18 Biological and Systematic Relationships of Social Parasitic *Leptothoracini* from Europe and North America

A. BUSCHINGER

Fachbereich Biologie, Zoologie, der Technischen Hochschule, Darmstadt, West Germany

Abstract: The biological and systematic relationships of European and North American *Leptothoracini* are described with special reference to the systematic position of the social parasitic species. Biological, ecological, ethological, and cytological methods revealed new aspects of relationships among the social parasites and between them and their host species. These relationships, established or presumed, are summarized in Fig. 1.

INTRODUCTION

The ant tribe *Leptothoracini* is, as all myrmecologists know, a group of ants whose systematics is in great confusion. Our main task is to elucidate the origin and evolution of social parasitic ways of life, and we therefore must concern ourselves with the systematics of these ants. I believe that the results of our studies reveal important new characters which may help to develop, in the future, a sound systematic basis for all the tribe. The comparison of related species from the two continents of Europe and North America has considerably advanced our conceptions of the *Leptothoracini* system. The social parasites are especially appropriate for such studies because they exhibit, apart from the ordinary characters of

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independent ants, a number of additional morphological and behavioural attributes which may help to explain relationships both with the host species and among the parasites themselves.

THE SOCIAL PARASITIC *LEPTOTHORACINI* AND THEIR HOSTS

Table I lists known social parasitic and independent *Leptothoracini* and their host–parasite relations. In this table the more familiar and older established names have been used to avoid confusion.

First, we have a number of *guest ants*, known in Europe under the genus name *Formicoxenus*, and living within the nests of *Formica* species. In North America there are two species: so-called *Leptothorax* (Buschinger, 1979a), all with essentially the same biology, and *Leptothorax provancheri*, living as a guest ant with *Myrmica* species. Secondly, there is a group of *workerless, permanently parasitic* species. In Europe we have *Doronomyrmex pacis*, *Leptothorax kutteri*, and *L. goesswaldi*, all living in queenright colonies of *Leptothorax acervorum* and clearly akin to this species. In 1977 I found a parasitic species in Canada which I described as *Doronomyrmex pocahontas* (Buschinger, 1979b), living in colonies of a so-called *Lept. muscorum*. The host species of all this group belong to the subgenus *Mychothorax* Ruzsky, or (following M. R. Smith, 1950) the subgenus *Leptothorax*. The North American *Leptothorax minutissimus* (Smith, 1942), with a similar mode of life, belongs to another subgroup of the genus *Leptothorax*. It parasitizes *Lept. curvispinosus*, a member of the subgenus *Leptothorax* s. str., or *Myrafant* sensu Smith. All the other social parasites are slavemakers, or can at least be suspected to be dulotic.

The well-known genus *Harpagoxenus* is represented by *H. sublaevis* in Europe and *H. canadensis* in North America. Both species, and supposedly also Mongolian *H. zaisanicus*, make slave raids on species of the subgenus *Mychothorax*. On the other hand, *H. americanus*, from North America, shows certain differences compared with *sublaevis* and *canadensis* and enslaves workers of three species of the subgenus *Leptothorax/Myrafant*. Until now, *H. americanus* was considered to belong to the genus *Harpagoxenus*, thus being more closely related to *Mychothorax*. The same holds true for another North American slavemaker, *Leptothorax duloticus*. Wilson (1975) stated that "*duloticus* is clearly a member of the holarctic *acervorum* group". *Chalepoxenus* is an exclusively European genus with about five described species. As my student, Mr. Ehrhardt, has recently

Table I. The social parasitic *Leptothoracini*, their hosts, present taxonomic status and known parasitic relationships.

