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Presidential Address: Parasitology: Retrospect and Prospect

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Introduction of President Rausch, by Gerald D. Schmidt

Ladies and Gentlemen, it is a distinct pleasure for me to introduce President Robert Rausch to you today. With the modesty characteristic of him, Professor Rausch asked me to make this introduction brief and unpretentious. That will be difficult, for the list of Bob's accomplishments is long. Also, because my admiration of him is so great, I find it hard not to carry on once I get started, but I'll try.

Robert Rausch earned his B.A. and D.V.M. degrees at Ohio State University, his M.S. at Michigan State University, and his Ph.D. at the University of Wisconsin. From 1949 through 1974, he progressed from Medical Parasitologist to Chief, Infectious Diseases Section, Arctic Health Research Center, U.S. Public Health Service in Alaska. He retired from the Public Health Service in 1974 with the rank of Veterinarian Director. He held several professorships during that time and since, and is currently Professor of Pathobiology at the University of Washington, along with four other appointments. He belongs to 20 professional organizations, and is a Fellow in five of them. He is a consultant, collaborator, or associate with other organizations too numerous to mention. During his years of tireless research he has published over 200 papers, on subjects ranging from garter snakes (his first paper), to bears (his 100th paper), to *Echinococcus* (his 205th paper). Some of you might not realize that Bob is also a mammalogist, and is as well known in that field as he is in parasitology.

It is natural and inevitable that honors and recognition should befall such a scientist. Foremost among them are: (1) the Henry Baldwin Ward Medal; (2) the Meritorious Service Medal of the U.S. Public Health Service; (3) the Lederle Prize, 5th Colombian Congress of Internal Medicine; (4) the K. F. Meyer Award, American Veterinary Epidemiology Association; (5) the Distinguished Service Award, Wildlife Disease Association; and (6) most recently, the first Arctic Science Prize, including a \$10,000 honorarium, given by the Alaskan North Slope Borough.

So you can see why I become enthusiastic when I talk about Robert Rausch. Ladies and Gentlemen, it is my honor to present your President, who will speak to us on "Parasitology: Retrospect and Prospect."

PARASITOLOGY: RETROSPECT AND PROSPECT

Until recently, few of us would have suspected that rotting logs on the forest floor represent complex biocenoses that may be essential in perpetuating organisms of great diversity and in the cycling of nutrients, on which the well-being of the forest depends (Maser and Trappe, 1984). This perception of fundamental processes in old-growth forest has far-reaching implications, and it adds a new dimension that must be considered in the formulation of management-policy in the future. The understanding of natural processes involved in the decomposition of logs was based in part on an extensive body of knowledge that

represents the cumulative effort of many investigators in numerous disciplines over a long period of time. The faunas of such logs are both abundant and diversified; in addition to bacteria and fungi, components include nematodes, annelids, insects, and mites, as well as higher plants and vertebrate animals. About 300 species of insects have been found to be associated with fallen Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco, alone. The identity of involved organisms was required before the investigation of their functions and interactions could be undertaken.

As parasitologists, we usually are not confronted with problems of such complexity (or we do not recognize them), but we, too, strive to understand interactions—those ecological systems involving parasites and their hosts. We also must first know the organisms with which we are concerned before rational investigation of their at-

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Robert Rausch

tributes is possible. How parasites and their hosts interact is usually determined by observations in the field. The more fundamental processes involved in these interactions are usually investigated in the laboratory. During recent years, technological advances have led to a shifting of interests in research, with greater emphasis on the application of highly specialized procedures in the laboratory. Nonetheless, we still must rely on investigations in the field to complement laboratory investigation. Otherwise, we risk a loss of perspective.

My review considers some historical aspects of parasitology, in part as a reminder of the comparatively early and observational origins of our field of interest, in which natural history played an important methodological role, and in part to point out that some fundamental biological questions recognized and studied by our professional precursors around the middle of the last century still have not been resolved. On the whole, we are probably less competent as biologists, although we compensate to some extent by specialization. This review is intended to promote serious discussion, in consideration of the judgement that basic investigations at the organismic level have not been superseded, but that our knowledge in this area remains regrettably deficient. My remarks here are limited mainly to cestodes, particularly those in the family Taeniidae.

The ability to distinguish, name, and categorize the components of the given ecosystem of which he is a part must be a fundamental attribute of man. As is evident from the orally transmitted knowledge of the few surviving peoples whose cultures are usually termed "primitive," that trait must have been developed by the earliest social units engaged in cooperative efforts to subsist by means of hunting and gathering. One of these peoples is the Nunamiut, an inland group of Iñupik Eskimos, who 30 years ago were still nomadic hunters. These people knew and designated by name birds of about 100 species (Irving, 1953), although few were used in any way, and they also had a remarkable knowledge of the more obscure components of the arctic flora and fauna. They recognized bumble bees (igutchaq) and the warble fly of reindeer (igut-chachiaq), among other insects. Their awareness of the few parasites that accompanied them on their long-ago dispersal from eastern Asia is evident from their names for the organisms, and by a term for the sensations produced by the

ubiquitous pinworm, *Enterobius vermicularis*. For a tropical region, by comparison, the classification of mammals by the Aguaruna Jivaro in the Amazonian region of Peru is of interest (Patton et al., 1982).

