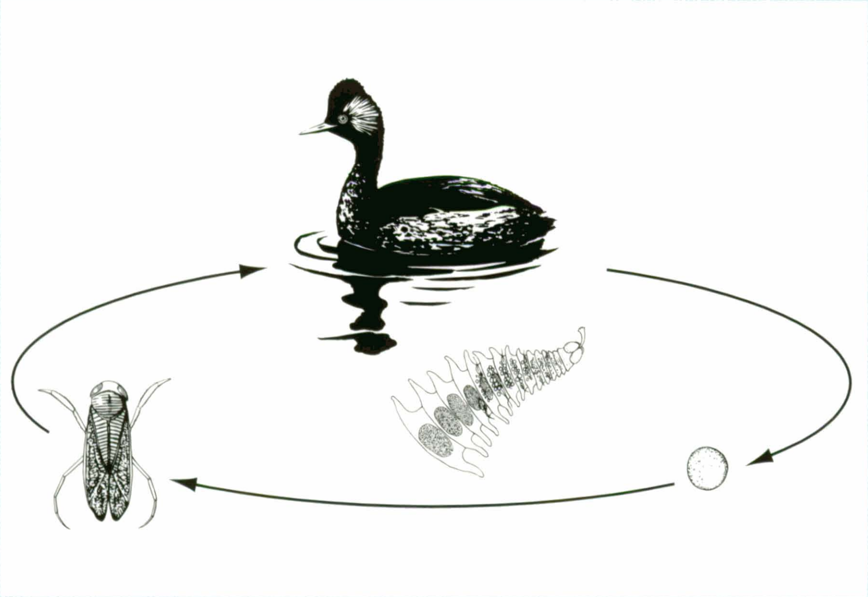
THE METAZOAN PARASITE FAUNA OF GREBES (AVES: PODICIPEDIFORMES) AND ITS RELATIONSHIP TO THE BIRDS' BIOLOGY

BY

ROBERT W. STORER



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The Metazoan Parasite Fauna of Grebes (Aves: Podicepediformes) and its Relationship to the Birds' Biology

by

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COVER

The life cycle of the cestode, *Tatria biremis.* The adult parasite (center), which reaches a length of approximately 2.5 mm, inhabits the anterior section of the small intestine of the definitive host, here an Eared Grebe (*Podiceps nigricollis*). A mean of 2,794 individual worms of this species has been found in 31 individual birds. The minute (0.02 mm) eggs are passed into the water, where they are presumably swept into the mouth of the intermediate host, a corixid bug (*Sigara*), by the insect's front legs. Grebes become infected by eating the bugs, which may teem in lakes where the birds breed.

This common parasite of grebes in the Northern Hemisphere belongs to the family Amabiliidae, all but one of whose 29 species are grebe specialists.

Original drawing by John Megahan from sources listed in the acknowledgments (p. 65).

ABSTRACT

Storer, R.W. 2000. *The Metazoan parasite fauna of grebes (Aves: Podicipediformes) and its relationship to the birds' biology. Misc. Publ. Mus. Zool., Univ. Michigan, 188:1-90, 10 figs., 7 tables.* The data base of this work consists of a list of the multicellular parasites known to infect grebes and a list of the known species of prey taken by each species of grebe. The former includes information on where in the bird the parasites are found, the distribution of the parasite species by continents, degree of host specificity, and life cycles (whether on fresh or salt water and lists of known intermediate and paratenic hosts). These data sets are used to show how the parasite faunas are related to the biology of the birds.

The aquatic existence of grebes and the wide range of prey taken by individuals and species of grebes are reflected in the wide range of helminths infecting the birds (113 species of digenes, 86 of cestodes, 13 of acanthocephalans, and 37 of nematodes, most of which have aquatic life cycles). One family, one subfamily (each with the exception of a single species), several genera, and 104 species of helminths are considered grebe specialists, as are most of the species of ectoparasites. Of the well-studied species of grebe helminth specialists, almost all have been found in more than one grebe species and many more in more than one grebe genus. This is believed related to the fact that even grebes adapted for taking particular kinds of prey will usually take many other kinds. Thus, where several species of grebes are sympatric, there is a considerable overlap in diet and consequently, overlap in the intermediate hosts ingested. On the other hand, most of the ectoparasites appear to be confined to single grebe species.

Grebes contain large numbers of intestinal helminths. In a study of these parasites of 91 grebes from the breeding grounds in Alberta (Stock 1985), all were found infected, with numbers ranging from 2 to 15 species and 112 to 33,169 individuals, the majority (96 percent) of which were cestodes.

Most grebes spend the breeding season on eutrophic bodies of water, which have an abundant supply of kinds and individuals of potential prey for the birds. More than half of the species of grebes winter on salt water where a variety of helminths with salt-water intermediate hosts can infect the birds, but unfortunately, very few grebes taken on salt-water habitats have been examined for parasites. Still other kinds of helminths may be acquired on bodies of water along the birds' migration routes. Most of the helminths that are obtained on fresh waters presumably are lost shortly after the birds' arrival on salt water and *vice versa.* What causes these changeovers in unknown, but it is suggested that the mechanisms for this are reversals of the salt gradient in the intestines. Eared Grebes coming to the highly saline Mono Lake on their molt migration after the breeding season presumably soon lose their helminth parasites.

Grebes have a unique habit of swallowing their own feathers which form pellets containing other indigestible materials and, when cast, are believed also to rid the stomach of nematodes that feed on the grebes' food there. A separate plug of feathers is lodged in the pyloric outlet of the stomach where it acts as a sieve preventing large pieces of indigestible material from passing through the intestine. This is believed to reduce the likelihood of parasites being dislodged from the wall of the gut.

Grebes are the only birds that do not nest on land but regularly build floating nests of material taken from the water. As a consequence, they are not known to be parasitized by animals like flies, fleas, bedbugs, and ticks that require a stay on land as part of their life cycle, and because of their limited physical contact with other birds, but few species of external arthropod parasites (12 mites and 13 lice) have been reported from them. Infections by several of these external parasites are thought to have resulted from crossovers from coots (*Fulica*).

Although grebes are found on all continents except Antarctica, with a minimum of three species on each, studies of their parasites have been few outside of the Northern Hemisphere. This is especially unfortunate because the greatest numbers of grebe species and endemics are found in South America. The virtual lack of information on the parasites of these birds severely limits the potential for parallel studies on the evolution of grebes and their parasites.

The parasites of grebes offer many possibilities for research from regional surveys and working out life cycles to studies on biogeography and evolution of these animals.

A data base for the parasites is available on the web.

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INTRODUCTION

In preparing accounts of grebes for the North American Bird Biographies (Storer 1992; Storer & Nuechterlein 1992), I found no general lists of grebe parasites. While hosts are regularly listed in studies of parasites, lists of parasites infecting an avian host or family of hosts are rare, and studies on the relationships between the avian hosts' biology with their parasite faunas, scarcer still. (Hoberg's study of the platyhelminth parasites of the Alcidae [1984] is a notable exception.) The unique or unusual aspects of the biology of grebes that might affect their suitability as hosts for internal or external parasites present an unusual opportunity to investigate how the life style of a group of birds may be related to that of the birds' parasite fauna.

The grebes have no known close relatives and are hosts to several groups of parasites seldom or never found in birds of other groups. Although no general assumptions can be made regarding coevolution of parasites and their hosts (Hoberg *et al.* 1997), how the evolution of these groups may have proceeded is of considerable interest and may provide clues to the hosts' relationships (Brooks & McLennan 1993; Baer 1957, for cestodes; Clay 1957, for lice).

Quite aside from their evolution in grebes, the parasites have much intrinsic interest. For instance, parasitic worms or helminths, usually have complex life cycles requiring one or more intermediate hosts before they can infect the definitive host in which sexual reproduction takes place. Their infective stages may also be accumulated in paratenic or "transport hosts," which differ from intermediate hosts in that no further development of the larval parasite occurs within them. These infective stages are often found in fishes. Because grebes serve as definitive hosts for parasites of those intermediate and paratenic hosts, they may adversely affect fisheries. Thus, their parasites have been much studied in countries with important fresh-water fisheries.

Because the terms intermediate host and paratenic host are defined from the point of view of parasitologists, I think it advisable to use the term infective host for any carrier of a stage that may infect an avian host. These may be the last intermediate host or paratenic hosts or both. For those studying the avian host, it is usually not significant which.

The more that is known about the biology of a parasite, the more we can learn from it about the biology of its avian hosts and *vice versa.* Ideally, we should know not only the identity of each host in the parasite's life cycle but also the behavior of the free-swimming larvae, how the parasite is transmitted to each stage in the cycle, the habitat in which this occurs, the specificity and range (both ecological and geographic) of each host. When these data are known for a species or group of birds, a surprising amount of information can be obtained from determining the parasite load in a sample of a single species of definitive host. Bartoli's (1989) study of the digenes found in a breeding population of the Yellow-legged Gull (*Larus cachinnans michahellis*) in Sardinia showed, among other things, not only what the birds were eating but in what habitats, differences in foraging between the sexes, and whence some of the birds came to the breeding grounds. The use of such a broad spectrum of information is natural history in the best sense.

On a broader scale, parasitology is one of the most integrative areas of biology. In particular, helminth parasites can "provide a new dimension to understanding ecological interactions, patterns of distribution, and the complex history of many geographic regions and biotas," and because they are "indicators of the historical and ecological development, temporal longevity, current health, and prospects for continuity of biotas" they are important in studies of biodiversity and in pointing out critical areas and biotas to conservationists (Hoberg 1997).

Most helminth parasites, which constitute by far the largest number of species parasitic in grebes, pass through one or more intermediate hosts before reaching the definitive grebe host. Because the last intermediate host or a paratenic host must be ingested by, or otherwise reach, a definitive host in order for the adult parasite to develop, it is clear that parallel lists of intermediate and paratenic hosts known for each parasite and of the prey species known for each species of grebe are needed to determine what parasites might be expected to infect any grebe species. Conversely, the presence of a parasite in a grebe may be useful in indicating consumption of a species of intermediate host that might not have been found in examination of stomach contents of the bird.

The more deeply I went into parasitology, the more questions arose about the relationships between the parasites and their hosts. These in turn led to ideas about what might be done with the information I had been collecting. What started out as a simple list has led to sets of data which could be analyzed in various ways and which could be expanded as new information became available. I am unaware that a similar study has been designed for any other group of birds and suggest that this work, with suitable modifications, might be useful in planning future studies.

Major sources. Rausch (1983) presents an excellent summary, including a brief history, of our knowledge of the biology of avian parasites. Yamaguti's *Systema Helminthum* (1958, 1959, 1961, 1963), contains world lists of the helminths and their vertebrate hosts and is basic in summarizing information up to the dates of the publication of the various parts, and Yamaguti (1971, 1975) updates the trematode volume of this work. The supplements to the Index-catalogue of Medical and Veterinary Zoology (U. S. Dept. Agric. 1966-1984) provide lists of hosts for parasites. Baruš *et al.* (1978) for the nematodes and Ryzhikov *et al.* (1985) for the cestodes and acanthocephalans also have been indispensable for this study. Dubinina's thorough monograph of the Ligulidae (1980) contains a wealth of information on this family of cestodes, and Ryzhikov & Tolkacheva's (1981) revision of the Acoleata is an up-to-date work on the systematics of the Amabiliidae and Dioecocestinae, the two groups of cestodes which, in the adult stage, are almost entirely confined to grebes. Valuable sources of information on life cycles are Schell (1985), Shoop (1988), and Yamaguti (1975) for digenes, Mackiewicz (1988) and Schmidt (1986) for cestodes, and Anderson (1988, 1992) for nematodes. Hyman (1951a,b) contains valuable information on the biology of the helminths up to the time of its publication. Crompton & Nickol (1985) provide an up-to-date account of the biology of acanthocephalans, and Sawyer (1986) of the leeches. Brooks *et al.* (1985, 1989) and Adamson

(1987) present phylogenetic analyses of the major groups of the digenes, and the nematodes, respectively. Hoffman (1967) is a useful source of information on the species of fishes known to be hosts of helminth larvae and McDonald (1969) for information of parasites of waterfowl also known to parasitize grebes. The theses by Gallimore (1964) and Stock (1985) contain much basic data on the intestinal helminths of North American grebes. For the lice, the check-list of Hopkins & Clay (1952), although long out of date, is still a major source of information on that group. Ash (1960) presents a general account of the biology of lice inhabiting birds. Edwards' revision of *Aquanirmus* (1965), the species of which are only known from grebes, is of special interest as the only study of a group of lice which is considered to have speciated on grebes. The mite genera, *Rhinonyssus* and *Ptiloxenus,* have also speciated on grebes and when better known, may well offer opportunities for parallel phylogenetic studies with the grebes. Bush *et al.* (1997) give useful definitions of population and community terms often used by parasitologists.

Grebes as Hosts for Parasites. The grebes form a well-defined and ancient avian family with a world-wide distribution. They were long thought to be nearest to the loons (Gaviidae), and this view is still held by some (*e.g.,* Cracraft 1982). On the other hand, molecular evidence supports the view that grebes have no close relations among Recent birds (Hedges & Sibley 1994). Although the known fossil record of the group only goes back to the Oligocene (Nessov 1992), the known fossil grebes are not sufficiently different from Recent ones to provide clues as to what the grebes' closest relatives might be, and on the basis of DNA-DNA hybridization studies, it is believed that grebes diverged from a basal stock of modern birds earlier in the Cenozoic than the Oligocene (Sibley & Ahlquist 1990).

The morphology, behavior, pattern of the downy young, ecology, and food habits of many of the species have been studied, and there is general agreement on the phylogenetic relationships among the species (cf. Storer 1967a, 1976; Fjeldså 1977, 1985), but to date, there have been no molecular studies which might be used to test these relationships. In addition, a major limitation for making studies of co-speciation and historical biogeography is the virtual lack of information on the parasite faunas of grebes in South America, which is believed to have been the center of radiation of the family (see below). Stock (1985) presented such a study, but it was based in part on Fig. 9.17 in Rich (1983) showing that five (unspecified) genera of grebes may have been known from the mid- to late Cretaceous. These genera are presumably ones that are now considered not to be grebes but part of the early radiation that resulted in the Hesperornithiformes. Hence, the radiation of grebes came after the breakup of Gondwanaland, on which Stock based much of his analysis.

The twenty-one Recent grebe species have been divided among six genera (Storer 1979). Since the publication of that list, a twenty first species, *Aechmophorus clarkii,* has been split from *A. occidentalis* (American Ornithologists' Union 1985). A seventh genus, *Podicephorus,* has been proposed by Bochelński (1994) for what was previously called *Podiceps major.* I think this proposal is justified on the basis of both morphological and behavioral grounds detailed in Sanders (1967) and Storer (1963a), and I use it here. The differences among these seven genera are sufficient to place them in two or three groups or tribes (Storer 1963b). There is thus a range of levels of relationships within the family from that of a tribe to that of subspecies. Grebes are found on all continents except Antarctica, with a minimum of three species on each. Several species are found on islands, and three flightless or nearly flightless species are or were confined to single lakes or lake systems. A list of the species and their distributions is found on Table 1.

Grebes probably arose in South America, where nine species, six of them endemic, are found. These endemics include the only two species of *Rollandia,* which is believed to be closest to the ancestral stock of the family (Storer 1976; Fjeldså 1977) and the monotypic genus *Podicephorus.*

The age of the group indicates that there was ample time for grebes to acquire parasites or for substantial coevolution to occur between hosts and parasites. Additionally, the wide geographic distributions of some grebes may enhance exposure to infections by a broad variety of parasites. The differences in parasite diversity between widely distributed species of grebes and those endemic to single lakes or islands offer possibilities for comparisons.

In size and diversity, the family of the grebes, the Podicipedidae, is comparable to that of the strictly marine diving birds, the Alcidae, the parasites of which have been studied extensively by Hoberg (1984, 1986) and with which interesting comparisons might be made.

Parasite faunas reflect the habits of the hosts. Grebes, which may seldom, if ever, come on land, are ideal hosts for parasitic worms with aquatic intermediate hosts. Grebes feed almost exclusively on aquatic animals, and the eggs of the parasites are excreted by the grebes directly into the water where they or their larvae can infect intermediate hosts. It is not surprising, therefore, that grebes carry a heavy load of tapeworms. It is not unusual to find large numbers of several species of this group of parasites in the intestines of a single bird (Stock 1985). The diversity of internal parasites is increased in the grebes that breed in fresh-water habitats and winter on salt water, because each of these habitats has its own contingent of parasites and their intermediate hosts not found in the other. The long association between these parasites and grebes is reflected in the large proportion of the genera and species of these worms that specialize in grebes.

Grebes' habit of picking up land-based insects from the surface of the water or from emergent vegetation may subject them incidentally to parasites with land-based life cycles. This may increase the parasite load of the grebes but is, of course, a dead end in the life cycle of the involved parasite.

Grebes rarely come in physical contact with other birds or their nests in situations in which exchange of external parasites might occur. Therefore, the crossover of these parasites from other species of birds to grebes must be very rare, and the known ectoparasite fauna of grebes is correspondingly low in species.

Some characteristics and adaptations of intermediate hosts. What makes a suitable intermediate host also needs to be considered. Many first intermediate hosts of helminths become infected by taking in eggs of the parasites. This may be by eating the eggs, in which case, the eggs must be able to pass through the mouth and without damage. For example,

Table 1. The Distribution of Grebe Species.

	Continent or major island						
	S.Am.	N.Am.	Euras.	Africa	Madag.	Austr.	N.Zeal.
Rollandia							
rolland	+E	-	-	-	-	-	-
microptera	+E	-	-	-	-	-	-
Tachybaptus							
novaehollandiae	-	-	-	-	-	+E	+ ←
ruficollis	-	-	+	+	+	-	-
rufolavatus	-	-	-	-	+E*	-	-
pelzelnii	-	-	-	-	+E	-	-
dominicus	+	+	-	-	-	-	-
Podilymbus							
podiceps	+	+	-	-	-	-	-
gigas	-	+E*	-	-	-	-	-
Poliocephalus							
poliocephalus	-	-	-	-	-	+E	+ ←
rufopectus	-	-	-	-	-	-	+E
Podicephorus							
major	+E	-	-	-	-	-	-
Podiceps							
auritus	-	+	+	-	-	-	-
grisegena	-	+	+	-	-	-	-
cristatus	-	-	+	+	-	+	+
nigricollis	+*	+	+	+	-	-	-
occipitalis	+E	-	-	-	-	-	-
taczanowskii	+E	-	-	-	-	-	-
gallardoi	+E	-	-	-	-	-	-
Aechmophorus							
occidentalis	-	+E	-	-	-	-	-
clarkii	-	+E	-	-	-	-	-
Total species	9(6E)	8(3E)	5(0E)	3(0E)	3(2E)	3(2E)	4(1E)
Total genera	5(2E)	4(1E)	2(0E)	2(0E)	1(0E)	3(0E)	3(0E)

+ = present. - = absent. E = endemic. * = extinct or extirpated. ← recently colonized.

among the insects, almost all hemiptera obtain their food by sucking plant or animal juices through fine, straw-like beaks which are unsuitable for taking in parasite eggs. However, members of one family of hemipterans, the water boatmen (Corixidae), have a simple mouth opening and feed by sweeping small objects into it with their brush-like forelegs (Griffith 1945). This method of feeding has made it possible for them to ingest eggs of the cestode, *Tatria biremis*. However, at least some corixids possess a crushing "masticator," which, if present in *Sigara*, intermediate hosts of *T. biremis*, must be passed without damage to the eggs. Most other members of the family Amabiliidae to which *Tatria* belongs, have nymphs of dragonflies and damselflies (Odonata) as intermediate hosts, and it has been suggested by Boertje (1974) that, in the nymph of the dragonfly, *Anax junius*, eggs of *Schistotaenia tenuicirrus* are swept into the intestine by action of the cloacal gills.

Larval schistosomes enter hosts by direct penetration of the skin. Obviously, the host's skin must be penetrable by the larva, and the internal environment of the host must be compatible for the schistosomes to mature.

It should be clear that the size of a last intermediate host may determine the maximum size of the infective stage of the parasite and/or the number of individual parasite larvae that can develop in it. In turn, the size of the infective stage can affect the length of time needed for the parasite to attain maturity in the definitive host and/or the ultimate size of the adult. The biology of an intermediate host can affect its abundance. Herbivores and other small species like detritus feeders near the base of the predation triangle are more numerous than predators near the apex, hence are more likely to be eaten, and in greater numbers, by a prospective definitive or paratenic host. On the other hand, larger predatory intermediate hosts are usually scarcer but may contain larger and/or more larvae. The trade-offs between these differences can be exemplified by the amabiliid tapeworms, *Tatria biremis* and *Schistotaenia tenuicirrus*. The former is a small species, whose intermediate hosts are water boatmen, abundant, small, algal or detritus feeding hemipterans, whereas the latter's intermediate hosts are the predacious nymphs of the very large dragonfly, *Anax junius*. *Tatria biremis* is found in very large numbers (up to several thousand) in a single Eared Grebe (Stock & Holmes 1987b), whereas *S. tenuicirrus* is found in much smaller numbers (up to 36) in a Pied-billed Grebe, *Podilymbus podiceps* (Boertje 1974).

Although no further development of the larval helminths occurs in paratenic hosts, these hosts are important in collecting numbers of the infective stages of parasites. In this way definitive hosts may get larger numbers of the parasites than they might by feeding directly on small intermediate hosts. The intermediate hosts of many helminths are copepods, ostracods and cladocerans, which may be too small to be taken, at least frequently, by grebes. However, when these small crustaceans are taken by snails, fishes, or other paratenic hosts that are more often taken by grebes, the chances of a grebe's becoming infected become much greater. For example, the tapeworm, *Dicranotaenia coronula,* presumably infects grebes when they eat snails, which in turn, eat the intermediate hosts, copepods and ostracods (McDonald 1969; Ryzhikov *et al.* 1985). This parasite is a specialist on waterfowl which, unlike grebes, have straining mechanisms in the bill and eat large numbers of small crustaceans. Snails, acting as paratenic hosts for this parasite, make them available to birds like grebes that take larger prey and thus increase the number of possible definitive hosts for the parasite, as well as parasites for the grebes.

This idea can be used in seeking unknown intermediate hosts of parasites. For example, if a fish-eating grebe is found to harbor a parasite whose intermediate hosts are known to be small crustaceans, one might look for fishes as paratenic hosts.

The role of anadromous and catadromous fishes in carrying infective stages of fresh-water parasites to marine hosts and *vice versa* does not appear to have received much attention. While this may often be a dead end for the parasite, it may be a significant cause of parasitism for the host. On the other hand, birds like many grebes, that breed on fresh water but migrate to salt waters for the winter, may be important in spreading parasites to stopovers on fresh waters enroute to and from the breeding grounds.

Purposes. The purposes of this work are first, to prepare a list of the species of both the internal and external metazoan parasites of grebes, with information on their distribution, location within or on the host, life cycles, including known intermediate and paratenic hosts, and degree of specificity for grebes as hosts; second, to prepare a list of the prey species of grebes for comparison with the lists of intermediate hosts of the parasites and to establish a data base to which new material may be added as it becomes available; third, to try to determine more specifically how grebes' parasite faunas may be related to the birds' morphology and aquatic way of life, including their food and foraging methods, their peculiar nesting habits, and the annual moves of many of them to and from fresh-water breeding habitats and salt-water winter quarters. Other questions such as the degree of host specificity, the possible coevolution of groups of parasite species with those of the hosts, and possible clues to the phylogenetic relationships of grebes with those of other groups of birds through similarity of their parasite faunas, may be considered. Finally, because the point of view of an ornithologist differs from that of a parasitologist, suggestions for further work will be made.

Methods. This review is based on the literature, much of which has been published in languages, many of them Slavic, unfamiliar to me. Furthermore, some are in obscure works, which have not been available on interlibrary loan. Therefore, I may have missed some host records. I hope not many.

Two major data sets have been assembled: a list of the species of parasites reported from grebes and a list of the species of prey reported taken by each species of grebe. Both lists include the names of numerous species of animals. In the various sources used, these animals may be identified to species, genus, family, or merely a higher group. Because of this disparity in the level to which these animals have been identified and the need to assemble records for all species of any genus, family, or higher group, it has been necessary to establish a system of classification that can be used consistently for these animals. Therefore, in order to make comparisons between prey of the birds and intermediate and paratenic hosts of parasites, I have given, as far as possible, genus, family, and two higher categories for each species. (In a few instances in which the lists of prey species and intermediate hosts from genera are very long, only the name of the genus may be given.) To distinguish the levels of classification, the name of the highest group is in bold face, the next highest in capital letters, the family name is in large and small capital letters, and the genus and species are in italics. In a few instances, such as the suborders of Odonata, subgroups are given in plain text.

What are given as the two highest groups depends to a large extent on the importance of the members of the group as hosts and/or prey. Therefore, above the family level, groups have been chosen largely on the basis of the number of species involved and the habits of members of the group that may affect their availability to grebes using different foraging techniques. Thus, phylum and class are used for the annelid worms, relatively few of which are involved, whereas class and order are used for the arthropods and mollusks, which are the two most important groups of intermediate hosts. Above the family level, most vertebrates are listed only by class, exceptions are made in the amphibians and reptiles, in which orders are used, and the fishes (all teleosts, except for a few lampreys) are listed only to family because grebes presumably select fishes on the basis of size and availability. For ease in reading, English names are used for higher groups for which the English group name is synonymous with and derived from the Latin one (*e.g.,* amphipods for Amphipoda). This has not been done for the orders of insects because some, like the Hymenoptera, consist of several groups with different English names. For the purposes of this work, consistency in which levels among the higher taxonomic ranks are used is immaterial, whereas consistency between the two data sets in the nomenclature of the animals and in which higher groups are used is essential for the computer analysis.

As groups of animals become better known, their classification and nomenclature change. Compilers of works on parasitology often list the hosts of a species of parasite from the literature without making certain that each host is always listed under the same name. As a consequence, the same host often appears in this literature under several names. The same problem arises in lists of the prey species of a definitive host. For this reason, I have found it necessary to standardize the nomenclature and classification of all the animals mentioned in this work in order to make computer-based analyses possible. This standardization has been both tedious and to a certain extent arbitrary.

In checking synonymies and assigning the families and other higher categories to which genera belong, I have used Vaught

(1989) for the mollusks and Robins *et al.* (1991) and Eschmeyer & Bailey (1990) for the fishes. For assistance in the systematics of other groups, I have relied on help from many colleagues acknowledged elsewhere (p. 65 Acknowledgments). Specialists on the various groups of parasites have been especially helpful in correcting errors in the taxonomy and nomenclature of the groups in which they specialize. In some instances, especially where authorities disagree, I have had to make arbitrary decisions but have tried to indicate divergent opinions.

Two subfamilies of aquatic insects belonging to primarily terrestrial families (the Donaciinae of the Chrysomelidae [Coleoptera] and the Nymphulinae of the Pyralidae [Lepidoptera] are listed separately and the other members of the former are listed as "Chrysomelidae, except Donaciinae." This is useful in indicating the greater availability of members of these subfamilies to foraging grebes and their possible use as intermediate hosts for parasites of aquatic birds.

The list for each major group of parasites is prefaced by a brief description of the biology of the group primarily for the benefit of non-parasitologists.

In the lists of helminth parasites, I have included as much of the following information as possible for each species:

A. The currently recognized name for the species of grebes known to be parasitized. Subspecific names are usually omitted. This list of grebe hosts is not intended as a list of all records for a given host, so usually only one record for each host is included. For a list of the scientific and English names of grebes and synonyms commonly used in the parasitological literature, see below (p. 6).

In parasitology, it is the practice to list the describer's name followed by a comma and the year in which description was published. I have followed this convention for original descriptions, although I have not used commas between the name of an author and date of publication of other references cited. I have not listed in the Literature Cited papers in which original descriptions were given unless information on hosts other than the type host or information on the life cycle of the parasite is included. Thus all references in which there is no comma between the name(s) of the author(s) and the date are included in the literature cited.

B. The location within the body of the definitive hosts (for the species of parasite as a whole).

C. Continents from which the species of parasite is known (from all hosts). Continents are used rather than zoogeographic regions because most grebe species either migrate from one such region to another or are resident in more than one region. Madagascar and New Zealand are added to the list of continents because each has one or more endemic species of grebe.

D. Whether the life cycle of the parasite is based on fresh water (FW), salt water (SW), brackish water (BW), or, in a few cases, is terrestrial (T). This may be complicated in instances in which the last (*i.e.*, infective) intermediate host or a paratenic host may move from fresh to salt water like the young of anadromous fishes (some salmonids and smelts) or *vice versa*, like the young of catadromous fishes (*e.g.*, eels), or may live in both habits (*e.g.*, some killifishes [*Fundulus*] and some sticklebacks [*Gasterosteus* and *Pungitius*]). In such cases, the habitat in which the parasite's egg is deposited and the first-stage larva reaches the first intermediate host is the one designated.

E. Known intermediate and paratenic hosts.

F. The degree of host specificity of the parasite. As defined in Hoberg (1986), "host specificity refers to the phenomenon in which species of helminths are limited in distribution to phylogenetically related hosts." However, It should be noted that host specificity must be decoupled from cospeciation. (See Hoberg *et al.* 1997 and references therein.) Because more than a few grebe parasites are known only from the original description or a very few collections, because little or nothing is known about the rates or intensities of infection by most grebe parasites, and because most of the species of parasites that are well studied are found to infect more than one grebe species or genus, I have devised the following classification which I think best suits the present situation. It consists of six degrees of increasing specificity: 0. Incidental or experimental infections, or immature stages found but species is not known to mature in grebes. 1. Generalist, species of parasites that is found commonly in more than one taxonomic group. 2. Specialist in other group(s), rare or occasional in grebes. 3. Specialist in grebes, rare or unknown in other groups. 4. Known only from type (grebe) host. 5. Known only from the original description. An asterisk opposite the name of the parasite indicates that it is a grebe specialist (categories 3-5). Because the categories tend to converge, a considerable degree of subjectivity was necessary in allotting them, and in many cases queries were added. This was often the case with category 5, when I found only the original description but could not be certain that no further collections had been reported. (For the few instances in which grebes act as intermediate hosts, information on specificity is not included.) This was also the case in category 2, in which it was often impossible to determine whether a parasite which was found to be common in a group of birds was also specific to that group. A special case is that of *Pelecitus fulicaeatrae* which is confined to coots and grebes. Because it is probably that this parasite originated on the former and was later transferred to grebes when its intermediate louse host crossed over to grebes, it is placed in category 2?

G. Frequently used synonyms of the name of the parasite, especially those used in records of the parasite from grebes.

When life-history information of a species of parasite is unknown, information inferred from a related species, followed by a question mark, may be included. Some parasites known to have intermediate hosts in fresh water are known to infect strictly marine birds such as auks. These birds presumably obtain infections from anadromous fishes (*e.g.*, some salmonids and smelt). In such cases, SW is also given with a question mark.

In the accounts of several species of parasites which have unusual life cycles, more detailed accounts are presented to give an idea of the diversity of these cycles found among the parasites of grebes.

Genera and species are listed alphabetically within each family. The names of subfamilies and subgenera are often omitted.

The lists of ectoparasites include the names of the parasite and of the hosts and the continents from which the parasites are known.

In the lists of prey of grebes, the species recorded are presented in the same system of classification as that used in the intermediate hosts. This has been done to permit parallel search and comparison by computer.

Parasites not identified to named species, those found in grebes not identified to species, those not known to mature in grebes, and those resulting from experiments or incidental infections (*e.g.*, in Zoos) are bracketed on the lists and are not included in the records used in the analyses.

