Taxonomy of the *Cecropia*-Inhabiting Ants in the *Azteca alfari* Species Group (Hymenoptera: Formicidae): Evidence for Two Broadly Sympatric Species

John T. Longino[1]

ABSTRACT. The numerous species of the genus *Azteca* constitute a large neotropical radiation of dolichoderine ants. All species are arboreal, nesting in external carton nests, cavities in dead trunks or branches, or in live stems. Of the latter, some exhibit obligate associations with specialized myrmecophytes. Myrmecophytic *Cecropia* trees are inhabited by several distinct species groups of *Azteca*. One of these is here defined and revised as the *Azteca alfari* species group, composed of two broadly sympatric, polytypic species: *A. alfari* sensu stricto and *A. ovaticeps*. The following new synonymy is proposed: *Azteca alfari* Emery = *A. alfaroi* race *lucidula* Forel = *A. virens* Forel = *A. alfari* subsp. *cecropiae* Forel = *A. alfari* var. *mixta* Forel = *A. alfaroi* var. *fumaticeps* Forel = *A. alfari* var. *curtiscapa* Forel = *A. foreli* race *breviscapa* Forel = *A. lynchi* Brèthes = *A. alfari* var. *argentina* Forel = *A. alfari* var. *langi* Wheeler = *A. alfari* subsp. *lucidula* var. *zonalis* Wheeler, and *Azteca ovaticeps* Forel = *A. alfari* var. *aequilata* Forel = *A. alfari* var. *aequalis* Forel = *A. alfari* subsp. *tuberosa* Forel. *Azteca alfaroi* race *lucida* Forel is raised to species, but excluded from the *A. alfari* group.

RESUMEN. Las hormigas dolichoderinas del género *Azteca* tienen una dispersión neotropical. Los especies son sumamente arbóreo, nidificando en panales de sustancia vegetal, en tallos secos, o en tallos verdes. Algunos de los especies que habitan tallos verdes forman asociaciones simbióticas con plantas mirmecófilas, incluyendo el género *Cecropia*. Algunos grupos-especies distintos de *Azteca* habitan arboles mirmecófilos de *Cecropia*. Aquí defino y reviso uno de estos grupos-especies, el grupo de *Azteca alfari*, compuesto de dos especies politípicos, de distribución amplia y simpátrica.

INTRODUCTION

Ants in the dolichoderine genus *Azteca* are major elements of neotropical forest ant communities (Forel, 1899). The numerous species exhibit a variety of nesting habits, inhabiting external carton nests, dead branches, dead cores of living trees, and live branches. The species that have attracted the most attention are those that form specialized associations with myrmecophytic plants, in particular those that inhabit *Cecropia* trees (reviews in Bequaert, 1922; Wheeler, 1942; Janzen, 1969, 1973; and Buckley, 1982). Lack of adequate species-level taxonomy for the *Azteca–Cecropia* association has delayed and obscured understanding of this prominent ant–plant system. Advances are being made in the taxonomy of *Cecropia* (*e.g.* Berg, 1978a,b), and here I present a first contribution to the taxonomy of *Cecropia*-inhabiting *Azteca*.

Forel (1878) established the genus *Azteca,* basing it on the polymorphic worker caste and features of the proventriculus. The weakly chitinized integument and the reflexed proventricular sepals allied *Azteca* with the genera *Iridomyrmex, Liometopum,* and *Tapinoma.* The definition of the genus has remained essentially unchanged, and as currently recognized the genus is almost certainly a monophyletic group within the Tapinomini (S.O. Shattuck, pers. comm.). Emery (1893) provided the first and as yet only revision of *Azteca,* recognizing 25 valid names. A flurry of disconnected descriptions followed, bringing the total to 155 available names (Kempf, 1972) but no real understanding of the genus.

1. Department of Biological Sciences, University of California, Santa Barbara, California 93106; Research Associate, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

Within the large genus *Azteca*, a few species are obligate inhabitants of *Cecropia* trees (Benson, 1985; Longino, 1989). These are *A. coeruleipennis* Emery, 1893, *A. constructor* Emery, 1896, *A. muelleri* Emery, 1893, *A. xanthochroa* (Roger, 1863), and *A. alfari* Emery, 1893. The latter three are species complexes with numerous infraspecific taxa. Species in the *A. alfari* complex can be distinguished from all other obligate *Cecropia* inhabitants by the lack of standing setae on the tibiae and scapes.

In this report, the *A. alfari* group is defined and revised. The species group is interpreted as a complex of two closely related, polytypic species, broadly sympatric in the Neotropics.

MATERIALS AND METHODS

COLLECTIONS

Collections are referred to by the following acronyms, following Arnett and Samuelson (1986).

LACM: Natural History Museum of Los Angeles County, Los Angeles, CA, USA
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
USNM: National Museum of Natural History, Washington, DC, USA

Much of the non-type material on which this study was based is from personal, LACM, and MCZC collections. Personally collected material from Costa Rica, Colombia, and Venezuela has been deposited in LACM and national collections of the countries of origin.

METHODS

Measurements were made at 63× magnification, with an ocular reticule, and are accurate to the nearest 0.01 mm. All measurements are presented in mm. Sculpture terminology generally follows Harris (1979). Drawings of queens and workers were made freehand using a Zeiss dissecting microscope with an eyepiece grid. Male antennae were illustrated by photographing either dry-mounted specimens or slide-mounted antennae and tracing from the projected negatives. The following characters are used:

HL: Head length (workers and queens), measured in frontal view (occipital border and anterior border of clypeus in same plane of focus) along the midline, from a point level with the posteriormost points of the occipital lobes to the anterior border of the clypeus.
HW: Head width (workers and queens), measured in frontal view across the widest portion of the head above the eyes.
SL: Scape length, not including basal neck and condyle.
EL: Eye length on longest axis.
WL: Weber's length (workers and queens), straightline distance from anteriormost point of pronotum (near pro-mesonotal suture for queens) to posteriormost point of metapleural lobe, accurate to 0.05 mm.

The following indices are reported:

CI: HW/HL
SI: SL/HW

The following setal counts are used:

GTC: Number of standing setae on second gastric (fourth abdominal) tergite exclusive of posterior row, including portion of tergite that wraps laterally to the ventral side of the abdomen. Counted on queens only. The posterior row continues up the lateral margins of the tergite (on the ventral surface of the gaster). When GTC > 5, the setae are usually somewhat symmetrically arranged on the abdominal dorsum, with fewer on the lateral portions of the tergite.
MSC: Number of standing 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. When more than 10 setae are present, counting is difficult and requires constant repositioning of the specimen. Counts are made up to 19 setae, after which specimens are scored as ≥20. Also, this character is subject to specimen age bias, due to rubbing and presumed progressive loss of setae.

Measurement data are presented in tabular form to aid in comparing the two species. In choosing material to measure, an attempt was made to minimize nonindependence of samples due to close genetic relatedness. Usually only one specimen per caste per colony was measured, and from at most three colonies per collecting site.

For worker measurements, a single worker was chosen from among the largest workers in a nest series. Interpretation of measurement data is difficult for the polymorphic workers of *Azteca*. There are prolonged ontogenetic and/or colony size-specific changes in worker size distribution and color (pers. obs.). Workers in incipient colonies are small and darkly pigmented. Larger and/or older colonies exhibit a great variability in color and maximum worker size, but the largest and lightest-colored workers are generally from very large colonies. Allometric head-shape change produces variable head shape both within and between colonies. These conditions make worker size and head shape poor taxonomic characters. Worker measurements are reported here to distinguish the *A. alfari* group from other species groups, rather than to differentiate species within the group.

The frequent occurrence of sympatric sibling species in the *A. alfari* group, coupled with imprecise designation and labeling of type material by early workers, has resulted in uncertainty regarding types, and occasionally syntype series consist of more than one species. I have found it necessary to make extensive use of lectotype designations to fix names and establish synonymy. For many taxa, I have designated lectotypes from what I judge to be a single nest series (based on data labels), from the available syntype material.

EVIDENCE FOR SYMPATRIC SPECIES

Azteca alfari group queens can be found in large numbers colonizing *Cecropia* saplings (Longino, 1989). Prior to dominance by a single colony, each internode of a sapling may house one or more founding queens. At several sites, I have found that *A. alfari* group founding queens occur in two discrete forms: one darkly pigmented and sparsely pi-
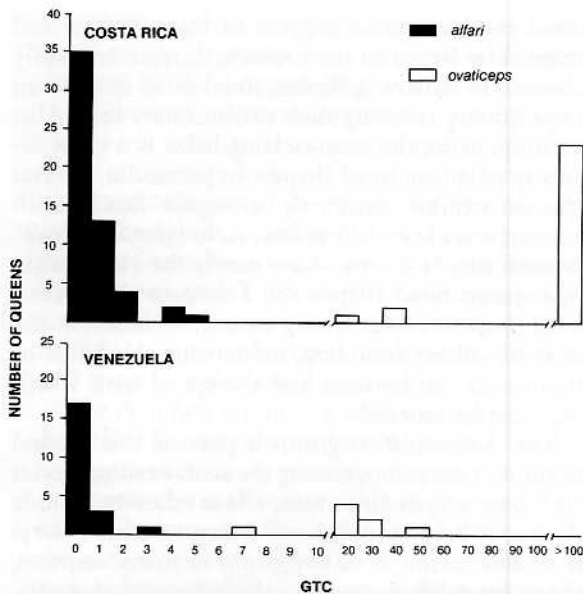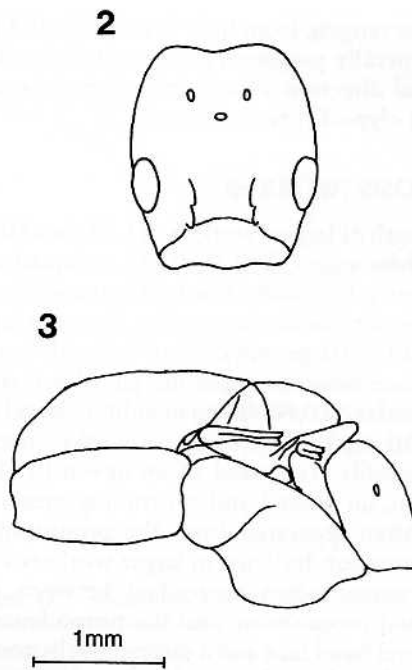
Figure 1. Bimodal distribution of GTC (number of setae on second gastric tergite of queens, exclusive of posterior row) for *Azteca alfari* group species. **A.** Samples of queens from throughout Costa Rica (see Material Examined under species treatments). **B.** Samples of queens from Venezuela, Estado Barinas.

