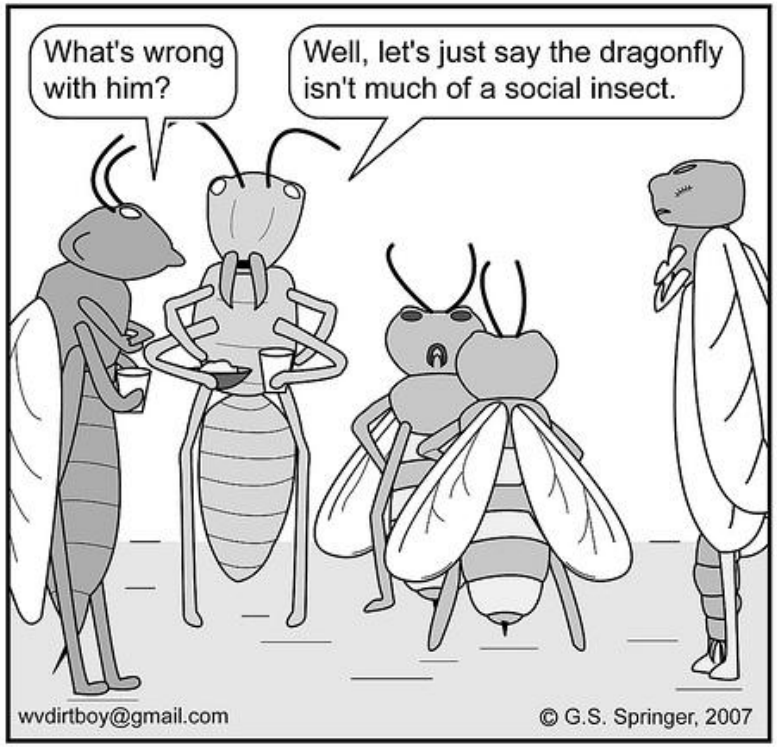
Social Insects

I. Insect sociality
II. Evolution of Eusociality (ants and termites)
III. Success of Eusocial Insects
IV. Ants
V. Ant plants



At An Insect Party

Degrees of Sociality

- Solitary: exhibit no social behavior - most arthropods

- Subsocial: adults care for their own offspring
    - Aphids: sacrificial sterile soldier caste
    - Thrips: cooperative brood care and foraging some soldier casts exist

Degrees of Sociality

- Communal: members of the same generation use the same nest without cooperating in brood care
    - Can allow “antisocial” behavior
- Presocial:
    - Quasisocial: members of the same generation use the same nest and cooperate in brood care
    - Semisocial: same as above plus reproductive division of labor (workers are usually sisters of the queen)

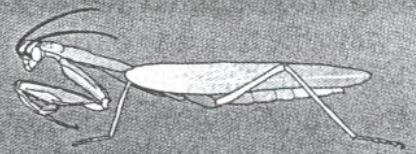
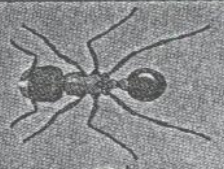
Eusociality

1. Cooperative brood care
2. Division of labor (caste system)
3. Overlap of generations (allows more contributing individuals)

Table 1.1. Taxa of insects and the number of times eusociality has evolved within each.

Insect Orders	Common Names	Frequency of Evolution of Eusociality
Hymenoptera	Ants, bees, wasps, and	11
Isoptera	Termites	1
Homoptera	Gall-forming aphids	1
Coleoptera	Bark-nesting weavils	1
Thysanoptera	Gall-forming thrips	1

