Exp Appl Acarol (2009) 49:45–84
DOI 10.1007/s10493-009-9287-6

Carcases and mites

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Received: 5 June 2009 / Accepted: 16 June 2009 / Published online: 24 July 2009

Abstract Mites are involved in the decomposition of animal carcases and human corpses at every stage. From initial decay at the fresh stage until dry decomposition at the skeletal stage, a huge diversity of Acari, including members of the Mesostigmata, Prostigmata, Astigmata, Endeostigmata, Oribatida and Ixodida, are an integral part of the constantly changing food webs on, in and beneath the carrion. During the desiccation stage in wave 6 of Mégnin's system, mites can become the dominant fauna on the decomposing body. Under conditions unfavourable for the colonisation of insects, such as concealment, low temperature or mummification, mites might become the most important or even the only arthropods on a dead body. Some mite species will be represented by a few specimens, whereas others might build up in numbers to several million individuals. Astigmata are most prominent in numbers and Mesostigmata in diversity. More than 100 mite species and over 60 mite families were collected from animal carcases, and around 75 species and over 20 families from human corpses.

Keywords Carrion · Carcass · Corpse · Cadaver · Animal decomposition · Necrophagy · Necrophagia · Succession · Post mortem interval

Introduction

Corpses of humans and carcases of animals represent biocenoses that are often composed of complicated food webs. Especially under the combined influence of residential bacteria from the gut and introduced blow or flesh flies, the decomposition of a recently deceased body can proceed very rapidly, resulting in a constantly changing habitat for necrophilous and necrophagous arthropods and other animals and fungi. These changes might be

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considered as a succession of microhabitats or seral sequences, microseres, which might be divided into a series of definable stages that might be called microseral stages. Insect species dominate the serially changing populations on carcases. However, mites are receiving increased recognition as a part of forensic biology (Frost et al. 2009; Perotti and Braig 2009a; Perotti et al. 2009b). Mites are also involved in most stages of decomposition of animal and human remains. This paper tries to list the most abundant mite fauna associated with decomposition.

Waves of arthropods

Early work on decomposition in forensic medicine was inspired by case observations of the arthropod fauna associated with exposed human corpses. Jean Pierre Mégnin in Paris, France, organised his observations in his book *La Faune des Cadavres [The Fauna of Carcases]*, where he observed that arthropods appear in 8 distinct waves on the carcases of humans. He illustrated this with 19 forensic case studies described in detail (Mégnin 1894). A short summary of the 8 waves was published a year later (Mégnin 1895). There remains an oddity in Mégnin's legacy. Specimens of the corpse fly *Hydrotaea capensis* recovered from 1 year-old corpses from the cemetery of Saint Nazaire in Paris were assigned by Mégnin to wave 5 and to an otherwise unknown wave 9 (Pont and Matile 1980). Over time, several more insect species have been added to the list of waves of arthropods (Table 1). In Mégnin's original observations, an entire wave, the sixth, was composed of only mites. Later on, Leclercq added mites also to the very first wave (Leclercq and Verstraeten 1993). Several other authors have added additional species to the list of waves. Porta in Parma, Italy, distinguished 9 waves of arthropods associated with ten stages of human decomposition. In his system, waves 6 and 7 were, among others, characterised by larvae, nymphs and adults of Acari. These 2 waves represent the initial and final pre-skeletal stages, each lasting for 3–4 months for exposed and for concealed corpses (Porta 1929). At the skeletal stage, only small numbers of adult mites were recovered by Porta.

Mégnin's appreciation of mites in a forensic context has been acknowledged early on by forensic entomologists and pathologists (Graells 1886; Ríos 1902a, b; Lecha-Marzo 1917; Porta 1929). However, the proposed succession of insects and Mégnin's interpretations were questioned over time by many (Strauch 1912; Wyss and Cherix 2006).

Mégnin's work on the arthropod succession on human corpses led him to describe several new species of mites and flies. Some of the species descriptions in *La Faune des Cadavres* are very brief and the associated drawings not particularly detailed. This has not been a problem in cases where subsequent workers have acknowledged Mégnin's species descriptions and included them in their revisions.

Serrator amphibius Mégnin (1894) is a revision by Mégnin himself of *Tyroglyphus rostro-serratus* Mégnin 1873 and should now be recognised as *Histiostoma feroniarum* (Dufour 1839) (Histiostomatidae, Astigmata). The identification of *Serrator necrophagus* Mégnin (1894) is more of a problem. Should it be considered as *Histiostoma necrophagus* (=? *necrophori* Dujardin) (Leclercq and Verstraeten 1988b)? According to OConnor (pers. comm.), *S. necrophagus* is a composite of *Histiostoma* and *Myianoetus* and as such unrecognisable.

The two species *Uropoda nummularia* Mégnin (1894) (? Uropodidae Kramer 1881, Mesostigmata) and *Trachynotus cadaverinus* Mégnin (1894) (? Trachyuropodidae Berlese 1917, Mesostigmata) had not been taken up by a systematic acarologist and their identity has remained a puzzle for a long time. Few authors have reproduced the characteristics of

Table 1 Based on 15 years of experience at the Paris morgue, Mégnin described 8 waves, squads or periods of arthropod succession on human corpses exposed to the air (escouades or séries des travailleurs de la mort [sections or series of death workers or gravediggers of nature (Gaudry 2002)])

Faunal succession as established by Mégnin on exposed human corpses	
1st wave – bodies fresh; normally, first 48 h but can last for 3 months after death	
Muscidae	
Musca domestica, house fly	
	M. autumnalis (=*M. corvina*), face or autumn house fly
Muscina stabulans (=*Curtonevra stabulans*), false stable fly	
Stratiomyidae	
	Hermetia illucens, black soldier fly
Phoridae	humpbacked or scuttle flies
Calliphoridae	
Calliphora vomitoria, holarctic blue blow fly	
	C. vicina (=*C. erythrocephala*), European bluebottle fly
	Chrysomya albiceps, blow fly
	Lucilia spp., greenbottle flies
	Protophormia terraenovae, bird's nest screwworm fly
	Phormia regina, black blow fly
Acari	mites
2nd wave – decomposition commenced, odour developing; 48–72 h but can last for the first 3 months after death	
Muscidae	
	Hydrotaea dentipes, sweat fly
Calliphoridae	
Lucilia caesar, golden greenbottle fly	
	Lucilia sericata (=*Phaenicia sericata*), sheep blow fly
	Cynomya mortuorum, bluebottle fly
Sarcophagidae	
Sarcophaga carnaria, grey flesh fly	
S. arvensis, flesh fly	
S. laticrus (=*Myophora laticrus*), flesh fly	
	S. (Liopygia) argyrostoma (=*Parasarcophaga argyrostoma*), flesh fly
Staphylinidae	
	Omalium rivulare, rove beetle
3rd wave – fats becoming racid, butyric fermentation; 3–6 months after death	
Dermestidae	
Dermestes lardarius, larder or bacon beetle	
D. frischi, common hide beetle	
D. undulatus, skin beetle	
Pyralidae	
Aglossa pinguinalis, grease moth	
A. caprealis, fungus or murky meal moth	
4th wave – caseous fermentation; 3–4 to 6–8 months after death	
Piophilidae	
Piophila casei, cheese skipper, jumping maggot	
P. petasionis, ham and cheese fly	

Table 1 continued

Faunal succession as established by Mégnin on exposed human corpses	
Anthomyiidae	
Chortophila vicina (=*Anthomyia vicina*), banded fly	
Anthomyia pluvialis, banded fly	
A. vesicularis, banded fly	
Cleridae	
Korynetes caeruleus (=*Corynetes violaceus*), bone beetle	
K. ruficornis (=*Corynetes coeruleus*), blue hide beetle	
Necrobia ruficollis (=*Corynetes ruficollis*), red-shouldered ham beetle	
N. rufipes (=*Corynetes rufipes*), red-legged ham beetle	
N. violacea, black-legged ham beetle, blue corynetes	
Staphylinidae	
	Omalium rivulare, rove beetle
Fanniidae	
Fannia scalaris (=*Anthomyia scalaris*), latrine fly	
Milichiidae	
	Madiza glabra, insect jackal
Syrphidae	
	Eristalis tenax, drone fly, rat-tailed maggot
	Brachyopa spp., hover flies
Ephydridae	
	Scatella fusca (=*Teichomyza fusca*), urine or urinal fly
Heleomyzidae	
	Tephrochlamys rufiventris, sun fly
Drosophilidae	vinegar flies
Sciaridae	dark-winged fungus gnats
Sepsidae	black scavenger flies
Sphaeroceridae	small dung flies
Trichoceridae	winter crane flies
5th wave – ammoniacal fermentation, black liquefaction, evaporation of sanious fluids; 4–5 to 8–9 months after death	
Piophilidae	
Thyreophora cynophila, skipper fly, considered extinct	
Centrophlebomyia anthropophaga (=*Thyreophora anthropophaga*), bone skipper, almost extinct	
	C. furcata, bone skipper
	Dasyphlebomyia stylata, skipper fly
Lonchaeidae	
Lonchaea nigrimana, lance fly	
Muscidae	
Hydrotaea capensis (=*Ophyra cadaverina* Mégnin,=*Ophyra anthrax*), dung or corpse fly	
H. leucostoma (=*Ophyra leucostoma*), black garbage or dump fly	
Phoridae	
Phora aterrima, scuttle fly	
	Triphleba spp., humpbacked flies
Silphidae	
Nicrophorus interruptus (=*Necrophorus fossor*), *burying beetle*	

Table 1 continued

Faunal succession as established by Mégnin on exposed human corpses
N. humator, black sexton beetle
N. investigator, banded sexton beetle
Necrodes littoralis (=*Silpha littoralis*), bent-legged silpha, shore sexton beetle
Oiceoptoma noveboracensis (=*Silpha noveboracensis*), small or margined carrion beetle
Silpha obscura, carrion beetle
Histeridae
Margarinotus brunneus (=*Hister cadaverinus, H. impressus*), clown beetle
Gnathoncus rotundatus (=*Saprinus rotondatus*), carrion beetle
Euspilotus assimilis (=*Saprinus assimilis*), clown beetle
Saprinus semistriatus, striped clown beetle
Hister foedatus, hister beetle
Leiodidae
Catops spp., round fungus beetle
Nitidulidae
Carpophilus spp., dried fruit beetles
6th wave – desiccation; 5–6 to 10–12 months after death
Mesostigmata
Dinychidae (Uropodidae)
Leiodinychus krameri (=*Uropoda nummularia* Mégnin) ?
Trachytidae
Uroseius acuminatus (=*Trachynotus cadaverinus* Mégnin) ?
Astigmata
Acaridae
Acarus siro (=*Tyroglyphus siro*, *Tyrolichus casei*)
Tyrophagus longior (=*Tyroglyphus longior*, *Tyroglyphus infestans*)
Histiostomatidae
Histiostoma feroniarum (=*Serrator amphibius* Mégnin, *Tyroglyphus rostro-serratus* Mégnin)
Serrator necrophagus Mégnin ?
Glycyphagidae
Glycyphagus destructor (=*Glyciphagus cursor* Mégnin, *Glyciphagus spinipes*)
7th wave – complete desiccation; after 8 months or 1–3 years after death
Pyralidae
Aglossa caprealis, fungus or murky meal moth
Tineidae
Tineola bisselliella, webbing clothes or carpet moth
Tinea pellionella, case-making clothes moth
Monopis laevigella (=*M. rusticella*), fur moth
Dermestidae
Attagenus pellio, fur beetle
Anthrenus museorum, museum beetle
Dermestes maculatus, leather, hide or bacon beetle
Nitidulidae
Omosita colon, pollen or sap beetle
Trogidae
Trox unistriatus, skin beetle

