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PHYLOGENY AND HISTORICAL BIOGEOGRAPHY
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Allan Christopher Carmichael

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PHYLOGENY AND HISTORICAL BIOGEOGRAPHY OF THE SCHISTOSOMATIDAE

By

Allan Christopher Carmichael

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1984

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ABSTRACT

PHYLOGENY AND HISTORICAL BIOGEOGRAPHY
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by

Allan Christopher Carmichael

Phylogenetic relationships of blood flukes of the trematode family Schistosomatidae were assessed and compared with host phylogenies in order to examine alternative hypotheses concerning coevolution and host shifting during phylogenetic history. Coevolution is suggested by congruence between host and parasite cladograms while patterns other than strict co-occurrence may indicate that host shifting occurred at some point in an organism's lineage.

Two analytic techniques were applied to morphological character state distributions in order to estimate parasite phylogenies: component analysis and Farris optimization. Polarity sequences for individual characters were determined on the basis of out-group comparison and ontogenetic arguments. Data sources included museum specimens and literature descriptions.

Before analyzing the relationships of schistosome genera, an out-group was designated in an analysis of

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the families of the suborder Strigeata. This analysis revealed the blood flukes of turtles, family Spirorchidae as the out-group of the Schistosomatidae. Family level analysis also called into question monophyly of the superfamily Schistosomatoidea by grouping the Clinostomatidae and Sanguinicolidae together as a sister lineage of the schistosomes and spirorchids. Analysis of host distributions suggested that a three-host life cycle involving pulmonate gastropods and vertebrate intermediate and definite hosts is a primitive pattern among the Strigeata.

Phylogenetic analysis of the Schistosomatidae revealed three major clades: one composed of the genera assigned to the subfamilies Bilharziellinae and Gigantobilharziinae, a second branch including members of the genus Macrobilharzia and a final clade involving all other members of the Schistosomatinae.

Examination of host distributions revealed a pattern of both host shifting and coevolution at both levels of host involvement. Pulmonates are the primitive intermediate host taxon and several shifts into prosobranch and opisthobranch gastropods are indicated. While it appears that birds primitively host the schistosomes, a minimum of two independent shifts into mammals have occurred. Within the Schistosomatinae, one shift is suggested by ancestors of Schistosoma and Orientobilharzia, while at least one other shift indicated is in the clade containing Bivitellobilharzia, Schistosomatium and Heterobilharzia. Biological

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ACKNOWLEDGEMENTS

I wish to express my appreciation to the members of my guidance committee, Drs. Donald O. Straney, James L. Edwards, John A. King and Jeffrey F. Williams for their support and enthusiasm during this study. As committee chairperson, Dr. Donald Straney provided invaluable training and encouragement in developing this research.

My studies were partially supported by the Department of Zoology and by a Doctoral Fellowship from the College of Natural Science, Michigan State University.

My parents, Allan and Jean Carmichael have provided continued support and encouragement throughout my graduate career. Finally, I would like to thank Terry Stein for his caring and support through all phases of this project.

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INTRODUCTION

Due to the nature and complexity of their life cycle, parasites have long evoked fascination from biological researchers and the general public alike. The close association between parasites and their hosts has intrigued evolutionary biologists for decades, but in the absence of a fossil record, biologists have done little more than speculate on the origin and evolution of the host-parasite interaction. The speciation mechanisms of parasitic organisms have received some attention (Price, 1980), but speciation studies have been constrained by a lack of knowledge concerning species boundaries and the common *a priori* assumption that parasite speciation is dependent upon prior host speciation. One area which, until recently, has been almost entirely neglected is that of parasite phylogeny.

This study was in part prompted by the development of modern systematic techniques that I used to generate parasite phylogenies independent of host bias. In addition to the baseline work in constructing a phylogeny for an unexamined group of trematodes, I addressed several questions of general interest to evolutionary biologists. My main concern was to evaluate what current distribution

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of parasites within their host organisms reveals about the pattern and process of parasite evolution. This question can be approached by examining the degree of overlap between independently derived phylogenies of parasites and their hosts. Areas of congruence may suggest a history of coevolution; discontinuities may indicate the occurrence of host shifts during lineage formation. Parasite evolution suggests a ready comparison with vicariance biogeography. An obvious parallel exists between the distribution of parasites in or on their speciating hosts and the geographic distribution of organisms on moving land masses. Host speciation can be likened to the formation of a geographic barrier which isolates parasite populations, while host shifts can be compared with organismal dispersal.

Before discussing these issues as well as the specific applications of modern systematic methods to my study, I will briefly review the history of evolutionary parasitology, addressing implications for my current study. I will also consider the problems inherent in conducting research on parasitic organisms, problems which in large part explain why many evolutionary questions have not been addressed to any great extent until recently.

Parasitism and Evolutionary Theory

Although definitions abound, parasitism generally designates a symbiotic (sensu Cheng, 1970) association of two organisms of different species in which one of

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the two is metabolically dependent upon the other. This characterization includes an array of organisms with diverse taxanomic affinities: viruses, bacteria, protozoans, "helminths," phytophagous insects, parasitoids, ectoparasitic arthropods, as well as numerous other taxa including coelenterates, molluscs and vertebrates. Although parasites taken as a whole do not form a natural group, Rensch (1959) and other evolutionary biologists have noted similar morphological trends in the evolution of many parasitic taxa. These include loss or reduction of limbs, sense organs, and certain organ systems, as well as an increased reproductive potential. Such similarities imply that related processes may be involved in the evolution and maintenance of parasitism in taxonomically distinct organisms.

Reflecting their common lifestyle, parasitic organisms are frequently treated in a collective manner that assumes they are governed by a unified set of biological principles. Questions concerning the evolutionary processes involved in deriving the morphological similarities that often characterize parasites have yet to be addressed in an empirical manner. For example, the environmental and evolutionary forces impinging upon a gut dwelling helminth and a phytophagous insect are almost certainly very different, although both are considered "parasites." Until a better understanding of the mechanisms of evolutionary change is available, I think it is wise to avoid <u>a priori</u> generalizations which encompass all parasitic organisms.

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For this reason, my comments here are restricted to the platyhelminth class Trematoda, which forms the basis of this research.

With regard to theoretical considerations, most of the focus of evolutionary parasitology has been directed toward accounting for the acquisition of a parasitic life-style by formerly free-living organisms. Faced with the lack of a fossil record which could be used to trace changes in morphology associated with parasitism, researchers have had to rely totally on extant organisms to aid in the construction of their hypotheses. Where available, comparisons with related free-living forms provide the basis for most theories of the origin of parasitism. Important contributions that consider the origins or platyhelminth parasitism include those of Cheng (1973), Noble and Noble (1976), Hyneman (1960), Llewellyn (1965), Janicki (1920), Fuhrmann (1928), and Freeman (1973). These authors have formulated elaborate scenarios to account for the acquisition of a parasitic lifestyle.

Some evolutionary studies have focused on recent parasite groups, but little empirical evidence has been bought to bear on questions concerning the mechanisms of change (Price, 1980). The process of speciation among parasitic organisms has received a moderate amount of attention, although many of the results are anecdotal (e.g., Inglis, 1971). Tabulations of the distributions of parasites and their host species have led to the

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formalization of three "rules" which neatly summarize the bulk of past thought on parasite speciation. The main theme present in each of these rules is that of an intimate association between host and parasite phylogeny. The "parasitic rules" are presented below in a summary taken from Noble and Noble (1976).

> The Eichler Rule. When a large taxonomic group (e.g., family) of hosts consisting of many species is compared with an equivalent group consisting of few representatives, the large group has the greater diversity of parasitic fauna.
>
> The Szidat Rule. The more specialized the host group, the more specialized are its parasites. Hence, the degree of specialization may serve as a clue to the relative phylogenetic ages of the hosts.
>
> The Fahrenholz Rule. Common ancestors of present-day parasites were themselves parasites of the common ancestors of present-day hosts. Degrees of relationship between modern parasites thus provide clues as to the parentage of modern hosts.

In every presentation of these "rules," the fact that numerous exceptions occur is mentioned (e.g., Noble and Noble, 1976). Relatively little attention has been paid to these exceptions, which may in fact outnumber the cases that follow the "rules." The concept of association by descent has been firmly entrenched since the early part of this century (reviewed in Stunkard, 1957), but few studies have objectively examined the relationship between host and parasite phylogenies. The views inherent in the parasitic "rules" have conceptually limited studies of the pattern and process of parasite evolution, since

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an a priori assumption of congruence between host and parasite phylogenies underlies each rule. Far too often the pattern observed in nature is forced to fit an interpretation of association by descent (e.g., Stunkard, 1970).

The most frequent manifestation of host biased taxonomy is seen in the naming of new parasite species. Multiple species of parasites are often designated when similar forms are recovered from different host species. Descriptions are frequently based on limited material without addressing questions of intraspecific variation. Thus inflated species reports result from the misinterpretation of normal variation within species. Problems such as these result from a lack of understanding of both individual and populational variation in morphology.

Variation

Species designations in parasitic trematodes seldom take into account the confounding influences of intra- and interspecific variability. For example, although many species distinctions are drawn on the basis of size, the factors which influence size are seldom, if ever, considered in a systematic context. Below I will review the existing literature concerning individual and populational variation in trematodes and discuss the importance of variability in systematic studies.

Probably the single most important factor influencing individual variability in parasites is the impact of the

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host organism (Wakelin, 1976). Host induced variation is poorly understood, at least in part because parasite ontogeny is difficult to observe independent of the host environment. Although the nutritional status of the host may have some effect on parasite morphology, host organisms impact the development of parasites primarily via immune defenses. The most frequently cited effects of immune repsonse are stunted growth and diminished reproductive output (Kennedy, 1975).

Host immune response may alter parasite morphology by affecting rates of growth and sexual maturation. Although in most cases the mechanisms of change remain poorly understood, it is likely that both humoral and cellular agents are involved (see Wakelin, 1976, for a discussion and bibliography concerning host response). The strength of the immune response differs between individuals of the same host species and is dependent upon numerous intrinsic and extrinsic factors. These factors include age of host, state of immune responsiveness due to concurrent infections, intensity of parasitic challenge and prior history of infection by the same or different species of parasite (Kennedy, 1975). In addition, rates of growth and development may be influenced by both inter- and intraspecific competition between parasites within a single host individual, as noted by Kennedy (1975). Finally, the nature and intensity of immune response varies between host species, providing different opportunities and

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challenges to invading parasitic organism. Thus the potential for variability in parasite morphology differs both within and between host species. Alterations in growth rate and reproductive output are reflected in a decrease in overall body size and the failure of reproductive organs to reach full development. Helminth species have historically been designated on the basis of minor morphological differences that are often metric in nature, but very few studies consider the effects of host response on the characteristics used in species descriptions.

Studies which document the morphological variability peculiar to a specific host-parasite system across its range of immunologic potentials are, to my knowledge, unavailable. Somewhat better data are available which chronicle the variability induced by different host species upon a single species of parasite, but the immunologic and/or competitive factors which result in differing morphologies have not been examined in most of these studies. For example, Haley (1962) examined some of the complexities of intraspecific variability and reviewed earlier work by Schiller (1959a, b, c) on morphological variability in hymenolepid tapeworms. In addition, several authors have examined intraspecific variability and its impact upon systematic studies of particular trematode groups. In a most comprehensive study, Blankespoor (1974) examined morphological variability in Plagiorchis noblei (Trematoda:

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Plagiorchiidae) which occurs naturally in the red-winged blackbird, Agelaius phoeniceus. He infected 51 species of birds and mammals with metacercariae reared in the laboratory and collected fifteen hundred adult worms from the 17 species of birds and mammals that were suitable hosts. The following previously used characters were unreliable in differentiating species within the genus: body size, size of suckers, position of oral sucker, length of esophagus, extent of vitellaria, size and position of gonads, and size and position of cirrus sac. The degree of variability in size or position in each character in Plagiorchis noblei overlapped the ranges given in descriptions of other species. Blankespoor did not comment on the proximal causes of the observed variability but he did note that Plagiorchis noblei failed to mature sexually in several host species. He concluded that the only stable adult characters which had been previously used in differentiating species of the group were the size ratio of suckers and intra-uterine egg size.

In a similar but less extensive study, Kinsella (1971) evaluated host-induced variation in Quinqueserialis quinqueserialis (Trematoda: Notocotylidae). On the basis of the variability revealed in his study, Kinsella revised the genus, reducing the number of species from five to three. Among the characters influenced by development in different host species were the pattern of uterine folding and certain body and sucker size ratios. Once

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again, both metric and positional characters which had previously been used in species descriptions proved unreliable due to extensive host induced variation.

Additional smaller scale studies address size variation in whole worms or their constituent organ systems. Bruce et al. (1961) found significant differences in the size of reproductive organs from Schistosoma mansoni maturing in twelve mammalian species exposed to infection. Differences in the degree of genital development (size of ovary, testes, etc.) were specifically examined by Berrie (1960), who raised Diplostomum phoxini, normally an avian parasite, in both birds and mice. Works by MacKenzie and McKenzie (1980), Pojmanska (1967) and Watertor (1967) focused primarily on host-induced size differences and their relationships to species level taxonomy of particular genera.

All of these studies examined either qualitative or quantitative characters routinely used in the differentiation of helminth species. Each study revealed levels of host-induced morphological variability which exceed the ranges commonly accepted when distinguishing species. These studies demonstrate clearly that until more information is available, characters which are defined by size differences should be avoided in phylogenetic analysis of trematode taxa.

Another aspect of variability that has particular importance in systematic studies is ontogenetic variability. In order to discern morpological changes due to an

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alteration of normal development, ontogenetic series must be compared using parasites raised in a number of different host individuals and/or species. Such series are available for very few trematode species.

The absence of adequate developmental information has led to the description of new "species" which are, in fact, different development stages of a single species. Goodchild and Martin (1969) provided a good example of the difficulties in discerning ontogenetic synonomy and the potential impact errors in the interpretation of development can have on trematode systematics. In their study of the trematode genus Spirorchis (Spirorchidae), the authors synonomized three previously described "species" as ontogenetic stages of the chelonian blood fluke Spirorchis scripta. The position of certain testes relative to the cecal bifurcation changes during the development of S. scripta and the observed variation overlapped the distinguishing features of the two other species.

One further level of variability seldom considered in the literature on parasitic helminths is that of intraspecific taxonomic variability. The concept of subspecies is virtually non-existent in parasite taxonomy. The geographic sampling of a species which is required to designate separate races is absent for all but a few helminths of medical importance. Where studies do exist, the characters examined are usually differences in biochemical markers or in ability to infect certain hosts, rather than strict

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morphological variation (see Taylor and Muller, 1976, and Taylor, 1965, for examples). In one of the few works which did consider morphology, Hsu and Hsu (1957) examined geographic variation in testes arrangement of Schistosoma japonicum. Depending on the locality, testes were either clustered or arranged in tandem. This level of variablity would have been used to define separate species of a less well understood organism. The importance of biochemical variation has not been integrated into the systematics of parasitic helminths, but the recent proliferation of such work indicates that information valuable to systematic studies will come from biochemical sources in the future (e.g., Ross et al., 1978).

Phylogentic Analysis

The problems of host induced and/or geographic variability have serious implications for evolutionary studies concerning host-parasite coevolution. Hypotheses of evolutionary process cannot be reasonably advanced when the taxa involved are inadequately known. At the species level, problems of variability may be addressed through detailed morphological studies that include data on both ontogenetic and host induced variation. If such detailed studies are unavailable, it may be more productive to conduct an analysis of parasite relationships at a higher taxonomic level which displays a more consistent pattern of variation. Genus and family level characters are less

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likely to involve size differences of the sort shown to vary in the studies I have mentioned. In any case, the first step in any study of host-parasite coevolution should involve careful construction of a parasite phylogeny that takes into account the problems of morphological variation.

The relatively recent rise of phylogenetic systematics has provided improved methods of inquiry aimed at discerning the patterns of relationships among organisms. The concepts of phylogenetic or cladistic analysis were first articulated by the German entomologist Willi Hennig during the early 1950s, but did not have a major impact upon systematic thought until translated into English (Hennig, 1966). The theories advanced by Hennig have been greatly developed and expanded during the past decade. A detailed discussion of current cladistic theory and methodology is available in a number of recent texts including Wiley (1981), Eldredge and Cracraft (1980), and Nelson and Platnick (1981).

In the present study, I chose cladistic analysis as the best method of producing the parasite phylogeny on which I based my inquiry into host-parasite coevolution. The strength of cladistic methodology lies in a detailed analysis of the patterns among the various characters, in this case, morphological attributes of the organisms under study. The distribution of each character or character state across taxa constitutes an individual evolutionary statement. It is the careful knitting together of these individual statements across characters upon

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which a phylogeny is based. Most of the arguments in recent cladistic literature (for examples, see Funk and Books, 1981; and Platnick and Funk, 1983) related to how separate evolutionary statements are best integrated to form phylogenies. I chose one particular method, component analysis of Nelson and Platnick (1981), for use in the present study because it allows all possible configurations of the data to be examined; thus it does not limit a priori the statements that can be made concerning a given phylogeny.

Objectives of the Study

The unique nature of the host-parasite relationship presents a myriad of untapped opportunities for studies of the coevolutionary process (Mitter and Brooks, 1983). My research was prompted by the nearly total lack of modern phylogenetic methodology in studies of helminth systematics. Utilizing the techniques of phylogenetic analysis, I constructed a phylogeny for a particular group of parasites in order to examine hypotheses concerning the occurrence of coevolution. Areas of congruence between host and parasite phylogenies suggested a history of coevolution, while host-shifting was indicated where branching patterns were incongruent.

The group I examined was the trematode family Schistosomatidae. Because of the medical importance of some of its members, the family has been extensively studied

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(Warren, 1973) and it is clear that its members form a well-defined group. These blood flukes are distributed world wide and are found in both birds and mammals. This pattern of distribution in two distantly related host taxa suggested a basis for examining competing hypotheses of host-shifting and coevolution. Also, in contrast with the vast majority of parasitic trematodes, sufficient sources of data were available for use in this study in the form of museum specimens and literature descriptions.

With the possible exception of the human blood flukes Schistosoma mansoni and S. japonicum, most of the problems in species designation discussed previously pertain within the family Schistosomatidae. In addition, many species and a few genera have been described on the basis of a very limited sample, often consisting of one or a few worms from a single host. For these reasons, I decided to perform my analysis at the generic level, since most genera are morphologically distinct and form discrete assemblages. In cases where there were questions concerning the congeneric status of certain species, I examined these species separately.

By choosing to perform my analysis at the generic level, I partially avoided the difficulties presented by host-induced variation because schistosome genera show clear morphological boundaries. To further minimize confounding problems of variation, in choosing characters I focused upon major morphological structures which varied

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between genera but which were consistent within each genus. Even in doing so, inconsistencies appeared in descriptions of certain characters in the literature. It is not always clear whether or not these inconsistencies represent natural variation or inaccurate observation. I have addressed such problems individually as they appear in my description of characters.

In evaluating the relationships of genera within the family Schistosomatidae, it was necessary to have some understanding of the systematic status of related taxa to perform an out-group analysis. The schistosomes have traditionally been grouped with the other two families of blood flukes from vertebrates, the Sanguinicolidae of fishes and the Spirorchidae of turtles. Since there are no detailed systematic studies examining the relationships between the families of blood flukes, I first performed family-level phylogenetic analysis in order to determine the out-group of the Schistosomatidae.

Having a phylogeny I addressed the following questions about schistosome evolution:

1. To what degree are host and parasite phylogenies congruent? In order to answer this question, I compared the phylogenies of parasite taxa and their definitive hosts on the basis of published reports. In part due to an extensive fossil record, vertebrate phylogeny is one of the most robust phylogenies in the literature. Although relatively little information is available

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with regard to intermediate host phylogeny, broad patterns of molluscan host distribution allowed for some degree of comparison.

2. What was the relative importance of host-shifting versus coevolution in the phylogenetic history of the Schistosomatidae? Coevolution is suggested by congruence between host and parasite cladograms, while patterns other than strict co-occurrence may indicate that host-shifting occurred at some point in an organism's lineage.

3. What is the relationship between phylogenetic analysis of host-parasite distributions and historical biogeography? In the recent literature, there has been a strong association between cladistic analyses and historical biogeography (for a summary, see Cracraft, 1983). The main emphasis has been on the principles of vicariance biogeography which examine patterns of organismal distribution under the hypothesis that observed taxonomic boundaries arose through geographic isolation, for example, as a result of continental drift. Vicariance biogeography is based on a model of allopatric speciation and has a parallel in discussions of host-parasite coevolution. Under such a model, parasite speciation is dictated by prior host speciation, just as host speciation is dictated by the isolating events of changing land masses. Therefore, I examined the extent to which parasite

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distributions reflect vicariant isolating effects of host speciation as well as changes in geographic distribution as a result of continental drift.

Schistosomatidae: Natural and Systemtic History

Blood flukes of the family Schistosomatidae belong to the platyhelminth class Trematoda, subclass Digenea, most of which are completely endoparasitic in vertebrates. Digenetic trematodes are characterized by a complex life cycle involving the production of several different larval stages which develop in one or more intermediate hosts (Figure 1). Asexual reproduction frequently occurs in several larval stages.

In all digenetic trematodes, a miracidium develops in the trematode egg and, upon hatching, constitutes the first free-living stage. Miracidia of most species are characterized by a body covered with ciliated epidermal plates (Figure 1); the number and arrangement of the epidermal plates have frequently been used in determining relationships among trematode taxa. The miracidium is either eaten by or penetrates an invertebrate, most frequently a gastropod mollusc. Within the mollusc serving as an intermediate host, the miracidium undergoes metamorphosis to the next larval stage, which may be either a sporocyst or redia. Rediae are characterized by the presence of a pharynx and intestine, which are absent in sporocysts. Sporocysts produce either another generation

Figure 1. Generalized life cycle of the strigeiform trematode Diplostomum baeri (Diplostomatidae) (adapted from Olsen, 1974).

A. Adult

B. Operculate egg

C. Miracidium

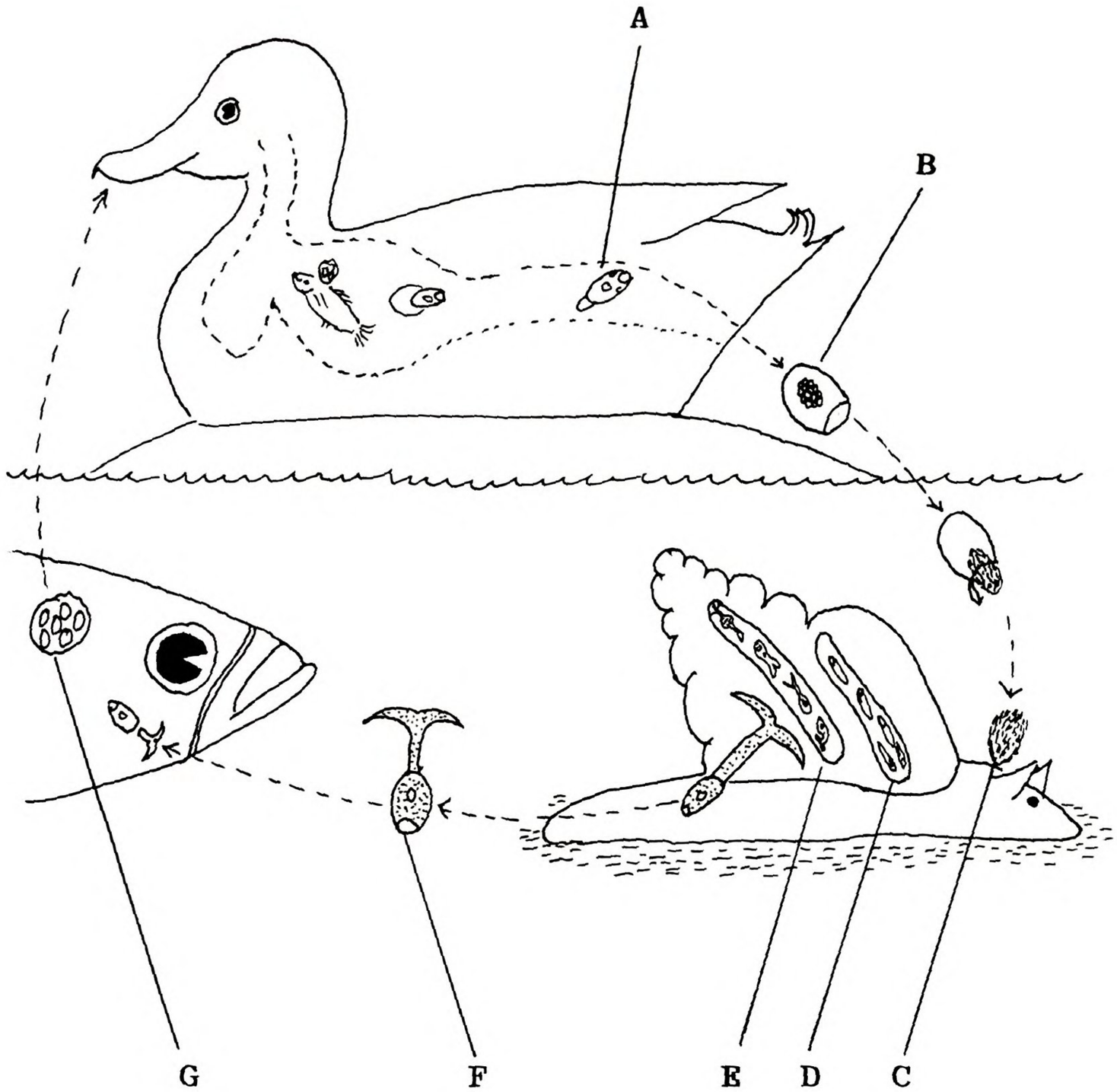
D. Sporocyst

E. Redia

F. Cercaria

G. Metacercaria

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of sporocysts (daughter sporocysts) or a generation of rediae. Two generations of rediae may also occur. Depending upon the trematode species, either sporocysts or rediae produce cercariae. The cercarial stage of most trematodes leaves the mollusc and after a brief free-living period encysts in or on either vegetation or a second intermediate host, or penetrates the definitive host directly. In cases where encystement occurs, the infective stage is called a metacercaria. The metacercaria transforms into a sexually mature adult when ingested by a definitive vertebrate host. The second intermediate host is eliminated in trematodes which penetrate their final host directly.

Above the generic level, much of trematode systematics rests upon a framework based on larval characteristics. LaRue (1957) utilized larval morphology to construct the first substantive higher taxonomy of the digenetic trematodes. On the basis of detailed developmental studies, LaRue divided the trematodes into two major groups according to patterns of cercarial excretory bladder formation. Within the group retaining an epithelial bladder, LaRue erected the suborder Strigeata (order Strigeatida) to contain the Clinostomatidae, the blood flukes (Sanguinicolidae, Spirorchidae and Schistosomatidae) and the so-called strigeiform families (Strigeidae, Diplostomatidae, Proterodiplostomatidae, Cyathocotylidae, etc.). Families within the Strigeata possess a distinctive cercarial morphology in which the tail terminates in a prominent fork.

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The terminal branches of the tail are termed furcae, thus giving rise to the name furcocercous cercariae.

In the present study, I have accepted LaRue's suborDinal classification as a basis upon which to conduct my analysis. In a study which was relatively sophisticated for the time in which it was conducted, LaRue examined consistent patterns of larval variation and utilized detailed developmental information in constructing his taxonomy. LaRue avoided simplistic analyses of adult morphology, the stage in which problems of homoplasy and host induced variation appear to be most prominent. Most importantly, LaRue's higher classifiction of the digenetic trematodes is, for the most part, not based on host relationships; thus host bias at least at the ordinal level appears minimal. Because of these aspects of LaRue's study, I felt his taxonomic framework provided a reasonable place to begin a search for the outgroup of the Schistosomatidae.

The families within the suborder Strigeata are usually divided into three superfamilies (LaRue, 1957). These are the Strigeoidea containing the strigeiform trematodes, the Clinostomatoidea, consisting of the Clinostomatidae and the Schistosomatoidea, composed of the three blood fluke families (Sanguinicolidae, Spirorchidae and Schistosomatidae). The relationships between superfamilies have been discussed only briefly in the literature. Without supplying data in support of his hypothesis, Short (1983)

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suggested that the strigeiform families and clinostomes are more closely related to each other than to the blood flukes. In a recent phylogenetic analysis, based on life history stages, Brooks et al. (1983) proposed that the clinostomes are primitive relative to a clade containing the blood flukes and strigeiform families.

Largely on the basis of their blood inhabiting life-style, the schistosomes have traditionally been grouped with the other two families of vertebrate blood flukes. Ohdner (1912) was the first worker to suggest that the blood flukes from endo- and exothermic vertebrates were related; Ward (1921) also voiced this opinion. In addition to host environment, certain morphological similarities between the families were noted, consisting of the absence of a pharnyx and apparent loss of the redial stage.

Life cycle features are actually poor indicators of relationship among the blood fluke families because the strigeiform trematodes also lack rediae and thus the character is not unique to blood flukes. It is useful to note that this is the sole character upon which Brooks et al. (1983) unite the Schistosomatoidea and Strigeoidea.

Early attempts to clarify relationships between the blood fluke families were rooted in the evolutionary concepts and methodologies of the day. Reflecting a trend that was popular among evolutionary theorists until fairly recently, a number of evolutionary "series" were proposed using the blood fluke families, in which various recent

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forms were thought to have given rise to other recent forms. At a time when very little information on any group of trematodes was available, Ohdner (1912) proposed the evolutionary series Liolope-Haplotrema-Bilharziella-Ornithobilharzia-Schistosoma. In this series, the spirorchid Haplotrema from turtles formed an important connecting genus between the nonblood fluke Liolope (Liolopidae) from amphibians and the more advanced schistosomes of homeotherms. The liolopids are no longer considered to be closely related to the blood flukes, and it is also interesting to note that the blood flukes of humans are considered to be derived from bird-inhabiting ancestors in this series. In addition, the sanguinicolids do not figure at all into Ohdner's scheme.

In a summary of his earlier papers, Mehra (1950) suggested that the spirorchid subfamily Haplotrematinae formed the primitive stock which gave rise to the Sanguinicolidae along one line and the Schistosomatidae along another. In proposing this sequence, Mehra differed from the majority opinion expressed most clearly by Stunkard (1921, 1923, 1970), who saw a logical derivation of spirorchids from sanguinicolids, and of schistosomes from spirorchids. This progressive series was quite compatible with interpretations of host evolution and Stunkard went as far as to suggest that the blood flukes were an ancient group, antedating the origin of birds and mammals.

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Families within the Strigeata show considerable variability with regard to life cycle pattern. Host and larval stage distributions for the families of the suborder Strigeata on which I focus in my analysis are presented in Table 1. All of these families possess an invertebrate intermetiate host and a vertebrate definitive host. Except for some questionable reports of sanguinicolid cercariae developing in pelecypods and annelid worms, invertebrate hosts are always gastropod molluscs. In addition, an intermediate vertebrate host, and thus a metacercariae stage, occurs in all families other than the three blood flukes. Fish usually serve as the intermediate vertebrate hosts, although amphibians (tadpoles) may serve this role for a few species in the families Strigeidae and Diplostomatidae (Dubois, 1938). Finally, cercariae develop from daughter sporocysts in all families except the clinostomes, where a redial stage is present.

Relative to the Schistosomatidae, comparatively little is known about the biology of the other blood flukes. Although sanguinicolids are found in a diversity of marine and freshwater fishes, very few life cycles appear in the literature. While relatively more information is available concerning spirorchids inhabiting freshwater turtles, virtually nothing is known about marine species. Smith's (1972) review of the sanguincolids and spirorchids remains the only major work published on either family in recent years.

TABLE 1

HOST DISTRIBUTION OF FAMILIES IN THE

TABLE 1

HOST DISTRIBUTION OF FAMILES IN THE SUBORDER STRIGEATA

Family	Invertebrate Intermediate Host	Vertebrate Intermediate Host	Final or Definitive Vertebrate Host
Strigeidae	Pulmonata	Fish Amphibians (Tadpoles)	Birds Mammals
Diplostomatidae	Pulmonata	Fish Amphibians (Tadpoles)	Birds Mammals
Proterodiplostomatidae	Pulmonata	Fish	Crocodilians
Cyathocotylidae	Pulmonata	Fish	Reptiles Birds Mammals
Clinostomatidae	Pulmonata	Fish	Birds Crocodilians
Sanguinicolidae	Pulmonata Prosobranchia Annelid worms? Pelecypods?		Fish
Spirorchidae	Pulmonata Prosobranchia		Turtles
Schistosomatidae	Pulmonata Prosobranchia Opisthobranchia		Birds Mammals

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In contrast with the other blood flukes, the family Schistosomatidae has received considerable attention, due no doubt to its human inhabiting members. Blood flukes of the family Schistosomatidae comprise a well-defined group in which all members are dioecius. Although dioecius species and even genera occur in other familes of digenetic trematodes, the schistosomes are unique in that the sexes are separate in all species.

The first species of schistosome was recorded by Rudolphi (1819) and was named Distoma canaliculatum; this avian blood fluke is currently assigned to the genus Ornithobilharzia. The description of the first human schistosome, Distoma haematobium by Bilharz in 1852 was followed by a long period of taxonomic confusion. The genus of the human blood flukes was assigned various names including Schistosoma (Weinland, 1858), Gynaecophorus (Diesing, 1858), Bilharzia (Cobbold, 1859) and Thecosoma (Moquin-Tandon, 1860). The names Schistosoma and Bilharzia were used interchangeably until 1954, when the International Commission on Zoological Nomenclature ruled the generic name of the group Schistosoma, while the term "bilharziasis" should be used to designate the disease.

Stiles and Hassal (1898) assigned the schistosomes to the subfamily Schistosominae of the family Fasciolidae. Loss (1899) raised the group to family rank, the Schistosomidae, and Poche (1907) grammatically revised the family name, replacing it with the term Schistosomatidae. A

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major breakthrough in understanding this group came in 1913 when Miyairi and Suzuki demonstrated the life cycle of S. japonicum.

Price (1929) provided the first major summary of the family, which at that time contained nine genera and 24 species. He divided the family into two subfamilies on the basis of relative length of the gynacophoric canal. The two subfamlies erected by Price, the Schistosomatinae and the Bilharziellinae, are still accepted by most authors, although there have been frequent modifications of the Bilharziellinae. This subfamilial split does not follow lines of host affinity; the Schistosomatinae are found in both birds and mammals, while the Bilharziellinae are strictly avian.

Mehra (1940) raised the genera Gigantobilharzia and Dendritobilharizia to subfamily rank: The Gigantobilharziinae and Dendritobilharziinae. Although this separation was accepted by both Skrjabin (1951) and Yamaguti (1971) in their volumes on digenetic trematodes, there is a major problem with Mehra's division. Although his rationale is not entirely clear, the subfamily Gigantobilharziinae was apparently distinguished due to Mehra's incorrect assumption that the cirrus pouch was absent in the genus. The subfamily Dendritobilharziinae was recognized on the basis of the extensive dendritic branches on the common cecum. Farley (1971) pointed out that females in both subfamilies possess a genital pore which opens at the

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extreme anterior end, next to the mouth. On the basis of this arrangement which is unique within the family, Farley grouped the two genera into a single subfamily, the Gigantobilharziinae.

The only major deviation from this higher taxonomic framework comes from Azimov (1970), who grouped the three families of vertebrate blood flukes into a single order, the Schistosomatida. The schistosomes were divided "on the basis of morphological and ecological peculiarities" into two families: the Schistosomatidae of mammals and the Ornithobilhariidae of birds. This host-based scheme of classification has not been accepted widely and to my knowledge has been used only by Smith (1972).

In a comprehensive manner, Farley (1971) summarized the literature up to that time and gave a taxonomic history of generic classification of the Schistosomatidae. He also synthesized both generic and specific taxonomies and listed known schistosome species. In reading Farley's summary, it is clear that although generic limits are fairly well defined, there is much confusion with regard to species designation. With two exceptions discussed below under Methods, my analysis will utilize Farley's generic designations, presented in Table 2 along with host distributions. Farley's work stands in sharp contrast with that of Yamaguti (1971), who provided the summary of digenetic trematodes most widely used today. Since little or no attention is paid to problems of intraspecific

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TABLE 2

FARLEY'S (1971) CLASSIFICATION OF THE SCHISTOSOMATIDAE AND HOST DISTRIBUTIONS

Subfamilies and Genera	Intermediate Hosts	Definitive Hosts
Schistosomatinae		
Schistosomatium	Pulmonata Lymnaeidae	Rodentia
Bivitellobilharzia	Pulmonata Lymnaeidae	Proboscidea
Heterobilharzia	Pulmonata Lymnaeidae	Carnivora
Orientobilharzia	Pulmonata Lymnaeidae	Artiodactyla
Schistosoma	Pulmonata *Lymnaeidae Planorbidae *Prosobranchia	Artiodactyla Primates Rodentia *Carnivora *Insectivora
Austrobilharzia	Prosobranchia	Anseriformes Charadriiformes
Macrobilharzia	?	Pelecaniformes
Ornithobilharzia	Prosobranchia	Charadriiformes
Bilharziellinae		
Bilharziella	Pulmonata Planorbidae	Anseriformes *Rallidae *Charadriiformes *Pelecaniformes *Podicipediformes
Trichobilharzia	Pulmonata Lymnaeidae *Physidae	Anseriformes *Passeriformes

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Table 2 (continued)

Subfamilies and Genera	Intermediate Hosts	Definitive Hosts
Gigantobilharziinae		
Gigantobilharzia	Pulmonata Physidae Planobidae *Opisthobranchia	Anseriformes *Passeriformes *Charadriiformes *Ardeiformes *Podicipediformes
Dendritobilharzia	?	Anseriformes *Pelecaniformes

*Occurs in less than ten percent of the reports.

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variation in most studies, Yamaguti's uncritical acceptance of just about any named species or genus has led to an over-inflated view of the family.

It is clear from this brief review that a critical approach is needed in order to determine the out-group of the Schistosomatidae. In addition, research to date adds little or no information to considerations of host relationships and their bearing on schistosome evolution. A clearer understanding of the relationships between families and genera is needed in order to discuss questions of evolutionary pattern and process.

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METHODS

Selection of Taxonomic Samples

The first step in any phylogenetic study is determining the taxonomic level at which the organisms in question are to be analyzed. This is often not an easy task since the validity of previously defined taxonomic boundaries is often questionable, and sampling techniques of earlier studies unclear. Carlton (1980) provided a useful discussion of these problems in his analysis of the neotomine-peromyscine rodents, where he utilized large population samples of nominal species and adopted the exemplar method of Sneath and Sokal (1973) in his characterization of species and genera. In the present study, my attempt to use Carlton's methodology met with a number of difficulties.

With the exception of the human infecting schistosome species, large population samples are unavailable for blood flukes. All that is available for the majority of schistosomes are published descriptions and/or type specimens. Specific and even generic descriptions are frequently based on one or a few specimens and the majority of preserved specimens appear to reside in private collections that are not widely accessible.

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METHODS

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The general lack of understanding concerning intraspecific variability and morphological species boundaries further complicated my selection of taxa for analysis. This, coupled with an extremely host-biased proliferation of species names makes the concept of "species" as currently used in parasitology questionable at best.

To cope with these difficulties, I chose to perform my analysis at the generic level. As I have previously discussed, I feel that the schistosome genera represent coherent systematic units. In nearly all cases, these units can be unamibuously differentiated on the basis of morphological characters. Where generic characters are unclear, I performed separate analyses on conflicting species or species groups. Analysis at the generic level was facilitated because at least some specimens from the majority of genera were available from the U.S. National Helminthological Collection which resides at the Animal Parasitology Institute of the U.S.D.A. I used these specimens to supplement and confirm the presence of morphological characters mentioned in published descriptions. Thus museum specimens and descriptions from the literature were the major sources of morphological data in this study.

I limited my character analysis to relatively gross morphological traits which varied between genera but were constant within genera. I was forced to rely totally upon published descriptions in determining the characters

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of certain poorly known genera (e.g., Bivitellobilharzia and Afro-Asian Macrobilharzia).

In addition, I had at my disposal numerous specimens of Schistosomatium douthitti, Schistosoma mansoni and S. japonicum that assisted greatly in interpreting material prepared by other researchers. My choice of morphological characters was limited by the nature of the available material. Certain potentially useful characters which show consistent variation, such as tegumental spination, require special preparation for clear observation and therefore were not examined because I did not have access to previously unstained material. Because they are best observed on living specimens, larval characters were taken entirely from published descriptions.

I chose to follow a modified version of Farley's (1971) interpretation of the family Schistosomatidae. Farley carefully synonymized previous descriptions and grouped the schistosomes into a series of morphologically discrete genera. I varied from his scheme in two instances where character incongruities indicated that the proposed genera were actually more complex than prior observations suggested. The first exception is the genus Sinobilharzia, a name used by Dutt and Srivastava (1961) to designate Ornithobilharzia odhneri (Faust, 1924). Although Farley placed this species in the genus Austrobilharzia, I feel it is safer to regard it as a monotyic genus based on features to be discussed in the survey of characters.

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The second exception concerns African and Indian reports of the genus Macrobilharzia. Although I have retained the Old World forms in the genus Macrobilharzia, I have analyzed them separately due to inconsistencies between Old and New World descriptions. The fourteen genera of schistosomes examined are listed in Appendix I along with the specimens and/or species descriptions used in assembling information on each genus.

In order to analyze relationships within the Schistosomatidae, I needed to determine an appropriate family to be used as an out-group. To do this, I performed an analysis of the eight families within the suborder Strigeata, as defined by LaRue (1957). The character states and their distributions used in this analysis were taken from reviews of the families given by Yamaguti (1971), Dubois (1938), Smith (1972), Price, (1929), and Schell (1970). In assessing family level character state transformations, I utilized other famlies within the order Strigeatida as out-groups of the Strigeata.

Character Descriptions and Analytic Methods

In contast with many systematic studies, there was little previous work on comparative trematode morphology available that I could use as a guide in choosing characters for my analysis. Trematode taxonomy rests on an ill-defined framework in which host relationships, morphology and life history patterns have been knit together to form

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a scheme of relationships. I found few useful characters within this taxonomic framework. The characters that I have defined for analysis are relatively gross morphological attributes, some of which display well defined ontogenetic patterns. I have utilized two methods of determining polarity sequences for multistate characters used in the various analytic methods: out-group analysis and ontogeny.

