

Notes on the New World allopatric beetle genus *Mycotrupes* (Scarabaeoidea: Geotrupidae) and on *Geotrupacarus mycotrupetes* (Krantz & Mellott) (Acari: Macrochelidae), an early derivative phoretic mite associate of *Mycotrupes gaigei* Olson & Hubbell in southeastern United States

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ABSTRACT

The five described species of the flightless, allopatric geotrupid beetle genus *Mycotrupes* are restricted to deep sand ridges in peninsular Florida and to adjacent, elevated sand hill habitats along the juncture of the Piedmont and the Atlantic Coastal Plain in southern South Carolina and Georgia, USA. Based on examination of major museum collections of all five described *Mycotrupes* species, it was concluded that *Geotrupacarus mycotrupetes*, a distinctive, early derivative macrochelid mite phoretic on *Mycotrupes gaigei*, does not occur on any of the other four described species of *Mycotrupes*, nor have other species of *Geotrupacarus* been found on any of these beetles, all of which (like *Myco. gaigei*) are isolated and allopatric in their own sand ridge or sand hill habitats. It also was determined that *Geotrupes egeriei* Germar, a winged, widely distributed geotrupid beetle that co-occurs with *Myco. gaigei* in Florida and which is strongly attractive to *G. mycotrupetes* in laboratory settings, has not expanded the range of *G. mycotrupetes* beyond peninsular Florida.

Keywords *Mycotrupes*; *Geotrupacarus*; *Geotrupes*; allopatry; arenicolity; kairomones; reproductive strategy; niche integrity; hypervolume

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INTRODUCTION

Mycotrupes LeConte

The geotrupid beetle genus *Mycotrupes* (Fig. 1) comprises five flightless, relict, allopatric species that occupy deep, well-drained sand ridges overlying porous limestone in peninsular Florida (Woodruff 1973) and a narrow, more northerly elevated sand hill zone separating the Atlantic Coastal Plain from the adjacent Piedmont in South Carolina and Georgia, a zone referred to as the Fall Line (Fig. 2). *Mycotrupes* species are efficient burrowers, often tunneling down through sand to depths exceeding six feet (Howden 1954, 1955). Their sandy habitat is mostly a xeric, open woodland in which the most abundant trees are turkey and bluejack oaks that originally served as the understory for a great pine forest that thrived there in earlier times. Clumps of seedling oaks and low shrubs surrounded by quantities of dead leaves, along

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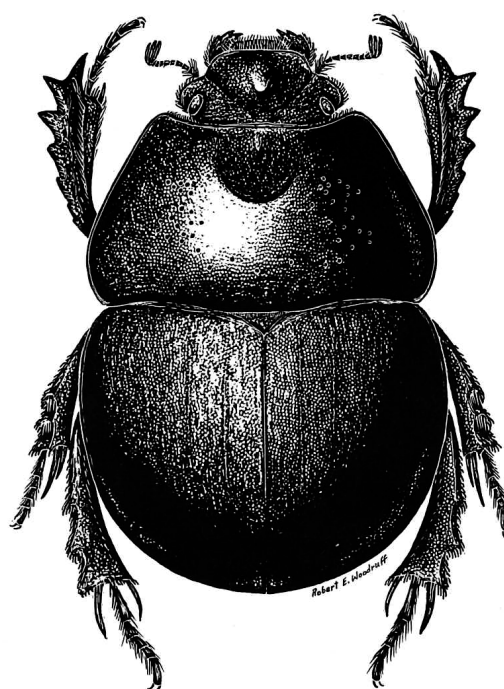


Figure 1 *Mycotrupes gaigei* Olson & Hubbell (from Woodruff 1973).

with a scattering of grasses and various herbs, also are common there (Olson & Hubbell 1954). *Mycotrupes* species are generalist feeders that take advantage of virtually any available organic food substrate in their heterogenous environment: dung, decaying fungi, plant litter, and even exposed soft tissue of acorns. As noted by Beucke (2009), reliance on a particular food source where its availability from year to year or season to season often is unpredictable would be a risky strategy for a genus whose members are flightless and consequently restricted in their searching capacity. According to Howden (1955, 1963), flightlessness in *Mycotrupes* arose early in the development of the genus and is a consequence of metathoracic wing degradation, coupled with median fusion of the prothoracic elytrae.

