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Phoresy and Mites: More Than Just a Free Ride

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Abstract

Mites are masters at attaching to larger animals, often insects, in a temporary symbiosis called phoresy that allows these tiny animals to exploit patchy resources. In this article, we examine phoresy in the Acari, including those that feed on their carriers in transit, from a broad perspective. From a phylogenetic perspective, phoresy has evolved several times from free-living ancestors but also has been lost frequently. Rotting logs appear to be the first patchy resource exploited by phoretic mites, but the evolution of rapid life cycles later permitted exploitation of short-lived resources. As phoresy is a temporary symbiosis, most species have off-host interactions with their carrier. These relationships can be highly complex and context dependent but often are exploitative of the carrier's resources or progeny. Transitions from phoresy to parasitism seem widespread, but evidence for transitions from obligate phoretic parasitism to permanent parasitism is weak.

1. INTRODUCTION

Deutonymph: the third life stage of mites after the egg

Free living: describes mites with no life stages that attach to carriers or hosts

Natal habitat: the place where eggs are laid and most or all immature stages develop

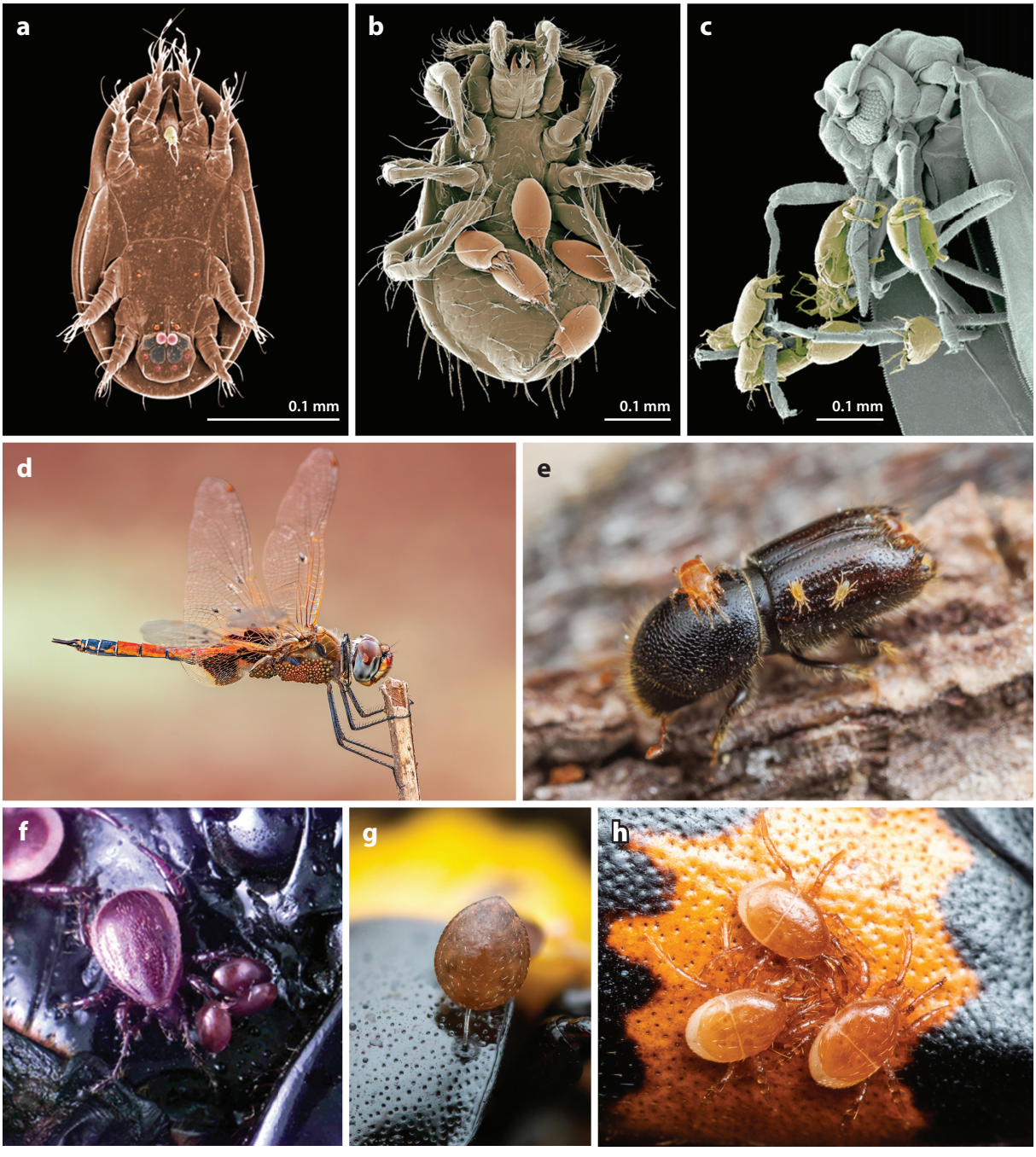
Mites include the smallest of all terrestrial arthropods, are the most diverse group of the Arachnida, and have infiltrated more habitats than the Insecta (142). Part and parcel of this acarine conquest and radiation is phoresy, their ability to hitch a ride on larger animals. Initially, phoresy was considered to include any relationship in which one animal transported another, even ants carrying their young; in which the relationship was temporary; and in which feeding on the carrier did not occur (82). However, Janet (55) struggled with the divide between phoresy and parasitism. *Antennophorus* species seem to be phoretic, but adult mites ride beneath the heads of ants, where they feed by deceiving their carrier into trophallaxis (40), while also being transported to new nests where their young develop as inquilines.

