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In the Eye of the Cyclops: The Classic Case of Cospeciation and Why Paradigms are Important

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ABSTRACT: Scientific disagreements due to empirical problems—not enough data, not enough of the critical type of data, problems in analyzing the data—are generally short-lived and resolved in the next cycle of data production. Such disagreements are thus transitory in nature. Persistent scientific conflicts, on the other hand, do not necessarily mean some facts are correct and some are wrong, nor do they mean that we do not have enough information. More often, such persistent conflicts mean that the conceptual frameworks used by different groups of researchers are insufficient to resolve apparent conflicts in the data. The latter seems to be the case with persistent disagreements about the phenomenon of cospeciation, wherein there has historically been no framework that allows us to understand speciation by host switching when the host and parasite lineages involved are of equal ages. This situation can now be resolved with the emergence of what has become known as the “*Stockholm Paradigm*.” In short, re-examination of what has been dubbed the “classic case of cospeciation” shows that divergent views of cospeciation are subsumed and reconciled within the larger explanatory framework of the *Stockholm Paradigm*. The implications are considerable, given the need to have a fundamental understanding of faunal structure, assembly, and distribution in addition to an understanding of the historical and evolutionary drivers of diversity within the current arena of accelerating environmental change, ecological perturbation, and emerging infectious diseases.

KEY WORDS: cospeciation, co-accommodation, *Stockholm Paradigm*, host switching, ecological fitting, taxon pulses, coevolution, pocket gophers, lice.

Most parasitologists, like most scientists, undertake their research within conceptual frameworks that they rarely, if ever, think about and that they never question. This is not a novel insight, with philosophers of science having long noted that most scientists eschew philosophy while nevertheless relying heavily upon it to do their work. The usual response by parasitologists to being questioned about the philosophical basis for their work is that they expect to collect such high-quality data that the data will “speak for themselves” and provide an answer to whatever problem they are investigating. Data, however, rarely speak for themselves and, in fact, the very question of what constitutes valid data has a strong philosophical basis that is rarely acknowledged. As David Hull stated in his classic book *Science as a Process* (Hull, 1988), when scientists are in dispute, each side will claim that it can know what it needs to know (i.e., it can gather the essential data) while the other side can never know what it needs to know (i.e., cannot gather the proper data)—an approach that inevitably leads to conflict. Philosophy,

embodied in the form of conceptual frameworks, allows for the possible resolution of such conflicts because it aids us in adjudicating data and, more importantly, because it helps us differentiate between apparent and real disagreements in our observations. In this commentary we discuss a case central to the comparative phylogenetic study of parasites and coevolution in the context of such a philosophical framework, that of parasite and host cospeciation. The implications are considerable, given the need to have a fundamental understanding of faunal structure, assembly, and distribution along with the historical and evolutionary drivers of diversity in an arena of accelerating environmental change, ecological perturbation, and emerging infectious diseases (for recent reviews, see Brooks and Hoberg, 2013; Hoberg and Brooks, 2013; Brooks et al., 2014).

Brooks (1979) discussed two elements of parasite evolution that could be examined phylogenetically. One of these was the extent to which parasite and host speciation events were correlated in space and time—for cases in which hosts and parasites speciated together, Brooks coined the term *co-speciation*. The other element of parasite evolution, which Brooks termed *co-accommodation*, had to do

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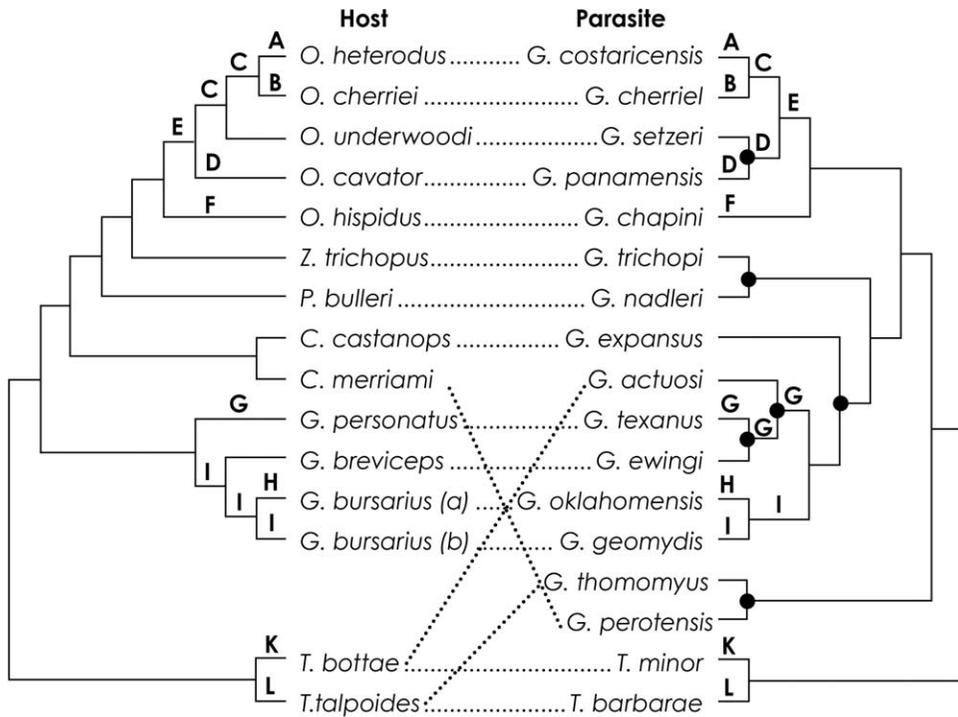


