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rbt@cariari.ucr.ac.cr
Universidad de Costa Rica
Costa Rica

Zara, F. J.; Fowler, H. G.
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Universidad de Costa Rica
San Pedro de Montes de Oca, Costa Rica

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Pheidole in the New World: A Dominant, Hyperdiverse Ant Genus

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Review with a special emphasis on the Brazilian *Pheidole* ant fauna and megadiversity distribution in American countries

Completing his academic career the way he began, one of the most outstanding scientists of this century, Edward O. Wilson, published his formidable monographic revision of the New World *Pheidole*. Though formally retired since 1997, Wilson continues to labor as Emeritus Pellegrino University Research Professor of the Museum of Comparative Zoology of Harvard University. Dr. Wilson is well known to biologists and ecologists as the author of *Sociobiology, Biophilia, Island Biogeography*, among others. Wilson, in spite of this breadth of vision and synthesis, is the foremost living myrmecologist. To those who know him, the sheer passion that he shares for ants he extends to all other living beings, and it is this commitment which has highlighted his Biodiversity advocacy, and he is now one of its principle spokesmen. His monumental revisionary monograph of *Pheidole* follows last year's publication of *The Future of Life* (Wilson 2002), the most accessible and impassioned of his appeals to humans to take heed of the millions of other species that make the planet habitable.

Pheidole in the New World is Wilson's masterful revision of the species rich ant genus that he has scrutinized for 16 years, as known to all friends and myrmecologists. To deal with the enormous number of species, Wilson defines the term "Hyperdiversity" to describe the species-richness of *Pheidole.* Hyperdiversity is employed by Wilson to discuss "when a genus or family … contains exceptionally large number of species with reference to plant and animal diversity as a whole." The large number of species is to be expected as *Pheidole* is the dominant taxon of New World ant ground ant assemblages (Fowler 1994), but some species are also arboreal and others have symbiotic relationships with myrmecophytes. Indeed, *Pheidole* is now the most species-diverse group of New World organisms after beetles (Chrysomelidae and Curculionidae). Placed in another light, Levi (2002), Wilson's colleague at the Museum of Comparative Zoology, estimates 1500 species of araenid spiders divided into 65 genera, 47 in Brazil, as occurring in the New World and these data show how hyperdiverse is the genus *Pheidole*.

The origin of these omnipresent faunal elements is still unclear. *Pheidole* has a world-wide distribution, although it is apparently dominant in the New World (Wilson 1976, Fowler 1994). The oldest fossil is from Oligocene shales of North America (Carpenter 1930), and is not common in the Dominician ambers (Baroni Urbani 1995). 2N chromosome numbers of the studied species range in the neighborhood of 20, although an Indian species has a diploid number of 42, not allowing for a clear interpretation. Old World diversification is however much lower than that found in the New World. Sister groups are presently interpreted as being *Aphaenogaster,* or the Indonesian *Chimaeridris*. Thus, much more research is needed to clarify the origin of this highly successful genus.

Wilson recognizes 624 *Pheidole* species in the Western Hemisphere. However, he notes that "undescribed species … were still pouring in to the Harvard Collection as (this) monograph went to press" suggesting that

many more species undoubtedly exist. This monumental binary key revision was in part supported by the world's taxonomists, which provided type specimens, the oldest dating from 1826. Wilson's research depended upon local collaborators who shipped him samples from collections throughout the United States, Latin America, and Europe, resulting in 337 new species. But, how does one organize such a monumental venture? Wilson began by dividing the taxa into 19 species groups, 2 of which are of Old World origin (*megacephala* and *teneriffana* both from Africa) but represented in the New World. One species group includes social parasitic forms, most of which are from Argentina and should grow as more myrmecological research continues in the New World.

Pheidole is spread through 35 New World countries, but the number of species, as well as the relative percentage of all species, varies greatly (Table 1). How does Brazil fit into the distribution of New World *Pheidole*? Is the mega-diversity of Brazil (Mittermeier and Werner 1990) also found in this highly speciose group? Indeed, the documented Brazilian *Pheidole* fauna represents 24.3% of its total diversity (152 species), followed by Mexico 18.6% (116 species), Costa Rica 18.1% (113 species), Colombia 15.2% (95 species), Peru 12.5% (78 species) and the USA 12.2% (76 species) (Fig. 1). These values, however, only consider the absolute number of species for each country. Furthermore, the superficial area and the collecting effort varies greatly among countries. In order to minimize differences in the number of species per area of any country, we created an index to estimate the relative megadiversity of species of New World *Pheidole,* by dividing the total number of recorded species per country by the number of 10º latitudinal bands of each country from 50º N to 50º S. The highest relative megadiversity of species of *Pheidole* was found in Costa Rica, followed by Panama, Peru, Mexico, Colombia, Brazil, Ecuador, EUA, Trinidad, and Guatemala independently of their surface area (Fig. 2, Table 1). These data clearly show the high collecting effort in Costa Rica and Panama, two countries well studied by Wilson. Brazil's sixth position indicates that this country may exhibit a large *Pheidole* diversity, depending on increased collecting effort.