During the twentieth century, authors devised more restrictive definitions. Intraspecific transport was dropped, species that feed on the host continued to be excluded, and some definitions precluded development during transit—while also suggesting that movement should be from a less to a more suitable habitat (36). Since then, however, these definitions have increasingly broadened again. For the purposes of this review, we prefer the definitions of Camerik (21) and Walter & Proctor (142), with slight modification: Phoresy is a temporary symbiosis where one life stage of a smaller animal (the phoretic) attaches to another larger animal (the carrier) for dispersal. We emphasize that the symbiosis is temporary and usually interspecific. Thus, phoretics can have an additional interaction with a carrier; in this review, we discuss examples of mutualists, commensals, parasites, and parasitoids with a phoretic symbiosis within their life cycle. In addition, although the outcome of phoresy is dispersal, we do not exclude negative impacts on the carrier. Thus, impeding movement of the carrier or feeding from the host are still within the realm of a phoretic relationship.

Our preferred definition is, however, more restrictive than that of Bartlow & Agosta (7), which includes parasites such as ticks. Ticks may disperse to new habitats on hosts; however, this appears to be incidental, and we exclude these species. Our definition does include those parasites for which dispersal is integral to the relationship with the host, particularly those that are parasitic in only one life stage. This includes the highly diverse Parasitengona (larval parasites), several groups of Astigmata with parasitic deutonymphs, and groups such as the Heterozerconina and Paramegistidae that are parasitic as adults. We emphasize that phoresy is a symbiosis executed by one life stage. In mites, this is usually either a deutonymph or an adult (**Figure 1**). Exceptions are explicable. For instance, the flower-inhabiting mite *Hattena panopla* lives in flowers, and adults ride on visiting honeyeaters. As the duration of each flower is shorter than the life cycle of the mites, immature mites are also phoretic—but by riding on phoretic adult mites, a rare case of intraspecific phoresy (127).

In contrast, there is little question as to whether a mite is free living or phoretic. Free-living mites that occasionally appear on larger animals are termed accidental phoretics (1) or facultative phoretics (21). Accidental phoresy can be ecologically significant, as exemplified by the surprising number of ground-dwelling Oribatida found on birds (81) and beetles (100). Indeed, the earliest purported case of phoresy, from the Carboniferous Period (121), could be an accidental association between an oribatid and an insect.

Various authors have tried to classify phoretic relationships into subtypes (e.g., 132, 134, 144); the most enduring of these classifications is the division into facultative and obligate phoresy (1). The terms themselves are unfortunate, as phoretic species must, at some time, make an obligatory movement from the natal habitat. In this spirit, Camerik (21) redefined facultative phoresy as equivalent to accidental phoresy, while separating obligate phoretics into species that exhibit frequent obligate phoresy (i.e., in short-term habitats) and those exhibiting infrequent obligate phoresy (i.e., in long-term habitats).



(*Caption appears on following page*)

Figure 1 (*Figure appears on preceding page*)

Phoretic mites. (*a*,*b*) Astigmata: (*a*) phoretic deutonymph, ventral view; (*b*) on ologamasid mite venter. (*c*) Heterostigmata: *Polyphagotarsonemus latus* adults on *Bemisia tabaci*. (*d*) Parasitengona: *Arrenurus* water mite larvae on venter of *Tramea loewii*. (*e*) Parasitidae deutonymph (*left*) and Ereynetidae adults (*right*) on six-spined bark beetle, *Ips calligraphus*. (*f*) Mesostigmata, Trigynaspida: *Megisthanus thorelli* and Fedrizziidae adults on passalid beetle. (*g*) Mesostigmata, Uropodina: phoretic deutonymph, attached by anal pedicel. (*h*) Mesostigmata: *Poecilochirus* deutonymphs on *Nicrophorus* carrion beetle. Panels *a–c* copyright DE Walter. Panel *d* copyright Narelle Power and Damian White. Panel *e* copyright Clarence Holmes. Panel *f* copyright Anthony O'Toole. Panel *g* copyright Benjamin Fabian. Panel *h* copyright Jason Headley. All images used with permission.

It has been several decades since the last reviews of phoresy in various groups of Acari (3, 14, 31, 52, 53, 58, 103). The phylogeny of mites is now better resolved, allowing us to explore phoresy within a phylogenetic framework. We look for patterns within the major groups of phoretic mites, and across the Acari, before exploring three important aspects of phoresy: the impact on carriers, phoresy as part of a dynamic relationship between the mite and its carrier, and the evolution of other symbioses from phoresy.

2. THE ORIGINS OF PHORESY

Mites comprise two monophyletic superorders, Acariformes and Parasitiformes, which are of uncertain affinity to each other and other arachnid groups (66, 111). Associations with insects have formed multiple times in both groups, sometimes exhibiting highly specialized morphologies and phoretomorphic stages (142).

2.1. Acariformes

Acariform mites have a significant fossil record starting from the early Devonian Period (134). These early forms occurred mostly in soils, with the exception of Triassic records of plant-parasitic Eriophyoidea (125). None are obviously phoretic or otherwise symbiotic with insects until the Cretaceous Period. By this time, the major insect-associated lineages of acariform mites, Parasitengona (29, 73), Heterostigmata (61, 92, 93), and Astigmata (68) (**Figures 2** and **3**), are known from fossils.

These three major lineages have completely different associations with insects. Furthermore, several other groups have formed phoretic associations with insects, illustrating the propensity for mites to independently form phoretic relationships.

2.1.1. The Parasitengona. The Parasitengona comprise approximately 12,000 spp. that are almost all parasites as larvae and predators thereafter (38, 136). They include the chiggers (Trombiculoidea), which usually parasitize vertebrates; the water mites (Hydrachnida), which usually parasitize adult aquatic insects (**Figure 1*d***); and several other families that parasitize terrestrial arthropods. The natal habitat is often not patchy or ephemeral, being a large body of water or a general habitat through which the mites search for prey. However, the free-living stages may occupy ephemeral habitats, such as temporary ponds (18) or nests (133). Thus, dispersal between these habitats as parasitic larvae is an essential part of their life cycle and possibly integral to the evolution of this unique life history (146).

