ECOLOGICAL RELATIONS OF THREE *ATTA* SPECIES IN PANAMA

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Abstract. Of the three *Atta* species of Panama (*sexdens* L., *cephalotes isthmicola* Weber and *colombica tonsipes* Santschi), *sexdens* is a grassland species as it is in South America, and the other two are forest or forest-grassland ecotone species. While *sexdens* and *tonsipes* may nest in the same general grassy area, *sexdens* extends along the sandy Pacific shore, and the other two nest primarily in clay. A unique relationship in the heart of the city of Colon on the Atlantic side was a colony of *isthmicola* surrounded by colonies of *tonsipes*. Their leaf-bearing files were separate and they were mutually hostile. The main plaza of Panama City on the Pacific side has been occupied by *sexdens* despite the gradual extinguishing of foraging areas by buildings. Barro Colorado Island has *isthmicola* and *tonsipes* occupying similar habitats. Personal records since 1938 are noted.

Usually the species of the leaf-cutting ant, *Atta,* occupy well-defined and separate areas (Fig. 1) throughout their range from Texas and Louisiana to Argentina and Uruguay. The gap between *texana* Buckley in Texas and the northernmost extent of *mexicana* F. Smith in Arizona is several hundred miles wide. In Uruguay *sexdens* L. is found to the north and on the rolling pampas while *vollenweideri* Forel is found only close to the Rio Uruguay, according to Carbonnel (pers. commun.). The much closer relations of *sexdens* and *cephalotes* L. in Brazil have been described by Borgmeier (1959) and Gonçalves (1960), and in Guyana and Venezuela in Weber 1946, and 1947. There is generally a well-defined ecological difference, *sexdens* being found in grassland or the grassland-forest ecotone and *cephalotes* occurring in the forest. In Guyana *sexdens* seemed more an ant of sandy soil and *cephalotes* an ant of clay, but this is not always consistent. The three species of Panama (Weber 1941, 1956, 1968) are *sexdens, cephalotes isthmicola* Weber and *colombica tonsipes* Santschi (Fig. 2).

It should not be assumed that the ranges of any *Atta* are stabilized. All fluctuate with changes in climate and for more obscure reasons. In part it may be that the species and the genus have evolved in relatively recent times compared with such genera as *Myrmicocrypta* and *Sericomyrmex*. They clearly have more flexibility in meeting climatic change.

HUMAN INFLUENCES ON *ATTA* DISTRIBUTION

Humans have a marked influence on the distribution of both *Acromyrmex* and *Atta* throughout the Americas. The reverse effect of the ants on humans has been noted (*e.g.,* Weber 1947, 1966).

A probable and unusual relationship in Panama has been due to the concentration of human migrations and populations in this narrow area. According to Bennett (1968), the first humans probably arrived about 20,000 years ago and must have possessed fire. Shifting cultivation may have appeared 5,000 years ago, including the cutting and burning of forest. As many as one million Indians may have been engaged in cultivating and fire-drives for hunting when Europeans appeared. Large areas then were in grassland or in second-growth shrubs and trees. Soon the Indian population was greatly reduced and second-growth forest greatly increased. We are now in a stage when grassland and second-growth vegetation are becoming reestablished.

The effect on *Atta* distribution of these changes was probably to increase the extent of *sexdens* during spread of grasslands, to increase the extent of *tonsipes* during spread of woodlands and perhaps to leave *cephalotes* and *isthmicola* to relatively untouched hilly or mountainous summits. As ecological islands were formed, the possibility of creation of *tonsipes* and *isthmicola* arose.

DISTRIBUTION OF *ATTA* IN PANAMA

ATTA SEXDENS

I saw *Atta sexdens* first in Panama in 1938, when it was seemingly the dominant animal in the heart of Panama City in the Plaza de Lesseps (Figs. 3, 5). The Plaza de Lesseps is close to the cities of Ancon and Balboa in the Canal Zone and is at the foot of Ancon hill that has the Tivoli Hotel. The trees around the hotel were planted after the building of it, at the time the Panama Canal opened. Man-made plantings of trees extend along the Canal and have become the normal habitat of *Atta colombica tonsipes* (Fig. 4).

On 16 June 1938 there were 14 aggregates of craters distributed over every part of the park. Some craters were 30 cm in diameter and 10 cm high. The 14 aggregates appeared to represent separate colonies, and the ants were noted as completely overrunning the park, which then had much grass as well as trees. The ants foraged for a variety of substrate and climbed such trees as *Ficus* for leaves and fruit.