Figure 1. Phylogenies of pocket gophers and lice (redrawn and modified from Hafner and Nadler, 1988, 1990) with phylogenetically incongruent nodes highlighted. Each of these represents a case of speciation by host-switching.

with the evolution of the various parameters associated with host specificity (a subset of what Janzen [1985] termed *ecological fitting*). Brooks made two fundamental assertions regarding these two elements: (1) cospeciation and co-accommodation were not the same thing so that, for example, presumptive host specificity (especially host range) could not be used as a surrogate for cospeciation (and vice versa); and (2) that cospeciation could only be documented by finding congruence between host and parasite speciation events in a phylogenetic comparison. In short, cospeciation means that hosts and parasites are the same age, and that departures from cospeciation are episodes of speciation by host switching, in which case the hosts and parasites are not of the same age.

Nearly a decade after Brooks coined the term cospeciation, Hafner and Nadler (1988) published a phylogenetic analysis of a group of mammals and a group of lice parasitizing them. After comparing the phylogenetic trees of each group based on molecular data and assessing the ages of the host and parasite lineages based on genetic divergence estimates, Hafner and Nadler concluded that their work represented the best-documented case of cospeciation to date. However, these workers did not cite Brooks

(1979) as the source of the term cospeciation, with good reason, as even a cursory comparison of the phylogenetic trees published (Hafner and Nadler, 1988) showed substantial points of disagreement, each of which according to the proposal by Brooks (1979) would have been interpreted as a case of speciation by host switching and not cospeciation (Fig. 1). Hafner and Nadler (1990) subsequently made it clear that two factors were more important than either the congruence or incongruence of host and parasite phylogenetic trees for their conception of cospeciation. These factors were narrow host range and the equivalence of genetic divergence, which Brooks (1979) had associated with co-accommodation as opposed to cospeciation. Hafner and Nadler (1990) reasoned that parasite species limited to a single host species, and host and parasite lineages exhibiting equivalent genetic divergence, must be the same age. Moreover, if they were of the same age, they then reasoned they must be the products of cospeciation. Significantly, Hafner and Nadler (1990) acknowledged that the genetic divergence data were not actually equivalent but explained away the apparent discordance based on the assumptions that (1) the problem was due to discrepancies in the

parasite data, and (2) parasites had higher reproductive rates, and thus accumulated mutations more rapidly, than did the hosts. It is at this point that complications begin to arise with their analysis.

Because Hafner and Nadler (1990) already “knew” that theirs was a case of cospeciation, they knew exactly how to fix the parasite data to bring them into line with the host data, even though their original study showed significant disagreement between the host and parasite phylogenies. In terms of cospeciation *sensu* Brooks (1979), there is only about 50% cospeciation in the phylogenies presented by Hafner and Nadler (1990) and, accordingly, their data support the decoupling of co-accommodation—indicated by the equivalence of genetic divergence and narrow host range from cospeciation—indicated by the degree of concordance–discordance in the phylogenetic trees of hosts and parasites. That is, if there is a 50% departure from cospeciation, then this explains the discrepancies in the genetic divergence data between hosts and parasites noted by Hafner and Nadler (1990), and perhaps the data did not need to be “fixed” after all. Hafner and Nadler (1988), in contrast, argued that the lack of concordance between host and parasite phylogenies was due to error in inferring one or both phylogenies.

As outlined above, we thus have two different conceptual frameworks at play, neither of which can accommodate all the available evidence comfortably. Interestingly, however, the conflict of interpretation arises from points of agreement within the two frameworks. It has been widely assumed (e.g., Brooks, 1988; Brooks and McLennan, 1991, 1993) that if it is cospeciation, then the hosts and parasites are the same age and, if they are of the same age, it is cospeciation. Conversely, if it is not cospeciation, then hosts and parasites are not of the same age and, if they are not of the same age, it is not cospeciation. The two frameworks thus seem to agree that there cannot simultaneously be narrow host range, equivalent genetic distances, and parasite speciation by host switching.