Edaphic: associated with the soil

Saproxylic: feeding on dead or decaying wood

2.1.2. The Heterostigmata. The Heterostigmata are a large, ecologically diverse group of mites with numerous associations with insects, including phoresy and permanent parasitism (58) (**Figure 2**). Early lineages associate closely with edaphic habitats and the nests of saproxylic social beetles, i.e., Passalidae and Scolytinae (Tarsocheylidae, Heterocheylidae). Beetles are common carriers, but the Pygmephoroidea include numerous myrmecophiles (8). Fungivory predominates throughout the group, with adults traveling on insects between habitats rich with mycelia (48, 58).

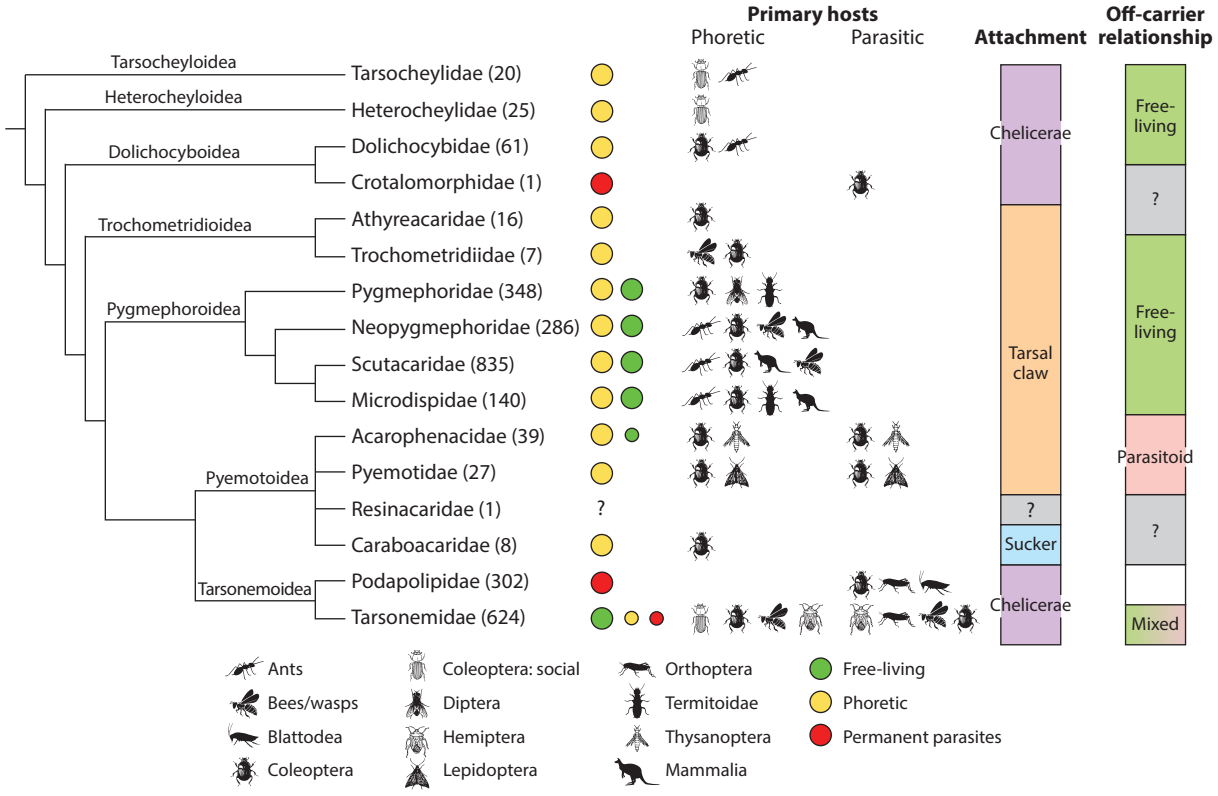


Figure 2

Phylogeny of Heterostigmata (84): species diversity (updated from Reference 148), primary host relationships (smaller circles indicate less representation), primary carriers or hosts (up to four, from most to least important), attachment method of phoretics, and primary off-carrier relationship.

However, in later branches, egg parasitoidism is prevalent, especially in the Pyemotoidea, where adult females ride a host and attack eggs as they are laid.

Early derivative taxa attach to carriers with their chelicerae (Tarsocheylidae, Heterocheylidae, Dolichocyboidea), as do the derived Tarsonemoidea (**Figure 2**). Permanent parasitism arises only in Tarsonemoidea (58, 84), notably the Podapolipidae, a radiation found primarily on beetles and orthopteroids (118, 131). Attachment to carriers via chelicerae may thus be a preadaptation to parasitism. Within most Trochometridioidea, Pygmephoroidea, and Pyemotoidea, attachment occurs via a claw-like structure at the tip of the tarsus (often a phoretomorph) that clasps the setae of the carrier. Notable variants are the bizarre Caraboacaridae, in which females attach via chelicerae and coxal suckers (59), and *Paracarophenax* (Acarophenacidae), which secrete a glue-like plug that they pinch for attachment (143).

The Heterostigmata present a shift from phoresy back to free-living lifestyles, a surprising theme also found in the other major groups exhibiting phoresy. The Tarsonemidae have made the shift most spectacularly, with numerous nonphoretic fungivorous and phytophagous taxa among phoretic lineages (84). Of the phoretic taxa, the best known are those within the nests of scolytine beetles that spread pathogenic bluestain fungi in sporothecae (48). However, some tarsonemids have more intimate or curious symbioses with their carriers. *Iponemus* are egg parasitoids of their scolytine beetle carriers (83), several tarsonemellines cause galls in figs and are transported on

Phoretomorph: a heteromorphic phoretic stage with a morphology differing from nonphoretic forms of the same stage

