Suprageneric taxonomy, appeasement behavior, sex ratio
and other aspects of the biology
of the myrmecophilous beetle *Thorictus grandicollis*
(Dermestidae, Thorictinae)

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Abstract

Following an overview of the literature on the systematic position of the Thorictidae sensu lato, *we show, on morphological grounds, that they constitute a natural group, considered as the subfamily Thorictinae of the Dermestidae. The Thorictinae are divided into two tribes: the Thorictini (comprising the myrmecophilous genera* Thorictus, Macrothorictus *and* Afrothorictus) *and the Thaumaphrastini (comprising the free-living genus* Thorictodes). *Although larval characters seem to place the Thorictinae closest to the Dermestinae, the morphological organization of the adult greatly differs. Differential diagnoses of these subfamilies and tribes are given as well as comments on the relevance of certain characters.*

The extant knowledge of the biology of Thorictus foreli *WASMANN, the sole Thorictini species which has been studied, is summarized.*

The guest beetle, Thorictus grandicollis *GERMAR, displays characteristic appeasement behavior when handled by ants. Turning on its back, the beetle immobilizes itself, uncovering its thoracic lateroventral trichomes, allowing them to be investigated and licked by the ants. This particular behavior and the absence of phoresis on the host's antennae distinguish* T. grandicollis *from* T. foreli. T. grandicollis *does not follow its hosts' trail. Its European populations have an extremely female-biased sex ratio.*

Résumé

Taxonomie supragénérique, comportement d'apaisement, sex-ratio et autres aspects de la biologie du Coléoptère myrmécophile **Thoríctus grandicollis** *(Dermestidae, Thorictinae).*

Après un survol de la littérature relative à la position systématique des Thorictidae sensu lato, *on montre, sur la base d'observations morphologi-*

ques, que ce groupe est naturel. Ce groupe est considéré ici comme une sous-famille des Dermestidae, les Thorictinae, et est divisé en deux tribus: les Thorictini (comprenant les genres myrmécophiles Thorictus, Macrothorictus *et* Afrothorictus*) et les Thaumaphrastini (comprenant le genre libre* Thorictodes*). Bien que les caractères larvaires rapprochent les Thorictinae des Dermestinae, l'organisation morphologique des adultes diffère grandement. Des diagnoses énumèrent les caractères différentiels de ces sous-familles et tribus, et la pertinence de certains caractères est discutée.*

Les connaissances relatives à la biologie de Thorictus foreli WASMANN*, la seule espèce de Thorictini jusqu'ici étudiée, sont résumées.*

Le Coléoptère myrmécophile Thorictus grandicollis GERMAR *présente un comportement d'apaisement lorsqu'il est abordé par les Fourmis: il se place sur le dos et s'immobilise en découvrant ses trichomes thoraciques latéroventraux, que les ouvrières peuvent alors inspecter et lécher. Ce comportement particulier et l'absence de phorésie sur les antennes des Fourmis distinguent* T. grandicollis *de* T. foreli. T. grandicollis *ne suit pas les pistes de ses hôtes. Par ailleurs, les populations européennes de* T. grandicollis *ont une sex-ratio extrêmement biaisée en faveur des femelles.*

Introduction

The genus *Thorictus* GERMAR, up to now, comprises 131 known species distributed all over Africa (with the exception of the tropical forests and Madagascar), in the Canary and Madeira islands and from Mediterranean Europe eastward to Burma (JOHN & ANDREAE, 1967 and JOHN's later papers). The species of *Thorictus* and those of two closely-related endemic South African genera, *Macrothorictus* ANDREAE and *Afrothorictus* ANDREAE, constitute a morphologically homogeneous group of myrmecophilous beetles.

These small beetles (their length ranges from 1.45 to 3.60 mm) have an ovoidal or elongated-round shape, are wingless and possess at each side of their body a set of opposite trichomes along the junction of the mesothorax and the metathorax. In addition, some species have trichomes situated at the posterolateral angles of the prothorax. The two endemic genera can be distinguished from *Thorictus* by their elongated legs (ANDREAE, 1967) which could be an adaptation to life in the dryest parts of South Africa.

Except for a fragmentary knowledge of their hosts' identity (HETSCHKO & WASMANN, 1925; ANDREAE, 1967), virtually all that we know about the biology of these myrmecophiles is based on one North African species, *Thorictus foreli* WASMANN. This beetle presents noteworthy phoretic behavior: by means of its mandibles it fastens itself on an antenna of its host, *Cataglyphis bicolor* (Formicinae). Astonishingly, no further biological research has been carried out on this group of myrmecophiles since the thesis of BANCK (1927).

While searching for myrmecophiles in the Spanish eastern part of the Pyrenees, we were fortunate to find two individuals of another species,

Thorictus grandicollis GERMAR, with their hosts. We were able to observe, to some extent, their behavior in a laboratory. The interaction of this species with its hosts was found to be very different from that of *T. foreli*, therefore interesting to describe, despite the fact that only two individuals were observed.

First of all, the taxonomic status of the group known as the family Thorictidae *sensu lato*, which comprises the three myrmecophilous genera (including *Thorictus*) and the free-living genus *Thorictodes*, needs some clarification. According to some authors, this group constitutes a distinct family, while others distinguish two families, the Thorictidae, which comprise the myrmecophilous genera, and the Dermestidae, which include the free-living genus. However, there is a growing consensus about placing the entire group (the Thorictidae sensu lato) within the Dermestidae, although no satisfactory reasons have been given. Therefore, following an historical review of the question, it is considered useful to give detailed diagnoses of the suprageneric components of the Thorictidae s.l., as they form part of the Dermestidae, and of the subfamily considered to be the nearest, the Dermestinae. In order to do this, we made use of some new differential characters associated with the hidden abdominal sclerites. We do not intent to discuss here the status of forms such as *Rhopalosilpha wasmanni* ARROW, 1929, originally perceived as distant (it was placed in the Silphidae), but which might be related to the Thorictidae s. l. (cf. CROWSON, 1951, 1955 and edition of 1967).

In the course of our morphological study we also found that there was no male among the 46 preserved individuals of *Thorictus grandicollis* at our disposal, which would point to the extraordinarily female-biased sex ratio of this beetle.

Hopefully, this article will encourage further research into the areas of interest partly developed here.

1. Suprageneric taxonomy of the Thorictidae sensu lato

1.1. Overview of the most important literature

The genus *Thorictus* GERMAR, 1834 was placed in a family of its own by WOLLASTON (1854) and later on, another genus, containing a free-living species, *Thorictodes heydeni* REITTER, 1875, was added to this family by its describer. Before the larvae were sufficiently known, the systematic position of the Thorictidae was uncertain, the best allocation seeming to be that of the superfamily Bostrychoidea, by VAN EMDEN (1924) and HINTON (1945).

The larva of *Thorictodes heydeni* REITTER was described in 1924 by VAN EMDEN and that of *Thorictus foreli* WASMANN, in 1926, by REICHENSPERGER, but it was only with the thorough description of the larva of the until then enigmatic *Thaumaphrastus karanisensis* BLAISDELL by ANDERSON (1949) that a decisive step was accomplished. ANDERSON (*op. cit.*) showed

the essential relationships of this species, particularly with the genus *Dermestes*, and placed it in a new subfamily of the Dermestidae, the subfamily Thaumaphrastinae.

Soon after, VAN EMDEN (1951) showed that *Thaumaphrastus karanisensis* BLAISDELL, 1927 was a synonym of *Thorictodes heydeni* and that the genera *Thorictodes* and *Thorictus* were closely related on the basis of the adult and larval features observed. He considered these genera to be sufficiently distinct from other groups to form a separate family (Thorictidae) and difficult to be united to the Dermestidae or to one of the families of Bostrychoidea, with which he thought that it could have the closest relations.

The classification work of CROWSON (1951, 1955 and its edition of 1967; 1959) was phylogenetically oriented and this led him to place *Thorictus* and *Thorictodes* in the Dermestoidea by keeping them in a family separate from the Dermestidae, "largely in deference to tradition", although CROWSON agreed with ANDERSON's view. The two genera were retained in the Thorictidae by VOGT (1967) and this family was maintained, without comments, in the superfamily Dermestoidea in the authoritative surveys of the biology of the Coleoptera of CROWSON (1981 and 1986 edition) and of PAULIAN (1988), as well as by DELVARE & ABERLENC (1989) in their key to the families of African and tropical American insects.