On 8 July 1954 *sexdens* was noted as dominating the Plaza as in 1938. The ants were harvesting remnants of human food. There were many craters but nearly all were closed because of intermittent rain. By 1955 a major building program initiated by the national government reduced the foraging area markedly. In March 1957 the ants survived by going up the concrete steps leading to recreational areas and entered cracks in the concrete. They were also surviving at the base of a high bamboo hedge. In 1966 the ants had ceased to be dominant animals but were persisting at a taxi stand, by benches under trees and in the cultivated grass of the soccer playing fields.

Other habitats of sexdens *in Panama.*—In addition to the Plaza de Lesseps site in Panama City, *sexdens* was noted to the northeast of Panama City in 1954 and later. The sites in 1954–57 were close to the shore of the Bay of Panama, including Paitiila Point, in dry, llanos-type

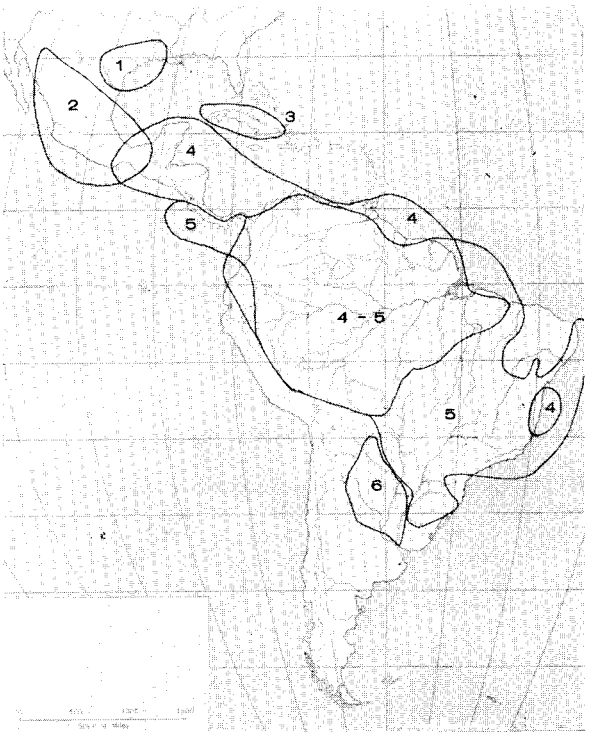

FIG. 1. Approximate distribution of six species of *Atta* indicated by the areas encircled. Brazilian distribution after Gonçalves (1960). Six additional species are found in Brazil. The western boundaries of *Atta* in South America have not clearly been established. Within a geographical area the ranges of *sexdens* and *cephalotes* are ecological. 1. *Atta texana* Buckley. 2. *Atta mexicana* F. Smith. 3. *Atta insularis* Guerin. 4. *Atta cephalotes* L. 5. *Atta sexdens* L. 6. *Atta vollenweideri* Forel.

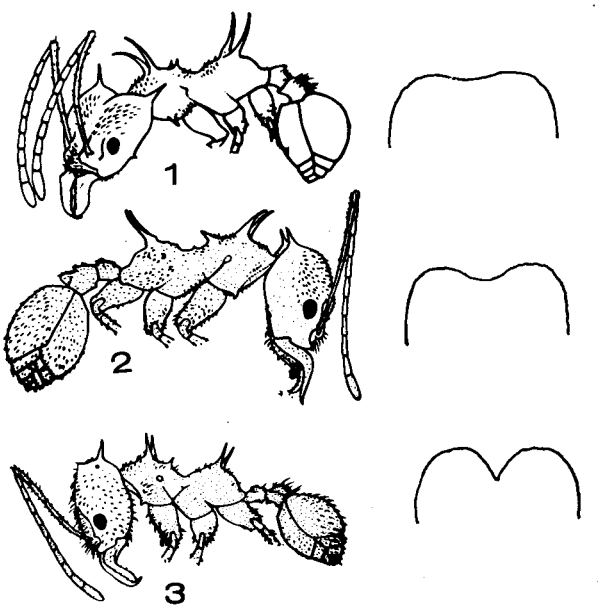

FIG. 2. Side view of three Panamanian *Atta* workers: Outline of occipital margins of largest soldier caste at right. 1. *Atta cephalotes isthmicola* Weber. 2. *Atta colombica tonsipes* Santschi. 3. *Atta sexdens* L. The occipital spine or tubercle on the front of the occiput is characteristic.

vegetation. The ants also nested in hilly country back from the shore and infested banana and other cultivations. Their adaptability to drought was well shown by a colony excavated 23 March 1957. The drought had lasted since mid-December, and the red clay surface was deeply fissured in many places. The superficial chambers were unoccupied and the gardens were deeper than 60 cm, although the soil at this depth was damp enough for gardens. Elsewhere, and closer to high tide, a garden with sexual brood was at a depth of 27 cm.

