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Phoresy in animals: review and synthesis of a common but understudied mode of dispersal

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ABSTRACT

Phoresy is a type of interaction in which one species, the phoront, uses another species, the dispersal host, for transportation to new habitats or resources. Despite being a widespread behaviour, little is known about the ecology and evolution of phoresy. Our goal is to provide a comprehensive review of phoretic dispersal in animals and to bring renewed attention to this subject. We surveyed literature published between 1900 and 2020 to understand the extent of known higher-level taxonomic diversity (phyla, classes, and orders) and functional aspects of animals that use phoretic dispersal. Species dispersing phoretically have been observed in at least 13 animal phyla, 25 classes, and 60 orders. The majority of known phoronts are arthropods (phylum Euarthropoda) in terrestrial habitats, but phoronts also occur in freshwater and marine environments. Marine phoronts may be severely under-represented in the literature due to the relative difficulty of studying these systems. Phoronts are generally small with low mobility and use habitats or resources that are ephemeral and/or widely dispersed. Many phoronts are also parasites. In general, animals that engage in phoresy use a wide variety of morphological and behavioural traits for locating, attaching to, and detaching from dispersal hosts, but the exact mechanisms behind these activities are largely unknown. In addition to diversity, we discuss the evolution of phoresy including the long-standing idea that it can be a precursor to parasitism and other forms of symbioses. Finally, we suggest several areas of future research to improve our understanding of phoresy and its ecological and evolutionary significance.

Key words: animal–animal interaction, animal-mediated dispersal, arthropod, dispersal host, hitch-hiking, parasitism, phoront, species interaction, symbiosis, zoochory

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I. INTRODUCTION

From the several cases now given, there can, I think, be no doubt that living bivalve shells must often be carried from pond to pond, and by the aid of birds occasionally even to great distances. (Darwin, 1882)

In his final publication, Darwin (1882) described several species of freshwater bivalves that use their shells to attach to the bodies of ducks, beetles, frogs, and newts. He hypothesized that the bivalves were using these other animals for dispersal, and that this could explain the observation that individuals from distant areas were remarkably similar in appearance and in fact the same species. Over a century later, it is clear that Darwin was remarking on the dispersal behaviour now known as phoresy (Lesne, 1896).

Dispersal is a critical component in the life history of most organisms. Dispersing away from one area to another can affect not only the fitness of individuals, but also the genetics of populations and the distribution and abundance of species (Bowler & Benton, 2005; Clobert *et al.*, 2012). Dispersal by both parents and offspring can, for example, decrease competition with conspecifics, reduce the probability of inbreeding, and allow populations to respond to environmental change (Bowler & Benton, 2005; Jackson & Sax, 2010; Clobert *et al.*, 2012). It can also decrease density-dependent predation and disease, which has been shown for some plant species (Connell, 1970; Janzen, 1970; Comita *et al.*, 2014). Phoresy, or phoresis (from the Greek 'phoresis' meaning 'being carried'), has been defined traditionally as a type of animal-mediated dispersal where an animal, the phoront, searches for and attaches to another animal, the dispersal host, for the sole purpose of being transported to a 'suitable' habitat (i.e. a habitat that supports continued survival and reproduction; Farish & Axtell, 1971). A second, more recent definition is not necessarily restricted to animals, with phoresy being "a phenomenon in which one organism (the phoretic) receives an ecological or evolutionary advantage by migrating from the natal habitat while superficially attached to a selected interspecific host for some portion of the individual phoretic's lifetime" (Houck & OConnor, 1991, p. 613). These definitions are similar but differ in the context under which they consider phoresy to occur. Specifically, Farish & Axtell (1971) consider phoresy to involve dispersal to and from any suitable habitat, whereas Houck & OConnor (1991) are more restrictive and consider only dispersal from the natal habitat. Both definitions agree that the goal of phoresy is dispersal and that, unlike parasites that consume parts of their hosts, phoronts are essentially passive 'hitchhikers' that have little or no net negative effects on their hosts (although, as discussed in later sections, this may not always be true and in some instances the lines between phoresy and other forms of symbioses can be blurred).

The goal of this paper is to assess the diversity of animals using phoretic dispersal through both taxonomic and functional lenses to reveal previously overlooked patterns of this relatively understudied type of species interaction and mode of dispersal. To date, there have been dozens of reviews on specific taxa, for example lice (Keirans, 1975a, 1975b), mites (Houck & OConnor, 1991), pseudoscorpions (Poinar, Curcic, & Cokendolpher, 1998), and nematodes (Giblin-Davis, Kanzaki, & Davies, 2013), but no large-scale comprehensive review of this subject. First, we briefly review the concept of phoresy and present a working definition. Next, we present a synthesis of the literature to reveal the higher-level taxonomic breadth (phyla, classes, and orders) of known phoretic animals and the functional similarities among them. In the discussion that follows, we speculate on the evolution of phoresy including the long-standing idea that it can be a precursor to parasitism and other types of symbiotic relationships. We end by offering suggestions for future research needed for an improved understanding of phoresy and its ecological and evolutionary significance.

II. WHAT IS PHORESY?

(1) Stages of phoretic dispersal

Phoresy generally comprises three distinct stages that are each critical for success of the phoront: locating a dispersal host, attaching to the host, and detaching from the host. If a phoront is unable to complete one of these stages, dispersal will fail.

(*a*) Stage 1: locating the host

Recognizing a suitable host is the first step to phoretic dispersal. To do so, phoronts must perceive host-specific cues. These may be cues related to being in the right habitat or sensing the proper host species or host developmental stage. The majority of species with documented cases of host-related cues are arthropods (Table 1). The cues that have been documented have been mostly chemical, although it seems likely that other types of cues involving visual, tactile, and auditory information are common but unrecorded. Examples include lice that use CO_2 released by their hippoboscid fly host (Harbison *et al.*, 2009), wasps that use sex pheromones produced by their moth host (Arakaki *et al.*, 1997), and nematodes that use volatiles and cuticular hydrocarbons emitted by their hosts (Hong & Sommer, 2006*a*; Krishnan *et al.*, 2010; Okumura, Tanaka, & Yoshiga, 2012). To locate

Table 1. List of phoretic orders of animals identified during the literature survey. Examples are arranged by phylum, subphylum, class, and order. We also list up to three families and indicate if there are more known. Common dispersal hosts, ecosystem and microhabitat type, and examples of specific traits used for phoresy are also given. Column labelled 'Phoretic stages observed' summarizes the phoretic behavioural stages that have been observed for at least one species within each group: 1, locating dispersal host; 2, attaching to the host; 3, detaching from the host (see Section II.1). Although all three behavioural stages are required, not all stages have been documented for most groups (see text for details). See Section III.1 for references used for taxonomic classifications

Phylum	Subphylum	Class	Order	Families	Common name	Life stage(s) involved	Major ecosystem	Microhabitat of phoront	Common dispersal host(s)	Phoretic stages observed	Examples of traits	Reference(s)
Euarthropoda	Chelicerata	Arachnida	Trombidiformes	Dolichocybidae, Microdispidae, Scutacaridae, and many others	Mites	Adults, nymphs	Terrestrial, freshwater	Nests, plants, flowers, feathers, hair, carrion, dung, fungi	Various arthropods, birds, and mammals	1, 2, 3	Enlarged claws, response to chemical cues, recognize cues for detachment	Magowski (1995); McLachlan, Ladle, & Bleay (1999); Soroker *et al.* (2003); Macchioni *et al.* (2005); Moser *et al.* (2005, 2010); Nims *et al.* (2008); Hodgkin, Elgar, & Symonds (2010); Khaustov & Trach (2014); Loghmani, Hajiqanbar, & Talebi (2014); Liu *et al.* (2016); Khaustov (2017); Baumann, Ferragut, & Šimić (2018); De Lillo *et al.* (2018); Baumann *et al.* (2018); Khaustov, Hugo-Coetzee, & Ermilov (2018); Azhari, Hajiqanbar, & Talebi (2018); Khaustov & Frolov (2018a, 2018b); Navabi, Hajiqanbar, & Mortazavi (2018); Kontschán & Hornok (2019)

Table 1. *(Cont.)*

Phylum	Subphylum	Class	Order	Families	Common name	Life stage(s) involved	Major ecosystem	Microhabitat of phoront	Common dispersal host(s)	Phoretic stages observed	Examples of traits	Reference(s)
Euarthropoda	Chelicerata	Arachnida	Mesostigmata	Dermanyssidae, Uropodidae, Macrochelidae, and many others	Mites	Adults, nymphs	Terrestrial	Nests, plants, flowers, feathers, hair, carrion, dung, fungi	Various arthropods, birds, and mammals	1, 2, 3	Modified chelicerae and claws of legs, anal pedicels, specific phoretic life stages, response to chemical cues	Moss (1966); Schabel (1982); Brown & Wilson (1992); Flechtmann & Baggio (1993); Seeman & Walter (1995); Gibbs & Stanton (2001); Bajerlein & Błoszyk (2003, 2004); Owen & Mullens (2004); Moser *et al.* (2005, 2010); Niogret, Lumaret, & Bertrand (2006); Lindquist & Moraza (2008); Nims *et al.* (2008); Perotti & Braig (2009); Hodgkin *et al.* (2010); López-Orozco & Cañón-Franco (2013); Bajerlein, Witaliński, & Adamski (2013); Fronhofer *et al.* (2013); Gettinger & Gardner (2017); Paraschiv, Martínez-Ruiz, & Fernández (2018); Kontschán (2018); Kontschán & Hornok (2019); Konwerski, Gutowski, & Błoszyk (2019)
Euarthropoda	Chelicerata	Arachnida	Ixodida	Ixodidae	Ticks	Larvae, nymphs	Terrestrial	Mammals and birds	Beetles, flies	2	Unknown	Petrova & Basikhin (1993); Flechtmann & Baggio (1993); Saloña-Bordas *et al.* (2015)

