Mem Inst Oswaldo Cruz, Rio de Janeiro, Vol. *95*, Suppl. I: 99-107, 2000

Parasite Systematics in the 21st Century: Opportunities and Obstacles

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Thanks to the phylogenetic systematics revolution, systematic parasitology is poised to make significant contributions in tropical medicine and public health, biodiversity science, and evolutionary biology. At the same time, the taxonomic impediment is acute within parasitology. Both systematists and non-systematists must be interested in working towards common goals and establishing collaborative efforts in order to re-vitalize and re-populate systematic parasitology.

Key words: parasites - systematics - biodiversity

As we move into the 21st century, interest in parasites has never been greater. Parasites are becoming recognized as significant players in the evolutionary game, and are being seen as excellent model systems for general evolutionary studies. On the negative side, the great hopes of half a century ago for eradicating parasitic disease have been dashed, parasitic disease of humans, livestock, and wild biodiversity threatened with extinction represent a major concern for most countries, and for the vast majority of human beings on this planet.

As we learn each day more about the importance of the documented portions of the biosphere, we realize that we have not documented, and thus do not understand, more than a fraction of that diversity. We often have no idea what we might be losing, and incomplete information on how to manage what remains, including known and potential parasitic disease agents. Biologists advocate extreme caution in human development projects linked to loss of habitat and diversity because our ignorance may lead us to make mistakes both in the short and long term. At the same time, biologists understand that caution cannot become a synonym for stasis or inaction. Once a species becomes extinct, we can never recover it, and its potential to play a role in the survival of our species is lost forever. Each species that we lose may represent an irreversible loss of socio-economic potential, and may restrict our survival options for the future. Each species lost also represents an irreversible loss of the evolutionary potential that has been the source of biotic recovery from ecological perturbations and environmental disasters on a global scale in the past (Jablonski 1991). Whether we are faced with an acute crisis or a chronic condition, the proportions of the problem are greater than we imagined 50 years ago. All parasitologists have a role to play as we re-define our relationship with the organisms whose biology fascinates us so much. This is especially true for systematic parasitology.

THE OPPORTUNITY: VALUING SYSTEMATICS

Systematists provide two kinds of information. The first of these is the names and characteristics of our (slowly) growing list of all known species. Species are the fundamental units of biodiversity, genealogical information systems that store and transmit the information leading to the emergence of ecosystems with their complex interactions. Without this information, biological science could not proceed. All biological research begins with one or more names of species, and it is systematists and their reseaarch who make certain that we all know what we are talking about when we use names like *Plasmodium falciparum* or *Schistosoma mansoni.* Parasitology has a rich tradition in both basic and applied research, and the centrality of systematic information for both has long been recognized. This is the reason that the Instituto Oswaldo Cruz has been a major source of basic systematic research as well as one of the world's leading centers for research in tropical medicine.

Systematists provide far more than the indispensible lists of names and keys for identification and diagnosis. They also provide the framework for all comparative studies in biology, both basic and applied. The only illustration ever to appear in any edition of *Origin of Species* is a phylogenetic tree. Darwin did not consider this to be simply a pictorial metaphor for evolution, but envisioned that such depictions could be crucial elements of biological explanation. The predictable parts of biological systems are the stable biological

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Received 7 August 2000
Accepted 4 September 2000

elements, both form and function, autecological and synecological, that have persisted through evolutionary time, even though they may be seen as operating on ecological time scales (e.g. Brooks 1985, Brooks & McLennan 1991, 1993, Brooks et al. 1995). This predictive power of taxonomy is embodied in the phylogenetic classifications of taxonomists (Simpson & Cracraft 1995).

