# Caste and Division of Labor in Leaf-Cutter Ants (Hymenoptera: Formicidae: *Atta*)

## I. The Overall Pattern in *A. sexdens*

Edward O. Wilson

Museum of Comparative Zoology Laboratories, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138, USA

**Summary.** *Atta sexdens* was selected for close study because its caste and polyethism systems, which are among the most complex found in all ants, can be expected to provide an estimate of the upper limits of colonial organization in these insects.

A total of 29 tasks were identified. These are performed by an estimated four physical castes, of which three are further subdivided into temporal castes to make a total of at least seven castes overall (Figs. 1–11 and Table 1).

The physical castes of *A. sexdens* were defined on the basis of 'role clusters,' which are more or less segregated or distinctively shaped sets of polyethism curves. The four castes can be characterized broadly according to role as gardener-nurses, within-nest generalists, forager-excavators, and defenders, respectively (Fig. 12). This discretization is only partial, and finer, arbitrary subdivisions at the lower end of the size scale are possible.

The physical castes have been generated by a large evolutionary increase in size variation accompanied by the adoption of relatively elementary rules in allometry and alloethism. The increase in caste diversity beyond that possessed by monomorphic attines serves the relatively narrow primary function of cutting and treating fresh vegetation for use as the fungal substrate. The material is processed and the fungus cultured in an assembly-line fashion, with the succession of tasks (gathering, degrading, and implanting of substrate, followed by implanting and care for the fungal hyphae) being performed by ever smaller workers (Fig. 13).

The rules of allometry and alloethism create far less caste diversity than would be possible by a few additional minor evolutionary adjustments in larval growth and allometry during adult development (Fig. 17). Evidence is presented for the existence of secondary roles possessed by various size ensembles in addition to the primary roles, and for the suboptimal performance of a few size classes. These two phenomena are considered to result from the simplicity and hence restrictiveness of the allometry and alloethism rules (see Discussion).

Polyethism has evolved further than polymorphism: the alloethic curves rise and descend more steeply than the size-frequency distributions and they are generally steeper than the allometric curves drawn for any selected pair of physical measurements.

A technique is introduced by which the functions of previously unstudied or poorly understood organs can be inferred. It consists of noting in which size classes the organs are maximally developed, then determinig the labor specializations of the size classes. The method is shown to work in the cases of pronotal spination, poison sac, postpharyngeal gland, metapleural gland, and mandibular gland, and it is extended in a speculation concerning the functions of other exocrine glands (Fig. 16).

A distinction is made between fixed tasks, which are attended by relatively limited age-size ensembles of workers, and flexible tasks, which are attended by ensembles that vary in size (and perhaps age) according to the objects treated during the performance of the task (Fig. 15).

The concept of the primitive caste is introduced; it is the size class that most resembles related monomorphic species and performs the most generalized services for the colony. Evidence is presented that in *A. sexdens* this class is composed of workers with head widths around 1.4–1.6 mm.

## Introduction

One of the key questions of modern evolutionary biology is whether natural selection is sufficient to

have produced the observed complexity of the living world within the time estimated from the geological record. Microevolution by natural selection has been repeatedly demonstrated in field and laboratory studies, and the rules of its dynamics are reasonably well understood. But can these dynamic processes be extrapolated to account for macroevolution in full, without resorting to some additional, as yet undefined genetic force? This question assumes a special importance in the case of the insect societies, which have added the origin of complex social organization on top of ongoing morphological and physiological change.

The problem of macroevolution in the insect societies can be translated into a more tractable form as follows: How well organized are the insect colonies? To make an estimation we need to know the basic rules of relative growth and behavioral differentiation among age-size classes that generate caste and division of labor. These rules are the components that change during genetic evolution. In some cases they are constructed so that only small alterations in their specification can cause large effects in morphogenesis and behavioral differentiation (Oster and Wilson 1978). A program of study of the organization of insect societies should consequently include three principal goals: (a) the detailed analysis of caste and division of labor that defines their underlying rules in morphogenesis and behavioral differentiation, (b) a phylogenetic comparison of species designed to estimate the rate of evolutionary change in the rules, and (c) ergonomic analyses that estimate the efficiency (the 'fit') of the rules with reference to the requirements imposed by the environment.

The fungus-growing ants (tribe Attini) are an exceptionally favorable group for this three-part analysis. They are a diversified group of approximately 200 species in 11 genera that collectively range from Argentina to New Jersey. The two leaf-cutter genera, *Atta* and *Acromyrmex,* are the dominant herbivorous animals in most habitats of the New World tropics and also rank among the leading agricultural pests. The natural history of several of the genera is well known, and most species can be readily cultured in the laboratory (Weber 1972, 1979). I selected the leaf-cutter genus *Atta* because it has the most phylogenetically advanced and complex caste system and division of labor among the Attini and possibly among the ants as a whole. I had previously noted that most or all of the complexity is arrayed along a single allometric curve and bimodal size-frequency distribution (Wilson 1953; Oster and Wilson 1978). I gambled that it could be reduced to a manageably small set of rules in morphological and behavioral development. If this indeed is the case, we might obtain some

sense of the ceiling of evolution in caste and division of labor within the Attini, and thence a valuable reference point in estimations of evolutionary rate. Furthermore, as I hope to be able to demonstrate in a later report (Wilson 1980), the ability to map the system into a one-dimensional array makes it possible to determine whether the species is in fact at the optimum in a purely ergonomic sense.

In order to make the conception of this research program clearer, it will be useful to repeat the definition of three terms about which some confusion is possible. *Allometry* is the size relation between two body parts that can be expressed by $y=bx^a$, where $a$ and $b$ are fitted constants. Physical castes in ants are universally based on allometry with $a \neq 1$ (Wilson 1953). *Alloethism* is the comparable phenomenon in behavioral response: the probability of performance of a specific task as a function of body size. In *Solenopsis,* for which the first actual alloethic curves have been drawn (Wilson 1978), no simple mathematical formula is apparent that might be used to characterize such curves generally. Allometry is the quantitative relation that can be used to characterize polymorphism, or physical caste systems, while alloethism is the quantitative relation that can be used (in conjunction with data on change of behavior with aging) to characterize polyethism, or the division of labor. *Ergonomics* is the quantitative study of work, performance, and efficiency; it is based in good part on data concerning caste and division of labor (Oster and Wilson 1978).

A *caste* can be broadly defined as any set of colony members, smaller than the total colony population, that specialize on particular tasks for prolonged periods of time. Castes are invariably delimited as groups of individuals of a particular size, age, or both. In the case of continuous variation in these traits, the limits of the sets are necessarily arbitrary, but they can at least be made repeatable through the characterization of modes, extreme range, variance, and other statistical properties. I have chosen to define a *task* as a set of actions that flow from one to the next in such an integrated sequence that for the sequence to be halted by one worker and resumed by another worker would result in a substantial loss of time or efficiency. Thus for a trail-laying worker to halt halfway home and turn over the rest of the performance to another worker would be such an interruption; trail laying constitutes a single task from inception to completion. In contrast, the shift from recruiting to leaf cutting is a clear break between the end of one task and the start of another. So is the step from the final processing of substrate particles to the implantation of fungi on them, or the shift from grooming a nestmate to feeding a larva.

## Materials and Methods

The present study was based on a colony of *Atta sexdens* (Linné) collected by Neal A. Weber at Timehri, Guyana, in 1970. *A. sexdens* is the most widely distributed of the *Atta* species, ranging from Argentina to Panama (Borgmeier 1959). Because of its economic importance, it has been the subject of an unusual amount of field investigation, much of which is relevant to the present investigation (Eidmann 1932, 1935, 1937; Stahel and Geijskes 1939; Jacoby 1944; Autuori 1956; Butenandt et al. 1959; Weber 1972; Schade 1973). During 1978, when the study was conducted, the colony contained the original mother queen and approximately 7,000 workers. Parallel but less detailed studies were conducted with smaller colonies of *Atta cephalotes*. The results from this closely related species are fully consistent with those on *A. sexdens*.

