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Journal of Natural History

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tnah20>

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Available online: 17 Feb 2007

To cite this article: J.T. Longino (1991): Taxonomy of the Cecropia-inhabiting Azteca ants, *Journal of Natural History*, 25:6, 1571-1602

To link to this article: <http://dx.doi.org/10.1080/00222939100770981>

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Taxonomy of the *Cecropia*-inhabiting *Azteca* ants

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(Accepted 1 August 1991)

Cecropia trees and several species of the ant genus *Azteca* form the most conspicuous ant–plant association in the Neotropics. The taxonomy and biology of the *Cecropia*-associated *Azteca* are reviewed. A key to queens is provided for the 13 species known to be obligate inhabitants of *Cecropia* trees, and a key to workers for the five species known from Costa Rica. Taxonomic changes include four new species and extensive synonymy. Individual species accounts contain taxonomic, behavioural, and ecological information. Evolutionary relationships among the species, and the community ecology of the *Cecropia*–*Azteca* association, are discussed.

KEYWORDS: *Azteca*, *Cecropia*, ant–plant relationships, taxonomy, Neotropics.

Introduction

The most prominent ant–plant association in the Neotropics is between *Cecropia* trees and *Azteca* ants (Bequaert, 1922; Wheeler, 1942; Benson, 1985). *Cecropia* trees are common throughout the Neotropics, where they often dominate second growth vegetation (Uhl *et al.*, 1981; Brokaw, 1987). Most of the species of *Cecropia* are specialized myrmecophytes, and the occupants are most often ants in the genus *Azteca*. The genus *Azteca* (subfamily Dolichoderinae) is strictly Neotropical and strictly arboreal (Emery, 1893, 1912; Forel, 1928; Hölldobler and Wilson, 1990), the many species comprising a diverse element of the arboreal ant fauna. A subset of the species form obligate associations with particular plant lineages, and a subset of the latter choose *Cecropia*.

The *Cecropia*–*Azteca* association is actually an interacting community of species (Harada and Benson, 1988; Longino, 1989a; Davidson *et al.*, 1991; Longino, 1991; Davidson and Fisher, 1991). National parks, biological research stations, mountainsides, even mosaics of degraded second growth and agricultural land, will typically have more than one species of *Cecropia* growing sympatrically. Although individual mature trees are usually dominated by a single colony of *Azteca*, a population of trees may support up to five *Azteca* species, all obligate inhabitants of *Cecropia*. Individual *Cecropia* saplings may contain founding queens of several species, all vying to dominate the tree. Ecological questions are now being asked of this ant–plant community: how do the *Azteca* species coexist? Are there patterns of host choice or habitat choice by founding queens? Do ant species differ in their fitness effects on host trees?

Because this ant–plant relationship is increasingly a subject of ecological study, the need for a current taxonomy is paramount. The purpose of this report is to provide an

updated taxonomy and an identification guide for the *Azteca* species that are obligate *Cecropia* inhabitants. No claim to monophyly is proposed for the taxa treated here, although issues of character change and phylogeny are addressed in the discussion. Phylogenetic analysis plays a primary role in examining scenarios of adaptation, and it is hoped that this taxonomic work will also provide a foundation for future studies in systematics.

The taxonomy presented here relies almost entirely on queens, and on relatively few character systems: head measurements and shape, pilosity distribution, petiole shape, and body colour. After more than 150 nominal taxa had been described in the genus *Azteca*, most of them from workers only, Wheeler and Bequaert (1929) belatedly stated 'Apparently the females [queens] furnish more reliable characters for identification than the workers in the genus *Azteca*', a statement with which I strongly concur. 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 (personal observation). In contrast, queens are much less intraspecifically variable, yet exhibit strong interspecific differences. Within a single locality, species with strongly differentiated queens may have workers that are barely distinguishable. The *Cecropia* ants are no exception.

Queens of *Cecropia* ants are much more readily collected than queens of most other species of *Azteca*. *Cecropia* saplings, which are easily sampled and split open, often contain dozens of founding queens spread throughout the multiple internodes. What species are present in an area can be quickly assessed by examining saplings. However, workers that may be present in these incipient colonies bear little resemblance to workers of the same species from mature colonies. Obtaining samples of both workers and sexuals from mature colonies is much more difficult, requiring branch samples in some cases, destruction of an entire tree in others. Worker samples from the surface of a tree are adequate for identification (assuming a mature colony) only when the local community has been well sampled, and subtle features differentiating sympatric species are not obscured by geographic variation.

Azteca alfari and *A. ovaticeps* together form a species group which was established and revised previously (Longino, 1989b). They are included here in the key to species, and brief species accounts contain some new information, but a more thorough treatment of synonymy, morphological variation, and geographic range may be found in the earlier revision.

Methods

Observations were made at 63 × magnification with a Zeiss dissecting microscope. Measurements are accurate to the nearest 0.01 mm. All measurements are presented in mm. Drawings were made with a camera lucida attachment.

The abundance and distribution of pilosity are important taxonomic characters. Unless otherwise indicated, pilosity on drawings is not stylized, but is an accurate representation of particular specimens. Only setae visible in a single plane of focus were drawn, and typically only those projecting beyond a border. For example, face-view figures of the head show only those setae projecting beyond the margins, and not those situated more medially on the frons.

The head is assumed prognathous for purposes of terminology and orientation. Sculpture terminology generally follows Harris (1979).

The following measurements and abbreviations are used:

- HW Head width, measured across the widest part of the head (not including eyes).
 HL Head length, measured from the posteriormost point on an occipital lobe to the anteriormost point of the *lateral* clypeal lobe on the same side. Note that this measurement is not the typical head length measurement of myrmecologists, which is along the median axis. The measurement used here obviates the need to (1) extrapolate to a point mid-way between the occipital lobes, and (2) see clearly the anteromedian clypeal border, which is often obscured by closed mandibles.
 SL Scape length, not including basal condyle and neck.
 CI Cephalic index (HW/HL).
 SI Scape index (SL/HW).

Collections are referred to by the following acronyms.

- BMNH British Museum (Natural History), London, UK.
 FSCA Florida State Collection of Arthropods, Gainesville, Florida, USA.
 HAHC H. A. Hespeneide, personal collection.
 IBCR Instituto Nacional de Biodiversidad, Costa Rica.
 IZAV Instituto de Zoología Agrícola, Facultad de Agronomía, Universidad Central de Venezuela, Maracay, Venezuela.
 LACM Los Angeles County Museum of Natural History, Los Angeles, CA, USA.
 MACN Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina.
 MCSN Museo Civico de Storia Naturale 'Giacomo Doria', Genoa, Italy.
 MCZC Museum of Comparative Zoology, Cambridge, MA, USA.
 MHNG Museum d'Histoire Naturelle, Geneva, Switzerland.
 MZSP Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.
 NHMB Naturhistorisches Museum, Basel, Switzerland.
 NHMW Naturhistorisches Museum, Vienna, Austria.
 PSWC P. S. Ward Collection, University of California, Davis, CA, USA.
 USNM National Museum of Natural History, Washington, DC, USA.

Unless otherwise indicated, material examined is from LACM, or, if collected by P. S. Ward, from PSWC.

All new species names are to be considered nouns in apposition and thus invariant.

Check list and known distributions

(For full synonymy of *A. alfari* and *A. ovaticeps*, see Longino, 1989b.)

alfari Emery. Mexico to Argentina.

= *bicolor* Emery, syn. nov.

aragua sp. nov. Venezuela.

australis Wheeler, stat. nov. Amazonia to Peruvian, Bolivian Andes.

coeruleipennis Emery. Mexico to Costa Rica.

constructor Emery. Mexico to Guyana.

= *emmae* Forel, syn. nov.

= *guianae* Wheeler, syn. nov.

isthmica Wheeler, stat. nov. Panama.

lattke sp. nov. Venezuela.

merida sp. nov. Venezuela.

muelleri Emery. Southern Brazil.

= *nigella* Emery, syn. nov.

= *wacketi* Emery, syn. nov.

- = *brunni* Forel, syn. nov.
- = *janeirensis* Forel, syn. nov.
- = *nigridens* Forel, syn. nov.
- = *gibbifera* Forel, syn. nov.
- ovaticeps* Forel. Costa Rica to Brazil.
- petalocephala* sp. nov. Bolivia.
- salti* Wheeler, stat. nov. Colombia.
- xanthochroa* (Roger). Mexico to Panama.
- = *costaricensis* Wheeler, syn. nov.

Key to species

Queens

- 1a Scapes and tibiae devoid of erect setae 2
- 1b Scapes and tibiae setose 3
- 2a Second gastral tergum with <6 setae, exclusive of posterior row; clypeus setose, but never with a dense brush (Fig. 1); scape relatively short (median SI 0.57, range 0.54–0.65, n=25) *alfari*
- 2b Second gastral tergum with >20 setae, exclusive of posterior row (Costa Rica), or clypeus with a dense brush of setae (South America) (Fig. 2); scape relatively long (median SI 0.61, range 0.59–0.67, n=19) *ovaticeps*
- 3a Body colour solid black or dark brown 4
- 3b Body colour solid orange, mottled orange, or brown with mottled orange mesosoma 6
- 4a Head much longer than broad (CI <0.85, Figs 19, 45) *coeruleipennis*
- 4b Head relatively shorter (CI >0.85, Figs 17, 18, 45) 5
- 5a Mesosoma and face with dense brush of setae, continuous from ocelli to occipital lobes and on anteriormost mesoscutum, average height of setal brush (perpendicular to surface) on both face and mesoscutum >0.30 mm (Fig. 3) *constructor*
- 5b Mesosoma and face with more typical, less dense setae, setae less dense or absent between ocelli and occipital lobes, and on anteriormost mesoscutum, average height of setae on mesoscutum <0.25 mm *lattke*
- 6a HL >1.90 mm, if near this value, CI <0.85 (upper group of species in Fig. 45) 7
- 6b HL <1.85 mm, if near this value, CI >0.90 (lower group of species in Fig. 45) 12
- 7a Ventral surface of petiole evenly setose for entire length (Figs 26, 27, 30, 31) 8
- 7b Ventral surface of petiole with setae unevenly distributed, coarse setae mainly clustered near anterior peduncle, underlying fine setae feeble (Figs 23–25) 11
- 8a Petiole in posterior view weakly setose, with few and/or very short projecting setae (Figs 26, 27) 9
- 8b Petiole in posterior view strongly setose, with abundant projecting setae of irregular lengths (Figs 30, 31) 10
- 9a Head strongly flattened (Fig. 21), sides of head above eyes with abundant erect setae (Fig. 12) *petalocephala*
- 9b Head less flattened (Fig. 22), sides of head above eyes bare (Figs 7–9) *australis*
- 10a Mandibles subopaque, sides of head weakly to moderately convex, HW >1.70 mm (Figs 13, 14) *merida*
- 10b Mandibles smooth and shiny, sides of head flat, HW <1.65 mm (Fig. 11) *aragua*
- 11a Petiole in posterior view with 0–5 long, delicate setae (Figs 23, 24) *xanthochroa*
- 11b Petiole in posterior view with about 8 long, coarse setae (Fig. 25) *salti*
- 12a Mandibles feebly striate, HW <1.60 mm (Figs 16, 45), colour uniform orange *isthmica*
- 12b Mandibles shagreened, opaque, HW >1.65 mm (Figs 15, 45), colour burnt orange mottled with brown *muelleri*

Workers

The following key applies primarily to Costa Rica. The portion treating *A. alfari* and *A. ovaticeps* will work to an extent for all of the Neotropics, but even in Costa Rica, where many worker samples have been examined, a few collections are intermediate and cannot be assigned with confidence to one species or the other. The key for the

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remaining species, those with setose appendages, will probably work for Costa Rica to Mexico, but worker-based species distinctions are too poorly known for Panama southward, and will probably have to be investigated region by region.

- 1a Scapes and tibiae devoid of erect setae 2
 1b Scapes and tibiae setose (these are fine and difficult to see on *A. coeruleipennis*) 3
 2a Mesonotum densely covered with setae of irregular lengths (median number of setae > 20, but some with as few as 10, $n = 40$); workers typically concolorous yellow-brown *ovaticeps*
 2b Mesonotum less setose (median number of setae 8, range 2–17, $n = 66$) (Fig. 44); colour highly variable between colonies: concolorous yellow-brown, bicoloured with darker head, or concolorous brown *alfari*
 3a Uniformly yellow; weakly polymorphic, largest worker HW < 1.05 mm (Fig. 39); appendage pilosity fine, difficult to see; in profile mesonotum drops to a shelf anterior to propodeal suture, metanotal area and basal face of propodeum in the same plane (Fig. 43); Mexico to Pacific coast dry forest of Costa Rica *coeruleipennis*
 3b Colour otherwise; strongly polymorphic, largest worker HW approaching 1.40 mm; appendage pilosity coarse and conspicuous; widespread in Costa Rica 4
 4a Largest workers approaching queen in colour, sides of head orange with extensive infuscation medially; sides of head more rounded (Figs 36, 37); in mature colonies, workers often emerge from fissure 2–3 m above ground level *xanthochroa*
 4b Largest workers uniform brown; head more quadrate (Fig. 38); in mature colonies, no fissure maintained near ground level; on disturbance, workers emerge from fissures near the first tree branches, blackening the trunk in a massive response *constructor*

Species accounts

Azteca alfari Emery 1893

(Figs 1, 20, 35, 40, 44)

Azteca alfari Emery, 1893: 338. Lectotype, Paralectotype workers: Jiménez, Atlantic slope, Costa Rica (Alfaro) [MCSN] (Lectotype designation by Longino, 1989b).