Specimens reported in the literature to be in collections of the U. S. National Museum (USNM) and the U. S. Dept. of Agriculture (USDA) are now in the U. S. National Parasite Collection (USNPC), Agricultural Research Service, Beltsville, Maryland. A recent account of the complex history of these collections can be found in Lichtenfels *et al.* (1992). As is customary in referring to this material, it is listed by the accession number. Parasite specimens in the H. W. Manter Laboratory, Lincoln, Nebraska, are referred to as HWM with their accession numbers. Specimens of birds in the collections of the University of Michigan Museum of Zoology are referred to as UMMZ with their catalogue numbers.

To facilitate searching and analyses, the basic data on each named parasite species have been put into a computer data base. These data include, where known, the class, order, and family, geographic range, habitat in which the parasite is transmitted (salt, fresh, or brackish water), degree of host specificity, site of infection in the grebe host, and intermediate, paratenic, and grebe hosts of each parasite species. A list of the known prey species of each grebe species is also in the data base. Separate records for each species of parasite and grebe have been created and manipulated using the program FileMaker Pro (Claris Corp. 1994). This is available on the web at <web<http://www.ummz.lsa.umich.edu/curators/rwstorer/>

Pogue (1994) has written "A person who uses jargon where simple English would do is trying to underscore the listener's ignorance." I would go further and believe that it is a duty of scientists to reach as wide a readership as possible by presenting the results of their research in simple yet precise terms. Jargon is too often used to make simple ideas sound complex and thus can be a form of elitism or, more simply, snobbery. Simplicity and directness of expression are especially important in writing up the results of interdisciplinary work such as this. I have therefore tried to use technical terms as seldom as possible and to define many of them. On the other hand, because this work may well be read by some for whom English is not the first language, I have tried, where possible, to use scientific names of species and names based on scientific names for higher categories.

The Scientific and English names of grebes. Over the last century, there have been many changes in the scientific names of grebes, especially at the generic level. The following list of scientific names is based on Storer (1979). Thus, *Tachybaptus* is the currently accepted generic name for the species that has been referred to as *Podiceps ruficollis* in most of the parasitological literature, and *T. novaehollandiae* is the currently accepted name for Australasian populations that were formerly included in *T. ruficollis*. *Poliocephalus,* which formerly included the species now in *Tachybaptus,* is currently used only for the Hoary-headed Grebe and the New Zealand Dabchick, once also included in *Podiceps*. The Short-winged Grebe, *Rollandia microptera* was formerly placed in the monotypic genus *Centropelma,* and the monotypic genus *Limnodytes* proposed for *Tachybaptus dominicus* has not been accepted. The name, *Podiceps caspicus,* was widely used for *P. nigricollis* until it was placed on the Official Index of Rejected and Invalid Names by the International Commission on Zoological Nomenclature (I. C. Z. N., 1955). *Aechmophorus clarkii* was not recognized as a distinct species until 1985, hence records for *A. occidentalis* presumably may include some from *A. clarkii*. The Great Grebe (formerly *Podiceps major*) has recently been placed in a monotypic genus (*Podicephorus*) by Bocheński (1994), which I consider valid, although I do not accept Bocheński's proposal to elevate *Podiceps grisegena holboellii* to specific rank for reasons I have presented elsewhere (Storer 1996). The generic name, *Colymbus,* was used for the loons (*Gavia*) in the Old World literature and for the grebes (*Podiceps*) in that of the New World until 1972, when *Colymbus* was placed on the Official Index of Rejected and Invalid Generic Names in Zoology by the International Commission on Zoological Nomenclature (I. C. Z. N., 1972). It is therefore difficult or impossible to know which group was meant by *Colymbus* before that date unless a specific name was given with it. The only specific name which is in the synonymy of both grebes and loons is *arctica* (*-us*) which has been applied to the Horned Grebe, as well as to the Arctic Loon. Although the generic name used with it usually indicates to which group the bird belongs, when listed as a species of *Colymbus,* it cannot always identified to order. In some instances in which *Colymbus* was used without a specific name, I have tried to determine whether it referred to *Podiceps* or *Gavia*. This has meant listing a few species known from loons but not from grebes. These are bracketed like other species not known to occur naturally in grebes.

Where two English names are given in the following list, the first is the one used in this paper.

Aechmophorus clarkii (Lawrence 1885), Clark's Grebe.
Aechmophorus occidentalis (Lawrence 1885), Western Grebe.
Podicephorus major (Boddaert 1783), Great Grebe.
Podiceps auritus (Linnaeus 1758), Horned or (in the Old World) Slavonian Grebe.
Podiceps cristatus (Linnaeus 1758), Great Crested Grebe.
Podiceps gallardoi Rumboll 1974, Hooded Grebe.
Podiceps grisegena (Boddaert 1783), Red-necked Grebe. Holboell's Grebe has been used widely for the North American subspecies.
Podiceps nigricollis Brehm 1831, Eared or (in the Old World) Black-necked Grebe.
Podiceps occipitalis Garnot 1826, Silvery Grebe.
Podiceps taczanowskii Berlepsch & Stolzmann 1894, Puna Grebe.
Podilymbus gigas Griscom 1929, Atitlán Grebe or Giant Pied-billed Grebe.
Podilymbus podiceps (Linnaeus 1758), Pied-billed Grebe.
Poliocephalus poliocephalus (Jardine & Selby 1827), Hoary-headed Grebe.
Poliocephalus rufopectus (Gray 1843), New Zealand Dabchick.
Rollandia microptera (Gould 1868), Short-winged or Flight-

less Grebe.
Rollandia rolland (Quoy & Gaimard 1824), White-tufted or Rolland's grebe.
Tachybaptus dominicus (Linnaeus 1766), Least Grebe.
Tachybaptus novaehollandiae (Stephens 1826), Australian Little Grebe.
Tachybaptus pelzelnii (Hartlaub 1861), Madagascar Little Grebe.
Tachybaptus ruficollis (Pallas 1764), Little Grebe or Dabchick.
Tachybaptus rufolavatus (Delacour 1932), Alaotra Little Grebe.

THE PARASITIC WORMS OR HELMINTHS OF GREBES

The parasitic worms or helminths of grebes belong to four major groups of animals: the Digenea (digenes) or flukes, the Cestoda or tapeworms, the Acanthocephala or spiny-headed worms, and the Nematoda or roundworms. Almost all of these parasites have complex life histories involving one or more intermediate hosts. Some also are found in paratenic hosts. With very rare exceptions, grebes are the definitive host. Exceptions include the Little (*Tachybaptus ruficollis*), Great Crested (*Podiceps cristatus*), Red-necked (*P. grisegena*), and Eared (*P. nigricollis*) grebes, which have been reported to contain larvae of the trematode, *Strigea falconis,* whose definitive hosts are diurnal birds of prey. The Little Grebe has also been found to contain larvae of the nematode, *Gnathostoma spinigerum,* whose usual definitive hosts are dogs and cats, but which is occasionally found in humans.

In recent years extensive work on the systematics of helminths has appeared, but much still remains to be done. Some 30,000 species of helminths have been described, yet several thousand probably remain to be named. Many of the described species are known from a single collection and/or from poorly preserved material, so some may prove to be synonymous with better-known species. In addition, the life cycles of many species remain to be worked out.

Because of the importance of helminth parasites to the health of humans and their domestic and game animals, far more time and money has been expended on their study than on that of wild animals and birds. In the case of grebes and other fish-eating birds, much of the work on parasites has been done in eastern Europe, where there are important fresh-water fisheries. The results of many of these studies have been published in Slavic languages. The inability of many parasitologists outside of this region to read Slavic languages and the difficulty of obtaining some of these publications have resulted in less than optimal communication between parasitologists in different regions, and all too often Western parasitologists have ignored much of the important work done in the former Soviet Republics. Poor communication also has made it difficult or impossible to assemble types and other materials needed for thorough revisions of "difficult" groups.

Progress in the study of grebe parasites also has been hampered by the difficulty of keeping these birds in captivity (Callegari 1956), which increases the problems of making experimental studies of the parasites' life cycles.

THE DIGENES (DIGENETIC TREMATODES) OF GREBES

The digenetic trematodes, (Phylum Platyhelminthes, Subclass Trematoda, Infraclass Digenea) are parasitic flatworms, the adults of which have a complete digestive system but lack an epidermis. The names come from the Latin roots *di-* or two and *gen-* birth or origin which refer to the complex life cycle involving one or more intermediate hosts and Greek word *trema* or hole, which refers to the cavity in the adhesive organs. The group is large, consisting of some 200 families, 1,800 genera, and more than 8,000 named species. Of the groups of trematodes, members of only one, the Infraclass Digenea or digenes, are known to parasitize grebes. Almost all digenes are endoparasites of vertebrates and unlike the other two groups of trematodes, have complex life cycles involving three or four larval stages and from two to four hosts (Shoop 1988).

Although they vary enormously in size and shape, adults of these flukes are typically flat and have two disc-like suckers, one around the mouth and one on the ventral side of the body. Members of a few groups have a single sucker (*e.g.,* the true monostomes) or lack suckers (*e.g.,* the cyclocoelids). Members of the family Echinostomidae, in addition to the suckers, have a collar of spines at the anterior end of the body.

Almost all digenes are hermaphroditic. (The Schistosomatidae are a notable exception.) Copulation (mutual or not) or self-fertilization may occur. In most species, the eggs pass from the definitive host into the water. There, the first larval stage, a miracidium, hatches from the capsule, (or in the case of the Plagiorchioids, the egg is eaten and the miracidia hatch in the first intermediate host). The miracidia are minute, ovoid objects, which swim by means of cilia. Free-living ones penetrate the first intermediate host, a mollusk, almost always a snail, in which asexual reproduction in larval stages (mother and daughter sporocysts and/or mother and daughter redia), occurs. Like the adults, redia have digestive tracts and feed actively on the host's tissue. This asexual reproduction results in the production of large numbers of the next larval stage, the cercaria. Although some cercariae encyst on objects (often the shell or operculum of a snail, or at least in some notocotylids, plants) in the water, most have tails and swim about until they are eaten by or penetrate a second intermediate host. This is often a crustacean, insect larva, or fish, but sometimes a second, or the same snail, or in the case of *Strigea falconis* and some of its relatives, an amphibian larva. In the second intermediate host the cercaria encysts and transforms into a metacercaria, which is like a small copy of the adult, except that the reproductive systems are incompletely developed or in an immature state. The definitive host acquires the parasite by eating the second intermediate host or an object on which the cercariae encyst. Most adult flukes are found in the host's digestive tract or appendages to it, such as the lungs, liver, bile duct, and Bursa of Fabricius, but some are found in the blood vessels, coelom, air sacs, head cavities, or eyes. Strigeids have the most complex life cycle of the digenes, which involves a special (mesocercarial) larval stage, and a third intermediate host (See Fig. 2, p. 15.).

Approximately one half of the species of digenes reported from grebes appear to be specialists in that group (*i.e.*, grebes are the usual or only known definitive hosts). Of these specialists more than half are reported from only one species of grebe and many, known only from the original description, may prove synonymous with other species. It is therefore likely that the number of grebe specialists will prove smaller than now recognized when the species of parasites are better known. It is also likely that when more collections of the parasites are made, fewer species will be known to parasitize single species of grebes.

The classification to the family level used here is based on that of Brooks *et al.* (1993). Unless otherwise indicated, the species of grebes known to be hosts are taken from Yamaguti (1958, 1971) and the life cycles from Yamaguti (1975) and references therein. McDonald (1969) was useful in providing lists of intermediate hosts. Pages for citations in the last are given because the work is not indexed.

Subclass Trematoda: Infraclass Digenea (Digenes)

Order Paramphistomiformes

Family Notocotylidae

Notocotylus attenuatus (Rudolphi, 1809)

In *Podiceps cristatus* (Kibakin 1965), *P. auritus, P. grisegena* (Gallimore 1964). Generalist (1), rare in grebes. In intestines and caeca. FW. Cosmopolitan. Intermed. hosts, **mollusks**: GASTROPODS, Bithyniidae (*Bithynia* [*"Bulimus"*]), Lymnaeidae (*Galba, Lymnaea*), Planorbidae (*Planorbarius* [*"Coretus"*], report from *Planorbis rotundatus* considered an error [Yamaguti 1975]). Cercaria from snails encyst on objects in water, including shells and opercula of snails. Birds obtain parasites by ingesting objects to which cysts are attached.

Paramonostomum bucephalae Yamaguti, 1935

In *Podiceps grisegena* (McDonald 1969:259), *P. nigricollis.* (Kostadinova *et al.* 1988). Caeca. FW? Eurasia. Intermed. hosts, snails? then, encyst on objects in water? Common in anatids, rare in grebes (2).

Paramonostomum caeci Smith & Hickman, 1983

In *Poliocephalus poliocephalus* (Smith & Hickman, 1983). Caeca. BW. Austr. Intermed. hosts, **mollusks:** GASTROPODS, Hydrobiidae (*Coxiella*) then encyst on shells of snails and other objects (Smith & Hickman, 1983). Definitive hosts presumably become infected by eating snails on which larvae have become encysted. Generalist, also in waterfowl (1).

Paramonostomum elongatum Yamaguti, 1934

In *Tachybaptus ruficollis* (Mirzoeva 1980). Caecum? FW? Eurasia. Intermed. hosts, snails? then encyst on objects in water? Also in swans. Presumably a generalist (?1).

Order Echinostomiformes

Superfamily Cyclocoeloidea

Family Cyclocoelidae

**Corpopyrum jaenschi* (Johnston & Simpson, 1940)

In *Tachybaptus novaehollandiae, Poliocephalus poliocephalus* (Yamaguti 1958). Abdominal air sacs. FW. Austr. Intermed. hosts, **mollusks:** GASTROPODS, Planorbidae (*Ameria* Johnston & Simpson, 1940). Grebe specialist (3). Sometimes placed in genus *Harrahium.*

Tracheophilus cymbium (Diesing, 1850)

In *Podilymbus podiceps.* Oronasal passages. FW. Asia, N. Amer., S. Amer. Single intermed. hosts, **mollusks:** GASTROPODS, Bullinidae (*Indoplanorbis exustus*), Planorbidae (*Helisoma trivolvis,* [also in *Planorbis corneus* and *P. planorbis* Szidat 1932]) in which first two larval stages are found. Common in anatids, one record each in *Podilymbus podiceps, Capella,* and *Himantopus* (2). Life cycle in Stunkard (1934) and (as *"Typhlocoelum cymbium,"* Sreekumaran & Peter 1973). Also, under what is probably a synonym, *T. sisowi* (*fide* S. C. Schell, pers. comm.), by Szidat (1932) and McDonald (1969:127-128). *Cymbium* is a noun in apposition *fide* Yamaguti (1971).

Transcoelum oculeum (Kossack, 1911)

In *Podiceps cristatus* (Kostadinova *et al.* 1988). In "trachea." FW. Eurasia. Intermed. hosts, **mollusks:** GASTROPODS, Lymnaeidae (*Galba, Radix*), Planorbidae (*Planorbis*), then encyst in visceral cavity of same snail. Common in infraorbital sinus of gruiformes and charadriiformes, rare in grebes (2). Described in *Hyptiasmus.*

Typhlocoelum cucumerinum (Rudolphi, 1809)

In *Podiceps cristatus* (McDonald 1969:125-127). Trachea, bronchi, lungs, nasal cavity, esophagus. FW? Eurasia, Afr., N. Amer., Austr. Intermed. hosts? Specialist in anatids, rare in grebes (2).

Superfamily Psilostomoidea

Family Psilostomidae

Psilochasmus oxyurus (Creplin, 1825)

In *Poliocephalus poliocephalus,* (Mawson *et al.* 1986). Small intestine. SW. Eurasia, N. Afr., Austr. Intermed. hosts, **mollusks**: GASTROPODS, Bithyniidae (*Bithynia*), Hydrobiidae (*Hydrobia, Littoridina*), cercariae encyst on inner surface of shell or in mantle tissue of same or other snails. Definitive hosts become infected by eating snails. Common in anatids, rare in grebes (2). Life cycle in Szidat (1957) and Wišniewski (1958).

[*Psilostomum* sp. "A" S. J. Smith, 1981.

In *Poliocephalus poliocephalus,* (Mawson *et al.* 1986).]

[*Psilostomum* sp. "B" S. J. Smith, 1981.]

In *Poliocephalus poliocephalus,* (Mawson *et al.* 1986).]

Family Cathaemasiidae

Ribeiroia ondatrae (Price, 1931)

In *Podilymbus podiceps, Podiceps auritus, P. grisegena, Aechmophorus occidentalis* (Gallimore 1964). In esophagus, proventriculus. FW. N. Amer., Afr. Intermed. hosts, **mollusks:** GASTROPODS, Planorbidae (*Helisoma*), then lateral line canal, nasal cavities and beneath scales of FW **fishes:** Centrarchidae (*Ambloplites rupestris, Lepomis gibbosus, L. macrochirus, Micropterus dolomieu*), Ictaluridae (*Ameiurus*), Percidae (*Perca flavescens*) (Beaver 1939b). Generalist. (1), also in loons. *R. thomasi* (McMullen, 1938), is a synonym for the cercaria.

Superfamily Echinostomoidea

Family Philophthalmidae

In most eye flukes of the nominate genus, the hermaphroditic adult lives in the orbital cavity. The eggs produced contain miracidia which hatch upon reaching water. These larvae inject a preformed redia into a snail in which as many as three generations of redia may be produced. These in turn give off cercariae, which on leaving the snail, encyst on hard surfaces including items the definitive avian host may eat. Warmth in the bird's throat stimulates the metacercaria to leave the cyst and migrate by way of the lacrymal duct to the bird's orbit where they develop into the adult (Nollen & Kanev 1995).

Philophthalmus lucipetus Rudolphi, 1819; Braun, 1902

In *Podiceps cristatus* (as *P. oshmarini* Shigin 1957). Conjunctival sac. FW. Eur. Intermed. hosts, snails? Generalist (1). Nollen & Kanev (1995) present a summary of information on the biology and taxonomy of this genus but point out that much more work on the taxonomy is needed.

Family Echinostomidae

Echinochasmus amphibolus Kotlán, 1922

In *Podiceps grisegena, P. nigricollis* (Vaidova 1965). FW? Intestines? Europe. Intermed. hosts? Generalist (1).

**Echinochasmus coaxatus* Dietz, 1909

In *Tachybaptus ruficollis* (McDonald 1969:149-150), *Podiceps grisegena, P. cristatus, P. nigricollis.* Small intestine. FW. Eurasia. Intermed. hosts, **mollusks:** GASTROPODS, Bithyniidae (*Bithynia tentaculata*), Lymnaeidae (*Lymnaea auricularia*), metacercaria encyst on FW mollusks (McDonald *loc. cit.*), which are eaten by FW **fishes:** Cobitidae (*Cobitis taenia*), Cyprinidae (*Abramis* [*"Blicca"*] *bjoerkna*), *Alburnus alburnus, Rutilus rutilus, Scardinius erythrophthalmus, Tinca tinca*), Gasterosteidae (*Pungitius pungitius*), Gobiidae (*Gobius, Neogobius*), Percidae (*Perca fluviatilis*), and experimentally in *Alburnus, Rutilus,* and Poeciliidae (*Poecilia* [*"Lebistes"*] *reticulata*). Grebe specialist (3), also in ducks and *Ciconia.*

**Echinochasmus colymbi* Oshmarin, 1950

In *Podiceps grisegena* (type host), *Tachybaptus ruficollis, P. cristatus, P. nigricollis* (Čanković *et al.* 1983b). Small intestine, cloaca, and Bursa of Fabricius. FW? Eurasia. Intermed. hosts, snails? then? Grebe specialist (3). Sometimes placed in genus *Episthmium. Episthmium mathevossianae* Shakhtakhtinskaya, 1957 is a synonym *fide* McDonald (1969:154).

**Echinochasmus dietzevi* Issaitschikoff, 1927

In *Tachybaptus ruficollis, Podiceps nigricollis* (Brglez 1976), *P. grisegena* (Yamaguti 1958), *P. cristatus* (Kostadinova *et al.* 1988). Small intestine. FW? Eurasia. Intermed. hosts, snails? then? Grebe specialist (3), rare in anatids and *Larus.*

**Echinochasmus donaldsoni* Beaver, 1941

In *Podilymbus podiceps* (type host, type and paratype in USNPC Nos. 036723.00 & 036724.00), *Podiceps auritus, P. nigricollis, Aechmophorus occidentalis* (Gallimore 1964). Grebe specialist (3). Duodenum. FW. N. Amer. Intermed. hosts, **mollusks:** GASTROPODS, Amnicolidae (*Amnicola*), cercariae from snails taken by respiratory currents into the mouth and pharynx of a variety of FW **fishes:** Amiidae (*Amia calva*), Cyprinidae (*Notropis* spp., *Phoxinus* [*"Pfrille"*] *neogaeus*), Gasterosteidae (*Culaea* [*"Eucalia"*] *inconstans*), and experimentally in Centrarchidae (*Lepomis macrochirus* [*"Helioperca incisor"*]), Ictaluridae (*Ameiurus nebulosus*), Percidae (*Perca flavescens*), Poeciliidae (*Poecilia* [*"Lebistes"*] *reticulata, Poecilia* [*"Mollienesia"*] *latipinna*), Umbridae (*Umbra limi*), encysting on the gill filaments (Beaver 1941).

**Echinochasmus fotedari* Chishti & Mir, 1989

In *Tachybaptus ruficollis,* type and only known host (?5). Intestines. FW? Asia (Kashmir). Intermed. hosts, snails? then?

Echinochasmus japonicus Tanabe, 1926

In *Tachybaptus ruficollis* (McDonald 1969:150-151). Intestine. FW. Asia. Intermed. hosts, **mollusks:** GASTROPODS, Bithyniidae (*Bithynia "Bulimus" striatulus, Hydrobioides "Parafossarulus" manchouricus*) then **fishes:** Bagridae (*Fluvidraco*), Cobitidae (*Misgurnus*), Cyprinidae (*Abbottina, Acheilognathus, Brevigobio, Carassius, Gnathopogon, Hemibarbus, Ischikauia, Opsarichthys, Pseudorasbora, Pseudoperilamphus, Rhodeus, Sarcocheilichthys, Zacco*), Eleotridae (*Mogurnda, Odontobutis*), Gobiidae (*Chaenogobius*), *Percidae* (*Coreoperca* [*"Coresperca"*]), Plecoglossidae (*Plecoglossus*), Pleuronectidae (*Limanda*), Salangidae (*Salangichthys, Salanx*), Siluridae (*Silurus*); **amphibians:** ANURANS, tadpoles, Ranidae (*Rana*). Generalist (1).

Echinochasmus mordax (Loos, 1899)

In *Podiceps auritus,* (Bittner & Sprehn 1928), *P. cristatus.* (Kostadinova *et al.* 1988). Small intestine. FW? Eurasia. Afr. Intermed. hosts, snails? then? Generalist (1).

**Echinochasmus podicepensis* (Bhardwaj, 1962)

In *Tachybaptus ruficollis.* FW? Asia (India). Midgut. FW. Intermed. hosts? Type and only known host (?5). Described in *Monilifer.*

Echinochasmus ruficapensis Verma, 1935

In *Tachybaptus ruficollis.* Intestine. FW? Eurasia. Intermed. hosts, snails? then? Also in *Nycticorax.* ?Generalist (?1).

Echinochasmus spinulosus (Rudolphi, 1809)

In *Tachybaptus ruficollis,* (Čanković *et al.* 1983b), *Podiceps auritus, P. grisegena, P. cristatus, P. nigricollis.* Small intestine. FW? Eurasia. Intermed. hosts, snails? then? Also in *Gavia, Alca,* and *Cepphus,* and occasionally ducks. Reports of this parasite from *Alca* and *Cepphus* suggests that anadromous fishes may act as second intermediate hosts. Generalist (1). Sometimes placed in genus *Monilifer* or considered a synonym of *Mesorchis spinosa* (*e.g.,* by McDonald 1969:159).

**Echinochasmus squamatus* Mendheim, 1940

In *Podiceps cristatus.* Type and only known host (?5). Intestines. FW? Eur. Intermed. hosts, snails? then?

Echinoparyphium aconiatum Dietz, 1909

In *Podiceps auritus* (McDonald 1969:163-164). Small intestine. FW. Eurasia, N. Amer. Intermed. hosts, **mollusks:** GASTROPODS, Bithyniidae (*Bithynia*), Lymnaeidae (*Lymnaea*); PELECYPODS, Pisidiidae (*Sphaerium*), then these plus GASTROPODS, Physidae (*Physa*), Planorbidae (*Anisus, Planorbarius*), Viviparidae (*Viviparus*), and, experimentally, in **amphibians:** ANURANS, Ranidae (*Rana*). Generalist (1), rare in grebes.

[*Echinoparyphium baculus* (Diesing, 1850)

Yamaguti (1958, 1971) lists *"Colymbus"* as a definitive host. This presumably refers to a loon or loons because McDonald (1969:165) lists *Gavia arctica* and *G. stellata,* but no grebes as such hosts.]

[*Echinoparyphium recurvatum* (Linstow, 1873)

In *Podiceps* sp. (McDonald 1969:172-175). Intestines. FW. Cosmopolitan. Intermed. hosts, **mollusks:** GASTROPODS, Bullinidae (*Bulinus*), Lymnaeidae (*Galba, Lymnaea,* [incl *"Bulimnea"*], *Radix*), Physidae (*Physa*), Planorbidae (*Anisus, Disculifer* [*"Spiralina"*], *Gyraulus, Planorbis*), Valvatidae (*Valvata*), Viviparidae (*Viviparus* [*"Paludina"*]); then GASTROPODS, Bullinidae (*Bulinus, Indoplanorbis*), Dreissenidae (*Dreissena*), Lymnaeidae (*Lymnaea*), Physidae (*Physa*), Planorbidae (*Anisus, Bathyomphala, Gyraulus, Planorbarius, Planorbis*), Valvatidae (*Valvata*); PELECYPODS, Pisiidae (*Musculina* [*"Musculinium"*], *Pisidium, Sphaerium* incl. *"Cyclas"*); **amphibians:** ANURANS, Bufonidae (*Bufo*), Hylidae (*Hyla*), Pelobatidae (*Pelobates*), Ranidae (*Rana*) hosts from McDonald (1969: *loc. cit.*). Generalist (1), common in waterfowl and shorebirds, rare or incidental in grebes (report needs checking).]

Echinostoma echiniferum (La Valette, 1855)

In *Tachybaptus ruficollis* (*"Podiceps minor"* Yamaguti 1971.) Intestines? FW. Europe. Intermed. hosts, cercaria in **mollusks:** GASTROPODS, Viviparidae

(*Viviparus* [*"Paludina"*] *viviparus* Yamaguti 1971), then? Generalist (1), rare in grebes, also in shorebirds and ducks.

*_Echinostoma intermedium_ (Mehlis in Creplin, 1846)

Podiceps grisegena, P. cristatus (Bittner & Sprehn 1928). Intestine. FW? Presumably Germany. Intermed. hosts? Grebe specialist (3). Possibly a synonym of a better-known species.

Echinostoma revolutum (Froelich, 1802)

In *Tachybaptus ruficollis* (McDonald 1969:192, as *E. paraulum*), *Podiceps cristatus* (Nicoll 1923), *P. auritus, P. grisegena, P. nigricollis* (Gallimore 1964). Intestines, caeca. FW. Cosmopolitan. Intermed. hosts, **mollusks:** GASTROPODS, Lymnaeidae (*Galba* [*"Fossaria"*], *Lymnaea, Pseudosuccinea, Stagnicola*), then these and other GASTROPODS Bithyniidae (*Bithynia*), Bullinidae (*Bulinus, Indoplanorbis*), Physidae (*Aplexa, Physa*), Planorbidae (*Ameria,* [*"Amerianna"*] *Anisus, Bathyomphalus, Biomphalaria, Gyraulus, Helisoma, Planorbarius, Planorbis*), Pleuroceridae (*Semisulcospira*), Valvatidae (*Valvata*), Viviparidae (*Viviparus* [*"Paludina"*]), PELECYPODS Cardiidae (*Cardium*), Corbiculidae (*Corbiculina*), Pisidiidae (*Musculium, Pisidium, Sphaerium*); and **flatworms**: TURBELLARIANS, Planariidae (*Planaria*), then **?crustaceans:** ?AMPHIPODS, ?Gammaridae (*Eogammarus* [*"Anisogammarus"*] *locustoides*); **amphibians:** ANURANS, tadpoles. Bufonidae (*Bufo*), Ranidae (*Rana*), and **reptiles**; FW. TURTLES (Kanev 1994), hosts from McDonald (1969:193-196). Life cycle in Kanev (1994). Generalist (1). (Little host specificity, Beaver 1937, but anatids "natural definitive hosts in Australia" *fide* Johnston & Angel 1941.) *E. paraulum* Dietz, 1909, and *E. trivolvis* (Cort, 1914) are synonyms *fide* Kanev (1994) *contra* Huffman & Fried (1990) who use *E. trivolvis* for this species.

[*Echinostoma* sp.

In *Poliocephalus poliocephalus.* (Mawson *et al.* 1986.) FW? Austr. Intermed. hosts?]

*_Episthmium wernickii_ (Marco del Pont, 1926)

In *Rollandia rolland* [*"Podiciper americanos"*]. Type and only known host (?5). FW? Intestine. S. Amer. Intermed. hosts, snails? then? Described in *Echinostoma.*

*_Euparyphium pindchi_ Khan & Chishti, 1984

In *Tachybaptus ruficollis* [*"Podiceps roficollis capensis"*]. Type and only known host (?5). Intestine. FW? Asia (Kashmir). Intermed. hosts?

Hypoderaeum conoideum (Bloch, 1782)

In *Tachybaptus ruficollis* (Vaidova 1965). Excretory system. FW. Eurasia, Afr., N. Amer. Intermed. hosts, **mollusks:** GASTROPODS, Lymnaeidae (*Lymnaea*), Planorbidae (*Planorbarius, Planorbis*), then encyst in these plus Physidae (*Physa*), Planorbidae (*Anisus, Gyraulus*), Viviparidae (*Viviparus*), PELECYPODS. Pisidiidae (*Pisidium, Sphaerium*), and **amphibians:** ANURANS, Ranidae ("frog tadpoles"). Generalist (1), common in anatids.

Hypoderaeum gnedini Bashkirova, 1941

In *Podiceps cristatus* (McDonald 1969:204), *Tachybaptus ruficollis* (Vaidova 1978). Intestines. FW? Eurasia. Intermed. hosts, snails? then ? Common in anatids (2), rare in grebes and *Fulica.* Citation in Yamaguti (1971) to *"Colymbus"* as a definitive host presumably refers to *P. cristatus.*

*_Mesorchis argentinensis_ (Sutton, Lunaschi & Topa, 1982)

In *Rollandia rolland, Podicephorus major.* Type host not specified. Grebe specialist (3). Intestines and caeca? FW? S. Amer. (Argentina) Intermed. hosts, snails? then, fishes?