2

3

1mm

Figures 2, 3. *Azteca ovaticeps* (syntype queen). **2.** Frontal view of head. **3.** Lateral view of mesosoma.

lose and the other lightly pigmented and densely pilose (here referred to *A. alfari* sensu stricto and *A. ovaticeps,* respectively).

In Costa Rica, a character that separates the two species is the number of standing setae on the second gastric (fourth abdominal) tergite, exclusive of the posterior row. A survey of 81 queens from localities throughout Costa Rica reveals a strongly bimodal distribution for this character (Fig. 1). For a quantitative character such as seta number, a unimodal distribution would be expected were the sample from a single panmictic population. A sample from Venezuela revealed less differentiation based on abdominal setae (Fig. 1), but queens were strongly differentiated into two forms by the presence or absence of a dense brush of setae on the clypeus (Figs. 6, 11).

That the *alfari* group is composed of two sympatric species is also suggested by Harada (1982). In her study of *Cecropia*-inhabiting ants of Brazil, she observed a "brown form" and a "black form" of *A. alfari* queens from the Manaus area. Although color is not diagnostic, *A. ovaticeps* queens are usually light to dark brown, whereas *A. alfari* queens are typically black.

Alternative explanations for dimorphism include ecotypic variation in phenotype or intraspecific genetic polymorphism. Ecotypic variation is an unlikely explanation for the two forms because of the fine spatial scale on which they co-occur. Colonies of the two species are found inhabiting adjacent trees, and saplings frequently contain queens of both species. Intraspecific genetic polymorphism cannot be ruled out, but no cases of intracolonial

polymorphism have been observed, either among siblings or between colony queens and offspring. The two forms are probably non-interbreeding sympatric populations; they are different species.

AZTECA ALFARI GROUP

DIAGNOSIS (QUEEN)

Obligate inhabitants of Cecropia trees; head longer than wide (HL 1.50–1.72, CI 0.778–0.863), sides evenly convex, and occipital border neither broadly cordate nor deeply excavated (Fig. 2); scapes in repose fall about mid-way between upper margin of eye and occipital border (SL 0.71–0.85); eyes elliptical to somewhat reniform (EL 0.37–0.45); mandibles 7-toothed; mesosoma shape as in Figure 3; *mandibles largely nitid* with large, piligerous foveae, becoming alveolate at base; head, mesoscutum, and mesoscutellum densely and minutely punctate, dorsum of gaster minutely alveolate; body and appendages covered throughout with fine appressed pubescence; standing setae always present on dorsal and ventral surfaces of head, and on dorsum of pronotum, mesoscutum (often setae nearly absent), mesoscutellum, propodeum, petiole, and first gastric tergite; second gastric tergite always with a posterior row of setae, setae variably present anterior to this; standing setae variably present on femora, but *essentially absent on tibiae* (tibial setae, when present, restricted to the tibia apex, and rarely 1 to a few short setae irregularly placed elsewhere on the shaft); *scapes generally devoid of setae* except at apex, occasionally up to 10 short, subdecumbent setae of irregular lengths and spac-

ing; color ranging from light brown to solid black, color generally progressing from darker to lighter in a distal direction along extremities: legs, antennae, and clypeal region of head.

DIAGNOSIS (WORKER)

Head length of largest workers ≤1.38; head slightly longer than wide (CI 0.86–0.94), subquadrate to subtriangular (narrowed toward the mandibles); occipital border cordate to varying degree; scapes in repose fall ½ (large workers) to ⅘ (small workers) the distance between upper margin of eye and occipital border (SI 0.60–0.76); mandibles largely nitid with 8–10 teeth, depending on worker size; mesonotal profile composed of an upwardly sloping pronotum, an arched and protruding mesonotum that is often separated from the pronotum by a distinct anterior declivity, in larger workers a metanotal remnant often protruding between mesonotum and propodeum, and the propodeum with nearly level basal face and a distinct declivitous face of similar length; surface sculpture as in the queen; long-standing setae always present on the dorsum of the pronotum, mesonotum, propodeum, petiole, and gaster; scape and tibial pilosity as in the queen; color highly variable, ranging from concolorous brown, to light brown mesosoma and gaster with dark brown head, to concolorous light brown or yellow.

COMMENTS

Of the several character systems that Emery (1893) used to differentiate *Azteca* species, those I have found most useful are queen head shape and distribution of pilosity on queens and workers. I suspect that both systems are strongly influenced by natural selection, making them good taxonomic characters because of the resulting diversification, but difficult characters for phylogeny reconstruction because of the increased likelihood of convergence.

Most of the species that inhabit carton nests either externally (e.g. *A. barbifex, A. chartifex, A. traili*) or in hollow tree trunks (e.g. *A. instabilis, A. velox*) have abundant standing setae on the scapes and legs. Pilose tibiae are probably of great utility in the manipulation of shredded plant matter used in carton construction. I suspect that tibial pilosity and carton construction are plesiomorphic in the genus. *Liometopum*, a possible outgroup for *Azteca*, exhibits both these characters. The early Miocene *Azteca alpha* Wilson (1985), one of two known fossil *Azteca*, has hairy tibiae and is very similar to any number of modern *Azteca* species (pers. obs.). Several obligate *Cecropia*-inhabiting species—*A. muelleri, A. constructor, A. xanthochroa,* and *A. coeruleipennis*—have densely pilose tibiae and, I suspect, were derived from carton-nesting species.

In contrast, there are many species that inhabit the narrow stems and branches of live plants, and these exhibit various degrees of loss of tibial and scape setae (setae on the thoracic dorsum are rarely absent). In narrow galleries, tibial setae may be an impediment, favoring their evolutionary loss. Also accompanying the stem-nesting habit is a great diversity of queen head shapes. In particular, several species exhibit extremely elongate heads with straight sides (e.g. *A. fasciata, A. longiceps*). Worker head shapes do not show nearly the elaboration that queen head shapes do. I suspect that queen head shape is under strong natural selection at the time of colony founding, influencing the kinds of stems that can be used and the speed with which they can be entered.

The *Azteca alfari* group is part of this second portion of the genus, among the stem-nesting species with bare scapes and tibiae. Close relatives include *A. emeryi* Forel and *A. foreli* Emery. *Azteca emeryi* is similar to the *A. alfari* group in many respects, the striking difference being the extremely elongate, parallel-sided head of the *A. emeryi* queen. Worker heads are also somewhat elongated. At the time of Kempf (1972), *A. emeryi* was known only from the types. I have examined the types of this species, from a *Cecropia* tree at Cachveira Juruá, Amazonas, Brazil (Ule), and a worker series, tentatively identified as *A. emeryi*, from a *Cecropia* at Cocha Totora, Departamento Madre de Dios, Peru (Davidson). The latter is the only collection out of dozens of collections of *A. alfari* group colonies in the region. I predict, given the queen head shape, that *A. emeryi* will prove to be an only occasional occupant of *Cecropia* trees and a more specialized inhabitant of some other plant genus with narrower stems. *Azteca emeryi* may best be placed as a derived member of the *A. alfari* group, but I await further knowledge of this poorly known species.

Azteca foreli workers are very similar to *A. alfari* group workers in pilosity, size, and head shape. The primary difference is that the mandibles of *A. foreli* are densely sculptured, with a granular or striate appearance, in contrast to the shiny mandibles of the *A. alfari* group. *Azteca foreli* is very different behaviorally, nesting in hollow live stems of a variety of canopy trees. It has the unique habit of constructing completely closed carton galleries on trunk and branch surfaces, traversing the host tree between hollow stems.

I have not considered males in the definition of the *A. alfari* group. *Azteca* males are frail, similar to workers in size, and very much smaller than queens. A cursory examination of males from a variety of *Azteca* species revealed few sources of morphological variability. The phallus is comprised of the weakly sclerotized, largely membraneous aedeagus, flanked by pick-like volsellae, subsequently flanked by the swollen basiparameres, at the tip of which are the small, triangular parameres (terminology after Snodgrass, 1941). A distinct articulation often separates the paramere and basiparamere. Tergites IX and X are absent, and there are no pygostyles. The volsellae have acute tips in some

Table 1. Comparative measurements of *Azteca alfari* and *A. ovaticeps*. Ranges are given, followed in parentheses by median and sample size. All measurements are in mm. Characters in bold show the greatest separation between *alfari* and *ovaticeps*.