BEAL (1959, 1961) adopted a slightly different position. He agreed with the phylogenetic point of view of ANDERSON (1949) and CROWSON (1955) and kept *Thorictodes* and, implicitly, *Thorictus*, in the Dermestidae, but reduced this group of two genera to the rank of a tribe (Thorictini) because of the inadequateness of the tribal definitions in one of the subfamilies of the Dermestidae: the Anthreninae being left without any tribal categories, BEAL thought that it was better to reduce the existing subfamilies to tribes.

Other authors attributed a particularly high value to the apomorphic characters of the myrmecophilous species (i.e. the presence of trichomes and the short length of the metasternum). Therefore, they taxonomically clearly separated the myrmecophiles from the free-living species (*Thorictodes*). Thus, JOHN (1961, 1963) and ANDREAE (1967) retained only the myrmecophilous genera in the family Thorictidae, wrongly arguing that BEAL (1961) placed only *Thorictodes* in the Dermestidae. This policy was followed in MROCZKOWSKI's (1968) world catalogue of Dermestidae, in which only the genus *Thorictodes* was retained and placed in the subfamily Thaumaphrastinae, and in AITKEN (1975: *Thorictodes* in Dermestidae and *Thorictus* in Thorictidae). This segregation was maintained by LOHSE (1979) in *Die Käfer Mitteleuropas* and, later on, in the same faunal series, by KOCH (1989) (*Thorictodes australis* being erroneously cited in place of *T. heydeni*).

ZHANTIEV (1976) placed the free-living Palearctic Dermestidae species with adults devoided of ocelli in the subfamily Dermestinae, which comprises the tribes Dermestini (genus *Dermestes* LINNAEUS), Marioutini (ge-

nus *Mariouta* PIC) and Thaumaphrastini (genus *Thorictodes*). Recently, ZHANG & LIU (1988) also placed their new *Thorictodes* species from China in the tribe Thaumaphrastini, but without any justification (subfamily not cited).

Without particular explanations, LAWRENCE (1982) incorporated the family Thorictidae (*Thorictus* being cited) into the Dermestidae. Having taken into account the works of BEAL (1961) and LAWRENCE (1982), HALSTEAD (1986) reunited *Thorictus* and *Thorictodes* in a subfamily of the Dermestidae, the Thorictinae, and provided a useful key for its identification among adult beetles found associated with stored products throughout the world. Moreover, within the Dermestidae, LAWRENCE & BRITTON (1991) distinguished the subfamily Thorictinae among 6 other subfamilies, although without comments. In his very recent key to British Dermestids, PEACOCK (1993) followed HALSTEAD's policy.

Finally, it must be pointed out that LAWRENCE & NEWTON (1982) suppressed the superfamily Dermestoidea, which became included in the Bostrychoidea, on the grounds of cryptonephridism, aedeagus structure and lack of molar tubercle on the larval mandible.

1.2. Materials and methods

Morphology

Morphological investigations were made on dried museum specimens of *Thorictus grandicollis* GERMAR, *T. foreli* WASMANN (form *bonnairei* WASMANN) and *Thorictodes heydeni* REITTER kept in the collections of the Institut royal des Sciences naturelles de Belgique, on fresh beetles collected indoors (*Anthrenus verbasci* (L.), *Attagenus pellio* (L.), *Trogoderma* sp., *Anthrenocerus australis* (HOPE); the latter species was collected from Haybes, Dpt. Ardennes, France) or bred at Brussels University (*Dermestes haemorrhoidalis* KÜSTER).

Dried glued insects were relaxed by boiling them for a short period in acetic acid. This was also a prerequisite for checking the genitalia of the Thorictine species, whose sex cannot be distinguished externally. The morphology of the male chitinous parts was studied after dissecting and cleaning them in an aqueous KOH solution (5%). The spatial organization of the abdomen terminalia, including the articulation points between sclerites, was studied by microdissection in alcohol, as well as after temporarily mounting them in dimethyl hydantoin formaldehyde (DMHF).

Nomenclature

The authorships of suprageneric taxa are given owing to the P riciple of Coordination (Article 36 of the International Code of Zoological Nomenclature).

Owing to the interpretation of the Article 40 of the International Code, the family group name Thaumaphrastini has to be maintained in spite of the fact that its type genus is a junior synonym.

1.3. Results

The examination of the ventral thoracic structures and of the chitinous structures of or associated to the abdominal hidden segments shows that the former Thorictidae *sensu lato* form a natural group. This group is divided into two subgroups (tribes Thorictini and Thaumaphrastini) on the basis of thoracic and antennal structures. These two tribes form a subfamily of the Dermestidae, the Thorictinae, which is however very distinct from the Dermestinae in terms of adult thoracic and abdominal characters, although ANDERSON (1949) has shown that the two subfamilies are linked by larval characters.

We, here, provide differential diagnoses for the Thorictinae, the Dermestinae and the two Thorictine tribes. We also comment on some of the relevant distinctive characters.

A) Subfamily Thorictinae WOLLASTON, 1854

Selected synonymy: Colydiidae Thorictini sensu SEIDLITZ (1888, 1889). Thorictidae sensu REITTER (1875, 1880): GANGLBAUER (1899), HETSCHKO & WASMANN (1925), HINTON (1945), PAULIAN (1949), VAN EMDEN (1951), CROWSON (1951, 1955 and edition of 1967), VOGT (1967). Dermestidae Thorictini sensu BEAL (1959, 1961). Dermestidae Thorictinae sensu HALSTEAD (1986): LAWRENCE & BRITTON (1991), PEACOCK (1993).

Differential diagnosis:
Adult: wingless; scutellum absent; meso- and metathorax without clearly distinct episterna and epimera to be seen from a ventral view; hind coxae rounded or more or less ovate, without a groove for reception of femurs and not extending laterally (Fig. 1A,B,C); male without a specialized hair tuft on abdominal sternites 3 or 4; antennae, except the end club, able to be hidden in a groove between the edge of the mouthparts and the latero-dorsal edge of the head; compound eyes very weakly developed, rimmed by dorsal head cuticle; abdominal sclerites 8 and 9 poorly chitinized (mainly membranous), the sternites articulated on the tergites by their lateral extremities, the aedeagus passing between these sclerites (Figs 2A,B and 3A,B,C); abdominal parasternites membranous, except those corresponding to sternite 2 (that is, to the basal half part of first visible sternite); rectum provided with a chitinous armature and with recurved toothed processes, both structures reaching the anal region (Fig. 2A,B).

Larva: head without ocelli; body setae simple (except some short clubbed setae which are reported in *Thorictodes* by ANDERSON, 1949).