(Continues)

Table 1. *(Cont.)*

Phylum	Subphylum	Class	Order	Families	Common name	Life stage(s) involved	Major ecosystem	Microhabitat of phoront	Common dispersal host(s)	Phoretic stages observed	Examples of traits	Reference(s)
Euarthropoda	Chelicerata	Arachnida	Sarcoptiformes	Oppiidae, Chaetodactylidae, Trhypochthoniidae, and many others	Mites	Adults, nymphs	Terrestrial, freshwater	Nests, plants, flowers, feathers, hair, carrion, dung, fungi	Various arthropods, birds, and mammals	1, 2, 3	Specific phoretic life stages, ventral suckers (hypopodes), possible response to chemical cues	Behura (1956); Schabel (1982); Durden & Wilson (1991); Houck & OConnor (1991); Houck & Cohen (1995); Holte, Houck, & Collie (2001); Fashing & Chua (2002); Macchioni *et al.* (2005); Moser *et al.* (2005); Perotti & Braig (2009); Hodgkin *et al.* (2010); Okabe & Makino (2010); Sarangi, Gupta, & Saha (2014); Paraschiv *et al.* (2018); Waleckx *et al.* (2018); Ermilov & Frolov (2019)
Euarthropoda	Chelicerata	Arachnida	Araneae	Corrinidae	Spiders	Adults and immatures	Terrestrial	Ant nests	Winged sexual ants	2	Unknown	Ichinose, Rinaldi, & Forti (2004)
Euarthropoda	Chelicerata	Arachnida	Pseudoscorpiones	Chernetidae, Chthoniidae, Withiidae, and many others	Pseudoscorpions	Adults	Terrestrial	Animal nests, decaying trees	Insects, rodents, opilionids	1, 2	Use of pedipalpal chelae, silk harnesses, response to chemical cues, modified reproduction	Haack & Wilkinson (1987); Zeh & Zeh (1991, 1992, 1997); Magowski (1995); Poinar *et al.* (1998); Santos, Tizo-Pedroso, & Fernandes (2005); Francke & Villegas-Guzmán (2006); Szymkowiak, Górski, & Bajerlein (2007); Tizo-Pedroso & Del-Claro (2007); Finlayson *et al.* (2015); Fombong *et al.* (2016)

Table 1. *(Cont.)*

Phylum	Subphylum	Class	Order	Families	Common name	Life stage(s) involved	Major ecosystem	Microhabitat of phoront	Common dispersal host(s)	Phoretic stages observed	Examples of traits	Reference(s)
Euarthropoda	Chelicerata	Pycnogonida	Pantopoda	Pallenopsidae	Sea spiders	Adults, juveniles	Marine	Mesopelagic zone	Jellyfish	2	Unknown	Pagès, Corbera, & Lindsay (2007)
Euarthropoda	Hexapoda	Insecta	Phthiraptera	Philopteridae, Bovicoliidae, Trichodectidae, and many others	Lice	Adults, nymphs	Terrestrial	Feathers, hair	Insects	1, 2	Tarsal claws, mandibles, response to chemical cues	Hopkins (1946); Keirans (1975a, 1975b); Durden (1990); Macchioni *et al.* (2005); Harbison, Jacobsen, & Clayton (2009); Bartlow *et al.* (2016)
Euarthropoda	Hexapoda	Insecta	Siphonaptera	Ischnopsyllidae	Fleas	Adults	Terrestrial	Bats	Earwig (*Arixenia esau*)	2	Unknown	Marshall (1977); Hastriter *et al.* (2017)
Euarthropoda	Hexapoda	Insecta	Thysanaptera	Heterothripidae	Thrips	Adults, nymphs	Terrestrial	Flowers, moss, fungi	Treehopper	2	Unknown	Alves-Silva & Del-Claro (2011)
Euarthropoda	Hexapoda	Insecta	Coleoptera	Leiodidae, Staphylinidae, Meloidae, and a few others	Beetles	Adults, larvae	Terrestrial	Animal dung, animal nests	Rodents, shrews	1, 2	Specialized mandibles, attracts host	Roubik & Wheeler (1982); Peck (1982); Ashe & Timm (1987); Durden & Wilson (1991); Saul-Gershenz & Millar (2006); Crees & Debinski (2018); Topitzhofer *et al.* (2018); Scholtz, Basson, & Bologna (2018)
Euarthropoda	Hexapoda	Insecta	Hemiptera	Diaspididae, Adelgidae, Aphididae, and a few others	True bugs	Nymphs	Terrestrial	Plants	Insects	2	Hair suction cups	Takagi (2001); Magsig-Castillo *et al.* (2010); Gish & Inbar (2018); Leppanen & Simberloff (2018)
Euarthropoda	Hexapoda	Insecta	Lepidoptera	Pyralidae, Acrolophidae	Moths	Adults	Terrestrial	Animal dung	Rodents, sloths	2	Unknown	Waage & Montgomery (1976); Waage (1979); Davis *et al.* (1986)
Euarthropoda	Hexapoda	Insecta	Hymenoptera	Scelionidae, Trichogrammatidae	Parasitoid wasps	Adults	Terrestrial	Moth eggs	Insects	1, 2	Response to chemical cues	Clausen (1976); Arakaki, Wakamura, & Yasuda (1995); Arakaki *et al.* (1997); Huigens *et al.* (2009); Fatouros & Huigens (2011)

(Continues)

Table 1. *(Cont.)*

Phylum	Subphylum	Class	Order	Families	Common name	Life stage(s) involved	Major ecosystem	Microhabitat of phoront	Common dispersal host(s)	Phoretic stages observed	Examples of traits	Reference(s)
Euarthropoda	Hexapoda	Insecta	Diptera	Phoridae, Chironomidae, Simuliidae	Phorid flies, non-biting midges, blackflies	Larvae, eggs, pupae	Terrestrial, freshwater	Decaying organic matter, rivers, streams	Blowflies, molluscs, freshwater insects, fish, crustaceans	2	Proleg and abdominal hooks	Disney (1971); White, Weaver, & Fox (1980); Tracy & Hazelwood (1983); Tokeshi (1993); de Moor (1999); Callisto & Goulart (2000); Stauder & Kiel (2004); Batista-Da-Silva (2012); Inoue *et al.* (2015)
Euarthropoda	Hexapoda	Insecta	Trichoptera	Hydroptilidae	Caddisflies	Larvae	Freshwater	Rivers, streams	Crustaceans	2	Silk attachment mechanism	Lewis & Fairchild (1984)
Euarthropoda	Hexapoda	Insecta	Orthoptera	Unknown	Grasshoppers	Adults	Terrestrial	Grasslands	Sheep	2	Unknown	Warkus, Beinlich, & Plachter (1997)
Euarthropoda	Hexapoda	Insecta	Strepsiptera	Stylopidae	Twisted-wing parasites	Larvae	Terrestrial	Nests of hunting wasps	Hunting wasps	2	Unknown	Kathirithamby *et al.* (2012)
Euarthropoda	Hexapoda	Insecta	Neuroptera	Mantispidae	Mantid lacewings	Larvae	Terrestrial	Spider egg sacs	Spiders	2	Unknown	Redborg & Macleod (1983); O'Brien & Redborg (2007)
Euarthropoda	Hexapoda	Insecta	Blattodea	Blaberidae	Cockroaches	Adults, juveniles	Terrestrial	Ant nests	Ants	1, 2	Well-developed tarsal pads for attachment	Phillips, Zhang, & Mueller (2017)
Euarthropoda	Hexapoda	Collembola	Entomobryomorpha	Cyphoderidae, Sminthuridae	Springtails	Adults	Terrestrial	Ant tunnels	Ants	2	Unknown	Moser & Blomquist (2011); Penney *et al.* (2012)
Euarthropoda	Hexapoda	Collembola	Poduromorpha	Poduridae	Springtails	Unknown	Freshwater	Still water pools	Nutria	2	Unknown	Waterkeyn *et al.* (2010)
Euarthropoda	Hexapoda	Collembola	Symphypleona	Unknown	Springtails	Unknown	Terrestrial	Unknown	Nutria	2	Unknown	Waterkeyn *et al.* (2010)
Euarthropoda	Crustacea	Ostracoda	Podocopida	Cyclocyprididae, Limnocytheridae	Ostracods	Adults	Freshwater	Bromeliads	Frogs, snakes, mammals	2	Closes skin between shell	Seidel (1989); Lopez, Rodrigues, & Rios (1999); Lopez *et al.* (2002, 2005); Sabagh *et al.* (2011)
Euarthropoda	Crustacea	Hexanauplia	Cyclopoida	Lubbockiidae	Copepods	Adults, larvae	Marine	Deep ocean	Jellyfish	2	Unknown	Ohtsuka *et al.* (2009)
Euarthropoda	Crustacea	Hexanauplia	Lepadiformes	Lepadidae, Poecilasmatidae	Barnacles	Adults, larvae	Marine	Rocks and hard surfaces	Marine mammals, copepods, crabs	2	Unknown	Williams (1986); Arnbom & Lundberg (1995); Jacobsen, Scott-Holland, & Bennett (2013)
Euarthropoda	Crustacea	Hexanauplia	Sessilia	Coronulidae	Barnacles	Unknown	Marine	Rocks and hard surfaces	Dolphins	2	Unknown	Waerebeek, Reyes, & Alfaro (1993); Toth-Brown & Hohn (2007)
Euarthropoda	Crustacea	Branchiopoda	Anostraca	Chirocephalidae	Fairy shrimp	Eggs	Freshwater	Isolated lakelets	Trout	2	Can survive digestion process of fish	Beladjal, Dierckens, & Mertens (2007)