Our understanding of the knowledge of natural history of earlier peoples is based only on fragmentary records that extend back only a few thousand years. The Ebers Papyri have shown that the ancient Egyptians had a realistic perception of zoological systematics (von Oeffele, 1902). Their ability as observers is indicated by hieroglyphic inscriptions depicting the complete metamorphosis of frogs. Nor did parasites escape their attention. A veterinary papyrus excavated at Kahun, a city founded during the 12th Dynasty, contained a text on the warble fly of cattle, describing not only the behavior of animals when the eggs were being deposited, but also the resulting subcutaneous larvae (von Oeffele, 1901). Thus, the cycle of *Hypoderma bovis* was understood by the Egyptians more than 4,000 years ago. But knowledge gained can be knowledge lost. In Europe, it was not until the 17th Century that Francesco Redi conducted his experiment to demonstrate that fly larvae in exposed meat did not arise by means of spontaneous generation.

The acquisition by Europeans of realistic knowledge concerning natural history resumed around the beginning of the 16th Century, after an hiatus of more than 1,000 years from the end of the classical period. An interest in organisms that we designate 'parasites' began to have tangible expression around the end of the 16th Century. Based on the bibliography of cestodes published by Max Braun (1897), one can trace the development of helminthology from its beginning as part of general natural history to its present status as a separate branch of zoology. Commencing with the work of Felix Plater, in 1602, 143 publications concerning cestodes had appeared by the year 1800. An additional 172 were listed for the interval 1800 to 1851.

The year 1850 might be taken to mark the beginning of modern helminthology, for works published around that time by Carl Th. von Siebold, Friedrich Küchenmeister, Rudolf Leuckart, and several others, remain sources of useful information. An increasing interest in parasitology was manifest in the second half of the 19th Century, as shown by the publication of at least 964 works concerning cestodes from the period 1851 to 1894. During the century up to about 1950, most effort was devoted to taxonomy, elu-

cidation of cycles, and descriptive pathology. Thus, many of us have experienced the evolution of our discipline to its contemporary state.

It is the earlier investigative methods in helminthology to which I refer here, without making generalizations about parasites in the broad sense. Organisms of great diversity have been grouped under the subjective designation 'parasite.' Having devised that vague and imprecise category, we now attempt to apply a reductionist approach to justify its validity, and we explain parasite-host interactions by means of a vocabulary including such terms as 'strategy,' 'cost,' and 'reward.' Our loss of objectivity is deplorable. However, I am not concerned here as to whether a given organism can or cannot be called a parasite. Rather, I want to consider some of the problems that seem to have been overlooked in our eagerness (and obligation) to modernize. First, with respect to cestodes, it is evident that some fundamental questions are yet to be resolved in systematics. One example will suffice, that being the diversity of views concerning the discrimination and allocation of genera in the family Taeniidae. Reflecting the medical and veterinary importance of several species, members of this group have been intensively studied, so much so that by contrast, knowledge of other families is very much less, and many of their taxa are known only from original descriptions.

Because of the authoritative nature of major taxonomic works, misconceptions concerning taeniids have tended to be perpetuated; but also, much of the disorder with regard to the relationships of these cestodes can be attributed to differences in the concept of the genus as a taxonomic category. In the family Taeniidae, 2 subfamilies, Taeniinae and Echinococcinae, have been established (Abuladze, 1964). Beyond this point, agreement ceases; in the Taeniinae, 9 genera were recognized by Wardle and McLeod (1952); 8 by Yamaguti (1959); 5 by Joyeux and Baer (1961); and 11 by Abuladze (1964) (Table I). (The genus *Monordotaenia* Little, 1967 has replaced *Fossor* Honess, 1937, which was preoccupied.) Current concepts support the view that not more than 2 genera can be distinguished in the subfamily Taeniinae.

Four genera listed by Abuladze (1964) and others represent families other than Taeniidae. Cestodes of the genus *Cladotaenia* Cohn, 1901 occur in raptors; their larval stage, designated an armed plerocercoid, occurs in small mammals. *Cladotaenia* was removed to the family Dilepididae

TABLE I. *Genera previously assigned to the subfamily Taeniinae.*

Genus	Wardle and McLeod (1952)	Yamaguti (1959)	Joyeux and Baer (1961)	Abuladze (1964)
<i>Taenia</i> Linnaeus, 1758	X	X	X	X
<i>Multiceps</i> Goetze, 1782	X	X		X
<i>Taeniarhynchus</i> Weinland 1858	X	X		X
<i>Hydatigera</i> Lamarck, 1861	X	X		X
<i>Cladotaenia</i> Cohn, 1901	X	X	X	X
<i>Anoplotaenia</i> Beddard, 1911	X	X	X	X
<i>Dasyurotaenia</i> Beddard, 1912	X	X	X	X
<i>Paracladotaenia</i> Yamaguti, 1935	X		X (?)	X
<i>Fossor</i> Honess, 1937*	X	X		X
<i>Insinuatoraenia</i> Spasskii, 1948				X
<i>Tetratirotaenia</i> Abuladze, 1964				X