To the southwest of Panama City along and inland from the Pacific shore, the country was less modified by human activity and more characteristic of South American habitats, with *Acacia* and *Curatella*. A colony excavated 11 July 1954 was of a size indicating that it resulted from a nuptial flight 2 or 3 months earlier. Others were older and all were in gray sand. Mature colonies had long trails over wet, flat areas that in the long dry season would be sun-baked and arid. Many runways went completely underground. A large colony had persisted in *Acacia* scrub beside a pool, indicating that it would receive enough subsurface moisture during a drought when the pool would be absent.

In 1966, *sexdens* colonies in Long. 80°W, Lat. 8°25'N, extended close to high-tide level in the shade of scattered trees and bushes. Superficial chambers of a mature nest with fungus gardens extended within 8 cm of the surface in moist, loose sand. Young colonies on 2 August were less than 100 m from the most seaward mature colony and were in steep banks of barely moist clay with some shade of bushes. They appeared to have originated from nuptial flights of May–June because of their incipient gardens that were 20–33 mm in diameter. At Rio Hato, nearby in this coastal area in 1957, young colonies more nearly 6–8 months old were taken in largely dry sandy clay, indicating that the species may have several nuptial flights in the year. All such habitats were much drier or better drained than were those of *tonsipes* and *isthmicola* in Panama. The closest *sexdens* has been noted to *tonsipes* was at Juan Diaz, where the latter was in wet savanna in 1938 and *sexdens* was in drier areas nearby in the Panama City area. At Cerro Campana, some 50 miles from Panama City, *sexdens* nests on the dry plains and *isthmicola* above 2,000 ft in forest.

Atta colombica tonsipes

Santschi described *tonsipes* in 1929 as a variety of *colombica* from specimens taken by G. C. Wheeler (not W. M. Wheeler) at Bella Vista and Colon, Panama, in 1924. Since he did not know authentic type material of *colombica*, the relationships of the two forms are obscure. At any rate, I have studied the *tonsipes* type material and am satisfied that the common *Atta* of Panama is this, whatever the validity of the name.

The first collection that I made of *tonsipes* was on 16 June 1938 near the village of Juan Diaz. This must have been also approximately at the type locality known as Bella Vista. The Juan Diaz ants were nesting on a slight rise in wet savanna. The grass was high and lush. The ants had no distinct craters but were bringing up soil from under a large, dead and fallen tree.

At the present time *tonsipes* is definitely the common species in the entire Canal Zone area. It is figured by Martin et al. (1967) and occurs from the Atlantic to the Pacific sides (Fig. 4). The ruins of Old Panama had *tonsipes* in 1938, and at the nearby Marsh's Zoo the ants