traditional classification of insect sociality

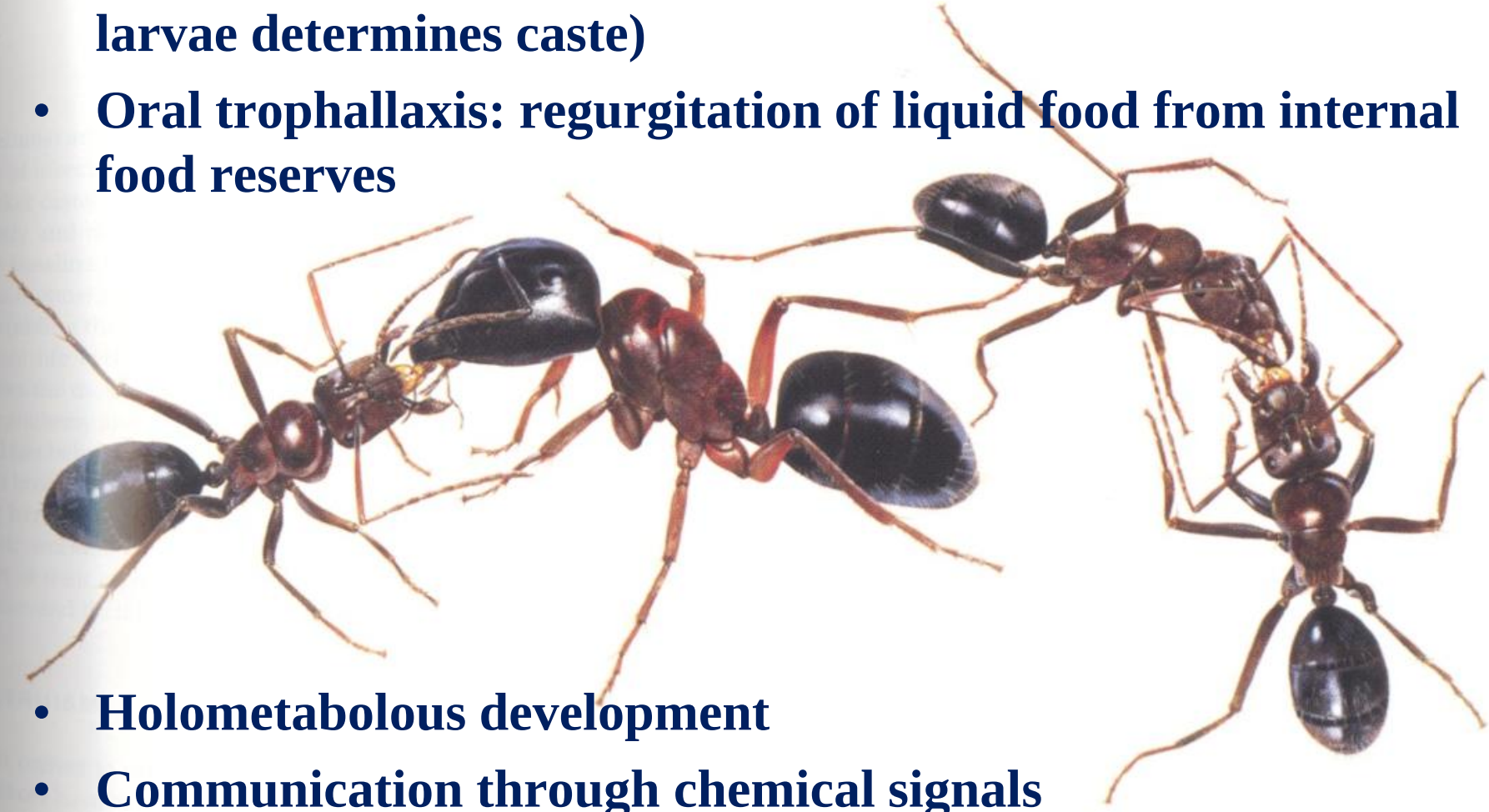
category		description	examples
solitary		• nonsocial • aggregate to mate or because of resource limitation	• most insects  praying mantis
presocial	subsocial	• parental care of immatures for at least part of lifecycle	• some stink bugs • some treehoppers • dung and carrion beetles • passalus beetles  carrion beetle
parasocial	communal	• members of same generation live together • no brood care	• gregarious caterpillars and sawflies • adult whirligig beetles • some bees  eastern tent caterpillar
parasocial	quasisocial	• members of same generation live together • cooperate in brood care	• some wasps • some bees  sweat bee
parasocial	semisocial	• members of same generation live together • cooperate in brood care • reproductive division of labor	• many wasps  paper wasp
eusocial		• overlapping generations • cooperate in brood care • reproductive division of labor	• all ants • all termites • many bees • many wasps  ant

Costa, J.T. and F.D. Fitzgerald. 1996. Developments in social terminology: semantic battles in a conceptual war. Trends in Ecology and Evolution 11:285-289

Costa, J.T. 1997. Caterpillars as social insects. American Scientist 85:150-159.

Ants (Hymenopterans, Formicidae)

- **100% of ant species are eusocial**
- **Trophogenic caste differentiation (food quality/quantity of larvae determines caste)**
- **Oral trophallaxis: regurgitation of liquid food from internal food reserves**



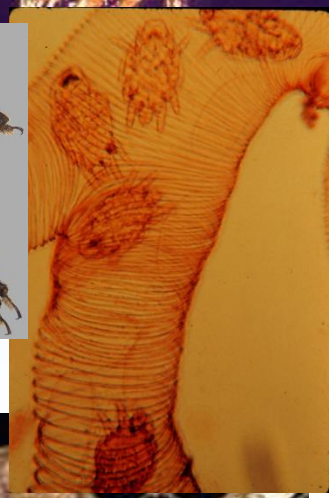
- **Holometabolous development**
- **Communication through chemical signals**

Pollination by bees (Apidae) > $14 Billion /year

CA has > 420,000 acres of Almonds requiring up to 1 million hives

In 2002 USA produced > $130 million of raw honey

Bees pollinate more than 16 percent of flowering plant species (~40,000 sp)



Threats to bees include:
Varroa mites – suck hemolymph and transmit RNA viruses
Tracheal mites – clogs trachea
Small hive beetle (Nitidulidae) - damage to comb, stored honey and pollen
American foulbrood – bacteria
Chalk brood – fungus

