

known, although most of the food requirements of the colony is probably provided by the symbiotic mealybugs in the form of honeydew (Buschinger et al., 1994). The ants rarely prey on insects outside the nests, whereas the other two species, *T. attenuata* and *T. nitida*, as well as *T. PSW-71* (the latter not having the bacterial pouch) were seen foraging on twigs and leaves for honeydew and small insects as is usual for most arboreal ants.

The reason for the presence of a very conspicuous culture of bacteria in the digestive system of these species is unknown. In general, bacterial microorganisms in social insects have been regarded as endosymbionts that play a role in the digestion of food compounds that the insect otherwise would not be able to use for its metabolism, or provide them with vitamins and other essential substances. We suppose that the bacteria could somehow recycle the nitrogen from uric acid which the Malpighian tubules release into the bacterial pouch, similar to the suggestions of Koor (1968) with respect to bacteria in the 'mixed segment' in certain termites. The well developed microvillar border as well as the presence of the intracellular vesicles may be indicative for a transportation function of this kind. Further studies on the precise dietary characteristics in these *Tetraponera* species will be needed.

Apart from the functional significance of the bacterial presence in various *Tetraponera* species is the very peculiar pouch organ in which these microorganisms occur. In contrast to all other social insects that contain bacteria in the digestive tract, the pouch in *Tetraponera* is a separate organ that can be considered a blind lateral extension of the main digestive tube, but that does not form part of the main trajectory the food follows. In cephalotine ants, the bacterial and fungal symbionts occur in the posterior region of the midgut and the anterior region of the intestine (Caetano and Cruz-Landim, 1985, 1987), where they are in direct contact with the passing food material. Even in many of the higher termites, that harbour their bacterial endosymbionts in a structurally complex mixed segment tube (Koor, 1968; Noirot and Noirot-Timothee, 1969), these microorganisms are still found in a part of the main lumen of the digestive tract.

The pouch in *Tetraponera* therefore represents a sheltered area, that moreover displays a fairly complex structural organization. A very obvious feature that is already externally visible is the extensive tracheal supply, of which histological observation reveals that tens of narrow tracheolar tubules penetrate into the lumen of the pouch, where they are entirely surrounded by the numerous bacteria. The penetrating branches appear to be formed by naked tracheoles that have lost their tracheolar cell lining, and become surrounded by the epithelium of the distal ectodermal epithelium only. The occurrence of such naked tracheoles has also been observed in other organs that are penetrated by tracheae, such as the rectum and flight muscles (Noirot and Noirot-Timothee, 1982). The close structural association between the bacterial mass and tracheoles is indicative for

an active metabolism that goes along with a high oxygen consumption. The bacteria show a very peculiar arrangement as they make contact with the tracheolar strands with their long axis perpendicular to the tracheoles, thus allowing a maximal number of bacteria to be in touch with the tracheoles. A similar organization of bacteria with a perpendicular orientation towards the rectal wall was also described in overwintering honeybee workers and in meliponine bees (Cruz-Landim, 1972, 1990), and towards the specialized part of the ileum in *Cephalotes* ants (Caetano, 1989).

The occurrence of a belt-like epithelial fold that connects the proximal and distal parts of the pouch to the best of our knowledge represents a unique structure in social insects. The 'mixed segment' in many of the higher termites equally contains two different epithelia (Koor, 1968), but the contact between these occurs in an oblique way and therefore is not as abrupt as in the *Tetraponera* pouch. The contact region between the two epithelia is the more interesting as the proximal microvillar epithelium has a mesenteric, endodermal origin, whereas the cuticle-lined distal epithelium is as an ectodermal formation. This ectodermal part appears as a distal cap that has no structural contact with any other ectodermal part. This peculiar organization inevitably must be the result of a complex ontogenesis, the understanding of which will require a study of the pouch development in the pupal or larval stage. Of special interest is the opening of the Malpighian tubules into the pouch at the proximal, endodermal part of the belt. Noteworthy in this regard is an early study of the digestive tract in ant larvae by Bonavita-Cougourdan and Poveda (1972). Although not dealing with any pseudomyrmecine ants nor with a pouch structure, this study reports on the complex junction of the endodermal midgut and the ectodermal hindgut during ontogenesis. In this case, the Malpighian tubules appear associated with the ectodermal hindgut part, which is in contrast to the unique situation in the *Tetraponera* pouch.

With respect to the occurrence of the bacterial pouch among the Pseudomyrmecinae, it is interesting that we found it in a couple of species belonging to a particular clade in the phylogenetic tree published by Ward (1991). It lacks in species belonging to other clades, such as *Tetraponera* PSW-71, *T. modesta* and *T. pilosa*, as well as in *Pseudomyrmex mexicanus* and *P. pallidus* (Buschinger et al., 1994), though as yet only very few species have been checked for its presence.

### Acknowledgements

We are very grateful to D. Corstjens and J. Cillis for their professional help in tissue preparation. P.S. Ward (Davis) kindly identified the *Tetraponera* species, and commented on the presence of the bacterial pouch in a particular clade of the Pseudomyrmecinae. D. Kramer (Darmstadt) helped to