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Pachycondyla luteola (Hymenoptera, Formicidae), an inhabitant of *Cecropia* trees in Peru

Abstract

Biological data of the rarely collected ponerine ant *Pachycondyla luteola* (ROGER, 1861) are presented. The „locus typicus" of this ant is corrected to Sarayacu, a mission at the Río Ucayali, Peru. The present known geographical distribution of the ant is limited to preandine lowland and submontane regions in Peru covered by evergreen and seasonal-evergreen tropical rain forest.

Ant colonies and colony founding queens were only found in the hollow stems of *Cecropia* trees and seedlings. The ants feed exclusively on Müllerian bodies produced by the plants in high numbers in special hair pads (trichilia) at the base of petioles of young leaves. Ant queens already colonize very young plants. The older colony is supposed to be functional polygynous, because in one examined nest three physogastric queens were found together. This social status has been rarely encountered in ponerine ants, and certainly has been evolved in context with the unusual nest habit. The species build up colonies which belong to the largest known for ponerine species in the world (several thousands of workers, possibly even between 10,000 and 100,000).

The benefits to the plants seem to consist primarly in a good protection against herbivores, not only insects but also vertebrates, because the ant is armed with a powerful sting. The pain of its stings in humans lasts longer than known from any other ant, and any other Hymenoptera as well. It is concluded that the protection against large herbivores is an advantage especially for *Cecropia* trees that grow slowly in small forest gaps at low light intensities.

Kurzfassung

Pachycondyla luteola (Hymenoptera, Formicidae), eine Bewohnerin von Cecropien in Peru

Die selten gesammelte Ponerine *Pachycondyla luteola* (ROGER, 1861) ist bisher nur aus immergrünen bis saisonal-immergrünen Regenwäldern des vorandinen Tieflandes und der submontanen Zone Perus bekannt geworden. Als „Locus typicus" dieser Ameise wird Sarayacu, eine Missionsstation am Río Ucayali in Peru bestimmt.

Die Kolonien und koloniegründenden Königinnen der Ameise wurden nur in hohlen Stämmen von Cecropien-Bäumen und ihren Jungpflanzen gefunden. Die Ameisen fressen ausschließlich Müllersche Körperchen, die die Pflanzen in großer Zahl in speziellen Haarpolstern (Trichilien) an der Basis junger Blattstiele produzieren. Die Ameisen-Königinnen besiedeln junge Cecropien bereits in einem sehr frühen Stadium. Die ältere Kolonie ist wahrscheinlich funktionell polygyn, da in einem näher untersuchten Nest drei physogastrische Königinnen zusammen lebten. Diese Form sozialer Organisation ist bei Ponerinen selten gefunden worden und scheint im Zusammenhang mit der ungewöhnlichen Lebensweise entstanden zu sein. *P. luteola* baut Koloniestärken auf, die zu den größten unter den Ponerinen überhaupt gehören (mehrere tausend Ar-

beiterinnen, wahrscheinlich sogar zwischen 10.000 und 100.000).

Der Nutzen für die Pflanzen liegt offenbar in einem guten Schutz gegenüber Herbivoren, Insekten wie Wirbeltieren, denn die Ameisen sind mit einem kräftigen Stachel ausgerüstet, dessen Stich eine längere Wirkung erzielt, als von irgéndeiner anderen Ameise oder Hymenoptere bekannt ist. Der Schutz gegen große Herbivoren scheint ein Vorteil speziell für langsam wachsende Cecropien in kleinen Baumsturzlücken im Innern des Waldes zu sein.

Resumen

Pachycondyla luteola (Hymenoptera, Formicidae), un habitante de *Cecropia* en Peru

Se presenta datos biológicos de la hormiga *Pachycondyla luteola* (ROGER, 1861). Como „locus typicus" de la hormiga esta fijado Sarayacu, una misión al lado del Río Ucayali en Peru. La distribución conocida se limite a bosques siempre verdes y estacional siempre verdes de la región preandina baja y submontañosa en Peru.

Las colonias de la hormiga y reinas colonizadoras fueron encontradas solamente dentro de troncos huecos de arboles y arbolitos de *Cecropia*. Las hormigas se alimentan exclusivamente de los corpúsculos de Müller que las plantas producen a las bases des pecíolos entre cojines de pelos especiales (trichilia) en grandes cantidades. Reinas ya colonizan cecropias muy pequeñas. Presuntamente la colonia establecida es funcionalmente polygyna, porque en un nido examinado vivieron tres reinas fisogastricas juntas. Este modo de organización social es raramente encontrado en Ponerinae y parace ser evolucionado en relación con el tipo de nido. Las colonias de esta especie forman parte de las mas grandes conocidas en hormigas de la subfamilia Ponerinae (unas millares de trabajadoras, probablemente 10.000-100.000).

Las plantas aprovechan de una buena protección contra animales herbívoros sea insectos o vertebrados porque las hormigas tienen una lanceta muy efectiva. El dolor de las picaduras dura mas tiempo que en cada otra especie de hormiga o de cualquier otra Hymenoptera conocida. Esta concluido que la protección contre herbívoros grandes es una ventaja especial para una especie de *Cecropia* que crece despacio en el interior del bosque con poca luz.

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1. Introduction

The biology of most of the hitherto approx. 2500 described neotropical ant species (KEMPF 1972) is poorly known or even not at all. This holds true even for larger species and includes such basic information as the nest site and nest type.

An astonishing example in this respect was, until recently, the ponerine *Pachycondyla luteola*. More than 1 cm in size, it apparently got known to science for the second time 115 years after its discovery (leg. L. PENA 1962). KOEPCKE (1972) reported for the first time that its colonies occupy a *Cecropia* and that two species of Icteridae (*Clypicterus oseryi* and *Ocyalus latirostris*) build their nests at leaves and petioles of *Cecropia* trees colonized by these ants. They are part of an interesting neotropical ant-plant-association and obviously build up the largest colonies among neotropical ponerines, probably even outnumbering the populous colonies of nomadic *Leptogenys* species of South-East Asia (MASCHWITZ et al. 1989). But nothing in detail was known about their biology up to the late 80s when DAVIDSON and co-workers started publishing results of their comparative work on ant-*Cecropia*-associations in south-eastern Peru (DAVIDSON et al. 1988, 1989, 1991, DAVIDSON & FISHER 1991, DAVIDSON & McKEY 1993).

The observations on *P. luteola* presented here were made during a two-year-field study (1983   1985) about the ant fauna at the biological station of Panguana/Peru.

2. Taxonomy and Distribution

Taxonomy

ROGER described this ponerine ant in the year 1861 from seven specimens under the name *Ponera luteola* in such a good manner that it can be recognized with great certainty already from his description. Very typical is the reddish brown or rusty color of the workers. Callow specimens are even yellow-red, hence the name. Workers are about 1.2 cm in size (combined head, thorax, petiolus and gaster length), the queens between 1.6 to more than 1.8 cm, and dark brown coloured. In the original description ROGER missed the weakly developed carina on the cheeks between the insertion of the mandibels and the compound eyes. This structure is better developed only in queens, and EMERY (1890) was the first to mention it. This character sets the species between the species of the pantropical genus *Pachycondyla* (SMITH, 1858) (=species without cheek carina) and the pure neotropical genus *Neoponera* (EMERY, 1901) (=species with clearly developed carina), hence explaining its taxonomic history:

Ponera luteola ROGER, 1861
Pachycondyla luteola (ROGER 1863, DALLA TORRE 1893)
Neoponera luteola (EMERY 1901, 1911, KEMPF 1972)

KEMPF (1964) already had profound doubts about the generic distinctness of *Neoponera* and *Pachycondyla*, and BROWN (1973) proposed the synonymy of *Neoponera* and other ponerine genera with *Pachycondyla*. HÖLLDOBLER & WILSON (1990) followed BROWN's opinion in their standard work.