Table 1 continued

Faunal succession as established by Mégnin on exposed human corpses
8th wave – debris; over 3 years after death
Tenebrionidae
Tenebrio molitor, yellow mealworm beetle
T. obscurus, dark mealworm beetle
Anobiidae
Ptinus brunneus, brown spider beetle

Species aligned to the left in the list represent the species originally identified by Mégnin (1894), species more to the right are additions made by subsequent workers (Johnston and Villeneuve 1897; Leclerq 1969; Smith 1973, 1986; Leclercq and Verstraeten 1993; Gaudry 2002). For some of the additional species, the assignment of a species to a particular wave varies with the locality and author. The systematics of species has been adapted to current use; the original and one of its synonyms, where appropriate, are in parentheses. Species names with '?' are discussed in the text. Where available, the vernacular name of the insect species is given, otherwise one of the common names of its family is used

Mégnin's species and often not in easily accessible publications, which might have contributed to them being overlooked (Ríos 1902b; Porta 1929). In addition, the mite name *T. cadaverinus* is sometimes confused with a beetle species. However, these species have finally been identified as quite common and widespread mites. Athias-Binche (1994) recognises *U. nummularia* as a synonym of the round grain or round brown mite, *Leiodinychus krameri* (G & R Canestrini 1882) (Dinychidae or Uropodidae) and *T. cadaverinus* as *Uroseius acuminatus* (CL Koch 1847) (Trachytidae), which can be phoretic on the phorid fly *Aphiochaeta rufipes*.

Mégnin differentiates between *Glyciphagus spinipes* Ch. Rob. and *Glyciphagus cursor* Mégnin (1894), both are now considered synonyms of the pilous or groceries mite *Glycyphagus (Lepidoglyphus) destructor* (Schrank 1781) (Glycyphagidae, Astigmata). Mégnin also differentiates between *Tyroglyphus longior* Gervais 1844 (Mégnin 1894) and *Tyroglyphus infestans* Berlese 1884 (Mégnin 1898), both are now synonyms of the seed mite *Tyrophagus longior* (Gervais 1844). However, the *Tyrophagus* species reported by Mégnin might have been a mixture of species (Perotti 2009).

The forensically important bulb mite species *Cœpophagus echinopus* depictured in detail in Mégnin's *La Faune des Cadavres* in 1894 is now recognised as *Rhizoglyphus echinopus* (Fumouze and Robin 1868) (Acaridae, Astigmata).

All species in the genus *Caloglyphus* Berlese 1923 will be listed as *Sancassania* Oudemans 1916 (Acaridae, Astigmata) (Samšiňák 1960). *Tyroglyphus mycophagus* Mégnin 1874 became *Caloglyphus mycophagus* and is now *S. berlesei* (Michael 1903). Some consider it one species, according to Hughes and Baker these are two species, and Moniez in 1892 has described a mite species as *Tyroglyphus mycophagus* that is now recognised as *S. chelone* Oudemans 1916.

In the early Spanish literature, mites of the genus *Carpoglyphus* (Carpoglyphidae, Astigmata) are listed as part of Mégnin's mite-rich sixth wave but have not been reported since then (Lecha-Marzo 1917).

The carrion or grave fly, *Ophyra cadaverina* Mégnin (1894) (Muscidae, Diptera), fifth wave, had been ignored by entomologists for some time. Around 85 years after the original publication in Mégnin's book, a bottle was discovered by accident in the Natural History Museum in Paris with insects collected from corpses and labelled 'Travailleurs de la Mort'.

The bottle also contained three specimens of *O. cadaverina* that allowed the identification of Mégnin's species as a junior synonym of *O. capensis* (Wiedemann, 1818; Pont and Matile 1980). Species in the genus *Ophyria* have meanwhile been transferred to the genus *Hydrotaea*, however, molecular studies place *Ophyria* species in a clade separate from *Hydrotaea* (Schnell e Schühli et al. 2004, 2007). The bottle must have been part of original material offered to the museum by Mégnin. Acarologists have not yet investigated whether some of the mites have been saved as well.

It is surprising that Mégnin didn't observe any mite species in wave 7, complete desiccation. The beetle species in this wave, *Dermestes* spp., *Trox* spp. and similar species, are well known for the large numbers and diversity of phoretic mites they carry (Perotti and Braig 2009b).

Some taxa such as the grease and fungi moths, may appear subsequently in 2 separate waves; first with wave 3, when the body fats started oxidising, particularly *Aglossa pinguinalis*, and later with wave 7, when the carcase has dried out, mostly *A. cuprealis*. The species composition of insects and mites will vary with the region, temperature, season, amount of light and shade, level of concealment, presence of vertebrate scavengers and other environmental peculiarities. Interestingly, the species composition might even change with time. For example, several species of bone skippers, *Thyreophora* species, are so specialised to later stages of the decomposition of large carcases that they have become extinct or are close to extinction. Decomposing bone marrow may be the preferred larval diet or the protection provided by large bones might be essential for the survival of the larvae. These species only remain in small pockets in countries like India (Kashmir) where their existence depends on the availability of later stages of decomposition of large animal carcases like horses (Michelsen 1983). One expects that Indian elephants might provide an even better habitat for these flies. Ironically, *Thyreophora* is not only a skipper fly genus threatened by extinction, it is also an extinct suborder of shield-bearing dinosaurs. During the time of Mégnin, sufficient numbers of large animals seem to have been allowed to decompose completely in nature to enable the species to survive. Through human intervention, most large animal carcases are now removed from the land before they reach advanced stages of decomposition. Changes in human behaviour influence which species participate in the decomposition process.

The time line of the 8 waves seems to have changed as well. Leclercq observed that the scuttle flies, Phoridae, no longer appear in wave 5 around 4–8 months after death but might arrive as early as week 3 and might also be found very late until several years after death. The mites no longer colonise the carcase as a compact wave between 6 and 12 months but in the experience of Leclercq, mites will arrive much earlier and more likely in 4 specific waves dependent on the physical state of decomposition of the carcase. He differentiates between the following appearances of the carcase as specific habitats for mites: 'outright liquid [franchement aquatiques]', 'semi liquid [semi-aquatiques]', 'a little bit wet [peu hydrophiles]' and 'in the process of desiccation or dry [milieu en voie de dessication ou desséché]' but didn't assign specific species to each habitat (Leclercq and Verstraeten 1988a, 1993; Leclercq 2002).

The waves of arthropods in Mégnin's system overlap with each other; they often form a continuum where it becomes difficult to say where one particular wave ends and a subsequent wave starts. Environmental conditions like the degree of drying out of the carcase or the impact of vertebrate scavengers might prevent several waves of arthropods arriving at a carcase. Many insect species are habitat specific. Ants (Hymenoptera), not mentioned in Mégnin's system, might be the numerically dominant species on a carcase under certain environmental conditions. And more critique has been expressed regarding individual waves and taxa. However, the acarological importance of this list is that most if not all of the insects arriving at the carcase might carry mites. Perhaps the easiest way to obtain a structured overview of the time line, the potential mite carriers and of the potential predators of mites still might be the use of Mégnin's system.

Stages of decomposition

Currently the state of a carcase is described by a state of decomposition rather than by a wave of arthropod colonisation. Five stages (Table 2) are most commonly recognised for exposed and concealed carcases as described by Goff (2009). Six stages of decay are proposed for the decomposition of pig carcases in water (Payne and King 1972).

Table 2 Terms of the most commonly recognised five stages of decomposition of vertebrate animals and humans

1 *Initial decay, fresh stage*
Carcase appears fresh externally but is decomposing internally due to the activities of bacteria, protozoa and nematodes present in the animal before death.
This stage begins at the moment of death and ends when bloating is first evident. The first organisms to arrive are blow flies and flesh flies. Eggs or larvae are deposited around the natural openings or wounds
2 *Putrefaction, bloated stage*
Carcase swollen by gas produced internally, accompanied by odour of decaying flesh.
Gasses produced by the metabolic activities of anaerobic bacteria first cause a slight inflation of the abdomen, and the corpse may later assume a fully inflated, balloon-like appearance. Internal carcase temperatures begin to rise as a combined result of putrefaction processes and metabolic heat of the fly larvae. Predatory taxa such as rove beetles arrive. Fluids seeping from natural body openings combined with ammonia produced by the fly larvae cause the soil beneath the carcase to become alkaline. Normal soil fauna will depart the area beneath the remains
3 *Black putrefaction, active decay, decay stage*
Flesh of creamy consistency with exposed parts black. Body collapses as gases escape. Odour of decay very strong.
The decay stage begins when the skin is broken, allowing gases to escape and the remains deflate. Diptera larvae from large feeding masses are the predominant taxa; Coleoptera arrive in numbers. Necrophagous and predatory taxa are observed in large numbers during the latter part of the stage. By the end of the stage, the blow and flesh flies will have departed the remains for pupariation. The fly larvae will have removed most of the flesh by the end
4 *Butyric fermentation, advanced decay, post-decay stage*
Carcase drying out. Some flesh remains at first, and cheesy odour develops. Ventral surface of body mouldy from fermentation.
Remains are reduced to skin, cartilage, and bones. Various beetle species will dominate and their diversity will increase; parasites and predators of beetles will increase as well. In wet habitats such as swamps and rain forests, beetles will be replaced by flies and other taxa
5 *Dry decay, dry decomposition, skeletal stage, remains stage*
Carcase almost dry to complete dry; slow rate of decay.
Only bones and hair remain. A gradual return of the normal soil fauna to the area beneath the remains. There is no definitive end point to this stage and some variations in the composition of the soil fauna may be detectable even years following the death depending on local conditions

Some stages have (almost) interchangeable names given by different authorities, like butyric fermentation and advanced decay; others like butyric fermentation and post-decay overlap only partially. The last term at each stage is the one used by Goff (2009). The rough description of the stages follows Bornemissza (1957) for guinea pigs. The more detailed description follows Goff (1993) for pigs and humans

Mites are numerous on carcases

Mites are not a rarity on carcases. A few examples and citations from the literature might illustrate this. Acarina are numerous on pig carcases (Gill 2005). Butyric fermentation and advanced decay will attract mites in such numbers that they become visible to the naked eye. However, they are often mistaken for mould, which is present at that time as well, or for fine sawdust, as is emphasised by one of the classical chapters on forensic entomology (Haskell et al. 1997). Large quantities of mites give a fluffy appearance to decomposing pigs (Anderson et al. 2002). In a study of 43 dog carcases in Tennessee (USA), mites were sometimes distributed on the upper surface of carcases (Reed 1958). Where any skin was left by the skin feeders of the previous stage, an immense number of tyroglyphid mites consumed the remainder leaving nothing but bones of guinea pigs (Bornemissza 1957). A very large number of Staphylinidae, Catopidae, Diptera and Acarina were collected from the carcases of bank voles (Nabagło 1973). Watson in Louisiana, USA, collected in pitfall traps under six alligators, three bears, six deer and six swine a total of 218,514 Parasitidae mites (Watson 2004). During the fresh stage of decomposition 23 Parasitidae plus 7 seed mites, during the bloating stage 1,427 Parasitidae plus 99 seed, 7 needlenose, 4 mushroom and 2 strawberry mites, during active decomposition 5,062 Parasitidae plus 87 seed and 23 needlenose mites, during advanced decomposition 51,418 Parasitidae plus 104 seed and 6 needlenose mites and during dry decomposition 160,584 Parasitidae plus 194 seed, 15 needlenose, 8 strawberry and 4 mushroom mites. Unfortunately, the identity of the mites behind these vernacular names remains unresolved.