* Preoccupied; = *Monordotaenia* Little, 1967.

by Fuhrmann and Baer (1943), whose action was supported by the work of Freeman (1959, 1973). For reasons not explained, this genus was replaced in the family Taeniidae by Joyeux and Baer (1961), and retained by Abuladze (1964). The genus *Paracladotaenia* Yamaguti, 1935 also was established for a cestode from a hawk. It was distinguished from *Cladotaenia* mainly by the absence of rostellar hooks, although *Cladotaenia* spp. characteristically lose the hooks if specimens are not fixed immediately following the death of the avian host. Schmelz (1941), a student of Baer, placed *Paracladotaenia* in synonymy with *Cladotaenia*, an action tacitly accepted by Yamaguti (1959). Again, for reasons not explained, Joyeux and Baer (1961) tentatively included *Paracladotaenia* in Taeniidae. Cestodes of the genera *Anoplotaenia* Beddard, 1911 and *Dasyurotaenia* Beddard, 1912 are known only from carnivorous marsupials in Australia or New Guinea, which formed a single land-mass at times of lowered sea-level during Pleistocene time. These differ from typical taeniids in form of rostellar hooks, structure of the embryophore, and in other details in the strobilar stage. Beveridge et al. (1975) determined that the larval stage of *Anoplotaenia* also occurs in metatherian mammals and resembles that of *Cladotaenia*. The affinities of these austral cestodes are uncertain, but I suggest that they represent a distinct group that arose in marsupials after Australia became separated from South America and Antarctica,

around 56 million years ago (Woodburne and Zinsmeister, 1982), and that their *Taenia*-like characteristics can be attributed to convergence. As might be expected on zoogeographic grounds, the family Taeniidae is represented in Australia only by species introduced by man.

Of the remaining 7 nominal genera in the subfamily Taeniinae, 1, *Insinuarotaenia* Spasskii, 1948, is distinctive in having a modified scolex, lacking rostellar hooks, which becomes deeply embedded in the intestinal wall of the host. The genus was established for cestodes from the European badger, *Meles meles* (L.). The larval stage is unknown. The description of a second species, *I. spasskii* Andreiko and Iun' Lian', 1963, from the mouse-weasel, *Mustela nivalis* L., seems clearly to have been based on specimens of *Taenia mustelae* Gmelin, 1780, from which the rostellar hooks had been lost (Andreiko and Iun' Lian', 1963).

Cestodes of 6 genera exhibit a high degree of morphological uniformity in the strobilar stage, some differing only in details of the scolex. Their larval stages are morphologically rather diverse, but all can be defined as a cysticercus or some modification thereof. Abuladze (1964) and others have utilized both larval and strobilar stages in distinguishing these genera; Verster (1969) considered all to be synonyms of *Taenia*.

The only taeniid lacking a rostellum is the common tapeworm of man, *Taenia saginata* Goeze, 1782, of which the larval stage is a cysticercus. For this cestode, the genus *Taeniarhynchus* Weinland, 1858 is still widely accepted, but the taxonomic significance of the lack of rostellum is much diminished by the observations of Žďárská (1976) and Šlais and Machnická (1976) that the primordia of a rostellum and hooks appear in the course of development of the cysticercus, and then regress.

The genus *Fossor*, now *Monordotaenia*, was established for *Taenia taxidiensis* Skinner, 1935, which is distinctive in having a single row of rostellar hooks. This cestode, of which the larval stage is a cysticercus, is known to occur only in the North American badger, *Taxidea taxus* (Schreber), and appears to be a member of a subgroup of species occurring in carnivores of the family Mustelidae. By analogy with *T. saginata*, primordia of a second row of hooks might be sought in developing cysticerci. The existence of any other taeniid having a single row of hooks has not been confirmed, although additional species of *Monordotaenia* have been recently named. Since at least 1 of these was based on

specimens from which the large hooks had been lost, descriptions of such taeniids should be viewed with doubt unless the presence of a single row of hooks has been confirmed in infective larvae.

Abuladze (1964) established the genus *Tetratirotaenia* for *Taenia polyacantha* Leuckart, 1856, on the basis of its peculiar larval stage, which he considered to resemble an armed tetrathyridium. It is, rather, a modified cysticercus that is somewhat advanced in development, and in which the bladder is reduced in size. *Taenia polyacantha* is unique among its congeners with respect to the mechanism of asexual reproduction.