Table 1. *(Cont.)*

Phylum	Subphylum	Class	Order	Families	Common name	Life stage(s) involved	Major ecosystem	Microhabitat of phoront	Common dispersal host(s)	Phoretic stages observed	Examples of traits	Reference(s)
Euarthropoda	Crustacea	Branchiopoda	Anomopoda	Chydoridae, Macrotrichidae, Daphniidae	Water fleas	Eggs	Freshwater	Isolated lakelets	Wild boar	2	Can survive digestion process	Vanschoenwinkel *et al.* (2008)
Euarthropoda	Crustacea	Ichthyostraca	Arguloida	Argulidae	Fish lice	Juveniles	Marine	Fish	Opossum shrimp	2	Unknown	Jackson & Marcogliese (1995)
Euarthropoda	Crustacea	Malacostraca	Decapoda	Pandalidae, Majidae, and Portunidae	Shrimp, spider crabs, swimming crabs, Columbus crabs	Larvae (zoea), juveniles	Marine	Sublittoral zones	Jellyfish, sea turtles	2	Unknown	Suzuki (1965); Marliave & Mills (1993); Dellinger, Davenport, & Wirtz (1997); Nogueira & Haddad (2005)
Euarthropoda	Crustacea	Malacostraca	Amphipoda	Hyalellidae, Gammaridae	Amphipods	Unknown	Freshwater	Lakes, ponds	Muskrat, beaver	2	Unknown	Peck (1975)
Euarthropoda	Myriapoda	Diplopoda	Polyxenida	Polyxenidae	Millipedes	Adults	Terrestrial	Bird nests on buildings	Birds	2	Unknown	Tajovsky (2001)
Nematoda	NA	Chromadorea	Rhabditida	Aphelenchoididae, Rhabditidae, Diplogastridae, and many more	Nematodes	Adults, larvae	Terrestrial	Plants, insects	Various insects, isopods, myriapods, annelids	1, 2, 3	Response to chemical cues, synchronous development, specific phoretic life stage	Poinar (1978); Georgieva (1993); Eng, Preisser, & Strong (2005); Moser *et al.* (2005); Sudhaus (2008); Krishnan *et al.* (2010); Okumura, Tanaka, & Yoshiga (2013); Shapiro-Ilan & Brown (2013); Zhao *et al.* (2013); Ramos Mertz *et al.* (2014); Tanaka *et al.* (2014); Kanzaki *et al.* (2014, 2018); Kanzaki, Giblin-Davis, & Ragsdale (2015); Kerchev *et al.* (2017); Carta & Thomas (2018); Foley *et al.* (2018)
Annelida	NA	Clitellata	Haplotaxida	Naididae	Annelids	Adults	Freshwater	Bromeliads	Frogs, snakes	2	Unknown	Lopez *et al.* (1999, 2005)
Annelida	NA	Clitellata	Arhynchobdellida	Erpobdellidae	Leeches	Unknown	Freshwater	Ponds	Salamander	2	Unknown	Khan & Frick (1997)
Annelida	NA	Clitellata	Rhynchobdellida	Glossiphoniidae	Leeches	Adults	Freshwater	Ponds	Crabs, frogs	2	Unknown	Maia-Carneiro *et al.* (2012); Badets & Du Preez (2014)
Annelida	NA	Polychaeta	Phyllodocida	Polynoidae	Polynoid polychaete	Unknown	Marine	Shallow waters	Sea cucumber	2	Unknown	Schiaparelli *et al.* (2010)
Mollusca	NA	Bivalvia	Unionoida	Unionidae	Mussels	Larvae	Freshwater	Streams, ponds	Fish	2	Closing shell on fin, forked holdfasts acting as anchor	Darwin (1882); Fryer (1961); Barnhart, Haag, & Roston (2008)

(Continues)

Table 1. *(Cont.)*

Phylum	Subphylum	Class	Order	Families	Common name	Life stage(s) involved	Major ecosystem	Microhabitat of phoront	Common dispersal host(s)	Phoretic stages observed	Examples of traits	Reference(s)
Mollusca	NA	Bivalvia	Cardiida	Cardiidae	Cockles	Unknown	Marine	Sheltered beaches	Shorebirds	2	Closing shell on bird feet	Green & Figuerola (2016)
Mollusca	NA	Bivalvia	Myida	Dreissenidae	Zebra mussel	Juvenile	Freshwater	Rivers, lakes	Killer shrimp	2	Attaching using byssal threads	Kenderov (2017)
Mollusca	NA	Bivalvia	Sphaeriida	Sphaeriidae	Fingernail clams	Juveniles	Freshwater	Lakes, ponds	Insects, salamanders	2	Closing shell on insect and salamander legs	Darwin (1882); Zelaya & Marinone (2012)
Mollusca	NA	Gastropoda	Patellogastropoda (subclass)	Lottiidae	Limpets	Adults	Freshwater	Lakes, isolated ponds	Freshwater and terrestrial insects	2	Unknown	Brewer (1975); Walther *et al.* (2008)
Mollusca	NA	Gastropoda	Neogastropoda	Nassariidae	Whelks	Juveniles	Marine	Rocky shores	Crabs	2	Unknown	Davenport *et al.* (2015)
Mollusca	NA	Gastropoda	Stylommatophora	Clausiliidae, Helicidae, Discidae, and others	Snails	Adults, juveniles	Terrestrial	Woodlands	Birds, frogs	2	Can survive digestion process of birds	Dorge *et al.* (1999); Simonová *et al.* (2016); Kolenda *et al.* (2017)
Mollusca	NA	Gastropoda	Hygrophila (superorder)	Lymnaeidae, Planorbidae,	Aquatic snails	Adults	Freshwater	Wetlands	Waterbirds	2	Unknown	van Leeuwen & van der Velde (2012)
Cnidaria	NA	Anthozoa	Actiniaria	Actinostolidae, Hormathiidae	Sea anemones	Adults	Marine	Sublittoral zones	Molluscs, hermit crabs	2	Unknown	Brooks & Mariscal (1986); Luzzatto & Pastorino (2006)
Platyhelminthes	Rhabditophora	Monogenea	Capsalidea	Capsalidae	Flukes	Unknown	Marine	Fish	Isopods	2	Unknown	Goto (1894)
Platyhelminthes	Rhabditophora	Monogenea	Mazocraeidea	Diclidophoridae	Flukes	Unknown	Marine	Fish	Isopods	2	Unknown	Llewellyn (1941)
Porifera	NA	Demospongiae	Spongillida	Spongillidae	Sponges	Gemmules	Freshwater	Ponds, lakes	Birds	2	Unknown	Van Leeuwen *et al.* (2017)
Rotifera	NA	Eurotatoria	Ploima	Brachionidae, Lepadellidae, and Lecanidae	Rotifers	Adults	Freshwater	Ponds, lakes	Mammals	2	Can survive digestion process	Vanschoenwinkel *et al.* (2008)
Rotifera	NA	Eurotatoria	Flosculariaceae	Conochilidae	Rotifers	Adults	Freshwater	Ponds, lakes	Mammals	2	Can survive digestion process	Vanschoenwinkel *et al.* (2008)
Bryozoa	NA	Phylactolaemata	Plumatellida	Plumatellidae	Bryozoans	Statoblasts	Freshwater	Ponds, lakes, rivers	Birds, insects	2	Hooks, spines	Ogbogu (1993); Okamura, Hartikainen, & Trew (2019)
Echinodermata	NA	Ophiuroidea	Amphilepidida	Amphilepididae, Ophiotrichidae	Brittle stars	Adults	Marine	Subtidal sandy areas	Jellyfish	2	Arm hooklets	Ohtsuka *et al.* (2009)
Entoprocta (Kamptozoa)	NA	Entoprocta	Solitaria	Urnatellidae	Kamptozoan	Larvae	Freshwater	River	Dobsonfly	2	Unknown	Tracy & Hazelwood (1983)
Tardigrada	NA	Eutardigrada	Apochela	Milnesium	Water bears	Adults, juveniles	Terrestrial, freshwater	Mosses, lichens	Birds	2	Unknown	Mogle *et al.* (2018)
Tardigrada	NA	Eutardigrada	Parachela	Hypsibiidae, Macrobiotidae	Water bears	Adults, juveniles	Terrestrial, freshwater	Mosses, lichens	Birds	2	Unknown	Mogle *et al.* (2018)
Tardigrada	NA	Heterotardigrada	Echiniscoidea	Echinsicidae	Water bears	Adults, juveniles	Terrestrial, freshwater	Mosses, lichens	Birds	2	Unknown	Mogle *et al.* (2018)

Table 1. *(Cont.)*

Phylum	Subphylum	Class	Order	Families	Common name	Life stage(s) involved	Major ecosystem	Microhabitat of phoront	Common dispersal host(s)	Phoretic stages observed	Examples of traits	Reference(s)
Chordata	Vertebrata	Actinopterygii	Perciformes	Echeneidae, Centrolophidae	Remora fish, butterfish	Adults, juveniles	Marine	Pelagic zones	Sharks, turtles, rays, jellyfish	2	Specialized mouthparts for attachment to marine animals	Sazima & Grossman (2006); Ohtsuka *et al.* (2009)
Chordata	Vertebrata	Actinopterygii	Siluriformes	Trichomycteridae	Pencil catfish	Unknown	Freshwater	Rivers	Catfish	2	Attachment with mouthparts	Zuanon & Sazima (2005)

NA, not applicable.

suitable hosts, phoronts may also alter their life history. Again, the known cues are chemical in nature. An example is nematodes parasitic on pine trees that use beetles as dispersal hosts (Zhao *et al.*, 2013). The nematodes use chemical cues given off by eclosing adult beetles to synchronize development with the mobile stage of their host. Chemical cues are also used to attract dispersal hosts. This is seen in larvae of the blister beetle *Meloe franciscanus* Van Dyke, which produce chemicals that mimic sex pheromones of their bee host (Saul-Gershenz & Millar, 2006).