Locus typicus

ROGER (1861) closed his description as follows: „7 ⚥ in der Kaiserl[ichen]. Sammlung zu Paris stammen von der Mission Sareyacu (Pampa del Sacramento) in Südamerika, von wo sie Mr. DE CASTELNAU mitgebracht."

The spelling of the location is wrong. The name should be correctly the Quechua word „sarayacu" (sara = maiz, yacu = water). The true position of this locality was never identified in the past. ROGER (1863) himself believed it to be in Uruguay, EMERY (1890) in Brazil (1911: Rio de Janeiro, Brazil), and KEMPF (1972) in Bolivia. All interpretations turned out to be wrong shown at once by the label of a syntype in the Museum of Comparative Zoology at Harvard: „Perou, Pampas del Sacramento, DE CASTELNAU 1847". This label must have been unknown to ROGER and other myrmecologists.

In modern maps of Peru the mentioned pampas are not found, but in a map added to the book of PORTILLO (1901). STIGLICH (1922) wrote about them: „Sacramento, chico y grande Hdas. en la Montaña de Paucartambo, Prov. de Pasco, Dist. de Ninacaca. Las Pampas del Sacramento son las vastas llanuras que se extienden al N y al E de la cuenca del Pachitea y en ella estan los salvajes cashibos....." STEPHENS & TRAYLOR (1983) defined this not sharply limited area according to the „Map of Hispanic America (MHA), American Geographical Society, New York, 1922-1952" as „SACRAMENTO, PAMPA DEL; Loreto/San Martin de. 400-500 m in plain E of Cordillera Azul, leftbank of Rio Ucayali drainage." ORTIZ (1974) gave a report about the discovery of this vast plain (=pampa), completely covered with forest, by some Franciscan friars on Corpus Christi Day (=dia del sacramento) in 1726.

The mission Sarayacu was founded in 1791 by the Franciscan FRANCISCO GIRBAL on the left bank of the Ucayali. It is situated at the northern border of the Pampas del Sacramento on a little elevation (165 m a.s.l.) on the right side of a little affluent (Caño Sarayacu) about 10 km apart from the Ucayali itself (STIGLICH 1922). The next larger settlement is Orellana about 20 km to the south. STEPHENS & TRAYLOR (1983) gave the coordinates with 6°44'S, 75°06'W and the altitude of 125 m a.s.l. according to the MHA. That is probably the altitude of the mouth of the caño into the Ucayali. ORTIZ (1974) reported the arrival of DE CASTELNAU to the mission (tome I: 304): „El año 1846 recibe [el padre PLAZA] en Sarayacu al expedicionario frances CASTELNAU..."

Distribution of *Pachycondyla luteola*

P. luteola is known only from the following locations in Peru: Sarayacu, Dep. Loreto (165 m); Panguana, Dep. Huánuco (220 m); Pozuzo, Dep. Cerro de Pasco (600 m), leg F. GESTR IV. 1985 and donated to the author; Cocha Cashu, Manu, Dep. Madre de Dios (400 m), leg. D. DAVIDSON XI. 1985 (see also DAVIDSON et al. 1991, DAVIDSON & FISHER 1991); Quincemil, Dep. Cusco (750 m), leg L. PENA XI. 1962 and IX. 1967; and Tambopata (200 m), Dep. Madre de Dios (DAVIDSON et al. 1991, DAVIDSON & FISHER, 1991). Thus, the geographical distribution of *P. luteola* so far known is confined to evergreen and seasonal-evergreen tropical rain forest of the lowland and submontane region of preandine Amazonian Peru (fig. 1).

Specimens are deposited in Musée d' Histoire Naturelle, Paris, Museum of Comparative Zoology, Cambridge, Mass., and Staatliches Museum für Naturkunde Karlsruhe.
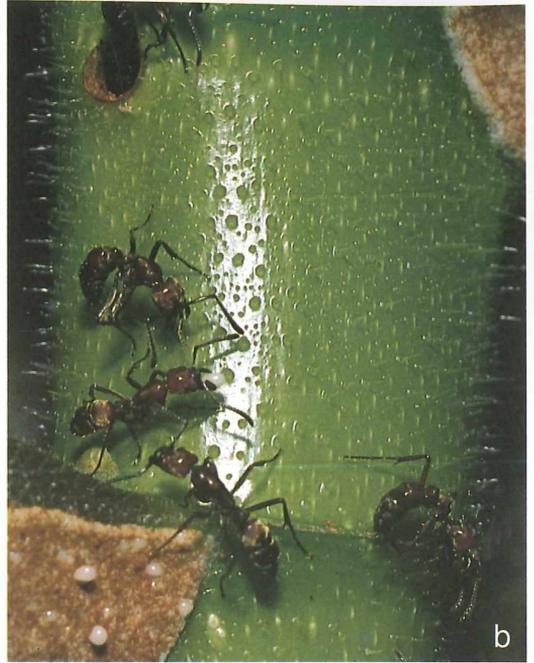
Plate 1. a) *Cecropia tessmannii* with a colony of *Pachycondyla luteola* in the garden of the biological station Panguana. b) Workers of *P. luteola* on the stem of the host *Cecropia*. Note Müllerian bodies (M.b.) in trichilium at the base of petiole (bottom), the worker with a recently harvested M.b. between the mandibles (middle), and the entrance of the nest (top). c) Look in the interior of an internodium of the *C. tessmannii* with numerous M.b. and larvae between them. d) Single larva feeding on M.b.

3. Study site and Material

Study site

The biological station Panguana (9°37'S, 74°56'W, Departamento Huánuco) is situated at 220 m a.s.l. at the left bank of the Río Yuyapichis, an affluent of the Río Pachitea. The average rainfall (7 years measurement) is 2403 mm (minimum 1998 mm, maximum 3004 mm), with 80% falling during the rainy season between October and April. The mean annual temperature at the forest border (station) is approx. 25 °C. For further details about the climate and soil types of Panguana see HANAGARTH (1981) and RÖMBKE & VERHAAGH (1992).

The vegetation zone at Panguana is classified as preandine hylaea (HUECK 1966); the region is naturally covered by seasonal-evergreen tropical rain forest (terra firme) and, to a small degree, by different inundation vegetation types (matorrales, HANAGARTH 1981). There are different anthropogeic biotopes (pastures, plantations, and secondary forests in different stages of succession) near the station, too.

Material

The results presented here are based on 6 collected or observed colonies, 8 colony-founding queens and 6 solitary queens. Voucher specimens are deposited under the indicated field numbers in the collection of the Staatliches Museum für Naturkunde Karlsruhe.

VFor 237 (25.7.83): 25 ♀♀ from a colony on a 4-5 m high *Cecropia* in a recent clearing of primary forest (total colony size was estimated to at least 2000 individuals). The ants remained on the cut *Cecropia* for approx. one week then disappeared with the whole brood. Whether they left the host plant with their brood or were eaten by animals is not known.

VFor 225 (5.10.83): 1 dealated ♀, solitary on a scrub in the garden behind the station.

VFor 433 (4.4.84): 1 ♀ from a colony in dense, 3-year-old secondary growth with numerous *Cecropia*.

VFor 456 (17.4.84): 1 alated ♀, at the station hut before noon.

VFor 489 (29.5.84): 1 dealated ♀ with two larvae and 6 eggs in the topmost internodium of a 70 cm high *Cecropia* in a secondary growth (no Müllerian Bodies, M.b. inside, but some in leaf trichilia). The internodium below contained a young nest of a *Camponotus* (*Tanaemyrmex*) species.