The deep sand ridges that shelter *Mycotrupes* species are believed to be remnants of ancient shorelines laid down during the alternating flooding/emergence episodes of the Pleistocene Epoch (Cooke 1945, Fig. 3). These sand ridges are isolated from one another by areas of poor drainage, shallow sand, swamps, marshes, rivers, low-lying dry timberland, or dense vegetative hammocks. Barriers such as these apparently were enough to produce the vicariance events that led to allopatry of *Mycotrupes* populations and to their subsequent speciation.

Hubbell (1954) presented a compelling evolutionary scenario for *Mycotrupes* in which he considered *Mycotrupes gaigei* Olson & Hubbell (Fig. 1) to be the most aberrant member of the genus, and its paleogeographic niche in western peninsular Florida (Fig. 2) to be the site where the genus made its first appearance during the late Tertiary. Hubbell's conclusions were later evaluated during the course of a molecular phylogenetic study of *Mycotrupes* by Beucke (2009), whose findings were based on nucleotide sequence data derived from a 481 base pair fragment of the Cytochrome Oxidase I gene taken from all five *Mycotrupes* species. Beucke's parsimony analysis revealed that the two Fall Line species, *Myco. retusus* (LeConte) and *Myco. lethroides* (Westwood), are basal to the other three described members of the genus (*Myco. gaigei*, *cartwrighti* O. & H. and *pedester* Howden), from which Beucke concluded that the genus originated on or close to the Fall Line, possibly during the Tertiary. He also concluded that, at some point after the sea level had fallen well below the level of the elevated Fall Line for