(*b*) Stage 2: attaching to the host

Attaching to and staying on the host is the second step in phoretic dispersal. Many phoronts have specific structures and life stages adapted for this task (Table 1). For example, mites in the infraorder Uropodina attach in the deutonymph stage using anal pedicels that stick to the dispersal host (Klompen, Lekveishvili, & Black, 2007; Bajerlein *et al.*, 2013). Mites in other groups also disperse in the deutonymph stage but attach to hosts using claws (Athias-Binche,- 1995) and suckers (Houck & OConnor, 1991; Seeman & Walter, 1995). Species in groups such as beetles (Roubik & Wheeler, 1982), pseudoscorpions (Zeh & Zeh, 1991), and lice (Marshall, 1981) use modified mouthparts to attach to hosts. Other mechanisms of attachment include bivalve shells and holdfasts (Darwin, 1882; Fryer, 1961; Seidel, 1989; Barnhart *et al.*, 2008). Some phoronts attach to very specific structures on their dispersal hosts. Mites from several families are transported in the abdominal pouches of bees and wasps (Houck & OConnor, 1991) and the pinewood nematode *Bursaphelenchus xylophilus* Steiner and Buhrer is transported in the spiracles of its beetle host (Zhao *et al.*, 2013). Many pseudoscorpions (Poinar *et al.*, 1998), mites (Bajerlein & Błoszyk, 2004), and nematodes (Moser *et al.*, 2005) attach under the elytra of beetles, perhaps because the area is well protected. Another example is the nematode *Caenorhabditis drosophilae* Kiontke, which attaches to a specific structure (an inflatable sac called the retracted ptilinium) on its fly host's head.

(*c*) Stage 3: detaching from the host

The final step of phoretic dispersal is detachment from the host. Little is known about how phoronts determine the right time or place to disengage from the host. Most information comes from mites (Table 1). *Brennandania lambi* Krczal is phoretic on mushroom flies (Diptera: Sciaridae and Phoridae). It only detaches from the host in the presence of one particular species of fungus (Clift & Larsson, 1987), suggesting a habitat-related cue. Another mite, *Histiostoma polypore* Oud., stays attached while the host develops from larva to adult. Upon death of the host, the mite uses cues given off by waxy secretions from the host to moult to the adult stage, after which it begins feeding on the dead host (Behura, 1956). The nematode *Caenorhabditis japonica* Kiontke, Hironaka & Sudhaus detaches from its adult hemipteran host in the

presence of host nymphs (Okumura *et al.*, 2013), maintaining synchrony and a continued association with the host. The precise mechanisms of detachment are almost entirely unknown. In mites, the structural integrity of anal pedicels used to attach to hosts is influenced by humidity; detachment occurs when the pedicel breaks during low humidity (Szymkowiak *et al.*, 2007).

(2) A working definition of phoresy

While phoronts may be passive hitch-hikers once attached, the process of finding and attaching to the host occurs along a spectrum of behaviours (as described in Section II.1) ranging from more active (e.g. moving towards the host) to more passive (e.g. sitting and waiting for the host). In the extreme, phoronts may simply wait for a dispersal host to pass by and make contact before attaching, as in the case of bivalves using their shells to clamp onto their hosts (Darwin, 1882; Barnhart *et al.*, 2008). According to Farish & Axtell (1971), phoresy specifically involves actively finding and attaching to a host; however, animals that sit and wait for hosts to find them are often reported as phoretic in the literature. For example, water fleas and rotifers are picked up by wild boar and transported to new areas (Vanschoenwinkel *et al.*, 2008) and eggs of fairy shrimp (*Chirocephalus diaphanous* Prévost) are swallowed by juvenile trout and transported among lakes *via* interconnecting streams (Beladjal *et al.*, 2007). Based on Farish & Axtell's (1971) definition, it is not entirely clear if some of these would be considered examples of phoretic dispersal. Instead, we agree with Houck & OConnor (1991) that a more expansive definition is needed that encompasses the full spectrum of host-seeking behaviours, from what might be considered 'actively searching' to 'more passively sitting and waiting'. At the same time, we believe Houck & OConnor's (1991) definition restricting phoresy to dispersal from the "natal habitat" is too narrow and instead agree with Farish & Axtell's (1971) more expansive view on this issue.

More recently, two broad definitions for phoresy have been offered. Camerik (2010, p. 334) defined phoresy as "a dynamic interspecific, temporary relationship whereby the phoretic…attaches to the host…for the duration of migration from one habitat to another, with the primary outcome being dispersal". Walter & Proctor (2013, p. 355) defined it as "a type of temporary symbiosis whose function is to allow a smaller individual (the phoretic) to move from one place to another on a larger individual (the host or carrier)". We believe these definitions are complementary, and that phoresy can be defined most broadly as *the behaviour of one organism (the phoront) to disperse from one location to another with the aid of another organism (the dispersal host) by attaching to that organism, regardless of whether the phoront actively searches for or more passively waits for the host*. Note that Camerik (2010) and some previous authors specifically restrict the definition of phoresy to interspecific interactions. While we restricted our review to interspecific cases, which represent the vast majority reported in the literature, we note that a small number of intraspecific cases have been reported, for example, aphid nymphs that attach to adults of the same species to disperse onto their food plants (Gish & Inbar, 2018).

(3) Similarity with dispersal in plants

Of course, animal-mediated dispersal is also used by many other types of organisms, including many species of plants [see reviews by Howe & Smallwood (1982), Vander Wall & Beck (2012) and Lichti, Steele, & Swihart (2017)]. The evolutionary and ecological significance of phoresy in animals is analogous to animal-mediated seed dispersal (zoochory) in plants. A seed attaching to or being carried by an animal functions in the same way as an animal attaching to another animal. Structures on seeds used for clinging to fur and feathers and energy-rich fruits and nuts used to attract dispersers can all be viewed as traits that function to move offspring away from parent plants (Howe & Smallwood, 1982). Likewise, as shown below, phoretic animals have a diversity of structures and other traits used to attract and attach to other animals. One major difference between seed dispersal and phoretic dispersal is that in many cases animals are offered nutritional rewards by plants to disperse seeds, resulting in mutualism. Interestingly, mutualism may also be the case in some phoretic systems (Kinn, 1980; Wilson & Knollenberg, 1987; Barbaro, Dutoit, & Cozic, 2001; Okabe & Makino, 2008), which we discuss below (see Section IV.2 and IV.4). Another major difference is that in animals, different life stages, including adults, can be the phoront, whereas in most plants it is only the seeds or spores that disperse. But despite the differences, whether speaking of plants or animals, both form and function converge to result in the organism being taken to other, possibly more favourable locations, such as seeds being taken to locations that favour germination and establishment (Howe & Smallwood, 1982; Wenny & Levey, 1998) or animals being taken to more resource-rich habitats (Saul-Gershenz & Millar, 2006). In the remainder of this review, we deal exclusively with phoresy in animals but acknowledge the fundamental similarities with zoochory in plants.

III. SURVEY OF THE DIVERSITY OF PHORONTS

(1) Surveying the literature

We used the following search terms to find records of phoretic dispersal by animals in the literature: 'phoresy animals', 'phoresis', 'phoresy', 'phoretic association', 'phoretic dispersal', 'animal-mediated dispersal', 'hitch-hiking', 'endozoochory', and 'ectozoochory'. We searched *Google Scholar* and *Web of Science* (1900–2020) initially between September and November 2014 and again in June 2020 to find new articles published since the initial search. Our goal was not to track down every single species or article on phoresy in the literature, but rather to uncover the major patterns of known diversity, and specifically to record all the taxonomic orders with animals known to be phoretic. In total, our search

produced more than 1,800 articles dealing with phoresy. We screened this initial collection of articles to identify studies reporting direct observations of phoretic associations, reviews, records, and checklists summarizing phoretic associations, and descriptions of behaviours and traits involved in phoretic dispersal. This exercise eliminated 475 articles that did not meet our criteria. We then scanned the remaining 1,325 articles to (*i*) record all animal orders with at least one species reported to disperse phoretically and (*ii*) provide ancillary information (e.g. behaviours, morphology, life stages, habitats, resources, dispersal hosts) on phoretic interactions for each group. Thus, not all articles that could have been cited are included in our review – again the goal was not to count every article or species, but to quantify ordinal-level diversity and capture the major patterns. Also note that we did not count the few papers that referred to epibionts or epizoic species as examples of phoresy since these animals, such as whale barnacles (Killingley, 1980; White, Morran, & de Roode, 2017), spend most of their lives living on the host rather than using the host for dispersal.