The Convention on Biological Diversity (CBD) (see Glowka et al. 1994) designated species as the fundamental units of biodiversity, and ecosystems management and sustainable development as the organizing principles for managing global biodiversity. Biologists and managers quickly realized that the current inventory of the world's species was far too limited to implement the mandate properly and that a critical shortage of trained taxonomists contributed directly to the problem (e.g., Gallagher 1989). The United Nations Environment Program (UNEP) in biodiversity called DIVERSITAS coined the term "the taxonomic impediment" to refer to this critical lack of global taxonomic expertise that prevents initiation and completion of biodiversity research programs (see SA2000 1994, Hoagland 1996, Blackmore 1996, PCAST 1998). In North America, this concern led to Systematics Agenda 2000 (SA2000), an intensive professional inventory of the value of taxonomic expertise to this planet, and a set of recommendations for revitalizing systematic biology and justifying the allocation of resources necessary to carry out such a revitalization (SA2000 1994, Brooks et al. 1995, Claridge 1995, Cracraft 1995, Davis 1995, Eshbaugh 1995, Jones 1995, Lauder et al. 1995, McNeely 1995, Miller & Rossman 1995, Prance 1995, Savage 1995, Simpson & Cracraft 1995, Wheeler 1995, Balick 1996, Blackmore 1996, Monson 1996, Oliver 1996, Richardson 1996, Rossman & Miller 1996, Vane-Wright 1996, Vecchione & Collette 1996). The 1998 and 2000 Conference of the Parties (COP) to the Convention on Biological Diversity endorsed a Global Taxonomy Initiative (GTI) to improve taxonomic knowledge and capacity to further country needs and activities for the conservation, sustainable use, and equitable sharing of benefits and knowledge of biodiversity (GTI 1999, Cresswell 2000). The GTI has three structural components: (1) systematic inventory, (2) predictive classifications, and (3) systematic knowledge bases.

GTI COMPONENT 1: SYSTEMATIC INVENTORY - DISCOVERING AND NAMING THE WORLD'S SPECIES

The CBD mandates that all signatory countires will undertake a national assessment of its biodiversity resources. Such national inventories are meant to be biodiversity development and conservation projects, a means for restoring global taxonomic capacity, and opportunities to study the health, reproductive, and nutritional requirements, as well as the ecology and evolution of a large number of wild species. Inventories can be carried out in a relatively small area, the site becoming a gigantic "mine canary" where the effects of global environmental change can be monitored across significant numbers of species and large pieces of integrated ecosystems, or for members of targeted taxa across many habitats. Parasites are useful for both types of inventories because of their significance as indicators of stable trophic interactions in ecosystems (including their use as biological tags) and as disease agents in humans, livestock, and wildlife.

Regardless of the focus of any inventory, the taxa examined should (1) be intrinsically important to humans, such as insect groups known to include important pollinators, biocontrol agents, or disease vectors, (2) be intrinsically important to ecosystems that humans want to preserve, (3) provide efficient means of learning something of importance, (4) be geographically widespread, and (5) provide opportunities for international networking of professionals, for collaborative research, and for training. It is easy to justify the inclusion of parasites in any inventory project under all these guidelines.

Taxa should be intrinsically important to humans - Parasites are agents of disease in humans, livestock, and wildlife, with attendant socio-economic significance. Parasites are significant components for assessing the risk of loss of bio-containment by introduced species, whether due to parasites of introduced species moving into the agriculutral landscape or wildlands and switching to native hosts, or parasites of native species moving out of the agricultural landscape or wildlands and infecting introduced, economically important host species. A special case involves the possibility of local people and tourists sharing parasites and parasitic diseases between themselves and between humans and non-human hosts. Some parasite species may provide revenue, as model systems for pharmaceutical companies or as bio-control agents. Additionally, we must understand parasite biodiversity within the context of global change (e.g., Dobson & Carper 1992, Hoberg 1997a,b, Brooks & Hoberg, 2000, Brooks et al. 2000).

Taxa should be intrinsically important to ecosystems that humans want to preserve - Parasites are significant regulators of host populations (e.g., Scott 1988, Gulland 1995), and are potent agents maintaining ecosystems integrity and stability (Dobson & Hudson 1986, Minchella & Scott 1991, Hudson et al. 1998). Complex feedback loops involving parasites, herbivores, and habitat structure in ruminant grazing systems further indicate the significance of parasites as determinants of community structure (e.g., Grenfell 1992). Parasites can also be important mediators of host behavior (Holmes & Bethel 1972). Introduced parasites may have unpredictable, and deleterious impacts on native species of hosts (Dobson & May 1986a,b, Woodford & Rossiter 1994, Vitousek et al. 1996). It is therefore important to be able quickly to distinguish native from introduced parasite species (Hoberg 1997a,b, Brooks et al. 2000).