The remaining genera, *Multiceps* and *Hydatigera*, also have been distinguished mainly by characteristics of the larval stage. As originally conceived, the genus *Multiceps* includes cestodes of which the larval stage is a polycephalic cysticercus, designated a coenurus. The concept of that genus was modified by Bondareva (1963), who included in *Multiceps* species such as *Taenia twitchelli* Schwartz, 1924 and *T. endothoracicus* Kirshenblat, 1948, in which the larval stage differs from a coenurus in both pattern of development and in ultimate form. In another cestode, *Taenia mustelae*, retained in the genus *Taenia* by Abuladze (1964), the larval stage may be either a cysticercus or a polycephalic coenurus, depending on species of intermediate host. I have found larvae of both forms in a single chipmunk, *Tamias townsendi* (Bachman), and have observed that occasionally, in massively infected muskrats, *Ondatra zibethica* (L.), the larval *T. mustelae* may be so pleomorphic as to make difficult assignment to a specific form. The type species of *Hydatigera* is *Taenia taeniaeformis* (Batsch, 1786), the common cestode of domestic cats. The diagnosis of *Hydatigera* does not accommodate strobilocysticerci that are polycephalic, as in *Taenia selousi* Mettrick, 1962. Both *Multiceps* and *Hydatigera* have been appropriately placed in synonymy with *Taenia* by Esch and Self (1965) and Verster (1969).

By the present assessment of common attributes, the subfamily Taeniinae would include only 2 genera, *Taenia* and *Insinuarotaenia*, which have a number of characteristics in common, and which form a natural group comparable in rank to the genus *Echinococcus*, in the subfamily Echinococcinae. The alternative to that arrangement would be the recognition of numerous monotypic genera differing only in minor details, an action that would obscure the phylogenetic relationship of the 2 subfamilies.

Obviously, the larval stages, or metacestodes, of members of the Taeniinae have been a major source of the taxonomic confusion. Gradually, the perspective is becoming prevalent that a high degree of morphological uniformity is characteristic of the strobilar stage and the diversity in the larval stage is attributable only to modification that has occurred in the basic form, the cysticercus. Modifications of that fundamental form include the capability, in several species of the genus *Taenia* as here conceived, of degrees of asexual multiplication, through production of multiple scolices or exogenous budding of vesicles. One of the most complex is exemplified by the ontogenic process involved in the multiplication of the larval *T. polyacantha*, which has been defined on the basis of recent experimental studies (R. L. Rausch and F. H. Fay, unpubl.). The infective cysticerci of *T. polyacantha* occur in moderate numbers free in the peritoneal cavity of arvicolid rodents. Following ingestion of the embryophore, the oncosphere localizes in the liver of the intermediate host, where initial development takes place. On about the sixth day post-exposure, the early-stage larvae pass from the liver to the peritoneal cavity, a process accompanied by the production of a considerable volume of ascitic fluid. At this time, the individual larva consists of a mass of minute vesicles, which increase in size over a period of a few days, and then become detached. Thereafter, the vesicles develop independently, each producing a single scolex at the pole opposite that by which it was previously attached. When fully developed, the larval cestodes are elongate, with segmented forebodies and much reduced caudal bladders. Although they do not multiply after removal from the initial intermediate host, such larvae are readily maintained by intraperitoneal transfer in rodents. These findings will be described in detail elsewhere.

If the discrimination of the various species and their allocation according to generic relationships present problems for taxonomists, the assessment of subspecific categories is even more difficult, and indeed the recognition of taxa at the infraspecific level has raised some questions of fundamental importance in helminthology. How can we ascertain whether a population is segregated as a distinct geographic or ecological race? In helminthology, infraspecific taxa have been variously designated as subspecies or biological strains, but sibling species may be involved in some cases. One example is the uncertain taxonomic status of nematodes in the

genus *Trichinella*. Evidence supporting the view that *Trichinella* is polytypic has been reviewed recently by Britov (1982), but Lichtenfels et al. (1983) concluded that reproductive isolation of the nominal species has not been confirmed. Among cestodes, the significance of biological variation in the taeniid genus *Echinococcus* has been a matter of controversy for at least 2 decades (Rausch, 1967; Thompson, 1978; Kumaratilake and Thompson, 1982).

The genus *Echinococcus* is represented by 4 species that are readily distinguished in the larval and strobilar stages by means of standard taxonomic criteria. As compared with *Taenia* species, these cestodes have very small strobilae, consisting of 2 to 6 segments. Because of the high productivity of protoscolices by asexual multiplication, they are often present in large numbers in the final host. In terms of egg-production, the large populations compensate for the relatively few eggs produced individually. Like species of *Taenia*, they are perpetuated by well defined predator-prey relationships existing between their respective final and intermediate hosts. In recent years, the question whether or not the nominal species of *Echinococcus* are reproductively isolated has been seriously considered, leading to confusion and to the expenditure of extensive investigative effort. That controversy serves to emphasize the existence and importance of other inadequacies in our knowledge of the biology of cestodes.

Two species, *Echinococcus granulosus* (Batsch, 1786) and *E. multilocularis* Leuckart, 1863, are indigenous in the northern hemisphere. I distinguish 2 forms of *E. granulosus*: the Northern form, for which deer (Cervidae) serve as intermediate host, and the European form, adapted to synanthropic hosts. The European form must be the most thoroughly studied of all cestodes, but nonetheless, our understanding of its fundamental biological characteristics is decidedly lacking. Particular controversy has arisen concerning the significance of local biological strains, and the mechanisms by which they occur. As do other taeniids, *E. granulosus* in the strobilar stage exhibits a range of statistically demonstrable but taxonomically insignificant morphological variation. All domestic ungulates appear to be susceptible to infection by the larval stage of the European form of *E. granulosus*, in which the degree of parasite-host compatibility is reflected in pleomorphism, productivity of protoscolices, and survival-time.

