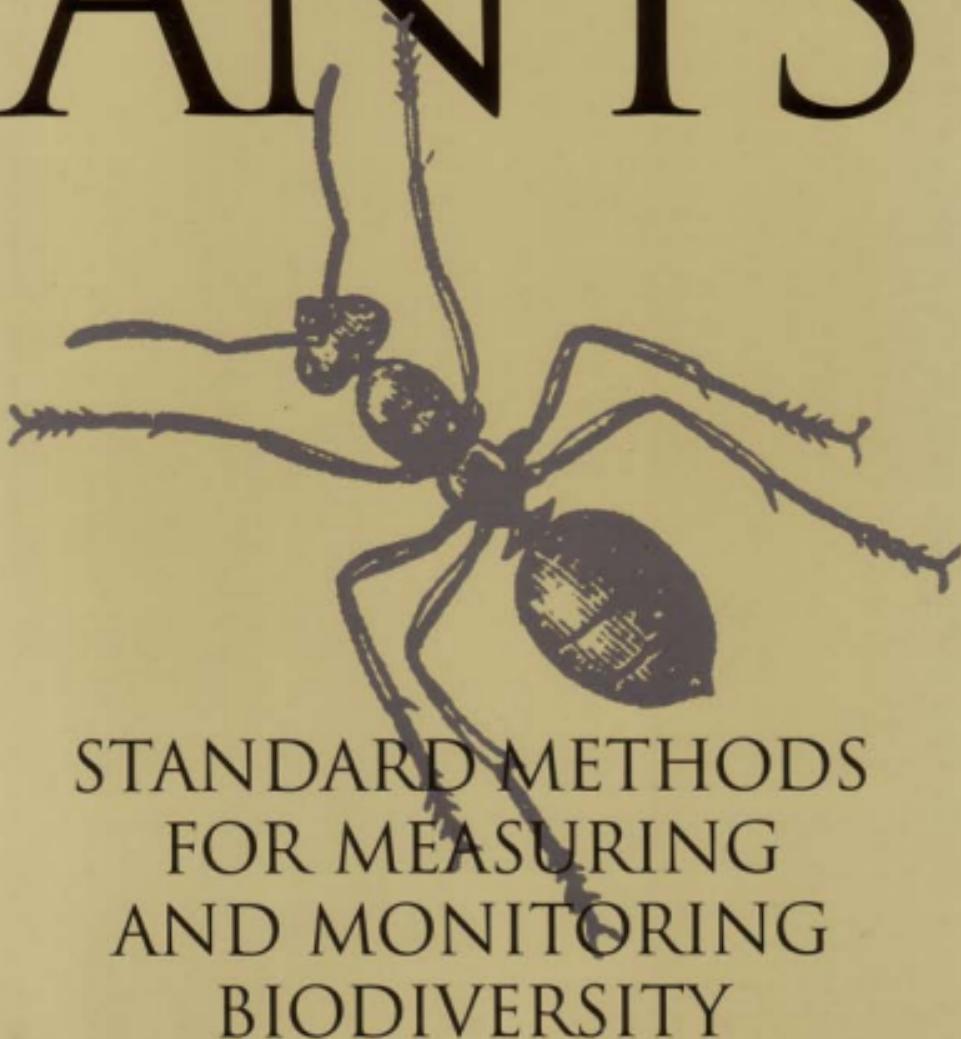


ANTS



STANDARD METHODS
FOR MEASURING
AND MONITORING
BIODIVERSITY

EDITED BY DONAT AGOSTI, JONATHAN D. MAJER,
LEEEANNE E. ALONSO, AND TED R. SCHULTZ

FOREWORD BY EDWARD O. WILSON



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AND MONITORING
BIODIVERSITY



Biological Diversity Handbook Series

Series Editor: Don E. Wilson

This series of manuals details standard field methods for qualitative and quantitative sampling of biological diversity. Volumes focus on different groups of organisms, both plants and animals. The goal of the series is to identify or, where necessary, develop these methods and promote their adoption worldwide, so that biodiversity information will be comparable across study sites, geographic areas, and organisms, and at the same site, through time.

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This book is dedicated to the memory of William L. Brown Jr.,
with affection, respect, and gratitude. For the inspiration you provided,
for the firm foundation you built for ant systematics, and especially
for your generous soul and irreverent good humor, we will never forget you, Bill.

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Diversity of Ants



William L. Brown Jr.



This chapter provides a background of taxonomic information for those who may be sampling ant diversity or dealing with other myrmecological matters (such as ant ecology) that demand some understanding of the challenge of identification of ant species. It is assumed that ants are chosen for biodiversity study mainly because they are ubiquitous and easily sampled, but also because identifying them is practicable as compared with identification of such other teeming taxa as mites and collembolans.

Although the last few years have seen great leaps forward in ant taxonomy—especially publication of *The Ants* (Hölldobler and Wilson 1990), *Identification Guide to the Ant Genera of the World* (Bolton 1994), and *A New General*

Catalogue of the Ants of the World (Bolton 1995b)—huge gaps still remain in our ability to identify given ant species with dispatch and confidence. The main challenges involve such immense and unrevised genera as *Camponotus*, *Crematogaster*, and *Pheidole*, plus various smaller but nevertheless dominant ground-dwelling taxa (Chapter 8). Some genera (e.g., *Pachycondyla*, New World *Pheidole*, the genera of the dacetonines) are currently under revision, as indicated by “forthcoming” in the list of identification aids in Chapter 12.

Ant Genera: An Overview

Table 5.1 summarizes general information about ant genera; some species may not conform to these generalizations. Numbers of

The author died shortly after completing this chapter.

Table 5.1 Distribution, Biology, and Ecology of the Ant Genera of the World^a

Genus	Subfamily	Tribe	Species	Distribution	Habitat	Microhabitat	Biology	Functional Group ^b	Keys
<i>Acanthogathus</i>	Myrmicinae		6	Neotropical		Nesting in litter	Predators of several arthropods	SP	Brown and Kempf (1969)
<i>Acanthomyops</i>	Formicinae	Myrmicinae	16	Nearctic		Subterranean	Tend homopterans	C	Wing (1968)
<i>Acanthomyrmex</i>	Myrmicinae	Myrmecini	11	Sri Lanka to Melanesia	Mesic forest		Seed harvesters, especially of ficus	TCS	Moffett (1986)
<i>Acanthoponera</i>	Ponerinae	Ectatommini	4	Neotropical	Mesic forest, savanna	Arboreal	Predators	TCS	Brown (1958)
<i>Acanthostichus</i>	Cerapachyinae	Acanthostichini	11	Neotropical, S Nearctic		Subterranean	Mass foraging predators of termites	C	MacKay (1996)
<i>Acromyrmex</i>	Myrmicinae	Attini	26	Neotropical, S Nearctic		Nesting in ground	Cultivators of fungi	TCS	Goncalves (1961); Fowler (1988) (<i>Moellerius</i>)
<i>Acropyga</i>	Formicinae	Plagiolepidini	56	Worldwide in tropics and warm temperate	Hypogaecic		Tend coccids	CS	Weber (1944) (Neotropical); Terayama (1985b) (Taiwan, Japan)
<i>Adelomyrmex</i>	Myrmicinae	?Myrmecini	8	Neotropical, Indo-Australian			Predators of mites	TCS	Smith (1947ab) (<i>Apyscho-myrmex</i> , Neotropical)
<i>Adetomyrma</i>	Ponerinae	Ponerini	1	S Madagascar			Predators	?	Ward (1994)
<i>Adlerzia</i>	Myrmicinae	Phaidolegotonini	1	Australia				?	Brown (1952)
<i>Aenictogiton</i>	Dorylinae	Aenictogitini	7	C Africa				TCS	Samisch (1923b); Brown (1975)
<i>Aenictus</i>	Dorylinae	Aenictini	100	E Mediterranean to E Australia		Army ants		TCS	Wilson (1964) (Indo-Australian); Gotwald (1982); Terayama and Yamane (1989) (Sumatra)
<i>Afroxyridis</i>	Myrmicinae	Pheidolegotonini	1	C, W Africa				?	Belshaw and Bolton (1994b)
<i>Agraulomyrmex</i>	Formicinae	Plagiolepidini	2	Afrotropical				?	Prins (1983)
<i>Alloformica</i>	Formicinae	Formicini	3	Tadzhikistan				?	Dlussky (1969: 219);
									Generalized foragers, . . .

<i>Allomerus</i>	Myrmicinae	Solenopsidini	3	Neotropical	Mostly nesting in plant cavities	?C	Wheeler and Mann (1942); Kempf (1975b); Bolton (1987)
<i>Amblyopone</i>	Ponerinae	Amblyoponini	64	World temperate and tropical	Predators, esp. of Chilopoda	C	Brown (1960); Baroni Urbani (1978a) (Mediterranean); Terayama (1987) (Taiwan); Lattke (1991) (Neotropical)
<i>Ancyridris</i>	Myrmicinae	Stenammini	2	Melanesia	Wet forest	?	?
<i>Anergates</i>	Myrmicinae	Tetramorini	1	Paleartic, adventive in Nearctic	Workerless parasites of <i>Terranomium caespitum</i>	?	Ettershank (1966)
<i>Aneuretus</i>	Dolichoderinae	Aneuretini	1	Sri Lanka	Predators	?	Wilson et al. (1956)
<i>Anillidris</i>	Dolichoderinae	Dolichoderini	1	S Neotropical		?	Santschi (1936, 1937)
<i>Anillomyrma</i>	Myrmicinae	Solenopsidini	2	Afrotropical, Indomalayan		?	Bolton (1987)
<i>Anisopheidole</i>	Myrmicinae	Pheidologetonini	1	Australia	Cryptic foragers	C	Ettershank (1966)
<i>Ankyloomyrma</i>	Myrmicinae	Leptothoracini	1	Afrotropical		?C	Bolton (1973a)
<i>Anochetus</i>	Ponerinae	Odontomachini	27	World tropics and warm temperate, except Nearctic	Arboreal Nesting in rotten logs	TCS SP	Brown (1978) (world); Lattke (1986) (Neotropical); Wang (1993) (China)
<i>Anomalomyrma</i>	Leptanillinae	Anomalomyrmini	4	Indomalayan	Cryptic predators	C	Taylor (1990a)
<i>Anonychomyrma</i>	Dolichoderinae	Dolichoderini	24	Indomalayan, Australia	Epigaeic and arboreal	DD	Shattuck (1992a, 1992b)
<i>Anoplolepis</i>	Fornicinae	Plagiopheidini	22	Afrotropical, S Palearctic, adventive in Indomalayan	Epigaeic Foragers	CS	Prins (1982) (custodiens group, partial)
<i>Antechinomyrma</i>	Myrmicinae	Solenopsidini	2	S Neotropical		?	Snelling (1975)
<i>Aphaenogaster</i>	Myrmicinae	Pheidolini	142	World except Afrotropical and South America	Generalized foragers	O	Smith (1961) (Niugini); Arnol'di (1976a) (USSR); Umphrey (1996) (Nearctic)
<i>Aphomomyrmex</i>	Formicinae	Brachymyrmeclini	1	Afrotropical	Arboreal, nesting in plant cavities	TCS	Snelling (1979b)
<i>Apomyrma</i>	?Leptanillinae	Aponymyrmini	1	Afrotropical	Hypogaeic Predators of geophilomorph Chilopoda	C	Brown et al. (1970)
<i>Apterostigma</i>	Myrmicinae	Attni	34	Neotropical	Nesting in ground Fungus cultivators	TCS	Lattke (1997)