For his twelfth case, Mégnin concluded: ‘the abundance of the Acarina, which were of an immense number, incalculable, on the leg of the mummy that we had to examine, proves that they were the principal agents of this mummification, without denying, however, that the abundance was helped by special environmental circumstances’ (Mégnin 1895). Von Niezabitowski (1902) also reported to always find larger numbers of mites belonging to the ‘Gamasidae’ (Mesostigmata) on human corpses but didn’t consider it to be characteristic. Mégnin’s first discovery of mites on and in a mummified newborn baby from the Paris area was followed by a report of a similar case from Montpellier in France (Brouardel 1879; Lichtenstein et al. 1885).

The early cases describe the mummified corpses to be covered by a brownish layer some 2 mm thick and made up exclusively of mite carcases, exuvia and faeces (Brouardel 1879; Perotti and Braig 2009b). Such a brownish layer has been reported from many more cases of mummified corpses of babies and adults. However, in many cases this layer was not microscopically examined and the possible presence of mites was not detected (Strauch 1928; Forbes 1942). The detection of the small black fly *Phora aterrima* (Phoridae) in such a brownish layer might distract from looking for mites. When baby pig carcases were put in burial pits, during the later part of advanced decomposition, mites became so numerous that they gave the carcase a mottled appearance; and during dry decomposition, ants, flies, Collembola and mites were the dominant fauna (Payne et al. 1968). Myriads of mites, Thysanura (now order Collembola) and dipteran puparia but no beetles nor dipteran larvae were found on a human corpse interred for 4 years only in a burial case but without coffin in a grave 3 feet deep (Motter 1898). In a more recent case, the corpse of a young female recently exhumed after 28 years yielded thousands of live Collembola together with large numbers of Acari (mites) of the family Glycyphagidae, and fly puparia (Merritt et al. 2007).

The only habitat where mites don’t seem to be numerous is on submerged carcases. In a study with baby pigs by Vance and colleagues, it was observed that during the collection process water mites and mayflies were typically found while searching the net holding the carcase after the net and carcase were recovered from submersion in a lake (Vance et al. 1995). The water mites detached readily during the first signs of carcase disturbance. In this study water mites were recovered in nine collections compared to amphipods in 19, mayflies in 20 and chironomids in 30 collections. However, Proctor expects freshwater mites to be of little forensic value in the estimation of post mortem intervals of submerged carcases (Proctor 2009).

Buried carcases

Corpses buried in graves only experience 4 waves of arthropod invasion (Mégnin 1887, 1894). In the introduction to the section on the fauna of buried and entombed corpses, Mégnin placed Acari next to Diptera, Coleoptera and Lepidoptera as constituents but did not elaborate further on any mite species that might be part of it, though he emphasised that the larvae of the mites were not visible to the naked eye. For the fourth and last wave of buried cases, the mite genera *Uropoda* and *Trachynotus* have been reported in the early literature (Lecha-Marzo 1917).

A total of 150 exhumations in the late eighteenth century in Washington, DC (USA) yielded eight mite species on 30 human corpses, interred from 3 to 71 years (Motter 1898). This is a very high recovery rate for mites compared with insect taxa. The highest recovery rate was achieved for rove beetles of the genus *Eleusis* (Staphilinidae, Coleoptera), which were found in 56 cases interred from 1 to 11 years, followed by scuttle flies (Phoridae, Diptera), which were found on 43 human corpses interred from 3 to 38 years. The most commonly found mite species was the new species *Uropoda depressa* (Uropodidiae, Mesostigmata) present on bodies interred from 3 to 11 years. Again, this species new to science has not yet been systematically evaluated by acarologists. A completely dry and crumpling corpse interred for 71 years in a wood coffin 1.8 m deep in sandy soil contained no insects; only '*Hypopus*' species, i.e. phoretic deutonynphs of several species in the family Acaridae (Astigmata) and a single snail, *Helicodiscus lineatus,* were present. In more recent exhuminations in France of shorter burial time, mites were reported from 3 of 22 human corpse, all in the stage of putrefaction and interred for 7–9 months (Bourel et al. 2004). Remarkably, conservation treatment applied to one of the corpses had no effect on the mite colonisation. Similarly, mites, springtails and puparia of coffin fly, *Conicera tibialis*, were collected from the embalmed body of a 28 year-old female with a gunshot wound to the head. The corpse was buried at a depth of 1.8 m in an unsealed casket that was placed inside an unsealed cement vault in a cemetery in Michigan, USA (Merritt et al. 2007).

Mites in decomposition studies

Mites have been observed in many decomposition studies but often referred to as Acari, Acarina or Acarida, for example: rabbits (Chapman and Sankey 1955), active and advanced decomposition, dry remains (Wolff et al. 2004); lizards and toads (Cornaby 1974); guinea pigs (Porta 1929); chickens, during all four or five stages of decomposition (Arnaldos et al. 2004; Horenstein et al. 2005); sparrows (Dahl 1896); pigs (Anderson et al. 2002; Grassberger and Frank 2004; Pérez et al. 2005; Schoenly et al. 2005; Kelly 2006); water mites on submerged pigs (Vance et al. 1995); sheep (Fuller 1934); mice and slugs (Kneidel 1984); voles (Nabagło 1973); crows, sparrows, striped field mice and baby pigs

(Fourman 1936); a study involving some 1,200 rodent carcases in Wytham Woods around Oxford (Putman 1978); herring gulls and great black-backed gulls (Lord and Burger 1984b); fish (Walker 1957; Watson 2004); mites of the family Parasitidae on wild bear, deer, alligator and wild pig carcases (Watson and Carlton 2003). Mites have also been noticed at crime scenes or associated with human corpses but not identified (Bianchini 1929; Magni et al. 2008).

In a study of the decomposition of baby pigs in Tennessee, USA, a total of 522 species representing 3 phyla, 9 classes, 31 orders, 151 families and 359 genera were identified (Payne 1965). Due to the need for a wide variety of taxonomic expertise, there is a tendency to report only a portion of the insects found on carrion based on the insect taxa previously published as forensically significant. This leads to a bias towards large, easily collected arthropods and avoidance of taxonomically difficult groups, i.e. Acari, Sphaeroceridae, Sepsidae, Histeridae, Drosophilidae, Piophilidae and many Staphylinidae (Gill 2005). This is also evident in the list of arthropod waves in Table 1, where authors indicated families instead of species. It is obvious that Acari—not being insects—should be the most difficult group of all for (forensic) entomologists. An extreme but fascinating case might demonstrate that even for arachnologists it might not be trivial to recognize a mite as such. *Brucharachne ecitophila* was initially described from a female specimen as the sole representative of the spider family Brucharachnidae. Reexamination revealed that the female spider specimen is actually a male dermanyssiod mite, now known as *Sphaeroseius ecitophilus* (Laelapidae, Mesostigmata) (Krantz and Platnick 1995). Along with size, the taxonomic difficulty of Acari might be the most important reason why mites are so often not reported in forensic and ecological studies of decomposition.

Mites are part of a food web

There are many ecological reasons why mites might be found on carcases. Mites will feed on successive waves of bacteria, algae and fungi that develop on the carcase. 'Cheese' mites that can be found feeding on cheese and ham, will feed on the caseous stage of carcases. Carcases pre-date cheese and ham in evolutionary terms. Species of macrochelid, parasitid, parholaspidid, uropodid and other mite families will prey on other mites, insects, and nematodes on the corpse. Nematodes have long been recognised as an integral part of animal and human decomposition but have been almost completely ignored by the forensic sciences. These nematodes, like the bacteria, algae and fungi, attract predatory mites to a carcase and then become as much part of the food web of a carcase as the nematodes. Other mite species specialise on the dry remains of the carcase. Several forensic web sources suggest that mites of the genus *Rostrozetes* (Haplozetidae, Oribatida) feed on dry skin in the later stages of decomposition. While a large diversity of mite species has been collected at later stages of decomposition and from dry skin (Table 3), there is currently no evidence for any *Rostrozetes* species being associated with animal or human remains. Several species of *Rostrozetes* are very common inhabitants of leaf litter and peatlands and are found on moss and fungi from tree trunks (Behan-Pelletier and Bissett 1994). Reports on associations of *Rostrozetes* with animal skin are very rare and restricted to parasitic infestations of living animals (Parker and Holliman 1971).

Burying and sexton beetles (*Nicrophorus* spp., Silphidae) bring mites of the genus *Poecilochirus* (Parasitidae, Mesostigmata) to a carcase. These mites have long been implicated in a symbiotic interaction with their carrier host. *Poecilochirus* can kill the eggs of blow flies, which are one of the main competitors of these beetles for the carcase. Blow

Table 3 Within the decompositional stages, families with mite species reported from human corpses are listed first followed in alphabetical order by other families reported only from animal carcases

Species	Family	Abundance	Host	Location	Habitat	Country	Season (month)	Reference
Fresh stage, initial decay								
Mesostigmata								
Arctoseius sp.	Ascidae		Pig	On	Grassland, bush	Spain	12–2	Castillo Miralbes 2002
Haemogamasus sp.	Haemogamasidae[a]		Pig	On	Grassland, bush	Spain	12–2	Castillo Miralbes 2002
	Laelapidae	Increasing	Chicken	Under	Woods	ME, USA		Wasti 1972
Glyptholaspis americana	Macrochelidae	Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
Macrocheles merdarius		Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
M. muscaedomesticae		Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
	Macrochelidae	Some	Pig	On, under	Several	HI, USA		Richards and Goff 1997; Avila and Goff 1998; Davis and Goff 2000
		Increasing	Chicken	Under	Woods	ME, USA		Wasti 1972
Parasitus sp.	Parasitidae		Pig	On	Grassland, bush	Spain	12–2	Castillo Miralbes 2002
Poecilochirus necrophori		High	Mice	On	Forest	MI, USA		Wilson 1983
P. silphaphila			Large carcases	On		MI, USA		Yoder 1972; Brown and Wilson 1994
	Parasitidae	Increasing	Chicken	Under	Woods	ME, USA		Wasti 1972
Fuscuropoda sp.	Urodinychidae	Abundant	Chicken	On	Farm	IA, USA		Rives and Barnes 1988
Sp 1–3	Uropodidae	Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
		Some	Pig	On	Several	HI, USA		Hewadikaram and Goff 1991; Avila and Goff 1998
Astigmata								
Acarus farris	Acaridae		Dog	Assoc.		Costa Rica		OConnor 2009
						NY, USA		OConnor 2009
A. siro	Acaridae	Common	Lizard, chicken	On	Woods	Nigeria		Iloba and Fawole 2006
	Acaridae	Moderate	Chicken	Under	Woods	MA, USA		Wasti 1972
			Chicken	On, under	Field	Spain	10–3	Arnaldos et al. 2004