Fundamental to the question of biological

strains is the mechanism by which fecundation takes place in cestodes. Among cyclophyllideans, the process of fertilization is not understood, except for the few that are dioecious. Self-fertilization is presumed to occur. Direct observation of specimens removed from the intestine of the final host may be misleading, since the occasional finding of segments in which the cirrus has been inserted into the adjacent vagina is not necessarily evidence of self-fertilization. One may find as well that the cirrus has perforated the wall of the genital atrium, or has been inserted into other tissues of the same or different strobilae. When cestodes are kept in water or physiological saline for a time, they may form an adherent mass as a result of the reciprocal insertion of cirri into any contiguous tissues. In the case of the larger ones, such as *Taenia* spp., appreciable force is required to pull apart such strobilae. Observations on the insertion of the cirrus by cestodes that have been removed from the host appear to have little value in the interpretation of the process of fertilization.

Indirect evidence supports the conclusion that cross-fertilization does indeed occur among cyclophyllidean cestodes, perhaps characteristically. Rausch and Maser (1977) determined that cestodes of the genus *Monoecocystus* Beddard, 1914 are protogynous, and that the seminal vesicle of a given segment becomes filled with spermatozoa as soon as the vagina is patent. In *M. americanus* (Stiles, 1895), host-specific in the porcupine, *Erethizon dorsatum* (L.), that condition was invariable in young strobilae in which the male genital organs had not yet become functional. Such cestodes had been inseminated from other, older strobilae in the same host. It is characteristic of this and other anoplocephaline cestodes that the population in a single host consists of numerous individuals at different stages of development, a mechanism that may ensure cross-fertilization.

Knowledge of ecological and behavioral attributes also supports the concept that cross-fertilization must occur. Among taeniids, the respective species attach within specific areas of the host-intestine, ensuring contact of strobilae. *Echinococcus granulosus* and *E. multilocularis*, in naturally and experimentally infected dogs and foxes, sometimes occur in small numbers, not widely spaced apart, but concentrated within a specific area of the jejunum. That distribution is evidently not regulated by adaptation to a specific biotope in the host-intestine. They attach farther anteriorly and posteriorly when greater

numbers are present; when infections are massive, involving many thousands of individuals, they are distributed more or less uniformly from the pylorus to the caecum. In suprainfections, established in dogs and foxes, members of 2 cohorts of a single species, or cestodes of both species, were intermingled. We do not know whether individuals of the 2 species of *Echinococcus* change their location after initial attachment in the intestinal mucosa.

An understanding of these processes is essential for comprehension of genetics and speciation in the cestodes. In *Taenia crassiceps*, which generates new vesicles by exogenous budding from the bladder-wall, Schiller (1973) determined that cysticerci exhibiting structural anomalies in the scolex multiplied readily in mice and produced normal progeny, from which he concluded that the germinative loci in the bladder-wall of such cysticerci were not genetically homogeneous. That work provides grounds for questioning the assumption that all individuals derived asexually from a single embryo are genetically uniform. In *Echinococcus*, an unusual phenotypic variation is never observed, nor do specimens exhibit combinations of characters that would make difficult their determination as 1 of the 4 species now distinguished. Individuals from widely separated localities in the northern hemisphere are readily identifiable as either *granulosus* or *multilocularis*, and morphological criteria serve equally well to distinguish the 2 neotropical species, *E. oligarthrus* (Diesing, 1863) and *E. vogeli* Rausch and Bernstein, 1972. The Northern form of *E. granulosus* seems to show a high degree of biological uniformity as well. Uniformity in morphological and biological characteristics in the natural population is indicative of an intensity of genetic homeostasis that may be attributable to gene-flow mediated by cross-fertilization.

The greater degree of biological variation in the European form of *E. granulosus* is evidently associated with synanthropy. Such diversity is not unique to this single species, but it occurs as well in members of the genus *Taenia* in synanthropic hosts. Under the natural conditions that still exist in the Arctic and the Subarctic, the cycles of *Taenia krabbei* Moniez, 1879 and *T. hydatigena* Pallas, 1766, like that of the Northern form of *E. granulosus*, involve the wolf and large deer as hosts (Sweatman and Plummer, 1957; Sweatman and Henshall, 1962). Verster (1969) demonstrated that *T. krabbei* is morphologically indistinguishable from *T. ovis* (Cobbold, 1869),

of which the cycle involves the dog and domestic sheep and goats. She consequently designated *T. krabbei* a subspecies of *T. ovis*. The form of *T. hydatigena* adapted to domestic ruminants and pigs has not been recognized formally at the infraspecific level. Experimental studies by Leikina et al. (1972) have demonstrated the existence of biological strains of the larval stage of *T. saginata*. These 3 species of *Taenia* as well as *T. solium* Linnaeus, 1758 probably will be found to have a range of biological variation comparable to that reported for the European form of *E. granulosus*.