Taxa should provide efficient means of learning something of importance - Parasites, especially those having complex life cycles involving more than one obligate host, are indicators of stable trophic structure in ecosystems (e.g., Marcogliese & Cone 1997). This is because all the biotic components necessary for completion of the life cycle must co-occur regularly in order to maintain any given parasite species. Knowing the complement of parasite species inhabiting any given host thus provides a means of rapid assessment of the breadth and form of trophic interactions of host species.

Taxa should be geographically widespread - Many parasite taxa are widespread geographically. At the same time, they are highly localized with respect to infecting particular hosts, which themselves may be the focus of particular inventory activities.

Taxa should provide opportunity for international networking of professionals, for collaborative research and for training - Parasite systematics is in serious trouble worldwide. Laboratory closures in the United Kingdom and elsewhere have eroded the infrastructure for taxonomy and systematics at a critical time. New survey opportunities, and recognition of the importance of parasites, may stimulate international collaboration and revitalization.

GTI component 2: predictive classifications – What is in a name?

A crucial element in preserving biodiversity within the context of the CBD is managing information about the 1.7 million species currently known and the millions yet to be discovered and described. The framework for such information systems must include the capability of making predictions about the characteristics of species based on what we know about the biology of close relatives. To do so requires knowledge of phylogenetic relationships, phylogenetic classification systems are the most effective framework for predictive information systems about organisms and their place in the biosphere (e.g., Wheeler 1990, 1993, Brooks & McLennan 1991, 1993, Faith 1991, 1992, 1996, Brooks et al. 1992, 2000, SA2000 1994, Stiassny 1993, Forey et al. 1994, Humphries et al. 1995, Simpson & Cracraft 1995). Although systematists have made major strides in understanding the interrelationships of life, corroborated phylogenetic hypotheses are still lacking for many groups. DIVERSITAS and SA2000 propose to coordinate international research to achieve a phylogenetic framework for all of life resolved to the family level by the year 2010. Phylogenetic analysis for the major groups of parasitic platyhelminths began appearing in 1985, results to 1992 were summarized in (Brooks & McLennan 1993), and many additional studies have been produced since then. These studies comprise a robust phylogenetic tree for the parasitic platyhelminths to family level more than a decade ahead of the SA2K-I agenda.

The past decade has seen the integration of phylogenetic information in all areas of evolutionary research, and a growing number of areas of applied research, providing common ground to serve the professional agendas of evolutionary biologists and ecologists as well as biodiversity and conservation managers. Why is this important? Set in a context of ongoing inventory, phylogenies can help us “buy time”. Using phylogenetic frameworks to make predictions can cut research and development, or planning and prioritization, time and costs (Brooks et al. 1992, Brooks 1998, Brooks & Hoberg 2000). Phylogenetic study of coevolutionary relationships can help us assess the suitability of proposed biological control agents, predict the epidemiology of emergent diseases, and recognize introduced species.

Understanding the evolutionary basis of disease resistance will come from comparison of closely related host species, one resistent and the other suspectible to a given pathogen, just as understanding the evolutionary basis for causing disease will come from comparison of closely related parasites, one pathogenic and the other not.

GTI component 3: managing systematic knowledge bases – Making the information available

Electronic data handling and interlinked knowledge systems are becoming the principal medium for all activities associated with applying systematic information in biodiversity studies and policies. The OECD Megascience Forum declared this critical need a global priority in mid-1998. Parasite systematists can contribute significantly in this area, establishing (1) *Phylogenetic Home Pages*, providing inter-linked phylogenetic trees, modified periodically as needed, for all groups of parasites, (2) *Species Home Pages*, providing for each species: (a) what is it (and how to distinguish it from others), (b) where is it, and (c) what is its natural history, and (3) *On-line Identification Guides and Keys*, designed to aid a large user community.