Azteca bicolor Emery, 1893: 341. Syntype workers: Paraguay (Balzan); syntype workers, queen: Brazil, Matto Grosso (Germain) [MCSN, USNM]. New Synonymy (examined; alate queen [MCSN] here designated Lectotype, remaining syntype workers excluded from types).

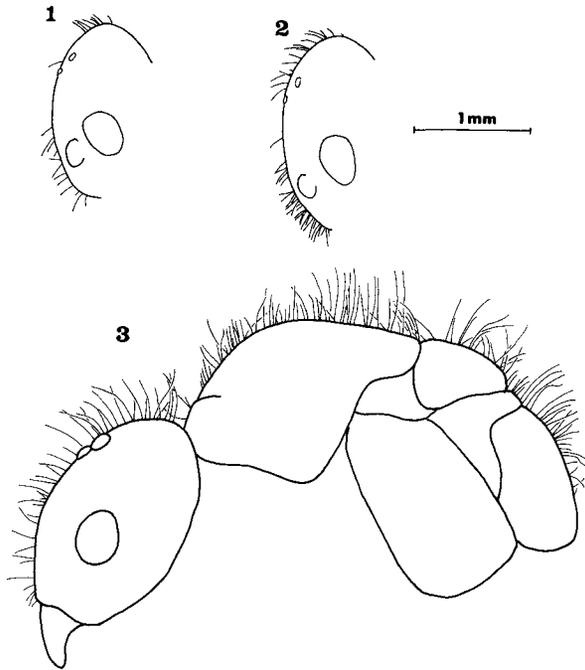
This species and its close relative, *A. ovaticeps*, have been revised by Longino (1989b). Subsequent examination of the syntype queen of *A. bicolor* revealed that it was a typical *A. alfari* queen. The syntype workers from Paraguay are not conspecific. The syntype workers from Brazil are small, probably from an incipient colony (and thus not nestmates of the lectotype queen) and cannot be identified with confidence.

Harada (1989) has described the colony structure of young colonies of *A. alfari*. Harada's study predates my *A. alfari* group revision, and thus her '*A. alfari*' does not distinguish between the two species in the group.

Azteca aragua sp. nov.

(Figs 11, 31, 45)

Holotype queen: Venezuela, Estado Aragua, Rancho Grande, 1100 m, 19 February 1969 (J. Salcedo) [IZAV]. Paratypes: 1 queen: Venezuela, Estado Aragua, Rancho Grande, 1100 m, 19 July 1967 (Poole) [MCZC]; 3 queens: same locality, 25–26 January 1978 (Heppner) [USNM]; 1 queen: same locality, 14 May 1975 (Salcedo and Clavijo) [IZAV]; 1 queen: same locality, 19 February 1969 (Salcedo) [IZAV]; 1 queen: Rancho Grande, Portachuelo, 1100 m, 24 April 1981 (Clavijo) [IZAV]; 1 queen: same locality and data (Clavijo and Chacon) [IZAV].



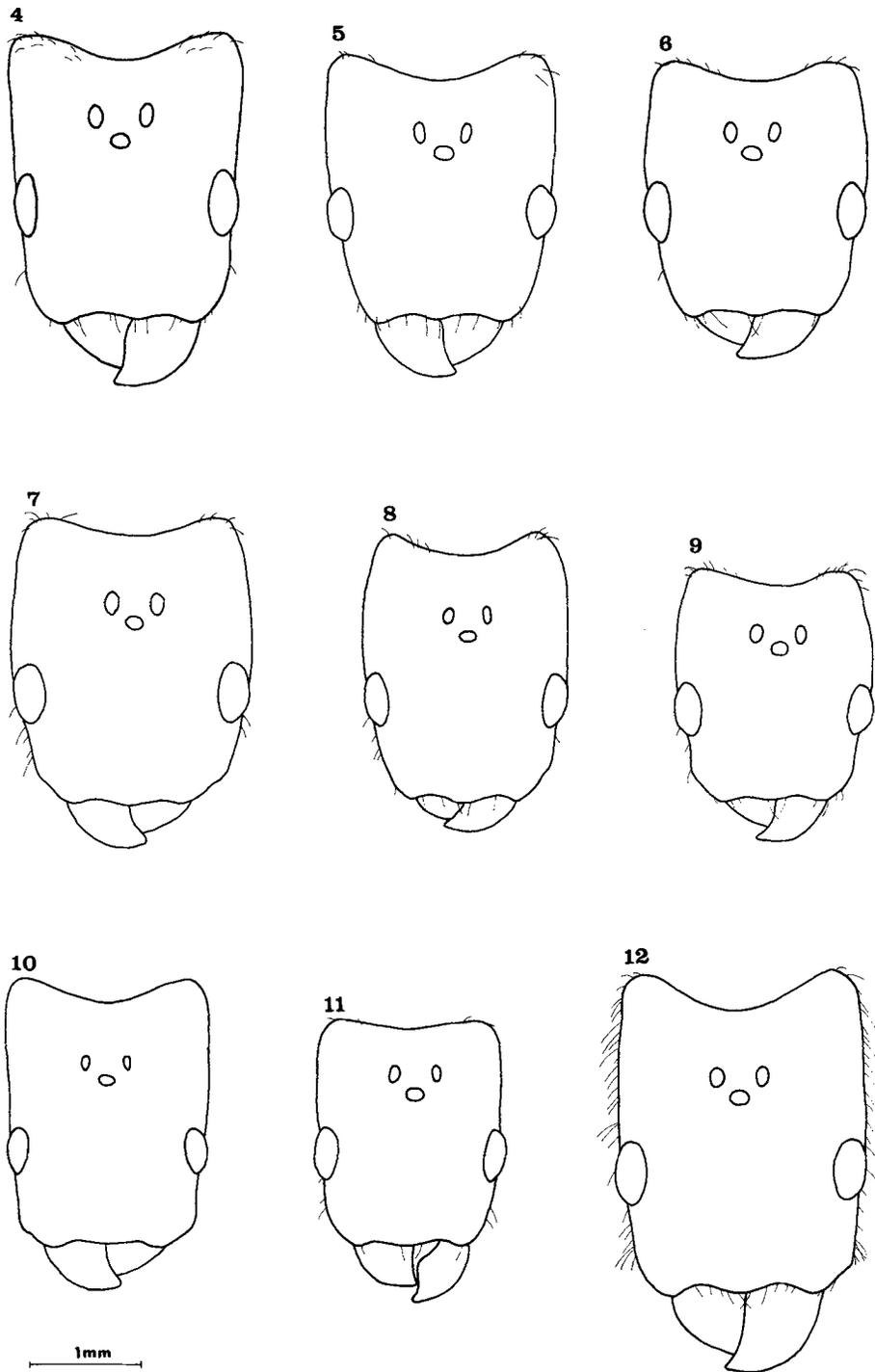
FIGS 1–3. *Azteca* queens: 1, *alfari* face in side view (Brazilian specimen); 2, *ovaticeps* face in side view (Brazilian specimen); 3, *constructor* head and mesosoma in side view.

Additional non-type material: 1 queen: Estado Carabobo, Palmichal, Canoabo, 1000 m (Bordón) [IZAV].

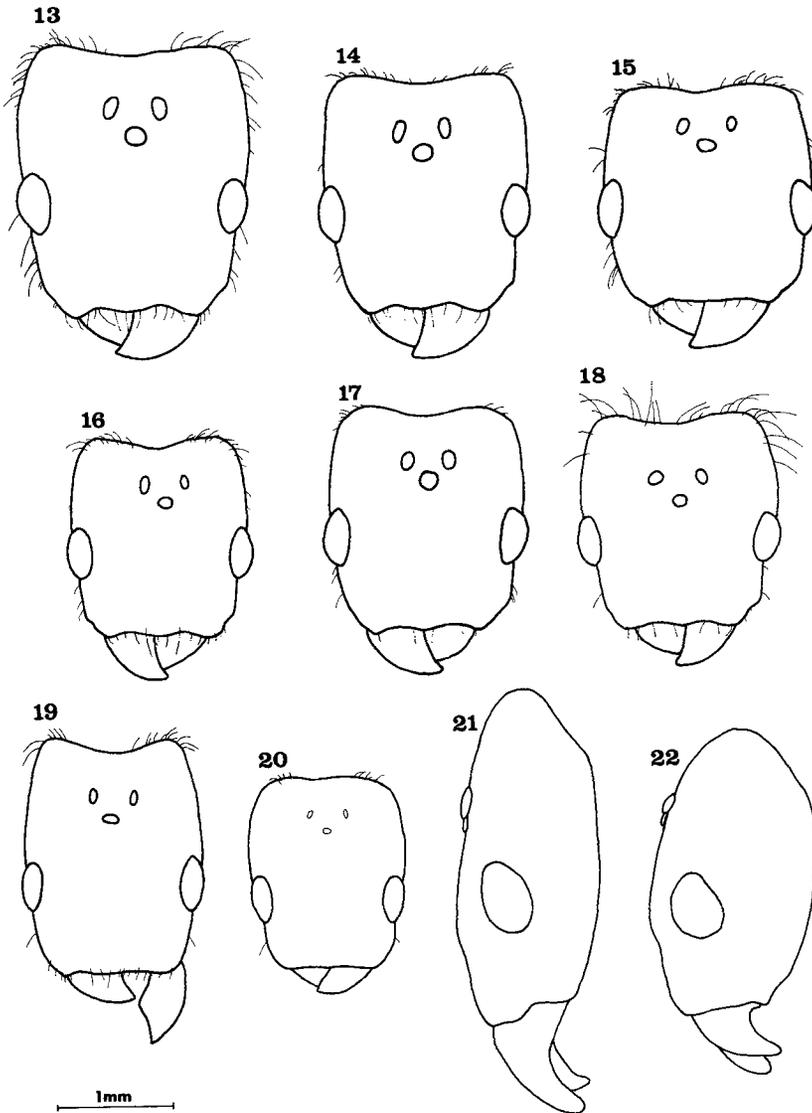
Queen measurements ($n=4$). HL 1.92–2.05, HW 1.49–1.64, SL 1.04–1.09, CI 0.76–0.85, SI 0.64–0.71.

Queen diagnosis. Head rectangular, longer than wide, sides flat. Mandibles smooth and shiny, with scattered puncta. Face sublucid, micropunctate. In full-face view, erect setae present on occipital lobes, absent on sides of head above eyes. Scapes and legs densely setose. Petiole subpyramidal in side view, with bluntly rounded apex, subangular in posterior view. Ventral margin of petiole with shallow lobe, lobe ending before posterior rim, leaving short peduncle. Setae on anterodorsal face and ventral surface of petiole abundant, of irregular length, not or weakly differentiated into long, coarse setae and short, fine setae. Dorsal setae projecting well beyond margins of petiole in posterior view, ventral setae evenly dispersed. Mandibles clear maroon; scapes and tibiae dark brown; head, mesosoma, and gaster burnt orange; sometimes head, and sometimes head and gaster, darker than mesosoma.

Comments. This species is known only from Venezuela's coast range, west of Caracas. All specimens are alate queens, collected around 1000 m elevation, at least one from a blacklight in cloud forest. No nest series has been collected, and it is not known for certain that this is a *Cecropia* ant. However, it is very similar to *A. merida*, differing only in the somewhat smaller size, flatter head sides, and shiny mandibles. *Cecropia palmatisecta* occurs in the same coast range, in cloud forest from 800 to 1000 m (Velásquez, 1972), and I predict that *A. aragua* is its main inhabitant (see discussion under *A. merida*).



FIGS 4–12. *Azteca* queens, face-view: 4, *xanthochroa* (Costa Rica); 5, *xanthochroa* (Guatemala); 6, *xanthochroa* (Mexico); 7, *australis* (Bolivia, 2000 m); 8, *australis* (Peru, 750 m); 9, *australis* (Brazil, <100 m); 10, *salti* (*the figure does not include pilosity. Written notes from examination of type suggest a setal pattern similar to *xanthochroa*); 11, *aragua*; 12, *petalocephala*.



FIGS 13–22. *Azteca* queens, face-view and side-view: 13 and 14, *merida*, showing size variation; 15, *muelleri*; 16, *isthmica*; 17, *latke*; 18, *constructor*; 19, *coeruleipennis*; 20, *alfari*; 21, *petalocephala*; 22, *australis*.