Pesticides

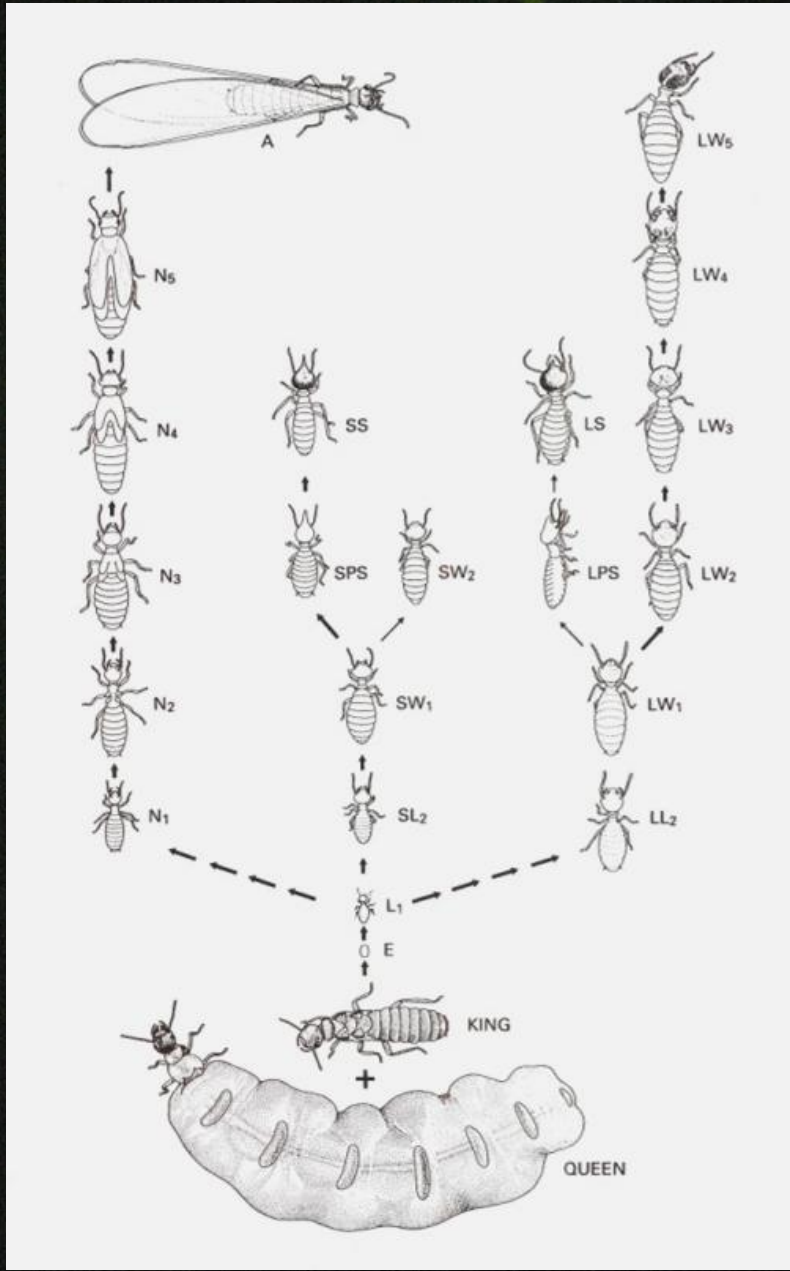
CCD

Neonicotinoid Pesticide Reduces Bumble Bee Colony Growth and Queen Production
Penelope R. Whitehorn, Stephanie O'Connor, Felix L. Wackers, and Dave Goulson
Science 1215025Published online 29 March 2012 [DOI:10.1126/science.1215025]

A Common Pesticide Decreases Foraging Success and Survival in Honey Bees
Mickaël Henry, Maxime Beguin, Fabrice Requier, Orianne Rollin, Jean-François Odoux, Pierrick Aupinel,Jean Aptel, Sylvie Tchamitchian, and Axel Decourtye
Science 1215039Published online 29 March 2012 [DOI:10.1126/science.1215039]

Termites (Isoptera)

- Important eusocial insects with complex life histories and colony structure.
- Usually associated with structural damage
- The Formosan subterranean termite (Rhinotermitidae) is local to New Orleans and can have underground colonies of up to 8 million individuals
  - Entomological Society of America. "Did Termites Help Katrina Destroy New Orleans Floodwalls And Levees?." Science Daily 15 October 2008.
  - Greg Henderson, a Professor at LSU AgCenter inspected 100 levee seems and found 70% evidence of infestation at London Ave Canal and 27% at 17th Street Canal
- Termites turn over at least as much soil as do earthworms in many tropical regions



Evolution of eusociality

… one special difficulty, which at first appeared to me insuperable, and actually fatal to the whole theory. I allude to the neuters or sterile females in insect-communities…

…This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that selection may be applied to the family, as well as to the individual, and may thus gain the desired end…

Altruism: self denying behavior performed for the benefit of others.

Kin selection: workers decrease personal survival and reproduction but increase survival and reproduction of genes they share with kin

Evolution of Eusociality

- Haplodiploidy in Hymenoptera: sisters are more related to each other than they would be with their own offspring

- Hamilton's Rule: rB > C, in which case selection will favor altruism

(r is the genetic relatedness of the recpient to the actor, B is additional reproductive benefit gained by the recipient, C = reproductive cost)

JBS Haldane: "I would lay down my life for 2 brothers or 8 cousins."