Sporothecae: special pockets for transporting ascospores

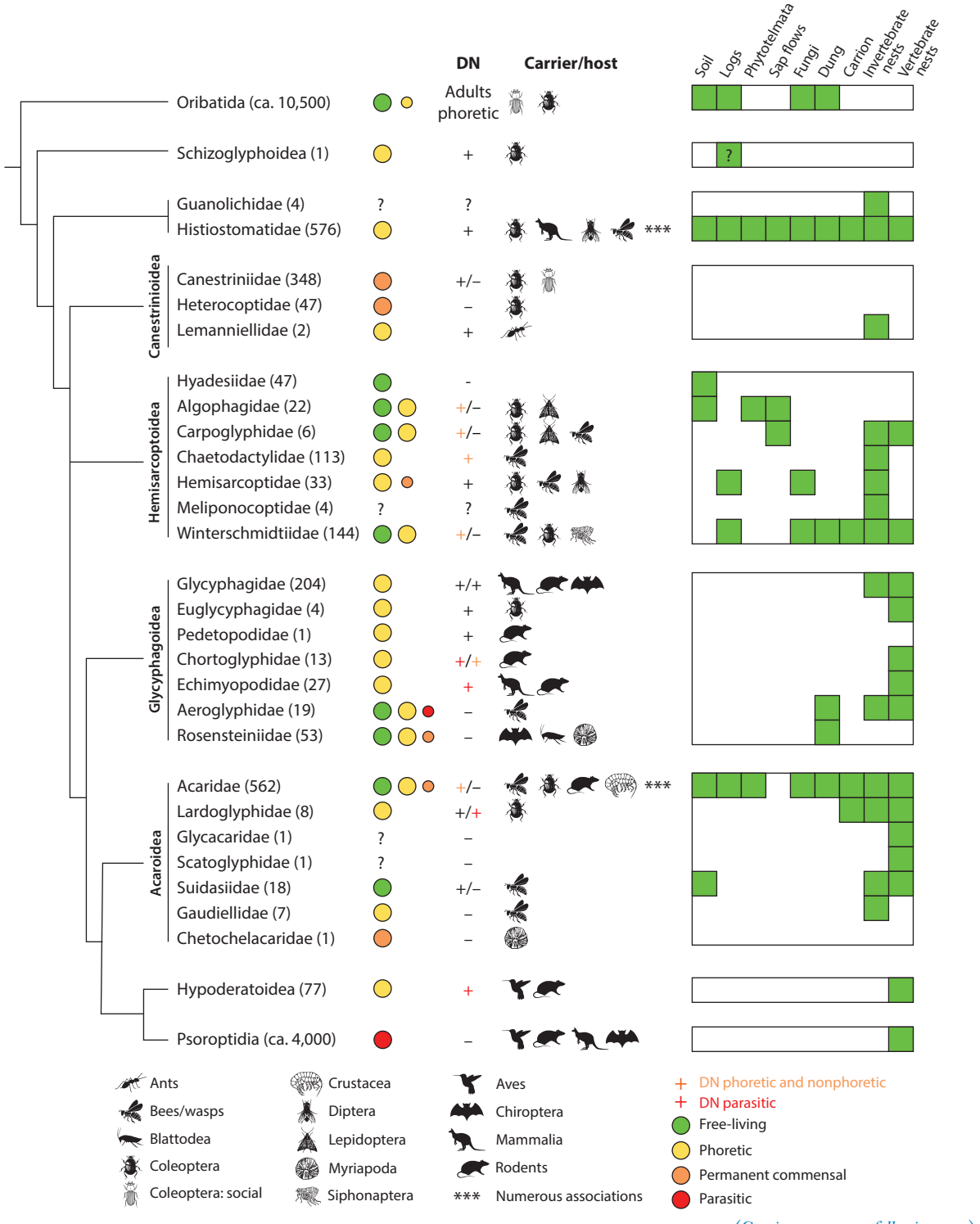


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Figure 3 (*Figure appears on preceding page*)

Phylogeny of Astigmata (105): species diversity (updated from Reference 123), primary host relationship (smaller circles indicate less representation), presence of deutonymphs (DN) [optional (*orange* +) or parasitic (*red* +)], primary carriers (up to four, from most to least important), and natal habitats for free-living and phoretic taxa.

fig wasps (56), and the wind-dispersed phytophagous pest *Polyphagotarsonemus latus* is phoretic on whiteflies (112) (**Figure 1*c***).

2.1.3. The Astigmata. The Astigmata present at least three remarkable shifts: first, from a probable edaphic free-living oribatid ancestor to a mite with a highly specialized deutonymph specifically adapted for phoresy; second, to permanent parasites of vertebrates (Psoroptidia); and third, from vertebrate parasites to nest inhabitants (Pyroglyphoidea, the house-dust mites) (26, 65, 66). The phylogenetic relationships of lower Astigmata, which are primarily associated with insects, are poorly resolved. In this review, we use previous morphological hypotheses (101) but acknowledge that more inclusive molecular studies will soon provide better resolution (26, 66).

Unlike Heterostigmatina, Astigmata have one primary attachment method via a ventral plate of suckers (**Figure 1*a*,*b***), although some groups have further modifications for clasping onto mammal hair (106). Purported early taxa (Schizoglyphoidea, Histiostomatoidea, Canestrinioidea, Hemisarcoptoidea) tend to be found on insects that utilize edaphic ephemeral habitats, but this pattern is less striking than in the Heterostigmata and Mesostigmata. Nevertheless, mammal and bird associates, with the natal habitat of nests, are primarily found in the Glycyphagoidea, Acaroidea, and Hypoderatoidea (**Figure 3**). In contrast to the Mesostigmata and Heterostigmata, beetle associations are less common than associations with bees and wasps, and few Astigmata are intimately associated with ants. However, the most diverse families (Acaridae, Histiostomatidae) often attach, probably in nonspecific relationships, to various insects as well as terrestrial vertebrates.