Continued on next page

Table 5.1 continued

Genus	Subfamily	Tribe	Species	Distribution	Habitat	Microhabitat	Biology	Functional Group ^b	Keys
<i>Asterogenys</i>	Myrmicinae	Dacetini	1 Indomalayan 3 Neotropical, Amazon basin, and Atlantic forest		Hypogaecic	Predators		Brown (1972); Brandão et al. (1999)	
<i>Asphinctanilloides</i>	Leptanilloidae	Leptanilloidini				Nomadic		C	
<i>Asphinctopone</i>	Ponerinae	Ponerini	1 Afrotropical	Rainforest floor		Predators		C	Brown (pers. obs.)
<i>Atopomyrmex</i>	Myrmicinae	Leptocephalini	3 Afrotropical					TCS	Bolton (1981b)
<i>Atta</i>	Myrmicinae	Attini	15 Neotropical and S Nearctic 1 Azerbaijan					TCS	Borgmeier (1959); Arnoldi (1930); Taylor (1979b)
<i>Aulacopone</i>	Ponerinae	Ectatommini			Nesting in ground Predators	Fungus cultivators		?	
<i>Axinidris</i>	Dolichoderinae	Dolichoderini	13 Afrotropical					?	Shattuck (1991)
<i>Azteca</i>	Dolichoderinae	Dolichoderini	70 Neotropical		Arboreal	Generalized foragers, visit extrafloral nectaries		DD	Longino (1991) (spp. inhabiting <i>Cecropia</i>)
<i>Bajcaridris</i>	Formicinae	Formicini	3 Algeria, Morocco					?	Agosti (1994a)
<i>Baracidris</i>	Myrmicinae	Stenammini	2 Afrotropical		Epigaecic			?	Bolton (1981b)
<i>Bariamyrma</i>	Myrmicinae	Stenammini	1 Neotropical		Forest floor			?	Lattke (1990)
<i>Basiceros</i>	Myrmicinae	Basicerotini	6 Neotropical		Mesic forest		Predators, esp. of termites	C	Brown and Kempf (1960); Brown (1974a)
<i>Belonopelta</i>	Ponerinae	Ponerini	2 Neotropical	Forest	Litter	Predators, esp. of campodeid diplura		?	Baroni Urbani (1975b); Brandão (1989) (Brazil)
<i>Blepharidatta</i>	Myrmicinae	Blepharidattini	2 Neotropical	Forest	Nesting in litter, in ground, or under stones	Scavengers		TCS	Kempf (1967c)
<i>Bondroitia</i>	Myrmicinae	Solenopsidini	2 Afrotropical					C	Bolton (1987)
<i>Bothriomyrmex</i>	Dolichoderinae	Dolichoderini	34 S Palearctic, India to Australia					CCS	Shattuck (1992b)
<i>Brachymyrmex</i>	Formicinae	Brachymyrmecini	40 Neotropical, Nearctic, adventive elsewhere					?	Santschi (1923a)
<i>Bregmatomyrma</i>	Formicinae	Bregmatomyrmecini	1 Indomalayan					CS	(out of date)
								?	

<i>Calyptomyrmex</i>	Myrmicinae	Stenammini	24	Afrotropical, Indo-Melanesian	?C	Baroni Urbani (1975a) (India); Bolton (1981a)
<i>Camponotus</i>	Formicinae	Camponotini	935	Worldwide	SC	Kusnezov (1951d) (Argentina); (Africa)
				Nesting in ground, Generalized foragers in dead wood, in and on trees		Kusnezov (1951d) (Argentina); Yasumatsu and Brown (1951, 1957)
						(<i>herculeanus</i> complex, E Palearctic); Hashmi (1973) (<i>Myrmothrix</i>); Dumper (1985) (<i>Kara-viaevia</i>); Snelling (1988)
						(<i>Myrmecoma</i> , Nearctic); Wang et al. (1989a, 1989b) (China); Robert- son (1990) (<i>fishhopilosus</i> group); Dumper et al. (1995) (<i>Karavaievia</i>); McArthur and Adams (1996) (<i>inigiceps</i> group, Australia); Radchenko (1996a) (Palearctic Asia); Mackay (1997) (<i>Myrmo- stenus</i>); Mackay and Mackay (1997) (<i>monti- vagus</i> group, <i>Myrmecoma</i>)
					O	Bolton (1982) (Afro-tropical); Radchenko (1995) (Palearctic)
<i>Cardiocondyla</i>	Myrmicinae	Leptothoracini	35	Warm Old World except Australia, adventive worldwide	C	Xu (1999)
				Afrotropical, Indomalayan, Neotropical		
<i>Carebara</i>	Myrmicinae	Pheidologetonini	18			
<i>Carebarella</i>	Myrmicinae	Solenopsidini	3	Neotropical	?C	Kempf (1975b)
<i>Cataglyphis</i>	Formicinae	Formicini	65	S Palearctic S to Ghana, E to N China, India	HCS	Agosti (1990, 1994a); Radchenko (1998) (Asia)
				Steppes and deserts		
				Nesting in ground, Scavengers		

Continued on next page

Table 5.1 continued

Genus	Subfamily	Tribe	Species	Distribution	Habitat	Microhabitat	Biology	Functional Group ^b	Keys
<i>Cataulacus</i>	Myrmicinae	Cataulacini	65	Afrotropical, Madagascar, Indomalayan	Arboreal, nesting in plant cavities			TCS	Bolton (1974a); Snelling (1979a)
<i>Centromyrmex</i>	Ponerinae	Ponerini	6	Neotropical, Afrotropical, Indomalayan	Nesting in termitaria	Cryptic predators of termites	C	Kempf (1967a) (Neotropical); Brown (pers. obs.)	
<i>Cephalotes</i>	Myrmicinae	Cephalotini	3	Neotropical	Arboreal, nesting in hollow tree trunks and branches	Some are pollen eaters	TCS	Kempf (1951, 1958a); Andrade and Baroni Urbani (1999)	
<i>Cerapachys</i>	Cerapachyinae	Cerapachyini	140	Worldwide in tropics and warm temperate		Army ants, predators of other ants	C, SP	Brown (1975) (world); Radchenko (1993) (Vietnam); Terayama (1996) (Japan)	
<i>Chalepoxenus</i>	Myrmicinae	Leptothoracini	8	Palearctic		Parasites on and slavemakers of <i>Lepiothorax</i>	?CCS	Kutter (1973); Buschinger et al. (1988) (W Palearctic); Radchenko (1989a) (USSR); Cagniant and Espadaler (1997a) (Morocco)	
<i>Cheliomyrmex</i> <i>Chelystruma</i>	Dorylinae Myrmicinae	Ecitonini Dacetini	4 1	Neotropical Neotropical	Army ants Predators		TCS	Borgmeier (1955) Brown (1950); Kempf (1960c); Bolton (pers. comm.)	
<i>Chimaeraeris</i> <i>Cladangoenus</i> <i>Cladomyrma</i>	Myrmicinae Myrmicinae Formicinae	Pheidolini Dacetini Brachymyrmecini	2 1 5	Indomalayan Afrotropical Indomalayan, West Malaysia and Borneo		Predators	TCS ?TCS, CS	Wilson (1989) Brown (1976a, 1976b) Agosti (1991); Agosti et al. (1999)	
<i>Codiumyrmex</i> <i>Colobostruma</i>	Myrmicinae Myrmicinae	Dacetini Dacetini	1 9	Neotropical Australia, Melanesia	Arboreal, nesting in internodes of trees and vines	Predators Predators of collembolans	SP ~~	Bolton (pers. comm.)	

<i>Creightoniella</i>	Myrmicinae	Basicerotini	1	Neotropical		C	Brown (1949d); Brown and Kempf (1960)
<i>Cremaatogaster</i>	Myrmicinae	Crematogastrini	427	World tropical and temperate		GM	Buren (1968b) (Nearctic); Onoyama (1998) (Japan)
<i>Cryptopone</i>	Ponerinae	Ponerini	8	World tropical and temperate		C	Brown (pers. obs.)
<i>Cylindromyrmex</i>	Cerapachyinae	Cylindromyrmecini	10	Neotropical		SP	Brown (1975); Andrade (1978)
<i>Cyphoidris</i>	Myrmicinae	Stenammini	4	Afrotropical		TCS	Bolton (1981b)
<i>Cyphomyrmex</i>	Myrmicinae	Atini	37	Neotropical, S Nearctic	Nest in ground	TCS	Kempf (1964, 1965 [<i>rimosus</i> group], 1968); Snelling and Longino (1992) (<i>rimosus</i> group)
<i>Dacatria</i>	Myrmicinae	Stenammini	1	Korea		?	Rigato (1994)
<i>Dacetinops</i>	Myrmicinae	Stenammini	7	Sundaland, Melanesia		?C	Taylor (1985)
<i>Daceton</i>	Myrmicinae	Dacetini	1	Neotropical		?SP	
<i>Decamorium</i>	Myrmicinae	Tetramorini	2	Afrotropical		?	Bolton (1976)
<i>Dendromyrmex</i>	Formicinae	Camponotini	7	Neotropical		SC	Mann (1916)
<i>Diacamma</i>	Ponerinae	Ponerini	33	India to N Australia		O	Emery (1897) (out of date); Brown (pers. obs.)
<i>Dicroaspis</i>	Myrmicinae	Stenammini	2	Afrotropical		C	Bolton (1981a)
<i>Dilobocondyla</i>	Myrmicinae	Leptocephalini	9	Indo-Melanesian		TCS	Wheeler (1924) (out of date)
<i>Dinoponera</i>	Ponerinae	Ponerini	6	Tropical South America	Forest, savanna	SP	Kempf (1971)
<i>Diplomorium</i>	Myrmicinae	Solenopsidini	1	Afrotropical			
<i>Discothyrea</i>	Ponerinae	Ectatommini	25	World tropical and warm temperate except Palearctic	Nesting in litter		?
<i>Doleromyrma</i>	Dolichoderinae	Dolichoderini	1	Australia			Bolton (1987)
<i>Dolichoderus</i>	Dolichoderinae	Dolichoderini	110	World tropical and temperate except Africa	Arboreal	Generalized foragers	C
							CCS

Continued on next page

Table 5.1 continued

Genus	Subfamily	Tribe	No. Species	Distribution	Habitat	Microhabitat	Biology	Functional Group ^b	Keys
				and Madagascar					(1993) (New World); Xu (1995b) (China)
<i>Dolichoderus</i>	Ponerinae	Ponerini	1	Afrotropical			Cryptic predators	?	Brown (1974d, 1974e)
<i>Dorisidris</i>	Myrmicinae	Dacetini	1	Cuba			Predators		Brown (1948)
<i>Doronomyrmex</i>	Myrmicinae	Leptocephalini	4	Palearctic, Nearctic			Parasitic on <i>Lepiothorax</i>	CCS	Kutter (1945) (Europe); Buschinger (1981)
<i>Dorylus</i>	Dorylinae	Dorylini	60	Afrotropical, Indomalayan			Army ants	TCS	Kusnezov (1951e)
<i>Dorymyrmex</i>	Dolichoderinae	Dolichoderini	50	Neotropical, Nearctic			Generalized foragers	O (?) some DD)	(S Neotropical); Snelling and Hunt (1975)
<i>Dysderognathus</i>	Myrmicinae	Dacetini	1	Indomalayan, W Malaysia			Predators	C	(1995a) (Nearctic)
<i>Echinopla</i>	Formicinae	Camponotini	24	Indomalayan, N Australia	Arboreal		Foragers	SC	Taylor (1968b)
<i>Ecton</i>	Dorylinae	Ectonini	12	Neotropical, S Nearctic	Epigaeic, form bivouacs		Army ants	TCS	Borgmeier (1955); Watkins (1976, 1982 [Mexico])
<i>Ephorella</i>	Dolichoderinae	Dolichoderini	1	Afrotropical				?	
<i>Ectatomma</i>	Ponerinae	Ectatommini	14	Neotropical	Forest, savanna	Nesting in ground, hollow trees	Predators, some thieves of other ants' brood, extrafloral nectaries	?O	Kugler and Brown (1982)
<i>Emeryopone</i>	Ponerinae	Ponerini	3	Israel, Indomalayan			Predators	C	Baroni Urbani (1975b) (as Belonopelta)
<i>Epeorus</i>	Myrmicinae	Solenopsidini	1	Indomalayan				TCS	Bolton (1987)
<i>Epimyrma</i>	Myrmicinae	Leptocephalini	11	Palearctic			Parasites of <i>Lepiothorax</i>	CCS	Buschinger (1989); Cagniant and Espadaler (1997a) (Morocco)
<i>Epirinus</i>	Myrmicinae	Dacetini	8	Palearctic (S Europe, E Asia), Afrotropical, Indomalayan			Predators	C	Brown (1948, 1949b); Bolton (1972 [world], 1983 [Afrotropical]); Cagniant and Espadaler (1997a) (Morocco)

