

MANDIBULAR WEAR IN *CAMPONOTUS CHROMAOIDES* WORKERS (HYMENOPTERA: FORMICIDAE)

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Abstract *Camponotus* colonies have a worker subcaste, consisting of major and minor workers. This designation is based on the width and height of the head (cephalic index, CI). Performance of tasks by workers results in wear of the mandibular teeth. A sample of workers was taken from a laboratory colony of *Camponotus chromaoides*. The CI was calculated to determine the major (CI 106.9) and minor (CI 83.6) workers. The objective of the study was to document the characteristics and extent of mandibular wear, and to divide the wear into distinct categories. Grade 1: little or no wear, Grades 3 and 5: moderate wear of the teeth, and Grade 7: absence of mandibular teeth. The absence of incisor and molar teeth may benefit rather than diminish foraging tasks of workers.

Key words Mandibular teeth, cephalic index, worker subcaste, foraging, carpenter ants.

INTRODUCTION

The mandibular teeth of insects wear during normal feeding as an immature and adult (Chapman and Boer 1995). Wear can be extensive and the original structure of the mandible may be worn away. This can result in a change in foraging behavior and other tasks. Excessive mandibular wear has been reported in grasshoppers (Chapman, 1964), leaf feeding and predaceous beetles (Raupp, 1985; Wallin, 1988), plant-piercing bugs (Roitberg et al., 2005; DePieri, 2010), leaf-cutter ants (Schofield et al., 2011), and aquatic insect larvae (Arens, 1990). Studies of mandibular wear in wood-infesting insects include investigations of the concentration of metals (Zn, Mn, Ca) in the mouthparts of termites (Stewart et al., 2011). There is little or no information on the mandibular wear sustained by carpenter ants (*Camponotus* spp.).

Camponotus is the largest ant genus with about 1,000 species worldwide; they are an economically important pest in tropical and temperate regions (Dukes and Robinson, 1982; Robinson, 2005). These large ants establish nests in wood or soil, and colonies can have several thousands of individuals (Pricer, 1908). Nest cavities and galleries in wood are excavated by the workers using their large mandibles. Fibrous shavings are removed and pushed out of galleries through openings, or packed into an unused cavity. Galleries are generally excavated in the direction of the wood grain, and in the sapwood portion of the wood. Walls of *Camponotus* galleries are smooth, which is the origin of the common name.

The objective of the research presented here was to document the characteristics and extent of mandibular wear in worker ants of *C. chromaoides*, and to divide the wear into distinct categories or grades based on the absence of mandibular teeth. The potential link between extensive mandibular and changes in foraging tasks is considered.

MATERIALS AND METHODS

Major and minor worker ants were randomly selected from a laboratory colony of *C. chromaoides*; 40 individuals from each of these castes were selected for a total of 80 workers.

Cephalic Index. The head of each worker was removed and the width across the occiput and the height (excluding the mandibles) were measured with an ocular micrometer. These measurements were used to calculate the Cephalic Index (CI) according to the formula: $CI = \text{Head width} \times 100 / \text{Head height}$. The index presented here is the mean.

Mandibular Wear. The mandibles of each worker were removed and the amount of wear was assessed and graded on a scale of 1, 3, 5, or 7. Grade 1 has no noticeable wear and all the teeth are intact, and grade 7 has extensive wear with the absence of all the teeth on the mandible.

RESULTS AND DISCUSSION

Mandible Wear and Cephalic Index

An analysis of variance of the amount of wear indicated that major workers (CI 106.9; range 97.0 to 126.4) had significant more than minor workers (CI 83.6; range 77.0 to 90.7). The right and left mandibles of major workers had significant ($P < 0.05$, $P < 0.001$, respectively) wear to their distal margin.

Mandibular wear has been documented for a variety of plant feeding, scavenging, and predaceous insects. Adult *Camponotus* species feed primarily on liquids. They use their large mandibles to crush solid food to extract liquids, and the mandibles are also used to excavate a nest cavity in soil and/or wood. While performing these tasks the major and minor workers in the colony wear the teeth on their mandibles. The extent of the wear can be graded on a scale based on the loss of mandibular teeth.

Mandible Structure

The mandibles of *C. chromaoides* workers are elongate and uniformly pigmented (Figure 1, A). The length of the mandible from the dorsal condyle to the tip of the incisor tooth (Fig. 1, It) is about twice the width. There are a series of molar teeth (Figure 1, Mt) along the distal margin. The two incisor teeth (Figure 1, It) are prominent and slightly longer than the three molar teeth below. The angle between the incisors and between them and the first molar tooth is about 30°. Right and left mandibles are nearly symmetrical. Because they are not used for grinding food the two sides do not fit into each other and are usually held apart at rest.

The sequence of mandible wear usually begins with changes in the molar teeth; the upper incisor is often the last to show significant wear. This tooth may have a higher level of hardness than the other teeth. Hillerton et al. (1982) reported the incisor tips can have nearly twice the hardness as other parts of the mandible, and Hillerton and Vincent (1982) reported the presence of zinc (Zn), a strengthening metal, in the mandibles of several ant species. Schofield et al. (2002) reported Zn in the mandibles of leaf-cutter ant (*Atta* sp.) workers, and in the mandibles of the odorous house ant, *Tapinoma sessile* (Schofield et al., 2003). The stiffness and thickness at the top edge of *C. chromaoides* mandibles may provide strength and resistance to wear or breaking of the upper incisor.