In Brazil, of the 19 species groups of *Pheidole* recognized by Wilson, only four are not present. The species groups *crassicornis*, *granulata* and *pilifera* are almost exclusively Nearctic. Additionally, the species group *teneriffana*, which is native to North Africa, has turned up in disturbed habitats in Cuba, Peru and California. Of the 15 species groups of *Pheidole* found in Brazil, *tristis*, *diligens*, *fallax* and *flavens* are, respectively, the most speciose and encompass 84% of the fauna. These species groups also represent the highest number of New World species, with *flavens* being the most species rich, followed by *tristis*, *fallax* and *diligens* (Fig. 3).

Of the 152 Brazilian species of *Pheidole*, 45.4% are apparently endemic to Brazil. Of these, 71% are known only from type localities, suggesting a broader geographic distribution, due to lack of systematic collections, or conversely restricted distributions which could lead to their rapid extinction without ever knowing their natural history. Of the total documented Brazilian fauna, 42.1% have unknown biologies, or in another words, 65.2% of the Brazilian species are endemic and with unknown biologies (Table 2), suggesting a formidable amount of natural history still ahead, as well as the probable discovery of more species. In spite of this fact, no *Pheidole* appear in the Red List of Threatened Species for Brazil (MMA 2003), which surprisingly has only three ant species listed.

Wilson graciously recognized many prominent myrmecologists who have worked largely solitarily in Latin America, by naming species after them, including the masters W.L. Brown and N. Kusnezov, and the present generation of myrmecologists J. Trager, W. MacKay, J. Lattke, C.R.F. Brandão, P. Oliveira, and H.G. Fowler. Wilson recognized the importance of the contributions in support of tropical conservation by Harrison Ford, Peter A. Seligmann and Sal Roush. Indeed, Wilson dedicated the

book to his deceased mentor, W.L. Brown, who began the revision of this genus with Wilson more than 20 years ago (Brown 1981).

Wilson meticulously illustrated by hand all species, and showed another innovation (Fig. 4). Wilson introduced anatomical markers which highlight keyed taxonomic characters and should greatly assist new myrmecologists, as well as more experienced ones by making explicit identifying traits.

A CD accompanies the printed book. The CD micrographically illustrates the species and should facilitate production of local and regional faunal keys. Combined with work underway at the Museum of Comparative Zoology and elsewhere, this additional innovation assures that such painstaking research will henceforth be refined and accelerated using digital imaging and genomics techniques, and then promptly disseminated to users worldwide by the Internet. In scholarly terms, it bridges the established science of biological systematics and its imminent future. However, the CD contains a mistake concerning the total number of *Pheidole* species in Brazil. Instead of 150 species presented in the CD list, we have detected that the book shows 152 species for Brazil, including *P. laevinota* (*diligens* group) and *P. nitidicollis* (*flavens* group).

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F.J. Zara[1] & H.G. Fowler[2]

1 UNESP, Campus do Litoral Paulista – Unidade de São Vicente, CEP 11330-900, São Vicente, SP, Brazil; fjzara@csv.unesp.br

2 Depto de Ecologia UNESP, Rio Claro - C. P. 199, CEP 13506-900, Rio Claro, SP, Brazil; hgfowler@rc.unesp.br

TABLE 1
Statistics of species richness and country characteristics used in our analysis

