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An integrated parasitology: revealing the elephant through tradition and invention

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The field of parasitology contributes to the elucidation of patterns and processes in evolution, ecology, and biogeography that are of fundamental importance across the biosphere, leading to a thorough understanding of biodiversity and varied responses to global change. Foundations from taxonomic and systematic information drive biodiversity discovery and foster considerable infrastructure and integration of research programs. Morphological, physiological, behavioral, life-history, and molecular data can be synthesized to discover and describe global parasite diversity, in a timely manner. In fully incorporating parasitology in policies for adaptation to global change, parasites and their hosts should be archived and studied within a newly emergent conceptual universe (the ‘Stockholm Paradigm’), embracing the inherent complexity of host–parasite systems and improved explanatory power to understand biodiversity past, present, and future.

Describing the elephant

How we adapt to accelerating disruption of the biosphere, including variation in the distribution, abundance, and emergence of pathogens and diseases (most often old diseases in new hosts), depends critically on our ability to identify and anticipate responses to perturbation of global ecosystems. Effective strategies require a thorough grounding in ecology and evolution [1]. Taxonomy provides the names that make it possible for informed discourse about the biosphere irrespective of concerns in conservation, disease ecology, agriculture and food production, and security [2]. A key observation of many biodiversity initiatives has been ‘no name = no information, wrong name = wrong information’ [3]. Systematics and taxonomy link evolution, ecology, and biogeography in a rich and

integrated tapestry describing global diversity. The dynamics of biodiversity cannot be explained in a comprehensive manner without a systematic foundation. Coping with the challenges of a changing biosphere is not only about systematics, but that systematics is also essential to the explanatory adequacy of the evolutionary and ecological framework that we use to interpret patterns and processes affecting biodiversity [4–7].

We have an opportunity to develop a relevant and integrated parasitology, from which success emerges through broad disciplinary support of systematic biologists and the collections on which they are dependent [7,8], and which are critical for research groups investigating climate change, biodiversity dynamics, and emerging disease [9–12]. However, few programs extend biodiversity information beyond the basics of taxonomic identification related to monitoring and surveillance. Although there are many rationales for wildlife parasitology, here we suggest a more general and integrated framework, bridging taxonomy, systematics, and historical ecology, contributing to powerful explanations and predictions about change in the biosphere [13–15]. A generation ago, Brooks and McLennan [16] applied that framework specifically to parasitology, but only a few research groups have explored these approaches. Research efforts are isolated in a manner consistent with the analogy of ‘the blind men and the elephant’. We remain balkanized across disciplines within parasitology, failing to ‘connect the dots’ across diverse expertise and divergent interests and, as a consequence, the explanatory tapestry is woven too slowly [17]. Parasitology progresses into increasingly narrow avenues, while aging scientific lineages are only inconsistently transferring traditional knowledge and skills. Furthermore in this maelstrom of reductionism, we are increasingly losing our basic capacities to pursue complex taxonomic questions because practitioners in this arena appear to be diminishing over time.

We can no longer afford this state of affairs. Parasitology can, and must, contribute appropriately as a general model system elucidating patterns and processes in evolution, ecology, and biogeography of fundamental importance across the biosphere. In addition, incorporation of parasitology in the

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development of policies for adapting to climate change, biodiversity alterations, and emerging disease, must bring together important capacities in a meaningful way. How we choose to address wildlife parasitology reflects larger options for the future and relevance of the discipline.

Systematics and the scope of the challenge

Brooks and Hoberg [18] detailed the compelling need to expand parasite systematics capacity, an exigency that remains to be realized. Systematics is the cornerstone for understanding past, present, and future patterns and processes across global biological communities. It provides the foundation for biodiversity knowledge that is needed to tackle a range of increasingly urgent and applied environmental challenges. The development and use of biodiversity knowledge by parasitologists, which to a great extent has encompassed free-living taxa [e.g., *Encyclopedia of Life* (www.eol.org) and *Global Biodiversity Information Facility* – <http://www.gbif.org>], have yet to become a global priority, despite decades of discussion at national and international levels. These resources could facilitate broad dissemination of critical parasite biodiversity information through use of common reference points and resources. As a result of research by the past generation, we recognize, document, and understand better the consequences of interacting crises for biodiversity perturbation and extinction, climate warming, and emerging infectious disease [3,7]. However, the scope of the problems facing humanity outstrips the knowledge gained by largely independent and competitive, rather than integrative and cooperative, efforts.