A1) Tribe Thorictini WOLLASTON, 1854

As it is defined here, this tribe only comprises the myrmecophilous genera *Thorictus* GERMAR, 1834 (type genus, with 131 known species), *Macrothorictus* ANDREAE, 1967 (6 species) and *Afrothorictus* ANDREAE, 1967 (monospecific).
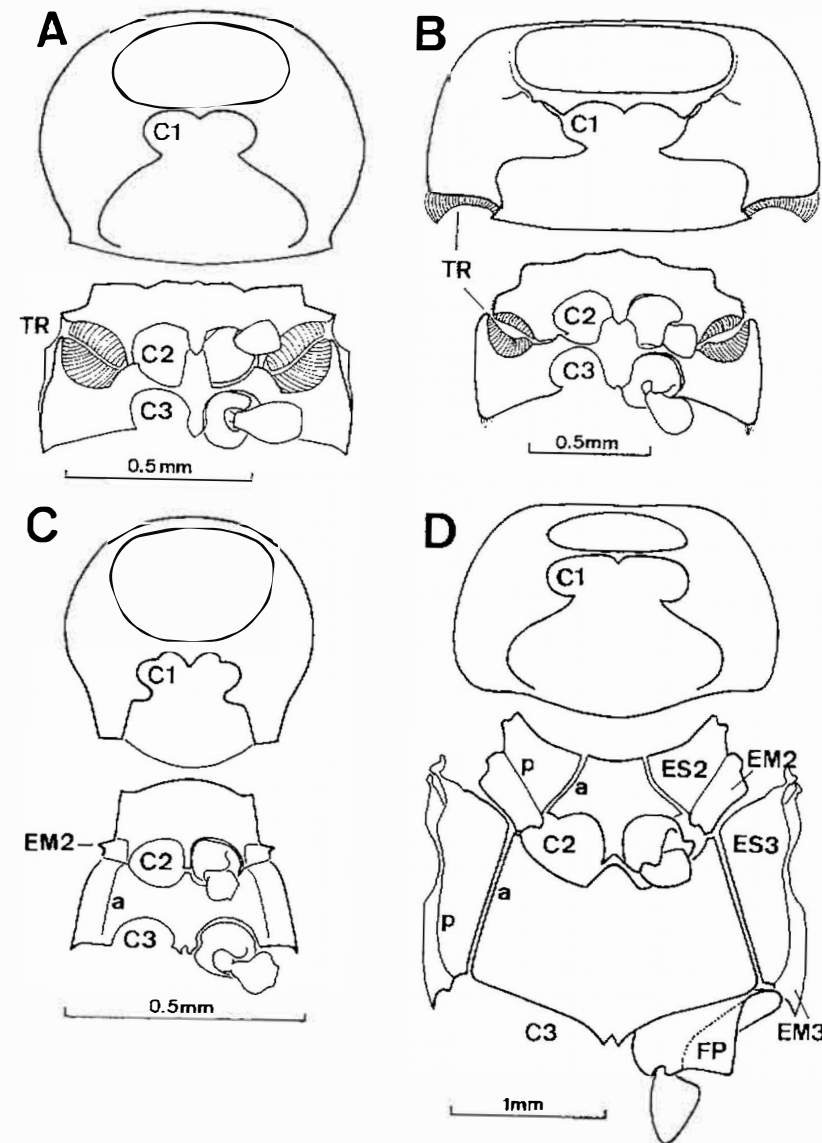
Fig. 1. Thorax of (A) *Thorictus grandicollis* (from Hyères, France), (B) *Thorictus foreli* (from Oued Miliane, Tunisia), (C) *Thorictodes heydeni* and (D) *Dermestes haemorrhoidalis*, ventral view. The prothorax (1) has been separated from the meso- (2) and metathorax (3). In Figure D, the sclerites have been slightly separated along the well-distinct anapleural grooves. Left meso- and metacoxae and trochanters are drawn in situ. a: anapleural suture; C: coxal cavity; EM: epimeron; ES: episternum; FP: femoral plate; TR: trichomes; p: pleural suture.

Synonymy: Thorictidae partim, sensu LACORDAIRE (1854, in its French formulation *Thorictides*, and without the genus *Pycnidium* ERICHSON, 1847). Thorictidae sensu JOHN (1963, 1965, 1967 and other papers): LOHSE (1979), KOCH (1989), MROCZKOWSKI (1968, by default), AITKEN (1975).

Differential diagnosis:

Adult: a set of opposite trichomes along each ventrolateral junction of mesothorax and metathorax (Fig. 1A,B). In some species, supplementary trichomes are situated at the posterolateral angles of prosternum and/or pronotum (Fig. 1B). There are no clear traces of pleural or anapleural sutures from a ventral view. Metasternum reduced in length, with the hind coxae therefore close to the median ones (Fig. 1A,B). Prothorax wider than its length, its posterior foramen wider than the anterior one (Fig. 1A,B). Antennal club with the posterior internal angle of segment 9 not distinctly discontinuous with the anterior angle of segment 8.

A2) Tribe Thaumaphrastini ANDERSON, 1949

Comprises only the free-living genus *Thorictodes* REITTER, 1875 (5 species).

Synonymy: Dermestidae Thaumaphrastinae ANDERSON, 1949: MROCZ-KOWSKI (1968), AITKEN (1975), LOHSE (1979). Dermestinae Thaumaphrastini: ZHANTIEV (1976). Dermestidae Thaumaphrastini: ZHANG & LIU (1988).

Differential diagnosis:

Adult: no trichomes. A poorly visible pleural suture separates the mesepimera (Fig 1C: EM2) from the rest of the mesosternum. There is also a trace of what seems to be the non-membranous remnant of the anapleural metathoracic suture, incomplete at its posterior end (Fig. 1C: a). Hind coxae are well separated from the median ones (Fig. 1C). Prothorax as long as or longer than wide, its anterior foramen wider or as wide as the posterior one (Fig. 1C). Antennal club with the posterior internal angle of segment 9 and the anterior angle of segment 8 distinctly discontinuous.

Remarks on the relevance of certain tribal characters

- There is no doubt that these tribes pertain to the same and distinct natural unit (Thorictinae) since the rectal chitinous lagging and the male hidden abdominal sclerites are similar. This can also be deduced from a comparison of our drawings (Figs. 2A,B) with those, which are less precise, of other species, illustrated in the literature (*Thorictus grandicollis* and *T. seriesetosus*: JOHN, 1963; *T. franzi*: JOHN, 1966; *T. namibensis*: JOHN & ANDREAE, 1967).

- *Thorictus* also differs from *Thorictodes* by having a stout mediolongitudinal process along the meso- and metasternum. The literature provides no information for the other Thorictini genera.

- In the literature the absence of eyes in *Thorictodes* is sometimes contrasted with their presence, even if strongly reduced, in the myrmecophi-

lous species. However, poorly developed lateral eyes exist in *Thorictodes heydeni* (VAN EMDEN, 1951; HALSTEAD, 1986), in *T. dartevellei* and in *T. bennetti* (JOHN, 1961).

- REITTER (1880) distinguishes *Thorictodes* from *Thorictus*, among other characters, by the absence of tibial spines. Some *Macrothorictus* species also lack tibial spines (ANDREAE, 1967).

- For each of the genera of the two tribes, the literature provides examples of species with a clearly 3-segmented antennal club and others with a 1-, or a 2- or an indistinctly segmented club. The sole species of *Afrothorictus* has a 3-segmented club.

B) Subfamily Dermestinae LATREILLE, 1807

Monotribal; it comprises the genera *Dermestes* LINNAEUS, 1758 (approximately 67 extant species) and *Montandonia* JACQUET, 1886 (monotypic).

Selected synonymy: Dermestidae Dermestini sensu BEAL (1959, 1961). Dermestinae Dermestini: ZHANTIEV (1976).

Differential diagnosis:

Adult: winged; scutellum present; meso- and metathorax with distinct episterna and epimera (separated by well-visible pleural sutures, at least on the mesothorax) and deep anapleural grooves (which are clearly membranous on the metathorax) (Fig. 1D); hind coxae transverse (laterally extending across hind margin of metepisterna), excavate for the reception of the femur, the anterior border of the groove expanded in a coxal or "femoral" plate (Fig. 1D: FP); male with a median tuft of hairs arising from a pit on 3rd and/or 4th visible abdominal sternite and associated with exocrine glands (cf. ZHANTIEV 1976); antennae (except end club) can be hidden between the edge of the mouthparts and the greatly developed compound eyes, which are not rimmed by head cuticle; abdominal sclerites 8 and 9 strongly chitinized. Unlike all other abdominal segments, sternite and tergite 9 articulate at their basal extremity (Figs. 2C and 3D), the aedeagus passing through the bended tergite 9 (Fig. 3D); all abdominal paratergites well chitinized and provided with short hairs; rectum provided on its anterior half with a smooth chitinous armature, thus not reaching its anal extremity (Figs. 2C and 3D).

Larva: head with distinct (lateral) ocelli; body setae complex ("rat-tailed" and "spear-headed" hairs).