	Species			
	alfari		*ovaticeps*	
Queens				
HL	1.51–1.69	(1.63, 26)	1.51–1.72	(1.59, 19)
HW	1.24–1.43	(1.35, 26)	1.20–1.39	(1.32, 19)
SL	0.71–0.81	(0.77, 25)*	0.73–0.85	(0.80, 19)
EL	0.39–0.45	(0.43, 13)	0.37–0.42	(0.40, 13)
WL	2.55–3.05	(2.80, 25)	2.70–3.15	(2.88, 16)
CI	0.778–0.856	(0.826, 26)	0.785–0.863	(0.820, 19)
SI	0.543–0.610	(0.573, 25)**	0.589–0.669	(0.608, 19)
GTC	**0–5**	**(0, 80)**	17–>100 (Costa Rica)	(>100, 26)
			2–42 (South America)	(14, 11)
Workers				
HL	0.80–1.38	(1.06, 32)	0.87–1.29	(1.10, 16)
HW	0.72–1.21	(0.96, 32)	0.77–1.16	(0.99, 16)
SL	0.53–0.74	(0.64, 24)	0.58–0.75	(0.71, 16)
CI	0.858–0.942	(0.905, 32)	0.870–0.914	(0.888, 16)
SI	0.603–0.734	(0.681, 24)	0.632–0.763	(0.715, 16)
MSC	**2–17**	**(8, 66)**	10–>19	(>20, 40)

* Outlier from Panama, 0.85.
** Outlier from Mexico, 0.649.

species and are blunt to somewhat knobbed in others. *Azteca alfari* group males exhibit slightly knobbed volsellae, as do many other *Azteca* species.

Azteca male antennae are composed of a short trapezoidal first segment (scape), a globular second segment, and variably shaped segments 3 to 13. The first and second segments are largely bare, whereas the remaining segments are densely covered with short setae. There is both intra- and interspecific variation in the size and shape of antennal segments, particularly segment 3. Although the shape of the third antennal segment is used to differentiate species within the *alfari* group (see below), diagnostic male characters for the *alfari* group as a whole are unknown.

In *Azteca* males preserved in alcohol, I have often observed what appear to be large eversible sacs between the anus and tergite VIII and between tergites VII and VIII. These sacs are probably associated with glandular products (Hölldobler and Engel-Siegel, 1982). I speculate that elaboration of antennal structure and abdominal glands results from a reliance on chemical communication during courtship and mating, replacing structural elaboration of genitalia as a reproductive isolating mechanism or feature subject to sexual selection (cf. Eberhard, 1985). This could be examined through comparative studies of *Azteca* mating behavior and pheromone chemistry.

SPECIES ACCOUNTS
Azteca alfari Emery, 1893
Table 1
Figures 1, 4–9, 14–21, 28–32, 37–42, 47

Azteca alfari Emery, 1893:138; syntype workers: Jiménez, Altantic slope, Costa Rica (Alfaro) [MCSN] (examined, one worker here designated as LECTOTYPE, remainder of nest series PARALECTOTYPES, other material excluded from type series).

Azteca alfaroi Emery; Emery, 1896:4 (description of queen).

Azteca alfaroi race *lucidula* Forel, 1899:113; syntype workers, queens, males: Trinidad (Urich); Guatemala, Retalhuleu (Stoll) [MHNG] NEW SYNONYMY (examined, one queen from Trinidad here designated as LECTOTYPE, remainder of nest series PARALECTOTYPES, other material excluded from type series).

Azteca virens Forel, 1899:115; syntype workers: Brazil, Amazonas, Pará (Göldi) [MCZC] NEW SYNONYMY (examined).

Azteca alfari subsp. *cecropiae* Forel, 1906:240; syntype workers: Brazil, Amazonas, Manaus (Göldi, Huber) [MHNG] NEW SYNONYMY (Huber series examined, one Huber worker here designated LECTOTYPE, other material excluded from type series).
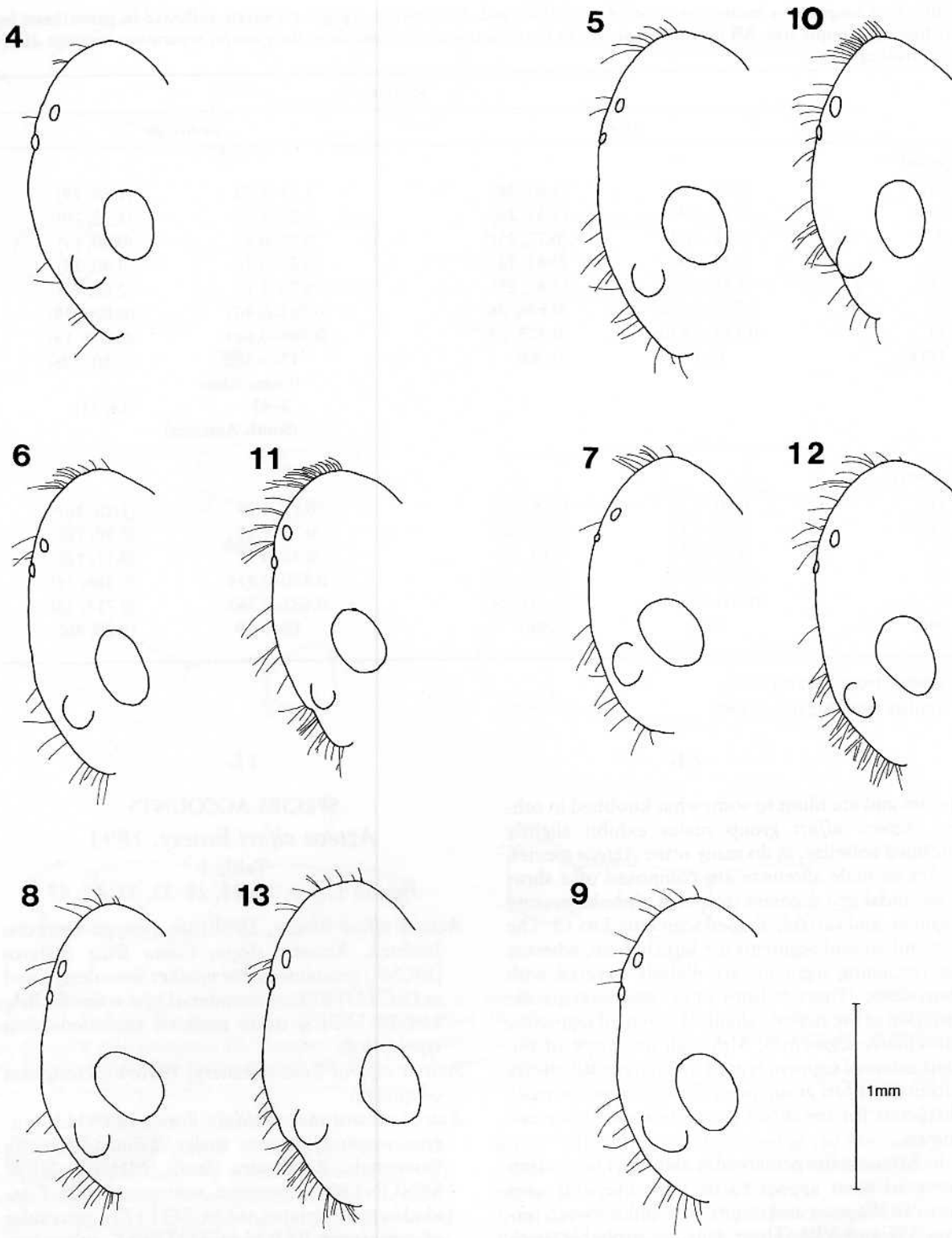
Figures 4–13. *Azteca alfari* group queens, lateral view of head. Setal patterns were drawn by focusing on the midline of the head and drawing all setae that were close enough to the plane of focus to be visible as a single seta. *A. alfari:* 4, Mexico; 5, Costa Rica; 6, Venezuela; 7, Brazil, Manaus; 8, Bolivia; 9, Paraguay (*A. mixta* lectotype). *A. ovaticeps:* 10, Costa Rica; 11, Venezuela; 12, Brazil, Pará (*A. ovaticeps* syntype); 13, Bolivia.

Azteca alfari subsp. *cecropiae* Forel; Forel, 1908: 387 (description of queen, male: Brazil, Campo Besso, near São Paulo (von Ihering) [MHNG] examined).

Azteca alfari var. *mixta* Forel, 1908:386; syntype workers, queens, males: San Bernardino, Paraguay (Fiebrig); Brazil, São Paulo (von Ihering) [MHNG] NEW SYNONYMY (examined, one

queen from Paraguay here designated LECTO-TYPE, remainder of nest series PARALECTO-TYPES, São Paulo series excluded from type series).

Azteca alfaroi var. *fumaticeps* Forel, 1909:250; syntype workers: Mexico, Buenaventura (Ross) [MHNG] NEW SYNONYMY (examined).

Azteca alfari var. *curtiscapa* Forel, 1912:51; syntype workers, queen: Panama (Christophersen); Costa Rica (no collector) [MHNG] NEW SYNONYMY (examined, one queen from Costa Rica here designated LECTOTYPE, remainder of nest series PARALECTOTYPES, Panama material excluded from type series).