Country	Species richness	Number of latitude bands of 10º covering each country	Country area (Km^2)*	Relative megadiversity Index Species/latitude 10º
Argentina	59	4	2.766.889	14.75
Brazil	152	5	8.511.965	30.6
Uruguay	4	1	186.925	4
Chile	1	5	751.625	0.2
Paraguay	9	2	406.750	4.5
Bolivia	34	2	1.098.575	17
Peru	78	2	1.285.215	39
Ecuador	53	2	461.475	26.5
Colombia	95	3	1.138.915	31.7
Venezuela	31	2	912.045	15.5
French Guiana	7	1	91.000	7
Suriname	8	1	163.820	8
Guyana	13	1	214.970	13
Trinidad	23	1	5.130	23
Curaçao (Dutch West Indies)	1	1	993	1
Panamá	46	1	78.515	46
Costa Rica	113	2	50.900	56.5
Nicaragua	11	1	148.000	11
Honduras	19	1	112.085	19
El Salvador	15	1	21.395	15
Guatemala	20	1	108.890	20
Belize	4	1	22.965	4
Bermudas	1	1	54	1
Cuba	12	2	114.525	6
Jamaica	7	1	11.425	7
Haití	4	1	27.750	4
Domenican Republic	7	1	48.440	7
Dominica	10	1	751	10
Puerto Rico	8	1	8.960	8
St. Kitts and Nevis	1	1	262	1
Bahamas	4	1	13.865	4
St. Vincent and The Grenadines	7	1	389	7
Grenada	4	1	345	4
USA	76	3	9.363.130	25.3
Mexico	116	3	1.972.545	38.7

(*) from Pauwels (1997)

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TABLE 2

Synoptic listing of what is known of the biologies and distributions of recorded Brazilian species of Pheidole

Group	Species	Known biology	Registered only in Brazil	Group	Species	Know biology	Registered only in Brazil
aberrans	*aberrans*	Yes	No	*flavens*	*flavens*	Yes	No
	cavifrons	Yes	No		*flavida*	No	Yes
	fracticeps	Yes	No		*goeldii*	No	Yes
	minensis	No	Yes		*guajirana*	Yes	No
biconstricta	*biconstricta*	Yes	No		*ligniocola*	No	No
	simplex	Yes	No		*lucaris*	Yes	Yes
	socrates	No	No		*minutula*	Yes	No
crassicornis	*ausency*	in	Brazil		*nana*	No	Yes
diligens	*angusta*	No	Yes		*nitella*	Yes	No
	blumenauensis	No	Yes		*nitidicollis*	No	No
	bruensi	Yes	No		*obtusopilosa*	Yes	No
	camptostela	No	Yes		*peltastes*	No	Yes
	cataractae	Yes	No		*pholeops*	Yes	No
	chrysops	Yes	No		*rudigenis*	Yes	No
	coffeicola	No	No		*schmalzi*	No	No
	cyrtostela	Yes	Yes		*sospes*	Yes	No
	diligens	Yes	No		*subreticulata*	No	Yes
	embolopyx	Yes	No		*tambopatae*	Yes	No
	fowleri	Yes	Yes		*termitobia*	Yes	Yes
	geraesensis	No	Yes		*tetrica*	No	Yes
	laevifrons	No	Yes		*victma*	No	Yes
	laevinota	Yes	No	*gertrudae*	*capillata*	Yes	No
	laidlowi	No	No		*gertrudae*	No	No
	lancifer	Yes	No		*jeannei*	Yes	Yes
	lemur	No	Yes	*granulata*	*ausency*	in	Brazil
	longiscapa	Yes	No	*lamia*	*colobopsis*	Yes	No
	longiseta	Yes	No	*megacephala*	*megacephala*	Yes	No
	oxyops	Yes	No	*perpusilla*	*perpusilla*	Yes	No
	peregrina	Yes	Yes	*pilifera*	*ausency*	in	Brazil
	perryorum	Yes	Yes	*pucntatissima*	*meinerti*	Yes	No
	pubiventris	Yes	No		*rugiceps*	Yes	No
	radoszkowskii	Yes	No	*scrobifera*	*mamore*	Yes	No
	reichenspergeri	No	Yes	*tachigaliae*	*mendicula*	Yes	No
	rochai	No	Yes		*pedana*	No	No
	rufipilis	No	Yes	*teneriffana*	*ausency*	in	Brazil
	sensitiva	Yes	No	*transversostriata*	*scolioceps*	Yes	No
	strigosa	Yes	Yes		*transversostriata*	Yes	No
	triconstricta	Yes	No	*tristis*	*alexeter*	Yes	Yes
	vafra	Yes	No		*allarmata*	Yes	No
	veletis	Yes	No		*alpinensis*	No	Yes
distorta	*bufo*	Yes	No		*ambigua*	No	Yes
	deima	No	Yes		*aper*	No	Yes
	dolon	Yes	No		*auropilosa*	No	No
	monstrosa	No	Yes		*avia*	No	Yes
fallax	*aenescens*	No	Yes		*bambusarum*	Yes	No
	alienata	No	Yes		*brevicona*	No	Yes
	araenoides	Yes	Yes		*brunnescens*	No	Yes
	arcifera	No	Yes		*bucculenta*	Yes	Yes
	cardinalis	Yes	Yes		*carapuna*	Yes	No
	claviscapa	Yes	No		*cephalica*	Yes	No
	cuevasi	Yes	No		*cramptoni*	Yes	No
fallax	*cursor*	Yes	No	*Tristis*	*descolei*	No	No
	eidmanni	No	Yes		*dyctiota*	Yes	Yes
	gigas	Yes	Yes		*fabricator*	Yes	No
	impressa	No	Yes		*fera*	No	Yes
	jacutifera	No	Yes		*fimbriata*	Yes	No