Remarks on the relevance of certain subfamily characters

Adults

- The proximal articulation of the male abdominal 9th sclerites in *Dermestes* clearly separates the Dermestinae from the Thorictinae, whose sclerites are laterally articulated. The *Dermestes* kind of articulation also exists in the Megatominae (*Anthrenocerus australis*), and, in the Anthreninae (*Anthrenus verbasci*), the 9th tergite even forms a complete ring.
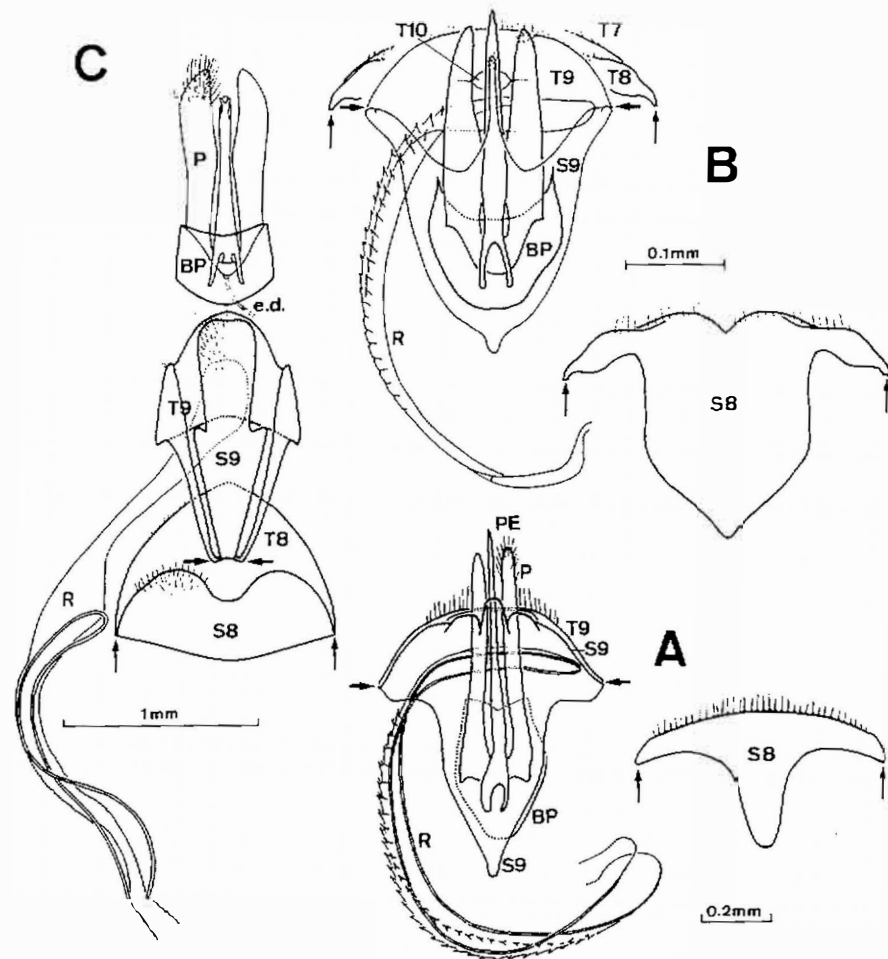
Fig. 2. Aedeagi and hidden abdominal chitinous structures of males of (A) *Thorictus foreli*, (B) *Thorictodes heydeni* and (C) *Dermestes haemorrhoidalis*, ventral view. Sternite 8 normally covers sternite 9 but is here shown apart. The rectum of *Dermestes* is shown to the left, as it is in reality, but of course has to pass between S8 and T8. The arrows point to the articulations of sternite 8 (narrow arrows) and 9 (wider arrows) with corresponding tergites. T8 is not drawn in Figure A. e.d.: ejaculatory duct; R: rectum; S: sternite; T: tergite; PE: penis; P: paramere; BP: basal piece of aedeagus.
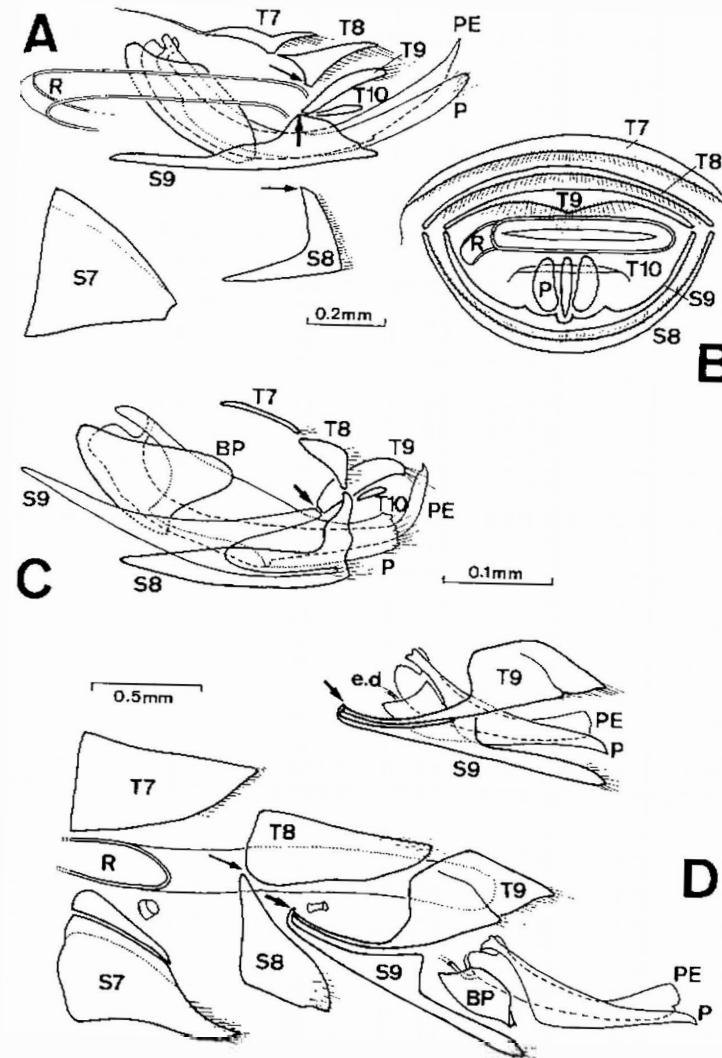
Fig. 3. Aedeagi and hidden abdominal sclerites (S7 is, however, apparent) of (A and B) *Thorictus foreli*, (C) *Thorictodes heydeni* and (D) *Dermestes haemorrhoidalis*, in left lateral view, except (B) which is seen in caudal view. In (A), sternites 7 and 8 are shown out of position. In (D), the abdominal segments have been separated and the eadeagus is seen in retracted and extended position. Notations and arrows as in Fig 2.

- The thoracic structure of the Dermestinae, with clear pleural sutures (at least on the mesothorax), very distinct anapleural grooves and with transverse hind coxae, is similar to that of other subfamilies, such as Attageninae (*Attagenus pellio*), Anthreninae (*Anthrenus verbasci*), and Megatominae (*Trogoderma sp.*, *Anthrenocerus australis*). This also clearly separates these subfamilies from the Thorictinae.

- The Dermestinae, as the other Dermestidae, are known to be cryptonephridic of the Bostrychoid type, that is, with Malpighian tubules having their ends applied in a bundle to one side of the rectum. However, BANCK (1927) found 6 free Malpighian tubules in *Thorictus foreli*. Free tubules are known to occur in near families (Derodontidae and Nosodendridae: CROWSON, 1955). The knowledge of the kind of nephridism in *Thorictodes* certainly should be of great taxonomic importance.

- Linked to this cryptonephridism is the presence of the smooth chitinous armature found on the wall of the anterior half of the rectum in *Dermestes* and which gives a solid support for the sack containing the bundle of the tubule's extremities (cf. POLL's (1932) study on *D. vulpinus*). Such a rectal armature exists in the Bostrychid *Sinoxylon sexdentatum* (POLL, 1932) but not in some Dermestid subfamilies which are however cryptonephridics of the same 'Bostrychoid' type: Attageninae (*Attagenus pellio*), Anthreninae (*Anthrenus verbasci*: present study and POLL, 1932), Megatominae (*Megatoma undata* (L.): POLL, 1932; *Anthrenocerus australis*; *Trogoderma sp.*). The more specialized rectal armature and spines of *Thorictus foreli* extend as far as the anal extremity and are likely to have another function. Furthermore, the rectum of *T. foreli* is provided with a caecum in mid-length (BANCK, 1927), which is also a noteworthy difference with other Dermestids.

- The differential characters given for the Dermestinae are those of *Dermestes*. They should be the same for *Montandonia*, which differs only by the exaggeration of some of them. However, the literature gives no information about specialized tufts of hairs on male abdominal sternites of *Montandonia latissima* (BIELZ) and JACQUET (1866) *thought* this species to be wingless.

- There are differences of lesser importance between Thorictinae and Dermestinae: in the Thorictinae there is no prosternal process between the procoxae and the mesosternum is anteriorly devoid of strong tegumental folds. In the Dermestinae there is a narrow cuticular process between the procoxae and the mesosternum is provided with strongly carenated tegumental folds between which the fore hips lie when at rest. (For the sake of clarity, these tegumental sculptures are omitted from Fig. 1D).

- The insertion of the trochanter on the femur is said to be very oblique in Dermestidae, but not in Thorictidae (CROWSON, 1955). However, we found no difference in the obliqueness of insertion between *Dermestes haemorrhoidalis*, *Thorictodes heydeni* and *Thorictus grandicollis*, where

the trochanter is inserted at about 55°-60° on the posterior femur. In *T. foreli* the angle is about 80°.

