

Pollen Eating, Storing, and Spitting by Ants

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A number of insects feed on pollen, but there are only a few, mainly episodic, records of pollen-eating ants. Worker ants do not fly and can reach only a limited number of flowers. We report here on a group of neotropical ants relying largely on pollen for their food. These ants walk short distances only and compensate for their incapacity to visit many flowers by licking wind-transported pollen from leaves. Pollen is regularly stored in the foregut as reserve and regurgitated to nestmates as food, and indigestible pollen membranes are disposed of outside the nest. We explain in this way the enigmatic production of "infrabuccal pellets" repeatedly described in the literature and thought until now to be a water retention mechanism. We show that storing of pollen in the crop is enabled by a sophisticated filtering mechanism of the alimentary canal.

There are only three published, explicit mentions of pollen-eating ants. All of them refer to two species of *Zacryptocerus*: *Z. texanus* [1, 2], confined to Texas and Nuevo León in Mexico and *Z. rohweri* [3], recorded from Arizona and from Sonora in Mexico. Together these two species are the two northernmost representatives of a tribe of neotropical ants (Cephalotini) currently containing 137 species in three genera.

We observed several Cephalotini in the field and kept laboratory colonies of the following seven Brazilian species: *Cephalotes atratus* (Linnaeus), *Zacryptocerus clypeatus* (Fabricius), *Z. pusillus* (Klug), *Z. angustus* (Mayr), *Z. borgmeieri* (Kempf), *Z. targionii* (Emery), and *Z. pallens* (Smith). All showed a marked prefer-

ence for (some species of) pollen among a variety of diets offered.

Under natural conditions most Cephalotini nest in dead parts of trees and walk slowly and over short distances only, rendering improbable an efficient exploitation even of the pollen produced by the tree that they inhabit. Foragers patrol and lick pollen from leaves [2, 3]. Our laboratory colonies systematically refused pollen kneaded by honeybees and pollen from ornamental flowers, which may suggest a preference for wind-dispersed pollen.