TABLE 2 (*Coninued*)

Synoptic listing of what is known of the biologies and distributions of recorded Brazilian species of Pheidole

Group	Species	Known biology	Registered only in Brazil	Group	Species	Know biology	Registered only in Brazil
	jelskii	Yes	No		*germaini*	No	Yes
	jujuyensis	No	No		*gibba*	No	Yes
	lovejoyi	Yes	Yes		*grandinodus*	No	Yes
	lucretii	No	Yes		*guilelmimuelleri*	No	No
	midas	Yes	No		*hetschkoi*	Yes	Yes
	nesiota	No	Yes		*lutzi*	Yes	Yes
	nitidula	No	No		*moseni*	Yes	Yes
	obscurior	Yes	No		*polita*	Yes	No
	paraensis	No	Yes		*praeses*	Yes	Yes
	punctithorax	No	Yes		*risii*	No	No
	puttemansi	No	No		*rosae*	Yes	No
	tijucana	No	Yes		*rutilana*	Yes	Yes
	trageri	No	Yes		*sarcina*	No	No
	valens	Yes	Yes		*schwarzmaieri*	No	No
	wallacei	No	Yes		*senilis*	Yes	Yes
	wolfringi	No	Yes		*sigillata*	Yes	Yes
flavens	*arhuaca*	Yes	No		*spininodis*	Yes	No
	asperithorax	Yes	No		*stulta*	Yes	No
	bidens	No	Yes		*subarmata*	No	No
	borgmeieri	Yes	Yes		*synarmata*	Yes	No
	dinophica	Yes	Yes		*tristicula*	Yes	No
	exigua	Yes	No		*tristis*	No	No