- JEANNEL (1955) wrongly stated that the aedeagi of *Thorictus* and of the Dermestidae (*Anthrenus*) lack a basal piece (named *lame basale*). A membranous basal piece is in fact present in the Thorictinae (*Thorictus*, *Thorictodes*), in the Dermestinae (*Dermestes*) (Figs. 2 and 3), in the Anthreninae (*Anthrenus verbasci*) and in the Trinodinae (*Trichelodes*: PEACOCK, 1978).

- In both tribes of the Thorictinae the parameres articulate on the penis (median lobe) rather than on the basal piece (Fig 3A,C), which is also a typical characteristic of the Dermestidae (Fig. 3D).

Larvae

- In *Dermestes*, the larval 10th abdominal segment always forms a clearly visible specialized pygopod with a completely sclerotized and pigmented ring. However, in the *Thorictodes heydeni* larva the 10th segment is short and membranous, consisting mostly of lobes around the anus (ANDERSON, 1949). No information exists for *Thorictus*.

- In *Dermestes* and other Dermestid larvae (REES, 1943), the setae of the anterior margin of the larval epipharynx are specialized (i.e. broader or leaflike) near the epipharynx midline. In *Thorictodes heydeni*, on the contrary, they are simple. No information exists for *Thorictus*.

- There are 3 apical teeth on the apex of the larval mandible in *Dermestes* (REES, 1947), 2 in *Thorictodes heydeni* (VAN EMDEN, 1924; ANDERSON, 1949) and, apparently only one ("stumpf einspitzig") in *Thorictus foreli* (REICHENSPERGER, 1926).

- A larval mandibular prostheca exists in *Dermestes* (REES, 1943) and in *Thorictodes heydeni* (ANDERSON, 1949). No information exists for *Thorictus*.

- The lacinia of the larval maxillae is bifid in *Dermestes*, in other Dermestidae (REES, 1943) and in *Thorictodes heydeni* (ANDERSON, 1949). However, it seems to be monofid in *Thorictus foreli*, according to the drawing of REICHENSPERGER (1926).

1.4. Conclusion and Discussion

Thoracic and antennal differences allow the division of the former Thorictidae sensu lato into two tribes, Thorictini for the myrmecophilous genera and Thaumaphrastini for the free-living one. These tribes form the subfamily Thorictinae of the Dermestidae.

The Thorictinae as defined here, have been related, in the literature, to the Dermestinae, because the adults of both subfamilies lack a median cephalic ocellus (but this is also the case for the genus *Trichelodes* of the Trinodinae: PEACOCK, 1978). We might add that the rectum of the Thorictinae and Dermestinae is lined with a chitinous armature (however not the

same and the Dermestine armature being found also in a Bostrychid), unlike some other Dermestid subfamilies. The larvae of Thorictinae and Dermestinae are provided with a pair of posterior tergal processes on the 9th abdominal segment (but these urogomphi are also present in the Orphilinae and in a near family, the Derodontidae) and with setae arranged in four rows on each side of abdominal segments (distinctly in *Dermestes* (REES, 1947) and less distinctly in *Thorictus foreli* (REICHENSPERGER, 1926) and *Thorictodes heydeni* (ANDERSON, 1949)).

However, even if we do not consider the trichomes, which are obvious adaptations to myrmecophily, the Thorictinae and the Dermestinae strongly differ in the organization of thoracic ventrolateral sutures and by the articulation of the 9th abdominal tergite with the 9th sternite.

The pterothoracic sutures, particularly the deep groove-like anapleural sutures of the Dermestinae and other subfamilies (e.g. Attageninae, Anthreninae, Megatominae) enable some mobility of the adjacent sclerites, a feature most probably linked to flight. The reduction or disappearance of these sutures and grooves in Thorictinae is probably linked to the loss of flight in this subfamily and, even further, in the Thorictini, to the strenghtening of the thoracic exoskeleton into a thick shield in order to protect against the biting of ants. The Thorictinae also totally differ from the Dermestinae in the way that the 9th tergite and sternite articulate on each other. The Dermestine kind of articulation is found in some other subfamilies.

There seem to be other remarkable differences between the Thorictinae and the rest of the Dermestids, such as the presence of free Malpighian tubules in *Thorictus foreli* (following BANKS, 1927). Dermestids are known to be cryptonephridics; however free Malpighian tubules are known to exist in the near families Nosodendridae and Derodontidae (CROWSON, 1955).

These differences show the need for a thorough cladistic study of the Dermestoidea or Bostrichoidea in order to gain more information on the phylogenetic relations and distances between their components. The remarks on the characters are likely to be useful for such an approach. In the meantime, we have conferred the rank of subfamily to the former Thorictidae (sensu lato), which we think is a logical and balanced decision. In doing so, we also align with the current trend of pushing downwards the status of other former myrmecophile families such as the Paussidae and the Clavigeridae.

When the status of a small group provided with a non-nominal name lowers from family to subfamily or tribe, its name becomes associated in the title of the paper with a better known family name, which then gives the reader an immediate idea of its phylogenetic relationships. The disadvantage lies in the difficulty of information retrieval because when a family name is present, usually only this name is kept as a distinct key word in some of the most read literature abstract indexes.

2. Biology

2.1. Overview of selected literature on *Thorictus foreli* and related species

Thorictus foreli frequently behaves as a phoretic by securing its mandibles to the basal third of a *Cataglyphis bicolor* worker or sexual antennal scape. The clypeus and mentum are said to be therefore characteristically grooved (ESCHERICH, 1898; BANCK, 1927). Attached in this position, the beetle does not feed and may be carried for days. Good illustrations of this behaviour are given in REICHENSPERGER (1926) and JOHN (1965). More rarely, the beetle secures itself to the host's tibiae or tarsi (ESCHERICH, 1902).

While attached to an ant's antenna, the beetle stays motionless except that sometimes it may straighten its body and appears then to regurgitate a droplet on the ant's antennal scape (BANCK, 1927).

Experiments showed that the stimuli inducing the beetle to attach itself and maintain its position on the antenna are appropriate form and movement of the object on which it can conveniently clamp its mandibles (BANCK, 1927).

The periods during which *T. foreli* is attached to an antenna alternate with periods during which the beetle stays on the ground or buries itself in the soil. On the basis of BANCK's data (1927, 20 observations), we calculated that the mean duration of the "antennal" periods is 6 days, with extremes ranging from 3 hours to 17 days (even up to 9 weeks according to another observation). During these antennal periods the beetle does not pierce the host's scape for feeding, contrary to the claim of WASMANN (REICHENSPERGER, 1926; BANCK, 1927). "Free" periods have a mean duration of 12 days (calculated on basis of BANCK's data, 18 observations), with extremes ranging from 1 to 37 days (even up to 5 months according to an observation by REICHENSPERGER, 1926).

Feeding occurs during the free moving periods and may lasts up to one week. The beetle eats fresh prey and older kitchen middens (cadavers) of the colony (REICHENSPERGER, 1926; BANCK, 1927). It may also lick freshly hatched and dead workers (ESCHERICH, 1902).

According to ESCHERICH (1898), the workers lick the beetle, or do not lick it (1902), while BANCK (1927) found that they eagerly lick the trichomes, where specialized tegumentary glands emit their secretions.

The ants may constantly transport the beetle for days (it may last as long as 9 days), one mandible being inserted in the laterodorsal trichome of the prothorax, the other in the trichome pit between the meso- and metathorax (BANCK, 1927).