Some Astigmata show intraspecific life stage plasticity in the deutonymph, which is skipped or takes a phoretic or sedentary form (71, 72, 104). Skipping the deutonymph allows for rapid population growth and thus resource exploitation, while the sedentary and phoretic forms provide security in time and space, respectively. Such plasticity is expected more often in cyclical or longer-lasting habitats with harsh periods or irregular resource replenishment (4, 37), characteristic of many habitats utilized by phoretic Astigmata.

2.1.4. Other independent derivations. Phoresy has evolved at least 10 times in the remaining Acariformes. The Oribatida are infrequently phoretic, but several wood-inhabiting species have adults that are phoretic on saproxylic beetles. Passalid beetles are the most common carriers, particularly of the Mesoplophoridae, which clamp onto setae with their folding, jackknife bodies (100). More passive phoresy occurs in other families, such as Oppiidae, Scheloribatidae, and Haplozetidae (34, 70, 122). Curiously, several Oppiidae are phoretic on dung beetles, an atypical habitat for oribatids (33), and myrmecophilous species must somehow move between ant nests (54).

In the Trombidiformes, phoretic relationships occur in some Cheyletidae (17), Ereynetidae (35) (**Figure 1*e***), and Iolinidae (140). Furthermore, other taxa form loose or poorly studied relationships with insects, such as Tydeidae on moths (140), Stigmaeidae on sandflies (149), and Dasythyreidae on click beetles (142). The phytophagous Eriophyoidea are wind dispersed, although pollinators may transport some species between host plants (41); more extraordinary are phoretic *Aceria pallida* that accompany their psyllid carrier not directly between host plants but to overwintering sites (87).

Life stage plasticity: the ability to vary developmental patterns according to environmental conditions

2.2. Parasitiformes

In contrast to the Acariformes, the earliest parasitiform fossil is Cretaceous (57). An earlier origin is expected, yet the lack of fossils, in tandem with a strong Gondwanan pattern for one of the earliest branches—the Holothyrida + Ixodida—gives credence to a late Cretaceous or early Cenozoic diversification (9). Whenever their origin, phoretic associations with insects are present within the earliest branches of Mesostigmata: Trigynaspida, Microgynioidea, Sejoidea, and Uropodina (**Figure 4**).

The Mesostigmata show three distinctive types of phoretic relationships (**Figure 4**). The first and earliest type comprises the Trigynaspida, which are phoretic as adults on insects, especially ants and wood-inhabiting beetles (62) (**Figure 1*f***). The exceptions are several free-living Cercomegistoidea that may represent prephoretic ancestors. Many trigynaspid mites live on their hosts even while their hosts are not dispersing and are thus in another nonphoretic symbiosis. Where they have been studied, the Celaenopsoidea, Cercomegistoidea, Fedrizzioidea, and Megisthanoidea are predators and scavengers and are thus commensal (20, 63, 128, 139); the other superfamilies are kleptoparasitic on carabid beetles or ants (40). Trigynaspids tend to live in long-lasting habitats, probably due to their relatively long life cycles of at least one month (63, 128, 139). They usually have no special adaptations for attachment and move freely over their hosts. Parasitic adults, such as the Paramegistidae (27), have evolved multiple times.

The second type involves several seemingly independent derivations of phoretic deutonymphs. The first of these are the Sejina and Uropodina, currently seen as two independent lineages that independently developed deutonymphs that attach via an anal pedicel (69) (**Figure 1*g***). As in trigynaspids, wood-inhabiting beetles are common hosts (60), as are ants for Uropodina (120). Both groups prefer long-lived habitats such as rotting wood and nests. The second group is a radiation in the otherwise free-living Parasitidae, the Parasitinae, which are phoretic as relatively unspecialized deutonymphs (**Figure 1*e*,*b***). Due to the relatively fast life cycles of parasitines, their natal habitats are often carrion, dung, and nests, and their carriers tend to be insects living in these habitats (74, 126). The Rhodacaroidea continue the deutonymphal pattern into the Gamasina: Some Ologamasidae are phoretic on mammals and inhabit their nests or are phoretic on carabid beetles; Halolaelapidae are phoretic on amphipods, beetles, and flies in wet habitats; and a large radiation of Digamasellidae are phoretic primarily on saproxylic beetles (85).

The third type encompasses four highly diverse groups of Mesostigmata: Ascoidea, Dermanyssoidea, Eviphidoidea, and Phytoseioidea. These mites are phoretic as adults and tend to have fast life cycles (approximately one week) (142). As such, these Mesostigmata are found primarily in carrion, dung, flowers, or other resources that quickly degrade (75, 85). However, this does not preclude them from exploiting longer-lasting habitats, especially the nests of insects (31, 107).

3. ADAPTATIONS FOR PHORESY: INNOVATION AND CONVERGENCE

Phoresy evolved a surprising number of times and in relationships with almost all winged insect orders, but primarily with beetles and nest-making Hymenoptera (**Figures 2–4**). The natal habitats of phoretic species are diverse, but phoresy appears to have initially evolved when a free-living edaphic species with a slow life cycle exploited the habitat of rotting logs. This habitat is among the longest lasting of all patchy environments (91). We hypothesize that rotten logs present an evolutionarily solvable problem: That is, dispersal between logs on foot could still be successful, but phoresy is more successful and therefore selected for. The three major phoretic groups, as well as Oribatida, share this ancestral habitat. The Parasitengona are an exception, rarely parasitizing log-inhabiting or nesting insects (38).

