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Why Ecologists Need Systematists: Importance of Systematics to Ecological Research[1]

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Abstract: Ecologists are concerned with population dynamics of organisms and with the spatial patterns of single or multiple populations. The goal of the ecologist is usually to explain the observed patterns in terms of processes. Field samples of nematodes from different habitats may contain similar but not identical specimens of a nominal taxon, and the systematist can help the ecologist decide whether the specimens are ecophenotypes of a single taxon or represent distinct species. A correct decision may be important or trivial, depending on the parameters and goals of the ecological study. When a precise identification is crucial to the success of the study, new biochemical methodologies of systematists may provide rapid and accurate diagnoses. Systematists can provide additional help in the assignment of taxa to trophic groups. For clarifying host–parasite associations, often a goal in ecological investigations, modern analytical methods of systematists can facilitate the ordering of systematic relationships.

Key words: coevolution, nematode species, taxa, trophic group.

Although ecologists differ as to the scope of their subject, and many approaches are possible, it is evident that since the 1970s evolutionary thinking has been integrated into ecological studies (5,16,23). Early ecology was mainly descriptive, but modern ecologists attempt to understand the origins and mechanisms of the interactions of organisms with each other and with the nonliving world (23). Recent ecology texts emphasize hierarchies of interaction and often emphasize population biology, the effects of natural selection on gene frequencies within populations, and how populations and communities interact with basic ecosystem processes (1,12,23). It is to be assumed that nematode ecologists embrace the same goals of moving from a descriptive phase toward explanations for the observed patterns.

Traditionally, a large gap has existed between ecology and systematics, despite the fact that ecologists working at the ecosystem level, community level, or below are absolutely dependent upon good taxonomic information (29). As ecologists study population changes in different habitats, or postulate reasons for differences in community structure, or concentrate on ecological processes and the taxa involved, it is essential that the basic data on the living organisms be accurate. Are the populations under study really populations of a single species, or are they distinct, sibling species with different life histories and responses to the environment? Are the species that comprise separate communities or ecosystems sufficiently well characterized to make the conclusions valid? In the past ecologists have tended to dismiss systematics as irrelevant (12). This was relatively easy for the ecologist interested in only one or a few species of well-studied plant and animal groups, because some taxonomist could usually be found willing to attach a name to the target organism. Studies of whole below-ground communities became popular in the 1970s and presented special problems to the general ecologist. During that period nematode systematists received many requests to "identify" specimens for ecologists engaged in large ecology projects dealing with soil organisms. In our own case, we do not recall a single instance in which an ecologist was willing to offer us any financial support in return for what would be a prodigious amount of time spent on his ecology project. Indeed, our participation was always considered peripheral

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and to be rewarded only by an occasional footnote. Such problems were recognized at a recent workshop sponsored by the National Science Foundation, where ecologists and systematists discussed priorities for collaborative work on soil organisms (29). In view of a current trend toward increased support for long-term ecological research (21) and of pressure for increased funding to study biodiversity (26,34), new funding opportunities may develop for broadly trained nematode systematists.

Nematode diagnoses should be as accurate as possible for studies of community structure. An example from our own research illustrates the kinds of difficulties one faces. Some years ago we were involved with a graduate student in an extensive study of nematode community structure of forest woodlots (17–19). Among the many taxa recovered from 18 mixed hardwood stands of varying composition, soils, physiography, and past management practices, sampled over a period of 2 years, we found two different forms of a *Mesodorylaimus* that differed only in size. One of them, which we characterized and called "M-1," was longer than 2.5 mm, whereas the other, which we called "M-4," was shorter than 2 mm. The deMan ratios (32) were similar and they were similar morphologically. Both forms occurred in two of our woodland sites, and adult specimens could be easily sorted into the two forms. The two sites where they both occurred tended to be wet; one had poor drainage and the other included a small stream that overflowed at times. Form M-1 occurred without form M-4 at one poorly drained site along a drainage ditch. Form M-4 occurred alone at four sites, which tended to be sites with better drainage (Table 1). It was tempting to consider these two forms ecophenotypes of a single species, with the larger form a response to wetter habitat conditions. This explanation would be acceptable to many nematologists, and probably would be preferred by most, but was it justified? How should we explain the sympatric occurrence of both forms in two of the habitats? Although many systematists in all animal groups feel that quantitative differences of the kind we observed are not sufficient for separating species, others have demonstrated that different means in quantitative data may signal species differences even though measurements overlap.