Experimental transfer from the host to other ant species did not induce aggressiveness in the ants (REICHENSPERGER, 1926).
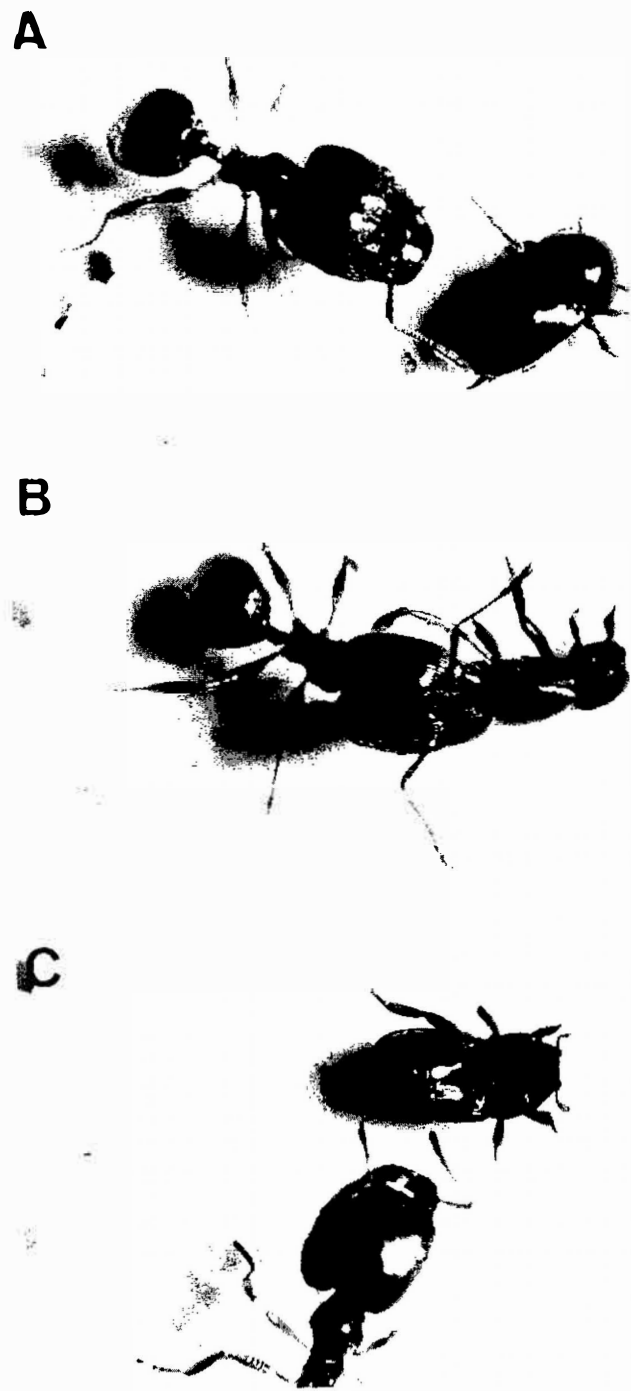
A

B

C

Fig. 4. Appeasement behavior of *Thorictus grandicollis* approached by a major worker of *Pheidole pallidula*. A: the worker antennates a passing beetle. B: the beetle turns itself on its back. C: once lying on its back, the beetle spreads its legs apart and its thoracic lateroventral trichomes are then antennated by the ant.

Copulation takes place after the male has intensively groomed the female's trichomes and elytra. The larva is indifferently tolerated by the ants and lives in the soil of the nest and feeds on kitchen middens and ant cadavers (REICHENSPERGER, 1926).

The adult of *T. foreli* thus appears to be a phoretic scavenger. As far as the other species are concerned, it is only known that some, such as *T. lethierryi* FAIRM., are antennophoretics, while others, such as *T. mauritanicus* LUC., have never been seen on the host's antennae (FOREL, 1894).

Astonishingly, two other species, *T. grandicollis* GERMAR and *T. indicus* GROUVELLE, have been found with stored food products (lentils, middlings; no other information) (AITKEN, 1975).

2.2. Behavioral relations of *Thorictus grandicollis* with its hosts

2.2.1. Material and methods

One of the two beetles we observed was found at El Port de la Selva (10.IV.1991), inside a nest of *Tetramorium semilaeve* (ANDRE) set under a stone on the gravel banks of the Riera de Romonac. Five nearby nests of the same ant species contained no beetle. This site appears to be very dry in summer.

The second beetle was found the same day, at Colera, just inside the rim of a *Pheidole pallidula* (NYLANDER) nest set under a stone lying on alluvial gravel mixed with clay, in an abandoned olive-plantation. No guest could be found in 25 other *Pheidole* and 4 *T. semilaeve* nests present in this site.

These two localities lie at sea level.

After having been collected, the beetles were kept separately in vials partly filled with moistened plaster and were observed in the laboratory after 6 to 10 days.

Each beetle was alternately deposited into an artificial ants' nest of each hosts' species through the humidification hole of the transparent cover. These two nests were made of Petri dishes half-filled with moistened plaster of Paris and contained about two hundred workers, a queen and, in the case of *T. semilaeve*, larvae and worker nymphs piles. The behavioral interactions were observed for hours under a stereomicroscope and photographed.

To observe the beetles' trail-following behavior, each of them was placed, for periods of 10 minutes, in contact with artificial circular trails. These were marked with trail pheromone solutions on circumferences (diameter: 3.2 cm) pencil-drawn on extra strong white paper and divided into 10° arcs. The pheromone solutions were deposited with a metallic pen. They were acetone extracts corresponding to 0.5 and 1.0 host workers' poison glands (from minor workers in the case of *P. pallidula*), without and with the addition of an equivalent amount of last sternite

extract. Last sternite extracts are known to be synergistic of the trail phe-romone in *T. semilaeve* and *P. pallidula* (CAMMAERTS & CAMMAERTS, 1990; DETRAIN & CAMMAERTS, 1991). The paper sheet with the trail cove-red the bottom of a small Petri dish in the center of which a beetle was deposited alone or with about twenty host workers. The trail-following behavior was checked under red light.

2.2.2. Results

Approach by the ants

The ants perceived the beetles from a short distance. They rarely appro-ached with open mandibles, this posture occurring mostly in *T. semilaeve*.

Appeasement behavior and licking

When dropped into a nest, when handled roughly by ants or simply antennated for the first time or after having been transported, the beetles did not immediately immobilize but turned themselves on their backs with their legs outstretched and stayed motionless for a long time (Fig. 4A-C). The antennae were the most often retracted. The typical position was with hind legs stretched rearwards along the abdomen, often with the tarsi nearly joined; the middle legs were stretched perpendicularly to the sagittal plane, and the fore legs were folded or stretched anterolaterally. This posture exposed the ventral face of the beetle to the ants and, more parti-cularly, uncovered its lateroventral trichomes (Fig. 5C,D). We name this particular behavior and posture of *T. grandicollis*, "appeasement beha-vior".

When the beetles remained motionless in this position, the ants began to lick all the accessible parts of their body, including the mouthparts (Fig. 5D) and tarsi, and particularly the trichomes (Fig. 5E) and pygidium although not spending much time there.

Due to the fact that the beetles very readily presented this particular "appeasement" behavior and so remained, their dorsal surface was not licked as often as the ventral surface (Fig. 5F).

The *T. semilaeve* workers more frequently licked the beetles than the minor and major *P. pallidula* workers.