<i>Epopostruma</i>	Myrmicinae	Dacetini	7	SE, SW Australia	Arboreal	Predators of collembolans	SP	Brown (pers. obs.)
<i>Eucryptocerus</i>	Myrmicinae	Cephalotini	3	Neotropical			TCS	Kempf (1951)
<i>Euprenolepis</i>	Formicinae	Lasiiini	6	Indomalayan			TCS	Brown (1953b)
<i>Eurhopalothrix</i>	Myrmicinae	Basicerotini	35	Neotropical, S Nearctic, Indomalayan, Australian	Nesting in litter	Predators	C	Brown and Kempf (1960); Taylor (1968b, 1980, 1990b) (Indo-Australian)
<i>Eutetramorium</i>	Myrmicinae	?Myrmicini	2	Madagascar			?	Alpert (pers. comm.)
<i>Forelius</i>	Dolichoderinae	Dolichoderini	17	Neotropical, S Nearctic	Epigaeic	Generalized foragers	DD,	Shattuck (1992a)
<i>Forelophilus</i>	Formicinae	Camponotini	1	Indomalayan			HCS	
<i>Formica</i>	Formicinae	Formicini	160	Nearctic, Palearctic: warm to cold temperate	Epigaeic	Generalized foragers, tend homopterans	SC	Kutter (1931)
							CCS,	Dlussky (1964)
							O	[exsecta group in USSR], 1965 [Mongolia, Tibet], 1967 [Pale- arctic]; Francoeur (1973) <i>fusca</i> group, Nearctic; Dlussky and Pisarski (1971) (Poland); Buren (1968a) (<i>san- guinea</i> group in Nearctic); Kupyanskaya (1980) (far eastern Russia); Wu (1990) (China)
<i>Formicoxenus</i>	Myrmicinae	Leptothoracini	7	Nearctic, Palearctic		Xenobiont, nesting in association with other ants	CCS	Francoeur et al. (1985) (world)
<i>Froggattella</i>	Dolichoderinae	Dolichoderini	2	Australia			DD	Shattuck (1992a, 1996b) (Australia)
<i>Gesomyrmex</i>	Formicinae	Gesomyrmecini	5	Indomalayan			'TCS	Cole (1949) (partial)
<i>Gigantiops</i>	Formicinae	Gigantiopini	1	Neotropical	Rainforest, savanna		'TCs	Kempf and Lenko (1968)

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Table 5.1 continued

Genus	Subfamily	Tribe	No.	Species	Distribution	Habitat	Microhabitat	Biology	Functional Group ^b	Keys
<i>Glamyromyrmex</i>	Myrmicinae	Dacetini	23	Neotropical, Afrotropical, Australia	Forest, savanna	Nesting in litter	Predators	C	Kempf (1960c) (Neotropical); Bolton (1983) (Africa)	
<i>Gnamptogenys</i>	Ponerinae	Ectatommini	102	Neotropical. S Nearctic, Oriental, India to Fiji	Forest, savanna	Nesting in the ground and rotten logs	Predators and scavengers	TCS	Lattke (1995) (New World); Brandão and Lattke (1990) (Ecuador); Xu and Zhang (1996) (China)	
<i>Goniomma</i>	Myrmicinae	Pheidolini	5	S Palearctic	Arid land		Seed harvesters	HCS	Santschi (1929) (out of date)	
<i>Gymnomyrmex</i>	Myrmicinae	Dacetini	7	Neotropical			Predators	C	Kempf (1959, 1960c); Bolton (pers. comm.)	
<i>Harpagoxenus</i>	Myrmicinae	Leptothoracini	3	Nearctic, Palearctic			Slavemaking parasites of <i>Leptothorax</i>	CCS		
<i>Harpegnathos</i>	Ponerinae	Ponerini	6	India to Philippines, Sundaland			Predators	SP	Bingham (1903) (S. Asia); out of date	
<i>Heteroponera</i>	Ponerinae	Ectatommini	15	Neotropical, Australia and New Zealand	Wet and mesic forests	Nesting in logs	Predators	?CCS	Brown (1958); Kempf (1962)	
<i>Huberia</i>	Myrmicinae	Myrmicini	2	New Zealand	Forest,	Nesting in sandy soil, litter	Generalized foragers	CCS	Brown (1958)	
<i>Hylomyrma</i>	Myrmicinae	Myrmicini	13	Neotropical	savanna		Generalized foragers	TCS	Kempf (1973a)	
<i>Hypoponera</i>	Ponerinae	Ponerini	150	Worldwide tropical and warm temperate	Forest, savanna	Nesting in litter	Generalized foragers	C	Brown (pers. obs.)	
<i>Indomyrma</i>	Myrmicinae	Stenammini	1	Peninsular India	Mesic forest			?C	Brown (1985)	
<i>Ireneopone</i>	Myrmicinae	Leptothoracini	1	Mauritius	Native forest		Generalized forager	?TCS	Donisthorpe (1946)	
<i>Idiomyrmer</i>	Dolichoderinae	Dolichoderini	55	Australia, Indomalayan			Generalized foragers	DD	Shattuck (1992a, 1992b, 1993) (<i>purpleus</i> group), (1996a) (<i>discors</i> group)	
<i>Ishakidris</i>	Myrmicinae	Phalacro-	1	N Romea			Nesting in leaf	C	Rölfsm (1982)	Predator
							Rainforest			

<i>Kartidris</i>	Myrmicinae	Pheidolini	SE Asia	Cryptic predators	TCS
<i>Kyldris</i>	Myrmicinae	Dacetini	India, China-Japan to New Guinea, Madagascar	Parasites of <i>Sirumigenys</i>	C
<i>Labidus</i>	Dorylinae	Ectonini	Neotropical to S Nearctic	Forest, savanna	TCS
<i>Lachnomyrmex</i>	Myrmicinae	Stenammini	Neotropical	Mesic forest	?TCS
<i>Lasiophanes</i>	Formicinae	Melophorini	Chile and Argentina	Epigaeic, forms bivouacs	CCS
<i>Lasius</i>	Formicinae	Lasini	Nearctic, Palearctic, temperate Oriental	Nesting in litter	CCS
<i>Lepisiota</i>	Formicinae	Plagiolepidini	S Palearctic, Afrotropical, Indomalayan	Generalized foragers	CCS
<i>Leptanilla</i>	Leptanillinae	Leptanillini	S Palearctic, Afrotropical, Indomalayan, Australia	Generalized foragers, tend homopterans	CCS
<i>Leptanillidae</i>	Leptanilloidinae	Leptanilloidini	Neotropical, Andes and foothills	Epigaeic, arboicolous, subterranean	[European <i>Cithonolasius</i>], 1992 [Palearctic <i>Lasius</i> s.s.]; Yamauchi (1978) (Japan)
<i>Leptogenys</i>	Ponerinae	Ponerini	Worldwide in tropics and some subtropics	Generalized foragers	Xu (1994a) (China)
<i>Leptomyrmex</i>	Dolichoderinae	Dolichoderini	Australia, New Caledonia, Melanesia W to Maluku	Cryptic mass predators	Xu (1994a) (China)
<i>Leptothorax</i>	Myrmicinae	Leptocephalini	Worldwide (Except Australia)	Hypogaeic	Baroni Urbani (1977)
				Predators of centipedes, nomadic	Brandão et al. (1999)
				Predators of isopods and mass-foraging predators, esp. of termites	Bingham (1903) (India); Bolton (1975a) (Africa)
					Wheeler (1934) (out of date)
					Bernard (1956)
					(W Europe); Kempf (1958c) (<i>Nesomyrmex</i> , Neotropical); Baroni Urbani (1978b) (<i>Macro-mischa</i> , Neotropical);

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Table 5.1 continued

Genus	Subfamily	Tribe	No. Species	Distribution	Habitat	Microhabitat	Biology	Functional Group ^b	Keys
<i>Linepithema</i>	Dolichoderinae	Dolichoderini	14	Neotropical, adventive worldwide in warm or temperate areas				Bolton (1982) (Afrotropical); Dlussky and Sosunov (1988) (<i>Tenuithorax</i> , USSR); Taylor (1989) (Australasian); Radchenko (1994a, 1994b) (C and E Palearctic); Cagniant and Espadaler (1997a) (Morocco); Terayama and Onoyama (1999) (Japan); MacKay (2000) (<i>Myrmecafant</i>)	
<i>Lionetopum</i>	Dolichoderinae	Dolichoderini	6	Nearctic, Palearctic, Oriental				DD	Wheeler (1905); Shattuck (1992a, 1992b)
<i>Liomyrmex</i>	Myrmicinae	Metaponini	8	Indomalayan				DD	Ettershank (1966)
<i>Lophomyrmex</i>	Myrmicinae	Pheidolini	4	Indomalayan				TCS	Rigato (1994b)
<i>Lordomyrma</i>	Myrmicinae	Stenammini	20	Indo-Melanesian to Japan				TCS	
<i>Loweriella</i>	Dolichoderinae	Dolichoderini	1	Australia				TCS	Shattuck (1992b)
<i>Machomyrma</i>	Myrmicinae	Pheidolgetonini	1	Australia				C	
<i>Manica</i>	Myrmicinae	Myrmicini	6	Nearctic, Palearctic, including Orient				CCS	Wheeler and Wheeler (1986) (Nearctic)
<i>Mayriella</i>	Myrmicinae	Stenammini	5	Oriental, Australian				?C	
<i>Megalomyrmex</i>	Myrmicinae	Solenopsidini	33	Neotropical	Forest, savanna	under leaves	Generalized foragers and nomads	TCS	Brandão (1990); Fernández and Donoso (1997)

<i>Melissotarsus</i>	Myrmicinae	Melissotarsini	4	Afrotropical, Madagascar	Nesting in or under tree bark	Tend coccids	?	Bolton (1982)
<i>Melophorus</i>	Fornicinae	Melophorini	21	Australia	Mostly xeric habitats	Nest in the ground	HCS	
<i>Meranoplus</i>	Myrmicinae	Meranoplini	55	Afrotropical, Madagascar, Oriental to Melanesia and Australia	Nesting in ground	Seed harvesters and general foragers	HCS	Bolton (1981a) (Afro- tropical); Taylor (1990c) (Australasian); Schödl (1998)
<i>Mesostroma</i>	Myrmicinae	Dacetini	6	Australia	Nesting in ground	Predators of collembolans	SP	Taylor (1973)
<i>Messor</i>	Myrmicinae	Pheidolini	106	Nearctic, Palearctic, Afrotropical, Oriental	Nesting in ground	Seed harvesters	HCS	Bernard (1954, 1979); M. Smith (1956a) (Nearctic, as <i>Ver-</i> <i>messor</i>); Arnol'di (1977); Tohmé and Tohmé (1981); Cagniant and Espadaler (1997b) (Morocco)
<i>Metapone</i>	Myrmicinae	Metaponini	16	Madagascar, Oriental to Melanesia, Australia	Nesting in hollow twigs and other plant cavities	Prey on termites	TCS	
<i>Microdacetum</i> <i>Monomorium</i>	Myrmicinae	Dacetini	2	Afrotropical			?C	Bolton (1983)
	Myrmicinae	Solenopsidini	296	Worldwide in tropics and warm temperate			GM,	DuBois (1981, 1986)
							HCS,	(Nearctic); Bolton
							CCS,	(1987) (Afrotropical);
							TCS	Radchenko (1997)
							TCS	Kempf (1960b); Mahyé- Nunes (1995)
<i>Mycetarotes</i>	Myrmicinae	Attni	2	Neotropical	Cultivators of fungi			
<i>Mycetophylax</i>	Myrmicinae	Attni	6	Neotropical	Coastal dunes	Nesting in ground	TCS	
<i>Mycetosoritis</i>	Myrmicinae	Attni	4	Neotropical, S Nearctic	Fungus cultivators		TCS	
<i>Mycoceropurus</i>	Myrmicinae	Attni	4	Neotropical	Fungus cultivators		TCS	Kempf (1963)
<i>Myopias</i>	Ponerinae	Ponerini	37	Oriental (N Thailand) to SE Australia	Predators of millipedes, 1 sp. on ants		C	Willey and Brown (1983), Brown (pers. obs.)
<i>Myopopone</i>	Ponerinae	Amblyoponini	1	Indomalayan to N Australia	Predator		C	