	Sister	Half-sister	Own son	Son of full sister	Queen's son (brother)	Son of half-sister
worker	0.75	0.375	0.5	0.375	0.25	0.125

Evolution of Eusociality

- Eusociality is also maintained by: maternal manipulation & competition/mutualism (benefits of colonial life)
- Isoptera: no effect of kinship
  - Intracolony interaction through trophallaxis to distribute gut symbionts after molting—encourages overlap of generations
- Workers in a colony will "police" non-queen eggs and destroy them, which is explained by Hamilton's Rule

	Sister	Half-sister	Own son	Son of full sister	Queen's son (brother)	Son of half-sister
worker	0.75	0.375	0.5	0.375	0.25	0.125

Success of Eusocial Insects

Eusocial

- Simultaneous performance of necessary tasks (foraging, feeding, offspring care, maintenance)
- Force and power of numbers
- Specialization of function=homeostatic regulation

Solitary

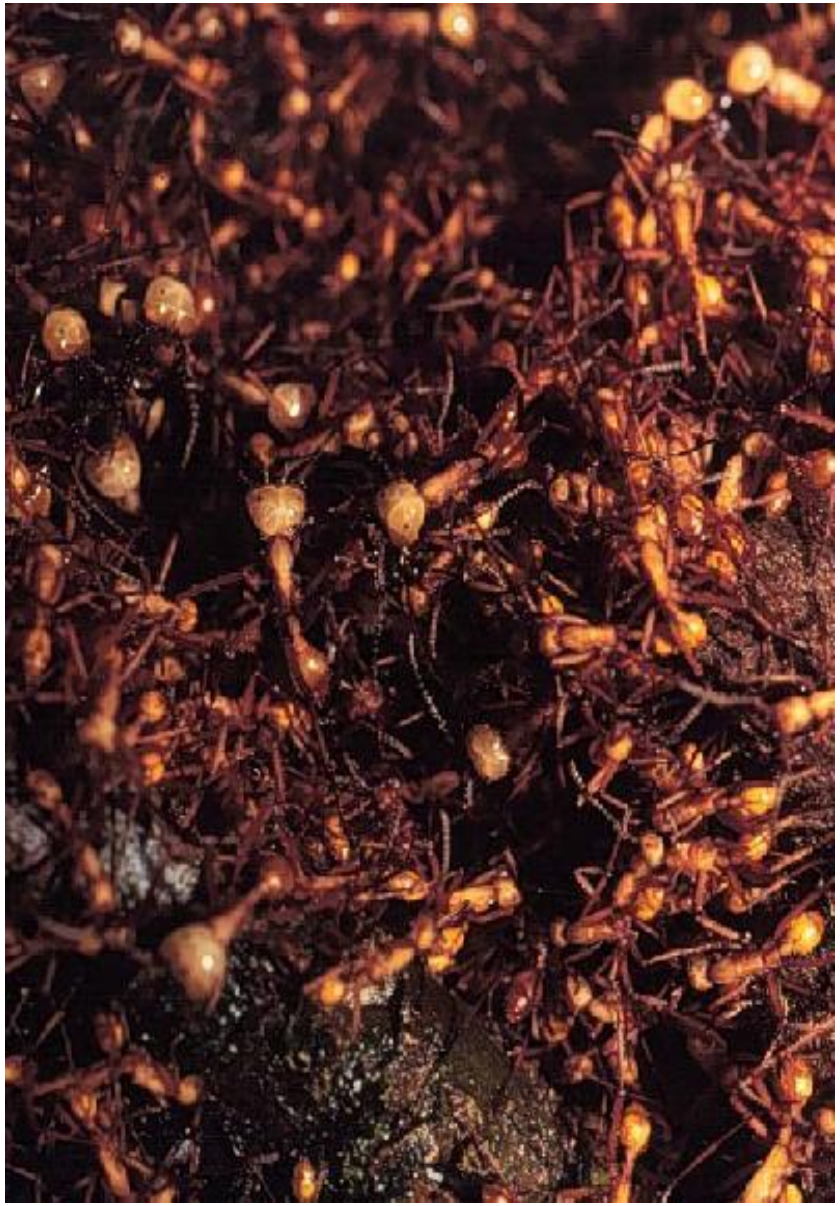
- Sequential performance of tasks = loss of time, higher effect of error & higher risk
- Solitary insect has less power against a large or more numerous predator or physical obstacle
- Little nest control of temperature, resource reserves, response to seasonal/climatic change

Ants are everywhere.

1/3 of the entire animal biomass of the Amazonian terra firma rain forest is composed of ants and termites, with each hectare containing in excess of 8 million ants and 1 million termites.

In Papua New Guinea, E.O. Wilson collected 172 species of ants in 59 genera in 1 square mile.

They are premier soil turners, channelers of energy, predators, seed dispersers, etc.



Eciton sp. (Army ants)

La Selva: 18 $\pm$ 4.5 per hectare

Protect .04 tons wet-weight leaves per hectare per year.