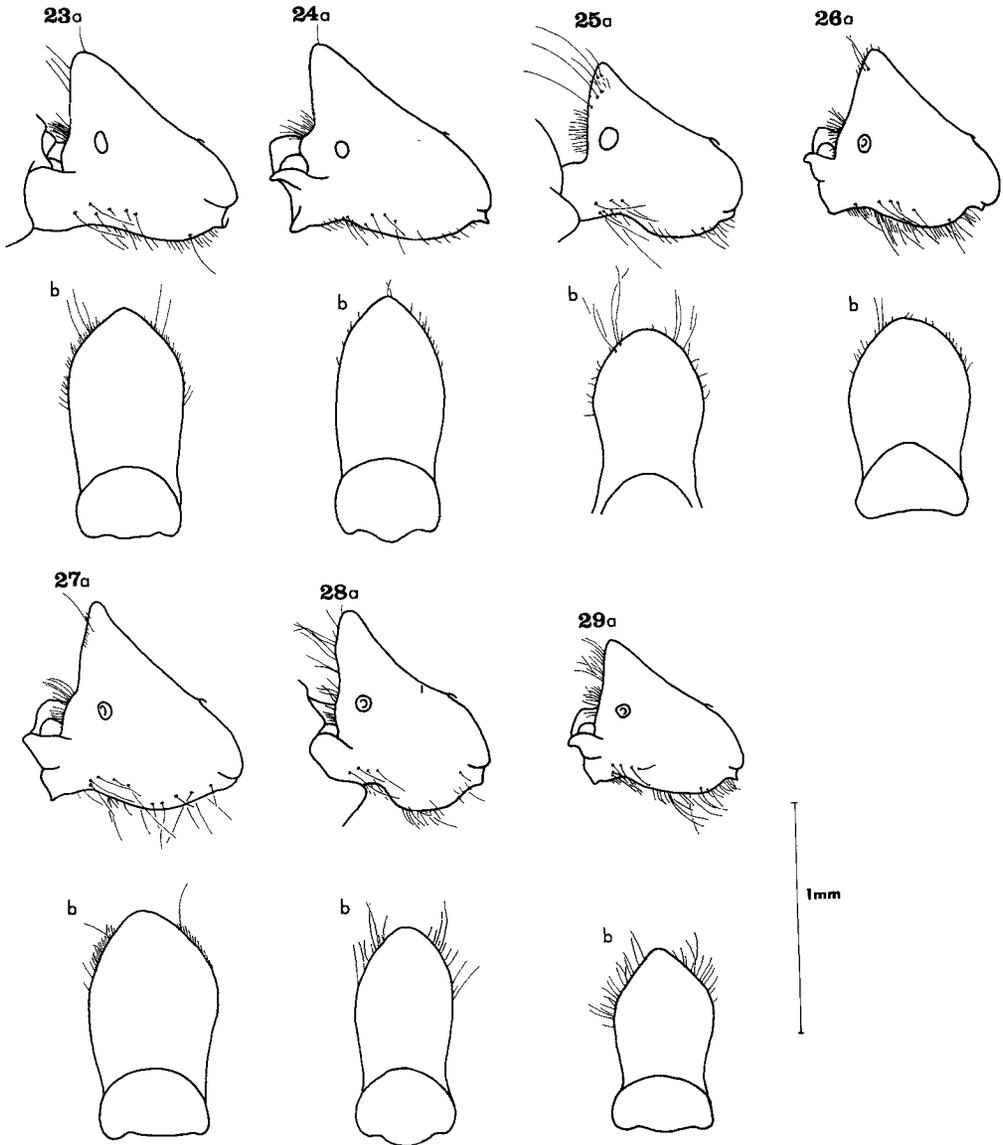
Azteca australis Wheeler, stat. nov.

(Figs 7, 8, 9, 26, 45)

Azteca xanthochroa subsp. *australis* Wheeler, 1942: 249. Syntype queens: Bolivia: Songo [=Dept. La Paz, Zongo?] (purchased from Staudinger and Banghaas); and Peru, Callanga [=Bolivia, Dept. La Paz, Challana?] (purchased from Staudinger and Banghaas) [MCZC] (examined, Songo queen here designated Lectotype).

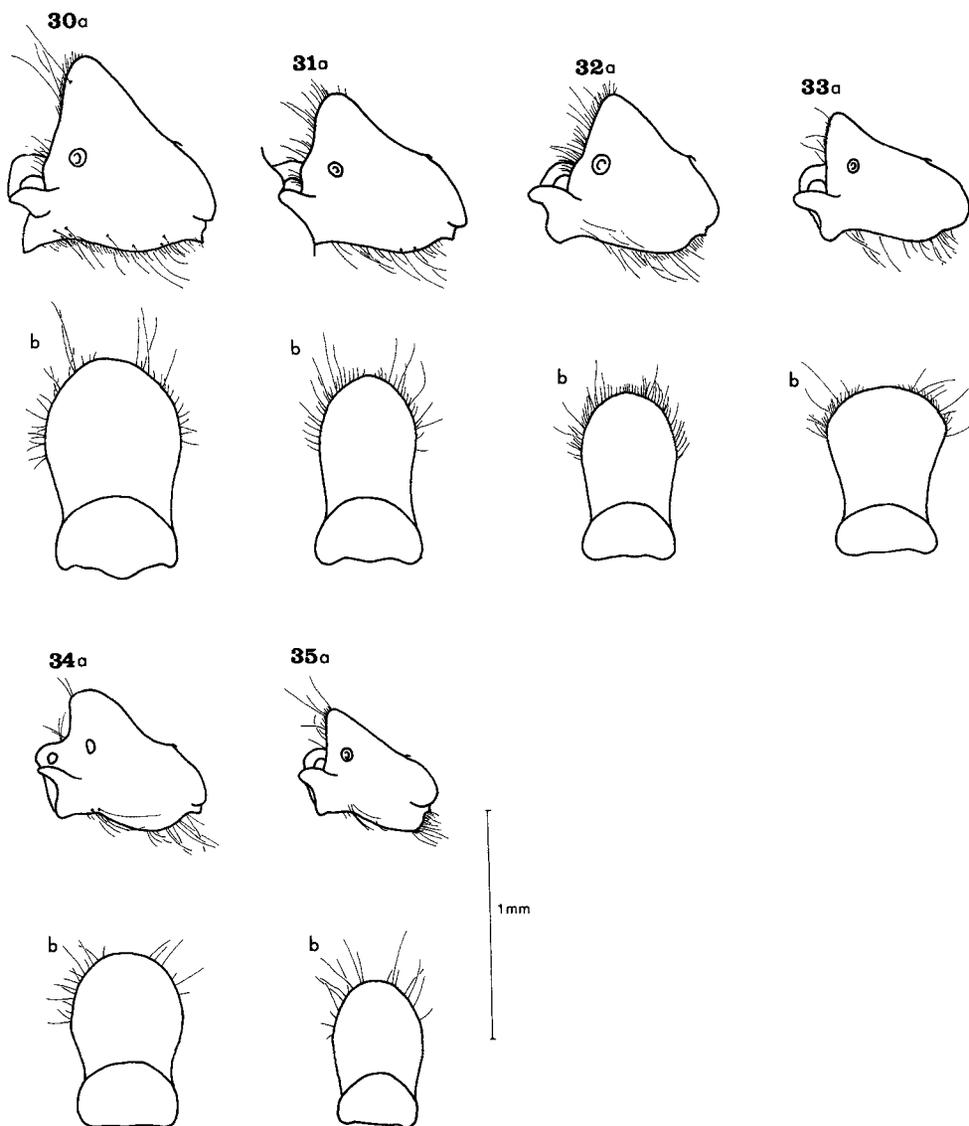
Azteca xanthochroa, in the sense of Harada, 1982; Davidson *et al.*, 1991; Davidson and Fisher, 1991 [misidentifications of *australis*].

Queen measurements ($n=12$). HL 1.94–2.46, HW 1.60–2.12, SL 1.00–1.20, CI 0.77–0.88, SI 0.55–0.66.



FIGS 23–29. *Azteca* queens, petiole in (a) side-view, and (b) posterior-view, with posterodorsal face perpendicular: 23, *xanthochroa* (Guatemala); 24, *xanthochroa* (Costa Rica); 25, *saltii*; 26, *australis*; 27, *petalocephala*; 28, *muelleri*; 29, *isthmica*.

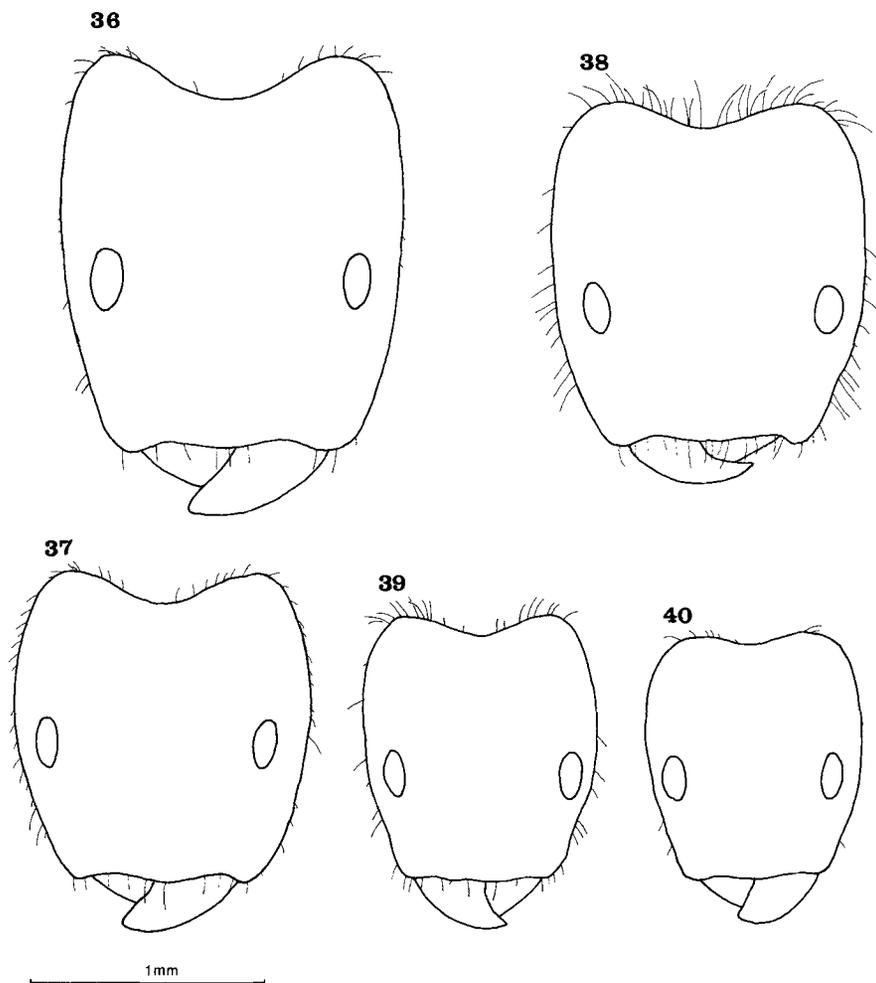
Queen diagnosis. Head subquadrate, longer than wide, sides weakly convex. Mandible very shiny with widely spaced small puncta. Face strongly shining, pubescence dilute to absent medially. In full-face view, short setae present on occipital lobes, lacking on sides of head above eyes. Scapes and legs densely setose. Petiole subpyramidal, bluntly triangular in side view, apex rounded in posterior view. Petiolar node with 0–5 delicate, long setae over sparse erect pubescence. Ventral margin of petiole with weak lobe, lobe ending before posterior rim, leaving a short peduncle. Coarse setae and erect pubescence abundant and evenly dispersed over ventral surface of petiole. Body colour orange, often with infuscation on face.



FIGS 30–35. *Azteca* queens, petiole in (a) side-view, and (b) posterior-view, with posterodorsal face perpendicular: 30, *merida*; 31, *aragua*; 32, *lattke*; 33, *constructor*; 34, *coeruleipennis*; 35, *alfari*.

Worker (based on two worker series from Manu National Park, Peru). Similar to workers of *A. xanthochroa* in all respects.

Comments. Queen size in this species varies geographically: those from the uplands of Peru and Bolivia (including types) are large; those from lowland Amazonia are small. Ward's collections from low and high elevation sites on the eastern slopes of Bolivia (see Material examined) exhibit this size difference, and I can detect no differences other than size. This species is very similar to the allopatric *A. xanthochroa* in the pyramidal petiole, the absence of abundant setae on petiolar node, the very dilute pubescence, and the frequently well-developed infuscation on the shiny face. The head shape is similar to

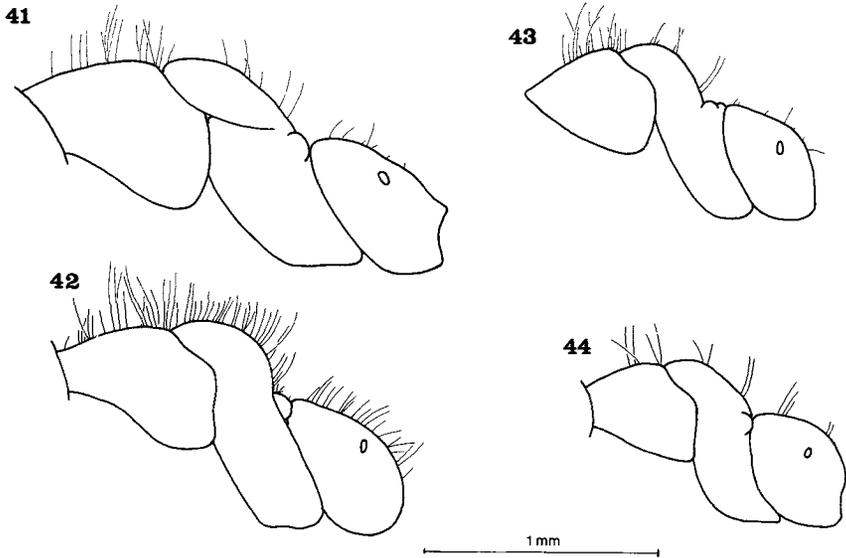


FIGS 36–40. *Azteca* workers, face-view: 36 and 37, *xanthochroa*; 38, *constructor*; 39, *coeruleipennis*; 40, *alfari*.

Mexican, the sculpture and colour to Costa Rican *A. xanthochroa*. *Azteca australis* consistently differs from *A. xanthochroa* in the more abundant, uniform pilosity on the ventral margin of the petiole.

Biology. *Azteca australis* is an obligate *Cecropia* inhabitant which occurs from Amazonian lowlands to 2000 m elevation montane forest in the Andes. In the context of community-level studies of *Cecropia* inhabitants, Davidson has frequently observed *A. australis* in Peru's Manu National Park. The following biological notes are from Davidson (personal communication):

In southeastern Perú, colonies of *Azteca australis* are most frequent on those *Cecropia* species which establish in relatively small forest light gaps. They are common on *C. ficifolia*, and are the sole associates of a second (yet unidentified) *Cecropia* species whose internodes are apparently too narrow and short to accommodate larger-bodied queens of two other ants (*Camponotus balzani* and



FIGS 41–44, *Azteca* workers, side-view of mesosoma: 41, *xanthochroa*; 42, *constructor*; 43, *coeruleipennis*; 44, *alfari*.