90/335 C-P (9.7.84): 1 dealated ♀ with 7 pupae, 7 larvae and 9 eggs in 45 cm height in a young *Cecropia* in secondary growth. Three internodia (total length 7 cm) were connected by holes in the nodial septa, a 6 x 3 mm large entrance was in the topmost internodium; no M.b. were found inside.

VFor 940a (3.4.85): 1 dealated ♀ at 6 p.m. at the stem of a *Cecropia* in the garden of the station (see VFor 940c). Held permanently contact with some workers through antennation. Also mutual oral contact was observed but no exchange of regurgitated food.

VFor 940b (19.4.85): 2 dealated ♀♀ (one of them still with wing remains) in close vicinity to the *Cecropia* in the garden but hidden in a rotten palm stem from which the *Cecropia* grew. One of them left the hiding-place loudly stridulating when disturbed.

VFor 940c (19.4.85): Complete nest from a 1.60 m high *Cecropia* (plate 1a, the same plant as VFor 940a,b) in the garden of the station (the plant was cut, put in a plastic bag and then poisened): 3 dealated physogastric ♀♀, 230 +/- 5 ♀♀, 1 not yet fully coloured ♂, 163 pupae, 241 larvae, 347 eggs, approx. 5800 M.b. (tab. 1), remains of an alien ant male and of a tree hopper (Membracidae), 1 living mite (Galumnidae, Oribatei). The bottom 80 cm of the plant were small, woody and uninha-

bited. The wider, inhabited 18 internodia (tab. 1) were all connected by holes in the nodial septa. The youngest internodium at the peak was still empty. The actual entrance was in the topmost inhabited chamber, but the lower ones still showed the pits of the former entrances, and occasionally the plant had two entrances. This slowly growing *Cecropia* had been colonized at least since a height of 50 cm.
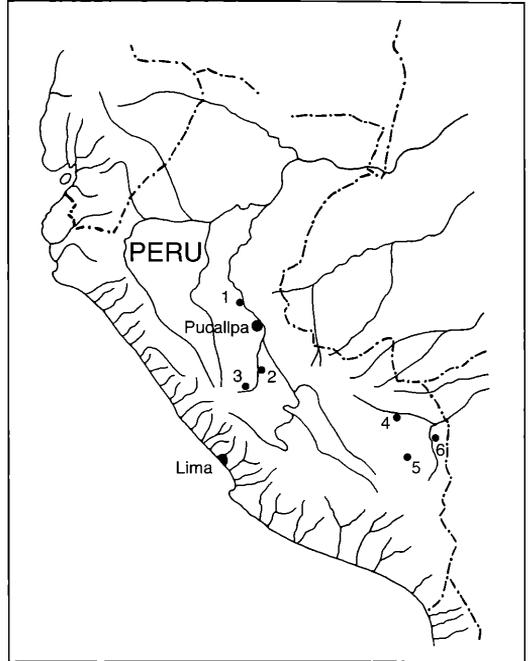
VFor 1033a-d (12.5.85): 4 dealated ♀♀ from one 20 cm high *Cecropia* with only 5 internodia from a small gap in a 20-year-old secondary forest; only the internodia 2 and 3 were interconnected by holes in the nodial septa:

a) In internodia 2 and 3 (counted from the bottom), 1 ♀ with 1 pupa, 9 larvae and 5 eggs. The larvae fed on M.b.; there were numerous mites (deuteronymphs of Tyroglyphidae, Acaridiae, Sarcoptiformes) inside the nest.

b) In the internodium above, 1 ♀ without brood and M.b.

c) In the top most internodium, 1 ♀ without brood but 4 M.b.; there were also some mites (Tyroglyphidae) in this internodium. All three ♀♀ had an entrance to the *Cecropia* for their own, in which often the head or antennae were seen. Knocking at the *Cecropia* occasionally caused them to leave the interior.

d) A fourth ♀ sat in front of the *Cecropia* on the forest ground and was stridulating. This specimen carried several phoretic Tyroglyphidae on the body.

VFor 1034 (12.5.85): 1 dealated ♀ with 9 pupae, 13 larvae and 12 eggs, but no M.b. in a 35 cm high *Cecropia* close to VFor 1033. The 4 topmost internodia were interconnected by holes in the nodia. The entrance (in the topmost internodium) was closed by a plug of soft material (chewed parenchym?).

Figure 1. Geographical distribution of *Pachycondyla luteola* in Peru: 1 – Sarayacu (Río Ucayali); 2 – Panguana (Río Yuyapichis), 3 – Pozuzo; 4 – Cosha Cashu, Manu Park; 5 – Quincemil; 6 – Tambopata Reserve.

Table 1. Distribution of brood and Müllerian bodies (M.b.) in the internodes (IN) of *Cecropia tessmannii* inhabited by *Pachycondyla luteola* (nest VFor 940). Numbers of internodes (IN) from top to bottom; magnitudes for M.b.: I = 1-100, II = 101-1,000; III = 1,001-2,000; size of larvae arbitrarily divided into large, middle sized, and small.

IN	M.b.	brood	remarks
1	II		inner ø=3.3 cm, 4 cm long
2	II	none	
3	III	none	IN 1/3 filled
4	II	large larvae	
5	II	large larvae	
6	I	large larvae/pupae	
7	I	large larvae/pupae	
8	I	large larvae/pupae	IN nearly filled
9	I	large larvae/pupae	IN nearly filled
10	I	large larvae/pupae	IN nearly filled
11	I	large larvae/pupae	IN nearly filled
12	I	large larvae/pupae	IN nearly filled
13	I	large larvae/pupae	IN nearly filled
14	II	small/middle sized larvae	
15	III	eggs	
16	I	eggs/small larvae	
17	I	eggs/small larvae	
18	I	few small larvae	water in IN; inner ø=1.8 cm, 4.5 cm long

VFor 1043 (12.5.85): 1 dealated ♀ without brood nor M.b. in the middle of three internodiums of a 20 cm high *Cecropia* in river bank vegetation (matorral) with the up to 11 m high grass *Gynerium sagittatum*. In the bottom internodium with closed entrance a dealated ♀ of *Azteca* sp. with eggs was found.
VFor 1045 (11.5.85): 1 ♀ from a colony on *Cecropia* in primary forest in a small gap caused by numerous colonies of *Myrmelachista* sp. on *Cordia* and *Duroia* trees.
VFor 1056 (14.5.85): 1 dealated ♀ without brood but some M.b. in a 1 m high *Cecropia* at the transition of matorral and terra firme forest.
VFor 1251 (1.7.85): 56 ♀♀, 69 pupae and 45 larvae from a nest (the rest of the completely sampled nest got lost) on a 2.5 m high *Cecropia* in primary forest in a nearly overgrown gap with *Cordia* and *Duroia* trees. Nesting scheme similar to that described from VFor 940c. Entry to the nest was in the topmost inhabited internodium. Brood was separated in pupae, larvae and eggs, too. There was no hint to other food than M.b. in the interior of the *Cecropia*. One worker held the head of a worker of *Cephalotes atratus* between its mandibles.
A further colony inside the primary forest could be shortly observed during a forest walk. The stem of the approx. 10 m high *Cecropia* was densely covered by workers. I estimate that this colony might have reached a number of approx. 10,000 workers.