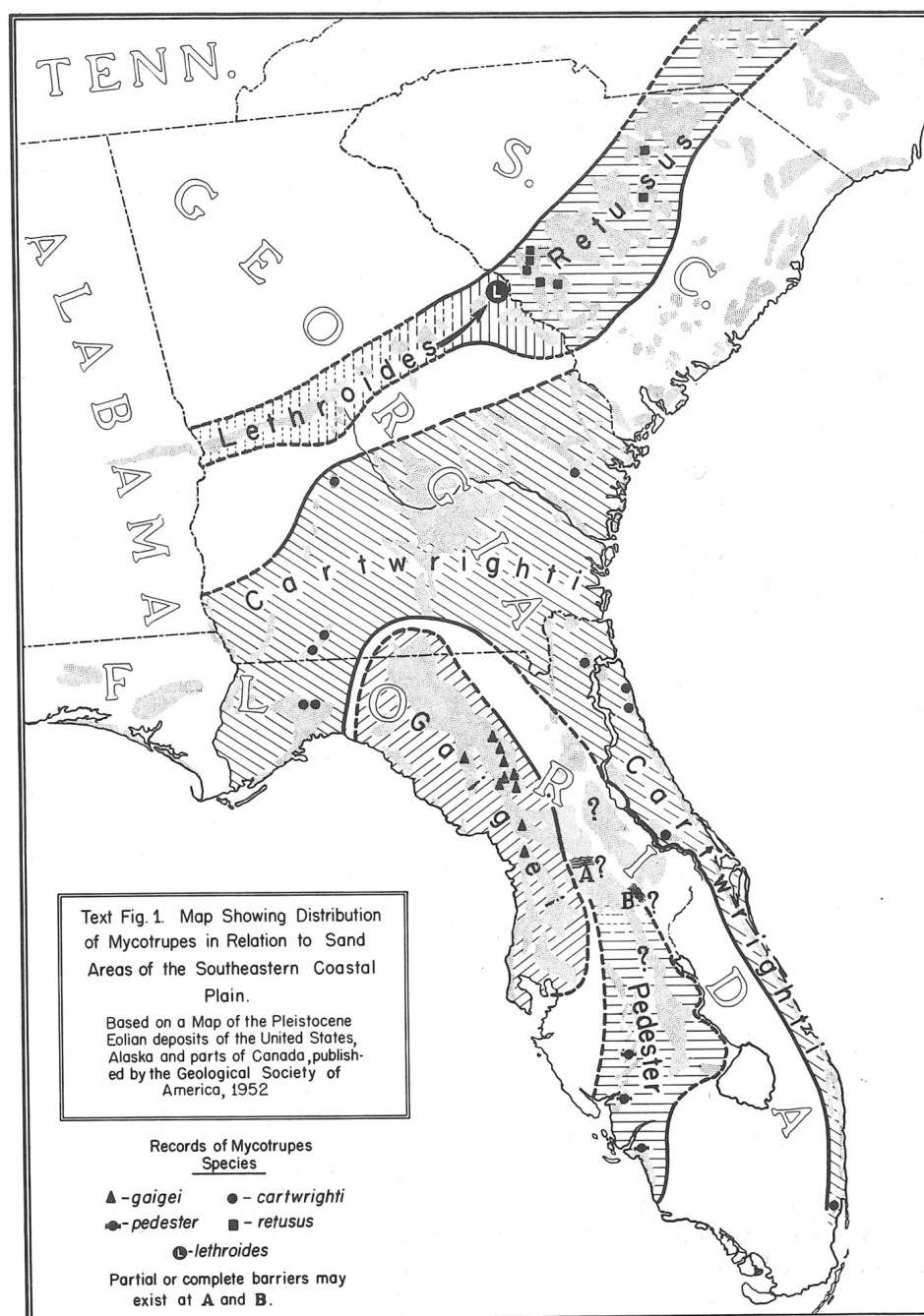


Figure 2 *Mycotrupes* species distribution in peninsular Florida and along the more northerly Fall Line (from Hubbell 1954, after Geol. Soc. Amer. 1952).

the last time in the late Pleistocene (Fig. 3), a southward dispersal of *Myco. retusus* gave rise to *Myco. gaigei*, *cartwrighti*, and *pedester*, along with a possible cryptic species in the *cartwrighti* lineage. Based on Beucke's findings, sea level changes generated by intermittent glaciation and melting events during the Pleistocene evidently played a major role in the evolution of *Mycotrupes*.

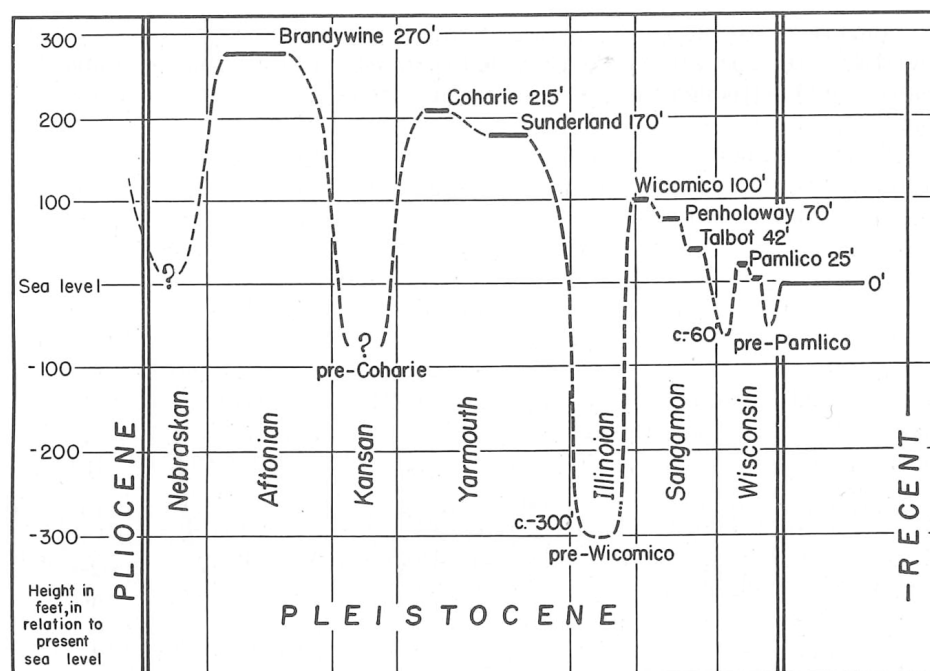


Figure 3 Diagram showing Pleistocene terraces (interglacial periods) and major sea level depressions (glacial periods), of the southeastern Coastal Plain and their presumed chronology (from Cooke 1945).