Social parasites	*Type*	*Nearest relatives*	*Hosts*
Formicoxenus spp.	Guest ants	*Mychothorax*	*Formica*
Leptothorax hirticornis, diversipilosus		*Mychothorax*	*Formica*
Leptothorax provancheri		*Mychothorax*	*Myrmica*
Doronomyrmex pacis, pocahontas	Workerless, permanent parasites	*Mychothorax*	*Mychothorax* (=*Leptothorax* M. R. Smith)
Leptothorax goesswaldi		*Mychothorax*	
Leptothorax kutteri		*Mychothorax*	
Leptothorax minutissimus		*Leptothorax*	*Leptothorax* (=*Myrafant* Smith)
Harpagoxenus sublaevis,	Slavemaker	*Mychothorax*	*Mychothorax*
H. canadensis, H. zaisanicus		*Mychothorax*	*Mychothorax*
Harpagoxenus americanus	Slavemaker	*Leptothorax*	*Leptothorax curvispinosus, ambiguus, longispinosus*
Leptothorax duloticus		*Leptothorax*	
Chalepoxenus spp. (5 species described)	Slavemaker	*Leptothorax* (?) or *Temnothorax* (?)	*Leptothorax* and *Temnothorax*
Epimyrma spp. (11 sp. described)		*Leptothorax*	*Leptothorax*
e.g. *E. goesswaldi*	Slavemaker		
e.g. *E. vandeli*	Permanent parasite	*Leptothorax*	*Temnothorax*
Myrmetaerus microcellatus (=*Myrmoxenus gordiagini* ?)	Permanent parasite (?)	*Epimyrma*/ *Leptothorax*	*Leptothorax*

found, these ants are also true slavemakers. Finally, in this list, we have the well-known genera *Epimyrma*, and *Myrmetaerus* (supposedly = *Myrmoxenus*), which all belong together as far as I can judge. Winter (1979b) has observed, for the first time, the slave raids of *E. goesswaldi*. All the *Epimyrma* species have hitherto been considered as permanent parasites which make no slave raids. It will be necessary to find out whether the other species are also slavemakers.*

The host species of *Epimyrma* are essentially the same as those of *Chalepoxenus*, i.e. *Leptothorax* s. str. species, except for three *Epimyrma* species which live together with *Temnothorax recedens*. *Myrmetaerus* (or *Myrmoxenus*), like most *Epimyrma*, have *Leptothorax* s. str. species as hosts.

THE NATURAL RELATIONSHIPS OF SOCIAL PARASITIC AND INDEPENDENT *LEPTOTHORACINI*

I shall now try to arrange these species and groups according to their natural relationships, with the aid of information that is largely new on their morphology, biology and ethology.

(a) Group Mychothorax (=Leptothorax *Smith, 1950)*

First, we can single out a group which has clear relationships with the well-known subgenus *Mychothorax* (Table II). Within this group, the guest ants of *Formica* species, in my opinion, represent a clearly distinct and well-defined genus, comprising *Formicoxenus nitidulus*, *orientalis*, *hirticornis* and *diversipilosus*. The close relationship between *F. nitidulus* and both North American species is shown by their common habit of living as guest ants in *Formica* mounds, by the occurrence of ergatoid, or workerlike, wingless males in all species, by the queen polymorphism with alate and intermorphic females, and by the functional monogyny of at least *F. hirticornis* and *F. nitidulus* (Buschinger, 1979a; Buschinger and Winter, 1976). *Leptothorax provancheri* may well belong to this genus, also we know too little about it to judge accurately.

The tree European workerless permanent parasites, *Doronomyrmex pacis*, *Lept. goesswaldi* (Buschinger, 1974) and *L. kutteri* (Buschinger, 1965) are very closely related. They live together with one common host species, and cross-breeding has been possible with *D. pacis* ♂♂ and *L. kutteri* ♀♀

* Recent field studies in the type locality of *E. vandeli* Santschi have confirmed that this species is really workerless and thus cannot be dulotic.

Table II. "Subgenus" *Mychothorax* and related social parasites.

