

Table 3. The four social parasites of *Leptothorax acervorum*
A linear evolutionary order cannot be established

	<i>L. acervorum</i>	<i>D. kutteri</i>	<i>D. goesswaldi</i>	<i>D. pacis</i>	<i>H. sublaevis</i>
Life habits	Independent, facultatively polygynous	Inquiline, facultatively polygynous	Parasitic, kills host queens, monogynous	Parasitic, sterilizes (?) host queens, monogynous	Dulotic monogynous
Morphological similarity	1	2	3	4	5
Karyotypes	n=13 (1)	n=23 or 25 (3)	n=ca. 28 (5)	n=26 (4)	n=20 (2)
Interspecifically effective ♀ sex-pheromone		x-----x		x-----x	
Hybridization possible		x-----x		x-----x	
<i>L. acervorum</i> : Host species (for <i>H. sublaevis</i> also <i>L. muscorum</i> and <i>L. gredleri</i>), <i>Doronomyrmex goesswaldi</i> , <i>D. kutteri</i> , <i>D. pacis</i> : Workerless parasites, <i>Harpagoxenus sublaevis</i> : Slave-maker.					

they all, according to EMERY's rule, should be closely related to the host species, and thus also among each other. Morphological, karyological and ethological evidence support this assumption (Tab. 3).

1. *Harpagoxenus sublaevis* is an actively dulotic species with a life history similar to that of *Chalepoxenus*, except for a different fighting technique: With secateur-like mandibles it cuts off the appendages of the host species workers when invading a colony for slave-raiding, or colony foundation. Apart from *L. acervorum* which is the most frequent host species, also *L. muscorum* and *L. gredleri* are enslaved.

A closely related North American species, *H. canadensis*, has a number of ill-defined slave species belonging to the *L. muscorum*-complex (BUSCHINGER 1966, 1968; BUSCHINGER et al. 1980; STUART and ALLOWAY 1983).

2. *Doronomyrmex kutteri* is a typical inquiline; it is workerless, and usually several reproductive queens coexist with the *L. acervorum* queens in a nest. Morphologically, *D. kutteri* has few particularities, it closely resembles the host species (BUSCHINGER 1965; ALLIES et al. 1986).

3. *Doronomyrmex goesswaldi* for a long time was believed also to represent a workerless inquiline living together with the host queens in polygynous *L. acervorum* colonies (BUSCHINGER 1974b). Recent field and laboratory results, however, revealed that the *D. goesswaldi* queen, soon after mating in August, penetrates a host colony, and during the next spring, while developing fertility, she slowly kills the colonies *L. acervorum* queens by cutting off their appendages. *D. goesswaldi*, thus, follows a similar strategy as *Epimyrmica* which throttles the host queens to death. No *goesswaldi* workers, however, are produced, and the species therefore is not a slave-maker (BUSCHINGER and KLUMP 1988). It may be termed a "murder-parasite" in the sense of FABER (1969).

4. *Doronomyrmex pacis* apparently represented a third inquiline of *L. acervorum*. It is usually found coexisting with host species females which, when dissected, prove to be inseminated, and corpora lutea in their ovaries show that they are, or at least were, functional queens. Often also host species sexuals are produced alongside of the parasites' offspring (BUSCHINGER 1971; BUSCHINGER et al. 1981). Recent observations of two colonies, however, revealed that the *acervorum* queens in nests infested by *D. pacis* apparently have a quite reduced fertility, without being physically damaged (BUSCHINGER unpubl.). Host species sexuals are reared for one or two years after the invasion of a colony by