Mesorchis denticulatus (Rudolphi, 1802)

In *Podicephorus major* (Torres *et al.* 1982, voucher in USNPC No. 076820.00), *P. nigricollis* (Kostadinova *et al.* 1988), *P. auritus, P. cristatus, P. grisegena* (McDonald 1969:156-157). Small intestine and caeca. FW, SW? Eurasia, N. Amer., S. Amer., Afr. Intermed. hosts, **mollusks:** GASTROPODS, Hydrobiidae (*Hydrobia ulvae*), then encyst on gills of **fishes:** Atherinidae (*Atherina pontica*), Cyprinidae (*Leuciscus idus*), Cyprinodontidae (*Fundulus heteroclitus* [FW, SW]), Gasterosteidae (*Gasterosteus aculeatus, Pungitius pungitius*), Gobiidae (*Pomatoschistus microps*). Generalist (1), also in *Gavia arctica.* Køie (1986) found differences between the adults and cercaria described by Nasir *et al.* (1968) and those found in her life-cycle study and in adults of *M. denticulatus* "as described from *Larus* spp. from northern Europe . . . indicating that the life cycle described by Nasir *et al.* (1968) belongs to another species of *Mesorchis.*" She also presented reasons for moving the species with avian definitive hosts formerly placed in *Stephanoprora* to *Mesorchis* and considered *M. pseudoechinatus* a synonym of *M. denticulatus.* Her conclusions are followed here. Yamaguti (1958:648 & 899; 1971:548) lists *"Colymbus,"* but not *Podiceps* or *Gavia* as definitive hosts for this species. McDonald (*loc. cit.*) lists species of both *Podiceps* and *Gavia,* so Yamaguti's references might refer to either or both.

*_Mesorchis podicipei_ (Etchegoin & Martorelli, 1997)

In *Podicephorus major* type and only known host (5). Small intestine. SW. S. Amer. (Argentina) (Etchegoin & Martorelli, 1997). Intermed. hosts? Described in *Stephanoprora,* but I follow Køie's (1986) recommendation to place all species of *Stephanoprora* with avian definitive hosts in *Mesorchis.*

Mesorchis polycestus Dietz, 1909

In *Aechmophorus occidentalis* (Matthias 1963). Small Intestine. FW?, SW? Eurasia, N. Amer. Intermed. hosts, snails? then fishes? Generalist (1).

Mesorchis spinosus (Odhner, 1910)

In *Podiceps cristatus* (Yamaguti 1971). Intestines. FW? Eur., Afr., N. Amer. Intermed. hosts, snails? Generalist (1). *Distoma spinulosum* Rudolphi, 1809, and *Stephanoprora gilberti,* Ward, 1917, are considered synonyms. The species has also been placed in the genera *Distoma, Echinochasmus, Echinostoma, Stephanoprora,* and *Monilifer.* (McDonald 1969:159).

*_Microparyphium ruficollis_ (Ishii, 1935)

In *Tachybaptus ruficollis.* Small intestine. FW? Asia (Japan). Intermed. hosts, snails? then? Type and only known host (?5). Described in the genus *Echinochasmus.*

[*Microparyphium shigini* Gubanov, 1954

In *Podiceps nigricollis* (as "[*Echinochasmus*] *schigini*" Vaidova 1978). Large intestine and Bursa of Fabricius. SW? Eur. Intermed. hosts? As this species was previously known only from *Uria lomvia,* the record from *P. nigricollis* requires checking.]

*_Nephrostomum robustum_ Pérez Vigueras, 1944

In *Tachybaptus dominicus.* Type and only known host (?5). Intestines. FW? N. Amer. (Cuba). Intermed. hosts, snails? then?

Paryphostomum radiatum (Dujardin, 1845)

In *Podiceps cristatus* (Chiriac 1965). Intestines. FW. Eurasia, Afr., Austr. Intermed. hosts, **mollusks:** GASTROPODS, Lymnaeidae (*Lymnaea, Radix*), Planorbidae (*Ameria* [*"Amerianna"*]), then FW **fishes:** Adrianichthyidae (*Oryzias*), Bovichtidae (*Pseudaphritis*), CYPRINIDAE (*Barbus, Carassius*), PLOTOSIDAE (*Tandanus*), POECILIIDAE (*Gambusia, Phalloceros*), **amphibians:** ANURANS MYOBATRACHIDAE (*Pseudophryne*). Cormorant specialist, rare in grebes (2).

[*Paryphostomum* sp.

In *Podicephorus major* (Torres *et al.* 1982). Gastrointestinal tract. SW? S. Am. Intermed. hosts?]

Patagifer bilobus (Rudolphi, 1819)

In *Tachybaptus ruficollis* (McDonald 1969:156). Small intestine. FW. Eurasia, Afr., S. Amer., Austr. Intermed. hosts, **mollusks:** GASTROPODS, PLANORBIDAE (*Planorbis planorbis*), then, experimentally, in LYMNAEIDAE (*Lymnaea* spp.). Specialist in Threskiornithidae, rare in grebes, *Anser*, and *Fulica* (2).

**Patagifer parvispinosus* Yamaguti, 1933

In *T. ruficollis*. Type and only known host (?5). Small intestine. FW? Eurasia. Intermed. hosts, snails, then?

[*Patagifer* sp.

In *Tachybaptus ruficollis*. Small intestine. juv. (Čanković 1983b).]

[*Patagifer* sp.

In *Poliocephalus poliocephalus* (Spines only. Mawson *et al.* 1986.) Austr.]

**Petasiger australis* Johnston & Angel, 1941

In *Tachybaptus novaehollandiae, Poliocephalus poliocephalus, Podiceps cristatus,* (Mawson *et al.* 1986.). Intestine. FW. Austr. Intermed. hosts, **mollusks:** GASTROPODS, PLANORBIDAE (*Ameria* ["*Amerianna*"] *pyramidata, A. pectorosa*), then snail or **fishes:** at least experimentally in ADRIANICHTHYIDAE (*Oryzias latipes*), CYPRINIDAE (*Carassius auratus*), ELEOTRIDAE (*Philypnodon grandiceps*), KUHLIIDAE, (*Nannoperca australis*), PLOTOSIDAE, (*Tandanus tandanus*), POECILIIDAE (*Gambusia affinis*), RETROPINNIDAE (*Retropinna semoni*). Grebe specialist (3). (Johnston & Angel 1941.)

[*Petasiger caribbensis* Nassi, 1980

Definitive host unknown, suggested to be *Podilymbus podiceps antillarum* by Nassi, 1980. FW. N. Amer., West Indies, (Guadeloupe). Intermed. hosts, **mollusks:** GASTROPODS, PLANORBIDAE (*Biomphalaria glabrata*), then FW **fishes:** CICHLIDAE (*Tilapia mossambica*) (introduced), and experimentlally also in POECILIIDAE (*Gambusia affinis, Poecilia reticulata, Xiphophorus helleri*).]

**Petasiger chandleri* Abdel-Malek, 1952

In *Podilymbus podiceps*. Type and only known host (?5). Duodenum. FW. N. Amer. Intermed. hosts, **mollusks:** GASTROPODS, PLANORBIDAE (*Helisoma corpulentum, H. pilsbryi*) then **fishes:** experimentally in CYPRINIDAE (*Notemigonus chrysoleucas, Notropis* sp., *Phoxinus* ["*Chrosomus*"] *eos, Semotilus atromaculatus*), CYPRINODONTIDAE (*Fundulus* sp.), ICTALURIDAE (*Ameiurus nebulosus*), PERCIDAE (*Etheostoma* ["*Poecilichthys*"] *exile, Perca flavescens* (Abdel-Malek 1953).

Petasiger coronatus Mendheim, 1940

In *Podiceps cristatus* (Vaidova 1978). Intestine. FW? Eur. Intermed. hosts, snails? then **annelids:** OLIGOCHAETES (in soil), GLOSSOSCOLECIDAE (*Criodrilus*). Also in *Anas* and *Gavia*. ?Generalist (?1). Has been placed in *Echinochasmus*.

**Petasiger floridus* Premvati, 1968

In *Podilymbus podiceps*. Type and only known host (?5). Intestine. FW? N. Amer. Intermed. hosts? Holotype and paratype USNPC Nos. 071150.00 & 071151.00.

**Petasiger grandivesicularis* (Ishii, 1935)

In *Tachybaptus ruficollis* (Kostadinova *et al.* 1988). Type and only known host (?5). Small intestine. FW? Eurasia. Intermed. hosts, **mollusks:** GASTROPODS, PLANORBIDAE (*Planorbis planorbis*), then FW **fishes:** experimentally in CYPRINIDAE (*Puntius nigrofasciatus, P. pentazona, P. tetrazona*) POECIIDAE (*Poecilia* ["*Lebistes*"] *reticulata, Xiphophorus helleri*)

**Petasiger lobatus* Yamaguti, 1933

In *Tachybaptus ruficollis*, type host, *Podiceps nigricollis* and *P grisegena* (Zhatkanbaeva 1971). Grebe specialist (3). Small intestine. FW? Asia. Intermed. hosts, snails? then? *P. brevicauda* Ishii is a synonym *fide* Yamaguti (1971).

**Petasiger megacanthum* Kotlán, 1922

In *Podiceps cristatus*, type host, *P. grisegena* (Yamaguti 1958), *Tachybaptus ruficollis* (Čanković *et al.* 1983b). *P. auritus* (McDonald 1969:211-212), *P. nigricollis* (Kibakin 1965). Small intestine. FW? Eurasia. Intermed. hosts, **mollusks:** GASTROPODS, PLANORBIDAE (*Helisoma*), then fishes: experimentally in CENTRARCHIDAE (*Ambloplites, Lepomis*), CYPRINIDAE (*Notropis*), ICTALURIDAE (*Ictalurus*), PERCIDAE (*Perca*), POECILIIDAE (*Poecilia* ["*Lebistes*"] *reticulata*), UMBRIDAE (*Umbra*). Grebe specialist (3).

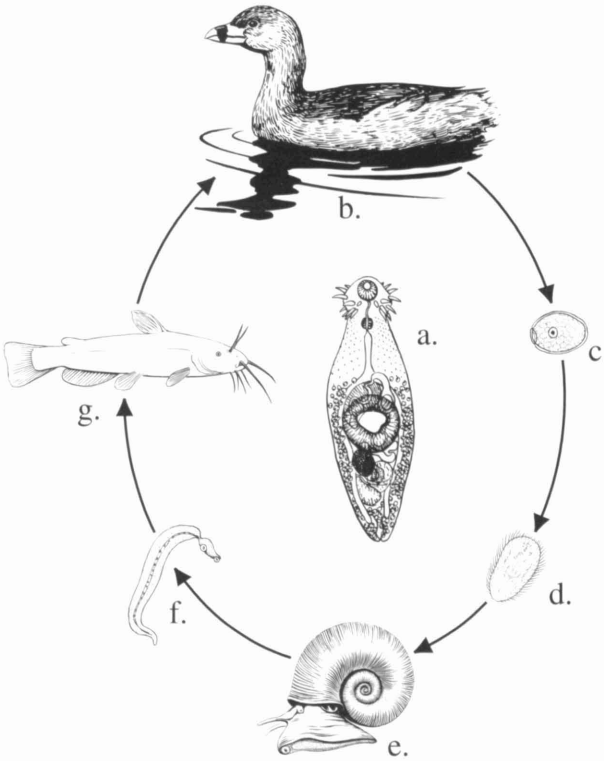

Figure 1. The life-cycle of the digene, *Petasiger nitidus*. The adult parasite (a) inhabits the intestine of the definitive host (b), here, a Pied-billed Grebe, from which the egg (c) is passed into the water. A miracidium (d) hatches from the egg and penetrates the first intermediate host (e), a planorbid snail. Cercariae (f) produced asexually in the snail are given off and are eaten by the second intermediate host (g), here, a bullhead (*Ictalurus*), where they encyst until eaten by the definitive host, in which they develop into the adult parasite. Original drawing by John Megahan from sources listed in the acknowledgments (p. 65).

**Petasiger neocomensis* Fuhrmann, 1928

In *Podiceps grisegena, P. cristatus* (Yamaguti 1958), *Tachybaptus ruficollis, P. nigricollis* (Čanković *et al.* 1983b), *P. auritus* (Leonov *et al.* 1965). Small intestine. FW? Eurasia. Intermed. hosts, snails? then? Grebe specialist (3). *Petasiger* is a masculine noun, hence Yamaguti's (1958), spelling of the specific name is correct *fide* H. D. Cameron (*in litt.*).

**Petasiger nitidus* Linton, 1928

In *Podilymbus podiceps* (Beaver 1939a), *Podiceps auritus* type host, *P. cristatus* (Vaidova 1965), *P. grisegena* (voucher in USNPC No. 079337.00), *P. nigricollis, Aechmophorus occidentalis* (Gallimore 1964). Intestines. FW. Eur., N. Amer. Intermed. hosts, **mollusks:** GASTROPODS, Planorbidae (*Helisoma antrosum, H. campanulatum*), then **fishes:** (at least experimentally in Centrarchidae (*Ambloplites rupestris, Lepomis macrochirus* [*"pallidus"*]), Cyprinidae (*Notropis hudsonius*), Ictaluridae (*Ameiurus nebulosus*), Percidae (*Perca flavescens*), Poeciliidae (*Poecilia* [*"Lebistes"*] *reticulata*), Umbridae (*Umbra limi.*) (Beaver 1939a). Grebe specialist (3). The life cycle is shown in Figure 1, p. 11.

**Petasiger novemdecim* Lutz, 1928

In *Tachybaptus dominicus* (voucher in USNPC No. 072003.00) type and only known host (4). FW. Intestines. S. Amer. Intermed. hosts, **mollusks:** GASTROPODS, Planorbidae (*Biomphalaria glabrata*), then **fishes:** Poeciliidae (*Poecilia* [*"Lebistes"*] *reticulata*). Life cycle in Nasir *et al.* 1972.

**Petasiger oschmarini* Kostadinova & Gibson, 1998

In *Podiceps grisegena* (type host) and *P. auritus.* FW. Duodenum. Asia (Kamchatka). Intermed. hosts? Grebe specialist (3). These specimens were formerly referred to *P. neocomensis,* but other records of that species from *P. grisegena* were not discussed.

**Petasiger pseudoneocomensis* Bravo-Hollis, 1971

In *Aechmophorus occidentalis* (paratype in USNPC No. 075526.00). Type and only known host (?5). FW?, SW? Intestines. Mexico. Intermed. hosts, snails? then fishes? (For ending of specific name, see under *P. neocomensis.*)

**Petasiger pungens* (Linstow, 1894)

In *"Podiceps fluviatilis"* (=*Tachybaptus ruficollis*). Type host. *"Colymbus nigricans"* (=*Podiceps auritus*), *P. cristatus.* (Yamaguti 1958; Kostadinova *et al.* 1988.) FW? Small intestine. Eur. Intermed. hosts, snails? then? Grebe specialist (3). (*P. australis* Johnston & Angel, 1941; *P. brevicauda* Ishii, 1935; *P. chandleri* Abdel-Malek, 1952; *P. floridus* Premvati, 1968; *P. grandivesicularis* [Ishii, 1935]; *P. lobatus* Yamaguti, 1933; *P. megacanthum* Kotlán, 1922; *P. neocomensis* Fuhrmann, 1928; *P. nitidus* Linton, 1928; and *Patagifer parvispinosus*, Yamaguti, 1933; are considered synonyms by Nasir *et al.* 1972, but most not by Nassi 1980 or Kostadinova *et al.* 1998. While it may be that combining of a few species in this group will prove desirable, the recent papers by Nassi 1980 and Kostadinova *et al.* (1998) suggest that the mass lumping of Nasir *et al.* [1972] is unwarranted.)

**Petasiger skrjabini* Bashkirova, 1941

In *Podiceps grisegena* (McDonald 1969:212-213), *P. cristatus.* Small intestine. FW? Eurasia. Intermed. hosts, snails? then? ?Grebe specialist. (?3), rare in ducks.

**Petasiger soochowensis* Ku, Chiu, Li & Chu, 1977

In *Tachybaptus ruficollis.* Type and only known host (?5). Small intestine. FW? Asia. Intermed. hosts, snails? then?

**Petasiger tientsinensis* Ku, Chiu, Li & Chu, 1977

In *Tachybaptus ruficollis.* Type and only known host (?5). Small intestine. FW? Asia. Intermed. hosts, snails? then?

Petasiger variospinosus (Odhner, 1910) Yamaguti, 1933

In *Podiceps cristatus* (Yamaguti 1971). In intestines. FW? Africa, Asia, Azerbaizhan. Intermed. hosts, snails? then? ?Specialist in cormorants and anhingas, rare in grebes (?2).

[Echinostomidae sp.?

In *Poliocephalus poliocephalus* (Mawson *et al.* 1986). Austr.]

Order Strigeiformes

Superfamily Clinostomoidea

Family Clinostomidae

Clinostomum complanatum (Rudolphi, 1814)

In *Podiceps cristatus* (Vaidova 1978). Buccal cavity and esophagus? FW. Cosmopolitan. Intermed. hosts, **mollusks**: GASTROPODS, Lymnaeidae (*Helisoma antrosum, H. campanulatum*), then FW **fishes:** Aphredoderidae (*Aphredoderus sayanus*), Blenniidae (*Blennius*), Centrarchidae (*Lepomis* [*"Eupomotis"*] *gibbosus, Micropterus dolomieu*), Cyprinidae (*Abramis* [*"Vimba"*] *vimba, Acheilognathus intermedia, Aspius aspius, Barbus, Carassius carassius, Cyprinus, Gobio gobio, Leuciscus* [*"Idus"*] *idus, Pseudogobio esocinus, Rutilus rutilus, Varicorhinus*), Percidae (*Perca fluviatilis, Stizostedion*), and experimentally in Cichlidae (*Tilapia*) and Poeciliidae (*Poecilia* [*"Lebistes"*] *reticulata*). Heron specialist, rare in grebes, also in other ciconiiforms, cormorants, pelicans, *Gallinula, Larus,* and man (2).

**Clinostomum pusillum* Lutz, 1928

In *Tachybaptus dominicus.* Type and only known host (?5). Buccal cavity and esophagus? FW?, S. Amer. Intermed. hosts, snails? then FW fishes?

Superfamily Schistosomatoidea

Family Schistosomatidae

Members of this family are unusual among digenes in that there is a single intermediate host (a FW or SW snail), the larvae penetrate the definitive host directly. The species are dioecious or functionally dioecious (gonochoristic). In the definitive host, the adults mature in the circulatory system within the liver before moving to other parts of the circulatory system.

Bilharziella polonica (Kowalewski, 1895)

In *Podiceps grisegena, P. cristatus* (Sulgostowska 1963). Hepatic portal, intestinal, and mesenteric veins. FW. Eurasia, N. Amer. Intermed. hosts, **mollusks:** GASTROPODS, Bithyniidae (*Bithynia* [*"Bulimus"*] *spiralina, Physopsis*), Planorbidae (*Anisus, Bathyomphalus, Planorbis, Planorbarius* [experimentally]). Specialist on waterfowl (2), uncommon in grebes, also in ciconiiformes, charadriiformes, and *Fulica.* For details of life cycle, see Khalifa (1972). Yamaguti (1971: 479) lists *"Colymbus"* and *Podiceps* as definitive hosts. McDonald (1969:96) lists *Podiceps* but not *Gavia,* so Yamaguti's record presumably refers to *Podiceps.*

Dendritobilharzia pulverulenta (Braun, 1901)

In *Podiceps nigricollis* (Gallimore 1964). Arterial system, most frequently in aorta and femoral arteries (Vande Vusse 1980). FW. Cosmopolitan, except Austr. Development direct? Waterfowl specialist, rare or occasional in *Fulica,* pelicans, and loons. Apparently rare in grebes (2). *D. anatinarum* Cheatum, 1941 is a synonym (Vande Vusse *op. cit.*)

**Gigantobilharzia elongata* (Brackett, 1940)

In *Podilymbus podiceps.* Type and only known definitive host (?5). In small veins of intestinal wall. FW. N. Amer. Intermed. hosts, **mollusks:** GASTROPODS, Planorbidae (*Gyraulus*). Cercariae (*Cercaria elongata*) penetrate skin of host. For information on life cycle, see Grodhaus (1965).

Gigantobilharzia monocotylea Szidat, 1930

In *Podiceps cristatus.* (Yamaguti 1958.) Intestinal veins. FW. Eurasia Intermed. hosts, snails? Generalist (1), also in *Anas* and *Larus.*

[*Trichobilharzia* sp.

One in *Podiceps nigricollis;* did not mature (0) (Stock 1985). FW. N. Amer. Intermed. hosts, snails?]

[Schistosomatidae sp.

Podiceps cristatus. (Mawson *et al.* 1986.) Intestinal veins? FW? Austr. Intermed. hosts, snails?]

Superfamily Strigeoidea

Family Cyathocotylidae

Cyathocotyle prussica Muehling, 1896

In *Tachybaptus ruficollis. Podiceps cristatus* (Čanković *et al.* 1984). Intestines. FW. Eurasia. Intermed. hosts, snails? then infective larvae in **amphibians:** ANURANS Ranidae (*Rana esculenta*). Common in ducks, rare in grebes (2).

**Cyathocotyle teganuma* Ishii, 1935

In *Tachybaptus ruficollis* type host, *Podiceps grisegena, P. cristatus* (Sudarikov *et al.* 1973). Grebe specialist (3). Small intestine. FW? Eurasia. Intermed. hosts, snails? then? Placed in *Duboisia* by Sudarikov *et al.* (1973).

[*Paracoenogonimus ovatus* Katsurada, 1914

In *Podiceps cristatus.* (Berlin Zoo. Odening 1963). Small intestine. FW. Asia. Intermed. hosts, **mollusks:** GASTROPODS, Bithyniidae (*Bithynia*), Viviparidae (*Viviparus*), then **fishes**: Acipenseridae (*Acipenser*), Cottidae (*Cottus*), Cyprinidae (*Abramis* [incl. *"Blicca,"*] *Alburnus, Aspius, Barbus, Carassius, Cyprinus, Leuciscus* [incl. *"Idus,"*] *Pelecus, Rhodeus, Rutilus* [*"Leuciscus rutilus"*], *Scardinius, Tinca, Vimba*), Esocidae (*Esox lucius*), Gasterosteidae (*Pungitius*), Lotidae (*Lota*), Osmeridae (*Osmerus*), Percidae (*Acerina, Perca, Stizostedion* [*"Lucioperca"*]), Salmonidae (*Coregonus, Salmo, Thymallus*), Siluridae (*Silurus*). Parasite of carnivores and birds of prey, rare in other birds, incidental in grebes (0).]

Family Diplostomidae

Diplostomum capsulare (Diesing, 1858) Bittner & Sprehn, 1928

In *Podiceps auritus, P. nigricollis* (Bittner & Sprehn, 1928). In muscles. FW? Presumably Europe. Also in *Nycticorax, Botaurus,* and *Crex*. Generalist (1). Possibly a synonym of a better-known species.

Diplostomum gavium (Guberlet, 1922) of Hughes, 1929

In *Podiceps auritus* (Leonov *et al.* 1965), *Tachybaptus ruficollis, P. grisegena, P. cristatus, P. nigricollis* (Čanković *et al.* 1983a). Stomach, duodenum, small intestine. FW? Eurasia, N. Amer. Intermed. hosts, snails? then fishes? Loon specialist (2), apparently uncommon in grebes. Some records of this species may refer to *Tylodelphys podicipina*. Yamaguti (1971) lists *"Colymbus"* and *"Podiceps"* as definitive hosts but *"Colymbus* [=*Gavia*] *immer"* and *"Colymbus* [=*Podiceps*] *grisegena"* in his his earlier (1958) work. Yamaguti's later reference to *Podiceps* probably comes from a report of the three other species of grebes cited by McDonald (1969:49). *Diplostomum gavium* of Dubois & Rausch, 1950 is a synonym of *Tylodelphys immer* Dubois 1961, which is apparently confined to loons.

Diplostomum mergi Dubois, 1932

In *Podiceps cristatus, P. grisegena* (Vaidova 1978). Small intestine, duodenum. FW. Eurasia. Intermed. hosts, **mollusks:** GASTROPODS, Lymnaeidae (*Lymnaea*), then in eye lens of FW **fishes:** Cyprinidae (*Abramis, Alburnus, Aspius, Carassius, Cyprinus, Pelecus, Rutilus, Scardinius*), Gobiidae (*Gobius*), Percidae (*Stizostedion* [*"Lucioperca"*]), Siluridae (*Parasilurus*). Common in anatids, rare or incidental in grebes and shorebirds (2).

[*Diplostomum scheuringi* (Hughes, 1929)

In *Podilymbus podiceps* (experimentally). Natural host unknown. Host specificity category (0). Intestine? FW. N. Amer. Intermed. hosts, **mollusks:** GASTROPODS, Planorbidae, then in vitreous chamber of FW **fishes:** Centrarchidae, Cyprinidae, Esocidae, Gadidae, Ictaluridae, Percidae, Percopsidae, Poeciliidae (*Gambusia affinis,* experimentally), Salmonidae, Siluridae, and **amphibians:** URODELES, Plethodontidae (*Pseudotriton*), Salamandridae (*Notophthalmus*). Holotype, paratype, and voucher in USNPC Nos. 078410.00, 078411.00, 078412.00.

Diplostomum spathaceum (Rudolphi, 1819)

In *Podiceps grisegena* (Zhatkanbaeva 1965), *P. cristatus* (Dubois 1970). Intestines. FW. Eurasia, N. Afr. Intermed. hosts, **mollusks:** GASTROPODS, Bithyniidae (*Bithynia*), Lymnaeidae (*Lymnaea, Radix*), then **fishes:** Acipenseridae (*Acipenser*), Anguillidae (*Anguilla*), Catostomidae (*Catostomus*), Cichlidae (*Cichlasoma*), Clupeidae (*Alosa, Caspialosa, Clupea*), Cobitidae (*Cobitis*), Cottidae (*Cottus*), Balitoridae (*Nemachilus*), Centrarchidae (*Lepomis macrochirus*), Cyprinidae (*Abramis* [incl, *"Blicca"*], *Alburnus, Aspius, Barbus, Capeotobrama, Carassius, Chalcalburnus, Chondrostoma, Cyprinus, Diptychus, Gila, Gobio, Lavinia, Leucaspius, Leuciscus* [incl. *"Idus,"*] *Orthodon, Pelecus, Phoxinus, Rutilus, Rhodeus, Scardinius, Schizothorax, Tinca, Triplophysa* [*"Diplophysa"*], *Vimba*), Esocidae (*Esox*), Gadidae (*Gadus*), Gasterosteidae (*Gasterosteus, Pungitius* [incl. *"Pygosteus"*)], Gobiidae (*Gobius*), Ictaluridae (*Ameiurus melas*), Lotidae (*Lota*), Osmeridae (*Osmerus*), Percidae (*Gymnocephalus* [*"Acerina"*], *Perca, Stizostedion* [*"Lucioperca"*], *Zingel* [*"Aspro"*]), Petromyzontidae (*Lampetra, Petromyzon*), Pleuronectidae (*Pleuronectes*), Salmonidae (*Coregonus, Salmo, Salvelinus, Stenodus, Thymallus*), Siluridae (*Parasilurus, Silurus*), Syngnathidae (*Nerophis, Syngnathus* [*"Siphonostoma"*]). Commonest in larids, apparently rare in grebes (2). Reports from marine birds (*Alca torda, Sula bassana, Spheniscus demersus*) may result from ingesting anadromous fishes infected in fresh water, but confirmation needed. Dubois (1970) considers the North American form *flexicaudum* (Cort & Brooks, 1928) and the Australian form *murrayense* (Johnston & Cleland, 1938) subspecies of *D. spathaceum.* Yamaguti (1971:649) reports this species from *"Colymbus"* and *Podiceps* and McDonald (1969:56) only from *Podiceps,* so both of Yamaguti's records presumably refer to *Podiceps.* The name *Cercaria helvetica,* has been used for the metacercaria.

Histeromorpha triloba (Rudolphi, 1819)

In *Tachybaptus ruficollis* (Vaidova 1965). The length of the intestines, most numerous anteriorly. FW. Eurasia, N. & S. Amer., Austr. Intermed. hosts, **mollusks:** GASTROPODS, Planorbidae (*Gyraulus hirsutus*), then in musculature of FW **fishes:** Atherinidae (*Atherina pontica*), Catostomidae (*Catostomus commersoni, C.* [*occidentalis*] *humboldtianus*), Cyprinidae (*Abramis* [*"Blicca"*] *bjoerkna, Carassius auratus, Leuciscus* [*"Idus"*] *idus, Notemigonus chrysoleucas, Pimephales notatus, Rutilus rutilus, Tinca tinca*), Esocidae (*Esox lucius*), Ictaluridae (*Ameiurus melas, A. nebulosus*). Life cycle in Hugghins (1954a,b). Common in cormorants (2), rare in grebes.

**Posthodiplostomum podicipitis* (Yamaguti, 1939)

In *Tachybaptus ruficollis.* Type and only known host (4). Small intestine Japan. FW. Intermed. hosts, **mollusks:** GASTROPODS, Physidae (*Physa*), then FW **fishes:** Adrianichthyidae (*Oryzias latipes.* experimentally, Yamaguti 1979). Described in the genus *Ornithodiplostomum,* in which Dubois (1970) places it.

[*Tylodelphys clavata* (v. Nordmann, 1832)

In *Podiceps cristatus,* experimentally (Niewiadomska

1964), Intestines? Eur. For a discussion of life cycle and systematics, also see Yamaguti, (1975).]

**Tylodelphys conifera* (Mehlis, 1846)

In *Tachybaptus ruficollis* (Vaidova 1978), *Podiceps auritus* (Leonov *et al.* 1965), *P. grisegena, P. cristatus, P. nigricollis.* Intestines, most numerous in anterior and mid sections. FW. Eur. Intermed. hosts, **mollusks:** GASTROPODS, Lymnaeidae (*Lymnaea*) then the eyes of FW **fishes:** especially *Perca fluviatilis.* Also in other Percidae (*Gymnocephalus* [*"Acerina"*] *cernuus, Stizostedion lucioperca*), Cyprinidae (*Abramis brama, A.* [*"Blicca"*] *bjoerkna, Carassius carassius, Rhodeus sericeus, Rutilus rutilus, Scardinus erythrophthalmus, Tinca tinca*), Esocidae (*Esox lucius*), Gobiidae (*Gobius gobius*), Lotidae (*Lota lota*), Salmonidae (*Coregonus albula*). Grebe specialist (3). The genus has been considered a subgenus of *Diplostomum* and is variously spelled *Thylodelphus, Thyelodelphys,* and *Tylodelphus* in the literature.

Tylodelphys elongata (Lutz,1928)

In *Tachybaptus dominicus*, type host, *Podilymbus podiceps* (Dubois & Macko 1972). ?Grebe specialist (?3). Intestines. FW. N. & S. Amer., Cuba. Intermed. hosts, snails? then fishes or amphibians? Also in *Jabiru.* Originally described in *Alaria. Diplostomum brevisegmentatum* Pérez Vigueras, 1944 is considered a synonym by Dubois (1970).

Tylodelphys excavata (Rudolphi, 1803)

In *Tachybaptus ruficollis, Podiceps cristatus, P. nigricollis,* (Čanković *et al.* 1983a). Small intestine, most numerous in anterior section. FW. Europe. Intermed. hosts, **mollusks:** GASTROPODS, Planorbidae (*Planorbis, Planorbarius* [*"Coretus"*] *corneus*), then in cerebrospinal system, brain, and subdural space in rachidial canal of **amphibians**: ANURANS, Bufonidae (*Bufo bufo*), Discoglossidae (*Bombina bombina*), Ranidae (*Rana esculenta, R. ridibundus, R. temporaria*). Generalist, most common in Ciconiiformes (1). Dubois (1966) considers earlier records of this parasite from grebes to apply to *T. podicipina.*

[*Tylodelphys glossoides* (Dubois, 1928)

"Colymbus asiaticus" was listed in Yamaguti (1971) as definitive host of *Glossodiplostomum* (=*Tylodelphys*) *glossoides.* Because I cannot find *"asiaticus"* in the recent synonymies of specific names of either *Gavia* or *Podiceps,* I think this is a *lapsus calami* for the loon, *C. arcticus.* (Although according to Ogilvie-Grant 1898, the specific name, *"arcticus,"* was sometimes applied to the Horned Grebe (*Podiceps auritus*) in the last century, in Europe, where the parasite was described, *Colymbus* was the generic name used for the loons at the time *glossoides* was described.)]