Pachycondyla luteola) which inhabit *Cecropia* in these same habitats. Although foundresses of *A. australis* also colonize *Cecropia* in larger riparian disturbances, their numbers there are far exceeded by those of *Azteca ovaticeps* on these hosts (*C. membranacea*, *C. polystachya*, and *C. engleriana*). The associations of *A. australis* with particular (habitat restricted) host species may be determined more by habitat than by host.

Foundresses of *A. australis* colonize their hosts by entering internodes via prostomata and then sealing these entrance holes. Colonies are founded claustrally, without access to Müllerian and pearl bodies. Along river and stream banks (where competition for hosts may be greatest?), multiple queens (2–10) commonly occur within individual internodes of *Cecropia*. In contrast, the vast majority of queens initiate their colonies individually on hosts of small forest light gaps. Even in habitats where colony founding is polygynous, host plants with established colonies of *A. australis* house only a single queen. Queens of this species produced larger but far fewer eggs over a 6-week period than did queens of *A. ovaticeps* on the same host plant (*C. membranacea*), but sample sizes for *A. australis* were extremely small. Workers of *A. australis* are more aggressive than those of *A. ovaticeps* when hosts are disturbed. *Azteca australis* workers will attack vines that contact host-plant stems and will defend their hosts against leafcutter ants in the genus *Atta* (though these ants are rare in flooded forests). Unlike some other obligate *Cecropia* ants, *A. australis* may not tend homoptera inside host-plant stems.

Additional material examined

BOLIVIA: department unknown: 'Bolivien' [printed label] [MCZC]; Beni: Estacion Biologica Beni, 42 km E San Borja, 210 m, 14°48'S 66°23'W (Ward no. 9084-2); La Paz: 13 km NNE Coroico, 16°04'S 67°41'W, 1050 m (Ward no. 9043); 9 km SW Coroico, 16°14'S 67°47'W, 2000 m (Ward no. 9107-2).

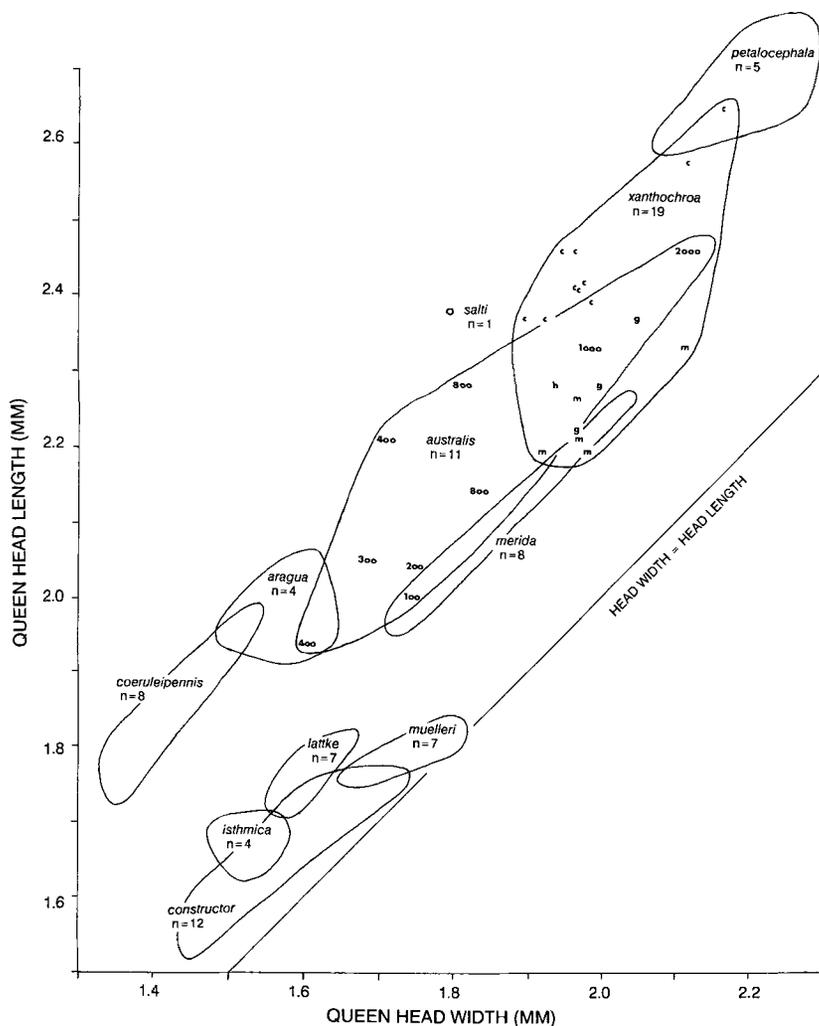


FIG. 45. *Azteca* queens, head length vs. head width. Closed curves circumscribe sets of n measurements for each species. For *xanthochroa*, individual measurements are shown, with the letter indicating country of origin: c = Costa Rica, h = Honduras, g = Guatemala, m = Mexico. For *australis*, individual measurements are shown only for queens with elevation data, the elevation being indicated on the figure.

BRAZIL: Amazonas: Lagoa, Janauacá (W. Buren no. 114F) [MCZC].

PERU: department unknown: Chauchamayo (WFH Rosenberg) [USNM]; Cuzco: Quincemil, 750 m (Pena) [MCZC]; Madre de Dios: Estacion Biologica Cocha Cashu, ca. 400 m (Davidson); Reserva Tambopata, 300 m (Davidson).

Azteca coeruleipennis Emery, 1893

(Figs 19, 34, 39, 43, 45)

Azteca coeruleipennis Emery, 1893: 130. Syntype workers, queens, males: Costa Rica, western slope (Alfaro) [label: 'Alajucla, Cecropia, III 90'] [MCSN] (examined, alate queen here designated Lectotype, 6 workers, 2 queens, 2 males Paralectotypes).

Queen measurements ($n = 8$). HL 1.74–1.98, HW 1.35–1.53, SL 0.90–1.03, CI 0.75–0.78, SI 0.65–0.68.

Queen diagnosis. Head subquadrate, longer than wide, sides flat to weakly convex. Mandible microalveolate, subopaque, with scattered small puncta. Face shining, densely micropunctate, medial pubescence dilute. In full-face view, abundant long setae on occipital lobes, lacking or a few very short setae on sides of head above eyes. Scapes with moderately abundant short setae, legs with dense, long, light-coloured, flexuous setae. Petiole low, blunt, anterior face nearly flat, perpendicular to horizontal axis, longer posterior face gradually curves to apex, apex slightly medially impressed (entire petiole shape as if a pyramidal petiole had been 'smeared' forward). Petiole in posterior view broadly rounded. Ventral margin of petiole with weak lobe, lobe ending before posterior rim, leaving a short peduncle. Setae which flank anterodorsal ligament of petiole long, projecting straight out (they look like cat whiskers when petiole removed and viewed anteriorly). Petiolar node with abundant, delicate, long setae that project beyond margin in posterior view. No underlying erect pubescence. Setae on ventral margin similar, of irregular length, clustered around juncture of lobe and anterior peduncle, and on posterior part of lobe. Body colour uniformly dark brown.

Worker. Weakly polymorphic. Mandibles strongly shining, with sparse, small puncta. Head shape and pilosity as in Fig. 39. In lateral profile, mesonotum rounded and projecting, drops abruptly to flat, relatively broad metanotal remnant, which is flanked by conspicuous metathoracic spiracles; metanotum continuous with flat basal face of propodeum, giving posterior portion of dorsal profile a step-like appearance (Fig. 43). Tibial setae abundant, but fine and difficult to see. Colour concolorous yellow.

Comments. Workers of *A. coeruleipennis* are often misidentified as *A. alfari* because of the small size, weak polymorphism, and light colour. Also, the tibial setae are very fine and easily overlooked. Wheeler (1942, and in MCZC collection) routinely misidentified *A. coeruleipennis* workers as *A. alfari* subspecies *lucida*. Workers of *A. constructor* have a similar mesosomal profile, but differ greatly from *A. coeruleipennis* in colour and pilosity.

Biology. *Azteca coeruleipennis* is an obligate inhabitant of *Cecropia* trees (Skwarra, 1934; Wheeler, 1942; Longino, 1989a), occurring from southern Mexico to north-western Costa Rica. Founding queens are found solely in *Cecropia* saplings, and large colonies occur in mature *Cecropia* trees. In Costa Rica, *A. coeruleipennis* is a common element of the *Cecropia*-inhabiting ant fauna in dry forest habitats, and exhibits abrupt declines at habitat boundaries (Longino, 1989a). In many dry forest areas the only *Cecropia* species is *C. peltata*, hence this is the host tree species in which I have most often seen *A. coeruleipennis*. I have twice encountered colonies in mature *C. obtusifolia* trees, and I have twice encountered founding queens in *C. insignis* saplings less than 2 m tall. Pleometrotic founding is rare: I have 22 records of lone foundresses from sapling internodes, and 1 record of 4 foundresses together in an internode. When a tree is molested bright yellow workers of rather uniform small size issue forth and descend the trunk, where they aggressively attack the intruder. In mature trees, colonies are polydomous, occupying primarily branch tips. Brood and alate sexuals are scattered throughout the colony space, the single colony queen occupying a central, well-protected site. Carton construction is absent (Longino, 1991).

Additional material examined

COSTA RICA: province unknown: Electriona (Alfaro) [MCZC]; San Lucas [MCSN]; *Guanacaste*: Santa Rosa National Park, 300 m (Longino nos. 411, 476, 515-s,

517-s, 518); north side Laguna Arenal, 10°32'N, 84°58'W, 570 m (Longino nos 1696, 1705-s); north side Laguna Arenal, 10°33'N, 84°54'W, 580 m (Longino no. 1731); *Limón*: Zent (Wheeler) [MCZC] [mixed series with *A. ovaticeps*; erroneous locality due to labelling error?]; *Puntarenas*: Pita, 200 m, 10°10'N, 84°55'W (Longino); Sarmiento, 200–300 m, 10°10'N, 84°52'W (Longino); Guacimal, 300–400 m, 10°13'N, 84°51'W (Longino); Guacimal, 500–600 m, 10°14'N, 84°51'W (Longino); Guaria, 700 m, 10°14'N, 84°51'W (Longino); 9 km S Santa Elena, 750 m, 10°15'N, 84°51'W (Longino nos 683, 684); 2.5 km SW Monteverde, 10°18'N, 84°50'W, 840 m (Longino no. 2547); Reserva Biologica Carara, 30 m, 9°47'N, 84°36'W (Longino nos 539-s, 581, 583-s, 2376-s); *San José*: 6 km SW Santiago, 9°50'N, 84°22'W, 1050 m (Longino nos 1550, 1551); 7 km SW Santiago, 9°49'N, 84°23'W, 820 m (Longino no. 1557); 1 km SW Santa Marta, 9°49'N, 84°23'W, 760 m (Longino nos 1558, 1560-s); Alto Palma, 9°47'N, 84°24'W, 950 m (Longino nos 1561, 1564-s); 2 km NE Guayabo, 9°52'N, 84°15'W, 1040 m (Longino no. 1569-s); 4 km S Santa Ana, 1150 m, 9°54'N, 84°11'W (Longino no. 1690-s); 2 km N Ciudad Colon, 790 m, 9°56'N, 84°15'W (Longino no. 1691-s); San José [MCSN].

GUATEMALA: Patulul (Wheeler) [USNM, MCZC] [some misidentified as *A. lucida*]; Escuintla (Wheeler) [MCZC] [some misidentified as *A. lucida*].

HONDURAS: *Comayagua*: 5 miles N Siguatepeque (Catton).

MEXICO: *Chiapas*: 47.2 miles SE Tonola (Janzen); *Oaxaca*: 4.2 miles S San Mateo Yetla (Snelling no. 73–118); 8 miles S Valle Nacional, 2400 ft (Snelling no. 73–106); Hwy. 175, 3.4 miles S Jacatepec, 2400 ft (Snelling); *Veracruz*: Mirador (Skwarra (nos. 69, 69a, 112, 113, 115, 132, 176, 176b, 176f, 257, 258, 259, 260, 262, 269, 436a) [MCZC, LACM]; Las Hamacas, 17 km N Santiago Tuxtla (E. O. Wilson nos 316, 317, 323) [MCZC].

Azteca constructor Emery, 1896

(Figs 3, 18, 33, 38, 42, 45)

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, Cañas Gudas [Prov. Puntarenas: Cañas Gordas?] (Pittier) [MHNG, MCZC]. New synonymy (examined).

Azteca constructor var. *guianae* Wheeler, 1942: 226. Syntype workers, queen: Guyana, Kartabo (Wheeler) [MCZC]. New synonymy (examined).

Queen measurements (n-12). HL 1.53–1.76, HW 1.45–1.73, SL 0.79–0.94, CI 0.92–0.98, SI 0.51–0.59.

Queen diagnosis. Head subquadrate, about as long as wide, sides convex. Mandibles microalveolate/striate, opaque, with scattered puncta. Face sublucid, micropunctate, with dense appressed pubescence. In full-face view, abundant setae on occipital lobes, very short, sparse setae on sides of head above eyes. Scapes and legs densely setose. Face between ocelli and occipital border, and entire mesosoma, including anteriormost sloping portion of mesoscutum, with dense brush of long setae; average height of setal brush (perpendicular to surface) on both face and mesoscutum >0.30 mm; individual setae to 0.50 mm long. Petiole low, blunt, posterior face much longer than anterior face; in posterior view low and wide, sides convex, dorsum flat to somewhat concave. Ventral margin of petiole with shallow lobe, lobe ending before posterior rim, leaving short peduncle. Pilosity on petiolar dorsum consisting of short erect pubescence beneath abundant long setae, conspicuously projecting beyond petiole in posterior view. Ventral surface of petiole with two clusters of long, coarse setae, one on lobe and one at juncture of lobe and anterior peduncle; no underlying short, fine setae. Colour entirely black.