Social parasites	*Type*	*Host*	*Distribution*
Formicoxenus nitidulus	Guest ants	*Formica* spp.	Europe
Formicoxenus orientalis		*Formica*	Asia
Formicoxenus hirticornis		*Formica*	N. America
Formicoxenus diversipilosus		*Formica*	N. America
Leptothorax provancheri		*Myrmica*	N. America
Doronomyrmex pacis	Workerless, permanent parasites	*Mychothorax acervorum*	Europe, alps
Doronomyrmex kutteri			Europe, central
Doronomyrmex goesswaldi			Europe, Alps
Doronomyrmex pocahontas		*M. "muscorum"*	N. America, Rocky Mountains
Harpagoxenus sublaevis	Slavemakers	*M. acervorum, muscorum, gredleri*	Europe, northern, central and eastern
Harpagoxenus zaisanicus		*M. muscorum*	Asia
Harpagoxenus canadensis		*M. "muscorum"* (2–3 spp.)	N. America, Canada

(Buschinger, 1972), and *L. goesswaldi* ♂♂ and *L. kutteri* ♀♀, both resulting with intermediate females. They also have similar karyotypes with haploid numbers between 23 and 28 chromosomes, differing greatly from *L. acervorum*, which has 13 chromosomes. Whether *Doronomyrmex pocahontas* really belongs to this group is not yet completely clear; however, the morphology of *pocahontas* is clearly that of a *Doronomyrmex*. Thus it seems possible to put them all together into the one genus *Doronomyrmex*.

Finally, *Harpagoxenus sublaevis* and *H. canadensis* are close relatives with similar karyotypes (20 chromosomes in *H. sublaevis*, and 18 in *H. canadensis*) and identical or very similar pheromones (Buschinger and Alloway, 1979). Mating between sexuals of the two species was observed, but their eggs did not develop. The two species also have identical raiding behaviour with tandem running as the recruitment method, and both have sharp, scissor-like mandibles which serve to dismember the workers of the host species when their nest is attacked.

All these social parasites, *Formicoxenus*, *Doronomyrmex*, and the two *Harpagoxenus* species, have close relations with the subgenus *Mychothorax*. This is indicated by several ethological and morphological features: the queens are rather slender with a narrow thorax, the ♂♂ are large and have long antennae which are necessary to contact the ♀♀'s antennae during mating. The ♀♀ are only a little smaller than the queens. Virgin queens of most species exhibit sexual calling behaviour while standing on top of any upright grass stem or twig etc. Finally, all these species, parasites as well as hosts, can be bred in short artificial annual cycles of only 3 or 4 months. A short hibernation of only 6 weeks is sufficient for the larvae to continue their development to sexuals and workers in a following warmer period. Altogether, this group represents a number of clearly related species and genera. The genera apparently have a holarctic distribution, similar to the distribution of other ant genera such as *Formica*, *Polyergus*, *Raptiformica*, *Lasius*.

(b) Group Leptothorax *s. str. (=*Myrafant *Smith, 1950)*

The second group is much more complex. It comprises, at first glance, all the genera or subgenera of the tribe *Leptothoracini* except these already mentioned in the first group. We shall concentrate on those subgroups which have known social parasites, namely the subgenus *Temnothorax*, the subgenus *Leptothorax* s. str. with 11-jointed antennae, and *Leptothorax* with 12-jointed antennae in females and workers, (the latter two groups forming

the subgenus "*Myrafant*" following Smith). The interrelationships of these groups are not well understood.

We can find a number of common features of all independent species of these 3 groups: they all have rather large queens, with a wide thorax, and comparatively much smaller workers. The males are normally smaller than the queens and have much shorter antennae than *Mychothorax* group males. The females, as far as is known, do not exhibit sexual calling behaviour near the nest; instead they seem to encounter the males in certain localities, in a swarm. There the females sometimes produce a short puff of poison gland secretion, which then stimulates the surrounding males to cluster around the female, until one of them succeeds in mounting her. As far as is known, all these species need a long hibernation of 4–5 months, and they cannot be bred in artificially shortened annual cycles. We also encounter most of these features in the social parasitic species belonging to this group. The main differences between *Temnothorax* and the two groups of *Leptothorax* are shown in Table III.