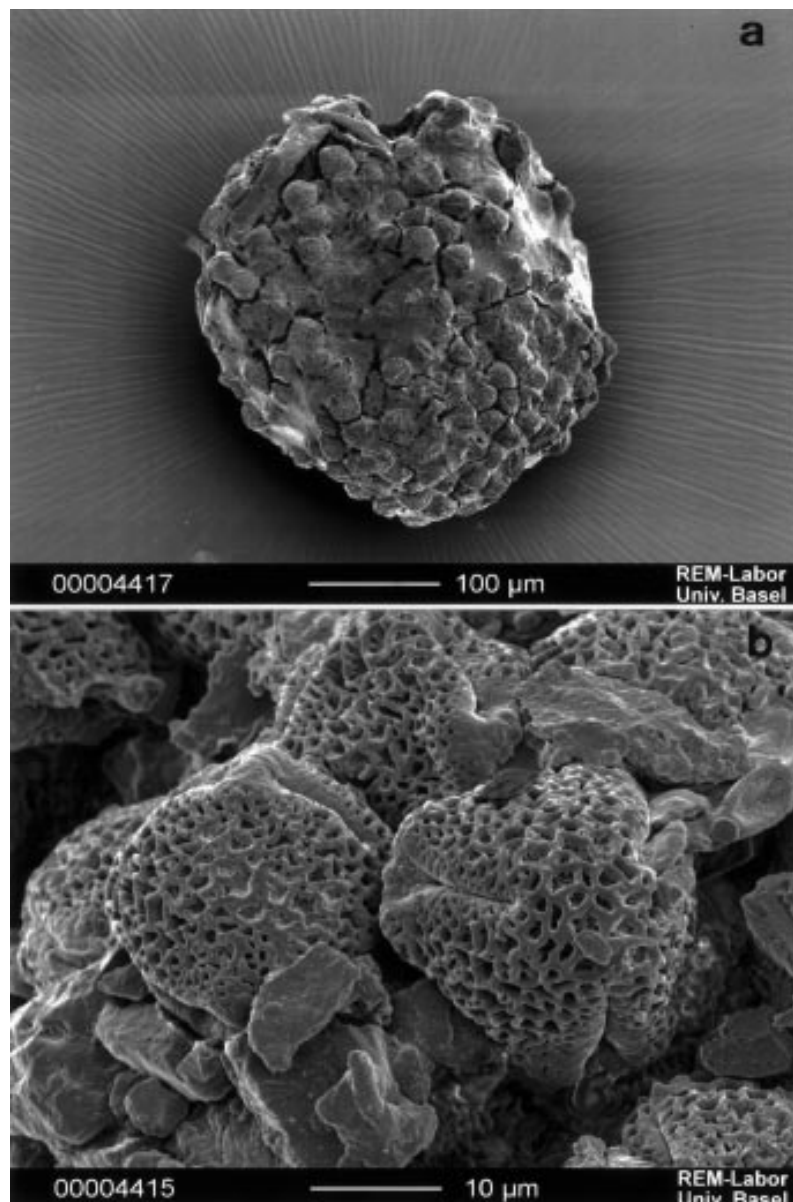


Fig. 1. a) Buccal pellet rejected outside the nest by *Cephalotes atratus*. b) Detail of the same showing unequivocal grains of pollen of *Hedera helix*

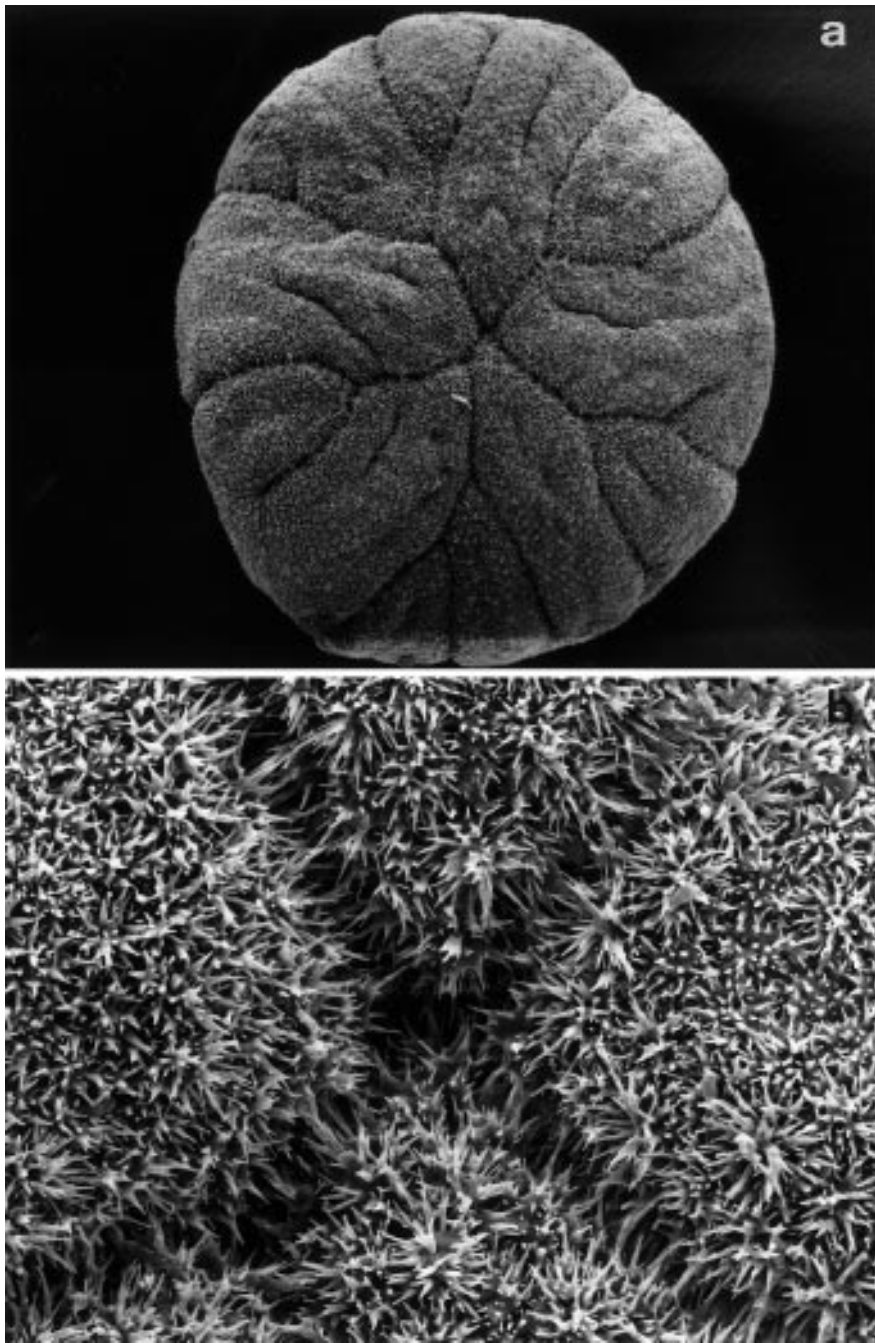


Fig. 2. a) *Zacryptocerus pusillus*, luminal surface of the proventricular bulb after removal of the proventricular shield. b) Detail of the pollen filtering bristles