***Geotrupacarus mycotrupetes* (Krantz & Mellott)**

Scarabaeoid beetles worldwide serve as hosts for a variety of mites, and *Mycotrupes* is no exception. *Geotrupacarus mycotrupetes* (Fig. 4), a mite originally described as a member of the genus *Macrocheles* by Krantz & Mellott (1968), is a large (>1,000 µm), distinctive phoretic form that attaches preferentially behind coxae I or in the gular area of *Myco. gaigei* in northwestern peninsular Florida. Like its beetle host, *G. mycotrupetes* is arenicolous and burrows with ease through sand substrates. In laboratory studies, it was observed to use its formidable burrowing capabilities in locating *Myco. gaigei* when the beetles and the mites were sequestered in separate wire mesh cages beneath the sand surface (Fig. 5), presumably in response to recognition of a kairomonal cue generated by the beetle host (Krantz & Royce 1994). Although it is clearly phoretic, the morphology and reproductive strategy of *G. mycotrupetes* point to a close phylogenetic relationship with early derivative, free-living macrochelid taxa best exemplified by the genus *Nothrholaspis* Berlese (Emberson 2010). Like *Nothrholaspis*, *G. mycotrupetes* lacks the subterminal bidentate tooth typically present on the cheliceral movable digit of more highly derived phoretic macrochelids, a structure coupled with an opposing ribbed platform on the fixed digit to form a complex for grasping a single hair of its host (Fig. 6). In addition, the lateral elements of the gnathotectum of *G. mycotrupetes*, like those of *Nothrholaspis* species, are broadly fused to a bifurcated central element (Fig. 4d) rather than being free and flaglike as in more highly derived forms. The female ventrianal shield (Fig. 4b) is narrow and oblong rather than being subtriangular or broadly rounded as in *Nothrholaspis* species (Emberson 2010), and the cribrum has narrow paranal extensions (Krantz, 2009) (overly abbreviated in Krantz & Mellott, 1968, Fig. 4b) that are more typical of early derivative lineages rather than being totally reduced to a narrow band of spicules confined to the posterior margin of the shield as in more highly derived macrochelids. Similar cribral extensions also occur in all postlarval immatures of *G. mycotrupetes* (Krantz 1990, Krantz & Royce 1992). Postepigynal platelets, again characteristic of more primitive lineages,