The colony was kept in a closed series of clear plastic chambers 14 cm × 19 cm and 9 cm high. Foraging workers were permitted to collect vegetation either from empty chambers or from an open tub surrounded by a water moat. A wide variety of materials were used, including leaves and flowers of several plant species and even wheat germ and other cereals. As the colony expanded over a period of eight years, the ants filled one chamber after another with characteristic spongelike masses of processed substratum, through which the symbiotic *Rozites* fungus grew luxuriantly.

Observations were conducted with the aid of an 8 × hand lens and swing-arm dissecting microscope at magnifications of up to 30 ×. Dissections were performed in insect Ringer's solution with the aid of watchmaker's forceps (Dumont no. 5) and insect pins set into the bases of applicator sticks. During the polyethism studies, live workers were not measured directly. Instead, their head width was estimated to the nearest 0.2 mm by reference to a standard array of preserved specimens whose head widths had previously been measured to the nearest 0.01 mm. The specimens were rank-ordered in rows according to size, at 0.2-mm intervals over the entire size range of the species (0.6 mm, 0.8 mm, ... 5.2 mm). Periodic checking with live ants removed for dissection proved that with a small amount of practice the technique can be made reliable, with more than 90% of ants being placed in the correct size class and the remainder being misplaced by a distance not exceeding one size class. The measurement used was the standard head width (HW) of ant taxonomy: the greatest width of the head viewed face on, with the measurement being taken at an exact right angle to the longitudinal axis of the head. In *Atta* the maximum breadth is close to the level of the eyes.

Larval length used in the study is the longest straight-line measure from one end of the body to the other of a larva lying in an ordinary relaxed, slightly curved posture.

## Results

### Basic Polyethism Data

In Table 1 are listed all of the tasks observed during approximately 100 h of observation of the *Atta sexdens* colony. Complete lists of tasks observed in earlier studies of other myrmicine species (*Leptothorax curvispinosus, Zacryptocerus varians, Pheidole dentata*) are added to enable comparison with the leaf-cutter ants. It should be noted that the tasks do not constitute the entire behavioral repertory; in complete ethograms of the other, non-attine species, the tasks make up only about half of the behavioral acts, with nonso-

**Table 1.** The tasks performed by the workers of the monomorphic myrmicine *Leptothorax curvispinosus*, dimorphic myrmicines *Zacryptocerus varians* and *Pheidole dentata*, and continuously polymorphic myrmicine *Atta sexdens*. *Leptothorax* data from Wilson and Fagen 1974; *Zacryptocerus* data from Wilson 1976a; *Pheidole* data from Wilson 1976b

| Task | *Leptothorax curvispinosus* | *Zacryptocerus varians* | *Pheidole dentata* | *Atta sexdens* |
|---|---|---|---|---|
| Exploring | × | × | × | × |
| Recruiting | | × | × | × |
| Cutting vegetation | | | | × |
| Carrying vegetation | | | | × |
| Degrading vegetation, first stage | | | | × |
| Degrading vegetation, second stage | | | | × |
| Implanting substrate particles | | | | × |
| Licking substrate | | | | × |
| Implanting hyphae | | | | × |
| Caring for hyphae | | | | × |
| Transporting hyphae | | | | × |
| Collecting prey or dead arthropods | × | × | × | |
| Collecting honeydew | × | × | × | |
| Refuse disposal | × | × | × | × |
| Reconstructing garden | | | | × |
| Transporting substrate | | | | × |
| Excavating | × | × | × | × |
| Carrying eggs and smallest larvae | × | × | × | × |
| Carrying small-intermediate larvae | × | × | × | × |
| Carrying large-intermediate larvae | × | × | × | × |
| Carrying pupae | × | × | × | × |
| Manipulating brood | × | × | × | × |
| Larval feeding | × | × | × | × |
| Assisting ecdysis | × | × | × | × |
| Allogrooming workers | × | | | × |
| Transporting workers | × | | | × |
| 'Parasol' riding | | | | × |
| Grooming queen | × | × | × | × |
| Feeding queen | × | × | × | × |
| Abdominal trophallaxis | | × | | |
| Defense against small invaders (e.g., ants) | × | × | × | × |
| Defense against large invaders (e.g., mammals) | | | × | × |
| Total number of tasks | 17 | 18 | 18 | 29 |
| Number of physical castes | 1 | 2 | 2 | 4 |
| Number of Temporal Castes | 2? | 2? | 3 | 3 |
| Total number of castes[a] | 2? | 3? | 4 | 7 |

[a] In *Pheidole dentata*, there are two physical castes, of which one is divided into two temporal castes, making a total of four castes (Wilson 1976b). In *Atta sexdens* four physical castes can be arguably distinguished (see Fig. 12), of which three are divided into at least two temporal castes (see Table 2); hence the estimated total number of castes is seven

cial functions such as self-grooming as well as distinct behavioral subcomponents of task performance making up the remainder.

The polyethism curves for the *A. sexdens* tasks and some subdivisions of the tasks are presented in

Figs. 1–11. These data have been evaluated in two ways. First, in Table 2, the tasks are grouped according to the modal size group of the workers that performed them, from 'caring for hyphae,' with a modal group of workers at head width (HW) of 0.6 mm, through exploring, recruiting, and other tasks attended by workers whose size-frequency distributions have an HW mode of 2.2 mm. In addition, the percentages of callow workers engaged in all of the 34 tasks and subtasks are given in Table 2. Callow workers are very young individuals whose integument is still lightly colored enough to distinguish them from older workers when examined at low magnifications. In ant species generally, callow workers spend almost all of their time within the nest interior and engage more frequently in brood care than do older workers. This has also proved to be the case in *A. sexdens*.

The second mode of evaluation is given in Fig. 12. When the polyethism curves are superimposed, they appear to fall into four role clusters. Three of the clusters are centered on head widths 1.0, 1.4, and 2.2 mm, respectively, and the fourth (*D*, defenders)
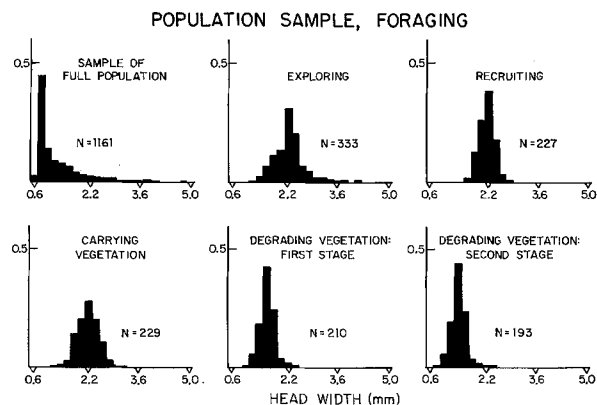


**Fig. 2.** Polyethism curves of vegetation cutting. *Cutting soft vegetation, rose petals* (data accumulated during trials on six days). *Cutting medium-hard vegetation, Andromeda* (data from one day). *Cutting hard vegetation, rose buds* (data from one day). *Cutting hard vegetation, Rhododendron leaves* (data from one day). *Cutting thin vegetation, Gypsophila sprays:* the stems of babies'-breath (*Gypsophila paniculatum*) are only about 1 mm thick and the flower heads are only about 4 mm across, yet approximately the same statistical array of relatively large medias climbed the sprays and did the cutting (data from four days)



