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Author for correspondence:
Sara B. Weinstein
e-mail: batrachoseps@gmail.com

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Independent origins of parasitism in Animalia

Sara B. Weinstein[1] and Armand M. Kuris[1,2]

[1]Department of Ecology, Evolution, and Marine Biology, and [2]Marine Science Institute, University of California, Santa Barbara, CA 93106, USA

SBW, 0000-0002-8363-1777

Nearly half of all animals may have a parasitic lifestyle, yet the number of transitions to parasitism and their potential for species diversification remain unresolved. Based on a comprehensive survey of the animal kingdom, we find that parasitism has independently evolved at least 223 times in just 15 phyla, with the majority of identified independent parasitic groups occurring in the Arthropoda, at or below the level of Family. Metazoan parasitology is dominated by the study of helminthes; however, only 20% of independently derived parasite taxa belong to those groups, with numerous transitions also seen in Mollusca, Rotifera, Annelida and Cnidaria. Parasitism is almost entirely absent from deuterostomes, and although worm-like morphology and host associations are widespread across Animalia, the dual symbiotic and trophic interactions required for parasitism may constrain its evolution from antecedent consumer strategies such as generalist predators and filter feeders. In general, parasitic groups do not differ from their free-living relatives in their potential for speciation. However, the 10 largest parasitic clades contain 90% of described parasitic species, or perhaps 40% of all animal species. Hence, a substantial fraction of animal diversity on the Earth arose following these few transitions to a parasitic trophic strategy.

1. Introduction

The potential for parasite diversification has been a topic of debate for over a century. Parasites may comprise nearly half of animal life on the Earth [1,2] and although the potential for adaptive radiations associated with the transition to parasitism is evident [2,3], how often this diversity arose remains unexplored. Did it occur frequently? Has it occurred recently? What was the pattern of speciation following these phylogenetic events?

Here we comprehensively survey the number of times parasitism has independently evolved from a non-parasitic ancestor. With this information, we analyse its distribution across all animal taxa, noting possible phylogenetic constraints on its evolution, consider the age of parasitic origins, reveal taxa where the evolution of parasitism appears to be most recently active, and compare speciation rates of parasitic taxa and their nearest relatives.

For parasites, the number and variety of available hosts and microhabitats therein create a diverse and unsaturated environment with the potential to promote continued diversification [3,4]. If the evolution of parasitism is associated with increased speciation, then in general, we should expect an increase in the species diversity of parasitic groups compared with their closest living non-parasitic relatives [5–7]. Sister clades are, by definition, the same age and, if extinction rates are assumed to be constant, then the difference in species numbers between the two groups should be due to different speciation rates [8]. This sister group comparison method has been used to show that diversification is associated with insect phytophagy, floral nectar spurs, sexual selection in birds and sexual conflict in insects [9–12].

2. Material and methods

For a critical analysis of parasite evolution, it is necessary to have an operational and biologically meaningful definition of parasitism. Here we consider only Animalia as both consumers and prey/hosts and define parasitism as a consumer interaction in which the consumer feeds on a single individual, the host, during at least one life-history stage [13]. This includes consumer strategies employed by parasitoids, parasitic castrators, macroparasites and pathogens but excludes micropredators, brood 'parasites', kleptoparasites, symbiotic egg predators, inquilines and non-feeding symbionts.

We identified monophyletic parasitic groups from an extensive literature search (electronic supplementary material, table S1 [14]). For each parasitic group, the non-parasitic sister clade was sought using available phylogenies (electronic supplementary material, table S2 [14]). Parasitic groups with no identifiable sister group, either due to lack of study or lack of consensus, were excluded from the species diversity analysis. We then identified the number of extant genera and species in each parasitic and non-parasitic group (electronic supplementary material, table S2 [14]), subtracting non-parasitic species nested within parasitic clades and vice versa [9]. Using the non-parametric Wilcoxon signed-rank test in R [15], we compared the log-transformed number of parasite and non-parasite species in each sister pair [16]. As this difference may decrease over time, we used Spearman's rank correlation coefficient to compare divergence age with species ratio, expressed as the log-transformed number of parasite species divided by the log-transformed number of free-living species [16,17]. We did not correct for taxonomic affiliation in these analyses, but explored taxonomic patterns in speciation signal in the electronic supplementary material, figures S1 and S2 [14].