Azteca foreli race *breviscapa* Forel, 1912:51 [nov. stat. of *Azteca foreli* race *championi* var. *breviscapa* Forel, 1899:112]; syntype workers: Costa Rica (Tonduz) [MCZC, USNM] NEW SYNONYMY (examined).

Azteca alfari var. *argentina* Forel, 1914:287; syntype workers: Argentina, Misiones, Santa Ana (Bruch) [MHNG] NEW SYNONYMY (examined).

Azteca lynchi Brèthes, 1914:93; syntype worker(s): Bolivia (Arribálzaga) provisional NEW SYNONYMY (not seen).

Azteca alfari var. *argentina* Forel; Gallardo, 1916: 115 (description of major worker and queen, not seen).

Azteca alfari subsp. *lynchi* Brèthes; Gallardo, 1916: 118 (lowered to subspecies).

Azteca alfari var. *fumaticeps* Forel; Wheeler, 1942: 218 (description of queen: Guatemala, Quirigua, 14.i.1912; and Puerto Barrios, 4.xii.1911 (Wheeler) [MCZC] examined).

Azteca alfari var. *langi* Wheeler, 1942:218; syntype workers, queens, males: Guayana, Kamakusa (Lang) [MCZC] NEW SYNONYMY (examined).

Azteca alfari subsp. *lucidula* var. *zonalis* Wheeler, 1942:222 (unavailable name); syntype workers, queens: Panama, Corozal, 21.xi.1911 (Wheeler) [MCZC] (examined).

DIAGNOSIS (QUEEN)

GTC < 6; 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 occiput (Figs. 4–9); clypeal setae sparse, never forming a dense brush (Figs. 4–9); mesoscutum with irregularly scattered setae to almost devoid of setae; SI generally ≤0.60; color usually black.

COMMENTS

The identity of true *A. alfari* was problematical. The type locality appeared in Emery's revision as Jimenez, Costa Rica. Two pins of worker series were examined from MCSN. One pin held a "typus" label, and a label with "Suerre" (a site within

2 km of Jimenez) and the identification "alfaroi" (an attempted emendation of *alfari* that appeared later). The other had a "Jimenez" locality label and a separate label with the identification "*alfari*," but no typus label. The two collections were not conspecific, consisting of the two commonly microsympatric species in the *A. alfari* group. Workers from the latter series, much more than the former, resembled Emery's 1893 illustration of *A. alfari*. A worker from the Jimenez series was chosen as a lectotype of *A. alfari* sensu stricto; the remaining workers on the pin were designated paralectotypes. The Suerre collection, now identified as *A. ovaticeps,* was excluded from the types of *A. alfari.*

Designation of a lectotype queen for *A. lucidula* was necessary because one "cotype" series of workers, queens, and males from Trinidad with label "Trinidad (Urich) sans No." was *A. alfari*, whereas a second "cotype" series of workers with label "Trinidad 59" was *A. ovaticeps*. I examined a single "cotype" worker from Retalhuleu, Guatemala (Stoll), that has standing setae on scapes and legs, which excludes it from the *A. alfari* group. A queen from the Trinidad "sans No." series was designated lectotype; the remaining workers, queens, and males in this series were designated paralectotypes, and all other series excluded from the types.

Forel described *A. virens* as being similar to *A. alfari*, with *A. virens*' outstanding feature being its green color. The body was described as partly translucent, and the green color came from within, recalling the color of green caterpillars. The collection was shipped from Pará "with the green stem of a plant." I examined syntypes at MCZC that were not green and were identical to typical *A. alfari*. I conjecture that the ant specimens were sent in fluid with the stem, perhaps in a plant preservative containing glycerine and acetic acid, and so obtained their translucent nature and green color.

I examined five workers from the Huber syntype series of *A. cecropiae,* one mutilated specimen at MCZC and four from MHNG. Of the four from MHNG, three were small and darkly pigmented, suggesting they came from an incipient colony. The fourth worker was larger and more lightly pigmented, and the mesonotal pilosity suggested *A. alfari*. This worker was designated lectotype. This collection almost certainly came from a sapling *Cecropia*. Given the prevalence of multiple colonization of saplings by queens of several species during the colony establishment phase (Longino, 1989) and the ease of obtaining mixed series when collecting from small saplings, I have not designated paralectotypes, and I have excluded all other material from the type.

Azteca lynchi was described from a Bolivian collection with no biological data. Gallardo (1916) placed *A. lynchi* as a subspecies of *A. alfari* with additional locality data of "Chaco boliviano." The original description and Gallardo's discussion describe sparse standing setae on the thoracic dorsum, suggesting *A. alfari* more than *A. ovaticeps*. I have

put *A. lynchi* in provisional synonymy with *A. alfari*.

MATERIAL EXAMINED

MEXICO: "Buenaventura" (Ross) [a rubber plantation on Isthmus of Tehuantepec]; *Colima:* 6 km NE Comala (Ward); *Jalisco:* 6 km NW El Tuito (Ward); *Michoacán:* 20 km S Uruapán (Ward); *Oaxaca:* 8 mi [13 km] S Valle Nacional, 2400' [730 m] (Snelling); Hwy. 175, 3.4 mi [5.5 km] S Jacatepec, 2400' [730 m] (Snelling); *Veracruz:* Mirador [80 km NW Veracruz] (Skwarra).

GUATEMALA: *Izabal:* Puerto Barrios (Wheeler); Quirigua (Wheeler); *Suchitepéquez:* Patulul (Wheeler).

HONDURAS: Ignacio (Mann); *Cortéz:* Choloma (Mann).

COSTA RICA: no specific locality (Tonduz); *Alajuela:* N side Volcán Arenal (Longino); *Cartago:* 4 km E Moravia (Longino); *Guanacaste:* 2 mi [3 km] E Tilarán (Janzen); 4 km W Sta. Cecilia (Longino); 6 km N Tilarán (Longino); N side Laguna Arenal (Longino); Parque Nacional Santa Rosa (Longino); *Heredia:* Finca La Selva (Janzen); 3–15 km S Pto. Viejo (Longino); *Limón:* 6 km WNW Pto. Viejo (Longino); Tortuguero (Longino); Reserva Biológica Hitoy Cerere (Longino); *Puntarenas:* San Vito de Java (Janzen); Rincón de Osa (Hogue); Sirena, Parque Nacional Corcovado (Longino); 9 km S Sta. Elena (Longino); Parque Nacional Manuel Antonio (Longino); Reserva Biológica Carara (Longino); *San José:* 1 km N Salitrales (Longino); 1 km SW Santa Marta (Longino); 2 km N Ciudad Colón (Longino); 4 km S Santa Ana (Longino); 5–7 km SW Santiago (Longino); Alto Palma (Longino).

PANAMA: no specific locality (Christophersen); *Canal Zone:* Barro Colorado Island (Zetek); Culebra (Wheeler); Corozal (Wheeler); Gatun (Wheeler); Monte Lirio (Wheeler); Red Tank (Wheeler); Rio Agua Salud (Wheeler); Summit (Krauss); *Chiriquí:* Bugaba (Champion); *Panamá:* Otoque I. (Wheeler); El Llano (Choe).

COLOMBIA: Isla Providencia (Janzen); *La Guajira:* Dibulla (Lallemand); *Magdalena:* Río Frio (Darlington); Sta. Cruz, C. Sta. Marta (Forel); 2 km ESE Minca (Longino); 5 km SE Río Frio (Longino); Cañaveral (Longino); *Tolima:* Armero (Peyton, Suarez).

VENEZUELA: no specific localty (Meinert); *Barinas:* 8–10 km WNW Sta. Barbara (Longino, Ward); 17 km SSW Ciudad Bolivia (Longino); *Miranda:* 2 km S Baruta (Longino); *Portuguesa:* San Rafael de Onoto (Longino); 3 km NNE Biscucuy (Longino); *Trujillo:* 15 km ESE Bocono (Longino); 18–19 km E Bocono (Longino); *Zulia:* El Tucoco, 45 km SW Machiques (Menke, Vincent).

TRINIDAD: no specific locality (Wheeler); no specific locality (Urich).

GUYANA: *Mazaruni-Potaro:* Kamakusa (Lang); Baracara (Wheeler); Kalacoon (Wheeler); *West Berbice:* Blairmount (Box).

SURINAME: "Paramaribo, Coppename River" (Reyne); *Paramaribo:* (Stahel).

PERU: *Madre de Dios:* Reserva Tambopata (Davidson).

BRAZIL: San Alberto (Bequaert); *Amazonas:* Flores, Manaus (Bequaert); Manaus (Huber); Manaus (Ward); *Bahia:* Bahia (=Salvador) (Ule); *Espirito Santo:* no specific locality (von Ihering); *Pará:* Pará (Göldi); *São Paulo:* São Paulo, Campo Basso (von Ihering).

BOLIVIA: *Beni:* Estación Biológica Beni, 42 km E San Borja (Ward); *La Paz:* 13 km NNE Coroico (Ward).

PARAGUAY: *Alto Paraná:* Puerto Bertoni (Strelnikou); Puerto Margarita, Río Monday (Strelnikou); *Cordillera:* San Bernardino (Fiebrig).

ARGENTINA: *Misiones:* Santa Ana (Bruch).