Out-group analysis is perhaps the most widely accepted method used as an independent criterion for evaluating evolutionary transformations (see Wiley, 1981, for complete discussion). Character states shared by a taxon and its out-group are assumed to have been inherited from a common ancestor, and thus are termed primitive (plesiomorphies). Character states absent in the out-group but present in some members of the taxon under study (apomorphies) may indicate relationship between those members. The problems in distinguishing homology and homoplasy are hopefully minimized by using this method.

The use of ontogeny as an independent criterion for establishing evolutionary transformations was formalized by Nelson (1978). Recently Fink (1982) discussed the conceptual relationship between ontogeny and phylogeny relative to systematic studies and considered the problems which heterochronic development posed for the evaluation of homology. Ontogenetic considerations of character state changes involve a robust adaptation of the biogenetic

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law in which it is assumed that apomorphic character states of a clade go through ontogenetic stages that are recognizable as plesiomorphic or embryonic states of that clade's more primitive relatives, primitive with respect to the character only. Since much of the higher taxonomy of digenetic trematodes is based on development of cercariae, rather detailed literature accounts were available for reevaluation.

I have coded the qualitative characters that form the basis of my analysis as nominal, discrete variables. Most characters express either presence/absence or degree of development of morphological structures and one character (testes number) is meristic.

To generate hypotheses of phylogenetic relationship, I utilized a combination of two methods of phylogenetic inference: component analysis and Farris optimization. Both are variations of the cladistic methodology proposed by Hennig (1966) and each requires an a priori determination of primitive and derived character polarities. Under the component analysis method of Nelson and Platnick (1981), the distribution of each character state across all taxa defines a "component" of node of a hypothetical cladogram. Figure 2, adapted from Straney (1980), illustrates how character state distributions are translated into components. These components are then knit together to form branching diagrams. I utilized Felsenstein's largest clique program to generate all possible combinations of

Figure 2. Translation of data on relationships into components and cladograms. The distribution of three character states (1-3) across four taxa (A-D) in (a) defines groups of taxa, or components (b). These components can be combined in a consistent manner to produce a cladogram (c), although the set of disarticulated components contains the same information as does the full cladogram. The branching diagrams assume that each taxon has been defined by other unspecified character states (from Straney, 1980).

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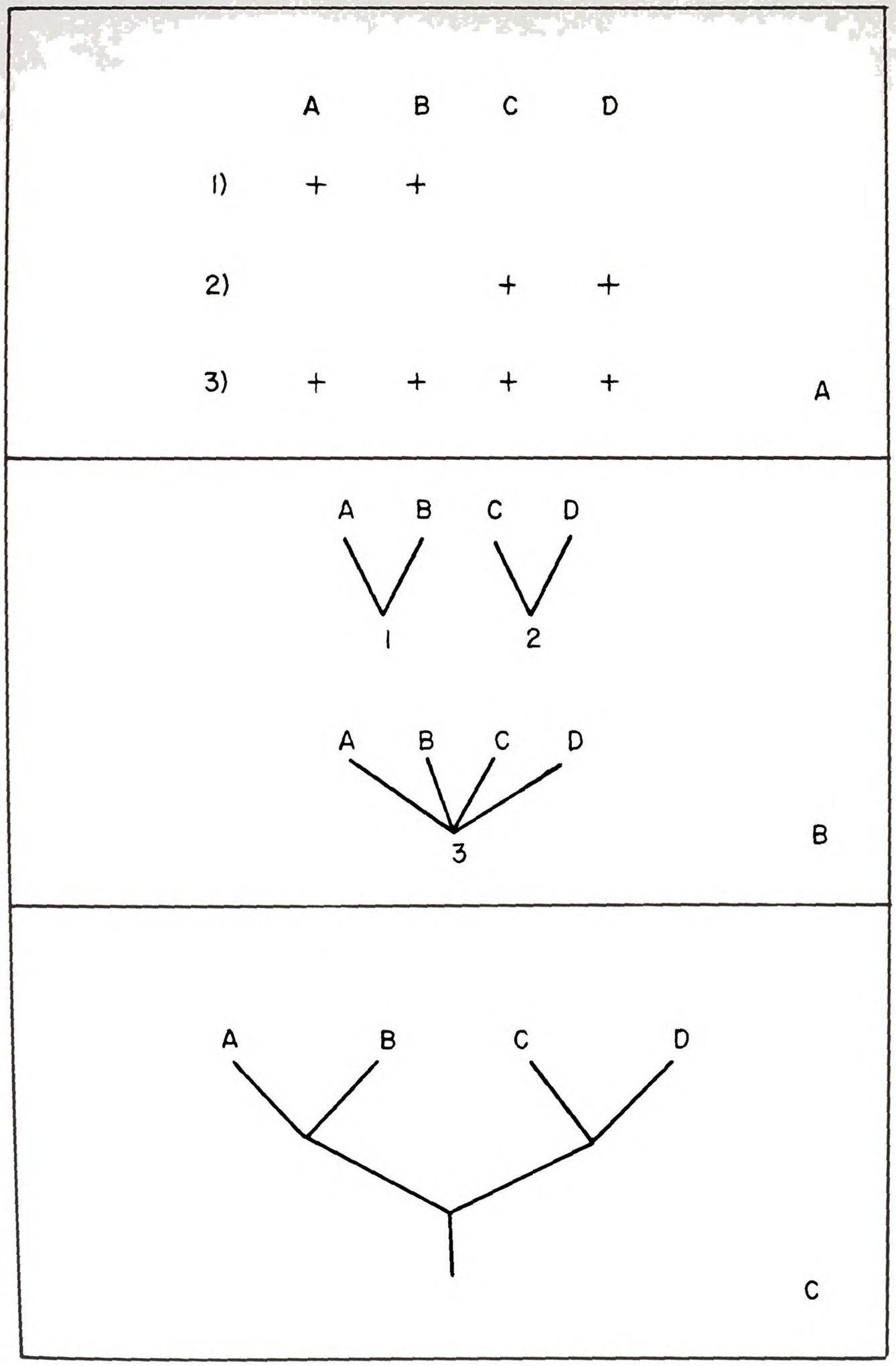

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the components defined by my data. This method generates a large number of cladograms for a given set of data. Arguing by analogy with experimental studies, cladograms containing the most highly replicated components are designated as a smaller subset for detailed analysis of character state distributions. For a more complete discussion of component analysis, see Nelson and Platnick (1981).

The version of the largest clique program used in this study was provided by Joseph Felsenstein of the University of Washington as part of his Phylogeny Inference Package for use on an Apple II Plus computer. For documentation as well as further information on the assumptions and methods of this technique, see Felsenstein (1978, 1979 and 1982).

After I chose a subset of cladograms that were corroborated because they included the most highly replicated component or components, I utilized the principles of Farris optimization to assign character state distributions. Farris optimization was proposed by Farris (1970) and formalized by Mickevich (1981) and is a parsimony method that seeks the branching diagram that minimizes the total number of character state transformations. Thus the cladogram involving the smallest number of steps is considered the most reasonable estimate of cladistic history (see Farris, 1983, for a discussion of parsimony). In actual fact, a number of minimal length cladograms may be generated. When I could not employ parsimony in choosing

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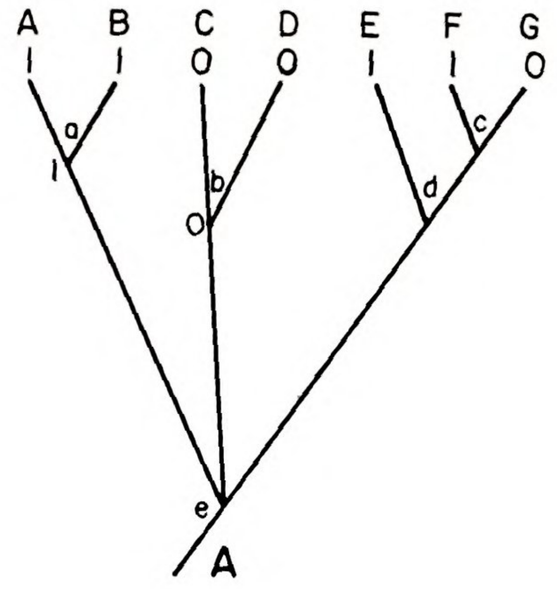
a preferred cladogram because the number of steps in each branching diagram was equal, I adapted the arguments of Hecht and Edwards (1977). Given two cladograms of equal length, I chose the one with the smallest number of branches defined by derived loss characters. The assumption made here is that two organisms are more likely to lose a structure in parallel (thus confounding the search for homology) than they are to evolve a new character state in parallel. In other words, I favored cladograms defined by complex, non-loss characters.

Fundamental to the workings of Farris optimization is the fact that no restrictions on the direction of evolutionary change are imposed, and therefore reversals from derived back to primitive states may occur. This greatly limits the number of parallel events which must be postulated to explain a given character distribution.

Under the optimization method, conflicting character state distributions are assigned to intermediate nodes of a given cladogram. This technique minimizes the total length of a cladogram, resolving multichotomies by combining branches and thus reducing the number of parallel evolutionary changes.

Figure 3A portrays a cladogram consisting of seven taxa (A-G), with the state distribution of a conflicting character occurring in the branch containing taxa E, F and G. The hypothetical character state at an ancestral node is unambiguous if all taxa derived from that ancestor

Figure 3. Farris Optimization.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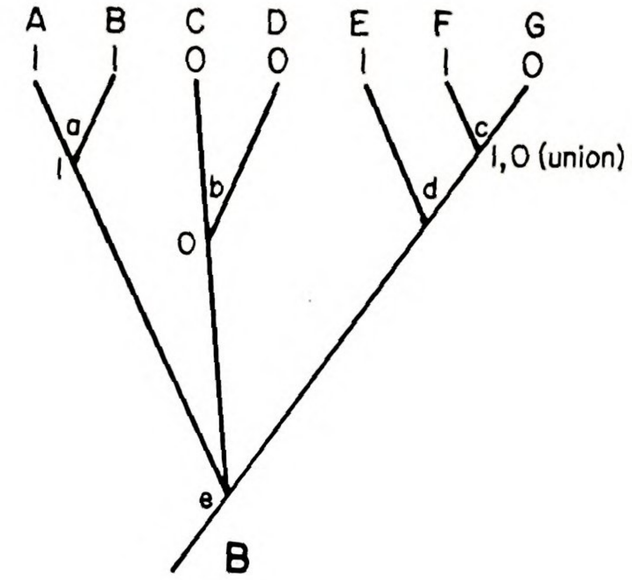
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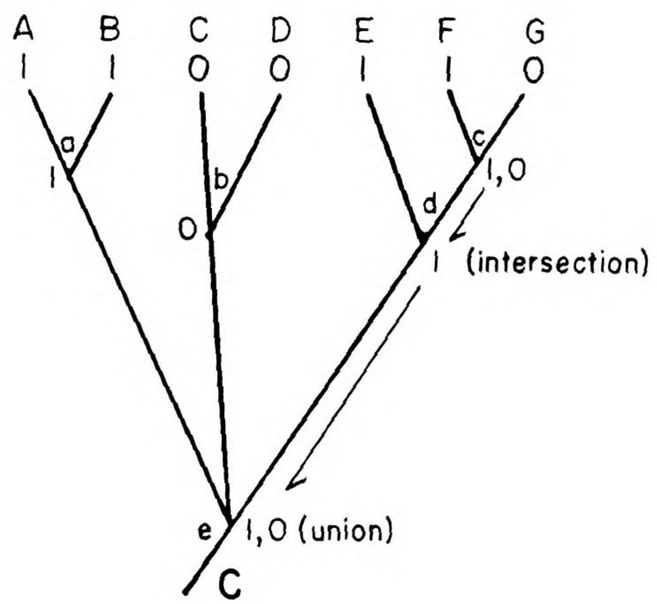
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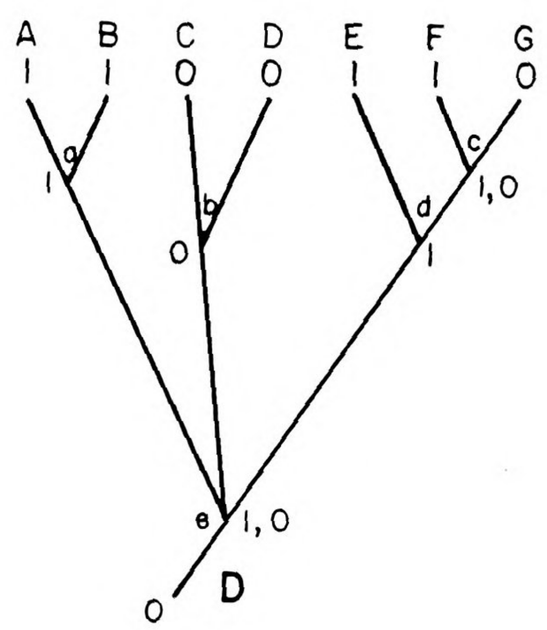
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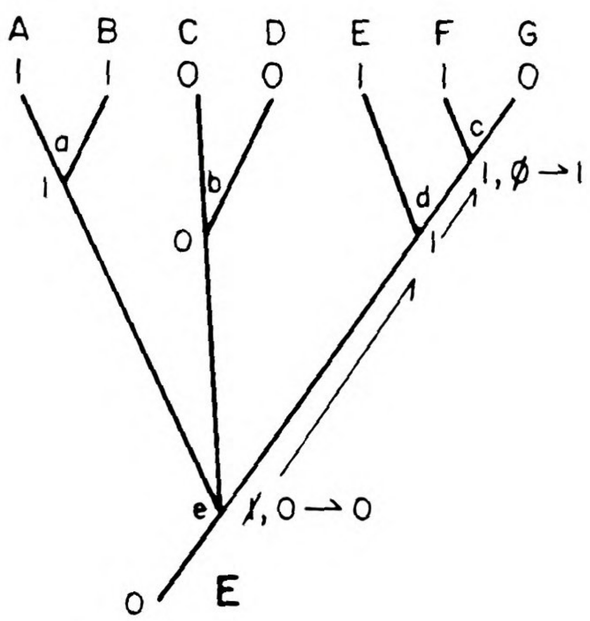
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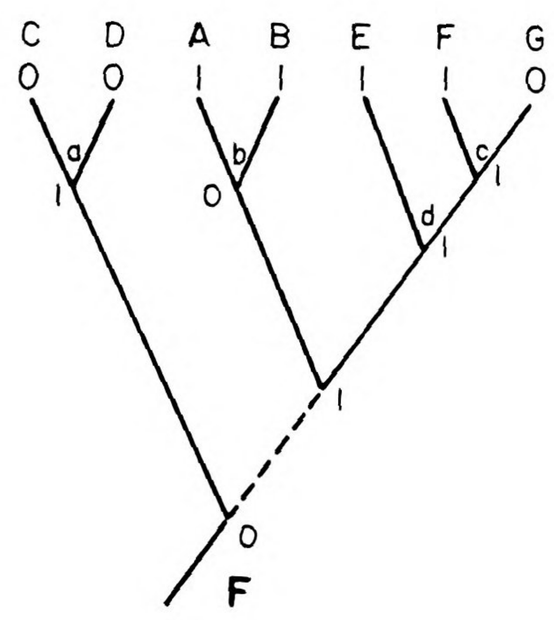
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have the same state. This point is illustrated by nodes a and b in Figure 3A, where the ancestral states 1 and 0, respectively, have been assigned. For the branch giving rise to taxa E-G, the ancestral node is provisionally assigned either the intersection of character states, or the union of states when no intersection occurs (Figure 3B, C). If any ambiguities remain, as in nodes c and e (Figure 3C), they are resolved by taking the intersection of the ambiguous node and its immediate ancestor. This process begins at the base of the cladogram and works up; the most ancestral state is always assumed to be primitive (Figure 3D). In Figure 3E, basal node e is assigned the primitive state. At this point, branches containing the derived state can be combined (Figure 3F). Optimized branches are illustrated by dashed lines. Thus, multichotomies are resolved and the number of parallel events is minimized. This procedure allows characters to undergo reversal to the primitive state (as in taxon G, Figure 3F) and therefore does not force evolution in one direction.

A major goal of this study was to examine hypotheses of cospeciation between parasites and their host taxa. The first step in the process consisted of an independent evaluation of the relationships between parasite genera described above. The next step involved comparing the phylogenetic relationships of host taxa with those of their parasite fauna, in a search for congruent branching patterns that would suggest a history of coevolution.

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At the class level, the phylogenetic relationships between vertebrate taxa are fairly well understood (McFarland et al., 1979). Existing phylogenies provided a basis for comparison with the family-level tree depicting the relationships within the suborder Strigeata.

Likewise, existing host phylogenies were used in assessing the phylogenetic congruence between schistosome host groups. While reasonable phylogenies exist for mammals (McKenna, 1975), the relationships among avian hosts as well as among the pulmonates (and molluscs in general) are far from clear. Although the modern approaches to avian systematics by Cracraft (1981) and to molluscan relationships by Hubendick (1978) are useful, I will address the limitations of these incomplete phylogenies in my discussion.

In my final analysis, I evaluated the preferred parasite phylogeny in light of vicariance biogeographic theory, which suggests that much of organismal evolution and distribution reflects a pattern of isolation during continental breakup. The concepts of vicariance biogeography have been extensively developed by Brundin (1966), Humphries (1981), Rosen (1978), and Nelson and Platnick (1981). These authors provide cladograms depicting continental breakup which I used in comparisons with organismal phylogenies generated in my analysis.

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THE STRIGEATA

Survey of Characters

My analysis and arguments concerning trematode phylogeny are presented in two sections. The 17 characters used in analysis of families in the suborder Strigeata are presented below followed by an analysis and discussion of family level relationships. The 24 characters used in my analysis of generic relationships within the Schistosomatidae begin on page 99. Each character is indexed by a number that serves to identify it in the various tables and figures. Character states are indicated by numbers in parentheses, the inferred ancestral (plesiomorphic) condition being (0) and derived (apomorphic) states consisting of positive numbers. Character state transformations usually follow numerical order, except in instances of furcating character state trees; in such cases, the immediately ancestral state is indicated next to the character state description. The majority of characters are two state variables, but some contain up to five character expressions. I have included discussions to clarify the nature of character variations and problems of homology, and to outline my rationale for determining character polarities. In some cases, this treatment will

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be extensive since argumentation of this sort is lacking in discussions of trematode phylogeny. As previously mentioned, all polarities have been determined on the basis of out-group comparison and ontogenetic arguments.

Family Level Characters

Character 1: Cercarial Body Form.

(0) Simple, straight tailed or tailless.

(1) Furcocercous, forked tails.

Out of the wide variety of cercarial body forms observed in nature (see Schell, 1970, for examples), members of the families in the suborder Strigeata all display a similar developmental pattern leading to a forked tailed, or furcocercous body form (Figure 4). The forked tailed condition is presumably derived from a primitive straight tailed or tailless ancestor. Ontogenetic studies by Hussey (1941), Cort (1917), and Kuntz (1950) indicate that development proceeds from tailless through straight tailed to a final forked tailed form. This character is unique to the order Strigeatida. The above-mentioned developmental studies are used as justification for Characters 2 and 3 as well.

Character 2: Length of Furcae.

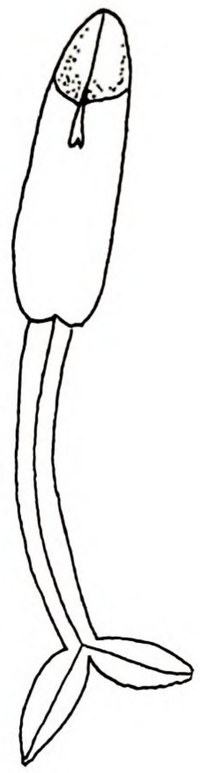
(0) Furcae short: Brevifurcate

(1) Furcae long: Longifurcate

Figure 4. Furcocercous cercariae.

A. Brevifurcate

B. Longifurcate



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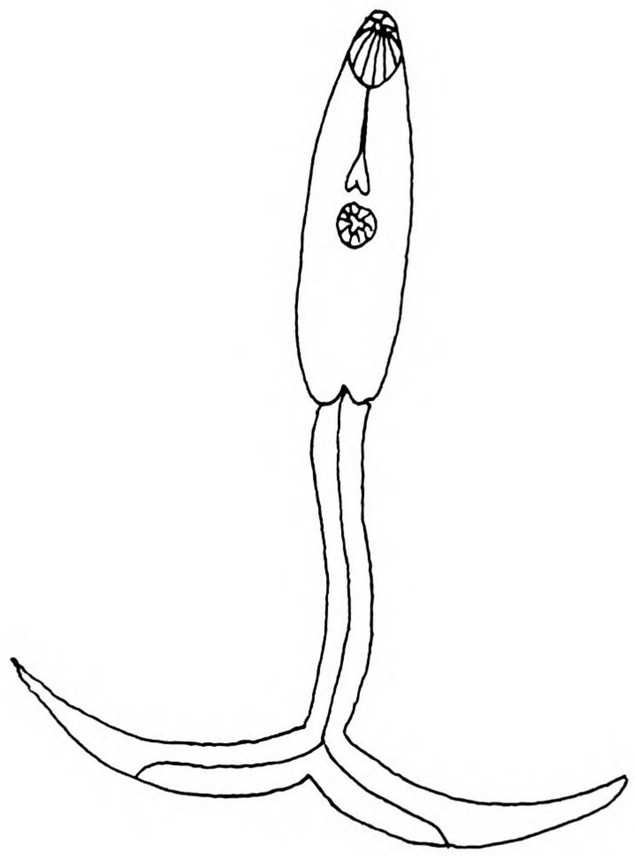

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As mentioned above, the presence of tail forks, or furcae, characterize cercariae of the Strigeatida. During the ontogeny of longifurcate forms the cercaria pass through a stage in which they resemble brevifurcate forms (Figure 4A). The simplest hypothesis therefore is that long furcae develop from extended growth of short furcae, resulting in a derived longifurcate morphology (Figure 4B).

Character 3. Position of Cercarial Excretory Pore.

(0) Terminal.

(1) Subterminal.

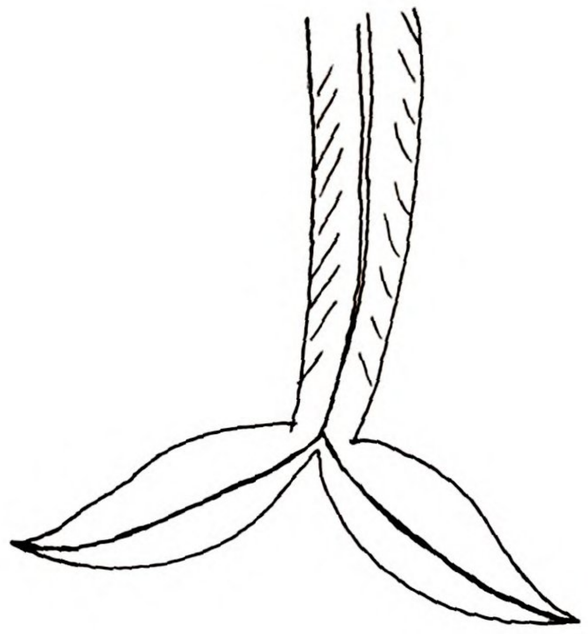
(2) Secondarily terminal.

Developmental studies show that cercariae possessing subterminal excretory pores (Figure 5B) pass through a stage in which the pores are at the tips of the furcae (Figure 5A). Further growth of the furcae produces lengthening beyond the excretory pores. This situation applies for all reports of development within cercariae of the Strigeata, with the exception of so called "vivax" cercariae belonging to the family Cyathocotylidae. Cercariae of this poorly understood family possess terminal excretory pores and are longifurcate. Although developmental studies (Anderson and Cable, 1950; Komiya, 1939) are rare, it appears safest to assume that the terminal pores of vivax cercariae are secondarily derived from the subterminal condition seen in other longifurcate cercariae. This hypothesis is clearly indicated in the developmental study

Figure 5. Position of cercarial excretory pore.

A. Terminal

B. Subterminal



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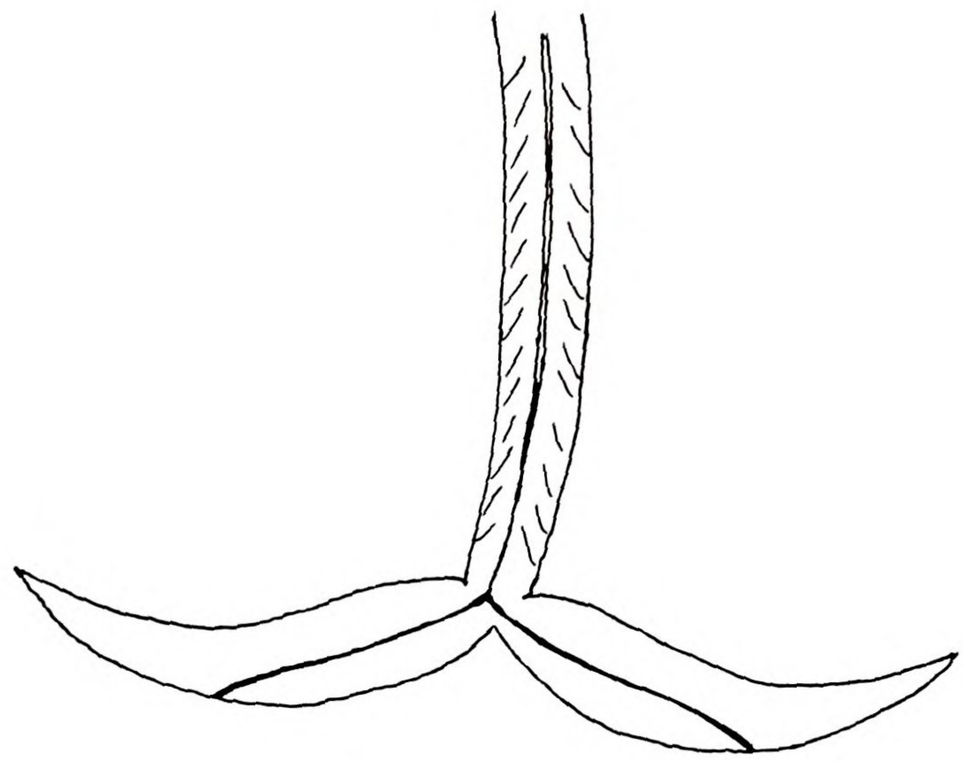

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of Linstowiella szidati by Anderson and Cable (1950). The pores begin at the tips of the furcae in early development, pass through a distinct subterminal phase and then move once again to the tips of the greatly elongated furcae.

Character 4. Site of Cercarial Development.

(0) Redia.

(1) Sporocysts.

Cercariae develop in a number of different larval precursors depending upon the family under examination. The most widespread pattern among trematodes as a whole is the production of cercariae from rediae which have in turn been produced from sporocysts. Within the Strigeata I consider the absence of the redial stage and subsequent production of cercariae from sporocysts as a derived loss condition because redia are widespread in the other families of the order Strigeatida. Among the families involved in this study, only the Clinostomatidae unambiguously possess a redial stage in their life cycle. Although all of the other families have been characterized by the lack of redial stage, there are inconsistencies in reports of the family Sanguinicolidae. Rediae are distinguished from sporocysts because they possess a muscular pharynx, which sporocysts lack (Figure 1). There are four reports of cercariae assigned to the family Sanguinicolidae that develop in rediae. All four reports are problematic, and only in the case of Cardicola (= Sanguinicola) davisi

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(Wales, 1958) has a complete life cycle been documented, although the published report is sketchy and many details are absent. McCoy (1929) and Croft (1933) reported that Cercaria brevifurca and C. whitentoni, respectively develop in rediae. ("Cercaria" is the generic name assigned to trematode cercariae of unknown affinities.) These cercariae possess a dorsal-median fin fold, common to both sanguinicolids and clinostomatids. Both cercariae appear to be classic sanguinicolid lophocercaria larvae, but adult stages which would distinguish these cercariae from clinostomatid larvae have not been described for these cercarial "species." Likewise, Cercaria hartmanae (Martin, 1952) and C. amphicteis (Oglesby, 1961), which develop in redia from annelid worms, are assumed to be sanguinicolids. Once again, the adult stages are undescribed and the cercariae possess certain morphological abnormalities which I will discuss in a subsequent section.

These three examples highlight the fact that the family Sanguinicolidae is poorly known and is, most likely, highly variable. In order to address the potential variability seen in the Sanguincolidae, I coded this character in two different manners, resulting in two different data sets which I analyzed separately. First, until more substantial instances of cercarial development in redia are reported, I scored the sanguinicolids for the derived state in which the redia is absent, as indicated by the majority of studies (see Smith, 1972, for an extensive

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bibliography). Secondly, I coded the sanguinicolids for the primitive state based on the limited reports of redial development because the primitive state occurs within the range of variation displayed by the taxon and the derived state shown by certain members of the family may have been independently achieved one or more times. Until more data are available, I cannot distinguish between the two alternative codings.

Character 5. Presence/Absence of Muscular Pharynx.

(0) Pharyngeate.

(1) Apharyngeate.

A muscular pharynx is found in both the cercariae and adults of most digenetic trematodes. It is absent and considered to be a derived loss character only in adults and cercariae of the schistosomes and spirorchids. The loss of a pharynx has assumedly occurred in parallel in adults of one genus (Apharyngostrigea) in the family Strigeidae, since the pharynx is present in cercariae (Oliver, 1940). There is one report of a pharynx present in the cercariae of the sanguinicolid Cardicola davisi (Wales, 1958). This is consistent with the reports of redial development in the same study, and although unique, there is currently no way to confirm or deny its validity. Accordingly, I will provide two codings of this character in two separate data sets, following the argument used in considering Character 4. It is useful to note that

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all pharyngeate lophocercariae (cercariae of the families Sanguinicolidae and Clinostomatidae that possess a dorsal-median fin fold) for which the adults are unknown are automatically considered to be clinostomatids. This may underestimate the occurrence of pharynges in the sanguinicolids. To further confuse matters, Agarwal (1959) notes that cercariae of the clinostomatid genus Clinostomum may lack a pharynx in both cercariae and adults. I assume that this is a unique loss event, since the majority of clinostomes possess pharynges.

Loss of the pharynx along with the absence of a redial stage were used to establish the superfamily Schistosomatoidea in the taxonomy of LaRue (1957).

Character 6. Miracidial Plate Pattern: Numbers of Plates in the Four Consecutive Tiers.

(0) 6,8,4,3.

(1) 6,6,4,2.

The miracidia of most trematodes are covered with tiers of ciliated plates. In nearly all families of the order Strigeatida, the number of plates in each of the four tiers is remarkably consistent: 6 in the first, 8 in the second, 4 in the third, and 3 in the fourth. Within the Spirorchidae, a presumably autapomorphic condition occurs in which the number of plates in rows two and four differ: 6,6,4,2.

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Character 7. Organization of Cercarial Anterior End.

(1) Oral sucker present, mouth terminal.

(1) Head-organ present, mouth subterminal.

The presence of an oral sucker and penetration gland ducts surrounding a terminal mouth in cercariae (Figure 6A) is widespread among the families in the order Strigeatida as well as in the cercariae of trematodes in general. In the three families of blood flukes and the clinostomes, the anterior end of the cercaria is modified to form what has been called a head-organ (Figure 6B). In this condition the oral sucker is absent, the mouth is subterminal and a series of penetration glands send ducts up to terminal openings. The head organ is found nowhere else among the trematodes, and I assume it to be a derived, homologous character state.

Character 8. Penetration Glands.

(0) One morphological type.

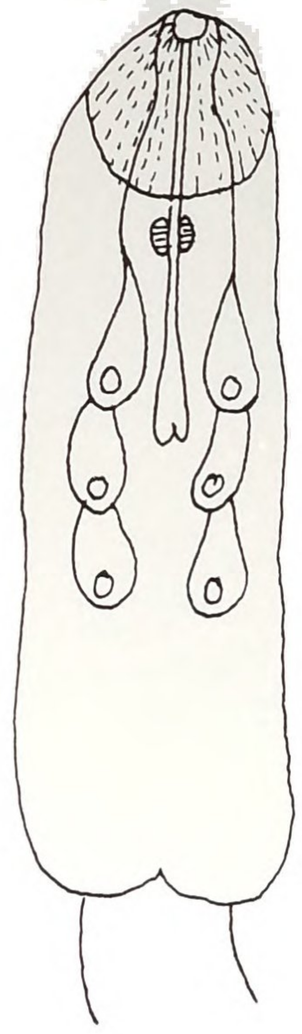
(1) Two morphological types.

The different types of penetration glands found in trematode cercariae are distinguished by their differential staining ability. Some glands have an affinity for basic stains while others take acidic stains. Most cercariae possess penetration glands of a single morphological (staining) type. In schistosomes and spirorchids, the glands are differentiated into an anterior mucoid group and a posterior lytic group. I will presume that the presence

Figure 6. Organization of cercarial anterior end.

A. Oral sucker present, mouth terminal

B. Head-organ present, mouth subterminal



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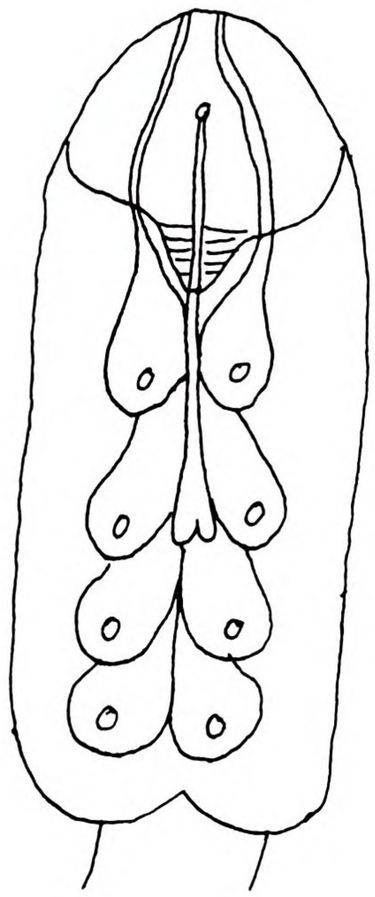

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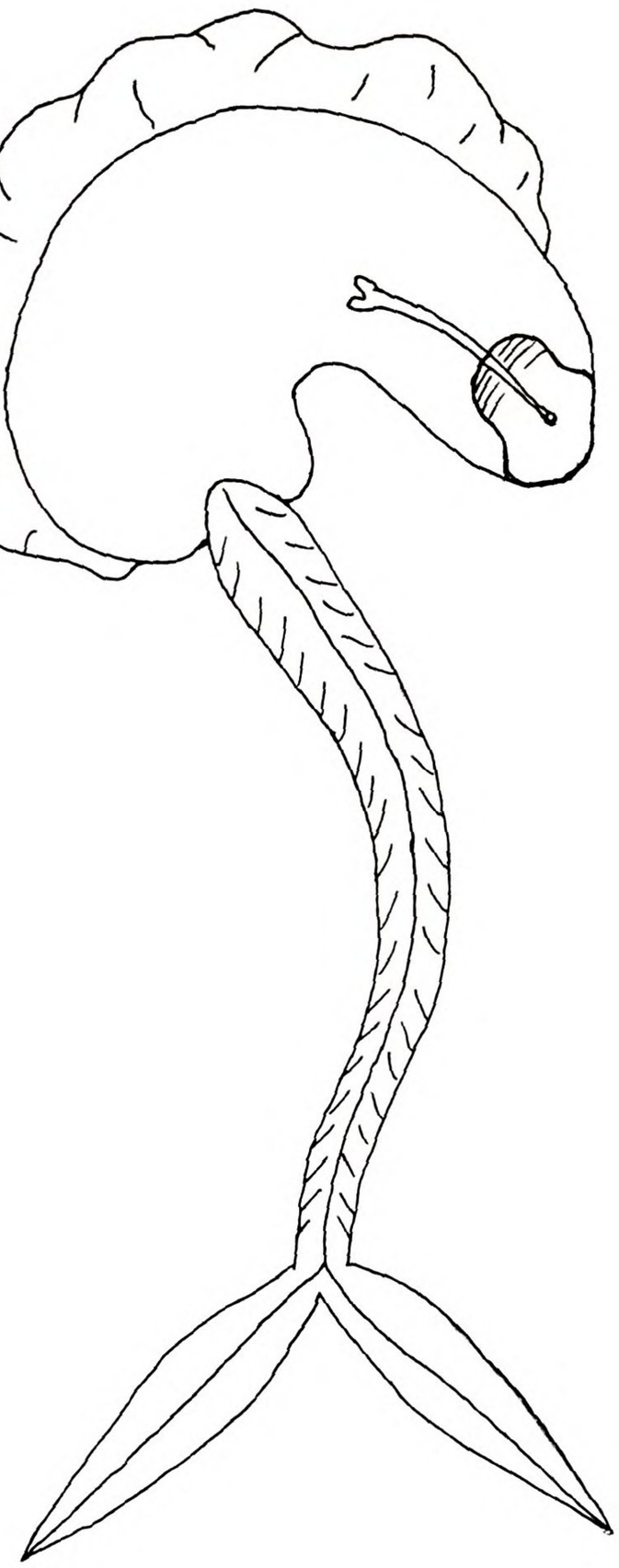
Figure 7. Lophocerous cercaria (=Lophocercaria).



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of these two gland types represents a homologous and derived condition, because this arrangement is found nowhere else among the Strigeatida.

Character 9: Cercarial Dorsal-Median Fin Fold.

(0) Absent.

(1) Present.

A prominant dorsal-median fin fold (Figure 7) is characteristic of sanguinicolid and clinostomatid cercariae. Collectively, cercariae possessing this character are known as lophocercariae. There are some reports of presumed sanguinicolid cercariae in which the fin fold may be absent (Cercaria solemyae, Martin, 1944, and C. amphicteis, Oglesby, 1961). In both cases, complete life cycles are unknown and the organisms are questionably assigned to the Sanguinicolidae. Until more complete life cycle information is forthcoming, I think it is safest to assume that the dorsal median fin fold is a derived structure shared by the two families.

Character 10. Egg Type.

(0) Operculate, tanned shell.

(1) Non-operculate, tanned shell.

(2) Non-operculate, thin, elastic shell; derived from state (0).

Operculate eggs with thick shells hardened by quinone tanning (Cheng, 1973) are widespread among families in the Strigeatida and among trematodes in general. The

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non-operculate eggs of schistosomes and sanguinicolids do not appear to be homologous and their modes of hatching differ substantially. Sanguinicolid eggs are elastic and thin shelled. They apparently remain in the fish host and hatch there, commonly in the gill filaments (Smith, 1972). In contrast, thick, quinone-tanned eggs of schistosomes leave the final host with the feces (and/or urine) and hatch in the external environment. I consider the eggs of schistosomes and sanguinicolids as independently derived, autamorphic characters because the details of miracidial hatching suggest that the loss of an operculum may not be homologous. In schistosomes, the top portion of the egg comes off upon hatching in a manner analogous to the opening of an operculum (Faust et al., 1934). In contrast, the eggs of sanguinicolids appear to disintegrate upon hatching, giving no suggestion of an operculumlike release mechanism (Ejsmont, 1926).

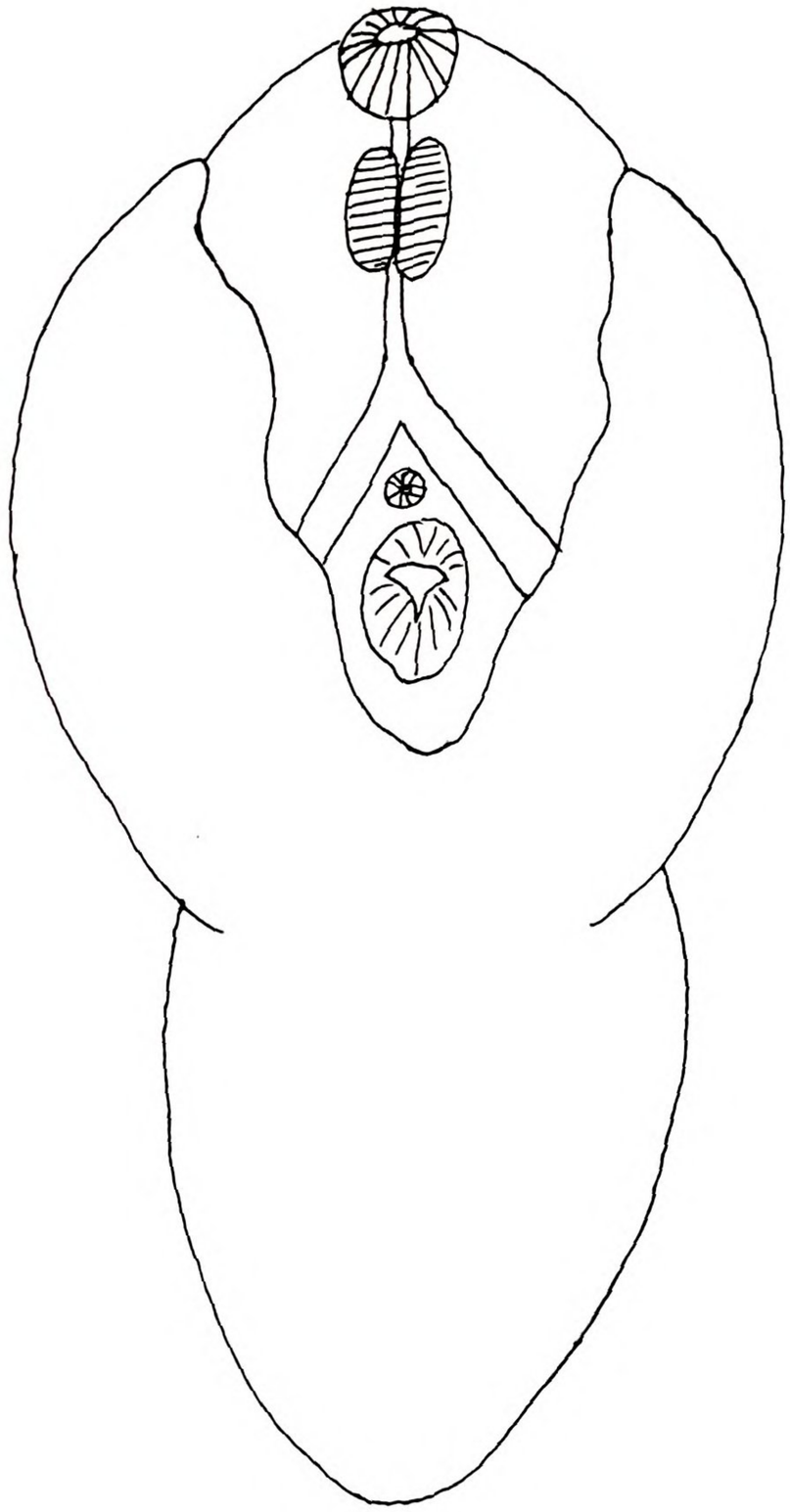
Character 11. Tribocytic Organ.