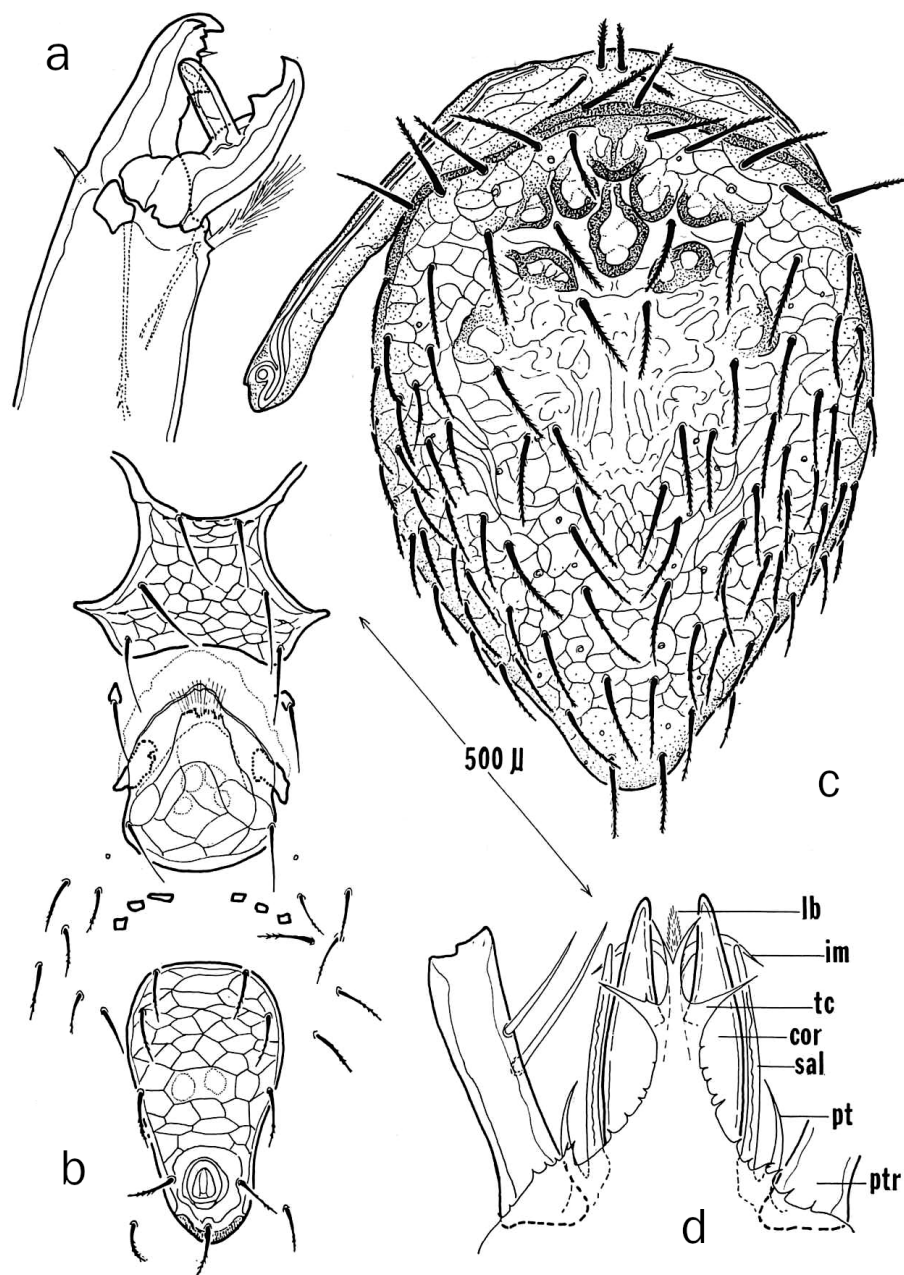


Figure 4 *Geotrupacarus myotrupetes* Krantz & Mellott. a – male chelicera; b – venter of female; c – dorsal and peritrematic shields of female; d – prodorsal aspect of female (tc=gnathotectum, cor=corniculum, lb=labrum, im=internal mala, sal=salivary stylus, pt=patrocinium, ptr=palptrochanter I) (from Krantz & Mellott 1968) (courtesy J. Kansas Entomol. Soc.).

are present in the female (Krantz 1998). Among the less obvious morphological features that define both described species of *Geotrupacarus* (*G. myotrupetes* and *peltotrupetes*) are the infrequent and often obscure barbs that ornament the subcapitular and ventral shield setae. Their obscurity is a consequence of some barbs being so closely aligned to their given seta that they are easily overlooked, as sometimes occurred in the original species descriptions (Krantz & Mellott 1968). Finally, the reproductive strategy of *G. myotrupetes* is more suggestive of

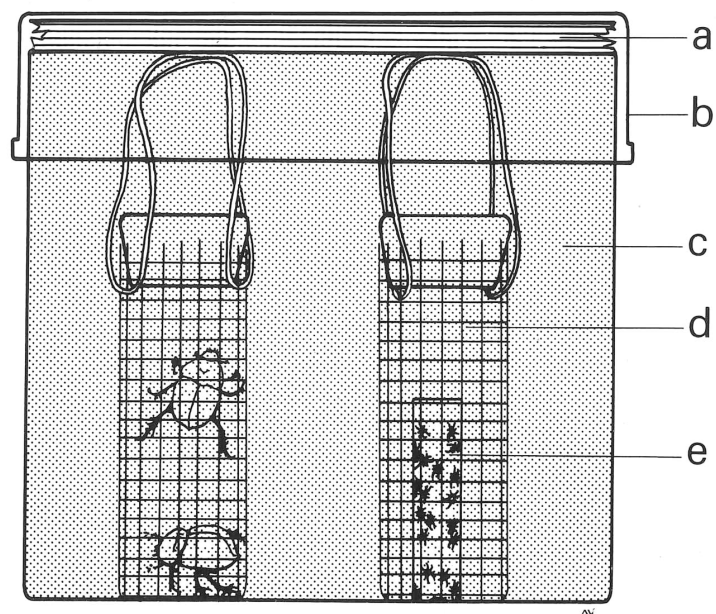


Figure 5 Test arena for verifying intergallery movement of *Geotrupacarus mycotrupetes* through a sand barrier (a=moistened paper towel layer, b=carton lid, c=sand, d=wire cylinder, e=shell vial) (after Krantz & Royce 1994).

primitive diplodiploidy or parahaploidy (*sensu* Norton *et al.* 1993) than of the arrhenotokous form of haplodiploidy common to most insect-associated phoretic macrochelids (Krantz & Royce 1994).