THE OBSTACLE: OVERCOMING THE TAXONOMIC IMPEDIMENT

I believe there are three misconceptions about modern systematics that have contributed to the taxonomic impediment within our discipline.

Basic and applied research have little in common

Many still believe that systematics is something done in the esoteric world of academia and evolutionary biology. In the real world of applied biology, such as fisheries and agriculture, as well as tropical medicine and public health, it is only necessary to have a name for the species you are studying. This misconception is not restricted to applied studies, many basic researchers in areas such as ecology and physiology have similar beliefs. And yet, all biodiversity is evolved biodiversity, so it makes sense that the most general referfence system one could have for basic and applied comparative studies is a phylogenetic one. This is the reason that comparative studies using phylogenetic information have exploded during the past decade. A growing number of applied researchers in parasitology have recognized this, and are using phylogenetic information in their studies. Unfortunately, the taxonomic impediment means that there are as yet few phylogenies for groups that include important parasites of humans and livestock (but see Barta 1989, Hoberg & Lichtenfels 1994, Hoberg et al. 2000, Nadler & Hudspeth 2000).

The solution to this problem has been for non-systematists to try to produce their own phylogenies, typically using sequence information from a gene or gene fragment being studied in the lab. Those data are often analyzed using whatever programs for tree-building are in the lab, or are known to members of the lab (many are very user-friendly). The vast majority of such trees in the literature today are not very robust. The missing part of the study is input by a professional systematist. A fully-trained modern systematist is someone who understands that when a program generates multiple equally parsimonious trees, there is a problem with the data, not the method of analysis implemented by the program. A fully-trained modern systematist can assess sequence data for sampling bias, missing data, site saturation, and alignment problems, and can generate combined analyses using information from many different sources. Finally, a fully-trained modern systematist can provide the most robust possible interpretation of the final results, helping members of a lab avoid the embarassment of claiming support for one particular theory when their own published data actually support the opposite (e.g., Brooks & McLennan 1992). In the long run, I think it will be more time- and cost-effective for modern molecular laboratories in tropical medicine and public health to hire one or more fully-trained modern systematists than to continue producing poor phylogenetic trees that will not lead to general consensus and will need to be re-done multiple times.

Parasite evolution differs from non-parasite evolution

Parasitology became an active part of evolutionary biology through an archaic theory of evolution called orthogenesis (Brooks & McLennan 1993), which flourished between 1890-1940 (Bowler 1983). Orthogenesis eventually failed because its proponents never developed a coherent theoretical framework and, more importantly, never proposed a plausible mechanism. Nevertheless, one of the central tenets of orthogenesis, that all biological systems are internally programmed to evolve towards overspecialization, secondary simplification, and eventual extinction, remains a powerful influence within parasitology because parasites were used as exemplars of orthogenetic trends. Two orthogenetic concepts about parasite evolution have become common modern assumptions about parasite evolution.

The first assumption is that parasites exhibit enormous levels of secondary simplification and character loss because of their life style. Given this trend, it is argued, if some parasite species lack a structure that is also lacking in the outgroups, the absence in the parasites must represent a convergent loss and should thus be coded appropriately. This type of a priori character polarization directly contradicts the polarization technique used by phylogenetic systematists called the Relative Apomorphy Rule or Outgroup Comparisons (see Wiley et al. 1991, Brooks & McLennan 1991). This rule states that any trait found in at least one member of the ingroup that also occurs in species outside the ingroup is plesiomorphic, or ancestral, relative to modifications of the trait restricted only to members of the ingroup. What does the empirical evidence tell us about these two different approaches (orthogenetic versus phylogenetic) to polarizing character "absence"? Although it is often assumed in many textbooks on evolution and parasitology that we "know" parasites exhibit massive secondary simplification, this assumption is not widely documented. In fact, the only empirical study ever performed to test this assumption (Brooks &

McLennan 1993) concluded that less than 11% of almost 2000 characters for various Neodermatan (parasitic platyhelminths) groups showed secondary loss. Subsquent studies (e.g., Pérez Ponce de León & Brooks 1995a,b, Pérez Ponce de León et al. 1997, Platt & Brooks 1997, León-Règagnon et al. 1996, 1998, 1999, Beveridge et al. 1999, Bray et al. 1999, Hoberg et al. 1999a,b, Ivanov & Hoberg 1999, Rego et al. 1999, Zamparo et al. 1999) have corroborated these findings.