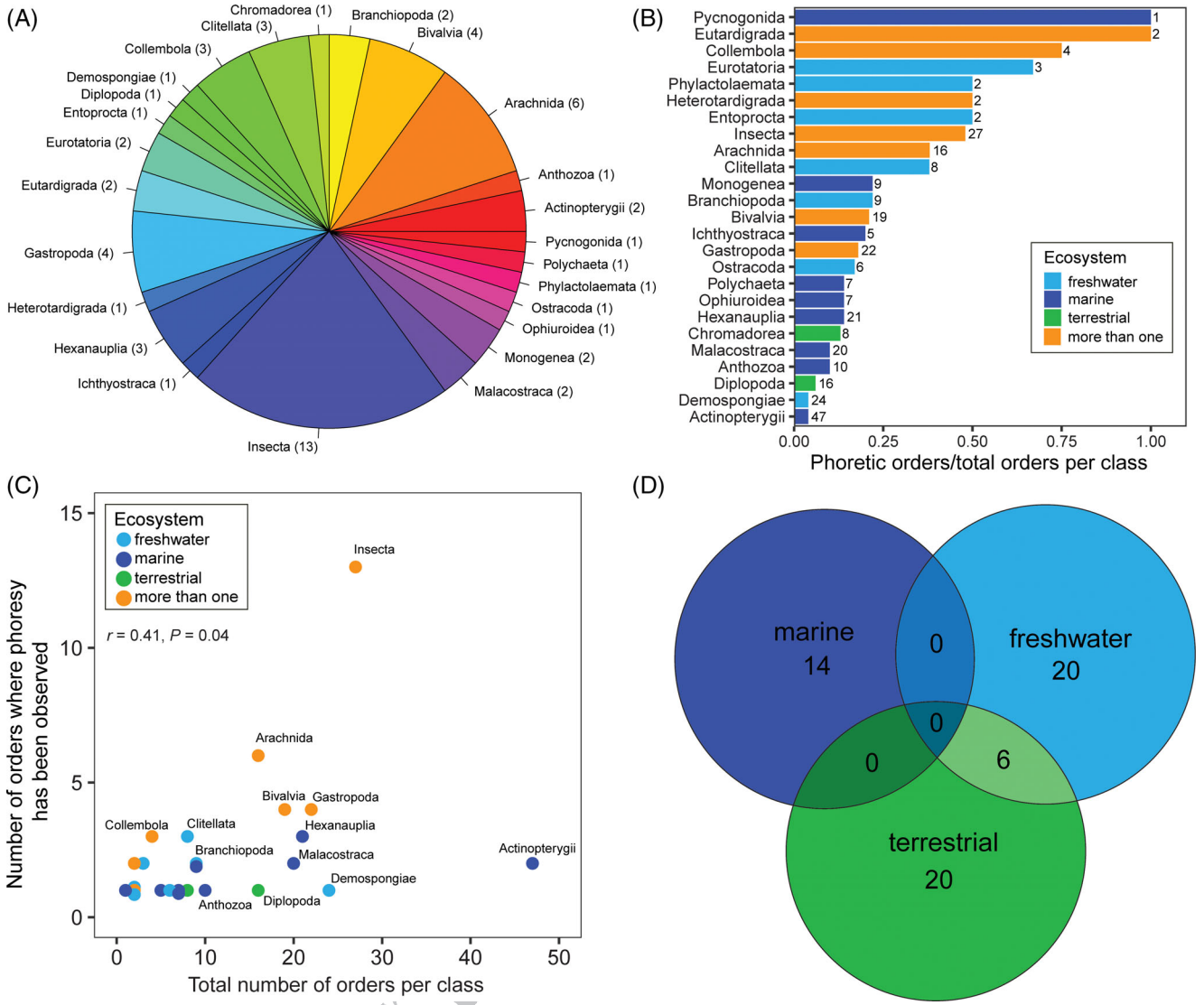
We chose to restrict our review to higher taxonomic levels because the diversity of known phoretic species is very large, and summarizing the information at this level was beyond our intended scope. For example, there are at least 212 species of phoretic mites that have been found by examining animal carcasses alone (Perotti & Braig, 2009). Note that many of the references herein contain more detailed information on the species involved in phoretic interactions. For our analysis, we focused on diversity at the level of orders within classes. This included comparisons of the absolute number of orders with known phoretic species per class and scaled comparisons of the relative number of orders with known phoretic species divided by the total number of orders per class. We obtained information on the total number of orders per class from the World Register of Marine Species (WoRMS Editorial Board, 2020) for marine taxa, freshwater taxa, taxa that fell into more than one category (Gastropoda, Bivalvia, Eutardigrada, Heterotardigrada), and the nematode class Chromadorea [cross-referenced with the World Database of Nematodes (Bezerra *et al.*, 2019)]. For the classes Arachnida, Insecta, Collembola, and Diplopoda, data were obtained from Wheeler *et al.* (2001), Brewer, Sierwald, & Bond (2012), Proctor *et al.* (2015), Beron (2018), and Leo *et al.* (2019). The name Entoprocta is used for both the phylum and class, which has two orders (Fuchs *et al.*, 2010; Conway, 2015; ITIS, 2020). For Arachnida, two sources differed in the number of orders: 15 (Proctor *et al.*, 2015) and 16 (Beron, 2018), and so we chose to use the most recent estimate. Finally, to obtain estimates of total numbers of phyla, classes, and orders in the animal kingdom, we used the WoRMS database (WoRMS Editorial Board, 2020). These data were compared with the numbers of phyla, classes, and orders where phoresy has been observed.

(2) Results of the survey

The results of our literature survey show that phoretic dispersal has been observed in multiple animal phyla (Table 1; and see Szymkowiak *et al.*, 2007), including at least two vertebrates [both are species of bony fish (Zuanon & Sazima, 2005; Sazima & Grossman, 2006)]. In total, we found 13 phyla (out of 33), 25 classes (out of 93), and 60 orders (out of 529) of animals in which at least one species has been recorded as dispersing phoretically (Table 1; note that within Gastropoda, the superorder Hygrophila and subclass Patellogastropoda were counted as orders for the purposes of this analysis). Most records are anecdotal and come from observational studies in which dispersal hosts were collected for another reason and phoronts were inadvertently found attached. Some records come from fossilized amber. Fossilized accounts of phoresy include mites, springtails, and pseudoscorpions (Magowski, 1995; Poinar *et al.*, 1998; Penney *et al.*, 2012), with some records of mites dating back 85 million years (Magowski, 1995), and pseudoscorpion records dating back 40 million years (Poinar *et al.*, 1998). A less commonly observed phoretic interaction described in the literature is hyperphoresy, which occurs when a phoretic individual itself carries another phoretic individual (Szymkowiak *et al.*, 2007). We found records of hyperphoresy in animals that involve mites attaching to other mites (Bajerlein & Błoszyk, 2003). A second example involves species of ciliates (Kingdom Chromista, Phylum Ciliophora) attached to ostracods, which are themselves attached to treefrogs (Sabagh *et al.*, 2011).

The majority of known phoretic animals are small invertebrates (Table 1). Of the 60 orders with known cases of phoresy, most are in the phylum Euarthropoda, with phoretic species spread across the terrestrial, freshwater, and marine environments (Table 1). The two classes across all animal phyla with the highest number of orders with observed phoresy are both from Euarthropoda: Insecta ($N = 13$ orders with phoretic species) and Arachnida ($N = 6$ orders). Two classes in the phylum Mollusca share the third highest rank: Gastropoda ($N = 4$ orders) and Bivalvia ($N = 4$ orders) (Fig. 1A). When scaled to the total number of orders per class (Fig. 1B), the highest relative diversity of phoronts is found in two relatively small groups: Class Pycnogonida (sea spiders) and Class Eutardigrada (tardigrades). The class Pycnogonida is composed of a single order, in which phoresy has been observed for some species, whereas both orders in the Class Eutardigrada have phoretic species. The second highest proportion of phoretic orders is found in another small group, Class Collembola (springtails), for which three out of the four total orders exhibit phoresy. Insecta and Arachnida also rank relatively high when scaled for total diversity (eighth and tied for ninth, respectively) with slightly less than half of the known orders in each class exhibiting the behaviour (Fig. 1B). On the other hand, Class Gastropoda ranks in the bottom half of all classes when scaled for total diversity, with less than a quarter of orders recorded exhibiting phoresy (Fig. 1B).

Out of the 60 orders where phoresy has been observed (11.3% of total animal orders), there is a positive correlation ($r = 0.41$, $P = 0.04$) between the number of orders with known records of phoresy and the total number of orders per class (Fig. 1C). This relationship suggests that in groups



Color Figure - Print and Online

Fig 1. (A) Pie chart showing the number of orders per class where phoresy has been observed (i.e. absolute diversity). (B) The number of known phoretic orders divided by the total number of orders per class (i.e. relative diversity). Numbers at the end of the bars represent the total number of orders in each class. (C) Correlation between the absolute number of known phoretic orders and the total number of orders per class ($r = 0.41$, $P = 0.04$). (D) Venn diagram of the number of known phoretic orders according to the major ecosystem inhabited. The six orders that are both terrestrial and freshwater represent two orders of mites, three orders of tardigrades, and the insect order Diptera.

with known phoresy, the behaviour is distributed among higher animal taxa roughly in proportion to their diversity.

By far the greatest number of orders and classes with known phoronts is in the phylum Euarthropoda. One explanation for the dominance of arthropods engaging in phoresy is that their small size, extreme diversity, and morphological traits that facilitate attachment (e.g. claws and mandibles; see Section II.1) favour its evolution in this group relative to others. Alternatively, phoresy may be more readily documented in arthropods relative to other species-rich groups such as molluscs for a variety of reasons including their ease of observation, especially in the terrestrial environment.

Within arthropods, insects dominate the number of orders known to exhibit phoresy, but the group most regularly associated with the behaviour is mites (Class Arachnida, Subclass Acari), and most research has been done on this group (Houck & OConnor, 1991; Table 1). Indeed, the majority (>800) of the articles found during our literature survey concerned mites. Mites have a diverse set of morphological and behavioural traits used for phoretic dispersal and are known to use a broad range of dispersal hosts including beetles, flies, bees, wasps, ants, bats, non-volant mammals, and birds. Phoretic mites have been implicated in increasing the transmission of Dutch elm disease among trees and entomopathogenic fungi among insects (Schabel, 1982; Moser *et al.*, 2010).

There are several mechanisms by which mites can be phoretic, including: females attaching using chelicerae, claws, and hooks; deutonymphs (the second nymphal life stage) attaching using chelicerae and claws; deutonymphs attaching using anal pedicels (secreted attachment stalks); and hypopodes (modified deutonymphs specialized for dispersal) attaching using suckers or claspers (Macchioni, 2007). Another order of arthropods, Pseudoscorpiones, also commonly use other invertebrates and mammals as dispersal agents, with species in at least ten out of 26 families known to engage in phoresy (Harvey, 2002, 2013; Tizo-Pedroso & Del-Claro, 2007).