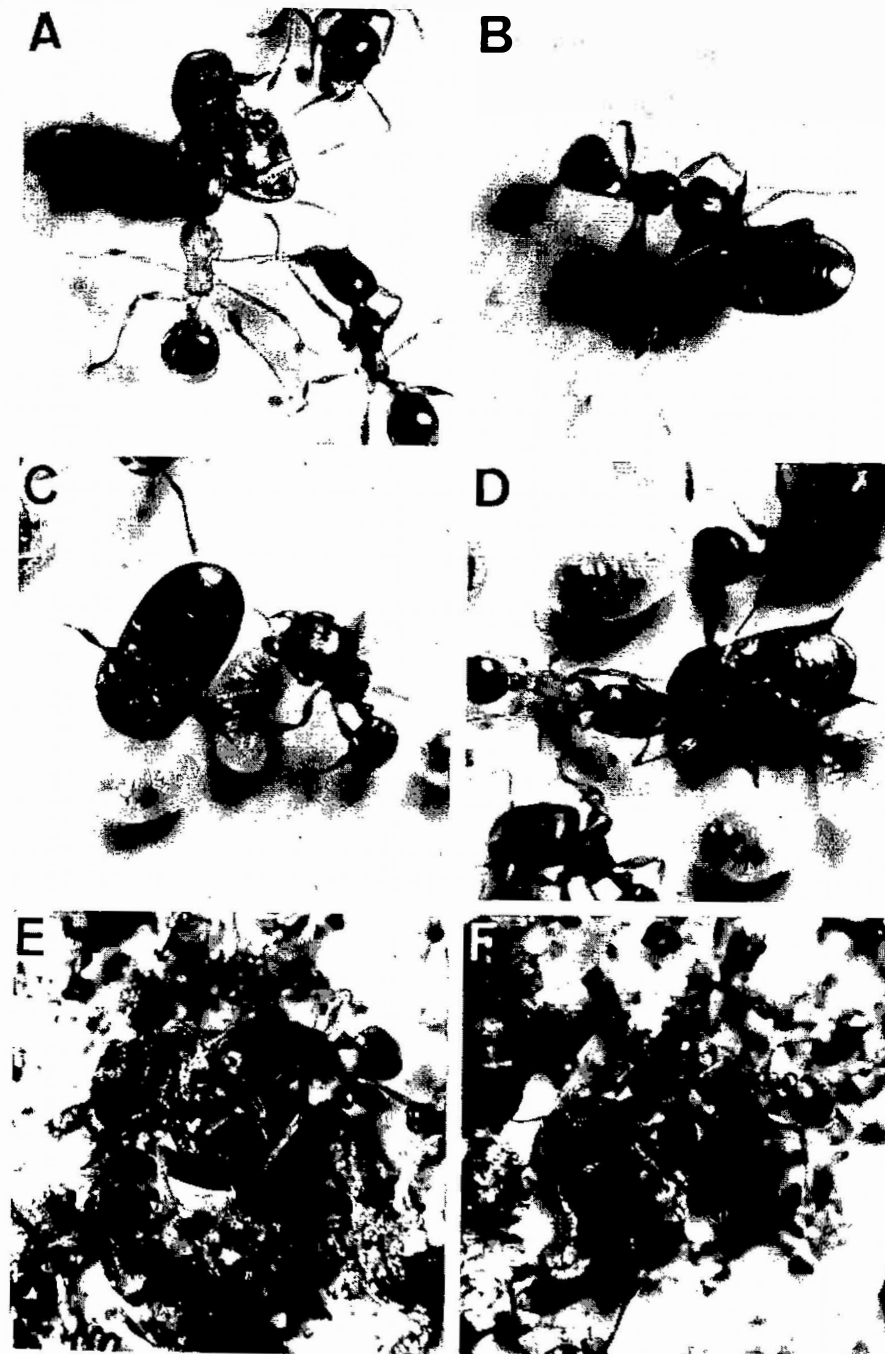The ants' licking behavior obviously cleaned the beetles' teguments.

Fig. 5. Interactions between *Thorictus grandicollis* and (A, B) *Pheidole pallidula* minor workers or (C-F) *Tetramorium semilaeve* workers. A: transport of the beetle, one of the worker's mandibles being inserted in the beetle's trichomes' pit. B: transport, the worker's mandibles grasping the basis of beetle's midlegs. C: after having been transported, a beetle was deposited next to a larva pile and displays the appeasement behavior. D: while displaying the appeasement behavior, the same beetle is approached by a worker which begins licking its mouthparts. E: a worker licks the thoracic latero-ventral trichomes of a beetle displaying the appeasement behavior amidst nest refuse materials. F: a worker licks the back of a beetle lying on its side.

When no longer touched by the ants, the beetles moved away or stayed motionless for some time on their back but then folded their legs.

Transport

Soon after having been licked, the beetles could be transported by the ants. Workers of *T. semilaeve* transported them onto or near the larvae piles, where the beetles took again the particular appeasement posture (Fig. 5C,D). The ants then licked the beetles again.

Although the ants could begin to transport the beetles by pulling them by the extremities of their legs, they mostly seized them transversely at the junction of the prothorax and mesothorax, thus in the trichomes vicinity (Fig. 5A). If carrying began by holding the beetles by the head and the fore part of their prothorax, the beetles were dropped, then seized as described above, before the transport resumed. The beetles could also be carried while being held in the ants' jaws at the proximal (coxal) part of the middle and hind legs, thus also at a place next to the lateroventral trichomes (Fig. 5B).

While being carried, the beetles kept their antennae and fore legs retracted but their middle and hind legs spread, in the manner of the appeasement behavior (Fig. 5A,B).

Beetle movement

After some time in the nest, the beetles could freely walk, without stopping or presenting the appeasement behavior when antennated.

During such movements, the beetle's head was deflected, only the antennae being seen from above and the beetle's middle and posterior femurs were rubbed against the trichomes, probably passively.

Biting

During licking sessions, *T. semilaeve* workers occasionally bit the beetles. Some of the bites looked like pinching, a harmless behavior also performed by either ant species, including major workers of *P. pallidula*.

Rest

When at rest, the beetles stayed with hidden antennae but with normally stretched middle and hind legs, the anterior part of the body staying lower than the posterior part. This posture allowed access to the trichomes.

When out of reach from the ants, the beetles could also stay motionless on their back, with folded legs. The ventral face of the femurs possess a shallow groove enabling the tibiae to be partly folded within them.

Ants were observed to rest while standing on a motionless beetle.

Feeding

The beetles were frequently seen amidst the kitchen middens, particularly in the *T. semilaeve* nest, but feeding was not observed.

When placed in the *T. semilaeve* nest, the beetles seemed neither interested in the corpse of a worker, a few hours dead and still licked by the ants, nor interested in a piece of cockroach cadaver aged about 12 hours.

The beetles showed no interest in *T. semilaeve* live worker larvae or nymphs.

Aggregation of ants

T. semilaeve workers were more likely to aggregate around the beetles than *P. pallidula* workers.

Trail following

The beetles perceived the trail of *P. pallidula* and of *T. semilaeve*: they stopped in front of it or rested on it.

However, they never followed the trails either marked with a poison gland extract, or with a poison gland plus a last sternite extract. Moreover, the additional presence of workers on the trail did not affect the beetles' performance.

2.3. Sex ratio

In order to examine the male hidden abdominal sclerites of *T. grandicollis*, we dissected all the available material (46 individuals) but encountered no male. The species' sex ratio in this sample is thus less than 0.02. The dissected beetles were clearly identified as females by their conspicuous genital styles on the extremities of hemisternites 9. A drawing of the male hidden sclerites of *T. grandicollis* is nevertheless given by JOHN (1963), however without information on the geographic origin of the beetle and on the male frequency.

The dissected specimens were the two collected by us and museum-preserved material collected in Europe (France, without locality, 3 specimens; Marseille, 1; St. Raphaël, 1; Toulon, 11; Hyères, 15; "Bola et Larrin", 3; Madrid, 3; Corsica, 7) These museum specimens are not dated or provided with data which can tell us how they were collected but the examination of their labels shows that at least nine different people collected them. It is thus likely that these beetles have been found at different periods of their life cycle, which should exclude a sex ratio bias due to a time-linked sexual behavior.

The highly significant biased sex ratio (two-tailed binomial test: $P < 0.00006$) which we found in *T. grandicollis* should be explained by particularities of the genetic dynamics of the species (see Discussion).

We could compare this aberrant sex ratio with that of the two other Thorictine species used in this study, by the examination of available

museum material and of the literature. We found the sex ratio of North African *T. foreli* to be 0.69, which, according to the size of the sample (n = 26), is not significantly different from the 0.50 equilibrium ratio (two-tailed binomial test: P = 0.08). When describing the male and female anatomy of this species, BANCK (1927) failed to notice anything special about its sex frequencies. Furthermore, we found that a European sample of the free-living *Thorictodes heydeni* had a sex ratio of 0.45 (n = 20), while a sample from India had a sex ratio of 0.46 (n = 86) (CHATTERJI & SARUP, 1959). The sex ratio of these two samples does not significantly differ from 0.50 (P = 0.83 and 0.26). The sample of 19 individuals on which ZHANG & LIU (1988) based the description of their new Chinese species, *Thorictodes brevipennis*, presents a sex ratio of 0.42, which is also not significantly different from the equilibrium ratio (P = 0.64).

2.4. Conclusions and discussion

Two important behavioral traits distinguish *T. grandicollis* from *T. foreli*.

Firstly, *T. grandicollis* never behaves as a phoretic on its hosts, while this is normal behavior in *T. foreli*.

Secondly, when approached or handled by an ant, *T. grandicollis* reacts by displaying remarkable and unique appeasement behavior: turning itself on its back and remaining motionless with its legs spread apart, it allows the lateroventral trichomes to be investigated and licked by the ants.

On the contrary, when knocked over or struck by the antennae of its host, *T. foreli* is reported to "feign death" with retracted legs. This behavior is said to ease the picking up of the beetle by the ants' mandibles (BANCK, 1927). Contrary also to *T. grandicollis*, *T. foreli* is reported to retract its legs when transported (BANCK, 1927).