Overall, the primitive characteristics of *G. mycotrupetes*, coupled with its unusual phoretic proclivities, lends credence to the concept that phoresy has arisen more than once in the Macrochelidae (Krantz & Royce 1992), and at the same time raises the question as to whether a phoretic association with a non-vagile host like *Myco. gaigei* could involve something other than transport to a fresh food substrate.

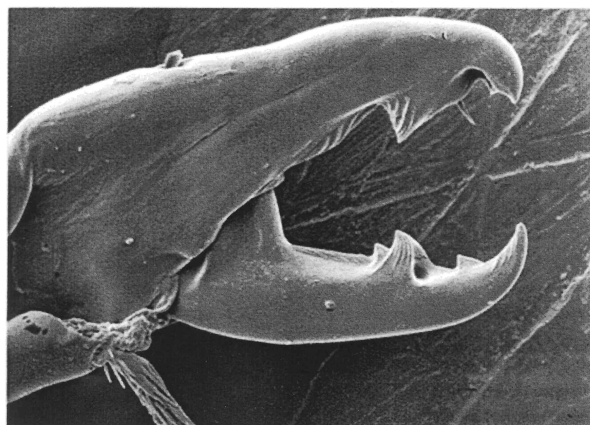


Figure 6 Female chelicera of *Macrocheles hallidayi* Walter & Krantz (from Walter & Krantz 1986) (courtesy Can. J. Zool.).

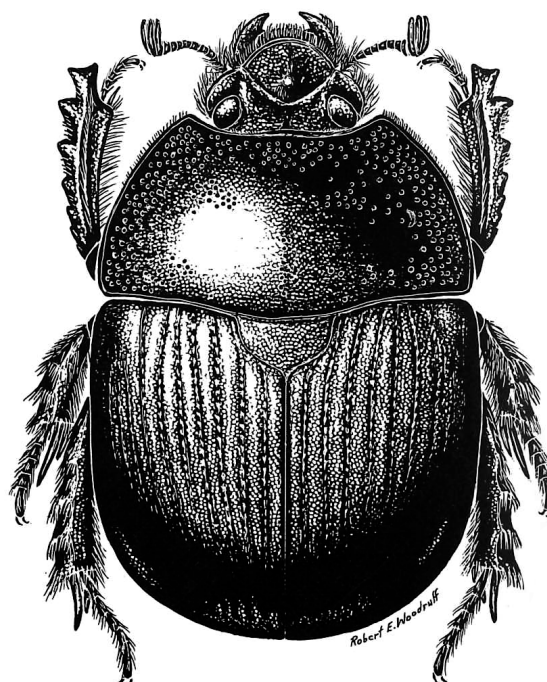


Figure 7 *Geotrupes egeriei* Germar (from Woodruff 1973).

Objectives

The major objectives of this study were to determine 1) whether *G. mycotrupetes*, originally described as phoretically specific on *Myco. gaigei*, occurs on any of the other four described species of *Mycotrupes* (viz., *retusus*, *lethroides*, *cartwrighti*, *pedester*); 2) whether other, heretofore undescribed, members of the genus *Geotrupacarus* occur on species of *Mycotrupes* other than *gaigei*; and 3) whether *G. egeriei* (Fig. 7), a winged, widely distributed geotrupid that co-occurs with *G. mycotrupetes* in Florida, and to which *G. mycotrupetes* is strongly attracted in laboratory settings, may have succeeded in expanding the range of *G. mycotrupetes* beyond Florida and the Fall Line.

Materials and methods

Although commonly observed in field collections, occurrence of *G. mycotrupetes* on *Myco. gaigei* tends to be erratic, which implies that verifying the presence of *G. mycotrupetes* on *Myco. retusus*, *lethroides*, *cartwrighti* or *pedester*, or confirming the presence of undescribed *Geotrupacarus* species on any of these beetles, would likely require access to relatively large numbers of specimens. Accordingly, requests for study material went out to four museums where significant geotrupid beetle collections were known to be located (see Acknowledgements for details). The recognized potential for *G. egeriei* to expand the range of *G. mycotrupetes* northward beyond Florida (see Objective 3, above) made *G. egeriei* an additional target of museum searches during the course of this study.