Bala ant *Paraponera clavata*

LEAF-CUTTER ANTS: Atta sp.

Economic important pests cont'd

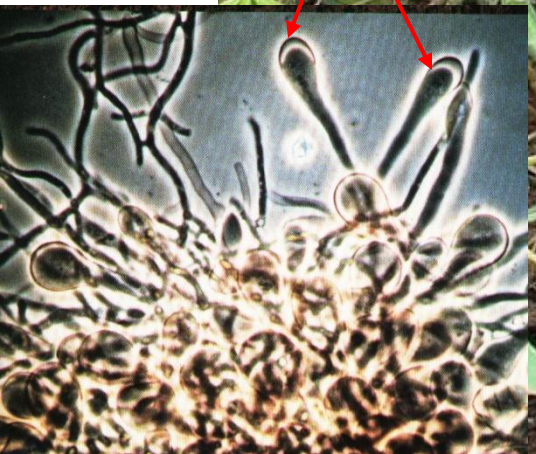
On various crops

Hymenoptera: Leaf-cutting ants

Atta sexdens

Damage on cassava plants

Gongylidia of fungus *Leucocoprinus gongylophora*



The thing ants fear most (even the Bala ant): Flies (Diptera)

Phorid fly
-Parasitoid
-attack wounded (or otherwise occupied) ants like *Atta*

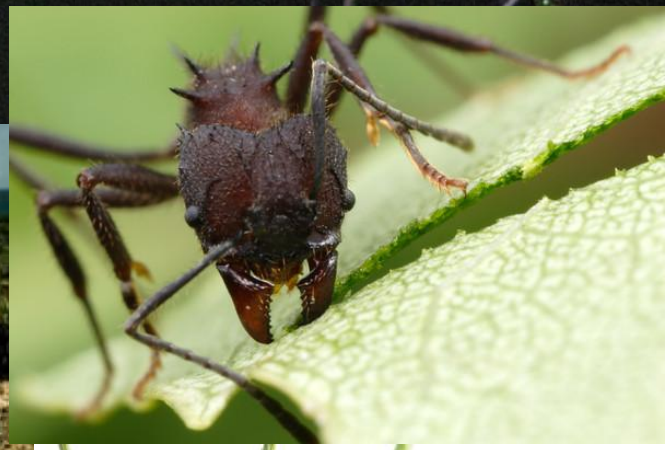
-Larvae move into ant's head to finish development

Ants (Hymenopterans, Formicidae)

- Colony size:
  - African Weaver Ant: A mature colony of up to 500,000 workers can be prevented from reproduction by a single queen
  - In other species the mature colony may be as small as 10 individuals.

Ants (Hymenopterans, Formicidae)

- Many food sources utilized, some species are predatory, some eat grains and seeds, some culture fungi
- High diversity of nest structures



Larval Development

- Larvae are completely dependent on workers
- May be fed through oral trophallaxis or placed directly on food source
- Specialized digestive castes exist in some species, larval saliva usually contains proteases and lipases while worker saliva may contain carbohydrates

Colony Development/Life Cycle
Foundation Stage

- Queen finds suitable nest site and constructs small nest chamber, sometimes multiple queens may found nest site (called pleometrosis).
- Starts egg-laying and takes care of first generation, developing larvae and pupae
- First generation of workers eclose and begin to take over feeding of the queen and colony maintenance.
- Early workers of many species are usually smaller in size

http://research.amnh.org/entomology/social_insects/ants/ant_colony_cycle.html

Ergonomic (growth) Stage

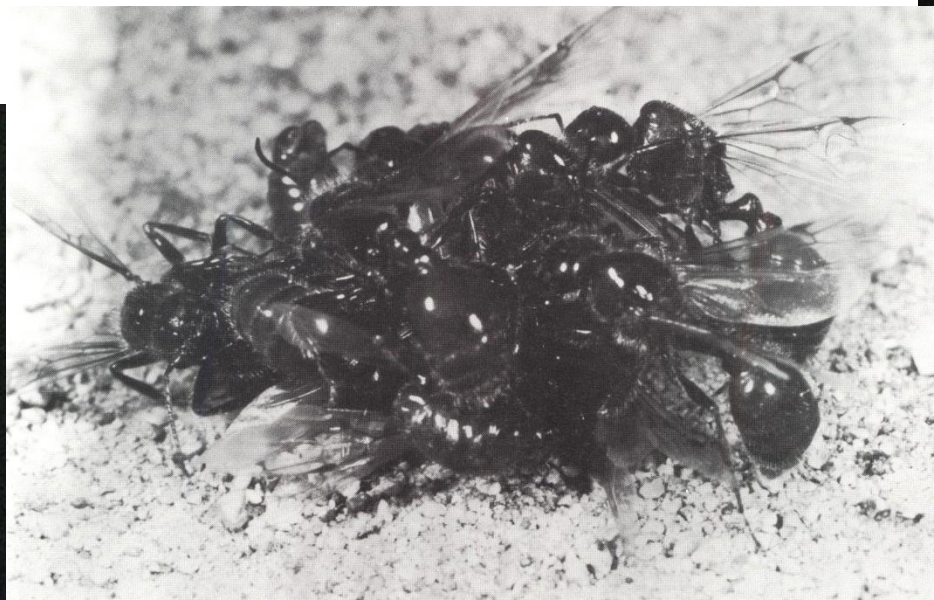
- Workers completely take over colony maintenance and feeding.
- Queen devotes herself entirely to egg-laying
- New castes begin to emerge
- Polymorphism, larger workers begin to appear, larger individuals may serve in defensive roles, soldiers for example
- Colony functions devoted to growth