**Fig. 1.** Polyethism curves of foraging and substrate preparation: the frequency distributions of workers of various sizes (head width estimated to the nearest 0.2 mm) engaged in several tasks. The number of workers in each sample (*N*) is also given. *Sample of full population:* the entire contents of one of five fungus chambers, removed after nearly all foragers had returned to the nest. *Exploring:* workers were observed as they first entered a foraging chamber newly attached to the artificial nest (data accumulated during trials on three days). *Recruiting:* workers observed laying odor trails from vegetation newly placed in the foraging chambers (data from 12 days). The trail pheromone originates from the poison gland sac and is emitted through the sting. *Carrying leaves:* workers were carrying freshly cut leaves from the foraging chamber (data from five days). *Degrading vegetation, first stage:* the ants were cutting and chewing relatively large fragments of leaves and petals shortly after they were brought into the garden chambers (data from five days). *Degrading vegetation, second stage:* The ants were chewing and licking leaf and petal fragments after the fragments had been reduced to diameters of 2 mm or less and were mostly discolored (data from 11 days)
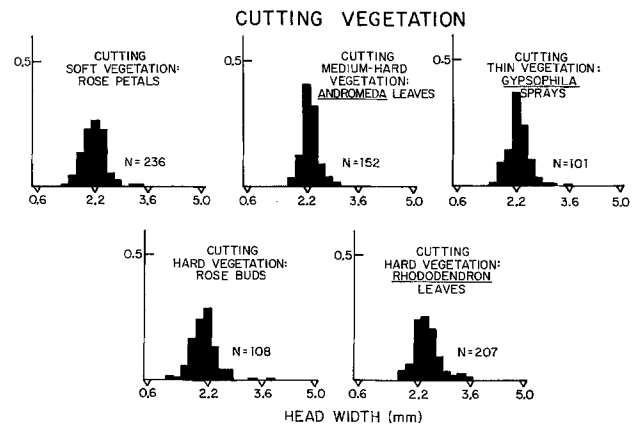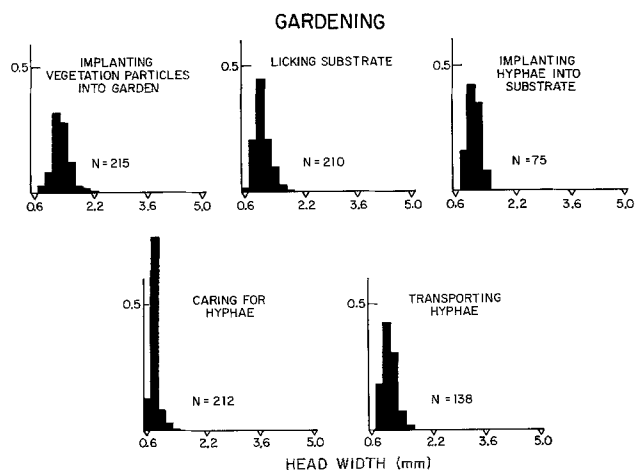


**Fig. 3.** Polyethism curves of gardening. *Implanting vegetation particles into garden:* the fragments of degraded vegetation, reduced to diameters of 2 mm or less, were inserted into the main substrate of the fungus gardens (data accumulated during nine days). *Licking substrate:* the implanted substrate fragments were further licked and chewed (data from nine days). *Implanting hyphae into substrate:* the workers were observed placing small tufts of *Rozites* hyphae onto the implanted substrate particles (data from eight days). *Caring for hyphae:* the workers were observed pulling, tamping, and licking hyphae already present on the substrate particles without, however, removing or eating the fungus (data from two days). *Transporting hyphae:* the workers were observed carrying tufts of hyphae to various destinations, including the larvae, queen, and other workers; the hyphae served as food or were implanted onto fresh substrate particles (data from eight days)
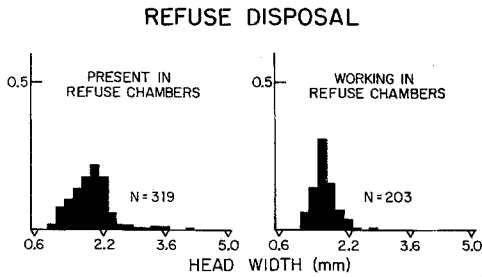
## REFUSE DISPOSAL



**Fig. 4.** Polyethism curves of refuse disposal. *Present in refuse chambers* (data accumulated during five days). *Working in refuse chambers:* digging in and carrying around dead nestmates, pieces of discarded substrate, and other forms of detritus (data from five days)
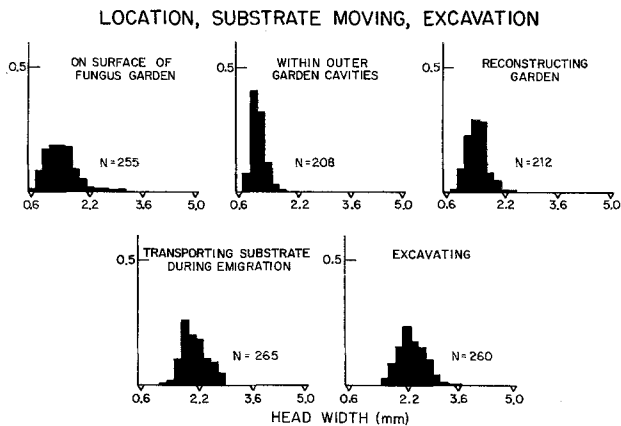
## LOCATION, SUBSTRATE MOVING, EXCAVATION



**Fig. 5.** Polyethism curves of location, substrate moving, and soil excavation. *On surface of fungus garden:* random sample of workers walking, resting, or working on outer surface of the fungus combs (data accumulated during two days). *Within outer garden cavities:* random sample of workers inside the outermost cavities of the fungus combs; these workers averaged larger in size than those in the inner cavities (data from four days). *Reconstructing garden:* reforming the fungus combs by pulling out pieces of hypha-bearing substrate, transporting them short distances, and reinserting them into the combs (data from ten days). *Transporting substrate during emigration:* when the colony absconded from a nest chamber, the workers tore away pieces of hypha-bearing comb and transported them to other chambers (data from three days). *Excavating:* digging up and carrying clusters of a mixture of soil, humus, and leaf litter during the excavation of this material within the nest chambers (data from one day)
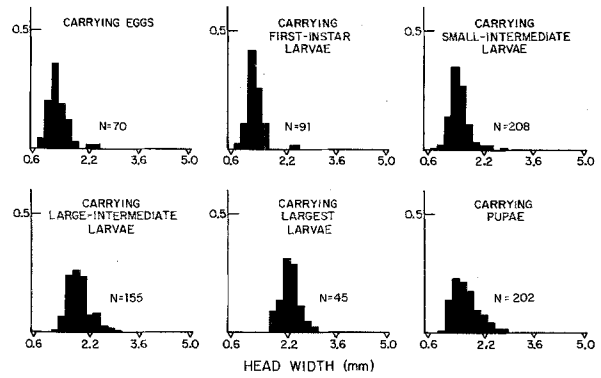
## BROOD TRANSPORT