While the conflict can perhaps be resolved in the traditional manner by declaring the evidence of one side “better” than the evidence of the other side, here we also find no comfort. Hafner and Nadler (1990), and later Hafner et al. (1994), demonstrated that genetic distance data used to infer and compare rates of evolution do not provide unambiguous support for their own view of cospeciation. “Knowing” that their system was the result of cospeciation, however, justified their post hoc assumption that parasite

reproductive rates are much higher than host reproductive rates (confounding reproductive rate with fecundity). Moreover, we know that host range data for the majority of parasites species is heavily affected by sampling bias and also that phylogenetic analyses are subject to constant update and modification based on new data and new taxa. As a result, none of the sources of data are free of potential shortcomings.

We do not dispute that cospeciation occurs widely in the biosphere. We believe, however, that cospeciation is only one mechanism among a complex array of drivers associated with such diversification (e.g., Hoberg, 1997; Hoberg and Klassen, 2002; Hoberg and Brooks, 2008). This view is contrary to more than a century of coevolutionary thinking about the nature of host–parasite assemblages, which has historically been heavily influenced by orthogenetic theories of evolution (Brooks and McLennan, 1993, 2002). In contrast to a gradual process of faunal assembly involving deep coevolutionary associations, an alternative view (summarized herein) is that the structure and diversification of complex faunas has been substantially driven by recurrent geographic events and host colonizations emerging from climatological and ecological perturbations manifested across the broad spatial and temporal scales of Earth history (e.g., Hoberg and Brooks, 2008, 2010). In short, depending on the temporal context of colonization, parasites may be older, younger, or the same age as their hosts regardless of their rate of molecular divergence, which may appear to be equivalent, delayed, or accelerated relative to that of the hosts (e.g., Hoberg, 2005). Moreover, episodic shifts in climate and environmental settings, in conjunction with ecological mechanisms and host switching, are also consistently found to be critical determinants of parasite diversification and faunal assembly (for comprehensive reviews, see Brooks and McLennan, 1993, 2002; Hoberg, 2005; Hoberg and Brooks, 2008, 2013; Agosta et al., 2010; Janz, 2011).

The pervasive nature of host colonization results in a “parasite paradox” based upon the recognition that parasites have restricted ranges (as resource specialists), and yet in the phylogenetic diversification of lineages (for example among helminths, arthropod ectoparasites, and other taxa) such shifts are common, can be inferred historically, and are directly observable in ecological time (Agosta et al., 2010). In this light, the patterns discovered by Hafner and Nadler (1988)—approximately 50% cospeciation and 50% speciation by host switching—seems to be the norm

and not the exception (see also Taylor and Purvis, 2003). If so, models designed specifically to promote maximum cospeciation (e.g., Paterson and Banks, 2001; Page, 2003; Demastes et al., 2012) provide an overly simplified idea about the macroevolutionary processes that have resulted in the structuring and assembly of the biosphere across evolutionary and ecological time. In this regard, Hafner and Nadler's study (1988) is critical: If the primary exemplar serving as the foundation for the maximum cospeciation paradigm is incorrect, the paradigm is refuted by the very evidence on which it has been based.

Now let us assume that, while the various sources of data are likely incomplete and likely contain some error, they are nevertheless sufficient to provide accurate insights into the evolution of this host–parasite system if the data are analyzed using methods that do not force the data into maximum cospeciation. Arguments about the need for, and development of, methodologies for assessing the macroevolutionary complexity of host–parasite associations have been presented elsewhere (e.g., Brooks and McLennan, 2002; Dowling et al., 2003; Brooks et al., 2004; Wojcicki and Brooks, 2004). In the case of the Hafner and Nadler data, simple inspection of the host and parasite phylogenies is sufficient to show substantial diversification by host switching.

Finally, it is important that we admit that existing conceptual frameworks are not capable of accommodating all of the data comfortably. The paradigm of maximum cospeciation may have persisted in part due to inertia verging on ennui—it may be a bad model, but it's the only one we have. From this, we must then conclude that the different interpretations of the “classic case of cospeciation” stem from shortcomings in the conceptual frameworks used to explain it and not necessarily in the data itself.

