

inoffensive ant *Strumigenys louisianae*) placed in the nest cavities.

(2) High Intensity. Both castes participate. The minor workers seize the intruder, usually by its appendages, and try to carry or to drag it from the nest. They also join the major workers in pushing the invader with their heads and in pinning it to the nest wall by pressing against it with their backs with legs extended. If these techniques do not work, numerous individuals of both subcastes gather around and form a solid plug, trapping the enemy; then, by squeezing and shoving, they gradually force it to the entrance and out of the nest. The major workers are the more effective in this mode of defence. Using its great saucer-shaped head (see Fig. 1) as though it were the blade of a bulldozer, one individual can block and push as effectively as two or more minor workers. Also, the major workers are more persistent once they have been activated, so that they become more heavily concentrated at the site of disturbance. The high intensity mode of defence was elicited in the laboratory by introducing workers of *Tetramorium caespitum*, which are approximately the same size as the *Zacryptocerus* minor workers, and by pushing dissecting needles into the midst of groups of workers.

Curiously, the *Zacryptocerus* showed no signs of using their stings, which are small but well developed. Nor was there any evidence of the employment of chemical defence, although the Dufour's and poison glands are typical in size for myrmicine ants and apparently normally developed. Intruders ejected from the nests invariably were able to walk away unharmed.

**Behaviour of the major workers and queens.** The major workers are very lethargic on almost all occasions except when defending the nest. Unlike the soldiers of *Camponotus (Colobopsis) fraxinicola* and *Pheidole dentata* (Wilson 1974 and unpublished), they are no more effective than minor workers in storing liquid food. This fact was ascertained by depriving a colony of honey for a period of 1 week, weighing a sample of ten minor workers and all of the six major workers, then feeding the colony to satiation for 2 days and weighing again. The average weight gain of the minor workers was 28.8 per cent, while that of the major workers was only 18.3 per cent, essentially the reverse of the situation in *C. fraxinicola*.

The *Zacryptocerus varians* major workers appear to function primarily in defence, and they deserve the title of soldiers. Yet they are

not wholly defensive automata. As indicated in Table I, the major workers sometimes wash and manipulate larvae and pupae. When the nest is broken open and the brood spilled out in the open air, the major workers join the minor workers in retrieving the immature forms. However, they are less effective in this role and retire more quickly to the interior of the nest.

The queens are even less active than the major workers. They are more sluggish than the queens of any ant species I have studied, standing immobile for long periods of time.

Both the major workers and the queens appear to live exclusively by liquid food regurgitated to them by the minor workers.

### Discussion

The six most distinctive features of the sociobiology of *Zacryptocerus varians* are listed in Fig. 2, and the inferred ultimate causations of these features are indicated by sequences of arrows. The key adaptations of the species are judged to be their exclusively arboreal life and their apparent extreme reliance on scavenging. To make the sequences logically complete, the two adaptations are suggested to have been initiated or at least shaped in part by competition from other species of ants specialized for more conventional modes of existence.

The preferred nest sites in dead twigs and branches are exceptionally dry. The *Zacryptocerus* colonies live in cavities that are consistently drier than the nest chambers of ground-dwelling ants, including many species that nest in desert soil. It seems probable that at least two peculiarities, the large size of the eggs and the partial consumption of infrabuccal pellets by the workers, are techniques to reduce water loss.

The 'turtle' defence strategy, which so markedly affects the anatomy of the ants as well as other aspects of their behaviour, is an efficient adaptation in two respects. First, the mandibles of a scavenger species, as opposed to a predaceous one, are likely to be blunt and short, rendering them less effective in defence. Those of *Zacryptocerus varians* have evolved to an extreme in this direction, so that when attacking an intruder the workers are able to do little more than seize a narrow appendage and hang on. As an alternative defence method the species has developed a squat body form with short, robust appendages. When workers are unable to escape more formidable enemies by running and hiding in the many crevices of the plants on which they forage, they can often