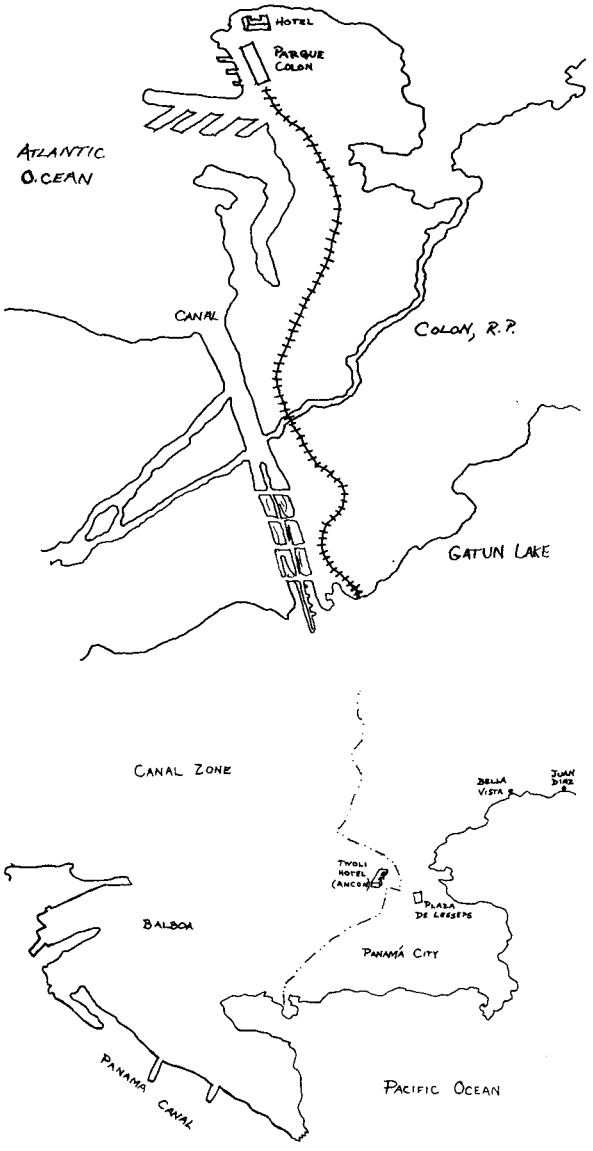

FIG. 3. Sketches of Colon (top) at the Atlantic side of the Isthmus of Panama and Panama City (bottom) at the Pacific side, from a map of the 1930's. The relations of two *Atta* species in each area are described in the text.

invaded the outdoor animal cages for corn and other food. In 1938 a large colony was at the end of Drayton trail on Barro Colorado Island (Table 1). The stomach of a basilisk lizard (*Basaliscus basaliscus* L.) from Rio Indio, Gatun Lake, had workers of this species.

A large *tonsipes* nest on Barro Colorado Island at Donato 4–5 in 1954 persisted into 1955 but both years was partially excavated in order to collect numbers of ants. On 4 July 1954 great numbers of the media caste were bringing out exhausted substrate, carrying it over forked tree branches as high as 1.9 m, then dropping the material to make a mound of several liters bulk. A similar nest at Snyder-Molino 2 (Fig. 6) had files of workers carrying exhausted substrate to a large rounded rock on a steep slope, then dumping the material so it rolled over the rock to form a pile of several liters below. The ants performed in this manner in June of both 1954

TABLE 1. Location of *Atta* nests on Barro Colorado Island, Panama Canal Zone, 1938–66

Sites[a]	1938	1954	1955	1957	1966
Laboratory clearing		*tonsipes*	*tonsipes*		
Snyder-Molino 1	*isthmicola*		*tonsipes*		*isthmicola*
" " 2		*tonsipes*	*tonsipes*	*tonsipes*	
Donato 4		*tonsipes*	*tonsipes*	*tonsipes*	
W. M. Wheeler 15	*isthmicola*				
Lake 5					*isthmicola*
Wheeler short-cut from Armour-Zetek	*isthmicola*	*isthmicola*	*isthmicola*	*isthmicola*	
Drayton end	*tonsipes*				
Barbour Lathrop 8					*tonsipes*
Armour 2			*isthmicola*		
Armour, Big Trees					*isthmicola*
R. Shannon 1					*isthmicola*
" " 11	*isthmicola*				
" " 16					*isthmicola*

[a]Identified by permanent markers along the trails named.

and 1955 and in March of 1957. We now know that the ant fungus had assimilated enough of the cellulose in the substrate so that it needed to be replaced.

Atta cephalotes isthmicola

This subspecies was described by me in 1941 from a 1938 Barro Colorado Island colony with queen, close to Snyder-Molino No. 1 post. Four colonies were seen in 1938 (Table 1) and a photograph of a large, mature nest at R. C. Shannon No. 11 appeared in my 1941 publication. By 1954 this nest was abandoned and *isthmicola* was seen only at the summit of the island (Wheeler trail short cut from Armour-Zetek trails). In 1954 *tonsipes* appeared to be more common and by 1954 specifically replaced the type colony of *isthmicola*. The latter had had the queen removed by me and would naturally have come to an end. The *tonsipes* had also replaced *Acromyrmex octospinosus* Reich in the laboratory clearing.

In 1966 Haines noted eight sites of *isthmicola*, mostly in the higher part of the island and we revisited the R. C. Shannon No. 11 site together, finding no *Atta* colony. We found that a 1957 site of a large *tonsipes* nest off Snyder-Molino No. 2 post (Figs. 6, 7) was unoccupied, but less than 20 m distant was an *isthmicola* colony. Clearly the ranges of the two on the island are unstable although no evidence of competition is available. Since both harvest the leaves of the same trees and these are always in abundant supply, the usual direct competition for food appears absent.

The isthmicola *and* tonsipes *relations*

Differing from all above relationships is an example found on 31 July 1966 in Colon, at the Atlantic entrance to the Panama Canal (Fig. 3). Here in the Parque Colon one nest of *isthmicola* was in the midst of other colonies of *tonsipes*, the common *Atta* here.