Table 3 continued

Species	Family	Abundance	Host	Location	Habitat	Country	Season (month)	Reference
Oribatida								
	Oribatids	Decline	Chicken	Under	Woods	MA, USA		Wasti 1972
Prostigmata								
Demodex brevis	Demodecidae	Decline	Human	On	Normal fauna	Worldwide		Desch 2009
D. folliculorum		Decline	Human	On	Normal fauna	Worldwide		Desch 2009
	Demodecidae	Decline	Most mammals	On	Normal fauna	Worldwide		Wilson 1844; Gmeiner 1908
	Bdellidae	Abundant	Chicken	Under	Woods	MA, USA		Wasti 1972
	Rhagidiidae	Abundant	Chicken	Under	Woods	MA, USA		Wasti 1972
	Trombidiidae	Moderate	Chicken	Under	Woods	MA, USA		Wasti 1972
			Pig	On	Bush	Spain	12–2	Castillo Miralbes 2002
Putrefaction, bloated stage—terrestrial								
Mesostigmata								
Arctoseius sp.	Ascidae		Pig	On	Grassland, bush	Spain	1–3	Castillo Miralbes 2002
Haemogamasus sp.	Haemogamasidae		Pig	On	Grassland, bush	Spain	1–3	Castillo Miralbes 2002
	Laelapidae	Fewer	Chicken	Under	Woods	ME, USA		Wasti 1972
Glyptholaspis americana	Macrochelidae	Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
Macrocheles merdarius		Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
M. muscaedomesticae		Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
	Macrochelidae	Some	Pig	On, under	Several	HI, USA		Richards and Goff 1997; Avila and Goff 1998; Davis and Goff 2000
	Macrochelidae	Fewer	Chicken	Under	Woods	ME, USA		Wasti 1972
Pachylaelaps sp.	Pachylaelapidae	Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
Parasitus sp.	Parasitidae		Pig	On	Grassland, bush	Spain	1–3	Castillo Miralbes 2002
Pergamasus sp.		Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
		Some	Pig	On, under	Several	HI, USA		Hewadikaram and Goff 1991
	Parasitidae	Fewer	Chicken	Under	Woods	ME, USA		Wasti 1972
		Common	Pig	On, under	Several	HI, USA		Richards and Goff 1997; Avila and Goff 1998

Table 3 continued

Species	Family	Abundance	Host	Location	Habitat	Country	Season (month)	Reference
Poecilochirus sp.		Some	Rabbit	On	Woods	CO, USA	7–8	De Jong and Chadwick 1999
Sp 1–3	Uropodidae	Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
		Some	Pig	On	Several	HI, USA		Hewadikaram and Goff 1991; Avila and Goff 1998
Astigmata								
Acarus siro	Acaridae	Common	Fish, frog,					
			Lizard, chicken	On	Woods	Nigeria		Iloba and Fawole 2006
Lardoglyphus zacheri	Lardoglyphidae or Acaridae		Deer	Assoc.		UT, USA		OConnor 2009
Prostigmata								
	Trombidiidae		Pig	On	Grassland, bush	Spain	9,1–3	Castillo Miralbes 2002
Ixodida								
	Ixodidae		Pig	On	Bush	Spain	5	Castillo Miralbes 2002
Putrefaction, bloated stage—freshwater								
Oribatida								
Hydrozetes sp.	Hydrozetidae		Pig	On		Canada		Hobischak and Anderson 2002
Black putrefaction, active decay								
Mesostigmata								
Cyrtolaelaps mucronatus	Rhodacaridae	One	Human (26 d)	On	Forest	Belgium	12	Leclercq 1978
Arctoseius sp.	Ascidae		Pig	On	Grassland, bush	Spain	2–4	Castillo Miralbes 2002
Haemogamasus sp.	Haemogamasidae		Pig	On	Grassland, bush	Spain	2–4	Castillo Miralbes 2002
Glyptholaspis americana	Macrochelidae	Abundant	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
Macrocheles merdarius		Abundant	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
	Macrochelidae	Abundant	Pig	On, under	Several	HI, USA		Richards and Goff 1997; Avila and Goff 1998; Davis and Goff 2000
Macrocheles sp.		20, 2	Rat	On, under		Germany		Schönborn 1963
Pachylaelaps sp.	Pachylaelapidae	Abundant	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989

Table 3 continued

Species	Family	Abundance	Host	Location	Habitat	Country	Season (month)	Reference
Parasitus stercorarius	Parasitidae	Common	Pig, sparrow,					
	Taxonomic position uncertain		Crow, mouse	On	Forest	Germany		Fourman 1936
Parasitus sp.			Pig	On	Grassland, bush	Spain	2–4	Castillo Miralbes 2002
Pergamasus sp.[b]		Abundant	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
		Abundant	Pig	On, under	Several	HI, USA		Hewadikaram and Goff 1991
Poecilochirus sp.		Common	Harbour seal	On	Rock	MA, USA	5–10	Lord and Burger 1984a
		Common	Rabbit	On	Woods	CO, USA	7–8	De Jong and Chadwick 1999
	Parasitidae	Abundant	Pig	On, under	Several	HI, USA		Richards and Goff 1997; Avila and Goff 1998
	'Gamasidae'	Large	Guinea pig	Under	Woods	W Australia	10–12	Bornemissza, 1957
Sp 1–3	Uropodidae	Abundant	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
			Abundant	Pig	On	Several	HI, USA	Hewadikaram and Goff 1991; Avila and Goff 1998
Astigmata								
Acarus siro	Acaridae	Common	Fish, frog, pig					
Sancassania berlesi		Abundant	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
Tyrophagus putrescentiae		Abundant	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
		Abundant	Pig	On	Several	HI, USA		Hewadikaram and Goff 1991
	Acaridae	Abundant	Pig	On	Several	HI, USA		Avila and Goff 1998
Spinanoetus spp. nov	Histiostomatidae		Common crow,					
			White-tailed deer	On		MI, USA		OConnor 2009
Pelzneria spp. nov			Mouse, crow,					
			White–tailed deer	On		MI, USA		OConnor 2009
	'Tyroglyphidae'	Some	Guinea pig	Under	Woods	W Australia	10–12	Bornemissza 1957

Table 3 continued

Species	Family	Abundance	Host	Location	Habitat	Country	Season (month)	Reference
Oribatida								
Galumna tarsipennata	Galumnidae		Chicken	On, under	Field	Spain	2–3	Arnaldos et al. 2004
Zygoribatula connexa	Oribatulidae		Chicken	On, under	Field	Spain	2–3	Arnaldos et al. 2004
Prostigmata								
	Trombidiidae		Pig	On	Grassland, bush	Spain	9–10,3–4	Castillo Miralbes 2002
Ixodida								
	Ixodidae		Pig	On	Grassland, bush	Spain	2–5	Castillo Miralbes 2002
Butyric fermentation, advanced decay								
Mesostigmata								
Arctoseius sp.	Ascidae		Pig	On	Grassland, bush	Spain	10,4	Castillo Miralbes 2002
Asca sp.		Scarce	Dog	In, on, under	Woods, pasture	TN, USA	1–12	Reed 1958
Proctolaelaps epuraeae		Many	Human (3 m)	On, under	Deciduous forest	Spain	8	Saloña et al. in prep.
Proctolaelaps sp. ?		Ten	Human (2 m)	On		Belgium	12	Leclercq and Verstraeten 1988b
Zerconopsis remiger		Many	Human (3 m)	Under	Deciduous forest	Spain	8	Saloña et al. in prep.
Hypoaspis aculeifer	Laelapidae	Many	Human (3 m)	On, under	Deciduous forest	Spain	8	Saloña et al. in prep.
Hypoaspis sp. ?		Ten	Human (2 m)	On		Belgium	12	Leclercq and Verstraeten 1988b
Glyptholaspis americana	Macrochelidae	Many	Human (3 m)	Under	Deciduous forest	Spain	8	Saloña et al. in prep.
		Common	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
Macrocheles glaber			Fox	On	Garden	England	10	Smith 1975
M. merdarius		Common	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
M. muscaedomesticae		One	Human (17 d)	On	Small wood	England	10	Easton and Smith 1970
		Some	Impala	On	Woods	South Africa	1–10	Braack 1986, 1987
		Common	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
Macrocheles sp.		Abundant	Dog	In, on, under	Woods, pasture	TN, USA	1–12	Reed 1958
		Increase	Chicken	Under	Woods	ME, USA		Wasti 1972
			Pig	On	Woods	SC, USA	8	Payne and Crossley 1966

Table 3 continued

Species	Family	Abundance	Host	Location	Habitat	Country	Season (month)	Reference
	Macrochelidae	Common	Pig	On, under	Several	HI, USA		Richards and Goff 1997; Avila and Goff 1998; Davis and Goff 2000
Gamasodes spiniger	Parasitidae		Fox	On	Garden	England	10	Smith 1975
'Gamasus' sp.		Many	Human (2.7 y)	On	Cask	Switzerland		Hunziker 1919
Paragamasus sp.		Many	Human (3 m)	Under	Deciduous forest	Spain	8	Saloña et al. in prep.
Parasitus fimetorum			Fox	On	Garden	England	10	Smith 1975
Parasitus sp.		Abundant	Dog	In, on, under	Woods, pasture	TN, USA	1–12	Reed 1958
		Increase	Chicken	Under	Woods	ME, USA		Wasti 1972
			Pig	On	Grassland	Spain	4	Castillo Miralbes 2002
			Pig	On	Woods	SC, USA	8	Payne and Crossley 1966
Pergamasus sp.		Scarce	Dog	In, on, under	Woods, pasture	TN, USA	1–12	Reed 1958
Phorytocarpais spp.		Abundant	Rabbit	On, under	Urban	Alex., Egypt	11–4	Tantawi et al. 1996
Poecilochirus carabi		Common	Human (35 d)	On		Belgium	8	Leclercq and Verstraeten 1988b
		Several	Human (2 m)	On beetle	Pine forest	Spain	11	
		Many	Human hanging	Under				Saloña-Bordas pers. comm.
P. necrophori		One	Human (17 d)	On	Small wood	England	10	Easton and Smith 1970
P. subterraneus		Common	Human (35 d)	On		Belgium	8	Leclercq and Verstraeten 1988b
Poecilochirus sp.		Common	Harbour seal	On	Rock	MA, USA	5–10	Lord and Burger 1984a
		Common	Rabbit	On	Woods	CO, USA	7–8	De Jong and Chadwick 1999
	'Gamasidae'	Large	Guinea pig	Under	Woods	W Australia	10–12	Bornemissza, 1957
Urobovella pulchella	Uropodidae	Many	Human (3 m)	On, under	Deciduous forest	Spain	8	Saloña et al. in prep.
Uroseius sp.			Pig	On	Grassland, bush	Spain	10	Castillo Miralbes 2002
Apionoseius sp.	Discourellidae	Medium	Dog	In, on, under	Woods, pasture	TN, USA	1–12	Reed 1958
	Idendity unclear							
Haemogamasus sp.	Haemogamasidae		Pig	On	Grassland, bush	Spain	10,4	Castillo Miralbes 2002
Melittiphis ? sp.		Rare	Dog	In, on, under	Woods, pasture	TN, USA	1–12	Reed 1958

