Queen or Worker, Which is the Original Honey Bee? (Hymenoptera: Apidae)

by

Christopher K. Starr[1]

ABSTRACT

Taking as a starting point the old controversy of whether the queen or worker of *Apis mellifera* represents the ancestral female bee, the question is posed: Which caste represents a greater departure from the primitive condition? A survey of 43 characters shows a somewhat more derived state overall in the queen than the worker. A closer look shows that derived character states more often represent a reduction than an elaboration of complexity. Consistent with their roles within the colony, workers show a general reduction in reproductive characters, while the queen has evolved away from a capacity for all other colony-maintaining activities.

It is now generally recognized that questions of caste are central to the understanding of social insects (Oster and Wilson 1978). These include the role of division of labor in the colony economy, the control of caste differentiation and the evolution of caste. For the honey bee, *Apis mellifera* Linnaeus, the most thoroughly studied insect species, attention to caste dates at least from the work of Aristotle more than 2300 years ago.

Since the general acceptance of Darwin's evolutionary theory, it has often been asked which caste of honey bees represents the solitary ancestral female. This question was especially surveyed by German bee keepers and entomologists earlier in this century, and much of the present essay is rooted in their controversy. There are 3 alternative answers to the question as posed:

1. The queen represents the primitive condition, while the worker is an evolutionary innovation since the origin of sociality.

This view was pointedly set forth by Demoll (1908) mainly on the basis of ontogenetic characters. He concluded that worker

[1]Department of Entomology, University of Georgia, Athens, GA 30602. Present address: Department of Entomology, Smithsonian Institution, Washington, DC 20560.

development includes the stages of queen development and goes beyond these. This necessarily leads to the prediction that no queen features can be derived from features arising at an earlier stage in the worker.

The problem with Demoll's imaginative hypothesis is not that this prediction was falsified by new facts, but that the larger theory on which it rested has not stood the test of time. Haeckel's Biogenetic Law, summarized in the dictum that "ontogeny recapitulates phylogeny", was already in trouble in Demoll's time and is now largely discredited in its original form (Gould 1977).

2. The worker represents the primitive condition.

I am not aware that anyone has taken this position strongly, which is raised here for the purpose of argument. Largely consistent with it is Wagner's (1904) view of the social insect queen as a social parasite of her workers. I have often heard entomologists use this same concept as a biologically realistic heuristic device in thinking about relations between colony mates. This is not quite the same, though, as calling the worker an ontogenetic or evolutionary forerunner of the queen, which evidently has not been taken as very probable.

3. Each caste represents a departure from the solitary female, so that neither is ancestral to the other.

This answer is so clearly in line with modern evolutionary ideas that to state it is to dissolve the controversy in its original form. My intention here is to utilize this conclusion to reformulate the question: Given that neither the queen nor worker is exactly the original honey bee, which has departed more from the primitive condition?

Even during the early German controversy, some participants took this more modern approach, at least with regard to behavioral characters. Weismann (1902) stated that the worker's behavior shows greater overall change. Buttel-Reepen (1915) and later Ribbands (1953) disputed this directly, stating that the worker shows all instinctive responses of the solitary female except for egg laying.

Lukoschus (1956a-c) examined the question in developmental terms, as had Demoll (1908), and concluded that the queen is the product of normal female development, while the worker results from a type of aberrant development peculiar to social insects. He gave special attention to development of the various glands, contending that it is differences in these which account for behavioral differences between castes. For this reason, Lukoschus regarded his treatment as more fundamental than that of Weismann, with whose conclusions his own nevertheless agreed (although he said that they did not). In a recent review of caste

Table 1. Comparison of character states of the queen and worker of *Apis mellifera*. Characters are grouped into general categories and are mostly taken from Demoll (1908), Zander & Becker (1925), Lukoschus (1956a-b), Ribbands (1953), Rembold (1974), Michener (1974), and Butler (1975). An asterisk indicates the apparently more derived character state.