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Table 5.1 continued

Genus	Subfamily	Tribe	No. Species	Distribution	Habitat	Microhabitat	Biology	Functional Group ^b	Keys
<i>Myrmecidris</i>	Pseudo-myrmecinae	Pseudo-myrmecini	1	Neotropical		Arboreal		TCS	Ward (1990)
<i>Myrmecia</i>	Myrmecinae	Myrmecini	89	Australia, 1 New Caledonia			Generalized predators	SP	Brown (1953c) (partial), (1990); Ogata and Brown (1991)
<i>Myrmecina</i>	Myrmicinae	Myrmecini	28	Nearctic, Palearctic to			Predators of mites	TCS, CCS	Brown (1949a) (N. America), (1967) (Nearctic); Terayama (1985a) (E Asia)
<i>Myrmecocystus</i>	Formicinae	Formicini	29	W Nearctic, mostly arid habitats			Generalized foragers, store honeydew in replete	HCS	Snelling (1976, 1982)
<i>Myrmecophynehus</i>	Formicinae	Melophorini	5	Australia		Mostly arboreal		CCS	
<i>Myrmelachista</i>	Formicinae	?Myrmelachistini	47	Neotropical		Mostly nesting in plant cavities		C	Kusnezov (1951b) (Patagonia)
<i>Myrmica</i>	Myrmicinae	Myrmicini	100	Nearctic, Palearctic, Oriental		Nesting in ground, Generalized foragers rotten wood	O	Menozzi (1939) (Himalaya, Tibet); Weber (1947, 1948, 1950b) (Nearctic, with synopsis of Palearctic; out of date); Arnol'di (1970 (European USSR)), 1976b [central USSR]; Kupyanskaya (1986), (lobicornis group of far eastern Russia); Seifert (1988b) (W Palearctic); Radchenko et al. (1997) (Poland); Radchenko et al. (1998) (<i>ritae</i>)	

<i>Myrmicaria</i>	Myrmicinae	Myrmicarini	31	Afrotropical, Indomalayan	Many arboreal	TCS
<i>Myrmicocrypta</i>	Myrmicinae	Attini	24	Neotropical	Cultivators of fungi; general foragers	TCS
<i>Myrmoteras</i>	Formicinae	Myrmoteraini	31	India to Sulawesi	Predators, mostly on forest floor	SP
<i>Mystrium</i>	Ponerinae	Amblyoponini	8	W Africa, Madagascar, Indomalayan to NW Australia	Predators, esp. of chilopoda	C
<i>Neivamyrmex</i>	Ectoninae	Ectonini	120	Neotropical, S Nearctic	Hypogaeic, forms bivouacs	TCS
<i>Neolepharidatta</i>	Myrmicinae	Blepharidattini?	1	India	Forest	Borgmeier (1955); Watkins (1976, 1982, 1985); Ward (1999b) (Nearctic)
<i>Neostruma</i>	Myrmicinae	Dacetini	6	Neotropical	Hypogaeic	Sheela and Narendra (1997)
<i>Nomamyrmex</i>	Dorylinae	Ectoninae	2	Neotropical	Predators, esp. of collembolans	C
<i>Noonilla</i>	Leptanillinae	Leptanillini	1	Melanesia	Army ants	Brown (1959)
<i>Nothidris</i>	Myrmicinae	Solenopsidini	3	S Neotropical	TCS	Borgmeier (1955); Watkins (1977)
<i>Nothomyrmecia</i>	Nothomyrmecinae	Nothomyrmecini	1	S Australia	Arid woodland	C
<i>Notoncus</i>	Formicinae	Melophorini	7	Australia	Nesting in ground, Nocturnal predators	CCS
<i>Notostigma</i>	Formicinae	Camponotini	3	Australia	foraging on trees	SC
<i>Ochetellus</i>	Dolichoderinae	Dolichoderini	4	Oriental to Australia, adventive in N America	Epigaeic	O
<i>Ochetomyrmex</i>	Myrmicinae	Ochetomyrmecini	4	Neotropical	Generalized foragers	Shattuck (1992a)
<i>Octostruma</i>	Myrmicinae	Basicerotini	10	Neotropical	Epigaeic	Kempf (1975b)
<i>Ocymyrmex</i>	Myrmicinae	Phedolini	37	Afrotropical	Nesting in ground	Brown and Kempf (1960); Palacio (1997) (Colombia)
					Mostly hot, arid sites	HCS
					Seed harvesters	Bolton and Marsh (1989)

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Table 5.1 continued

Genus	Subfamily	Tribe	No. Species	Distribution	Habitat	Microhabitat	Biology	Functional Group ^b	Keys
<i>Odontomachus</i>	Ponerinae	Ponerini	55	Worldwide in tropical and warm temperate, not W Palearctic		Epigaeic	Predators	O, ?SP	Brown (1976c, 1977b, 1978) (world); Deyrup et al. (1985) (SE United States); Wang (1993) (China)
<i>Odontoponera</i>	Ponerinae	Ponerini	2	Indomalayan				SP	Brown (pers. obs.)
<i>Oecophylla</i>	Formicinae	Oecophyllini	1	Afrotropical, Oriental to N Australia				TCS	
<i>Oligomyrmex</i>	Myrmicinae	Pheidolegotonini	93	Worldwide in tropics, rare in warm temperate		Nesting in arboreal, silk-woven leaf nests	Cryptic foragers, termite thief ants	C	Weber (1950a, 1952) (partial Afrotropical)
<i>Onychomyrmex</i>	Ponerinae	Amblyoponini	8	Australia			Mass predators	TCS	
<i>Opisthopsis</i>	Formicinae	Camponotini	13	N Australia, Melanesia			Generalized foragers	SC	
<i>Orectognathus</i>	Myrmicinae	Dacetini	29	Australia, Melanesia			Predators	SP	Taylor (1977, 1978b, 1979a, 1980)
<i>Overbeckia</i>	Formicinae	Camponotini	1	Indomalayan				SC	
<i>Oxyepoecus</i>	Myrmicinae	Solenopsidini	11	Neotropical		Nesting in leaf litter	Some spp. in nests of <i>Pheidole</i> spp.	TCS	Kempf (1974a)
<i>Oxyponomyrmex</i>	Myrmicinae	Pheidolini	9	S Palearctic			Seed harvesters	HCS	Santschi (1929)
<i>Pachycondyla</i>	Ponerinae	Ponerini	150	Worldwide in tropics and some warm temperate			Predators; 1 species also harvests seeds	Sp ^d	Brown (pers. obs.); Xu (1994b) (China)
<i>Paedalgus</i>	Myrmicinae	Pheidolegotonini	10	Afrotropical, Oriental				C	Bolton and Beishaw (1993)
<i>Papyrius</i>	Dolichoderinae	Dolichoderini	4	Melanesia, Australia				DD	Shattuck (1992a)
<i>Paraponera</i>	Ponerinae	Ectatommini	1	Neotropical		Nesting in ground, Predators, tend homopterans, foraging arboreally		?	
<i>Parapriopelta</i>	Ponerinae	Amblyoponini	1	S Neotropical					Kusnezov (1955); Brown (1960)
<i>Paratoniula</i>	Myrmicinae	Lemiothoracini	9	Indomalayan					Bolton (1988a)

<i>Paratrechina</i>	Formicinae	Lasini	107	Worldwide in tropics and temperate	Generalized foragers	O	Trager (1984) (Nearctic)
<i>Pentastruma</i>	Myrmicinae	Dacetini	2	Oriental	Predators	C	Brown and Boesvrt (1979)
<i>Perissomyrmex</i>	Myrmicinae	Myrmecinini	2	Central America, Oriental		TCS	Smith (1947) (Guatemala); Baroni Urbani and De Andrade (1993)
<i>Peronymex</i>	Myrmicinae	Leptocephalini	1	E Australia		TCS	Hartley (1994) (C. America)
<i>Petalomyrmex</i>	Formicinae	Brachymyrmecini	1	Afrotropical		TCS	Taylor (1970a)
<i>Phacota</i>	Myrmicinae	Solenopsidini	1	S Palearctic		?	Snelling (1979b)
<i>Phalacromyrmex</i>	Myrmicinae	Phalaenomyrmecini	1	Neotropical		?	Bolton (1987)
<i>Phasmomyrmex</i>	Formicinae	Camponotini	4	Afrotropical		?	Kempf (1960a)
<i>Phaolomyrma</i>	?Leptanillinae	?Leptanillini	1	Indomalayan		SC	
<i>Phedole</i>	Myrmicinae	Pheidolini	910	Worldwide in tropics and warm temperate	Most nesting in soil, some in rotten wood	C	Wheeler and Wheeler (1950); Petersen (1968)
<i>Pheidole</i>					Many seed harvesters, many omnivorous	GM	Kusnezov (1951c) (Argentina); Gregg (1958) (Nearctic); Ogata (1982) (Japan); Wilson (forthcoming) (New World); Zhou and Zheng (1999) (China)
<i>Pheidolegeton</i>	Myrmicinae	Pheidolegetonini	30	Afrotropical, India to Melanesia	Generalized and mass foragers	C	
<i>Philidris</i>	Dolichoderinae	Dolichoderini	7	Indo-Melanesian	Mainly arboreal, most nesting in plants	DD	Shattuck (1992a)
<i>Phrynoponera</i>	Ponerinae	Ponerini	3	Afrotropical	Foragers	SP	Wheeler (1922a) (out of date)
<i>Pilotrochus</i>	Myrmicinae	Phalaenomyrmecini	1	Madagascar	Predators	?	Brown (1977a)

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Table 5.1 continued

Genus	Subfamily	Species	Distribution	Habitat	Microhabitat	Biology	Functional Group ^b	Keys
<i>Plagiopeltis</i>	Formicinae	Plagiopeltidini	53 Old World tropics and temperate areas; adventive in New World		Generalized foragers	C	Radchenko (1980b) (USSR); Radchenko (1996b) (central and southern Palearctic)	
<i>Platythyrea</i>	Ponerinae	Platythyreini	37 Neotropical, S Nearctic, Old World tropics to S Australia	Arboreal	Predators, many on termites	SP	Brown (1975:4)	
<i>Plectroctena</i>	Ponerinae	Ponerini	17 Afrotropical		Predators on millipedes and their eggs	SP	Bolton (1974b)	
<i>Podomyrma</i>	Myrmicinae	Lepto thoracini	57 Indomalayan, Australia	Mostly arboreal, nesting in plant cavities		TCS, CCS		
<i>Poecilomyrma</i>	Myrmicinae	Lepto thoracini	1 Melanesia	Arboreal		TCS	Mann (1921)	
<i>Pogonomyrmex</i>	Myrmicinae	Myrmicini	58 Neotropical, Nearctic	Nesting in soil	Generalized foragers and seed harvesters	HCS	Kusnezov (1951a) (S Neotropical); Cole (1968) (Nearctic); Snelling (1981); Shattuck (1987) (<i>occidentalis</i> complex); Fernández and Palacio (1997) (Neotropical)	
<i>Polyergus</i>	Formicinae	Formicini	4 Nearctic, Palearctic		Parasites and slavemakers of <i>Formica</i>	SP	Wheeler (1968) (Nearctic); Agosti (1994a)	
<i>Polyrhachis</i>	Formicinae	Camponotini	477 S Palearctic, Afrotropical, Oriental to S Australia	Many arboreal, others nesting on the ground	Generalized foragers	SC	Hung (1967) (subgenera); Hung (1970), Bolton (1973b, 1973c) (Africa); Bolton (1975c) (species synonyms); Vachon (1989:xxv)	

