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Parasites, commensals and phoretics of *Timarcha* (Coleoptera: Chrysomelidae)

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ABSTRACT. A review of the known parasites, commensals and phoretics of the genus *Timarcha* is presented. Probably additional species of gregarines, nematodes and Hymenoptera will be found, but the review includes what is known from Western Europe and Western North America. Gregarine and *Heterorhabditis* nematode infections of North American *Timarcha* are reported here for the first time. So far, very few studies have been done on the effect of these parasites on their hosts.

Key words: entomology, bionomy, *Timarcha*, *Perilitus*, *Gregarina*, *Pseudamansia*, *Mermis*, *Heterorhabditis*.

INTRODUCTION

The genus *Timarcha*, with more than 100 species and approximately 50 acceptable subspecies (GOMEZ-ZURITA 2004; GOMEZ-ZURITA et al. 2000), remains an enigma among the Chrysomelinae. Its distribution in the Old World, surely the remains of a formerly much larger distribution, is limited to warmer Europe, south of the Quaternary glaciations (southern Baltic States and south of Scotland), North Africa, Turkey and to western North America from south of Canada to northern California. It does not go east farther than Montana and Idaho. The genus is missing in Asia (except Turkey) and seems to be a good example of vicariance (POINAR et al. 2002). *Timarcha* is apterous and, as *Meloe*, apterous in the pupal stage, which means a very old history of apterism. The elytra are fused as in the genus *Pimelia*. When the distribution of both genera coincides, there seems to be some kind of Muellierian mimicry between the two (JOLIVET 1997). *Timarcha* is extremely toxic, its blood being rich with anthraquinones,

and the Old World species, being most of them diurnal, except for *Metallochimarra* species, produces reflex bleeding abundantly when disturbed (JOLIVET and VERMA 2002). American species being all entirely nocturnal do not show autohaemorrhage. Being so toxic, *Timarcha* should be devoid of parasites, but on the contrary they are relatively abundant. Only their predators are absent, the bitter and toxic blood being strongly repellent to birds and lizards (HOLLANDE 1926). A list of predators of Chrysomelidae is given by COX (1996). According to literature (CARPENTER 1992), the genus *Timarcha* seem to be very ancient if we consider the Lower Jurassic fossils found in Siberia (*Timarchopsis czekanowskii* BRAUER, REDTENBACKER and GANGLBAUER), but their real relationships are still questionable. Generally black against a green background, *Timarcha* seems aposematic to potential predators. A few species have metallic reflects (*T. cerdo* STÅL in the US, *T. balearica* GORY in the Balearic islands and one species in Spain), but the basic color remains black.

Curiously, no flagellates, ciliates, trichomycetes (Eccrinales) are found in the intestine of Chrysomelidae, including *Timarcha*. Laboulbeniales, fungi known among many Chrysomelidae, as ectoparasites, have never been found in *Timarcha*. The following parasites, commensals and phoretics have been recorded on these beetles:

ENDOPARASITES OR PROTOLIAN PARASITES

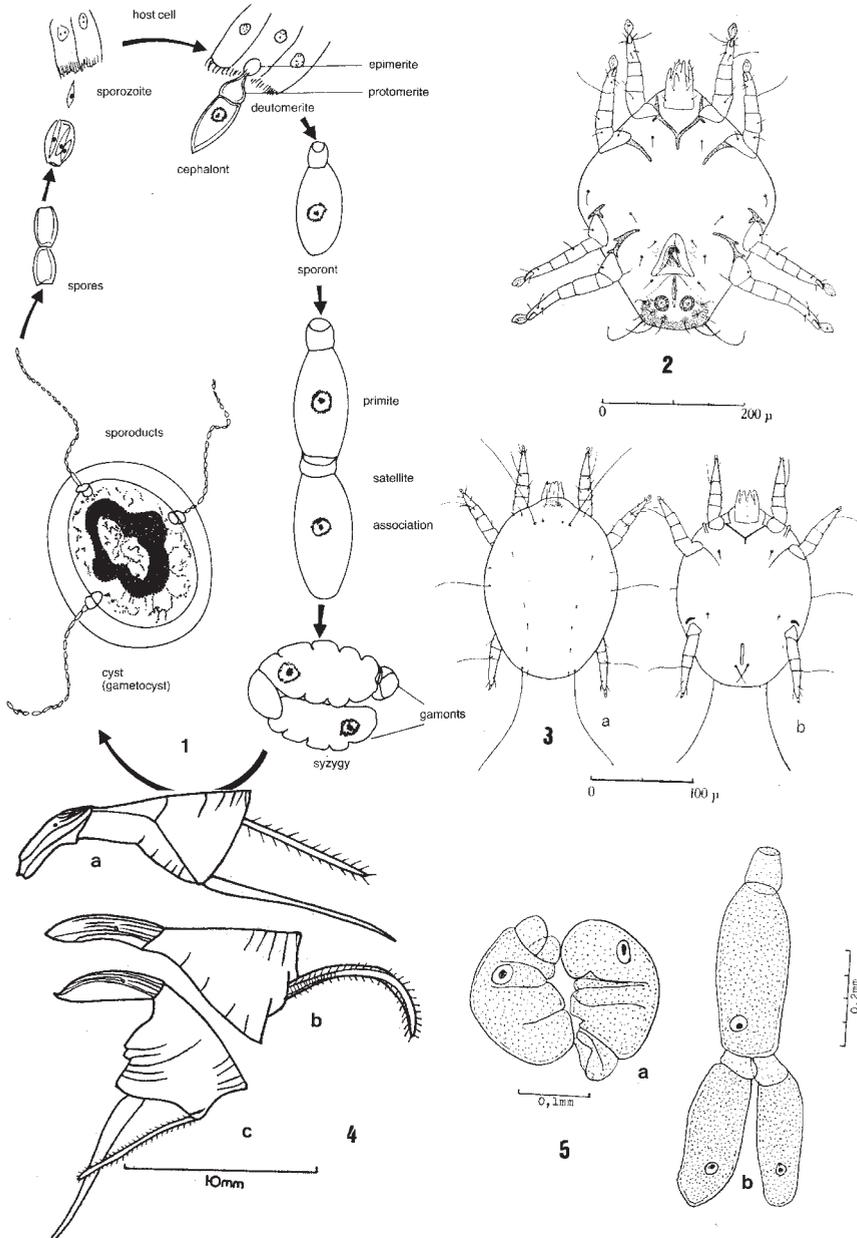
So far, parasitoids have been found in *Timarcha* in Europe only. They probably exist also in North America. Hymenoptera and nematodes have been found in Europe. So far, Nematomorpha have not been found among *Timarcha*. They are mostly linked with carnivorous beetles (Carabidae) and Orthoptera. So far, no Diptera (Tachinidae) or other families have been found among *Timarcha*, even though they are relatively common among *Chrysolina* and others.

Nematodes.

Among the Nematodes reported from Chrysomelidae (Mermithidae, Heterorhabditidae, Steinernematidae and Allantonematidae) (POINAR 1988), two of these groups are now known from *Timarcha*. Recently a *Mermis* sp. was collected from *Timarcha* (*Timarchostoma*) *obsoleta* LABOISSIÈRE from the Pyrenean mountains in France (POINAR et al. 2007). The specimen was found to contain 3 individual mermithid nematodes. The specimens seem to possess some characters of the *Hexameris* complex. Very probably the beetle was sterilized by the parasites. We report here the first record of a *Heterorhabditis* sp. attacking *Timarcha cerdo* STÅL in Oregon (Fig. 6). The nematodes live in the soil and attack the mature larvae as they prepare for pupation.

Braconidae.

Several Hymenoptera were found as protelian parasites of *Timarcha* (ABELOOS 1933 ; RICHARDS 1960; JOLIVET 1948 ; COX 1994). *Perilitus sicheli* (GIARD) and *Perilitus falciger* (RUTHE) are among the most often quoted from *Timarcha tenebricosa* FABRICIUS and other species in Western Europe. The larvae are visible in the haemocoel at an early instar. The pink *Perilitus* larvae, (around 30 per insect) are 7mm long and exit



1. Schematized representation of the life-cycle of *Gregarina munieri* (A. SCHNEIDER) (Apicomplexa : Gregarinidae) (after J. THÉODORIDÈS 1988); 2. *Pseudamansia chrysoelinus* (C. L. KOCH) (Acari : Canestriniidae). Male, ventral side (after COOREMAN 1950); 3. *Pseudamansia chrysoelinus* (C. L. KOCH). Larva : a) dorsal face ; b) ventral face (after COOREMAN 1950); 4. Gaster or metasoma (abdomen) of *Perilitus* spp., from left side (Hymenoptera : Braconidae). a) *P. dubius* (WESMAEL) ; b) *P. falciger* (RUTHE) ; c) *P. sicheli* GIARD (after RICHARDS 1960); 5. *Gregarina munieri* (A. SCHNEIDER). a) Syzygia ; b) Multiple association. (after J. THÉODORIDÈS 1955)

the adult *Timarcha* through the anal region and make yellowish cocoons on the sand. Before pupating inside the cocoon, *Perilitus* larvae evacuate a reddish meconium, stained with carotenoids and anthraquinones from *Timarcha* hemocoel.