Character	Queen	Worker
Development:		
Cell type in which reared	*special type	horizontal, hexagonal as for male
Fate of brood cell after emergence	*dismantled	retained
Food during development	hypopharyngeal and mandibular gland products only	*honey as well from about day 3.
Food quantity	ample	*reduced
Brain neurosecretion	present	*reduced
Corpora allata	similar to other holometabolous insects, little change after eclosion	*as in other social insect workers, continued enlargement during adult life
Corpus cardiacum	well developed	*reduced, about 1/3 as large in queen
Prothoracic glands	well developed	*reduced
Piping before emergence	*present	absent
Sensation and learning		
Facets per compound eye	*about 4900	about 6300
Position of ocelli	on upper frons	*at top of head
Size of antennal lobes, number of chemoreceptors per antenna	*smaller, about 1600	larger, about 2400
Corpora pedunculata	*smaller	larger

Table 1. Comparison of character states of the queen and worker of *Apis mellifera* (Continued).

Character	Queen	Worker
Brood Care		
Salivary glands	*absent	present
Mandibular glands	*much enlarged, new function in communication	present
Hypopharyngeal glands	*absent or vestigial	large
Postgenal glands	*absent, with at most a vestigial opening	present
Nest construction and maintenance		
Cutting edge of mandibles	with prominent tooth	*smooth
Wax glands	*absent	4 pairs
Cell building behavior	*absent	present
Nest cleaning behavior	*absent	present
Defense and aggression		
Shape of sting shaft	*curved	straight
Barbs on sting lancets	2-5, indistinct	*8-11, prominent
Scent gland	absent	*present
Nest defensive behavior	*absent	present
Tolerance of similar individuals	intolerant	*tolerant of colony mates
Foraging		
Tongue length	*short	long
Shape of paraglossae	primitive	*derived
Crop	simple	*elaborated as the "honey stomach"
Body hairiness	*reduced	well developed
Pollen brushes	*indistinct	well developed, each about 10 rows of long spines
Pollen presses	*absent	present

Table 1. Comparison of character states of the queen and worker of *Apis mellifera* (Continued).

Character	Queen	Worker
Corbiculae	*absent	present
Flight out of nest	*only to mate and swarm	regularly for various purposes
Foraging behavior	*absent	present
Food source communication	absent	*present
Reproduction		
Shape of abdomen	*elongate, narrow	similar to other bees
Ovarioles per ovary	*75-185, avg. about 150	1-30, avg. about 4
Condition of ovarioles	well developed	*atrophied, rarely functional
Spermatheca	well developed	*very small or absent
Accessory glands	large paired	*reduced to a small lobe
Mating behavior	present	*poor or absent
Egg laying behavior	efficient	*often poor

differentiation, Wilde and Beetsma (1982) similarly concluded that the honey bee worker undergoes a more derived form of development.

Any attempt to reach a general answer to the present question, whether in its original or new formulation, must consider as many characters as possible, in order to regard each caste in its entirety. This appears to have been 1 of Buttel-Reepen's (1915) points, and Demoll (1908), despite the weak theoretical underpinnings of his approach, was likewise interested in the whole bee. In the expansive spirit of these 2, then, let us review a range of physical, developmental, physiological, and behavioral characters in which the queen and worker honey bee differ and attempt to say in each case which caste is closer to the ancestral solitary female. Although this latter is no longer with us, we may take the character states common to modern solitary bees as a reasonable approximation of hers.

Table 1 compares the castes for 43 characters in each of which we can fairly designate 1 caste as more derived than the other. In this phenetic treatment we are not concerned with establishing

1 of the 2 states of any character as ancestral to the other. Rather, we are comparing their degree of departure from the ancestral condition, sometimes in different directions. The accessory glands provide a good example of this.

If we simply add up the asterisks in the columns of Table 1, we find the queen more derived in 24 characters and the worker more derived in 19 characters. If all characters are weighted equally, then, the worker is somewhat closer to the putative ancestral female. A closer or broader analysis would not likely change this general conclusion.

What can be said about how the queen differs from the ancestral bee? Michener's (1974) statement that her modifications mostly represent reductions or losses, rather than elaborations, is well supported in Table 1, in which 17 (71%) of her more derived character states are of this type. This is especially clear of behavioral characters which corroborates Buttel-Reepen's (1915) conclusion cited above. The worker likewise shows in a majority of her more derived character states that she has lost more than she as gained. The outstanding exception is the evolution of dances for food-source communication, which seems to be a singular accomplishment of workers.

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