(0) Absent.

(1) Present.

The tribocytic organ is a foliaceous or bulbous expansion of the anterior end (Figure 8) unique to four (perhaps more) families of strigeiform trematodes. Because of structural similarity, this complex organ is considered by Dubois (1938) to be homologous in the groups possessing it. I consider its presence a derived character.

Figure 8. Adult strigeiform trematode displaying the tribocytic organ.



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Character 12. Condition of Intestinal Cecae.

(0) Terminate blindly.

(1) United at posterior end.

Intestinal cecae which terminate blindly (Figure 9A) constitute the widespread condition in families of the order Strigeatida as well as in digenetic trematodes in general and are assumed to be the primitive condition. The cecae of all schistosomes and one genus of the morphologically diverse family Spirorchidae unite posteriorly to form a continuous loop (Figure 9B). I have coded the family Spirorchidae for the primitive condition, under the rationale that while partially retaining the primitive condition, one genus has independently developed the derived morphology in parallel with the schistosomes.

Character 13. Anterior Cecal Branches.

(0) Absent.

(1) Present.

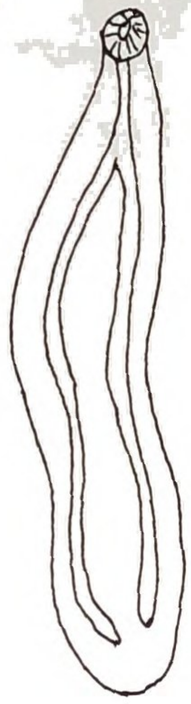
Anterior cecal branches (Figure 9C) are most likely a derived condition unique to the Sanguinicolidae. Anterior cecal branches appear to be absent in two poorly known genera, which may eventually prove to be congeneric. Chimaerohemecus trondheimensis has been reported twice (Van der Land, 1967 , and Drenske, 1968) from the rat-fish, Chimaera monstrosa, in the North Sea, while Orchispirium heterovitellatum has been reported once (Madhavi and Rao, 1967) from the ray, Dasyatis imbricatus in the Bay of

Figure 9. Condition of intestinal cecae.

A. Terminate blindly

B. United at posterior end

C. Anterior cecal branches present



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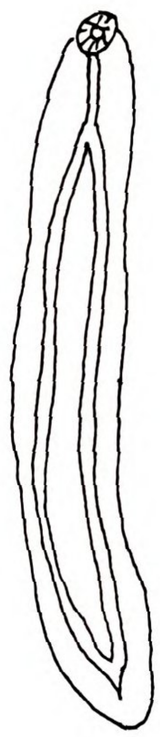

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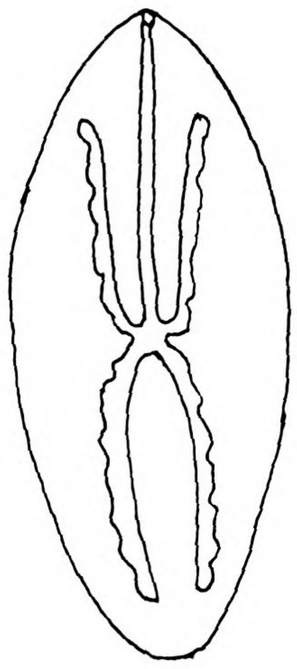

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Bengal. As of yet, these specimens are too poorly known to warrant a change in the character coding for the group, but they suggest that the family may not be as homogeneous as previously thought. There is some indication that anterior cecal branches may exist in reduced form in Orchispirium, which has a bulbous expansion on either side of the point where the esophagus meets the cecal bifurcation. A firm hypothesis of reduction and loss of the branches in these two genera must await further information and direct examination of specimens.

Character 14. Separation of Sexes.

(0) Monoecious.

(1) Dioecious.

Although dioecious species are rarely found in several trematode families (e.g., Didymozoidae) among the Strigeatida, only the Schistosomatidae possess separate sexes. In addition, this is the only trematode family in which all species are dioecious. It is likely that the dioecious condition arose independently in a number of trematode families and its occurrence in the schistosomes represents a uniquely derived condition within the Strigeatida.

Character 15. Esophageal Gland Cells.

(0) Absent.

(1) Present.

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With the exception noted below, esophageal gland cells (Figure 10) appear to be unique to the families Spirorchidae and Schistosomatidae and are coded as a derived character. Gland cells have been reported in the two aberrant sanguinicolids mentioned in the discission of Character 13: Chimaerohemecus trondheimensis and Orchispirium heterovitallatum. These two blood flukes are very poorly known and until more detailed morphological studies are available, I will assume that esophageal gland cells of sanguinicolids represent one or two derivations in a parallel with those of other blood flukes.

Character 16. Acetabulum (Ventral Sucker).

(0) Present in at least some life history stage.

(1) Absent in all life history stages.

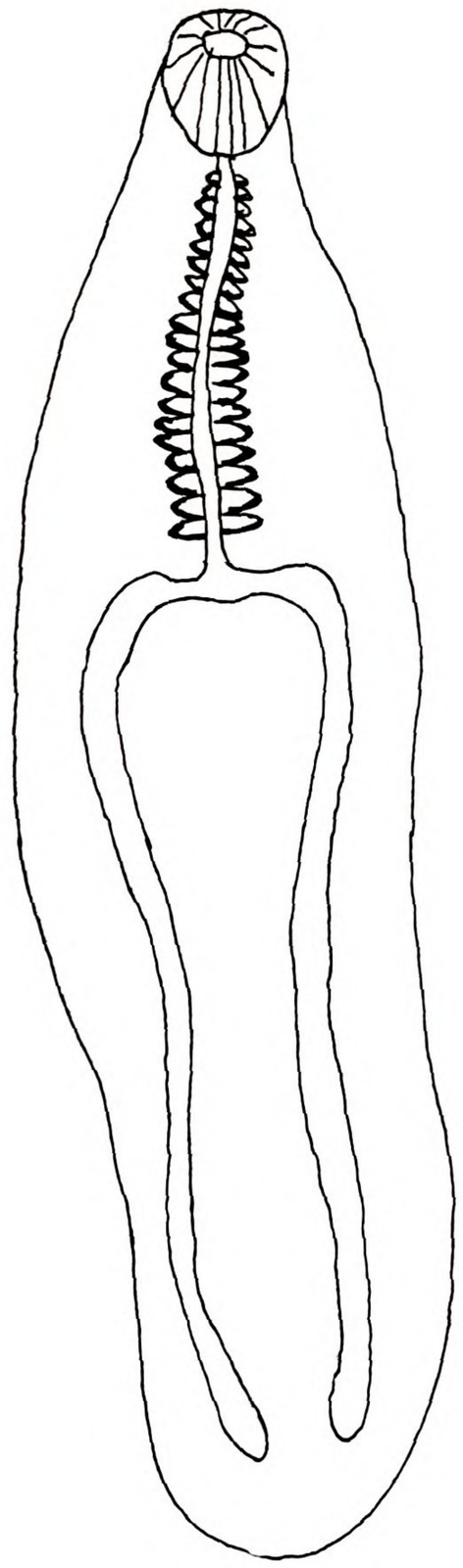
The acetabulum is found in nearly all digenetic trematode taxa. In the Schistosomatidae the acetabulum may be absent in adult worms (e.g., Gigantobilharzia) but its presence in cercariae indicates loss during metamorphosis into the adult stage. The acetabulum is never found in the sanguinicolids and I consider this a derived loss character.

Character 17. Genital Pore.

(0) Male and female ducts open into a common pore.

(1) Separate, monoecious.

Figure 10. Esophageal gland cells present.



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(2) Separate, dioecious; derived from state (0).

A common genital pore receiving both male and female ducts is found in nearly all trematode taxa and in all Strigeatida with the exception of the schistosomes and sanguinicolids. The arrangements seen in these two families are not likely to be homologous for two reasons. First, the sexes are separate in the Schistosomatidae, while both sets of reproductive organs are found in the same individual in the Sanguinicolidae. Secondly, in schistosomes the genital pore of each sex is located anterior to the reproductive organs, usually immediately behind the acetabulum. In sanguinicolids, the genital pores are located behind the reproductive organs, at the posterior end of the body. I consider these two conditions to be independent derivations from the primitive state.

Phylogenetic Analysis

I conducted an analysis of the phylogenetic relationships of families in the suborder Strigeata in order to determine the out-group of the Schistosomatidae. Because of the ambiguities present in data from the family Sanguinicolidae, I analyzed two different data sets in which the problematic characters received different codings. The derived state of Character 4 involves the loss of the redial stage. Among families of the Strigeata, only the clinostomes unambigiously possess rediae. Several

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questionable reports suggest that a redial stage may be present in certain sanguinicolid life cycles (see Character 4). Therefore in the first data set (Data Set I, Table 3), I scored the sanguinicolids as possessing the primitive redial stage, under the assumption that the majority of species have lost the redia in parallel with other families. Conversely, in Data Set 2 (Table 3), I score the sanguinicolids as having undergone a derived loss of the redia.

In a similar manner, the derived state of Character 5 designates loss of the pharynx in cercariae and adults. Once again, a pharynx is reported as present in a few sketchy reports of sanguinicolid cercariae (see Character 5). Therefore I have coded the sanguinicolid pharynx as present in the first data set and absent in the second. In the first data set, those sanguinicolids with no pharynx are presumed to have lost it in parallel with other families.

Both data sets listed in Table 3 consisted of 17 characters in a total of 37 states, designated for 8 families. The components specified by the character distributions are listed in Table 4. I have omitted single taxon components specified by autapomorphies from Table 4 because they do not aid in producing branching diagrams. To perform a component analysis, I used Felsenstein's largest clique program to generate all possible combinations of the components contained in Table 4. Computer analysis

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TABLE 3

CHARACTER STATE DISTRIBUTIONS OF THE STRIGEATA

DATA SET 1 Character State	Strigeidae	Diplostomatidae	Proterodiplo-stomatidae	Cyathocotylidae	Clinostomatidae	Sanguinicolidae	Spirorchidae	Schistosomatidae
1	1	1	1	1	1	1	1	1
2	1	1	1	1	0	0	0	0
3^1	1	1	1	1	0	0	0	0
3^2	0	0	0	1	0	0	0	0
4	1	1	1	1	0	0	1	1
5	0	0	0	0	0	0*	1	1
6	0	0	0	0	0	0*	1	0
7	0	0	0	0	1	1	1	1
8	0	0	0	0	0	0	1	1
9	0	0	0	0	1	1	0	0
10^1	0	0	0	0	0	0	0	1
10^2	0	0	0	0	0	1	0	0
11	1	1	1	1	0	0	0	0
12	0	0	0	0	0	0	0	1
13	0	0	0	0	0	1	0	0
14	0	0	0	0	0	0	0	1
15	0	0	0	0	0	0	1	1
16	0	0	0	0	0	1	0	0
17^1	0	0	0	0	0	1	0	0
17^2	0	0	0	0	0	0	0	1

*Data Set 2 differs in substituting the derived state for the starred characters.

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TABLE 4

COMPONENTS SPECIFIED BY CHARACTER STATE DISTRIBUTIONS OF THE STRIGEATA

Component	Families	Defining Character State
1	All families	1
2	Strigeidae, Diplostomatidae, Proterodiplostomatidae, Cyathocotylidae, Sanguinicolidae, Spirorchidae, Schistosomatidae	4 (Data Set 2)
3	Strigeidae, Diplostomatidae, Proterodiplostomatidae, Cyathocotylidae, Spirorchidae, Schistosomatidae	4 (Data Set 1)
4	Strigeidae, Diplostomatidae, Proterodiplostomatidae, Cyathocotylidae	2, 3[1], 11
5	Sanguinicolidae, Spirorchidae, Schistosomatidae	5 (Data Set 2)
6	Clinostomatidae, Sanguinicolidae, Spirorchidae, Schistosomatidae	7
7	Spirorchidae, Schistosomatidae	5, 8, 15 (Data Set 1) 8, 15 (Data Set 2)
8	Clinostomatidae, Sanguinicolidae	9

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of Data Set 1 generated two unique cladograms while Data Set 2 yielded three topologies.

The cladograms generated by the component analysis are illustrated in Figure 11. All five cladograms contain a quadrichotomy consisting of the four strigeiform families. Due to my character state designation, all four families have identical codings. I chose to accept this uninformative coding scheme because the strigeiform families were of interest only as potential outgroups. One other feature common to all five cladograms is the designation of the spirorchids as the sister taxon, and thus the outgroup, of the Schistosomatidae.

In Figure 11A and B, I assigned character state distributions to the two branching diagrams produced by Data Set 1; each contained 21 evolutionary steps. In Cladogram 1 (Figure 11A), Component 6 unites the clinostomes and the three blood fluke families on the basis of the shared cercarial head-organ (Character 7). Component 8 defines the clinostomes and sanguinicolids as sister groups because their cercariae possess a dorsal-median fin fold (Character 9). The tetrapod blood flukes (Schistosomatidae and Spirorchidae) form a terminal dichotomy defined by Component 7. Two character states contribute to Component 7: 8--derived penetration gland pattern and 15--presence of esophageal glands.

In depicting the clinostomes and sanguinicolids as a sister lineage to the schistosome-spirorchids, Cladogram

Figure 11. Component analysis of the Strigeata. Components are indicated by circled numbers. Gain of a derived character state is indicated by the symbol (X), reversal by (0). Optimized branches are indicated by dashed lines.

A. Cladogram 1, Data Set 1, 21 steps

B. Cladogram 2, Data Set 1, 21 steps

C. Cladogram 3, Data Set 2, 22 steps

D. Cladogram 4, Data Set 2, 22 steps

E. Cladogram 5, Data Set 2, 22 steps

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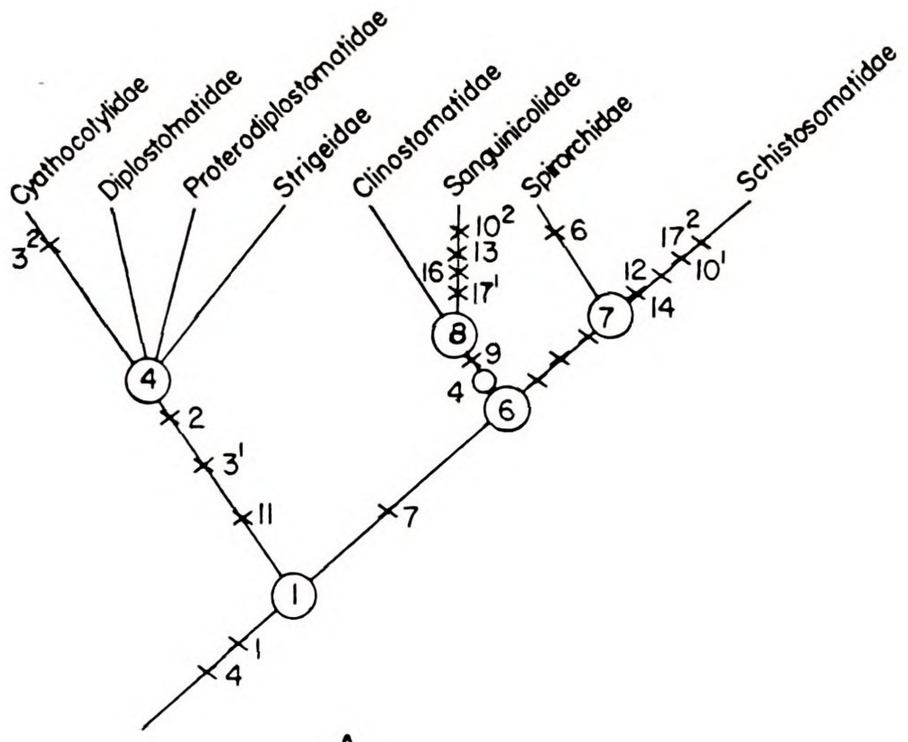

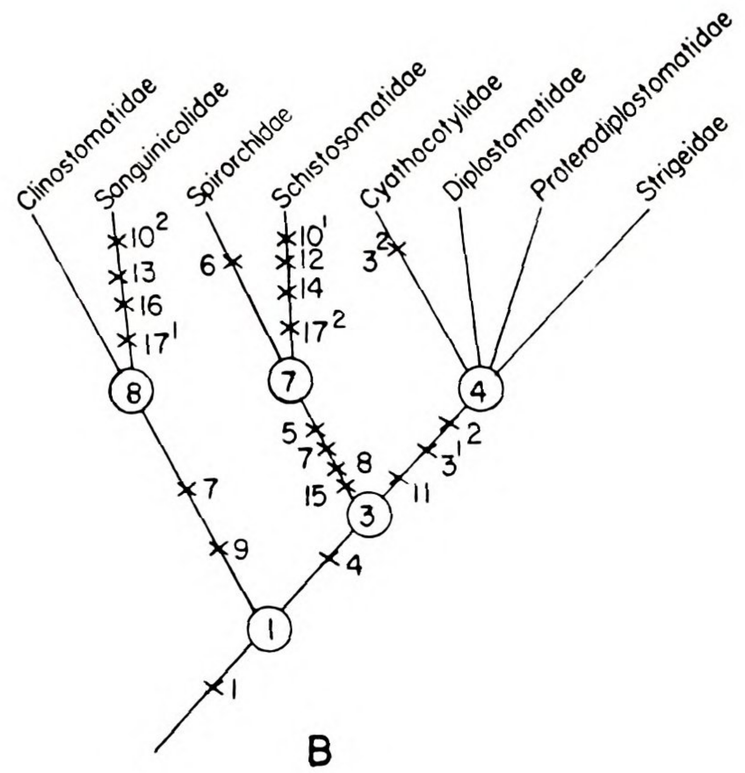


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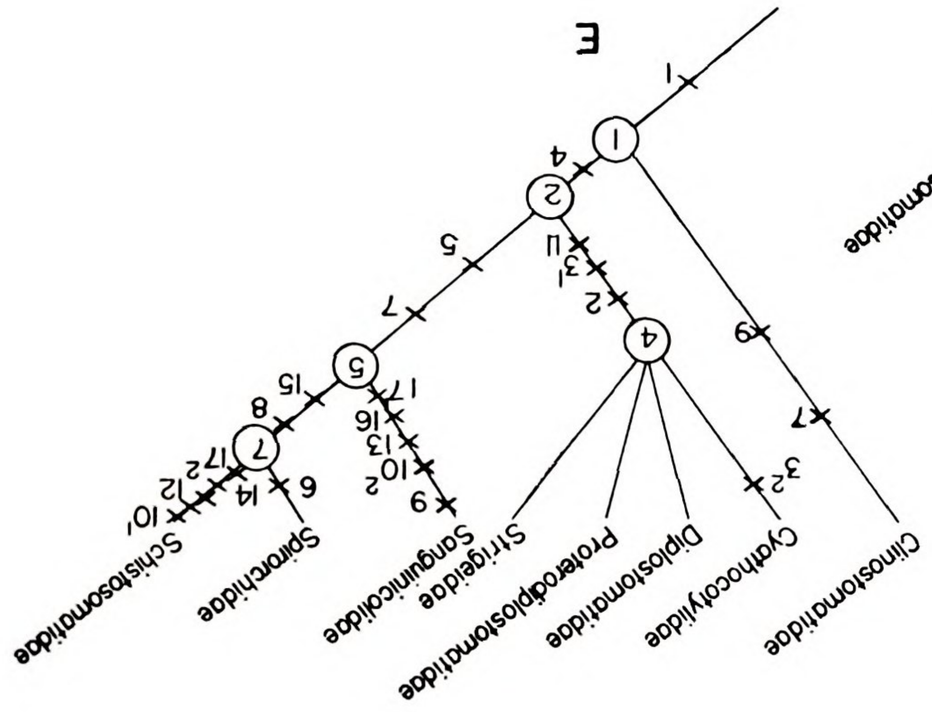
Xenotrichidae
Zoiostomatidae
Zygiellidae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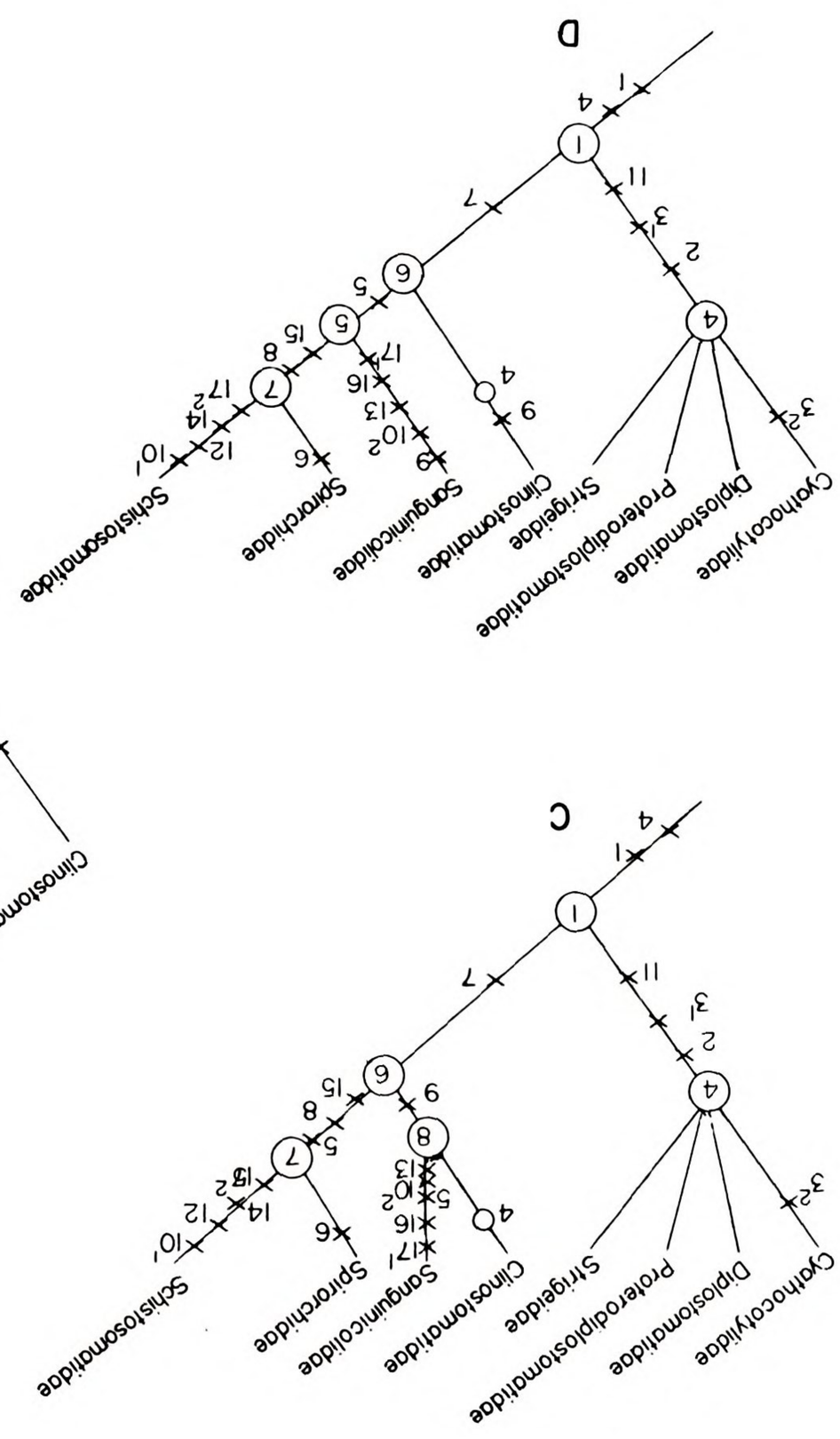
Proterodiplostomatidae
Strigeidae
Sanguinicolidae
Spirorchidae
Schistosomatidae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Strigeidae
Sanguinicolidae
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1 requires a parallel loss of the redial stage (Character 4) in the strigeiform families and tetrapod blood flukes. This branching sequence could also be explained by a reversal in which the redia reappeared in clinostome and sanguinicolid life cycle. The relationships portrayed in Cladogram 1 differ markedly from standard interpretations which place the three families of blood flukes in a single superfamily, the Schistosomatoidea.

The second cladogram produced by component analysis of Data Set 1 also differs from traditional taxonomy in that the clinostome-sanguinicolids form a sister group to a branch containing the tetrapod blood flukes and strigeiform families (Figure 11B). Component 3 removes the clinostomes and sanguinicolids since these taxa retain rediae (Character 4) and cercarial pharynx (Character 5). Cladogram 2 requires the parallel evolution of the cercarial head-organ (Character 7) in the clinostomes and blood flukes, or alternatively its loss in the strigeiform families.

The three cladograms generated from Data Set 2 each require 22 evolutionary steps. Cladograms 3 (Figure 11C) is identical in topology to Cladogram 1, and the defining components are the same in each case. Two conflicting character state distributions are indicated. First, a reversal to development in rediae (Character 4) occurs in the clinostomes and second, the pharynx is either lost in parallel in the sanguinicolids and tetrapod blood flukes

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or a reversal in which the pharynx reappears (Character 5) occurs in clinostomes.

Cladogram 4 (Figure 11D) approaches a more traditional view of blood fluke relationships. Once again, Component 6 groups together the clinostomes and blood flukes, but this time the blood flukes branch as a monophyletic lineage defined by Component 5. Here, derived loss of the cercarial pharynx (Character 5) designates a component which corresponds to the superfamily Schistosomatoidea. Two incongruent character state distributions occur in Cladogram 4. A reversal to redial development (Character 4) is indicated for the clinostomes and the dorsal-median fin fold (Character 9) either evolves in parallel in the clinostomes and sanguinicolids or arises in Component 6 and is subsequently lost in tetrapod blood flukes.

In Cladogram 5 (Figure 11E), Component 2 separates the clinostomes as the sister taxon of the other families in the suborder Strigeata based on a derived loss of the redial stage (Character 4). Once again, the superfamily Schistosomatoidea is designated by Component 5. The branching sequence of Cladogram 5 requires the parallel origin of two character states in both the sanguinicolids and clinostomes: Character 7--cercarial head-organ and Character 9--dorsal-median fin fold.

Both data sets produced alternative cladograms of equal length, thus eliminating parsimony as a criterion for choosing preferred cladograms. Instead I followed

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a modified interpretation of the arguments of Hecht and Edwards (1977), favoring cladograms defined by the fewest derived loss characters. My preferred topology in the case of each data set was the same: Cladogram 1 and 3 (Figure 11A and C). In both cladograms, the clinostomes are allied with the blood flukes on the basis of the derived cercarial head-organ. Similarly, the clinostomes and sanguinicolids group separately from the tetrapod blood flukes as a result of the dorsal-median fin fold. In contrast, cladograms which designate the blood fluke families as a monophyletic lineage do so on the basis of derived losses of the pharynx and redia. In addition, cladograms other than 1 and 3 require parallel evolution of complex structures such as the head-organ and dorsal-median fin fold, further reducing the confidence in them.

My analysis therefore suggests that the blood flukes are not a monophyletic lineage and thus brings current taxonomy of the superfamily into question. This analysis is based on only 17 characters, though, and additional information is necessary in order to settle the matter.

Phylogenetic Implications and Host Relationships

Although the precise relationships of the families in the suborder Strigeata are not entirely clear due to problematic accounts in the literature, the results of

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my analysis do pose questions with regard to current taxonomy and phylogenetic history of the group.

In the preferred cladograms the four strigeiform families cluster together as a sister group to the clinostome-blood fluke lineage. This arrangement differs markedly from the prevailing concept of these taxa (Figure 12), reviewed most recently by Short (1983). LaRue (1957) first proposed the subordinal ranking Strigeata to include the superfamilies Schistosomatoidea (containing the blood flukes), Strigeoidea (the strigeiform families), and Clinostomatoidea (the family Clinostomatidae); the latter two superfamilies are generally considered more closely related to one another than to the blood flukes (Figure 12). Studying LaRue's account, I have been unable to discover a specific morphological basis for his uniting the clinostomes and strigeiform families. I suspect that the classical arrangement of these taxa is based on life cycle patterns and an unstated desire to keep the "distinctive" and "advanced" blood flukes differentiated from other trematodes. In my analysis, the clinostomes and blood flukes are united on the basis of a derived modification of the anterior end of the cercariae known as the head-organ (Character 7). Clinostome and blood fluke cercariae are quite similar in most aspects of their morphology, although the characters contributing to this similarity (Characters 2 and 3) are scored as primitive in my analysis, and therefore not indicative of derived relationship. If, as

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Figure 12. Classical interpretation of relationships of the superfamilies of the Strigeata (after Short, 1983).

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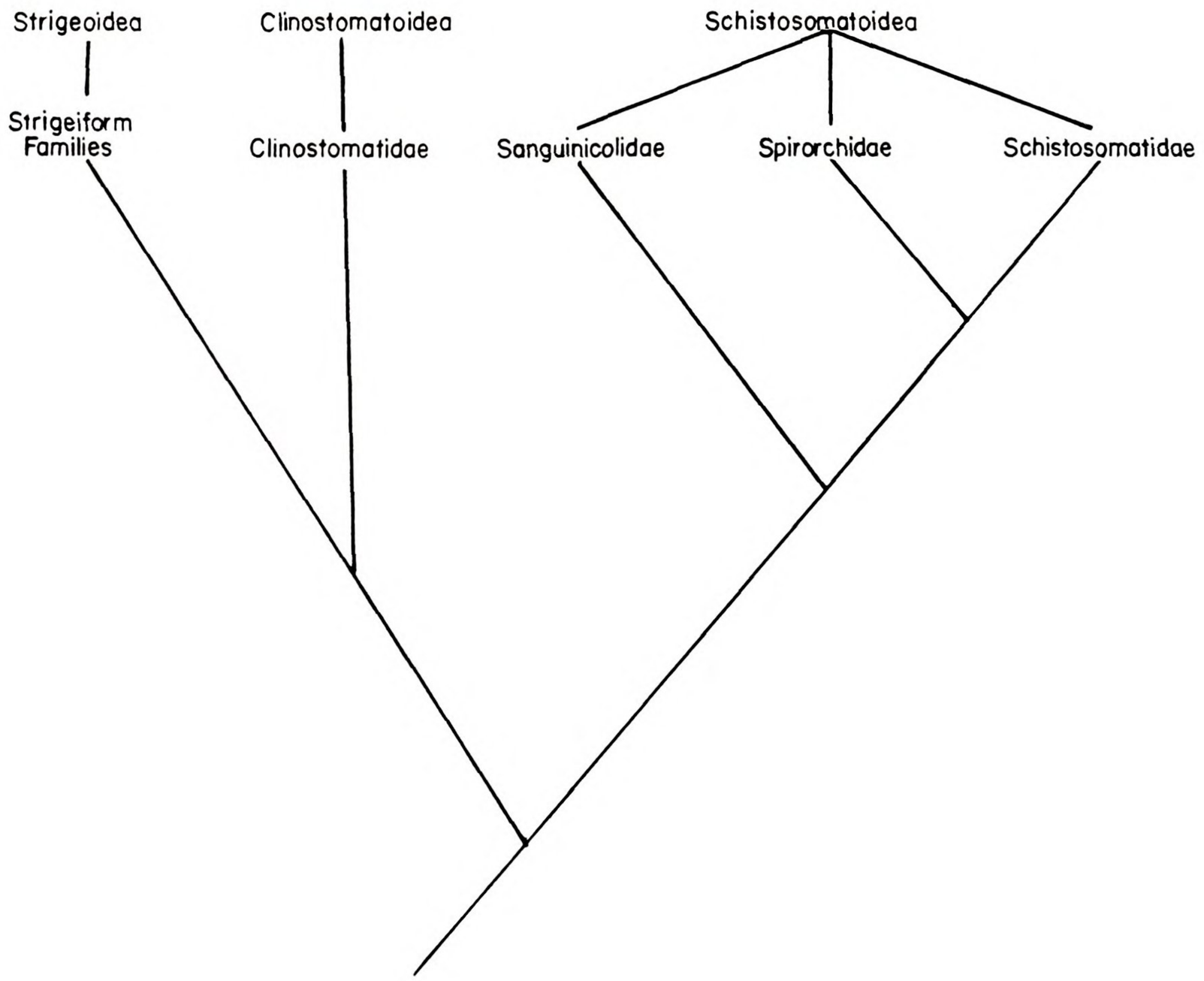

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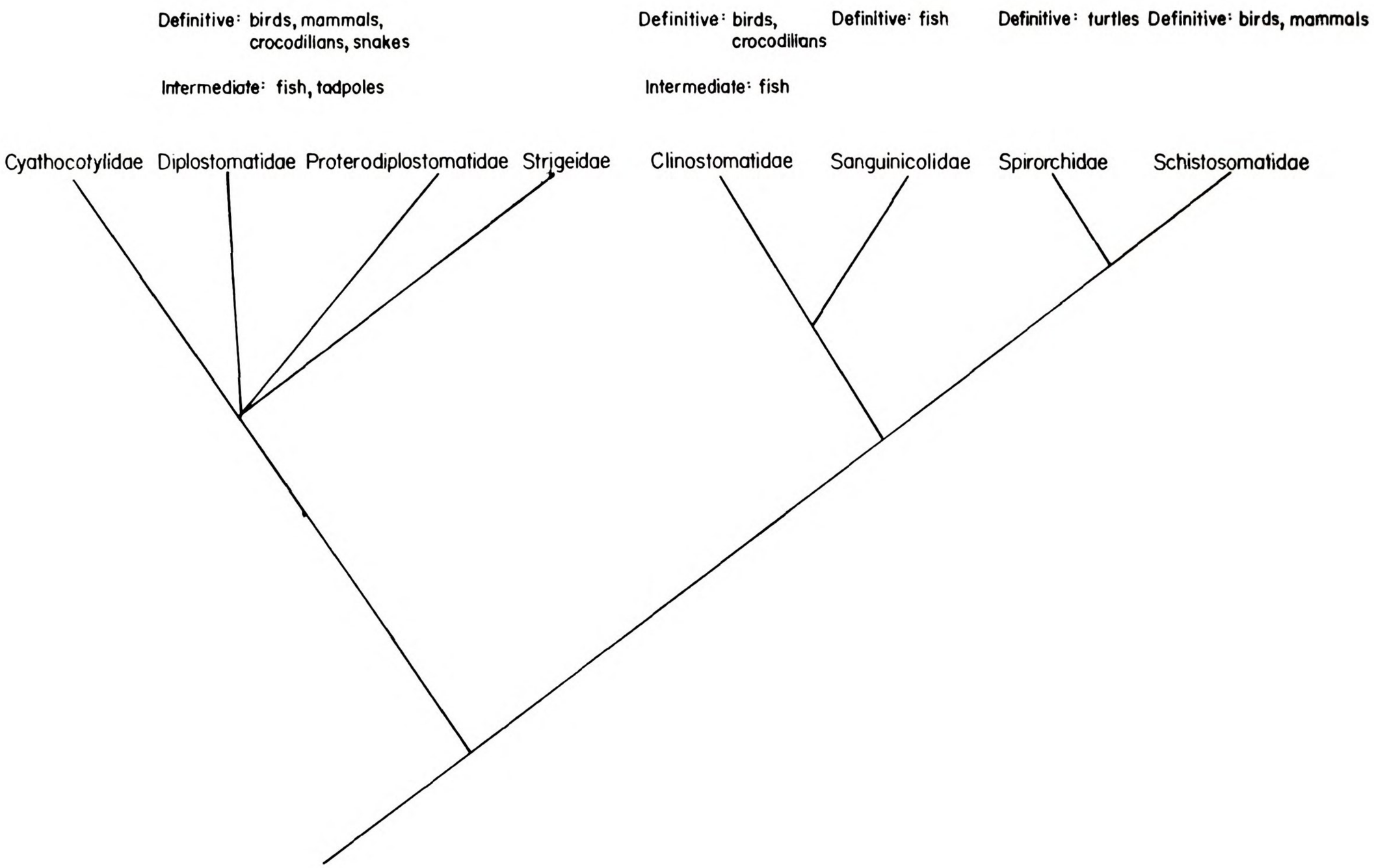
Brooks et al. (1983) suggest, the blood flukes (and clinostomes) are a paedomorphic lineage, then Characters 2 and 3 may well be secondary simplifications which are in fact synapomorphic in nature. If this turns out to be the case, the argument for a close relationship between the clinostomes and blood flukes would be strengthened.

One consistent trend in all cladograms was the placement of the spirorchids as the sister group to the schistosomes. Although this arrangement does reflect classical thinking, prior systematists have grouped the two taxa together on the basis of host relationship and life cycle similarity, rather than on shared morphological features. Synapomorphies which unite the schistosomes and spirorchids are penetration gland pattern (Character 5), presence of esophageal gland cells (Character 15), absence of the cercarial pharynx (Character 8) and loss of rediae (Character 7). This result establishes the blood flukes of turtles as the out-group which I will use in my analysis of the phylogenetic relationships of schistosome genera.

Having chosen the out-group of the Schistosomatidae, I examined hypotheses suggested by the preferred cladogram concerning historical patterns of host relationships. In Figure 13, host taxa are assigned to the terminal branches of the preferred cladogram. My discussion will focus upon the host relationship patterns of the clinostome-blood fluke alliance. As a result of an extensive phylogenetic analysis of the phylum

Figure 13. Vertebrate host distributions assigned to the preferred cladogram depicting relationships of the Strigeata.


Definitive: birds, mammals, crocodilians, snakes
Intermediate: fish, tadpoles
Definitive: birds, crocodilians
Intermediate: fish
Definitive: fish
Definitive: turtles
Definitive: birds, mammals
Cyathocotylidae
Diplostomatidae
Proterodiplostomatidae
Strigeidae
Clinostomatidae
Sanguinicolidae
Spirorchidae
Schistosomatidae

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Platyhelminthes, Brooks et al. (1983) suggested that complex life cycles are a defining characteristic of the Digenea and that simpler patterns represent internal derivations resulting from losses within specific lineages. For example, the metacercarial stage which encysts upon the vertebrate intermediate host is distributed widely outside of the Strigeata, but within the suborder it is found only in the clinostomes and strigeiform families. It appears most parsimonious to suggest loss within the Strigeata rather than multiple derivations in other families and orders. If in fact the three-host life cycle is found primitively in the clinostomes and strigeiform families, then the preferred cladogram (Figure 13) indicates that one vertebrate host has been lost in the life cycles of the three blood fluke families. Unless a reversal back to a three-host life cycle occurred in the clinostomes, the preferred cladogram suggests that there have been at least two separate losses of vertebrate hosts in blood fluke life cycles: one in the sanguinicolids and at least one in the tetrapod blood flukes.

Host distribution patterns portrayed in Figure 13 indicate that the ancestors of the Strigeata were inhabiting either modern tetrapods or their primitive ancestors prior to the splitting off of the spirorchid-schistosome branch, which now penetrate the definitive host directly. If one loss event accounts for the two-host life cycle in both spirorchids and schistosomes, then the loss is indeed

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ancient because turtles are thought to be a very early offshoot from the primitive reptilian stock which gave rise to other tetrapods.

Conversely, the sanguinicolids may have lost the final or definitive host. Ancestral sanguinicolids may have altered to penetrate their intermediate vertebrate host and develop directly rather than encysting in or on it.

Some support for this latter hypothesis is perhaps found in differences in the mechanics of host involvement in the three blood fluke families. The cercariae of all three families penetrate the host directly, but virtually nothing is known about this process other than in the Schistosomatidae. The way in which the eggs return to the external environment differs between the sanguinicolids and tetrapod blood flukes. In both the schistosomes and spirorchids, the eggs leave the vertebrate host in the feces, urine, or very rarely in a nasal discharge. In the sanguinicolids which have been studied, the eggs travel to the gill filaments where the miracidia hatch and penetrate to the exterior (Smith, 1972). These differences may reflect separate historical patterns of host inhabitation, or alternatively, they may reflect a long history of divergence accompanied by specific modifications for differing host environments. Specifically, the structure of the piscean circulatory system may require exit routes which differ from those needed in tetrapods.