TABLE 1. Occurrence (indicated by X) of two forms of *Mesodorylaimus* in Indiana forest woodlot sites with soils of different drainage characteristics.

Site designation†	Soil drainage rank‡	M-1 (large)	M-4 (small)
R	2		X
E	3		X
K	4		X
I	5		X
C (stream edge)	2	X	X
D	5	X	X
G (drainage ditch)	5	X	

† Data from Johnson et al. (17).
‡ Based on Indiana Soil Profile Ranking: 1 = excessively drained; 5 = very poorly drained.

We were not able to solve our dilemma, but in the data enumeration we kept the forms separate and treated them as separate entities. Fortunately, their numbers were small, relative to the totals for all 175 species found at the sites, so our decision whether to combine them or keep them separate did not affect the outcome of our ordinations in any important way (17–19). Interestingly, the state of the art with respect to the taxonomy of the *Mesodorylaimus* group at that time was such that we had to call the M-1 form *Laimydorus* 1 in a publication of the work (17) because species longer than 2 mm were categorically assigned to *Laimydorus* and species shorter than 2 mm were assigned to *Mesodorylaimus* (32).

Although our difficulty with the *Mesodorylaimus* forms did not drastically affect the outcome of that particular study, in some cases misidentification can lead to more serious problems. This is also the case in applied ecological research involving plant-parasitic nematodes. For such research the development of new techniques of diagnosis based on the use of biochemical data may be justified (7,10,24). As an

example, we are often told by well-trained field people working in our state that *Heterodera glycines,* or soybean cyst nematode (SCN), develops on several common weeds, including lambsquarter (*Chenopodium album* L.) and smartweed (*Polygonum* spp. L.). Sufficient variability occurs among SCN cysts from any field soil that a casual perusal of cysts from fields containing these weeds may not provide convincing evidence to prove or disprove the allegations. Several years ago, when confronted with such a claim, we collected roots from lambsquarter and smartweed in a particular field, as well as roots from soybean plants, and carefully removed female cyst nematodes from each collection of roots. We then obtained 2-D PAGE (two-dimensional polyacrylamide gel electrophoresis) protein patterns for each sample of female nematodes and discovered that each of the three protein samples produced a different pattern (Fig. 1). The pattern of the nematodes from the soybean roots was typical for *H. glycines,* but the patterns of the nematodes from the two weed species were different. Michigan isolates of cyst nematodes from lambsquarter and smartweed were subsequently studied using classical techniques over a period of approximately 3 years by G. Bird and L. Graney. These workers conclude that the isolate from smartweed is *Cactodera weissi,* whereas the isolate from lambsquarter is a new species of *Cactodera* (pers. comm.). We have compared protein patterns of our Indiana isolates with those from Michigan isolates and find similar protein patterns for all isolates taken from the same host species (Fig. 1). We therefore conclude that our two *Cactodera* species (one each from lambsquarter and smartweed) are the same as those in Michigan.

It can be argued that the answers to this dilemma *could* be found by classical means and that the protein patterns were not necessary. However, we had our answer within a few days, whereas the classical study by Bird and Graney took many months and required considerable taxonomic expertise. The availability of rapid methods of accurate diagnosis might have changed the conclusions of many published applied studies, e.g., Rivera and Crossan (25), and provided assurance about the identity of species in field plot experiments. It is likely that over the next decade many more methods for rapid diagnosis of plant-parasitic nematode species will be developed, including some that utilize DNA probes (24).