4. Results and Discussion

Nest, and colony founding

Pachycondyla luteola was regularly found in the vicinity of Panguana, although it was never especially searched for. KOEPCKE (1972) examined 6 colonies in Panguana. The ant colonies lived exclusively on *Cecropia* trees (plate 1). Whether this was only one *Cecropia* species or more could not be verified as *Cecropia* seedlings often resemble each other. As far as noted, the young colonized *Cecropia* trees were densely covered by rather long, stiff hairs (plate 1b). The local people know both the ant and the *Cecropia* on which it lives as „pungara" According to FERREYRA (1970), the *Cecropia* called „pungara" in Peru is *Cecropia tessmannii* MILDBR., but this still lacks confirmation. BERG (1978) questioned the specific distinctness of *C. tessmannii* from *C. membranacea* TRÉCUL. *P. luteola* is also not uncommon in the vicinity of Cosha Cashu, Manu Park, and the Tambopata Reserve, as DAVIDSON and co-workers examined 28 established colonies on *C. tessmannii* and 42 foundresses or incipient colonies on *C. tessmannii*, respectively 18 on *C. membranacea* (DAVIDSON et al. 1991, DAVIDSON & FISHER 1991). According to these authors, *C. tessmannii* and *C. membranacea* look very similar but have different ecological demands, *C. tessmannii* being a shade-tolerant, very slowly growing species typical for small forest gaps and edges of forest swamps (aguajales) of which only seedlings can be found in clearings and riverine vegetation. In contrast, *C. membranacea*, is a fast growing, light-demanding species of stream and river bank disturbances and clearings which cannot survive under light limited conditions. In comparison with *C. membranacea*, *C. tessmannii* has shorter internodes, larger Müllerian bodies (0.16 mg dry weight versus 0.09 mg), starts earlier with production of M.b. (on the average with the 6th leaf when seedling still has not reached 10 cm height versus *C. membranacea* that on average starts production of M.b. with the 16th leaf; DAVIDSON et al. 1991, DAVIDSON & MCKEY 1993). These authors found larger, established colonies only on *C. tessmannii* that grew in small forest gaps. Foundresses of *P. luteola* on *C. membranacea*, however, either died (possibly because of limited food supply) or were replaced by faster growing *Azteca* colonies on the same plant. In their investigation 90% of established *C. tessmannii* were colonized by *P. luteola* and 10% by *Camponotus balzani*, but both species excluded each other on the same tree. DAVIDSON et al. conclude that the long stiff hairs on the stem and, especially, the urticating hairs around the large prostomata favour large-bodied *P. luteola* queens over smaller-sized *Azteca* queens on *C. tessmannii*. But *C. membranacea* exhibits the same traits and is regularly occupied by *Azteca alfari, A. xanthochroa* and *Camponotus balzani* as are other ra-

pidly growing *Cecropia* species, too (DAVIDSON et al. 1989, 1991, DAVIDSON & FISHER 1991, DAVIDSON & McKEY 1993).

Keeping these results in mind, most likely the *Cecropia* trees in Panguana colonized by *P. luteola* were indeed *C. tessmannii*, and probably only a few *C. membranacea* (e.g. VFor 489, and 90/335 C-P from secondary growth, and VFor 1043 and VFor 1056 from the matorral). Only in two of the examined *Cecropia* other ants were found besides *P. luteola* (once *Camponotus* sp. and once *Azteca* sp., both in presumed *C. membranacea*). The young trees were already colonized by the foundresses when only few (4-5) internodes were present, and it happened that several queens colonized the same plant. Ant queens shed their wings after mating and search for a young *Cecropia* with still uninhabited internodes. Some also obviously seek reception in yet established colonies, and it seems reasonable to speculate that they even do this in the mother nest.

In all cases observed, the young queens entered the internodium through the prostoma, a thin preformed spot in the wall of each internodium, that is easily gnawed by the ants to make a round or elliptical (up to 6 x 3 mm) entrance (plate 1b). Queens primarily colonized only one internodium and normally did not close the prostoma as do *Azteca* queens with chewed parenchyma (however, see the observation with VFor 1034). They harvested M.b. very early and fed them to the young larvae and certainly consumed them theirselves (see VFor 1033 a,c). Queens of ponerine species have to nourish themselves during colony founding because they are not supplied with great amounts of reserve material as queens of many myrmicine, formicine and dolichoderine species are. Colony founding queens of *Pseudomyrmex ferruginea* also regularly leave the swollen thorns of acacias to collect Beltian bodies (JANZEN 1967). The observations on foundresses of *P. luteola* made by DAVIDSON et al. (1991) and DAVIDSON & FISHER (1991) were similar to the results from Panguana. They state that colony growth is very slow and possibly depends on the production of M.b. They found colonies with as few as 2 - 4 workers a full year after colonization. Colony growth might also depend on the rate of parasitation of the pupae by parasitoids (Chalcidoidea) that have easy access to the brood because of the unclosed prostoma (DAVIDSON & FISHER 1991).

Polygyny

Multiple colonization of young trees of different *Cecropia* species by queens of one or several different ant species is not uncommon, but normally only one colony survives with one queen (e.g. in *Azteca*). Deadly fights between the colony foundresses are indicated by the carcasses of *Azteca* or queens of other species often found inside the internodia. Obviously, *P. luteola* queens avoid deadly fights among each other - car-

casses or body parts were never found. Possibly, the young colonies on the same *Cecropia* later fuse, as it is known from the obligate *Acacia* inhabitant *Pseudomyrmex venefica*, too (JANZEN 1973). The result would be a polygynous colony.

The strongest hint pointing to a polygynous colony form are three dealated queens found in the completely examined colony on a *C. tessmannii* in the garden of the station (VFor 940c, plate 1). All three queens were physogastric. Because of the tubular construction of the 3rd and 4th abdominal segment this is indicated in ponerine ants by the telescopically spreading of the abdominal segments and the protruding of the intersegmental membranes. Physogastry was especially distinct in comparison with virgin not egg laying alated or dealated queens showing a „normal", non-physogastric abdomen. The dissection of two of the three physogastric queens revealed that the ovaries were fully developed and mature eggs were present. As the third, not dissected, queen showed an identical enlarged abdomen I assume that the colony had three reproductive queens at the time of examination. Unfortunately, it cannot be stated whether the queens stayed together or separately in the nest. All internodia of the *Cecropia* were interconnected by holes in the nodal septa, and eggs were found in three neighbouring internodia (tab. 1).

The observation at this nest on April 3rd, 1985 of a dealated queen communicating by antennal and oral contact with workers on the *Cecropia* stem may have been part of an adoption process of an alien queen. The colony did not yet produce queens on its own (there was only a single callow male inside when the nest was examined). Two other dealated queens were observed at the base of the same *Cecropia* on April 19 and April 20, 1985, possibly indicating that such adoption processes occur regularly.

Besides these observations, there are good theoretical reasons why *P. luteola* colonies are likely to be polygynous.Functional polygyny (facultative or obligatory one, for definitions see BUSCHINGER 1974) in which all queens of a colony contribute to the reproduction of alates can be achieved in different ways within an ant colony (HÖLLDOBLER & WILSON 1977, 1990):

– Several queens found a new colony together (= pleometrosis and primary polygyny).
– Queens found colonies independent from one each other, and later colonies adopt alien or own fertilized queens (= haplometrosis and secondary polygyny).
– Fertilized queens leave the nest with a number of workers for new nesting sites (= budding). Often, the daughter-colonies stay in contact with the mother-colony, thus resulting polydomous colonies.

Pleometrosis and primary polygyny have been interpreted in several cases to maximize fitness during the difficult period of colony founding, but often only one queen survives the fights which start later when colo-

nies grow (see e.g. TSCHINKEL & HOWARD 1983, RIS-SING & POLLOCK 1987). Transitions from primary to secondary polygyny are observed in species in which queens found colonies independently but young colonies soon fuse and later adopt additional queens, too. This is the case, for example, in *Pseudomyrmex venefica* living on bull-horn acacia (JANZEN 1973).