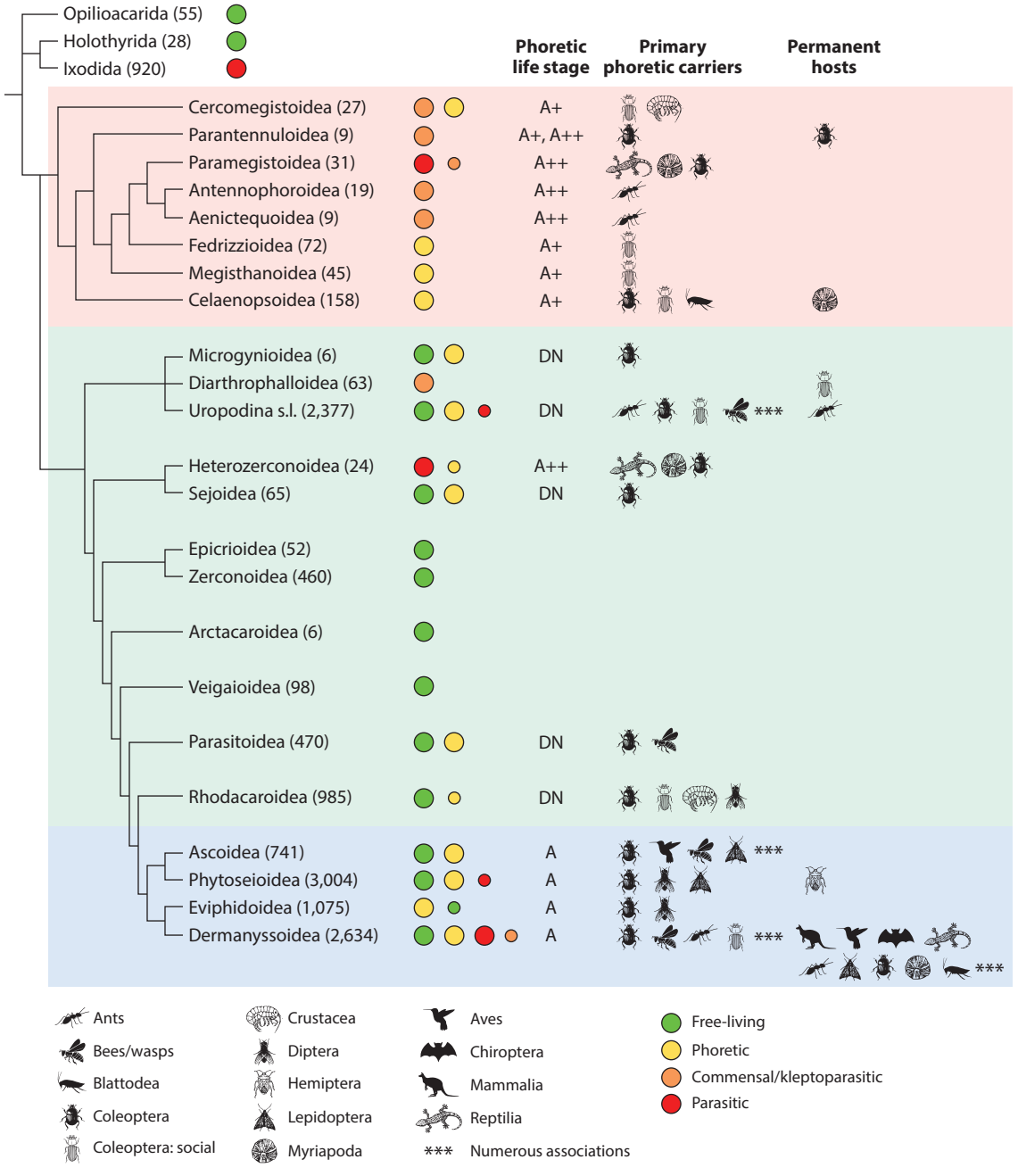

Figure 4

Phylogeny of Parasitiformes (28, 62, 69): species diversity (updated from Reference 11), primary host relationships (smaller circles indicate less representation), phoretic life stage, and primary carriers or permanent hosts. Shading indicates three types of phoretic relationships. Abbreviations: A, adult phoretic; A+, adults that also have a nonphoretic period on host; A++, phoretic parasites; DN, deutonymph phoretic.

Haplodiploid: a sex-determination system in which haploid males develop from unfertilized eggs, and diploid females develop from fertilized eggs

Phoretic parasite: species that is parasitic in one life stage while also being dispersed by its host

After rotting logs, phoretic species exploited all manner of habitats, including those that persist only for a matter of days or weeks. The key innovation seems to be faster life cycles (104). A mite's life cycle must be shorter than the duration of the resource. Thus, mites with slow life cycles, such as trigynaspids (128, 139) and oribatids (101), occupy long-lasting habitats. In contrast, the faster life cycles of higher Mesostigmata, Heterostigmata, and Astigmata—as little as a week (e.g., 78, 116, 126)—allow exploitation of short-lived resources such as dung, carrion, flowers, and sporocarps (104). These higher taxa also utilize long-lasting habitats, such as tree holes (37) and sap flows (44), although they tend to have slower life cycles.

The phoretic life stage is usually an adult or deutonymph. Phoretic adults are often females (88, 141), but both sexes are phoretic in species that have nonphoretic periods on their host (e.g., Trigynaspida; 130) or where males seek additional mates in new habitats (e.g., 42, 119). Phoresy by adults provides obvious advantages: Mated adult females or those with haplodiploid genetic systems (102) can establish colonies alone and exploit resources instantaneously. More significantly, their progeny can feast on ephemeral prey that also exploit the resource (e.g., nematodes, eggs, early-instar larvae). Thus, phoresy by adults dominates in species that exploit short-lived resources, whether it be the resources that the habitat presents (e.g., small prey, nectar) or the host's progeny (i.e., host eggs or provisions). Why do some species disperse as deutonymphs? We think that it is significant that the most morphologically specialized phoretic mites are deutonymphs. Immature mites do not need to find mates and bear young, and the specialized deutonymphs of Astigmata and Uropodina do not feed, allowing investment in adaptations for phoresy. The existence of a phoretic morph resistant to adverse conditions also permits some environmental resilience and life-cycle synchronization, which are ideal for life in a long-lived cyclic habitat. Furthermore, deutonymphs are smaller than adults and, in bisexual species, must disperse in groups to increase mating opportunity. If carrying mites incurs a cost to the insect, then perhaps having smaller nymphs reduces these impacts.