**Fig. 6.** Polyethism curves of brood transport. *Carrying eggs* (data accumulated during ten days). *Carrying first-instar larvae:* workers were recorded as they carried the smallest larvae, those with total body lengths of up to approximately 1.5 mm (data from ten days). *Carrying small-intermediate larvae:* workers were recorded carrying larvae approximately 1.5–3.0 mm in total length (data from nine days). *Carrying large-intermediate larvae:* workers were recorded carrying larvae approximately 3.0–5.0 mm in total length (data from 11 days). *Carrying largest larvae:* workers were recorded carrying larvae exceeding 5.0 mm in total length (data from eight days). *Carrying pupae:* workers were recorded carrying pupae (data from seven days; see also Fig. 15A)
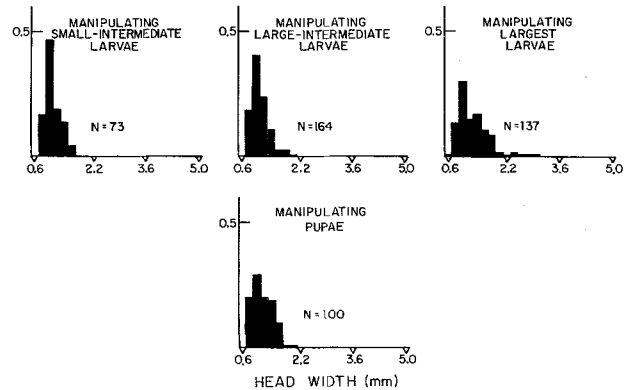
## BROOD MANIPULATION



**Fig. 7.** Polyethism curves of brood manipulation. *Manipulating small-intermediate larvae:* workers were recorded licking or turning over larvae approximately 1.5–3.0 mm in total length (data accumulated during seven days). *Manipulating large-intermediate larvae:* workers were recorded licking or turning over larvae approximately 3.0–5.0 mm in total length (data from nine days). *Manipulating largest larvae:* workers were recorded licking or turning over larvae exceeding 5.0 mm in total length (data from eight days). *Manipulating pupae:* workers were recorded licking or turning over pupae (data from ten days; see also Fig. 15B)

consists of a special skewed distribution. The groups can be characterized as follows:

*A) Gardeners and Nurses.* Centered on head width 1.0 mm: size ensembles of workers specialized on the

care of hyphae, final treatment and implantation of substrate particles, brood care, and parasol riding.

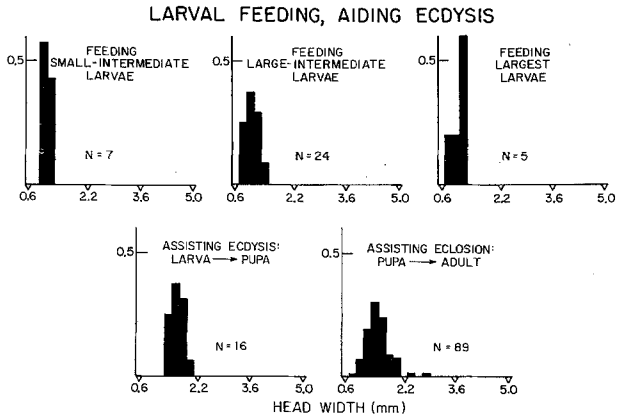*B) Within-Nest Generalists.* Centered on head width 1.4 mm: size ensembles of workers that perform a rela-

**Fig. 8.** Polyethism curves of larval feeding and assistance at ecdysis. *Feeding small-intermediate larvae:* workers were recorded as they regurgitated to larvae 1.5–3.0 in total length or fed tufts of hyphae to larvae in this size range (data accumulated during two days). *Feeding large-intermediate larvae:* workers were recorded as they regurgitated to larvae 3.0–5.0 mm in total length or fed tufts of hyphae to larvae in this size range (data from five days). *Feeding largest larvae:* workers were recorded as they regurgitated to larvae greater than 5.0 mm or fed tufts of hyphae to larvae in the same size range (data from two days). *Assisting ecdysis of larvae into pupae:* licking and pulling the final larval integument from the surface of newly formed pupae (data from three days). *Assisting eclosion of adults from pupal integument:* licking and pulling the old pupal integument from the bodies of emerging adults (data from three days)
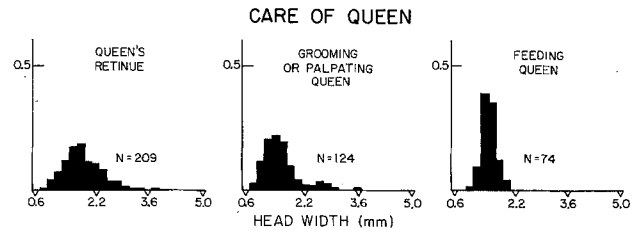


**Fig. 10.** Polyethism curves of queen care. *Queen's retinue:* resting or walking on the body of the queen; this category also includes the workers grooming the queen, for which a separate polyethism diagram is presented to the right (data accumulated during 11 days). *Grooming or palpating queen:* licking the queen with the glossa, touching her with the maxillary or labial palps, or both (data from ten days). *Feeding queen:* presenting queen with either a trophic egg, which is about twice the size of a queen-laid egg and is presumably laid by workers (17 of 29 feedings observed were with trophic eggs) or presenting the queen with a tuft of *Rozites* hyphae (12 of the 29 feedings were with tufts of hyphae) (data from seven days)
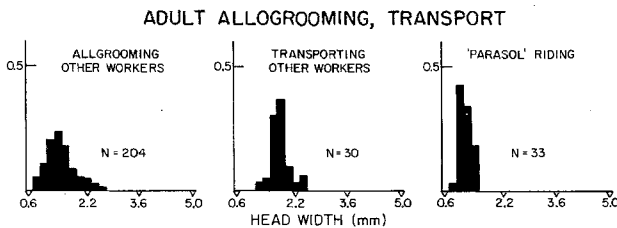


**Fig. 9.** Polyethism curves of adult allogrooming and transport. *Allogrooming other workers:* licking the surfaces of the bodies of other adult workers (data accumulated during six days). *Transporting other workers:* carrying live nestmates bodily (data from four days). *'Parasol' riding:* riding on the 'parasols,' or fragments of newly cut vegetation, being carried homeward by other workers (data from four days)
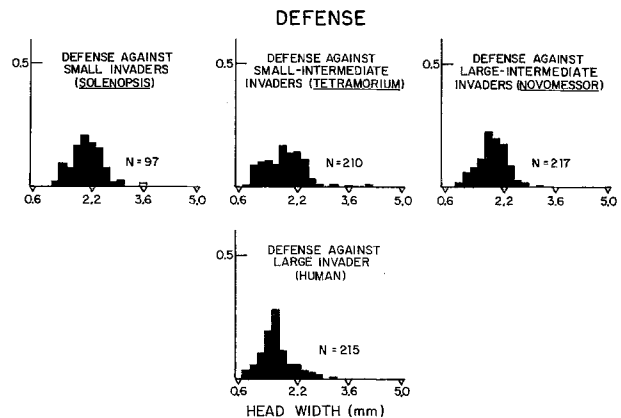


tively wide variety of tasks, including the degradation of vegetation prior to its incorporation into the garden, major reconstruction of the fungus combs, disposal of refuse, transport of other workers, assistance of the brood at ecdysis, and queen care.

*C) Foragers and Excavators.* Centered on head width 2.2 mm: size ensembles of workers that explore, recruit to new vegetation, cut and retrieve the vegetation, and excavate the nest.