**Tylodelphys podicipina* Kozicka & Niewiadomska, 1960

In *Podiceps auritus, P. grisegena* (voucher in USNPC No. 079338.00, from Alberta), *P. cristatus, P. nigricollis* (Kozicka *et al.* 1960), *Aechmophorus occidentalis* (Gallimore 1964). Small intestine. FW. Eur., N. Amer., Austr. Intermed. hosts, snails? then metacercaria in vitreous humor of eyes of FW **fishes**: Lotidae (*Lota lota*), Percidae (*Gymnocephalus* [*"Acerina"*] *cernuus, Perca fluviatilis*). Grebe specialist (3). Dubois (1970) considers examples from *P. grisegena holboellii* in Alaska to represent a distinct subspecies, *T. p. robrauschi* Dubois, 1969 (paratype USNPC No. 071346.00). Reports of *Diplostomum gavium* Guberlet, 1922, from grebes may represent this species.

Family Strigeidae

Apatemon gracilis (Rudolphi, 1819)

In *Tachybaptus ruficollis* (as *A. g. minor* Yamaguti, 1933; McDonald 1969:75), *Podiceps auritus, P. grisegena, P. nigricollis* (also voucher USNPC No. 079339.00), *Aechmophorus occidentalis* (Gallimore 1964). Duodenum and anterior part of small intestine. FW. Eurasia, N. & S. Amer., Cuba. Intermed. hosts, **mollusks:** GASTROPODS, Acroloxidae (*Acroloxus*), Bithyniidae (*Bithynia*), Lymnaeidae (*Lymnaea*), Planorbidae (*Anisus, Helisoma, Planorbarius, Segmentina*), Physidae (*Physa*), Viviparidae (*Viviparus*), then **annelids:** OLIGOCHAETES sp. LEECHES, Erpobdellidae (*Erpobdella* [*"Herpobdella"*]), Glossiphoniidae (*Glossiphonia* incl. *"Boreobdella," Helobdella, Hemiclepsis, Theromyzon*), Hirudinidae (*Haemopis*), Piscicolidae (*Piscicola*); **mollusks:** GASTROPODS, Lymnaeidae (*Lymnaea*); **insects:** ODONATA, Anisoptera, Aeschnidae (*Aeschna*); or **fishes:** Balitoridae (*Nemacheilus*), Cottidae (*Cottus*), Cyprinidae (*Acheilognathus, Culter, Gobio, Hemiculter*), Gasterosteidae (*Culaea*), Gobiidae (*Proterorhinus*), Eleotridae (*Mogurnda*). Specialist in anatids, locally common in grebes`(2). McDonald (1969:68-75) lists 10 subspecies of this parasite from waterfowl and the above snail, insects, and fishes as second intermediate hosts. Yamaguti (1975) lists only leeches as second intermediate hosts.

Apharyngostrigea cornu (Zeder, 1800)

In *Podiceps cristatus* (Vaidova 1978). Intestine. FW? Eurasia, N. Amer., Cuba. Intermed. hosts? Specialist in herons, rare in grebes (2).

Cotylurus cornutus (Rudolphi, 1808)

In *Tachybaptus ruficollis* (Vaidova 1978). Small intestine. FW, BW. Eurasia, N. Amer, S. Amer., Afr. Intermed. hosts, **mollusks:** GASTROPODS, Bithyniidae (*Bithynia*), Lymnaeidae (*Lymnaea*), Physidae (*Physa*), Planorbidae (*Anisus, Planorbarius, Planorbis*), then, **mollusks:** GASTROPODS, Lymnaeidae (*Lymnaea*), Planorbidae (*Planorbarius, Planorbis*), Viviparidae (*Viviparus*) and **annelids:** LEECHES, Glossiphoniidae (*Glossiphonia,* incl. *"Boreobdella," Helobdella, Hemiclepsis*), Haemopidae (*Haemopis* [*"Haemopsis"*]), Piscicolidae (*Piscicola*), Salifidae (*Salifa, "Herpobdella"*). Generalist, common in anatids and charadriiform birds, rare in grebes (1).

[*Cotylurus flabelliformis* (Faust, 1917)

In *Podilymbus podiceps* (experimentally, Campbell 1973). Intestines. FW. N. Amer. Intermed. hosts, **mollusks:** GASTROPODS, Lymnaeidae (*Lymnaea*), Planorbidae (*Helisoma*), Physidae (*Physa*), then the same or other snail. Common parasite of ducks. (0)]

[*Cotylurus* sp.

In *Podiceps grisegena* (Stock 1985). Small intestine. FW. N. Amer. "Generalist."]

Ichthyocotylurus erraticus (Rudolphi, 1809)

In *Podiceps auritus, P. grisegena, P. nigricollis, Aechmophorus occidentalis.* (Gallimore 1964). Intestines. FW. Eurasia, N. Amer. Intermed. hosts, **mollusks:** GASTROPODS, Lymnaeidae (*Lymnaea stagnatilis*) and experimentally in Valvatidae (*Valvata*), then **fishes**: Salmonidae (*Coregonus, Oncorhynchus, Salmo, Salvelinus, Thymallus*). Infection in birds presumably may also be obtained from salmonids in salt-water habitats. Generalist (1). also in *Spheniscus, Uria,* and *"Colymbus"* (Yamaguti 1958). Yamaguti (1971:676) lists *Gavia* as well. McDonald (1969:80) lists species of both *Podiceps* and *Gavia,* so it is not clear to which (or both) Yamaguti's references belong. Niewiadomska (1971) presents reasons for recognizing *Ichthyocotylurus* as distinct from *Cotylurus.*

Ichthyocotylurus pileatus (Rudolphi, 1802)

In *Podiceps cristatus* (as *"Strigea variegata"* Nicoll [1923]), *Aechmophorus occidentalis* (Gallimore 1964), and as *"C.*

medius” (Matthias 1963). Small intestine. FW, SW? Eurasia, N. Amer. Miracidia presumably penetrate FW **mollusks:** GASTROPODS. Metacercaria from the snails (*Tetracotyle pileata,* synonyms = *T. ovata* and *T. variegata*) are found in the peritoneum, swim bladder, ovaries, pericardial cavity, and eye muscles of a variety of FW **fishes:** Cyprinidae (*Alburnus alburnus, Abramis* [*“Blicca”*] *bjoerkna, A. brama, Carassius auratus, Phoxinus phoxinus, Rutilus rutilus, Tinca tinca*), Esocidae (*Esox lucius*), Osmeridae (*Osmerus eperlanus*), Percidae (*Gymnocephalus* [*“Acerina”*] *cernuus, Perca fluviatilis*). Metacercaria of this or *C. platycephalus* found in other FW **fishes:** Cottidae (*Cottus gobio*), Cyprinidae (*Abramis balleus, Carassius auratus, Cyprinus carpio, Gobio gobio, Leuciscus* [*“Idus”*] *idus, Leuciscus* [*“Squalius”*] *cephalus, L.* [*“S”*] *leuciscus, Scardinius erythrophthalmus, Tinca tinca, Vimba* [*“Abramus”*] *vimba*), Percidae (*Stizostedion* [*“Lucioperca”*] *lucioperca, S.* [*“L.”*] *volgensis*), Salmonidae (*Coregonus lavaretus*). Data from Yamaguti (1971). Specialist in Lari and Alcae, rare in grebes (2). Marine birds such as alcids may obtain this parasite from anadromous fishes such as smelt (*Osmerus*) or salmonids (*Salvelinus*). *Cotylurus medius* Dubois & Rausch, 1950 considered a synonym by Yamaguti 1958; and Dubois 1968).

Ichthyocotylurus platycephalus (Creplin, 1825) Szidat, 1928
In *Tachybaptus ruficollis* (Vaidova 1965a), *Podiceps cristatus* (Yamaguti 1958), *P. auritus, P. nigricollis, Aechmophorus occidentalis* (Gallimore 1964). Bursa Fabricii (most frequently [Gallimore 1964]), cloaca, rectum, large intestine. FW? Eurasia. Intermed. hosts? and see above under *I. pileatus.* Generalist (1), common in Lari, also in *Alca, Cepphus, Gavia,* etc. (McDonald 1969:83-84). Dubois (1968) divided *“C.”* (= *I.*) *platycephalus* into two subspecies, *C. p. communis,* from *Larus argentatus* in N. Amer. and the nominate race from Eurasia.

Parastrigea robusta Szidat, 1928
In *Tachybaptus ruficollis* (Vaidova 1965). Small intestine. Eurasia. N. Amer. FW. Intermed. hosts, **mollusks:** GASTROPODS, Planorbidae (*Anisus, Bathyomphalus, Gyraulus, Planorbis, Segmentina*), then **amphibians**: ANURANS, Bufonidae (*Bufo bufo*), Ranidae (*Rana arvalis, R. temporaria*) Yamaguti 1971, 1975. Common in anatids, rare in grebes (2).

Schwartzitrema pandubi (Pande, 1939)
In *Tachybaptus novaehollandiae, Poliocephalus poliocephalus, Podiceps cristatus* (Mawson *et al.* 1986). Small intestine. FW? Asia (India), Austr. Intermed. hosts, snails? then? Specialist in cormorants and anhingas, apparently less common in grebes (2). Has been placed in *Apatemon* and *Pseudostrigea. S. nigericus* and *Apatemon truonis* are synonyms.

Strigea falconis Szidat, 1928
In *Tachybaptus ruficollis, Podiceps cristatus* (as *Tetracotyle ardea,* Vaidova, 1965), *P. grisegena, P. nigricollis* (McDonald 1969:88-89). FW. This widespread (Eurasia, Afr., N. Amer.) parasite of diurnal raptors appears to be the only trematode for which grebes have been reported as intermediate hosts. **mollusks:** GASTROPODS, Planorbidae (*Anisus, Bathyomphalus, Planorbarius, Planorbis, Segmentina*) act as first intermediate hosts. Cercaria released by the snails penetrate the skin of **amphibians**: ANURANS, (tadpoles and adults). These are eaten by **reptiles:** SNAKES, **birds:** (of at least 13 orders), and **mammals**. In these third intermediate hosts, the metacercaria, known as *Tetracotyle ardea* (Matare, 1910), become encysted in the muscles and subcutaneous tissues. When the third intermediate host is eaten by a definitive host, the metacercaria are freed and become attached to the wall of the anterior and middle sections of the small intestine, where they mature. The adults of this parasite are specialists on diurnal birds of prey, including falcons and at least 13 genera of hawks. The systematics of this trematode has been complicated by the naming of several “subspecies” from definitive hosts of different groups of non-falconiform birds. Whether the differences among these forms are the result of development in different groups of birds or are based on genetic differences remains to be proved. This account is based on the nominate form. For further details see Dubois (1968). Yamaguti (1971:685) lists *“Colymbus”* and *Podiceps* as intermediate hosts of this species. McDonald (1969 *loc. cit.*) lists species of *Podiceps* but none of *Gavia,* hence Yamaguti’s records presumably refer only to species of grebes. The life cycle is shown in Figure 2.

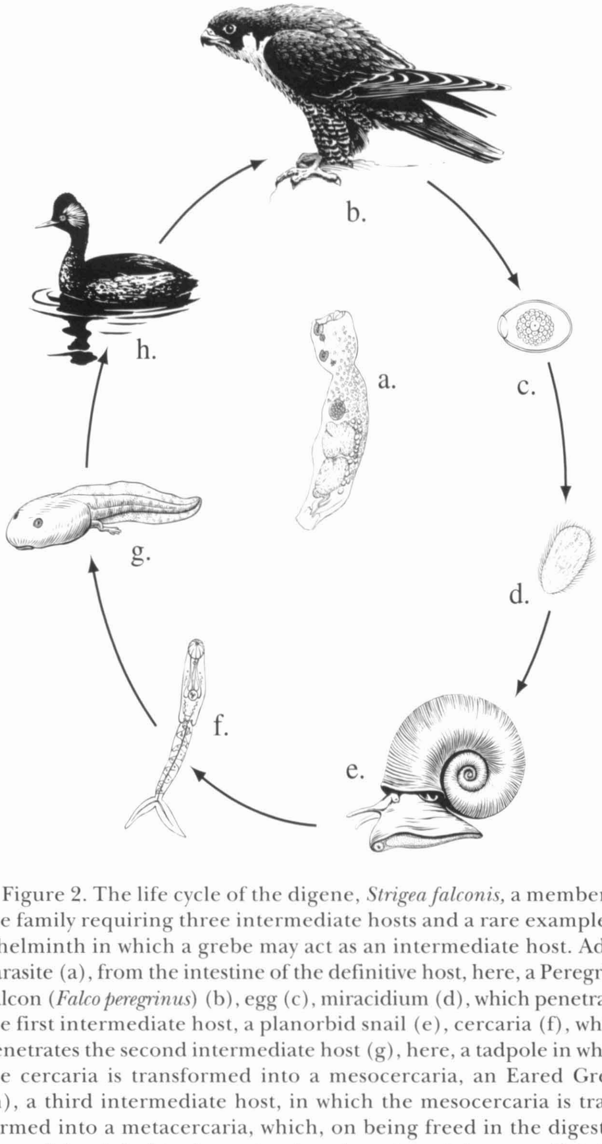

Figure 2. The life cycle of the digene, *Strigea falconis,* a member of the family requiring three intermediate hosts and a rare example of a helminth in which a grebe may act as an intermediate host. Adult parasite (a), from the intestine of the definitive host, here, a Peregrine Falcon (*Falco peregrinus*) (b), egg (c), miracidium (d), which penetrates the first intermediate host, a planorbid snail (e), cercaria (f), which penetrates the second intermediate host (g), here, a tadpole in which the cercaria is transformed into a mesocercaria, an Eared Grebe (h), a third intermediate host, in which the mesocercaria is transformed into a metacercaria, which, on being freed in the digestive tract of the definitive host, develops into the adult worm. Original drawing by John Megahan from sources listed in the acknowledgments (p. 65).

[Immature strigeids, did not mature
In *P. grisegena*. (Stock 1985.)]

Order Opisthorchiformes

Family Opisthorchidae

Metorchis orientalis Tanabe, 1920

In *Tachybaptus ruficollis*. Gall bladder. FW. Asia. Intermed. hosts, **mollusks:** GASTROPODS, Bithyniidae (*Bithynia* [*"Bulimus"*]), then **fishes:** Cyprinidae (*Pseudogobius, Pseudorasbora, Sarcocheilichthys*). Summaries in Yamaguti (1958), McDonald (1969:350-351). Generalist (1).

Metorchis xanthosomus (Creplin, 1846)

In *Tachybaptus ruficollis* (Čanković *et al.* 1984). Gall bladder. FW?, SW? Europe. Intermed. hosts, **mollusks:** GASTROPODS, Bithyniidae (*Bithynia*), then **fishes:** Balitoridae (*Nemachilus*), Cobitidae (*Cobitis*), Cyprinidae (*Phoxinus, Rhodeus*), Gasterosteidae (*Pungitius* [*"Gasterosteus"*] *pungitius*). Data from McDonald (1969:353). Generalist (1), also in loons, alcids, and other groups.

**Plotnikovia podilymbae* (Olsen, 1938)

In *Podilymbus podiceps* (type and paratype in USNPC Nos. 009057.00, 009058.00). Type and only known host (?5). Mesentery. FW? N. Amer. Intermed. hosts? Described in genus *Diasia*.

Family Heterophyidae

[*Apophallus muehlingi* (Jägerskiöld, 1889)

Yamaguti (1971:621) lists *"Colymbus"* as a definitive host. This presumably refers to Yamaguti's earlier (1958:702, 869) listing of *"Colymbus septentrionalis"* (=*Gavia stellata*). Another species of *Apophallus* (*A. brevis*) has been reported from loons, but not from grebes.]

Cercarioides humbargari (Park, 1936)

In *Podiceps grisegena* (Gallimore 1964, voucher in USNPC No. 072810.00), *Aechmophorus occidentalis* (USNPC No. 072815.00). Not previously reported from this species. Small intestine. SW. N. Amer. Intermed. hosts snails? then **fishes**: Atherinidae (*Leuresthes tenuis*). Generalist (1), also in larids and alcids. Described in *Galactosomum*.

Cryptocotyle concava (Creplin, 1825)

In *Podiceps cristatus, P. nigricollis* (Nicoll 1923), *P. grisegena* (McDonald 1969:332-333). Intestines. FW?, SW? Eur. Intermed. hosts, **mollusks:** GASTROPODS, Amnicolidae (*Amnicola*), then **fishes:** Atherinidae (*Atherina*), Bothidae (*Scophthalmus* [*"Rhombus"*]), Carangidae (*Trachurus trachurus*), Catostomidae (*Catostomus*), Gasterosteidae (*Gasterosteus*), Gobiidae (*Benthophilus, Gobius,* [incl. *"Mesogobius"*]), Mugilidae (*Mugil*), Mullidae (*Mullus*), Pleuronectidae (*Pleuronectes*), Syngnathidae (*Siphonostoma*). Data also from McDonald (1969: *loc. cit.*). Generalist (1), also in *Gavia*.

Cryptocotyle lingua (Creplin, 1825)

In *Podiceps auritus* (Nicoll, 1923). Anterior half of small intestine. SW. Eur., N. Amer. Intermed. hosts, **mollusks:** GASTROPODS, Hydrobiidae (*Hydrobia, Paludestrina*), Littorinidae (*Littorina*), then **fishes:** Atherinidae (*Menidia*), Bothidae (*Scophthalmus* [*"Lophopsetta"*]), Carangidae (*Trachinotus*), Clupeidae (*Brevoortia*), Cottidae (*Cottus, Hemitripterus, Myoxocephalus* [*"Cottus"*] *scorpius, Myoxocephalus* [*"Acanthocottus"*]), Gadidae (*Gadus, Microgadus, Pollachius* [*"Pallachius"*]), Gobiidae (*Gobius*), Labridae, (*Labrus, Tautoga, Tautogalabrus*), Lotidae (*Gaidropsarus* [*"Onos"*]), Mullidae (*Mullus*), Osmeridae (*Osmerus*), Pholidae (*Pholis*), Pleuronectidae (*Pleuronectes* [*"Pseudopleuronectes"*]), Pomatomidae (*Pomatomus*), Sciaenidae (*Menticirrus*), Scombridae (*Scomber*), Stromateidae (*Peprilus* [*"Poronotus"*]), Syngnathidae (*Syngnathus*), Zoarcidae (*Macrozoarces*). (Yamaguti 1958). Also in Cottidae ["sculpins"] and Osmeridae (*Hypomesus pretiosa,* Surf ["Silver"] smelt) and experimentally in Cottidae (*Leptocottus armatus, Oligocottus maculosus*), Pleuronectidae (*Platichthys stellatu*s, Ching 1978). Data also from McDonald (1969:335-336). Cercariae encyst under the skin of fishes, where black pigment in the cysts indicates "black-spot" disease (Stunkard, 1930). Common in Lari and Alcae: also found in canids (Rausch *et al.* 1990); rare in grebes and loons (2).

Metagonimus takahachii Suzuki, in Takahashi, 1929

In *Tachybaptus ruficollis*. Intestines? FW. Eurasia. Intermed. hosts, **mollusks:** GASTROPODS, Pleuroceratidae (*Semisulcospira libertina*), then metacercariae under scales of **fishes:** Cobitidae (*Misgurnus*), Cyprinidae (*Acheilognathus, Carassius auratus, C. carassius, Cyprinus carpio, Gnathopogon*), Percichthyidae (*Coreoperca*), Salangidae (*Salangichthys microdon*) family *incertae sedis* in Percoidei (*Lateolabrax japonicus*) (Yamaguti 1958, 1975). Generalist (1). *M. yokogawai* is a synonym *fide* Yamaguti 1971.

**Taphrogonimus holostomoides* (Mehlis in Creplin, 1846)

In *Podiceps cristatus*. Type and only known host (?5). "End gut." Eur. FW? Intermed. hosts? Position of genus uncertain, may =*Monostomum pingue* Mehlis in Creplin, 1846, *fide* Yamaguti 1958.

Family Pachytrematidae (Family not in Brooks *et al.* 1993. Placed here by Schell 1985.)

Pachytrema paniceum Brinkmann, 1942

In *Podiceps cristatus* (Čanković *et al.* 1984). Gall bladder. FW? Eur. Intermed. hosts? Parasite of gulls, rare in grebes (2).

[*Pachytrema* sp.

In *Poliocephalus poliocephalus*. (Mawson *et al.* 1986.) Gall bladder? FW? Austr. Intermed. hosts?]

Order Plagiorchiformes

Suborder Renicolata

Family Renicolidae

Renicola pinguis (Mehlis in Creplin, 1846)

In *Podiceps cristatus* (Bittner & Sprehn 1928). *P. auritus, P. grisegena* (Leonov *et al.* 1965). Kidney. SW? Eurasia. Intermed. hosts, marine mollusks? then fishes? Generalist (1), also in *Gavia stellata*.

[Family Orchipedidae]

[*Orchipedum tracheicola* Braun, 1901

In *Podiceps auritus, P. grisegena, P. nigricollis,* did not mature (Gallimore 1964). Trachea. FW? Eur., N. Amer. Intermed. hosts? Generalist? Also in ducks. (0)]

Suborder Plagiorchiata

Superfamily Microphalloidea

Family Microphallidae

Atriophallophorus coxiellae S. J. Smith, 1974

In *Poliocephalus poliocephalus* (Mawson *et al.* 1986). Small intestine and rectum. BW. Austr. Intermed. hosts, **mollusks:** GASTROPODS, Hydrobiidae (*Coxiella badgerensis*) (S. J. Smith 1974) then **?crustaceans**. Generalist (1). Also in coot (*Fulica*) and plovers (*Charadrius* spp.).

Levinseniella cruzi Travassos, 1921

In *Rollandia rolland* (Martorelli 1988). Caeca. FW?, SW? Amer. Intermed. hosts, **mollusks:** GASTROPODS, Hydrobiidae (*Littoridina* [*"Heleobia"*] *parchappei*), then FW?, SW? **crustaceans:** DECAPODS, Palaemonidae (*Palaemonetes argentinus*). Generalist (1), also in *Anas* and *Himantopus*. (Martorelli 1988) and *Vanellus* and the cricetid rodent, *Scapteromys aquaticus* (Martorelli *et al.* 1996). A SW life cycle for what may be this species involving a **mollusk:** GASTROPOD, Olividae (*Olivella*) as first intermed. host, a **crustacean:**

DECAPOD, Hippidae (*Emerita*), as second intermed. host, and shorebirds *Limosa* and *Catoptrophorus* as definitive hosts was reported by Young (1938).

Levinseniella tasmaniae (S. J. Smith, 1974)

In *Poliocephalus poliocephalus* (Mawson *et al.* 1986). "Mainly caecum; also intestine and rectum." BW. Austr. Probable intermed. hosts, **mollusks:** GASTROPODS, Hydrobiidae (*Coxiella badgerensis*), then **crustaceans:** AMPHIPODS, Ceinidae (*Austrochiltonia australis*) (S. J. Smith 1974). Generalist (1), also in ducks (*Anas* spp.) and plovers (*Charadrius* spp.).

Maritrema calvertense S. J. Smith, 1974

In *Poliocephalus poliocephalus* (Mawson *et al.* 1986). "Lower intestine, caeca, and rectum." BW. Austr. Probable intermed. hosts, **mollusks:** GASTROPODS, Hydrobiidae (*Coxiella badgerensis*), then **crustaceans**: AMPHIPODS, Ceinidae (*Austrochiltonia australis*) (S. J. Smith 1974). Generalist (1), also in ducks (*Anas* spp.) and plovers (*Charadrius* spp.).

Maritrema oocystum (Lebour, 1907)

In *Tachybaptus novaehollandiae* (Mawson *et al.* 1986, voucher from *"Podiceps ruficollis"* USNPC No. 070994.00). Intestines? SW? Austr. Intermed. hosts, snails? then, crustaceans? Generalist (1).

Pseudospelotrema japonicum Yamaguti, 1939

In *Podiceps grisegena, P. nigricollis* (Gallimore 1964). Caeca, intestines. SW. Asia, N. Amer. (Rim of North Pacific.) Intermed. hosts, snails? then, **crustaceans**: DECAPODS, Cancridae (*Cancer magister*) (Ching 1991) and AMPHIPODS, ?Gammaridae (*"Anisogammarus"*) Yamaguti (1975). Sometimes placed in *Maritrema* Generalist (1). Also in ducks and an alcid (*Cepphus*).

Family Prosthogonimidae

Prosthogonimus cuneatus (Rudolphi, 1809)

In *Tachybaptus ruficollis* (Nicoll 1923), *Podiceps auritus, P. cristatus,* P. *nigricollis* (McDonald 1969:276-277). In Bursa Fabricii, cloaca, large intestine, oviduct. FW. Cosmopolitan. Intermed. hosts, **mollusks:** GASTROPODS, Bithyniidae (*Bithynia*), Planorbidae (*Anisus, Gyraulus, Planorbarius*), Viviparidae (*Viviparus*), then **insects:** ODONATA, Zygoptera, Coenagrionidae (*Platycnemis*), Anisoptera, Aeschnidae (*Anax*), Libellulidae (*Cordulia* [incl. *"Epitheca"*], *Leucorrhinia, Libellula, Sympetrum*), data largely from McDonald (1969:276-277), see also Macy (1965). There has been some confusion regarding intermediate hosts of this and the next species, and the two are sometimes considered conspecific. (See McDonald 1969:276; Yamaguti 1975:258.) Generalist (1). Yamaguti (1971:567) lists *"Colymbus"* and *Podiceps,* but not *Gavia.* McDonald (1969:277) lists only grebes. Presumably, the reference to *Colymbus* in Yamaguti is to species of *Podiceps.*

Prosthogonimus ovatus (Rudolphi, 1803)

In *Tachybaptus ruficollis, Podiceps nigricollis* (McDonald 1969:279-282), *P. grisegena* (Nicoll 1923). Generalist (1). Usually in Bursa Fabricii, also in cloaca, large intestine, and oviduct. FW. Cosmopolitan. Intermed. hosts, **mollusks:** GASTROPODS, Bithyniidae (*Bithynia*), then nymphs and adults of **insects**: ODONATA, Zygoptera, Coenagrionidae (*Ischnura, Platycnemis*), Anisoptera, Aeschnidae (*Aeschna, Anax, Gomphus*), Libellulidae (*Cordulia, Epicordulia, Erythemis* [*"Mesothemis"*], *Leucorrhinia, Libellula, Macrodiplax* [*"Tetragonuria"*], *Pachydiplax, Platythemis, Sympetrum*). Adult flukes reach the oviducts of domestic chickens, turkeys, ducks, and geese, causing females to lay soft-shelled eggs in which adult flukes may be found (Boddeke 1960). Yamaguti lists *"Colymbus"* and *Podiceps* as definitive hosts. The former presumably also refers to *Podiceps* because McDonald (1969:281) lists grebes but no loons as such hosts.

Superfamily Plagiorchioidea

Family Plagiorchiidae

Plagiorchis laricola Skrjabin, 1924

In *Podiceps grisegena* (Leonov *et al.* 1965), *P. nigricollis* (McDonald 1969:317-319). Duodenum, small intestine, rectum. FW? Eurasia. Intermed. hosts, **mollusks:** GASTROPODS, Lymnaeidae (*Lymnaea stagnatilis*), then **crustaceans:** AMPHIPODS, Gammaridae (*Gammarus*), ISOPODS Asellidae (*Asellus*), and aquatic larvae of **insects**: EPHEMEROPTERA, Baetidae (*Cloeon*), ODONATA, Zygoptera, Coenagrionidae (*Enallagma* in adults also), Anisoptera, Aeschnidae (*Aeschna*), TRICHOPTERA, Limnophilidae (*Limnophilus*), COLEOPTERA Dytiscidae (*Dytiscus*), DIPTERA, Chaoboridae (*Chaoborus* [*"Corethra"*]), Tabanidae (*Tabanus*), and experimentally in Culicidae (*Aedes, Culex*). Data also from McDonald (1969:317-319). Generalist, rare in grebes (1).

Plagiorchis maculosus (Rudolphi, 1802)

In *Podilymbus podiceps, Podiceps grisegena* (Gallimore 1964). Intestine, caecum. FW. Euras., N. Amer. Intermed. hosts, **mollusks:** GASTROPODS, Lymnaeidae (*Lymnaea stagnatilis, Radix auricularis*), Valvatidae (*Valvata*), Viviparidae (*Viviparus* [incl. *"Paludina"*]), then larvae and adults of aquatic **insects:** DIPTERA, Chaoboridae (*Chaoborus crystallinus*), Chironomidae (*Chironomus thummi, Psectrotanypus varius*), Culicidae (*Culex pipiens*). Data also from McDonald (1969:319-320). Generalist, most common in passerine birds (1).

[Superfamily Dicrocoelioidea]

[Family Cephalogonimidae]

[?*Cephalogonimus* sp.

In *Poliocephalus poliocephalus* (Mawson *et al.* 1986.) Intestines? Austr. Parasites of amphibians and reptiles (Yamaguti 1958), record probably based on misidentification (0).]

Superfamily Telorchioidea

Family Ochetosomatidae (Formerly Stomylotrematidae)

**Lobogonimus skrjabini* Filimonova, 1973

In *Podiceps grisegena* (type host). Small intestine. FW? Eurasia. Intermed. hosts? Genus and species only known from original description (5).

Pygidiopsis genata Looss, 1907

In *Podiceps cristatus* (McDonald 1969:330-331). Intestine. FW. Eurasia, N. Afr., N. Amer. Intermed. hosts, **mollusks:** GASTROPODS, Thiaridae (*Thiara*), then **fishes:** Atherinidae (*Atherina*), Cichlidae (*Astatotilapia, Hemichromus, Tilapia*), Cyprinidae (*Barbus, Scardinius*), Gobiidae (*Neogobius*), Mugilidae (*Mugil*), Pleuronectidae (*Pleuronectes*), Poeciliidae (*Gambusia*). Generalist (1), most common in fish-eating birds and mammals.

**Stomylotrema grebei* Mathur, 1950

In *Tachybaptus ruficollis.* Type and only known host (?5). Intestines? FW? Asia. Intermed. hosts, aquatic insects?

Family Eucotylidae (Family *incertae sedis*)

Eucotyle cohni Skrjabin, 1924

In *Tachybaptus ruficollis* (Vaidova 1978), *Podiceps auritus* (Gallimore 1964), *P. grisegena, P. nigricollis.* Urinary tubules. FW? Eurasia, N. Amer. Intermed. hosts? ?Generalist. (?1). Also in *Gavia arctica* and ducks.

**Eucotyle hassalli* Price, 1930

In *Podiceps auritus.* Type and only known host (?5). Urinary tubules. FW? N. Amer. Intermed. hosts, snails?

[*Eucotyle nephritica* (Mehlis in Creplin, 1846)
In *"Colymbus" arcticus* (=*Gavia arctica*). Also known from an anatid (*Netta rufina*) McDonald (1969:271). Not known from grebes.]

Eucotyle popowi Skrjabin & Evranova, 1942
In *Podiceps cristatus* (McDonald 1969:271-272). Urinary tubules. FW? Eurasia. Intermed. hosts, snails? ?Specialist in anatids. rare in grebes (?2).

Tanaisia fedtschenkoi Skrjabin, 1924
In *Tachybaptus ruficollis.* (Vaidova 1965). Urinary tubules. FW? Eurasia, N. Amer. Intermed. hosts, snails? Generalist, rare in grebes (1).

Tanaisia integerriorcha Saidov, 1954
In *Tachybaptus ruficollis.* (Vaidova 1965). Kidney. FW? Eurasia. Intermed. hosts, snails? Specialist in larids, rare in grebes (2).