Unusually, protonymphs are never the phoretic stage, and phoretic larvae exist only as the phoretic parasites of Parasitengona. We hypothesize that enough resources must be accumulated to invest in a specialized and resilient life stage, as in the Astigmata, or the preadult stage, as in the Sejina, Uropodina, Parasitidae, and basal Gamasina.

4. PHORESY AND THE DIVERSIFICATION OF MITES

Phoresy allows mites to exploit a plethora of resources that are otherwise unobtainable, permitting numerous radiations throughout the three major lineages that have evolved phoresy. Thus, phoretic mites contribute significantly to the diversity of the Acari. However, free-living and parasitic mites outnumber phoretic mites significantly: Almost all Oribatida are free living (101), and most Trombidiformes and Mesostigmata are free-living or permanent parasites (**Figures 2–4**). Therefore, phoresy itself has not promoted unusual rates of speciation. Indeed, the greater dispersal ability may promote panmixis in populations, reducing fragmentation as experienced by soil-dwelling free-living mites. In permanent parasites, host specificity and on-host microhabitat specificity likely promote speciation. Phoretic mites could experience similar pressures, but probably only in nests and environments where the natal habitat requires species-specific adaptations for tracking the life cycle of hosts, and where options for carriers are limited.

5. INTERACTIONS BETWEEN MITES AND THEIR CARRIERS

Phoresy is a temporary relationship that is frequently regarded as commensal. As mites rely on their carrier for safe transit, the smooth, flattened bodies of many phoretic mites may have evolved to minimize impact on their carrier. However, numerous phoretic mites have bodies with little

modification, and those of Uropodina attach via stalks, thus nullifying aerodynamic benefits to their carrier. Occasionally, mite loads hinder the movement of their carrier (e.g., 64, 89), and some mites feed on host tissues in transit (e.g., 51, 115) or prey on phoretic nematodes (76). Despite these few examples of negative impacts or feeding, the mite is still phoretic: It is a single life stage moving between habitats on a carrier.

Context dependent: describes a symbiosis that is conditional, changing its nature according to certain biotic or physical factors

Phoretic mites rely on their carrier for transport, and in most cases, the natal habitat for mites is the same as their carrier. Therefore, we expect insignificant or even beneficial symbioses (43, 107, 145), particularly cleaning and protective mutualisms (e.g., 13, 108), in the shared natal habitat. However, numerous examples of negative symbioses exist. For instance, the heterostigmatic families Pyemotidae and Acarophenacidae contain parasitoids of the eggs of their carriers (32, 98), *Chaetodactylus* kills the young of mason bees (94), *Trochometridium* kills the larva of various bees and then feeds on the resulting fungal growth (from spores carried by the mites) (24), and *Macrocheles muscaedomesticae* eats the eggs and first-instar larvae of its muscid fly carrier (39). In this section, we discuss four well-studied systems: the mite–fungus community of scolytine bark beetles, the hummingbird–flower mites, *Poecilochirus* on carrion beetles, and mites in the acarinaria of bees.

The community of mites living with bark beetles is a complex system of several species of mites, fungi, and beetles (47, 48, 113). Most work focuses on southern pine beetle (*Dendroctonus frontalis*) and its phoretic mites, particularly *Tarsonemus*. Beetles and *Tarsonemus* both actively disperse wood-pathogenic fungi upon which the beetle larvae and mites rely. However, mites also actively transport the beetle-antagonistic bluestain fungus, which can outcompete beetle-mutualistic fungi. Thus, the *Tarsonemus*–beetle relationship has mutualistic benefits, by supplementing transmission of beneficial fungi, that are weak at best; this relationship instead tends to be indirectly antagonistic when *Tarsonemus* transmits bluestain fungi (45, 46). Indeed, evidence for mite–beetle mutualisms is weak and is only inferred from the vast diversity of mites with bark beetles, some of which presumably prey on *Tarsonemus*; however, others are predatory of their own carriers (96).

Several groups of Mesostigmata have colonized flower–pollinator systems, where they consume nectar and pollen and are phoretic on floral visitors (19, 42, 95, 127). The best known of these mites are the hummingbird–flower mites, which dash up the bills of hummingbirds and hide in their nares until the hummingbird visits the next suitable flower (19, 22). Unlike the other systems, the mites do not share the natal habitat directly; however, they compete with hummingbirds for the same nectar, removing up to half of the resource (79) and potentially altering foraging behavior (80). Thus, hummingbird–flower mites rob resources from their carrier while providing no benefit in return.

The mites of both carrion beetles and eumenine wasps are examples of protective mutualisms, where mites attack competing flies and parasitic wasps, respectively. However, this harmonious relationship has a sinister side. In both cases, the relationship is context dependent, shifting between mutualistic and antagonistic according to biotic and/or physical conditions.

Carrion beetles (*Nicrophorus*) compete with calliphorid flies for the corpses of small mammals, but only carrion beetles regularly carry parasitid mites (*Poecilochirus* spp.; **Figure 1*b***). These mites feed on the eggs of calliphorid flies and are thus beneficial to beetles, but the mites also attack the eggs of their hosts (12, 15) and compete for carrion (99, 124, 137). The mites are thus in a conditional relationship with their hosts, being disadvantageous in the absence of blowflies but often advantageous when blowflies are present (137, 145).

Several bees and wasps have pits or pockets (acarinaria) in which they carry mites. Given that these structures seemingly encourage phoretic mites, surely these mites should be beneficial. However, numerous mites riding in acarinaria feed on their carrier's progeny or provisions (23; **http://idtools.org/id/mites/beemites/index.php**). Thus, instead of transporting beneficial mites, acarinaria could instead be a structure for skewing mite loads as social bees depart their natal

nest (67). Unfortunately, we know little about the impact of most of these mites; one of the best-studied relationships is that of the eumenine wasp *Allodynerus delphinalis* and its mite *Ensliniella parasitica* (108–110). These mites feed on the hemolymph of juvenile wasps and, at high densities, cause mortality of their carrier (110). However, at lower densities, the mites have little impact and, when the parasitoid wasp *Melittobia acasta* is present, defend juvenile wasps by attacking and sometimes killing the parasitoid (108).

