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RESOURCE TRACKING IN NORTH AMERICAN *TELORCHIS* SPP. (DIGENEA: PLAGIORCHIFORMES: TELORCHIDAE)

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ABSTRACT: We examine the evolution of host specificity for species of *Telorchis*, using the methods developed by researchers studying phytophagous insect–plant systems. Optimization of “generalist” compared with “specialist” onto the phylogeny for *Telorchis* revealed ambiguous patterns, depending on how the 2 terms were defined. Regardless of that definition, most of the evolutionary diversification of this group has been carried out within eucryptodiran turtles, the ancestral host group. From that plesiomorphic background, there appears to have been 2 episodes of specialization by way of a host switch into caudates (ancestor of *T. stunkardi* + *T. sirenis*) and snakes (*T. auridistomi*), and 1 episode of exuberant expansion producing a true generalist (*T. corti*). These results, which indicate that most species of *Telorchis* are tracking widespread plesiomorphic resources, mirror those reported for phytophagous insects and their plants. We believe that establishing a dialogue between the two research groups will be mutually beneficial to both and will strengthen our understanding of the complex factors underlying the evolution of coevolutionary associations.

Biologists have been fascinated by the observation that although members of different taxa tend to be associated with one another more than with members of other taxa, those associations are rarely absolute. Sometimes an associate species switches hosts, and a new kind of association begins. This begs the question, when host switching does occur, is it just a random phenomenon (based, for instance, on spatial proximity), or are there more stringent guidelines concerning who is and who is not an acceptable new host? Researchers working with phytophagous insect–plant systems have attempted to answer this question by beginning with the assumption that the insects are tracking a particular resource offered by their plant host(s). If the new host species possesses the same resource as does the colonizer’s ancestral host (Jermy, 1984), the new host is simply more of the same habitat (Janzen, 1985). The expansion of the host range may appear to indicate that the associate species is becoming a generalist, when in fact it has not changed its resource preference at all (“faux generalists”: Brooks and McLennan, 2002). Second, the associate may speciate on the colonized host species but may still be tracking the plesiomorphic resource. In this case we may be fooled into thinking that a different specialist has evolved when it has not. Such a dynamic produces clades of specialists on the same resource, regardless of whether the ancestral resource is plesiomorphically (e.g., Taber and Pease, 1990; Berenbaum and Passoa, 1999) or convergently (e.g., Becerra, 1997; Köpf et al., 1998) widespread. Finally, an associate species may colonize a host species with a novel resource. If the colonizer already possesses a trait that allows it to access the novel resource (plesiomorphic trait, apomorphic function) it may establish itself on the new species. If the colonizer does not speciate, it has expanded its resource base. In this case, appearances will not be misleading because the colonizing species really has added a novel resource to its list (has become more of a generalist).

Several recent overviews of parasite evolution (Brooks and McLennan, 1993; Poulin, 1998; Trouvé et al., 1998) suggest that host–parasite systems may not differ fundamentally from the insect–plant coevolutionary associations. Parasitologists, however, have traditionally viewed the host species as “being” the resource rather than viewing the host species as “having”

the resource. Is this distinction likely to make any difference to explanations about the evolution of particular groups of parasites? If, on the one hand, the host species is the resource, then there is a straightforward relationship between host specificity and resource specialization, i.e., the number of host species used by a given parasite indicates its degree of specialization. If, on the other hand, the target resource is a characteristic of the host species (for example, habitat provided by the lungs or the intestine) and not the species itself, the relationship between host specificity and specialization may be complex and historically contingent (Brooks and McLennan, 1993, 2002; Adamson and Caira, 1994; first suggested in a phylogenetic systematic context by Brooks, 1979). In this view, a parasite species showing pronounced host specificity may indicate either cospeciation or peripheral isolates speciation, in which some members of the ancestral population have managed to colonize a host representing a novel (apomorphic) resource, have adapted to that resource, and have speciated as a result (McLennan and Brooks, 1993, 2002; Funk et al., 1995a, 1995b, 1995c; Funk, 1998). The situation is equally complex for parasites inhabiting numerous host species. Such parasite species may be true generalists, that is, they are capable of using a variety of different resources. In other cases the parasite uses the same resource in each host species, so it is actually a resource specialist. It only appears to be a generalist because researchers are recording the number of host species and not the underlying resource that each host is providing.

Researchers working with phytophagous insects and their host plants have amassed a substantial amount of data concerning the dynamics involved in the origin, maintenance, and diversification of coevolutionary associations (e.g., Pellmyr, 1992; Futuyma et al., 1993, 1994, 1995; Bernays and Chapman, 1994; Thompson, 1994; Funk et al., 1995a, 1995b, 1995c; Sperling and Feeny, 1995; Armbruster, 1997; Funk, 1998; Janz and Nylin, 1998; Janz et al., 2001). We believe that it might be useful to apply the techniques used by these researchers to host–parasite systems to ask whether there are any differences between the 2 types of coevolutionary associations. We need 2 things to pursue this investigation: species-level phylogenetic trees for various groups of parasites and a substantial amount of information about preferred hosts for each species being studied. Such information is rare for groups of parasites, but

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the North American species of *Telorchis* represent a suitable exemplar group.