The Parque Colon had eight shade trees arranged in two rows of four each and extending between Calle 3 and 5 along the Calle de Enfrente. The trans-Isthmian railroad comes up to the park. At the Calle 3 end of the park, *tonsipes* was nesting under the first tree of four and on the Canal side. Under the second tree on this side was *isthmicola*. Under the third tree on the Canal side was another *tonsipes* nest, and the *Atta* runways under the two trees were as close as 19 m. Craters of the two species were 44 m apart. Under the fourth tree on the Canal side was another *tonsipes* about 21 m from the second *tonsipes* nest. Still farther seaward

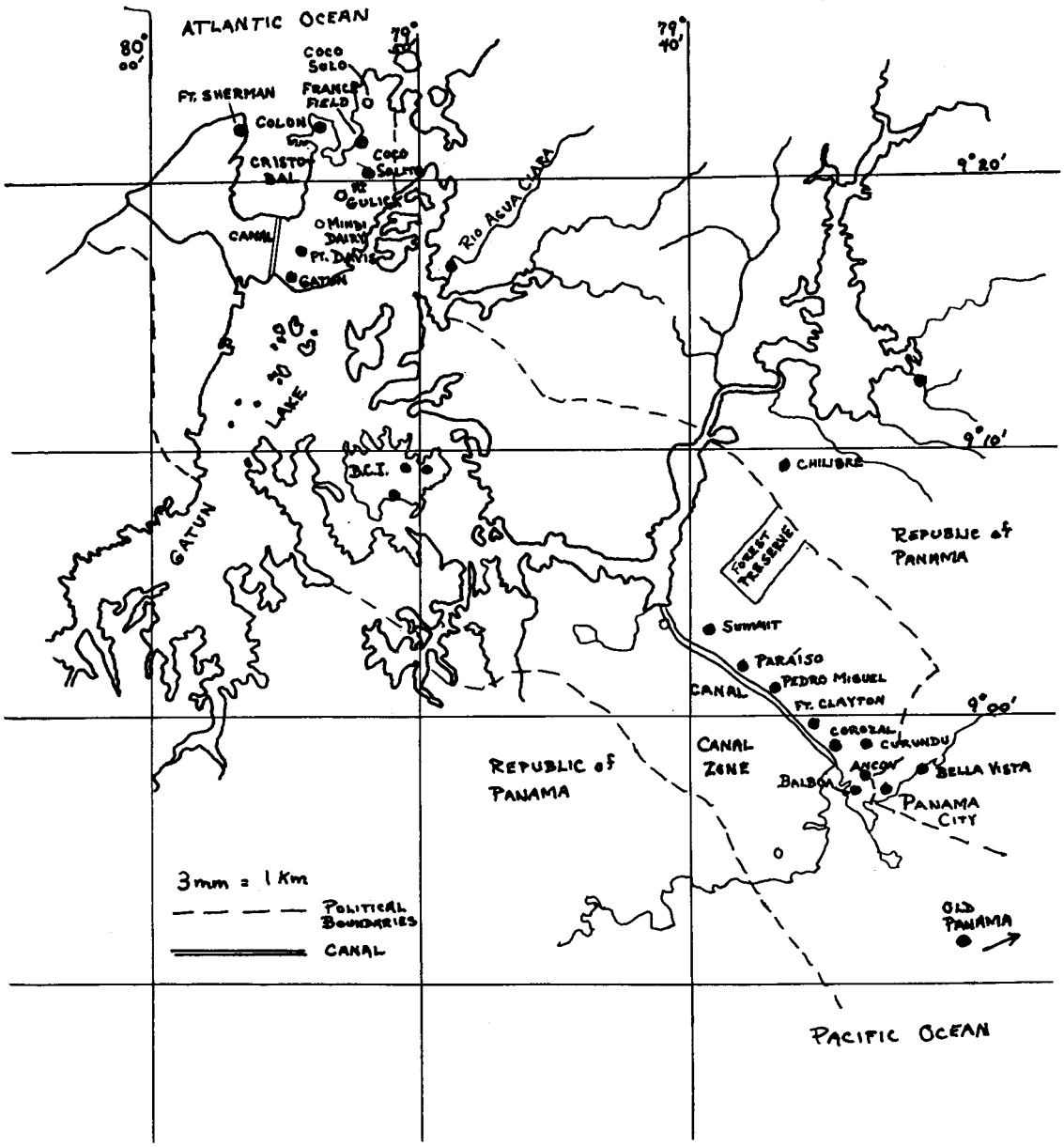

FIG. 4. Distribution of *Atta colombica tonsipes* in the Panama Canal Zone area. Other localities are known within the range shown. Panama City has *sexdens* rather than *tonsipes*.

and on the grounds of the Hotel Washington was another thriving *tonsipes* colony. The ants then were climbing coconuts at the very seawall and harvesting the flowers. Their files of workers descending the smooth trunks were occasionally sprinkled with spray from the ocean waves.