Mandibular Wear Scale

The wear of the mandibles of the major and minor workers was divided into four categories based on loss of the incisor and molar teeth. The amount of wear was graded on a scale: 1, 3, 5, or 7.

Grade 1 (Figure 1, A). These mandibles show little or no wear of the incisor or molar teeth. There is a 30° groove between the second incisor and the first molar tooth. Individuals with this amount of wear may be recently emerged workers that have not excavated galleries in wood or soil.

Grade 3 (Figure 1, B). These mandibles show wear on all the mandibular teeth. Most or all teeth have rounded tips, some have broken tips. Angle at the base of the incisor teeth is wider than 30°.

Grade 5 (Figure 1, C). Mandibles of these workers have sections without distinct teeth; there are gaps in the row of molar teeth and one or both of the incisor teeth is worn or broken off.

Grade 7 (Figure 1, D). There is little or no evidence of teeth on either mandible. When the incisor tooth is present it is rounded and without a cutting angle. The distal face of these mandibles is straight or a curved ridge, which seems more suited for cutting than for gauging substrates.

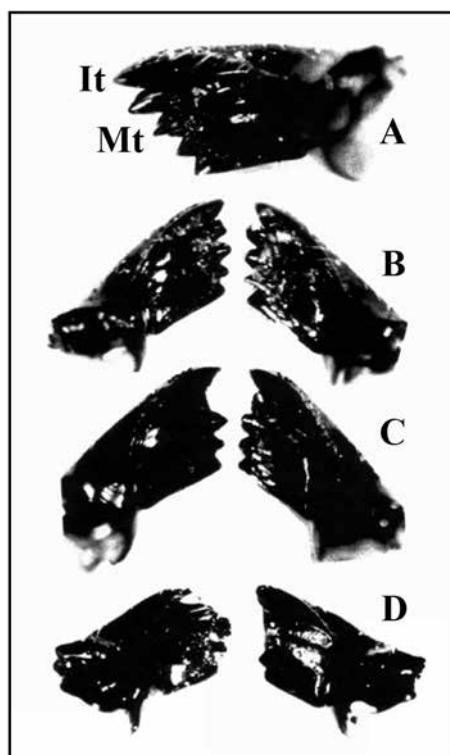


Figure 1. Mandibles of major and minor workers of *Camponotus chromaoides*. It – Incisor teeth; Mt – Molar teeth. Mandible wear scale: A, Grade 1; B, Grade 3; C, Grade 5; D, Grade 7 (major worker).

Mandible Function

The structure of the mandible is generally linked to the type of food the insect eats (Chapman and de Boer, 1995). Predatory species have long mandibles with pointed incisors, and a molar region with teeth for tearing apart prey. Phytophagous species have short mandibles and reduced molar and incisor teeth, which are suited for gouging leaf surfaces and chewing plant fibers (Chapman and de Boer, 1995). The mandibles of some saturniid caterpillars have a combination of teeth and ridges that tear away small fragments of leaf (Bernays and Jansen, 1988). The mandibles of *C. chromaoides*, and probably most *Camponotus* species, are between the predaceous and plant feeding forms. This intermediate form has short incisor and molar teeth that provide the capacity to gouge the surface of wood to create the smooth galleries and the fragments of wood (frass) characteristic of carpenter ant nests (Robinson, 2011).

The extreme mandible wear, Grade 7 (Figure 1, D) in workers in this study, may provide an advantage in dismembering insects and returning parts back to the primary nest site. Grade 7 mandible

wear often results in a smooth edge along the molar margin after the teeth have eroded or broken off. This type of continuous ridge enables *Heterocampa obliqua* caterpillars to cut segments out of leaves, and enables the carabid, *Elephrus cupreus* to cut and remove fragments of prey.

Tasks and Tools

Pricer (1908) reported that the initial tasks of the major workers of *C. pennsylvanicus* and *C. chromaoides* (as *C. ferrugineus*) were primarily inside the nest and involved caring for brood and perhaps gallery excavation. However, Fowler and Roberts (1980) observed major and minor workers foraging away from a *C. pennsylvanicus* nest. They reported that minor workers primarily tended aphids for honeydew, while major workers foraged on the ground and in trees for insects. This change in task from housekeeping to foraging may reflect a change in the tools (mandibles) the workers have. Mandibles may not be effective in maintaining and extending galleries in wood when they are worn and lack sharp teeth. Schofield et al. (2011) reported that leaf-cutter ant (*Atta cephalotes*) workers with 10% mandibular wear switched their foraging task from leaf cutter to leaf carrier.

Instead of wear resulting in reduced utility of major and minor workers, it may increase foraging efficacy when they transition from being inside the nest to outside. When wear reaches Grade 5 and 7 (Figure 1, C, D) mandibles may be better suited for slicing pieces of insect prey than gouging wood in galleries. While forage on the ground or in trees they may encounter disabled insects and can carve out pieces of flesh to be returned to the nest.

Foraging worker from a nest of *C. pennsylvanicus* carried parts of cicadas, plant bugs, beetles, and wasps (Fowler and Roberts, 1980). Cutting the cuticle and flesh of these insects may be more effective using mandibles with an edge than mandibles with teeth.

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