ECTOPARASITES

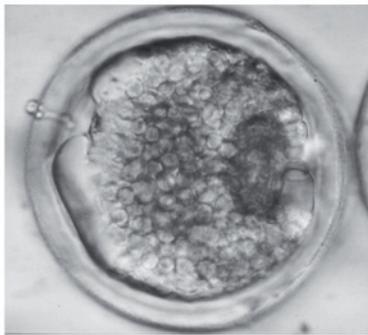
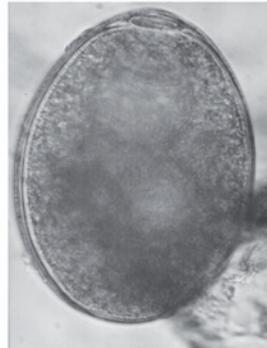
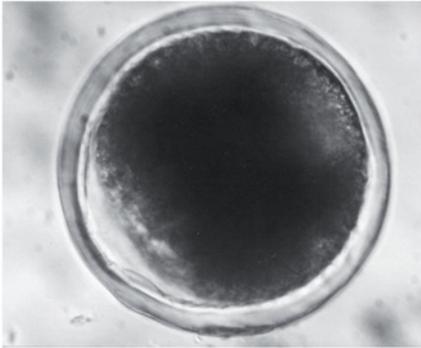
Phygadeuon punctiventris Thomson (Ichneumonoidea, Phygadeuontinae) has been reported from *Timarcha nicaeensis* VILLA, a beetle from southern France (JOLIVET 1954 ; COX 1994). These Hymenoptera are generally idiobiont ectoparasitoids. An idiobiont is a parasitoid that prevents further development of the host by paralyzing or killing it.

Another ectoparasitoid has been found on the larvae of *Timarcha cerdo* STÅL in Oregon by George POINAR (2003) : *Lestodiplosis grassator* (FYLES), a Cecidomyiidae. The cecidomyiid larvae remains on the surface of the beetle, usually between the thoracic and abdominal segments of the larva, puncturing the host's cuticle and feeding on released hemolymph (POINAR and JOLIVET 2004). The parasites are often semi-immersed in a pool of the host's hemolymph. As they mature, the larvae eventually migrate to other locations on the beetle and a zone of melanized subdermal tissue surrounds the original feeding site. Upon completion of their development, the cecidomyiid larvae leave the host and enter the sand where pupation occurs. All the beetle larvae die after the cecidomyiid larvae have completed their development. The body cavity of the *Timarcha* larvae is filled with bacteria at the time of death.

COMMENSALS

We can place the Gregarines (Apicomplexa) among the commensals. They absorb osmotically some of the gut contents, but normally cause no damage to their hosts. Intestinal pH varies along the intestine from 5.6 to 7.4 (PRASAD et al. 1991). This results in the specific distribution of the species from the anterior part to the posterior part of the host intestine. Several species of *Gregarina* have been found among the world Chrysomelidae, but so far only *Gregarina munieri* (A. SCHNEIDER) has been found along the middle and posterior part of the intestine of the *Timarcha* in the New and the Old World. The trophozoites are generally found in the mid-intestine and the gamonts and cysts in the posterior intestine. Practically, all the species of *Timarcha* contain Gregarines. Among the Chrysomelidae, in general, several families of Apicomplexa have been found : Gregarinidae, Hirmocystidae and Actinocephalidae (THÉODORIDÈS 1988). Most of the records of gregarines in chrysomelids are from adult beetles, but they can be found also in the larval stages. Infestation occurs early, mainly with the ingestion of leaves soiled with excreta containing cysts.

Let us also remember that *Gregarina munieri* is not exclusive to *Timarcha* spp., but it has been found also among many chrysomelids from diverse subfamilies as well as from some Curculionidae. At least eight species of *Gregarina* have been found among the Chrysomelidae, but so far even *Gregarina crenata* (BHATIA and SETNA), common among *Chrysolina*, has never been found in *Timarcha*. We report the first gregarines from North American populations of *Timarcha cerdo* STÅL. (Figs. 7-9).