In most cases of permanent, i.e. secondary polygyny a selective advantage for the colony as a whole is supposed (group selection; OSTER & WILSON 1978) which surpasses the importance of the kin selection (e.g. BU-SCHINGER 1974, HÖLLDOBLER & WILSON 1977, NONACS 1988). That means, the adoption of new, mostly alien queens must have advantages for the established colony and for the queens seeking adoption, as well. For the foundresses the chance for reproduction seems to be better in an established colony because nest sites, i.e. young *Cecropia* are limited in number. For colonies, in general, a number of ecological reasons are discussed in which a polygynous social organization is favored (see e.g. WILSON 1963, 1971, 1974 JANZEN 1973, BUSCHINGER 1974, HÖLLDOBLER & WILSON 1977, 1990, WARD 1983, VARGO 1988). For *P. luteola* the following reasons are likely to be important:

1. While the reproductive capacity of most ponerine queens is rather limited (in comparison to ant species from other subfamilies) polygyny enables a ponerine species to increase its colony size rapidly enough which, on the other hand, is necessary for complete occupation and defense of the steadily growing nest (=*Cecropia* tree).
2. Polygyny prolongs the lifetime of a colony independently of the individual lifetime of the single queen. Thus, a *Cecropia* can be colonized by the same colony over several decades.
3. The *Cecropia* trees occupied by *P. luteola* are long-living nest sites but unpredictable in space and limited in number.
4. The effective breeding size of the population increases which is especially important for rare species and those limited to very special or rare habitats.

At present it is not known whether the supposed polygyny in *P. luteola* is an obligatory or a facultative one, in the latter case being a plastic response to a different resource availability (i.e. amount of production of M.b.) or competiton (i.e. for limited *Cecropia* number) as observed in several plant-ants (see literature in DAVIDSON & MCKEY 1993).

The estimated number of up to 10,000 or more workers within colonies on adult *Cecropia* trees is very unusual for ponerines. DAVIDSON & MCKEY (1993) even estimate colony sizes up to 100,000 workers on mature *C. tessmannii* trees that reach a stature of 30 - 35 m after several or even many decades. Thus, they constitute the largest ponerine colonies in the neotropis, possibly even in the world, rivaling with nomadic *Leptogenys* colonies in South-East Asia (MASCHWITZ

et al. 1989). Reasons for the normally small colony size (several dozens to some hundreds; WILSON 1971, HÖLLDOBLER & WILSON 1990) in ponerines are:

1. Colonies most frequently are monogynous (for exceptions see e.g. WARD 1981, PEETERS & CREWE 1985).
2. Queens most often do not differ very much in size from that of the workers and are often replaced by ergatogynes or gamergates (= reproductive individuals with worker-like habits; e.g. PEETERS & CREWE 1985, WILDMAN & CREWE 1988).
3. Ponerine species are mainly predacious and often restricted in their diet (see overwievs in BRIAN 1983 and HÖLLDOBLER & WILSON 1990).
4. Hunting and prey transport is mainly done by single workers or by just some few after tandem recruitment. Group and mass recruitment are seldom developed (e.g. in *Megaponera*, *Pachycondyla*, *Leptogenys*, *Ectatomma*) and is often associated with a special diet (e.g. very large prey, or other social insects) and/or nomadic behaviour (WHEELER 1936, WILSON 1958, 1971, HÖLLDOBLER & WILSON 1990).

The first two points limit the egg production, the third and fourth the food supply for the brood. All points together result in small to medium colony sizes. Exceptions like nomadic monogynous *Leptogenys* species (MASCHWITZ et al. 1989) are certainly not food restricted, and in *P. luteola*, possibly all four points do not match: Colonies are supposingly polygynous, queens and workers differ quite much in size, the ants feed exclusively on a plant product which is always available (see below), and the ants must not hunt but just collect M.b. from the plant.

Nutrition

Obviously, *P. luteola*'s diet consists exclusively of Müllerian bodies (M.b.), which are produced in special hair pads (trichilia) at the base of the petioles (plate 1b). Analyses of M.b. of *Cecropia peltata* revealed that, in contrast to other cells of *Cecropia* containing starch as reserve carbohydrate, they are rich in glycogen that is stored in plastid derivates (RICKSON 1971). Because M.b. also contain protein and lipids, *Cecropia* trees offer their ants a complete diet, which makes them independent of other nutritional resources.

M.b. produced by *Cecropia tessmannii* are white and average 1.0 x 1.3 mm in size (plate 1c,d). They weigh on average 0.16 mg, i.e. they have double or triple the size of those of most other *Cecropia* species mainly colonized by *Azteca* ants. More than 50% of the trichilia of a plant were actively producing M.b. in greenhouse experiments, and production was declining with leaf age (DAVIDSON et al. 1991, DAVIDSON & FISCHER 1991). Therefore, it is not surprising that the ants always shift the nest entrance to the topmost internodia close to the most productive trichilia. For *P. luteola* foundresses it might even be vital to stay outside the plant as short time as possible.

Workers of *P. luteola* pull the M.b. with their mandibles out of the trichilia as soon as they are ripe and project from the hairs. Sometimes they even try to pull them out when they still deeply stick in the trichilia (same observations were made for *Azteca* by BEQUAERT 1922). The workers carry the M.b. immediately into the interior of the *Cecropia* (plate 1b). In the complete examined nest (VFor 940) they were stored in the first three internodes and distributed to the other internodia with brood (tab. 1, plate 1c). The whole plant contained approx. 5800 M.b., i.e. on average, 12 per adult ant or larva.

During the opening of nests, several times larvae were found feeding directly on M.b. (plate 1d). The larvae are of the pogonomyrmecoid type with ectatommoid mandibles and have a very distinct „neck", giving the head much mobility. (This is a character believed to be typical for *Pachycondyla* species and to separate them from *Neoponera* species, WHEELER & WHEELER 1976). There were few hints in the nests on possible other food than M.b. taken by *P. luteola*: In nest VFor 940 remnants of a treehopper (Membracidae) and of a male ant were found; and one worker (in nest VFor 1251) held the head of a *Cephalotes atratus* ant between the mandibles. But except for one worker that was found sitting 20 cm apart from the base of a *Cecropia* cleaning itself (after it had fallen from the plant?) workers never could be observed away from their host plant. Additionally, DAVIDSON & FISHER (1991) found out that *P. luteola* rejected standard ant baits like tuna and cheese. Thus, it seems more likely that workers kill other insects because they had invaded the *Cecropia* rather than to feed on them. In contrast to *Cecropia* trees occupied by *Azteca,* scale insects were never encountered inside the plants.

Mutualistic advantages

Mutualistic advantages in plant-ant-associations are known from many cases (see for recent reviews e.g. BEATTIE 1984, JOLIVET 1986, HUXLEY & CUTLER 1991, DAVIDSON & McKEY 1993).

The relationship between *P. luteola* and *C. tessmannii* obviously is obligatory for the ant and of great advantage: The plant offers a nest site that grows with increasing colony size and plenty of food. On the other hand, the plant is protected by hyperaggressive ants, which are easy to stimulate and very vigilant. Access to abundant carbohydrate-rich food is apparently often linked with an increased colony size and aggression in ants (DAVIDSON & McKEY 1993). During the day workers always patrol over the stem and in lower number over the leaves. At the slightest disturbance they get excited searching the whole surface of the plant for the source of the disturbance. This is already the case when somebody approaches the plant. The ants seem to be able to detect the human smell (and probably that of other vertebrates, too). JANZEN (1967) suppo-

sed the same for *Pseudomyrmex ferruginea*. The reaction of the ants is stronger and lasts longer if the plant is touched. Also at night, there are always some workers sitting on top of the plant and close to the entrance, which react and alert nestmates at the slightest disturbance.