The second orthogenetic-based assumption about parasite biology is that species with common specialized lifestyles evolve the same set of characters independently. Thus, because we are dealing with parasites therefore we should expect high levels of correlated homoplasy. Some have even rejected highly robust phylogenetic analyses by asserting that it is not surprising to find a single most parsimonious result with a very low level of convergent evolution that is, nonetheless, an incorrect depiction of phylogenetic relationships. To correct for this "problem", characters "known" to be adaptations to parasitism should be eliminated *a priori*. For example, Rieger and Tyler (1985) suggested that similar structures in taxa sharing similar environments should be coded *a priori* as independently evolved. Such suggestions ignore the basic Darwinian notions that homologies can be adaptations and that adaptation need not produce homoplasy. As well, the past decade has witnessed the accumulation of a substantial amount of evidence indicating that Darwin was correct in asserting that most similarities in structure, function, and preferred environment are due to common ancestry (e.g., Wanntorp et al. 1990, Harvey & Pagel 1991, Brooks & McLennan 1991). Finally, Ronquist's (1994) study on the evolution of inquilinism in cynipid hymenopterans showed that removal of characters associated with parasitic lifestyle did not alter the phylogenetic assessment that inquilinism had arisen only a single time in the group. There is thus no reason to exclude any "adaptive" character from any analysis (Brooks & McLennan 1994).

Brooks and McLennan (1993) proposed that there is no such thing as "parasite evolution". There is only "evolution" and those species we call parasites are simply the most fascinating representatives of that general process producing and affecting all of life (see also Poulin 1997). In addition, if parasites are like all other species in general evolutionary terms, they fit a set of criteria indicating that they should be included in all biodiversity inventories. Parasites are critically important as: (1) ecological/trophic indicators, (2) historical indicators of phylogeny, ecology and biogeography (3) contemporary and historical probes for biodiversity research, and (4) model system to explore theoretical issues and generalities in evolutionary biology, ecosystem and community structure, biogeography, adaptation and radiation, modes of speciation, and life history within a comparative framework (Brooks & Hoberg 2000 and references therein). Substantial contributions by parasitological research to biodiversity inventories extend from the accretion of novel information from standard surveys established over the past 200 years, to sophisticated research programs for systematics, ecology, biogeography, and evolutionary biology, based on organismal and molecular approaches.

Molecular data are better than morphological data for phylogenetic analysis

Researchers using phylogenetic information must be familiar enough with the methodology responsible for the construction of that tree in order to assess its potential strengths and weaknesses. For example: (1) some published diagrams are not the phylogenetic trees that are best supported by the data, (2) some information cannot be interpreted phylogenetically (e.g., genetic distances, immunological distances, DNA-DNA hybridization), and (3) some published trees represent only one of many equally parsimonious representations of the data. There is a simple solution to this problem. All published trees must be accompanied by descriptions of goodness-of-fit statistics, optimization assumptions used, the number of equally parsimonious solutions and, if there is more than one tree, why the tree presented is the preferred one. If they are not based on phylogenetic systematic analysis, the reason should be stated, especially if the answer is "phylogenetic systematic analysis produced too many trees, and this other methods gives me only one, so I prefer it". or "phylogenetic systematic analysis did not support the answer I bleieve in, so I used another method which produced results more similar to my preconceived notions".