We previously suggested that maximum cospeciation should be replaced by an empirical framework that reveals both historical complexity and contingency (e.g., Brooks and McLennan, 2002; Dowling et al., 2003; Brooks et al., 2004; Wojcicki and Brooks, 2004; Hoberg and Brooks, 2008, 2010, 2013) and such a framework appears to be emerging. Resolution of the parasite paradox emerges from articulation of the *Stockholm Paradigm* (Brooks et al., 2014; Hoberg and Brooks, 2015; Hoberg et al., 2015), a view that integrates evolutionary and ecological processes in the biosphere while providing new insights into the nature of the macroevolutionary mechanisms driving diversification, persistence, and the distribution of complex systems. This paradigm

provides a framework or model unifying the seemingly disparate dynamics of macroevolution, ecological processes, biogeography, and faunal assembly across plant–insect and host–parasite systems and emanates from the core contributions of four academic generations of researchers at Stockholm University (for reviews, see Brooks and McLennan, 2002; Agosta et al., 2010; Janz, 2011). In this view of the biosphere, recurrent episodes of geographic expansion at local to regional scales, the mosaic assembly of faunas, host colonization, and shifting patterns of specialization serve as determinants of faunal diversity over time (e.g., Hoberg and Brooks, 2008). In short, 4 things determine this diversification: (1) Host switching is a central phenomenon and results from phenotypic flexibility and the phylogenetic conservatism in traits for resource exploitation, essentially host preference, as described in *Ecological Fitting* (Janzen, 1985; equals co-accommodation of Brooks, 1979). Host shifts via ecological fitting (prior to the evolution of novel capacities for host utilization) allow expansion of host range by specialists; (2) Acquisition of a novel array of hosts becomes the downstream antecedent for alternation in the evolution of generalists and new specialists as described in the *Oscillation Hypothesis* (Janz and Nylin, 2008; Nylin et al., 2014); (3) More generally, dynamic faunal assembly through the temporal and spatial generation of novel combinations of interacting species within the *Geographic Mosaic Theory of Coevolution* (Thompson, 2005) occurs. Responses among assemblages of hosts, parasites, and pathogens (e.g., helminths of vertebrates or phytophagous insects) to ecological disruption, or to a crucible of accelerating change such as that occurring with climate alteration, are governed by equivalent processes of expansion, geographic colonization, or range contraction across spatial scales through evolutionary and ecological time (e.g., Hoberg and Brooks, 2008, 2010; Hoberg et al., 2012); and (4) The dynamic nature of *Taxon Pulses* (Erwin, 1985; Halas et al., 2005), driven by climate change and large-scale ecological perturbation, acts as the precursors and drivers of biotic mixing, mosaic faunal assembly, and episodes of rapid host switching including outbreaks of emerging infectious diseases (Brooks and Hoberg 2007, 2013; Hoberg and Brooks, 2008, 2013; Agosta et al., 2010).

Significantly, this view of processes linking evolution, ecology, and biogeography accommodates insights about the age and history of the assemblage of contemporary pocket gophers and the nature of

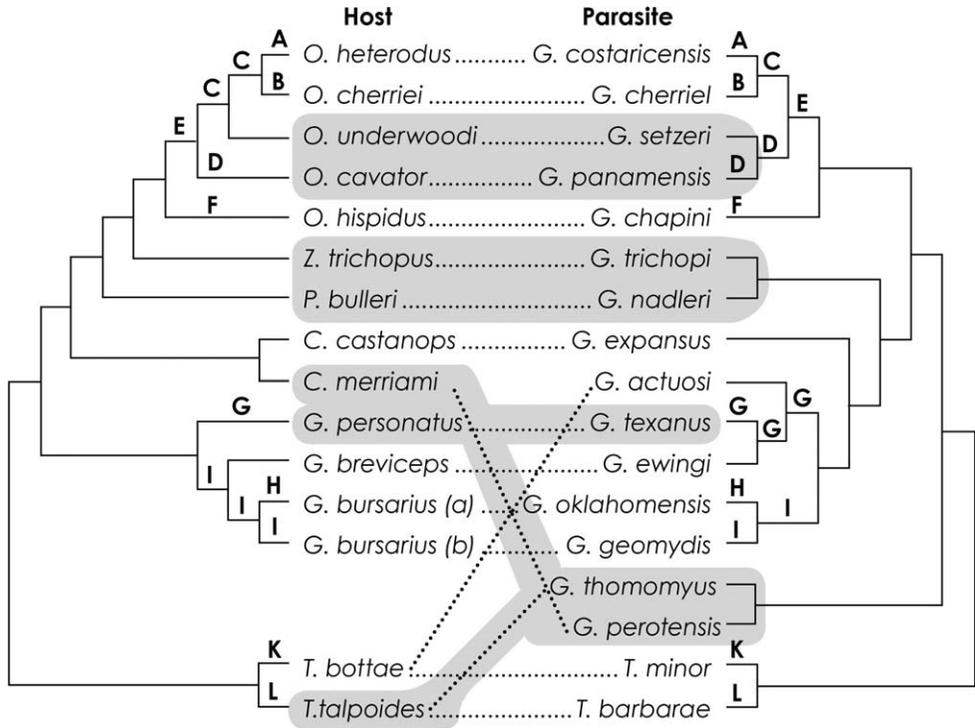


Figure 2. Phylogenies of pocket gophers and lice (redrawn and modified from Hafner and Nadler, 1988, 1990) with episodes of host-switching circled. Note the pattern of alternating episodes of cospeciation and episodes of host-switching predicted by the *Stockholm Paradigm*.