Worker. Mandibles strongly shining to feebly microalveolate. Head shape and pilosity as in Fig. 38. Mesosomal profile as in Fig. 42. Dorsal pilosity dense, variable in length, frequently shorter than that depicted in Fig. 42. Mesosoma mottled brown; head either the same colour, or more often a contrasting uniform dark brown.

Comments. *Azteca constructor* queens exhibit a striking feature which makes them immediately recognizable. They bear a dense brush of long setae on the face and occipital lobes, and on the entire mesosomal dorsum. The syntype queens of *A. emmae* and *A. guianae* exhibit the dense setal brush, and are in no way exceptional among the hundreds of *A. constructor* specimens I have examined. Forel (1908a) reported *A. emmae* from the oceanic island Isla de Coco (Costa Rican territory), based on a single collection of worker(s) from A. Alfaro. This locality was subsequently cited by Emery (1919) and Kempf (1972). Additional ant collections from Isla de Cocos were examined by Emery (1919) and Wheeler (1919), and no *Azteca* were found. I failed to find in Forel's collection the Alfaro material from Isla de Coco, and I consider the record highly suspect.

In Costa Rica, workers of *A. constructor* can be most easily confused with those of *A. xanthochroa* (see discussion under *A. xanthochroa*).

Biology. This *Cecropia* ant occurs from Guatemala south through lower Central America, continuing across coastal lowlands of northern South America eastward to Guyana. In Costa Rica it occurs throughout the country, in a wide variety of habitats and in a variety of *Cecropia* species. I have found queens in *Cecropia* saplings from sea level to 1500 m. Queens occur abundantly in saplings of *C. peltata*, *C. obtusifolia*, and *C. insignis*, and I have occasionally found queens in saplings of *C. polyphlebia*, a non-mymecophytic cloud forest species which does not harbour *Azteca* colonies when mature. In the lowlands, *A. constructor* colonies are common in mature trees of *C. peltata* on the Pacific coast and *C. obtusifolia* on the Atlantic coast. In the Atlantic lowlands, mature *C. insignis* trees are dominated by *A. ovaticeps* (D. and D. Clark, personal communication, and personal observations). This contrasts with the uplands, where in relatively undisturbed forest *C. insignis* is the only myrmecophytic *Cecropia* species. In these upland sites, saplings are filled with queens of *A. constructor* and *A. xanthochroa*, which implies that nearby mature trees of *C. insignis* must harbour reproductive colonies of *A. constructor*. Thus, host plant use appears to vary with region and elevation.

In South America I have found *A. constructor* only in *C. peltata* (see discussion under *A. merida*).

Pleometrosis at colony founding is very common, particularly at upland sites, and I have found up to 10 queens in a single internode. Mixed-species associations are common, with queens of *A. constructor* and *A. xanthochroa* inhabiting the same internode. Colonies at a stage where there are hundreds of workers and the queen has become physogastric are generally monogynous, but I have twice observed colonies at this stage with two physogastric queens. In both cases the queens have been close together in the central carton nest of the colony. Multiple physogastric queens in young colonies are apparently common in Monteverde, Costa Rica (D. Perlman, personal communication). I have dissected two mature colonies of *A. constructor*, and both were monogynous.

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 Homoptera. 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, 1991).

In spite of the commonness of this widespread species I know of only three collections with associated workers, alate queens, and males: the type series of *A. constructor*, the type series of *A. emmae*, and one of my dissections mentioned above. The paucity of such collections no doubt results from the aggressive behaviour of workers and the extreme concentration of queens and males in the central carton nest.

Additional material examined

COLOMBIA: *Magdalena*: Cañaveral, 11°19'N, 73°56'W, < 50 m (Longino nos 705, 724, 725-2, 729); El Campano, 11°07'N, 74°06'W, 1300 m (Longino no. 740); 2 km ESE Minca, 11°08'N, 74°06'W, 780 m (Longino no. 754-s); 5 km SE Rio Frío, 10°53'N, 74°08'W, 50–200 m (Longino no. 791-s).

COSTA RICA: no specific locality (Tonduz) [USNM]; *Alajuela*: 4.5 km E Monteverde, 1200 m, 10°18'N, 84°46'W (Longino no. 126); Rio Peñas Blancas, 10°19'N, 84°43'W, 800 m (Longino nos 1599-s, 2523); Rio Peñas Blancas, 10°19'N, 84°43'W, 950 m (Longino nos 1648, 1651, 1653-s); *Cartago*: 9 km ESE Moravia, 9°48'N, 83°22'W, 700 m (Longino nos 927, 928, 931); 8 km ESE Moravia, 900 m, 9°48'N, 83°23'W (Longino no. 935-s); 7 km ESE Moravia, 1150 m, 9°48'N, 83°23'W (Longino nos 938-s, 939-s); *Guanacaste*: Santa Rosa National Park, 10°50'N, 85°38'W, 300 m (Longino nos 447-s, 448-s, 514-s); north side Laguna Arenal, 10°30'N, 84°57'W, 670 m (Longino no. 1692); north side Laguna Arenal, 10°32'N, 84°58'W, 570 m (Longino nos 1700-s, 1701-s, 1703-s, 1705-s, 1706-s); 2 miles E Tilaran [10°29'N, 84°57'W] (Janzen); 2 miles W Tilaran [10°28'N, 84°59'W] (Janzen); 6 miles S Cañas, Taboga [10°20'N, 85°12'W] (Janzen); 23.3 miles S Cañas [probably Rio Lagartos, 10°10'N, 84°55'W] (Janzen); *Heredia*: 10°20'N, 84°04'W, 500 m (Longino no. 199-s); 13 km S Puerto Viejo, 300 m, 10°20'N, 84°01'W (Longino nos 1082, 1083); 15 km N Volcan Barba, 1100 m, 10°16'N, 84°05'W (Longino no. 1375-s); 17 km S Puerto Viejo (Rara Avis), 10°18'N, 84°02'W, 600 m (Longino nos 2252-s, 2255-s, 2256-s, 2258-s, 2259-s, 2262-s); La Selva (Janzen); La Selva (Davidson CR-39); *Limón*: Tortuguero, < 5 m, 10°32'N, 83°31'W (Longino nos 359-s, 360); Reserva Biológica Hitoy Cerere, 100 m, 9°40'N, 83°02'W (Longino no. 975-s); *Puntarenas*: Corcovado National Park (Longino); Corcovado National Park (Davidson CR-93, 116, 103, 102, 99); Rincon de Osa (Hogue); Golfito (Truxal and Menke); nr Villa Neily (Hogue); 4 km S San Vito, 8°47'N, 82°58'W, 1200 m (Longino nos 2391-s, 2392-s); San Vito (Janzen); Reserva Biológica Carara, 9°47'N, 84°36'W, 30 m (Longino nos 573, 577, 2376-s); Manuel Antonio National Park, 9°23'N, 84°09'W, < 40 m (Longino nos 624, 648-s); Monteverde, 1190–1500 m, 10°18'N, 84°48–9 (Longino) [dozens of collections, including nos 685, 1976-s, 2384, 2461, 2465, 2472, 2476, 2478, 2479, 2480, 2482, 2485, 2488, 2489, 2490, 2496, 2498, 2499, 2538, 2539]; 2 km SSE Monteverde, 1150 m, 10°17'N, 84°48'W (Longino no. 1046); Santa Elena, 1100 m, 10°19'N, 84°51'W (Longino); Pita, 200 m, 10°10'N, 84°55'W (Longino); Sarmiento, 200–300 m, 10°10'N, 84°52'W (Longino); Guacimal, 300–400 m, 10°13'N, 84°51'W (Longino); Guacimal, 500–600 m, 10°14'N, 84°51'W (Longino); *San José*: 5 km SW Santiago, 9°50'N, 84°21'W, 1120 m (Longino nos 1545, 1546); 6 km SW Santiago, 9°50'N, 84°22'W, 1050 m (Longino nos 1548-s, 1549-s); Alto Palma, 9°47'N, 84°24'W, 950 m (Longino no. 1564-s); 1 km N Salitrales, 9°46'N, 84°24'W, 850 m (Longino no. 1565); 2 km NE Guayabo, 9°52'N, 84°15'W, 1040 m (Longino no. 1569-s); 4 km S Santa Ana, 1150 m, 9°54'N, 84°11'W (Longino no. 1690-s).

GUATEMALA: *Izabal*: Quirigua (Wheeler) [MCZC].

PANAMA: *Canal Zone*: Culebra (Wheeler); Ancon (Wheeler) [MCZC]; Barro Colorado Island (Wheeler nos 704, 743) [MCZC].

TRINIDAD: no specific locality (Wheeler) [MCZC].

VENEZUELA: *Trujillo*: 19 km E Boconó, 9°13'N, 70°06'W, 600 m (Longino nos 1844, 1846-s); *Barinas*: 10 km WNW Sta. Barbara, 7°51'N, 71°16'W, 280 m (Longino nos 1916, 1922).

Azteca isthmica Wheeler stat. nov.

(Figs 16, 29, 45)

Azteca xanthochroa subsp. *isthmica* Wheeler, 1942: 249. Syntype workers, queen: Panama, Canal Zone, Rio Agua Salud (Wheeler no. 121) [MCZC] (examined).

Queen measurements ($n = 4$). HL 1.63–1.69, HW 1.49–1.57, SL 0.85–0.89, CI 0.88–0.93, SI 0.56–0.59.

Queen diagnosis. Head subquadrate, longer than wide, sides flat to weakly convex. Mandibles shiny, feebly striate to variable extent, with scattered puncta. Face sublucid, micropunctate, pubescence dilute. In full-face view, short setae present on occipital lobes, variably present on sides of head above eyes. Scapes and legs densely setose. Petiole pyramidal, apex subangular in lateral and posterior views. Ventral margin of petiole with shallow lobe, lobe ending before posterior rim, leaving short peduncle. Pilosity on anterodorsal face of petiole abundant, projecting well beyond margins of petiole in posterior view, of irregular length, not differentiated into long, coarse setae and short, fine setae. Ventral surface of petiole with setae evenly dispersed, irregular length, not or weakly differentiated into long, coarse vs. short, fine setae. Mandibles maroon, rest of head and body uniform yellow–brown.

Comments. This small-queened species is known only from Panama and Colombia. From present knowledge, *A. isthmica* is allopatric with *A. xanthochroa* to the north, *A. australis* to the south, and *A. salti* and *A. merida* to the east. However, further collecting in regions between the currently known ranges is warranted, and may reveal parapatric or narrowly sympatric distributions. In spite of its occurrence on Barro Colorado Island, one of the most studied patches of tropical forest in the world, nothing is known of the biology of this species beyond its occurrence in *Cecropia* trees.

Additional material examined

PANAMA: *Canal Zone*: Monte Lirio (Wheeler) [MCZC]; Barro Colorado Island (Wheeler no. 704) [MCZC]; Barro Colorado Island (N. Banks) [MCZC]; *Panamá*: El Llano, 300 m (Choe) [Longino pers. colln.].

COLOMBIA: *Cundinamarca*: nr La Mesa, ca. 1200 m (W. L. and D. E. Brown) [MCZC].

Azteca lattke sp. nov.

(Figs 17, 32, 45)

Holotype queen: 15 km ESE Boconó, 9°11'N, 70°09'W, 1160 m, 23–24 August 1987, roadside vegetation, in *Cecropia libradensis* (Longino no. 1835) [MCZC].

Paratypes: 1 queen, same data as holotype except second growth forest, in *Cecropia* sapling (Longino no. 1820) [IZAV]; 2 queens, same data as holotype except in *Cecropia*

sapling (Longino no. 1836-s) [LACM]; 2 queens, 18 km E Boconó, 9°13'N, 70°07'W, 6–800 m, 25 August 1987, roadside vegetation, in *Cecropia* sapling (Longino no. 1856-s) [LACM]; 1 queen, 14 km ESE Boconó, 9°12'N, 70°09'W, 1500–1850 m, 25 August 1987, roadside vegetation, in *Cecropia palmatisecta* (Longino no. 1860-s) [MCZC].

Queen measurements ($n=7$). HL 1.71–1.81, HW 1.56–1.66, SL 0.92–0.96, CI 0.90–0.92, SI 0.57–0.60.

Queen diagnosis. Head subquadrate, about as long as wide, sides flat to weakly convex. Mandibles feebly microalveolate, sublucid, shiny near masticatory margin, with scattered puncta. Face sublucid, micropunctate, with appressed pubescence becoming sparse medially. In full-face view, setae projecting from occipital lobes, absent on sides of head above eyes. Scapes and legs densely setose. Petiole subpyramidal, in lateral view low, apex bluntly triangular; in posterior view broadly rounded. Ventral margin of petiole with shallow to moderately produced lobe, lobe ending before posterior rim, leaving short peduncle. Setae on anterodorsal face and ventral surface of petiole abundant, consisting of short erect pubescence beneath abundant long setae; dorsal setae projecting well beyond margins of petiole in posterior view, ventral setae evenly dispersed. Colour entirely dark brown.

Comments. This species is known only from Venezuela, from the coast ranges and the Cordillera de Merida. I have collected it only as incipient colonies in *Cecropia* trees, and I have seen alate queens that others have taken at lights, etc. A few of my collections were with small workers, but there are no collections of queens associated with workers from mature colonies. Further discussion is under *A. merida*.