3. Results and discussion

Parasitism has evolved at least 223 times in Animalia (figure 1). Although this estimate is influenced by how parasitism is defined, this value is substantially larger than previous estimates of 'about 60' [22,23]. The minimum estimate we provide here will probably increase as relationships within Metazoa are better resolved, unknown life-history strategies are described and new species are discovered. Of the 223 identified parasitic origins, 186 (83%) occur at or below their present taxonomic rank of family and 113 (51%) occur at or below the level of genus. However, 90% of parasite species diversity occurs in the 10 largest parasitic clades, all of which appeared prior to the Mesozoic. These deeply rooted lineages reveal that parasitism is not the sort of specialization that theory predicts is an ephemeral dead end [24,25]. While the majority of parasitic species are included in persistent and morphologically distinctive hierarchical clades, the majority of unique evolutions of parasitism are at or below the family level. At first glance, 223 acquisitions of parasitism may appear to be a frequent transition, but once divided across the 7.7 million extant animal species, this evinces its rarity. Rarer still is the loss of parasitism, which has occurred only among mites [26,27], Hymenoptera [28,29], nematodes [30] and unionid mussels [31]. This loss occurs most commonly when the parasitic life stage is lost from a complex life cycle, as opposed to a trait reversal from a parasitic to a non-parasitic consumer strategy.

Parasites are present in 15 (43%) of the generally recognized 35 animal phyla, with metazoan human parasites derived from 12 unique lineages in four phyla. At the phylum level, the number of species correlated with the number of independent origins of parasitism ($F_{1,33} = 30.83$,

$p < 0.0001$). However, the number of transitions to parasitism was not determined by only the number of species in a clade. For example, although beetles are the most diverse arthropod order (and include 10 parasitic lineages), the majority of independent origins of parasitism within arthropods occur within the mites and flies. Outside of Arthropoda, the nematodes, flatworms, molluscs and annelids are also noteworthy, each containing at least nine uniquely evolved parasitic groups.

Parasitism-prone groups, notably flies and mites, typically include free-living species that exhibit diverse and flexible trophic strategies, with predation, saprophagy, necrophagy and facultative parasitism observed within the same genus. Our estimates of parasitic origins in these groups probably underestimate the number of relatively recent transitions, particularly for diverse, but understudied groups such as turbellarians, mites, copepods and flies. These taxa are often outside the purview of parasitology, but may provide the best models to understand the origin and evolution of parasitism.

Although some parasites are exclusively parasitic, the majority of parasitic species have free-living stages. Many origins of parasitism, particularly among insects, are protelean with free-living adults arising from parasitic juveniles. The flexible larval feeding strategies seen in many of the most parasite-prone groups may be a gateway to protelean parasitism. Although many of these protelean parasites are parasitoids, the transition to a macroparasite strategy could occur if larger host species are subsequently parasitized [31]. Although macroparasites and parasitoids have historically been studied in independent fields, insights into parasite evolution could be gained through comparative examination of parasitoid evolution and life history [13,32].

About half the animal phyla lack parasitic species. Most notably, the deuterostomes do not include parasitic representatives (with the exception of some pearlfishes). Phyla whose habitats are primarily meiofaunal have no known parasitic representatives (Gastrotricha, Gnathostomulida, Kinorhyncha, Loricifera, Priapulida, Micrognathozoa), nor does the Brachiopod-Phoronida lineage. Parasitism is also absent among the Bryozoa despite its frequent epizoic/host-associated habitats. Although many species have independently converged on a worm-like morphology and symbiotic associations, the evolution of parasitism appears to require a confluence of both symbiotic and trophic interactions [33]. Some trophic strategies may represent greater barriers to parasitism and we hypothesize that the restricted niche space of a symbiosis may constrain the evolution of parasitism from consumer strategies such as generalist predators, filter feeders or deposit feeders.