THE TAPEWORMS (CESTODES) OF GREBES

The cestodes (Phylum Platyhelminthes, Class Eucestoda) are endoparasitic flatworms lacking a mouth and digestive tract. The name is derived from the Latin *cestus*, a girdle. There are approximately 5,000 described species (Hoberg 1997).

The adults of virtually all species are found in the intestines of vertebrates, where they absorb food through the surface of their bodies. The adult worm may be from less than 1 mm to 20 meters in length, white or yellowish in color, and usually tape-like in appearance, although there is considerable difference in proportions among species. The head or scolex is a small enlargement on the anterior end and is usually equipped with attachment structures — hooks and/or sucking depressions of several kinds. Behind the head is a short neck from which a series of segments or proglottids proliferate. In most species, each proglottid contains one or two complete sets of reproductive organs of both sexes. Fertilization is usually within a proglottid, but may be between proglottids of the same or a different worm. The sexes are in separate animals in *Dioecocestus,* a genus largely confined to grebes, and a few other genera, including *Gyrocoelia,* one species of which has been reported from a grebe.

Cestode life cycles are complex, usually requiring one (Cyclophyllidea) or two (Pseudophyllidea and at least some Tetraphyllidea) intermediate hosts. In the latter case, the first intermediate host is a crustacean and the second, usually a fish. In the Cyclophyllidea, the intermediate host is usually an arthropod. Grebes become infected with the parasites by eating intermediate or paratenic hosts containing the cestode larvae.

Asexual reproduction in the intermediate host of cestodes is not common but has been extensively studied in the cyclophyllidean *Echinococcus.* It has also been found in some other hymenolepidids and some dilepidids and the amabiliid, *Tatria uralensis* (B.B. Georgiev *in litt.*). For details see below under that species.

Contrary to general belief, what damage cestodes may cause to the host is not so much the utilization of some of the host's food but physical damage to the lining of the intestines. Light infections usually cause little such damage, but in massive ones like those sometimes found in grebes and waterfowl damage may be considerable (*e.g.*, Stock & Holmes 1987a).

Cestodes are the most abundant intestinal parasite of grebes. In his study of the intestinal helminths of 91 grebes of four species in Alberta (the Western [*Aechmophorus occidentalis*], Red-necked [*Podiceps grisegena*], Eared [*Podiceps nigricollis*], and Horned [*Podiceps auritus*] grebes), Stock (1985) found each bird parasitized by from two to 15 species and from 112 to 33,169 individuals of parasitic worms, 96 percent of which were cestodes.

In the following list, the cestode systematics at the generic and specific levels is based primarily on Schmidt 1986 and Czapliński *et al.* 1994. Other major sources are Yamaguti 1959; Dubinina 1966; Ryzhikov & Tolkatcheva 1981; and Ryzhikov *et al.* 1985. In comparing the generic-level taxonomy within the Cyclophyllidea (especially in the Dilepididae and Hymenolepididae), major differences can be found. Unless otherwise indicated, references for intermediate and definitive hosts are from Ryzhikov *et al.* 1985, and unless otherwise or more specifically stated, adult worms are found in the intestines.

A recent paper by Hoberg, Gardner & Campbell (1999) including a cladistic analysis of the orders of the Eucestoda, does much to clarify the systematic relationships among the major groups of tapeworms parasitizing vertebrates. Another by Hoberg, Jones & Bray (1999) based on comparative morphology advances our knowledge of the relationships of the families within the Cyclophyllidea and provides new hypotheses for co-evolution in vertebrates, and one by Mariaux (1998) on a molecular phylogeny of the Eucestoda also contains valuable new information on the systematics of the group.

Class Eucestoda
Order Pseudophyllidea
Family Diphyllobothriidae

Digramma interrupta (Rudolphi,1810)
In *Podiceps auritus* (Yamaguti 1959), *P. grisegena, P. cristatus,* and experimentally, *P. nigricollis* (McDonald 1969:364). FW. Eurasia. Intermed. hosts, **crustaceans:** COPEPODS, CYCLOPIDAE (*Acanthocyclops, Cyclops strenuus, Eucyclops* [experimentally], *Macrocyclops, Paracyclops*), DIAPTOMIDAE *Acanthodiaptomus* and *Eudiaptomus* [experimentally], *Diaptomus*), FAMILY? (*Heterocopa*), then FW **fishes:** CYPRINIDAE (*Abramis brama, A. sapa, Barbus lacerta, Carassius auratus, C. carassius, Cyprinus carpio, Gobio gobio, G. albipinnatus, Leuciscus brandti, Rhodeus sericeus, Rutilus rutilus, Saurogobio dabryi*). Generalist as adults (1). The name, *D. alternans,* is sometimes used for this species, *e.g.*, by Schmidt (1986). The genera *Digramma, Ligula,* and *Schistocephalus* are sometimes placed in a separate family, the Ligulidae (*e.g.*, by Dubinina 1966; Ryzhikov *et al.* 1985).

Diphyllobothrium ditremum (Creplin,1825)
In *Podiceps grisegena.* FW, SW? Eurasia. Intermed. hosts, **crustaceans:** COPEPODS, CYCLOPIDAE (*Cyclops strenuus*), DIAPTOMIDAE (*Diaptomus gracilis*), then **fishes:** especially SALMONIDAE (*Coregonus albula, C. pidschian, C. sardinella, C. wartmanni, Salmo trutta, Salvelinus alpina, Thymallus thymallus*); less often LOTIDAE (*Lota lota*), and OSMERIDAE (*Osmerus eperlanus*). Generalist as adults (1). Common in gulls and loons.

**Diphyllobothrium podicipedis* (Diesing,1854)
In *Tachybaptus ruficollis* type and only known host (?5). FW, SW? Europe. Intermed. hosts? Sometimes consid-

ered a synonym of *D. ditremum*.

Ligula colymbi Zeder, 1803

In *Podilymbus podiceps* (Rausch 1983); *Tachybaptus ruficollis, Podiceps auritus, P. grisegena, P. cristatus, P. nigricollis*. FW. Eurasia, N. Amer. Intermed. hosts, experimentally in **crustaceans:** COPEPODS, Cyclopidae (*Acanthocyclops, Cyclops* [incl. "*Mesocyclops,*"] *Eucyclops, Microcyclops*), Diaptomidae (*Diaptomus, Eudiaptomus*), then FW **fishes:** especially Cobitidae, (*Cobitis taenia, Nemachilus kuschakewitschi, N. stoliczkai, N. strauchi,* and ?*N. dorsalis*). Less often in Cyprinidae (*Gobio gobio, Barbus brachycephalus, Leucaspius delineatus*). Generalist (1), most common in grebes. Dubinina (1966) divides *Ligula* into five species (two of which are unnamed) each of which is considered a specialist on a different group of fishes as intermediate hosts. Schmidt considers *Ligula* monotypic, with *L. intestinalis* the only species.

Ligula intestinalis (Linnaeus, 1758)

In *Aechmophorus occidentalis* (Stock & Holmes 1987b), *Podilymbus podiceps* (Pérez-Ponce de Leon *et al.* 1992, and vouchers in USNPC Nos. 007859.00, 029673.00), *Tachybaptus ruficollis, Podiceps auritus, P. grisegena* (voucher in USNPC No. 079328.00), *P. cristatus, P. nigricollis*. Large and small intestines, kidney (Shigin 1957). FW. Cosmopolitan. Intermed. hosts, **crustaceans:** COPEPODS, Cyclopidae (*Acanthocyclops, Cyclops, Macrocyclops, Microcyclops,* and, experimentally, in *Eucyclops* and *Mesocyclops*), Diaptomidae (*Diaptomus,* and, experimentally, in *Eudiaptomus*), then FW **fishes:** Atherinidae (*Chirostoma attenuatum, C. consocium, C. estor, C. ocotlanae* [Pérez-Ponce de Leon *et al.* 1992]), Catostomidae (*Catostomus ardens, C. catostomus, C. commersoni*), Centrarchidae (*Micropterus dolomieu*), Cyprinidae (*Abramis ballerus, A.* ["*Blicca*"] *bjoerkna, A. brama, A. sapa, Alburnoides bipunctatus, Alburnus alburnus, A. charusini, A. filippii, Barbus barbus, B. lacerta, Chalcalburnus chalcoides, Gobio gobio, Gila atraria, Hybognathus nuchalis, Hybopsis plumbeus, Leuciscus cephalus, L. idus, L. leuciscus, Mylocheilus caurinus, Notropis cornutus, N. hudsonius* (Lawler 1964), *Pelecus cultratus, Phoxinus brachyurus, P. phoxinus, Pimephales notatus, P. promelas, Ptychocheilus oregonensis, Rhodeus sericeus, Richardsonius balteatus, Rutilus rutilus, Scardinius erythrophthalmus, Schizothorax argentatus, S. intermedius, Varicorhinus capoeta*), Goodeidae (*Goodea atripinnis, Lermichthys multiradiatus, Poblana alchichicae, Xenotoca variata* [Pérez-Ponce de Leon *et al.* 1992]), Osmeridae (*Osmerus mordax*), Percidae (*Perca flavescens* [Lawler 1964]), Salmonidae (*Prosopium williamsoni, Salmo gairdneri*). List of genera of fish hosts "not verified by recent classification" in McDonald (1969:367). Generalist (1). *Ligula monogramma* (Voucher from *P. auritus* in USNPC No. 007971.00) is a synonym. Some of these records from grebes may refer to *L. colymbi*.

[*Ligula pavlovskii* Dubinina, 1959

In *Podiceps cristatus* (experimentally). Definitive host in nature Little Tern, *Sterna albifrons*. FW. Basin of Black Sea. Intermed. hosts, ?**crustaceans:** ?COPEPODS, then, FW **fishes:** Gobiidae (*Benthophilus stellatus, Neogobius kessleri, N. fluviatilis, Pomatoschistus microps*). Adults little known Dubinina (1966). Specialist in terns (0).]

Schistocephalus pungitii Dubinina, 1959

In *Podiceps auritus, P. grisegena, P. cristatus*. FW?, SW? Eurasia, N. Amer. Intermed. hosts, **crustaceans:** COPEPODS, Diaptomidae (*Diaptomus salinus*) and, experimentally, in Cyclopidae (*Acanthocyclops, Cyclops, Macrocyclops*), then **fishes:** (specialist on *Pungitius,* Gasterosteidae). In definitive hosts a generalist (1), parasitizing fish-eating ducks, gulls, terns, and shorebirds, as well as grebes.

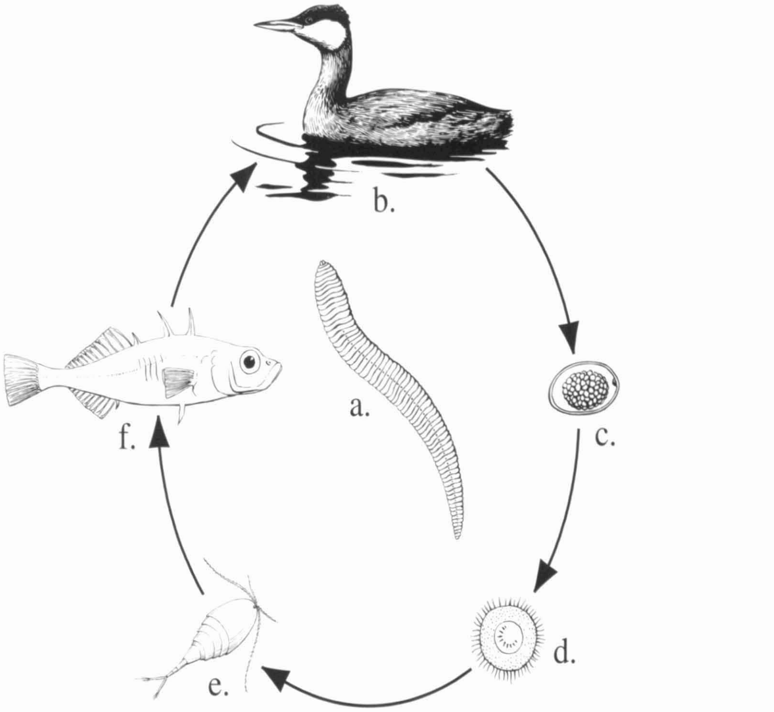

Figure 3. The life cycle of the pseudophyllidean tapeworm, *Schistocephalus solidus*. Young adult (a) from the intestine of the definitive host, here a Red-necked Grebe (b). The egg (c) is passed into the water where it hatches into a coracidium (d). This is eaten by the first intermediate host, a copepod, *Cyclops* (e), which in turn is eaten by the second intermediate host, a stickleback, *Gasterosteus,* (f). An infected fish is eaten by the definitive host, a grebe, in which the worm reaches maturity. This cestode is unusual in that while many kinds of copepods and fish-eating birds act as first intermediate and definitive hosts, respectively, the second intermediate host is almost invariably a stickleback of the genus *Gasterosteus*. Original drawing by John Megahan from sources listed in the acknowledgments (p. 65).

Schistocephalus solidus (Mueller, 1776)

In *Tachybaptus ruficollis* (McDonald 1969:369), *Podilymbus podiceps* (Linton 1927, voucher in USNPC No. 007860.00), *Aechmophorus occidentalis* (Matthias 1963), *Podiceps auritus, P. grisegena* (voucher in USNPC No. 079325.00), *P. cristatus, P. nigricollis*. Small and large intestines. FW, SW? Eurasia, Iceland, Greenland, Afr., N. Amer. Intermed. hosts, **crustaceans:** COPEPODS, Cyclopidae (*Acanthocyclops, Cyclops, Eucyclops,* and, experimentally, in *Macrocyclops, Mesocyclops*), Diaptomidae (*Diaptomus,* and, experimentally, in *Eudiaptomus*), then **fishes:** Gasterosteidae, (specialist on *Gasterosteus,* also in *Culaea inconstans* [Hoffman 1967]) and possibly "Cottidae, *Cottus gobio, C. kaganowskii,* etc." [Dubinina 1966]). McDonald (1969:370) lists unverified reports from other genera. Some species of these (*e.g., Salmo*) may act as sources for marine hosts. In definitive hosts, a generalist (1) found in a variety of fish-eating birds, some marine (*e.g.,* Procellariidae and Alcidae), as well as some mammals. The life cycle is shown in Figure 3.

Order Tetrabothriidea

Family Tetrabothriidae

Although no life cycle for a member of this marine family has been worked out, it is thought that three stages are involved: first, crustaceans, then, cephalopods and/or teleost fishes, and finally, marine birds and/or mammals as definitive hosts (Hoberg 1987).

Tetrabothrius macrocephalus (Rudolphi, 1810)

In *Aechmophorus occidentalis* (Stock & Holmes 1987b), *P. nigricollis* (Immature worms only, Gallimore 1964), *Tachybaptus ruficollis*, *Podiceps auritus*, *P. grisegena* (voucher USNPC No. 079327.00), *P. cristatus*. Intestine. Presumably SW. Cosmopolitan. Generalist (1), found commonly in loons, grebes, and gulls and as an incidental parasite of shags (but not cormorants), anatids, and alcids (Hoberg pers. comm.). Ryzhikov *et al.* (1985) consider *T. immerinus* (Abildgard, 1790) formerly used for this species, a *nomen oblitum* and *T. perfidus* Joyeux & Baer, 1934, a synonym.

[*Tetrabothrius* cf. *torulosus* Linstow, 1888

In *Podiceps grisegena*. SW. Asia (Kamchatka, Spasskaya *et al.* 1973), Pacific Ocean in both Northern and Southern hemispheres. Because the identification by Spasskaya *et al.* was tentative and this parasite is otherwise known from albatrosses, Hoberg (pers. comm.) considers this identification to be incorrect.]

[*Tetrabothrius* sp.

In *Podicephorus major.* (Torres *et al.* 1982). Gastrointestinal tract. S. Am. SW. Because it is not clear that the cestode reported in this paper from *Pelecanus thagus* was the same as that found in *Podicephorus major* and because this is the only report of any species of *Tetrabothrius* from any pelican, Hoberg (pers. comm.) considers the report incorrect.]

Order Cyclophyllidea

Family Dioecocestidae

Subfamily Dioecocestinae

This group is variously placed in the Amabiliidae, with that group in the Acoleidae, as a separate family, or subfamily, or in a family with other dioecious cestodes. See Jones (1994) for a review of its taxonomic history. Jones' arrangement is followed here. With the exception of the type species, *Dioecocestus paronai,* Fuhrmann, 1900, confined to glossy ibises (*Plegadis*), members of this genus are grebe specialists. The genus and family are sometimes spelled *Dioicocestus* and Dioicocestidae, respectively. The genera *Hamulocestus* Spasskii, 1992 (type *D. asper*), and *Neodioecocestus* Siddiqi, 1960 (type *D. cablei*), are not considered valid by Jones (1994).

The reproductive biology of the family is known from studies by Clerc (1907, 1920) and Jögis (1978a, 1978b) summarized in Ryzhikov & Tolkatcheva (1981). In at least *D. asper,* it is usual to find only a single pair per bird. Several immatures, which do not develop, may also be found. Thus, regardless of how many individuals may occur in the original infection, only one pair matures. B.B. Georgiev (*in litt.*) adds that he thinks the young may wait to replace dead adults and thus maintain the reproductive period of the infection beyond the life span of the first mature pair. I think that the presence of several individuals in the initial infection is important in increasing the chances that both sexes may be included and thus that a pair can be formed.

Ryzhikov & Tolkatcheva further cite Jögis' (1978a or 1978b?) finding of three cysticercoids of the strobilocercoid type in the stomach of a Red-necked Grebe (*Podiceps grisegena*). This type of cysticercoid contains not only a scolex, but also an immature strobila of 10-20 proglottids. These cysticercoids reach a length of 9-17 mm and can be sexed by the presence of a cirrus sac in the males. These "larval" proglottids do not mature in the adult worm and are believed to function in providing a larger absorptive surface for the early development of the cestode in the definitive host. (*Taenia taeniaeformis,* a common parasite of the domestic cat, is a textbook example of this type of cysticercoid.)

**Dioecocestus acotylus* Fuhrmann,1904

In *Tachybaptus dominicus,* type and only known host (4). Middle of small intestine. FW? N. Amer. (common in southern Texas), S. Amer., West Indies. Intermed. hosts?

**Dioecocestus asper* (Mehlis, 1831)

In *Tachybaptus ruficollis, Podiceps auritus, P. grisegena* (including reports as *"P. rubricollis"*), *P. cristatus, P. nigricollis.* FW. Eurasia, N. Amer. Grebe specialist (3). Intermed. hosts? Jögis (1978a) studied the development of cysticercoids of this species in a definitive host. Because of the large size of these cysticercoids and the composition of the invertebrates in the diets of grebes, Jögis suggested the nymphs of dragonflies (Anisoptera) as likely intermediate hosts. [Comparing the diets of glossy ibises with those of grebes, I independently came to the same conclusion.] *Dioecocestus novaeguineae* Fuhrmann,1914, considered a synonym by Ryzhikov *et al.* (1981). *Dioecocestus fuhrmanni* Linton, 1925 considered a synonym (Holmes, pers. comm.). The host specificity to *P. grisegena* in North America and the apparent lack of it in Eurasian grebes suggest that the Old and New World populations may represent different species.

**Dioecocestus cablei* (Siddiqi, 1960)

In *Tachybaptus ruficollis,* type and only known host (5). FW? Asia (India). Intermed. hosts? Known from a single male specimen. May be a synonym of *D. asper* (Jögis 1978b).

**Dioecocestus fevita* Meggitt, 1933

In *Tachybaptus ruficollis,* type and only known host (?5). FW? Asia (India). Intermed. hosts? May be a synonym of *D. asper* (Jögis 1978b).

**Dioecocestus novaeguineae* Fuhrmann, 1914

In *Tachybaptus novaehollandiae, T. ruficollis* [As *Podiceps capensis*]. FW? Austr. (New Guinea). Intermed. hosts? Grebe specialist (3).

**Dioecocestus novaehollandiae* (Krefft, 1873)

In *Tachybaptus novaehollandiae* Mawson *et al.* (1986). Type and only known host (?5). FW? Austr. Intermed. hosts?

[**Dioecocestus* sp.

In *Poliocephalus poliocephalus.* FW? Austr. Mawson *et al.* (1986).]

Subfamily Gyrocoeliinae

[*Gyrocoelia* sp.

In *Poliocephalus poliocephalus.* FW? Austr. Mawson *et al.* (1986).]

Family Amabiliidae

With the exception of the monotypic nominate genus, which is confined to flamingos, all known species of this family are grebe specialists. Although subject of several revisions, the latest at the species level by Ryzhikov & Tolkatcheva (1981) and at the generic level by Jones (1994), the group is in need of much study based on more material than is currently available. Although Jones (*op. cit.*), considered the genus *Pseudoschistotaenia* Fotedar & Chishti, 1976, a synonym of *Schistotaenia,* I prefer to retain it until a new name is provided for *P. indica,* Fotedar & Chishti, 1976, preoccupied by *Schistotaenia indica* Johri, 1959.

**Diporotaenia colymbi* Spasskaya, Spassky & Borgarenko, 1971
In *Tachybaptus ruficollis.* Type and only known host (?5). Asia (Tajikistan). FW. Intermed. hosts?

**Laterorchites bilateralis* (Fuhrmann, 1908)
In *Tachybaptus dominicus,* type and only known host (?5). FW? Cuba. Intermed. hosts? Sometimes placed in the Dilepididae.

**Pseudoschistotaenia indica* Fotedar & Chishti, 1976
In *Tachybaptus ruficollis,* type and only known host (?5). FW? Asia (Kashmir). Intermed. hosts? (The original description is an abstract; a fuller description is in Fotedar & Chishti 1980.)

**Pseudoschistotaenia pindchii* Fotedar & Chishti, 1977
In *Tachybaptus ruficollis,* type and only known host (?5). FW? Asia (India). Intermed. hosts?

**Ryjikovilepis dubininae* (Ryzhikov & Tolkatcheva, 1981)
In *Podiceps grisegena, P. cristatus, P. nigricollis* (Ryzhikov & Tolkatcheva 1981). FW. Eurasia. Grebe specialist (3). Intermed. hosts, **insects:** ODONATA, Zygoptera, AGRIONIDAE (*Agrion hastulatum*) (Kukashev 1985). Formerly placed in the genus *Tatria.* For generic placement, see Gulyaev & Tolkatcheva 1987.

**Schistotaenia colymba* Schell, 1955
In *Podiceps auritus,* type host, *P. nigricollis* (Stock & Holmes 1987b, voucher USNPC No. 079332.00), *Tachybaptus ruficollis, P. grisegena, P. cristatus.* (Ryzhikov & Tolkatcheva 1981), *Podilymbus podiceps* (Voucher WHML No. 33323). Small intestine. FW. Asia, N. Amer. Grebe specialist (3). Intermed. hosts, **insects:** ODONATA, Zygoptera, COENAGRIONIDAE (*Ischnura elegans*) (Kukashev 1985). *Tatria antipini* Mathevossian & Okorokov, 1959, is a synonym *fide* Ryzhikov & Tolkatcheva (1981). Sometimes placed in subgenus *Paraschistotaenia.* (WHML. 33323, formerly listed as *S. macrocirrus,* is this species *fide* J. M. Kinsella, pers. comm.)

**Schistotaenia indica* Johri, 1959.
In *Tachybaptus ruficollis,* type host. *Podiceps auritus.* FW? Asia (India, Tajikistan). Intermed. hosts? Grebe specialist (3).

**Schistotaenia macrocirrus* Chandler, 1948
In *Podilymbus podiceps* (type host, type and paratype in USNPC. No. 037065.00, and voucher HWML 33322), *P. cristatus* (Ryzhikov & Tolkatcheva 1981). Grebe specialist (3). FW. Eurasia?, N. Amer. Intermed. hosts? Because Ryzhikov & Tolkatcheva (1981) consider *S. tenuicirrus* a synonym of this species, it is not clear to which the report from *P. cristatus* refers. It appears to be the only report for either species from Eurasia.

**Schistotaenia macrorhyncha* (Rudolphi, 1810)
In *Tachybaptus dominicus* (Vigueras 1960). *Tachybaptus ruficollis, Podiceps auritus, P. grisegena, P. cristatus, P. nigricollis.* FW. Eurasia, N. Amer., West Indies. Grebe specialist (3). Intermed. hosts, **insects:** ODONATA, Anisoptera, LIBELLULIDAE (*Somatochlora metallica* [Vojtková 1971]). *Schistotaenia indica* Johri, 1959, *sensu* Borgarenko, 1972, a synonym *fide* Ryzhikov & Tolkatcheva 1981.

**Schistotaenia mathevossianae* Okorokov, 1956
In *Tachybaptus ruficollis, Podiceps auritus, P. grisegena.* FW. Asia (Urals, Uzbekistan). Grebe specialist (3). Ryzhikov & Tolkatcheva (1981) consider *T. erschovi* Mathevossian & Okorokov, 1959, and *T. jubilaea* Okorokov & Tkachev, 1973, synonyms of this species, although Ryzhikov *et al.* (1981) do not. Ryzhikov & Tolkatcheva (*op. cit.*) and Schmidt (1986) followed here. Sometimes placed in subgenus *Paraschistotaenia.*

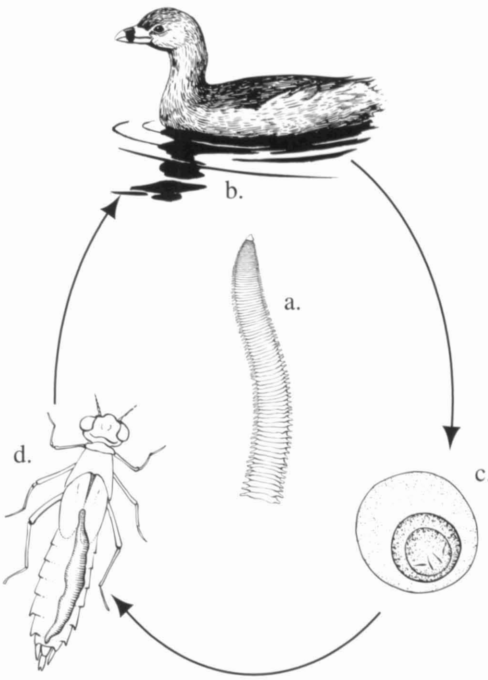

Figure 4. The life cycle of the cyclophyllidean cestode, *Schistotaenia tenuicirrus,* a member of the family Amabiliidae, which consists almost exclusively of grebe specialists. The adult worm (a) inhabits the intestine of a Pied-billed Grebe (b), which passes eggs (c) of the parasite into the water, where they are taken in by the intermediate host, possibly with water taken into the cloaca for use in jet propulsion, (d) a dragonfly nymph (*Anax junius*) in which they develop into the large strobilocercoid larva, which can be seen here in the abdomen of the nymph. This larva matures in the intestine of the grebe after the nymph is eaten. Original drawing by John Megahan from sources listed in the acknowledgments (p. 65).

**Schistotaenia rufi* Sulgostowska & Korpaczewska, 1969
In *Tachybaptus ruficollis.* Type and only known host (?5). FW? Eur. (Poland). Intermed. hosts? Sometimes placed in subgenus *Paraschistotaenia.*

**Schistotaenia scolopendra* (Diesing, 1856)
In *Tachybaptus dominicus* (type host), *Podilymbus podiceps* (Baer 1940), *Podiceps cristatus* (Ryzhikov & Tolkatcheva 1981). Grebe specialist (3). FW? Eurasia?, S. Amer., West Indies. Intermed. hosts? Report from *P. cristatus* (Ryzhikov & Tolkatcheva 1981) needs verification.

**Schistotaenia srivastavai* Rausch, 1970
In *Podiceps grisegena,* type host (holotype, paratype, and voucher in USNPC Nos. 063135.00, 063136.00, 079321.99), *P. auritus, P. nigricollis* (Stock & Holmes 1987b). Small intestine. FW. Asia, N. Amer. Grebe specialist (3). Intermed. hosts, **insects:** ODONATA, Zygoptera, AGRIONIDAE (*Agrion armatum, A. hastulatum, A.* sp.), COENAGRIONIDAE (*Enallagma cyathigerum, Erythromma najas, Ischnura pumilo, I.* sp., *Sympycna* sp.) (Kukashev 1989). This is the *"Schistotaenia* sp." of Gallimore (1964). Sometimes placed in subgenus *Paraschistotaenia.*

*_Schistotaenia tenuicirrus_ Chandler, 1948

In _Podilymbus podiceps_ (type host) (and vouchers HWML Nos. 21659 and 31349, the latter identified by J. M. Kinsella, pers. comm.), _Podiceps auritus, Corvus brachyrhynchos_ (once) (Chandler 1948), _Podiceps grisegena_ (Stock & Holmes 1987b). Grebe specialist (3). Ant. small intestine. FW. N. Am. Intermed. hosts, **insects:** ODONATA, Anisoptera, AESCHNIDAE (_Anax junius_). Type and paratype in USNPC Nos. 037066.00, 037067.00. Life cycle in Boertje 1974, 1975, and shown in Figure 4. Sometimes considered a synonym of _S. macrocirrus_ Chandler 1948. (See above under that species.)

*_Tatria acanthorhyncha_ (Wedl, 1855)

In _Tachybaptus dominicus_ (McDonald 1969:373), _T. ruficollis, Podiceps auritus, P. grisegena, P. cristatus, P. nigricollis,_ Grebe specialist (3), exceptionally in _Fulica atra, Aythya nyroca._ FW. Eurasia, Afr., N. Amer. Intermed. hosts, **insects:** ODONATA, Zygoptera, AGRIONIDAE (_Agrion puella_), COENAGRIONIDAE (_Enallagma cyathigerum, Pyrrhosoma nymphula_), and, experimentally in **crustaceans:** CYCLOPIDAE (_Macrocyclops albidus_). _Tatria azerbaijanica_ Mathevossian & Sailov, 1963, and _T. fuhrmanni_ Solomon, 1932, considered synonyms by Borgarenko & Gulyaev (1990).

*_Tatria appendiculata_ Fuhrmann, 1908

In _Tachybaptus dominicus,_ type and only known host (4). FW? S. Amer., West Indies. Intermed. hosts?

*_Tatria biremis_ Kowalewski, 1904

In _Aechmophorus occidentalis_ (Stock & Holmes 1987b), _Tachybaptus ruficollis, Podiceps auritus, P. grisegena_ (voucher USNPC No 079329.00), _P. cristatus, P. nigricollis_ (voucher USNPC No. 079330.00). Small intestine. FW. Eurasia, N. Amer. Grebe specialist (3). Intermed. hosts, **insects:** HEMIPTERA, CORIXIDAE (_Sigara concinna_) (Kukashev 1983) (The life cycle is shown on the cover, with legend on page ii.) Split into 2 subspecies, _T. biremis major_ and _T. b. minor_ (Korpaczewska & Sulgostowska, 1974) on the basis of size. _T. b. minor_ raised to rank of species by Gulyaev 1990a. (_T. b. major_ then became _T. biremis._) The two species combined by Ryzhikov & Tolkatcheva 1981, and by Ryzhikov _et al._ 1985, the arrangement followed here. _Hymenolepis lintonella_ Fuhrmann, 1932 is a synonym _fide_ Joyeux & Baer (1950).

*_Tatria biuncinata_ (Joyeux & Baer, 1943)

In _Tachybaptus ruficollis, Podiceps auritus._ Intestine. FW. Eurasia, N. Afr. Intermed. hosts, **insects:** EPHEMEROPTERA. "larve d'Ephéméridé sp." Grebe specialist (3).This, the type of the genus _Joyeuxilepis_ Spasskii, 1947, is a cysticercoid described by Joyeux & Baer (1943) and in more detail by Joyeux & Gaud (1945) from an unidentified mayfly nymph in Morocco. Adults from Tajikistan described by Borgarenko _et al._ (1972). Formerly considered a synonym of _Tatria decacantha_ Fuhrmann, 1913. For a discussion, see Borgarenko & Gulyaev (1990). Listed as _Echinorhynchotaenia biuncinata_ in the subfamily Echinorhynchotaeniinae of the Hymenolepididae by Schmidt (1986).

