

OBSERVATIONS ON THE GENUS *TERATANER* IN  
MADAGASCAR (HYMENOPTERA: FORMICIDAE)

BY GARY D. ALPERT

Museum of Comparative Zoology  
Harvard University, Cambridge, MA 02138

INTRODUCTION

The present study was inspired by the analysis of endemism in Malagasy ants by William L. Brown (1973). The rare myrmicine ant genus *Terataner*, presently with twelve described species, is known only from the Ethiopian and Malagasy zoogeographical regions. Bolton (1981) revised the Ethiopian species of *Terataner*, and provided illustrations and a key to workers. In the same paper, Bolton described a new species of *Terataner* from Madagascar and included an illustrated key to workers from the Malagasy region. An ongoing study of Malagasy *Terataner* resulted in the discovery of many new species (Alpert, in prep.) and the first natural history data on any of the ants in this group. This new information separates *Terataner* into two distinct groups with fundamental biological differences.

The first group, containing four closely related arboreal species, occurs only in tropical West Africa. According to Bolton (1981, pers. comm.), these species construct nests in rotten parts of standing timber, often located a considerable distance above the ground. The males in this group are unknown and the female reproductives, although presently undescribed, are morphologically typical ant queens. No other biological information is available on this group of ants.

The second, much larger, group of *Terataner* species nests near the ground and inhabits preformed plant cavities, such as hollow twigs and burrows of wood-boring insects. One species occurs in the Transvaal of South Africa, one in East Africa, one in the Seychelles, and five are currently recognized in Madagascar. The males, known from only a few species, are morphologically unusual. The newly discovered queens are wingless ergatoid

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forms, distinguishable externally from workers only by very subtle characters. This extreme ergatoid condition is rare among ants in general (Peeters and Crewe 1985, Hölldobler and Wilson 1990), and particularly rare in the Myrmicinae (Bolton 1986, Brandao 1987, Peeters 1991). Observations on these Malagasy *Terataner* contribute to our understanding of the evolutionary biology of the genus, as well as the biogeography and biodiversity of ants from Madagascar.

#### MATERIALS AND METHODS

In a forthcoming revision of Malagasy *Terataner* (Alpert, in prep.), species names are given to the forms designated *T. sp. a-d* in this study. Individual foragers of *T. sp. a* were first discovered by William L. and Doris E. Brown, in 1977, in a vanilla plantation near the town of Sambava on the northeast coast of Madagascar. Subsequent trips by the author to the coastal lowlands and foothills of the Masoala Peninsula in the northeast of Madagascar (February 1990 and 1991, July 1992) were successful in locating colonies of this species as well as three other species of *Terataner* (*alluaudi*, *foreli* and *sp. b*). In August of 1992, colonies of two additional species were studied, one from the Ankarana Reserve in the north (*sp. c*), and the other (*sp. d*) from the Lokobe Forest, Nosy Be in the northwest of Madagascar.

Complete *Terataner* colonies were collected into both 80% alcohol and Bouin's preservative. Field notes and photographs were taken of each nest site location. Field observations were made on foragers from each species, and representative colonies were brought back to the laboratory for further studies.

Colonies were located by following individual workers returning to their nests and by searching the ground for twig nests. Ants entering twigs in search of prey items were occasionally mistaken for returning foragers. Nests sites were confirmed only when *Terataner* ant brood was found associated with workers. After nest collection, the immediate area was examined for colony fragments, returning foragers and other ant nests.

Workers and ergatoid reproductives in a colony were dissected under a light microscope to determine their degree of reproductive development. The degree of ovarian development was measured,

and those with developed ovaries were examined for the presence of external queen characters.

## RESULTS

Foragers of three undescribed species of *Terataner* were found at field study sites but their nests were not located. Data from complete colonies of six species; two previously described and four undescribed, are included in this study:

*T. alluaudi*, the most common *Terataner* in northern Madagascar, is a large (7.3 mm) black species with conspicuous orange legs. It is found from just above sea level (20 m) on the northeast and northwest coasts to about 500 m inland. It ranges from 12°S near Antsiranana (Diego Suarez: type locality) in the north, to a latitude of 15°S near Marofinaritra.

*T. foreli* is a medium-sized (5.3 mm) black and orange species distributed along the eastern coast of Madagascar from 14°S to 19°S latitude and from 50 to 800 meters altitude. Morphologically, it is more variable than other species presently known from Madagascar, and has the widest distribution.

*T. sp. a* is very similar to *T. alluaudi* but is larger (7.9 mm) and has black, rather than orange, legs. *T. sp. a* has only been collected from the northeast coast of the Masoala Peninsula. Occurring in forested foothills from 50 m to 100 m altitude, its habitat is threatened by the advance of agriculture at these lower elevations.