<i>Ponera</i>	Ponerinae	Ponerini	33	Nearctic, Palearctic, Indo-Australian	Predators of small arthropods	C	Brown (1960) (New World Indo-Australian); Terron (1974) (Afrotropical)
<i>Prenolepis</i>	Formicinae	Formicinae	8	Neotropical, Nearctic, Paleartic, Oriental, Indomalayan	Generalized predators	CCS	Taylor (1967) (world); Terayama (1996) (Japan)
<i>Prionopelta</i>	Ponerinae	Amblyoponini	12	Worldwide in tropical and subtropical, except Paleartic	Predators, esp. of small chilopoda	C	Taylor (1967) (world); Terayama (1996) (Japan)
<i>Pristomyrmex</i>	Myrmicinae	Myrmecinini	36	Afrotropical, Mauritius, Oriental to E Australia	Generalized foragers and specialized predators	TCS	Bolton (1981b) (Afrotropical); Xu (1995a) (China)
<i>Proatia</i> <i>Probolomyrmex</i>	Myrmicinae	Stenammini	1	Indomalayan	Nesting in soil	TCS	Rigato (1994a)
	Ponerinae	Playthyreini	13	World tropics except Madagascar	Nesting in leaf litter	C	Taylor (1965); Brown (1975) (world); Terayama and Ogata (1988) (Japan); Agosti (1994b) (Neotropical)
<i>Proceratium</i>	Ponerinae	Ectatommini	29	Worldwide in tropics and temperate	Predators of spider and other arthropod eggs	C	Brown (1958 [world], 1979 [Malagasy]); Terron (1981) (Africa); Ward (1988) (New World)
<i>Procryptocerus</i>	Myrmicinae	Cephalotini	39	Neotropical	Nesting and foraging arboreally	TCS	Kempf (1951, 1957)

Continued on next page

Table 5.1 continued

Genus	Subfamily	Tribe	Species	Distribution	Habitat	Microhabitat	Biology	Functional Group ^b	Keys
<i>Proformica</i>	Formicinae	Formicini	24	Palearctic		Epigaeic	Generalized foragers	?	Agosti (1994a) (references to regional keys)
<i>Prolasius</i>	Formicinae	Melophorini	19	Australia, New Zealand in dead wood	Subtropical rainforest	Epigaeic, nesting and soil	Generalized foragers and seed harvesters in forest	CCS	McAreavey (1947) (out of date)
<i>Protalaridris</i>	Myrmicinae	Basicerotini	1	Mountains of Colombia and Venezuela	Mesic forest		Predators	C	Brown (1980a, 1980b)
<i>Protanilla</i>	Leptanillinae	Anomalomyrmecini	2	Indomalayan			Predators	C	Taylor (1990a)
<i>Protomognathus</i>	Myrmicinae	Leptocephacini	1	Nearctic			Parasites and slavemakers of <i>Leptocephax</i>	CCS	
<i>Psalidomyrmex</i>	Ponerinae	Ponerini	6	Afrotropical			Predators, perhaps of lumbricid worms	C	Bolton (1975b)
<i>Pseudaphomomyrmex</i>	Formicinae	Brachymyrmecini	1	Indomalayan		Arboreal			
<i>Pseudodaatta</i>	Myrmicinae	Attni	1	Neotropical			Workerless parasites of <i>Acromyrmex</i>	?TCS	Wheeler (1922b)
<i>Pseudolasius</i>	Formicinae	Lasini	48	Afrotropical, Oriental to N Australia		Living in <i>Acromyrmex</i> nests		TCS	Weber and Anderson (1950) (Afrotropical); Xu (1997) (China)
<i>Pseudomyrmex</i>	Pseudomyrmecinae	Pseudo-myrmecinae	118	Neotropical and S Nearctic		Epigaeic	Cryptic foragers	TCS	Kempf (1958b [<i>gracilis</i> group], 1960c [<i>tenius</i> group], 1961b [groups of <i>tenius</i> , <i>oculatus</i> , <i>pallens</i> , and <i>latinoduslocula-</i> <i>tus</i> and <i>sutillissimus</i> groups], 1990 [generic revision], 1993 [<i>Acacia-</i> <i>inhabitans</i> <i>macracanthus</i>]

<i>Pseudonotoncus</i>	Formicinae	Melophorini	2	Australia	Woodland	Generalized foragers	CCS
<i>Quadristruma</i>	Myrmicinae	Dacetini	2	Melanasia, ?adventive in Neotropical	Predators	C	Brown (1949b); Bolton (1983)
<i>Recurvidris</i>	Myrmicinae	Pheidologenotini	7	Indomalayan	Generalized foragers	C	Bolton (1992)
<i>Rhopalomyia</i>	Myrmicinae	Melissoatarsini	3	Oriental	Nesting and foraging in and under bark	?	Xu (1999) (China)
<i>Rhopalothrix</i>	Myrmicinae	Basicerotini	10	Neotropical, Indo- melanesian, NE Australia	Predators	C	Brown and Kempf (1960) (world); Taylor (1990b) (Indo-Australian)
<i>Rhopromyrmex</i>	Myrmicinae	Tetramorini	10	Afrotropical, Oriental to NE Australia	Generalized foragers	?	Bolton (1986)
<i>Rhytidoponera</i>	Ponerinae	Ectatommini	102	Australia and Melanesia W to S Philippines	Generalized predators	O	Clark (1936) (Australia; out of date); Ward (1980) [Impressa group], 1984 [New Caledonian]
<i>Rogeria</i>	Myrmicinae	?Stenammini	27	Neotropical, S Nearctic, Indo-Melanesian	Nesting in leaf litter	Generalized foragers	TCS
<i>Rombonella</i>	Myrmicinae	Leptothoracini	8	Indo-Melanesian, Australian	Grassland	Kugler (1994)	
<i>Rossomyrmex</i>	Formicinae	Formicini	2	S Palearctic	Nesting in ground Parasites and slavemakers of <i>Formica</i>	?	Smith (1953a, 1953b, 1956b); Taylor (1990d)
<i>Rostromyrmex</i>	Myrmicinae	Solenopsidini?	1	Indomalayan	Lowland rainforest	Litter, nesting in rotten wood	TCS
<i>Rotastruma</i>	Myrmicinae	Leptothoracini	2	Indomalayan	Probably arboreal	Rosciszewski (1994) (Malaysia)	
<i>Sanischella</i>	Formicinae	Santschiellini	1	Afrotropical		TCS	
<i>Scyphodon</i>	Leptanillinae	Anomalomyrmini	1	Indomalayan		Bolton (1991)	
<i>Secostruma</i>	Myrmicinae	Tetramorini	1	Indomalayan	Nesting in soil,	?	?TCS
<i>Sericomyrmex</i>	Myrmicinae	Atini	19	Neotropical	some in rotten logs	Bolton (1988a)	
<i>Serrastruma</i>	Myrmicinae	Dacetini	12	Afrotropical	Predators, mainly of collembolans	TCs	
						C	Bolton (1983)

Continued on next page

Table 5.1 continued

Genus	Subfamily	Tribe	No. Species	Distribution	Habitat	Microhabitat	Biology	Functional Group ^b	Keys
<i>Simopelta</i>	Ponerinae	Ponerini	14	Neotropical		Nesting in leaf litter	Mass predators of ants	C	Gottwald and Brown (1966); Brown (pers. obs.)
<i>Simopone</i>	Cerapachyinae	Cerapachyini	16	Afrotropical, Madagascar, Indo-Malaysian			Mass predators of ants	SP	Brown (1975)
<i>Smithistruma</i>		Dacetini	122	Worldwide in tropics and warm temperate	Litter	Predators, mainly of collembolans		C	Brown (1953a, 1964) (world); Bolton (1983) (Afrotropical); Ward (1988) (W Nearctic); Terayama et al. (1995) (Taiwan); Terayama et al. (1996); Ogata and Onoyama (1998) (Japan)
<i>Solenopsis</i>	Myrmicinae	Solenopsidini	180	Worldwide in tropics and warm temperate		Nesting in ground, Generalized foragers and sand mounds and thief ants (mainly <i>geminata</i> group), and litter	C ^e , TCS	Snelling and Hunt (1975) (Chile); Thompson and Johnson (1989) (Florida); Ross and Trager (1990) (<i>saevisima</i> complex); Trager (1991) (<i>geminata</i> group); Dlussky and Radchenko (1994) (C Palearctic)	
<i>Sphinctomyrmex</i>	Cerapachyinae	Cerapachyini	23	Afrotropical, Indomalayan to Australia, SE Brazil			Mass predators of ants	C	Brown (1975)
<i>Stegomyrmex</i>	Myrmicinae	Stegomyrmecini	3	Neotropical	Mesic forest	Nesting in soil	Predator of eggs of millipedes	C	Diniz (1990)
<i>Stenamma</i>	Myrmicinae	Stenammini	42	Neartic, Palearctic, Oriental			Generalized predators	CCS	Yasumatsu and Murakami (1960) (Japan); Smith (1962) (C America); Coddington (1972)

<i>Stereomyrmex</i>	Myrmicinae	Leptocephalini	1	Sri Lanka	Generalized foragers	TCS
<i>Stigmachus</i>	Formicinae	Plagiolepidini	48	Australia	CCS	McAreavey (1957) (out of date)
<i>Streblognathus</i>	Ponerinae	Ponerini	1	South Africa	Predators of tenebrionid beetles	SP
<i>Strongylognathus</i>	Myrmicinae	Tetramorini	25	Paleartic	Parasites and slavemakers of <i>Tetramorium</i>	Pitsarski (1966); Baroni Urbani (1969) (<i>huberi</i> group, Paleartic); Radchenko (1985, 1991) (USSR)
<i>Strumigenys</i>	Myrmicinae	Dacetini	190	Worldwide in tropics and warm temperate areas, except W Paleartic	Predators, esp. of collembolans	C
<i>Talaridris</i>	Myrmicinae	Basicerotini	1	Neotropical	Predator	C
<i>Tapinoma</i>	Dolichoderinae	Dolichoderini	60	Worldwide in tropics and temperate regions	Generalized foragers	O,
<i>Tanuidris</i>	Myrmicinae	Agroecomyrmecini	1	S Neotropical		DD
<i>Technomyrmex</i>	Dolichoderinae	Dolichoderini	60	Old World tropics, 1 sp. adventive worldwide	Generalized foragers	?C
<i>Teleutomyrmex</i>	Myrmicinae	Tetramorini	2	Paleartic	Workerless parasites of <i>Tetramorium</i>	TCS
<i>Terataner</i>	Myrmicinae	Leptocephalini	15	Afrotropical, Madagascar	Mostly arboreal, in plant cavities	Kutter (1950); Tinaut (1990)
<i>Teratomyrmex</i>	Formicinae	Lasiusini	1	E Australia	Mesic forest	Bolton (1981b)
<i>Tetraenomyrma</i>	Myrmicinae	Stenammini	1	Borneo	Foraging on leaves of shrubs	TCS
				Nesting in forest litter	Nesting in forest litter	McAreavey (1957)
						Bolton (1991)