In many ecological studies that include nematode communities, nematodes are sorted into trophic groups prior to analysis (29). The activity of sorting into groups has many pitfalls, because little is known about the feeding habits of most nematode species, particularly in the dorylaimid groups that are not known parasites of higher plants. One solution at present is to assign a species to the same trophic group where close genealogical relatives have been placed, based upon actual laboratory observations of feeding activities of the latter. Two problems with this approach are that 1) the ecologist must have some knowledge of the taxonomic groups in order to make the proper analogy and 2) feeding information is available for only a fraction of the species found. Although it is often stated that most dorylaims are large, possess an elongate cylindrical esophagus and large hollow spear, and are predaceous (8), this is an oversimplification that might lead to misassignment to a trophic group. For example, most leptonchid nematodes are relatively small, do not have the "typical" dorylaimid esophagus, and are probably able to feed on fungus hyphae only, owing to their exceedingly slender stylets. The fact that *Tylencholaimellus* and *Tylencholaimus* (often numerous in soil communities) possess a swollen posterior esophagus that may appear bulb-like, and stylet flanges that are knobbed, causes species of these genera often to be characterized as "tylenchs," if a trained nematode systematist is not consulted. Over the years we have attempted to culture representatives of dorylaimid and other groups found in our ecological studies, and in some cases have been successful (Table 2). A number of published reports