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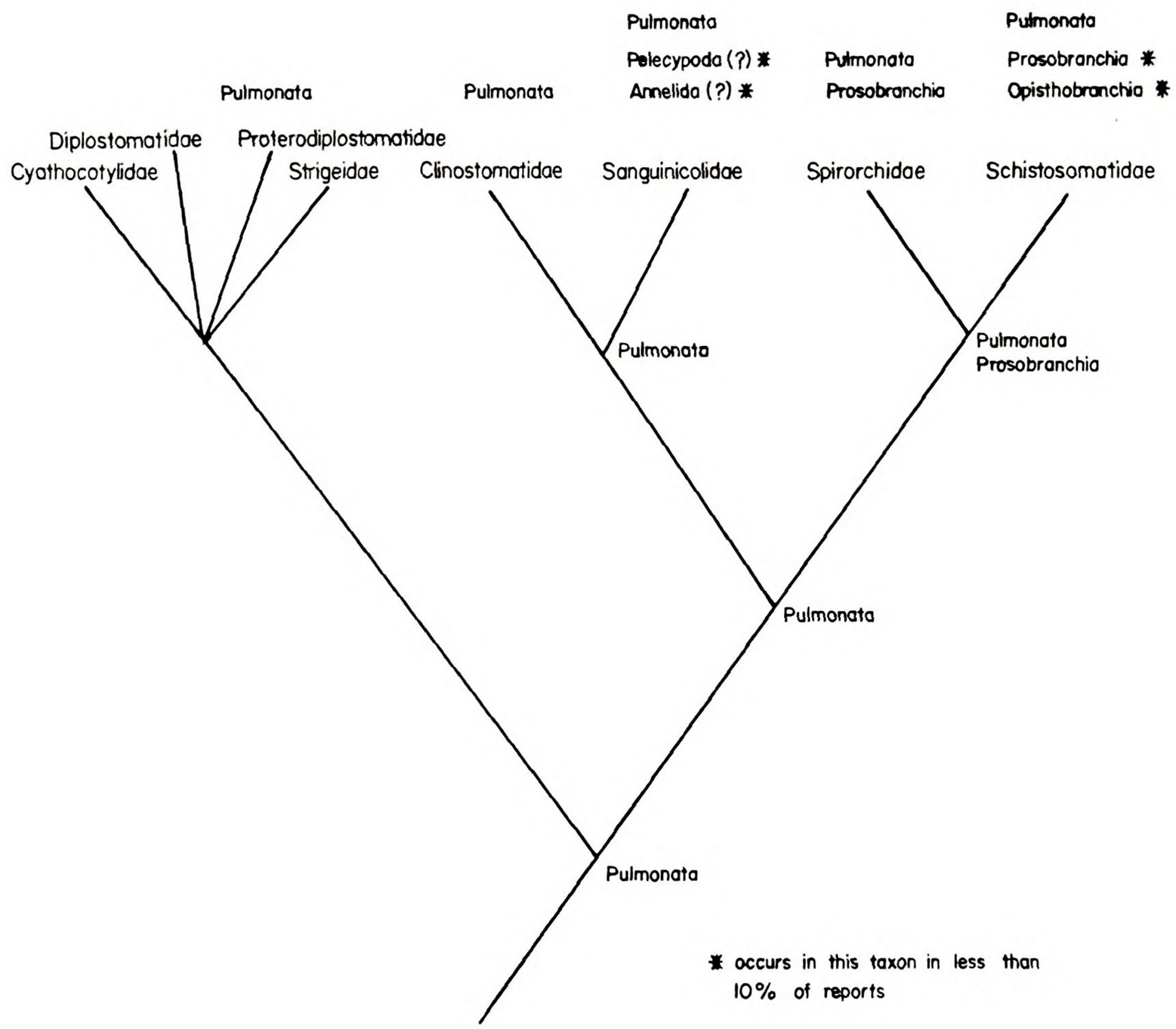
An alternative and perhaps less parsimonious hypothesis could view the current piscean hosts of the sanguinicolids as the ancestral definitive host. In this case, the primitive life cycle would have involved two fish as vertebrate hosts, and the intermediate fish would have been eliminated.

Although I favor the first hypothesis which suggests that the sanguinicolids lost the definitive vertebrate host while the tetrapod blood flukes eliminated the intermediate vertebrate host, further information on sanguinicolid biology is needed before more definite conclusions are made. A detailed analysis of phylogenetic and host relationships of the strigeiform families might provide additional data pertinent to this discussion.

The phylogenetic implications of intermediate invertebrate host relationships of the Strigeata are tentative at best since the life cycles of non-schistosome blood flukes are so poorly known. Figure 14 depicts the intermediate host distributions represented by the preferred cladogram of familial relationships. Larval development has been reported for at least some members of all families as occurring in the strictly freshwater molluscan class Pulmonata. Sanguinicolid-like cercariae have been reported from non-gastropod hosts in marine environments, particularly annelids and pelecypods (Smith, 1972). Unfortunately, complete life cycles are unavailable and therefore definite identifications are lacking. Spirorchids are recorded only from pulmonate snails, but since adults

Figure 14. Intermediate invertebrate host taxa assigned to the preferred cladogram depicting relationships of the Strigeata.



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of many species are found in marine turtles, prosobranch gastropods and perhaps non-gastropod invertebrates must also be involved.

In a manner similar to that used in character analysis, I utilized Farris optimization to assign intermediate host taxa to interior nodes of the preferred cladogram. Despite the limitations imposed by incomplete data, certain generalizations can be drawn from intermediate host distributions. Figure 14 indicates that pulmonate gastropods are the primitive hosts of the Strigeata. Since pulmonates are considered derived relative to prosobranchs (Purchon, 1977), this implies that up to three independent invasions of prosobranchs may have occurred in the history of the Strigeata. The occurrence of the primitive intermediate host taxon in the life cycles of all three families of blood flukes suggests that at least one independent invasion of prosobranch gastropods has occurred in each family. This may be related to the invasion of the marine habitat by these groups, because although prosobranchs are found in fresh water, they are presumed to have originated in salt water, where the majority of taxa now reside (Purchon, 1977).

Summary

A definite hypothesis of the relationships within the Strigeata is not available at present, but my results favor cladograms which group the clinostomes and

sanguinicolids and differ significantly from classical thought in breaking up the superfamily Schistosomatoidea. Cercariae of the sanguinicolids and clinostomes possess a complex dorsal-median fin fold which unites the two families. Most the cercariae positively assigned to both families are virtually identical, with the questionable exception of the absent pharynx in some sanguinicolids.

If the pharynx and redial stage do turn out to be present in some sanguinicolids, this would further support separating the sanguinicolids from the tetrapod blood flukes. Brooks et al. (1983) use the loss of the redial stage to unite the blood flukes and strigeiform families. A cladogram defined by this derived loss character appeared in my analysis, but I preferred branching diagrams supported by the presence, rather than absence of morphological characters.

Alternatively, if the pharynx and redia are absent in sanguinicolids, then this absence would support the traditional view of the blood flukes as a monophyletic group. In any case, the blood flukes are presently united solely on the basis of derived loss characters, and any such monophyletic grouping must postulate the parallel evolution of the synapomorphic dorsal-median fin fold in the clinostomes and sanguinicolids.

My analysis indicates that three-host life cycles involving pulmonate molluscs and vertebrate intermediate and definitive hosts are primitive characteristics of

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the Strigeata. Although the monophyletic nature of the Schistosomatoidea is open to question, my analysis did show that the tetrapod blood flukes are sister groups, with the Spirorchidae forming the out-group of the Schistosomatidae. Inconsistent species descriptions and incomplete life cycle data constrain further speculation at the present time. Detailed cercarial descriptions will most likely be the key to clarifying ambiguous character codings and thus the family relationships of the Strigeata.

THE SCHISTOSOMATIDAE

Survey of Characters

The 24 characters used in my analysis of the Schistosomatidae are presented below, followed by discussions of schistosome phylogeny and host relationships. The explanation of terminology presented at the beginning of the survey of Family Level Characters (page 47) also applies here.

Genus Level Characters

Character 1. Testes Shape.

(0) Compact.

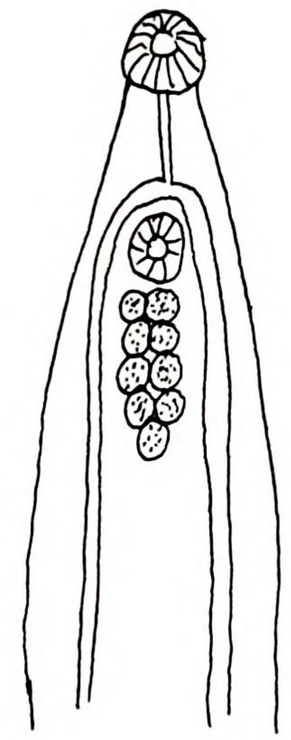
(1) Lobulate.

Within the out-group, the Spirorchidae, the testes occur in a variety of forms ranging from globular to elongate and spiraled (as the familial name implies). In all cases, the testes occur as discrete units with a more or less solid outline. In a similar manner, schistosomes generally possess discrete, roughly ovoid testes (Figure 15A). An exception to this pattern occurs in the genus Schistosomatium where the testes are lobulated and diffuse (Figure 15B). Thus in contrast with the discrete testes displayed by spirorchids and most schistosomes, the

Figure 15. Shape of testes.

A. Compact

B. Lobulate



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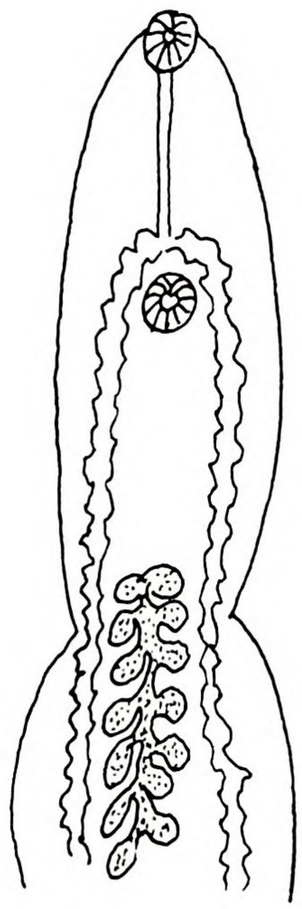

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lobulated testes of Schistosomatium appear to represent a derived, autapomorphic state.

Character 2. Testes Location.

(0) Testes lie between cecal branches.

(1) Testes lie along common cecum.

The blood flukes of turtles and the majority of digenetic trematodes possess testes which lie between the cecal branches (Figure 16A). In all schistosomes, the cecal branches unite posteriorly to a greater or lesser degree to form a common cecum. The testes are located either between the paired cecae as in spirorchids or they may lie on either side of the common cecum (Figure 16B). I will therefore consider the condition in which testes lie alongside the common cecum to be derived relative to testes which lie between the cecal arms.

Character 3. Dendritic Branches on Paired Cecae.

(0) Absent.

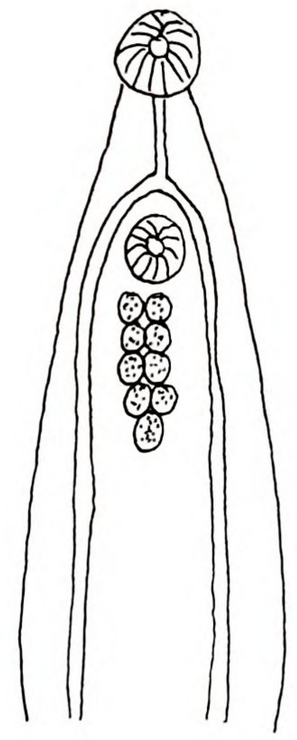
(1) Present.

Among blood flukes, dendritic branches on the paired cecae (Figure 17) are found only in the genera Schistosomatium and Heterobilharzia. I assume that the condition is homologous, although more detailed developmental and histological data would be necessary to confirm this. In both genera, the condition is dispayed more prominently in the female. A similar condition occurs, presumably

Figure 16. Location of testes.

A. Between cecal branches

B. Along common cecum



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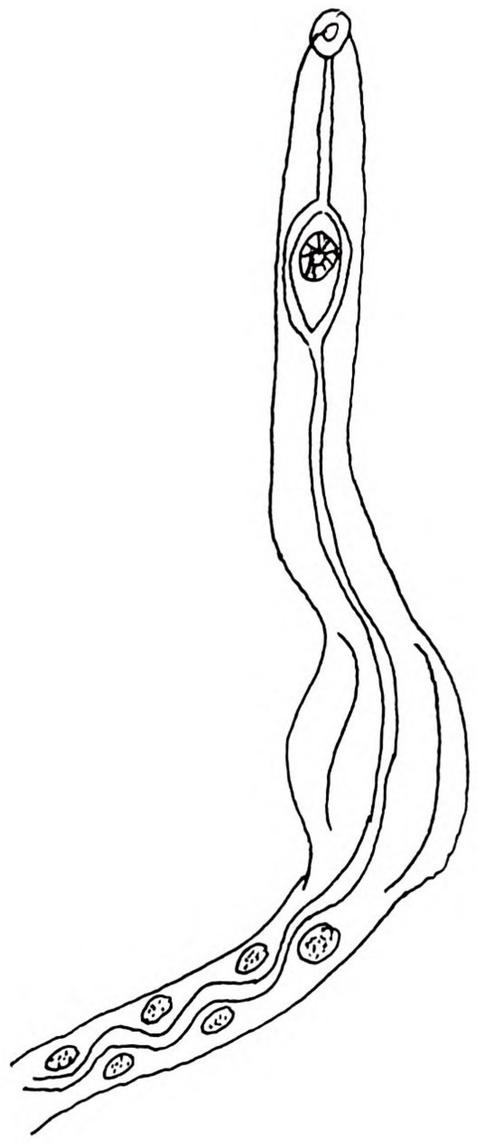

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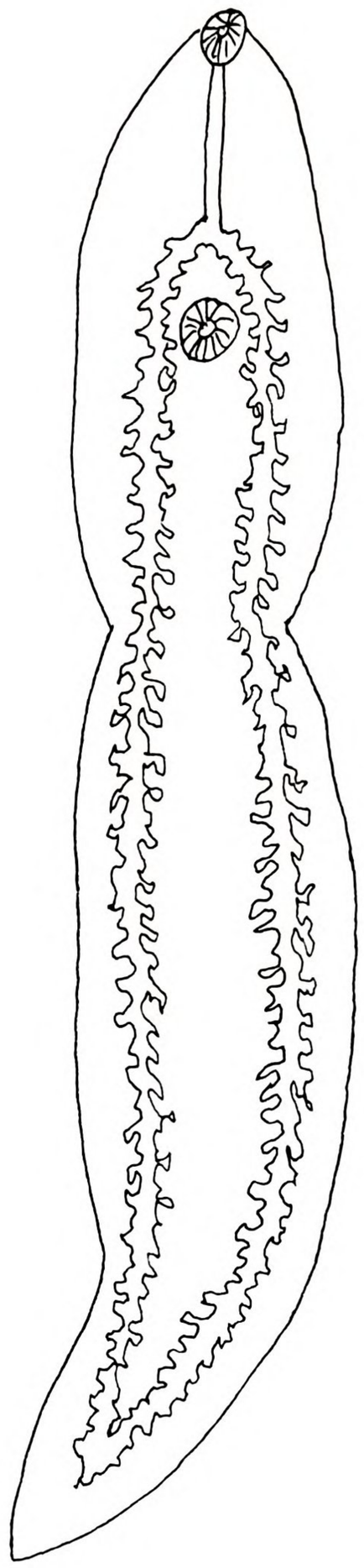
Figure 17. Dendritic branches present on paired cecae.



cae.

in parallel, in the clinostome genus Clinostomoides (Yamaguti, 1971).

Character 4. Gynacophoric Canal.

(0) Absent.

(1) Present, running the length of the body.

(2) Present, surrounding the genital pore only; derived from state (1).

(3) Present, restricted to the posterior one-half of the body; derived from state (1).

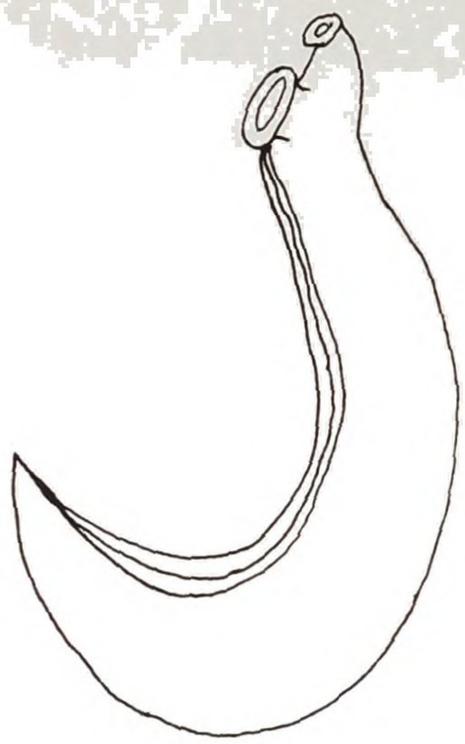
The gynacophoric canal is formed in male schistosomes by an infolding of the sides of the body. This characteristic structure is found only in schistosomes and gives the family its name. It is absent in the flat-bodied genus Dendritobilharzia which I will conservatively score for the primitive condition since there is no obvious way to distinguish between primitive absence and derived loss. The remaining schistosome genera can be placed in one of three categories, depending upon the extent of development of the canal. In the most simple arrangement, e.g., Schistosoma, the body walls fold inward for much of the length of the worm (Figure 18A). This may be accompanied by muscular thickening to a greater or lesser degree; this muscularization is apparently used to keep pairs intact while in the blood vessels of hosts. Variation in the extent of muscularization suggests further

Figure 18. Form of Gynacophoric Canal.

A. Running the full length of the body

B. Surrounding genital pore only

C. Restricted to the posterior one-half of the body



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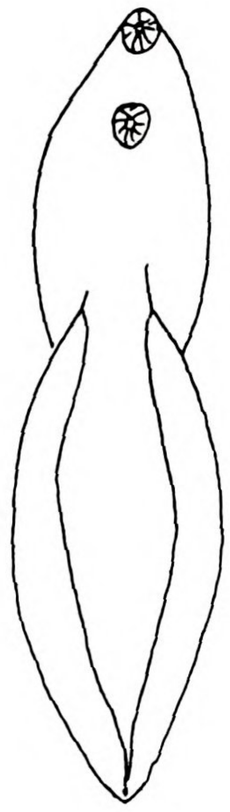

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refinement of this character, but histological data are needed for confirmation. I consider this state of the canal to be primitive relative to the following two canal arrangements. I feel that this is a relatively safe assumption, since the following genera all possess derived body forms not represented elsewhere in the Schistosomatidae or Spirorchidae.

The first of these two derived canal arrangements occurs in the genera Trichobilharzia and Gigantobilharzia. In these two highly elongate genera, the canal is represented by a short anterior muscular expansion surrounding the genital opening (Figure 18B). In the genus Schistosomatium, the canal is limited to the posterior one-half of the body (Figure 18C) in correlation with the derived position of the male genital pore (see Character 10). In the absence of further information as to the development of the canal in these three forms, I consider the latter two to be independent derivations from the simple canal which runs the length of the body.

The genus Bilharziella is somewhat problematic since reports on the length or actual presence of the canal vary. Khalifa (1972) reports that in B. polonica, the edges of the body have a tendency to roll inward and that the actual canal is short and located in the region of the testes. Lal (1937) reports a well developed canal running the length of the body in B. indica. Based on these reports and my own observations that suggest some

folding of the body wall, I think it is safest to score this genus for the widespread, simple gynacophoric canal. Interpretation of the length of the canal can vary according to degree of relaxation and state of preservation, and since there are reports indicating the presence of a full canal (Lal, 1937), I will assume it is present until clear evidence to the contrary is presented.

Character 5. Adult Oral Sucker.

(0) Present.

(1) Absent.

The oral sucker is present in all members of the out-group family, Spirorchidae, and in most schistosomes. I therefore consider its absence a derived loss. The oral sucker is always absent in members of the genus Dendritobilharzia. It is usually reported as absent in the genus Gigantobilharzia, but reports vary. Najim (1956) reviews the problem and observes that the oral sucker is present in one or both sexes in at least G. monocotylea and G. gyrauli. Brackett (1942) reported it absent in G. lawayi, but it is clearly present on one specimen (#44862) deposited by Brackett in the U.S. National Helminth Collection. In light of these conflicting reports, it is evident that the primitive state occurs more than once in the range of variation shown in the genus Gigantobilharzia. I have therefore scored the genus as primitive

and assumed that the loss of the oral sucker has occurred one or more times within the genus.

Character 6. Adult Acetabulum (Ventral Sucker).

(0) Present.

(1) Absent.

The ventral sucker, or acetabulum, is present in cecariae in all schistosomes and spirorchids for which the life cycle is known. It is absent in the adults of two genera: Gigantobilharzia and Dendritobilharzia. It is apparently lost during the process of penetration and maturation. I consider the absence of the acetabulum to be a derived loss character.

Character 7. Ovary Shape.

(0) Ovary globular, or weakly coiled at the anterior end.

(1) Ovary weakly coiled throughout.

(2) Moderately coiled ovary; derived from state (1).

(3) Highly coiled ovary; derived from state (2).

(4) Coiled ovary with prominent lateral loops; derived from state (2).

In its most widespread form in the out-group and in the order Strigeatida as a whole, the ovary is a simple globular structure with a relatively smooth outline. I have therefore labeled this simple, globular ovary shape

Figure 19. Ovary shape.

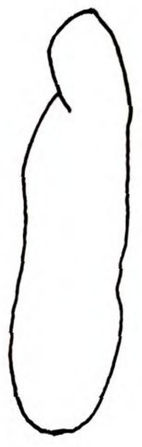
A. Globular or weakly coiled

B. Weakly coiled throughout

C. Moderately coiled

D. Elongate and highly coiled

E. Coiled, with prominent lateral loops



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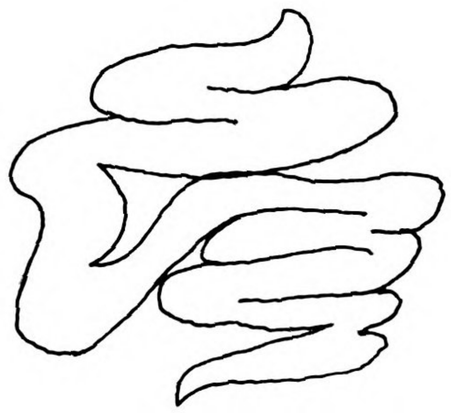

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as the primitive character state. Within the Schistosomatidae, the ovary is either simple and globular or more or less coiled to form a spiraled structure. Support for the suggestion that the simple ovary represents the primitive state comes from developmental studies. The detailed ontogenetic study of Schistosomatium douthitti by El-Gindy (1951) shows that the ovary forms first as a globular structure and then elongates the coils during the final stages of development. In the genus Schistosoma, ovary shape is variable ranging from pyriform in S. japonicum to elongate with a slight "torting" of the anterior end in S. mansoni (Price, 1929). Basch (1981) reports that when sexual maturation of S. mansoni is incomplete, a pyriform ovary similar to the one seen in S. japonicum is retained. These studies imply that spiraling of the primitive globular ovary occurs as a terminal addition to the development sequence. Coiling occurs to variable degrees in all genera of schistosomes and below I will explain my coding of character states based on degree of coiling.

In the genera Schistosoma and Orientobilharzia, certain species have simple globular ovaries while all other genera show some degree of coiling (see Dutt and Srivastava, 1961, for a review of ovary morphology in the Schistosomatidae). Although problematic, the most conservative coding for the two genera is for the primitive state with independent derivations of a partially coiled ovary in

certain species of both genera (Figure 19A). The genus Bilharziella is highly consistent in displaying an ovary which is only slightly coiled with one major coil running the whole length of the ovary (Figure 19B) (Kowalewski, 1886; Khalifa, 1972, etc.). I have coded this condition for derived state (1): Ovary slightly coiled.

The majority of schistosome genera possess ovaries that are moderately coiled (Figure 19C) consisting of four or more coils packed tightly together (e.g., Austrobilharzia). Although there is variation in the length and degree of coiling, I have scored schistosomes with moderately coiled ovaries as possessing the same character state. It is likely that the degree of coiling in the report of a given species would be affected by the age of the worm as well as its ability to mature in a particular host species. Lack of information on individual variation makes further refinement of this character unreasonable at the present time. Further research on growth and development in a range of species might yield useful information.

Despite the above mentioned ambiguity, two extreme variations indicate that separate codings are in order. In two genera (Trichobilharzia and Ornithobilharzia), the ovary is extremely elongate and loosely coiled (Figure 19D). I scored this condition as an independent derivation from state (2) because sparse developmental data indicates elongation during ontogeny (McMullen and Beaver, 1945).

In the genera Heterobilharzia and Dendritobilharzia, the coiled ovary is thrown into a series of prominent lateral loops (Figure 19E). I coded this condition as independently derived from state (2) until additional developmental information is available that might suggest otherwise.

Character 8. Arrangement of Vitelline Follicles.

(0) Follicles scattered between and/or outside of paired cecae.

(1) Follicles paired along both paired cecae.

(2) Follicles paired along common cecum; derived from state (0).

In the spirorchids and other families of the Strigeata, the vitelline or yolk producing glands are scattered in a diffuse manner between or lateral to the two cecal branches (Figure 20A). This arrangement occurs in a number of schistosome genera and I considered it to be primitive. Two additional arrangements also occur and I scored these as independently derived from the primitive condition. The genus Bivitellobilharzia derives its names from the paired arrangement of the vitellaria (Figure 20B) which surround each of the cecal branches (Vogel and Minning, 1946). This distinctive arrangement is also found in the genera Schistosomatium and Heterobilharzia. Although the paired arrangement is not as distinct as in the published report of Bivitellobilharzia mentioned above, it is clearly evident in developing Schistosomatium as

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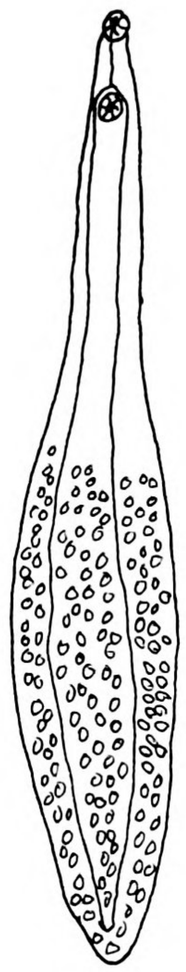
Figure 20. Arrangement of vitelline follicles (=vitellaria).

A. Scattered

B. Paired along both paired cecae

C. Paired along common cecum

D. Unpaired



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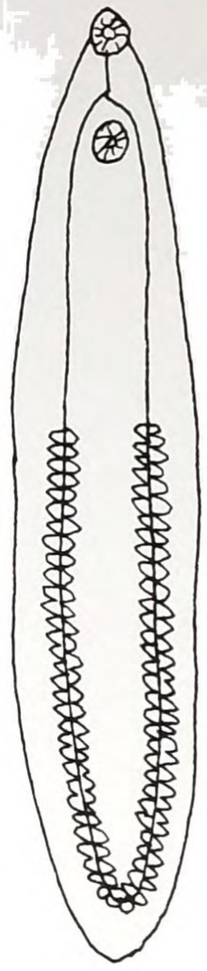

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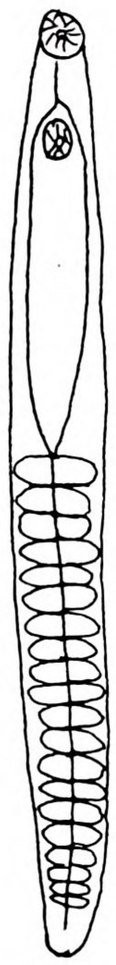

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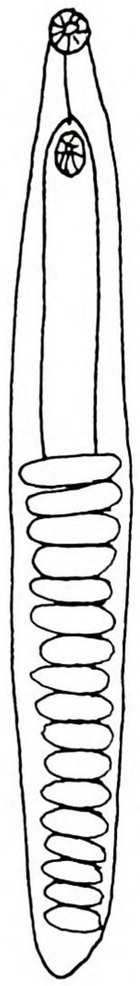

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portrayed by El-Gindy (1951) and in the specimens of Heterobilharzia that I examined (U.S.N.H.C. #39420).

Another equally distinct arrangement is seen in the genera Schistosoma, Ornithobilharzia, Austrobilharzia, and Orientobilharzia. In these genera, the vitellaria form prominent lobes which are paired on either side of the common cecum (Figure 20C). Although the length of the common cecum may vary, the vitelline arrangement is quite consistent.

A fourth vitelline pattern consisting of single, large vitellaria arranged in tandem (Figure 20D) has been reported at least three times in the literature. One of these reports, that of Faust (1924) concerning Ornithobilharzia odhneri, has generated considerable controversy. Dutt and Srivastava (1961) erected the new genus Sinobilharzia to house this species based on the peculiar vitelline structure and a few inconsistencies in genital arrangement. Farley (1971) considered O. odhneri to be an aberrant member of the genus Austrobilharzia. Although the reported genital arrangements have their own problems (discussed later), subsequent authors have failed to point out the inconsistencies between Faust's illustration and his written description of the vitellaria. Faust's Figure 2 portrays a female O. odhneri with large ovoid vitelline follicles spanning the width of the body and is the basis for Dutt and Srivastava's (1961) taxanomic action. In contrast, on page 551, Faust reports "the paired vitelline

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follicles occupy a large portion of the body from the posterior position to the sub-distal region" (emphasis added). Faust stated that he based his description on a total of nine male and four female worms. There were no females present in the type material I received from the U.S. National Helminth Collection (#60990), which consisted of nearly all the reported specimens (fragments made the exact number difficult to determine).

I suspect that the written description is correct and that an error was made in illustrating the material. Given that the number of male specimens which I examined nearly matches the total number of worms on which Faust based his description, I speculate that the testes of a male worm were mistakenly illustrated as vitellaria. From my own observations, the testes are large and span the width of the body, resembling closely the illustrated structures. This species has not since been reported in the literature.

Two other reports describe schistosomes with a single row of vitellaria. In his description of Ornithobilharzia filamenta, McLeod (1940) stated that "the vitellaria are in the form of a single row of numerous relatively large follicles, each of which is almost as wide as the body." The photomicrographs which accompany the report are not particularly revealing, and no mention is made of the relationship of the vitellaria to the common cecum. Since no further note is made of this aberrant arrangement,

I can only conclude that the paired vitellaria have been interpreted as a single structure, a description which seems plausible if the common cecum did not stain prominently enough to demarcate the two lobes.

The final report of an avian schistosome with an aberrant vitelline structure comes from an incomplete note published by Young (1937), involving an unidentified schistosome from the marbled godwit (Limosa fedoa). The author describes the vitellaria as, "occupying about 2/5 of the body, . . . somewhat pyriform in shape and filling most of the diameter of the worm." The description was based on a single pair of worms, and these specimens were destroyed during sectioning before a positive identification could be made. Although these specimens appear to belong to the genus Ornithobilharzia, no special attention was given to the peculiar arrangement and once again no reference to the common cecum was made.

As in the previous two accounts, the information in Young's report is sufficiently incomplete that an error in interpretation of such limited material cannot be ruled out. Until more substantial information is available, I am not willing to recognize a separate character for these questionable reports of aberrant vitelline structure. For the purpose of analysis, I have included O. odhneri under the separate genus Sinobilharzia, a placement which differs from Farley (1971) who included the species in the genus Austrobilharzia. This listing is based on Faust's

report of genital differences, not on vitelline structure. These genital differences have their own associated problems and I will discuss these in a later section (Character 14, below).

Character 9: Dendritic Branches on Common Cecum.

(0) Absent.

(1) Present.

Dendritic branches from the common cecum (Figure 21) appear to be autapomorphous relative to the out-group and are restricted to the genus Dendritobilharzia. The life cycle of this genus is unknown and thus information pertaining to the development of these branches is unavailable.

Character 10. Position of Testes and Genital Pore.

(0) Testes and genital pore immediately post-acetabular.

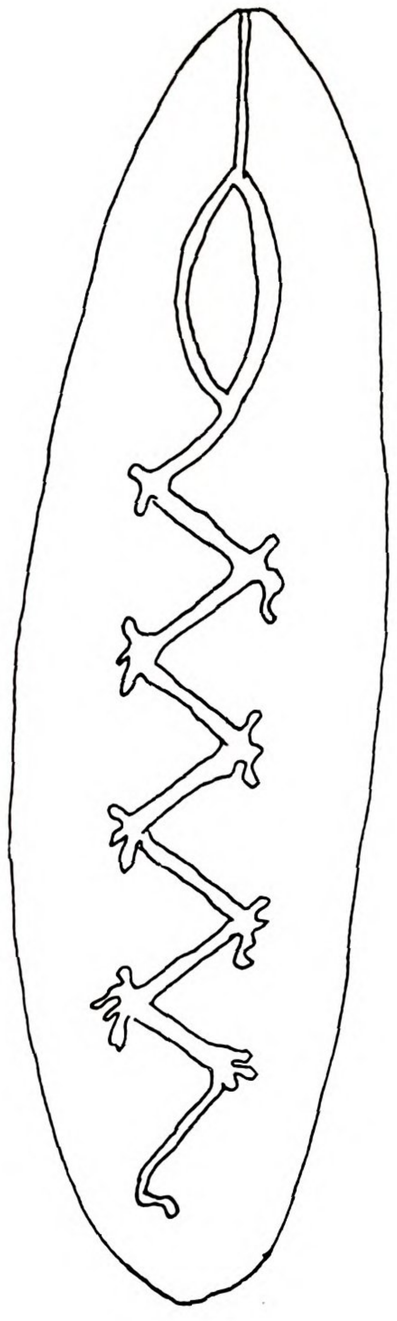
(1) Testes and genital pore located in the middle of the body, not associated with the acetabulum.

(2) Testes located in the posterior end of the body; genital pore immediately post-acetabular; derived from state (0).

In schistosomes, the testes are located either between the cecal branches or along the length of the common cecum (see Character 2). In the former situation, the testes

Figu

Figure 21. Presence of dendritic branches on the common cecum of Dendritobilharzia.



and genital pore are located immediately behind the acetabulum in the majority of genera (Figure 22A). Two exceptions to this pattern occur. In the genus Schistosomatium, the genital pore and testes are located in the middle of the body, well behind the acetabulum (Figure 22B). In the genus Heterobilharzia, the testes are found in the posterior end of the body and are connected by a long vas deferens to the genital pore which is situated immediately behind the acetabulum (Figure 22C).

Developmental data presented by El-Gindy (1951) show that in Schistosomatium the testes and terminal genitalia form early in development between the cecal branches immediately behind the acetabulum. During subsequent development, the whole complex moves posteriorly and comes to lie in the middle of the body. Thus the early developmental stages of Schistosomatium resemble the final adult stage of the majority of genera, in which the testes lie between the cecae. Based on this information, I suggest that the pattern seen in Schistosomatium is derived relative to other schistosomes.

Although developmental data are lacking for Heterobilharzia, it seems likely that a third developmental pattern is involved and I have scored it as independently derived from the primitive, intercecal condition.

Figure 22. Position of testes and genital pore.

A. Immediately post-acetabular

B. Located in the middle of the body

C. Testes located in the posterior end of the body; genital pore immediately post acetabular

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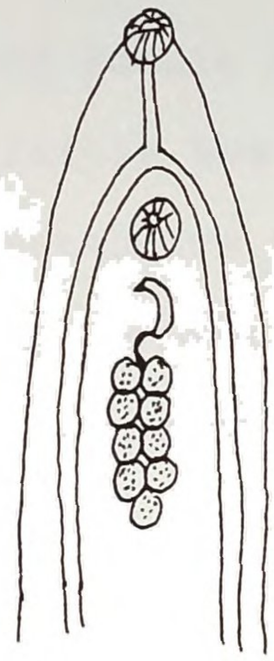

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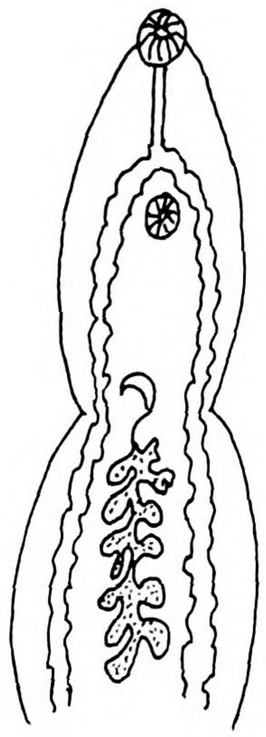

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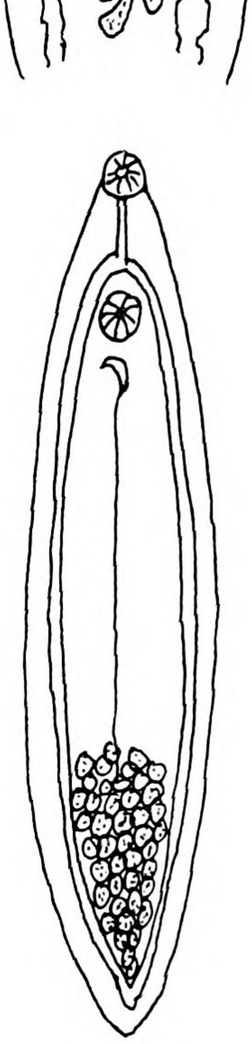

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Character 11: Position of Female Genital Pore.

(0) Immediately behind the cecal bifurcation and acetabulum.

(1) Genital pore opens at extreme anterior end, anterior to cecal bifurcation and acetabulum, when present.

In the spirorchids and nearly all schistosomes, the genital pore lies posterior to the cecal bifurcation and acetabulum, where present (see Character 10, Figure 22A). In two genera, Dendritobilharzia and Gigantobilharzia, the female genital pore lies anterior to the cecal bifurcation and close to the oral opening (Figure 23). Based on out-group comparison, I assumed this to be a derived state.

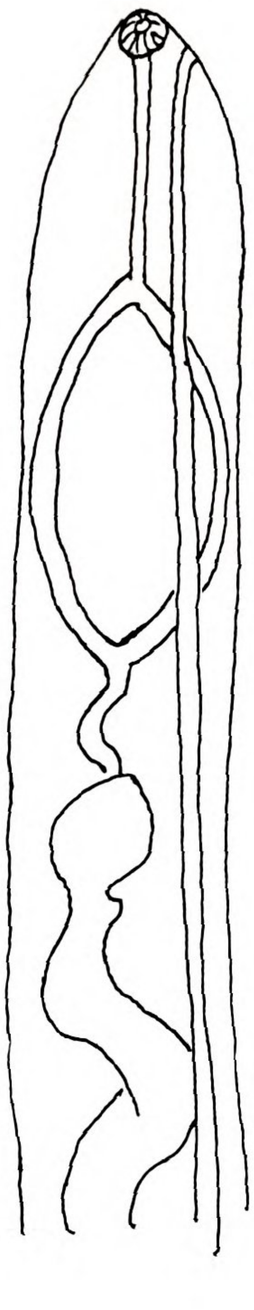
Character 12. Number of Eggs in the Uterus.

(0) One to ten eggs.

(1) More than fifty eggs.

Trematodes in general are noted for their high reproductive capacity which is often evidenced by enormous egg output by individual females. Among the strigeiform trematodes, there is a tendency toward the production of a few (<10) relatively large eggs. The spirorchids always have one or, at the very most, a few (<5) large eggs present in the uterus. The widespread occurrence of a single egg in the uterus of most blood flukes will therefore be considered the primitive state. Members

Figure 23. Position of female genital pore in Dendritobilharzia and Gigantobilharzia.



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of at least five schistosome genera have sac-like uteri packed with many (50-100+) eggs. This is true for all species of the four genera (Macrobilharzia, Heterobilharzia, Schistosomatium and Dendritobilharzia) I have scored as possessing the derived state. Species in the genus Schistosoma generally contain a single egg, but some members (e.g., S. japonicum) may contain over a hundred. Since the primitive state is present in the range of variation seen in Schistosoma, I assume that the presence of multiple eggs in some species represents one or more independent derivations of the state. That multiple egg production in the genus Schistosoma is not homologous with that of other schistosome genera is also indicated by the arrangement of the eggs in the uterus. In S. japonicum, for example, the eggs are loosely packed, generally in tandem, in a very long, straight uterus. In the other genera, the eggs are densely packed in an enlarged, sac-like uterus which tends to fold and bend along its length.

Characters 13-17 report on details of genital morphology, which are generally the most difficult morphological traits to observe using conventional straining techniques. Information on many of these characters is not present in a substantial number of descriptions. The majority of authors fail to explain whether or not they feel a structure is truly absent or whether their technique was insufficient to distinguish presence or absence. In my

own experience, certain structures (e.g., prostate cells) are extremely difficult to distinguish on many mounted worms; it is clear that histological examination would have been much more useful. In most cases, histological data were not available and I had to rely on inconsistent literature descriptions and mounted worms stained by researchers other than myself.

Faced with this inconsistent data, I needed to formulate a standard method of coding problematic genital characters. I decided to use a synthesis of all available data on a given genus. I took information from all available species descriptions, as well as from museum specimens. In recording the presence or absence of a structure, I assumed that it was more likely to be overlooked in a description than to be reported as present when it actually was not. Therefore, if a given structure was reported in at least two species descriptions or was observed by myself in museum material, I coded it as present. My decisions were influenced by the quality of a given description and/or museum specimen, since certain authors provided much more detail in their accounts than others. Overall, I am satisfied with this approach and feel it gives a reasonable picture of the morphology of each genus; at worst, this approach provides hypotheses to be examined by future workers. Problems arose mainly when a generic designation relied on a single description (e.g., Sinobilharzia and Bivitellobilharzia). These and other

significant problems are discussed under individual characters.

I used a similar argument in determining transformation series in genital Characters 13-17. All of the characters are present in some form in the spirorchids and most other families of the Strigeata. These structures show a bewildering pattern of variation in presence or absence in digenetic trematodes as a whole, as well as in their sister group, the Monogenea. Although numerous and highly specific genital autapomorphies exist, it seems unlikely that the presence of common genital structures (e.g., prostate, seminal receptacle, cirrus, etc.) which serve the same function and display similar morphologies represents independent derivation in so many lineages. I have therefore scored absence of these genital characters as derived from the schistosomes, in the hope that a biologically meaningful pattern of derived loss states will be revealed.

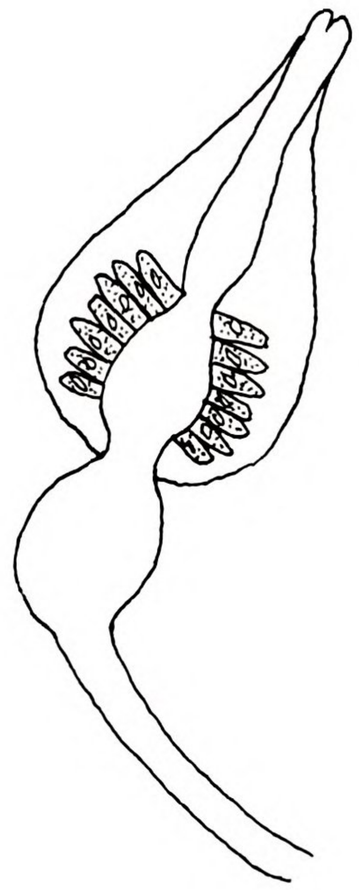
Character 13. Prostate Gland Cells.

(0) Present.

(1) Absent.