Continued on next page

Table 5.1 continued

Genus	Subfamily	Tribes	No. Species	Distribution	Habitat	Microhabitat	Biology	Functional Group ^b	Keys
<i>Tetramorium</i>	Myrmicinae	Tetramorini	415	Worldwide in tropics and temperate but adventive only in S America		Generalized foragers	O	Bolton (1976 [partial], 1977 [Indo-Australian], 1979 [Madagascar, New World], 1980 [African]); Wang et al. (1988)	
					(China); Radchenko and Arakelian (1990) (<i>ferox</i> group, Caucasus); Radchenko (1992) (USSR); Cagniant (1997) (Morocco)			TCS	Ward (1990); Wu and Wang (1990) (China)
<i>Tetraponera</i>	Pseudo-myrmecinae	Pseudo-myrmecini	78	Old World tropics and warm temperate, except Europe	Mainly forest	Arboreal, nesting in plant cavities			
<i>Thaumatomyrmex</i>	Ponerinae	Ponerini	6	Neotropical	Forest, savanna	Nesting in litter and bromeliads	Predators of polyxenid millipedes	SP	Kempf (1975a)
<i>Tingomyrmex</i>	Myrmicinae	Dacetini	1	Neotropical		Nesting in litter	Predators	C	Mann (1926)
<i>Trachymyrmex</i>	Myrmicinae	Attini	41	Neotropical, S Nearctic		Nesting in soil	Cultivators of fungi, nests covered with straw, specialized entrances	TCS	
<i>Tranopelta</i>	Myrmicinae	Ochetomyrmecini	4	Neotropical	Nesting and foraging underground or cryptically	Hypogaeic predators of termites		?C	
<i>Trichoscapa</i>	Myrmicinae	Dacetini	150	Worldwide tropical and warm temperate		Predators, mostly of collembolans		C	Brown (1953a); Bolton (1983, unpublished)
<i>Tricyrtus</i>	Myrmicinae	Leptothoracini	1	Indomalayan				TCS	Bolton (1994) (male only)
<i>Turneria</i>	Dolichoderinae	Dolichoderini	6	Melanesia, NE Australia	Arboreal, nesting in plant cavities			TCS	Shattuck (1990, 1992b)

<i>Typhlomyrmex</i>	Ponerinae	Typhlomyrmecini	5	Neotropical	Forest	Nesting in rotten logs	Predators	C	Brown (1965)
<i>Vollenhovia</i>	Myrmicinae	Metaponini	50	China to N Australia, Madagascar		Many nesting under bark or in cavities in logs		TCS	
<i>Vombisidris</i>	Myrmicinae	Leptocephalacini	12	Indomalayan to E Australasia		Mostly arboreal, nesting in plant cavities		TCS	Bolton (1991)
<i>Waismannia</i>	Myrmicinae	Blepharidatini	8	Neotropical, adventive in W Africa, New Caledonia, Galápagos		Arboreal, nesting in soil or rotten logs	Generalized foragers	TCS	
<i>Willowsiella</i>	Myrmicinae	Leptocephalacini	2	Melanesia, E Australia				TCS	Taylor (1990d)
<i>Xenomyrmex</i>	Myrmicinae	Metaponini	3	Neotropical, S Nearctic		Arboreal, nesting in plant cavities		TCS	Taylor (1990e)
<i>Yavonna</i>	Leptanillinae	Leptanillini	1	S Palearctic, Oriental				TCS	Creighton (1957)
<i>Zacryptocerus</i>	Myrmicinae	Cephalotini	71	Neotropical, S Nearctic				TCS	
						Arboreal, nesting in plant cavities	Some are pollen eaters	C	Kugler (1986)
								TCS	Kempf (1951, 1952, 1958a, 1967d, 1973b)

^aCompiled by the author, with comments added by D. Agosti, A. N. Andersen, C. R. F. Brandão, and X. Espadaler. Functional groups designated to the genera by Andersen (Chapter 3). For further explanation see text.

^bC, cryptic species; DD, dominant Dolichoderinae; GM, generalized Myrmicinae; H/C/TCS, hot/cold/tropical climate specialists; O, opportunists; SC, subordinate Camponotini; SP, specialist predators.

^cC applies to subgenus *Ceropachys*; SP to subgenera *Lipponera* and *Phyracaces*.

^dMost are SP; subgenus *Brachypomera* is TCS.

^eC applies to subgenus *Diplorhoptrum* only.

species for each genus are largely derived from Bolton (1995a, 1995b), but these numbers have been modified in a few cases where the count is likely to be changed in the near future by the creation of new species, named and unnamed, the existence of which are known to me now. Of course, numbers of species will continue to change in the future. Another drastic change will be a reduction in the number of genera of Dacetonini, which are now deemed excessive by Bolton (1999). Functional groups of the genera have been provided by Anderson (Chapter 3).

Ant Taxonomy: The State of the Art

Characters

Taxonomists (or for that matter most dictionaries) fail in the definition of *character* as it applies to biosystematics. For me, a character is any trait of use in making a comparison. The comparison may be made between different parts of the same organism, but here we are mainly interested in comparisons between whole organisms and populations of them. Thus we accept the distinction between characters and their states, though we may simply use *character* as shorthand for *character state*.

A major change in formicid systematics since 1950 has been the acceleration of the discovery and employment of new characters, a function at least as important as the description of new taxa. In higher-level classification, Barry Bolton's investigations of morphological characters, particularly those of the abdominal segments of the worker caste, leap immediately to mind. He has not neglected other tagmata and other castes, and his sample of the genera and species has been extensive and documented, at least as far as the numbers of species reviewed for each character are concerned. Explicit listing of the species examined for such studies has become a welcome standard.

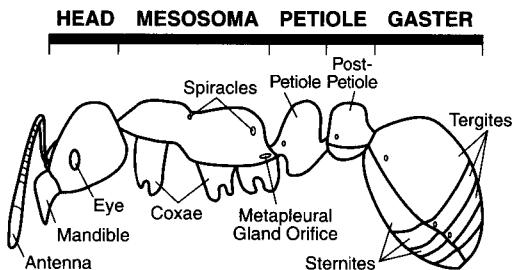


Figure 5.1. Body parts of an ant.

The ancestors of ants were apparently some kind of aculeate wasp, perhaps a vespoid, as claimed by Brothers (1975) and Brothers and Carpenter (1993), but it is probable that the ancestral ant, like most living ants, differed from wasp ancestors by possessing a metapleural gland (Fig. 5.1) far back and down low on each side of the alitrunk (Grimaldi et al. 1997). This relatively obscure feature typically consists of a group of secretory cells that duct separately into an atrium under a more or less obvious bulla having a variously shaped aperture to the exterior on each side of the alitrunk. Its products have disputed functions, one of which may be to protect the insects against microorganisms and fungal spores inhabiting the substrate (Maschwitz 1974). In some ants—notably the carpenter ants and a few others—the metapleural gland has been secondarily lost or reduced.

A much more obvious trait of the family Formicidae, to which all ants belong, is the nodiform or scalelike shape of the second true abdominal somite of the waist, called the petiole (Fig. 5.1), which is separated by a more or less apparent constriction from the following somite (A3), also called the postpetiole, particularly whenever it itself is separated by a constriction from the following somite (A4). The trouble with using the petiole as an ant-diagnostic character is partly that there exist various wasps, often wingless ones, that have developed a nodiform petiole, and some, such as the mullid Apterogyna, that even have a postpetiole. In

such cases, the lack of a metapleural gland and other characters must be used to distinguish them from ants.

To reduce confusion in the naming of successive somites in the region of the waist and beyond, we call them by their sequence as ancestral abdominal units, with the propodeum being the first (actually it is T1, the tergum of the first true abdominal somite, which in Hymenoptera: Apocrita is fused with the thorax to form the alitrunk). Many specialists on apocritan Hymenoptera use *mesosoma* instead of *alitrunk*, after Michener (1944:167). However, *alitrunk* has been in use at least since J. B. Smith's *Glossary* of 1906, and probably much longer. It is used in such well-known works as *The Insects of Australia and New Zealand* by Tillyard (1926) and Torre-Bueno's *Glossary of Entomology* (1937, 1989; Tulloch 1962) as well as several foreign glossaries. When I wrote to Michener to ask why he had avoided use of *alitrunk*, he replied simply that he had not known about it.

The petiole is the second true abdominal segment, and the postpetiole, if present, is the third. The remaining abdominal segments together form the gaster. The somites are of course ancestrally rings, each formed of a dorsal plate, the tergum, and a ventral plate, the sternum; these are often called tergite and sternite (e.g., Gauld and Bolton 1988). A handy convention calls the somites of the true abdomen A1, A2, A3, . . . ; their terga T1, T2, T3, . . . ; and their sterna S1 (although S1 has been lost in the apocritan ancestors of ants), S2, S3, Each plate is more or less distinctly divided in the axial direction into regions, particularly an anterior one (the pretergite or presternite, which is the band fitting into the preceding somite and normally at least partly covered by it) and a main exposed region (which I call the tergite or sternite, and Bolton calls the posttergite and poststernite). (I reason by analogy with the mesothoracic sclerites prescutum and scutum,

and because the term *posttergite* or *-sternite* is logically reserved for specialized posterior segmental belts found in many ants.)

Bolton (1990a) has given a special name, *helcium*, to the much-narrowed "presegment," or pretergite with presternite, of the third abdominal segment. The structure of the helcium, especially its sternum, has become important in ant phylogeny and taxonomy (e.g., Agosti 1991).

Other abdominal characters of importance are the fusion or lack of it between the tergum and sternum of each of the second (A2) through fourth (A4) somites, and the structure of their presclerites when present. In Bolton (1990a) and subsequent papers on ant phylogeny by Bolton (1990c, 1990d) and Baroni Urbani, Bolton, and Ward (1992) (hereafter referred to as BBW), the characters are presented in a splendid series of illustrations that should be standard references.

Phylogenies

In the central study of the series, BBW offer a matrix for 68 characters of all adult castes and larvae, with coding binary (0 or 1). (I do suggest that, for making the often complex task of following binary character states easier for the reader, absence of a state might be coded 0 and its presence 1, mnemonic advantage thus outweighing other considerations.) The highlights of the resulting cladogram and classification are presented, with my comments, in the following sections.

THE EXTENDED ARMY ANT CLADE. Aenictinae, Cerapachyinae, Dorylinae, and Ecitoninae, plus Aenictogitoninae and Leptanilloidinae (considered as subfamilies), are placed in a monophyletic cluster, with a more-inclusive cluster being the (Leptanillinae + Ponerinae) and then the next, Apomyrminae. Of these, the first four form the doryline section, while the Aenictogitoninae, Apomyrminae, and Leptanilloidinae are all monogeneric, incompletely known taxa

that are probably best considered as tribes of uncertain position.

In his important study of the cerapachyines, Bolton (1990a) made a reasonable case for their separation from the Ponerinae and their inclusion in a “doryline section” also containing subfamilies Dorylinae, Ecitoninae (Brown 1973), and Aenictinae (Bolton 1990c), considered to be monophyletic as based on eight shared derived character states. This relationship is reinforced by the circumstance that most species sufficiently well known are predators with a preference for formicid prey; all follow the army ant lifestyle except *Acanthostichus* and *Cylindromyrmex*, termitotherous specialists; the last may not be nomadic and badly needs study. Of course, we must be aware that the army ant lifestyle could be the basis for a convergent adaptive syndrome of morphological states in some or all four of the subfamilies of the doryline section, a possibility demonstrated by the partial homoplasies of syndromes in species of such disparate ponerine genera as *Leptogenys*, *Onychomyrmex*, and *Simopelta*. However, the unity of the doryline section, with the cerapachyines near the base of the lineage, is a concept that has been developing at least since Emery (1901), and myrmecologists are probably comfortable with it. In fact, it seems reasonable now to suggest that the “doryline section” is equivalent to one subfamily bearing the prior name Dorylinae.

ANEURETINAE, DOLICHODERINAE, AND FORMICINAE. *Aneuretinae*, Dolichoderinae, and Formicinae form a second cluster at a distance from the first. These taxa had already received attention from Shattuck (1992c), who found them to be monophyletic in a cladistic analysis. There is substantial accord among ant specialists in regarding dolichoderines and aneuretines as related; the question has become whether they are separate subfamilies (Clark 1951; Wilson et al. 1956) or whether, as treated traditionally,

the Aneuretini are a tribe within the Dolichoderinae. BBW maintained the subfamily status rather hesitantly “in accord with contemporary usage,” because they could not list any strong morphological shared derived states to bolster Aneuretinae (BBW, pp. 313, 315–316). Though the sting is present in *Aneuretes* and variously reduced in Dolichoderinae, it seems to me that the ensemble of differences between the two is not strong enough to maintain Aneuretini as more than a tribe of Dolichoderinae.