Additional material examined

VENEZUELA: *Aragua*: Rancho Grande, 1100 m (Heppner) [USNM]; *Miranda*: 2 km S Baruta, 10°25'N, 66°53'W, 1200 m (Longino nos 1939-s, 1940, 1941); *Tachira*: San Cristobal, Est. del INOS, La Parada [IZAV]; Rio Frio, 600 m (Clavijo, Chacon and Ayala) [IZAV].

Azteca merida sp. nov.

(Figs 13, 14, 30, 45)

Holotype alate queen: Venezuela, Estado Trujillo, 15 km ESE Boconó, 9°11'N, 70°09'W, 1160 m, 23–24 August 1987, ex *Cecropia palmatisecta* (Longino no. 1832) [MCZC]. Paratypes: 10 workers: nestmates of holotype, same data; 10 queens: Venezuela, Estado Trujillo, 14 km ESE Boconó, 9°12'N, 70°09'W, 1500–1850 m, 25 August 1987, ex *Cecropia palmatisecta* saplings (Longino no. 1860-s) [IZAV, LACM, MCZC, USNM, BMNH, FSCA, MZSP, UCDC, MCSN, MHNG].

Queen measurements ($n=8$). HL 1.97–2.26, HW 1.71–2.03, SL 1.06–1.20, CI 0.87–0.90, SI 0.59–0.65.

Queen diagnosis. Head subquadrate, longer than wide, sides weakly to moderately convex. Mandibles feebly microalveolate, subopaque, with scattered puncta. Face sublucid, micropunctate. In full-face view, abundant setae on occipital lobes, erect setae present but less abundant on sides of head above eyes. Scapes and legs densely setose. Petiole subpyramidal in side view, with bluntly rounded apex, broadly rounded in posterior view. Ventral margin of petiole with shallow lobe, lobe ending before posterior rim, leaving short peduncle. Setae on anterodorsal face and ventral surface of

petiole abundant, of irregular length, not or weakly differentiated into long, coarse setae and short, fine setae. Dorsal setae projecting well beyond margins of petiole in posterior view, ventral setae evenly dispersed. Mandibles dark maroon, rest of head and body uniform orange or variably mottled with dark brown; when mottled, mesosoma is contrastingly lighter than head and gaster.

Worker (based on Longino no. 1832, the only worker–queen associated sample). Mandibles weakly microalveolate on basal half, shiny on distal half to masticatory margin. Basal face of propodeum convex, metanotal remnant not flat or co-planar with propodeum (similar to Fig. 41). Sides of head above eyes with abundant erect setae, similar to Fig. 38. Mesosomal dorsum densely pilose, similar to Fig. 42. Colour light yellow–brown, with very faint infuscation medially on frons, faint mottling on mesosoma.

Biology. This species is known only from collections I made on the eastern slopes of the Cordillera de Merida in Venezuela, where its range possibly corresponds to that of *Cecropia palmatisecta*.

At one site in Trujillo state I examined *Cecropia* along an elevational transect from 600 to 1850 m (*Cecropia* taxonomy follows Velásquez, 1972). *Cecropia peltata* occurred around 600 m, followed by *C. libradensis* from 600 to 1000 m, and *C. palmatisecta* from 1000 to 1850 m. Above this, non-myrmecophytic *C. telenitida* continued to above 2000 m. The transition from *C. libradensis* to *C. palmatisecta* also corresponded to a habitat shift from relatively disturbed agricultural land (small coffee plantations) to relatively undisturbed montane forest. *Azteca alfari* dominated samples from below 1000 m, with occasional *A. constructor* from the lowest elevations. At the 1000 m ecotone, where most collecting effort was concentrated, mixed saplings of *C. libradensis* and *C. palmatisecta* along a roadside contained colonies of *A. alfari*, *A. lattke*, and *A. merida*. Incipient colonies of each ant species were found in saplings of both tree species. A sample of *C. palmatisecta* saplings from 1000 to 1850 m yielded dozens of *A. merida* queens, only one *A. lattke* queen, and no queens of *A. alfari* or *A. constructor*. *Azteca merida* was found at one other site, in Lara state, also in *C. palmatisecta*.

The results of this survey suggest that, at least in the Cordillera de Merida, three ecologically similar *Azteca* species, *A. constructor*, *A. lattke*, and *A. merida*, have ranges corresponding to three *Cecropia* species, *C. peltata*, *C. libradensis*, and *C. palmatisecta*, with the ant–plant species pairs spatially segregated along an elevational gradient. *Azteca alfari* is ecologically distinct from the above three, perhaps a parasite on the *Cecropia*–*Azteca* system, and preferring frequently disturbed habitats (Longino, 1989b). It coexists with the above species when forested and agricultural habitats are adjacent, explaining its absence above 1000 m on the above transect. Similar community patterns, with correlated abrupt transitions between habitats, *Cecropia* species, and *Azteca* species, have been documented elsewhere (Longino, 1989a; Davidson and Fisher, 1991; and see Discussion below).

On a hillside covered with *C. palmatisecta* trees, many or possibly all with *A. merida* colonies, I cut down a 10 m-tall tree. There was a bulge in the trunk about half-way up, and inside the bulge was a spindle-shaped carton nest containing brood and several alate queens. I did not examine the nest in sufficient detail to ascertain whether a colony queen was present. The workers were extremely aggressive, enormous numbers pouring forth from the hole I cut in the trunk and covering the carton nest in a dense mat. This type of nest structure is similar to that seen in *A. muelleri*, *A. xanthochroa*, and *A. constructor*.

Additional material examined

VENEZUELA: *Lara*: 5 km SW Guarico, 9°36'N, 69°50'W, 1350 m (Longino nos 1799-2, 1800); *Trujillo*: 15 km ESE Boconó, 9°11'N, 70°09'W, 1160 m (Longino nos 1809-s, 1812, 1813, 1815-s, 1819, 1821, 1823-s, 1830-s, 1834, 1836-s, 1837-s).

Azteca muelleri Emery

(Figs 15, 28, 45)

Azteca muelleri Emery, 1893: 331. Syntype workers, queens: Brazil, Santa Catarina (Müller, Hetschko); and Brazil, Rio de Janeiro (Göldi) [MCSN, MHNG] (examined; Müller queen here designated Lectotype [MHNG]; same Müller series: 2 queens [MHNG], and 1 queen, 3 workers [MCSN] Paralectotypes).

Azteca nigella Emery, 1893: 332. Holotype (unique syntype?) worker: Brazil, Santa Catarina (Hetschko) [MCSN]. New synonymy (examined).

Azteca muelleri var. *wacketi* Emery, in Forel, 1908b: 391. Syntype workers, males: Brazil, São Paulo (v. Ihering) [label: 'Estação de Rio Grande, São Paulo, Ihering, Cecropia'] [MCSN]. New synonymy (examined; worker here designated Lectotype, remaining 11 workers, 3 males Paralectotypes).

Azteca muelleri var. *nigridens* Forel, 1908b: 392. Syntype workers: Brazil, state of Rio de Janeiro, Colonia Alpina (Göldi) [MHNG]. New synonymy (examined).

Azteca ulei var. *gibbifera* Forel, 1908b: 392. Syntype workers: Brazil, São Paulo (v. Ihering) [MHNG]. New Synonymy (examined).

Azteca muelleri var. *brunni* Forel, 1909: 251. Holotype (unique syntype) worker: Brazil, Bahia State, Bahia [label 'Salvador'] [MHNG]. New synonymy (examined).

Azteca muelleri var. *janeirensis* Forel, 1912: 48. Syntype workers: Brazil, Prov. Rio de Janeiro (Göldi, Sampaio); and Bolivia [MHNG]. New synonymy (examined; worker, label 'Sera Vermella, Prov. Rio (Göldi)' here designated Lectotype).

Azteca muelleri var. *nigella* Emery; Emery, 1912: 34.

Queen measurements ($n=7$ or 8). HL 1.76–1.83, HW 1.66–1.80, SL 0.97–1.04, CI 0.94–1.00, SI 0.57–0.59.

Queen diagnosis. Head subquadrate, about as long as wide, sides flat or weakly convex. Mandibles alveolate/striate, opaque, with scattered puncta. Face sublucid, micropunctate, with dense appressed pubescence. In full-face view, abundant setae on occipital lobes, erect setae present but less abundant on sides of head above eyes. Scapes and legs densely setose. Petiole pyramidal, apex subangular in lateral, tall and subangular in posterior view. Ventral margin of petiole with strong, deep lobe, lobe ending before posterior rim, leaving short peduncle. Pilosity on dorsal and ventral surfaces of petiole not differentiated into long, coarse setae and short, fine setae; anterior face of petiolar node with abundant fine setae of irregular lengths, ventral surface with similar setae roughly grouped in two clusters, one medially on ventral lobe, one around juncture of lobe and anterior peduncle. Head dark brown, lighter brown near antennal insertions, lateral portions of clypeus, sides of head; rest of body mottled burnt orange.

Worker. Mandibles shagreened, opaque. Head shape and mesosomal profile similar to *A. coeruleipennis* (Figs 39, 43). Sides of head above eyes with abundant erect setae. Pilosity on mesosomal dorsum similar to *A. constructor* (Fig. 42). Colour of head and mesosoma yellow or light brown; mandibles red-brown to deep maroon, often contrasting sharply with yellow head.

Comments. The worker of *A. muelleri* is relatively distinctive among *Azteca* species. The combination of shagreened mandibles and setose sides of the head is rare among *Azteca* species. The distinctiveness of this species allowed me to establish synonymy

based solely on workers in some cases, and to resolve whether the 'Salvador' label on *A. brunni* referred to El Salvador in Central America, or the old name for Bahia in Brazil. The holotype worker of *A. brunni* is clearly *A. muelleri*, and no similar workers are known from Central America.

The type of *A. nigella* is a single small brown worker, which alone cannot be distinguished from any number of *Azteca* species (including *A. muelleri*). In the original species description, Emery describes a worker and then states 'due esemplari raccolti dall'Hetschko'. In the Emery collection I found only one worker under *A. nigella*, but under *A. muelleri* I found a typical *A. muelleri* queen with the same data. Hetschko probably obtained a queen and a small worker from an incipient colony in a *Cecropia* sapling, and Emery, unaware of the gradual change in worker size and colour that occurs as *Azteca* colonies grow, considered the worker a new species. H. v. Ihering (1907), who had experience in the field, also surmised that collections identified as *A. nigella* were simply immature *A. muelleri* colonies.

Biology. This species is the classic *Cecropia* ant, the one first studied by F. Müller (1876, 1880–81), and subsequently by Schimper (1888), von Ihering (1907), and Eidmann (1945). It is known only from southern Brazil, where it colonizes *Cecropia adenopus*. Colonies form a spindle-shaped carton nest in the bole, which causes a bulging deformity in the trunk. This nest structure is illustrated in von Ihering, Wheeler (1910), and Eidmann, and is very similar to the nest structure of *A. constructor* described by Longino (1991).

Additional material examined

BRAZIL: Kajahi [or Kajahy, or Majahi, various spellings on labels] [MHNG]; Rio de Janeiro: 'Rio Janeiro' (Göldi) [MCSN]; Santa Catarina: no specific locality [LACM]; no specific locality (Schmalz) [MCSN]; Blumenau (Möller) [MHNG]; São Paulo: São Paulo [MHNG]; Ilha Victoria (v. Ihering) [MHNG].

Azteca ovaticeps Forel

(Fig. 2)

Azteca alfari var. *ovaticeps* Forel, 1904a: 44. Syntype queens, workers: Brazil, Pará (Göldi) [MHNG, MCZC] (examined).

Azteca alfari var. *aequalis* Forel, 1906: 239. Syntype workers: Brazil, Pará, Obidos (Göldi); and Brazil, Mexiana Island, Amazon delta (Hagmann) [MHNG, USNM] (synonymized by Longino, 1989b: 8, one MHNG Hagmann worker here designated Lectotype).

Comments. This species and its close relative, *A. alfari*, have been revised by Longino (1989b). Queens and males of the Hagmann series of *A. aequalis*, from which the lectotype was chosen, were incorrectly identified as syntypes in my earlier revision (the original description was based on workers only). The error is corrected here with the designation of a worker lectotype.

Azteca petalocephala sp. nov.

(Figs 12, 27, 45)

Holotype queen: Bolivia, La Paz: 9 km SW Coroico, 16°14'S, 67°47'W, 2000 m, 7 September 1987, ex *Cecropia*, montane rainforest edge (Ward no. 9108) [MCZC]. Paratypes: 6 queens: same data except Ward no. 9107-1 [UCDC, LACM, MCZC, USNM]. Additional non-type material: small workers accompanying holotype queen.

Queen measurements ($n=5$). HL 2.60–2.75, HW 2.09–2.29, SL 1.37–1.49, CI 0.80–0.86, SI 0.60–0.68.

Queen diagnosis. Head rectangular, strongly dorsoventrally flattened, longer than wide, sides flat. Mandibles densely microalveolate, opaque, with scattered puncta. Face feebly shining, densely micropunctate. In full-face view, occipital lobes and entire sides of head with abundant erect setae. Scapes and legs densely setose. Petiole pyramidal, apex bluntly triangular in side view, subangular in posterior view. Petiolar node with 2 long setae over erect pubescence. Ventral margin of petiole with weak lobe which slopes to posterior rim, no short peduncle posteriorly. Ventral surface of petiole with abundant coarse setae, dispersed evenly, no underlying erect pubescence. Head dark brown with lighter regions around antennal insertions and posterior margin of clypeus, rest of body burnt orange, degree of darkness variable, but always contrasting with darker head.

Comments. This species is known only from the type locality, where incipient colonies were collected from *Cecropia* saplings. It is sympatric with *A. australis* at this site.