Results and discussion

More than 400 mite collections taken from all five described *Mycotrupes* species offered convincing support for the conclusion that *G. mycotrupetes* is phoretically specific to *Myco. gaigei*. No other species of *Geotrupacarus* were found on any of the 133 available specimens of *Myco. retusus*, *lethroides*, *cartwrighti* and *pedester*, nor was there any evidence to suggest that *G. egeriei* had carried *G. mycotrupetes* beyond its normal Florida range. It should be noted here that available *Myco. gaigei*, *Myco. cartwrighti* and *G. egeriei* specimens (282, 73, 104) far outnumbered the more narrowly distributed and less often collected *Myco. pedester*, *lethroides* and *retusus* (28, 15, 17), leaving room for speculation as to whether additional collections of the latter three species might reveal a broader host distribution for *G. mycotrupetes*, or verify the presence of other species of *Geotrupacarus*.

Geotrupacarus mycotrupetes seems to have defied a major precept of phoresy in choosing a host beetle that is flightless and presumably unable to carry it to fresh food substrates. Also, the incidental recovery of other phoretic *Macrocheles* species on four of the five species of *Mycotrupes* (*Myco. lethroides* excepted) and of phoretic Eviphididae on three species of *Mycotrupes* (*Myco. pedester* and *Myco. retusus* excepted), leaves unanswered the question as to what benefit can be expected from a relationship between these highly derived phoronts and flightless, reclusive allopatric beetles that spend much of their lives in deep sand burrows. Clearly, there are factors involved in these relationships that have yet to be resolved.

The strong attraction of *G. mycotrupetes* to *G. egeriei* in laboratory settings (Figs. 8a, b) belies the virtual absence of the mite from field collections of *G. egeriei* beyond Florida. This seeming contradiction illustrates the overarching importance of niche integrity and habitat dimension in natural ecological systems. Moving beetles from their natural habitat to an alien laboratory environment is disruptive not only for the beetles, but for their acarine phoronts as well, and may account for the unexpected high boarding levels of *G. mycotrupetes* on *Geotrupes egeriei* (at most an incidental host under natural conditions) in mite boarding tests on beetle candidates in both individual and group choice experiments (Krantz & Mellott 1972).

In their natural habitats, scarabaeoid beetle species each occupy an n -dimensional universe in which they respond in given ways to biotic and abiotic signals inherent to that universe. Hutchinson (1957) referred to these n -dimensional universes as hypervolumes. Each