Synanthropy as a phenomenon to be considered in parasitology is a comparatively recent and important development. The processes involved in animal husbandry, beginning in the Palaearctic more than 10,000 years ago, led to the formation of new assemblages of hosts, to which the various taeniid cestodes become adapted. Completion of their cycles was enabled by the sustained association of the domesticated wolf (the dog) with domestic ungulates, and man became involved via what we deem now to be undesirable sanitary conditions. Only in the north, the host-assemblage consisting of the dog and the domesticated reindeer was but an extension of the coexisting natural assemblage. At some point, man acquired 2 species of *Taenia*, for which cattle and pigs serve respectively as intermediate hosts. These cestodes, no less than all other taeniids, are perpetuated by a predator-prey relationship, however we may perceive it. It is of interest that all other species in the family Taeniidae occur in the strobilar stage in fissiped carnivores. The precursors of these species in man have not been identified.

In actuality, the cosmopolitan distribution of the European form of *Echinococcus granulosus* and the aforementioned species of *Taenia* perpetuated in synanthropic hosts is artificial, and resulted from the global dispersal of domestic animals from Europe and Asia, most importantly since the end of the 15th Century. The possibility may exist that *E. granulosus* was introduced much earlier in Australia, with dogs accompanying the original immigrants. Remains of dogs have been found in archaeological sites dating back about 5,000 years (White and O'Connell, 1982). However, the immigrant people are not known to have had other domestic animals that could have served as intermediate host for the cestode in the course of their dispersal. Nonetheless, repeated introductions of the cestode to Australia must have occurred. World-

wide, the subsequent appearance of local biological strains does not seem remarkable, and indeed might be the expected consequence of response to selection pressures imposed through practices of animal husbandry. An example of an apparent adaptation in the European form of *E. granulosus* is based in part on our findings in experimentally infected elk (moose), *Alces alces* (L.), and reindeer, wherein it was determined that the larval stage of the Northern form of the cestode develops slowly, with production of protoscolices beginning after about 2 years. The larval stage of the European form develops more rapidly in some domestic ungulates. Selection for more rapid development in such animals might be expected, since they usually are slaughtered at a relatively young age. By contrast, animals as old as 7 to 9 years usually make up a significant component of populations of elk and reindeer. In them, the rate of infection by the larval *E. granulosus* increases with age. Response to selection pressures in synanthropic hosts would seem to be favored by genetic heterogeneity of the cestodes. As natural environments are more and more altered globally, we probably shall be increasingly concerned with synanthropic associations, involving organisms of increasing diversity.

While the phenomenon of synanthropy is a relatively recent one, non-artificial assemblages of host-specific helminths and their mammalian, and other, hosts may be of great age. That comprehension can provide some perspective of the ancient origins of the parasite-host interactions in which we, as a species, also are a part. Research in this area has received little emphasis but is becoming more feasible as knowledge accumulates in such fields as glaciology and palaeontology. Helminths themselves are not well suited to fossilization, and none was mentioned in the review of fossil parasites by Moodie (1923). An exceptional case was the report by Dubinina (1972) of the nematode *Strongylus edentatus* (Looss, 1900) in a horse from frozen deposits on the upper Indigirka River, for which an age of about 33,000 years B.P. was established. According to Lazarev (1980), the late Pleistocene horse in northeastern Siberia represented the species *Equus lenensis* Rusanov. *Strongylus edentatus* is a cosmopolitan nematode in domestic horses, and it occurs in wild equine animals as well. More recently, Vereshchagin (1975) reported the presence of a nematode of the genus *Cobboldia* Leiper, 1910 (preoccupied; = *Cobboldina* Leiper, 1911), from the remains of a mam-

moth found on the Shandrin River in Siberia. Extant species of *Cobboldina* occur in the tree hyrax, *Dendrohyrax arboreus* (Smith) (Perissodactyla: Procaviidae), and in the hippopotamus, *Hippopotamus amphibius* L., in Africa (see Round, 1968). Despite the rarity of such fossil material, the relative ages of assemblages consisting of mammals and their host-specific helminths can sometimes be established by correlations with intercontinental dispersals of mammals. The distributional histories of mammals are most readily traced when dispersals have taken place across intermittent land-connections such as Beringia, for which the chronologies have been determined (Rausch, 1977).

An example of the synthesis involved in tracing distributional histories is that of the small lagomorphs of the genus *Ochotona*, the pikas, which serve as final host for helminths of several host-specific genera (Gvozdev et al., 1970). The ochotonid and leporid lines diverged during the Eocene, and the earliest confirmed ochotonids are known from the Oligocene of Europe, dating to about 25 million years ago (Thenius, 1980). In the Recent fauna, the family Ochotonidae is represented by a single extant genus, *Ochotona*, with about 17 species in Eurasia and 2 in North America. The 2 nearctic species are evidently derived from a precursor that dispersed into North America via Beringia near the end of the penultimate glacial period more than 100,000 years ago. This mammal was accompanied by various helminths representing genera known exclusively from pikas. These included a cestode of the genus *Schizorchis* Hansen, 1948 and nematodes representing 5 genera (*Cephaluris* Akhtar, 1947; *Eugenuris* Shul'ts, 1948; *Labiostrongylus* Akhtar, 1941; *Muriellus* Dikmans, 1939; and *Graphidiella* Olsen, 1948). Pikas had spread widely in North America by the beginning of the last glacial period, about 70,000 years ago, during which the population was divided into northern and southern segments by the continental ice. That disjunction in range has persisted to the present time. Divergence in the 2 populations led to speciation, which was paralleled in helminths of some of the genera mentioned. This is an excellent example of parallel cladogenesis in a mammal and its helminths. It is of interest that, after a period of more than 100,000 years, the host-specific helminths recorded from pikas in North America represent exclusively the original genera of palaearctic derivation.