**Fig. 11.** Polyethism curves of defense. *Defense against small invaders (Solenopsis):* workers were recorded as they attacked workers of a very small Ecuadoran species of thief ant, S. *(Diplorhoptrum)* sp., placed in the nest chambers; the *Solenopsis* were about the size of the smallest *Atta* workers (data accumulated during eight days). *Defense against small-intermediate invaders:* workers were recorded as they attacked pavement ants, *Tetramorium caespitum,* which are about the same size as small *Atta* workers (head widths 1.2 mm) (data from four days). *Defense against large-intermediate invaders:* workers were recorded as they attacked desert ants, *Novomessor cockerelli,* which are about the size of an *Atta* media worker with head width 2.8 mm (data from one day). *Defense against large invader (human):* I removed the lid of a garden chamber and blew on the comb to stir up the workers thoroughly, then placed my hand on the comb; the ants crawling onto the hand during the first 30 s were recorded (data from one day)

**Table 2.** Modal class of the size-frequency distribution (polyethism curve) according to the task addressed by the workers in the distribution. Information on the location of the task and the frequency of very young (callow) workers is also given

| Modal head width (mm) of the workers addressing tasks | Tasks addressed by the workers | Location of the tasks | Frequency of very young (callow) workers among the workers addressing the task |
|---|---|---|---|
| HW 0.8 mm | Caring for hyphae | Over all fungus garden | > 0.005 |
| HW 1.0 mm | Larval feeding | Brood areas in fungus garden | 0? |
| | Manipulating brood | Brood areas in fungus garden | > 0.027–0.130[a] |
| | Licking substrate | Over all fungus garden | > 0.029 |
| | Implanting hyphae | Over all fungus garden | 0? |
| | Transporting hyphae | Over all fungus garden | 0? |
| | 'Parasol' riding | Outside nest | 0? |
| HW 1.2 mm | Implanting substrate particles | Over all fungus garden | > 0.102 |
| | Carrying eggs and first-instar larvae | Brood areas in fungus garden | > 0.118 |
| HW 1.4 mm | Degrading vegetation, second stage | Over all fungus garden | 0.063 |
| | Reconstructing fungus garden (shared with HW 1.6) | Over all fungus garden | 0.019 |
| | Assisting ecdysis (shared with HW 1.6) | Brood areas in fungus garden | 0.125–0.146[a] |
| | Grooming queen | Vicinity of queen | 0.006 |
| | Feeding queen (shared with HW 1.6) | Vicinity of queen | 0.013 |
| | Carrying small-intermediate larvae | Brood areas in fungus garden | 0.144 |
| HW 1.6 mm | Degrading vegetation, first stage | Over all fungus garden | 0.005 |
| | Refuse disposal | Refuse chambers | 0 |
| | Reconstructing fungus (shared with HW 1.4) | Over all fungus garden | 0.019 |
| | Feeding queen (shared with HW 1.4) | Vicinity of queen | 0.013 |
| | Assisting ecdysis (shared with HW 1.4) | Brood areas in fungus garden | 0.125–0.146[a] |
| | Transporting workers (shared with HW 1.8) | Over all nest and outside | 0 |
| | Defending against large invader (human) | Over all nest | 0.009 |
| HW 1.8 mm | Transporting substrate (shared with HW 2.0 and 2.2) | Over all fungus garden | 0.219 |
| | Defending against small invaders (ants) (shared with HW 2.0 and 2.2) | Over all nest | 0 |
| | Carrying large-intermediate larvae | Brood areas in fungus garden | 0.090 |
| | Transporting workers (shared with HW 1.6) | Over all nest and outside | 0 |
| HW 2.0 mm | Defending against small invaders (ants) (shared with HW 1.8 and 2.2) | Over all nest | 0 |
| HW 2.2 mm | Exploring | Outside nest | 0 |
| | Recruiting | Outside nest | 0 |
| | Cutting vegetation | Outside nest | 0 |
| | Carrying vegetation | Outside nest | 0 |
| | Defending against small invaders (shared with HW 1.8 and 2.0) | Over all nest | 0 |
| | Excavating | In soil next to nest | 0 |
| | Carrying largest larvae | Brood areas in fungus garden | 0.044 |
| HW > 3.0 mm | [Both inside and outside the nest, the very young (callow) individuals among these large media and major workers are relatively inactive. The older workers are virtually limited to defense, at which they are not numerically predominant but nevertheless highly efficient; thus they are considered to constitute part of a distinct physical caste.] | | |

[a]  Range of frequency values according to brood stage

*D) Defenders.* Broadly distributed and entailing more of the large medias and (in larger, free-living colonies) majors in the largest size classes. It is equally valid, and perhaps more consistent with the conventional definition of caste, simply to distinguish all workers over head width 3.0 mm as a specialist group of 'soldiers.'

Clearly there is overlap between not only the polyethism curves within a role cluster, but also to a lesser extent among the role clusters themselves. Individuals of the same size, and even the same individuals, perform multiple functions. However, the probability that a given worker will be engaged in a particular task is a strong function of her size. Furthermore,
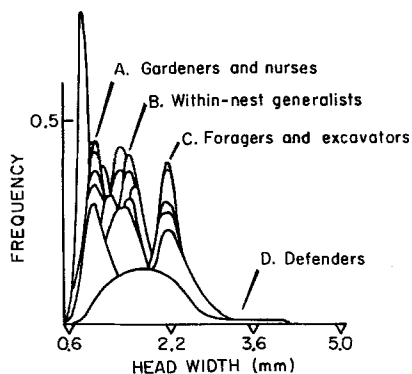
**Fig. 12.** The polyethism curves smoothed by eye and superimposed, showing the partially discretized physical caste system that exists on the continuous size variation of *A. sexdens* workers. Three tasks, transport of brood, transport of substrate, and allogrooming of other workers, have been omitted because of the broad participation of the size classes. The polyethism curves are interpreted as constituting four role clusters, which are labeled *A–D* in the figure. It is also valid to distinguish workers over head width 3.0 mm as a specialist group of 'soldiers,' while recognizing that other size groups also assist in defense. (Further explanation in the text)



**Fig. 13.** The 'assembly-line' processing of vegetation depends on an intricate division of labor among the minor and media workers. Medias gather the vegetation, and a succession of ever smaller media and minor workers process it and use it to cultivate fungal hyphae. The polyethism curves are smoothed versions of the histograms depicted in Figs. 1–3

the physical caste system appears to be partially discretized, in spite of the fact that size varies continuously among workers. The phenomenon is not so strongly marked as that noted earlier in the discretized temporal caste system of *Pheidole dentata* (Wilson 1976b), but its consequence is the same: as size in *A. sexdens* workers increases (parallel to the increase in age among *P. dentata* workers), the workers shift from one *cluster* of tasks to another. The tasks within a cluster are spatiotemporally close to one another. Thus workers in *A* (gardeners and nurses) take care of the substrate particles, the hyphae that grow upon them, and the larvae and other immature forms scattered in cavities through the garden. Workers in *C* (foragers and excavators) are active mostly outside the main nest, where they gather fresh vegatation and excavate new portions of the nest.

By combining the information on the discretized physical castes, summarized in Fig. 12, and the information on frequency of callow workers (Table 2), it is possible to make a first, preliminary estimate of the number of castes in *A. sexdens*. Aside from the queen, the sole reproductive caste, and the larvae, which may serve some as yet unknown trophic function, the colony appears to be divided into four physical castes, of which three (all of the clusters except *D*, the defenders) are further subdivided into at least two ergonomic subgroups according to age, that is, callows versus older workers. The total number of castes, physical plus temporal, is therefore judged to be seven. However, it must be stressed that this is only a rough, preliminary estimate that is likely to
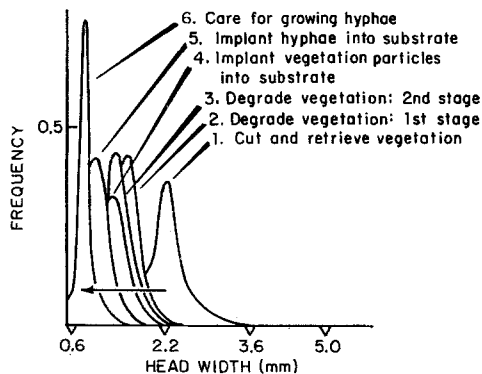
be on the low side. The discretization is only partial, and finer divisions of role clusters might be possible at the lower end of the size scale.