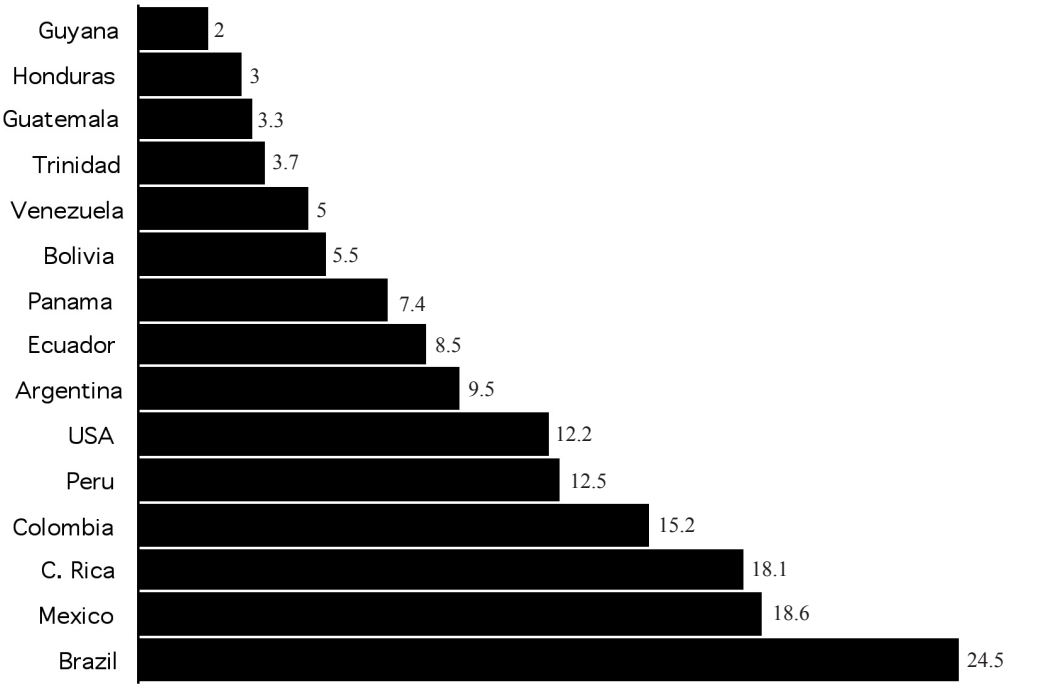

Fig. 1. The 15 New World countries with the largest number of species of *Pheidole*. Numbers above bars indicate the relative percentage of each country to the total number of species recognized by Wilson (2003).

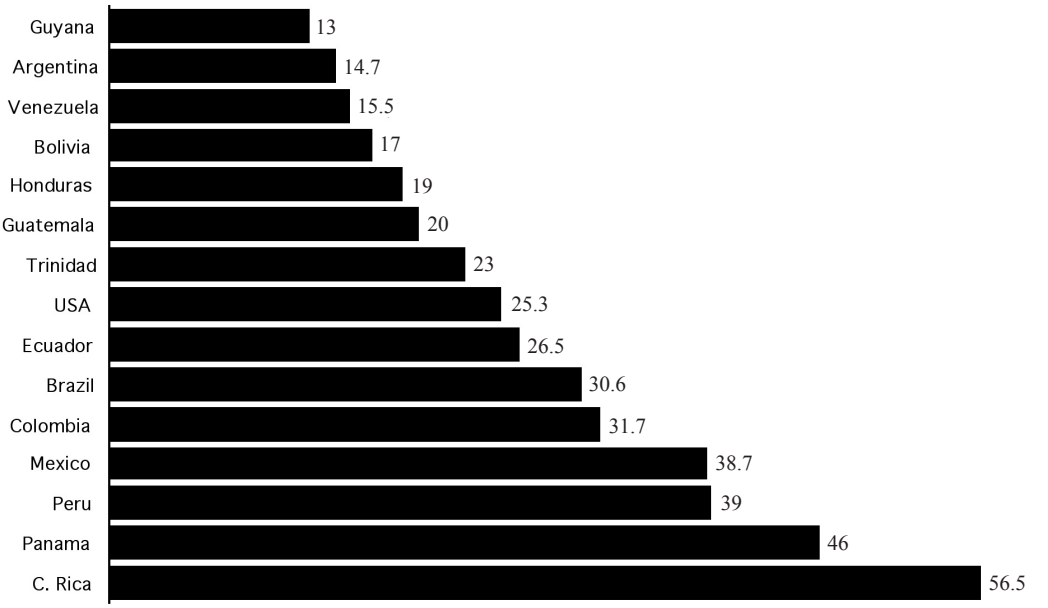

Fig. 2. Relative *Pheidole* megadiversity (number of species/number of 10º latitudinal bands from 50ºN to 50ºS) for the 15 most speciose countries of the New World.