Table 3 continued

Species	Family	Abundance	Host	Location	Habitat	Country	Season (month)	Reference
Gamasellus sp.	Rhodacaridae or Ologamasidae	Rare	Dog	In, on, under	Woods, pasture	TN, USA	1–12	Reed 1958
Zercon sp.	Zerconidae	Rare	Dog	In, on, under	Woods, pasture	TN, USA	1–12	Reed 1958
Astigmata								
Myianoetus diadematus	Histiostomatidae	Mass occ.	Human (1.3 y)	On	Basement	Germany		Russell et al. 2004
Acarus siro	Acaridae	Common	Fish, frog, pig					
			Lizard, chicken	On	Woods	Nigeria		Iloba and Fawole 2006
Cosmoglyphus sp.		Common	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
Sancassania berlesei		Many	Human (3 m)	Under	Deciduous forest	Spain	8	Saloña et al. in prep.
		Common	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
Sancassania sp. nov		Common	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
Sancassania sp. nov			Deer, raccoon	On		USA		OConnor 2009
Sancassania sp.		Few	Dog	Under	Woods, pasture	TN, USA	1–12	Reed 1958
		Abundant	Pig	On	Burial pit	SC, USA	6–11	Payne et al. 1968
Tyrophagus putrescentiae		Common	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
		Common	Pig	On	Several	HI, USA		Hewadikaram and Goff 1991
Lardoglyphus zacheri	Lardoglyphidae or Acaridae		Bird	Feathers under		TX, USA		OConnor 2009
	'Tyroglyphidae'	Immense	Guinea pig	Under, on	Woods	W Australia	10–12	Bornemissza 1957
	Acaridae	Common	Pig	On	Several	HI, USA		Avila and Goff 1998
Oribatida								
Platynothrus peltifer	Camisiidae	Many	Human (3 m)	Under	Deciduous forest	Spain	8	Saloña et al. in prep.
		Few	Dog	Under	Woods, pasture	TN, USA	1–12	Reed 1958
Minunthozetes semirufus	Mycobatidae	Many	Human (3 m)	Under	Deciduous forest	Spain	8	Saloña et al. in prep.
Malacanothrus sp.	Malacanothridae	Few	Dog	Under	Woods, pasture	TN, USA	1–12	Reed 1958
Ceratoppia bipilis	Ceratoppiidae	Few	Dog	Under	Woods, pasture	TN, USA	1–12	Reed 1958
	Liacaridae	Common	Pig	On	Several	HI, USA		Hewadikaram and Goff 1991
Medioppia pinsapi	Oppiidae		Chicken	On, under	Field	Spain	10–12	Arnaldos et al. 2004

Table 3 continued

Species	Family	Abundance	Host	Location	Habitat	Country	Season (month)	Reference
Oribatula tibialis	Oribatulidae		Chicken	On, under	Field	Spain	10–12	Arnaldos et al. 2004
	Oribatida spp.	Common	Pig	On	Several	HI, USA		Davis and Goff 2000
		Few	Dog	Under	Woods, pasture	TN, USA	1–12	Reed 1958
		Few	Dog	Under	Woods, pasture	TN, USA	1–12	Reed 1958
Prostigmata								
Lephus spp.	Erythraeidae		Pig	On	Woods	SC, USA	8	Payne and Crossley 1966
Penthaleus major	Eupodidae	Few	Dog	Under	Woods, pasture	TN, USA	1–12	Reed 1958
	Trombidiidae		Pig	On	Grassland, bush	Spain	10	Castillo Miralbes 2002
Ixodida								
Dermacentor variabilis	Ixodidae	Few	Dog	Under	Woods, pasture	TN, USA	1–12	Reed 1958
	Ixodidae		Pig	On	Bush	Spain	4	Castillo Miralbes 2002
Dry decomposition, skeletal stage								
Mesostigmata								
Leiodinychus krameri	Dinychidae (Uropodidae)	Myriads	Human (>1 y)	On, in	Cellar	France		Mégnin 1894
		Common	Human	On		Canada		Johnston and Villeneuve 1897
Holostaspis sp.	Laelapidae	Common	Human (11 y)	On	Grave	DC, USA		Motter 1898
Hypoaspis sp.		Common	Human (20–30 y)	On	Grave	DC, USA		Motter 1898
		Common	Dog (3 m)	On	Grave	DC, USA		Motter 1898
Laelaps (Iphis) sp.		Common	Human (11 y)	On	Grave	DC, USA		Motter 1898
Melittiphis ? sp.		Rare	Dog	In, on, under	Woods, pasture	TN, USA	1–12	Reed 1958
Glyptholaspis americana	Macrochelidae	Common	Human (53 d)	Soil	Clothing	HI, USA	3–5	Goff 1991
		Common	Cat	On, under	Xero + mesophytic	HI, USA		Early and Goff 1986; Goff 1989
Macrocheles glaber		One	Human (3 m)	On		Belgium	6	Leclercq and Verstraeten 1988b
M. merdarius		Common	Human (53 d)	Soil	Clothing	HI, USA	3–5	Goff 1991
		Common	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989

Table 3 continued

Species	Family	Abundance	Host	Location	Habitat	Country	Season (month)	Reference
M. muscaedomesticae		Common	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
		Some	Impala	On	Woods	Sth Africa	1–10	Braack 1986, 1987
Macrocheles sp.		Abundant	Dog	In, on, under	Woods, pasture	TN, USA	1–12	Reed 1958
		Abundant	Small animals[f]	On	Oak forest	IL, USA	4–11	Johnson 1975
	Macrochelidae	Common	Pig	On, under	Several	HI, USA		Richards and Goff 1997; Avila and Goff 1998; Davis and Goff 2000
Pachylaelaps sp.	Pachylaelapidae	Common	Human (53 d)	Soil	Clothing	HI, USA	3–5	Goff 1991
		Common	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
'Gamasus' sp.	Parasitidae	Common	Human (30–40 y)	On	Grave	DC, USA		Motter 1898
		Common	Dog (3 m)	On	Grave	DC, USA		Motter 1898
Parasitus sp.		Abundant	Dog	In, on, under	Woods, pasture	TN, USA	1–12	Reed 1958
		Common	Small animals[f]	On	Oak forest	IL, USA	4–11	Johnson 1975
Pergamasus sp.[c]		Scarce	Dog	In, on, under	Woods, pasture	TN, USA	1–12	Reed 1958
		Abundant	Small animals[f]	On	Oak forest	IL, USA	4–11	Johnson 1975
Poecilochirus sp.		Common	Rabbit	On	Woods	CO, USA	7–8	De Jong and Chadwick 1999
Uroseius acuminatus	Trachytidae	Common	Human (3 y)	On, in		France	5	Mégnin 1894
Uropoda depressa	Uropodidae Identity unclear	Common	Human (3–7 y)	On	Grave	DC, USA		Motter 1898
Uropoda sp.		Common	Dog (3–5 m)	On	Grave	DC, USA		Motter 1898
Sp 1–3	Uropodidae	Common	Human (53 d)	Soil	Clothing	HI, USA	3–5	Goff 1991
		Common	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
			Common	Pig	On	Several	HI, USA	Hewadikaram and Goff 1991; Avila and Goff 1998
Asca sp.	Ascaidae	Scarce	Dog	In, on, under	Woods, pasture	TN, USA	1–12	Reed 1958
Apionoseius sp.	Discourellidae Identity unclear	Medium	Dog	In, on, under	Woods, pasture	TN, USA	1–12	Reed 1958
Gamasellus sp.	Rhodacaridae or Ologamasidae	Rare	Dog	In, on, under	Woods, pasture	TN, USA	1–12	Reed 1958

Table 3 continued

Species	Family	Abundance	Host	Location	Habitat	Country	Season (month)	Reference
Zercon sp.	Zerconidae	Rare	Dog	In, on, under	Woods, pasture	TN, USA	1–12	Reed 1958
Astigmata								
Acarus immobilis	Acaridae	Common	Human (1.3 y)	On	Basement	Germany		Russell et al. 2004
			Raccoon	On		OH, USA		OConnor 2009
A. siro		Common	Human (3 y)	On, in	Rural	France	5	Mégnin 1894
		Myriads	Human (>1 y)	On, in	Cellar	France		Mégnin 1894
		Common	Fish, frog, pig					
			Lizard, chicken	On	Woods	Nigeria		Iloba and Fawole 2006
Acarus (Tyroglyphus) sp.		Common	Human (3 y)	On	Grave	DC, USA		Motter 1898
Cosmoglyphus sp.		Common	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
Rhizoglyphus echinopus		Myriads	Human (>1 y)	On, in	Cellar	France		Mégnin 1894
		Abundant	Human (2 y)	On	Urban	France	10	Mégnin 1894
		Common	Human (2–3 y)	Bulbs of lily	Garden, burrial	France		Mégnin 1894
Sancassania berlesei		Abundant	Human (3–8 m)	On, in	Urban	France	1	Brouardel 1879
		Abundant	Human (7–8 y)	On	House	France		Mégnin 1894
		784	Human (3 m)	On		Belgium	6	Leclercq and Verstraeten 1988b
		Abundant	Human (3.5 m)	On		Belgium	1	Leclercq and Verstraeten 1988b
		Common	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
Sancassania sp. nov		Common	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
Sancassania sp. nov			Deer, raccoon	On		USA		OConnor 2009
Sancassania sp.		Few	Dog	Under	Woods, pasture	TN, USA	1–12	Reed 1958
Tyrophagus longior		Abundant	Human (3–8 m)	On, in	Urban	France	1	Brouardel 1879
		Abundant	Human (7–8 y)	On	House	France		Mégnin 1894
		Very rare	Human (1 y)	On	House	France	1	Mégnin 1894