The above examples show how assumptions of relationships based on feeding or a limited number of observations can be misleading. In each example, the multitrophic interactions are more complex than was first thought: Few, if any, phoretic mites exist in a single phoretic-carrier system, and some are extraordinarily complex. For example, beetles and sunbirds transport four phoretic mite species, with the mites themselves transporting fungal spores, to protea flowers, where only some mite species utilize the fungi for food (138). The interactions among players in these multipartite symbioses are difficult to disentangle, but phoretic mites tend to build exploitative relationships with their carriers that are only mutualistic under certain conditions. Nevertheless, stable commensal or mutualistic relationships may occur; however, these have been little studied, and we encourage work on the impact of more mundane phoretics on their carriers.

6. EVOLUTIONARY TRANSITIONS FROM PHORESY

Phoresy is a logical intermediate life history because it requires elements of parasitism (host finding and attachment) but no adaptations for feeding, breeding, and transfer between hosts (3, 5, 49, 132). Phylogenetic evidence generally supports this pivotal position, as lineages of permanent symbionts arise consistently within or as sister to lineages exhibiting phoresy (**Figures 2–4**). Significant exceptions are deep branches, most notably the ticks and Parasitengona, which have no known phoretic intermediary (9, 146).

Two pathways to parasitism are possible: via the phoretic symbiosis itself or via the off-host symbiosis. The former involves the phoretic stage first becoming a phoretic parasite, while the latter involves other stages shifting to parasitism, or another permanent symbiosis, while maintaining a phoretic stage. The relative importance of each pathway is difficult to disentangle, and we suspect that both pathways have played a significant role.

Examples of phoretic mites sometimes feeding from their hosts, such as *Macrocheles* (90, 114, 115) and *Hemisarcoptes cooremani* (51), are purported transitional relationships leading to parasitism. However, we see these relationships as a step toward obligate phoretic parasitism; i.e., feeding on the carrier is required for further development. For the next step, phoretic parasites must abandon their ancestral feeding habits and shift to living and breeding on their hosts. However, examples of this transition are elusive. Water mites with parasitic nymphs and adults do not parasitize their chironomid carrier but instead shift to mollusks (30) or sponges (25). In the Glycyphagoidea (Astigmata), the specialized deutonymphs were originally insect phoretics, but a putative transformation series from vertebrate phoretics to endofollicular phoretics and finally to endofollicular phoretic parasites occurred. None, however, have abandoned the natal habitat of the nest. Similarly, the Hypoderatidae are regressive deutonymphal parasites within the tissues of birds and rodents, but, where they are known, active stages develop in nests. Therefore, phoretic parasites with highly modified life histories and morphologies may not transition easily to permanent parasitism, but, as in the example of the Hypoderatidae, the probable sister to the Psoroptidia (103), when they do so it may allow an extraordinary radiation.

A shift toward parasitism by nonphoretic stages first requires a more intimate off-host relationship, of which a nest is the most intimate of all. Significant lineages of bird and mammal parasites may have followed this pathway, such as the Dermanyssoidea (117), Cheyletoidea (16), and Psoroptidia (6). The same pathway seems likely for some permanent symbionts of insects

found on nesting beetles (e.g., Diarthrophallidae on Passalidae) and social bees (e.g., Varroidae on Apidae) and Uropodina with unmodified deutonymphs in ant colonies (77). However, some permanent symbionts of insects have no links with nests, such as the Otopheidomeninae (moths; 86) and Podapolipidae (chrysomelid beetles; 129) or have ambiguous ancestral host relationships (e.g., Canestriniidae, possibly on carabids; 105). Thus, these lineages may have arisen through phoretic parasitism by adults, coupled with selection to remain on hosts that did not utilize concentrated resources, thus making new hosts difficult to locate.

Phoresy is readily reversible, with free-living taxa arising frequently within otherwise phoretic lineages (**Figures 2–4**). In Heterostigmata, each family of Pygmephoroidea reverted to free living (8), as have Tarsonemidae and possibly the Acarophenacidae. Surprisingly, several Astigmata and Uropodina also reverted to free living, despite their heteromorphic phoretic deutonymphs. Most Astigmata accomplished this reversion by skipping the deutonymph, which often shows plasticity in its expression (71). Similarly, some Uropodina have phoretic and nonphoretic deutonymphs (2), and adult phoretomorphs occur in some Heterostigmata (97) and Mesostigmata (10). The optional expression of these stages suggests that they could be lost easily. Phoretic parasitism is also lost frequently in the Parasitengona, primarily within water mites (135) but also in terrestrial groups (147). Thus, phoresy has evolved frequently as a means of exploiting patchy resources, but it seems to be just as easily lost, representing reversions to free-living lifestyles where food is presumably harder to find but more evenly distributed.

SUMMARY POINTS

1. Phoresy is a temporary symbiosis where a larger animal transports a single life stage of a smaller animal.
2. Feeding may occur on the carrier and is obligate in the larval parasites of Parasitengonina, deutonymphal vertebrate parasites of the Astigmata, and some kleptoparasitic and parasitic Mesostigmata.
3. Rotting logs are an ancestral habitat, with faster life cycles in derived taxa allowing exploitation of shorter-lived resources.
4. Phoresy is usually part of another symbiosis with the carrier, which can be a complex, context-dependent relationship that nevertheless tends to be exploitative of the carrier's progeny or its resources.
5. Phoresy has evolved multiple times—although just once in Astigmata and perhaps Heterostigmata—but is also lost frequently.
6. Permanent parasitism has evolved from numerous phoretic lineages but rarely, if ever, from lineages with parasitic phoretic stages.

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