diversification in the gopher–louse model. The family Geomyidae, endemic in the Nearctic, comprises an assemblage of rodents exhibiting highly sedentary habits, considerable stability in geographic range, and numerous species and subspecies that are characterized by strong partitioning at local scales (Kurtén and Anderson, 1980; Patton, 2005). Exceptional levels of local variation have been demonstrated in this system. For example, within the *Thomomys bottae*–*Thomomys umbrinus* complex (common name–common name), 213 subspecies had been recognized (Hall, 1981; Álvarez-Casteñda, 2010). Although the geomyid fossil record is known from the Miocene, rapid divergence and radiation within the tribes Geomyini and Thomomyini extends to near 5 million years ago (MYA), coinciding with the origins of 5–6 generic-level lineages (Russell, 1968; Spradling et al., 2004). Contemporary diversity among pocket gophers is limited to the temperate zone, and the current geographic range indicates restriction south of the Laurentide–Cordillera during sequential glacial maxima over the extent of the late Pliocene and Quaternary. The diversification and origins of extant species assemblages in this group represents a

primary radiation limited to a relatively brief temporal window between 4.2 and 1.8 MYA (Spradling et al., 2004). Thus, a burst of diversification for genera and species of pocket gophers, and presumably their louse parasites, coincided with a substantial regime of episodic variation in climate and habitat perturbation.

Cyclical shifts in climate through alternating glacial–interglacial and stadial–interstadial episodes have been identified as primary drivers for range expansion–contraction, isolation (often in restricted refugia), and the initiation of secondary contact, and such shifts have appeared to act as a principle environmental driver of geographic and host colonization among assemblages of mammals (other vertebrates) and their parasites since the Pliocene (e.g., Avise, 2000; Hoberg and Brooks, 2008; Galbreath et al., 2009; Shafer et al., 2010; Hoberg et al., 2012). Significantly, a re-examination of associations among pocket gophers and lice using a method (PACT: Wojicki and Brooks, 2004) independent of a model of maximum cospeciation produces an evolutionary scenario involving a history of alternating episodes of host colonization and

cospeciation (Fig. 2). Consequently, a general climatological and regional chronology, in which episodes of dynamic climate change have strongly determined patterns of diversification and distribution, provides a more robust explanation for radiation within this assemblage (e.g., Hoberg and Brooks, 2010) than does classical coevolution alone and is consistent with the expectations of the *Stockholm Paradigm*.

As noted above, traditional paradigms of narrow association by descent in host–parasite systems predict that the potential for host colonization is minimal and that coevolutionary processes should provide substantial buffers or protection from emerging infectious diseases. This expectation is embodied in the idea that switching and successful exploitation of a novel host should rarely occur given the degree of intense coadaptive responses (and specificity) that characterizes these associations. A cospeciation paradigm leads to two logical conclusions: (1) host switches should be infrequent; and (2) when host colonization does occur, it must be a direct consequence of genetic changes that have enhanced the ability by a parasite or pathogen to exploit a novel host or host assemblage. These assumptions become focused in discussions about climate change and emerging diseases, which then emphasize the possible mechanisms by which climate or environmental perturbation can lead to such novel genetic variation (and provide an ecological arena in which these may enhance host exploitation). The expectation, however, remains that host shifts will be exceptional (relative to background), even during periods of accelerating climate forcing, simply because rare genetic innovations must serve as the precursors for emerging diseases.

In contrast, the interacting phenomena at the core of the *Stockholm Paradigm* allow for the prediction that events of emergent diseases—for example among macro- and microparasites of humans, livestock, crops (we include in this novel pest phytophagous insects and parasitoids of beneficial insects), and wildlife—will be common rather than rare events during episodes of climate change and the resultant general breakdown in mechanisms of ecological isolation. In these instances, host switching is driven initially by ecological fitting based only on genetic capabilities already within the system in contrast to being limited by the potential development of novel genetic capacity. Ecological fitting is active in a broad arena across a large fitness space (*Sloppy Fitness Space*: Agosta, 2006; Agosta and Klemens, 2008, 2009; Agosta et al., 2010) represented by potential hosts from which the parasites and patho-

gens have been historically precluded via both spatial and temporal isolation as well as via circumstances of origin. In this view, climate change and the associated biotic expansion (or habitat contraction and increasing host sympatry and density) serve to drive the breakdown in mechanisms of ecological isolation, broadening access in the *Sloppy Fitness Space* and within which switching events would be expected to occur more rapidly and often. Hoberg and Brooks (2010) have demonstrated elsewhere that processes for geographic expansion (invasion) and host colonization are equivalent in space and time and, thus, that historical dynamics for complex host–parasite systems reveal the potential for such rapid change in contemporary assemblages.