Table 3 continued

Species	Family	Abundance	Host	Location	Habitat	Country	Season (month)	Reference
		Common	Human (3 y)	On, in	Rural	France	5	Mégnin 1894
		Myriads	Human (>1 y)	On, in	Cellar	France		Mégnin 1894
		Myriads	Human	On	House, trunk	France		Mégnin 1898
		Common	Human	On, in		Canada		Johnston and Villeneuve 1897
T. putrescentiae		Abundant	Human (1.3 y)	On	Basement	Germany		Russell et al. 2004
		Common	Human (53 d)	Soil	Clothing	HI, USA	3–5	Goff 1991
		Common	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
		Common	Pig	On	Several	HI, USA		Hewadikaram and Goff 1991
Tyrophagus sp.		Common	Human (18 m)	On, around	House	France	3	Mégnin 1894
		Common	Human (2 y)	On	Urban	France	6	Mégnin 1894
T. (Hypopus) sp.		Common	Human (20–71 y)	On	Grave	DC, USA		Motter 1898
	Identity unclear							
		Acaridae	Few	Human (summer)	Alps	France	10	Leclercq and Verstraeten 1992
		Common	Pig	On	Several	HI, USA		Avila and Goff 1998
Glycyphagus destructor	Glycyphagidae	Very rare	Human (1 y)	On	House	France	1	Mégnin 1894
		Common	Human	On		France		Mégnin 1894
	Glycyphagidae	Large	Human (28 y)	On	Embalmed	MI, USA		Merritt et al. 2007
Histiostoma feroniarum	Histostomatidae	Common	Human	On		France		Mégnin 1894
		Common	Human	On		Canada		Johnston and Villeneuve 1897
H. necrophagus		Common	Human	On		France		Mégnin 1894
	Composite species, unrecognisable	Common	Human	On		Canada		Johnston and Villeneuve 1897
H. sachsi		Two	Human (3 m)	On		Belgium	6	Leclercq and Verstraeten 1988b
Histiostoma sp.		One	Human (3 m)	On		Belgium	6	Leclercq and Verstraeten 1988b
		Common	Human (53 d)	Soil	Clothing	HI, USA	3–5	Goff 1991
		Common	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989

Table 3 continued

Species	Family	Abundance	Host	Location	Habitat	Country	Season (month)	Reference
Myianoetus ? sp.		Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
	Histostomatidae	Common	Pig	On, under	Several	HI, USA		Richards and Goff 1997; Avila and Goff 1998
Lardoglyphus radovskyi	Lardoglyphidae		Human	Pelvis,	Mummy	NV, USA		Baker 1990
	or Acaridae			Gut content				Radovsky 1970
L. robustisetosus			Human	Gut content	Mummy	Chile		Baker 1990
L. zacheri		Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
			Racoon	On		USA		OConnor 2009
Czenspinskia transversostriata	Winterschmidtiidae	Common	Human (53 d)	Soil	Clothing	HI, USA	3–5	Goff 1991
		Common	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
Oribatida								
Aphelacarus acarinus	Aphelacaridae		Human	Remains	Tomb	Spain		Hidalgo-Argüello et al. 2003
Hoplophora (Tritia) sp.	Euphthiracaridae	Common	Human	On	Grave	DC, USA		Motter 1898
Platynothrus peltifer	Camisiidae	Few	Dog	Under	Woods, pasture	TN, USA	1–12	Reed 1958
Ceratoppia bipilis	Ceratoppiidae	Few	Dog	Under	Woods, pasture	TN, USA	1–12	Reed 1958
	Galumnidae	Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
Rostrozetes spp.[d]	Haplozetidae	Common	Skin of animals	On				
	Haplozetidae	238	Rat	On	Campus	Cameroon	2–3	Feugang Youmessi et al. 2008
	Liacaridae	Common	Pig	On	Several	HI, USA		Hewadikaram and Goff 1991
Malacanothrus sp.	Malacanothridae	Few	Dog	Under	Woods, pasture	TN, USA	1–12	Reed 1958
	Oribatida spp.	Common	Pig	On	Several	HI, USA		Davis and Goff 2000
		Few	Dog	Under	Woods, pasture	TN, USA	1–12	Reed 1958
		Increase	Chicken	Under	Woods	MA, USA		Wasti 1972
Prostigmata								
Cheyletus eruditus	Cheyletidae	Abundant	Human (>1 y)	On	Cellar	France		Mégnin 1894

Table 3 continued

Species	Family	Abundance	Host	Location	Habitat	Country	Season (month)	Reference
	Podapolipidae		Human	Remains	Tomb	Spain		Hidalgo-Argüello et al. 2003
	Tarsonemoidea		Human	Remains	Tomb	Spain		Hidalgo-Argüello et al. 2003
Tarsotomus sp. nov	Anystidae	Abundant	Rabbit	On, under	Urban	Alexandria, Egypt	7–8	Tantawi et al. 1996
Erythraeus sp.	Erythraeidae		Pig	On	Woods	SC, USA	8	Payne and Crossley 1966
Penthaleus major	Eupodidae	Few	Dog	Under	Woods, pasture	TN, USA	1–12	Reed 1958
Trombidium sp.	Trombidiidae	Common	Small animals[f]	On	Oak forest	IL, USA	4–11	Johnson 1975
Ixodida								
Dermacentor variabilis	Ixodidae	Few	Dog	Under	Woods, pasture	TN, USA	1–12	Reed 1958
			Pig	On	Woods	SC, USA	8	Payne and Crossley 1966
Undetermined stage								
Mesostigmata								
Epicrius mollis	Epicriidae	Male	Small animal	On	Alder forest	Poland	8	Gwiazdowicz and Klemt 2004
E. thanathophilus			General, human?	On				Porta 1929
Celaenopsis cuspidatus	Celaenopsidae		General, human?	On				Porta 1929
Cornigamasus lunaris	Parasitidae	Few	Small animal	On	Alder forest	Poland	8	Gwiazdowicz and Klemt 2004
Holoparasitus calcaratus		Few	Small animal	On	Alder forest	Poland	8	Gwiazdowicz and Klemt 2004
Paracarpais furcatus			General, human?	On				Porta 1929
Pergamasus crassipes		Few	Small animal	On	Alder forest	Poland	8	Gwiazdowicz and Klemt 2004
Pergamasus sp.[e]		Hundreds	Rat	On	Copse, grassland	England	8–12	Collins 1970
		Decrease	Rat	Under	Copse, grassland	England	8–12	Collins 1970
Poecilochirus sp.		Common	Rat	On	Field	CO, USA	7–8	De Jong and Hoback 2006
	Parasitidae	Common	Bear, deer, Alligator, pig	On		LA, USA		Watson 2004

Table 3 continued

Species	Family	Abundance	Host	Location	Habitat	Country	Season (month)	Reference
	Gamasida	Some	Pig	On	Several	HI, USA	1–4	Davis and Goff 2000
Asca craneta	Ascidae	Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
Gamasellodes bicolor		Few	Small animal	On	Alder forest	Poland	8	Gwiazdowicz and Klemt 2004
Iphidozercon gibbus		Some	Small animal	On	Alder forest	Poland	8	Gwiazdowicz and Klemt 2004
Proctolaelaps sp. nov		Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
Zerconopsis decemremiger		Some	Small animal	On	Alder forest	Poland	8	Gwiazdowicz and Klemt 2004
	Ascidae	Some	Pig	On, under	Several	HI, USA		Richards and Goff 1997; Avila and Goff 1998
	Digamasellidae	Some	Pig	On	Several	HI, USA		Avila and Goff 1998
	Digamasellidae	As control	Turtle	Under	Woods	MA, USA	6–8	Abell et al. 1982
	Diplogyniidae	Increasing	Turtle	Under	Woods	MA, USA	6–8	Abell et al. 1982
	Eviphidae	Some	Pig	On	Several	HI, USA		Avila and Goff 1998
Hypoaspis (Cosmolaelaps) vacua	Laelapidae	Some	Small animal	On	Alder forest	Poland	8	Gwiazdowicz and Klemt 2004
	Laelapidae	146, large	Turtle	On, under	Woods	MA, USA	6–8	Abell et al. 1982
		Increase	Rat	Under	Copse, grassland	England	8–12	Collins 1970
		Some	Pig	Associated	Several	HI, USA		Richards and Goff 1997
Macrocheles sp.	Macrochelidae	Hundreds	Rat	On	Copse, grassland	England	8–12	Collins 1970
Macrocheles sp. N			Rodents	On		USA		Krantz and Whitaker 1988
M. agilis			Carrion	In		Australia		Halliday 2000
M. lagodekhensis group		Several	Roe deer	On		Slovakia	4, 5,7	Mašán 1993
M. matrius			Weasel	On		MT, USA		Krantz and Whitaker 1988
M. mykytowyczi			Fish, squid, carrion	In	Forest	Australia		Halliday 2000
M. nataliae (=melisii)			Vole	On		Lithuania		Hyatt and Emberson 1988
			Small mammals	On		USSR		Bregetova and Koroleva 1960

Table 3 continued

Species	Family	Abundance	Host	Location	Habitat	Country	Season (month)	Reference
M. peckorum			Carrion trap	On		Australia		Halliday 2000
M. spatei			Squid	On		Australia		Halliday 2000
M. tessellatus			Squid	On		Australia		Halliday 2000
	Macrochelidae	Increase	Rat	Under	Copse, grassland	England	8–12	Collins 1970
	Ologamasidae	Some	Pig	Associated	Several	HI, USA		Richards and Goff 1997
	Paraholaspidae	Some	Pig	Associated	Several	HI, USA		Richards and Goff 1997
Phytoseius hawaiiensis	Phytoseiidae	Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
	Phytoseiidae	Increasing	Turtle	Far, under	Woods	MA, USA	6–8	Abell et al. 1982
	Podocinidae	Some	Pig	Associated	Several	HI, USA		Richards and Goff 1997
	Rhodacaridae	Decrease	Rat	Under	Copse, grassland	England	8–12	Collins 1970
Trachytes aegrota	Trachytidae	Several	Small animal	On	Alder forest	Poland	8	Gwiazdowicz and Klemt 2004
	Uropodidae	As control	Turtle	Under	Woods	MA, USA	6–8	Abell et al. 1982
		Increase	Rat	Under	Copse, grassland	England	8–12	Collins 1970
Veigaia nemorensis	Veigaiidae	Few	Small animal	On	Alder forest	Poland	8	Gwiazdowicz and Klemt 2004
	Veigaiidae	Some	Pig	On	Several	HI, USA		Richards and Goff 1997; Davis and Goff 2000
Prozercon kochi	Zerconidae	Few	Small animal	On	Alder forest	Poland	8	Gwiazdowicz and Klemt 2004
Astigmata								
	Acaridae	As control	Turtle	Under	Woods	MA, USA	6–8	Abell et al. 1982
Lardoglyphus sp.	Lardoglyphidae or Acaridae	Some	Impala	On	Woods	South Africa	1–10	Braack 1986
	Astigmata	Decrease	Rat	Under	Copse, grassland	England	8–12	Collins 1970
Oribatida								
	Achipteriidae	Decrease	Rat	Under	Copse, grassland	England	8–12	Collins 1970
	Ceratozetidae	Increasing	Turtle	Under	Woods	MA, USA	6–8	Abell et al. 1982
		Decrease	Rat	Under	Copse, grassland	England	8–12	Collins 1970
	Eremaeidae	One	Rat	On	Field	CO, USA	7–8	De Jong and Hoback 2006
	Euzetidae	Decrease	Rat	Under	Copse, grassland	England	8–12	Collins 1970