6. Nematodes of the genus *Heterorhabditis* sp. parasitizing larvae of *Timarcha cerdo* in Oregon, USA ;
 7-9. Stages of a gregarine parasite of *Timarcha cerdo* adults in Oregon

PHORETICS

Some Canestriniidae mites have been found under the elytra of the Old World *Timarcha*: *Pseudamansia chrysomelinus* (C. L. KOCH) (COOREMAN 1950; JOLIVET 1952; THÉODORIDÈS 1955). Rarely they are found on the sternites, but generally they remain inside the subelytral cavity. They feed on desquamations of the skin (exudophagous), on skin fungi (fungivorous) and eventually on dry blood after reflex bleeding. The mites can be very abundant. Several families of mites are known as ectoparasites or phoretics of Chrysomelidae, but Canestriniidae are the most frequent among Chrysomelinae, Cassidinae, Hispinae ; however, they also parasitize Carabidae and other beetle families. (SANTIAGO-BLAY and FAIN 1994).

DISCUSSION

Timarcha has very toxic blood rich in anthraquinones. That and reflex bleeding of diurnal species prevent them from being attacked by predators. However, there are a certain number of protelian parasites, commensals and phoretics. Only one species of Gregarines in Europe is known from these beetles and it can also be found on American species. Probably more parasites exist, but even Braconidae are not always common among the species. Rarity of *Timarcha* is mostly due to the destruction of the habitat of one apterous species, unable to recolonize lost areas. The beetle is also very sensitive to pesticides and urbanization.

THOMAS et al. (1999a & b) and THOMAS and DE MEEUS (2006) have studied the reactions to parasitism of the Atlantic species *Timarcha maritima* PERRIS. For the Hymenopteran *Perilitus sicheli*, THOMAS et al (1999a), the following conclusions were reached: the prevalence of infection was higher in unpaired males and females than in paired individuals, although this result was significant only for males. The infection did not modify the size of the hosts, since the infection starts at the larval instar. The infection of females reduced significantly the fecundity, if not killing them before oviposition. Males were unable to detect or avoid infected females as sexual partners.

Dealing with the effect of the parasitism (commensalism) of *Gregarina munieri* (A. SCHNEIDER), in the gut of *Timarcha maritima* PERRIS, THOMAS et al. (1999b) conclude that the « parasite-related assortative pairing in this beetle could result from parasitized females being less fecund and parasitized males less competitive ». Theoretically, gregarines are supposed not to do any harm to the Coleoptera hosts: however sometimes they seem to cause some mortality among Diptera or Orthoptera. As mentioned by THOMAS (1999b), it seems that when the midgut is completely occluded by trophozoites, the gregarines alter the nutrition of the host. Gregarines are far from having a harmless effect on *T. maritima*, in case of severe infections, which are not rare. They have a major effect on fecundity at an interpopulation scale. Parasites also are theoretically expected to create assortive mating (homogamy) among hosts, between heavily or lightly parasitized individuals. It seems that males, at least in the laboratory, avoid heavily infected females and prefer the less parasitized females (more fecund). There seems also to be some homogamy regarding the parasitic load. Also THOMAS and DE MEEUS

(2006) have detected a decreased capacity in movement for the parasitized males. The fact that males are more heavily infected than females has been already observed by ZUK (1987) with gryllids. With *Timarcha maritima*, THOMAS et al., (1999b) observed also less ability in movement for the heavily parasitized males. The conclusion of THOMAS and DE MEEUS (2006) is that *Gregarina munieri* exerts a major influence on *T. maritima* ecology. The role of the external (phoretic) parasite, the mite *Pseudamansia chrysomelinus*, is always weak whatever the population considered. Previous authors observed that *T. maritima* displays a phenotypic variability along the Atlantic coast of France and a part of this variability could be interpreted as linked with the variation in infection level of *Gregarina munieri* (THOMAS et al. 1999a and b). Unfortunately, *Timarcha normanna* REICHE which is as abundant along the western Norman coast as *T. maritima* in the Atlantic, has never been studied from this viewpoint.

CONCLUSIONS

As mentioned earlier, species of the genus *Timarcha* are actually becoming rarer everywhere, due certainly to pesticides, urbanization, habitat fragmentation, drought, but also probably to parasitism which can greatly reduce populations in a given area, especially already weakened populations. Hymenoptera are certainly the most dangerous since such parasitism is always fatal. A wingless population is of course more vulnerable than a winged one. The genus, often considered as a living fossil, should be considered as in danger and accordingly protected.

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