A key feature of *Atta* social life disclosed by these data is the close association of both polymorphism and polyethism with the utilization of fresh vegetation in fungus gardening. The elaborate caste system and division of labor that are the hallmark of the genus *Atta* are an essential part of the specialization on fresh vegetation. And, conversely, the utilization of fresh vegetation is the raison d'être of the caste system and division of labor.

An additional but closely related major feature is the 'assembly-line' processing of the vegetation, in which the medias cut the vegetation and then one group of ever smaller workers after another takes the material through a complete processing until, in the form of 2-mm-wide fragments of thoroughly chewed particles, it is inserted into the garden and sown with hyphae (see Fig. 13).

*Caste Specialization*

Figure 14 A presents still another use of the polyethism data. When the polyethism distribution modes are plotted as a function of size, the maximum diversity of tasks is found to be concentrated not at the lower extreme (head width 0.6–1.0 mm), where the greatest number of workers is concentrated, but nearer the center, in the region HW 1.2–2.2 mm. The same result is obtained when the absolute number
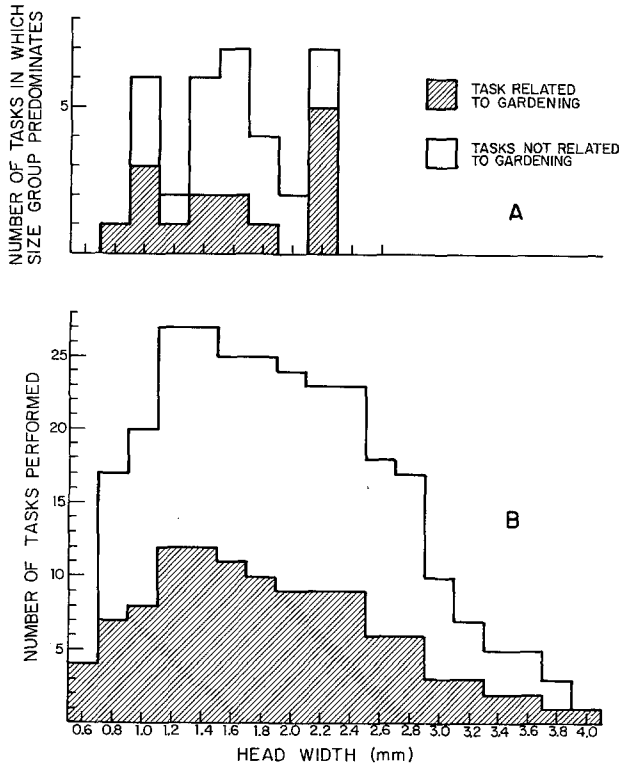
Fig. 14. A The frequency of polyethism curves with modes falling in various size classes. B The frequency of tasks performed by workers in the various size classes



Fig. 15A and B. The relation between worker size and size of pupa carried during brood transport (A) and size of pupa licked and turned over during brood manipulation (B). Pupal transport is an example of a flexible task, and pupal manipulation is an example of a fixed task (see Discussion)

of tasks performed (regardless of the frequency of performance) is plotted as a function of total size (see Fig. 14B). Another way of expressing the result is to note that the extreme size classes, that is, those with HW less than 1.2 mm and greater than about 2.4 mm, are the most specialized.

The polyethism curves reveal that alloethism – the relative likelihood of a particular response as a function of size – is moderate to strong in the great majority of tasks. A particularly striking example of steeply changing alloethism occurs in the gardening behavior of the smallest size classes. Workers of HW 0.6–0.8 mm strongly favor care of the hyphae, but are only moderately interested in the substrate particles. Those of HW 1.0 mm spend a great deal of time working on substrate particles, but are relatively disinterested in the hyphae themselves. Finally, workers at HW 1.4–1.6 mm have little interest in either task.

A point of interest that will be expanded in the Discussion is the difference in the pattern of response with reference to brood manipulation (licking and turning the brood pieces over) as opposed to brood transport. As shown in Fig. 15, only workers within a relatively narrow size range manipulate pupae; this is approximately the same range of workers that feed
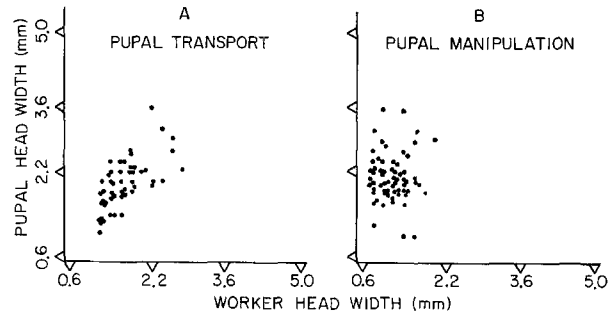
Fig. 15A and B. The relation between worker size and size of the larvae. Workers across a somewhat wider size range carry pupae from one location in the fungus garden to another, or from one site to another during emigration. Of equal interest, the size of the transporter appears to be correlated with that of the pupa being carried.

Although I do not yet have quantitative documentation, the following primary alloethism rule appears to apply also to the general level of activity: the amount of time spent by a worker in motion and attending to tasks is inversely proportional to the size of the worker. The minims (HW 0.6–1.0 mm) are the most active and industrious, while the large medias and majors (HW greater than 2.6 mm) are the least industrious. The intermediate size classes fall between these two extremes in level of activity.

*Analysis of Organ Function*

Figure 16 presents data that can be used as part of a new technique for the physiological analysis of division of labor. I have found that *disproportionate variation in the size of organs as a function of total body size reflects the function of the organs and can thus be used as a first clue concerning the roles of previously unstudied or experimentally intractable organs.* This technique can be especially useful in the study of exocrine glands, the functions of which are often difficult to adduce by ordinary experimental procedures. The method employed is the following. Polyethism curves for all of the colony tasks are derived for most or all of the size variation – on which the physical caste system is based. Then the proportion of the organs of interest is measured relative to body size. Finally, the possibility is considered that tasks performed by size groups with the largest proportional development of the organ are in fact served by
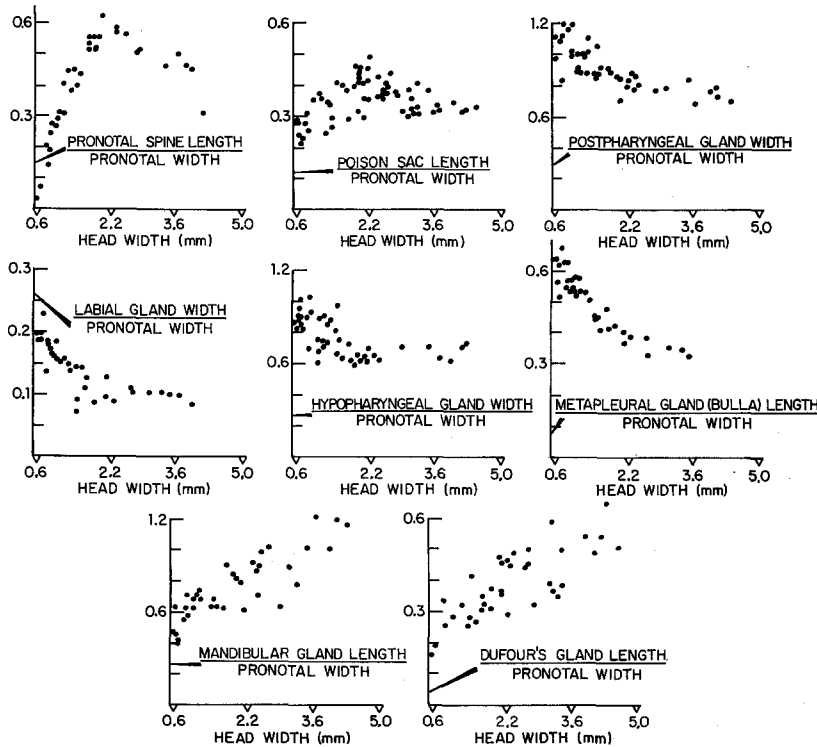
Fig. 16. The relation between worker size and the proportions of selected organs of known and unknown functions. The *caption and vertical axis* of each diagram give the ratio of the size of the organ to the pronotal width, a standard measure of overall body size subject only slightly to allometry. As explained in the text, data of this kind can be used as clues to the functions of problematic organs

the organ. The general validity of the method can be tested by determining whether tasks do match the known functions of the organs that have been successfully deciphered by other means. The hypotheses concerning the functions of hitherto unknown organs can be tested by experiments that attempt to demonstrate those roles indicated by the behavioral repertories of the size groups in which the organs are maximally developed.