Corresponding to the high aggression and vigilance of *P. luteola* the rate of damage by herbivores on colonized *C. tessmannii* is low. Two intensely examined trees showed no leaf damage. While sampling the *Cecropia* nest VFor 940 only two arthropods could be detected on the leaves: a small salticid spider, and a small beetle. Also in the study of DAVIDSON & FISHER (1991), *C. tessmannii* presented the lowest number of herbivorous insects on the leaves among all examined *Cecropia* species.

P. luteola offers its host plant not only a good protection against phytophagous insects but, in contrast to *Cecropia* colonizing *Azteca* species, also against phytophagous vertebrates by means of its powerful sting. The stings of *P. luteola* are very painful for humans as I could learn by own experience. The skin burned and swelled, the intense pain lasted in one case (sting in the belly) 2 hours, in another case about half an hour. More interesting than the acute pain, that is known from other ponerines as well (SCHMIDT 1986), is the long lasting residual pain. The sting in the belly was felt for a whole week. KOEPCKE (1972) reported a two weeks lasting pain. Thus, the sting has a longer effect than of any other ant known to the author including several other species of *Pachycondyla*, *Odontomachus*, *Pseudomyrmex*, and even *Paraponera clavata*, the most painful of all. According to SCHMIDT (1986, tab. 16), the pain even lasts for a longer time than in any other hymenopteran so far known.

Cecropia trees colonized by *Azteca* ants have been observed to suffer damage from monkeys and sloths (BEQUAERT 1922, WHEELER & BEQUAERT 1929, WHEELER 1942, BERG 1978, JOLIVET 1986). Whereas *Azteca* workers defend their colony only by biting and chemical repellents, which seem to be tolerable at least for some time for larger animals with dense fur or thick skin, the sting of *P. luteola* is strong enough to penetrate vertebrate skin not protected by dense fur. The pain of the sting should repell every animal intending to climb the *Cecropia*, and the pain lasts long enough to accelerate a learning process to avoid this „dangerous tree" in the future. DAVIDSON states that the stings reinforce vertebrate learning for a period of 7 to 10 weeks (DAVIDSON & McKEY 1993).

JANZEN (1967) already made the observation that large mammals like deers (*Mazama*), donkeys and cattle avoid to browse on *Acacia*, which are colonized by painful stinging *Pseudomyrmex ferruginea*. In Africa, *Tetraponera* living on *Barteria fistulosa* defend their trees also with stings against big herbivores and are successful even against elefants (JANZEN 1972).

During his study on *Acacia* ants JANZEN (1967) ob-
served that the herbivores learned the intensive, for a
human even in 3 m distance still detectable odour of
rancid onions that is part of the alarm pheromone of *P.
ferruginea*, and avoided the colonized *Acacia* even at
night. A similar displeasant odour is released by the
Tetraponera on *Barteria*, too. *P. luteola* does not pos-
sess such a smell, but a similar function may have the
striking stridulation of the workers. Even for the human
ear it is audible up to a distance of several decimeters.
The workers are stridulating nearly all the time while
patroling over the plant or harvesting Müllerian bodies,
but immediately intensify it, if they feel a disturbance
by a mecanical stimulus or just by detecting a strange
odour.
Ponerine ants stridulate with the abdominal tergites III
and IV, and 48% of examined ponerine species pos-
sess the necessary structures (MARKL 1973, 1983,
1985). In most cases the stridulation of ants is not au-
dible for humans because the frequences are too high,
and sound energy and range are too low. This is also
the reason why ants certainly cannot detect air con-
ducted sound but only receive vibrations through di-
rect contact or a substrate (e.g. MARKL et al. 1977,
STUART & BELL 1980, MARKL 1983, 1985). Some large
ponerine ants, however, produce sounds similar to
chirping that are audible for humans, too (SHARP 1893,
HOWSE 1984, and own observations). Stridulation in
ants has been observed in a whole array of situations
e.g. when movements were restricted, when ants got
buried alive, in fights with other ants, in queens after
copulation to keep males away, when capturing large
prey, during recruitment, while feeding other ants
(trophallaxis), during nest movements, and other
„stress“ situations (see e.g. MARKL 1967, SPANGLER
1967, MARKL et al. 1977, ZHANTIEV & SULKANOV 1977,
MARKL & HÖLLDOBLER 1978, STUART & BELL 1980). In
Megaponera foetens, a large African ponerine, stridu-
lation has been interpretated as aposemantic signal
against predators (MASTERS 1979, HOWSE 1984).
These communication signals have a low intensity, a
low range, and a low capacity to provoke a specific re-
action (=low range signals). However, they can be pre-
cisely tuned, are not energy expensive, only effective
as long they are directly practised, do not immediately
alert to many nestmates, and cannot be used by ene-
mies. Thus they are especially suited to function as
alarm system respectively as trigger and/or amplifier of
other communication systems in the often highly com-
partmented nests of social insects (MARKL 1983, 1985).
In *P. luteola* at least two functions of the stridulation
seem to be obvious:
1. As alarm system via a substrate, such as the stem
and leaves of a *Cecropia*. Possibly, the hollow stem of
the plant additionally amplifies these signals. An ana-
logous alarm system is known from several *Campono-
tus* species that „knock“ with the tip of their abdomen

or with the mandibels against the thin wooden walls of
their nests in trees (FUCHS 1976) or against the walls
of their silk nests (*Camponotus senex*, pers. observati-
on). In such strongly compartmented nests vibrations
as communication form are possibly more effective
and better tunable than chemical substances. The
same seems to be plausible for the *Cecropia* nest, a
hypothesis worth to be tested.
2. As aposemantic acoustical signal against verte-
brates which approach the host plant. This could be
important against terrestrial herbivores and any bigger
animal able to damage young *Cecropia* trees mecha-
nically, but especially against arboreal herbivores like
iguanas, coendus, monkeys or sloths. Although
Cecropia trees contain considerable amounts of tan-
nins (DAVIDSON & FISHER 1991) and are often densely
covered by stiff hairs their leaves are consumed by dif-
ferent mammals, e.g. the primates *Alouatta* and *Ateles*
(HLADIK & HLADIK 1969) or the three-toed sloths *Bra-
dypus variegatus* and *B. tridactylus*. The latter are
known to consume leaves of *Cecropia* trees regularly
(the Brazilian name „imbauba“ for *Cecropia* means
„sloth tree“, WHEELER 1942) and stay sometimes for
several day in a single tree (BEEBE 1922, SUNDQUIST &
MONTGOMERY 1973, HUSSON 1978: 251). It is not known
whether sloths also consume leaves of *Cecropia* inhabi-
ted by *P. luteola*. An acoustical warning signal which
vertebrates are likely to learn quickly would be especial-
ly valuable against nocturnal herbivores such as coen-
dus, two-toed sloths and partly three-toed sloths.
At last, it should be mentioned that according to DA-
VIDSON et al. (1988) *P. luteola* facultatively prunes
vines and other plants that got attached to the host
tree. The authors could observe this behaviour when
other ants, especially predacious or behaviourally
competing species, occurred on these plants. In Pan-
guana, workers of the examined nest in the garden
neither showed any interest to vines experimentally
brought in contact with the *Cecropia* nor to a winding
Pueraria phaseoloides (Fabaceae) which was clim-
bing the stem of the *Cecropia*. As most *C. tessmannii*
grow under shaded conditions, vines that climb over
them are expected to be rare anyway.