When I picked up workers of *isthmicola* from a foraging file, using clean forceps and picking up the leaf section with ant attached rather than touching the ants, and dropped them in the file of *tonsipes*, there was immediate hostility. This was equally true of the ant alone, when first shaken from the leaf as when dropped with leaf. The dropped ant would run wildly about and leave the alien ant trail as directly as possible. The ants in file immediately sensed the presence of an alien and ran to attack it. Both species clearly recognized the differences in odor of the trails, which in these cases were on the concrete paving of the park and not physically altered by the ants. The results were the same when *tonsipes* workers were similarly dropped in an *isthmicola* file.

It would appear that the *isthmicola* nest was the result of a female from a nuptial flight in some wooded area perhaps several hundred meters distant. Or it could have been a female carried on an automobile or train during its flight. The time must have been short enough so that it could dig into the soil for momentary safety and deposit its indispensable nucleus of the fungus garden. By accident, the female must have crawled or descended into an area where files of *tonsipes* were not foraging. The first *isthmicola* ants to emerge must also have had time to establish their own trails before the

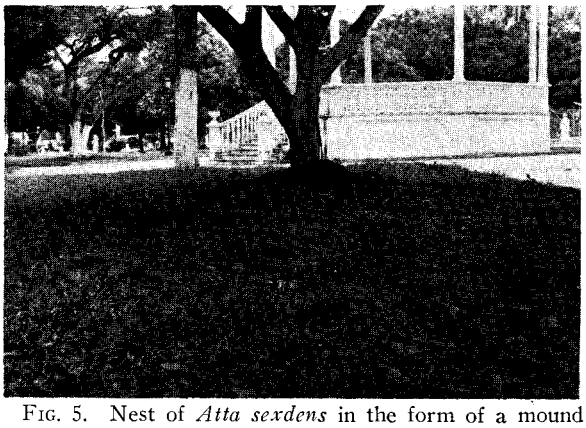

FIG. 5. Nest of *Atta sexdens* in the form of a mound of craters at the base of a tree in the Plaza de Lesseps, Panama City, Panama, as it was on 1 July 1938. At the present time the ants are still in this city square, but their activities have been much restricted by the major building program in the intervening years. Many of the attractive city squares throughout the Americas still contain nests of leaf-cutting ants.

first contacts between the species. In general, attine ants show tolerance for one another when the contacts are brief. The crossing of files of two *Atta* species, however, would probably not be tolerated.

THE FUNGUS

The fungus gardens in nature and the fungus as cultured on artificial media look much alike in the three species. There are always minor differences when comparing one garden with another in *Atta,* even within the same colony. A young garden will be darker than a senile one. The most recently formed portions, which are mostly on the upper septa of the cells, have a scantier mycelial coat than the paler basal part. In the dry season, the senile basal cells have the staphylae, or masses of inflated hyphal ends, resembling miniature golf balls. These are a particularly concentrated form of ant food for adults and larvae.

Each species will eat the fungus of the others as cultured in the laboratory, but this is not necessarily conclusive evidence that the species of fungus is the same. In the field, temporarily captive ants of one species will eat the fungus from a fresh piece of the garden of another species, and this shows a more significant relationship of the fungi as grown by the ants. It also shows a close relationship of the chemical nature of the ant secretions. In no case have identifiable sporophores from any *Atta* species been reared from artificial culture. At the present time the best that can be said is that the three *Atta* culture the same or very closely related strains of one fungus species.

GEOGRAPHICAL AND SYSTEMATIC NOTES

The Central American *Atta* fauna has not yet been the subject of detailed study and the following notes are offered in the hope that they will assist in the identification of these conspicuous and important insects.

Forel, in the *Biologia Centrali-Americana* of 1899–1900, listed four species of *Atta* from Central America. They were *sexdens* of Costa Rica, Panama and South America; *cephalotes* from Mexico south to South America; *columbica* (incorrect spelling for *colombica*) of Guatemala, Costa Rica, Panama and Colombia; and *fervens* of Texas south to Colombia and Surinam. The latter clearly consisted of at least three species as understood now: *texana, mexicana* and *cephalotes.* What he called *colombica* may in large part be the subspecies *tonsipes* described later by his younger associate, Santschi.