Despite the superficial similarities of the members of the *unifasciatus* group and the *curvispinosus* group, and the very different morphology of *Temnothorax*, which look more like a *Pheidole*, I am inclined to suppose a

Table III. Differences between *Temnothorax* and *Leptothorax* sensu stricto subgroups.

Group	*Body hairs*	*No. of antennal segments*	*No. of queens*	*Main species and their distribution*	
Temnothorax	Long, tapering	13(♂) 12(♀♀)	Monogynous	*L. recedens*	Europe, mediterranean
Leptothorax "*unifasciatus* group"	Short, blunt	13(♂) 12(♀♀)	Mainly obligatorily monogynous	*L. unifasciatus* *L. nigriceps* *L. affinis* *L. tuberum* *L. nylanderi*	Europe, central and mediterranean
				L. texanus *L. nitens* *L. nevadensis*	Southern North America
Leptothorax "*curvispinosus* group"	Short, blunt	12(♂) 11(♀♀)	Facultatively polygynous	*L. curvispinosus* *L. ambiguus* *L. longispinosus* *L. schaumi*	Southern North America
				L. flavicornis	Europe, mediterranean

closer phylogenetical relationship between *Temnothorax* and the *unifasciatus* group. The 11-jointed *curvispinosus* group, in my opinion, could be more distant from both, and could have evolved convergently to its *unifasciatus*-like appearance. One argument in favour of this opinion is that most of the species with 12-jointed antennae, including *Temnothorax*, are strictly monogynous, whereas all species with 11-jointed antennae are facultatively polygynous, as far as this is known. On the other hand, it is very unlikely that these three groups represent subgenera as far distant from each other as the subgenus *Mychothorax* is from them. We shall see how the social parasites link the group together.

Let us first consider the North American social parasites of the

Table IV. Subgenera *Leptothorax* sensu stricto, and *Temnothorax*, and their social parasites.

Social parasite (no. of antennal segments)	*Type*	*Host species (no. of antennal segments)*	*Distribution*
Leptothorax minutissimus (11)	Permanent parasite, workerless	*L. curvispinosus* (11)	N. America
Harpagoxenus americanus (11)	Slavemaker	*L. curvispinosus*, *L. ambiguus*, *L. longispinosus* (11)	N. America
Leptothorax duloticus	Slavemaker		N. America
Epimyrma goesswaldi (11)	Slavemaker	*L. unifasciatus* *L. nigriceps* (12)	Europe, southern and central
Other Epimyrma spp.	?	Other *Leptoth.*	
Epimyrma vandeli, kraussei (11)	?	*Temnothorax* (12)	Europe, southern
Myrmetaerus microocellatus (12)	?	*L. lichtensteini* (12)	Europe, southern
Chalepoxenus spp. (12)	Slavemaker	*L. unifasciatus* *L. nigriceps* *and others* (12)	Europe, southern
Chalepoxenus spp. (12)	?	*L. flavicornis* (11)	Dalmatia
		Temnothorax (12)	Greece

11-jointed *Leptothorax* (Table IV). *Leptothorax minutissimus* (Smith, 1942) there seems to be a clear descendant of its host *Leptothorax curvispinosus*. We do not know very much about its behaviour, but it lives together with the host colony queens, and resembles them so much that it looks just like a microgyne of *curvispinosus*.

Harpagoxenus americanus is a slavemaker which enslaves three host species. It may be surprising to find this species here, far from the other *Harpagoxenus* species. However, there are so many differences between *americanus* and the other *Harpagoxenus* species that I am sure they are *not* congeneric.