Reproductive Stage

- New queens and males begin to appear within colony (usually winged, alates)
- Alates often leave colony in mass to find mates
- Timing of mass flights is usually specific to each species, time of day and time of year
- Males are short-lived

Reproductive Stage

- Females of many species mate with more than 1 male, males are unable to produce enough sperm for successful colony (atrophied testes)
- Apterous males or females may exist in some species, colony fission involved in new colony formation
- Colony reverts back to ergonomic stage after reproductive stage
- Colony may only be able to survive for a few months following loss of the queen



Inquilines & Parasites

- Inquiline: an organism that shares a home of another (usually for nutritional benefit)

- Wasmannian Mimicry: chemical or tactile mimetic features that allow integration into a host nest

Table 1: CATEGORIES OF ANT-PLANT INTERACTIONS (Modified from Keeler)

INTERACTION	PLANT BENEFIT/LOSS	ANT BENEFIT	EXAMPLES
Mutualism (Myrmecophytes)	Defended against herbivores (and some epiphylls)	Shelter and food	*Acacia-Pseudomyrmex* *Cecropia-Azteca* *Piper-Pheidole*
Mutualism	Defended against herbivores	Food (extrafloral nectaries)	*Solanum*-ants *Ipomoea*-ants
Mutualism (Myrmecophytes)	Nutrients	Shelter and food	Ant gardens-*Camponotus* *Myrmecodia-Iridomyrmex*
Commensalism	Nothing	Food (extrafloral nectaries)	*Passiflora auriculatum* - various ants
Commensalism	Nothing	Shelter	*Witheringia asterotricha - Crematogaster*
Mutualism (Myrmecochory)	Seeds are dispersed	Food	Many plants-*Tapinoma*
Mutualism	Gametes are delivered (pollination)	Food	*Leporella fimbriata - Myrmecia*
"Predation"	Leaf tissue, floral structures, or seeds lost	Food	Various plants-*Atta* Various plants-*Pogonomyrmex*
Indirect interactions	Various (can be both positive and negative)	Various	*Desmanthus illinoensis - Crematogaster lineolata*

Ant-Plant Interactions

- Myrmecochory (Seed Dispersal)
- Pollination (quite rare)
- Leaf-cutter ants
- **Myrmecophily**
  - Ant-mediated protection
  - Myrmecotrophy

Extrafloral Nectaries (EFNs)

-Many plants have extrafloral nectaries on young leaves or fruits
-Very common among tropical species

EFN on new vine tip

Jumping spider visiting Passiflora efn

Myrmecophytic Strategies

Protection-based

- Acacia, Cecropia, etc.
- Predominantly terrestrial
- Plants are defended against herbivory and competition
- Ants may receive shelter and specialized food bodies or extrafloral nectar

Nutrition-based

- Myrmecodia, Hydnophytum
- Predominantly epiphytic
- Plants obtain nutrients from ants through stems or root systems
- Ants receive nesting sites or nest structural support, as well as food bodies or nectar

Protection-based Mutualisms

- Many terrestrial myrmecophytes, such as this bull's horn Acacia, offer shelter and food rewards in return for the protective territoriality of their inhabitant ants

Pseudomyrmex ants and Acacia

- Ants nest in the hollow swollen thorns
- They eat lipid-rich Beltian bodies that grow on the tips of new leaves
- They get carbohydrates and amino acids from extrafloral nectar