There are several records of Cephalotini producing “infrabuccal pellets” [4] of doubtful nature. These pellets are stored in the foregut and are either chewed by the ants themselves [5, 6], or offered to larvae [3, 5, 6] or other workers [6], or dropped outside the nest [5, 7]. Ant males do not forage

outside the nest, and in our laboratory colonies they also receive pellets from workers. Considering that apparently similar pellets have been reported for other arboreal ants, it has been suggested that the pellets represent a water conservation device [5, 6]. The same water conservation hypothesis

has also been used to explain the contrary, i.e., the fact that pellets have been not observed in some species [8]. SEM examination of cephalotine pellets revealed that they are packages of nearly intact pollen grains (Fig. 1). The Cephalotini do not have bacteria capable of hydrolyzing cellulose in the intestine [9], a fact suggesting that indigested pollen should be found in the gut. We searched for pollen in the mid- and hindgut of all laboratory species and of others collected in the field, but in vain. At the junction of fore- and midgut adult Cephalotini possess a peculiar proventriculus, the morphology of which is only partly understood, and the precise function of which remains unknown [10–12]. Seen from the luminal surface, the bulb resembles a spherical cushion with radial infoldings, covered with pointed cuticular structures described as star-shaped folds [10], broom-shaped hairs [11], or tree-shaped spines [12] (Fig. 2). The bulb is made out of irregular septa associated with longitudinal and circular musculature (Fig. 3). The longitudinal and circular musculature, by working independently in free haemocoel within each septum, allows independent motion of the septa probably resulting in a greater efficiency and better regulation of the pumping function common to all Hymenoptera.

Our efforts to obtain SEM images of the cuticular structures over the septa failed until we realized that they are covered by a hard, transparent sheath nearly invisible under strong illumination. We believe that this corresponds to the “dry food” which Emery in 1888 [11], had to remove in order to see the broom-shaped hairs. The sheath is visible in previously published micrographs [12], but it has not been described, and no hypothesis on its function has been formulated.

Histological sections proved the sheath to be a cap composed of a cuticular layer of variable thickness, traversed by perpendicular canals, and covered by a thin, external layer of epidermal cells. It is connected to the crop, and it completely embraces the proventriculus, making possible a filtering of particles between its internal surface and the moving spines on the proventriculus. We suggest the term