Azteca ovaticeps Forel, 1904
Table 1
Figures 2, 3, 10–13, 22–27, 33–37, 43–47

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

Azteca alfari var. *aequilata* Forel, 1904b:691; syntype workers, male: Brazil, Amazonas, Juruá Miry (ex *Cecropia* No. 5588), and Cachveira Juruá (ex *Cecropia* No. 5587), Juruá (Ule) [MHNG] NEW SYNONYMY (examined, one worker from *Cecropia* No. 5587 here designated LECTOTYPE, remainder of these two series and a third series with queens PARALECTOTYPES).

Azteca alfari var. *aequalis* Forel, 1906:239; syntype workers, queens, males: Brazil, Pará, Obidos (Göldi); and Brazil, Mexiana Island, Amazon delta (Hagmann) [MHNG, USNM] NEW SYNONYMY (examined, one MHNG Hagmann queen here designated LECTOTYPE, remainder of nest series PARALECTOTYPES, Göldi material excluded from type series).

Azteca alfari subsp. *tuberosa* Forel, 1906:240; syntype workers, queen: Brazil, Ceará (Diaz da Rocha) [MHNG, MCZC] NEW SYNONYMY (examined).

Azteca alfari var. *aequalis* Forel; Forel, 1908:387 (description of queen, male: Brazil, Amazon delta, Mexiana Island (Hagmann) [MHNG], examined).

DIAGNOSIS (QUEEN)

GTC > 10, and/or clypeus bearing a dense brush of setae; dorsal surface of head, when viewed in profile, often with setae bridging the gap between the ocellar region and the occiput, and often with

setae extending up from the clypeus almost to the ocellar region (Figs. 10–13); mesoscutum usually with even vestiture of standing setae; SI > 0.588; color variable.

COMMENTS

I examined material of *A. aequilata* which included the two published syntype series and a third series from Juruá Miry (labeled "(Ule) 26" by Forel) which contained queens. Due to their being from the same site, and appearing nearly identical (and thus almost certainly conspecific), I have designated all three series paralectotypes to accompany the single lectotype worker. Including the third series serves to incorporate queens into the type material.

MATERIAL EXAMINED

COSTA RICA: *Alajuela:* N side Laguna Arenal (Longino); *Guanacaste;* N side Laguna Arenal (Longino); Parque Nacional Santa Rosa (Longino); *Heredia:* Finca La Selva (Janzen); Carrillo, Parque Nacinal Braulio Carrillo (Longino); 3–15 km S Pto. Viejo (Longino); *Limón:* Zent (Wheeler); Suerre (no collector, probably Alfaro); 6 km WNW Pto. Viejo (Longino); Reserva Biológica Hitoy Cerere (Longino).

VENEZUELA: *Barinas:* 8–10 km WNW Sta. Barbara (Longino, Ward); 17 km SSW Ciudad Bolivia (Longino).

TRINIDAD: Caroni (Wheeler); no specific locality (Urich).

PERU: *Madre de Dios:* Cocha Totora (Davidson); Colpa Quebrada, nr Cocha Cashu (Davidson); Estación Biológica Cocha Cashu (Davidson); Tayacome (Davidson); Reserva Tambopata (Davidson).

BRAZIL: *Amazonas:* upper Purus (Huber); lower Purus (Huber); Cachveira Juruá (Ule); Juruá Miry (Ule); *Ceará:* Ceará (Rocha); *Pará:* Pará (Göldi, Bequaert); Pará, Obidos (Göldi); Mexiana Island (Hagmann).

BOLIVIA: *Beni:* Estación Biológica Beni, 42 km E San Borja (Ward); *La Paz:* 13 km NNE Coroico (Ward).

VARIATION OF *A. ALFARI* AND *A. OVATICEPS*

On *A. alfari* queens, the density of setae on the dorsum of the head and on the mesoscutum increases from north to south. The setae are very sparse on specimens from Mexico in particular. The position of the posterior row of setae on the second gastric tergite varies in distance from the posterior margin, being displaced anteriorly on many South American specimens. Some queens from Mexico are light brown rather than black.

In contrast to *A. alfari*, density of setae on *A. ovaticeps* queens is highly variable and decreases from north to south. In Costa Rica, most queens have a uniform covering of an estimated 200 setae on the second gastric tergite and an even, dense vestiture of setae on the mesoscutum. Three Costa Rican queens exhibit a reduced GTC, between 10 and 40 (Fig. 1), but general abundance of setae elsewhere allies them with *A. ovaticeps*. The possibility of introgression or hybridization should be entertained. The head, in profile, usually exhibits abundant setae on the occiput, which spreads down the front bridging the gap between the occiput and the setae of the ocellar region.

In South American *A. ovaticeps*, general body pilosity is always less than the Costa Rican material, is highly variable, and can approach the state of *A. alfari*. GTC is always very reduced compared to Costa Rican material but is still usually 10 or more, distinguishing *A. ovaticeps* from *A. alfari*. Setae on the second gastric tergite are usually somewhat symmetrically arranged on the dorsal surface of the abdomen. The head, in profile, may or may not have setae bridging the gap between the occiput and the ocellar region.

The most reliable *A. ovaticeps* character throughout South America is a dense brush of setae on the clypeus, and the cuticle is always light brown beneath the brush, even if the rest of the body is black. To appreciate this character, it is best to have comparative material of *A. alfari*. Material of *A. alfari* and *A. ovaticeps* from two sites in Bolivia (Ward collection) was the most difficult to separate. Body color (black) and overall pilosity were very similar. GTC for four *A. alfari* queens was 0, 0, 0, and 3, whereas for three *A. ovaticeps* queens it was 2, 9, and 11. However, the seven queens clearly differed in the presence or absence of a clypeal brush.

Workers of *A. alfari* and *A. ovaticeps* are not always distinguishable. Earlier taxonomy of the *A. alfari* group relied heavily on worker head shape, a character which shows nearly continuous variation and is rarely used in this revision (Figs. 14–27). There is a tendency for *A. alfari* workers to have more triangular heads (Figs. 14, 18–20), but the significance of this needs to be evaluated in the context of allometric shape change related to worker size.

The two species are most distinguishable by degree of pilosity, particularly on the mesonotum (Figs. 28–36). When multiple samples are available from a locality where both species occur, they are usually easily separable into *A. alfari* and *A. ovaticeps*. The former have a "clean" look, with relatively few, long setae of somewhat regular length, whereas the latter have a "scruffy" look, with many setae of irregular lengths. Geographic variation obscures this difference when examining single collections from scattered localities. MSC values for the *A. alfari* group as a whole (Fig. 37) exhibit a pronounced bimodal distribution, but there is a zone of overlap between the two species. Species determinations for the zone of overlap in Figure 37 were made by association of workers with sexuals, or by "gestalt"
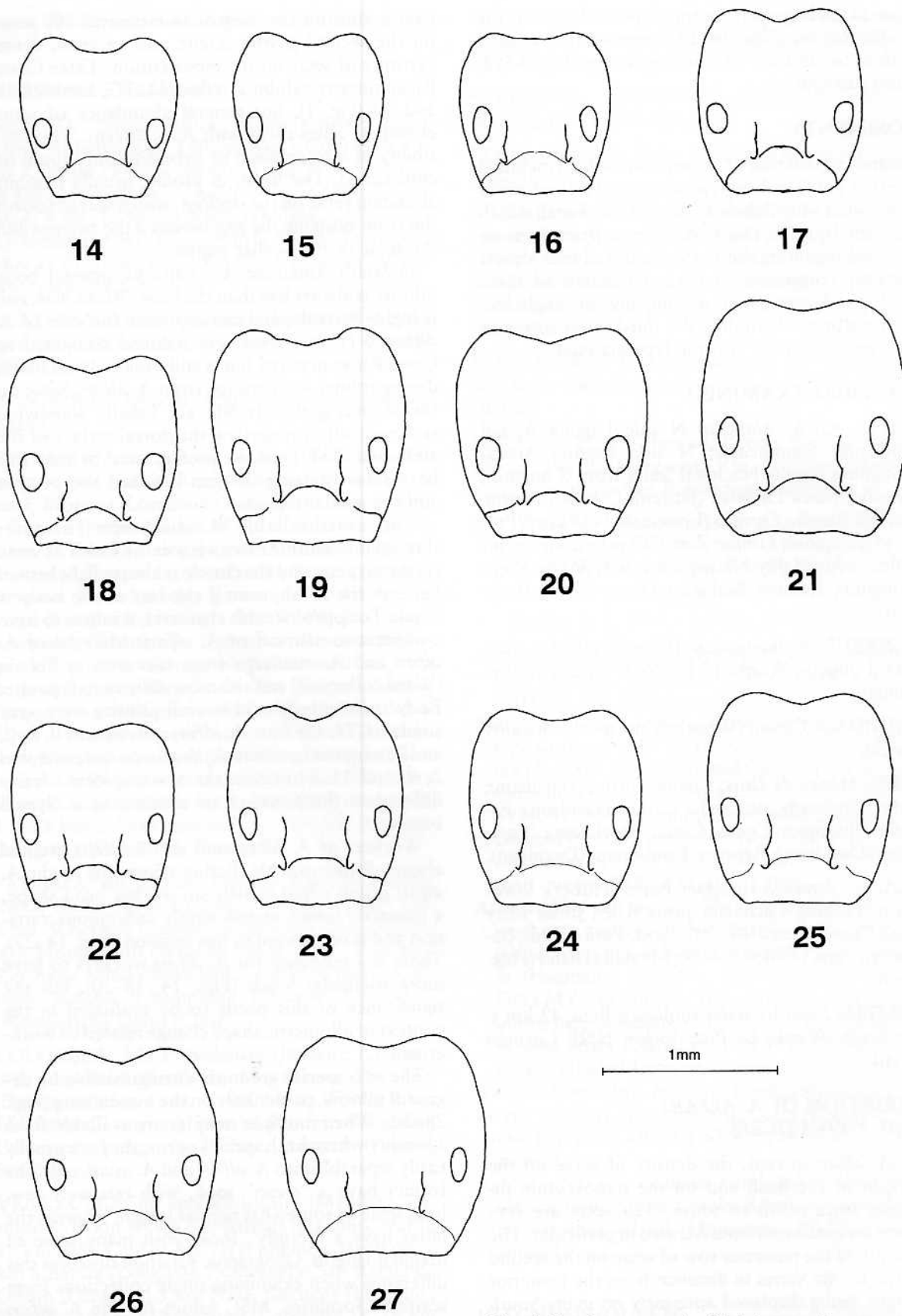
Figures 14–27. *Azteca alfari* group workers, frontal view of head. Top 2 rows are *A. alfari*; bottom 2 rows are *A. ovaticeps*. **14.** Costa Rica (*A. alfari* lectotype). **15.** Mexico (*A. fumaticeps* syntype). **16.** Brazil (*A. cecropiae* lectotype). **17.** Paraguay (*A. mixta* paralectotype). **18.** Argentina (*A. argentina* syntype). **19.** Costa Rica. **20.** Venezuela. **21.** Mexico. **22.** Venezuela. **23.** Peru. **24.** Brazil (*A. tuberosa* syntype). **25.** Brazil (*A. aequilata* lectotype). **26.** Brazil (*A. ovaticeps* syntype). **27.** Costa Rica.