*_Tatria decacantha_ Fuhrmann, 1913

In _Aechmophorus occidentalis_ (Stock & Holmes 1987b), _Tachybaptus ruficollis, Podiceps auritus, P. grisegena_ (voucher USNPC No. 079323.00), _P. cristatus, P. nigricollis._ Grebe specialist (3), also "coot" = grebe sp? in Africa, exceptionally in herons (_Ardea_). Small intestine. FW. Eurasia, N. Amer., Afr. Intermed. hosts, **insects:** ODONATA (nymphs), Zygoptera, AGRIONIDAE (_Agrion_ sp.), COENAGRIONIDAE (_Coenagrion hastulatum, C. vernale, C. puella, C. pulchellum, Enallagma cyathigerum, Ischnura elegans, I. pumilo, Lestes virens, L. dryas, L. sponsa, Pyrrhosoma nymphula_), Anisoptera, AESCHNIDAE (_Aeschna cyanea_), LIBELLULIDAE (_Libellula quadrimaculata, Sympetrum depressiusculum_). The name, _Joyeuxilepis biuncinata_ (Joyeux & Baer, 1943), has been erroneously applied to this species.

*_Tatria decacanthoides_ (Borgarenko & Gulyaev, 1991)

In _Tachybaptus ruficollis,_ type and only known host (?5). Intestine. FW. Asia (Tajikistan). Intermed. hosts? Described in the genus _Joyeuxilepis._

*_Tatria duodecacantha_ Olsen, 1939

In _Podilymbus podiceps_ (holotype and paratypes in USNPC Nos. 009282.00, 009283.00), _Podiceps nigricollis_ (WHML No. 23182). FW? N. Amer. Intermed. hosts? Redescribed by Schultz (1940). Considered a synonym of _T. appendiculata_ by Ryzhikov & Tolkatcheva (1985). Recognized by Schmidt (1986). Grebe specialist (3).

*_Tatria fimbriata_ (Borgarenko, Spasskaja & Spassky, 1972)

In _Podiceps grisegena,_ type and only known host (?5). FW? Asia (Tajikistan). Intermed. hosts?

*_Tatria fuhrmanni_ Solomon, 1932

In "coot" (presumably a grebe). FW? Afr. Intermed. hosts? Known only from original description (5).

*_Tatria iunii_ Korpaczewska & Sulgostowska, 1974

In _Podiceps nigricollis,_ type host, _Tachybaptus ruficollis._ FW? Europe. Grebe specialist (3). Intermed. hosts?

*_Tatria jubilaea_ Okorokov & Tkachev, 1973

In _Tachybaptus ruficollis, Podiceps auritus._ FW. Eurasia (Russia). Grebe specialist (3). Intermed. hosts, **insects:** ODONATA (nymphs), Zygoptera, AGRIONIDAE _(Agrion pulchellum)._

*_Tatria mircia_ Gulyaev, 1990

In _Podiceps nigricollis,_ type and only known host (?5). FW? Eurasia. Intermed. hosts?

*_Tatria octacantha_ Rees, 1973

In _Tachybaptus ruficollis,_ type and only known host (5). FW. Eur. (England). Intermed. hosts, **insects:** ODONATA (nymphs), Zygoptera, COENAGRIONIDAE (_Enallagma cyathigerum, Pyrrhosoma nymphula_) (Rees, 1973). Placed in genus _Joyeuxilepis_ by Borgarenko & Gulyaev (1990).

*_Tatria pilatus_ (Borgarenko & Gulyaev, 1991)

In _Tachybaptus ruficollis, Podiceps auritus_ (Borgorenko & Gulyaev 1991). Small intestine. FW. Asia (Tajikistan). Intermed. hosts? Known only from these grebes (3). Described in the genus _Joyeuxilepis._

*_Tatria skrjabini_ Tretyakova, 1948

In _Tachybaptus ruficollis._ Type and only known host (4). FW? Eurasia (southern Transural region). Intermed. hosts? Listed in Ryzhikov & Tolkatcheva (1981) as _"Tatria_ sp. Korpaczewska & Sulgostowska, 1974."

[*_Tatria uralensis_ (Gulyaev, 1989)

Larvae in **insects:** ODONATA, Anisoptera, AESCHNIDAE (_Aeschna cyanea_). FW. Eurasia (Southern Urals). Adult and definitive hosts unknown. Presumably a grebe specialist (?3). The odonate nymph becomes infected by eating the entire uterine capsule containing several dozen eggs. Each egg produces blastocysts in which a continuous production of scoleces occurs until the nymph is eaten by the definitive host. These "mother blastocysts" and "daughter cysticercoids" are analogous with the mother and daughter rediae of digenes. According to B.B. Georgiev (_in litt._), there are approximately 1,000 scoleces per blastocyst and several blastocysts per infected dragonfly nymph. Gulyaev found but three of 1,130 *Aeschna* nymphs infected. This low rate may be balanced by the high reproductive rate in the intermediate host.]

Family Dilepididae

Paricterotaenia porosa (Rudolphi,1810)

In *Podiceps nigricollis.* FW? Eurasia, N. Amer. Intermed. hosts? Specialist in lari, uncommon in grebes (2). Sometimes placed in the genus *Choanotaenia.*

Lateriporus clerci (Johnston, 1912)

In *Podiceps grisegena.* FW. Eurasia, N. Amer. Intermed. hosts, **crustaceans:** AMPHIPODS, GAMMARIDAE (*Gammarus lacustris*). Specialist in lari, occasional in grebes and ducks (2). The adult *"Lateriporus* sp." of Gallimore (1964) is this species (Denny 1969).

Lateriporus skrjabini Mathevossian, 1946

In *Podiceps nigricollis,* did not mature (Stock 1985), *P. grisegena, P. nigricollis,* (Denny 1969). FW. Eurasia, N. Amer. Intermed. hosts, **crustaceans:** AMPHIPODS, GAMMARIDAE (*Gammarus lacustris*). Specialist in lari, occasional in grebes (2). The immature *"Lateriporus* sp." of Gallimore (1964) are this species.

Liga lencoranica Sailov, 1962

In *Tachybaptus ruficollis, Podiceps cristatus.* FW? Eurasia. Intermed. hosts? Specialist in lari, occasional in grebes (2). Has been placed in *Anomotaenia.* May prove to be a synonym of *A. hydrochelidonis* Dubinina,1954.

Neovalipora parvispine (Linton, 1927)

In *Podiceps grisegena.* SW? Eurasia, Iceland, N. Amer. Intermed. hosts? Loon specialist, occasional in grebes and gulls (2).

Paradilepis urceus (Wedl, 1855)

In *Podiceps cristatus.* FW? Eurasia, Afr. Intermed. hosts? Ciconiiform specialist, occasional in grebes and several other groups (2).

[Dilepididae sp.?

In *Tachybaptus novaehollandiae* (Mawson *et al.* 1986.). Austr.]

Family Hymenolepididae

There is much confusion in the literature about the systematics of this family, but Vasileva *et al.* (1996a, 1996b,1998, 1999, in press a, b) have revised the genera *Pararetinometra, Mackoja* and *Confluaria,* and described the genus *Dollfusilepis* which, like other genera of this family which are grebe specialists (*Lobatolepis, Mackoja, Parafimbriaria* and *Podicipitilepis*), they consider confined to grebes. These authors are cited for the host records that they have verified, and, as indicated earlier, records at the end of each list of definitive hosts without references are from Ryzhikov *et al.* 1985 and have not been verified.

Subfamily Fimbriariinae

Fimbriaria fasciolaris (Pallas, 1781)

In *Podiceps cristatus* (McDonald 1969:404), *P. grisegena, P. nigricollis.* Duodenum to caeca (Szelenbaum-Cielecka *et al.* 1988). FW. Cosmopolitan. Intermed. hosts, **crustaceans:** COPEPODS, CYCLOPIDAE (*Acanthocyclops, Cyclops* [incl. *"Mesocyclops,"*] *Eucyclops, Macrocyclops, Paracyclops*), DIAPTOMIDAE (*Diaptomus*), OSTRACODS, CYCLOCYPRIDAE (*Cyclocypris,* experimentally), CYPRIDAE (*Cypria*), CYPRIDOPSIDAE (*Cypridopsis,* experimentally), CYPRIDINIDAE? *Physocypris fadeevi,* and AMPHIPODS, GAMMARIDAE (*Gammarus, Pontogammarus*), TALITRIDAE (*Hyalella azteca*) (Denny 1969), **insects:** EPHEMEROPTERA, BAETIDAE (*Cloeon*), not verified. Specialist in anatids, occasional in grebes, cormorants, and other birds (2).

Subfamily Hymenolepidinae

Aploparaksis crassirostris (Krabbe, 1869)

In *Tachybaptus ruficollis,* (Petrova 1978). Intestine. FW, T. Eurasia, Afr. Intermed. hosts, **annelids:** OLIGOCHAETES, LUMBRICULIDAE [FW] (*Lumbriculus*), LUMBRICIDAE [T] (*Eiseniella*) (Ryzhikov *et al.* 1985). Specialist in Charadrii, rare in grebes (2). The generic name is sometimes spelled *Haploparaksis.*

Aploparaksis filiformis Spassky, 1963

In *Podiceps grisegena* (Malakhova 1985), *P. cristatus, P. nigricollis.* Intestine. FW? Eurasia. Intermed. hosts? Specialist in Charadrii? Occasional in grebes (2). Not listed in Schmidt (1986).

Aploparaksis furcigera (Nitzsch in Rudolphi, 1819)

In *Tachybaptus ruficollis, Podiceps cristatus, P. nigricollis.* Small intestine, caeca, rectum (Szelenbaum-Cielecka *et al.* 1988). FW. Eurasia, N. Amer. Intermed. hosts, FW **annelids:** OLIGOCHAETES, LUMBRICULIDAE (*Lumbriculus,* Harper 1930), TUBIFICIDAE (*Limnodrilus,* experimentally). Specialist in anatids, uncommon in fish-eating birds (2).

Aploparaksis larina (Fuhrmann, 1921)

In *Podiceps nigricollis* (Movsesyan 1987). Small intestine, caecum. FW? Eurasia, N. Amer., Austr., Antarctica? Intermed. hosts? Specialist in larids (2), rare in grebes and herons. Described in *Haploparaksis.*

[*Biglandatrium biglandatrium* Spasskaya, 1961

In *"Podiceps* sp." Ryzhikov *et al.* 1985. Intestine. FW? Eurasia. Intermed. hosts? Loon specialist (2). Records from grebes probably in error.]

Cloacotaenia megalops (Nitzsch in Creplin, 1829)

In *Podiceps cristatus.* In cloaca. FW. Cosmopolitan. Intermed. hosts, **crustaceans:** OSTRACODS, CYPRIDAE (*Cypris pubera, Eucypris* sp.). Common in anatids, rare in grebes (2). Its presence in *Podiceps cristatus* suggests that there may be a paratenic host, possibly a fish.

**Confluaria capillaris* (Rudolphi, 1810)

In *Podiceps auritus* (type host as *Colymbus auritus* L.), *P. nigricollis, P. grisegena, P. cristatus, Tachybaptus dominicus* (type host of *C. capillaroides* [voucher in USNPC No. 049741.00] all verified by Vasileva *et al.* 1999), intestine. FW? Iceland, Eur., Central Asia (Kazakhstan), S. Amer. (Brazil) Intermed. hosts? Has been placed in genera *Dicranotaenia, Dubininolepis, Hymenolepis, Taenia, Variolepis* and *Wardium.* Grebe specialist (3). Joyeux & Baer (1950) considered it confined to grebes. Reports from hosts other than grebes are erroneous or doubtful (Vasileva *et al.* 1999) who have redescribed this species and synonymize *C. capillarioides* (Fuhrmann, 1906) with it. Reports of this cestode from the West Indies and Central America evidently come from Fuhrmann's description of the range of the definitive host, *T. dominicus* (B. B. Georgiev, in litt.).

**Confluaria furcifera* (Krabbe, 1869)

In *P. grisegena* (as *P. rubricollis,* type host *fide* Vasileva *et al.* in press b) (Stock & Holmes 1987b, voucher USNPC No. 079326.00), *P. nigricollis* (Vasileva *et al.* in press b), *Podilymbus podiceps* (Gallimore 1964), *Aechmophorus occidentalis* (Stock & Holmes 1987b), *Podiceps auritus.* Reports from *Tachybaptus ruficollis,* and *P. cristatus* need confirmation. Intestine. FW. Eurasia, N. Amer., Afr. Intermed. hosts? Formerly placed in the genera *Dimorphocanthus, Diplacanthus, Dubininolepis, Hymenolepis* and *Variolepis.* It seems highly unlikely that a grebe specialist could depend on the ingestion of cladocerans to infect fish-eating definitive hosts. The high frequency of occurrence and large numbers of individuals reported by Stock & Holmes (1987b) in the piscivorous *Aechmophorus occidentalis* suggest that fishes may act as second intermediate or paratenic hosts. Obligate parasite of grebes (3). Redescribed by Vasileva *et al.* in press a.

**Confluaria japonica* (Yamaguti, 1935)

In *Tachybaptus ruficollis, Podiceps grisegena* (Vasileva *et al.* in press a). Intestine. FW? Eurasia, N. Afr. Intermed. hosts? Grebe specialist (3). *Haploparaksis chikugoensis* Sawada & Kifune, 1974, is a synonym *fide* Ryzhikov *et al.* (1985). Has also been placed in genera *Dicranotaenia, Dubininolepis, Hymenolepis,* and *Variolepis.* Redescribed by Vasileva *et al.* (in press a).

**Confluaria multistriata* (Rudolphi, 1810)

In *Tachybaptus ruficollis* (as *Colymbus minor,* type host) and *Podiceps nigricollis, P. auritus, P. cristatus* (Vasileva *et al.* in press a), *P. grisegena.* Intestine. FW. Eurasia, Afr? Intermed. hosts, **insects:** EPHEMEROPTERA, Baetidae (*Cloeon*). Has been placed in genera *Colymbilepis, Dicranotaenia, Dimorphocanthus, Drepanidotaenia* (subgenus), *Dubininolepis, Hymenolepis, Taenia* and *Variolepis.* Grebe specialist (3). Redescribed by Vasileva *et al.* (in press a) who consider Solomon's report from Africa requires confirmation.

**Confluaria podicipina* (Szymanski, 1905)

In *Podiceps auritus* (type host), *Tachybaptus ruficollis, P. nigricollis* (voucher in USNPC No. 079334.00) and verified by Vasileva *et al.* in press b, who consider Linton's [1927] reports from *P. auritus* and *P. grisegena holboelli* incorrect), *Aechmophorus occidentalis* (Stock & Holmes 1987), *P. grisegena, P. cristatus.* Intestine. FW, SW. Eurasia, N. Amer. Intermed. hosts, **crustaceans:** FW CLADOCERANS, Chydoridae (*Eurycercus lammelatus*), Daphniidae (*Ceriodaphnia reticulata, Simocephalus exspinosus*) (Ryzhikov *et al.* 1985), and SW PHYLLOPODS, Artemiidae (*Artemia salina*) in Tengiz Lake, Kazakhstan (Maximova 1981). Grebe specialist, incidental in *Aythya fuligula* (3). Has been placed in *Dicranotaenia, Dimorphocanthus, Dubininolepis, Hymenolepis, Microsomacanthus* and *Variolepis.* The listing of this species from *Aechmophorus occidentalis* and its occurrence in *Podiceps grisegena* suggest that fishes or larger aquatic invertebrates than cladocerans may act as second intermediate or paratenic hosts. Redescribed by Vasileva *et al.* in press b, who consider *C. spasskii* Ablasov in Spasskaya, 1966, a synonym.

**Confluaria* n. sp. Vasileva, Georgiev & Genov, in press a.

In *Podiceps cristatus.* Small intestine. FW? Europe Intermed. hosts, **crustaceans:** CLADOCERANS, Chydoridae (*Eurycercus lamellatus*), Daphniidae (*Ceriodaphnia reticulata, Simocephalus exspinosus*). Grebe specialist (3).

[**Confluaria* sp. Vasileva, Georgiev & Genov, in press b.

In *Tachybaptus ruficollis.* Small intestine. FW? Europe. Intermed. hosts? More material needed for description. Presumably grebe specialist (3)]

Dicranotaenia coronula (Dujardin, 1845)

In *Podiceps nigricollis* (Akhumian 1966), *P. grisegena* (Malakhova 1985), *P. cristatus.* Small intestine, caecum. FW. Eurasia, N. Amer., Afr. Intermed. hosts, **crustaceans:** COPEPODS and OSTRACODS, (many species. See references in Ryzhikov *et al.* 1985.); **mollusks:** GASTROPODS, Lymnaeidae (*Lymnaea ovata, L. palustris, L. peregrina, L. vulgaris*) believed to be paratenic hosts. Specialist in anatids, occasional in grebes, pelicans, and gulls (2).

**Dicranotaenia paraporale* (Podesta & Holmes, 1970)

In *Podiceps nigricollis* (type host, holotype in USNPC No. 070729.00), *P. auritus, P. grisegena* (voucher in USNPC No. 079324.00), *Aechmophorus occidentalis* (Stock & Holmes 1987b). Posterior third of small intestine. FW. N. Amer. Intermed. hosts, **crustaceans:** AMPHIPODS, Talitridae (*Hyalella azteca*). Life cycle in Podesta & Holmes (1970b). Known only from grebes (3). This is the "*Dicranotaenia* sp." of Gallimore (1964) *fide* Podesta & Holmes (1970b). Described in *Wardium*

Diorchis elisae (Skrjabin, 1914)

In *Podiceps nigricollis* (Tolkatcheva 1975). Ileum (Szelenbaum-Cielecka *et al.* 1988). FW. Eurasia, N. Amer. Intermed. hosts, **crustaceans:** OSTRACODS, Cypridae (*Heterocypris incongruens*), (Grytner-Ziecina & Olszewska 1989). Described in *Aploparaksis.* Specialist in anatids, rare in grebes (2).

Diorchis inflata (Rudolphi, 1819)

In *Podiceps cristatus.* Jejunum to caeca and rectum (Szelenbaum-Cielecka *et al.* 1988). FW. Eurasia, Afr., N. Amer. Intermed. hosts, **crustaceans:** COPEPODS, Diaptomidae (*Diaptomus, Eudiaptomus*), OSTRACODS, Cyclocyprididae (*Cyclocypris*), Cyprididae (*Cypris, Eucypris*), Cypridopsidae (*Cypridopis*). Specialist in anatids and rallids, occasional in grebes (2).

**Diorchis skarbilowitschi* Shakhtakhtinskaya, 1952

In *Podiceps grisegena,* type and only known host (?5). Intestine? FW? Eurasia. Intermed. hosts?

Diorchis spinata Mayhew, 1929

In *Tachybaptus ruficollis.* Intestine. FW? Eurasia, N. Amer. Intermed. hosts, **crustaceans:** COPEPODS, Diaptomidae (*Arctodiaptomus salinus, A. bacilifer*), OSTRACODS, Cyprididae (*Hungarocypris madaraszi* and, experimentally, in *Heterocypris incongruens*). Specialist in anatids, rare in grebes (2).

[**Diorchis* species "O" Stock, 1985

In *Podiceps auritus, P. grisegena, P. nigricollis* (Voucher in USNPC No. 079335.00). On the basis of the definitive hosts, this is the undescribed species of *Diorchis* listed by Gallimore (1964).]

[**Diorchis* species "P" Stock, 1985

In *Podiceps auritus, P. nigricollis* (Voucher in USNPC No. 079336.00), *Aechmophorus occidentalis.*]

**Dollfusilepis hoploporus* (Dollfus, 1951)

In *Podiceps cristatus,* type and only known host (4). Intestine? FW?, SW? Eur., N. Afr. (Morocco). Sometimes placed in genera *Dubininolepis, Variolepis,* or *Wardium. Hymenolepis capillaris* (Rudolphi, 1810) of Joyeux & Baer 1950, is this species *fide* Vasileva *et al.* (1998).

Drepanidotaenia lanceolata (Bloch, 1782)

In *Tachybaptus ruficollis, Podiceps cristatus, P. nigricollis.* Small intestine. FW. Cosmopolitan. Intermed. hosts, **crustaceans:** COPEPODS, Cyclopidae (*Acanthocyclops, Cyclops, Eucyclops, Macrocyclops, Mesocyclops, Paracyclops,* family? *Tropocyclops,* Diaptomidae (*Diaptomus*), OSTRACODS (rarely). Paratenic hosts, **mollusks:** GASTROPODS, Lymnaeidae (*Lymnaea*). Specialist in anatids, occasional in grebes, loons, and other birds (2).

Dubininolepis rostellatus (Abildgaard, 1790)

In *Podiceps grisegena* (Yamaguti 1959), *P. auritus.* Intestine. FW? Eurasia, N. Amer. Intermed. hosts? Loon specialist, rare in grebes (2). Formerly in genera *Armadoskrjabinia* and *Microsomacanthus.*

Dubininolepis swiderskii (Gasowska, 1932)

In *Podiceps auritus.* Intestine. FW? Eurasia. Intermed. hosts? Loon specialist, rare in grebes and gulls (2). Formerly placed in the genera *Microsomacanthus* and *Variolepis,* but see Vasileva *et al.* 1998).

[*Hymenolepis woodsholei* Fuhrmann, 1932
Considered a synonym of *Confluaria furcifera* by Joyeux & Baer 1950) and Voge & Read (1954) and a species inquirenda by Vasileva *et al.* (ms).]

[*Hymenosphenacanthus* sp. 1, Gallimore, 1964
In *Podiceps grisegena, P. nigricollis.* Intestine? FW? N. Amer. (Alberta). Presumably a species of *Cladogynia,* in which genus *Hymenosphenacanthus* is placed by Khalil *et al.* 1994.]

**Lobatolepis lobulata* (Mayhew, 1925)
In *Podilymbus podiceps* (type host, vouchers in USNPC No. 051159.00, and HWML Nos. 30295, 30296, 13217); *P. gigas* (Gallimore & Holmes 1965). Small intestine. FW. N. Amer., West Indies. Intermed. hosts? Described in *Hymenolepis,* has been placed in *Wardium.* Grebe specialist (3). Known only from *Podilymbus.* (WHML Nos. 30295 and 30296 were originally identified as *Idiogenes,* and 23217 as *Hymenolepis* sp. but belong to this species *fide* J. M. Kinsella, pers. comm.)

**Mackoja podirufi* (Macko, 1962)
In *Tachybaptus ruficollis, Podiceps nigricollis.* Small intestine. FW? Eur. Intermed. hosts? Known only from these grebes (3). Described in genus *Echinocotyle.* Redescription and new records in Vasileva *et al.* (1996b).

Microsomacanthus compressus (Linton, 1892)
In *Podiceps grisegena* (Schmidt 1986), *Tachybaptus ruficollis, P. nigricollis.* Intestine. FW. Eurasia, N. Amer. Intermed. hosts, **crustaceans:** COPEPODS, CYCLOPIDAE (*Acanthocyclops, Cyclops, Macrocyclops, Mesocyclops*); paratenic hosts, **mollusks:** GASTROPODS, LYMNAEIDAE (*Lymnaea*), PLANORBIDAE (*Anisus, Planorbis*), VALVATIDAE (*Valvata*), VIVIPARIDAE (*Viviparus*). Specialist in anatids, occasional in grebes (2).

Microsomacanthus microskrjabini Spassky & Yurpalova, 1965
In *Podiceps grisegena* (specimen in USNPC No. 079333.00), *Aechmophorus occidentalis* (Denny 1969). Intestine. FW. Eurasia, N. Amer. Intermed. hosts, **crustaceans:** AMPHIPODS, GAMMARIDAE (*Gammarus lacustris*) (Denny 1969). Specialist in anatids, rare in grebes (2). This is the "*Nadejdolepis* sp." of Gallimore (1964) *fide* J. C. Holmes (*in litt.*).

Microsomacanthus pachycephalus (Linstow, 1872)
In *Podiceps grisegena* (Linton 1927). Intestine. FW. Eurasia, N. Amer. Intermed. hosts, **crustaceans:** COPEPODS, DIAPTOMIDAE (*Diaptomus*). Specialist in anatids, rare in grebes (2).

[*Microsomacanthus* ("*Echinatrium*) species Y" Stock, 1985
In *Podiceps nigricollis.* Did not mature. Presumably a species of *Microsomacanthus* in which genus *Echinatrium* is placed by Khalil *et al.* 1994.]

[*Microsomacanthus* species "T" Stock, 1985.
In *Podiceps nigricollis,* did not mature.]

[*Microsomacanthus* species "W" Stock, 1985
In *Podiceps nigricollis,* did not mature.]

[*Microsomacanthus* species "Z" Stock, 1985.
In *Podiceps nigricollis,* did not mature.]

**Parafimbriaria micrantha* Gulyaev, 1990
In *Podiceps grisegena, P. nigricollis.* Gulyaev (1990b). Small intestine? FW? Eurasia. Intermed. hosts? This species is the Old World representative of *P. websteri.* Genus confined to grebes (3).

**Parafimbriaria websteri* Voge & Read, 1954
In *Podiceps nigricollis* (type host). (HWML No. 23183). Also in *P. grisegena, P. auritus* (Gallimore 1964). Small intestine. FW?, SW? N. Amer. Intermed. hosts? Grebe specialist (3). (WHML 23183 formerly listed as *Paradilepis* sp. is this species *fide* J. M. Kinella, pers. comm.)

**Pararetinometra lateralacantha* Stock & Holmes, 1981
In *Podiceps grisegena* (type, paratype, and voucher in USNPC Nos. 076524.00, 076525.00, 079322.00), *P. nigricollis, Aechmophorus occidentalis* (Stock & Holmes 1987b), *P. nigricollis,* Bulgaria (Vasileva *et al.* 1996a). Anterior fifth of small intestine (Stock & Holmes, 1981). FW. Eur., N. Amer. Intermed. hosts? This is *Hymenosphenacanthus* sp. "2" of Gallimore (1964). Grebe specialist (3). Placed in the genus *Cladogynia* by Czapliński & Vaucher (in Khalil *et al.* 1994), but see Vasileva *et al.* (1996a) for further description of species and reasons for maintaining the genus *Pararetinometra.*

**Podicipitilepis laticauda* (Yamaguti, 1956)
In *Tachybaptus ruficollis,* type and only known host (?5). Small intestine. FW? Eurasia. Intermed. hosts? Monotypic genus confined to grebes. Has been placed in the genus *Variolepis.* See Vasileva *et al.* (1996b) for comparison with *Mackoja.*

Retinometra macracanthos (Linstow, 1877)
In *Podiceps cristatus* (McDonald 1969:490). Small intestine. FW? Eurasia, N. Amer. Intermed. hosts? Formerly placed in genera *Hymenosphenacanthus* and *Cladogynia.* Specialist in anatids, rare in grebes (2).

*[*Retinometra* species "A" Stock, 1985
In *Podiceps grisegena.* Intestine? FW? N. Amer. (one specimen). Listed as grebe specialist by Stock & Holmes, 1987b. This is presumably a species of *Cadogynia* in which Khalil *et al.* (1994) place *Retinometra* and may be the same as Gallimore's *Hymenosphenacanthus* sp. "1"]

Wardium amphitricum (Rudolphi, 1819)
In *Podiceps grisegena.* Intestine. FW?, T? Eurasia, N. Amer. Intermed. hosts, **annelids:** OLIGOCHAETES [T], GLOSSOSCOLECIDAE (*Criodrilus lacuum*). Specialist in scolopacids, rare in grebes (2). Sometimes placed in genera *Dicranotaenia* and *Limnolepis.*

Wardium cirrosum (Krabbe, 1869)
In *Podiceps auritus, P. nigricollis.* Intestine. FW?, SW? Eurasia, N. Amer. Intermed. hosts? Specialist in larids (2), occasional in grebes. Has been placed in genera *Haploparaxis* (=*Aploparaksis*) and *Dicranotaenia.*

Wardium fusum (Krabbe, 1869)
In *Podiceps nigricollis* (Zhatkanbaeva 1965), *P. grisegena.* Intestine. FW?, SW? Eurasia, N. Amer. Greenland, Austr. Intermed. hosts? Specialist in larids, occasional in grebes (2). Also reported from a rodent (*Arvicola terrestris*) by Merkusheva (1965). *Hymenolepis pseudofusa,* Skrjabin & Mathevossian, 1942, is a synonym.

Subfamily Diploposthinae

Diploposthe laevis (Bloch, 1782)
In *Tachybaptus ruficollis, Podiceps grisegena, P. cristatus, P. nigricollis.* Small intestine. FW. Cosmopolitan. Intermed. hosts, **crustaceans:** COPEPODS, CYCLOPIDAE (*Acanthocyclops* [experimentally], *Macrocyclops, Mesocyclops*), OSTRACODS, CYPRIDOPSIDAE (*Cypridopsis,* experimentally), CYPRIDAE (*Heterocypris*). Specialist in anatids, uncommon in grebes (2). Sometimes placed in the Acoleidae.

THE SPINY-HEADED WORMS (ACANTHOCEPHALANS) OF GREBES

The acanthocephalans comprise a phylum of obligate endoparasites. Adults of most species are less than 10 mm long and whitish in color. The name is derived from the Greek *akantha* for spine and *kephale* for head and refers to the spine-covered proboscis, which can be retracted into the body. Hooks and spines also may occur elsewhere on the body. Like the tapeworms, spiny-headed worms lack mouths and digestive tracts and absorb nutrients through the surface of the body. The developmental stages include, first the acanthor, which develops within the egg membrane or shell while the latter is still in the body of the female. After being shed with the intestinal contents of the definitive host and eaten by an intermediate host, the acanthor hatches and penetrates this host's intestinal wall. Once through this, it grows and, through a series of changes, during which it is usually referred to as an acanthella, it reaches a stage known as a cystacanth, when it has all the structures of the adult and is infective to a new definitive host. Thus, unlike the digenes, spiny-headed worms have no active free-living stage. The sexes are in different individuals, and individuals of either sex may mate with more than one individual of the other. Male acanthocephalans often produce a "copulatory cap" over the vulva of the female, which can prevent multiple matings. As far as known, all mature in the digestive tract of vertebrates and have a single intermediate arthropod host. Again unlike many parasitic flatworms, no asexual reproduction occurs in the intermediate host, although infective larvae may accumulate in paratenic hosts. For an up-to-date account of the biology of the group, see Crompton & Nickol (1985).

Intermediate hosts for acanthocephalans parasitizing terrestrial vertebrates are usually insects whereas those parasitizing aquatic ones are usually crustaceans. Paratenic hosts may be vertebrates of any group from fishes to mammals, but aquatic birds, including grebes, have not been proved to be such. In the family Polymorphidae, the only family of acanthocephalans known to parasitize grebes, fishes are known to be paratenic hosts for species of the genera *Corynosoma, Filicollis* and *Southwellina,* and probably are for species of *Andracantha,* for which the life cycles are unknown, because *A. phalacrocoracis* is a widespread parasite in the piscivorous Pelagic and Red-faced shags (*Phalacrocorax pelagicus* and *P. urile*), and of *Polymorphus*, several species of which have been well studied (Schmidt, in Crompton & Nickol, 1985).