MATERIALS AND METHODS

Macdonald and Brooks (1989) provided names and synonyms for 11 North American *Telorchis* species and a phylogenetic tree with a consistency index of 94%. Subsequently, Friedenfelds et al. (1994) synonymized *T. auridistomi* and *T. dollfusi*, so we have combined host records for both under *T. auridistomi*. Searching the primary literature from 1900 to the present produced the list of vertebrate hosts for each species. The list of the source articles is available on request from D.R.B. Published reports that did not include the species name of the parasite or its host were eliminated from this analysis.

We used an approach designed by researchers studying insect–plant systems (e.g., Janz, 1999; Janz et al., 2001) in which host specificity is investigated using phylogenetic comparisons on different levels of taxonomic resolution for the host groups. So, for example, *T. stunkardi* inhabits 6 host species, which can in turn be clumped to 2 larger host categories (Caudata and Emydinae). Ancestral conditions were estimated using phylogenetic optimization procedures (Brooks and McLennan, 1991, 2002; Wiley et al., 1991, in press). Possible bias in host specificity associated with uneven sampling was investigated using a simple regression analysis comparing the number of reported hosts with the number of published reports of the parasite. Statistical analyses were performed using Statview 5.0.1, implemented on a MacIntosh G4 computer.

RESULTS

Regression analysis using all species of North American *Telorchis* (Fig. 1a) indicated a strong association between the number of reported hosts and the number of published reports of the parasite species. One possible interpretation of this result is that a parasite species might be categorized as a “specialist” because of incomplete knowledge about host range. Closer examination of the data, however, indicated that the analysis was biased because of the inclusion of the extremely “host-rich” *T. corti*. Removing *T. corti* eliminated any significant association (Fig. 1b). Differences in host specificity (as estimated by the number of inhabited host species), therefore, do not appear to be an artifact of incomplete knowledge.

Figure 2 depicts the number and the names of the documented host species for each North American *Telorchis* species. To optimize this information onto the tree, we must categorize each *Telorchis* species as a generalist or a specialist. If we use the most conservative definition of a specialist (only 1 host used by the parasite species), then the entire *Telorchis* clade can be categorized as “generalists.” A less conservative interpretation, however, considers the specialists to have a low number of host species and the generalists to have a large number of host species. This, of course, is an arbitrary distinction. Clearly *T. corti* is a generalist under any definition. If all other species are categorized as “specialists (1–6 hosts),” then the optimization is simple: being a specialist is plesiomorphic for the clade with 1 transition to the generalist lifestyle. Narrowing the definition of a specialist to include only species with 4 or fewer hosts produces the macroevolutionary pattern depicted in Figure 2. The plesiomorphic state for the clade is still a specialist, but there are now 3 postulated independent transitions to a generalist (*T. corti*, *T. stunkardi*, and *T. robustus*). If a specialist is defined as a species with 3 or fewer hosts, then the macroevolutionary pattern is reversed; being a generalist is the plesiomorphic condition for the “clade with 4 independent transitions to being a

FIGURE 1. Results of regression analysis of number of reported hosts against number of times the parasite species was documented in the literature, including (a) or excluding (b) the extreme generalist *T. corti*.

specialist” (*T. sirenis*, *T. angustus*, *T. scabrae*, and the ancestor of *T. singularis* + *T. attenuatus*).

DISCUSSION

It was impossible to unambiguously determine whether being a specialist or a generalist was the plesiomorphic condition for the North American *Telorchis* clade. Depending on how many host species and parasite species were assigned to the designations of a specialist and a generalist, the macroevolutionary patterns indicate a range from “all species are generalists” to “specialist plesiomorphic with 1 transition to generalist.” This confusion stems, in part, from the assumption that the host species is the resource being used by the parasite. Researchers working with insect–plant systems have solved this problem, in part, by beginning from the perspective that the host has the resource and then combining host plants into larger monophy-

FIGURE 2. Optimizing specialist (open box) compared with generalist (black box) onto the phylogenetic tree for *Telorchis* (McDonald and Brooks, 1989). Specialist, any species with 1–4 hosts. Bold lines, specialist.

letic groupings. Although this kind of analysis initially appears somewhat arbitrary, it is in fact based on the biological assumption that insects are tracking particular resources and that the chemical composition of these resources is identical, or at least highly similar, in closely related plant species. Studies elucidating the actual compounds being tracked by various insect groups support this hypothesis (see e.g., Sperling and Feeny, 1995). Following this protocol we clumped *Telorchis* hosts into 3 major clades, eucryptodiran turtles (Chelonia: Eucryptodira), caudatan amphibians (Amphibia: Caudata), and colubrid snakes (Serpentes: Colubridae), and optimized these host groups above the phylogenetic tree for the parasites (Fig. 3). For the sake of discussion, we are assuming that turtles are the plesiomorphic hosts for the North American clade. To confirm this hypothesis, we need a robust phylogeny for all members of *Telorchis*. If that analysis confirms that turtles are the plesiomorphic hosts for the clade, then there have been 2 episodes of specialization by way of a host switch into caudates (ancestor of *T. stunkardi* + *T. sirenis*) and snakes (*T. auridistomi*), and 1 episode of exuberant expansion producing a true generalist (*T. corti*).