Nematodes are another large group of invertebrates with records of many species engaging in phoresy (Table 1). Two families of nematodes, Rhabditidae and Diplogastridae, engage in endophoresy by entering protected cavities on the bodies of insects, including the rectum and genital chamber (Sudhaus, 2008; Giblin-Davis *et al.*, 2013). Other species enter the excretory system of earthworms (Annelida) (Poinar, 1978) or the guts and intestines of snails (Petersen *et al.*, 2015) for dispersal. Many free-living nematodes use a specific larval form, the dauer larva, for phoresy. Dauer larvae are arrested third-stage larvae (L3) that are non-feeding. In parasitic nematodes, the infective larvae are also arrested L3 larvae that are non-feeding. Both dauer larvae of free-living nematodes and infective larvae of parasites are resistant to harsh environmental conditions such as those encountered during dispersal or infection (Sudhaus, 2008; Crook, 2014). Because of the similarity of the L3 larval stages, it has been suggested that phoresy was a precursor to parasitism in nematodes (Rogers & Sommerville, 1963; Sudhaus, 2008; Ogawa *et al.*, 2009; Crook, 2014).

In terms of major ecosystems, phoretic species are found in all three habitat realms: terrestrial (Poinar *et al.*, 1998; Tizo-Pedroso & Del-Claro, 2007; Krishnan *et al.*, 2010), freshwater (Seidel, 1989; Vanschoenwinkel *et al.*, 2008), and marine (Arnbom & Lundberg, 1995; Luzzatto & Pastorino, 2006) (Table 1). Of the orders known to exhibit phoresy (Table 1), more than 75% are terrestrial or freshwater (Fig. 1D). Six orders [Diptera, two orders of mites (Trombidiformes and Sarcoptiformes), and three orders of tardigrades (Echinsicidae, Apochela, Parachela)] contain records of both terrestrial and freshwater species. Based on these data, phoresy appears to be more taxonomically widespread in both the terrestrial realm (N= 26 orders) and freshwater realm (N= 26 orders) than in the marine realm (N= 14 orders). In fresh water, many arthropods, such as ostracods, and the larvae of non-biting midges (Chironomidae) and blackflies (Simuliidae) (de Moor, 1999; Stauder & Kiel, 2004) are phoretic. Midges alone are known to attach to molluscs, fish (Tokeshi, 1993), stoneflies, mayflies, damselflies, and dragonflies (White *et al.*, 1980) (Table 1). Among marine species, pandalid shrimps (Pandalidae), copepods (Lubbockiidae), and sea spiders (Pallenopsidae) use jellyfish as dispersal hosts, and cockles (Cardiidae) use shorebirds (Table 1). The lower number of marine taxa known to engage in phoresy compared to terrestrial and freshwater taxa may be because the marine environment is somehow fundamentally different (e.g. strong water currents assist with dispersal of many species; Highsmith, 1985). However, a more probable explanation is a sampling bias due to the relative difficulty of documenting phoretic events in marine systems. This means the extent of phoresy in these systems is probably far greater than currently known. For example, marine diversity includes many small, sedentary animals with low mobility and many large, high-mobility animals, with vast distances between some habitat types. These characteristics seem likely to promote the evolution of phoretic dispersal in the marine environment more than current observations would suggest.

(3) Some common characteristics among phoronts

Although diverse taxonomic groups use phoresy as a method of dispersal, our literature survey reveals several characteristics that are common among phoronts (Table 1). First, we found several cases that involve what might be considered as a sit-and-wait strategy. Of the 60 orders with known phoronts, 18 had at least one example of 'sit-and-wait'; interestingly, most are from the marine and freshwater environments, including bryozoans, sponges, rotifers, and bivalves that wait to be picked up by a host (Vanschoenwinkel *et al.*, 2008; Zelaya & Marinone, 2012; Van Leeuwen *et al.*, 2017; Okamura *et al.*, 2019). Thus, most observed cases of phoresy appear to involve some form of actively searching and attaching to the host. Second, the habitats/resources used by phoretic species are often patchy or ephemeral, such as animal dung, isolated lakes and ponds, fungi, bromeliads, or hosts to parasitize. Third, most phoronts are small and lack a highly mobile life stage, which presumably makes it inherently difficult to disperse to widely spaced or ephemeral habitats or hosts.

Phoresy is not, however, strictly limited to organisms with low mobility; it also occurs in species with at least one mobile life stage (Table 1). For example, many species of insects that are aquatic during the larval stage (e.g. non-biting midges, blackflies, caddisflies) are phoretic even though they can fly as adults. Some mobile adult moths (Waage & Montgomery, 1976), beetles (Ashe & Timm, 1987), and parasitic wasps (Arakaki *et al.*, 1995) also disperse *via* phoresy (Table 1). Species in which otherwise mobile adults engage in phoretic dispersal may require specific habitats or resources that are highly aggregated, ephemeral, or difficult to find. For example, adult *Cryptoses choloepi* Dyar moths that live and feed on the dung of sloths use these mammals as dispersal hosts (Waage & Montgomery, 1976). Sloths occur at low densities and climb down trees to defecate infrequently; thus, their dung is a patchy and ephemeral resource (Waage & Montgomery, 1976). Even though adult moths can fly, the time and energy cost to finding dung is presumably reduced by hitching a 'free ride' and being taken directly to the resource.

Along with widely dispersed habitats, small body size, and low mobility, many phoronts are also parasites (Keirans, 1975a, 1975b; Saul-Gershenz & Millar, 2006;

Bartlow *et al.*, 2016), some being phoretic on a different species than they parasitize and others parasitizing the same host species or individual (e.g. Arakaki *et al.*, 1995; Houck & Cohen, 1995; Bartlow *et al.*, 2016). In fact, one hypothesis is that phoresy has been a precursor to the evolution of parasitism in some systems (Osche, 1956; Houck & OConnor, 1991; Athias-Binche & Morand, 1993; Houck, 1994; Blaxter, 2003; Sudhaus, 2008; Crook, 2014; see Section IV.4). Like other phoronts, phoretic parasites generally have patchy, widely dispersed and ephemeral resources – their hosts. While highly mobile parasites (e.g. with free-living adult stages, mobile larvae, or intermediate hosts) may disperse and find hosts with relative ease, more 'permanent' parasites with little or no mobility may be especially likely to engage in phoresy on non-host species. Some evidence for this pattern has been found in lice. Lice exhibit a range of mobilities from highly mobile to relatively immobile, and species with the ability to move independently off a host may be less likely to engage in phoretic dispersal (Bartlow *et al.*, 2016).

In some cases, the lines between phoresy and parasitism are blurred (Parmentier & Michel, 2013). For example, some parasitoid wasps are known to use adults of the insect eggs they parasitize for dispersal (Arakaki *et al.*, 1997; Fatouros & Huigens, 2011). Since the host eggs are small, inconspicuous, and can be separated by long distances (Fatouros & Huigens, 2011), hitching a ride on adults and simply waiting for eggs to be laid effectively eliminates the need to search for new hosts to parasitize. In this case, parasitoid wasps are parasitizing the same species as their dispersal host, but are not parasitizing the individual to which they are attached. In other cases, phoronts may be parasitizing the dispersal host itself, further blurring the lines and hinting at an evolutionary transition from phoresy to parasitism. An example is the mite *Hemisarcoptes cooreman* Thomas. Once thought to be using beetles for the sole purpose of phoretic dispersal, *H. cooreman* are now known to parasitize the beetles by consuming haemolymph (Houck & Cohen, 1995). These fuzzy lines between phoresy and parasitism lend more credence to the long-standing idea that phoretic interactions can precede evolutionary transitions to more intimate symbiotic relationships.

IV. EVOLUTION OF PHORETIC DISPERSAL

(1) Is phoresy 'risky'?

Phoresy has been said to be a 'risky' strategy for dispersal (de la Rosa, 1992; Lopez *et al.*, 2005; Bartlow *et al.*, 2016; Nolan & Delaplane, 2017). The behaviour involves attaching to another organism and relying on that organism for transport to a suitable habitat or, in the case of phoretic parasites, to a suitable host. To accomplish this, phoronts must successfully complete the three stages of phoresy outlined in Section II.1: locate the host, attach to the host, and detach from the host at an appropriate location. These three stages appear to require precise cues and mechanisms of attachment and detachment in at least some cases, and failing to complete any of the stages will result in failure to disperse.

If phoresy is a 'risky' strategy for dispersal, then why did it evolve? Risk is relative. All that matters from an evolutionary perspective is that dispersing *via* phoresy is more likely to be successful than dispersing under one's own power or not dispersing at all. The behaviour is distributed widely throughout the animal kingdom (Table 1; Fig. 1), suggesting multiple independent origins. Studies of specific taxa, including blister beetles (Bologna & Pinto, 2001; Bologna *et al.*, 2008; Di Giulio *et al.*, 2014) and acarid mites (OConnor & Pfaffenberger, 1987), *show evidence for its repeated origins within multiple clades. For the behaviour to evolve* independently multiple times, the benefits must sometimes outweigh the risks. Some hypothesized advantages of phoresy for the phoront include reduced energetic costs (Houck & OConnor, 1991), reduced dispersal times (Krishnan *et al.*, 2010; Bartlow *et al.*, 2016), directed dispersal to specific habitats (Fronhofer *et al.*, 2013), and protection from predators (Badets & Du Preez, 2014) and harsh environmental conditions (Liu *et al.*, 2016). The ultimate risk of phoresy is death, such as falling off mid-transport, being wounded or killed by the host, or ending up at the wrong location. For example, avian wing lice that fall off their hippoboscid fly hosts likely die quickly, since they desiccate rapidly off a host (Johnson & Clayton, 2003). Other risks involved in phoresy include reaching a habitat with few available resources or one already heavily colonized by competitors. But as long as some individuals survive and reproduce, phoretic dispersal can emerge and persist evolutionarily, despite the inherent risks involved in the behaviour.