Well developed prostate gland cells surround the intromittent organ (Figure 24) in all members of the subfamilies Bilharziellinae and Gigantobilharziinae (Farley, 1971). They are present in reduced form in the genus Dendritobilharzia and were reported only in the most recent,

Figure 24. Cirrus surrounded by prostate cells.



highly detailed analysis of this genus, presented by Ulmer and VandeVusse (1970). In another relatively recent report, prostate cells were found by Short and Holliman (1961) in Austrobilharzia penneri, although they are not mentioned in prior works on this genus. As mentioned earlier, I chose to separately analyze Old and New World forms assigned to the genus Macrobilharzia. Prostate cells were recorded from African (Fain, 1953), and Indian (Baugh, 1963) forms, but not from the poor accounts of North American (Price, 1931) and South American (Kohn, 1964) worms. There is one report of prostate cells in Schistosoma japonicum (Tada, 1928) but because both the species and genus are so well studied and prostate cells are never again reported, I consider this an error. Prostate cells appear to be absent in all other genera. They are never mentioned in any works on the genus Heterobilharzia and since I was not able to observe them on mounted slides (U.S.N.H.C. #14572 and #39420), I assume that they are absent.

Character 14. Cirrus.

(0) Present.

(1) Absent.

The intromittent organ, or cirrus (Figure 24), is definitely absent in only two genera: Schistosoma and Orientobilharzia (Price, 1931, and Dutt and Srivastava, 1961). In these well-studied genera, the seminal vesicle terminates at the genital pore and an eversable cirrus

is absent. I have tentatively scored the cirrus as absent in Bivitellobilharzia because it is not mentioned in the extremely vague report of Vogel and Minning (1940). In general, the male genital arrangement of Bivitellobilharzia resembles that of Schistosoma, but the genus has been reported only twice and until further data are available, I think the given coding is most appropriate.

Although the intromittent organ is not mentioned by Faust (1924), I scored the cirrus as present in Sino-bilharzia. I did so because the cirrus pouch described by Faust was clearly visible in museum specimens (U.S.N.H.C. #60990), and in all other schistosomes which possess a cirrus pouch, the cirrus is also present.

Character 15: Male Genital Complex.

(0) Cirrus pouch, internal and external seminal vesicle present.

(1) Cirrus pouch and coiled internal seminal vesicle present.

(2) Cirrus pouch very small, surrounding terminus only; external seminal vesicle present; derived from state (0).

(3) Cirrus pouch and a relatively small, straight seminal vesicle present; derived from state (0).

(4) Cirrus pouch absent; seminal vesicle small and globular; derived from state (0).

The male genital apparatus is a complex set of organs, and the interrelationship of the constituent parts is unclear. In addition to the prostate and cirrus, the following structures may be found in a number of combinations: cirrus pouch, internal seminal vesicle (within the cirrus sac), external seminal vesicle (outside the cirrus sac), and seminal vesicle proper (in the absence of the cirrus sac). The evolutionary relationships of these component parts are unclear; for example, in the absence of histological data, it is currently impossible to determine if the seminal vesicle proper represents an internal or external seminal vesicle or combination of both after the loss of the cirrus pouch. Instead of recording the presence and absence of individual structures, I recorded the male terminal genitalia as a complex since at least five distinct patterns occur. Since all the above mentioned structures are found in the out-group, I coded as primitive those genera in which all are present. States 1-4 consist of different combinations of these structures and are coded as independent derivations. It is likely that a more informative pattern of relationship exists but until considerably more information is available, the approach I have taken seems most conserative.

(4) Cirrus pouch absent; seminal vesicle small and globular; derived from state (0).

The male genital apparatus is a complex set of organs, and the interrelationship of the constituent parts is unclear. In addition to the prostate and cirrus, the following structures may be found in a number of combinations: cirrus pouch, internal seminal vesicle (within the cirrus sac), external seminal vesicle (outside the cirrus sac), and seminal vesicle proper (in the absence of the cirrus sac). The evolutionary relationships of these component parts are unclear; for example, in the absence of histological data, it is currently impossible to determine if the seminal vesicle proper represents an internal or external seminal vesicle or combination of both after the loss of the cirrus pouch. Instead of recording the presence and absence of individual structures, I recorded the male terminal genitalia as a complex since at least five distinct patterns occur. Since all the above mentioned structures are found in the out-group, I coded as primitive those genera in which all are present. States 1-4 consist of different combinations of these structures and are coded as independent derivations. It is likely that a more informative pattern of relationship exists but until considerably more information is available, the approach I have taken seems most conserative.

Character 16: Laurer's Canal.

(0) Present.

(1) Absent.

Laurer's canal is a structure of undetermined function which is found in female trematodes. It was formerly thought to be a rudimentary vagina, but evidence supporting this hypothetis is lacking. Laurer's canal is absent in Schistosoma and Orientobilharzia. It is not mentioned in any description of Macrobilharzia and although I feel the data are not conclusive for this genus, I coded its absence as a derived loss. The canal is reported as present in at least some representatives of all other genera, and is consistently reported as present in all genera in subfamilies other than the Schistosomatinae.

Character 17: Seminal Receptacle.

(0) Present.

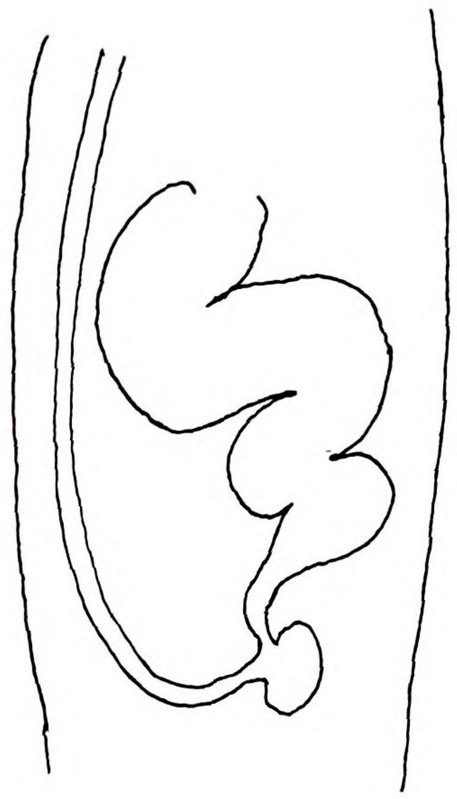
(1) Absent.

Although it is seldom mentioned, the seminal receptacle (Figure 25) has been reported for the genus Schistosoma on more than one occasion (i.e., Faust et al., 1934; Sinha and Srivastava, 1956). The only group in which the seminal receptacle is consistently reported as absent is the genus Orientobilharzia. Although previously mounted specimens which I examined showed no trace of the structure, a vaguely suggestive object was observed in one specimen of O. turkestanicum which I stained and mounted (U.S.N.H.C. #45820).

Figure 25. Size and shape of seminal receptacle.

A. Simple and sac-like

B. Enlarged; long and sinuous



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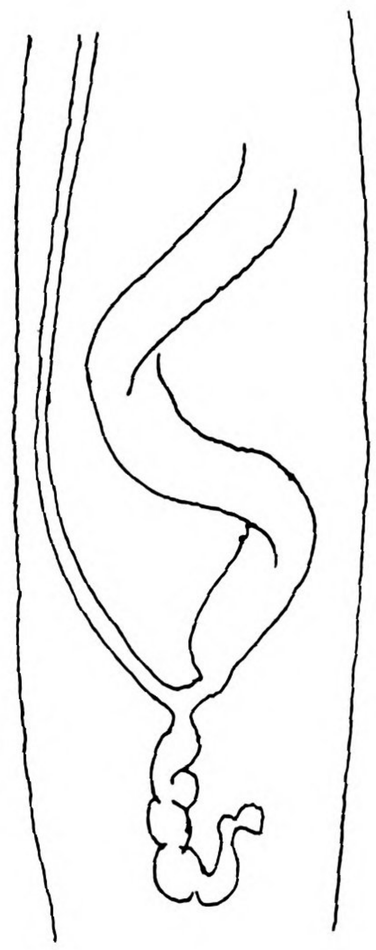

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Although I have coded its absence as a derived loss in Orientobilharzia, further study on more extensive material may reveal the presence of the seminal receptacle in the genus.

Character 18. Size and Shape of Seminal Receptacle.

(0) Simple and sac-like.

(1) Englarged; long and sinuous.

When present in spirorchids, the seminal receptacle is always small and globular. It is described in two different ways, as either an expansion of the germiduct, or as a separate sac-like outpocketing from the duct (Price, 1934; Mehra, 1939). In schistosomes, the seminal receptacle is usually a small, globular sac arising from the germiduct (Figure 25A). I have scored the enlarged and convoluted seminal receptacle which occurs in three genera (Trichobilharzia, Gigantobilharzia and Dendritobilharzia) as derived condition (Figure 25B).

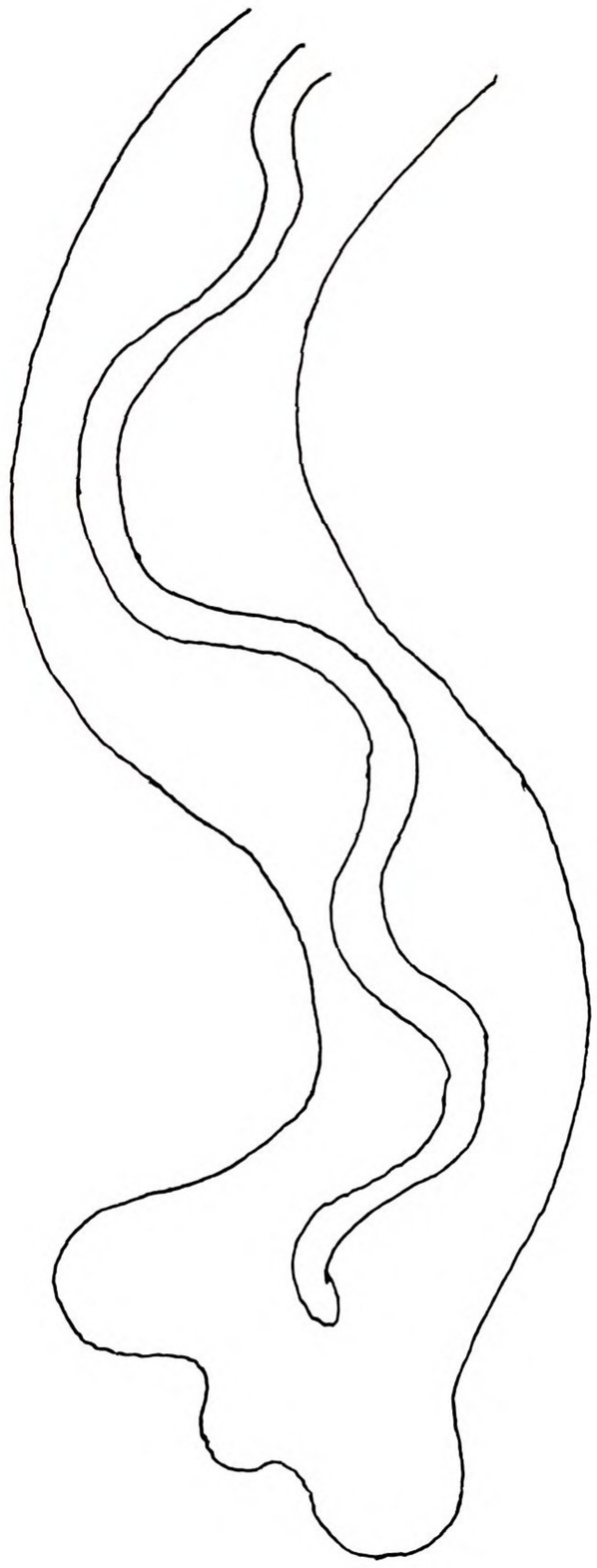
Character 19: Spatulate Projections of Posterior Extremity.

(0) Absent.

(1) Present.

Nearly all reports for the genus Trichobilharzia depict a modification of the posterior end of the body (Figure 26) which is variously described as spatulate, fan-like, and bulb or club-like. I suspect the extent to which the projections are manifested is dependent upon the degree of contraction of an individual worm during

Figure 26. Spatulate projections of posterior extremity of Trichobilharzia.



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preservation. It is generally reported as present in males, but McMullen and Beaver (1945) report it in both sexes for T. physellae, T. ocellata and T. stagnicolae. It is possible that further examination of this large and complex genus will yield useful information pertaining to interspecific variation in the size and shape of the posterior extremity.

In his description of the subfamily Gigantobilharziinae (genus Gigantobilharzia only), Yamaguti (1971) mentioned lobe-like lateral projections of the posterior end in both sexes. This is apparently due to Odhner's original description of the genus Gigantobilharzia (Odhner, 1910) in which a modification of the posterior end was reported. Nearly all subsequent reports of the genus describe a blunt or tapering terminus. Lal (1937) and Farley (1963) mention dilated or swollen posterior ends on G. egreta and G. lawayi respectively, but at least Farley clearly distinguished the condition he observed from the spatulate structures seen in Trichobilharzia. Likewise, my own limited observations indicate that spatulate modifications are restricted to the genus Trichobilharzia. I have scored their occurrence as an autopomorphy.

Character 20. Location of Male Genital Pore.

(0) Seminal vesicle relatively simple; genital pore located just posterior to the acetabulum.

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(1) Seminal vesicle elongated; genital pore well behind the acetabulum but anterior to the cecal reunion.

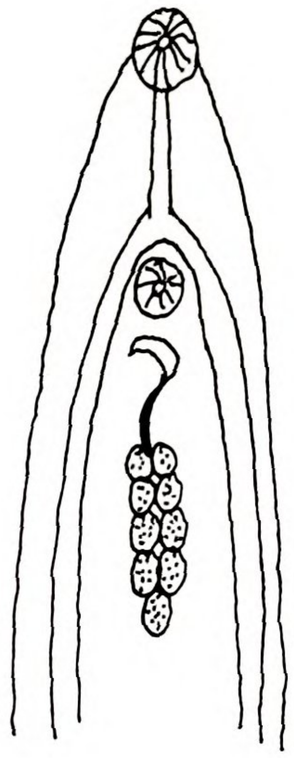
(2) Seminal vesicle elongated; genital pore well behind the acetabulum and cecal reunion; derived from state (1).

Although the seminal vesicle is somewhat enlarged in a few spororchids, it never achieves the enlarged and elongate condition seen in some members of the Bilharziellinae and Gigantobilharziinae. In the genera Trichobilharzia and Gigantobilharzia, the seminal vesicle is extremely long and the genital pore lies well behind the acetabulum and/or cecal reunion (Figure 27B). This situation differs from the general condition displayed by schistosomes; sparse developmental information in McMullen and Beaver (1945) indicates that early development of the genital primordia occurs just behind the acetabulum and that the genital pore moves posteriorly as the seminal vesicle grows and lengthens. This developmental sequence suggests that the condition just described is derived relative to the arrangements seen in the Schistosomatinae, where the genital pore lies just posterior to the acetabulum (Figure 27A). A somewhat intermediate condition coded as such, is displayed by the genera Bilharziella and Dendritobilharzia. In these genera, the seminal vesicle is moderately enlarged and the genital pore lies between the cecal branches, anterior to the cecal reunion. This

Figure 27. Location of male genital pore.

A. Immediately post-acetabular

B. Well behind acetabulum and cecal reunion



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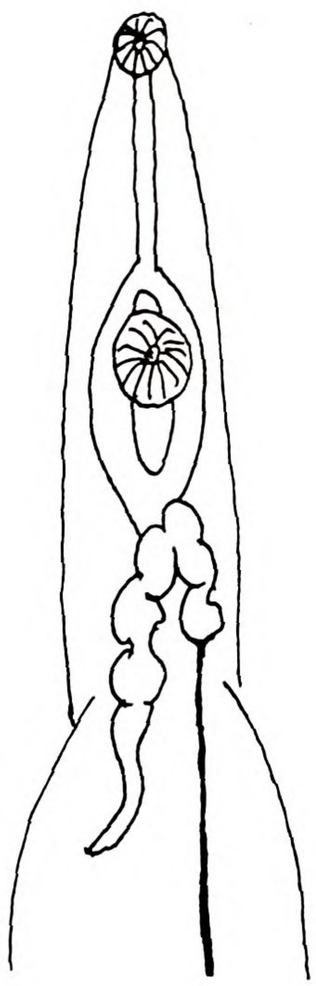

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coding consists of a somewhat bold hypothesis, and more detailed developmental data would provide a stronger basis for the hypothesis of relationship.

Character 21. Length of Common Cecum; Male.

(0) Common cecum short; fused only at posterior end.

(1) Cecae fused for at least half of the body length.

Character 22: Length of Common Cecum; Female.

(0) Common cecum short, fused only at posterior end.

(1) Common cecum long and straight.

(2) Common cecum long and sinuous; derived from state (0).

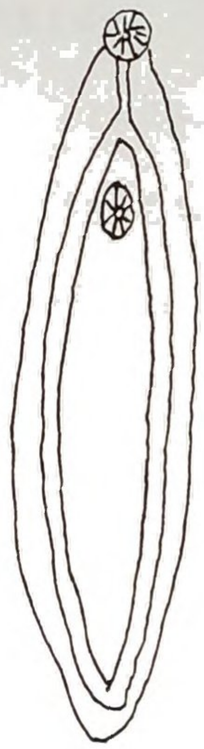
In the out-group, cecal branches usually remain unfused at the posterior extremity. Stunkard (1923) reported a few instances of fusion in the normally unfused genus Spirorchis. Sporadic occurrences of fused cecae may be related to the elongate body form characteristic of blood-inhabiting flukes. In schistosomes,the cecal arms always fuse but the relative length of the fused cecum varies in two ways. First, the paired cecae may fuse only at the posterior extremity, resulting in a very short common cecum (Figure 28A). I consider this condition to be primitive, since fusion occurs late in development and results in an arrangement similar to that seen in the above

Figure 28. Length of common cecum.

A. Short

B. Long and straight

C. Long and sinuous



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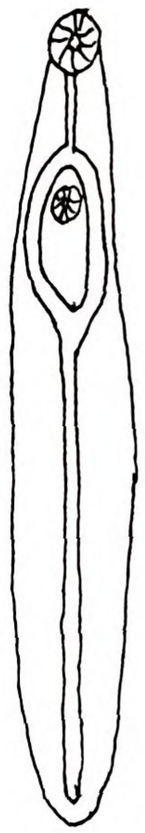

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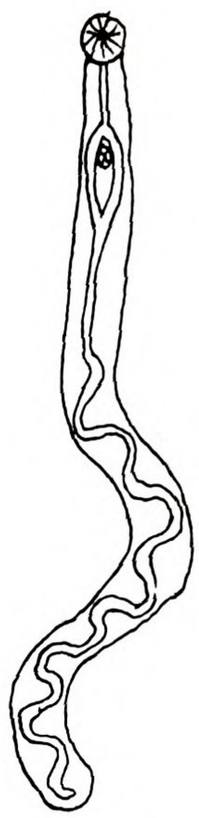

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mentioned aberrant spirorchids. The second pattern involves a long common cecum which runs at least half the length of the body (Figure 28B). In this case, the cecal branches fuse early in development and subsequent elongation occurs along the common cecum. Cecal length may vary between the sexes of a given genus; therefore I have used separate characters for male and female worms.

In addition to variation in length, females with long cecae can be further subdivided into a group in which the cecum is straight (Figure 28B) and a group in which the cecum is sinuous (Figure 28C). Limited ontogenetic information (McMullen and Beaver, 1945; Cort, 1921; and Faust et al. 1934) suggests that fusion occurs later in development in the sinuous group than in taxa with straight cecae. I have tentatively coded these two states as independently derived, until I obtain more informative data.

Character 23. Condition of the Acetabulum.

(0) Simple.

(1) Areolated.

In spirorchids and the majority of schistosomes, the acetabulum is a simple, sucker-like structure. Exceptions to this occur in reports of both African and Asian Macrobilharzia. The acetabulum of the Indian form is described by Baugh (1963, p. 306) as follows: "the ventral sucker has a scalloped margin -- this is a consequence of its peripheral area being marked into a series of

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areolae, usually seventeen or eighteen in number. This areolated periphery of the ventral sucker is an outstanding morphological and distinguishing character of the fluke." Fain (1955, p. 357) described the acetabulum of the African form as possessing "17 á 22 festons." The presence or absence of this autapomorphic character in American forms is unclear; since areolae are not mentioned, I have scored the acetabulum as simple. In an intriguing but inconclusive report, Kohn (1964) pictures this genus with segmented acetabulae. Since no special reference is made in the text, this "segmentation" may just be pictured for artistic effect, emphasizing the three dimensional nature of the organ. Once again, further information is necessary in order to clear up this ambiguity.

Character 24: Testes Number.

(0) 2.

(1) >2, <10.

(2) >10, <30.

(3) >30, <100.

(4) >100, <200.

(5) <200.

The presence of two testes is the pattern most frequently encountered among digenetic trematodes. Spirorchids usually have two testes, but numbers may vary from one to many. Schistosomes always have more than two, and often up to many hundred testes. In scoring this character,

I assumed the condition of multiple testes was achieved independently in the two above mentioned families, since spirorchids possess the primitive condition of two testes within the range of variation displayed by the family.

In determining a transformation series based on the number of testes within genera of the Schistosomatidae, I took a number of factors into consideration. The number of testes in a given individual varies according to the age (Chu and Cutress, 1954) and size of the worm; the latter is particularly true of the filiform genera. In the introduction, I discussed the present knowledge of factors (suitability of host environment, competition, etc.) which influence growth and development, and thus indirectly influence testes number. Unfortunately, it is nearly impossible to determine the age of a sample taken from a wild-caught host. Since most species descriptions are based on samples taken from one or a very few host individuals, the chance of encountering immature worms may bias the estimate of testes number downward for a given genus. In addition, it is impossible to assess the suitability of a particular host species with regard to parasite development when descriptions are based on small samples.

Taking these factors into account, I based my estimate of testes number on the upper two-thirds of the range of variability shown by all species of a given genus. This approach resulted in the six non-overlapping categories

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listed at the beginning of this section, each derived in sequence from the state immediately previous to it. Genera with fewer testes (<100) showed less variability than those with numerous testes, as might be expected. I realize that in my attempt to compartmentalize data on testes number, I run the risk of obscuring true natural variability. Although subject to reevaluation in the future, I feel my hypothesis of relationship is reasonable at present.

Phylogenetic Analysis

The data matrix presented in Table 5 consists of 24 characters in a total of 64 states, designated for 14 genera. For the purpose of computer analysis, I included a hypothetical ancestor scored for the primitive state of all characters. With two exceptions, I followed the generic taxonomy of Farley (1971). The first exception is in the genus Macrobilharzia, where I found enough inconsistencies in reports of Old and New World forms to merit a separate analysis of each. Macrobilharzia is the most poorly described avian taxon within the Schistosomatidae; my separation of forms may simply represent the general lack of knowledge of the group.

The second deviation from Farley's taxonomy is my use of the name Sinobilharzia for his Austrobilharzia odhneri, which had originally been described in the genus Ornithobilharzia. As I discussed under individual

TABLE 5

CHARACTER STATE DISTRIBUTIONS OF THE SCHISTOSOMATIDAE

Character State	Schistosoma	Bivitellobilharzia	Heterobilharzia	Orientobilharzia	Schistosomatium	Austrobilharzia	Macrobilharzia (New World)	Macrobilharzia (Old World)	Ornithobilharzia	Sinobilharzia	Bilharziella	Trichobilharzia	Gigantobilharzia	Dendritobilharzia
1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	1	1	1	1
3	0	0	1	0	1	0	0	0	0	0	0	0	0	0
4^1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
4^2	0	0	0	0	0	0	0	0	0	0	0	1	1	0
4^3	0	0	0	0	1	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0	0	1
6	0	0	0	0	0	0	0	0	0	0	0	0	1	1
7^1	0	1	1	0	1	1	1	1	1	1	1	1	1	1
7^2	0	1	1	0	1	1	1	1	1	1	0	1	1	1
7^3	0	0	0	0	0	0	0	0	1	0	0	1	0	0
7^4	0	0	1	0	0	0	0	0	0	0	0	0	0	1
8^1	0	1	1	0	1	0	0	0	0	0	0	0	0	0
8^2	1	0	0	1	0	1	0	0	1	1	0	0	0	0

17	0	0	0	1	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	1	1	1

Table 5 (continued)

Character State	Schistosoma	Bivitellobil-harzia	Heterobil-harzia	Orientobil-harzia	Schistoso-matium	Austrobil-harzia	Macrobilharzia (New World)	Macrobilharzia (Old World)	Ornithobil-harzia	Sinobilharzia	Bilharziella	Trichobil-harzia	Gigantobil-harzia	Dendritobil-harzia
9	0	0	0	0	0	0	0	0	0	0	0	0	0	1
10^1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
10^2	0	0	1	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	1	1
12	0	0	1	0	1	0	1	1	0	0	0	0	0	1
13	1	1	1	1	1	0	1	0	1	1	0	0	0	0
14	1	1	0	1	0	0	0	0	0	0	0	0	0	0
15^1	0	0	0	0	0	1	1	0	0	0	0	0	0	0
15^2	0	0	0	0	0	0	0	1	1	1	0	0	0	0
15^3	0	0	1	0	1	0	0	0	0	0	0	0	0	0
15^4	1	1	0	1	0	0	0	0	0	0	0	0	0	0
16	1	0	0	1	0	0	1	1	0	0	0	0	0	0
17	0	0	0	1	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	1	1	1

Table 5 (continued)

Character State	Schistosoma	Bivitellobil-harzia	Heterobil-harzia	Orientobil-harzia	Schistoso-matium	Austrobil-harzia	Macrobilharzia (New World)	Macrobilharzia (Old World)	Ornithobil-harzia	Sinobilharzia	Bilharziella	Trichobil-harzia	Gigantobil-harzia	Dendritobil-harzia
19	0	0	0	0	0	0	0	0	0	0	0	1	0	0
20^1	0	0	0	0	0	0	0	0	0	0	1	1	1	1
20^2	0	0	0	0	0	0	0	0	0	0	0	1	1	0
21	0	0	0	0	0	0	0	0	0	0	1	1	1	1
22^1	1	0	0	1	0	1	0	0	1	0	0	0	0	0
22^2	0	0	0	0	0	0	0	0	0	0	1	1	1	1
23	0	0	0	0	0	0	0	1	0	0	0	0	0	0
24^1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
24^2	0	1	1	1	1	1	1	1	1	1	1	1	1	1
24^3	0	1	1	1	0	0	1	1	1	1	1	1	1	1
24^4	0	0	0	0	0	0	1	1	0	0	0	1	1	1
24^5	0	0	0	0	0	0	1	1	0	0	0	0	1	0

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characters, inconsistencies in the published description suggest that a separate analysis of this species is a more cautious approach than Farley's lumping of the taxon.

The components specified by character distributions in the data matrix are listed in Table 6. I have not included single taxon components specified by autapomorphies in Table 6 since they do not contribute information useful in generating branching diagrams. In order to perform a component analysis, I used Felsenstein's largest clique program to generate all possible combinations of the components contained in Table 6. The computer analysis generated 66 unique cladograms.

I limited detailed analysis to the fourteen cladograms which contained Component 12, consisting of the taxa Bilharziella, Trichobilharzia, Gigantobiharzia and Dendritobilharzia. Component 12 is specified by four derived character states, more replicates than occur for any other component. (No components are specified by three character states, four are specified by two, and the rest by one character state.) These derived states are: 2^1--testes located on either side of common cecum; 20^1--male genital pore located well behing the acetabulum, 21--common cecum in male greater than one half of the total body length; and 22^2--female common cecum long and sinuous. In addition to the number of replications, all four states represent derived gains as opposed to losses, lending further

TABLE 6

COMPONENTS SPECIFIED BY CHARACTER STATE DISTRIBUTIONS OF THE SCHISTOSOMATIDAE

Component	Genera	Defining Character State
1	All taxa	24^1
2	Bivitellobilharzia, Heterobilharzia, Orientobilharzia, Schistosomatium, Austrobilharzia, Macrobilharzia (N.W.), Macrobilharzia (O.W.), Ornithobilharzia, Sinobilharzia, Bilharziella, Trichobilharzia, Gigantobilharzia, Dendritobilharzia	24^2
3	Schistosoma, Bivitellobilharzia, Heterobilharzia, Orientobilharzia, Schistosomatium, Austrobilharzia, Macrobilharzia (N.W.), Macrobilharzia (O.W.), Ornithobilharzia, Sinobilharzia, Bilharziella, Trichobilharzia, Gigantobilharzia	4^1
4	Schistosoma, Heterobilharzia, Schistosomatium, Austrobilharzia, Macrobilharzia (N.W.), Macrobilharzia (O.W.), Ornithobilharzia, Sinobilharzia, Bilharziella, Trichobilharzia, Gigantobilharzia, Dendritobilharzia	7^1
5	Bivitellobilharzia, Heterobilharzia, Orientobilharzia, Macrobilharzia (N.W.), Macrobilharzia (O.W.), Ornithobilharzia, Sinobilharzia, Bilharziella, Trichobilharzia, Gigantobilharzia, Dendritobilharzia	24^3

Table 6 (continued)

Component	Genera	Defining Character State
6	Bivitellobilharzia, Heterobilharzia, Schistosomatium, Austrobilharzia, Macrobilharzia (N.W.), Macrobilharzia (O.W.), Ornithobilharzia, Sinobilharzia, Trichobilharzia, Gigantobilharzia, Dendritobilharzia	7^2
7	Schistosoma, Bivitellobilharzia, Heterobilharzia, Orientobilharzia, Schistosomatium, Macrobilharzia (N.W.)	13
8	Ornithobilharzia, Sinobilharzia, Heterobilharzia, Schistosomatium, Macrobilharzia (N.W.), Macrobilharzia (O.W.), Dendritobilharzia	12
9	Macrobilharzia (N.W.), Macrobilharzia (O.W.), Trichobilharzia, Gigantobilharzia, Dendritobilharzia	24^4
10	Schistosoma, Orientobilharzia, Austrobilharzia, Ornithobilharzia, Sinobilharzia	8^2
11	Schistosoma, Orientobilharzia, Austrobilharzia, Ornithobilharzia	22^1
12	Bilharziella, Trichobilharzia, Gigantobilharzia, Dendritobilharzia	$2, 20^1$ $21, 22^2$
13	Schistosoma, Orientobilharzia, Macrobilharzia (N.W.), Macrobilharzia (O.W.)	16
14	Macrobilharzia (N.W.), Macrobilharzia (O.W.), Gigantobilharzia	24^5

Table 6 (continued)

Component	Genera	Defining Character State
15	Trichobilharzia, Gigantobilharzia, Dendritobilharzia	18
16	Macrobilharzia (N.W.), Ornithobilharzia, Sinobilharzia	15^{2}
17	Schistosoma, Bivitellobilharzia, Orientobilharzia	$14, 15^{4}$
18	Bivitellobilharzia, Heterobilharzia, Schistosomatium	8^{1}
19	Heterobilharzia, Schistosomatium	$3, 15^{3}$
20	Austrobilharzia, Macrobilharzia (N.W.)	15^{1}
21	Heterobilharzia, Dendritobilharzia	7^{4}
22	Ornithobilharzia, Trichobilharzia	7^{3}
23	Gigantobilharzia, Dendritobilharzia	6, 11
24	Trichobilharzia, Dendritobilharzia	$4^{2}, 20^{2}$

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confidence to my decision to focus attention on cladograms containing Component 12.

Three of the character states defining Component 12 involve the cecum. I cannot rule out the possibility that these states are in some way developmentally or functionally correlated since detailed ontogenetic sequences are unavailable for nearly all genera. I think it is not unreasonable to treat each character state separately. Variation in cecal fusion and testes location both within and between genera suggest some support for my approach. Patterns of cecal fusion differ significantly between genera, and within a given genus, the cecum may be fused in females and separate in males (e.g., Schistosoma), fused in both sexes (e.g., Bilharziella), or unfused in both sexes (e.g., Macrobilharzia). Likewise, testes distribution and number vary consistently, and variability is particularly marked in genera in which the cecum is unfused. Testes may be tandem and numerous (e.g., Orientobilharzia), few and clustered midbody (e.g., Schistosomatium), numerous and clustered terminally (e.g., Heterobiharzia), etc. Thus a broad sample of comparative development data is needed before the question of correlation among these character states is resolved.

After narrowing my analysis to 14 cladograms based on the replication of Component 12, I then assigned character state distributions to each branching diagram using

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Farris optimization. The fourteen branching diagrams are presented in Figure 29A-N. In these cladograms, groups defined by actual components are illustrated using solid lines, while optimized branches are indicated by dashed lines. The total number of evolutionary changes in character states or steps is indicated along with each cladogram.

The fourteen cladograms can be viewed as two sets of seven branching diagrams each, the sets differing only in the placement of two taxa. In Cladograms 1-7, Component 24 defines a terminal dichotomy consisting of the genera Trichobilharzia and Gigantobilharzia, while in Cladograms 8-14, Component 23 describes a terminal dichotomy of Dendritobilharzia and Gigantobilharzia. In each case, two character state changes are involved; thus exchanging Trichobilharzia and Dendritobilharzia does not alter the total number of steps in each corresponding pair of cladograms.

The character state distributions in the fourteen resulting cladograms offered no clear avenues along which to further narrow the field of choices. In the absence of other criteria, I invoked parsimony to choose the cladogram which made the fewest statements about character state change during evolution (Farris, 1983).

Two minimum length cladograms, each with an equal number of steps, result from the use of parsimony: preferred Cladograms 2 and 9 (Figure 29B, I), with 64

Figure 29. Component analysis of the Schistosomatidae. Components are indicated by circled numbers. Gain of a derived character state is indicated by the symbol (X), reversal by (0). Optimized branches are indicated by dashed lines.

A. Cladogram 1, 71 steps

B. Cladogram 2, 64 steps

C. Cladogram 3, 68 steps

D. Cladogram 4, 66 steps

E. Cladogram 5, 67 steps

F. Cladogram 6, 69 steps

G. Cladogram 7, 77 steps

H-N. Cladograms 8-14 correspond with Cladograms 1-7 but contain Component 23 in place of Component 24.

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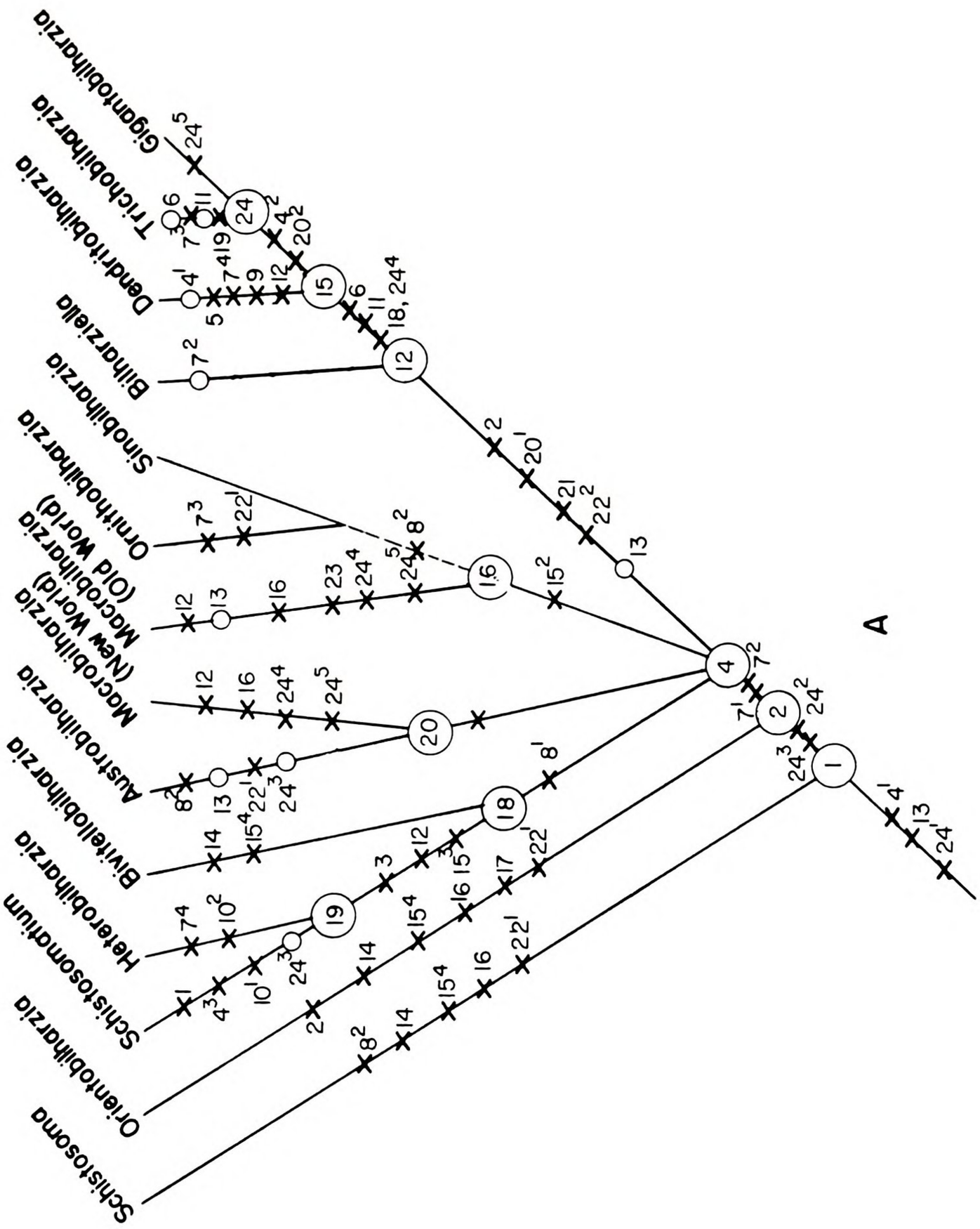
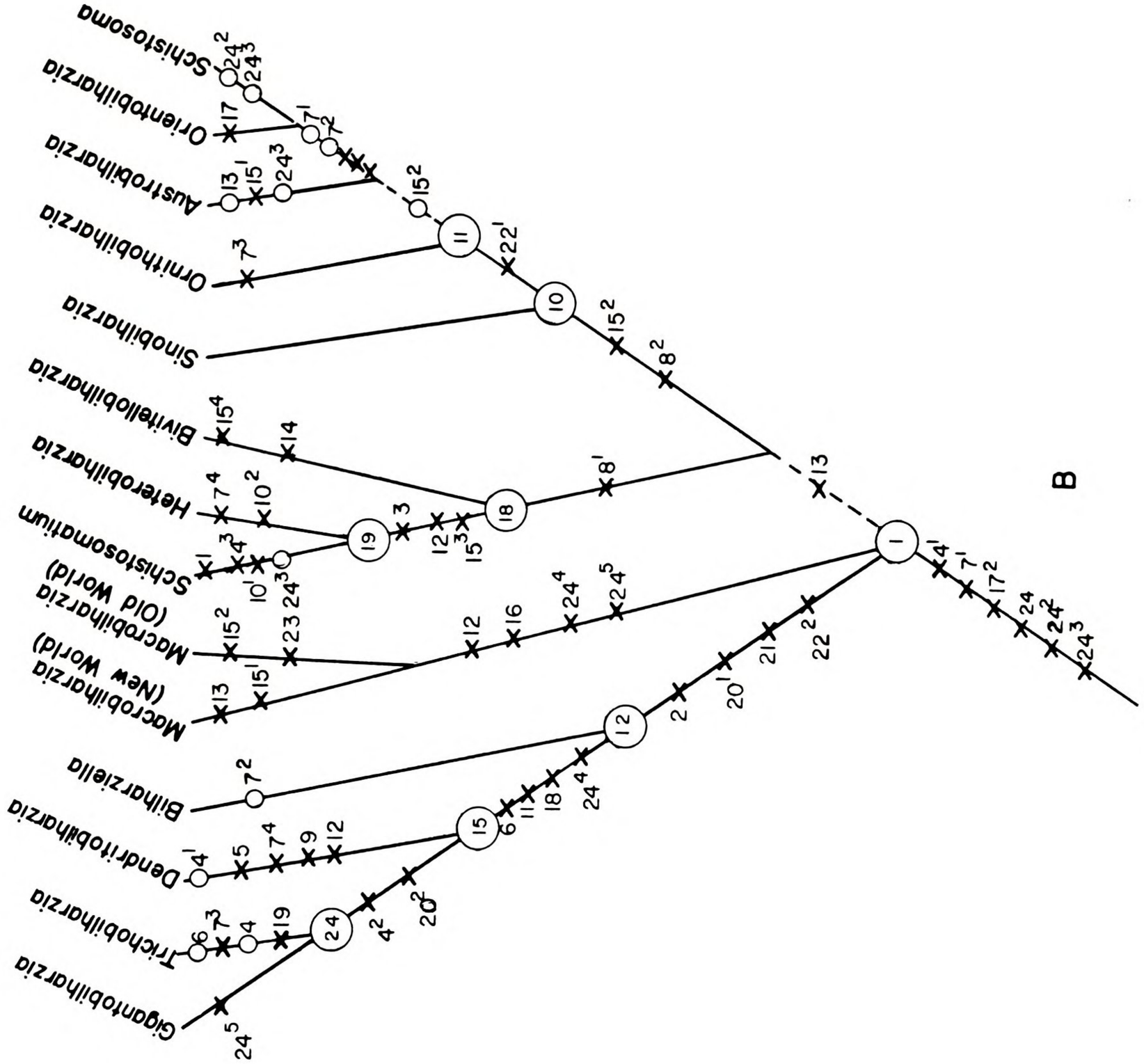
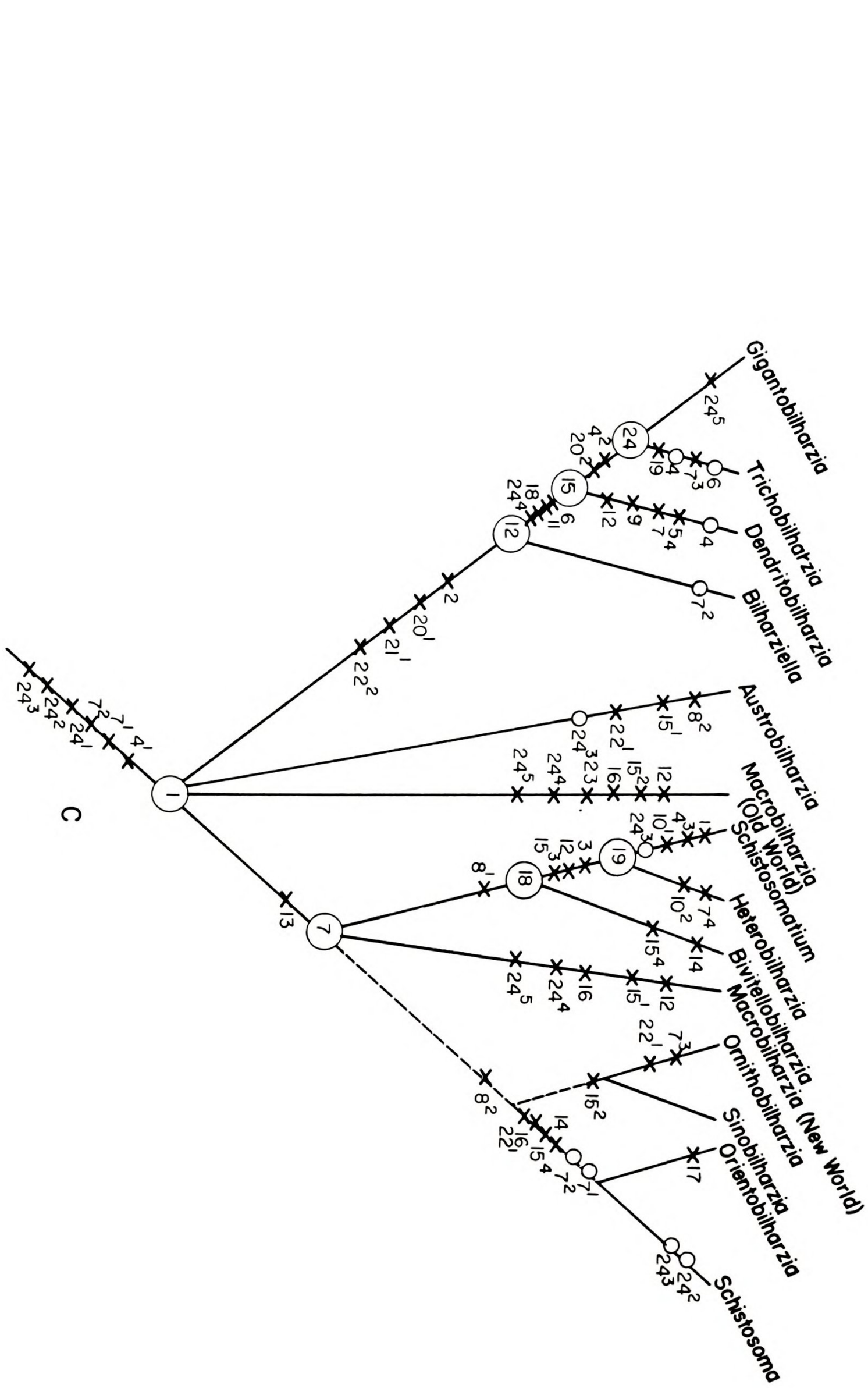
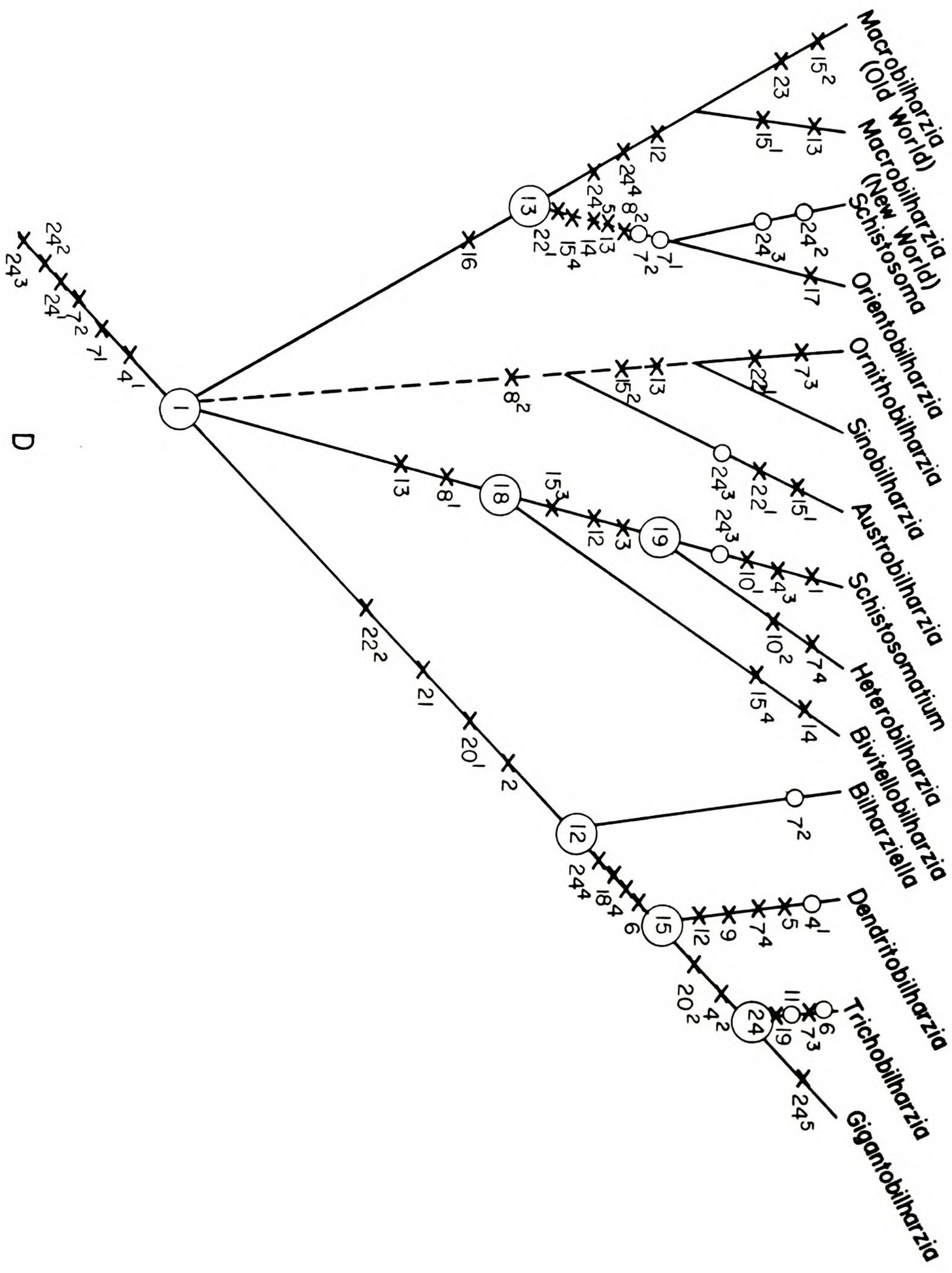