Longino: *Cecropia*-inhabiting Ants
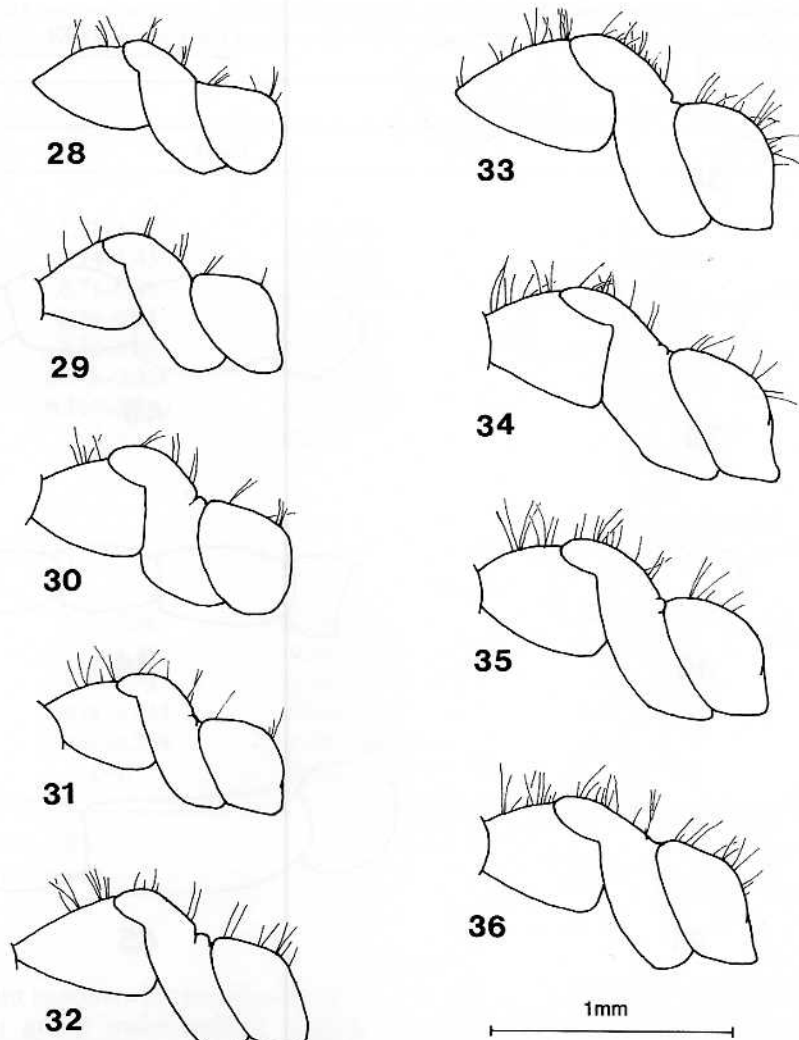
Figures 28–36. *Azteca alfari* group workers, lateral view of mesosoma. Setal patterns were drawn, as for queen head profiles, by focusing on the midline. Left-hand column is *A. alfari*; right-hand column is *A. ovaticeps*. **28.** Mexico (*A. fumaticeps* syntype). **29.** Costa Rica (*A. alfari* lectotype). **30.** Panama. **31.** Brazil (*A. cecropiae* lectotype). **32.** Paraguay (*A. mixta* paralectotype). **33.** Costa Rica. **34.** Brazil (*A. aequilata* lectotype). **35.** Brazil (*A. ovaticeps* syntype). **36.** Brazil (*A. tuberosa* syntype).

developed from multiple samples from one locality. Some of the overlap is probably due to loss of setae on older specimens of *A. ovaticeps*.

Figures 38–46 illustrate male antennae across the geographic range of *A. alfari* and *A. ovaticeps*. From Costa Rica to Paraguay, *A. alfari* exhibits a highly asymmetrical third antennal segment, with a pronounced distal lobe (Figs. 39–42). There is variation in the degree of development of the asymmetry. Figure 40 shows the most extreme reduction of the lobe observed in six separate collections of males from Venezuela. In contrast, *A. ovaticeps* males exhibit a much more cylindrical third segment (Figs. 43–46). In South America there is almost no trace of asymmetry, the segment being very cylindrical (Figs. 44–46). In Costa Rica the third segment is more swollen and exhibits greater asymmetry (Fig. 43), but Costa Rican *A. alfari* exhibit the greatest asymmetry observed (Fig. 39) and are distinct from
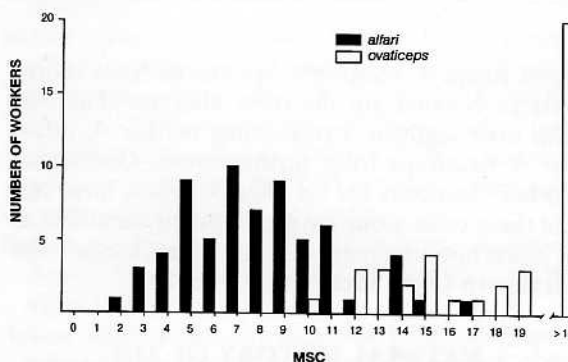
Figure 37. Distribution of MSC values (number of mesonotal setae on workers) for *Azteca alfari* and *A. ovaticeps*. Seven of the *A. ovaticeps* specimens with MSC < 20 were old, collected before 1910, and have probably experienced seta loss through wear.
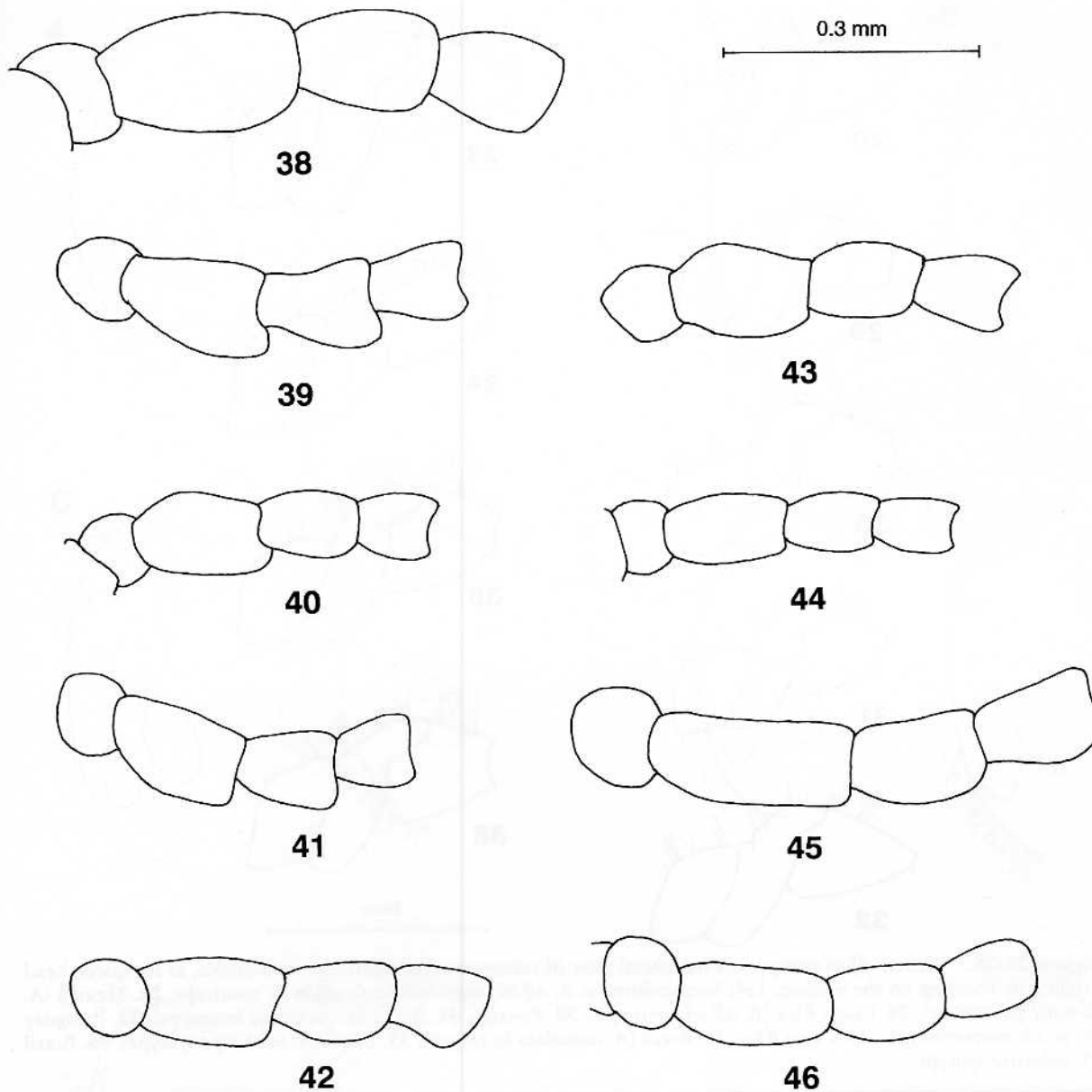
Figures 38–46. Male antennae, segments 2–4. Antennae are oriented to show maximum width of segment 3. Silhouettes are drawn without the dense fringe of setae. *Azteca alfari*: **38**, Mexico; **39**, Costa Rica; **40**, Venezuela; **41**, Trinidad (*A. lucidula* paralectotype); **42**, Paraguay (*A. mixta* paralectotype). *Azteca ovaticeps*: **43**, Costa Rica; **44**, Venezuela; **45**, Brazil (*A. aequilata* paralectotype); **46**, Brazil (*A. aequalis* paralectotype).