Hafner and Nadler's phylogenetic data (1988) show clear evidence of alternating episodes of cospeciation and speciation by host switching (Fig. 2), an interpretation counter to the prevailing model. Most parasitologists, and many others in the broader zoological community as well, have accepted or promoted the idea that host–parasite associations and their development are strongly linked to coevolution and cospeciation (reviewed in Klassen, 1992; Brooks and McLennan, 1993). A generality for association by descent emerged from the initial development of concepts about evolution and the seemingly tight connections demonstrated between hosts and parasites, although exceptions or departures from this orthodoxy have long been noted for insect–plant systems (Kellogg, 1913; for a review, see Brooks and McLennan, 1993). Nevertheless, adherence to a core paradigm of maximum cospeciation (e.g., Demastes et al., 2003; Hafner et al., 2003; Page, 2003; Demastes et al., 2012) has continued even in the face of considerable empirical evidence to the contrary (e.g., reviewed in Hoberg, 1997; Brooks and McLennan, 2002; Hoberg and Klassen, 2002; Hoberg and Brooks, 2008). In light of the *Stockholm Paradigm*, there is no conflict in the data, and the perceived conflict between the two views of cospeciation disappears, each subsumed in a larger conceptual framework capable of explaining the observable outcomes more fully.

SUMMARY

Scientific disagreements due to empirical problems—not enough data, not enough of the critical type of data, problems in analyzing the data—are generally short-lived and resolved in the next cycle of data production. Such disagreements are thus transitory. Persistent scientific conflicts do not necessarily

mean some facts are correct and some are wrong, nor do they mean that we do not have enough of them. More often, such conflict means that the conceptual frameworks used by the different groups of researchers involved are insufficient to resolve the apparent conflicts in the data. In the case presented herein there has been, until recently, no framework that has allowed us to have speciation by host switching and equal ages of lineages. That situation has now changed, and re-examining what has been dubbed the “classic case of cospeciation” shows that it is in fact better interpreted as a classic case of the *Stockholm Paradigm* in action.