*T. sp. b* is a small (4.5 mm), entirely black species, closely related to *T. foreli*. It has only been found along the northeast coast of the Masoala Peninsula and a few kilometers inland.

*T. sp. c* is restricted to the Lokobe forest, a "Réserves Naturelles Intégrales" along the southeast coast of Nosy Be, an island off the northwest coast of Madagascar. The protection of this reserve is vital to the survival of this ant.

*T. sp. d* is restricted to the Ankarana forest in the "Réserves Spéciales" of north central Madagascar. The protection of this reserve is vital to the survival of this ant. Figure 1 illustrates the distribution of *Terataner* species included in this study.

### *Colony Composition*

All six *Terataner* species nest in plant cavities, typically in dead branches or twigs that are on the ground or in bushes close to the

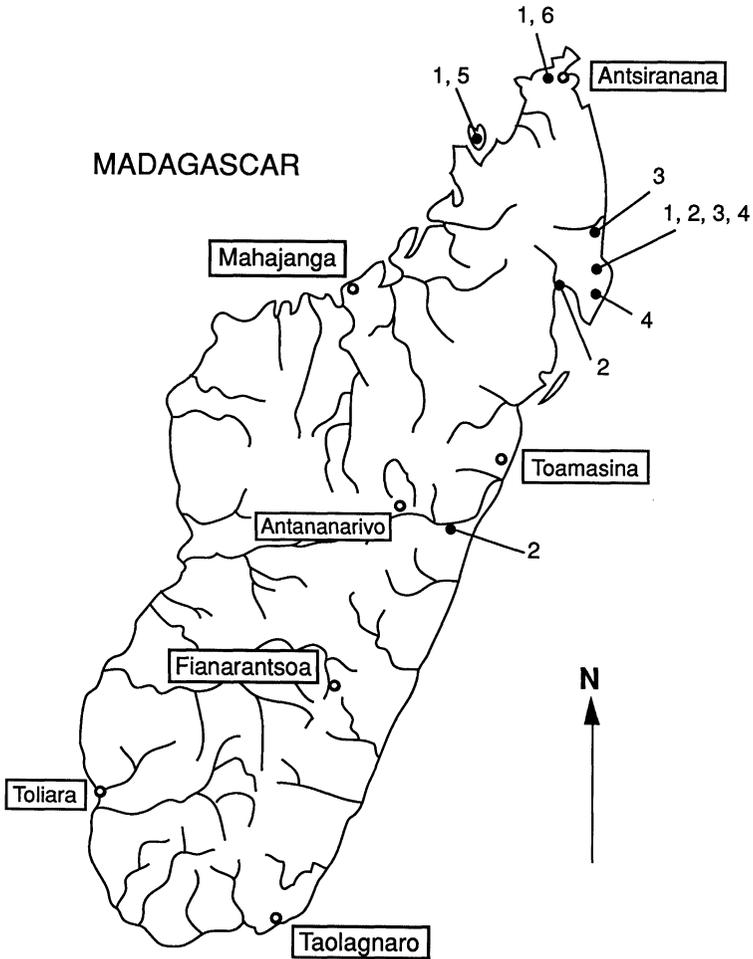


Figure 1. Distribution of *Terataner* in Madagascar. (*T. alluaudi* = 1; *T. foreli* = 2; *T. sp. a* = 3; *T. sp. b* = 4; *T. sp. c* = 5; *T. sp. d* = 6)

ground. Different species of *Terataner* were often found nesting within a meter of one another in the same habitat. *T. alluaudi*, a widespread species, was found sympatrically with *T. foreli* and the more restricted species *T. sp. a*, *T. sp. b*, *T. sp. c*, and *T. sp. d*. Larvae, pupae and adults were packed together into a central cavity.

Only one or two entrances were found per nest, and these openings were typically guarded by workers. During nest analysis, no predators, parasites, or inquilines were found. Occasionally, stored insect booty were found cached at one end of the nest.

Seven complete nests of *T. alluaudi* were collected (Table 1). The nest sites of *T. alluaudi* consisted of a dead branch on the ground (4 cases), or a dead branch resting in vegetation close to the ground (3 cases).

Table 1. *T. alluaudi* colony size and composition.

Nest #	Eggs	Larvae	Workers	♀-Pupae	♂-Pupae	Males	Ergatoid ♀
1	65	130	78	48	.2	3	5
2	0	14	9	1	0	0	3
3	19	16	17	1	0	0	1
4	26	29	32	7	0	1	1
5	17	19	18	1	0	0	1
6	25	11	19	2	0	0	1
7	10	15	18	0	0	0	1

Nine complete colonies of *T. foreli* were collected (Table 2). *T. foreli* colonies typically were found in small twigs resting directly on the ground.

Table 2. *T. foreli* colony size and composition.