Protection-based Mutualisms

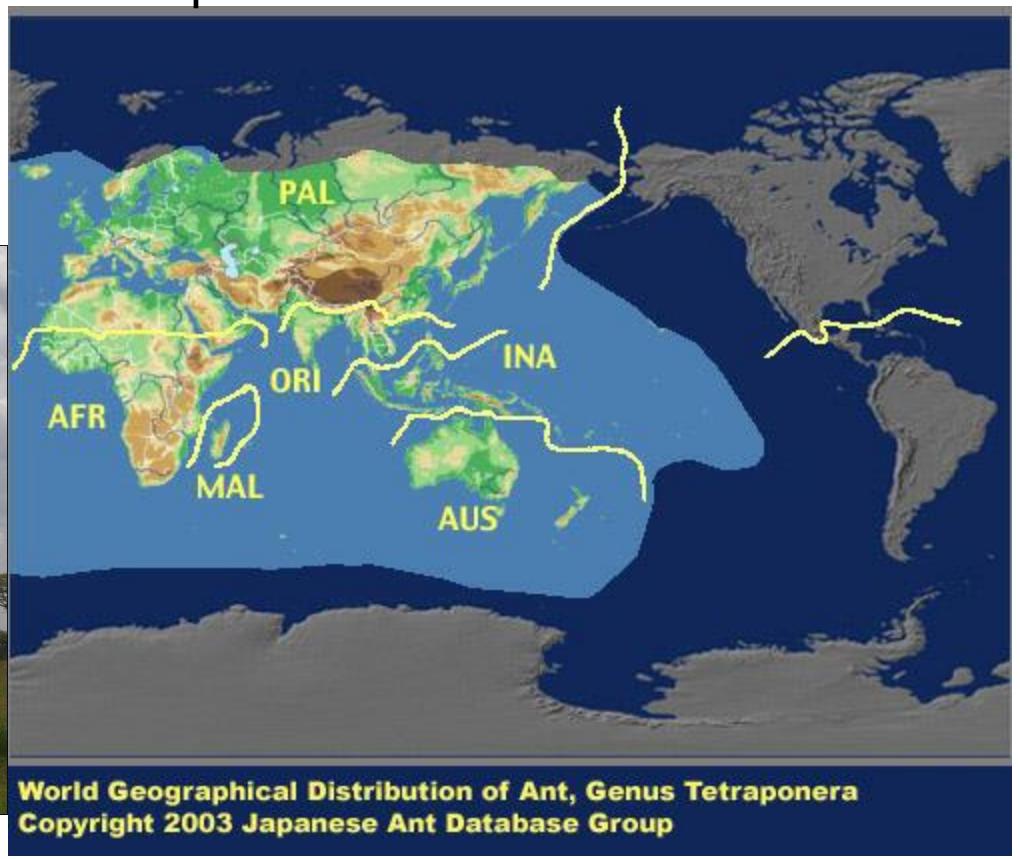
Subfamily Pseudomyrmecinae: Pseudomyrmex Neotropics

Bullhorn acacia and ant mutualism: ant-cleared area around tree, Costa Rica.

Protection-based Mutualisms

Acacia ant mutualists include

Subfamily Pseudomyrmecinae: Tetraponera and Pseudomyrmex in Old World



Protection-based Mutualisms

Cecropia mutualists include aggressive Azteca (Subfamily Dolichoderinae) ants

The ants nest in the hollow stem and feed on Mullerian bodies

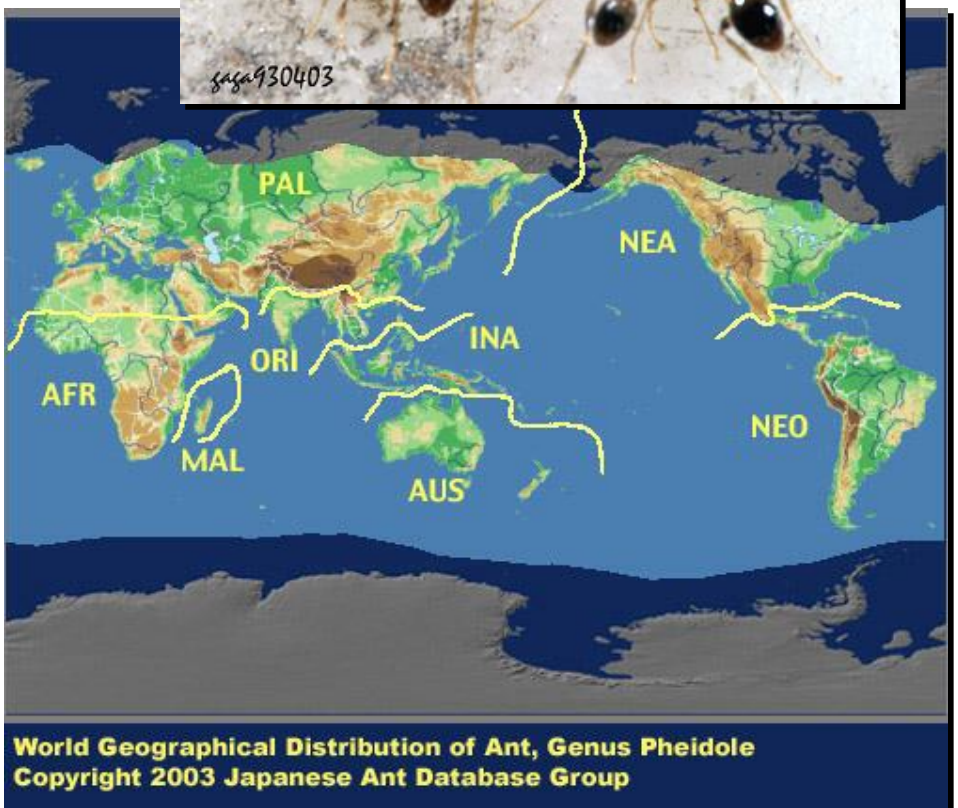
Cecropia

Can receive significant portion (up to 90 percent) of N budget from Azteca ants!