Corynosoma semerme and *C. strumosum* are of interest because both are characteristic parasites of pinnipeds, but are found rarely in grebes and other fish-eating birds, in which they are not known to mature. The occurrence of these acanthocephalans in these birds can be accounted for by their eating either marine or anadromous fishes, many of which, such as herring, salmon, and smelt, are known paratenic hosts for these parasites, or by eating fishes that prey on these fishes. Many of the fish-eating birds that act as hosts for these parasites breed in fresh-water areas but winter in marine habitats. Thus they can acquire the parasites in either place. However, it should be noted that although birds may become infected by feeding on intermediate hosts on either fresh or salt water, no species of acanthocephalan is known to have a life cycle in both environments.

Although spiny-headed worms are found in all major groups of vertebrates including those living on land and in fresh water and marine environments, they are a rather small group compared with other groups of parasitic worms. The recent classification by Amin (in Crompton & Nickol, 1985) lists just under 950 species in three classes, eight orders, 22 families, and 125 genera. Of these, but 14 species in five genera of a single family have been reported from grebes.

At least in grebes, acanthocephalans tend to be much less numerous than tapeworms, digenes, and nematodes inhabiting the same hosts. When Stock (1985) examined 91 grebes of four species for intestinal parasites, he found a maximum infection rate per parasite species per grebe species and a maximum mean number of parasites per bird for cestodes to be 100% and 2,794 individuals, for digenes, 94% and 1,025 individuals, for nematodes, 88% and 57 individuals, and for acanthocephalans, 12% and six individuals, although Gallimore (1964) found up to 112 individuals of *Polymorphus paradoxus* a single grebe.

Acanthocephalans appear to show more specificity for intermediate hosts than for paratenic or definitive hosts. None is known to be specific for grebes, and three of the 14 species found in grebes have also been found in mammals. In addition, several species found in grebes are not known to mature in these hosts.

Major sources of data for the following list of the acanthocephalans known to parasitize grebes are from Yamaguti (1963), host lists in the *Index Catalogue of Medical and Veterinary Zoology*, the *Zoological Record*, and Crompton & Nickol 1985. The classification is that of Amin in the last. With the kind assistance of R. M. Bailey, the names of fishes that act as paratenic hosts (listed by Schmidt in Crompton & Nickol) have been brought up to date to agree with Robins *et al.* (1981) and other recent publications. Where the names of fishes differ from those in Schmidt, the latter are given in quotation marks. Only references for intermediate hosts not listed by Schmidt are given. Obvious typographical errors are merely corrected. Unless otherwise indicated, host records are from Ryzhikov *et al.* (1985).

Phylum Acanthocephala
  Class Palaeacanthocephala
    Order Polymorphida
      Family Polymorphidae
        Andracantha mergi (Lundström, 1941)
          In *Podiceps grisegena, P. cristatus.* Intestine. SW. Eurasia, N. Amer. Intermed. hosts? Paratenic hosts? Generalist (1), also in *Gavia immer, Mergus serrator,* and *Cepphus grylle.* Formerly placed in the genus *Hemiechinosoma.* Described in *Corynosoma* in which it is placed by McDonald (1969:661).
        Corynosoma anatarium Van Cleave, 1945
          In *Podiceps grisegena.* Intestine. FW?, SW? Eurasia, N. Amer. Intermed. hosts? Paratenic hosts? Generalist (1).
        Corynosoma constrictum Van Cleave, 1918
          In *Podiceps grisegena* (Stock 1985, voucher in USNPC No. 079341.00). Intestine. FW. N. Amer. Intermed. hosts, **crustaceans:** AMPHIPODS, TALITRIDAE (*Hyalella azteca*) (Podesta & Holmes 1970a). Paratenic hosts? Generalist (1), common in anatids, also in coots (*Fulica*) and mink (*Mustela vison*).
        [*Corynosoma semerme* (Forssell, 1904)
          In *Tachybaptus ruficollis, Podiceps grisegena.* Intestine, most often at anterior part of large intestine. SW. Eurasia, Atlantic and Pacific oceans, near Austr. Intermed. hosts, **crustaceans:** AMPHIPODS, LYSIANASSIDAE, (*Pontoporeia*). Second intermediate and paratenic hosts, a wide variety of SW, and some anadromous and catadromous

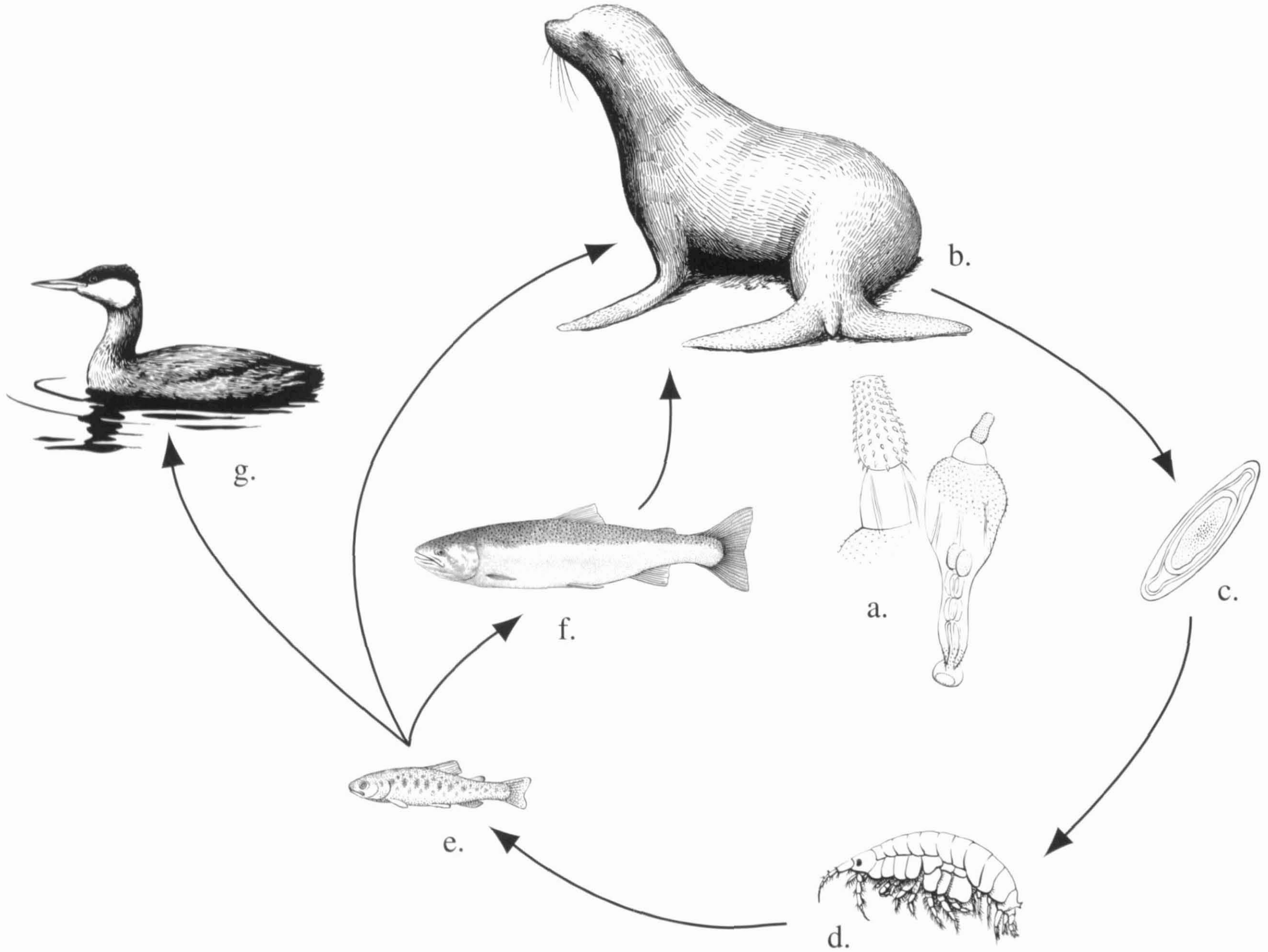

Figure 5. The life cycle of the acanthocephalan, *Corynosoma strumosum,* a marine species which occasionally infects grebes, the parasite is not known to complete its life cycle in birds. The adult worm (a) inhabits the intestine of a marine mammal, here a California Sea Lion (b), which passes the acanthor larva encased in the egg shell (c) into the water, where it is eaten by the first intermediate host, an amphipod, *Pontoporeia* (d). This in turn is eaten by a second intermediate host, here, a young salmon, *Onchorhynchus* (e). This may grow and be eaten by the definitive host or reach it by way of a paratenic host, which may be a predatory fish, such as a large salmon (f). Grebes (g) may become infected by eating the second intermediate host, but because the parasite is not known to mature and produce eggs in fish-eating birds, this is a dead end in its life cycle. Original drawing by John Megahan from sources listed in the acknowledgments (p. 65).

fishes: ANARHICHADIDAE (*Anarhichas* [SW]), ANGUILLIDAE (*Anguilla anguilla* [FW, SW]), BOTHIDAE (*Scophthalmus* [*"Rhombus"*] *maximus* [SW]), CLUPEIDAE (*Clupea harengus* [SW], *C. h. pallasi* [*"membras"*] [SW]), COTTIDAE (*Gymnocanthus ventralis, Myoxocephalus* [*"Cottus"*] *quadricornis* [SW], *M.* [*"C."*] *scorpius* [SW]), CYCLOPTERIDAE (*Cyclopterus lumpus* [SW]), CYPRINIDAE (*Abramis* [*"Blicca"*] *bjoerkna* [FW], *Leuciscus* [*"Idus"*] *idus, Tinca tinca* (*as Corynosoma "smerine"* Hoffman [1967] [FW]), ESOCIDAE (*Esox lucius* [FW]), GADIDAE (*Eleginus navaga* [SW], *Gadus* [*morhua*] *callarias* [SW], GASTEROSTEIDAE (*Pungitius pungitius* [FW, SW]), LOTIDAE (*Enchelyopus cimbrius* [*"Onos cumbrinus"*] [SW], *Lota lota* incl. "*L. vulgaris*" [FW]), MERLUCIIDAE (*Macruronus novaezelandiae* [SW]), OPHIDIIDAE (*Genypterus blacodes* [SW]), OSMERIDAE (*Osmerus* [*mordax*] *dentex* [FW, SW], *O. eperlanus* [FW, SW]). PETROMYZONTIDAE (*Lampetra japonica* [FW, SW]), PLEURONECTIDAE (*Liopsetta glacialis, Pleuronectes flesus* [SW, FW], *P. limanda* [SW], *P. platessa* [SW]), SALMONIDAE (*Coregonus albula* [FW, BW], *C. lavaretus* [FW, BW], *Oncorhynchus nerka* [FW, SW], *Salvelinus alpinus* [FW, SW], STICHAEIDAE (*Lumpenus fabricii* [SW]), ZOARCIDAE (*Zoarces viviparus* [SW]). Reports from FW fishes probably erroneous (McDonald 1969:663-664). Immature stages in mink (*Mustela vison*). Common in marine mammals, rare in cormorants, herons, mergansers, and other fish-eating birds, in which it is not known to mature.]

[*Corynosoma strumosum* (Rudolphi, 1802)

In *Podiceps grisegena.* Small intestine. SW. Eurasia, N. Amer., S. Amer. Intermed. hosts, **crustaceans:** AMPHIPODS, LYSIANASSIDAE (*Pontoporeia*) and second intermediate hosts, and, probably, paratenic hosts, marine and anadromous or catadromous **fishes:** ANGUILLIDAE (*Anguilla anguilla* [FW, SW]), ATHERINIDAE (*Atherina pontica* [FW, SW]), BOTHIDAE (*Scophthalmus maximus* [SW]), CLUPEIDAE (*Caspialosa* spp. [FW], *Clupea harengus* [SW]), CONGRIDAE (*Conger conger* [SW]), COTTIDAE (*Cottus aeneus, C. bubalis, Leptocottus armatus* [FW, SW], *Myoxocephalus quadricornis* [SW], *M. scorpius* [SW]), CYCLOPTERIDAE (*Cyclopterus lumpus* [SW]), ESOCIDAE (*Esox lucius* [FW]), GADIDAE (*Gadus* [*morhua*] *callarius* [SW], *G. macrocephalus* [SW], GASTEROSTEIDAE (*Gasterosteus aculeatus, Pungitius pungitius* [both FW, SW]), LOPHIIDAE (*Lophius piscatorius* [SW]), *Lota lota* [incl. *L. vulgaris*] [FW]), OSMERIDAE (*Osmerus mordax* [*"dentex"*] [FW, SW], *O. eperlanus* [FW, SW], *Spirinchus* [*"Osmerus"*] *lanceolatus* [FW, SW]), Petromyzontidae (*Caspiomyzon wagneri* [FW], *Lampetra fluviatilis* [FW], *Petromyzon* sp. [FW, SW]), Pleuronectidae (*Pleuronectes* [*"Lepidopsetta bileneata"*] *bilineatus* [SW], *P. flesus* [FW, SW], *P. limanda* [SW], *Platichthys stellatus* [FW, SW]), Salmonidae (*Coregonus lavaretus* [FW, BW], *C. sardinella, Oncorhynchus gorbuscha* [FW, SW], *O. nerka* [FW, SW], *Salmo trutta* [FW, SW], *Salvelinus alpinus* [FW, BW]), Sciaenidae (*Sciaena schlegeli* [?SW]), Syngnathidae (*Syngnathus cucculentus* [SW?]), Trachinidae (*Trachinus draco* [SW]), Zoarcidae (*Zoarces viviparus* [SW]); and **reptiles:** SNAKES, "aquatic snake." Juvenile forms have been found in mink (*Mustela vison*), blue fox (*Alopex*), and "seal bear" (presumably the Polar Bear [*Thalassarctos*]). Reports from FW fishes may be based on misidentification of the larvae, or, in the case of predators like *Esox,* by eating fishes that move from SW to FW. Common in marine mammals rare in fish-eating birds, in which they are not known to mature; also reported from canids and man (Rausch *et al.* 1990)].

Filicollis anatis (Schrank, 1788)
In *Tachybaptus ruficollis, Podiceps cristatus* (McDonald 1969:666-668), *P. auritus, P. nigricollis.* Small intestine. FW. Eurasia. Intermed. hosts, **crustaceans:** ISOPODS, Asellidae (*Asellus aquaticus, Asellus* sp.) and paratenic hosts, ?DECAPODS, Astacidae (*Astacus*), **fishes:** Anguillidae (*Anguilla anguilla* [FW, SW]). Generalist (1), common in anatids, also in coots (*Fulica*) and birds of several other orders. Formerly placed in the family Filicollidae.

Polymorphus acutis Van Cleave & Starrett, 1940
In *Podiceps grisegena* (McDonald 1969:669), *P. nigricollis.* (Smogorzhevskaya *et al.* 1965 [Not seen.]), *P. auritus.* Intestine. FW?, SW? Eurasia. N. Amer. Intermed. hosts? Paratenic hosts? Generalist (1), common in anatids.

Polymorphus chasmagnathi Holcman Spector, Mane Garzon & Dei Cas, 1977
In *Rollandia rolland* (Vizcaino 1989). Intestine. SW to BW. S. Amer. Intermed. hosts, **crustaceans:** DECAPODS, Grapsidae, (*Chasmagnathus granulata*), paratenic hosts? Generalist (1), also in *Plegadis* and *Fulica.*

Polymorphus contortus (Bremser in Westrumb, 1821)
In *Podiceps grisegena* (Denny 1969). Intestine. FW. Eurasia, N. Amer. Intermed. hosts, **crustaceans:** AMPHIPODS, Gammaridae, (*Gammarus lacustris*), Talitridae (*Hyallela azteca*), paratenic hosts? Generalist (1), common in anatids.

[*Polymorphus formosus* Schmidt & Kuntz, 1967
In *Tachybaptus ruficollis* (Schmidt & Kuntz, 1967, vouchers in USNPC Nos. 062945.00, 062946). Stomach. FW. Asia (Taiwan). Intermed. hosts, **crustaceans:** DECAPODS, Palaemonidae, *Macrobrachium* sp. Described from domestic ducks. Cystacanths found in stomach of *T. ruficollis.* Not known to mature in grebes. Natural host unknown. ?Generalist (0).]

Polymorphus magnus Skrjabin, 1913
In *Podiceps grisegena* (Khokhlova 1978). Intestine. FW. Eurasia. Intermed. hosts, **crustaceans:** AMPHIPODS, Gammaridae (*Carinogammarus roeselii* [Vojtková 1971], *Gammarus bergi, G. lacustris, G. maeoticus, G. pulex, G. wilkitzkii*), paratenic hosts? Generalist (1), common in anatids and charadriiformes, also in loons (*Gavia*), other birds, and muskrat (*Ondatra*).

Polymorphus marilis Van Cleave, 1939
In *Podiceps grisegena, P. nigricollis, Aechmophorus occidentalis* (did not mature, Stock 1985), in *P. grisegena,* (Denny 1969). Intestine. FW. Eurasia, N. Amer. Intermed. hosts, **crustaceans:** AMPHIPODS, Gammaridae (*Gammarus lacustris*), paratenic hosts? Generalist (?1), common in anatids.

Polymorphus meyeri Lundström, 1942
In *Podilymbus podiceps* (Voucher, HWM No. 35113). Intestines. FW? Eur., N. Amer. Intermed. hosts? Also rarely in ducks (?2).

Polymorphus minutus (Goeze, 1782)
In *Podiceps grisegena* (Khokhlova 1978), *Tachybaptus ruficollis* (Brglez 1977). Large and small intestines. FW, SW. Eurasia, N. Amer. Intermed. hosts, **crustaceans:** AMPHIPODS, Gammaridae ([FW] *Carinogammarus roeselii, Gammarus fossarum, G. lacustris, G. limnaeus, G. pulex, G. wilkitzkii* [SW], *G. duebeni. G. oceanicus, G. salinus, G. zaddachi* [Lehtonen *et al.* 1994]) and DECAPODS, Astacidae (*Cambarus*). Paratenic hosts, **"fishes."** Generalist in birds, including alcids and land birds. Commonest in anatids and Charadriiformes (1). *P. boschadis* (Schrank, 1788) is a synonym.

Polymorphus paradoxus Connell & Corner, 1957
In *Podiceps auritus, P. grisegena, P. nigricollis, Aechmophorus occidentalis* (Gallimore 1964). Intestine. FW. N. Amer. Intermed. hosts, **crustaceans:** AMPHIPODS, Gammaridae (*Gammarus lacustris,* Denny 1969), paratenic hosts? Generalist (1), also reported from muskrat (*Ondatra*) and beaver (*Castor*).

Southwellina hispida (Van Cleave, 1925)
In *Tachybaptus ruficollis* (Yamaguti 1963). Intestine. FW, SW. Eurasia, N. Amer., Galapagos Is. Intermed. hosts, **crustaceans:** DECAPODS, Palaemonidae (*Palaemon squilla, Macrobrachium*). Paratenic hosts, a variety of cold-blooded vertebrates, including **reptiles:** SNAKES, Colubridae (*Elaphe quadrivirgata*), **amphibians:** ANURANS, Ranidae (*Rana nigromaculata*), and **fishes:** Bothidae (*Paralichthys lethostigma* [FW, SW]), Cyprinidae (*Carassius* [*"Cyprinus"*] *carassius* [FW]), Cyprinodontidae (*Fundulus grandis* [FW, SW]), Eleotridae (*Mogurnda obscura* [SW]), Gobiidae (*Rhinogobius* sp. [FW]), Pleuronectidae (*Pleuronectes "passer"* [=*flesus*], Sciaenidae (*Sciaenops ocellatus* [FW, SW]). Generalist (1), also in herons. Sometimes placed in the genus *Arhythmorhynchus.*

[Acanthocephala sp.
In *Podilymbus podiceps.* Intestine. FW? N. AM. (Iowa). Voucher in USNPC No. 029675]

THE ROUND WORMS (NEMATODES) OF GREBES

The nematodes (from *nema*, genitive, *nematos,* the Greek word for thread) comprise a phylum of wormlike animals. They are perhaps the most ubiquitous animal group. Free-living forms can be found from the arctic to hot springs and in soil, fresh water, and salt water, while parasitic ones inhabit both plants and animals.

Typical nematodes are round in cross section and taper toward each end. They vary in length from less than a millimeter to more than several meters. Most have a smooth cuticle and lack pigment, appearing white or yellowish. Unlike tapeworms, the sexes are separate in most species. Males tend to be smaller than females and are curved at the posterior end.

Although often found in the intestines, nematodes resemble digenes and differ from cestodes and acanthocephalans in frequently being found in other parts of the body. This is possible because they have complete digestive systems and feed actively. Some nematodes are found under the integument of the gizzard or in the esophagus, lungs, liver, kidneys, muscles, or bloodstream. Adults of *Pelecitus fulicaeatrae,* which parasitize grebes and coots, are found coiled around the ankle joint. Some nematodes found in the stomach of birds may feed directly on the host's food rather than on the tissues of the host itself.

All true nematodes undergo four molts and pass through four larval stages before becoming adult. Otherwise, members of this group are notable for the variety of their life cycles. In many free-living forms, these cycles are simple, the eggs developing into larvae, which pass through the four stages, all rather similar to the adult, before becoming mature. Most parasitic nematodes pass through one or more intermediate hosts before becoming infective and passing to the definitive host in which the reproductive stage occurs. Some may also occur in paratenic hosts. In direct life cycles, the definitive host may swallow eggs or larvae, or the latter may enter the host through the skin. One grebe (*Tachybaptus ruficollis*) has been reported as an intermediate host for a nematode, *Gnathostoma spinigerum,* the definitive hosts of which are dogs, cats, and, occasionally, humans.

It has been estimated that 16,000 species of nematodes have been described in 2,300 genera and 256 families, but that the total number of described species eventually may reach 40,000 (Anderson 1992). Nematodes are currently placed in two classes and nine orders. Grebes have been reported to be parasitized by members of both classes, four orders, 11 families, 22 genera, and approximately 47 species. These numbers will need adjustments as some described species are synonymized, undescribed species are discovered, and grebes are found to harbor other nematode species.

Nematode parasites of grebes are largely limited to species whose larval stages or intermediate hosts live in water, although a few forms with terrestrial intermediate hosts may be acquired from terrestrial hosts in or on the surface of the water.

The degree of host specificity in nematodes parasitizing grebes is small. Most species found in grebes are either generalists (19) or are common in other groups but rare in grebes (9). Six species considered grebe specialists are reported from two or three genera and from three to six grebe species. Three others are known only from the original description and the type host, a grebe.

Several groups of genera of nematodes are badly in need of revision (*e.g.*, the ascaridoids, especially the genus *Contracaecum,* the trichostrongyloids, and some strongyles). Because of this, for the following list of the nematodes known to parasitize grebes, I have taken the work of Baruš *et al.* 1978 as a starting point. References to hosts not included in that work are listed in the Literature Cited. A review of the life cycles of the Capillariidae is given in Moravec *et al.*, 1987. Up-to-date summaries of life cycles of all groups are found in Anderson (1992), whose classification of major groups is followed in this list. The arrangement of species not found in Anderson (1992) generally follows Baruš *et al.* (1978).

- Class Nematoda
  - Subclass Adenophorea
    - Order Enoplida
      - Superfamily Dioctophymatoidea
        - Family Dioctophymatidae
          - *Eustrongylides mergorum* (Rudolphi, 1809)

            In *Tachybaptus ruficollis* (as *E. elegans,* Yamaguti 1935), *Podiceps auritus, P. cristatus.* Walls of proventriculus. FW? Eurasia, N. Amer. Intermed. hosts, aquatic oligochaetes (**annelids:** OLIGOCHAETES FAMILY?), then FW **fishes:** ESOCIDAE, (*Esox lucius*). Generalist (1). Considered a *species inquirenda* in revision by Measures 1988a, who considered *E. elegans* (Olfers, 1816) a synonym.
          - *Eustrongylides tubifex* (Nitzsch, 1819)

            In *Tachybaptus ruficollis, Podiceps cristatus.* In tumors in wall of proventriculus. FW. Eurasia, N. Amer., S. Amer. Intermed. hosts, **annelids:** OLIGOCHAETES [FW], TUBIFICIDAE (*Limnodrilus hoffmeisteri, Tubifex tubifex*), then **fishes:** CENTRARCHIDAE (*Ambloplites rupestris, Lepomus gibbosus*), CYPRINIDAE (*Rutilus rutilus*), GOBIIDAE (*Gobius* sp.), PERCIDAE (*Perca flavescens*). Generalist (1). Females produce eggs 10 to 17 days post infection, then die. Life cycle geared to brief periods spring and fall when migrating birds visit lakes where intermed. hosts live. (Measures, 1988b, c, d).
      - Superfamily Trichinelloidea
        - Family Trichuridae
          - Subfamily Capillariinae

            Most of the following list follows the arrangement of Baruš & Sergejeva 1990a, b, c). According to Anderson, (1992:544), the classification of this group "is one of the most difficult and unsatisfactory in the Nematoda." In the case of grebes, this is especially true of the genus *Baruscapillaria.* The only species of this genus mentioned by Anderson (1992) is *B. obsignata* which is said to be found in pigeons and galliform birds and to have direct development. The species reported from grebes are believed to have oligochaetes as intermediate hosts (R. C. Anderson, *in litt.*).
            - *Baruscapillaria carbonis* (Rudolphi, 1819)

              In *Podiceps grisegena, P. nigricollis.* Small and large intestines. FW? Eurasia. Intermed. hosts, ?**annelids:** OLIGOCHAETES. Generalist (1).
            - *Baruscapillaria mergi* (Madsen, 1945)

              In *Tachybaptus ruficollis.* Caeca, rectum, rarely small intestine. FW? Eurasia. Intermed. hosts ?**annelids:** OLIGOCHAETES. Specialist in anatids (especially mergansers), also in *Gavia* and *Ardea* (2). The prevalence in fish-eating birds indicates that fishes may act as intermediate or paratenic hosts.
            - *Baruscapillaria obsignata* (Madsen, 1945)

              In *Podiceps cristatus* (Kibakin 1965), *P. auritus, P. grisegena* (voucher as *"Capillaria obsignata"* in USNPC No. 079343.00), *P. nigricollis, Aechmophorus occidentalis* (Stock & Holmes 1987b). Small intestine, rarely caeca. Eurasia, Afr., N. Amer., S. Amer. Development direct in pigeons and galliform birds, the only hosts given for this species by Anderson (1992). Intermed. hosts for grebes, ?**annelids:** OLIGOCHAETES. Generalist, most common in waterfowl. (1). Records for this species in grebes "require reviewing" (Baruš & Sergejeva 1990c).

Baruscapillaria podicipitis (Yamaguti, 1941)

In *Podiceps grisegena* (Alekseev *et al.* 1968), *Tachybaptus ruficollis, P. auritus, P. cristatus, P. nigricollis.* Intestines and caeca. FW? Eurasia, N. Amer., Austr. Intermed hosts, ?**annelids:** OLIGOCHAETES. Generalist, common in grebes and ducks, rare in gulls (1). In genus *Capillaria* in Uchida *et al.* 1991.

**Baruscapillaria ryjikovi* (Daiya, 1972)

In *Tachybaptus ruficollis, Podiceps grisegena, P. nigricollis.* Small intestine and caeca. FW? Eurasia. Intermed. hosts, ?**annelids:** OLIGOCHAETES. Known only from grebes (3).

Capillaria anatis (Schrank, 1790)

In *Podiceps grisegena.* Caeca, rarely small intestine. T? Eurasia, N. Amer., S. Amer. Intermed. hosts, soil **annelids:** OLIGOCHAETES?, Family? (*Aporroectodea* (="*?Aporrectodea*") *caliginosa*), or direct life cycle (McDonald 1969:546). Generalist, rare in grebes (1). Placed in the genus *Thominx* by Baruš *et al.* (1978).

[*Capillaria michiganensis* Read, 1949

In *Podiceps auritus, P. grisegena, P. nigricollis* (Gallimore 1964). FW? Eurasia, N. Amer. Intermed. hosts? Generalist (1), described from the muskrat (*Ondatra zibethica*). Stock & Holmes (1987b) reported only *Capillaria* (=*Baruscapillaria*) *obsignata* from the same area. Both reports gave high infection rates. It seems likely that both refer to the same species. All other reports of *C. michiganensis* are from *Ondatra.*]

[*Capillaria* sp.

In *Poliocephalus poliocephalus, Podiceps cristatus.* FW? Austr. (Mawson *et al.* 1986). Intermed. hosts?]

[*Capillaria* sp.

In *Podicephorus major* (Torres *et al.* 1982). Gastrointestinal tract. SW? S. Am. Also in *Larus dominicanus.*]

Eucoleus contortus (Creplin, 1839)

In *Podiceps auritus, P. nigricollis* Gallimore (1964), *Tachybaptus ruficollis, P. grisegena, P. cristatus.* Esophagus. FW? Cosmopolitan. In mucous membrane of the oral cavity, esophagus, and crop. Development direct, or Intermed. hosts ?**annelids:** OLIGOCHAETES. Generalist (1). (According to Baruš & Sergejeva, 1990b, information on life cycles in the literature does not apply to this species as they define it.) *Capillaria pachyderma* (Linstow, 1877) is a synonym, although the the capillariids referred by Gallimore (1964) to this species appear to be *Baruscapillaria obsignata.* Sometimes placed in genus *Thominx.*

Subclass Secernentea

Order Strongylida

Superfamily Trichostrongyloidea

Family Amidostomidae

Subfamily Amidostominae

Amidostomum anseris (Zeder, 1800)

In *Tachybaptus ruficollis.* Under cuticle of gizzard. FW. Cosmopolitan. Life cycle direct; birds swallow larvae, which may also penetrate skin. Parasite of anatids, rare in grebes (2).

Amidostomum fulicae (Rudolphi, 1819)

In *Podiceps cristatus* (Kibakin 1965), *Tachybaptus ruficollis, P. nigricollis.* Under cuticle of gizzard. FW. Eurasia, Afr., N. Amer. Life cycle direct. *Amidostomum raillieti* is considered a synonym by Baruš *et al.* 1978. Parasite of coots (*Fulica*), rare in grebes (2). Also reported from ducks.

Subfamily Epomediostominae

Epomidiostomum uncinatum (Lundahl, 1848)

In *Tachybaptus ruficollis, Podiceps grisegena, P. cristatus.* Under cuticle of gizzard. FW. Cosmopolitan. Life cycle direct. Parasite of waterfowl, rare in grebes (2).

Order Ascaridida

[Superfamily Heterakoidea]

[Family Heterakidae]

[Subfamily Heterakinae]

[*Heterakis gallinarum* (Schrank, 1788)

In *Podiceps* sp. (Baruš *et al.* 1978). T, FW? Cosmopolitan. Caeca. Direct development through ingesting eggs or indirect from eating earthworms containing larvae (R. C. Anderson, *in litt.*). Common parasite of gallinaceous birds, probably incidental in grebes (0).]

Superfamily Ascaroidea

Family Anisakidae

Subfamily Anisakinae

Contracaecum andersoni Vevers, 1923

In *Tachybaptus ruficollis.* Small intestine. FW? Eurasia, S. Amer. Intermed. hosts, ?copepods, then ?fishes. Generalist (1).

Contracaecum microcephalum (Rudolphi, 1809)

In *Podiceps auritus, P. grisegena, P. cristatus.* Stomach, intestine. FW. Cosmopolitan. Intermed. hosts, **crustaceans:** COPEPODS, Cyclopidae (*Cyclops*), then fry of FW **fishes:** Cobitidae (*Misgurnus*), Cyprinidae (*Alburnus, Cyprinus, Scardinius*), Esocidae (*Esox*), or **insects:** ODONATA (nymphs), Zygoptera, Agrionidae (*Agrion*), Coenagrionidae (*Coenagrion*), Anisoptera, Aeschnidae (*Anax*); DIPTERA, Chironomidae (*Chironomus*). FW fishes may also act as paratenic hosts. Generalist, most common in Ciconiiformes (1).