Costa Rican *A. ovaticeps*. Specimens from southwestern Mexico are the most aberrant (Fig. 38), with male segment 3 resembling neither *A. alfari* nor *A. ovaticeps* from further south. Queen and worker characters are very like *A. alfari*, however, and these collections are provisionally identified as *A. alfari* until the nature of character change from Mexico to Costa Rica is better known.

NATURAL HISTORY OF THE
A. ALFARI GROUP

The two *A. alfari* group species are obligate *Cecropia* inhabitants. Wheeler (1942) referred to *A. alfari* (sensu lato) as the "Cecropia ant *par excel-*

lence." All collections described in the literature or examined by me were either collected from *Cecropia* or lack biological data. Types of *A. alfari* were from *Cecropia* trees on the Atlantic slope of Costa Rica. The lectotype of *A. cecropiae* was collected "from a *Cecropia*," and the von Ihering collections from near São Paulo were "from swamp *Cecropia*." The paralectotype series of *A. mixta* was from Fiebrig's (1909) study of *Cecropia* in Paraguay. Syntypes of *A. fumaticeps* were from Ross's (1909) study of *Cecropia* in Mexico. Syntypes of *A. breviscapa*, *A. langi*, and *A. zonalis* were from *Cecropia*. Syntypes of *A. aequilata* were collected by Ule from *Cecropia* trees along the Juruá in Brazil.

This species group is nearly coextensive with *Ce-*

cropia trees, except at high elevations and on islands where *Cecropia* has colonized without ants (Janzen, 1973). It occurs from southern Mexico to Paraguay and northern Argentina, and on several Caribbean islands. It is generalized in its use of *Cecropia* species, even within microhabitats. I have observed colonies of *A. alfari* inhabiting *C. obtusifolia* Bertoloni, *C. peltata* L. and *C. insignis* Liebmann in Costa Rica, and *C. peltata*, *C. palmatisecta* Cuatrecasas, and *C. libradensis* Cuatrecasas in Venezuela. I have collected *A. ovaticeps* from *C. obtusifolia*, *C. peltata*, and *C. insignis* in Costa Rica and from *C. peltata* in Venezuela.

The *A. alfari* group as a whole is found in more disturbed habitats than other obligate *Cecropia* inhabitants such as *A. muelleri*, *A. constructor*, and *A. xanthochroa* (Benson, 1985; Longino, unpubl. obs.). The two species within the *A. alfari* group, although frequently occurring in adjacent trees, may also exhibit slightly different habitat preferences with respect to each other. *A. alfari* sensu stricto is found in habitats at the high end of the disturbance spectrum. In Costa Rica, *A. alfari* is the most frequently encountered species in *Cecropia* trees along roadsides and pasture edges, in areas that are far from forest or forest patches. It also occurs in and around forest patches, but there it occurs at a lower frequency, sharing *Cecropia* populations with several other *Azteca* species (Longino, 1989). *Azteca alfari* also exhibits a wide geographical range, occurring at the tropical/subtropical transitions in Mexico and Paraguay. This species' presence at the geographical and climatic limits of the ant–*Cecropia* association may be related to its affinities for disturbed, open habitats in the center of its range.

In contrast, *A. ovaticeps* seems to be associated more with wet forest habitat or, at least, forest edge, and its geographic range is smaller and more centrally located. Although perhaps associated with disturbance in the form of treefall gaps or shifting river edges, it does not seem to thrive in areas of continual anthropogenic disturbance. At the La Selva biological station in Costa Rica it is the most common *A. alfari* group species, whereas at other sites farther from intact forest *A. alfari* sensu stricto is more abundant. Judging from old collections, *A. ovaticeps* was very common along river margins in the Amazon basin. With increasing human disturbance, *A. alfari* may be much more common in this area than it used to be. Davidson has made dozens of collections of ants from *Cecropia* trees at and around Cocha Cashu Biological Station in Manu National Park, Peru, an extremely remote area with almost no human disturbance; all have been *A. ovaticeps*. In contrast, her collections from the nearby Tambopata reserve, a site with somewhat more disturbance, contain an *A. alfari* queen in addition to many *A. ovaticeps* queens.

A long-standing debate revolves around whether the ant–*Cecropia* association is a mutualism (reviewed in Bailey, 1922; and Janzen, 1969). Recent studies suggest that the *A. alfari* group may be less

Figure 47. Distribution of *A. alfari* and *A. ovaticeps*.

effective than other *Azteca* species in defending *Cecropia* trees from herbivores (Andrade and Carauta, 1982; Andrade, 1984). In Costa Rica, *A. alfari* group species are slow to respond to mechanical disturbance of their nest trees, and their nest trees suffer increased herbivory and reduced growth relative to trees inhabited by other obligate *Cecropia* ants (Longino, unpubl. obs.).

SPECIES EXCLUDED FROM THE
A. ALFARI GROUP
Azteca lucida Forel NEW STATUS

Azteca alfaroi race *lucida* Forel, 1899:113; syntype workers: Guatemala, Pantaleon, 1700' (Champion) [MHNG] (examined).

The syntype workers have standing hairs on the tibae, and the major workers have large, subquadrate, nearly glabrous heads, completely unlike the heads of major workers in the *A. alfari* group. In the description, Forel states that *A. lucida* was collected from *Cecropia*, but the labels I observed on the syntypes contain no biological data. The syntypes may or may not have been collected from a *Cecropia*, but there is no evidence that this species is an obligate inhabitant.

DISCUSSION

Recent taxonomic studies of ants are revealing the frequent occurrence of broadly sympatric sibling species (*e.g.* Trager, 1984; Ward, 1985). Some may view this as a simple swing of the pendulum from lumpers to splitters, but this form of splitting is fundamentally different from that of Forel, Wheeler, and others. The uncontrolled proliferation of

names occurring in the early part of this century was largely based on geographic variation with no critical evaluation of character variation within or between regions. Current studies frequently split within regions and lump across regions, the opposite of past practice. Recent discoveries in ant taxonomy have, in part, been due to an increased abundance and availability of museum material. But a more important factor has been the thorough examination of local ant communities. Knowledge of sympatric ant communities gives the first clue to the presence of sibling species, because subtle species differences within a site are not masked by geographic variation.

In this paper, ecological evidence of microsympatric discrete morphologies has been used to justify the delineation of two species. The differences between the two species can be very subtle, and I might not consider them an adequate basis for species distinction were it not for the ecological evidence. The primary differences at any one site are degrees of pilosity, but the details of seta abundance and distribution are highly variable geographically.

Many taxonomists have a biological species concept in mind when describing species. Members of a species are presumed to be united by potential or actual gene flow. When lineage concepts are added, members of a species are presumed to share ancestry unique to them. Thus, a first hypothesis in this study is that A. alfari and A. ovaticeps satisfy these conditions, being two reproductively isolated lineages, each with its own unique ancestor and each reproductively continuous throughout its range. However, the two "species" as defined here are in reality two phenetic clouds of correlated characters of museum specimens and should not automatically be assumed to be two monophyletic lineages. The following alternatives could complicate the story and should be evaluated in future studies of the A. alfari group.

Either or both species could be composed of numerous sibling species, their distributions being allopatric, parapatric, or largely parapatric with narrow zones of sympatry. The geographic variation observed could thus be due to species differences. Within A. alfari, there are morphological gaps among material from Mexico (e.g. A. fumaticeps), Central America (e.g. A. alfari sensu stricto), northern South America and Amazonia (e.g. A. virens, A. cecropiae), and southern South America (e.g. A. mixta). Within A. ovaticeps, there are fairly striking differences among material from Costa Rica, Venezuela, Amazonia, Peru, and Bolivia. These geographic gaps in morphology are accompanied by gaps in material examined, however; and the nature of character change in those gaps remains unknown.