From this and similar cases, the evidence seems to indicate that most host-specific helminths rep-

resent stable species of ancient origin. With reference to the relative age of the taeniids, an examination of the history of the mammalian fauna of South America permits some useful inferences about *Echinococcus* species. As was expressed by the title of a recent book by George Gaylord Simpson (1980), the mammalian fauna of South America existed in 'splendid isolation' for a period beginning about 65 million years ago until Tertiary time, when caviomorph rodents and platyrrhine primates appeared in the fossil record. Some immigration of mammals from North America began about 7 million years ago. The phenomenon known as the Great American Interchange began about 3 million years ago, with the formation of the Panamanian Isthmus (Marshall et al., 1982).

As part of that Interchange, carnivores of the families Canidae and Felidae of North American origin appeared in South America during the early Pleistocene (Webb and Marshall, 1982), where they underwent extensive radiation. The Recent fauna of South America includes at least 11 species of canids, of which all but 1 represent endemic genera (Honacki et al., 1982). The gray fox, *Urocyon cinereoargenteus* (Schreber), has spread relatively recently as far south as northern Colombia and Venezuela. Cats of 10 species occur in South America. The geographic ranges of a few of these include, or formerly included, southern regions of North America. Only the cougar, *Felis concolor* L., probably a late Pleistocene immigrant to South America, now occurs widely on both continents.

The family Taeniidae has few representatives in South American carnivores. The cycles of the 2 endemic species of *Echinococcus* involve caviomorph rodents as intermediate hosts, indicating an early origin of the respective cestode-host assemblages. The strobilar stage of *Echinococcus vogeli* is known to occur naturally only in the bush dog, *Speothos venaticus* (Lund), and indeed, no other South American canid appears to be capable of preying on the large rodent, the paca, *Cuniculus paca* L., that serves as intermediate host. Rodents of the genus *Dasyprocta* are thought to be the typical intermediate hosts of *E. oligarthrus*, but since this cestode occurs also in small cats of various species, rodents smaller than agoutis are considered as well to serve as intermediate host, and in fact, the larval stage has been recorded from spiny rats, *Proechimys* spp. (D'Alessandro et al., 1981). The biology of these assemblages requires much more study.

The 3 species of the genus *Taenia* known to

FIGURE 1. The approximate distribution of *Echinococcus multilocularis* in central North America (shaded). The southern border of the zone of tundra is indicated by the heavy line.

occur naturally in neotropical carnivores live in members of the family Felidae. These cestodes, *Taenia omissa* Lühe, 1910, *T. macrocystis* (Diesing, 1850), and *T. pseudolaticollis* Verster, 1969, appear to be of comparatively recent nearctic origin, since all occur widely in wild cats in North America. The known intermediate hosts of 2 of these are among species of mammals that also spread into South America during the late Pleistocene. The cycle of *T. pseudolaticollis* is not known. In addition, taeniids that are perpetuated in synanthropic hosts have become widely es-

tablished in South America following their introduction by Europeans. The consequences of introduction of the European form of *E. granulosus* are well known.

From geochronological data, one can infer that the 2 neotropical species of *Echinococcus* were derived from a precursor or precursors already present in canids and/or felids in North America by early Pleistocene time. Although the relationships of the 4 recognized species of *Echinococcus* are obscure, the marked differences in structure of the larval stage in all are indicative of early

divergence. In contrast, the absence of any endemic species of *Taenia* in neotropical carnivores indicates that this genus was not represented in the early Pleistocene precursors of these mammals.

Dispersal of helminths is still going on—but much faster, as global alteration of ecosystems takes place. Again, the taeniid *Echinococcus multilocularis* can be cited; this organism is extending its range in Japan, in central North America, and perhaps in southern Asia. About 20 years ago, *E. multilocularis* was known in North America only from the prairies of the Arctic and the Subarctic, where it is a common cestode in the arctic fox, *Alopex lagopus* (L.). The cycle is completed through the predator-prey relationship existing between the fox and arvicolid rodents. The zone of boreal forest to the south evidently constituted an ecological barrier to its spread, since the diversity of prey utilized there by the red fox, *Vulpes vulpes* (L.), does not seem to sustain the cycle. That this barrier had been breached became apparent in 1964, when the cestode was found to have become established in mammalian populations in North Dakota. Its occurrence in that region might be attributable to the importation of infected dogs from the Arctic, or to natural spread from the north. Evidence exists to support the second alternative. Certainly, it is difficult to believe that this helminth could have been overlooked if it had been an indigenous component of the fauna of the central plains region. Moreover, its geographic range in central North America is quite small relative to that of suitable mammalian hosts (Fig. 1).