5. Conclusion

Pachycondyla luteola is one of the very few ponerine
ant species known to nest regularly in myrmecophytes
DAVIDSON & MCKEY (1993). In *P. luteola* several life
traits are uncommon for a ponerine ant: The nest site,
the completely vegetarian diet in form of glycogen rich
Müllerian bodies that *Cecropia tessmannii* produces in
abundance, and also the presumed functional poly-
gyny. It is concluded that these traits enable the spe-
cies to build up the most populous ponerine colonies
in the world. For the *Cecropia* species colonized by

this ant there seems to be an additional advantage compared to associations of *Cecropia* trees and *Azteca* ants. Besides pruning vines and eliminating herbivorous insects as do *Azteca* species, *P. luteola* also protects its host plant effectively against herbivorous vertebrates because of its powerful sting which produces a long residual pain. Certainly, the birds nesting on *Cecropia* trees colonized by *P. luteola* profit from fewer predators in these trees (KOEPCKE 1972).

Thus, the possession of this ant is likely to facilitate *C. tessmannii* to grow, though slowly, even at localities, where other *Cecropia* species cannot survive, like very small gaps in the primary forest. Because protection of myrmecophytes by ants is often far from being perfect (see e.g. VERHAAGH 1988), at such places where low light intensities limit the growth of a plant, the loss of photosynthetic active (leaf) surface is certainly more disastrous compared with a place with plenty of light. Light flooded forest edges or river banks are sites where most of the fast growing *Cecropia* species live with *Azteca* ants as inhabitants. DAVIDSON et al.(1991) and DAVIDSON & MCKEY (1993) therefore conclude that it is advantageous for slowly growing, shade tolerant myrmecophytes to invest early during their development in biological protection, i.e. ants, against herbivores. Such an association is likely to be species-specific, as in *C. tessmannii* and *P. luteola*. In contrast, associations between rapidly growing *Cecropia* species and *Azteca* ants often seem to be habitat-specific (HARADA & BENSON 1988, LONGINO 1989, DAVIDSON et al. 1991, DAVIDSON & FISHER 1991, DAVIDSON & MCKEY 1993).

6. Literature

BEATTIE, A. J. (1984): The evolutionary ecology of ant-plant mutualism. – Cambridge (Cambridge Univ. Press).

BEEBE, W. (1926): The three-toed sloth *Bradypus cuculliger cuculliger* WAGLER. – Zoologica, **7**: 1-67

BEQUAERT, J. (1922): Ants in their diverse relations to the plant world. – Bull. Amer. Mus. Nat. Hist., **45**: 333-621.

BERG, C. C. (1978): Espécies de *Cecropia* da Amazônia brasileira. – Acta Amazonica, **8**: 149-182.

BRIAN, M. V. (1983): Social insects. Ecology and behavioural biology. – London (Chapman & Hall).

BROWN, W. L. Jr. (1973): A comparison of the hylean and Congo-west African rain forest ant faunas. – In: MEGGERS, B. J., AYENSU, E. S. & DUCKWORTH, W. D. (Eds.): Tropical forest ecosystems in Africa and South America: A comparative review: 161-185; Washington (Smithsonian Inst. Press).

BUSCHINGER, A. (1974): Monogynie und Polygynie in Insektensozietäten. – In: SCHMIDT, G. H. (Ed.): Sozialpolymorphismus bei Insekten: 862-896; Stuttgart (Wissenschaftliche Verlagsgesellschaft).

DALLA TORRE, C. G. DE (1893): Catalogus hymenopterorum. Vol. VII Formicidae. – Leipzig (Engelmann).

DAVIDSON, D. W. & FISHER, B. L. (1991): Symbiosis of ants with *Cecropia* as a function of the light regime. – In: HUXLEY, C. R. & CUTLER, D. K. (Eds.): Ant-plant interactions: 289-309; Oxford (Oxford University Press).

DAVIDSON, D. W., FOSTER, R. B., SNELLING, R. R. & LOZADA, P. W. (1991): Variable composition of some tropical ant-plant-symbioses. – In: PRICE, P. W., LEWINSOHN, T. M., FERNANDES, G. W. & BENSON, W. W. (Eds.): Plant-animal interactions. Evolutionary ecology in tropical and temperate regions: 145-162; New York (Wiley).

DAVIDSON, D. W., LONGINO, J. T. & SNELLING, R. R. (1988): Pruning of host plant neighbors by ants: an experimental approach. – Ecology, **69** (3): 801-808.

DAVIDSON, D. W. & MCKEY, D. (1993): The evolutionary ecology of symbiotic ant-plant relationships. – J. Hym. Res., **2** (1): 13-83.

DAVIDSON, D. W., SNELLING, R. R. & LONGINO, J. T (1989): Competition among ants for myrmecophytes and the significance of plant trichomes. – Biotropica, **21**: 64-73.

EMERY, C. (1890): Voyage de M. E. SIMON au Venezuela. Formicides. – Ann. Soc. Ent. France, (6) **10**: 55-76.

EMERY, C. (1901): Notes sur les sous-familles des dorylines et ponerines. – Ann. Soc. Ent. France, **45**: 32-54.

EMERY, C. (1911): Formicidae: Ponerinae, fasc. 118. – In: WYTSMAN, P. (Ed.): Genera Insectorum. – Brüssel.

FERREYRA, R. (1970): Flora invasora de los cultivos de Pucallpa y Tingo Maria. – Lima.

FUCHS, S. (1976): The response to the vibration of the substrate and reactions to the specific drumming in colonies of carpenter ants (*Camponotus*, Formicidae, Hymenoptera). – Behav. Ecol. Sociobiol., **1**: 155-184.

HANAGARTH, W. (1981): Vergleichend-ökologische Untersuchungen an epigäischen Arthropoden aus Naturbiotopen und Kulturland im tropischen Regenwald Perus. – Dissertation Hamburg.

HARADA, A. Y & BENSON, W. W. (1988): Espécies de *Azteca* (Hymenoptera, Formicidae) especializadas em *Cecropia* (Moraceae): distribução geográfico e considerações ecológicas. – Revta bras. Ent., **32**: 423-435.

HLADIK, A. & HLADIK, C. M. (1969): Rapports trophiques entre vegetation et primates dans la forêt de Barro Colorado (Panama). – Terre Vie, **1**: 29-117.

HÖLLDOBLER, B. & WILSON, E. O. (1977): The number of queens: an important trait in ant evolution. – Naturwissenschaften, **64**: 8-15.

HÖLLDOBLER, B. & WILSON, E. O. (1990): The ants. – Berlin (Springer).

HOWSE, P. E. (1984): Alarm, defense and chemical ecology of social insects. – In: LEWIS, T. (Ed.): Insect communication: 151-167; London (Academic Press).

HUSSON, A. M. (1978): The mammals of Suriname. – Leiden (Brill).

HUXLEY, C. R. & CUTLER, D. F. (Eds.) (1991): Ant-plant interactions. – Oxford (Oxford University Press).

JANZEN, D. H. (1967): Interaction of the Bull's-horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. SMITH) in eastern Mexico. – Univ. Kansas Sci. Bull., **47**: 315-558.

JANZEN, D. H. (1972): Protection of *Barteria* (Passifloraceae) by *Pachysima* ants (Pseudomyrmecinae) in a Nigerian rain forest. – Ecology, **53**: 885-892.

JANZEN, D. H. (1973): Evolution of polygynous obligate acacia-ants in western Mexico. – J. Anim. Ecol., **42**: 727-750.