Table 3 continued

Species	Family	Abundance	Host	Location	Habitat	Country	Season (month)	Reference
	Galumnidae	Increasing	Turtle	Far, under	Woods	MA, USA	6–8	Abell et al. 1982
	Hypochthoniidae	Increasing	Turtle	Far, under	Woods	MA, USA	6–8	Abell et al. 1982
	Mycobatidae	Decrease	Rat	Under	Copse, grassland	England	8–12	Collins 1970
	Nothridae	3, small	Turtle	On, under	Woods	MA, USA	6–8	Abell et al. 1982
		Decrease	Rat	Under	Copse, grassland	England	8–12	Collins 1970
	Oppiidae	Decrease	Rat	Under	Copse, grassland	England	8–12	Collins 1970
	Oribatulidae	Decrease	Rat	Under	Copse, grassland	England	8–12	Collins 1970
Prostigmata								
Erythraeus sabulosus	Erythraeidae		General, human?	On				Porta 1929
	Anystidae	Few	Rat	On	Field	CO, USA	7–8	De Jong and Hoback 2006
	Bdellidae	Some	Pig	Associated	Several	HI, USA		Richards and Goff 1997
	Camerobiidae	Some	Pig	On	Several	HI, USA		Avila and Goff 1998
Cunaxa sp.	Cunaxidae	Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
	Ereynetidae	Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
		Some	Pig	On	Several	HI, USA		Avila and Goff 1998
	Eupodidae	Some	Pig	Associated	Several	HI, USA		Richards and Goff 1997
Pygmephorus sp.	Pygmephoridae	Some	Impala	On	Woods	South Africa	1–10	Braack 1986
	Pygmephoridae	Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
		Some	Pig	On	Several	HI, USA		Avila and Goff 1998
	Rhagidiidae	Increasing	Turtle	Under	Woods	MA, USA	6–8	Abell et al. 1982
		Some	Pig	Associated	Several	HI, USA		Richards and Goff 1997
	Scutacaridae	Some	Cat	On, under	Xero + mesophytic	HI, USA	3–5	Early and Goff 1986; Goff 1989
	Tarsonemoidea	Some	Pig	On	Several	HI, USA		Avila and Goff 1998
	Prostigmata	Decrease	Rat	Under	Copse, grassland	England	8–12	Collins 1970
Endeostigmata								
	Terpnacaridae	Some	Pig	On	Several	HI, USA		Avila and Goff 1998

Table 3 continued

Species	Family	Abundance	Host	Location	Habitat	Country	Season (month)	Reference
Ixodida								
Dermacentor variabilis	Ixodidae	Few	Bear	On		LA, USA	12–2	Watson 2004

In many reports, particular mites species or taxa dominate in a single stage of decomposition but are also recorded in lower numbers in the adjacent preceding and subsequent stage. To increase clarity, the presence in these adjacent stages is not recorded in the table unless the species is dominant in more than one stage. The description of abundance tries to follow the original wording of the authors. If mites are abundant, one might expect several hundred thousand to several million specimens per carcase. For a few cases of human corpses, the estimated post mortem interval is given between parentheses in the column of host designation and the month the corpse was discovered in the season column

[a] As the name implies, these are blood-feeding mites but are also present during later stages of decomposition

[b] It is unusual for species in this genus to concentrate in huge proportions

[c] It is unusual for species in this genus to concentrate in huge proportions. This genus is also very easy to confound with *Poecilochirus* or *Parasitus* species for a non-acarologist

[d] Erroneous reports on websites; there is no evidence for Rostrozetes species being involved in animal decomposition or associated with carcases

[e] It is unusual for species in this genus to concentrate in huge proportions. This genus is also very easy to confound with *Poecilochirus* or *Parasitus* species for a non-acarologist

[f] Small animals: grey squirrel, fox squirrel, juvenile cottentail rabbit, cat, opossum; mites found on all carcases (Johnson 1975)

fly maggot activity also renders the medium of the carcase alkaline, which is detrimental to the beetles. By reducing the amount of blow flies, the mites create a habitat more suitable for their phoretic hosts. However, this line of reasoning of a strictly mutual interaction is increasingly being questioned by acarologists. *Poecilochirus* mites might feed more on the carcase than on the blow fly eggs. *Poecilochirus davydovae* has now been recognized as a specialist predator feeding on the eggs of its beetle carrier, *Nicrophorus vespilloides* (Blackman 1997).

Some mite species will end up at a carcase as incidentals, as species that use the corpse as a concentrated resource extension of their normal habitat; springtails (Collembola), spiders (Araneae), centipedes (Chilopoda), and wood lice (Isopoda) fall also in this category. However, mites as incidentals might be a minority group. Many mite species arrive at a carcase through phoresy on a necrophagous or necrophilous insect. The phoresy is often highly taxon specific. Many mite species arriving by phoresy are likely the product of evolutionary adaptation to a specialized food source and habitat, the opposite of incidental (Athias-Binche 1994; Perotti and Braig 2009b). But if mites are incidental, they might become the centre point of trace analysis in a forensic setting.

Oligospecific infestations

The importance of mites on carcases becomes even more pronounced under conditions of concealment or expedited dehydration, when the normal succession of arthropod waves is disrupted. Such situations often occur indoors. Carcases then decompose often completely under the action of a single or a few species of insects or mites. Insect species recorded in mono—or oligospecific infestations of human remains include the grey flesh fly *Sarcophaga carnaria* (=*Musca carnaria;* Sarcophagidae; Bergeret 1855), the brown house or false clothes moth *Hofmannophila pseudospretella* (=*Borkhausenia pseudospretella;* Oecophoridae; Forbes 1942), the corpse fly *Hydrotaea capensis* (Muscidae; Turchetto and Vanin 2004) or beetles. A case published by Schroeder et al. (2002) found that the leather or hide beetle *Dermestes maculatus* (Dermestidae) had almost skeletonised an indoor corpse in Germany within 5 months. A similar situation might have occurred involving the larder or bacon beetle *D. lardarius* in Denmark and the USA (Voigt 1965; Lord 1990). The first forensic case where mites have been used to estimate a post mortem interval involving a mummified corpse of a new-borne baby girl is also a case where one or two mite species were the only arthropods found on the corpse other than larvae of the grease moths *Aglossa* spp. (Pyralidae) (Brouardel 1879; Perotti 2009). The sprinkling or injection with lead arsenate of two human corpses found in the French Alps not only misled police dogs, but also prevented practically any insect infestation (Leclercq and Verstraeten 1992). The lead arsenate did not stop the bacterial decomposition. The bodies were mummified possibly through the effect of a dry and hot summer. With the exception of a very few fly larvae of miniscule size, the corpses carried only mites of the family Acaridae (=Tyroglyphidae), and even the mites were not in great numbers. In a more recent case reported from Germany, a child corpse found wrapped in plastic in a basement of a home was only associated with a mass occurrence of mites (Russell et al. 2004; OConnor 2009).

Human corpses may be mosaics

To assign a human corpse or any large carcase to a certain stage of decomposition might not be as straightforward as might be expected, especially, if the carcase is considered from an ecological point of view. Human body parts may be covered to varying degree with clothing that can have a drastic impact on decomposition. Exposed body parts like the face and hands might be skeletonised whereas clothed parts might still have most of the soft tissues in active or advanced stages of decay. Other parts of a carcase might develop adipocere or grave wax and enter a stage of mummification. This might be the case as much for an exposed body as for a body buried in a coffin. Particularly, woollen socks used to dress corpses in coffins have regularly delayed decomposition of soft tissue parts to a large degree. Clothed parts remained delayed in decomposition or preserved when exhumed after two or more years (Hunziker 1919). A human corpse sometimes might represent a mosaic of different stages of decomposition occurring simultaneously rather than a neat single stage. Often it is then just the biggest body part or the body part most advanced in the process of decomposition that determines the stage of decomposition represented in reports or in listings. The arthropod fauna present on such a corpse will reveal an increasing diversity the more carefully it is investigated. The more elaborate the clothing or other means of concealment, the stronger the impact on the decomposition process.

The influence of clothing, wrapping and physical trauma such as knife wounds on the decomposition and arthropod succession has been studied in detail with pigs in central South Africa (Kelly 2006). The presence and absence of Acari during decomposition was recorded but not systematically analysed. A recent case of a child whose corpse had been wrapped in a pullover and plastic bag and hidden in a basement is illustrative (Russell et al. 2004). A water film formed on the inside of the plastic wrapping that generated a habitat characteristic of liquid decomposition at the transition between bloating stage and active decay. This liquid environment supported the mass occurrence of *Myianoetus diadematus* (Astigmata). At the same time, the rest of the body was at an advanced stage of decomposition characterised by the astigmatid mites *Tyrophagus putrescentiae* and *Acarus immobilis*; the corpse was probably 1–1.5 years post mortem. When the plastic bag was removed from the body, the *M. diadematus* colony collapsed through dehydration.

Mites dominate in diversity and in numbers during the stages of butyric fermentation and dry decomposition. The low number of listings in the table for earlier stages of decomposition might be misleading. In the study of Johnson on small animals, all the mites were first recognised during the bloating stages but became very common during the dry decomposition stage (Johnson 1975). The mite presence spans four stages of decomposition. In a study with highly compromised chicken carcases with the flesh partially removed, Mesostigmata, Astigmata and Prostigmata were collected during the fresh stage (Arnaldos et al. 2004).

Human mites

Healthy humans will carry one or two species of symbiotic mites, *Demodex brevis* and *D. folliculorum* (Demodecidae, Prostigmata), the mites of sebaceous or fat glands and hair follicles (Desch 2009). These mites have been found on human corpses since their discovery in 1844 (Wilson 1844). Table 3 only gives exemplary references, for a more comprehensive account please see Perotti and Braig (2009a). Parasitic mites of humans do not feature during the fresh stage of Table 3, because humans have very few parasitic mites that are not incidental occurrences stemming from individual case reports. The best representative of a parasitic mite associated with humans is the scab mite *Sarcoptes scabiei* (Sarcoptidae, Astigmata). The sister species *S. bovis* of cows and *S. equi* of horses cause milker's and cavalryman's itch in humans during an abortive superficial infection.

Cheyletiella blakei (Cheyletidae, Prostigmata) of cats, *C. furmani* and *C. parasitivorax* of rabbits and *C. yasguri* of dogs are mange mites, also known as walking dandruff, that might feed on epidermal keratin of humans and cause an abortive infection (Beesley 1998). Many chigger mites (Trombiculidae, Prostigmata) belonging to the genera *Trombicula*, *Neotrombicula*, *Eutrombicula*, *Leptotrombicula* and *Ascoschoengastia* may be encountered in the larval stage. These chiggers might feed on humans as an alternative host for a few days but are perhaps better regarded, like ticks and dermanyssid mites, as micropredators rather than as human parasites (Ashford and Crewe 2003). The species *Eutrombicula belkini* was central in linking a suspect to a murder scene in a case in California (Prichard et al. 1986; Turner 2009).

Environment, microhabitats, size of carcase

The impact of the habitat on the appearance of visible waves of Acari became evident in a comparative study using small pigs (around 9 kg) in three contrasting tropical habitats (Shalaby et al. 2000). Acari first became obvious 7–8 days post mortem in a mesophytic habitat, intermediate between dry and wet vegetation. At 11 days post mortem, Acari followed in the rain forest habitat of Oahu, Hawai'i (USA). Around 19–20 days post mortem, the pigs in the mesophytic and rain forest habitat experienced a second wave of mites; and pigs in an arid, xerophytic habitat received their first wave of mites.

Studies of the insects associated with small carcases have been characterised by dramatic variations in the carrion-feeding fauna (Blackith and Blackith 1990). Even small variations in the size of the carcase may have an influence on the stage at which mites are obvious. For very small pigs of 8.4 kg, nymphs and adults of Acaridae (Astigmata) and Macrochelidae (Mesostigmata) and adults of Liacaridae (Oribatida) were dominant during the postdecay stage, 12–16 days post mortem, whereas the same mite population occurred during the remains stage, 14–30+ days post mortem, for a pig carcase of 15.1 kg (Hewadikaram and Goff 1991).