Petalomyrmex phylax is an obligate plant ant in Africa, the queen of which has a strongly flattened head. McKey (1984) proposed that the flattened head is an adaptation that allows the queen to use a slit-shaped entrance hole, excluding queens of competing species of plant ants with broader heads. The same process may be driving the evolution of head shape in some *Cecropia* ants. The strongly flattened head of *A. petalocephala* is unique among *Cecropia* ants, although it is approached by *A. xanthochroa* and *A. salti*, and *A. xanthochroa* queens are known to use slit-shaped entrance holes. The main competitors in these systems are probably *A. australis* for *A. petalocephala* and *A. constructor* for *A. salti* and *A. xanthochroa*. The flat-headed condition also occurs in another group of arboreal ants from the Neotropics, *Camponotus* subgenus *Myrmostenus*. These ants are known only from queens, but I predict they will prove to be specialist plant ants.

Azteca salti Wheeler, stat. nov.

(Figs 10, 25, 45)

Azteca xanthochroa subsp. *salti* Wheeler, 1942: 250. Syntype workers, queens: Colombia, Sierra Nevada de Santa Marta, Vista Nieve, 5000 ft (Salt) [MCZC] (examined).

Queen measurements. HL 2.38, HW 1.80, SL 1.26, CI 0.76, SI 0.70.

Queen diagnosis. Head rectangular, longer than wide, sides flat. Mandibles largely shiny with widely spaced small puncta. Face strongly shining, pubescence dilute to absent medially. In full-face view, short setae present on occipital lobes, lacking on sides of head above eyes. Scapes and legs densely setose. Petiole pyramidal, apex bluntly triangular in side view, rounded in posterior view. Petiolar node with a conspicuous, projecting clump of 5–6 long, coarse setae on each side. Ventral margin of petiole with weak lobe, lobe ending before posterior rim, leaving a short peduncle. Coarse setae clustered around juncture of lobe and anterior peduncle, absent medially, 2 posteriorly. Ventral erect pubescence similarly clustered anteriorly and posteriorly, with a medial gap. Body colour orange, with infuscation on face.

Comments. This species is known only from the type series, collected from 'internodes of young *Cecropias*' (Wheeler, 1942) at a montane site in the Sierra Nevada de Santa

Marta, Colombia. It is very similar to Costa Rican *A. xanthochroa*, differing in the shape and dorsal pilosity of the petiole.

***Azteca xanthochroa* (Roger)**

(Figs 4, 5, 6, 23, 24, 36, 37, 41, 45)

Liometopum (?) *xanthochroum* Roger 1863: 167. Holotype (unique syntype) queen: Mexico. *Iridomyrmex xanthochrous* (Roger); Mayr, 1866: 497 (partim) [Mexican workers described; later found to be a different species].

Liometopum instabile, in the sense of Mayr, 1877: 870 (partim) [*xanthochroa* incorrectly synonymized under *instabile*].

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

Azteca xanthochroa (Roger); Emery, 1896: 2 [description of Costa Rican workers; exclusion of Mexican workers described in Mayr 1866].

Azteca xanthochroa (Roger); Wheeler, 1942: 248 [description of workers from Guatemala].

Azteca xanthochroa var. *costaricensis* Wheeler, 1942: 248 [for Costa Rican workers described by Emery, 1896: 2 as *xanthochroa*]. Syntype workers: Costa Rica, Limón province, Jimenez (Alfaro) [label: 'Jimenez, C.R. v.95'] [MCSN, NHMW]. New synonymy (examined; NHMW worker here designated Lectotype, second worker on same pin and 4 MCSN workers Paralectotypes).

Queen measurements ($n=19$). HL 1.19–2.65, HW 1.90–2.17, SL 1.18–1.37, CI 0.79–0.91, SI 0.59–0.70.

Queen diagnosis. Head subquadrate, longer than wide, sides flat to weakly convex. Face strongly shining, pubescence dilute to absent medially. In full-face view, short setae present on occipital lobes, lacking on sides of head above eyes. Scapes and legs densely setose. Petiole pyramidal, apex subangular in posterior view. Petiolar node with 0–5 long setae over sparse erect pubescence. Ventral margin of petiole with weak lobe, lobe ending before posterior rim, leaving a short peduncle. Coarse setae clustered around juncture of lobe and anterior peduncle, absent medially, 0–2 posteriorly. Ventral erect pubescence similarly clustered anteriorly and posteriorly, with a medial gap. Body colour orange, often with infuscation on face.

Worker. Mandibles strongly shining (Costa Rica) or with basal half faintly micro-alveolate (Mexico). Head shape and pilosity as in Figs 36, 37. Mesosomal profile and pilosity as in Fig. 41. Mandibles light to dark red–brown; head orange with variable extent of infuscation clouding frons medially; mesosoma similar to head, mottled orange–brown.

Comments. Mexican queens and Costa Rican queens differ in head shape and mandible sculpture. Mexican queens have shorter heads with more rounded sides, and the mandibles are shagreened, opaque. Costa Rican queens have longer, strongly rectangular heads, and the mandibles are strongly shining, with sparse puncta. However, the few Guatemalan queens I have examined are somewhat intermediate in head shape and mandible sculpture, and a few Costa Rican queens exhibit faint shagreening on the mandibles. I am interpreting the specimens from western Panama northward as one polytypic species.

Medium-sized workers of *A. xanthochroa* are darker and more pilose than the large workers, and are very similar to workers of *A. constructor* (compare Figs 37, 38). At some upland wet forest sites in Costa Rica, where *A. xanthochroa* colonies appear somewhat stunted (see below), worker series of *A. xanthochroa* and *A. constructor* are nearly indistinguishable.

Biology. In Costa Rica, *A. xanthochroa* is one of the most common *Cecropia* ants in wet forested areas. In the Atlantic lowlands, colonies are most frequently found in *C. obtusifolia*, a common tree of disturbed areas. *Cecropia insignis*, a tree more often in primary forest, is dominated by *A. ovaticeps*. As one moves up-slope, both *C. obtusifolia* and *A. ovaticeps* drop out, and *A. xanthochroa* is then frequently found in *C. insignis*, throughout the rest of its elevational range (up to 1100 m in the Peñas Blancas Valley east of Monteverde). Above this limit, *C. insignis* is replaced by the non-myrmecophytic *C. polyphlebia*. Founding queens may be found in *C. polyphlebia* saplings, well above the elevational limit of *C. insignis*, but never in mature trees. These queens are presumably doomed dispersants from lower elevations. On the Pacific slopes of northwestern Costa Rica a narrow band of *C. obtusifolia* separates cloud forest *C. polyphlebia* from the common *C. peltata* which is throughout the seasonally dry lowlands. *Azteca xanthochroa* is common in this narrow band, but does not occur at lower elevations where *C. peltata* dominates (Longino, 1989a).

Emery (1896) records Alfaro's observations of *A. xanthochroa* in Costa Rica. Alfaro observed *A. xanthochroa* running with abdomen raised, a behaviour that distinguished it from other *Cecropia* ants in Costa Rica. He observed that the nest entrance was a longitudinal fissure, and found carton septa inside the chambers. He further claimed that the species was less aggressive, and did not bite the collector's hand.

Longino (1991) describes nest architecture and worker behaviour. In *C. obtusifolia*, colonies maintain a longitudinal fissure near the base of the tree, from which very large workers emerge when the tree is disturbed. These larger workers bite 'the collector's hand' only infrequently, perhaps because they have difficulty manoeuvring their large heads or obtaining a grip with their large mandibles (Perlman, personal communication). Many smaller workers emerge from branch tips, however, and these are very aggressive and readily bite. All reproduction is concentrated in a single carton nest in the bole. Internal communication is maintained with all branch tips, which contain only workers, coccoid homoptera, and cached muellerian bodies. Nest structure appears quite different in *C. insignis*, perhaps due to the much thicker wood of the bole, or to the fact that it is inhabited mainly at higher elevations where it is much cooler and wetter. For example, in the Peñas Blancas Valley (800–900 m), colonies are smaller and less aggressive. They occur high in the tree, sometimes in only a portion of the crown, and they do not maintain a basal fissure.

Additional material examined

COSTA RICA: Province unknown: La Fuente (Alfaro) [LACM, USNM, MCSN]; no spec. loc., ex col. Emery, Col. T. Pergande [USNM, possible syntypes of *costaricensis*]; *Alajuela*: Rio Peñas Blancas, 10°18'N, 84°42'W, 940 m (Longino); Rio Peñas Blancas, 10°19'N, 84°43'W, 800 m (Longino nos 1516-s, 1517-s, 1605-s, 1620, 2517, 2518-s, 2520, 2525); 10 km E Monteverde, 10°19'N, 84°43'W, 950 m (Longino no. 1653-s); N side Laguna Arenal, 10°30'N, 84°43'W, 480–500 m (Longino nos 1710-s, 1712, 1716, 1718-s, 1720-s); *Cartago*: 4 km E Moravia, 1200 m, 9°49'N, 83°25'W (Longino no. 902-s); 8 km ESE Moravia, 900 m, 9°48'N, 83°23'W (Longino no. 935-s); 7 km ESE Moravia, 1150 m, 9°48'N, 83°23'W (Longino nos 938-s, 939-s); Turrialba (SS & D Duckworth) [USNM]; *Guanacaste*: 4 km W Santa Cecilia, 250 m, 11°04'N, 85°27'W (Longino no. 427-s); N side Laguna Arenal, 10°32'N, 84°58'W, 570 m (Longino nos 1698-s, 1700-s, 1701-s, 1702, 1703-s, 1706-s); N side Laguna Arenal, 10°32'N, 84°53'W, 570 m (Longino no. 1707-s); 2 miles E. Tilaran (Janzen); 2 miles W Tilaran (Janzen); *Heredia*: Zona Protectora, 500 m, 10°20'N, 84°04'W (Longino nos

176, 178); 15 km S Pto. Viejo, 500 m, 10°19'N, 84°02'W (Longino no. 1076); 17 km S Puerto Viejo, 10°18'N, 84°02'W, 600 m (Longino nos 2236, 2240-s, 2241-s, 2242-s, 2243-s, 2244-s, 2245-s, 2246-s, 2249-s, 2250-s, 2251-s, 2252-s, 2253-s, 2254-s, 2255-s, 2256-s, 2257-s, 2259-s, 2260-s, 2261-s, 2263-s, 2264-s, 2265-s, 2266-s); 16 km N Volcan Barba, 950 m, 10°17'N, 84°05'W (Longino no. 1371-s); 15 km N Volcan Barba, 1100 m, 10°16'N, 84°05'W (Longino no. 1375-s); Horquetas, 10°21'N, 83°58'W, 50 m (Longino no. 2173); Estacion Biologica La Selva, 10°26'N, 84°00'W, 50 m (Longino nos 2419, 2420, 2441); La Selva (Janzen); La Selva (Davidson CR-20); *Limón*: Tortuguero, < 5 m, 10°32'N, 83°31'W (Longino nos 341-s, 356); Tortuguero, 10°35'N, 83°31'W, 5 m (Longino nos 2105-s, 2125-s); Reserva Biologica Hitoy Cerere, 100 m, 9°40'N, 83°02'W (Longino nos 964, 975-s); 6 km WNW Pto. Viejo, 50 m, 9°40'N, 82°49'W (Longino nos 1029, 1031-s, 1038-s); Los Diamantes [near Guapiles], 350 m (J. Robertson); Guapiles (Hampton); *Puntarenas*: Monteverde, 10°18'N, 84°48–9'W, 1190–1460 m (Longino nos 1976-s, 2383, 2385, 2386, 2387, 2388, 2462, 2464, 2473, 2474, 2475, 2477, 2481, 2484, 2487, 2491, 2492, 2493, 2494, 2495, 2497, 2502, 2503, 2535, 2536, 2537, 2540, 2546); Guacimal, 500–600 m, 10°14'N, 84°51'W (Longino); 2 km SSE Monteverde, 1150 m, 10°17'N, 84°48'W (Longino no. 1045); Reserva Biologica Carara, 9°47'N, 84°35'W, 400 m (Longino no. 2196); 4 km S San Vito, 8°47'N, 82°58'W, 1200 m (Longino nos 2391-s, 2392-s); San Vito (Janzen); Corcovado National Park (Davidson CR-48, 94); Golfito (Truxal & Menke); *San José*: 2 km NE Guayabo, 1040 m, 9°52'N, 84°15'W (Longino no. 1569-s); Parque Nacional Braulio Carrillo, Carrillo, 600 m, 10°09'N, 83°57'W (Longino no. 2099).

GUATEMALA: *Alta Vera Paz*: 30.3 Cacao, Trece Aguas (Barber & Schwarz) [MCZC]; *Esquintla*: Esquintla (Wheeler) [MCZC]; *Izabal*: Quirigua (Wheeler) [USNM, MCZC]; Puerto Barrios (Wheeler) [MCZC]; *Suchitepéquez*: Patulul (Wheeler) [MCZC].

HONDURAS: Province unknown: San Juan Pueblo [USNM]; *Colón*: Puerto Castillo (Bequaert) [MCZC, USNM].

MEXICO: State unknown: Teh., St. Lucrecia (Mann) [USNM]; *Oaxaca*: Palomares (Petrunkevitch [?, illeg.]) [MCZC]; 8 miles S Valle Nacional B-4, 2400 ft (Snelling nos 73-106, 73-107); *Tabasco*: Teapa [MHNG]; *Veracruz*: Mirador (Skwarra) [MCZC, LACM]; Las Hamacas, 17 km N Santiago Tuxtla (Wilson no. 323) [MCZC]; Fortin de las Flores (Snelling no. 73-120); Estacion Biologica Los Tuxtlas near San Andres Tuxtla (G. Ibarra M. no. 2372); Los Tuxtlas (G. Ibarra nos 1997, 2003).