Nest #	Eggs	Larvae	Workers	♀-Pupae	♂-Pupae	Males	Ergatoid ♀
1	3	3	8	1	0	0	1
2	10	23	12	2	0	0	1
3	11	10	7	1	0	0	1
4	0	6	10	0	0	0	1
5	15	16	10	6	0	0	1
6	1	7	12	2	0	0	1
7	9	40	19	6	0	0	1
8	0	8	22	6	0	0	1
9	1	7	11	3	0	0	1

Four complete nests of *T. sp. a* were collected (Table 3). The branches used for nests by *T. sp. a* were always suspended above the ground by vegetation.

Table 3. *T. sp. a* colony size and composition.

Nest #	Eggs	Larvae	Workers	♀-Pupae	♂-Pupae	Males	Ergatoid ♀
1	27	74	9	13	0	0	1
2	14	22	13	6	0	0	1
3	6	36	19	0	0	0	1
4	12	61	32	3	0	0	1

Eight complete nests of *T. sp. b* were collected (Table 4). *T. sp. b* nests close to the ground in the stems of bushes, or on the ground in small twigs.

Table 4. *T. sp. b* colony size and composition.

Nest #	Eggs	Larvae	Workers	♀-Pupae	♂-Pupae	Males	Ergatoid ♀
1	0	25	27	3	1	0	1
2	20	21	46	9	0	1	1
3	66	110	89	16	3	0	1
4	24	65	55	12	0	0	1
5	47	89	24	6	6	0	1
6	20	41	22	16	0	0	1
7	39	41	28	17	0	0	1
8	21	8	19	3	0	0	1

Eight complete nests of *T. sp. c* were collected (Table 5). Nests were found in twigs on the ground, or in small stumps close to the ground.

Table 5. *T. sp. c* colony size and composition.

Nest #	Eggs	Larvae	Workers	♀-Pupae	♂-Pupae	Males	Ergatoid ♀
1	3	41	21	5	0	1	1
2	1	4	5	0	0	0	1
3	0	15	10	0	0	0	1
4	8	25	6	2	0	0	1
5	1	6	4	0	0	0	1
6	0	21	15	4	0	0	1
7	0	6	4	1	0	0	1
8	3	28	16	1	0	0	1

Three complete nests of *T. sp. d* were collected (Table 6). Nests were found in small twigs resting on the ground.

Table 6. *T. sp. d* colony size and composition.

Nest #	Eggs	Larvae	Workers	♀-Pupae	♂-Pupae	Males	Ergatoid ♀
1	10	37	11	3	0	0	1
2	5	23	8	1	0	0	1
3	0	9	3	0	0	0	1

*Ergatoid Queens*

No morphologically normal alate or dealate queens occur in any of the Malagasy *Terataner* species. Colonies are almost always monogynous with a single reproductive, an ergatoid queen, that differs only slightly from corresponding workers (Fig. 2). This remarkable reproductive lacks both wings and ocelli, and has an almost normal, worker-like thorax. The ergatoid queen is externally distinguishable from workers only by very subtle characters (e.g., small spines or tubercles below the mesonotal groove; a unique pattern of rugae on the sides of the pronotum) that vary among species. Ergatoid queens have ovaries bearing two to three

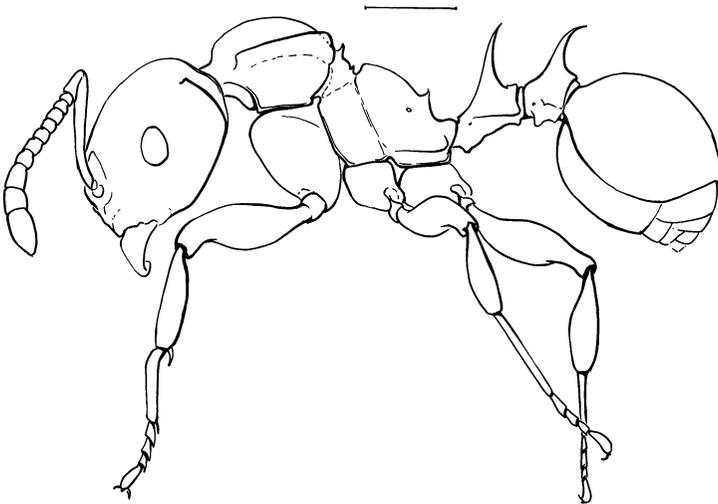


Figure 2. Ergatoid queen of *Terataner alluaudi*.  
Scale line, 1.0 mm.

ovarioles, and each ovariole contains a string of oocytes undergoing oogenesis. In contrast, no oocytes are present in workers.

### *Males*

Males were rare in colonies, never surpassed four per colony, and were found in only three of the six species. *Terataner* males are morphologically distinctive (Fig. 3). The alitrunk is unusually shaped such that the wings are attached abnormally low on its sides, yet the male is still capable of flight. The middle pair of legs is reduced in size relative to the other two pairs of legs. Males were present in nests throughout this study (July, August, February and March). When nests were opened for analysis, males sometimes took flight. It is unknown whether males mate inside nests or whether they mate in the field with ergatoid queens.