Although the end goal is dispersal, other important activities (e.g. reproduction) may take place during phoresy in some species. For example, the pseudoscorpion *Cordylochernes scorpioides* L. has a phoretic association with the giant harlequin beetle *Acrocinus longimanus* L. The beetles are attracted to decaying trees on which pseudoscorpions wait until freshly laid beetle larvae develop into adults. The pseudoscorpions can wait 3–5 generations until beetle larvae develop (Zeh & Zeh, 1997). After adult beetles eclose, male and female pseudoscorpions rush to attach to the beetle's abdomen to disperse phoretically. While attached, males force rival males off the beetle to dominate the abdomen and gain access to females. Therefore, the dispersal host can also serve as a site for reproduction and an arena for sexual selection (Zeh & Zeh, 1997).

(2) Effects on dispersal hosts

Despite being a strategy that seemingly only benefits the phoront, phoresy may have more effects on dispersal hosts than generally assumed. For example, phoretic mites of the genus *Poecilochirus* normally have no negative impact on their burying beetle (*Nicrophorus* spp.) hosts, except at high densities (Wilson & Knollenberg, 1987). The beetles bury carcasses, such as mice, and use them to feed their developing larvae.

Fly (*Calliphora* spp.) larvae, which are also buried during this process, feed on shallowly covered carcasses, thereby taking resources away from the beetles. At normal densities, mites phoretic on beetles can actually reduce competition with flies by consuming them, thus indirectly increasing beetle performance (Springett, 1968; Wilson & Knollenberg, 1987). However, it is hypothesized that at high densities, phoretic mites may decrease beetle performance by consuming beetle larvae (Wilson & Knollenberg, 1987). A second example is the remarkable case of mutualism between the potter wasp *Allodynerus delphinalis* Giraud and the mite *Ensliniella parasitica* Vitzthum (Okabe & Makino, 2008). After phoretic dispersal, mites attached to wasps actually defend the wasp's offspring against attacks from species of parasitoid wasps. The mites feed on the haemolymph of the potter wasp larvae, but do not kill them, and may even go on to become phoretic on the individual they fed on after it becomes a winged adult. A final example is mites (*Dendrolaelaps neodisetus* Hurlbutt) phoretic on southern pine beetles (*Dendroctonus frontalis* Zimmerman). Beetles with phoretic mites harbour fewer endoparasitic nematodes, possibly because the mites feed on the nematodes (Kinn, 1980).

Despite these examples, research into phoretic interactions has generally ignored the dispersal host side of the equation. Are the effects of phoronts on their hosts mostly neutral as generally assumed? What role does density dependence (i.e. how many individuals are physically attached to the host) play in the effects of phoronts on their hosts (e.g. Moser, 1976; Gupta & Borges, 2019)? Answering these and related questions will help develop a better understanding of the evolution of these interactions from the viewpoint of both phoronts and hosts. In addition to the examples listed above, Walter & Proctor (2013) documented numerous examples of adverse effects of phoretic mites on their dispersal hosts, including, but not limited to, negative impacts on their movement, reproduction, feeding, breathing, growth rates, and longevity [see Table 9.4 of Walter & Proctor (2013) for a complete list]. If phoronts have more adverse effects on their hosts than generally assumed (Walter & Proctor, 2013; Wang & Rozen, 2019), then questions regarding the evolution of host defence mechanisms and the potential for coevolutionary interactions between phoronts and hosts are worth investigating. For example, hippoboscid flies groom themselves to remove lice (Harbison *et al.*, 2009; Bartlow *et al.*, 2016). Do other dispersal hosts use similar mechanisms to prevent phoronts from attaching? Have phoronts evolved counter defences? In carabid beetles that harbour external mites, Gudowska *et al.* (2016) showed that compared with mite-free individuals, infested beetles exhibited a different pattern of respiration. Specifically, beetles infested with mites used more discontinuous gas exchange (DGE) which is characterized by extended periods where the spiracles are closed and no respiration occurs. This result is consistent with the 'strolling arthropod' hypothesis proposed by Miller (1974) who posited that complete closure of the spiracles during DGE is a mechanism to prevent other organisms and foreign objects from blocking or entering the tracheal system. How general is this pattern in arthropods and what role might it play in the evolution of phoronts and their dispersal hosts?

(3) Host associations

Like parasites, phoronts show wide variation in host specificity (White *et al.*, 2017), from one species of dispersal host (e.g. the wasp *Telenomus euproctidis* Wilcox) to many (e.g. the mite *Histiogaster arborsignis* Woodring). The classical evolutionary model of parasite–host and other types of symbiotic relationships is that they are primarily the result of coevolution, where reciprocal selection pressures favour the evolution of increasing specialization among interacting species [see Janz (2011) for a recent review]. This high degree of specialization is expected to lead to widespread cospeciation and therefore phylogenetic congruence between parasites and their hosts: if the host goes extinct, so does the parasite. In this view, parasites are trapped in an inherent evolutionary 'dead-end' as a result of specializing on their hosts (Moran, 1988; Wiegmann, Mitter, & Farrell, 1993; Kelley & Farrell, 1998). More recently, this way of thinking about species associations has been challenged on both conceptual and empirical grounds (Hoberg & Brooks, 2008; Agosta, Janz, & Brooks, 2010; Janz, 2011; Araujo *et al.*, 2015; Braga *et al.*, 2018; Nylin *et al.*, 2018; Brooks, Hoberg, & Boeger, 2019). For parasites and other symbionts, it is now clear from both theory and data that there is frequent switching to evolutionarily unrelated hosts (Agosta, 2006; Nylin *et al.*, 2018), and that this host switching is a fundamental part of the evolutionary dynamics of these systems (Hoberg & Brooks, 2008; Agosta *et al.*, 2010; Janz, 2011; Araujo *et al.*, 2015; Braga *et al.*, 2018; Brooks *et al.*, 2019).

Compared to parasitism and other forms of symbioses, there have been relatively few studies on the evolution of host associations in phoretic systems. If phoretic interactions are primarily commensal, with phoronts having little to no impact on their hosts, then reciprocal coevolutionary interactions like those that occur between other symbionts are likely rare. However, if phoronts have more impacts on their hosts than generally assumed, as suggested by the evidence discussed in Section IV.2, then the potential for coevolutionary dynamics like those seen in other systems becomes greater. Groups where evolutionary relationships between phoronts and dispersal hosts have been examined to some degree include acarid mites (OConnor & Pfaffenberger, 1987), beetles and hymenopterans (Eggleton & Belshaw, 1993), remora fish (O'Toole, 2002), and nematodes (Giblin-Davis *et al.*, 2003). Like other forms of symbioses, a common theme among these studies is that host switching by phoronts has been a primary mechanism behind the colonization of new dispersal hosts. In the case of phoretic parasites, this may also be a stepping stone to parasitizing new hosts (see also Clayton & Johnson, 2003; DiBlasi *et al.*, 2018).

In general, the potential for host switching is driven by the interaction of ecological opportunity to encounter new potential hosts and the inherent capabilities of parasites (or in this case phoronts) to use new hosts (Agosta &

Klemens, 2008; Agosta *et al.*, 2010; Araujo *et al.*, 2015; Brooks *et al.*, 2019). The formation of new species associations through host switching is one manifestation of ecological fitting (*sensu* Janzen, 1985), which is the process where organisms respond or 'fit' to novel conditions, such as encountering a new potential host, using inherited traits they already possess (Agosta & Klemens, 2008). Compared to parasites, phoronts appear to have fairly superficial relationships with their dispersal hosts: they use them as a vehicle for transport, but are typically not directly dependent on them for energy. In addition, the kinds of morphological traits used by phoronts to attach to dispersal hosts (e.g. claws, shells, mouthparts) could make it relatively easy for new hosts to be exploited. For these reasons, it seems likely that host switching by ecological fitting is a common phenomenon in the evolution of phoretic systems, especially during periods of widespread environmental change. This prediction is supported by the relatively few studies on the evolution of host associations in the phoretic systems cited above. It is also supported by experiments showing that phoronts can use a wider variety of dispersal hosts than observed in nature (Palevsky *et al.*, 2001; Nehring, Müller, & Steinmetz, 2017) and observations of native phoronts using recently introduced species as dispersal hosts (e.g. mites on introduced millipedes in Europe and North America; Farfan & Klompen, 2012). Host switching has also been implicated as a means for the incidental introduction of phoretic species to new geographic areas with potential impacts on humans and native species (Okabe *et al.*, 2010; Farfan & Klompen, 2012; Shaw, 2012; Giblin-Davis *et al.*, 2013). For example, the pinewood nematode *Bursaphelenchus xylophilus*, which causes pine-wilt disease, was introduced to Japan around 1905. After switching to a native dispersal host, the longhorn beetle *Monochamus alternatus* Hope, the nematode caused massive tree mortality throughout Japan and spread across Asia and Europe (Giblin-Davis *et al.*, 2013). In sum, the potential for host switching in phoretic systems seems high. However, more studies are needed at both ecological (e.g. experiments on the ability of phoronts to use alternative hosts) and evolutionary (e.g. co-phylogenetic studies of phoretic associations) scales to understand this potential and the general dynamics of how phoretic systems evolve.

(4) A precursor to parasitism?