PANAMA: *Bocas del Toro*: Changuinola District (G. C. Wheeler nos 136 D,h,j) [Wheeler pers. colln]; *Chiriquí*: Bugaba, 800–1500 m (Champion) [MHNG].

Discussion

Phylogeny

Phylogenetic hypotheses are cursory given the present state of knowledge. The character systems used here for species-level taxonomy—head shape, pilosity, and colour—are probably prone to frequent homoplasy, and determining polarity of character states is problematic.

The hairless appendages, the small queen size, the deep ventral lobe on the queen petiole, and the polydomous nesting habits of *A. alfari* and *A. ovaticeps* set them apart from the other taxa treated here. One or more of these character states may be apomorphic, allying the *A. alfari* group with other stem-nesting *Azteca* species such as *A. forelii* and *A. longiceps*.

Mottled orange to pure orange queen coloration, if a synapomorphy, unites *A. xanthochroa*, *A. isthmica*, *A. salti*, *A. aragua*, *A. merida*, *A. australis*, *A. petalocephala*, and *A. muelleri* in one lineage, which I will refer to as the *A. muelleri* complex. These taxa also have large, subpyramidal petioles, a possible apomorphic character state. Petioles of most other taxa in the genus are either more flattened and scale-like, or smaller, lower, and more blunt (like *A. coeruleipennis*). With the exception of *A. australis* and *A. petalocephala*, these taxa are allopatric or parapatric. They tend to be found in montane regions, and could represent a lineage which has been split up as a result of Central and South American mountain-building during the Tertiary.

Azteca lattke shares all the characters of the *A. muelleri* complex, except that its queens are solid black. In fact, the queen petiole looks very much like the petioles of *A. aragua* and *A. merida*. Thus, *A. lattke* could prove to be a member of the *A. muelleri* complex, with a colour reversal.

Azteca constructor shares several characters—short head, dense pilosity, and the formation of a central carton nest in the tree bole—with members of the *A. muelleri* complex, but all of these characters may be plesiomorphic. The extremely long dorsal pilosity is apparently an autapomorphy; I have seen it in no other *Azteca* species. The petiole shape is completely unlike members of the *A. muelleri* complex, and is reminiscent of *A. gnava*, a Costa Rican species that forms large ant gardens (and may be close to or synonymous with *A. ulei*).

Azteca coeruleipennis exhibits a perplexing mix of characters. The small worker size and the polydomous nesting habit are similar to *A. alfari*. The head shape and pilosity is reminiscent of an *A. muelleri* complex species. The petiole shape is unique, but is closest to other species of stem-nesting *Azteca* such as *A. belti*, *A. pittieri*, and *A. patruelis*.

To conclude, the precise relationships of these taxa are far from known, but it is very likely that at least two lineages are represented whose most recent common ancestor was not an obligate *Cecropia* inhabitant. I propose that the *A. muelleri* complex arose from an ancestor that nested in dead branches or in external carton nests, while the *A. alfari* group arose from an ancestor that nested in live stems of trees. *Azteca constructor* could represent a third colonization of *Cecropia*, from an ancestor that made ant gardens. Alternatively, it may represent a basal lineage, with a plesiomorphic petiole shape, from which the more pyramidal petiole of the *A. muelleri* complex was derived.

Ecology

Local regions support two to five *Cecropia*-inhabiting *Azteca* species (Table 1). Competition appears to be intense, with multiple queens and multiple species initiating colonies in individual saplings and vying for dominance (Longino, 1989a; Davidson *et al.*, 1989). What mechanisms might lead to coexistence of species in the face of competition for the same limited resource? The answer is probably some form of niche partitioning based on preference for particular habitats and/or *Cecropia* species.

As I have described in the species accounts, the *Azteca* species in Table 1 are not randomly distributed with respect to habitat or *Cecropia* species. In at least three regions, Costa Rica, Venezuela, and Peru (Davidson *et al.*, 1991; Davidson and Fisher, 1991), there are three-way correlations between habitat, *Azteca* species, and *Cecropia* species. Davidson and Fisher (1991) discussed possible adaptive explanations for the correlations, relying on plant defence theory. Here I discuss possible proximate mechanisms. The following causes could generate the observed patterns: (1) habitat characteristics could determine *Azteca* distribution, (2) habitat characteristics could

Table 1. *Cecropia*-inhabiting *Azteca* communities by region. Species are represented by the first three letters of their specific epithet (see Checklist).

Central America	alf	ova	xan	con	—	coe
Panama, Colombia	alf	—	ist	con	—	
Sierra Nevada de Santa Marta	alf	—	sal	con	—	
Coast ranges of Venezuela	alf	—	ara	con	lat	
Cordillera de Merida, Venezuela	alf	ova	mer	con	lat	
Peru, Bolivia, Amazon Basin	alf	ova	aus	—	—	pet
Southeastern Brazil	alf	—	mue			

determine *Cecropia* distribution, (3) *Azteca* species could influence *Cecropia* distribution, and (4) *Cecropia* species could influence *Azteca* distribution.

Habitat effect on *Azteca*. Habitat features include temperature, rainfall, seasonality, and disturbance regime, all of which probably influence distributions of *Azteca* and *Cecropia*. Cold, wet conditions may determine the upper elevational limit for many *Azteca* species. The diversity and abundance of the genus as a whole drops quickly with increasing elevation, but certain *Cecropia* ants are exceptional in attaining elevations of 2000 m. In elevational transects, *Cecropia* ants always far exceed all other members of the genus. Differential tolerance of cold, wet conditions among obligate *Cecropia* ants could result in elevational habitat partitioning based on climate alone. Examples where high elevation tolerance may promote coexistence are *A. salti* vs. *A. constructor* in Colombia, *A. aragua* or *A. merida* vs. *A. lattke* vs. *A. constructor* in the two Venezuelan sites, and *A. petalomymex* vs. *A. australis* in Bolivia.

The long seasonal drought of tropical dry forest may have adverse effects on *Cecropia* ants by decreasing host-tree muellerian body production, and by decreasing internode humidity to damaging levels. *Azteca coeruleipennis* may be a tropical dry forest specialist, with adaptations for tolerating prolonged drought. I examined branches of several *A. coeruleipennis*-inhabited trees during the dry season, and observed that exit holes were very few and very small. Leafy branch tips were perforated by one or two active entrances, often 10 or more internodes back from the terminal sheathing stipule. In contrast, other *Azteca* species typically maintain five or more active entrances in the terminal 10 internodes. Occupied branch sections which contained alate queens bore active entrances which were only large enough for workers. Larger tunnels were excavated in the internode walls, but these ended blindly within a millimetre of the surface, as though the final perforation were suspended until wet season and/or the time of flight of new queens. Control of entrance size and abundance may be an adaptation for reducing water loss.

Disturbance regime is probably a major factor affecting *Azteca*–*Cecropia* communities. Frequent disturbance may favour an *Azteca* species that reproduces early at the expense of tree defence, while infrequent disturbance may favour species with greater investment in tree defence and consequence delayed reproduction. Widely spaced disturbances may favour the production of many small queens for long-distance dispersal. Closely spaced disturbances may favour the production of fewer, larger queens for greater competitive ability.

I think a major pattern in *Cecropia*–ant communities is caused by disturbance regime. Throughout the Neotropics, *A. alfari* dominates *Cecropia* trees on frequently chopped roadsides and agricultural land, while other *Azteca* species dominate *Cecropia* trees in primary forest or very old second growth forest. Three characteristics

of *A. alfari* favour its dominance in areas of frequent and large disturbance: early reproduction in small trees, small queen size (the smallest of the *Cecropia* ants), and weak defence of host tree. In contrast, most of the other species (where known) reproduce only in the boles of large trees, have larger queens, and are strong defenders of their host trees.

Azteca ovaticeps, a close relative of *A. alfari*, is enigmatic. It shares behavioural features and size with *A. alfari*, but tends to occur in areas of frequent disturbance which are embedded in primary forest: river margins in Brazil and Peru, new roadcuts or new clearings in otherwise forested areas of Costa Rica and Venezuela (Longino, 1989b). *Azteca ovaticeps* is also more geographically variable than *A. alfari*. The following historical scenario would explain the current distribution and character of *A. alfari* and *A. ovaticeps*. The *A. alfari* group initially may have been a set of allopatric populations, each confined to small areas of high natural disturbance. One of these populations may have been particularly well-suited to a very high disturbance regime, expanding in concert with human habitat alteration in the Neotropics and, through secondary contact, becoming sympatric with the other populations. This expanding population, now called *A. alfari*, would be very uniform over a large range. The remaining populations, now collectively called *A. ovaticeps*, would exhibit the ancestral pattern of allopatry and geographic variation.

Habitat effect on *Cecropia*. The same habitat factors which potentially influence ant distribution are likely to influence *Cecropia* distribution through their actions on fruit dispersal, germination, and survivorship. *Cecropia* species often show pronounced elevational zonation, perhaps due to climatic effects. *Cecropia* are probably affected by disturbance regime, some species being clearly 'weedy', invading large man-made disturbances, others being 'forest' species, occurring more often in gaps in primary forest.

Given that the same habitat features might influence the distribution (and segregation) of *Azteca* species and *Cecropia* species, the observed ecological 'preference' (meaning correlation) of certain *Azteca* species for certain *Cecropia* species could result from independent but similar responses to these habitat features. Alternatively, biotic interactions between trees and ants might cause the species sorting and association.

***Azteca* effect on *Cecropia*.** An ecological correlation between *Azteca* species and *Cecropia* species could result from ant effects on their host trees, in which interspecific variation in ant defensive behaviour has demographic consequences for the *Cecropia* population. At La Selva Biological Station in Costa Rica, a strong pattern of host association is observed. Populations of small *C. obtusifolia* trees in young second growth vegetation, at the edge of the station property, contain the four *Azteca* species *A. xanthochroa*, *A. constructor*, *A. alfari*, and *A. ovaticeps*, each of them common. In contrast, large *C. obtusifolia* trees in old second growth forest contain only *A. xanthochroa* and *A. constructor*. This pattern may result from differential mortality of trees during succession, the relatively undefended trees inhabited by *A. alfari* and *A. ovaticeps* succumbing to herbivory and vine encroachment.

***Cecropia* effect on *Azteca*.** Finally, correlations between tree species and ant species could result from tree effects on ants. Chemical or anatomical features of *Cecropia* trees could influence *Azteca* distribution, independent of habitat effects. Tree effects on *Azteca* could manifest themselves as host-specific searching by founding queens, or differential mortality of *Azteca* species following colonization. If either of these

processes occur, they are not absolute. Founding queens are generalists with respect to species of *Cecropia* sapling, and will even colonize saplings of non-myrmecophytic species. Mature colonies of a single species of *Azteca* may be found inhabiting several *Cecropia* species in a region. However, tree species could still have differential effects on *Azteca* in a non-absolute way. Founding queens may exhibit a preference for certain tree species that is a function of motivation, such that failure to find a suitable host tree within a particular time results in addition of species to their search profile. Even if queens are absolutely generalized in their search for *Cecropia* saplings, fitness effects could produce patterns. Two *Azteca* species might have reversed competitive relationships in two *Cecropia* species. Each *Azteca* species would dominate in areas dominated by its preferred tree species, but abutting distributions or mixed populations of the two tree species would be indeterminate with respect to species of ant occupant. The elevational zonation of *Azteca* species that was described under *A. merida* could result from such a process.

At La Selva Biological Station, another feature of the pattern of host association may be explained by interspecific variation in *Cecropia* characteristics. In primary forest and old second growth, large *C. obtusifolia* trees are dominated by *A. xanthochroa* or *A. constructor*, while the intermingled population of large *C. insignis* trees is dominated by *A. ovaticeps*. *Cecropia insignis* appears to rely less on ant protection than *C. obtusifolia*. Relative to *C. obtusifolia*, its trichilia are more irregular and they appear later on saplings. In contrast to *C. obtusifolia*, young trees occupied by *A. alfari* and *A. ovaticeps* do not appear more herbivore-damaged or vine-covered than those occupied by *A. xanthochroa* or *A. constructor*. *Azteca ovaticeps* may be favoured in *C. insignis* because (1) *C. insignis* does not require strong ant defence to survive, and (2) *A. ovaticeps* is somehow competitively superior at colonizing *C. insignis*. *Cecropia obtusifolia* may be dominated by *A. xanthochroa* and *A. constructor* because it requires aggressive ant defence to survive, regardless of competitive relationships among ant species at colonization.

Most of the above speculations regarding the community ecology of the *Azteca*–*Cecropia* association can be framed as hypotheses amenable to experimental test. This taxonomic work should facilitate such ecological studies and encourage additional systematic investigations which will clarify the evolutionary history of this most conspicuous ant–plant relationship.

Acknowledgements

Numerous people have helped me in my studies of *Cecropia* ants in the northern Neotropics, most notably Lisa Ellis, Dan Perlman, Nalini Nadkarni, and a large number of OTS and University of California students. My development of species concepts for the southern Neotropics has depended almost entirely on the work of Ana Harada in Brazil, and the collections of Diane Davidson from Peru and Phil Ward from Bolivia. This work relies heavily on the legacy of effort contained in taxonomic collections; over a century of past collectors and curators deserve some credit. The following contemporary curators were extremely helpful in the loan of specimens and during museum visits: C. Besuchet, D. Burckhardt, and I. Löbl (MHNG), B. Bolton (BMNH), V. Raineri (MSNG), M. Brancucci (NHMB), M. Fischer (NHMW), S. Cover (MCZC), D. Smith (USNM), R. Snelling (LACM), and P. Ward (U.C. Davis). The Millers provided assistance at the Allyn Museum. This work was supported by National Geographic Grants 2900-84 and 4064-89 to Longino, and NSF Biological Research Resources Program grant BSR-8800344 to LACM (Hogue).

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