Schistosoma
Orientobilharzia
Austrobilharzia
Ornithobilharzia
Sinobilharzia
Bivitellobilharzia
Heterobilharzia
Schistosomatium
(Old World)
Macrobilharzia
(New World)
Macrobilharzia
Bilharziella
Dendritobilharzia
Trichobilharzia
Gigantobilharzia
B


Gigantobilharzia
Trichobilharzia
Dendritobilharzia
Bilharziella
Austrobilharzia
Macrobilharzia (Old World)
Schistosomatium
Heterobilharzia
Bivitellobilharzia
Macrobilharzia (New World)
Ornithobilharzia
Sinobilharzia
Orientobilharzia
Schistosoma
C


Macrobilharzia (Old World)
Macrobilharzia (New World)
Schistosoma
Orientobilharzia
Ornithobilharzia
Sinobilharzia
Austrobilharzia
Schistosomatium
Heterobilharzia
Bivitellobilharzia
Bilharziella
Dendritobilharzia
Trichobilharzia
Gigantobilharzia
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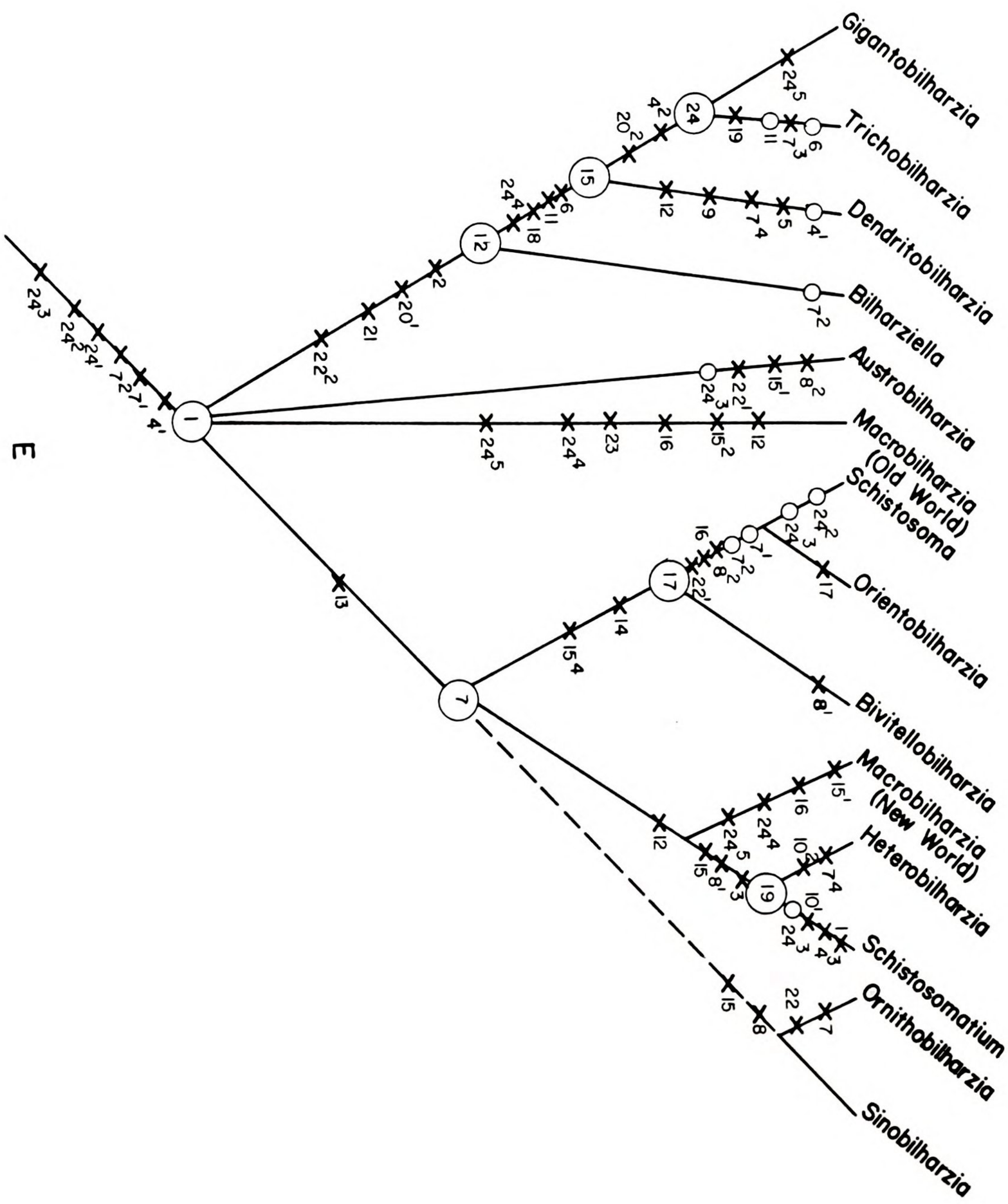
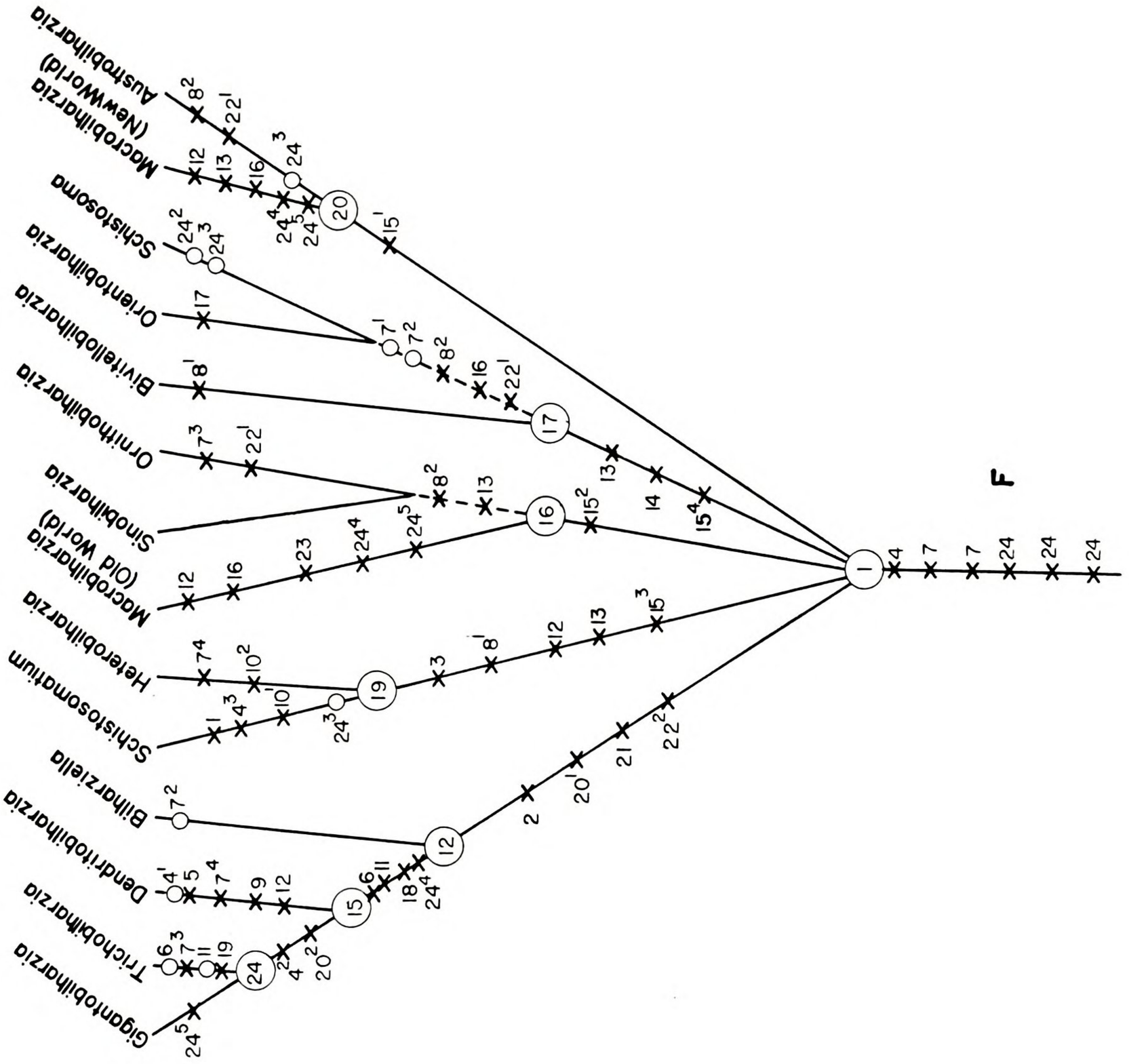

E
Gigantobilharzia
Trichobilharzia
Dendritobilharzia
Bilharziella
Austrobilharzia
Macrobilharzia (Old World) Schistosoma
Orientobilharzia
Bivitellobilharzia
Macrobilharzia (New World) Heterobilharzia
Schistosomatium
Ornithobilharzia
Sinobilharzia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4 7 7 24 24 24
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8² 22¹ 3 24 16 13 12 24⁴ 24⁵ 24² 15¹
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8¹ 7³ 22¹ 7¹ 7² 8² 16 22¹ 13 14 15⁴
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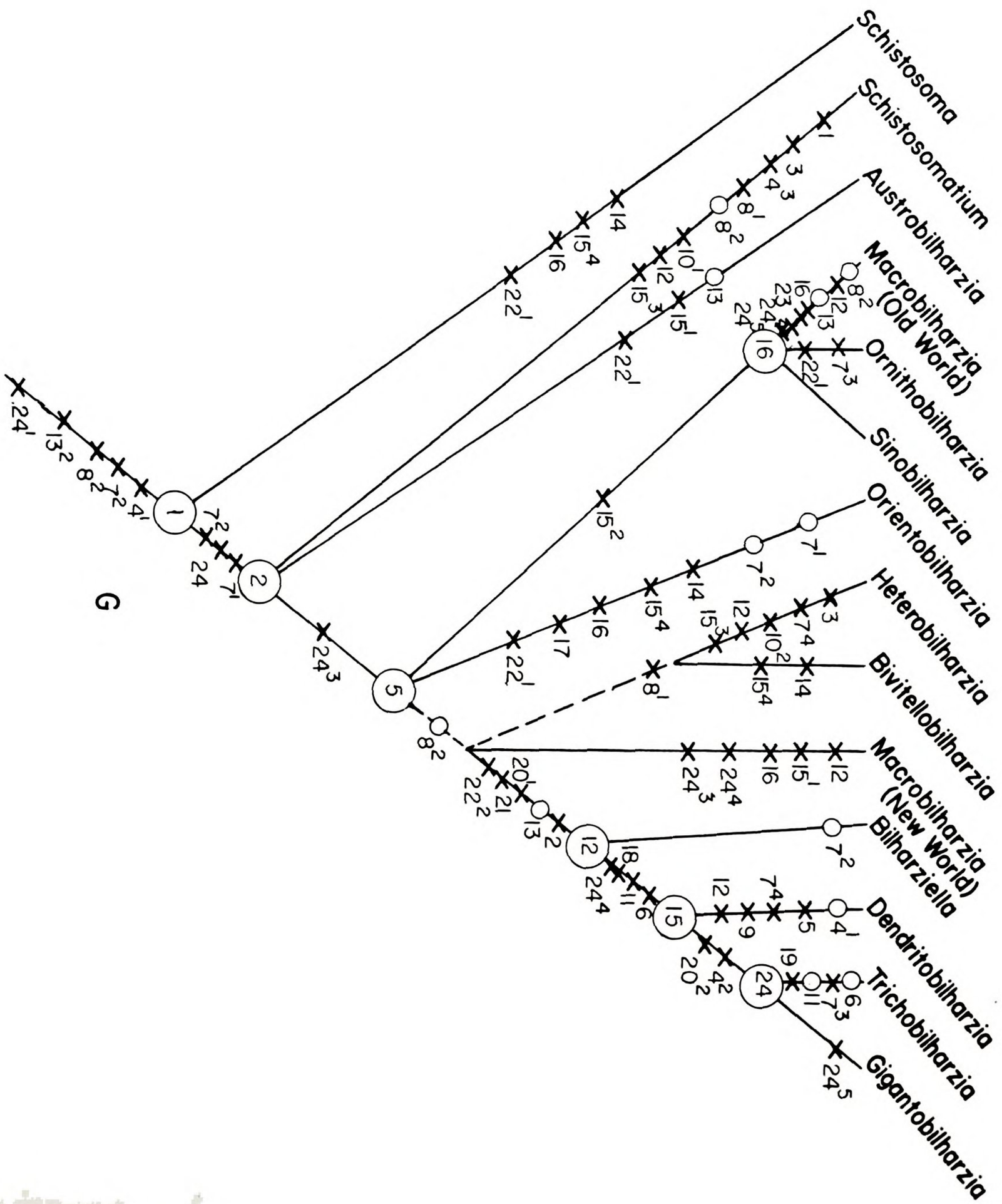
8² 13 15² 12 16 23 24⁴ 24⁵
19
74 10² 1 4³ 10 24³ 3 8¹ 12 13 15³
12
7² 2 20¹ 21 22² 11 24⁴ 18 6 11
15
4¹ 5 7⁴ 9 12 24³ 20² 2⁴
24
6 7³ 11 19 24⁵
Macrobilharzia (New World)
Austrobilharzia
Macrobilharzia
Schistosoma
Orientobilharzia
Bivitellobilharzia
Ornithobilharzia
Sinobilharzia
Macrobilharzia (Old World)
Heterobilharzia
Schistosomatium
Bilharziella
Dendritobilharzia
Trichobilharzia
Gigantobilharzia


Schistosoma
Schistosomatium
Austrobilharzia
Macrobilharzia (Old World)
Ornithobilharzia
Sinobilharzia
Orientobilharzia
Heterobilharzia
Bivitellobilharzia
Macrobilharzia (New World)
Bilharziella
Dendritobilharzia
Trichobilharzia
Gigantobilharzia

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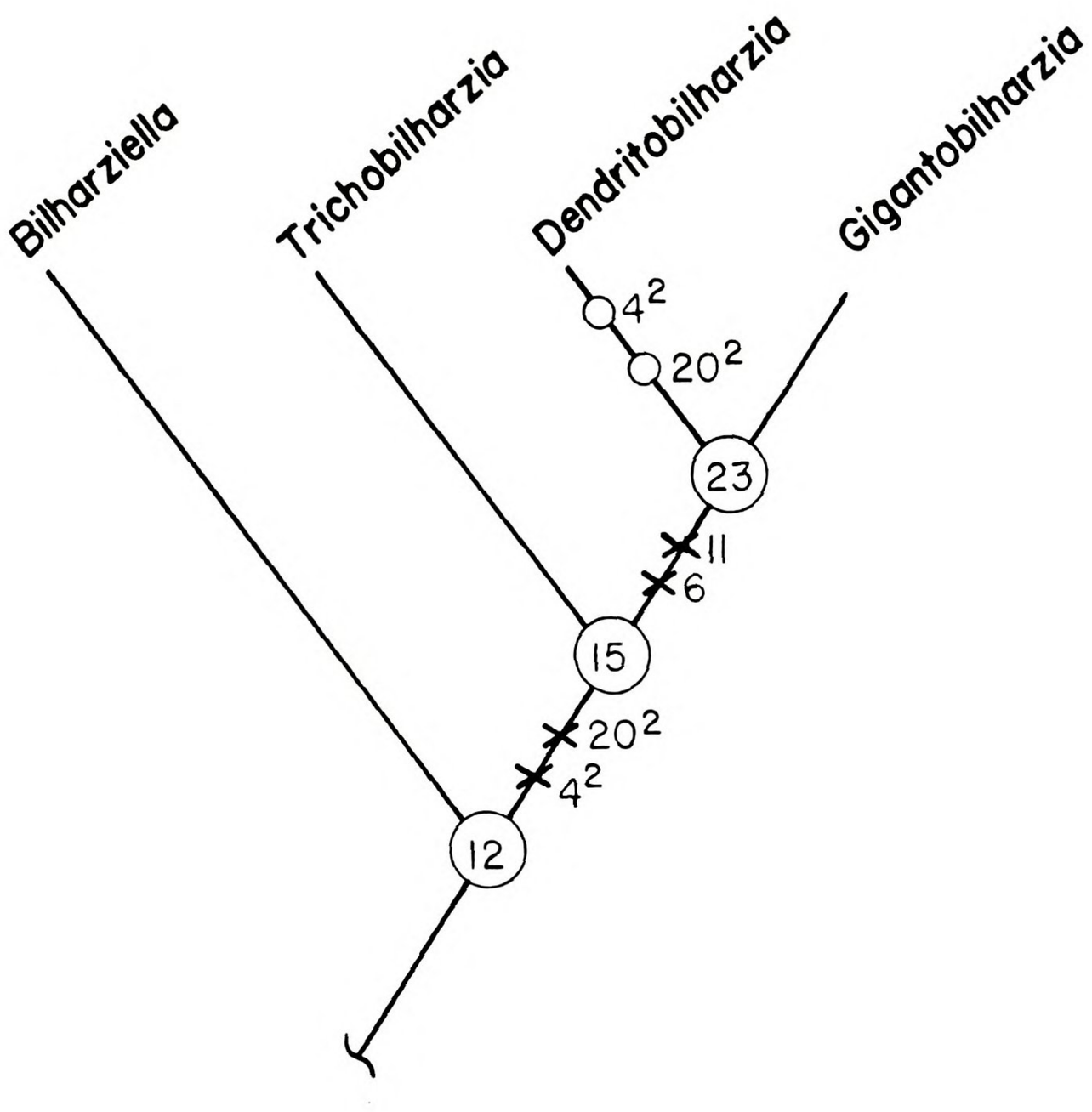
Bilharziella
Trichobilharzia
Dendritobilharzia
Gigantobilharzia
4²
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23
11
6
15
20²
4²
12

H-N

evolutionary steps in each. I will discuss the implications of the character state changes described by these branching diagrams and then briefly compare them to the other 12 cladograms for which state changes were analyzed.

The preferred cladograms each contain a basal trichotomy consisting of one branch composed of genera assigned to the subfamilies Bilharziellinae and Gigantobilharziinae, a second clade including Old and New World members of the genus Macrobilharzia, and a final branch which involves all other genera of the Schistosomatinae.

The relationships indicated by the basal portion of the preferred cladograms differ somewhat from conventional interpretations of schistosome subfamilies. Genera of the Bilharziellinae and Gigantobilharziinae are generally considered more closely related to one another than to members of the Schistosomatinae; therefore placement of their constituent genera on the same branch is not surprising. Within the branch defined by Component 12, however, the arrangement of genera brings into question the traditional division into two subfamilies. Also, the genus Macrobilharzia branches separately from the rest of the genera assigned to the subfamily Schistosomatinae, where it has been traditionally placed.

In Cladogram 2, Gigantobilharzia, Trichobilharzia and Dendritobilharzia are separated from the primitive genus Bilharziella and form a component defined by three character states: 18^{1}--seminal receptacle is long and

sinuous, 24^4--greater than 100 but less than 200 testes, and an optimized character: 11--female genital pore opening at the extreme anterior end. Component 24 defines a terminal dichotomy consisting of the genera Trichobilharzia and Gigantobilharzia. Two derived character states describe Component 24: 4^2--gynacophoric canal limited to the region of the genital pore and 20^2--genital pore located behind a greatly enlarged seminal vesicle. Character 11 reverses to the primitive state in Trichobilharzia, resulting in the genital pore opening behind the acetabulum. Because of the freedom Farris optiminzation allows in interpreting the nature of character state changes, the derived state of Character 11 can alternatively be viewed as a parallel derivation in Dendritobilharzia and Gigantobilharzia. Either intepretation results in the same number of steps.

The terminal dichotomy that appears in Cladogram 2 differs from the traditional interpretation of the subfamily Gigantobilharziinae (Farley, 1971). Trichobilharzia rather than Dendritobilharzia shares a most recent common ancestor with Gigantobilharzia. In contrast, Cladogram 9 incorporates Component 23 which is composed of the two genera Farley (1971) places in the Gigantobilharziinae: Gigantobilharzia and Dendritobilharzia. Two character states defined Component 23: 6--derived loss of the adult acetabulum, and 11--female genital pore located at the extreme anterior end.

The nonparsimonious character state distributions indicated by Component 23 can be interpreted in two ways. In one case, Dendritobilharzia is defined by the loss of two derived character states found in Trichobilharzia and Gigantobilharzia: Complete loss of the gynacophoric canal (Character State 4^2) and reversal to a shortened seminal vesicle (Character State 20^2). Under the alternative interpretation, both Character States 4^2 and 20^2 arise in parallel in Trichobilharzia and Gigantobilharzia. In either case, the total number of evolutionary steps remains the same and until further data are available, I can find no basis to choose a single preferred branching diagram between Cladograms 2 and 9.

In preferred Cladograms 2 and 9, the genus Macrobilharzia branches independently of the Schistosomatinae. Optimization resolves a portion of the multichotomy present after component analysis by uniting Old and New World Macrobilharzia in a single clade. Although Old and New World forms appear similar, much of their resemblance occurs in primitive character states. Interestingly, four optimized states define a component that unites the genus. Two of these states (24^4, 24^5) refer to the extremely large number of testes that Macrobilharzia shares in parallel with most members of Component 12. One character refers to the large number of eggs in the uterus (Character 12) and is shared in parallel with the genera Heterobilharzia, Schistosomatium and Gigantobilharzia.

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The final optimized character state (16--derived loss of the Laurer's canal) is also found in parallel in Schistosoma and Orientobilharzia. I consider the absence of the Laurer's canal in Macrobilharzia questionable since it is overlooked in many reports and the few accounts available for the genus are sketchy at best. Additional descriptions will hopefully clarify the status of Macrobilharzia relative to other genera.

Remaining genera traditionally assigned to the Schistosomatinae are united in an optimized branch combining Components 10 and 18 on the basis of a derived loss of the prostate complex. This is a problematic scoring since the prostate is often hard to detect and a reversal in which the prostate appears apparently occurs in the genus Austrobilharzia. The prostate is also lost in New World Macrobilharzia or was perhaps overlooked in the few existing descriptions.

To date, there have been no systematic studies examining the relationships of genera within the Schistosomatinae. In discussions of the subfamily, mammalian and avian genera are usually treated separately; therefore it is interesting to note that my analysis separates mammalian genera in two components, one of which contains avian genera as well. Schistosomatium, Heterobilharzia and Bivitellobilharzia comprise Component 18. These three mammalian taxa share a derived vitelline structure found no where else among the Strigeata. It consists of a set of vitelline

glands on either side of both paired cecae (Character State 8^1). The Afro-American genus Bivitellobilharzia is one of the most poorly known schistosomes and details of genital morphology, which in my analysis arise in parallel with Schistosoma and Orientobilharzia, are vaguely described in the literature.

Component 19 appears in all of the 14 initially preferred cladograms and consists of the monotypic genera Heterobilharzia and Schistosomatium. These two North American genera are united on the basis of three characters. Both share a state in which the paired cecae possess lateral diverticulae (Character 3) and both have a nearly identical arrangement of the male genitalia (Character State 15^3) which consists of a simple cirrus pouch and a straight seminal vesicle. One optimized character (Character 12) describes Component 19 on the basis of numerous eggs in the uterus.

A different vitelline arrangement, paired glands on either side of the common cecum (Character State 8^2) describes Component 10. This component consists of the genera Sinobilharzia, Ornithobilharzia, Austrobilharzia, Orientobilharzia and Schistosoma. Optimized Character State 15^2 describing male genital morphology also defines Component 10. Component 11, consisting of Ornithobilharzia, Austrobilharzia, Orientobilharzia and Schistosoma nests within Component 10, and is defined by Character State 22^1--female common cecum long and straight. The

quadrichotomy produced by Component 11 is resolved during optimization. Loss of Character State 15^2 creates an optimized branch containing the trichotomy Austrobilharzia, Schistosoma and Orientobilharzia. Finally, an optimized component containing Schistosoma and Orientobilharzia is described by three derived loss character states (14, 15^4, 16) and two reversals (7^1, 7^2) which result in the primitive state of Character 7 occurring in the terminal dichotomy.

In addition to Cladograms 2 and 9, I assigned character state distributions to the 12 other cladograms which contained Component 12 (Figure 29A, C-H, J-N). The number of evolutionary steps contained in each of these cladograms ranged from 66 to 77. Differences in the patterns of the 12 additional cladograms reflect the inclusion of components incompatible with those present in Cladograms 2 and 9.

Eight (Cladograms 1-4, 8-11; Figure 29A-D, H-K) of the total 14 cladograms are similar to one another in possessing Component 18, made up of the mammalian genera Schistosomatium, Heterobilharzia and Bivitellobilharzia. When Component 18 is absent, four cladograms (Cladograms 5 and 12, 6 and 13) group Bivitellobilharzia with Schistosoma and Orientobilharzia. These three genera make up Component 17, defined by two character states: 15^4--male terminal genitalia simplified by derived loss, and 14--derived loss of the cirrus. Thus Component 17 groups

together the predominantly Old World mammalian schistosomes, keeping separate the North American genera found in mammals.

Cladograms 2 and 9 differ from the other 12 cladograms in that they include Component 10, composed of Sinobilharzia, Ornithobilharzia, Austrobilharzia, Schistosoma and Orientobilharzia. The absence of Component 10 allows for the inclusion of a number of other components which significantly alter cladistic relationships. In Cladograms 1 and 8, an inclusive component (defined by Character States 7^1--slightly coiled ovary, and 7^2--moderately coiled ovary) separates the genera Schistosoma and Orientobilharzia as basal branches. This placement contrasts markedly with Cladograms 2 and 9, where terminal placement of the two genera requires the reversal to more primitive states of a number of characters, including Character 7. In Cladograms 1 and 8 (Figure 29A and H) as in all cladograms which separate Old and New World Macrobilharzia (Cladograms 1 and 8, 3 and 10, 5 and 12, 6 and 13, 7 and 14), the number of parallel steps is increased. A major basal separation in Cladograms 3 and 10 is forced by Component 7, which separates Austrobilharzia and Old World Macrobilharzia from other genera of the Schistosomatinae on the basis of Character 13--derived loss of the prostate. Component 13 clusters the Old and New World Macrobilharzia with the genera Schistosoma and Orientobilharzia in Cladograms 4 and 11 and is defined by Character 16 (derived loss of Laurer's canal).

In Cladograms 5 and 12, New World Macrobilharzia group with the North American mammalian schistosomes on an optimized branch defined by the large number of eggs in the uterus (Character 12). Cladograms 6 and 13 share a basal multichotomy and include a number of components absent in Cladograms 2 and 9, such as Components 16 and 20.

Finally, Cladograms 7 and 14 base three major nodes on components described by character states referring to testes number (Character States 24^1, 24^2 and 24^3). This results in the early branching off of taxa with low testes numbers: Schistosoma, Schistosomatium and Austrobilharzia.

All of the 12 non-preferred cladograms include components that increase the number of postulated evolutionary changes. Interestingly, of the branching diagrams proposed by this analysis, the arrangement of taxa in the preferred cladograms differs least from currently proposed subfamilial relationships within the Schistosomatidae (Farley, 1971). Nonetheless, the results of this analysis bring into focus questions concerning host relationships of taxa previously assigned to the subfamily Schistosomatinae. Although avian and mammalian genera appear in the same clade, they cluster into discrete units which reflect host class affiliation.

Systematic Implications

The cladistic relationships proposed herein are in no way the final word on schistosome phylogeny and I expect further data to refine and perhaps redefine the phylogenetic structure I propose. This is particularly true since relatively few characters or character states define many branches of my preferred cladogram. Although I would like to have more data available before attempting a complete taxonomic revision of the family, two reinterpretations of current systematics are worth mentioning.

I see no utility in retaining the subfamilial rankings of Dendritobilharziinae and Gigantobilharziinae. Cladistic analysis clearly indicates inclusion of the genera contained in these two subfamilies in the subfamily Bilharziellinae. Accordingly, in subsequent discussion I will consider the subfamily Bilharziellinae to contain the genera Bilharziella, Trichobilharzia, Gigantobilharzia and Dendritobilharzia. Further study is needed to clarify relationships within the Bilharziellinae, particularly with regard to the genera Gigantobilharzia and Dendritobilharzia which share a unique terminal opening of the female genital pore. Here and throughout the study, more complete information on cercarial characteristics will help with the differentiations I wish to make.

The subfamily Schistosomatinae is probably a polyphyletic grouping as currently defined. A conservative change would involve removing the genus Macrobilharzia

to its own subfamily, which could be named the Macrobilharziinae. The genus is poorly understood and it retains many primitive character states. I am currently unable to clarify its relationship to the other two schistosome subfamilies. For the present time, I have chosen to retain the mammalian genera Schistosomatium, Heterobilharzia and Bivitellobilharzia in the subfamily Schistosomatinae. Further research may suggest their removal based on a number of derived character states which differentiate them from the other members of the subfamily.

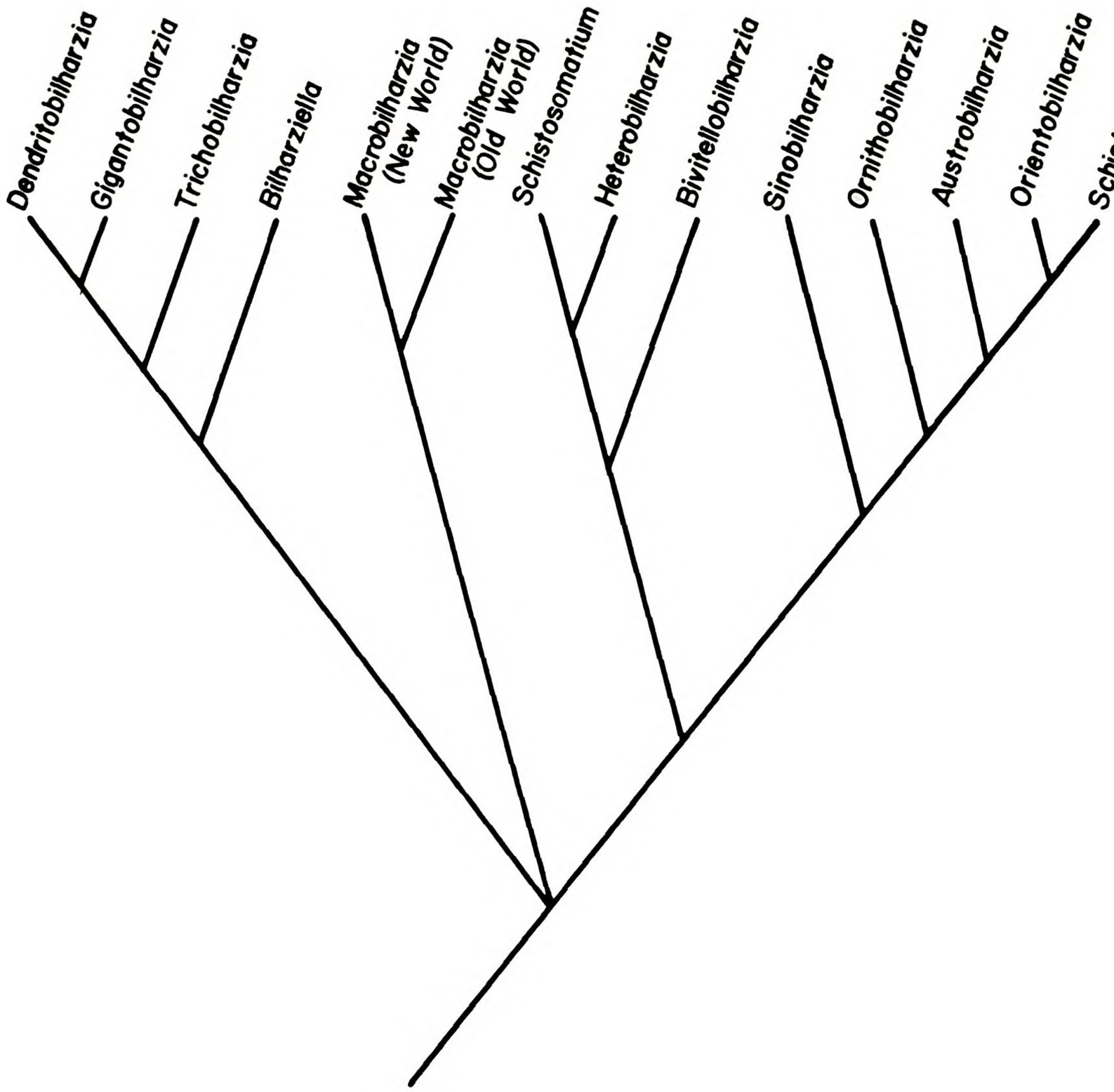
I have already discussed the problems with current definitions of the genera Macrobilharzia and Sinobilharzia. These genera await further data which will clarify their status. In Appendix 1, I have listed the genera recognized in this study and most of the reports describing "species" within each genus. In a few cases, I have noted generic synonomies which do not exist in the current literature, but for the most part I have not commented on the validity of described species. An understanding of the status of the species in all genera will only be achieved following considerable study of morphological variability and genetic species boundaries. Although some progress has been made, the area of speciation biology in schistosomes offers many unanswered and intriguing questions for the future of parasite systematics.

Phylogenetic Results

Phylogenetic analysis of character state evolution in the Schistosomatidae provided me with two preferred cladograms that I feel represent the best estimate of schistosome phylogeny. The two preferred cladograms differ in the placement of the genus Dendritobilharzia. Largely for ease of interpretation, in the following analysis I will focus on the cladogram that places Dendritobilharzia and Gigantobilharzia as the terminal node in the Bilharziellinae (Figure 30). I tend to favor this placement based on the peculiar derived location of the female genital pore but switching Dendritobilharzia and Trichobilharzia does not alter the results of host and geographic analyses.

To examine hypotheses of cospeciation and host shifting, I examined patterns of congruence between the distributions of hosts superimposed upon parasite phylogenies in comparison with independently derived theories of host relationships. If coevolution has been a theme in schistosome evolution, then some degree of congruence would be expected between parasite and host phylogenies, either at the intermediate or definitive host level, or both. Incongruities between host and parasite phylogenies tend to deny hypotheses of coevolution, and suggest rather that host shifting has been a factor during parasite evolution.

Figure 30. Preferred cladogram depicting the phylogenetic relationships of the Schistosomatidae.



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Vertebrate Host Relationships

Figure 31 depicts the preferred cladogram of the phylogenetic relationship of the schistosomes with avian and mammalian host taxa assigned to the terminal nodes. Host taxa are usually presented at the ordinal level, since in most cases a number of families and/or genera are inhabited. Two of the three basal branches, the subfamilies Macrobilharziinae and Bilharziellinae, contain members which occur only in avian hosts. The third branch includes both birds and mammals as hosts. Of the two lineages in the third branch, one occurs only in mammals while the other is primitively found in birds and secondarily occurs in mammals.

From the outset, it appeared likely that host shifting was involved at some time in the evolutionary history of the schistosomes because the two major definitive host groups, birds and mammals, are only distantly related, having been separated from one another by several reptilian lineages during their phylogenetic history. To determine which taxon is likely to be the primitive host group for the lineage, host taxa can be treated in a manner analogous to conflicting character states (Mickevich, 1981). Working at the level of vertebrate class, I applied a Farris optimization procedure in which ancestral hosts were assigned to interior nodes. Results of the optimization procedure indicate that birds are the primitive hosts of the schistosomes and that a minimum of two shifts into mammals have

Figure 31. Vertebrate host distributions assigned to the preferred cladogram depicting relationships of the Schistosomatidae. References documenting host distributions are presented in Appendix I.