This technique appears especially promising in the case of *Atta sexdens*. In every instance where the function of an organ was known among the set of organs chosen for measurement, the organ proved to be maximally developed in the size classes that specialize on the tasks served by the organ. As shown in Fig. 16, the pronotal spines – representative of spination over the entire body – are proportionally longest in the size classes (HW 1.6–2.6 mm) that spend the greatest amount of time foraging outside the nest and hence are exposed most frequently to predators and competitor ants. In larger colonies, the foraging classes fall primarily in the HW range 1.8–2.6 mm. My parallel studies with *A. cephalotes* have shown that in the smallest, youngest colonies the foraging size class is HW 1.6 mm (Wilson, unpublished data). Of special interest is the maximum development of the poison gland sac in the same size range. Independent studies have shown that the sac is used to store methyl-4-methylpyrrole-2-carboxylate, the recruit-

ment trail pheromone of other *Atta* species, and they provide some indirect evidence that the same substance is also used by *A. sexdens* (Tumlinson et al. 1971; Riley et al. 1974; Robinson and Cherrett 1973). Recent tests using artificial trails have confirmed that the poison gland sac is the source of the recruitment trail substance in *A. sexdens* (Wilson, unpublished data). As depicted in Fig. 1, workers in this size range (HW 1.8–2.6 mm) are indeed the ones that do the great bulk of recruitment by means of odor trails. To take another example, the postpharyngeal gland is the source of larval food in species of ants that have been studied in this respect (review in Wilson 1971). And it turns out that in *A. sexdens* the postpharyngeal gland is proportionately largest in the smallest size classes, at HW 0.6–1.2 mm, which include the workers that feed larvae by regurgitation. The metapleural gland produces substances, including phenylacetic acid, that inhibit alien fungal and bacterial growth within the *A. sexdens* nest (Maschwitz et al. 1970). Finally, the mandibular gland is known to produce the alarm substances citral and 5-methyl-3-heptanone in species of *Atta*, including, in at least the case of the methylheptanone, *A. sexdens* (Butenandt et al. 1959; Blum et al. 1968). As shown in Figure 16, it is proportionately largest in the largest size classes of *A. sexdens*, which are specialized for colony defense.

With these relations confirming the utility of the

method, one might consider as a working hypothesis the following general roles for the remaining organs depicted in Fig. 16: the secretions of the labial and hypopharyngeal glands might function in brood care or fungus gardening, while those of Dufour's gland could be used in defense or alarm communication (or both). The technique might also be used to infer the roles of sensory organs. Jaisson (1972), for example, states that the sensilla ampulacea and s. coeloconica of the antennae vary according to worker size in *Atta laevigata*, although he has provided no numerical data.

### Emigration

Finally, an interesting pattern of polyethism was observed during emigrations of parts of the laboratory colony. Absconding from one nest chamber to another was induced on two occasions when I introduced ten *Tetramorium caespitum* workers for studies of defensive behavior. After about 30 min the *Atta* workers began moving back and forth out of the invaded chamber along an odor trail, carrying large numbers of eggs, larvae, and pupae. The size range of the carriers was broad and correlated with the size of the brood object, as illustrated in Fig. 15A. Approximately 1 h later, when almost all of the brood had been transferred, a small number of workers began to tear off pieces of fungus comb and transport this material to the new chambers. The carriers in this case were a peculiar group. As shown in Fig. 5, they were mostly medias with HW 1.6–2.6 mm (mode 1.8 mm), and a very high proportion (21.9%) were callows.

### Discussion

The fungus-growing ants of the tribe Attini are of exceptional interest because, to cite the familiar metaphor, they alone among the ants have achieved the transition from a hunter-gatherer to an agricultural existence. But this major shift did not require an elaborate caste system. The great majority of attine genera and species, including the presumably most primitive forms belonging to *Cyphomyrmex* (see Weber 1972), are monomorphic. As I believe I have demonstrated in the present report, the complex caste system and division of labor of *Atta* represent a much narrower, more idiosyncratic adaptation to the collecting of fresh vegetation as a novel form of fungal substrate. Most of the monomorphic attines utilize decaying vegetation, insect remains, or insect excrement as substrates, in other words, materials ready made for fun-
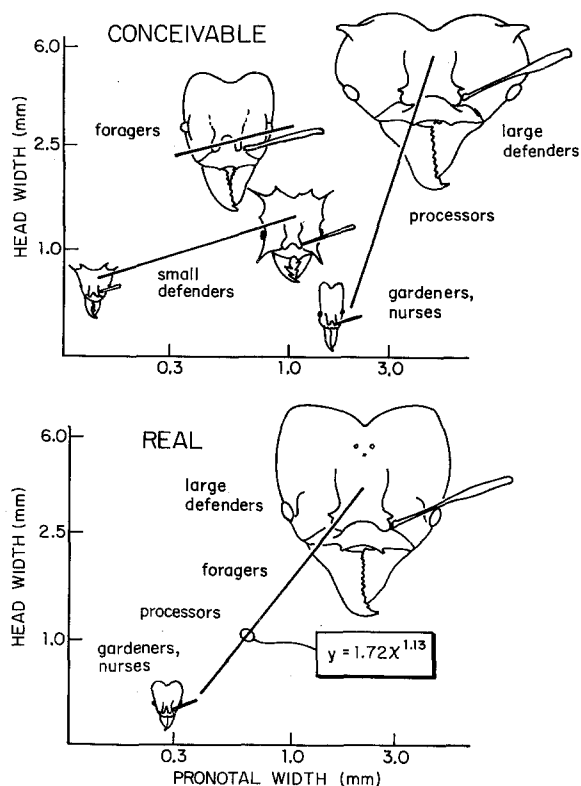


**Fig. 17.** A conceivable array of *Atta* castes compared with the actual array in *A. sexdens*. Ant species conceivably could evolve multiple allometric curves that generate castes precisely fitted to various tasks as illustrated in the *upper, imaginary figure*. However, even in the unusually complex *A. sexdens* system, all ant castes are generated by a single allometric curve for any given pair of measurements; this true situation in *A. sexdens* is illustrated in the *lower figure*. The *curve* shown, for head width as a function of pronotal width, is based on 211 measurements and was fitted by the least-squares method. The more complete formula, with standard deviations of the fitted constants, is $y=1.725$ ($\pm0.006$) $\times$ exp. $1.130(\pm0.008)$. The plot shown is double-logarithmic

gal growth. Fresh leaves and petals, on the other hand, require a whole series of special operations before they can be converted into substrate. They must be cut down, then chopped into fine pieces, next chewed and treated with enzymes, and finally incorporated into the garden combs. The evidence now shows that the most distinctive castes of *Atta* have evolved as specialists to perform successive operations in this processing of fresh vegetation.