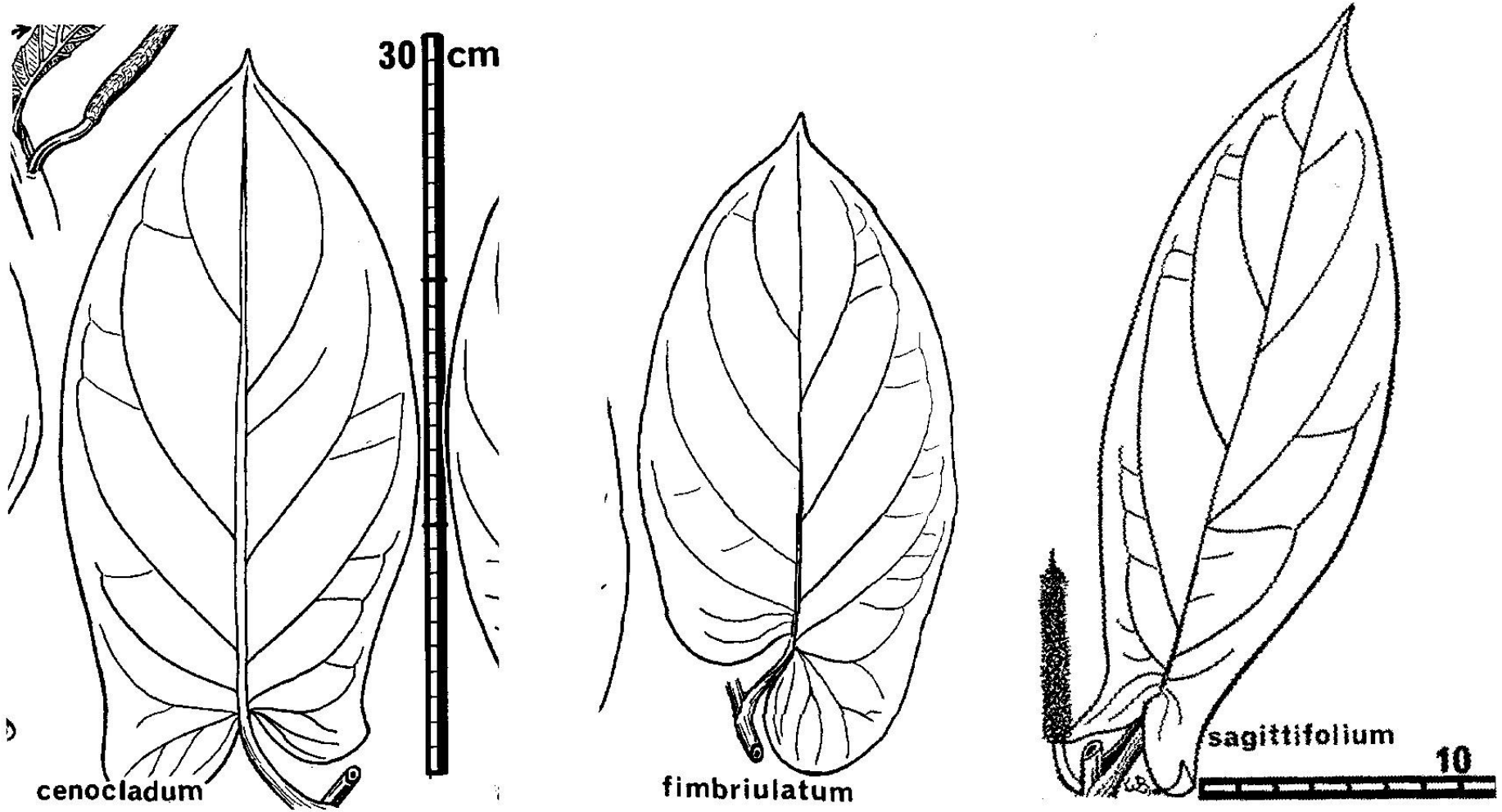
Protection-based Mutualisms

Subfamily Myrmicinae

Pheidole ants and Piper



Piper Ant-Plants



From Burger 1971

Piper cenocladum

Pheidole bicornis in *Piper*, Costa Rica, Barva Transect 500m, Feb'03. Colln. JTL4935. Image by J. Longino.

Pheidole bicornis in *Piper*, Costa Rica, Corcovado, Dec'81. Colln. JTL5Dec81/1000. Image by J. Longino.

Pheidole bicornis in *Piper*, Costa Rica, Barva Transect 500m, Feb'03. Colln. JTL4935. Image by J. Longino.

Pheidole bicornis in *Piper*, Costa Rica, Corcovado, Dec'81. Colln. JTL5Dec81/1000. Image by J. Longino.

Piper immutatum

Piper pterocladum

Piper pterocladum

Piperaceae: Piper biseriatum

Piper biseriatum

Piper imperiale

Melastomataceae : Tococa guianensis

Tococa guianensis

Melastomataceae: Clidemia allardii

Nutrition-Based Mutualisms

- Hollow chambers develop in the tuberous stem bases of Hydnophytum formicarum in Southeast Asia provide nesting sites for symbiotic ants

Epiphytic Myrmecotrophs

Southeast Asian ant-plants including Myrmecodia and Hydnophytum have specific ant mutualists– *Iridomyrmex* and *Philidris*