LITERATURE CITED

- Agosta, S. J.** 2006. On ecological fitting, plant-insect associations, herbivore host shifts, and host plant selection. *Oikos* 114:556–565.
- Agosta, S. J., and J. A. Klemens.** 2008. Ecological fitting by phenotypically flexible genotypes: implications for species associations, community assembly and evolution. *Ecology Letters* 11:1123–1134.
- Agosta, S. J., and J. A. Klemens.** 2009. Resource specialization in a phytophagous insect: no evidence for genetically based performance tradeoffs across hosts in the field or laboratory. *Journal of Evolutionary Biology* 22:907–912.
- Agosta, S. J., N. Janz, and D. R. Brooks.** 2010. How generalists can be specialists: resolving the “parasite paradox” and implications for emerging disease. *Zoologia* 27:151–162.
- Álvarez-Casteñeda, S. T.** 2010. Phylogenetic structure of the *Thomomys bottae-umbrinus* complex in North America. *Molecular Phylogenetics and Evolution* 54: 671–679.
- Avise, J. C.** 2000. *Phylogeography: The History and Formation of Species*. Harvard University Press, Cambridge, Massachusetts. 447 pp.
- Brooks, D. R.** 1979. Testing the context and extent of host–parasite coevolution. *Systematic Zoology* 28:299–307.
- Brooks, D. R.** 1988. Macroevolutionary comparisons of host and parasite phylogenies. *Annual Review of Ecology and Systematics* 19:235–259.
- Brooks, D. R., A. P. G. Dowling, M. G. P. van Veller, and E. P. Hoberg.** 2004. Ending a decade of deception: a valiant failure, a not-so-valiant failure, and a success story. *Cladistics* 20:32–46.
- Brooks, D. R., and E. P. Hoberg.** 2007. How will climate change affect host–parasite assemblages? *Trends in Parasitology* 23:571–574.
- Brooks, D. R., and E. P. Hoberg.** 2013. The emerging infectious disease crisis and pathogen pollution: a question of ecology and evolution. Pages 215–229 in K. Rohde (ed.). *The Balance of Nature and Human Impact*. Cambridge University Press, Cambridge, U.K.
- Brooks, D. R., E. P. Hoberg, W. A. Boeger, S. L. Gardner, K. E. Galbreath, D. Herczeg, H. H. Mejía-Madrid, S. E. Rácz, and A. T. Dursahinhan.** 2014. Finding them before they find us: informatics, parasites, and environments in accelerating climate change. *Comparative Parasitology* 81:155–164.
- Brooks, D. R., and D. A. McLennan.** 1991. *Phylogeny, Ecology and Behavior: A Research Program in Comparative Biology*. University of Chicago Press, Chicago, Illinois. 441 pp.
- Brooks, D. R., and D. A. McLennan.** 1993. *Parascript: Parasites and the Language of Evolution*. Smithsonian Institution Press, Washington, DC. 429 pp.
- Brooks, D. R., and D. A. McLennan.** 2002. *The Nature of Diversity: An Evolutionary Voyage of Discovery*. University of Chicago Press, Chicago, Illinois. 668 pp.
- Demastes, J. W., T. A. Spradling, and M. S. Hafner.** 2003. The effects of spatial and temporal scale on analysis of cophylogeny. Pages 221–239 in R. D. M. Page (ed.). *Tangled Trees: Phylogeny, Cospeciation, and Coevolution*. University of Chicago Press, Chicago, Illinois.
- Demastes, J. W., T. A. Spradling, M. S. Hafner, G. R. Spies, D. J. Hafner, and J. E. Light.** 2012. Cophylogeny on a fine scale: *Geomydoecus* chewing lice and their pocket gopher hosts, *Pappogeomys bulleri*. *Journal of Parasitology* 98:262–270.
- Dowling, A. P. G., M. G. P. van Veller, E. P. Hoberg, and D. R. Brooks.** 2003. A priori and a posteriori methods in comparative evolutionary studies of host–parasite associations. *Cladistics* 19:240–253.
- Erwin, T. L.** 1985. The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. Pages 437–472 in G. E. Ball (ed.). *Taxonomy, Phylogeny, and Biogeography of Beetles and Ants*. W. Junk, Dordrecht, The Netherlands.
- Galbreath, K. E., D. J. Hafner, and K. R. Zamudio.** 2009. When cold is better: climate-driven elevation shifts yield complex patterns of diversification and demography in an alpine specialist (American pika, *Ochotona princeps*). *Evolution* 63:2848–2863.
- Hafner, M. S., J. W. Demastes, T. A. Spradling, and D. L. Reed.** 2003. Cophylogeny between pocket gophers and chewing lice. Pages 195–220 in R. D. M. Page (ed.). *Tangled Trees: Phylogeny, Cospeciation, and Coevolution*. University of Chicago Press, Chicago, Illinois.
- Hafner, M. S., and S. A. Nadler.** 1988. Phylogenetic trees support the coevolution of parasites and their hosts. *Nature* 332:258–259.
- Hafner, M. S., and S. A. Nadler.** 1990. Cospeciation in host–parasite assemblages: comparative analysis of rates of evolution and timing of cospeciation events. *Systematic Zoology* 39:192–204.
- Hafner, M. S., P. D. Sudman, F. X. Villablanca, T. A. Spradling, J. W. Demastes, and S. A. Nadler.** 1994. Disparate rates of molecular evolution in cospeciating hosts and parasites. *Science* 265:1087–1090.
- Halas, D., D. Zamparo, and D. R. Brooks.** 2005. A historical biogeographical protocol for studying diversification by taxon pulses. *Journal of Biogeography* 32: 249–260.
- Hall, E. R.** 1981. *The Mammals of North America*. Wiley and Sons, New York, New York. 1,181 pp.
- Hoberg, E. P.** 1997. Phylogeny and historical reconstruction: host–parasite systems as keystones in biogeography and ecology. Pages 243–261 in M. Reaka-Kudla, D. E. Wilson, and E. O. Wilson (eds.). *Biodiversity II:*

Understanding and Protecting Our Biological Resources. Joseph Henry Press, Washington, DC.