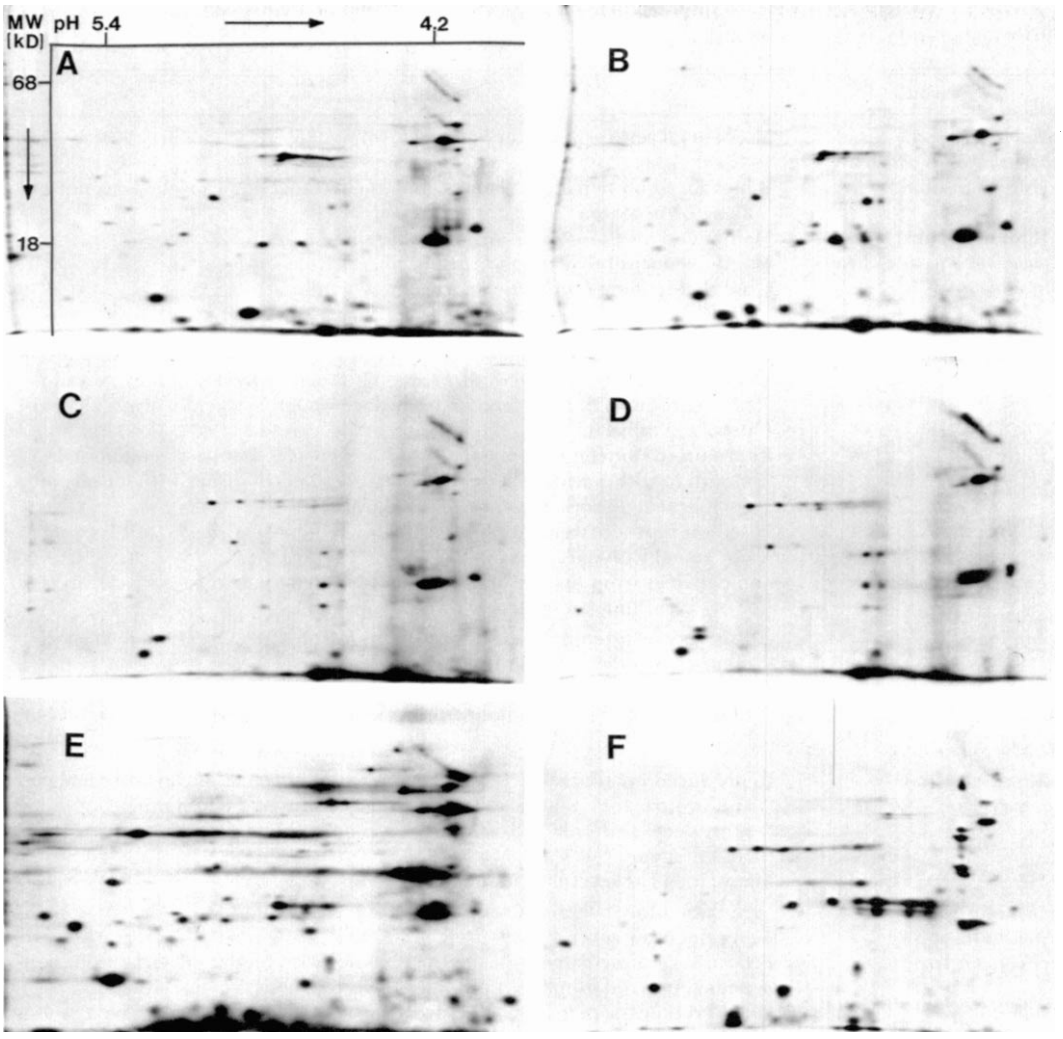

FIG. 1. Two-dimensional polyacrylamide gel electrophoresis patterns from cyst nematodes that occur together in midwest soybean fields. A, B) *Cactodera* isolates from lambsquarter. A) Indiana. B) Michigan. C, D) *Cactodera* isolates from smartweed. C) Indiana. D) Michigan. E) Typical pattern for soybean cyst nematode. F) Pattern for clover cyst nematode isolate from Indiana.

of observations of feeding in culture exist (e.g., 8,9,13–15,22,27,28,33), and additional reports of this type would help place assignments of nematodes to trophic groups on a firmer foundation, although it is always possible that a given species behaves differently in nature.

Ecologists have been interested in the topic of coevolution for some years. The word coevolution was actually used first by ecologists (6) to refer to the joint evolution of two or more taxa that have close ecological relationships but do not exchange genes, and in which reciprocal selective pressures operate to make the evolution of either taxon partially dependent on the other (23). Brooks (2), a systematist and parasitologist, redefined coevolution as a combination of two processes: coaccommodation between host and parasite with no implication of host or parasite speciation; and cospeciation indicating concomitant host and parasite speciation. Brooks showed that the two phenomena can be sorted out by means of a phylogenetic (i.e., cladistic) analysis of both host and parasite. If cospeciation has occurred, the two cladograms will be congruent, or at least par-

TABLE 2. Genera and species of dorylaimid and mononchid nematodes maintained in agar cultures in our Purdue laboratory at various times.†

Taxon	Feeding notes
Actinolaimus spp.	Maintained several years on *Panagrellus redivivus.*
Aporcelaimellus obscurus (Indiana isolate)	Reproduced on nematodes, mites, and enchytraeid egg capsules, but not on algae or protozoa.
(Other isolates)	Maintained on *P. redivivus* for several years.
Coomansus spp. (or close)	Maintained several years on *P. redivivus.*
Discolaimus sp.	Observed feeding on *Plectus* sp.
Eudorylaimus:	
E. meridionalis	Reproduced on all prey nematodes offered (*Acrobeloides, Plectus, Cylindrolaimus, Aphelenchus, Aphelenchoides* spp.); also seen to feed on mites, but did not reproduce; did not feed or reproduce on enchytraeid worms, algae, or protozoa offered.
E. irritans	Reproduced only on *Cylindrolaimus* and *Acrobeloides,* but survived about 1 month in dishes with other prey nematodes and in dishes with either mites, enchytraeid worms, algae, or protozoans.
E. circulifer	Based on reproduction observed, probably fed on *Acrobeloides,* but feeding not actually observed.
Eudorylaimus spp.	Some species from diverse areas of the world maintained for several years on *P. redivivus* (but no success with other species).
Labronema spp.	All six species attempted survived well on *P. redivivus.* Occasionally a specimen seen to feed also on fungus spores.
Leptonchus sp.	Twice observed feeding on fungus (hyphae and spores). Fed 15 minutes at a time. We could not maintain culture long enough to achieve reproduction.
Mesodorylaimus:	
M. pseudobastiani (or close)	Reproduced on all six species of prey nematodes (listed above) and on algae and protozoa. Possibly also fed on fungus cultures. Fed on mites but didn't reproduce. Fed only 2–3 seconds at a time and had difficulty puncturing cells of algae.
Mesodorylaimus spp.	Maintained for several years on *P. redivivus.*
Mononchus spp.	Maintained for several years on *P. redivivus.*
Mylonchulus spp.	Maintained for several years on *P. redivivus.*
Nyglolaimus sp.	Fed on several nematode species; made holes with teeth and sucked out contents (observed esophagus pulsating). No reproduction in cultures.
Pungentus sp.	Survived on prey nematodes for several months, but feeding not seen and reproduction not achieved in our cultures.
Thonus spp.	Cultures of several species maintained for many years on *P. redivivus.*
Tylencholaimus sp.	Observed feeding on fungus hyphae. Eggs observed in agar.