The placement of the Formicinae with the dolichoderine lineage is a more important matter. Judging from the BBW phylogeny, most of the characters shared by the two subfamilies are probably in the ancestral state. Unique derived (autapomorphic) characters of Formicinae are the presence of the acidopore, or “venom nozzle,” and the disarticulation of the sting from its lancets (a stage of sting reduction beyond the most extreme condition in the Dolichoderinae). Associated with this, but not coded, are the production of formic acid uniquely by formicids and what is patently a whole series of characters of the venom production and storage apparatus. On their side, the Dolichoderinae (including Aneuretinae) uniquely have Pavan’s gland and also share the lack of an unfused furcula in the sting apparatus. The coding of these complex characters on a simple binary basis is to me one of the unreal aspects of cladistic syntheses, at least as we have them for ants.

Another character, BBW No. 38, is the sclerotized versus flaccid condition of the proventriculus. Coding “according to Eisner (1957) could be an oversimplification” puts it mildly, since the proventriculus of *Dolichoderus* (=*Hypoclinea*) was characterized by Eisner (1957:453, and his Figs. 7, 17–20, and 97) as of the flaccid type, “still conform[ing] to the basic structural plan of *Myrmecia*, *Pseudomyrmex*, and *Aneuretes*, except that the plicae have become sclerotized toward the base of the bulb.” But the subfamilies Dolichoderinae and For-

micinae were both coded by BBW as of the sclerotized type. Considering the details of Eisner's review of proventricular morphology, I find it difficult to avoid a conclusion of completely independent evolution of the two morphoclines, regardless of the apparent similarity of some intermediate stages. From all this, I find that close relationship of Formicinae to Dolichoderinae is unlikely even by strict cladistic standards. As is mentioned by BBW, Emery (1925b) provides an interesting commentary on proventricular evolution of formicines versus dolichoderines, but it is worth noting that in his time the function of the organ was not well understood. I would place the Formicinae at an early split in the ant phylogram, mainly on the basis of the complex derived condition of the sting apparatus and the many ancestral states of characters, such as body articulation, antennal and palpal segmentation, and retained worker ocelli. Dolichoderinae seem to me to be a separate lineage, convergently morphoclinal to Formicinae in consonance with their commitment to the adaptive zone of exploiters of sugary fluids.

MYRMECIINAE, PRIONOMYRMECINI, AND NOTHOMYRMECIINAE. Myrmeciinae, Prionomyrmecini, and Nothomyrmeciinae are placed as terminal taxa on a monophyletic stem, shared at the next lowest node with Pseudomyrmecinae, and at the next lowest with Myrmicinae. Of the fossil *Prionomyrmex*, there is little to argue against in its placement in Myrmeciinae. Concerning Nothomyrmeciinae, things are less certain. Clark (1951:16) started by putting the monotypic *Nothomyrmecia* into a separate subfamily in a key that was rather offhanded, for example, giving subfamily rank to Amblyoponinae, Discothyreinae, Eusphinctinae, and Odontomachinae. Brown (1954b) tended to over-emphasize the difference between Nothomyrmeciinae and Myrmeciinae when he split all the living ants into two branches ("myrmecoid complex" and "poneroid complex") and

placed *Myrmecia* in one complex and *Nothomyrmecia* in the other. This was at a time when only the two type specimens of Nothomyrmecia were known but hardly available for study. Due to the efforts of Taylor (1978a) and a series of colleagues, the celebrated *N. macrops* was rediscovered, and it is now one of the best known of all ants. Although its differences from *Myrmecia* are at once apparent, more and more similarities have also been found (e.g., Billen 1990). In addition the BBW opinion that "absence of a postpetiole in *Nothomyrmecia* is undoubtedly primary" need not be accepted unreservedly, because this segment is small and just might represent a reversal of the condition in *Myrmecia*. My original peek did give me the impression that *Nothomyrmecia* was somewhat like lower formicines in habitus, but I would now find it easier to accept placement in a tribe within the Myrmeciinae.

PSEUDOMYRMECINAE. Pseudomyrmecinae were placed by BBW and by Ward (1990) in their cladograms as arising near the *Myrmecia* group of taxa, and for the time being this placement seems reasonable to me, as it did in 1954. Monophyly with the next lowest step, Myrmicinae, is much less appealing.

MYRMICINAE. Myrmicinae, the most speciose of the subfamilies, was placed by BBW and by Ward (1990) next to Pseudomyrmecinae. Both taxa have A3 postpetiolate, that is, reduced in size and pinched off from A4 by a constriction, which has probably long caused them to be considered as allied. Brown (1954b:28 and later papers) has favored a myrmicine derivation from ponerine ancestors, possibly Ectatomminae, but the finding by Gotwald (1969), Bolton (1990a), Ward (1990), and BBW that Ponerinae have the tergum and sternum of A4 completely fused seems to weigh heavily against this origin because Myrmicinae do not show complete fusion (but sometimes have the pretergite of A4

fused to its presternite, BBW No. 26). The A4 fusion character is now somewhat diminished by the finding by Ward (1994) of the new Malagasy genus *Adetomyrma*, which, though ostensibly a rather typical amblyoponine ponerine, has the terga and sterna of A3 and A4 unfused. In an honest and earnest probe of the phylogenetic implications of the possibility that tergosternal fusion may be reversed in this (and other) instances, Ward offers Fig. 45, a cladogram assuming reversibility. This schema is fascinating in that it depicts the possibility that Myrmicinae is monophyletic with "remaining Ponerinae," that is, remaining after Amblyoponini is relegated to a neighboring terminal branch on the same stem. It is interesting to compare this tree with one I drew up rather negligently five years ago for a poster exhibit, in which the Myrmicinae are derived from within or near the Ponerinae. The position of the Formicinae is of course entirely different; Ward was not dealing with that issue in 1994. Now a finding by Hashimoto (1996) based on skeleto muscular characters also concludes that Ectatommini, Myrmicinae, and Ponerinae are closely related, perhaps sister groups, and incidentally that the amblyoponine petiole may not be a retention of the typhoid wasp state, but a reversal of a previous formicid condition of petiolar postconstriction.

APOMYRMINI. Apomyrmini, a problematic monogenic tribe, is probably best considered as an anomalous Leptanillinae for the time being.

Two Lessons

For me, two lessons to be learned from a consideration of the recent history of phylogenetic reconstructions of the ant family are that (1) cladistic techniques are not as robust for ants as had been hoped, perhaps partly owing to problems of coding and discreteness of characters; and (2) characters involving the articulation or fusion, and expansion or reduction, of abdominal segments may be especially subject, even if

only rarely, to reversal. About problem (1), I can only suggest that each character be scanned for complexity, i.e., for whether multiple characters are involved, and for its suitability to be shoehorned into a rigid binary system. For (2), I urge more careful consideration of possible adaptive reasons for particular character states and transitions between them—in short, bolder application of the much-derided "Just-So Stories." Such application might even help to bring phylogeny back into biology. Ward is thinking along these lines when he briefly discusses possible reasons for reversal of tergosternal fusion, though he does not find examples among several taxa with dichthadiygne queens that might be expected to evolve an expandable gaster. It is worth noting, though, that BBW (p. 317) regard the loss of tergosternal fusion in A3 of ecitonine males as secondary!

Be that as it may, reversal of the fusion could conceivably have other adaptive reasons. For example, if a lineage of ants began a behavioral shift toward feeding prominently on sugary fluids, such as nectar or honeydew, flexibility and dissociation of some segments of the abdomen could be at a selective premium. On the other hand, increased commitment to predation might favor strengthening and fusion of integumental elements at the expense of ability to store fluids internally, as seems true of many if not all Ponerinae. Formicinae and Dolichoderinae may be lineages that have taken the fluid-food path and retained or evolved anew separated terga and sterna, while Ponerinae, the dorylines with Cerapachyinae, and the minor predatory subfamilies (usually) have fusion at least in A3.

At the Front with Revisionary Taxonomy

Taxonomy in the "old days" was largely accomplished on a faunal basis, especially when tropical colonialism was in flower. Collections made by missionaries, official travelers, and

others were sent back to a specialist in the home country—a Frederick Smith, a Gustav Mayr, a Carlo Emery, an Auguste Forel—who then duly produced a paper on “New and Little-Known Ants Collected by Mr. Whatusisname in Southern Whereverland,” replete with descriptions of new species and varieties, and, fairly often, new genera. This system, practiced by specialists who communicated and exchanged specimens all too rarely, produced such a confused welter of taxa that it was a wonder that Emery could make as much sense of it as he managed to do with his fascicles in the *Genera Insectorum* (1910, 1911, 1913, 1921, 1922, 1925a). Even so, the synonymy and other confusion resulting from the compartmental colonial-faunal approach left a mess that thwarted most efforts at effective identification or inventory of ant species, particularly in the larger genera. I need only mention the examples of *Camponotus*, *Crematogaster*, *Pheidole*, and *Solenopsis* to make this point about identifiability, even to this very day.

For a half century this state of affairs has been changing. The Era of Revision has happily arrived with a vengeance. By keeping descriptions of new species largely within the context of world- or at least continentwide revision, genus by genus, we have been able to avoid most of the duplicate description and consequent synonymy of the old days. The process of revision as it is understood today means to gather large collections in the field, compare them with the type specimens in the classical collections to fix their names, and generally sort out all the species. The output is monographs of whole genera, tribes, or even subfamilies, with keys to genera and species, illustrations, and other identification aids by now familiar to all. These monographs allow others to make accurate identifications for the first time, so that one result of the appearance of a revision is a subsequent flock of descriptions of new species. If these descriptions are carefully carried out with-

in the context of the revision itself, that is all to the good. The best result of a revision is the encouragement of new revisions.

Some Cases in Point. Subfamily Ponerinae has been revised in a series of steps, primarily by Brown since 1952, all listed in Bolton’s *Catalogue*. A major part of this study dealing with the subtribe Poneriti, which has been long delayed, deals with the expanded version of *Pachycondyla*, consisting of nearly 150 valid species after extensive synonym pruning. This and allied genera contain many ground-dwelling species. Other parts deal with the large genera *Leptogenys* and *Hypoponera*—the latter a genus of great interest to this manual because of its abundance in leaf litter samples. The African *Leptogenys* have already been completed for the known species by Bolton (1975a). *Hypoponera*, separated from the smaller genus *Ponera* by Taylor (1960), is a real challenge because of the great uniformity of the many species, and because ergatoid queens commonly resemble the workers of different species. In addition some adventives are common and widespread in both hemispheres.

MacKay revised *Acanthostichus* (1996) and added several species to this New World genus of termitotheres.

Following Bolton’s (1990b, 1990d) works on the Cerapachyinae and Leptanillinae, nothing has been done on the latter, though Taylor has had excellent descriptions of *Anomalomyrma* and *Protanilla*, with fine illustrations, in manuscript for two decades. Their descriptions are ascribed to Taylor in Bolton’s paper, but the real authorship is confused. *Scyphodon*, known only from the tiny male, has been found again in Borneo, and its peculiar mandibles suggest that it is the male corresponding to the worker of *Protanilla*.

Revisionary work on the Pseudomyrmecinae by Ward (1985, 1989, 1990) following useful partial revisions by Kempf (1958–1967) has been completed for the Neotropical species.

Probably the largest bloc of unrevised species is genus *Pheidole*, of which the Nearctic species have been partly revised by Gregg (1959). Wilson has revised the New World species of this genus, which is principally tropical in the New World, and after synonymic debridement has found 335 new species, or approximately one-tenth of the known New World ant fauna! This revision is essentially complete, with illustrations, and will be published in 2000 by Harvard University Press. *Pheidole* is of course another of the prevalent ground-dwelling taxa; in most tropical forests, it is the dominant one in terms of individuals (Chapter 8). In Africa, *Pheidole* has many species, but fewer than it does in the Americas; in Asia, Melanesia, and Australia there are more species, but it is not yet known how the number compares with that in tropical America.

Charles Kugler's (1994) revision of *Rogeria* is another first full examination of a long-neglected myrmicine genus, and his study of the sting apparatus of Myrmicinae (1978) plus later papers on the sting promise to be of importance as more taxa are examined.