Regardless of the resolution of the basal host type, our anal-

ysis indicates that most of the evolutionary diversification of this group has been carried out within what might be called "turtle resource space." In addition to the 2 major shifts in host specificity into caudatans and snakes, there has been a substantial amount of host shifting within turtle resource space. That shifting, however, occurs predominantly within the Emydinae (Testudinoidea: black boxes in Fig. 4), with occasional movement either into another testudinoidean (Chelydridae: grey box in Fig. 4) or into a trionychoidean (Trionychidae: white box in Fig. 4), the sister group of the Testudinoidea. Within turtle resource space, then, host switching is at once widespread and yet constrained to Eucryptodirans. Note also that all the new hosts are occupied by *T. corti*. The pattern is similar for Serpentes; all *Telorchis* species that are associated with snakes are found within colubrids. Host specificity of *Telorchis* species thus appears to be at the level of major tetrapod groups and not of individual species. In other words, as suggested initially for insect-plant systems (for a close parallel, see Janz et al., 2001), the parasite may be tracking a widespread ancestral resource and not a given host species. What we require now are studies delineating the actual resource that the parasites are tracking.

FIGURE 3. Examining the evolution of host specificity by grouping hosts on a higher taxonomic level (Eucryptodira, Colubridae, Caudata). It is difficult to determine the ancestral host type for the clade (it could be either Eucryptodira or Caudata). To resolve this problem, we need to include data from sequential sister-groups to the North American *Telorchis* group. Bold lines, preference limited to 1 major type of host group.

FIGURE 4. Examining the evolution of host specificity by incorporating information about the phylogenetic relationships among host groups (depicted to the right of the phylogenetic tree for the parasites) at a lower taxonomic level. Host switching in these parasites has occurred primarily within the Emydinae and secondarily among their close relatives, the Chelidridae and Trionychoidea, all eucryptodiran turtles.

For example, if the colonizer is tracking a plesiomorphic resource, both it and its sister species should be able to survive in each other's hosts, just as has been documented for insect-plant systems (Futuyma, 1991; Futuyma et al., 1993, 1994, 1995; Funk et al., 1995a, 1995b, 1995c). Studies performed in laboratory settings have demonstrated that at least some parasite species are capable of surviving in many different hosts, including hosts with which they are never associated in nature (Watertor, 1967; Blankespoor, 1974; O'Grady, 1987).

Telorchis corti and its closest relatives are perhaps the most interesting members of this group. By exhibiting the largest number of hosts and the broadest phylogenetic range of hosts by far, *T. corti* differs markedly from its closest relatives, *T. angustus* and *T. auridistomi*. Unlike *T. angustus* and *T. auridistomi*, *T. corti* has no autapomorphies, a condition used by some phylogenetic systematists to identify a persistent ancestor (Wiley, 1981; Wiley and Mayden, 1985; Brooks and McLennan, 1991, 1993, 2002). If *T. corti* is the persistent ancestor of *T. angustus* and *T. auridistomi*, it is possible that these changes in host range were associated with the speciation of the latter 2 species. Both species are sympatric with *T. corti* and do not exhibit any obvious differences in preferred location in the host intestine. *Telorchis angustus* occurs only in hosts also known to be inhabited by *T. corti* and, thus, may be the product of true sympatric speciation, presumably isolated from its sympatric ancestor *T. corti* by an autapomorphic genital pore position (Macdonald and Brooks, 1989). *Telorchis auridistomi*, on the other hand, occurs in colubrid hosts not known to host *T. corti*, suggesting that *T. auridistomi* may be the result of peripheral speciation, i.e., speciation by colonization. These inferences, of course, are on the basis of the assumption that *T. corti* is indeed 1 widespread species, not a species complex, and that its broad host range was achieved before the evolution of *T. angustus* and *T. auridistomi*, as indicated by phylogenetic optimization (Fig. 2). To pursue this question further, molecular phylogeographic studies of *T. corti*, which has over a dozen synonyms, need to be undertaken. We also need a robust phylogenetic tree for all species of *Telorchis* to pinpoint the full scope and breadth of host switching, both within and among different host resource types, in this clade.

This study, although preliminary, supports the hypothesis that such different systems as helminth-vertebrate and insect-plant associations may exhibit common macroevolutionary patterns and thus may be subject to, and formed by, common evolutionary dynamics (Brooks and McLennan, 1993, 2002). We believe that the establishment of a dialogue between the 2 research groups will be mutually beneficial to both and may strengthen our understanding of the complex factors underlying the evolution of coevolutionary associations.

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