† We recognize the anecdotal nature of these feeding notes, but include them in the hope that they will be useful to nematologists.

tially so (2–4); if they are discordant, the present-day associations are best interpreted as coaccommodation, rather than cospeciation (Fig. 2).

Chapters dealing with coevolution in ecology texts of the 1970s do not as a rule mention systematics at all; indeed, the subject matter included deals largely with the phenomenon of coaccommodation (11,23). The two aspects of coevolution, as defined by Brooks (2), have been mingled over the years, producing a muddled literature. A recent compilation of papers by ecologists and systematists (31) suggests that the situation has changed. Ecologists who reviewed the book wrote, "With the development of increasingly rigorous methods and new kinds of data for inferring genealogical relationships among species, systematics is emerging from a period of eclipse to take its rightful place as an essential integral party to *evolutionary studies* [italics added]. There is increasing recognition that the study of both adaptive and nonadaptive traits cannot be divorced from the historical analysis that systematics in-

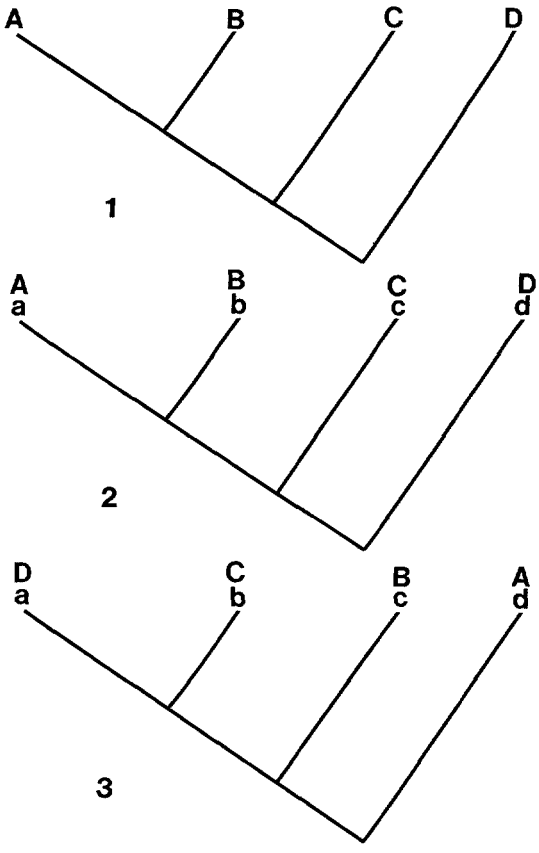

FIG. 2. Cladograms depicting two of the possible coevolutionary relationships between hosts and parasites. Hosts are represented by uppercase letters and parasites by lowercase letters. 1) Phylogenetic relationships of a four-species monophyletic host taxon. 2) Host cladogram and parasite cladogram coincide, indicating narrow coaccommodation and cospeciation. 3) Host and parasite cladograms discordant, indicating narrow coaccommodation and no cospeciation. Redrawn with permission from Brooks (2).

cludes among its subjects" (12). Although it may come as a surprise to many systematists that they are only now admitted as integral parties to *evolutionary studies,* confusion over the term coevolution has been shared by systematists. A general recognition that the phylogeny of a plant-parasitic nematode taxon cannot be recovered from the host associations of members of that taxon in the absence of cladograms for the nematode and host groups should result in a more precise approach to the subject of coevolution of nematodes and plants (20,30).

For animal parasite–host associations in which each host harbors a number of different kinds of parasites of some specificity, Brooks (4) has devised interesting methods for deriving host-group cladograms by means of cladograms for the several parasite groups. The host relationships revealed by the cladograms may suggest in turn relationships for still other parasite groups. Brooks (4) suggested that his approach of "historical ecology" complements the "evolutionary ecology" of ecologists (1,11,23). Based on actual data for animal parasites, Brooks (4) has concluded that ecological diversification lags behind morphological diversification historically, and that degree of specificity is not a reliable indicator of the age of an association. These observations should be of interest to nematologists and ecologists alike.

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