JOLIVET, P (1986): Les fourmis et les plantes – Un exemple de coevolution. – Paris (Boubee).

KEMPF, W. W. (1972): Catálogo abreviado das formigas da região neotropical. – Studia Ent., **15**: 3-343.

KOEPCKE, M. (1972): Über die Resistenzformen der Vogelnester in einem begrenzten Gebiet des tropischen Regenwaldes in Peru. – J. Orn., **113** (2): 138-160.

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

MARKL, H. (1967): Die Verständigung durch Stridulationssignale bei Blattschneiderameisen. I. Die biologische Bedeutung der Stridulation. – Z. vergl. Physiol., **57**: 299-330.

MARKL, H. (1973): The evolution of stridulatory communication in ants. – In: Proc. VII Congr. IUSSI: 258-265; London.

MARKL, H. (1983): Vibrational communication. – In: HUBER, F. & MARKL, H. (Eds.): Neuroethology and behavioral physiology: 332-353; Berlin (Springer).

MARKL, H. (1985): Manipulation, modulation, information, cognition: some of the riddles of communication. – In: HÖLLDOBLER, B. & LINDAUER, M. (Eds.): Fortschritte der Biologie Bd. 31: Experimental behavioral ecology: 163-194; Stuttgart (Fischer).

MARKL, H. & HÖLLDOBLER, B. (1978): Recruitment and food-retrieving behavior in *Novomessor* (Formicidae, Hymenoptera). II. Vibration signals. – Behav. Ecol. Sociobiol., **4**: 183-216.

MARKL, H., HÖLLDOBLER, B. & HÖLLDOBLER, T. (1977): Mating behavior and sound production in harvester ants (*Pogonomyrmex*, Formicidae). – Ins. Soc., **24**: 191-212.

MASCHWITZ, U., STEGHAUS-KOVAC, S., GAUBE, R. & HÄNEL, H. (1989): A South East Asian ponerine ant of the genus *Leptogenys* (Hym., Form.) with army ant life habits. – Behav. Ecol. Sociobiol., **24**: 305-316.

MASTERS, W. M. (1979): Insect disturbance stridulation: its defensive role. – Behav. Ecol. Sociobiol., **5**: 187-200.

NONACS, P. (1988): Queen number in colonies of social Hymenoptera as a kin-selected adaptation. – Evolution, **42** (3): 566-580.

ORTIZ, D. (1974): El Pachitea y el Alto Ucayali: Visión histórica de dos importantes regiones de la selva peruana, T. 1 – Lima.

OSTER, G. F. & WILSON, E. O. (1978): Caste and ecology in the social insects. – Princeton (Princeton Univ. Press).

PEETERS, C. P. & CREWE, R. M. (1985): Worker reproduction in the ponerine ant *Ophthalmopone berthoudi*: an alternative form of eusocial organization. – Behav. Ecol. Sociobiol., **18**: 29-37.

PORTILLO, D. P (1901): Las montañas de Ayacucho y los ríos Apurimac, Mantaro, Ene, Perene, Tambo y Alto Ucayali. – Lima.

RICKSON, F. R. (1971): Glycogen plastids in Müllerian body cells of *Cecropia peltata* – a higher green plant. – Science, **173**: 344-347.

RISSING, S. W. & POLLOCK, G. B. (1987): Queen aggression, pleometrotic advantage and brood raiding in the ant *Veromessor pergandei* (Hymenoptera: Formicidae). – Anim. Behav., **35**: 975-981.

RÖMBKE, J. & VERHAAGH, M. (1992): About earthworm communities in a rain forest and an adjacent pasture in Peru. – Amazoniana, **12** (1): 29-49.

ROGER, J. (1861): Myrmicologische Nachlese. – Berl. Ent. Z., **5**: 163-174.

ROGER, J. (1863): Verzeichnis der Formiciden-Gattungen und Arten. – Berl. Ent. Z., **7**: 1-64.

SCHMIDT, J. O. (1986): Chemistry, pharmacology, and chemical ecology of ant venoms. – In: PIEK, T. (Ed.): Venoms of the Hymenoptera: 425-508; London (Academic Press).

SHARP, D. (1893): On stridulation in ants. – Trans. Ent. Soc. Lond., 1893: 199-213.

SPANGLER, H. G. (1967): Ant stridulations and their synchronization with abdominal movement. – Science, **155**: 1687-1689.

STEPHENS, L. & TRAYLOR, M. A. Jr. (1983): Ornithological gazetteer of Peru. – Cambridge, Mass. (Harvard Univ.)

STIGLICH, G. (1922): Diccionario geográfico del Peru. – Lima.

STUART, R. J. & BELL, P. D. (1980): Stridulation by workers of the ant, *Leptothorax muscorum* (Nylander) (Hymenoptera: Formicidae). – Psyche, **87**: 199-210.

SUNQUIST, M. E. & MONTGOMERY, G. G. (1973): Activity patterns and rates of movement of two-toed and three-toed sloths (*Choloepus hoffmanni* and *Bradypus infuscatus*). – J. Mammal., **54**: 946-954.

TSCHINKEL, W. R. & HOWARD, D. F. (1983): Colony founding by pleometrosis in the fire ant, *Solenopsis invicta*. – Behav. Ecol. Sociobiol., **12**,:103-113.

VARGO, E. L. (1988): Effect of pleometrosis and colony size on the production of sexuals in monogyne colonies of the fire ants. – In: TRAGER, J. C. (Ed.): Advances in myrmecology: 217-225; Leiden (Brill).

VERHAAGH, M.(1988): „Parasitierung" einer Ameisen-Pflanzen-Symbiose im neotropischen Regenwald? – Carolinea, **46**: 150; Karlsruhe.

WARD, P. S. (1981): Ecology and life history of the *Rhytidoponera impressa* group. I. + II. – Psyche, **88**: 89-126.

WARD, P. S. (1983): Genetic relatedness and colony organisation in a species complex of ponerine ants. 1. Phenotypic and genotypic composition of colonies. – Behav. Ecol. Sociobiol., **12**: 285-299.

WHEELER, G. C. & WHEELER, J. (1976): Ant larvae: review and synthesis. – Mem. Ent. Soc. Washington, **7**: 1-108.

WHEELER, W. M. (1936): Ecological relations of ponerine and other ants to termites. – Proc. Amer. Acad. Arts Sci., **71**: 159-243.

WHEELER, W. M. (1942): Studies of neotropical ant-plants and their ants. – Bull. Mus. Comp. Zool., **90**: 1-262.

WHEELER, W. M. & BEQUAERT, J. (1929): Amazonian myrmecophytes and their ants. – Zool. Anz., **82**: 10-39.

WILDMAN, M. H. & CREWE, R. M. (1988): Gamergate number and control over reproduction in *Pachycondyla krugeri* (Hymenoptera: Formicidae). – Ins. Soc., **35** (3): 217-225.

WILSON, E. O. (1958): The beginnings of nomadic and group-predatory behavior in the ponerine ants. – Evolution, **12** (1): 24-31.

WILSON, E. O. (1963): Social modifications related to rareness in ant species. – Evolution, **17** (2): 249-253.

WILSON, E. O. (1971): The insect societies. – Cambridge, Mass. (Belknap).

WILSON, E. O. (1974): The population consequences of polygyny in the ant *Leptothorax curvispinosus*. – Ann. Ent. Soc. Amer., **67**: 781-786.

ZHANTIEV, R. D. & SULKHANOV, A. V. (1977): Sounds of ants of the genus *Myrmica* (Russian with Englisch summary). Zool. Zh., **56**: 1255-1258.