Emery had the same Central American species in the *Genera Insectorum* in 1921 except that he considered *texana* and *mexicana* as subspecies of the Cuban *insularis,* a hardly tenable position.

Later writers such as Mann in 1922 tended to list the common *Atta* as *cephalotes* (Honduras) although Skwarra in 1934 figured a *mexicana* nest from Mirador, Mexico.

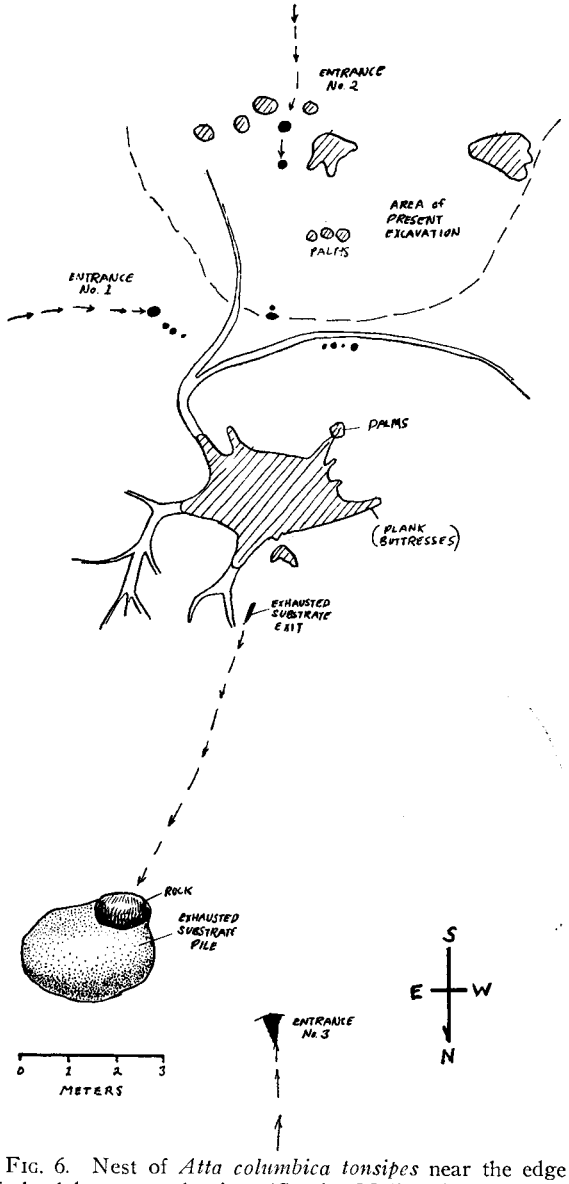

FIG. 6. Nest of *Atta columbica tonsipes* near the edge of the laboratory clearing (Snyder-Molino 2) of Barro Colorado Island, Panama Canal Zone, on 24 December 1957, after a sketch by David Klingener. The nest has since disappeared and one of *Atta cephalotes isthmicola* was in the general area in 1966.

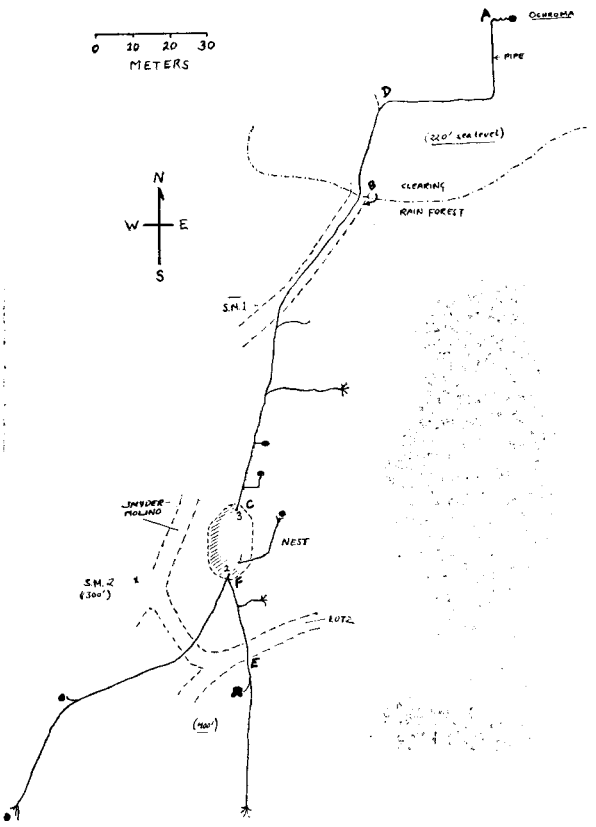

FIG. 7. Trail system of the nest in Fig. 6 on 24–25 December 1957, extending into the laboratory clearing, after a sketch by David Klingener.