Wrigley and Hatch (1976) summarized records concerning the southward dispersal of arctic foxes in years when arvicolid rodents were scarce in the tundra bordering Hudson Bay. They reported, for example, that in 1974, a migrant fox was killed in Manitoba about 1,000 km south of the nearest tundra, and only about 135 km north of the border of North Dakota. The presence of *E. multilocularis* in foxes along the shore of Hudson Bay has been documented by Choquette et al. (1962). The embryophores expelled by migrant foxes would of course be a potential origin of new endemic foci. On the temperate prairies of North America, this cestode is being perpetuated mainly by the red fox, with rodents of the genera *Microtus* and *Peromyscus* serving as intermediate host (Fig. 1).

It appears that the southward spread of *E. multilocularis* has been a process influenced by

events initiated some 200 years ago. At the time of colonization of eastern North America by Europeans, the red fox evidently was not present east of the Rocky Mountains, but was introduced there from Europe by early colonists, for the purpose of hunting. Reference to such introductions was made by Richardson (1829). In his report on the zoology of Ohio, Kirtland (1838) remarked that the red fox had not been present formerly in that state, but that it had become numerous as well as troublesome by 1838. The modifications brought about by the clearing and cultivation of land in Manitoba and Ontario south of Hudson Bay produced habitat suitable for both red foxes and rodents that were formerly absent or uncommon. *E. multilocularis* probably spread southward in that region, or endemic foci were established and eventually coalesced. The fatal case of alveolar hydatid disease in a resident of Manitoba, reported by James and Boyd (1937), has puzzled physicians and helminthologists alike; its occurrence does not seem unusual when viewed with respect to such a pattern of dispersal.

Cases of alveolar hydatid disease have been reported recently in northern India, in the People's Republic of China, in Tunisia, and in Iraq; all represent new records of distribution for the cestode. Whether such records are indicative of the dispersal of *Echinococcus multilocularis* brought about by ecological changes or are attributable to improved medical service and a greater general awareness of parasitic diseases is uncertain. Perhaps these combine as factors. Its recent introduction and spread on the Island of Hokkaido is unquestionable. In the United States, the opportunity exists for precisely tracing its changing pattern of occurrence in wild animals. Our knowledge thus far has been derived from intermittent, local surveys and expository data such as I have considered.

Some of these problems are not unresolved perplexities of long standing, but concern relatively new epidemiologic concepts. In this respect, world-wide conditions have been described recently by Heyneman (1984). I shall further emphasize that globally, the combined effects of increasing human populations, deterioration of human habitat, and growing abuse of our remaining natural areas can be expected to enhance the transmission of pathogenic parasites, bring about new and different problems, and offset some past successes in prevention and control of parasitic diseases. Most of us contemplate with alarm the destruction of forest in the

Amazon Basin and in southeastern Asia. Most of us, too, know the factors that contribute to the rapid desertification of the sub-Saharan region of Africa, with its appalling toll in human misery and devastation of life. A brief summation of the difficulties that exist to forestall any effective action in the Sahel was given by Walsh (1984); "A shortage of money. A shortage of good concepts of what to do. And an inability to implement good concepts." We should at least have known what not to do. Whether it be the enhanced transmission of parasitic diseases or other adverse effects, our ecological errors are attributable to our rudimentary comprehension of ecosystems, by which human populations ultimately are sustained.

In this paper, I have dealt largely in retrospect, discussing methodology and some of the long-standing problems that could be viewed and conceivably resolved within the conceptual frame of the natural historian in parasitology. It is more important now than ever that we reassume this disposition; probably one of the most significant changes that we can make within our discipline is to begin, or to renew, if you prefer that term, an effort to view parasite-host associations at the same level and with the same intellectual probes that Maser and Trappe (1984) have applied in their perception of old-growth forest. A continuing emphasis on understanding of natural processes in parasitology, and communicating this comprehension, are absolute needs. It is critical that we as parasitologists remain diversified, with some individuals concentrating on parasites at the organismic level and on ecological studies in the natural environment.

Recently, the National Research Council (1983) reported an assessment of manpower needs and career opportunities in the field aspects of vector biology. It was recognized that few inducements and favorable circumstances exist for developing competence in field biology relating to vector-transmitted diseases. A conclusion was that the number of vector biologists is woefully inadequate to meet our needs, both nationally and internationally. The trend in other areas of parasitology, *sensu lato*, appears to have been like that in medical entomology. Not only is our national effort in parasitology comparatively modest—and this can be said of Canada as well—but the numbers of parasitologists competent to accomplish investigations in the field are diminishing. Their replacement cannot be a short-term enterprise. As parasitologists, we ought to change

this, to combine the new technology with objective investigations in natural history, since we bear the responsibility for the course taken by our profession to meet future obligations. In the sense that we are living in 1984, we are also part of some global problems that are difficult to define, let alone to solve. We need to achieve a better balance between laboratory-oriented and field-oriented research if we are to train investigators capable of discerning interactions in complex ecosystems. For the future, I believe that this is a *sine qua non*.

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