The tribe Dacetonini, exceedingly common in tropical litter samples, has also been under stepwise revision by Brown (preliminary revision in 1948, plus many later papers) and by Bolton for the Afrotropical species. Bolton is now engaged in a major revision of the classification of the tribe, and it is clear that many of the smaller genera, particularly among the short-mandibulate forms that once seemed so distinct, are now compromised by the more recent discovery of intermediate species. This tribe is astonishingly diverse in tropical forests, especially the largest genus *Strumigenys*, with hundreds of species worldwide, mostly in leaf-litter and rotten wood. There are probably fifty endemic species of this genus on Madagascar, only one of which has been described and named (B. Fisher, pers. comm.). I have revised the New World species and have a large, incom-

plete manuscript covering the known Indo-Australian species.

The genera of the Basicerotini were included in the Dacetonini in the Emery-Wheeler classifications, and the tribe was set up by Brown (1949d) and revised by Brown and Kempf (1960) for the world. A supplement to the revision of *Basiceros* was produced by Brown (1974g), who also described the genus and species *Protalaridris armata* from the northern Andes (Brown 1980a, 1980b). Scattered Neotropical species were published from time to time by various authors, and major groups of basicerotine species were studied for the Indo-Australian area by Taylor (1968a, 1968b, 1970b, 1980, 1990b), bringing the total of Paleotropical species to 26.

Excellent recent revisions of Dolichoderinae are those by Shattuck: genera *Turneria* (1990), *Axinidris* (1991), and *Iridomyrmex* (1992a); a generic revision of Dolichoderinae (1992b); and two Australian species groups of *Iridomyrmex*. References are contained in his catalogue (Shattuck 1994). This work is exemplary in its treatment of a long-confused subfamily; the author recognizes 912 currently valid species, including Aneuretinae and a few fossils.

In Formicini, the tribe Myrmoteratini, with the single genus *Myrmoteras*, has attracted successive revisers, perhaps because of its easily recognizable and distinctive species, originally few in number. After limited pre-1980 efforts, reviews were published by Moffett (1985) and then Agosti (1992), primarily consisting of diagnoses of new species. The species count has reached the astounding number of 31. Agosti (1994a) has extended research to the classification of the tribe Formicini and to the species-level taxonomy of *Cataglyphis* (1990) and *Cladomyrma* (1991).

Paratrechina remains to be revised; the only large regional revision is by Trager for North America (1984), but this is a frequently encoun-

tered ground-dwelling genus in most tropical forests.

Other large genera known to be rich in ground-dwelling species are *Tetramorium*, *Monomorium*, and *Solenopsis* (Chapter 8). The first two of these are predominantly Old World in distribution; they have been revised by Bolton (1986–1988) in a very useful series of contributions. *Solenopsis* (including *Diplorhoptrum* sensu Baroni Urbani 1968), is a very common and speciose genus in the New World tropics, but much less so in the Old World. Creighton's review of the tropical species really dealt only with the larger fire ants of the *saevisima* group. Trager (1991) revised the same group, and his revision has largely been superseded since, but the many species of the small-sized groups, composing the thief ants (subgenus *Diplorhoptrum*), are without modern revision. Treatment of these requires massive collections of nest series containing queens, and if possible males, because the workers are often devoid of striking differences.

Then there are the Attini, fungus cultivators of the Americas, predominantly the tropics. Their diversity is being studied by Schultz and colleagues (Chapela et al. 1994; Hinkle et al. 1994; Schultz and Meier 1995; Mueller et al. 1998; Schultz 1998; Wetterer et al. 1998), who are also determining the mode of co-evolution of the ants with their fungi, venturing into comparative studies of the ant larvae and also of DNA.

Other taxa, such as *Camponotus*, *Crematogaster*, and *Pseudomyrmecinae*, are certainly common and ubiquitous in the tropics, but they are less closely tied to the leaf litter and tend to be arboreal.

Army ants, although often common and conspicuous in tropical forest, usually occur unevenly in samples, but they and other less densely distributed genera often are indicators of particular conditions or habitats, so they clearly should and will receive attention in sur-

veys. The New World Ecitoninae were revised by Borgmeier (1955), with additional taxonomic studies by Watkins (1976, 1982, 1985).

Much more could be said about the systematics of particular groups and particular taxonomists, but many of these studies are based on work performed in study areas outside the forest litter zone and are often published in languages and journals not readily accessible to most workers. China now has a number of specialists on ant systematics, but as far as I have seen they have not focused on revisions, but rather on random detection and description of new species from the Chinese fauna. In Japan the local fauna is also emphasized, but some workers are now commencing revisionary work in the Asian tropics and elsewhere, and experts such as Imai and Kubota are the leaders in the field of ant karyology. The world revisionary initiative has been strong in South America and Australia, with revisers of the caliber of Brandão, Lattke, Shattuck, and Taylor, but there are still not very many of them.

Systematic Infrastructure

The year 1950 was a turning point for world ant taxonomy; in that year Creighton published *The Ants of North America*, the first major work to apply the Modern Synthesis (Mayr 1942) to the family. This meant that the “quadrinomial” system of the last century, congealed in Emery’s great *Genera Insectorum* fascicles of 1910–1929 and kept relatively unchanged in the works of W. M. Wheeler and his contemporaries, was abandoned—we hope forever! The quadrinomial (four-name) system in the Formicidae—almost unique in the persistence of its application to species-group taxa of names for genus, species, subspecies, and variety—was really a pentanomial (five-name) system, because in practice it routinely used a fifth infrageneric category, the subgenus. Thus we suffered such monstrosities as *Lasius (Chthono-*

Lasius) umbratus mixtus aphidicola; today this species is represented (in North America) by *Lasius umbratus*. Although many pentanomials and quadrinominals are still listed in catalogues and regional lists, almost everyone agrees that they should be eliminated. Under the International Code of Zoological Nomenclature, changes in the status of the variety have helped mightily in this direction, and in my opinion they could help still further by removing the subspecies category from Linnaean nomenclature (Wilson and Brown 1953).

The elimination of the subgenus as a formally named category is a worthy goal in systematic biology, and one that is well on the way to realization in ant systematics (Brown 1973). For nomenclatorial purposes the International Rules recognize the subgenus as equivalent to a genus. The confusion that results when generic names are synonymized or found to be homonyms reveals subgenera to be dangerous as well as merely inconvenient and burdensome: witness the recurrent case of *Cryptocerus* and its subgenera. Most myrmecologists seem to be moving in the direction of using informal species groups instead of subgenera, and groups serve every purpose except to satisfy the cravings of authorship. In practice, formicid taxonomy is fast becoming binomial again, after two centuries.

Another nomenclatorial issue is the ending for subtribal names, which in the beetles and other groups has unfortunately settled on *-ina*, this neither unambiguously plural nor uncommon as an ending of generic names, and identical in the vernacular of most European languages with the already overburdened *-ine* (e.g., Ponerinae, ponerine; Ponerini, ponerine; Ponerina, ponerine). I have discussed the problem (Brown 1958) and suggested instead the subtribal ending *-iti*, which does not have the disadvantages of *-ina* and enjoys much better classical credentials. Bolton feels that the subtribal category may be unnecessary in ant

systematics. I think he is wrong in this, and I believe that, in a taxonomy increasingly based on phylogeny, fine subdivisions such as the subtribe will be needed more and more.

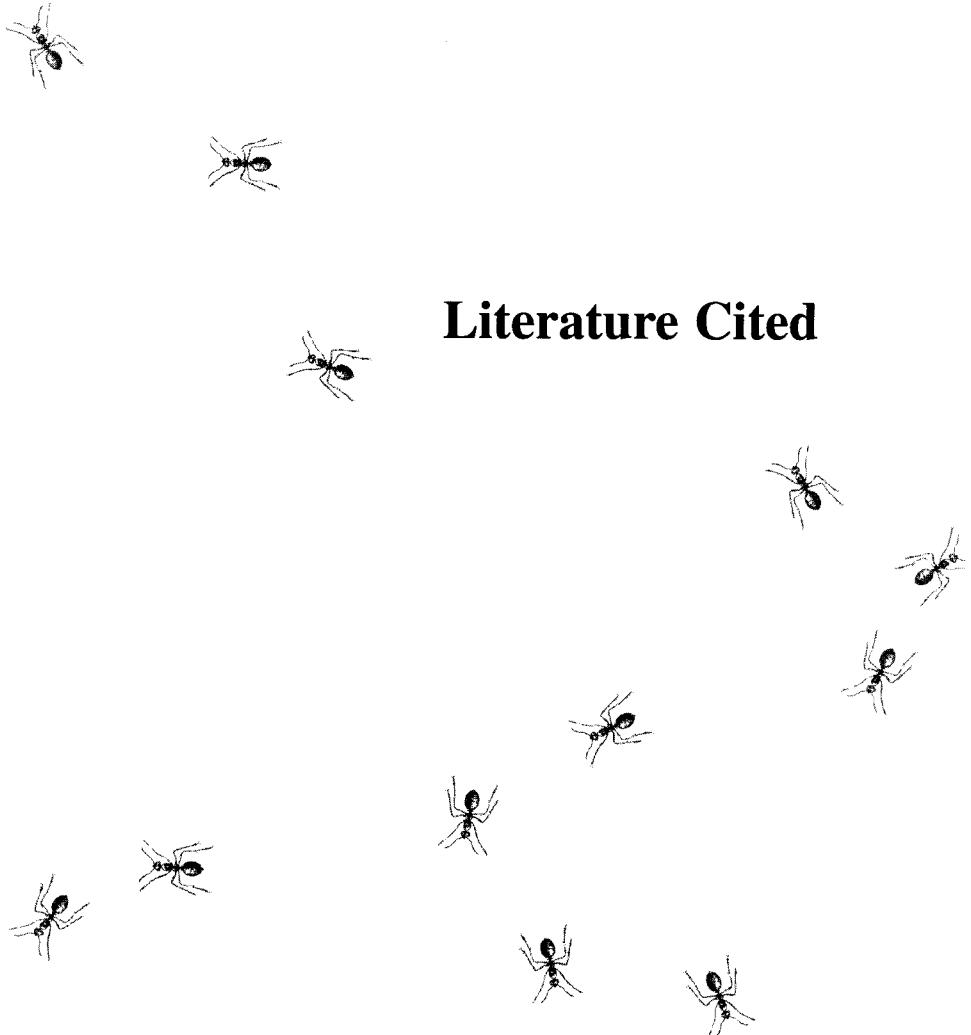
One more practice needs attention: the superfluous citation of authors with the ant name, either with the species binomial or just the genus. I used to teach this practice in taxonomy courses until at last I asked myself: What is its purpose? The author's name has almost become part of the true scientific name of the organism for many who publish research papers, in or outside systematics (true even for many journal editors!), but the Rules state that the author is not part of the scientific name. Author citation has scant reference value in practice, though it is often put forward as a rationale. Abandonment or radical deemphasis of author citation would save much time, effort, and page space; would cut down on the clutter of titles, lists, and captions that slavish citations now engender; and would facilitate computer searching through bibliographies. The rule I follow in this case is to give the author's name only when the instance normally calls for a full bibliographic citation of author, date, volume, and page.

Looking Ahead

We can discern some of the taxonomic needs expected to arise in the future, and the likely responses to them; indeed this manual defines some of them. Requirements of litter ecology overlap, but there is much more to ant systematics than the litter inhabitants. Genera such as *Camponotus*, *Crematogaster*, *Paratrechina*, and *Solenopsis* are all there waiting, but it cannot be said that they make very attractive subjects for Ph.D. theses. The hope is that a Bolton or a Shattuck will soon have the courage (and time and money) to take them on. There is also the matter of phylogeny and major taxon relationships. More characters will have to be found

and studied. Some of these will be molecular genetic, but their study will not be all that simple, as Crozier (1990) hints in his review of the prospects for mitochondrial DNA research on phylogeny and populations. If these dual tasks of defining species and developing new charac-

ter systems continue apace, we may look forward to dramatic advances in ant systematics and phylogenetics that will favorably impact diverse biological disciplines, including the field of biodiversity assessment that is the focus of this book.



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