As complex as this system is compared with other ant systems, it is still based on surprisingly elementary rules of allometry and alloethism. To make this point clearer, I have juxtaposed in Fig. 17 the properties of the true *A. sexdens* system with those of an imaginary, more complex system that could be generated by only slightly more elaborate rules. Ant species in general and *A. sexdens* in particular have thus been re-

markably restrained in the elaboration of their castes. They have relied on a single rule of deformation to create physical castes, which translates into a single allometric curve for any pair of specified dimensions such as head width versus pronotal width or, as illustrated in Fig. 16, exocrine gland size versus pronotal width. The *Atta* could have created a more complex and precise array of castes by programming an early divergence of developing larval lines along with differing allometry among those lines at pupation, producing the effect illustrated in the upper diagram of Fig. 17. But neither the *Atta* nor to my knowledge any of the many kinds of polymorphic ants have ever done so.

Behavior follows similarly elementary rules. The polyethism curves presented in Figs. 1–11 are all of relatively simple form. They are unimodal and show only limited amounts of skewing. These properties suggest the existence of underlying alloethism functions of fundamental simplicity: for each behavior, a monotonic rise of responsiveness to a peak along the size range is followed by a monotonic decline.

To summarize this part of the discussion, even though *A. sexdens* possesses one of the most complicated caste systems found in the ants, it has not evolved anywhere close to the conceivable (and I believe evolutionarily attainable) limit. There are far more tasks than castes: by my first crude estimate (Table 1) seven castes cover 29 tasks. Furthermore, one can discern another important phenomenon in *A. sexdens* that constrains the elaboration of castes: polyethism has evolved further than polymorphism. That is, the alloethic curves rise and descend more steeply than the size-frequency distributions and they are generally steeper than the allometric curves drawn for any selected pair of physical measurements. As a consequence, ensembles specialized on particular tasks are more differentiated by behavior than by age or anatomy.

As illustrated in Figs. 1–11, *A. sexdens* created its division of labor primarily by greatly expanding the size variation of the workers, while adding a moderate amount of allometry and a relatively much greater amount of alloethism.

With these limitations of *Atta* caste evolution in mind, it is useful to consider the evidences of suboptimality in colonial organization. Since the castes have not been discretized physically, and since size variation is continuous from one extreme to the other, it is quite possible that certain size groups are truly intermediate between groups that contribute maximally to the colony welfare. They may exist only because it is energetically too expensive to build in developmental rules that reduce or eliminate them

(see the formal discussion of the concept of fidelity costs in Oster and Wilson 1978). One such size class could be the workers with HW (head width) 1.4 mm. Unlike those with HW 1.6 mm, these ants are too small to cut fresh vegetation. In beginning colonies of *A. cephalotes,* they are actually less numerous than workers with HW 1.6, which do the first cutting for the little fungus garden; thus in *A. cephalotes* incipient colonies, some adjustment of the size-frequency distribution appears to have been made (Wilson, unpublished observations). The small number of workers of HW 1.4 mm found in the foraging columns have no known role. Other roles played by workers of HW 1.4 mm within the nest, including the later stage of degrading vegetation, are shared prominently with workers of HW 1.2 and 1.6 mm. If all workers of HW 1.4 mm were to be replaced by equal numbers of workers of HW 1.2 and 1.6 mm, it is possible that colony fitness would improve slightly or at least remain unaffected. Another possible suboptimal class consists of the workers of HW 3.0–3.4 mm, which are too large to be energetically efficient leaf cutters (see Wilson 1980), but smaller than and presumably less effective in defense than the largest medias and majors (HW > 3.4 mm).

A related concept suggested by the present study is the distinction that can be drawn between primary and secondary functions of castes. As stressed earlier, the primary role of the increased size variation and moderate allometry of *A. sexdens* is the utilization of fresh vegetation as a fungal substrate. Fine details in allometry and alloethism have been adjusted to accommodate other functions such as brood care and defense. Thus the head of the media worker (HW 1.6–3.0 mm) is ideally suited for scissoring off pieces of vegetation. The heads of large medias and majors, the workers that defend the nest but do not cut vegetation, are nevertheless of the same basic design as those of the foragers, differing mostly in the possession of more massive adductor muscles and mandibular glands. The minor workers (HW 0.6–1.2 mm) with their relatively tiny stature and forceps-like mandibles, are plainly well-suited for fungal care, the single most time-consuming activity of the *A. sexdens* colony. Their role as parasol riders, during which they may be defending the larger foraging workers from parasitic phorid flies (Eibl-Eibesfeldt and Eibl-Eibesfeldt 1967) is evidently secondary. In this sense, the morphological adaptations of the various castes to their secondary roles are probably suboptimal.

Another concept that has emerged during the analysis of *A. sexdens* is the distinction between fixed and flexible tasks. A fixed task is one attended by a relatively limited ensemble of workers, defined by

size or age. Even if the nature of the task is altered
– for example, the objects handled in the performance
of the task may become either smaller or larger –
the same size ensemble ('caste') performs the work.
A flexible task is one in which the ensemble attending
to it is distinctly more variable in age and size compo-
sition; as the nature of the task is altered, the workers
handling it are different in age, size, or both. An
excellent example of this distinction is shown in Fig.
15. The size of workers carrying pupae is strongly
correlated with the size of the pupae, but this is not
the case for workers grooming and turning over pupae
in the brood pile, a task performed principally by
minor workers in the HW 0.8–1.4 mm size class. Ad-
ditional examples of fixed tasks are foraging, vegeta-
tion cutting, substrate processing, fungal care, and
larval feeding. Additional examples of flexible tasks
are egg and larval transport, adult transport, and
defense.

Finally, I wish to introduce a more speculative
but potentially significant concept, the hypothesis of
a primitive caste. We have seen that the *Atta* caste
system is based on an increase in size variation and
allometry fitted primarily to the utilization of fresh
vegetation. Is it possible that one size group is closest
to the ancestral, monomorphic attine species in anato-
my and behavior? No doubt even this segment of
the size range has been modified in evolution to ac-
commodate the new demands of the altered way of
life, yet it would be of interest to learn whether such
a segment exists and to what extent it still bears the
mark of its earlier, more generalist existence. Two
criteria can be applied. The first is the degree of mor-
phological resemblance to less modified, mono-
morphic species in the same genus or tribe. The sec-
ond is the behavioral resemblance to the monomor-
phic species, which can be translated into the total
number of tasks performed by various size groups
in the advanced species as well as their generality.
The primitive caste is expected to resemble related
species and to perform the largest number of tasks,
including especially those that are primitive with ref-
erence to the group of species as a whole rather than
serving the specialization that characterizes the ad-
vanced species.

By these criteria, I would judge workers of about
HW 1.4–1.6 mm to be the primitive caste in *Atta*,
for the following reasons. Workers of about HW 1.2–
1.8 mm more closely resemble such monomorphic at-
tine genera as *Myrmicocrypta, Sericomyrmex,* and
*Trachymyrmex* in size and head shape than do *A.
sexdens* workers outside this size range. And as can
be seen in Fig. 14, the greatest number of tasks are
performed by workers in the size range HW 1.2–

2.4 mm. Moreover, the tasks not related to either
the gathering of fresh vegetation (the specialization
of HW 1.8–2.8 mm) or gardening are the greatest
concern of workers in the size range HW 1.4–1.6 mm.
If any single segment of the total worker size range
were required to continue the life of a colony single-
handedly, workers in the range HW 1.4–1.6 mm
would be most likely to succeed.

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