The appeasement behavior of *T. grandicollis* should not be confused with thanatosis with irregularly positioned legs, which often occurs when insects are roughly handled or dropped from some height (e.g. in the Pselaphid *Claviger testaceus*: CAMMAERTS 1991a). Personal observations also enable us to say that most of the free-living small beetles which encounter ants immobilize themselves with their legs retracted under their body, so presenting the least possible surface of their back to the ants. However, when myrmecophilous beetles are investigated for the first time by ants, most of them stand upright, motionless on their legs, and do not crouch (e.g. three species of Staphylinids: HÖLLDOBLER & WILSON, 1990 and the Pselaphid *Claviger testaceus*: CAMMAERTS, 1991a).

The use of the term "appeasement behavior" for *T. grandicollis* requires further clarification as we did not experimentally prove that this behavior inhibited the limited aggressiveness of the workers. This term seems, however, to be correct because the sole instances where *T. grandicollis* was found to retract its legs was in the absence of ants. (Appeasement

glands or substances appearing to suppress aggressive behavior in the ants are reported in the pygidium of the Staphylinids *Atemeles pubicollis*, *Lomechusa strumosa* and *Dinarda dentata* (HÖLLDOBLER & WILSON, 1990).

The biting of *T. foreli* by ants is not reported in the literature, unless this behavior has been confused with the grasping of the beetle before its transport. *T. grandicollis* was rarely bitten by its hosts. Biting the guest is known to occur for most myrmecophiles after they are transferred from one society to another. However, biting might also have a meaning other than aggressiveness. This is the case for the Clavigerine Pselaphid *Claviger testaceus* after it has spent a long time in a host's society. Then biting still constitutes 40% of the occurrences of the host's behavioral units and 11% of the time spent by the host when interacting with the beetle (CAMMAERTS, 1991b).

We never observed *T. grandicollis* in the act of feeding but for *T. foreli* it is known that very long periods of fasting may alternate with feeding periods (REICHENSPERGER, 1926; BANCK, 1927).

No interaction was seen between *T. grandicollis* and the queens of either host species.

T. grandicollis does not follow the trail of its hosts, a fact which may be explained by a morphological characteristic. The distance between the extremities of the beetle's antennae does not exceed 1 mm, which is probably less than the width of the active space of the trail pheromone. This fact together with the lack of lateral mobility of the head could hinder *T. grandicollis* following a trail by osmotropotaxis.

Another guest of *P. pallidula*, the Tenebrionid *Dichillus minutus*, does not follow the trail of its host (CAMMAERTS *et al.*, 1989 and further unpublished work). Both *Dichillus* and *Thorictus* are slow moving and have a great resistance to desiccation (as may be inferred from their thick cuticle) and a low host specificity (unpublished observations for *D. minutus*). The latter two characteristics mean that these beetles are not obliged to rapidly find another nest when outside nor to follow a trail. Unlike *T. grandicollis* and *D. minutus*, another guest of *P. pallidula*, the Paussine Carabid *Edaphopaussus favieri*, follows the host's trail very well, although this behavior needs to be aroused by the presence of ants on the trail (CAMMAERTS & CAMMAERTS, 1992). Contrary to the two other beetles, *E. favieri* is highly host specific and has weak teguments, making it sensitive to dessication (CAMMAERTS *et al.*, 1990). These two reasons may explain why *E. favieri*, and not *T. grandicollis* or *D. minutus*, follows the host trail.

T. grandicollis has a surprisingly highly female-biased sex ratio. As the genetics of the Thorictinae are not known, we can only try to give an explanation by reference to unrelated organisms.

Besides the particular case of thelytokous parthenogenesis, female-biased sex ratios are common among small arthropods with specialized microhabitate requirements, such as those distributed in strongly structured demes. Empirical evidence and mathematical modelling show that such a bias may

be attributed to an allele coding for it and to any factor that affects the productivity of the trait group (WILSON & COLWELL, 1981). Models taking into account the effect of high local mate competition (LMC) and level of inbreeding in diploid or haplo-diploid species show that when the number of foundresses is nearly equal to one, the sex ratio tends to be around zero (HAMILTON, 1967; HERRE, 1985; BULMER, 1986). The more extreme-biased sex ratios thus appear when the population size is strongly reduced.

The very low sex ratio of the European populations of *T. grandicollis* is thus consistent either with thelytoky or with the existence of isolated sub-populations with very few individuals. The latter seem to be the case. The discovery of such an extremely biased sex ratio should prompt future research to look at the population structure of *T. grandicollis*, particularly the number of males and females per ant's nest and if the species reproduces or not parthenogenetically.

Apart from the sex ratio, the only certainties that can help us to understand the reproductive biology of *T. grandicollis* are that the two sexes are wingless (we could not verify it for the male, but the contrary has never been specified in the literature), are very slow moving and that the species has "island" specialized microhabitat requirements (the scattered host's nests).

The only other *Thorictus* species whose biology is somewhat known, is *T. foreli*. Although wingless, this species does not appear to have a biased sex ratio. Its phoretic behavior on the workers' antennae is likely to facilitate its dispersal among hosts' nests and, so, possibly prevents it from having structured populations. In fact, *T. foreli* has also been found attached to the antennae of sexuals (ESCHERICH, 1902).

The sex ratio of the free-living *Thorictodes heydeni* also appears to be in equilibrium. This wingless species does not spread by phoresis but, at present, thanks to the world trade of stored food products (it has been found associated with a very wide variety of plant products and even with fish and bone meal). Another species of *Thorictodes*, *T. brevipennis*, seems to have a balanced sex ratio and might also be associated with stored food products, as can be inferred from the paper of ZHANG & LIU (1988).

Our fragmentary knowledge of the interactions between *T. grandicollis* and its hosts prevents us from drawing reliable conclusions about the status of the beetle in the ants' societies. Social integration is, however, unlikely, *T. grandicollis* having been found in nests of very different Myrmicinae such as *Pheidole pallidula*, *Tetramorium semilaeve* (this work), *T. "caespitum"*, *Aphaenogaster testaceopilosa*, *Messor barbara* and even *Monomorium solomonis* (HETSCHKO & WASMANN, 1925). It may also be interesting to point out that experiments showed that *T. foreli* can be accepted by at least 8 different ant species belonging to 2 subfamilies (REICHENSPERGER, 1926; BANCK, 1927) and that it may be transported and deposited by its host ant on the kitchen middens, like a piece of refuse (BANCK, 1927).

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Crabroniens du Chili des genres *Podagritus* SPINOLA, 1851 et *Rhopalum* STEPHENS, 1829 (Hymenoptera: Sphecidae)

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Résumé

Dans les collections de Sphécides Crabronini *provenant du Chili que j'ai pu étudier jusqu'ici, j'ai reconnu 15 espèces de* Podagritus SPINOLA, 1851, *et 6 espèces de* Rhopalum STEPHENS, 1829. *La plupart sont endémiques ou retrouvées seulement dans des régions voisines de l'Argentine. Leur comparaison a permis de revoir la définition des deux genres et de justifier plusieurs synonymies indiquées précédemment d'une manière préliminaire.*
Les espèces suivantes sont nouvelles: Podagritus colchagae, Rhopalum chinquense, collectum, nahuelbutae, *et d'Argentine:* kovacsi. *Une combinaison nouvelle s'impose:* Physoscelus longinodus SPINOLA, 1851, = Podagritus longinodus *(*SPINOLA*). La combinaison* Podagritus magellanus LECLERCQ, 1957 *est rétablie, ce n'est pas un* Rhopalum.
Un néotype est désigné pour trois des espèces de Rhopalum *pour lesquelles du matériel originel a été cherché en vain:* Physoscelus brevinodus SPINOLA, 1851, Physoscelus crassinodus SPINOLA, 1851, *et* Crabro claudii JANVIER, 1928.
On n'a pas connaissance de l'existence au Chili d'espèces d'autres genres de Crabronini.

Introduction

Les premières étapes de l'étude des Crabroniens du Chili datent de SPINOLA (1851), REED (1894) et KOHL (1905). Vinrent ensuite les recherches de Paul HERBST, habitant Valparaiso, qui vers 1920 préparait une publication mais ne mena pas son projet à terme. On eut ensuite les observations éthologiques de JAFFUEL & PIRION (1926) et surtout celles de JANVIER (1928).

J'admis qu'il faut classer les espèces connues de ces auteurs et d'autres trouvées aussi au Chili, certaines dans le genre *Podagritus*, les autres dans