- Hoberg, E. P.** 2005. Coevolution in marine systems. Pages 327–339 in K. Rohde (ed.). *Marine Parasitology*, (Chapter 8, Coevolution and Speciation). CSIRO, Sydney, Australia.
- Hoberg, E. P., and D. R. Brooks.** 2008. A macroevolutionary mosaic: episodic host-switching, geographic colonization, and diversification in complex host–parasite systems. *Journal of Biogeography* 35:1533–1550.
- Hoberg, E. P., and D. R. Brooks.** 2010. Beyond vicariance: integrating taxon pulses, ecological fitting and oscillation in historical biogeography and evolution. Pages 7–20 in S. Morand and B. Krasnov (eds.). *The Geography of Host–Parasite Interactions*. Oxford University Press, Oxford, U.K.
- Hoberg, E. P., and D. R. Brooks.** 2013. Episodic processes, invasion, and faunal mosaics in evolutionary and ecological time. Pages 199–213 in K. Rohde (ed.). *The Balance of Nature and Human Impact*. Cambridge University Press, Cambridge, U.K.
- Hoberg, E. P., and D. R. Brooks.** 2015. Evolution in action: climate change, biodiversity dynamics and emerging infectious disease. *Philosophical Transactions of the Royal Society B* 370:20130553. <http://dx.doi.org/10.1098/rstb.2013.0553>
- Hoberg, E. P., S. J. Agosta, W. A. Boeger, and D. R. Brooks.** 2015. An integrated parasitology: revealing the elephant through tradition and invention. *Trends in Parasitology*. Elsevier Ltd. <http://dx.doi.org/10.1016/j.pt.2014.11.005>
- Hoberg, E. P., K. E. Galbreath, J. A. Cook, S. J. Kutz, and L. Polley.** 2012. Northern Host–Parasite Assemblages: History and Biogeography on the Borderlands of Episodic Climate and Environmental Transition. D. Rollinson and S. I. Hays (eds.). *Advances in Parasitology* 79:1–97.
- Hoberg, E. P., and G. J. Klassen.** 2002. Revealing the faunal tapestry: coevolution and historical biogeography of hosts and parasites in marine systems. *Parasitology* 124(Supplement):S3–S22.
- Hull, D. L.** 1988. *Science as a Process*. University of Chicago Press, Chicago, Illinois. 586 pp.
- Janz, N.** 2011. Ehrlich and Raven revisited: mechanisms underlying codiversification of plants and enemies. *Annual Review of Ecology, Evolution, and Systematics* 42:71–89.
- Janz, N., and S. Nylin.** 2008. The oscillation hypothesis of host plant-range and speciation. Pages 203–215 in K. J. Tilmon (ed.). *Specialization, Speciation, and Radiation: The Evolutionary Biology of Herbivorous Insects*. University of California Press, Berkeley, California.
- Janzen, D. H.** 1985. On ecological fitting. *Oikos* 45:308–310.
- Kellogg, V.** 1913. Distribution and species-forming of ectoparasites. *American Naturalist* 47:129–158.
- Klassen, G. J.** 1992. Coevolution: a history of the macroevolutionary approach to studying host–parasite associations. *Journal of Parasitology* 78:573–587.
- Kurtén, B., and E. Anderson.** 1980. *Pleistocene Mammals of North America*. Columbia University Press, New York. 442 pp.
- Nylin, S., J. Slove, and N. Janz.** 2014. Host plant utilization, host range oscillations and diversification in nymphalid butterflies: a phylogenetic investigation. *Evolution* 68:105–124.
- Paterson, A. M., and J. Banks.** 2001. Analytical approaches to measuring cospeciation of host and parasites: through the glass darkly. *International Journal for Parasitology* 31:1012–1022.
- Page, R. D. M.** (ed.). 2003. *Tangled Trees: Phylogeny, Cospeciation, and Coevolution*. University of Chicago Press, Chicago, Illinois. 350 pp.
- Patton, J. L.** 2005. Family Geomyidae. Pages 859–870 in D. E. Wilson and D. M. Reeder (eds.). *Mammal Species of the World, A Taxonomic and Geographic Reference*, 3rd ed. Johns Hopkins University Press, Baltimore.
- Russell, R. J.** 1968. Evolution and classification of the pocket gophers of the subfamily Geomyinae. University of Kansas Publications, Museum of Natural History 16:475–579.
- Shafer, A. B. A., C. I. Cullingham, S. D. Côté, and D. W. Coltman.** 2010. Of glaciers and refugia: a decade of study sheds new light on the phylogeography of northwestern North America. *Molecular Ecology* 19:4589–4621.
- Spradling, T. A., S. V. Brant, M. S. Hafner, and C. J. Dickerson.** 2004. DNA data support a rapid radiation of pocket gopher genera (Rodentia: Geomyidae). *Journal of Mammalian Evolution* 11:105–125.
- Taylor, J., and A. Purvis.** 2003. Have mammals and their chewing lice diversified in parallel? Pages 240–261 in R. D. M. Page (ed.). *Tangled Trees: Phylogeny, Cospeciation, and Coevolution*. University of Chicago Press, Chicago, Illinois.
- Thompson, J. N.** 2005. *The Geographic Mosaic of Coevolution*. University of Chicago Press, Chicago, Illinois. 443 pp.
- Wojcicki, M., and D. R. Brooks.** 2004. Escaping the matrix: a simple and powerful algorithm for comparative phylogenetic studies in coevolution. *Cladistics* 20:341–361.