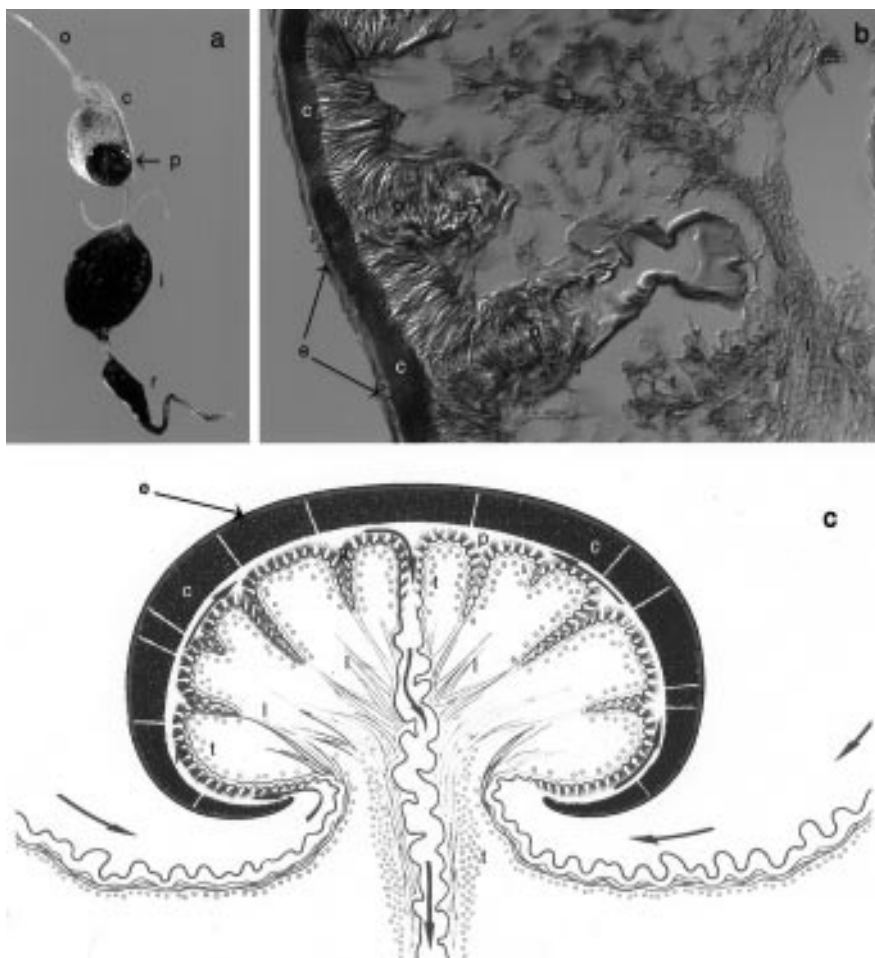


Fig. 3. a) Alimentary canal of *C. atratus* showing the oesophagus (*o*), the crop (*c*), the proventriculus (*p*) seen in transparency within the crop, the ileum (*i*) and the rectum (*r*). b) Detail of a longitudinal section of the proventriculus of *Z. clypeatus* displaying the proventricular shield composed of a cuticular layer (*c*) with its epidermal cells (*e*), the septa with longitudinal (*l*) and transverse muscles (*t*) in large, empty spaces, and the pollen filtering bristles (*p*). c) Schematic reconstruction of the cephalotine proventriculus in longitudinal section, lettering as in b). Curved arrows, the flux of liquid nutrients from which intact pollen grains are excluded. The shield is attached to the bulb by pillars omitted from the drawing

“proventricular shield” for this sheath. This structure, by preventing transfer of solids to the midgut, allows efficient packing of pollen in the foregut for transmission to nestmates when undigested and for elimination through the mouth after digestion. The nutrient-rich internal part of the pollen is presumably digested through the pores of the pollen membrane as in honeybees [13]. In honeybees, the pollen passes through the whole intestine and is excreted through the anus [14]. After reaching the midgut it can

no longer be regurgitated to nestmates. The honeybee proventriculus likewise has an important musculature moving independently four lips armed with a fine comb of hairs [15] but no shield. It is generally accepted that these structures “indicate the remarkable superiority of this organ in the honeybee” [14]. The honeybee proventricular organization, under normal circumstances, allows retention of pollen in the crop for ca. 3–12 h [16]. Our laboratory colonies of Cephalotini, when fed exclusively with a sugar solution, continued regurgitating pol-

len pellets for weeks after they had been collected in the field.

Regurgitation of liquid food from the foregut is widespread in ants. We explain the presence of the unique proventricular shield and filtering bristles of the Cephalotini by the need to collect and transmit to nestmates a solid food available only in microscopic particles. The cephalotine mechanism allows storage and better exploitation of a protein-rich and virtually unlimited resource of food: wind-transported pollen. This adaptation may account for the species richness of these noncompetitive and nonaggressive ants in the neotropical region.

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1. Creighton, W.S.: *Psyche* 70, 133 (1963)
2. Creighton, W.S.: *Psyche* 74, 34 (1967)
3. Creighton, W.S., Nutting, W.L.: *Psyche* 72, 59 (1965)
4. Wheeler, W.M., Bailey, I.W.: *Trans. Amer. Phil. Soc.* 22, 235 (1920)
5. Wilson, E.O.: *Anim. Behav.* 24, 354 (1976)
6. Cole, B.J.: *Ins. Soc.* 27, 265 (1980)
7. Wheeler, D.E.: *Psyche* 91, 171 (1984)
8. Corn, M.L.: Thesis, Cambridge: Harvard University 1976
9. Yurman, D., Dominguez-Bello, M.G.: *Folia Microbiol.* 38, 515 (1993)
10. Forel, A. *Bull. Soc. Vaud. Sci. Nat.* 15, 337 (1878)
11. Emery, C.: *Z. Wiss. Zool.* 46, 378 (1888)
12. Caetano, F.H.: *Papéis Avulsos Zool.* 35, 257 (1984)
13. Whitcomb, W. Jr., Wilson, H.F.: *Agric. Exp. Sta. Univ. Wisconsin, Res. Bull.* 92, 1 (1929)
14. Bailey, L.: *Proc. R. Ent. Soc. London* 29, 119 (1954)
15. Snodgrass, R.E.: *Anatomy of the honey bee*. Ithaca; Comstock 1956
16. Bailey, L.: *J. Exp. Biol.* 29, 310 (1952)