The seasons can have a huge impact on the stage of decomposition at which mites become obvious. In a study in a farmland area in the north of Spain using pigs exposed to the sun, mites became obvious at the fresh stage during winter, at the bloating stage during spring, at the active decomposition stage during autumn, and remained absent even at the advanced stage of decomposition during summer (Castillo Miralbes 2002). However, in experiments with chicken carcases with the flesh partially removed and the viscera present showed the highest numbers of mites (687) during summer and advanced decomposition followed by spring (216); winter had 190 mites during the earlier stage of decomposition and autumn showed overall the lowest numbers (Arnaldos et al. 2004). The chicken carcases were put in an agricultural field around Murcia in southeastern Spain. The impact of the season on the abundance of mites on a carcase also becomes evident if the numbers of mites are put in relation to other major sarcosaprophagous arthropods. The percentual contribution of mites to the fauna on the chicken carcases can almost be as high as that of flies during the summer, and during winter still much higher than that of beetles: spring: 42% Diptera, 33% Hymenoptera, 9% Collembola, 5% Acari, 3% Coleoptera; summer: 29% Hymenoptera, 22% Diptera, 21% Acari, 14% Collembola, 5% Coleoptera; autumn: 55% Collembola, 37% Diptera, 3% Hymenoptera, 2% Coleoptera, 1% Acari; winter: 41% Diptera, 39% Collembola, 8% Acari, 2% Coleoptera, Hymenoptera and Psocoptera, each (major constituents only) (Arnaldos Sanabria 2000; Goff et al. 2004).

The pig study also showed that carcases exposed to the sun during autumn contained mites at the active or advanced stage of decomposition, whereas carcases kept at the same time in a shadowed environment 300 m away already had mites at the bloating stage. The differences might be explained to a great extent by the scotophilic or heliophilic behaviour of the insects carrying the mites. Both, shadow and lower temperatures facilitate early mite colonisation of carcases in the pig experiments. The fact that many mite species are photonegative can make the collection of mites during daylight or in direct sunlight difficult and unrepresentative for the actual diversity and abundance present. The seasons also have some influence on the families of mites colonising the carcase.

Hard ticks (Ixodidae) were only found during spring at the bloated stage and at active decomposition in the shadow, and during winter at active decomposition in the sun. Since ticks are obligate parasites of living animals, the presence of ticks might reflect the activity of scavengers at that time (Castillo Miralbes 2002). The study with chickens confirms the presence of hard ticks only during spring time (Arnaldos et al. 2004). A comprehensive study on the influence of shade and sun exposure with pigs was performed in Edmonton, Canada (Anderson et al. 2002). Careful records on the presence or absence of mites during decomposition were kept but mites were not systematically differentiated.

Mite dispersal

The importance of phoresy for the introduction of mites to carcases has repeatedly been emphasised; for review, see Perotti et al. (2009a). Often overlooked is the fact that these mites also have to leave the carcase again at a certain time. Skin beetles (Trogidae) can become so heavily overloaded that their mites also infest and cover larval stages, which have no functional role in phoresy. The infestation can become so severe that the beetles end up dead in and around the carcase. This has also been observed for skin beetles on pig carcases and beetles in general on dog carcases (Reed 1958; Gill 2005). *Macrocheles* species go to their beetle species. *Parasitus* and *Poecilochirus* species jump on everything that moves and easily saturate the phoretic host. Details of mite-host associations can be found in Perotti and Braig (2009b). The end of a wave of either mites or their insect carriers might be judged by the level of mite infestation on a particular carrier.

Another aspect of dispersal is the analysis of mites that were already present before death. Very few studies have addressed this point. One study on pigs in Nigeria observed that the ticks present naturally on the pig left the pig to find a new host as the bloated stage approached (Iloba and Fawole 2006). Humans carry mites in hair follicles and skin pores but also on their clothing (Desch 2009; Perotti and Braig 2009a). The diversity of mites found in buildings and homes might gain forensic importance (Frost et al. 2009; Solarz 2009; Colloff 2009).

Using furred or feathered animals in forensic experiments as substitutes for human bodies poses some problems for the investigation of mites. A study of mites on rat species showed that many parasitic mite species present in the fur during life are still recovered from the dead animals (Ramsay and Paterson 1977). Even feather mites were found on the rats. The diversity of known mite species associated with fur and feathers is huge and might represent only 20% of the actual number. For example, there are more than 2,000 feather mite species described belonging to 44 genera and 33 families. Only pigs, elephants, rhinoceroses, mole rats, whales and hippopotamuses share naturally the nakedness with humans. Mexican hairless dogs and sphinx cats might be alternatives but have no advantage over pigs. Unfortunately, the only decomposition study on elephants did not consider mites (Coe 1978).

The soil below

Mites might be the most abundant soil invertebrates beneath a carcase (Anderson and VanLaerhoven 1996). Bornemissza (1957) studied the impact of decomposing guinea pigs on the natural soil fauna beneath the carcases in Perth, Western Australia. He graphically showed that on the soil surface and in the soil to a depth of 15 cm, the natural mite fauna together with most other arthropod taxa seem to mainly disappear 5–6 days into the decomposition process and reappear some 3 months later. The complete absence of oribatid mites or subterranean springtails such as *Onychiuris* and *Tullbergia* spp. indicated that the reduction of the typical soil fauna was very severe. It was greatest under the oral and anal parts of the carcase. These graphs and this information have been widely cited in the forensic entomological literature suggesting that the fauna beneath a carcase might be highly impoverished during most of the decomposition process and therefore of little forensic interest. This, however, might actually have been exceptional and should not be generalised. Bornemissza, citing Kühnelt (1950), also states that in Europe mites are only present during the final stages of decomposition. We don't see any evidence for such assertions. However, we have no doubt that soil mites under carcases will display geographical behavioural variation, caused by climatic or edaphic factors (Dadour and Harvey 2008). Reed (1958) in a study with dogs in Tennessee described that soil samples taken beside carcases teemed with mites. At various times mites were piled in layers several individuals thick on the putrefactive substance under carcases. They were most abundant during warm and hot weather, but during the winter a few mites could generally be found under each carcase.

In a study with cats on the island of Oahu, Hawai'i, Goff not only demonstrated large quantities of mites but also showed that changes in mesostigmatid populations (Macrochelidae, Parasitidae, Uropodidae and Pachylaelapidae) in samples of soil and litter removed from under the carcases could be correlated with post mortem intervals (Goff 1989). Goff reported on a homicide case where soil was found in the hood of a jacket that had been associated with the skull of a child of approximately 30 months of age recovered from a shallow grave on a narrow ledge on the side of Koko Head Crater on Oahu (Goff 1991). This is the third case in a comparative study by Goff of human decomposition ranging from 8 to 53 days post mortem reported earlier (Goff and Odom 1987). The soil exhibited a rich diversity of mite taxa that had previously been found on and under pig and cat carcases. The taxa are listed in Table 3. Although the acarine fauna considered in this case was not by itself definitive of a specific post-mortem interval, it served to provide valuable supporting data for the refining of the estimate toward the lower end of the window defined by the insects collected from the corpse (Goff 1991). The insect data suggested a period between 51 and 76 days. Presence of only adults of two species of Macrochelidae was consistent with an interval of 22–60 days. Presence of numbers of *T. putrescentiae* was characteristic of a time period greater than 48 days. Other mite species present were not definitive of any time period for this case. There was a total of 97 mites/10 cm^3 of soil for this sample, a number corresponding to an interval of 48–52 days in decomposition studies previously conducted. Based on the estimated post mortem interval, the authorities requestioned the father of the child. In his subsequent confession he put the time of death at the 53rd day prior to the collection of the samples (Goff 1991).

In a study with bank vole carcases in a wooded park in Poland with acid soil, it was noticed that carcases left on the surface experienced mite infestations during the initial stages of decomposition and during the final residual stages with little mite participation during active decomposition. However, when the carcases were buried in a 25–30 cm deep hole, mites dominated during active decomposition and residual stages but not during the initial process (Nabagło 1973).

The soil of a large wooded area in Massachusetts during summer harboured mites of the families Acaridae (Asigmata), Digamasellidae, Laelapidae, Uropodidae (Mesostigmata), and Nothridae (Oribatida) under turtle carcases as well as in control samples (Abell et al. 1982). Northridae were found in very small numbers and Laelapidae in large numbers also on the turtle carcases themselves. The forest consisted of a mixture of deciduous trees primarily made up of red oak and red maple with some American beech and white pine. The soil beneath the carcases contained in addition the following families: Ceratozetidae (Oribatida), Diplogyniidae (Mesostigmata) and Rhagidiidae (Prostigmata), while soil far from the carcases also contained the families Galumnidae, Hypochthoniidae (Oribatida) and Phytoseiidae (Mesostigmata). The dominant family on the turtles and in the soil beneath exposed carrion was Laelapidae.

Payne et al. (1968) compared the mite families on surface exposed baby pigs and baby pigs in burial pits at depths varying from 50 to 100 cm. Twenty-six of 48 arthropod species were not implicated in above-ground carrion succession, but were found only on buried pigs; among these were the mite families Uropodidae and Acaridae.

Mummies might harbour mites belonging to the Tarsonemidae (Prostigmata) and/or mites in general that are associated with a practice of food storage, food gifts or the use of raw cotton to wrap the corpse, oribatid mites that often originate from soil contaminations, or mites that might be derived from plant material in general or leaves of coca added to the corpse (Leles de Souza et al. 2006; Mendonça de Souza et al. 2008; Baker 2009).

Coprolites and faeces

Corpses also come with faeces, and faeces attract mites. A great diversity of mites has been collected from inside human mummies (Baker 2009). Practically no work has been done on the mites attracted to relatively fresh faeces of human corpses. It seems that more acarological information is available on coprolites of human and animal mummies (Radovsky 1970; Kliks 1988; de Candanedo Guerra et al. 2003) or 6,500 year-old *Demodex* mites in regurgitated pellets of raptors (Fugassa et al. 2007). Radovsky identified deutonymphs of *Myianoetus* nr *dionychus* and *Anoetostoma oudemansi* (Histiostomatidae, Astigmata) and an acarid tritonymph in a human coprolite (Radovsky 1970). Mass occurrence of *M. diadematus*, a species related to *M.* nr *dionychus*, was recently reported from the corpse of a human baby wrapped in a plastic bag (Russell et al. 2004). The histiostomatid and acarid mites found there might have been attracted by the fresh faeces; however, mites of these two families might also have been ingested with food and passed in the faeces, something that happens unnoticed but perhaps frequently in most human cultures (Radovsky 1970).

Acknowledgments The authors appreciate the funding of research on forensic acarology by the Leverhulme Trust. Additional information was kindly provided by M. Lee Goff, Paola Magni, Marta I. Saloña-Bordas and Francis D. Feugang Youmessi. The authors like to thank Mariló Moraza and Barry M. OConnor for advice and reviewing an earlier version of the manuscript.

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