We compared diversification of parasitic and free-living species with a sister group analysis of 45 independently derived parasitic groups from nine of the 14 phyla containing parasitic species. A total of 147 750 parasite species and 464 650 non-parasitic species were included in the sister group comparisons, representing 41% of Earth's described animal biodiversity. No significant difference was found between the number of parasitic species and the number of non-parasitic species originating from each node (Wilcoxon signed-rank test, $p = 0.495$). Consistent results were obtained when the analysis was repeated using genera instead of species to control for a potential bias in species description rates ($p = 0.395$) and age of divergence had no effect on the speciation ratio (r_s) $= -0.01$ ($p = 0.944$).

Parasitism is clearly linked to spectacular speciation in groups like Hymenoptera and Platyhelminthes [3,34].

Figure 1. Origins of parasitism across Animalia. Bar plot of the natural log transformed number of independent acquisitions of parasitism within Metazoa, Arthropoda and Insecta, arranged according to taxonomic affiliation [18–21]. Bar shading denotes the per cent of the group that is parasitic and bar width is proportional to the $\log_{1000}$ transformed number of species per group. D, Deuterostomia; Pr, Protostomia; L, Lophotrochozoa; E, Ecdysozoa; Ch, Chelicerata; Cr, Crustacea; He, Hexapoda; Pa, Palaeoptera; Po, Polyneoptera; Co, Condylognatha; Ho, Holometabola.

However, the overall diversification pattern of parasitic groups did not differ from what was seen in their non-parasitic relatives (figure 2), consistent with previous analyses of more limited taxonomic groups [16]. Sister group analyses have two inherent flaws: power is reduced if the sister group is also diversifying [9], and using species counts as a proxy for speciation rates assumes equivalent species description rates and extinction rates. The overall similarity seen in
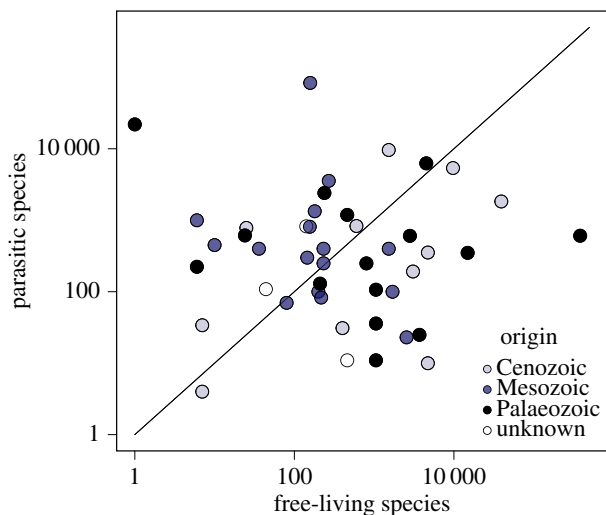
Figure 2. Plot of sister group pairs. Each point represents a single parasite/non-parasite pair with the number of free-living species as the x-coordinate and the number of parasite species as the y. The line represents a one-to-one relationship such that pairs with an equal number of free-living and parasite species are plotted on the line. (Online version in colour.)

free-living and parasitic diversification could be due to either equal speciation rates or much higher speciation rates balanced by equivalently high extinction rates. Some of the more recently derived parasitic clades, such parasitic flies in the family Sarcophagidae and mites within the superfamily Dermanyssoidea [35], may provide the best model systems

for addressing these questions. However, the taxonomic affiliation and basic natural history of these groups are frequently the least studied.

Investigations of metazoan parasitology are dominated by the study of helminths in the few clades resulting from ancient and spectacularly diverse radiations. By contrast, the most frequent diversification of parasitic groups occurs among the arthropods. The majority of these groups represent relatively recent transitions to parasitism suggesting that parasitism may evolve more frequently than is assumed, but only a few of these events persist and lead to speciose radiations. A substantial fraction of Earth's biodiversity is parasitic, thus, more comprehensive explorations of parasite evolution would contribute much to our understanding of the evolution of life.

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