It has long been thought that phoretic associations may have been a precursor to the evolution of parasitism in some systems (Osche, 1956; Rogers & Sommerville, 1963; Houck & OConnor, 1991; Athias-Binche & Morand, 1993; Houck, 1994; Houck & Cohen, 1995; Blaxter, 2003; Giblin-Davis *et al.*, 2003; Sudhaus, 2008; Schmid-Hempel, 2013; Crook, 2014; Petersen *et al.*, 2015; White *et al.*, 2017). Phoronts are predisposed to transition from phoretic relationships with dispersal hosts to other relationships such as parasitism and mutualism. Phoretic mites and nematodes may be especially good groups to study the transition from phoresy to parasitism (Athias-Binche & Morand, 1993; Houck & Cohen, 1995; Kiontke & Sudhaus, 2006; Sudhaus, 2008). Both have a diversity of species with free-living, parasitic, and phoretic lifestyles. For example, in free-living nematodes, third-instar dauer larvae are non-feeding and resistant to harsh environmental conditions (McSorley, 2003). In phoretic species, this stage is used for dispersal, while in parasitic species the same stage is used for infection (Sudhaus, 2008; Ogawa *et al.*, 2009; Crook, 2014). The dauer hypothesis suggests that phoretic larvae were an evolutionary precursor to parasitism (Rogers & Sommerville, 1963; Crook, 2014).

In cases where phoresy has been a precursor to parasitism, it seems likely the transition begins with the phoront simply attaching to the host for dispersal but then later developing the ability to exploit host resources for growth and reproduction. The aforementioned mite *H. cooreman* is perhaps an example of this transition. It was first thought to be phoretic on beetles, but was then found to be a parasite that consumes host haemolymph (Houck & Cohen, 1995). Further experiments suggested that the host beetles also acquire nutrients from the phoretic mites, which led Holte *et al.* (2001) to hypothesize an evolutionary transition from phoresy to parasitism to mutualism in this system. In phoretic nematodes, necromeny may have been key in the transition to parasitism for some species (Kiontke & Sudhaus, 2006; Hong & Sommer, 2006*b*; Dieterich & Sommer, 2009; Luong & Mathot, 2019). Necromeny is the process in which dauer larvae of nematodes attach to a live host and, after the host dies (from non-phoretic causes), feed on microbes on the decaying carcass. Parasitism could follow if the nematodes begin to obtain resources from the living host (Dieterich & Sommer, 2009). To our knowledge, no studies have explicitly tested this hypothesis.

Two major mechanisms are thought to facilitate the evolutionary transition from phoretic interactions to parasitism and other forms of symbioses. First, dispersing on or in another animal can provide a relatively stable microenvironment, from which may emerge selection for more permanent or obligate phoront–host interactions (Hairston & Bohonak, 1998; Schmid-Hempel, 2013). Second, dispersing on or in another animal can provide access to a consistent and predictable supply of nutrients, which again may create selection for more obligate relationships such as parasitism (Houck, 1994).

A stable microenvironment and predictable resources are benefits that can also be offered by nest commensalism, where organisms live inside the nests of other animals. Nest commensals, such as beetles, pseudoscorpions, and mites experience stable microclimates and predictable sources of food such as ectoparasites and dead skin (Ashe & Timm, 1987; Proctor & Owens, 2000; Roubik, 2006). Phoresy may have evolved in some nest commensals in the context of colonizing new nests (Ashe & Timm, 1987). Alternatively, nest commensalism could theoretically arise from phoresy, where initial exposure to nests is a by-product of phoretic dispersal. Groups including phoretic beetles and pseudoscorpions that live in host nests may be especially useful to test these ideas.

V. OUTSTANDING QUESTIONS AND FUTURE DIRECTIONS

Some major outstanding questions about phoresy to emerge from our review are listed below.

(1) What are the fundamental traits, behaviours, and cues involved in the different stages of phoresy discussed in Section II.1?
(2) To what extent does the observed diversity of phoretic animals reflect actual diversity?
(3) Are phoronts mainly commensals, with little to no impact on their dispersal hosts, or do they have more impacts on their hosts than is generally assumed?
(4) To what degree and how often are the lines between phoresy and parasitism/mutualism blurred?
(5) What is the role of coevolution in phoretic systems? If phoronts are mainly commensals, then the potential for coevolution is limited, but if they have more effects on hosts than generally assumed, then coevolutionary dynamics become more likely.
(6) To what degree are phoronts host specific? How readily do phoronts switch hosts? What is the role of host switching in the evolution of phoretic associations? In parasite–host systems, host switching (as opposed to cospeciating in tandem with hosts) is a frequent and widespread mechanism behind the formation of these interactions (and examples of cospeciation are actually rare) (for an extensive review of this subject see Brooks *et al.*, 2019). We would expect comparable or even greater rates of host switching in phoretic systems.
(7) How often has phoresy been a precursor to parasitism or mutualism (and possibly *vice versa*) in the evolution of these associations?

In closing, to address the questions outlined above and to understand phoresy better in general we encourage research in the following areas:

(1) *Continued and intensified exploration of the taxonomic and functional diversity of phoretic interactions, including mechanisms of attachment, transport, and detachment from the host.* Presumably, one reason phoretic interactions are relatively understudied is because of the difficulty of observing the behaviour of small organisms in the field and tracking them over large distances. Therefore, inventive approaches will be needed to begin to gain a better understanding of the basic biology of phoretic dispersal. In the laboratory, more functional studies of a greater diversity of phoronts and their hosts are needed to elucidate the mechanisms used to disperse, but obtaining a better understanding of the ecological and evolutionary consequences of dispersing will require some highly creative manipulations in the field.
(2) *Phylogenetic studies of macroevolutionary relationships between phoronts and hosts.* Compared to parasite–host, insect–plant, and other forms of symbioses (see Nylin *et al.*, 2018; Brooks *et al.*, 2019), there has been relatively little work done using modern systematic phylogenetics to build phylogenies for phoronts and their hosts. Not only are these phylogenies needed to help understand the evolution of phoresy within certain groups (see point 4 below), but also to compare patterns between phoronts and their hosts that can be indicative of phenomena such as host switching and cospeciation (for an extensive review see Brooks & McLennan, 2002). As stated previously, we expect host switching to be common (and cospeciation to be rare) in the evolution of phoretic associations.
(3) *Assessment of the potential for host switching and the limits of host specificity in phoretic systems.* While phylogenetic analysis may provide insights into the frequency of host switching in the evolutionary history of phoretic associations, experiments are needed to gain a better understanding of the potential for phoronts to use new hosts and the degree to which realized host range (observed host use) is a subset of fundamental host range (Agosta *et al.*, 2010; Brooks *et al.*, 2019). In particular, more experiments like those of Palevsky *et al.* (2001) and Nehring *et al.* (2017) testing the abilities of phoronts to use novel hosts are needed, especially with species closely related to and/or found in similar habitats to their actual hosts. Such experiments are relatively common in the literature on plant-feeding insects (e.g. Janz, Nyblom, & Nylin, 2001; Cipollini & Peterson, 2018; Peterson *et al.*, 2020) and can provide a roadmap for how to study this in the context of phoresy.
(4) *Tests of long-standing hypotheses that phoresy can be a precursor to parasitism and other forms of symbioses, and possibly* vice versa. Strong inferences about the direction and context of evolutionary transitions (e.g. from phoresy to parasitism) require phylogenies to map the characters of interest (Brooks & McLennan, 2002). So far, character mapping has been carried out to only a limited degree in the context of the evolution of phoresy (e.g. Eggleton & Belshaw, 1993; O'Toole, 2002), and in the transition from phoresy to parasitism (e.g. Blaxter, 2003; Kiontke & Sudhaus, 2006).
(5) *Research from the perspective of dispersal hosts regarding both positive and negative consequences of phoretic interactions.* An example is the clever experiment by Gudowska *et al.* (2016) that manipulated phoront loads to study effects on dispersal host respiration. Challenging the assumption that phoronts are generally commensals with little or no impacts on their dispersal hosts will be critical to developing a better understanding of the ecological and evolutionary context of these interactions.

VI. CONCLUSIONS

(1) Many animals are small, have limited mobility, or have patchy or ephemeral habitats and resources. To

disperse, some animals have evolved a phoretic lifestyle, taking advantage of other animals for a 'free ride'. The potential advantages of this 'free ride' include reduced energetic and time costs, directed dispersal to specific habitats or resources, and increased protection from natural enemies and abiotic conditions.

(2) Phoretic dispersal is analogous to zoochory in plants and has been documented in at least 13 animal phyla, 25 classes, and 60 orders. A broad definition includes a spectrum of animal behaviours, from phoronts that actively search for or attract dispersal hosts to those that passively sit-and-wait for hosts to make physical contact.

(3) Animals that engage in phoresy use a wide variety of morphological and behavioural traits for locating, attaching to, and detaching from dispersal hosts. However, the exact mechanisms and specific chemical, visual, auditory, or tactile cues used for these activities are largely unknown.

(4) The majority of known animal phoronts are terrestrial arthropods. It is unclear if known diversity reflects actual diversity or a sampling artefact emerging from the relative ease of documenting these interactions in terrestrial environments. It seems likely that the diversity of phoretic interactions is largely undocumented in all environments, especially the marine environment, which is more difficult to study and is likely underrepresented in the current literature.

(5) In closing, we encourage research in the following areas: continued and intensified exploration of the taxonomic and functional diversity of phoretic interactions, including mechanisms of attachment, transport, and detachment from the host; phylogenetic studies of macroevolutionary relationships between phoronts and hosts; assessment of the role of host switching and host specificity in phoretic systems; tests of long-standing hypotheses that phoresy can be a precursor to parasitism and other forms of symbiosis, and possibly *vice versa*; and research from the perspective of dispersal hosts regarding both positive and negative consequences of phoretic interactions.

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