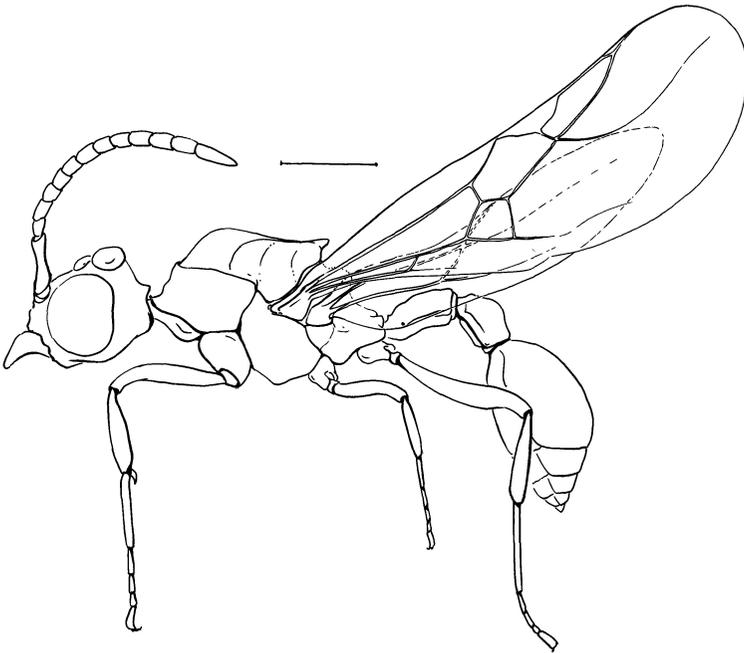


Figure 3. Male of *Terataner alluaudi*.  
Scale line, 1.0 mm.

*Foraging Behavior*

All species are diurnal, active from sunrise to sunset. During the months of January, February and March, the warm, rainy season in Madagascar, foraging activity was much greater than during July and August, which are cool and dry. Foragers for all six species spend most of their time searching the upper surface of vegetation close to the ground. When found, nests were usually located less than 5 meters from these foragers. Although *Terataner* workers forage individually, they will also sometimes initiate small group raids.

*T. alluaudi* raided other ants and termites that were nesting inside branches. *T. foreli* was found attacking small insects and beetle larvae in branches by chewing their way into the wood to reach their prey. *T. sp. a* was observed bringing in and caching large numbers of lepidoptera larvae as well as termites and other insects. *T. sp. b* was observed bringing in dismembered parts of insects. *T. sp. c*, and *d* were not observed raiding and their food sources are unknown.

## DISCUSSION

Ergatoid queens, reported for the first time in the genus *Terataner*, are present in all six Malagasy species studied. Thus the most probable mode of colony founding in these ants is budding, where a mated ergatoid queen and some workers leave an established nest and occupy a nearby plant cavity. Flightless queens severely restrict the dispersal ability of these ants and may account, in part, for the limited geographic distributions of some of these species. This mode of reproduction, combined with their preference for forested habitats, means that Malagasy *Terataner* may be extremely vulnerable to habitat destruction. Malagasy *Terataner* share other ecological similarities: 1) small colony size, ranging from 3 to 89 workers; 2) workers that are general predators which group raid the nests of other ants, termites, and attack live insects; and 3) nest sites in plant cavities such as twigs and hollow branches close to the ground. The presence of spider and clerid beetle mimics of several *Terataner* species (Alpert, unpublished data) suggests that workers are distasteful and/or formidable to vertebrate predators.

The significance of the disjunct biogeographical distribution of this genus is an open question. Have a few species dispersed to Madagascar from Africa and then secondarily radiated in a land devoid of driver ants and other competitors? Or, is *Terataner* a relict genus that was once widespread and is now restricted to a portion of the Ethiopian and Malagasy regions? It will be interesting to discover whether the Transvaal and East African *Terataner* have ergatoid queens similar to Malagasy species, or normal queens similar to those in West Africa. Many more species of *Terataner* may be discovered when Madagascar is studied further. The ant biodiversity of this region of the world is far greater than expected based upon the number of described taxa (P. Ward, pers. comm.). If conservation efforts are successful, further research may answer some of these unresolved questions.

#### SUMMARY

*Terataner* species in Madagascar are very different from those in West Africa. West African *Terataner* are arboreal and have normal, alate queens. In Madagascar, colonies nest in plant cavities near the ground, and reproduction is by means of ergatoid queens that are very similar to workers. Workers forage for live insect prey, and often group raid the nests of ants and termites. Males are morphologically unusual and are rare. This is the first report of ergatoid queens in the genus *Terataner*.

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