H. americanus has a highly different karyotype with only 11 chromosomes in the haploid set, compared to 18 or 20 in *H. canadensis* or *H. sublaevis*, and it makes raids with a group recruitment towards the target colony, not with tandem running. The sexual behaviour of *americanus* resembles that of the other members of this *Leptothorax* group, and its sexual pheromone is not "understood" by *H. sublaevis* or *canadensis* males (Buschinger and Alloway, 1979). The males have short antennae, which is characteristic for this whole group, and the wing venation of *americanus* females, too, resembles more that of the host species than that of any *Mychothorax* group female. *H. americanus* therefore should be in a separate genus, or in a genus which should also include the following species. *Leptothorax duloticus* (Wesson, 1937, 1940), enslaves the same three host species as *H. americanus*, it makes use of essentially the same group recruitment technique, and its sexual behaviour and morphological characters correspond with those of *H. americanus*. There is only one major difference: unlike *americanus*, the *duloticus* workers have completely dentate mandibles, and they fight by vigorously stinging the defending host colony workers during a raid. These slave raids of both *H. americanus* and *L. duloticus* were first described by Wesson (1937, 1939, 1940).

Winter (1979) has observed the raids of the European *Epimyrma goesswaldi*. The main characteristics of these raids are group recruitment and sting fighting. Moreover *Leptothorax duloticus* and *Epimyrma goesswaldi* look surprisingly similar in appearance. Morphological characters and the identical raiding behaviour make me suspect a rather close relationship between *L. duloticus* and the genus *Epimyrma*. We do not know whether other *Epimyrma* species are also slavemakers, but I think that dulosis is the primary mode of parasitic life in this genus. Incidentally, *Epimyrma* is the first example of a social parasitic group which might link together the *Leptothorax* groups: all *Epimyrma* species have 11-jointed antennae, like *L.*

duloticus. Their European host species, however, belong to the 12-jointed subgroup, and three *Epimyrma* species parasitize *Temnothorax recedens*.

We know little about *Myrmetaerus microcellatus*. It lives together with a 12-jointed *Leptothorax* and also has 12-jointed antennae. According to Walter Faber (personal communication) I know that the *Myrmetaerus* females found their colonies like *Epimyrma*, killing the host colony queen. The results of Fischer's karyotype studies (personal communication) are a further argument to suppose *Myrmetaerus* and *Epimyrma* to be congeneric,