The availability of robust and explicit estimates of phylogeny is the primary limiting resource in all comparative studies, basic and applied. This situation is further exacerbated by the fact that systematists and non-systematists have traditionally focused their attention on different groups of organisms. There is room for optimism, information about phylogenetic systematic methods in parasitology is being disseminated more widely (e.g., Pérez-Ponce de León 1997, Pérez Ponce de León et al. 1997) phylogenetic trees are being produced at a more rapid, there is an increased breadth of taxa being investigated, including those of general conceptual interest to evolutionary biologists, and we are finally beginning to build a large enough database to compare the outcomes of analyses based upon morphological and molecular data. These results are encouraging because, when the data are subjected to rigorous phylogenetic analysis, they generally tend to produce congruent trees (e.g, Hoberg et al. in press, Leon-Regagnon et al. 1999, Nadler & Hudspeth 2000), although it make take some time for such agreement to be apparent and accepted (see e.g., Brooks et al. 1985, Brooks 1989a,b, Brooks & McLennan 1993, Zamparo et al. in press, Baverstock et al. 1991, Blair 1993, Rohde et al. 1993, Littlewood et al. 1999).

I believe that two things are responsible for the perception that molecular data are superior to morphological data for phylogenetic analysis. The first is that most morphologically-based parasite systematists are not using any kind of phylogenetic methods in their work. This leads to the view that morphology is used for descriptive purposes and molecular data are used for phylogenetic studies. The second is that fewer and fewer expert morphologists are being trained. Consequently, there are fewer and fewer parasitologists available to take advantage of new approaches to comparative morphological study, including novel types and sources of characters. When I began my phylogenetic studies, no one believed that we would find enough morphological traits to even make an initial tree, much less corroborate it, for any group of parasitic helminths. We enter the 21st century with a robust phylogenetic hypothesis at least to family level for all the Neodermata, based on more than 2,500 morphological characters, and an overall CI of approximately 70%. It is truly an exciting time, because I believe we have just begun to tap this rich resource of information about phylogenetic relationships. At the same time, we are already beginning to accumulate the necessary molecular data, gene by gene, to produce a truly robust framework.

CONCLUSIONS: TURNING OBSTACLES INTO OPPORTUNITIES

The growing number of phylogenetically informed studies in basic and applied parasitology highlight some harsh realities: (1) although their number is growing, well supported phylogenies are still rare, (2) the groups that have attracted phylogeneticists are rarely the groups that have attracted non-systematists and (3) the number of active systematists decreases yearly. The solution to these problems requires a groundswell of support from non-systematists (1) supporting the training and hiring of more phylogeneticists, (2) providing more support for museum collections and museum systematists and (3) becoming better versed about phylogenetic methodology. Systematists, for their part, must (1) provide more and larger data bases, integrating both molecular and morphological data, (2) encourage students to work on groups that are classically of interest to non-systematists, and (3) develop better ways to explain their ideas to a naive, but enthusiastic, audience. In other words, there must be active collaboration based on mutual respect between systematists and non-systematists.

Human beings preserve what they value and ignore what they do not value. Clearly, the value of systematics has been overlooked, especially in parasitology, there is a decreasing number of systematists, and those still left provide little phylogenetic information to enhance the research programs of non-systematists. Saving biodiversity and promoting human socio-economic development is a complex problem, requiring networks of people and of research programs. Networks require common language and discourse, as well as collaborative development of theory and research programs. Fully-trained modern systematists are the masters of a language powerful enough to faciliate such necessary discourse.

Parasite taxonomists need to present a better case to those who do not yet understand how valuable systematic information is for them. The GTI represents a useful framework for accomplishing this general goal. In order to make this goal a reality, parasitologists must overcome serious internal and traditional biases associated with various forms of exclusionary behavior commonly associated with the social systems known as universities and research institutes.

ACKNOWLEDGEMENTS

To Dr José Rodrigues Coura, Director, and Dr Hooman Momen, for the invitation to participate in the Centenary Celebration of the Instituto Oswaldo Cruz. To Deborah McLennan and David Zamparo for discussions during the writing of this article. To the Natural Sciences and Engineering Research Council of Canada for 20 years of support for my research on the evolution of parasites.

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