tonduzi*. The only difference is that the scape and tibiae of *A. jelskii* lack erect setae. The scape and tibiae of *A. tonduzi* have an inconspicuous but distinct series of short erect setae. There is variation in queen head size in South America. A queen from Venezuela is smaller than queens of *A. tonduzi* (HLA 1.01mm versus 1.10–1.16mm, respectively); two queens, one from Peru and one from Bolivia are similar in size to *A. tonduzi* queens (HLA 1.16–1.17mm).

Additional material examined. BOLIVIA: *Beni*: Cavinas, Feb 1922 (M. B. Lopez) — alate queen [USNM]; **PERU**: *Madre de Dios*: Manu National Park, 12°S, 71°W, 400m, Sep–Nov 1994 (D. Yu) — alate queen, worker; Cocha Totora, Manu National Park, 25 Oct 1986 (D. W. Davidson) — worker [LACM]; *San Martín*: La Perla, 21km NNE Tarapoto, 6°19'S, 76°17'W, 220m, 23 Aug 1986 (P. S. Ward) — alate queen [UCDC]; **TRINIDAD**: no specific locality (Urich) — worker [MCZC]; **VENEZUELA**: Puerto Cabello (A.

Forel) — worker [MHNG]; *Barinas*: Ticoporo, 8°02'N, 70°46'W, 240m, 28 Aug 1987 (J. Longino) — workers, queens.

Azteca sericea (Mayr 1866)

Iridomyrmex sericeus Mayr 1866:498. Syntype workers: Mexico, in pseudobulbs of *Schomburgkia tibicinus* (Heller) [NHMW] (examined).

Liometopum instabile (F. Smith) (part): Mayr 1878:870.

Azteca sericea Mayr: Emery 1893:134.

Azteca instabilis var. mexicana Emery, 1896a:3 [n. nov. for *Iridomyrmex xanthochrous* Mayr 1866:497 (not Roger 1863)]. Syntype workers: Mexico (Norton) [NHMW] (examined). NEW SYNONYMY.

The history of the name *mexicana* is complicated. Roger (1863) described *A. xanthochroa* based on a single queen from Mexico. Mayr (1866) described workers from Mexico as the workers of *xanthochroa*. Emery (1893) examined these workers, identifying them as *xanthochroa* and making *xanthochroa* a variety of *instabilis*. Emery (1896a), having discovered that *xanthochroa* was a species distinct from *instabilis*, reidentified these same workers as a new variety, *instabilis* var. *mexicana*. In the Mayr collection, under "*instabilis* Sm. var. *xanthochroa* Rog.," are several pins with Emery determination labels. The only Mexican material among these are two workers, with labels "Mex, Norton," identified by Emery as "*A. instabilis* var. *xanthochroa*." These are the syntypes of *mexicana*, and when I examined them I added red labels stating "syntypus *Az. mexicana* Emery 1896, det. J. Longino 1990." I compared the workers directly with the types of *A. sericea*.

To confuse matters, a series labeled "Mexico, No. 211," with red type labels indicating they are types of *instabilis mexicana* has been distributed to American museums. Specimens from LACM have an additional label indicating they are from the Pergande collection. I have examined specimens of this series from MCZC and LACM; and AMNH type labels on the MCZC material suggest there is also material at AMNH. These are not syntypes of *mexicana*. I identify them as *A. pittieri*.

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