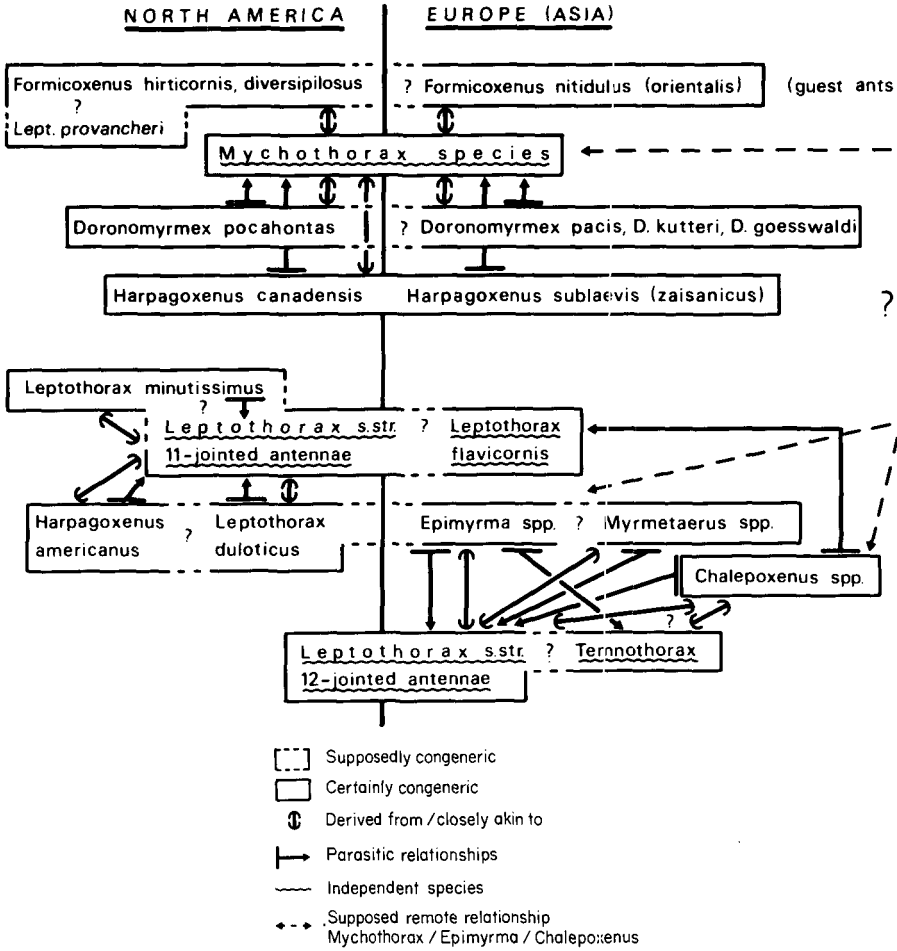

Fig. 1. Supposed relationships between social parasitic Leptothoracini and their host species groups from Europe and North America on the basis of morphological, ethological, cytological and ecological facts described in the text.

they all have a haploid number of 10 chromosomes and the karyotypes look very similar.

Lastly there is the genus *Chalepoxenus*; Ehrhardt (personal communication) has found this to be also a slave-making genus. It enslaves the same 12-jointed *Leptothorax* as *Epimyrma*. However, its raiding characteristics are a mixture of what we know from *Harpagoxenus sublaevis* and *Epimyrma*: recruitment is performed by tandem runs, but fighting by use of the sting. *Chalepoxenus*, again, is a genus which connects three subgroups of *Leptothorax*: most species live together with members of the *unifasciatus* group. However, Walter Faber has found a species in Yugoslavia, which is not yet described, living together with *Leptothorax flavicornis*, the only European *Leptothorax* s. str. with 11-jointed antennae, and in April 1980 I found a *Chalepoxenus* species living together with *Temnothorax* near Tiros (Peloponnesus).

Figure 1 summarizes, provisionally, the new information and supposed interrelations discussed here. Rather closely related groups surround the independent *Mychothorax* species, and in this group the European and North American species rather clearly belong to a few holarctic genera.

Among the second group there are, apart from the morphological differences of the three independent subgroups, also differences in their distribution. The 11-jointed *Leptothorax* predominate in the New World, whereas the 12-jointed species have a higher number of species in Europe and Asia. However, as already noted, the social parasites link together the three subgroups, and, at least *Lept. duloticus* and *Epimyrma* among the social parasites seem to form a linkage across the Atlantic. Of course, while constructing such hypothetical connections, I am conscious of having considered only the American and the European faunas and I am well aware of the fact that we know only very little about the *Leptothoracini* parasites of all Asia.

I cannot say whether there will be similar relationship across the Pacific, and it would be highly interesting to compare, for example, *Harpagoxenus zaisanicus* from Mongolia with *H. sublaevis* and *H. canadensis*. This lack of information, too, is the main reason why we cannot yet decide whether the relationships of European and North American *Leptothoracini* are due to former connections of the two faunas via the Bering bridge, or via the North Atlantic. In the latter case we could possibly speculate about a splitting of the southern *Leptothorax* sensu stricto group early in the Tertiary period, with the opening of the Atlantic.

Finally, this table indicates a weak connection between *Mychothorax*

and *Epimyrma*/*Chalepoxenus*. This means that there are a few, faintly visible, morphological similarities between these genera, mainly concerning the thoracic structures of the queens. It is more a subjective interpretation that these social parasites may represent the recent descendants of an extinct common ancestor of the two big groups.

Using characters other than purely morphological ones, we can thus approach a natural system, and I am sure that this will be possible, not only with the *Leptothoracini*, but also with other, similarly difficult groups of social insects.

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