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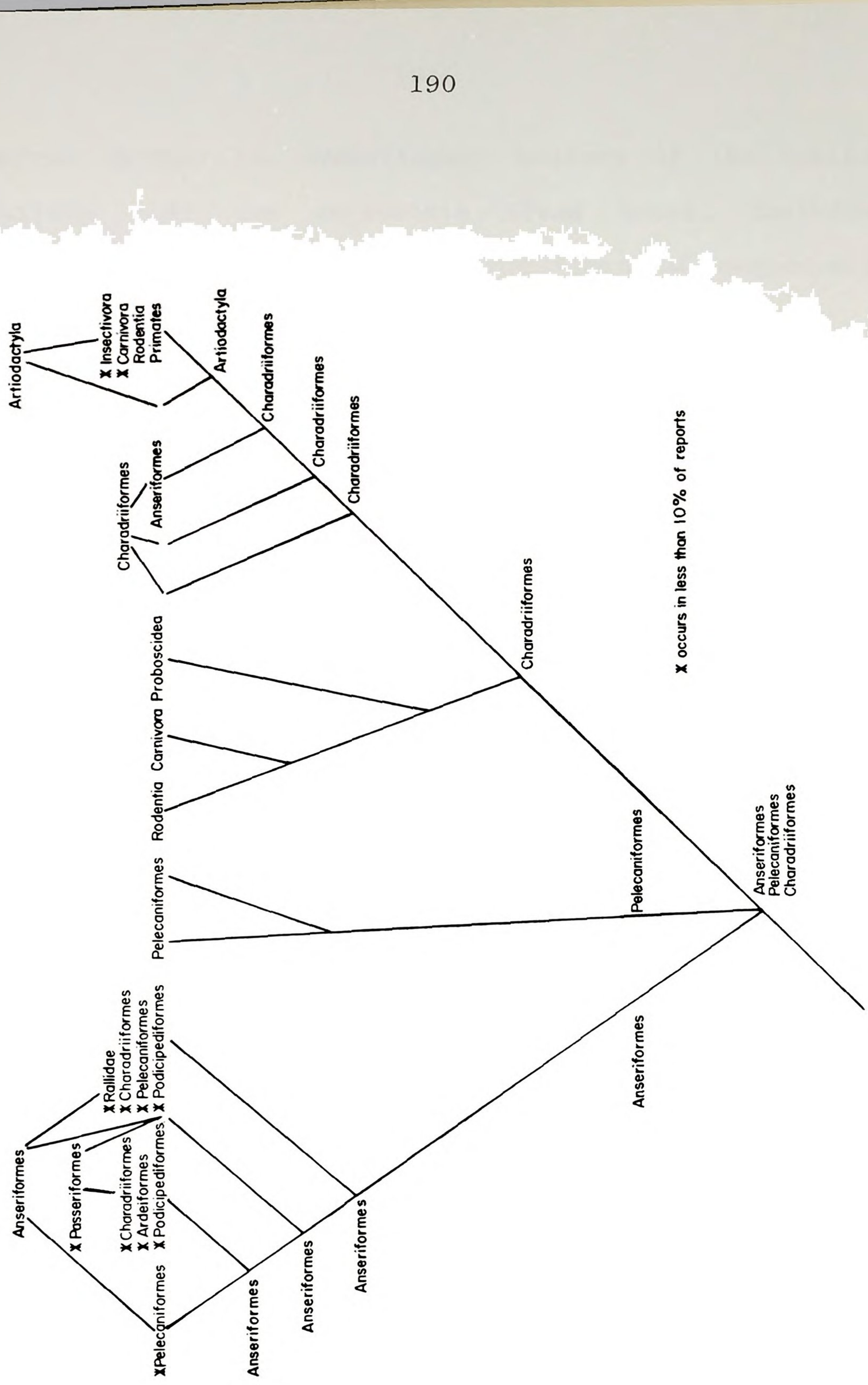

occurred during the evolutionary history of the Schistosomatidae. At the vertebrate class level, therefore, host shifts are suggested but questions of cospeciation must be addressed within each vertebrate lineage.

Optimization indicated that three avian orders or their ancestors served as hosts for the three lineages of the preferred cladogram. These three avian taxa are the Anseriformes (ducks and geese) which host members of the Bilharziellinae, the Pelecaniformes (cormorants and anhingas) which host the genus Macrobilharzia, and the Charadriiformes (gulls, terns and shorebirds) which host avian taxa assigned to the Schistosomatinae. Optimization does not designate a single basal taxon but rather results in a union of the three avian orders.

Although the interrelationships between orders of birds are at best poorly known (Cracraft, 1981), the orders portrayed here are not considered to have shared a recent phylogenetic history. It is impossible to rule out host shifts between avian host taxa, but a parsimonious interpretation of definitive host relationships suggests that the common ancestor of the anseriforms, charadriiforms and pelecaniforms hosted the ancestor of modern schistosomes. Relatively broad host specificity may explain reports of minor hosts (birds reported in less than ten percent of accounts) among aquatic birds; until more data are available, I cannot determine if minor host taxa represent shifts or chance infections.

The pattern of mammalian distribution portrayed in Figure 31 suggests a minimum of two independent shifts into mammals. One invasion gave rise to an ancestor of the genera Bivitellobilharzia, Heterobilharzia and Schistosomatium, while an ancestor of Schistosoma and Orientobilharzia invaded mammals at a later date. Unlike avian blood flukes, mammalian genera show a high degree of specificity at the level of host order, with the exception of the genus Schistosoma. Even so, this specificity does not readily appear to reflect phylogenetic congruence with mammalian host evolution (see Simpson, 1945, and McKenna, 1975, for reviews of mammalian phylogeny). The five or six major mammalian orders involved share common ancestors very early in the evolution of placental mammals, perhaps suggesting an early origin of the shifts which gave rise to mammalian lineages. Much more recent host shifts at the level of individual species or species groups probably account for the distribution of some Schistosoma in primates, rodents and carnivores.

Intermediate Host Relationships

Although missing data in the form of unreported host taxa may affect the analysis of definitive host relationships, its impact upon the understanding of intermediate host biology is more readily apparent. Intermediate life history stages have not been described for the genera Dendritobilharzia, Macrobilharzia (Old and New World forms)

and Sinobilharzia. Figure 32 depicts the known intermediate host distributions of the Schistosomatidae. Members of three gastropod subclasses serve as hosts: Opisthobranchia, Prosobranchia and Pulmonata. The latter two taxa are by far the most common, and the majority of blood flukes are found in the pulmonate families Planorbidae and Lymnaeidae.

Farris optimization (Figure 32) indicates that the pulmonates are the primitive hosts of the schistosomes. At least one host shift has occurred into opistobranchs by some members of the genus Gigantobilharzia: two researchers, one in Europe and one in North America, have recovered Gigantobilharzia cercariae from marine opistobranchs (Donges, 1964, and Leigh, 1955). The genera Austrobilharzia and Ornithobilharzia occur only in marine prosobranch gastropods (Farley, 1971). While the majority of flukes in the genus Schistosoma occur in planorbid pulmonates, two closely related species, S. japonicum and S. mekongi, are found in freshwater prosobranchs. Figure 32 also depicts a shift back into pulmonates by the genera Schistosoma and Orientobilharzia.

All schistosomes recorded from pulmonates are found in one or more of three closely related families: Physidae, Planorbidae, and Lymnaeidae. Certain genera (e.g., Gigantobilharzia, Trichobilharzia and Schistosoma) are found in more than one pulmonate family. Unless host shifting among pulmonate families has occurred after the

Figure 32. Intermediate host distributions assigned to the preferred cladogram depicting relationships of the Schistosomatidae. References documenting host distributions are presented in Appendix I.

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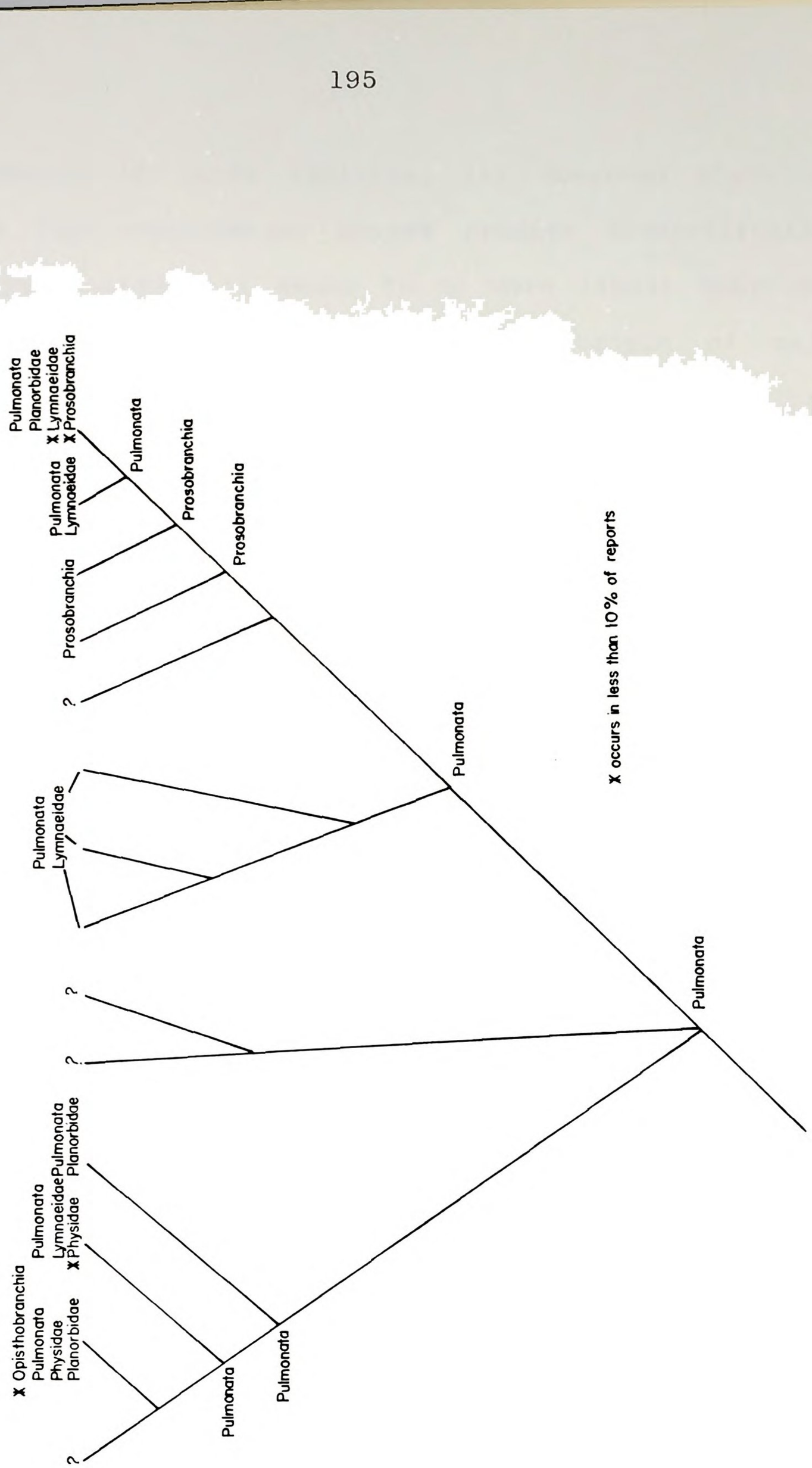


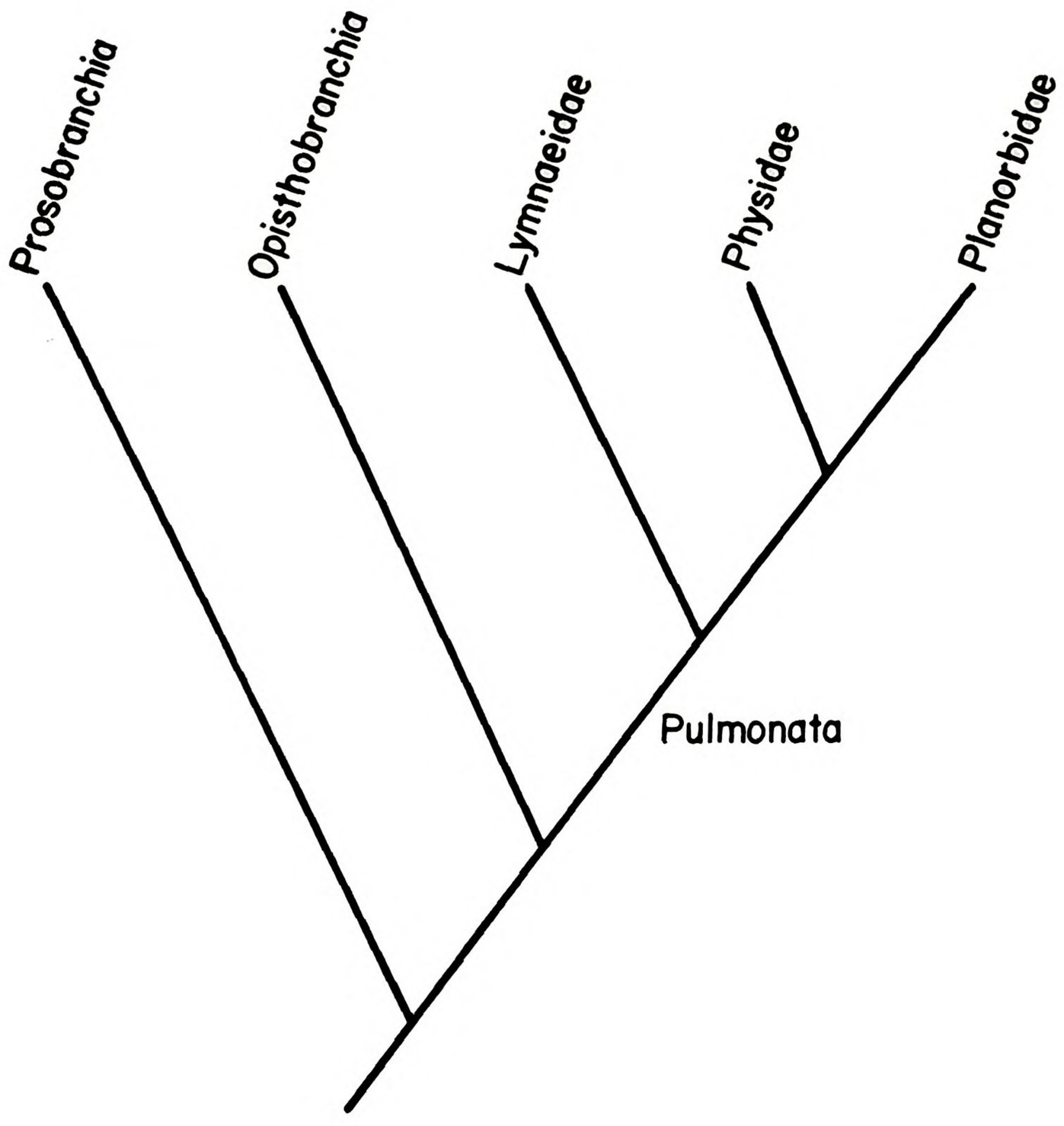
establishment of those families, the observed distribution suggests that schistosome genera predate diversification of the pulmonates. It seems to me more likely that some host shifting has occurred since the origin of major molluscan lineages; the Jurassic origin of the three pulmonate families (Zilch, 1959) significantly predates the origin of eutherian lineages of mammalian definitive hosts (Lillegraven et al., 1979).

With the exception of Davis' monography on the pomatiopsid snails (Davis, 1979), there are no other published discussions of gastropod phylogeny which utilize cladistic methodology. Figure 33, assembled from information in Fretter and Peake (1978), depicts current thinking on the relationships among the gastropod taxa of interest in this study. This phylogeny offers little useful information for my analysis, since schistosome evolution seems primarily associated with pulmonate gastropods, accompanied by an amount of shifting among host taxa (Figure 32) and detailed phylogenies of the pulmonata are unavailable.

Biogeographic Relationships

Cladistic analysis of organismal distributions has become an increasingly important technique in reconstructing phylogenetic history. This methodology is based primarily on an analysis of organismal distribution relative to continental drift theory. Brooks (1978) demonstrated

Figure 33. Probable phylogenetic relationships of the molluscan intermediate hosts of the Schistosomatidae (adapted from Fretter and Peake, 1978).



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er and Peake,

the utility of this methodology in a parasitological context in his study of the cestode fauna of crocodilians. I examined the geographic distributions of the schistosomes in an attempt to understand the potential relationship between host dispersal and vicariant pattern.

In order to examine biogeographic pattern, I assigned geographic locations to the terminal nodes of the preferred cladogram (Figure 34) in a manner analogous to that used in the host analyses. The geographic locations consisted of continental or subcontinental land masses. I compared the cladogram of schistosome distributions to a recently proposed cladogram (Figure 35) depicting the sequence and relationship between land masses during continental breakup (Humphries, 1981). There is no apparent congruence between the two cladograms or between portions of them.

Farris optimization produces a basal grouping of land masses (Figure 34) that bears no resemblance with proposed historical land masses with the exception of Pangea. In fact, a Pangean origin of the schistosomes is consistent with the ages of host inhabitation implied in the previous analyses. Ancestral schistosomes appear to have inhabited the common ancestors of modern host orders; host shifts from birds to mammals apparently occurred before the origin of modern orders. Conservative estimates place the origin of common ancestral hosts prior to or at the beginning of the breakup of Gondwanaland (Lillegraven et al., 1979, Van Tyne and Berger, 1976).

Figure 34. Farris optimization of schistosome geographic distributions. References documenting geographic distributions are presented in Appendix 1.

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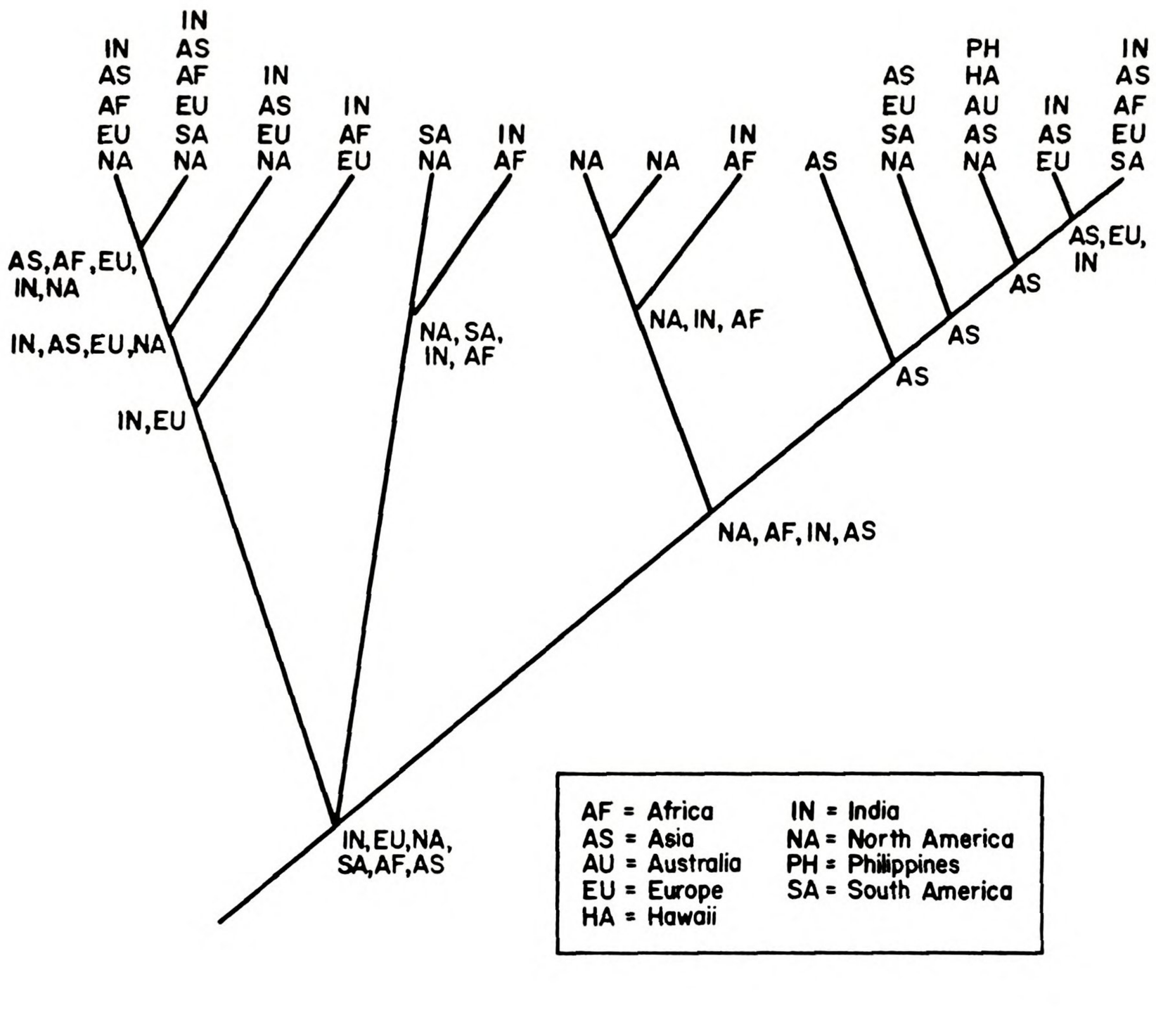

Figure 35. Proposed sequence of relationships between land masses during continental breakup (adapted from Humphries, 1981).



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It also seems likely that some geographic dispersal has occurred via migratory birds since continental breakup. This possibility is suggested by the widespread distribution of avian schistosomes relative to those genera inhabiting mammals. With the exception of Schistosoma, mammalian genera are restricted to either the Old or New World, while several avian genera are nearly circumpolar in distribution.

Evolution of the Schistosomatidae

A Synthesis

In this section, I will present an overview of schistosome evolution set in a context of phylogenetic and evolutionary history. I will attempt to unite the information generated in this study into a cohesive framework chronicling patterns of evolutionary change.

The blood flukes along with other families in the trematode suborder Strigeata form a well defined lineage based primarily upon cercarial morphology. Phylogenetic analysis indicates that a three host life cycle, involving one invertebrate and two vertebrate hosts may be the primitive developmental pattern for the group. Loss of one vertebrate host may have subsequently occurred in each of the three blood fluke families.

The primitive invertebrate intermediate hosts of the lineage appear to be members of the freshwater molluscan class Pulmonata. Clinostomes and all strigeiform families

have been reported only from pulmonates. The three families of blood inhabiting flukes all contain some members which develop in marine molluscs other than pulmonates, and in sanguinicolids, development probably occurs in annelid worms as well. I suggest that the occurrence of non-pulmonate intermediate hosts in the life cycles of the three blood fluke families represents independent host shifts by certain members of each family. These host shifts are correlated with and may have accompanied invasion of marine habitats by formerly freshwater parasites. I will consider this point in more detail in my discussion of the family Schistosomatidae.

Within the Strigeata, the clinostomes and blood flukes appear to form the sister group of the strigeiform families. Although the spirorchids and schistosomes clearly form a monophyletic lineage, the relationships of the clinostomes and sanguinicolids to each other and to the tetrapod blood flukes is ambiguous. I feel that current evidence does not support the classical interpretation of monophyly of the blood flukes. Characters which unite the blood flukes involve morphological loss and certain reports indicate the major characters lost (absence of pharynx and redial stage) may be present in some members of the Sanguinicolidae. In contrast, a complex cercarial body form, the lophocercaria allies clinostomes and sanguinicolids.

I favor an interpretation in which the clinostomes and sanguinicolids form a monophyletic sister group of the tetrapod blood flukes. All four families were derived from a common ancestor which utilized a three host life cycle. Therefore, this suggests that clinostomes retained the primitive developmental pattern while at least two independent losses of a vertebrate host stage occurred in the blood flukes.

Presuming that the sanguinicolids and clinostomes shared a recent common ancestor, I suggest that it was the second or definitive vertebrate host which was lost by the sanguinicolids. Rather than encysting upon the surface of the intermediate piscean host, perhaps ancestors of the sanguinicolids penetrated into the host directly and completed their life cycle. This interpretation differs markedly from the classical view which sees development in the host circulatory system as a major reason for uniting the blood fluke families in a single superfamily.

The origin of direct penetrating by the spirorchid-schistosome ancestor most likely predated the diversification of the common reptilian ancestor which gave rise to modern host groups. In this case, the encysting phase associated with a vertebrate intermediate host was eliminated and penetration of the final reptilian host occurred directly.

At least two blood fluke lineages appear to have coevolved with different derivitives of early reptiles.

One lineage, the Spirorchidae, was isolated in turtles or their ancestors while the schistosomes developed in the reptilian ancestors of modern birds. At some point prior to the diversification of early avian lineages, the ancestors of modern schistosomes added a major evolutionary novelty in the form of dioecy, a synapomorphic character which defines the family.

The family Schistosomatidae may have had its orign in Pangea prior to continental breakup, as suggested by the current world-wide distribution of the family. Modern schistosomes may have shared a common ancestral host found in the avian lineage which gave rise to anseriform, charadriform and perhaps pelecaniform birds. Of the three recent schistosome lineages, two are found only in birds, while one utilizes both birds and mammals as hosts. Within the Schistosomatinae, cladistic analysis suggests that distribution in mammals is the result of at least two separate host shifts during the evolutionary history of the schistosomes.

Character analysis clearly defines genera of the subfamily Bilharziellinae as a monophyletic group. Anseriform birds (ducks, geese and swans) or their ancestors appear to be the primitive hosts of the Bilharziellinae. Although the optimization procedure labeled one avian order as primtively hosting the subfamily, within most genera host specificity seems somewhat loose and several other avian taxa appear as minor hosts in distributional

records (Figure 31). It appears that an ecological rather than systematic theme relates the different minor host taxa, that is, hosts recorded from less than ten percent of reports for a given genus. This theme is apparent in the observation that, to a greater or lesser degree, all of the avian hosts are found in aquatic habitats. The non-aquatic passerines (perching birds) that are found as minor hosts in the genera Trichobilharzia and Giganto-bilharzia are the only exceptions to an aquatic trend. The lack of relationship among the birds inhabited, as well as the number of different host species infected in certain families (e.g., Anatidae), imply that it is largely the fact of living in an aquatic habitat that determines which host species are infected. The underlying ordinal trends suggest that certain avian groups may serve as more suitable hosts than others, but the overall lack of specificity makes more definite statements difficult at the present time.

Limited distributional records indicate that passerine hosts occur in the morphologically similar genera Giganto-bilharzia and Trichobilharzia (Ito, 1960; Byrd, 1957; Najim, 1950; and Brackett, 1942). I feel it is impossible to determine whether these reports represent chance invasions of bathing birds or whether they indicate a close relationship between the two genera. Following the arguments used in determining character state distributions, the fact that anatids, the primitive hosts of the lineages,

occur in both Trichobilharzia and Gigantobilharzia suggests independent invasions of passerines. Evolution from an anseriform inhabiting ancestor may have been followed by shifts into passerines by a few species in each genus.

Pulmonate gastropods of several families (Figure 32) serve as intermediate hosts for members of the Bilharziellinae and at least one shift into opisthobranch gastropods occurred in the genus Gigantobilharzia. I suspect that a better understanding of species relationships within schistosome genera will reveal more detailed patterns of coevolution with different pulmonate families. Currently, incomplete life cycle data and poorly defined species boundaries hamper this inquiry.

Distributional records for members of the subfamily Macrobilharziinae are restricted to birds in the order Pelecaniformes. Anhingas serve as hosts in the Americas, while cormorants host Macrobilharzia in both Africa and India. Formerly placed in separate families, cormorants and anhingas are currently grouped in the family Phalacrocoracidae (Cracraft, 1981). Distributional data suggest an historical pattern of coevolution. Cormorants and anhingas each occur on both sides of the Atlantic Ocean. Present parasite distributions imply either isolation in different divisions of the Phalacrocoracidae following continental breakup or extinction in one host group in each portion of the disjunct range. Further information in the form of additional host records and more detailed

morphological study may aid in distinguishing between these hypotheses.

Macrobilharzia retains more primitive morphological characters than any other schistosome genus. Therefore, it is interesting to note that the host order, Pelecaniformes is considered by most workers to be primitive relative to the other major schistosome host groups, the Anseriformes and Charadriiformes (Cracraft, 1981). Thus host distribuion of the Macrobilharziinae may conform to a modified version of the Szidat Rule, in which parasites retaining primitive traits inhabit host groups which also possess primitive morphological attributes. In this case, host data may suggest a resolution of the basal trichotomy in the preferred cladogram of schistosome relationships (Figure 31). Although I would like to see morphological evidence to confirm this resolution, the Macrobilharziinae may represent the earliest offshoot from a primitive schistosome ancestor.

In the third schistosome subfamily, the Schistosomatinae, charadriiform birds appear as primitive hosts and at least two shifts of mammalian hosts have occurred in the phylogenetic history of the group. One avian genus, Austrobilharzia, is frequently reported from anseriform as well as charadriiform birds. This observation suggests an avenue for further study to determine whether inhabiting different host orders reflects undetected morphological differences within the genus.

Avian members of the subfamily Schistosomatinae develop in prosobranch gastropods, while with two exceptions, mammalian genera retain the primitive schistosome intermediates, pulmonate gastropods. Shifts by avian taxa into prosobranch snails may have accompanied or precipitated invasion of a new habitat, the marine environment.

Within the Schistosomatinae, an early shift into mammals may have occurred by the common ancestor of Schistosomatium, Heterobilharzia and Bivitellobilharzia. The two genera of North American blood flukes, Schistosomatium and Heterobilharzia are clearly more closely related to one another than to other genera of schistosomes. Both genera are primarily restricted to their rodent and carnivore hosts, respectively. Within host orders, however, specificity breaks down and members of various families serve as hosts. For example, microtine, peromyscine and zapodid rodents host Schistosomatium, while raccoons, feral dogs and bobcats are the commonly reported hosts of Heterobilharzia (see references in Appendix 1). In the case of North American schistosomes, host distribution does not offer clear evidence of systematic affiliation of the parasite taxa. The relationships of rodents to other mammalian taxa remain unclear after years of study, and no author has closely associated rodents with carnivores (McKenna, 1975). The lack of clear relationships among host taxa suggest a shift into mammals by the ancestors of North American blood flukes very early in placental

history. Alternatively a shift by the ancestors of one genus may have given rise to a new parasite taxon in a different host group.

Host relationships of the Afro-Indian genus Bivitellobilharzia, as with most aspects of the genus, are problematic. The genus is known on the basis of two descriptions, one from a wild caught African elephant (Loxodonta africana) on display in a German zoo and one very vague account from an elephant (Elephas maximus) in India. If, as I suggested earlier, the host shift which established the mammalian lineage containing Bivitellobilharzia took place early in placental evolution then the relationship of the genus to the North American blood flukes is not unfeasible. All three host orders shared a common ancestor at some point in their history, but our current knowledge of this phase of mammalian history is fragmentary at best. Alternatively, and perhaps more feasibly, a host shift into the ancestor of modern elephants may account for the distribution seen today.

A second shift into mammals occurred with the ancestors of the genera Orientobilharzia and Schistosoma. These two genera are quite similar in morphology, differing only in the number of testes and the absence of a seminal receptacle in Orientobilharzia. The genus Orientobilharzia is Eurasian in distribution and found entirely in bovids. The genus Schistosoma appears quite diverse relative to other members of the family. There are approximately

17 described species of Schistosoma (Davis, 1980), more than in any other schistosome genus except Trichobilharzia. This relatively large number of species may simply reflect the great amount of attention the genus has received due to the fact that some species parasitize humans. The possibility exists that other genera may have species which have not been reported.

Species diversity in Schistosoma appears to be related to variations in infectivity to different host taxa (Wright, 1960). Specificity and strain variation seems most pronounced at the intermediate host level; in contrast, the genus and certain species show the greatest diversity of definitive host species to be found in the family. Schistosoma mansoni, for example, has been reported naturally from humans, non-human primates, insectivores and many rodents.

Intermediate host relationships of the genus Schistosoma have received considerable attention. The genus occurs primarily in planorbid pulmonates, but at least two species, S. japonicum and S. mekongi, have shifted into prosobranch snails. It was, in fact, the occurrence of S. mekongi in a previously undetected prosobranch snail that alerted researchers to the separate taxonomic status of this parasite (Bruce and Santasiri, 1980). Detailed studies subsequently demonstrated morphological and biochemical differences that resulted in specific differentiation.

The genus Schistosoma is widespread in distribution across Asia, southern Europe, Africa and South America. The range of one species in particular has drawn a considerable amount of attention: S. mansoni is found in both Africa and South America, where it develops in closely related snails of the genus Biomphalaria. On both continents, a variety of mammalian hosts is infected, with various rodents and man reported most frequently (Kuntz, 1955). Studies show that Old and New World forms are interfertile, although varying degrees of intermediate host specificity exist in different populations, both within and between continents (Kuntz, 1955).

The transoceanic distribution of S. mansoni has classically been interpreted as the result of an introduction from Africa into South America via the slave trade (Cheng, 1973). Recently, Davis (1980) presented an alternative vicariant explanation. Based on his studies of gastropod biogeography, Davis proposed that populations of S. mansoni inhabiting snails of the planorbid genus Biomphalaria were isolated on opposite sides of the Atlantic following the breakup of Gondwanaland. Separation of Africa and South America was complete by the late Cretaceous, between 70 and 100 M.Y.B.P. (Lillegraven et al., 1979). By the early Cretaceous, members of many modern genera of planorbids and lymnaeids were present (Zilch, 1959) and a vicariant explanation for the distribution of Biomphalaria seems feasible. The genus Biomphalaria has speciated

extensively on both sides of the Atlantic since its original separation (Davis, 1980). The situation with S. mansoni requires more careful consideration. Davis is proposing that not only the genus Schistosoma but also the species S. mansoni have been separated by the Atlantic Ocean for at least 70 million years. S. mansoni has failed to undergo speciation in the Neotropics and it remains interfertile with African forms after all this time. This would be a remarkable example of stasis.

Although the intermediate hosts of S. mansoni have changed little since the time of continental breakup, mammalian hosts have changed radically. At the time of the separation of South America and Africa, none of the modern placental orders which serve as hosts had yet evolved (Lillegraven et al., 1979). Indeed, the placentals which were isolated in South America gave rise to groups which later became extinct (e.g., Meridiungulata); modern placental groups (e.g., rodents, carnivores, etc.) are presumed to have reached South America at a later date. In the Neotropics, S. mansoni is found in several native rodents as well as in introduced exotics such as Rattus and Homo (Kuntz, 1955), but it is not found in remnants of the archaic mammalian fauna, the didelphoid marsupials. It is clear therefore that if S. mansoni has been isolated in South America since the breakup of Gondwanaland, shifts into modern placental mammals are necessary to explain current host distribution patterns. Much more recent

shifts would have to be postulated to explain the occurrence of S. mansoni in Rattus and Homo, two genera with relatively recent histories in the Neotropics.

Given the information available, I think it is likely that S. mansoni was introduced to South America following the arrival of Old World people. The presence of suitable snail intermediates which appear to show a vicariant distribution pattern allowed for successful colonization in the New World. Perhaps the most compelling evidence in support of this hypothesis are the observations that Old and New World populations of S. mansoni are interfertile, and while species diversity in Africa is high, the genus has not undergone speciation during the proposed millions of years of isolation in South America. It also seems likely that the current distributions of human infecting Schistosoma reflect the range limits of suitable intermediate hosts, since human dispersal has, in essence, been cosmopolitan.

Analysis geographic patterns indicates that avian schistosomes tend to be quite widely distributed (Figure 34). This trend appears to be correlated with the greater mobility of birds relative to mammals, and many avian schistosomes inhabit migratory waterfowl, gulls and shorebirds. Also, at least at the generic level, most avian schistosomes inhabit, at least facultatively, a wide range of water dwelling birds, further increasing the probability of widespread distribution. The wide distributions of

avian blood flukes suggest that intermediate host specificity may be relatively weak, thus allowing cycles to be established in new habitats when introduced by migrating birds. Unfortunately, the intermediate host biology of most avian schistosomes is quite poorly known, so this suggestion awaits further study.

In contrast with avian forms, mammalian schistosomes tend to be more limited in their geographic (and host taxonomic) distributions. This correlates with the more limited mobility of their hosts, and may also relate to narrower definitive and/or intermediate host specificity.

In summary, the available information suggests that the schistosomes are an ancient group which have been associated with modern vertebrate lineages throughout their evolutionary history. The vagaries of extinction and host shifting have obscured patterns of ancient association. In addition, the mobility of avian hosts as well as the broad specificity displayed by avian forms may contribute to the lack of a coherent biogeographic pattern. Wright (1960) suggested that intermediate host speciation patterns constrain schistosome evolution, but much more information is required before evaluating the impact of intermediate hosts on schistosome biogeography. If schistosomes are, in fact, an ancient group, then it appears that intermediate host relationships have remained stable at least at the family and often genus level while major vertebrate lineages have evolved and gone extinct.

This is suggested by the observation that recent pulmonate host genera are identifiable in the fossil record prior to the orign of nearly all modern vertebrate host taxa.

Biological Considerations

The observation that parasite species preferentially infected certain host taxa suggested to early researchers that host-parasite relationships reflect a history of coevolution. Biochemical and physiological adaptation of the parasite and its host constitute one aspect of coevolution but it is the historical context of the host-parasite interaction which I examined in this study. Phylogenetic analysis utilizing cladistic methodology provided a set of techniques which I used to test the hypothesis that the phylogeny of the Schistosomatidae reflects a history of coevolution with their vertebrate and invertebrate hosts.

Phylogenetic analyses did, in fact, reveal an overall pattern of coevolution at both levels of host involvement. This coevolutionary pattern appears to be an ancient one which was established prior to the origin of modern host groups. The extreme age of the host-parasite relationship is suggested by the observation that parasite specificity is most pronounced at the level of host order and that within each vertebrate class, the orders which serve as hosts are only distantly related. Although the lack of a close relationship among host orders could also be

explained by postulating recent host shifts, until further evidence to the contrary is available, coevolution may be a more parsimonious explanation.

While coevolution has been the dominant theme in the phylogenetic history of the schistosomatidae, host shifting also played a prominent role in structuring current host distributions. My analysis indicated that shifts from birds into mammals were involved in establishing at least two schistosome lineages. At the intermediate host level, the ancestors of one avian lineage shifted into marine prosobranch snails, and several species in genera which generally develop in pulmonates shifted to either prosobranch or opisthobranch gastropods.

Further study at the species level may reveal additional evidence of host shifting. Minor host taxa may, in fact, represent relatively recent host shifts by particular species or species groups, but more adequate sampling along with complete life history data is needed to determine whether host shifts have actually occurred.

The results of my research differ from other recently published cladistic analyses of parasite phylogenies in that host shifting appears to have played a significant role in determining present relationships. Studies by Brooks and his coworkers (summarized in Mitter and Brooks, 1983) describe complex patterns of coevolution, generally focusing on species relationships within particular parasite genera. I suspect that the difference in the frequency

of reported host shifts lies in the taxonomic level at which the various studies were conducted. By analyzing generic relationships, I maximized the chances of detecting the effects of host shifting which occurred over an extended period of evolutionary history. The studies by Brooks and his coworkers focused on speciose parasite taxa which display a narrow range of host specificity; thus groups in which the likelihood of finding a coevolutionary pattern is higher.

My research suggests that host shifts have played a role in speciation and lineage formation during the evolution of the schistosomes. This observation raises questions concerning the interrelationships of host specificity, host shifts and speciation mechanisms. At the vertebrate host level, many schistosomes infect and successfully reproduce in novel species (Bruce et al., 1961), but it appears that relatively few infections of new host taxa have led to speciation. As the growing body of literature on parasite ecology indicates, complex behavioral and biochemical factors function to maintain the intricate balance which characterizes most host-parasite systems (Price, 1980; Holmes, 1983). Davis (1980) noted that trematode biology necessitates genetic adaptation to both snail and vertebrate hosts within an environment suitable for this three-way interaction. To understand the role of host shifts in parasite speciation, research will have to focus on the factors which change the balance between

host and parasite, thus providing the isolating mechanism necessary to initiate speciation. Mechanisms may involve shifts in the timing of reproduction in the altered immune environment of a novel host or simply a transfer of the system by the host into a different ecological habitat (e.g., marine life zone) and away from the main parasite population. Also, a change in the site of development within a host species may sufficiently alter the course of a life cycle to initiate isolation. For example, the majority of schistosomes mature in the portal system of their vertebrate hosts. In contrast, within the Bilharziellinae, the morphologically aberrant genus Dendritobilharzia reproduces in the major anteries that leave the heart of its anseriform hosts (Ulmer and Vande Vusse, 1976, Vande Vusse, 1980). Novel behavioral patterns that precipitate entering a new environment within a host individual may be accompanied by shifts in the timing of reproduction which temporally isolate a parasite from its surrounding population. Questions concerning isolating mechanism are addressed most appropriately at the species level where fine scale differences in host distribution patterns can be used to examine relatively recent speciation events. With its complexities of host distribution at both the intermediate and definitive host level, the genus Schistosoma suggests a starting point for such detailed studies of speciation.

The question of the role of host specificity in the evolution of the schistosomes has received considerable attention at the intermediate host level. Wright (1960) suggested that schistosome evolution was dependent upon prior evolution of the snail host. He based this statement on his observations of certain species in the genus Schistosoma. Wright's proposal may partially explain species proliferation in the genus Schistosoma, but Davis (1980) pointed out that schistosomes have in no way cospeciated to match the post-Cretaceous radiation seen in modern gastropod lineages.

Different species and genera of blood flukes show very different patterns of intermediate host specificity. Species of the African Schistosoma complex are interfertile but show a high degree of intermediate host specificity (Kuntz, 1955). In contrast, the widespread monotypic genus Schistosomatium is found in a number of species of lymnaeid snails, and worms from a given local can successfully infect several different gastropod intermediates (Malek, 1977). Variations in host specificity may represent different ecological strategies which have evolved in response to environmental factors or intrinsic host attributes such as immune reaction. Broad host specificity may reduce the likelihood that a parasite will closely track evolutionary subdivisions of changing intermediate host lineages. The ability to infect many different host species may play a crucial role in schistosome survival

under unstable environmental conditions, but it may not provide the set of circumstances which favor cospeciation. Resolution of species boundaries will be the necessary first step in examining the role of host specificity and parasite speciation.

To study the speciation process of trematodes in more detail, we will need to obtain a much better understanding of the nature of morphological character state change during evolution. Conventional wisdom suggests that morphological simplification is a major feature of parasite evolution (Baer, 1951). Simplification may characterize certain parasite groups, particularly arthropods, but it is difficult to posit large scale simplification when faced with the bewildering diversity of cercarial morphologies displayed by parasitic trematodes (Schell, 1970). It seems more likely that trematodes have added complex life stages during evolution from relatively simple free living platyhelminths.