The Costa Rican Atta *species*

The three Panama species occur also in Costa Rica but there are several subspecies of *cephalotes* (Weber 1957). Santschi described *erecta* in 1929 as a variety of *cephalotes* and I have examined the type material. Unfortunately soldiers were not among the types so that it is difficult to be sure what the form is. It is not *isthmicola* or *tonsipes*, and of course *sexdens* is very different. Most authorities have been content to identify as *cephalotes* a complex of forms whose soldiers have broad heads with a shallow sulcus between the occipital lobes, the lobes being variably shiny on the sides. The minima and media workers are shiny or slightly dull. I took this at Pt. Limon, Bataan, Zent, Turrialba and San José and have specimens from Orosi and Alajuela.

The common *Atta* at LaLola (near Bataan and Zent) in 1956 seemed to be *Atta colombica tonsipes* so that in lowland Costa Rica as in Panama the ecological relations between *cephalotes* and *colombica* remain to be determined.

The third species, *sexdens*, must be confined to the arid and semi-arid Pacific drainage.

The Colombian species

The species in Colombia have close relations to those above and little has been published. It is possible that *Atta cephalotes* subsp. *opaca* Forel, known from Colombia, occurs in Costa Rica. I took this in Lat. 6°40'N, Long. 76°10'W at 1020 m but took more typical *cephalotes* at Buenaventura on the Pacific coast. Specimens sent to me from Ibaqué, Dept. Tolima in Lat. 4°26'N, Long. 75°14'W at 1250 m are typical *isthmicola*. At sea level at Turbo, Gulf of Uraba in Lat. 8°N and close to Panama, I collected what may well be the typical *colombica*. The llanos would also have *sexdens* and *laevigata* F. Smith, and I was sent specimens of *sexdens* from Suraita, Lat. 6°6'N, Long. 73°38'W.

Differences Between the Species

The three species are readily separated when a series of workers including the soldier caste is available (Fig. 2). Technically the soldier belongs to the worker caste but has a disproportionately large head and has defensive functions. Comparison should be made between individuals of approximately the same size.

The soldiers may be separated as follows:

1a. Head broadly and feebly impressed in the middle of the occipital border.....*cephalotes* or *isthmicola*
1b. Head sharply impressed in the middle.....2
2a. Front of head on each occipital lobe with an angularity .....*sexdens*
2b. Front of head smooth on the occiput.....*tonsipes*

The spines and tubercles of the thorax are of little use in classification because of their variability.

Workers of medium to large sizes may be separated as follows:

1a. Front of head on each side with an occipital spine or tubercle.....*sexdens*
1b. Front of head on each side smooth.....2
2a. Body dull red-brown, densely and finely punctate; concolorous .....*tonsipes*
2b. Body largely smooth and shining.....3
3a. Concolorous .....*cephalotes*
3b. Thorax markedly darker than head.....*isthmicola*

The spines of the thorax may have some use in classification but are highly variable.

Added differences in the Panama fauna often include a larger and paler soldier caste in *isthmicola* that also tends to have the occipital lobes somewhat smooth and shining on the sides.

The soldiers of *tonsipes* and *sexdens* are always duller than those of *isthmicola*, and only in old colonies do occasional individuals attain a size comparable to the common size of those in mature *isthmicola* or other *cephalotes* nests. Shiny workers of the media sizes are likely *cephalotes* or *isthmicola* in Costa Rica or Panama.

Future Research

Enough has been sketched above to indicate some of the unusual opportunities for worthwhile ecological research on *Atta* in the Panama area. The relations with man in the past as well as the present in the cities and surrounding country, the relationships between the species, the exact distribution of the mature colonies, the very origin of the subspecies and the detailed mapping of such continuing biological reserves as Barro Colorado Island and Cerro Campana are among the feasible projects. Any mature nest in itself is the center of an ecological unit of considerable complexity that justifies a major study.

Acknowledgments

David Klingener and Graham B. Fairchild in 1957 and Bruce Haines in 1966 gave welcome assistance in field work. Michael M. Martin and colleagues in 1966 pursued related biochemical interests to mutual benefit. Aided by NSF Grant GB-5346.

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