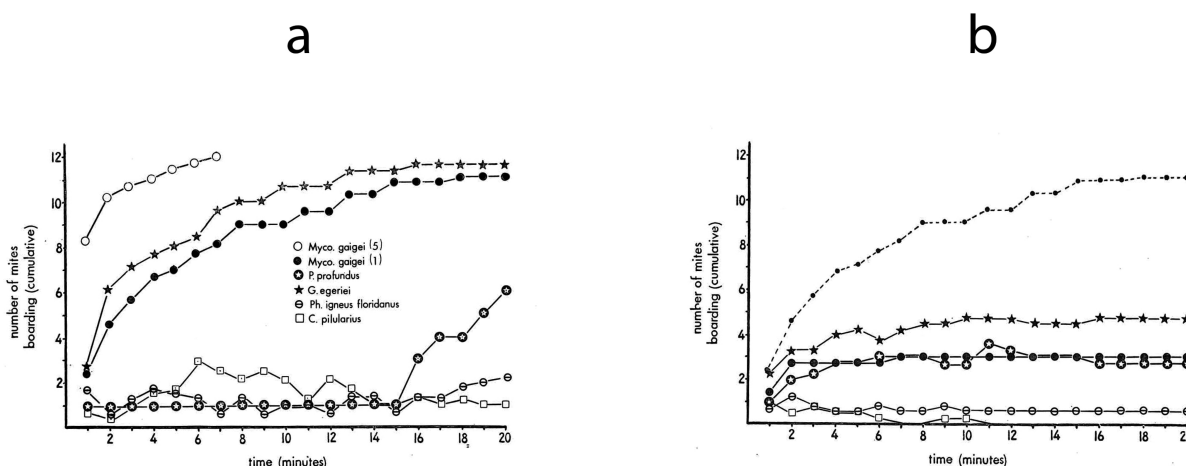


Figure 8 Mean cumulative boarding rates of *Macrocheles mycotrupetes* (four replicates of 12 mites each). a – boarding rates on individual beetle species in five separate experiments (see insert for graph symbols), plus one test using five *Mycotrupes gaigei* (open circles); b – mite boarding rates on *Mycotrupes gaigei*, *Pelotrupes profundus*, *Geotrupes egeriei*, *Phanaeus igneus floridanus* and *Canthon pilularius* when offered in combination. Small solid circles connected by broken line in Figure 8b show boarding rate of individual *M. mycotrupetes* on *Myco. gaigei* alone (latter taken from Figure 8a) (after Krantz & Mellott 1972).

scarabaeoid species maintains an insularity based on its hypervolume, an insularity that also provides the conditions for niche integrity of their phoretic acarine associates (Krantz 1991). Chemical signals in the form of beetle-generated kairomones are a particularly important dimension for phoretic acarines occupying the n -dimensional universe of their host. In the laboratory setting referred to earlier, it appears that attraction of *G. mycotrupetes* to a given beetle species was based primarily on recognition of a class of kairomones common to both *Mycotrupes* and *Geotrupes* (Krantz & Mellott 1972, Krantz 1998). A study of the chemical structure of this compound in *Mycotrupes* cuticle (Krantz *et al.* 1991) revealed that it corresponds in some respects to the major dihydroxy wax ester found in uropygial fluid, an oily substance produced in a gland near the anal vent of many birds and used by them to waterproof their feathers. Based on that study, the kairomonal attractant in the cuticle of *Myco. gaigei* was tentatively identified as a dihydroxy wax or its diol ester.

Finally, in regard to *G. egeriei* and the four other scarabaeoid beetle species whose levels of attractiveness to *G. mycotrupetes* in the laboratory were referred to by Krantz & Mellott (1972), the loss of niche integrity occasioned by transfer of test beetles from the field to a laboratory setting apparently left *G. mycotrupetes* with only one recognizable dimension to which it could respond—the chemical dimension. Future laboratory studies on phoretic responses of mites to prospective hosts should therefore consider niche integrity and dimension as major variables when creating experimental systems.

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I acknowledge with pleasure the receipt of beetle specimens, alcoholic mite collections, and pertinent tabular data on mites taken from *Mycotrupes* species and from *G. egeriei* provided by curators of four major geotrupid collections in the US and Canada. Paul Skelley, Head Curator of the Florida State Collection of Arthropods in Gainesville, kindly sent data sheets and 62 alcoholic collections of *G. mycotrupetes* and other gamasines from all five *Mycotrupes* species, and E. Richard Hoebeke, Associate Curator and Collections Manager of the University of Georgia Collection of Arthropods in Athens provided 20 mite-laden *Mycotrupes* and *Geotrupes egeriei* beetles for study. Mite data on 53 *Mycotrupes* and 29 *Geotrupes egeriei* collections were generously provided by Frédéric Beaulieu and Wayne Knee, Acari Unit Curator and Curator Assistant at Ottawa's Canadian National Collection of Insects, Arachnids and Nematodes. I am grateful to François Génier, Curator of the Canadian Museum of Nature in Ottawa, who sent essential data on mites from 290 *Mycotrupes* and 71 *G. egeriei* specimens housed in CMN, a small subset of the vast geotrupid collection bequeathed to the Museum by the late Henry F. Howden, a world specialist on the Geotrupidae. My thanks also to Brett Ratcliffe, Curator of the University of Nebraska Beetle Collection, who provided mite specimens from *G. egeriei* during the early days of this project, and to Chris Marshall, Curator of the Oregon State Arthropod Collection in Corvallis, who shared information on pertinent museum collections and made the OSAC collection of geotrupids available to me for study. Finally, I thank the late Robert Woodruff, author of many fine works on Florida scarabs, for his advice and encouragement when I first delved into the complex and fascinating world of Florida scarabaeoids and their equally fascinating acarine phoronts.

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