It was clear from the beginning of my research that homoplasy, loss and reversal were prominent themes in the evolution of the schistosomes and of trematodes in general. For example, male terminal genitalia of all parasitic trematodes appear to be homologous. Cestodes and both monogenetic and digenetic trematodes possess a presumably homologous series of organs which include a cirrus, prostate, seminal vesicle, etc. The presence or absence of one or more of these structures varies between

and within families in all three platyhelminth classes. Because of this intrafamilial variation, I avoided using most male genital characters in my family level analysis. Within the Schistosomatidae, I attempted to discern patterns of derived loss using careful outgroup comparison. It was in part because of the apparent frequency of character loss that I was inclined to favor cladograms defined by evolutionary gains rather than losses.

The study of changes in developmental timing that result in heterochronic evolution may offer some insight into the pattern of loss and reversal displayed by trematodes. Paedomorphosis is one form of heterochrony that has frequently been associated with discussions of parasite evolution(DeBeer, 1958; Gould, 1977), but few examples of heterochronic development have been documented. In my study of the Schistosomatidae, certain character state changes imply that the host shift by the ancestor of Orientobilharzia and Schistosoma was accompanied by heterochronic changes in morphology. Fink (1982) carefully developed the argument that heterochrony can only be detected in an organism once the phylogeny containing that organism has been determined. One set of circumstances which alert a researcher to the potential occurrence of heterochrony is the appearance of apparently primitive characters rather than the expected derived ones at an anomalous place on the chosen cladogram, such as the terminal nodes of a derived lineage. Reversals to the

primitive ovary condition (Character States 7^0 and 7^1) define the branch containing the genera Schistosoma and Orientobilharzia. Also, the primitive condition of reduced testes number (Character State 24^1) is found terminally in Schistosoma. Although the evidence is not overwhelming, it does suggest that further inquiry into the nature of heterochronic change in these mammalian genera is appropriate.

Heterochrony may explain what appears to be the frequent loss and reversal in genital characters displayed in comparisons between trematode families and genera. Although genes coding for morphological characters are not expressed, they are still present in the genome and may become functional later in a given phylogeny (Kollar and Fisher, 1980). In order to test this hypothesis, large scale examination of the patterns of character state change will have to be based on detailed studies of morphological development. I feel that developmental studies are likely to be the key to understanding the complexity of homoplasy in trematode evolution. In addition, resolution of homoplasic characters will generate additional sources of data which will aid in producing reliable phylogenies.

In proposing the "parasitological method" nearly twenty years ago, Hennig (1966) acknowledged the value of parasite data in constructing host phylogenies. In a converse manner, parasitologists have often relied almost

exclusively on host relationships when determining parasite phylogenies. When carefully constructed phylogenies of both hosts and parasites are derived independently of one another, a process of reciprocal illumination may clarify relationships at both levels and focus further attention on problematic branch points. Congruence between host and parasite phylogenies can form the basis for more detailed studies of coevolution, while areas of incongruity offer evolutionary biologists models for examining the role of host shifts and sympatric speciation.

APPENDIX 1

APPENDIX 1

Specimens and species descriptions used in assembling character state, host and geographic distributions for genera of the family Schistosomatidae.

Schistosoma	
mansoni	Faust et al. (1934)
japonicum	Tada (1928)
curassoni	Brumpt (1931); Gretillat (1962, 1964)
bovis	Khalil (1924)
margrebowiei	LeRoux (1933)
haematobium	Schwetz (1951)
intercalatum	Schwetz (1951)
incognitum	Sinha and Srivastava (1956, 1960)
rodhaini	Fripp (1967); Saoud (1966)
hippopotami	Thurston (1963)
edwardiense	Thurston (1964)
Bivitellobilharzia	
loxodontae	Vogel and Minning (1940)
nairi (=*Schistosoma n.*)	Mudaliar and Ramanujachary (1945)

Heterobilharzia	
americana	U.S.N.H.C. #s 14532, 39420 Lee, H.-F. (1962); Price (1943)
Orientobilharzia	
turkestanicum (=Ornithobilharzia t.)	U.S.N.H.C. #s 45820, 40932 Dutt and Srivastava (1961); MacHattie (1934); Skrjabin (1913)
bomfordi	Montgomery (1906)
harinasutai	Kruatrachue et al. (1965)
dattai (=Ornithobilharzia d.)	Dutt and Srivastava (1952)
Schistosomatium	
douthitti	Tanabe (1923); Price (1929); El-Gindy (1951)
Austrobilharzia (=Microbilharzia)	
chapini	U.S.N.H.C. #27888
terrigalensis	U.S.N.H.C. #46655
(=A. variglandis and Microbilharzia variglandis)	Johnston (1917); Chu and Cutress (1954); Stunkard and Hinchcliffe (1952)
(=A manitobensis and A. canadensis)	McLeod (1937)
penneri	U.S.N.H.C. #39070 Short and Holliman (1961)
pricei (=Ornithobilharzia p.)	U.S.N.H.C. #29718 Wetzel (1930)
bayensis	Tabangui (1933)

Macrobilharzia (New World)	
macrobilharzia	U.S.N.H.C. #27887 Travassos (1922); Price (1931); Kohn (1964)
Macrobiharzia (Old World) (=Ornithobilharzia)	
baeri	Fain (1955)
phalacrocoraxi	Baugh (1963)
Ornithobilharzia	
canaliculata	Dutt and Srivastava (1961); Macko (1961); Witenberg and Lengy (1967); Travassos (1942)
(=O. intermedia)	Odhner (1912)
(=O. filamenta and O. aviani)	McLeod (1940)
Sinobilharzia	
odhneri (=Ornithobilharzia o. and Austrobilharzia o.)	U.S.N.H.C. #s 60990, 601015 Faust (1924)
Bilharziella	
polonica	U.S.N.H.C. #14732 Baer (1932); Price (1929); Kowalewski (1886); Khalifa (1972); Ohdner (1912); Szidat (1929a,b)
indica (=Chinhuta i.)	Mehra (1940); Lal (1937)
lali	Baugh (1963)
*Trichobilharzia (=Pseudobilharziella)	
brevis	U.S.N.H.C. #60715 Bash (1966)
crecci (=Jilinobilharzia c.)	Lui and Bai (1976)

jequitibaensis	Rios Leite et al. (1978)

**Gigantobilharzia

lawayi	U.S.N.H.C. #s 44862, 44863 Brackett (1942); Farley (1963)
huronensis	U.S.N.H.C. #37334 Najim (1950, 1956)
huttoni	U.S.N.H.C. #37473 Leigh (1955)

Dendritobilharzia

pulverulenta	U.S.N.H.C. #s 46655, 75331 Ejsmont (1929); Cheatum (1941); Ulmer and Vande Vusse (1970); Vande Vusse (1980)
asiaticus	Mehra (1940)

*For additional species and references, see Farley (1971) and Fain (1956).

**For additional species and references, see Farley (1971) and Fain (1960).

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Agarwal, S. M. 1959. Studies of the morphology, systematics and life history of Clinostomum giganticum n. sp. (Trematoda: Clinostomatidae). Ind. J. Helminthol. 11:75-115.

Anderson, D. J. and R. M. Cable. 1950. Studies on the life history of Linstowiella szidati (Anderson) (Trematoda: Strigeatoidea: Cyathocotylidae). J. Parasitol. 36:395-410.

Azimov, D. A. 1970. A revision of the systematics of the Schistosomatata Skryabin and Schulz, 1937. Zool. Zh. 49:1126-1131.

Baer, J. G. 1932. Contribution à la faune helminthologique de Suisse. Rev. Suisse Zool. 39:1-57.

Baer, J. G. 1951. Ecology of Animal Parasites. Univ. Illinois Press, Urbana.

Basch, P. F. 1966. The life cycle of Trichobilharzia brevis n. sp. an avian schistosome from Malaya. Z. Parasitenkd. 27:242-251.

Basch, P. F. 1981. Cultivation of Schistosoma mansoni in vitro. II. Production of infertile eggs by worm pairs cultured from cercariae. J. Parasitol. 67:186-190.

Baugh, S. C. 1963. Contributions to our knowledge of digenetic trematodes VI. Z. Parasitenkd. 22:303-315.

Berrie, A. D. 1960. The influence of various definitive hosts on the development of Diplostomum phoxini (Strigeida, Trematoda). J. Helminthol. 34:205-210.

Bilharz, T. 1852. Fernere Beobachtungen uber das die Pfortades des Menschen bewohnende Distomum haematobium und sein Verhaltniss zu gewissen pathologischen Bildungen, aus brieflichen Mittheilungen an Professor v. Siebold vom 29 Marz 1852. Ztschr. f. wissensch. Zool. Leipz. 4:72-76.

Blankespoor, H. D. 1974. Host induced variation in Plagiorchis noblei Park, 1936 (Plagiorchiidae: Trematoda). Am. Midl. Nat. 92:415-433.

Brackett, S. 1942. Five new species of avian schistosomes from Wisconsin and Michigan with the life cycle of Gigantobilharzia gyrauli (Brackett, 1940). J. Parasitol. 28:25-42.

Brooks, D. R. 1978. Evolutionary history of the cestode order Proteocephalidae. Syst. Zool. 27:312-323.

Brooks, D. R. 1980. Allopatric speciation and non-interactive parasite community structure. Syst. Zool. 30:192-203.

Brooks, D. R.; D. R. Glen and R. T. O'Grady. 1983. Phylogenetic analysis of the Digenea (Platyhelminthes: Cercomeria) with comments on their adaptive radiation. Unpublished manuscript.

Bruce, J. I.; L. M. Llewellyn and E. H. Sadun. 1961. Susceptibility of wild mammals to infection by Schistosoma mansoni. J. Parasitol. 47:752-756.

Bruce, J. I. and S. Sornmani, eds. 1980. The Mekong Schistosome. Malacological Review, Whitmore Lake, Michigan.

Brumpt, E. 1931. Description et duex bilharzies de mammiféres africans, Schistosoma curassoni sp. inquir et Schistosoma rodhaini n. sp. Ann. Parasitol. 9:325-328.

Brundin, L. 1966. Transantarctic relationships and their significance, as evidenced by Chironomid midges. Kungl. Svenska Velenskapsa-kademiens Handingar Fjarde series, 11:1-472.

Byrd, E. E. 1957. Bilharziella littlebi (Byrd, 1956), a blood fluke (Digenea: Schistosomatidae: Bilharziellinae) from the chestnut-sided warbler, Dendroica pennsylvanica (Linnaeus). J. Parasitol. 43:374-376.

Carlton, M. D. 1980. Phylogenetic relationships in Neotomine-Peromyscine rodents (Muroidea) with a reappraisal of the dichotomy within New World Cricetinae. Misc. Pub. Mus. Zool. U. Mich. 157:1-146.

Cheatum, E. L. 1941. Dendritobilharzia anatinarum n. sp., a blood fluke from the mallard. J. Parasitol. 27:165-170.

Cheng, T. C. 1970. Symbiosis. Pegasus Press, New York.

Cheng, T. C. 1973. General Parasitology. Academic Press, New York.

Chu, G. W. T. C. and C. E. Cutress. 1954. Austrobilharzia variglandis (Miller and Northrup, 1926) Penner, 1953, (Trematoda: Schistosomatidae) in Hawaii with notes on its biology. J. Parasitol. 40:517-524.

Cobbold, T. S. 1859. On some new forms of entozoa. Trans. Linn. Soc. London 22:363-366.

Cort, W. W. 1917. Homologies of the excretory system of the forked-tailed cercaria. J. Parasitol. 4:49-57.

Cort, W. W. 1921. The development of the Japanese blood fluke, Schistosoma japonicum Katsurada, in its final host. Amer. J. Hyg. 1:1-28.

Cracraft, J. 1981. Toward a phylogenetic classification of the recent birds of the word (class Aves). Auk 98:681-714.

Cracraft, J. 1983. Cladistic analysis and vicariance biogeography. Amer. Sci. 71:273-281.

Croft, J. W. 1933. A description of Cercaria whitentoni, n. sp. Trans. Amer. Micros. Soc. 52:259-266.

Davis, G. M. 1979. The origin and evolution of the gastropod family Pomatiopsidae, with emphasis on the Mekong River Triculinae. Monogr. Acad. Nat. Sci. Phila. 20:1-20.

Davis, G. M. 1980. Snail hosts of Asian Schistosoma infecting man: evolution and coevolution. Pp. 195-238 In The Mekong Schistosome (J. I. Bruce and S. Sornmani, eds.). Malacological Review, Whitmore Lake, Michigan.

DeBeer, G. R. 1958. Embryos and Ancestors. Oxford Univ. Press, London.

Dienske, H. 1968. A survey of the metazoan parasites of the rabbit-fish, Chimera monstrosa L. (Holocephali). Netherlands J. Sea Res. 4:32-58.

Diesing, K. M. 1858. Revision der Myzhelminthen Abt. Trematoden. Sber. Öst Akad. Wiss., Wein. 32:307-390.

Dönges, J. 1964. Gigantobilharzia suebica n. sp. (Trematoda), ein Dermatitiserreger beim Menschen. Z. Parasitenkd. 24:65-75.

Dubois, G. 1938. Monographie des Strigeida (Trematoda). Mem. Soc. Neuchât. Sc. Nat. 6:1-535.

Dutt, S. C. and H. D. Srivastava. 1952. On the morphology and life history of a new mammalian blood fluke -- Ornithobilharzia dattai n. sp. (preliminary report). Parasitology 42:144-149.

Dutt, S. C. and H. D. Srivastava. 1961. A revision of the genus Ornithobilharzia Odhner (1912) with the creation of two genera Orientobiharzia Dutt and Srivastava (1955) and Sinobiharzia Dutt and Srivastava (1955) (Trematoda: Schistosomatidae). Ind. J. Helminthol. 13:61-73.

Ejsmont, L. 1926. Morpholoische, systematische und entwicklungsgeschichtliche Untersuchungen an Arten des Genus Sanguinicola Plehn. Bull. Int. Acad. Pol. Sci. Lett. Cl. Sci. Math. Nat. 9-10:877-966.

Ejsmont, M. L. 1929. Über zei Schistosomatidengattungen der Vögel. Bull. Acad. Pol. Sc. et Lettre Cl. Sc. Math et Nat. S. B. Nat (II):389-403.

Eldredge, N. and J. Cracraft. 1980. Phylogenetic patterns and the evoutionary process. Columbia Univ. Press, New York.

El-Gindy, M. S. 1951. Post-cercarial development of Schistosomatium douthitti (Cort 1914) Price 1931 in mice, with special reference to the genital system (Schistosomatidae-Trematoda). J. Morph. 89:151-177.

Fain, A. 1955. Un nouveau schistosome du Comoran au Ruanda-Urundi (Congo Belge) -- Ornithobilharzia baeri n. sp. Acta Tropica 12:357-360.

Fain, A. 1956. Les schistosomes d'oiseaux du genre Trichobilharzia Skrjabin et Zakharow, 1920 au Ruanda-Urundi. Rev. Zool. Bot. Afr. 54:147-178.

Fain, A. 1960. Nouveaux schistosomes d'oiseaux du genre Gigantobilharzia Odhner. Ann. Parasit. Hum. Comp. 35:292-304.

Farley, J. 1963. A redescription of Gigantobilharzia lawayi Brackett, 1942. J. Parasitol. 49:465-467.

Farley, J. 1971. A review of the family Schistosomatidae excluding the genus Schistosoma from mammals. J. Helminthol. 45:289-320.

Farr, M. M. and V. G. Blankemeyer. 1956. Trichobiharzia brantae n. sp. (Trematoda: Schistosomatidae) from the canada goose (Branta canadensis L.). J. Parasitol. 42:320-325.

Farris, J. S. 1970. Methods for computing Wagner trees. Syst. Zool. 19:83-92.

Farris, J.S. 1983. The logical basis of phylogenetic analysis. Pp. 7-36 In Advances in Cladistics, Volume 2. (N. I. Platnick and V. A. Funk, eds.). Columbia Univ. Press, New York.

Faust, E. C. 1924. Notes on Ornithobilharzia odhneri n. sp. from the asiatic curlew. J. Parasitol. 11:50-55.

Faust, E. C., C. A. Jones and W. A. Hoffman. 1934. Studies on schistosomiasis mansoni in Puerto Rico. III. Biological Studies. The mammalian phase of the life cycle. P. R. J. Pub. Health Trop. Med. 10:133-196.

Felsenstein, J. 1978. Cases in which parsimony or compatibility methods will be positively misleading. Syst. Zool. 27:401-410.

Felsenstein, J. 1979. Alternative methods of phylogenetic inference and their interrelationship. Syst. Zool. 28:49-62.

Felsenstein, J. 1982. Numerical methods for inferring evolutionary trees. Quar. Rev. Biol. 57:379-404.

Fink, W. L. 1982. The conceptual relationship between ontogeny and phylogeny. Paleobiology 8:254-264.

Freeman, R. S. 1973. Ontogeny of cestodes and its bearing on their phylogeny and systematics. Adv. Parasitol. 2:481-557.

Fretter, V. and J. Peake, eds. 1978. Pulmonates, Vol. 2A: Systematics, evolution and ecology. Academic Press, London.

Fripp, P. J. 1967. On the morphology of Schistosoma rodhaini (Trematoda, Digenia, Schistosomatidae). J. Zool. Lond. 151:433-452.

Fuhrmann, O. 1928. Trematoda In Handbuch der Zoologie (W. Kukenthal and T. Krumbach, eds). Berlin.

Funk, V. A. and D. R. Brooks, eds. 1981. Advances in Cladistics, Volume 1. N. Y. Botanical Garden, Bronx.

Goodchild, G. C. and V. L. Martin. 1969. Speciation in Spirorchis (Trematoda: Spirorchiidae) infecting the painted turtle Chrysemys picta. J. Parasitol. 55:1169-1173.

Gould, S. J. 1977. Ontogeny and Phylogeny. Belknap Press, Cambridge.

Gretillat, S. 1962. Etude du cycle èvolutif du schistosome des Ruminants domestiques de l'uest Africain et confirmation de l'Espèce Schistosoma curassoni Brumpt 1931. Ann. Parasit. Hum. Comp. 37:557-568.

Gretillat, S. 1964. Différences morphologiques entre Schistosma bovis (Souche de Karthoum) et Schistosoma curassoni (Souche de Mauritanie). Rev. Elev. Med. vét. Pays Trop. 17:429-432.

Haley, A. J. 1962. Role of host relationships in the systematics of helminth parasites. J. Parasitol. 48:671-678.

Hecht, M. K. and J. L. Edwards. 1977. The methodology of phylogenetic inference above the species level. Pp. 3-51 In Major Patterns of Vertebrate Evolution (M. K. Hecht, P. C. Goody, and B. M. Hecht, eds.). Plenum Press, New York.

Hennig, W. 1966. Phylogenetic Systematics. Univ. of Illinois Press, Urbana.

Heyneman, D. 1960. On the origin of complex life cycles of digentic trematodes. Pp. 133-152 In Libro Homenaje al Dr. Edwardo Caballero y Caballaro. Sec. Educ. Publ., Int. Politic. Nac., Esc. Nac. Cienc. Biol., Mexico, D.F.

Holmes, J. C. 1983. Evolutionary relationships between parasitic helminths and their hosts. Pp. 161-185 In Coevolution (D. J. Futuyma and M. Slatkin, eds.). Sinauer Associates, Sunderland.

Hsu, H. F. and S. Y. Li Hsu. 1957. On the intraspecific and interstrain variations of the male sexaul glands of Schistosoma japonicum. J. Parasitol. 43:456-463.

Hubendick, B. 1978. Systematics and comparative morphology of the Basommatophora. Pp. 1-48 In The Pulmonates (V. Fretter and J. Peake, eds.). Academic Press London.

Humphries, C. J. 1981. Biogeographical methods and the southern beeches (Fagaceae: Nothofagus). Pp. 177-207 In Advances in Cladistics (V. A. Fund and D. R. Brooks, eds.). N. Y. Botanical Garden, Bronx.

Hussey, K. 1941. Comparative embryological development of the excretory system in digenetic trematodes. Trans. Amer. Micros. Soc. 60:171-210.

Inglis, W. G. 1971. Speciation in parasitic nematodes. Adv. Parasitol. 9:185-223.

Ito, Y. 1960. Studies on Trichobilharzia corvi (Yamaguti, 1941). I. Morphological studies on the adult. Jap. J. Parasitol. 9:556-563.

Janicki, C. V. 1920. Grundlinien einer "Cercomer Theorie" zur Morphologie der Trematoden und Cestoden. Festsch. für Zschokke, Basel.

Johnston, S. J. 1917. On the trematodes of Australian birds. J. Proc. Roy. Soc. N. S. Wales 50:187-261.

Kennedy, C. R. 1975. Ecological Animal Parasitology. John Wiley and Sons, New York.

Khalifa, R. 1972. Studies on Schistosomatidae Looss, 1899 (Trematoda) of aquatic birds of Poland. I. On the life cycle of Bilharziella polonica Kowalewski 1895, with a discussion of the subfamily Bilharziellinae Price 1929. Acta Parasitol. Pol. 20:343-365.

Khahl, M. 1924. On the morphology of Schistosoma bovis. J. Helminthol. 2:81-86.

Kinsella, J. M. 1971. Growth, development and intraspecific variation of Quinqueserialis quinquerseralis (Trematoda: Notocotylidae) in rodent hosts. J. Parasitol. 57:62-70.

Kohn, A. 1964. Sôbre o genêro Macrobilharzia Travassos 1922 (Trematoda, Schistosomatidae). Mem. Inst. Osw. Cr. 62:1-6.

Kollar, E. J. and C. Fisher. 1980. Tooth induction in chick epithelium: Expression of quiscent genes for enamel synthesis. Science 207:993-995.

Komiya, Y. 1939. Die Entwicklung des Exkretionssystems einiger Trematodenlarven aus Alster und Elbe, nebst Bemerkungen über ihren Entwicklungszyklus. Z. Parasitenkd. 10:340-385.

Kowalewski, M. 1886. Studya Helminibologiszne. III. Bilharzia polonica sp. nov. Rozpr. Akad. Umiejet. 31:41-70.

Kruatrachue, M., M. Bhaibulaya and C. Harinasuta. 1965. Orientobilharzia harinasutai sp. nov., a mammalian blood flulke, its morphology and life cycle. Ann. Trop. Med. Parasitol. 59:181-188.

Kuntz, R. E. 1950. Embryonic development of the excretory system in fork-tailed cercariae of the schistosomes and in a blunt-tailed brachylaemid cercaria. Trans. Amer. Micros. Soc. 64:1-20.

Kuntz, R. E. 1955. Biology of the schistosome complexes. Am. J. Trop. Med. Hyg. 4:383-412.

Lal, M. B. 1937. Studies on the trematode parasites of birds. Part II. Morphology and systematic position of some new blood flukes of the family Schistosomatidae. Proc. Ind. Acad. Sci. 6:274-283.

LaRue, G. R. 1957. The classification of digenetic Trematoda: a review and a new system. Exp. Parasitol. 6:306344.

Lee, H. F. 1962. Life history of Heterobilharzia americana Price 1929, a schistosome of the raccoon an other mammals in southeastern United States. J. Parasitol. 48:728-739.

Leigh, W. H. 1955. The morphology of Gigantobilharzia huttoni (Leigh, 1953) an avian schistosome with marine dermatitis-producing larvae. J. Parasitol. 41:262-269.

LeRoux, P. L. 1933. A preliminary note on Bilharzia margrebowiei, a new parasite of ruminants and possibly man in northern Rhodesia. J. Helminthol. 11:57-62.

Liu and Bai. 1976. On bird schistosomes from Jilin Province Jilinobiharzia crecci gen. nov. sp. nov. (Schistosomatidae: Bilhariellinae) with a discussion of the taxonomy of the subfamily Bilharziellinae. Acta Zoologia Sinica 22:385-392.

Llewellyn, J. 1965. Evolution of parasitic plalyhelminths. Pp. 47-78 In Evolution of Parasites (A. E. R. Taylor, ed.). Blackwell Scientific Publications, Oxford.

Loss, A. 1899. Weiters Beiträge zur Kenntnis der Trematoden-Fauna Aegyptens. Zod. Jb. 12:521-784.

MacHattie, C. 1934. A preliminary note on the life history of Schistosoma turkestanicum Skryabin, 1913. Trans. Roy. Soc. Trop. Med. Hyg. 30:115-124.

MacKenzie, D. I. and C. E. McKenzie. 1980. Morphological variation in Plagiorchis noblei Park 1936 (Trematoda: Plagiorchiidae) from Tyrannus tyrannus and T. verticalis (Aves: Tyrannidae). J. Parasitol. 66:145-149.

Macko, I. K. 1961. Revision of the species Ornithobilharzia canaliculata (Rudolphi, 1819) (Trematoda: Schistosomatiae). Helminthologia 4:303-316.

Madhavi, R. and K. H. Rao. 1970. Orchispirium heterovitellatum gen. et. sp. n. (Trematoda: Sanguinicolidae) from the ray fish, Dasyatis imbricatus Day, from Bay of Bengal. J. Parasitol. 56:41-43.

Malek, E. A. 1977. Geographical distribution, hosts, and biology of Schistosomatium douthitti (Cort, 1914) Price, 1931. Can. J. Zool. 55:661-671.

Martin, W. E. 1944. Cercaria solemyae n. sp., probably a blood fluke, from the marine pelecypod, Solemya velum. J. Parasitol. 30:191-195.

Martin, W. E. 1952. Another annelid first intermediate host of a digenetic trematode. J. Parasitol. 38:356-359.

McCoy, O. R. 1929. Notes on Cercariae from Missouri. J. Parasitol. 15:199-208.

McFarland, W. N., F. H. Plough, T. J. Cade and J. B. Heiser. 1979. Vertebrate Life. Macmillan Publishing Company, New York.

McKenna, M. C. 1975. Toward a phylogenetic classification of the Mammalia. Pp. 21-46 In Phylogeny of the Primates (W. P. Luckett and F. S. Szalay, eds). Plenum Press, New York.

McLeod, J. A. 1937. Two new schistosomid trematodes from water birds. J. Parasitol. 23:456-466.

McLeod, J. A. 1940. Studies on cercarial dermatitis and the trematode family Schistosomatidae in Manitoba. Can. J. Res. 18:1-28.

McMullen, D. B. and P. C. Beaver. 1945. Studies on schistosome dermatitis. IX. The life cycle of three dermatitisproducing schistosomes from birds and a discussion of the subfamily Bilharziellinae (Trematoda: Schistosomatidae). Amer. J. Hyg. 43:128-154.

Mehra, H. R. 1939. New blood flukes of the family Spirorchidae Stunkard (Trematoda) from the marine turtle Chelone mydas of the Arabian sea with observations on the synonymity of certain genera and classification of the family. Proc. Nat. Acad. Sci. India 9:155-167.

Mehra, H. R. 1940. A new distome Enterohaematotrema n. g. and a new blood fluke Hemiorchis bengalensis n. sp. belonging to the family Spirorchidae (Stunkard) and a new species of the genus Dendritobiharzia Skrjabin and Zakharrow, belonging to the family Schistosomatidae Poche, with remarks on the evolution of the blood flukes. Proc. Nat. Acad. Sci. India 10:100-118.

Mehra, H. R. 1950. Evolution of the blood flukes and strigeid trematodes. Proc. Nat. Acad. Sci. India 19:9-38.

Mickevich, M. F. 1981. Quantitative phylogenetic biogeography. Pp. 209-222 In Advances in Cladistics, Volume 1 (V. A. Funk and D. R. Brooks, eds.). N. Y. Botanical Garden, Bronx.

Mitter, C. and D. R. Brooks. 1983. Phylogenetic aspects of coevolution. Pp. 65-98 In Coevolution (D. J. Futuyma and M. Slatkin, eds). Sinauer Associates, Sunderland.

Miyairi, K. and Suzuki, M. 1913. On the development of Schistosoma japonicum. Trop. Dis. Bull. 3:289-290.

Montgomery, R. E. 1906. Observations on bilharziosis among animals in India. II. J. Trop. Vet. Sci. 1:138-174.

Monquin-Tandon, A. 1860. Éléments de zoologie médicale. Paris.

Mudaliar, S. V. and G. Ramanujachary. 1945. Schistosoma nairi n. sp. from an elephant. Ind. Vet. J. 22:1-4.

Najim, A. T. 1950. Gigantobilharzia huronensis sp. nov., bird blood-fluke from goldfinch. J. Parasitol. 36:19.

Najim, A. T. 1956. Life history of Gigantobilharzia huronensis Najim, 1950. A dermatitis producing bird blood fluke (Trematoda: Schistosomatidae). Parasitol. 46:443-469.

Nelson, G. 1978. Ontogeny, phylogeny, paleobiology and the biogenetic law. Syst. Zool. 27:324-345.

Nelson, G. and N. I. Platnick. 1981. Systematics and Biogeography. Columbia Univ. Press, New York.

Noble, E. R. and G. A. Noble. 1976. Parasitology. Lea and Febiger, Philadelphia.

Odhner, T. 1910. Gigantobilharzia acotylea n. g. n. sp. ein mit den Bilharzien vervandter Blutparasit von enormer Länge. Zool. Anz. 35:380-385.

Odhner, T. 1912. Zum naturlichen System der digenen Trematoden. 5. Die Phylogenie des Bilharzia-Typus. Zool. Anz. 41:54-71.

Oglesby, L. C. 1961. A new cercaria from an annelid. J. Parasitol. 47:233-236.

Olivier, L. 1940. Life history studies on two strigeid tematodes of the Douglas Lake region, Michigan. J. Parasitol. 26:447-477.

Olsen, O. W. 1974. Animal Parasites. University Park Press, Baltimore.

Platnick, N. I. and V. A. Funk, eds. 1983. Advances in Cladistics, Volume 2. Columbia Univ. Press, New York.

Poche, F. 1907. Einige Bemerkungen zur Nomenclatur den Trematoden. Zool. Anz. 31:124-126.

Pojmanska, T. 1967. Variability of Leucochloridium paradoxum Carus (=L. heckerti Kagan, 1952) (Trematoda: Brachylaimidae) in natural and experimental conditions. Acta Parasitol. Pol. 14:381-398.

Price, E. W. 1929. A synopsis of the Trematode family Schistosomidae with descriptions of new genera and species. Proc. U.S. Nat. Mus. 75:1-39.

Price, E. W. 1931. Note on Macrobilharzia Travasos. J. Parasitol. 17:230-231.

Price, E. W. 1934. New genera and species of blood flukes from a marine turtle, with a key to the genera of the family Spirorchidae. J. Wash. Acad. Sci. 24:132-141.

Price, E. W. 1943. A redescription of Heterobilharzia americana Price (Trematoda: Schistosomatidae). Proc. Helminthol. Soc. Wash. 10:85-86.

Price, H. F. 1931. Life history of Schistosomatium douthitti (Cort). Amer. J. Hyg. 13:685-727.

Price, P. W. 1980. Evolutionary biology of parasites. Princeton Univ. Press, Princeton.

Purchon, R. D. 1977. The biology of the mollusca. Pergamon Press, Oxford.

Rensch, B. 1959. Evolution above the species level. Columbia Univ. Press, New York.

Rios Leite, A. C., H. M. de Araiýo Costa and J. O. Costa. 1978. Trichobilharzia jequitibaensis np. n. (Trematoda, Schistosomatidae) in Cairina moschata domestica (Anatidae). Rev. Brasil Biol. 38:843-846.

Rosen, D. 1978. Vicariant patterns and historical explanation in biogeography. Syst. Zool. 27:159-188.

Ross, G. C., V. R. Southgate and R. J. Knowles. 1978. Observations on some isoenzymes of strains of Schistosoma bovis, S. matheei, S. margrebowiei, and S. leiperi. Z. Parasitenkd. 57:49-56.

Rudolphi, C. A. 1819. Entozoorum synopsis cui accedunt mantissa duplex et indices locupletissimi. Berolini.

Schell, S. C. 1970. How to know the trematodes. W. M. C. Brown Co., Dubuque.

Schiller, E. L. 1959a. Experimental studies on morphological variation in the cestode genus Hymenolepis. I. Morphology and development of the Cysticercoid of Hymenolepis nana in Tribolium confusum. Exp. Parasitol. 8:91-118.

Schiller, E. L. 1959b. Experimental studies on morphological variation in the cestode genus Hymenolepis. II. Morphology and development of the strobilate

phase of Hymenolepis nana in different mammalian host species. Exp. Parasitol. 8:215-235.

Schiller, E. L. 1959c. Experimental studies on morphological variation in the cestode genus Hymenolepis. III. X-irradiation as a mechanism for facilitating analyses in H. nana. Exp. Parasitol. 8:427-470.

Schwetz, J. 1951. A comparative morphological and biological study of Schistosoma haematobuim, S. bovis, S. intercalatum Fisher, 1934; S. mansoni and S. rodhaini Brumpt, 1931. Ann. Trop. Med. Parasitol. 45:92-98.

Short, R. B. 1983. Presidential address: Sex and the single schistosome. J. Parasitol. 69:3-22.

Short, R. B. and R. B. Holliman. 1961. Austrobilharzia penneri, a new schistosome from marine snails. J. Parasitol. 47:447-452.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist. 85:1-350.

Sinha, P. K. and H. D. Srivastava. 1956. Studies on Schistosoma incognitum Chandler, 1926. I. On the synonomy and morphology of the blood fluke. Parasitology 46:91-100.

Sinha, P. K. and H. D. Srivastava. 1960. Studies on Schistosoma incognitum Chandler, 1926. II. On the life history of the blood fluke. J. Parasitol. 46:629-641.

Skrjabin, K. I. 1913. Schistosomum turkestanicum nov. sp., ein neuer parasit des Rindes aus Russisch-Turkestan. Zeit. Inf. Kran. Parasit. Krank. Hyg. Haus. 13:457-469.

Skrjabin, K. I., ed. 1951. Trematodes of animals and man. Principles of trematodology, Vol. V. Izdatelstro Akademii Nauk SSSR, Moscow.

Smith, J. W. 1972. The blood flukes (Digenea: Sanguinicolidae and spirorchidae) of cold-blooded vertebrates and some comparisons with the schistosomes. Helminthol. Abstr. A41:161-204.

Sneath, P. H. A. and R. R. Sokal. 1973. Numerical taxonomy W. H. Freeman and Co., San Francisco.

Stiles, C. W. and A. Hassall. 1898. An inventory of the genera and subgenera of the trematode family Fasciolidae. Arch. Parasitol. 1:81-99.

Straney, D. O. 1980. Relationships of phyllostomatine bats: Evaluation of phylogenetic hypotheses. Ph.D. thesis, Univ. California, Berkeley.

Stunkard, H. W. 1921. Notes on North American blood flukes. Amer. Mus. Novit. 12:1-5.

Stunkard, H. W. 1923. Studies on North American blood flukes. Bull. Amer. Mus. Nat. Hist. 75:165-221.

Stunkard, H. W. 1957. Host-specificity and parallel evolution of parasitic flatworms. Z. Tropenmed. Parasitol.

Stunkard, H. W. 1970. Trematode parasites of insular and relict vertebrates. J. Parasitol. 56:1041-1054.

Stunkard, H. W. and M. C. Hinchcliffe. 1952. The morphology and life history of Microbilharzia variglandis (Miller and Northrup, 1926). Stunkard and Hinchcliffe, 1951, avian blood-flukes whose larvae cause "swimmers itch" of ocean beaches. J. Parasitol. 38:242-265.

Szidat, L. 1929a. Die Parasiten des Hausgeflugels. 3. Bilharziella polonika Kow., ein im Blut schmarozender Trematode unserer Enten, seine Entwicklung und Uebertragung. Archiv. Gefluegelkunde 3:78-87.

Szidat, L. 1929b. Zur Entwicklungsgeschechte des Blutteremato den der Enten, Bilharziella polonica Kow. Zbl. Bakt. I Orig. 3:461-470.

Tada, S. 1928. On the development and structure of Schistosoma japonicum in the final host. Okayama Igakkai Zasshi 463:1-36.

Tanabe, B. 1923. The life-history of a new schistosome, Schistosomatium pathlocopticum Tanabe, found in experimentally infected mice. J. Parasitol. 9:183-198.

Taylor, A. E. R., ed. 1965. Evolution of Parasites. Blackwell Sci. Pub., Oxford.

Taylor, A. E. R. and R. Muller, eds. 1976. Genetic aspects of host-parasite relationships. Blackwell Sci. Pub., Oxford.

Stiles, C. W. and A. Hassall. 1898. An inventory of the genera and subgenera of the trematode family Fasciolidae. Arch. Parasitol. 1:81-99.

Straney, D. O. 1980. Relationships of phyllostomatine bats: Evaluation of phylogenetic hypotheses. Ph.D. thesis, Univ. California, Berkeley.

Stunkard, H. W. 1921. Notes on North American blood flukes. Amer. Mus. Novit. 12:1-5.

Stunkard, H. W. 1923. Studies on North American blood flukes. Bull. Amer. Mus. Nat. Hist. 75:165-221.

Stunkard, H. W. 1957. Host-specificity and parallel evolution of parasitic flatworms. Z. Tropenmed. Parasitol.

Stunkard, H. W. 1970. Trematode parasites of insular and relict vertebrates. J. Parasitol. 56:1041-1054.

Stunkard, H. W. and M. C. Hinchcliffe. 1952. The morphology and life history of Microbilharzia variglandis (Miller and Northrup, 1926). Stunkard and Hinchcliffe, 1951, avian blood-flukes whose larvae cause "swimmers itch" of ocean beaches. J. Parasitol. 38:242-265.

Szidat, L. 1929a. Die Parasiten des Hausgeflugels. 3. Bilharziella polonika Kow., ein im Blut schmarozender Trematode unserer Enten, seine Entwicklung und Uebertragung. Archiv. Gefluegelkunde 3:78-87.

Szidat, L. 1929b. Zur Entwicklungsgeschechte des Blutteremato den der Enten, Bilharziella polonica Kow. Zbl. Bakt. I Orig. 3:461-470.

Tada, S. 1928. On the development and structure of Schistosoma japonicum in the final host. Okayama Igakkai Zasshi 463:1-36.

Tanabe, B. 1923. The life-history of a new schistosome, Schistosomatium pathlocopticum Tanabe, found in experimentally infected mice. J. Parasitol. 9:183-198.

Taylor, A. E. R., ed. 1965. Evolution of Parasites. Blackwell Sci. Pub., Oxford.

Taylor, A. E. R. and R. Muller, eds. 1976. Genetic aspects of host-parasite relationships. Blackwell Sci. Pub., Oxford.

Thurston, J. P. 1963. Schistosomes from Hippopotamus amphibius L. I. The morphology of Schistosoma hippopotami sp. nov. Parasitology 53:49-54.

Thurston, J. P. 1964. Schistosomes from Hippopotamus amphibius L. II. The morphology of Schistosoma edwardiense sp. nov. Parasitology 54:67-72.

Travassos, L. 1922. Informacões sôbre a fauna helmintologica de Mato Grosso. Folha Med. 3:187-190.

Travassos, L. 1942. Contribuicões ao conhecemento dos "Schistosomatidae." Sobre "Ornithobilharzia canaliculata" (Rudolphi, 1819). Rev. Brasil Biol. 2:473-476.

Tubangui, M. A. 1933. Trematode parasites of Philippine Vertebrates, VI. Descriptions of new species and classification. Philipp. J. Sci. 52:167-197.

Ulmer, M. J. and F. J. Vande Vusse. 1970. Morphology of Dendritobilharzia pulverulenta (Braun, 1901) Skrjabin, 1924 (Trematoda: Schistosomatidae) with notes on secondary hermaphroditism in males. J. Parasitol. 56:67-74.

Van der Land, J. 1967. A new blood fluke (Trematoda) from Chimaera monstrosa L. Proc. Koninkl. Neder. Akad. van Wetenschappen Amsterdam 70:110-120.

Vande Vusse, F. J. 1980. A review of the genus Dendritobilharzia Skrjabin and Zakhorow 1920. (Trematoda: Schistosomatidae). J. Parasitol 66:814-822.

Van Tyne, J. and A. J. Berger. 1976. Fundamentals of Ornithology. John Wiley and Sons, New York.

Vogel, V. H. and W. Minning. 1940. Bilharziose bei Elephanten. Arch. Schiffs-u. Tropenhyg. 44:562-574.

Wakelin, D. 1976. Host Responses. Pp. 115-141 In Ecological Aspects of Parasitology (C. R. Kennedy, ed.). North-Holland Pub. Co., Amsterdam.

Wales, J. H. 1958. Two new blood fluke parasites of trout. Calif. Fish Game 44:125-136.

Ward, H. B. 1921. A new blood fluke from turtles. J. Parasitol. 7:114-128.

Warren, K. S. 1973. Schistosomiasis: The Evolution of a Medical Literature. Mass. Inst. Tech., Cambridge.

Watertor, J. L. 1967. Intraspecific variation of adult Telorchis bonnerensis (Trematoda: Telorchiidae) in amphibian and reptilian hosts. J. Parasitol. 53:962--968.

Weinland, D. F. 1858. Human Cestoides. Cambridge.

Wetzel, R. 1930. A new species of trematode worm of the genus Ornithobilharzia from a Canada goose. Proc. U.S. Nat. Mus. 78:1-4.

Wiley, E. O. 1981. Phylogenetics: the theory and practice of phylogenetic systematics. John Wiley and Sons, New York.

Witenberg, G. and J. Lengy. 1967. Redescription of Ornithobilharzia canaliculata (Rud.) Odhner, with notes on classification of the genus Ornithobilharzia and the subfamily Schistosomatinae (Trematoda). Israel J. Zool. 16:193-204.

Wright, C. A. 1960. Relationships between trematodes and molluscs. Ann. Trop. Med. Parasitol. 54:1-7.

Yamaguti, S. 1971. Synopsis of Digenetic Trematodes of Vertebrates, Vol. I and II. Keigaku Pub. Co., Toyko.

Young, R. T. 1937. Another record of avian schistosomes in North America. J. Parasitol. 23:295-296.

Zilch, A. 1959. Gastropoda, Vol. 2, Euthyneura. Pp. 1-834 In Handbook Palaozool. (O. H. Schindewolf, ed.).

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