Bacterial Ectosymbionts which Confer Motility: *Mixotricha paradoxa* from the Intestine of the Australian Termite *Mastotermes darwiniensis*

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Dedicated to Prof. Dr. Karl Otto Stetter on the occasion of his 65th birthday

1 Introduction

Because of their intestinal flora, termites are among the most important wood- and litter-feeding insects (Wood and Sands 1978; Abe et al. 2000; König and Varma 2005). The gut microbes play an indispensable role in the digestion of food. The dense gut microbiota can include a variety of prokaryotic and eukaryotic microorganisms from different systematic positions (König et al. 2002; Chap. 3). Due to the interesting microbial symbionts and their ecological importance in the global carbon cycle, termites have attracted the interest of many scientists from different disciplines.

Flagellates from the intestine of termites have branched off very early in the evolution of the eukaryotes. These species seem not to occur elsewhere in nature except in wood-eating roaches of the genus *Cryptocercus*. All protozoa of the termite gut belong to the oxymonads, trichomonads, and the hypermastigotes (Fig. 5.4; Honigberg 1970; Yamin 1979; Radek and Hausmann 1993; Viscogliosi et al. 1993; Berchtold and König, 1995; Brugerolle and König 1997; Dacks and Redfield 1998; Keeling et al. 1998; Kitade and Matsumoto 1998; Moriya et al. 1998; Ohkuma et al. 1998; Fröhlich and König 1999b; Brugerolle 2000; Brugerolle and Lee 2000a,b; Delgado-Viscogliosi et al. 2000). From 205 examined termite species, 434 species of flagellates have been described until 1979. The flagellates occur in high number in the paunch (10^3–10^7) and they can occupy more than 90% of the paunch volume (Berchtold et al. 1999). Only three species of the flagellate flora have been obtained in culture: *Trichomitopsis termopsidis* (Yamin 1978, 1980), *Trichonympha sphaerica* (Yamin 1981) from *Zootermopsis* sp. and *Trichomitus trypanoides* from

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Reticulitermes santonensis (Berchtold et al. 1995). Whether lower termites obligatory depend on the flagellates is a matter of debate. We observed several colonies of *Zootermopsis angusticollis* and one colony of *Kalotermes flavicollis*, which lived without flagellates.

The microbiota is not distributed randomly in the gut, but play certain roles in the degradation of lignocellulose and occupy distinct microhabitats. Electron microscopy studies of termite guts have shown that prokaryotes occur either suspended in the contents, located within or on the surface of flagellates, or they are attached to the gut wall (Breznak and Pankratz 1977; Czolij et al. 1984, 1985, 1986; König er al. 2002).

2 The Intestinal Microbiota of *Mastotermes darwiniensis*

The lower wood-feeding termite *Mastotermes darwiniensis* Froggatt (Fig. 5.1.) is the only living member of the family Mastotermitidae. Today, this species is restricted to Northern Australia, but mastotermitid fossil specimen from the Eocene and Miocene have been found in Central America, the Caribic region, Europe, and Australia (Thorne et al. 2000). Termites are assigned to 13 families and 282 genera (Table 5.1; Myles 1999). *Mastotermes darwiniensis* is believed to be the most primitive existing termite species (Gay and Calaby 1970). *Mastotermes darwiniensis* developed a complex symbiotic hindgut flora, which consists of protozoa (formerly named Archaezoa; Cleveland and Grimstone 1964; Brugerolle et al. 1994; Berchtold and König 1995; Fröhlich and König 1999a,b), Bacteria (Berchtold and König 1996; Berchtold et al. 1999), Archaea (Fröhlich and König 1999a,b) and yeast (Prillinger et al. 1996; Schäfer et al. 1996). Defaunation experiments showed that the protozoa appeared to be essential for the termites survival (Veivers et al. 1983). In amber containing the Miocene termite *Mastotermes electrodominicus*, a 20-million-year-old fossil microbial community consisting of protists, spirochetes, and other bacteria has been observed (Wier et al. 2002).

Despite their small volumes of about 0.5–10 µl, the hindguts of termites are morphologically complex systems. The digestive system of termites consists of the foregut with the crop and the gizzard, the midgut and the hindgut (Noirot and Noirot-Timotheé 1969; Noirot 1995). The hindgut consists of five segments (P1–P5): the proctodeal segment, the enteric valve, the paunch, the colon and the rectum. The paunch is the microbial fermentation chamber, but the colon also contains microorganisms. Some higher termites possess a