

Mueller and Weislo (1998) report an average colony size of 29.4 workers for a mixed sample of *C. longiscapus* and *C. muelleri*. However, when the colony sizes of these nests are recalculated by species, *C. muelleri* nests are found to contain twice as many workers (average  $43.8 \pm 27.57$  s.d. workers; range 6–109; N=106) than *C. longiscapus* nests (average  $22.7 \pm 12.33$  s.d. workers; range 4–58; N=67). This difference in observed nest size may be due in part to sampling bias: Because *C. muelleri* nests possess less conspicuous entrance auricles than do *C. longiscapus* nests (Figs. 8b and 8c), smaller colonies of *C. muelleri* may be less frequently noticed and collected in the field relative to smaller colonies of *C. longiscapus*. However, in a more recent survey of three populations in central Panama where both species occur sympatrically, conducted in June 1998, a special effort was made to locate and collect smaller nests. In this case the average number of workers per nest was  $14.6 \pm 9.73$  s.d. (range 0–40; N=76) for *C. longiscapus* and  $29.4 \pm 24.24$  s.d. (range 4–117; N=42) for *C. muelleri*. Thus, when the problem of size-biased sampling error is addressed and when nests of all sizes are sampled, sympatrically occurring *C. muelleri* nests are found to contain about twice as many workers as *C. longiscapus* nests.

For the subset of colonies with alates reported in Mueller and Weislo (1998), *C. muelleri* averaged 12.4 alates per nest (N=30), whereas *C. longiscapus* averaged only 7.8 alates per nest (N=56), a pattern paralleling the average worker colony-size differences between the two species. At locations where both species occur in mixed aggregations, alates were found in nests of both species during the early dry season (December to February) of 1996, and also during the wet season in July and August of 1997, suggesting temporal overlap of alate production between the two species at these times. However, collections of both species taken at the same sites in June 1998, at the start of the wet season, yielded only a single alate (a male) from 29 nests of *C. muelleri* and 101 alates of both sexes from 72 nests of *C. longiscapus* (Villesen et al., unpubl.). In addition, late dry-season collections from April 2001 yielded only six males from 34 nests of *C. muelleri* and 111 alates of both sexes from 32 nests of *C. longiscapus* (UGM, unpubl.). Although these data are inadequate for drawing firm conclusions, they suggest a scenario of partial reproductive isolation in which both *C. longiscapus* and *C. muelleri* produce alates during the wet season and early dry season (July to February), but in which only *C. longiscapus* (and not *C. muelleri*) produces sexuals during the late dry season and early rainy season (March to June). Additional data are needed from more extensive nest surveys conducted throughout the year, as well as from observations of mating flight times in both species. Pigmentation differences between males of the two species, noted above, may indicate time-of-day separation in alate flight times, a phenomenon known to occur between sympatric, closely related species of *Atta* (Mariconi, 1970; Weber, 1972; TRS and UGM, pers. obs.). Specifically, the lighter pigmentation in males of *C. muelleri* suggests nocturnal mating flights, whereas the darker pigmentation in males of *C. longiscapus* suggests diurnal mating flights.

## Discussion

*C. longiscapus* and *C. muelleri* are obviously very closely related, and are remarkably similar in terms of ecology, behavior, and morphology. The primary morphological differences separating these species suggest a common evolutionary pattern: Relative to *C. longiscapus*, *C. muelleri* appears to be more specialized for cryptic defense. Specifically, the surfaces of the head and alitrunk of *C. muelleri* are smoother and more rounded than are those of *C. longiscapus*. Carinae and tubercles are more reduced and the dorsal profile is less interrupted by sutures and grooves (Fig. 2b). This “streamlined” morphology in *C. muelleri* plausibly reduces the available points of purchase for the mandibles or grasping organs of an attacking, similarly-sized predator (e.g., another arthropod). In contrast to this general trend toward reduced sculpture, but in agreement with the general trend toward more efficient cryptic defense, sculpturing in two features in *C. muelleri* is increased over that found in *C. longiscapus*: the posterior postpetiolar tubercles are produced into teeth (Fig. 3b) and the hind femur is equipped with a pair of ventral carinae, forming a ventral groove, and with a ventral lobe (Fig. 4b). These features, which occur independently in other *Cyphomyrmex* species (Kempf, 1966), serve to protect vulnerable body parts that are commonly attacked by arthropod predators, particularly other ants; specifically, the postpetiolar tubercles protect the point of articulation between the postpetiole and the gaster; the metafemoral groove receives the tarsus and tibia when the leg is folded in the cryptic-defensive posture; and the metafemoral lobe protects the point of articulation between metatibia and metatarsus.

Thus, morphological features of *Cyphomyrmex* spp. in general and of *C. muelleri* in particular suggest adaptations to predation pressure from arthropod-sized predators. Such predation pressure, at least from above-ground (rather than subterranean) hunters, is also suggested by the unusual “auricle” nest-entrance morphology of *C. longiscapus* and *C. muelleri*, which may serve as a partial physical or even chemically protected barrier to surface-raiding arthropods, particular predatory ants. Likely examples of such predators include army ants in the subfamily Ecitoninae, which are known to significantly impact Neotropical ant colonies in general (Schneirla, 1971; Rettenmeyer, 1983; Gotwald, 1995; Kaspari, 1996). Published records of army ant predation specifically on fungus-growing ants other than *Atta* spp. are rare and include no raids on *Cyphomyrmex* spp. (Cole, 1939; Weber, 1945; Schneirla, 1958, 1971; Fowler, 1977; Mirenda et al., 1980; summarized in LaPolla et al., 2002). That the auricle nest entrance could serve to deter the entry of surface-raiding army (and other) ants is suggested by a single observation in Panama in 1996 in which a *Neivamyrmex* sp. raiding column, consisting of many thousands of workers, swarmed past the entrances of two *C. longiscapus* nests. Although many dozens of army ant workers climbed up the outside (i.e., ground-facing) surfaces of the auricles, none ventured onto the auricle rim or onto the frontal (outward) face adjacent to the nest opening (UGM, pers. obs.). If nest-entrance auricle morphology of *C. longiscapus* (Figs. 8a and 8b) is more efficient