The taxonomic impediment [18,19] remains the single greatest obstacle for parasitology to contribute meaningfully to efforts dealing with climate change, biodiversity alteration, and emerging disease. Contrary arguments, and the idea that sufficient taxonomic infrastructure exists, are based on skewed species estimates from the Catalogue of Life that do not include macro- and microparasites in any meaningful way [20,21]. These estimates may disregard as much as 50% of the species on this planet [17,22]. A more accurate accounting of biodiversity would emphasize the significance of parasites as drivers and mediators of interactions that shape ecosystems, food webs, host demographics, and behavior [23–25], affecting ecosystem assembly across the expanse of Earth history [4,26,27].

We estimate that no more than 10% of global pathogens have been documented [3]. As well, we have elucidated critical elements of evolution and ecology for a minority of those species that have been named. For example, approximately 75% of all named parasitic platyhelminthes are known only from their original descriptions, meaning one host, one place, one time [22]. Thus, in most situations, we cannot anticipate capacities for host switching, the primary source of disease emergence [6]. Human–wildlife interfaces expand through occupation of new habitats, the translocation and/or introduction of species for conservation, alteration and fragmentation of ecosystems under natural and anthropogenic forcing, and the cascading influence of climate change. These factors combine to create a geographic arena of pathogen emergence [3,11,28] that has been likened to an evolutionary minefield of potential emerging diseases [29].

We must reverse the diminishing emphasis on proficiency in comparative biology that underlies all applications of systematics and/or phylogenetic data. Morphological, physiological, behavioral, and life-history data can be integrated with molecular data to characterize species, and to discover and describe global parasite diversity in a timely manner. Those efforts provide essential data for understanding ecological and evolutionary frameworks and the temporal and spatial partitions that influence diversity [2,7,30]. Molecular toolkits, initially informed by authoritative identification of specimens, provide a relatively rapid means for assessment of parasite–host assemblages emphasizing, for example, the potential for intensive landscape sampling across large geographic scales necessary to identify range shifts in real time [31–33]. Relatively few individuals are proficient in more than a few of these areas, underscoring the need for cooperative networks of research groups with diverse interests and capacities [30,34]. We need collaborations to build and apply fundamental skills, develop capacity for producing synoptic morphological and molecular data, as well as analytical models applied in areas such as phylogeography and epidemiology of disease [35–39].

Cryptic diversity and its implications

Sorting biodiversity into morphospecies remains an essential bridge to higher systematics, measures of species richness, and expanding views of diversity. Morphology provides substantial insights into phylogeny, and resulting phylogenetic trees and historical hypotheses often share considerable congruence with molecular-based assessments [40,41]. By contrast, morphology can also confound [42], highlighting the importance of detecting and delimiting cryptic species for understanding responses to perturbation related to variation in physiological tolerances and resilience that may determine geographic distributions, potential host associations, and patterns of disease [2,43]. Molecular characterization of biodiversity does not constitute formal description, a process requiring considerable expertise and comparative resources usually linked to archival specimen collections. Although providing an avenue to address landscape-scale phenomena that are critical to understanding temporal and spatial distributions and transmission of pathogens [7], barcoding is not a panacea. Knowing the players in the biosphere is an initial step in exploring the mechanisms determining the panoply of biodiversity in this world [30,42] and is fundamental to many applications, including drug discovery and biological control [44].

Cryptic species are ubiquitous among parasitic groups. Their discovery has been bolstered by large-scale surveys and inventories specifically designed to explore limits of diversity [45–47]. Notable examples among helminth parasites include: anoplocephalid, catenotaeniid, and hymenolepidid cestodes of rodents and lagomorphs [48–54]; *Taenia* spp. cestodes in carnivorans [55,56]; hookworms and anisakine nematodes in marine mammals [57–59]; lungworms (Protostrongylidae) in ungulates [31]; and *Trichinella* spp. nematodes in mammals [60,61] (for comprehensive discussion, see [62]).

Discovery of cryptic diversity stems from observations of: (i) considerable morphological variation in a nominal species that (in the case of parasites) is not immediately

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