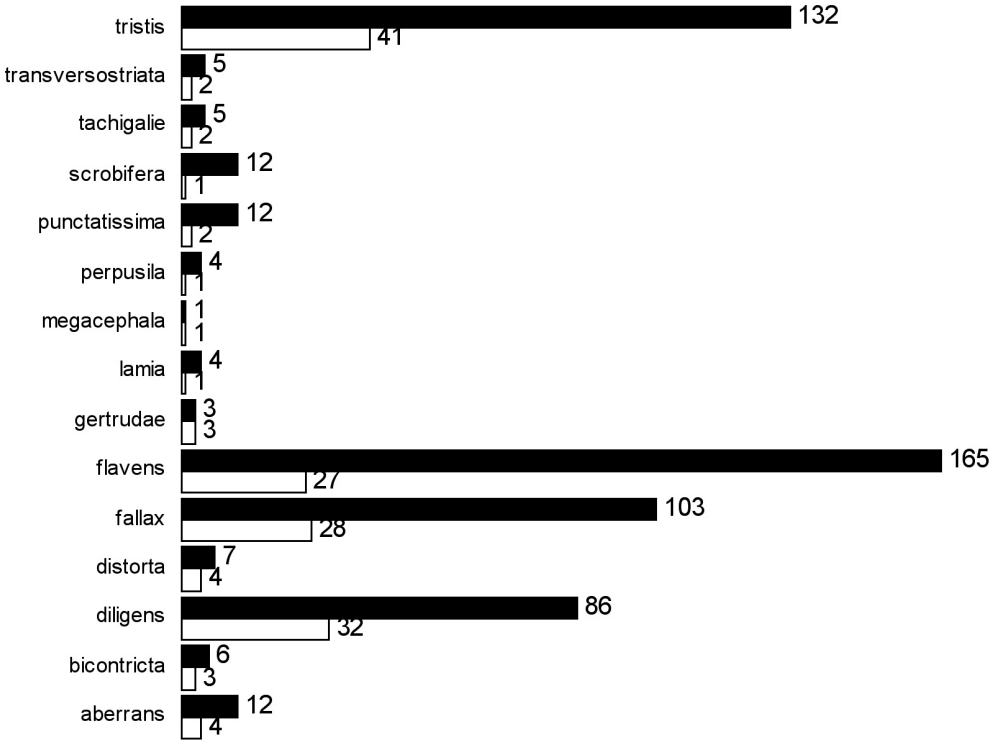

Fig. 3. Species richness of each 15 species groups of *Pheidole* found in Brazil (white bars) compared to the total New World species group (black bars).

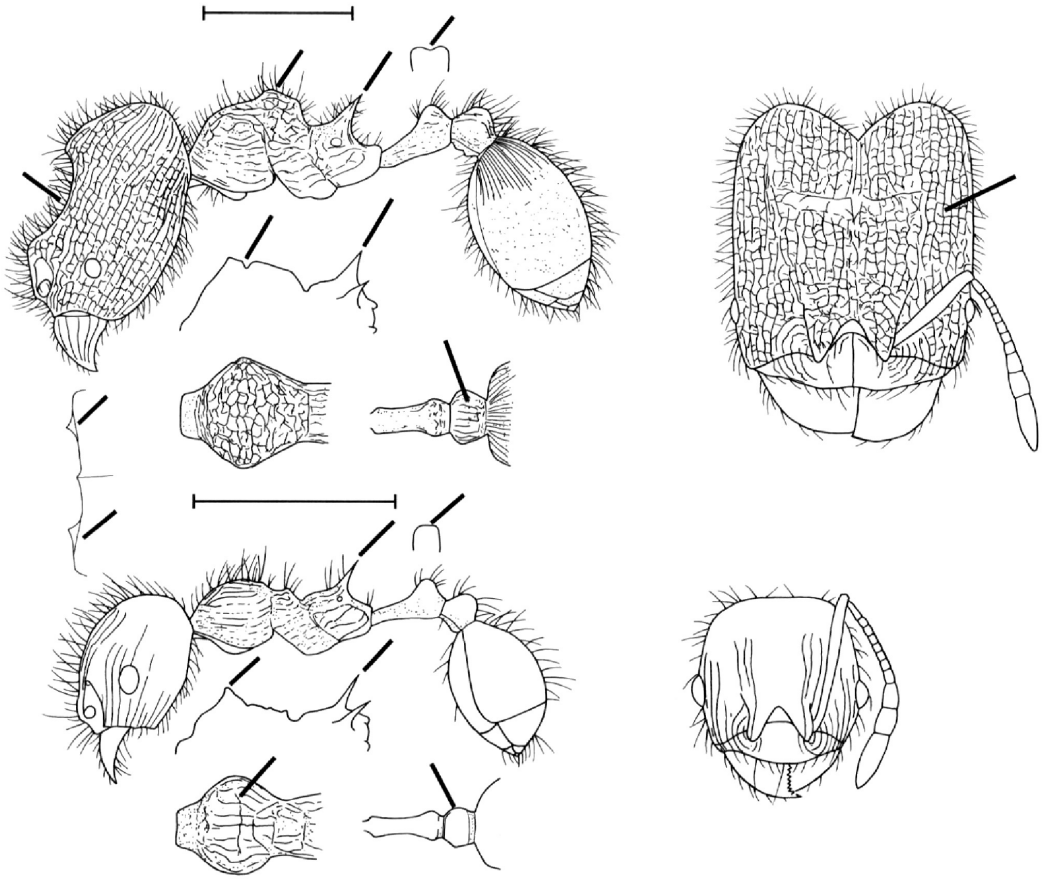

Fig. 4. Taxonomic markers used by Wilson to characterize anatomical features used in the identification keys.

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