The possibility of multiple sibling species raises an additional hypothesis: that one of the "species" defined here is paraphyletic with respect to the other. For example, one sibling species of the A. alfari lineage could have split, giving rise to a contemporary sibling species within A. alfari and the lineage that became A. ovaticeps. An even more intriguing possibility, although distressing to a taxonomist, is that one of the species is polyphyletic. For example, there could be selection favoring increased pilosity in some habitats, where A. alfari group queens are in frequent contact with competing species of Azteca (A. muelleri, A. constructor, and A. xanthochroa). There could be conditions scattered throughout the range of the widespread A. alfari lineage that favor the existence of a genetically isolated A. ovaticeps-like form. Azteca ovaticeps as defined here could have arisen numerous times independently, as distinct lineages descended from ancestral A. alfari-like populations.

With this much uncertainty regarding the status of the A. alfari group species, is this taxonomic treatment of the group justified? I think there are several reasons for the approach taken here. First, this study alerts investigators to the presence of sympatric species within the A. alfari group. Second, when two species are present, names are available for use in ecological and evolutionary studies. An investigator in Manaus, on reading an ecological study on A. ovaticeps and A. alfari in Costa Rica, will be able to make direct comparisons with the cognate species pair found locally. If new studies reveal multiple species within the current species boundaries, identities of the former A. alfari and A. ovaticeps can be established region by region, and a continuity can be maintained among literature using old and new nomenclature. Retaining the original nomenclature (prior to this study) has obvious drawbacks. Using the single name A. alfari for all A. alfari group members obscures the presence of sympatric species; using the multitude of infraspecific names not only obscures the presence of sympatric species but hinders comparability from region to region.

Hillis (1988) recognized three phases in the development of a taxonomic species concept, using the anuran Rana pipiens complex as an example. He termed these phases the "thesis of typological species, the reaction to typology or antithesis of polytypic species, and the synthesis of evolutionary species." For many groups of neotropical ants, taxonomy has stalled in phase one. A phase two approach has been taken in this report. I suspect that as additional material is obtained and molecular techniques provide additional characters, zones of sympatry will be found and a number of evolutionary species will emerge from each of my polytypic species.

Further understanding of the A. alfari group will require additional collections from mature colonies. I hope this study stimulates further collection throughout the range of the A. alfari group and encourages the collection of voucher material in ecological studies of the Azteca-Cecropia association.

ACKNOWLEDGMENTS

LITERATURE CITED

Andrade, J.C. de. 1984. Desempenho e distribuição de *Azteca alfari* (Formicidae) em *Cecropia lyratiloba* var. *nana* (Cecropiaceae) na restinga do Recreio dos Bandeirantes, Rio de Janeiro. *Atas da Sociedade de biologia do Rio de Janeiro* 24:11–15.

Andrade, J.C. de, and J.P.P. Carauta. 1982. The *Cecropia–Azteca* association: a case of mutualism? *Biotropica* 14:15.

Arnett, R.H., and G.A. Samuelson. 1986. *The Insect and Spider Collections of the World.* Gainesville, Florida: E.J. Brill/Flora & Fauna Publications, 220 pp.

Bailey, I.W. 1922. Notes on neotropical ant-plants. I. *Cecropia angulata,* sp. nov. *Botanical Gazette* 74: 369–391.

Benson, W.W. 1985. Amazon ant-plants. In *Amazonia,* eds. G.T. Prance and T.E. Lovejoy, 239–266. Oxford, England: Pergamon.

Bequaert, J. 1922. Ants of the American Museum Congo expedition. IV. Ants in their diverse relations to the plant world. *Bulletin of the American Museum of Natural History* 45:333–583.

Berg, C.C. 1978a. Cecropiaceae, a new family of Urticales. *Taxon* 27:39–44.

———. 1978b. Espécies de *Cecropia* da Amazônia brasileira. *Acta Amazônica* 8:149–182.

Brèthes, J. 1914. Note sur quelques Dolichodérines argentines. *Anales del Museo Nacional de Historia Natural de Buenos Aires* 26:93–96.

Buckley, R.C. 1982. Ant–plant interactions: a world review. In *Ant–Plant Interactions in Australia,* ed. R.C. Buckley, 111–162. The Hague: Dr. W. Junk.

Eberhard, W.L. 1985. *Sexual Selection and Animal Genitalia.* Cambridge, Massachusetts: Harvard University Press.

Emery, C. 1893. Studio monografico sul genere *Azteca* Forel. *Memorie della Royal Accademia delle Scienze dell'Istituto di Bologna* 5(3):119–152. 2 pls.

———. 1896. Alcune forme nouve del genere *Azteca* For. e note biologiche. *Bollettino dei Musei di Zoologia ed Anatomia comparata della R. Università di Torino* 11(230):1–7.

Fiebrig, K. 1909. *Cecropia peltata* und ihr Verhältnis zu *Azteca alfari,* zu *Atta sexdens* und anderen Insekten, mit einer Notiz über Ameisen-Dornen bei *Acacia cavenia. Biologisches Zentralblatt* 29:1–16, 33–55, 65–77, 5 pls.

Forel, A. 1878. Études myrmécologiques en 1878 (première partie) avec l'anatomie du gésier des fourmis.

Bulletin de la Société Vaudoise des Sciences naturelles 15:337–392, 1 pl.

———. 1899. Formicidae. *Biologia Centrali-Americana,* Hymenoptera 3:1–160.

———. 1904a. Miscellanea myrmécologiques. *Revue Suisse de Zoologie* 12:1–52.

———. 1904b. In und mit Pflanzen lebende Ameisen aus dem Amazonas-Gebiet und aus Peru, gesammelt von Herrn E. Ule. *Zoologische Jahrbücher. Abtheilung für Systematik, Geographie und Biologie der Thiere* 20:677–707.

———. 1906. Fourmis néotropiques nouvelles ou peu connues. *Annales de la Société Entomologique de Belgique* 50:225–249.

———. 1908. Ameisen aus São Paulo (Brasilien), Paraguay etc. gesammelt von Prof. Hern. v. Ihering, Dr. Lutz, Dr. Fiebrig, etc. *Verhandlungen der Zoologisch-botanischen Gesellschaft in Wien* 58:340–418.

———. 1909. Ameisen aus Guatemala usw., Paraguay und Argentinien (Hym.). *Deutsche entomologische Zeitschrift* 1909:239–269.

———. 1912. Formicides néotropiques. Part V. 4me sous-famille Dolichoderinae Forel. *Mémoires de la Société Entomologique de Belgique* 20:33–58.

———. 1914. Formicides d'Afrique et d'Amérique nouveaux ou peu connus. *Bulletin de la Société Vaudoise des Sciences naturelles* 50:211–288.

Gallardo, A. 1916. Las hormigas de la República Argentina: subfamilia Dolichoderinas. *Anales del Museo Nacional de Historia Natural de Buenos Aires* 28:1–130.

Harada, A.Y. 1982. Contribuição ao conhecimento do gênero *Azteca* Forel, 1878 (Hymenoptera: Formicidae) e aspectos da interação com plantas do gênero *Cecropia* Loefling, 1758. Thesis, Instituto Nacional de Pesquisas da Amazônia e Fundação Universidade do Amazonas, Manaus, Amazonas, Brasil.

Harris, R.A. 1979. *A Glossary of Surface Sculpturing.* Occasional Papers in Entomology, No. 28, 31 pp. California Department of Food and Agriculture.

Hillis, D.M. 1988. Systematics of the *Rana pipiens* complex: puzzle and paradigm. *Annual Review of Ecology and Systematics* 19:39–63.

Hölldobler, B., and H. Engel-Siegel. 1982. Tergal and sternal glands in male ants. *Psyche* 89:113–132.

Janzen, D.H. 1969. Allelopathy by myrmecophytes: the ant *Azteca* as an allelopathic agent of *Cecropia. Ecology* 50:147–153.

———. 1973. Dissolution of mutualism between *Cecropia* and its *Azteca* ants. *Biotropica* 5:15–28.

Kempf, W.W. 1972. Catálogo abreviado das formigas da Região Neotropical. *Studia Entomologica* 15:3–344.

Longino, J. T. 1989. Geographic variation and community structure in an ant–plant mutualism: *Azteca* and *Cecropia* in Costa Rica. *Biotropica* 21:126–132.

Ross, H. 1909. Pflanzen und Ameisen im tropischen Mexiko. *Naturwissenschaftlichen Wochenschrift* 8: 822–830.

Snodgrass, R. E. 1941. *The Male Genitalia of Hymenoptera.* Smithsonian Miscellaneous Collections, vol. 99, no. 14, 86 pp., 33 pls. Smithsonian Institution.

Trager, J. C. 1984. A revision of the genus *Paratrechina* (Hymenoptera: Formicidae) of the continental United States. *Sociobiology* 9:51–162.

Ward, P.S. 1985. The nearctic species of the genus *Pseudomyrmex* (Hymenoptera: Formicidae). *Quaestiones Entomologicae* 21:209–246.

Wheeler, W.M. 1942. Studies of neotropical ant-plants and their ants. *Bulletin of the Museum of Comparative Zoology, Harvard* 90:1–262.

Wilson, E.O. 1985. Ants of the Dominican amber (Hymenoptera: Formicidae). 3. The subfamily Dolichoderinae. *Psyche* 92:17–37.