Contracaecum micropapillatum (Stossich, 1890)

In *Tachybaptus ruficollis.* Stomach, intestine. FW. Eurasia, Afr., N. Amer., Austr. Intermed. hosts, **crustaceans:** COPEPODS, Cyclopidae (*Acanthocyclops, Cyclops, Eucyclops, Macrocyclops, Mesocyclops*), Diaptomidae (*Arctodiaptomus*); AMPHIPODS, Gammaridae (*Gammarus*), and fry of FW **fishes:** Cyprinidae (*Cyprinus carpio*). Paratenic hosts include **insects:** ODONATA (nymphs), Zygoptera, Agrionidae (*Agrion*), Coenagrionidae (*Coenagrion*), Anisoptera, Aeschnidae (*Aeschna, Anax*), **amphibians:** ANURANS, (tadpoles of "frogs," and **fishes:** Cyprinidae (*Abramis brama, Alburnus alburnus, Rutilus rutilus, Tinca tinca*), Poeciliidae (*Gambusia affinis*). Reports from experimental work by Semenova summarized in Anderson (1992). Generalist, most common in Pelecaniformes (1).

Contracaecum ovale (Linstow, 1907)

In *Tachybaptus novaehollandiae* (Mawson *et al.* 1986); *Podilymbus podiceps* (Gallimore 1964), *Aechmophorus occidentalis* (Stock & Holmes 1987b); *T. ruficollis, Podiceps auritus, P. grisegena* (voucher in USNPC No. 079342.00), *P. cristatus, P. nigricollis.* Stomach, small intestine. FW. Cosmopolitan. Intermed. hosts, **crustaceans:** COPEPODS, Cyclopidae (*Macrocyclops*), then **insects:** ODONATA (nymphs), Zygoptera, Agrionidae (*Agrion*), Coenagrionidae (*Coenagrion*) and fry of FW fishes. *C. nehli, C. podicipitis, C. ruficolle,* and *C. spasskii* considered synonyms of *C. ovale.* Generalist, common in grebes (1).

**Contracaecum praestriatum* Moennig, 1923.

In *Poliocephalus poliocephalus* (Mawson *et al.* 1986), *Tachybaptus ruficollis, Podiceps nigricollis.* Stomach? FW? Eurasia, Afr., Austr. Intermed. hosts? Reports from the Palearctic region need verification. Reported only from grebes (3). Possibly a synonym of *C. ovale.*

Contracaecum quincuspis Lucker, 1941

In *Tachybaptus dominicus* (voucher in USNPC No. 065658.00). FW. N. Amer. (Texas). Described from *Anhinga anhinga* (?2). Although McDonald (1969:589-591) lists *T. dominicus* as a host for *C. spiculigerum,* he makes no mention of *C. quincuspis.*

Contracaecum spiculigerum (Rudolphi, 1809)

In *Podilymbus podiceps* (Threlfall 1968), *Tachybaptus dominicus* (McDonald 1969:589-591), *T. ruficollis, Podiceps auritus, P. grisegena, P. cristatus, P. nigricollis.* Proventriculus, intestine, stomach. FW, SW. Cosmopolitan. Intermed. hosts, **crustaceans:** COPEPODS, Cyclopidae (*Cyclops, Macrocyclops, Mesocyclops* [FW], Family? (*Tigriopus,* experimentally [SW]), Diaptomidae (*Diaptomus*), [FW], AMPHIPODS, Gammaridae (*Gammarus*), **insects:** ODONATA, Zygoptera, Agrionidae (*Agrion*), Coenagrionidae (*Coenagrion*), DIPTERA Chironomidae (sp.) then **insects:** ODONATA (nymphs), Zygoptera, Agrionidae (*Agrion*), Coenagrionidae (*Coenagrion*), or **fishes:** Amiidae (*Amia*), Anguillidae (*Anguilla*), Atherinidae (*Labidesthes, Menidia*), Catostomidae (*Catostomus, Erimyzon, Ictobius*), Centrarchidae (*Archoplites, Centrarchus, Elassoma, Enneacanthus, Lepomis* [incl. *"Chaenobryttus"* and *"Sclerotis"*], *Micropterus, Pomoxis*), Centropomidae (*Centropomus*), Clupeidae (*Dorosoma*), Cottidae (*Myoxocephalus*), Cyprinidae (*Aspius, Gila, Notegonimus, Ptychocheilus, Rhinichthys, Ricardsonius*), Cyprinodontidae (*Fundulus, Jordanella*), Eleotridae (*Dormitator*), Esocidae (*Esox*), Ictaluridae (*Ictalurus, Noturus,* [*"Schilboeodes"*], *Pylodictis*), Labridae (*Tautogolabris*), Lepisosteidae (*Lepisosteus*), Nototheniidae (*Notothenia*), Percichthyidae (*Morone*), Percidae (*Etheostoma, Gymnocephalus* [*"Acerina"*], *Perca*), Pleuronectidae (*Pleuronectes* [*"Pseudopleuronectes"*]), Poeciliidae (*Poecilia* [*"Lebistes"*]), Polyodontidae (*Polyodon spathula*), Salmonidae (*Oncorhynchus, Salmo, Salvelinus*), Sciaenidae (*Aplodinotus grunniens*), Serranidae (*Roccus mississippiensis*), Siluridae (*Silurus*), experimentally in Poeciliidae (*Gambusia, Heterandria, Poecilia* [*"Lebistes"* and *"Mollienesia"*]). Paratenic hosts, **fishes:** Cyprinidae (*Tinca tinca*). Generalist in both FW and marine birds (1). *Contracaecum rudolphii* is a synonym.

[*Contracaecum* sp.

In *Tachybaptus rufolavatus* (Vassiliades 1970). Only larval stages found. FW? Madagascar. Intermed. hosts? (0).]

Subfamily Toxocarinae

Porrocaecum crassum (Deslongchamps, 1824)

In *Podiceps grisegena.* Stomach, small intestine. FW, T. Eurasia. Intermed. hosts, **annelids:** OLIGOCHAETES [T], Glossoscolecidae (*Criodrilus*), Lumbricidae (*Allolobophora, Dendrobaena, Eisenia, Eiseniella, Eophila, Octolasium*) infected, at least experimentally. Common in anatids, rare in grebes (2).

**Porrocaecum praelongum* (Dujardin, 1845)

In *Podiceps auritus,* type and only known host. Intestine. T?, FW? Europe, not reported since original description (5). Intermed. hosts? Status in question.

Porrocaecum reticulatum (Linstow, 1899)

In *Podiceps cristatus* (Chiriac 1965). Intestine. FW. Eurasia, N. Amer., Afr. Infective larvae in **fishes:** Cottidae (*Cottus* sp.), Cyprinidae (*Cyprinus carpio, Pelecus cultratus*). Heron specialist, rare in grebes (2).

Order Spirurida

Suborder Camallanina

Superfamily Dracunculoidea

Family Dracunculidae

Avioserpens mosgovoyi Supryaga, 1965

In *Tachybaptus ruficollis, Podiceps grisegena, P. cristatus.* In hypodermal tissue, especially in submaxillary region, where it forms tumors. Eurasia. FW. Intermed. hosts, **crustaceans:** COPEPODS, Cyclopidae (*Cyclops*), Diaptomidae (*Diaptomus*). Paratenic hosts, **insects:** ODONATA (nymphs), **fishes:** Cyprinidae (*Rutilus rutilus*), Gobiidae, Gasterosteidae, **amphibians:** ANURANS, "frogs." Generalist, most common in grebes and coots, also in ducks (1). Life cycle summarized in Anderson (1992).

Suborder Spirurina

Superfamily Gnathostomatoidea

Family Gnathostomatidae

Subfamily Gnathostomatinae

Gnathostoma spinigerum Owen, 1836

Third-stage larvae in muscles of *Tachybaptus ruficollis* in Japan, (Uchida *et al.* 1991). FW. Asia, Afr. Second stage larvae in **crustaceans:** COPEPODS, Cyclopidae (*Cyclops, Eucyclops, Mesocyclops, Thermocyclops*), third stage larvae in a wide variety of paratenic hosts (**fishes, amphibians, reptiles, birds,** and **mammals** and, experimentally, in crabs). Larvae transfer readily from one paratenic host to another. Definitive hosts, mainly dogs and cats, also humans. Life cycle in Anderson (1992).

[Superfamily Spiruroidea]

[Family Spiruridae]

[*Pseudocystidicola skrjabini* (Layman, 1933)

In *Podiceps nigricollis.* FW?, SW? Eurasia. (Lake Issyk-Kul, Kirgiziya). No details given. (Iksanov & Dikambaeva 1962). Intermed. hosts? This parasite of fishes is presumably incidental in birds (0).]

Superfamily Habronematoidea

Family Tetrameridae

Subfamily Tetramerinae

Tetrameres fissispina (Diesing, 1861)

In *Podiceps auritus, Aechmophorus occidentalis* (Gallimore 1964), *Tachybaptus ruficollis, P. grisegena, P. cristatus, P. nigricollis.* Proventriculus (females in glands, males in lumen, Gallimore 1964). FW. Cosmopolitan. Intermed. hosts, **flatworms:** TURBELLARIANS, Planariidae (*Planaria*), **annellids:** OLIGOCHAETES, Lumbricidae (*Eisenia*), **crustaceans:** AMPHIPODS, Gammaridae (*Gammarus*), CLADOCERANS, Daphniidae (*Daphnia*), ISOPODS, Asellidae (*Asellus*), Idotheidae (*Idothea* [experimentally]), OSTRACODS, Cypridae (*Heterocypris*), **insects:** EPHEMEROPTERA, Baetidae (*Cloeon*), ORTHOPTERA, Acrididae (*Gastrimargus* [*"Gastricnargus"*]), Blattidae (*Periplaneta*), DIPTERA, Chironomidae (*Chironomus* [*"Tendipes"*], *Cricotopus, Culicoides, Polypedilum* [*"Polipedium"*], *Procladius*). Paratenic hosts, **fishes:** Clupeidae (*Caspialosa brashnikovi*), Cyprinidae (*Rutilus rutilus, Scardinius erythrophthalmus*), Gobiidae (*Neogobius fluviatilis, N. melanostomum*), Percidae (*Stizostedion* [*"Lucioperca"*] *lucioperca*). Generalist (1). Life cycle in Anderson (1992).

**Tetrameres gubanovi* Shigin, 1957

In *Tachybaptus novaehollandiae* (Mawson *et al.,* 1986), *T. ruficollis* (Baruš & Zajíček 1967), *Podiceps grisegena, P. cristatus, P. nigricollis.* Esophagus, proventriculus. FW? Eurasia, Austr. Intermed. hosts, crustaceans? Apparently confined to grebes (3). Placed in *Tropisurus* by Baruš & Zajíček 1967.

Superfamily Acuarioidea

Family Acuariidae

Subfamily Acuariinae

Cosmocephalus obvelatus (Creplin, 1825)

In *Aechmophorus occidentalis* (Gallimore 1964 [as *C. firlottei*]), *Podiceps auritus, P. grisegena, P. cristatus, P. nigricollis*. Esophagus. FW, SW. Cosmopolitan, except S. Amer. (Reported from four genera of Alcids by Baruš *et al.* 1978). Intermed. hosts, **crustaceans:** AMPHIPODS, Crangonyctidae (*Crangonyx laurentianus*), Gammaridae (*Gammarus fasciatus*), Talitridae (*Hyalella azteca*). Paratenic hosts, **fishes:** Cottidae (*Cottus* sp.), Cyprinidae (*Notropis hudsonius, Semotilis atromaculatus*), Gasterosteidae (*Gasterosteus aculeatus*), Osmeridae (*Osmerus mordax*). *Gasterosteus* and *Osmerus,* which are found in both fresh and salt water, may be source of infection in marine habitats. Life cycle in gulls in Wong *et al.* 1982b. Species redescribed by Anderson *et al.* (1981), who consider *C. diesingi* and *C. firlottei* synonyms. Generalist, most common in gulls (1).

Echinuria uncinata (Rudolphi, 1819)

In *Tachybaptus ruficollis, Podiceps auritus, P. grisegena, P. cristatus, P. nigricollis*. Proventriculus, especially near the gizzard. FW. Cosmopolitan. Intermed. hosts, **crustaceans:** primarily CLADOCERANS, Daphniidae (*Daphnia, Simocephalus* and, experimentally, *Ceriodaphnia*), also in CONCOSTRACANS, Lynceidae (*Lynceus brachyurus*) and, at least experimentally, AMPHIPODS, Gammaridae (*Gammarus*), ISOPODS, Asellidae (*Asellus*), and OSTRACODS, Cypridae (*Heterocypris*). Common in ducks, in which infections may be fatal. Rare in fish-eating birds (2). Life cycle summarized in Anderson (1992).

[*Dispharynx* sp.

Immatures in *Podiceps nigricollis* (Gallimore 1964). Only record from grebes. Probably incidental from land-based intermediate hosts or based on a misidentification (0).]

Paracuaria adunca (Creplin, 1846)

In *Podiceps grisegena* (Smogorzhevskaya 1990), *Tachybaptus ruficollis, P. auritus, P. cristatus, P. nigricollis.* Most numerous near junction of proventriculus and gizzard. FW. Eurasia, N. Amer. Intermed. hosts, **crustaceans:** AMPHIPODS, Crangonyctidae (*Crangonyx laurentianus*), Gammaridae (*Gammarus duebeni*), Talitridae (*Hyalella azteca*). Paratenic hosts, **fishes:** Cyprinidae (*Notropis hudsonius, Semotilus atromaculatus,* and, experimentally, *Carassius auratus*), Gasterosteidae (*Culaea inconstans*). Life cycle in gulls in Anderson *et al.* (1982). Wong *et al.* (1982a) consider *adunca* type and only member of genus and *P. tridentata* (Linstow, 1877) a synonym. Report of infective larvae of *P. "tridentata"* found in **insects:** COLEOPTERA (larvae) Tenebrionidae (*Pimelia subglobosa, Tentiria taurica*). Baruš *et al.* (1978) probably based on misidentifications. If *P. tridentata* is included in this species and if records from *Cyclorrhynchus psittacula* and *Aethia pygmaea* are correct, it must be transmitted in salt water. In that case anadromous species of *Osmerus* would be likely second intermediate hosts. Often placed in genus *Cosmocephalus.* Common, widespread parasite of fish-eating birds, generalist (1).

Rusguniella elongata (Rudolphi, 1819)

In *Podiceps grisegena, P. cristatus, P. nigricollis.* Esophagus and gizzard. FW? Eurasia, N. Afr. Intermed. hosts? Generalist (1). *Rusguniella skrjabini* is considered a synonym by Baruš *et al.* 1978.

**Rusguniella wedli* Williams, 1929

In *Tachybaptus ruficollis, Podiceps cristatus, P. nigricollis.* Proventriculus, under parietal layer of peritoneum, muscles of femur, kidneys. Eurasia. FW? Intermed. hosts? Apparently confined to grebes (3). Considered a synonym of *R. elongata* by Smogorzhevskaya 1990.

[*Skrjabinoclava decorata* (Solonitsin, 1928)

In *Podiceps auritus, P. cristatus.* Proventriculus. FW?, SW? Eurasia. Intermed. hosts? Specialist in shorebirds, reports from grebes and passerine birds need verification. (0)]

[*Skrjabinoclava horrida* (Rudolphi, 1809)

In *Tachybaptus novaehollandiae* (Mawson *et al.* 1986). Proventriculus. FW?, SW? Eurasia, Cuba, Austr. Intermed. host? Common in shorebirds, reports from grebes and larids need verification. (0).]

[*Syncuaria ciconiae* (Gilbert, 1927)

In *Tachybaptus ruficollis* (Baruš *et al.* 1978). Under cuticle of gizzard. FW? Eurasia. Intermed. hosts? Specialist in storks, report from grebe needs verification. (0).]

**Syncuaria decorata* (Cram, 1927)

In *Podiceps auritus,* type host. *Aechmophorus occidentalis* (Gallimore 1964), *Tachybaptus ruficollis, P. grisegena, P. cristatus, P. nigricollis.* Under cuticle of gizzard, proventriculus. FW? Eurasia, N. Amer. Intermed. hosts? Grebe specialist, one report from *Aythya fuligula* (3). Genus revised by Wong *et al.* (1986). Formerly placed in the genus *Decorataria.*

**Syncuaria longialula* Wang, 1976

In *Podiceps nigricollis,* type and only known host (?5). Proventriculus? FW?, SW? Asia (China). Intermed. hosts?

Syncuaria squamata (Linstow, 1883)

In *Tachybaptus ruficollis.* In muscles of gizzard. FW. Eurasia, N. Amer. Austr. Intermed. hosts, **crustaceans:** OSTRACODS, Cypridae (*Cypris pulera*), experimentally in Cyclocypridae (*Cyclocypris ovum*), Cypridopsidae (*Cypridopsis vidua*), then **fishes:** as obligate paratenic hosts (experimentally in Cyprinidae [*Carassius auratus*] Wong *et al.* 1987). Cormorant specialist, rare in grebes (2). Placed in genus *Skrjabinocara* by Baruš *et al.* 1978.

[*Syncuaria* sp.

In *Tachybaptus novaehollandiae, Podiceps cristatus.* Austr. Mawson *et al.* 1986. Further identification needed.]

Subfamily Seuratiinae

Streptocara crassicauda (Creplin, 1829)

In *Tachybaptus novaehollandiae, Poliocephalus poliocephalus* (Mawson *et al.* 1986), *Aechmophorus occidentalis* (Gallimore 1964), *T. ruficollis, Podiceps auritus, P. grisegena, P. cristatus, P. nigricollis.* Under cuticle of gizzard. FW, SW. Eurasia, N. Amer., Austr. Intermed. hosts, **annelids:** LEECHES, Erpobdellidae (*Nephelopsis*), **crustaceans:** AMPHIPODS, Gammaridae (*Gammarus lacustris, G. triacanthus* [FW], *G. locusta, G. maeoticus* [SW]), Talitridae (*Hyalella azteca* [FW]). Paratenic hosts, **fishes:** Clupeidae (*Caspialosa braschnikowi*), Cyprinidae (*Carassius carassius, Phoxinus perenurus, Rutilus rutilus, Scardinius erythrophthalmus*), Gobiidae (*Neogobius fluviatilis, N. melanostomus*), Percidae (*Stizostedion* [*"Lucioperca"*] *lucioperca*). Life cycle in Denny 1969; Laberge *et al.* 1989. For a revision of *Streptocara,* see Gibson (1968). Generalist (1). Widespread in waterfowl.

**Streptocara recta* (Linstow,1879)

In *Tachybaptus ruficollis* (Yamaguti 1935), *T. novaehollandiae, Poliocephalus poliocephalus,* (Mawson *et al.* 1986), *Podiceps auritus* (voucher USNPC No. 070943.00), *P. cristatus* (Smogorzhevskaya 1990), *P. nigricollis* (McDonald 1969:646). Under cuticle of gizzard? FW? Eurasia, N. Amer., Austr. Intermed. hosts, ?**crustaceans:** AMPHIPODS, then ?**fishes.** Grebe specialist (3). Considered a *species inquirenda* by Baruš *et al.* 1978. Probably a synonym of *S. crassicauda.*

Superfamily Filarioidea

Family Onchocercidae

Subfamily Dirofilariinae

Pelecitus fulicaeatrae (Diesing, 1861)

In *Tachybaptus ruficollis* (Yamaguti 1935), *Podiceps auritus, P. grisegena* (vouchers in USNPC Nos. 077837.00, 079934.00, and, as *Spirofilaria podicipitis,* 056301.00), *P. nigricollis* (Bartlett & Greiner 1986), *P. cristatus.* Larvae in skin of shank, adults under the skin, coiled around ankle joints. Eurasia, N. Amer., Afr. Intermed. hosts, **insects:** PHTHIRAPTERA, Amblycera, MENOPONIDAE (*Pseudomenopon*) (Bartlett & Anderson 1987). Specialist in coots, also in grebes (2). For list of other hosts, see Bartlett and Greiner (*op. cit.*). *Spirofilaria podicipitis* (Yamaguti 1935) is a synonym (Vanderburgh *et al.* 1984). Subspecies *P. f. grisegenae* named by Bartlett & Anderson (1989b) from *P. grisegena* in N. Amer. The life cycle of this nematode is of special interest because the adults and larvae are extremely cold hardy and can withstand freezing (Bartlett 1992); the adults are capable of reproducing for only a brief period, which is believed to prevent overinfection and death of the intermediate host; and they live on in the ankle joint, where if they died, they could not be resorbed and presumably would cause arthritis and eventually the death of the bird (Anderson & Bartlett 1994).

Subfamily Splendidofilariinae

**Carinema bilqeesae* Gupta & Jaiswal, 1989

In *Tachybaptus ruficollis,* type and only known host (5). Body cavity. Asia (India). FW? Intermed. hosts?

THE EXTERNAL PARASITES OF GREBES

Three groups of external parasites of grebes are included in this work: the leeches (Hirudinea), the mites (Acari) and the lice (Phthiraptera). The few records of leeches actually taken from grebes probably make the frequency with which these parasites feed on grebes seem less than it is.

Although the mites and lice of grebes have not been well studied, what is known about them indicates that the number of species that eventually may be found on these birds will not be large. Still, collections of these arthropod groups from grebes in the Southern Hemisphere, and especially South America, might double the number of species known from these birds.

THE LEECHES (HIRUDINEA) OF GREBES

The leeches (Phylum Annelida, Class Hirudinea) are carnivorous or parasitic segmented worms. The name comes from the Latin word, *hirudo* (genitive *hirudinis*), for leech. These worms are an offshoot of the oligochaete worms, the group including the earthworms, and, like the earthworms, they are characterized by a clitellum. This is a transient, slightly raised, differently colored band covering some of the anterior segments of the body. When the eggs have been laid, the clitellum produces a cocoon, which, with the eggs, slips over the head of the worm. The life cycle is direct, the newly-hatched young resembling the adults. For a detailed account of the biology of leeches and an extensive bibliography, see Sawyer (1986).

The group contains approximately 250 species and is of worldwide distribution. Most leeches inhabit fresh water, although some are marine and others are found in wet forests. All can crawl and some can swim, but the most familiar form of locomotion is "inching" rather like that of a geometrid caterpillar, which in leeches is accomplish by means of a sucker on each end of the body.

Most leeches are predators on aquatic invertebrates, but several groups are blood-sucking parasites of vertebrates. Like almost all blood-feeding animals, including vampire bats, sanguivorous leeches produce anticoagulants. Leeches are known to transmit trypanosomes and other disease-producing organisms, especially in fishes.

Members of one genus of parasitic leeches, *Theromyzon,* called "duck leeches," parasitize a variety of water birds, including grebes. These leeches are said to be attracted by heat and by the odor of the oil-gland secretion, which the birds spread on their feathers in the process of preening (Sawyer 1986:576). Once on the bird, the leeches move forward, following the lie of the feathers, to the head where, most frequently, they attach themselves in the nasal passages, or more rarely, around the eyes. In the latter case, there is a tendency for both adult and young leeches to attach themselves under the nictitating membrane and for young, also to attach themselves under the eyelids. In both sites, they are safe from removal by the hosts' scratching. Leeches in the nasal passages are also safe from this scratching, but small leeches sometimes are ejected by the birds' sneezing. Leeches entering through the nares may penetrate further into the body (trachea, lungs). Other uncommon places of attachment include the mouth, legs, feet, breast and cloaca. Parasitism by leeches is known to result in blindness or death of waterfowl, especially the young (*e.g.,* Bartonek & Trauger 1975).

Although genera of parasitic leeches tend to be specific to major groups of vertebrates, there appears to be little, if any, host specificity within some of these groups. In the case of *Theromyzon,* waterfowl (Anatidae) are the most frequent victims, although coots, grebes, loons, gulls, herons, and some other birds are also attacked. The high frequency of attack on waterfowl is probably more a matter of these birds' relative abundance and ease of access to the leeches than one of specificity. Perhaps because leeches drop off their hosts between feedings and because it is easier to collect leeches when they are free in the water than when they are feeding, host records, especially of birds other than waterfowl, are scarce in the literature.

From the very few records, it might be thought that leeches rarely feed on grebes, but Gallimore's study (1964) shows that where a species of *Theromyzon* is common, all local species of grebe may be subject to attack by these parasites.

What host records there are, support Sawyer's statement (1986:576) that species of *Theromyzon* are not specialists when it comes to the type of water bird they parasitize.

In the past, there has been much confusion regarding the identification of North American species of *Theromyzon.* Most of this has been cleared up by Davies & Oosthuizen

(1993) and Oosthuizen & Davies (1992, 1993), but care must be taken to bring earlier identifications into line with the above-cited works. In many instances, this will require reexamination of the material on which the records are based. This is especially true of those with the male and female gonopores separated by two annuli (*fide* Davies *in litt.*).

Synonyms. In earlier literature, references to species of *Theromyzon* Philippi, 1867 can be found under the genera *Clepsine* Savigny, 1822, *Glossiphonia* Johnson, 1816, *Protoclepsine,* Moore, 1898, and *Protoclepsis* Livanov, 1902.

Theromyzon biannulatum Klemm, 1977, new name for *T. occidentalis* Moore, 1912, preoccupied by *T. occidentalis* Verrill, 1874, is considered a *nomen nudum* by Oosthuizen & Davies (1993).

Theromyzon sexoculatum (Moore, 1891) = *T. tessulatum fide* Oosthuizen & Davies (1993).

Theromyzon lineatum Sciacchitane, 1963 = *T. cooperi fide* Oosthuizen (1993).

The Leeches reported to feed on grebes

Class Hirudinea
  Order Rhynchobdellida
    Family Glossiphoniidae
      Placobdella ornata (Verrill, 1872)
        On *Podiceps auritus* (Moore 1964). Found among the feathers "partly distended with blood." FW. N. Amer. Turtle specialist. One record on grebes. Presumably rare or incidental on waterbirds.
      Theromyzon cooperi (Harding, 1932)
        On *Tachybaptus ruficollis* (Oosthuizen & Fourie 1985) FW. Afr.
      Theromyzon "occidentalis" (Verrill, 1874)
        On *Podilymbus podiceps* (Sooter 1937). FW. N. Amer. (Iowa). This record presumably is referable to one of the four recognized species of *Theromyzon* with two annuli between the male and female gonopores. (See Oosthuizen & Davies 1993.)
      Theromyzon tessulatum (O. F. Müller, 1714)
        On *Podiceps cristatus* (Mann 1951). FW. N. Amer., Eurasia.
      Theromyzon "trizonare" Davies & Oosthuizen, 1993
        On *Podilymbus podiceps, Podiceps auritus, P. grisegena, P. nigricollis, Aechmophorus occidentalis* (Gallimore 1964). The same records of the first four reported also by Moore (1964), and the last (without reference to the source) by Moore (1966). In nasal cavity. FW. N. Amer. (Alberta). These specimens, originally identified as *T. rude* (Baird, 1863), are probably referable to this species, but I have been unable to find their whereabouts so that their identification could be checked.

THE MITES (ACARINA) OF GREBES

The Acari (mites and ticks) form a varied group of small to very small arthropods, typically classified into two orders. The number of species is estimated in the millions, but only a few have been described. Approximately one-half the described species of acarines are associated with other animals, the remainder occupying almost every conceivable niche available to small arthropods. Such habitats include soil, detritus, plant substrates, and both fresh and salt water. Plant-associated mites may feed on cellular contents or phloem sap, and many produce galls or cause serious damage to crops. Many mites are predaceous and may be beneficial in preying on injurious mites and small insects. Some acarines, like ticks, chiggers, and follicle mites are found on humans and their livestock, where they may cause itching or mange, or may act as vectors of disease. On avian hosts, parasitic and ectoparasitic (commensal) mites may occur in a wide range of habitats including the surface of the feathers or skin, feather follicles, subcutaneous tissues, nasal passages, lungs, and air sacs. Some even enter the lumen of the feather quills where they feed on the quill matrix itself or pierce the quill wall and feed on tissue fluid. One group, in the family Cheyletidae includes species that are predaceous on other quill-inhabiting mites.

The basic (and presumably ancestral) life cycle consists of an egg, one or two six-legged stages (prelarva and larva), one or more (usually three) eight-legged nymphal instars (protonymph, deutonymph, and tritonymph), and the adult. Viviparity and suppression of instars have evolved in some groups, reaching an extreme in some forms in which the female gives birth to mature adults.

Although mites are perhaps the most widespread of parasitic arthropods, the number of species known from grebes is small and limited to forms inhabiting the nostrils (6) and feathers (6). This is presumably a result of grebes' extremely aquatic habits and limited physical contact with other birds or places frequented by other birds on land.

Mites belonging to both the orders Parasitiformes and Acariformes inhabit the nasal passages of grebes. Species of the parasitiform family Rhinonyssidae and the acariform family Ereynetidae have adapted to this habitat. Although similar in their microhabitat choice, mites of these two lineages are otherwise quite different. The rhinonyssids move slowly in the mucus of the nasal passages, whereas the ereynetids are covered with a hydrophobic cuticle and move about actively on the surface of this mucus. Rhinonyssids feed on host blood by piercing through the mucus membranes with highly modified mouthparts. The feeding habits of the Ereynetidae are unknown, although blood is not typically observed in their digestive tracts.

The life histories of the two groups of nasal mites also differ, although both are presumably viviparous. The rhinonyssids alternate feeding with non-feeding instars. The non-feeding larva is followed by a feeding protonymph, a short-lived non-feeding deutonymph, and the feeding adult. The intranasal Ereynetidae also exhibit life-cycle compression, having a feeding larva followed directly by the adult. The nymphal stages are represented by layers of cuticle laid down during the period between the larval instar and the molt to the adult.

The mites associated with feather habitats belong to three families in the order Acariformes, all of which are believed to have arisen from a common, feather-inhabiting ancestor. The quill-wall mites (Laminosioptidae) are associated with the basal part of the feathers. These mites have been most often collected between the sheath and the rachis of developing quills. Because such mites appear trapped, it seems more likely that their natural habitat is the feather follicle itself. The food of quill-wall mites is unknown. Members of the other two families live between adjacent barbs of feathers, often in great numbers. Species in the family Analgidae typically inhabit the plumulaceous (downy) barbs of body contour feathers and the basal parts of flight and tail feathers. Analgid mites often have modified hook-like processes on their legs which enable them to maneuver among these barbs. Species in the family Ptiloxenidae, in contrast, inhabit the spaces between the barbs of the pennaceous parts of the flight and tail feathers. These mites show strongly modified morphological adaptations to this habitat including the elongated, flattened body and enlarged, sucker-like pretarsi which are pressed against the barbs to maintain the mites' positions.

All feather-inhabiting mites exhibit a life cycle only slightly modified from the ancestral acariform pattern. Eggs are glued to feathers in highly specific locations, and the prelarval instar is passed in the egg. The larva and two active nymphal instars are followed by the adult. The deutonymphal instar is suppressed in these taxa.

The food of feather mites is little known. Small projections of feather barbules have been found in the digestive tracts of some analgid mites, while algae, fungal spores, and other detritus are also observed, especially in parasites of aquatic birds. It seems most likely that the major component of the diet is the oil with which birds dress their feathers. Because feather mites often occur in very high population density, it is unlikely that most groups of external, feather-inhabiting mites are in any way detrimental to their hosts.

I am much indebted to Barry M. OConnor for rewriting and expanding the above account to include much information that is not generally available. RWS.

The classification of the feather mites is that of Gaud & Atyeo 1996.

Order Parasitiformes
Suborder Mesostigmata
Superfamily Dermanyssoidea
Family Rhinonyssidae Nasal mites.

The species of this family are quite variable. This has led to considerable splitting, which has been countered by much lumping. To date, there is no experimental evidence of non-genetic variation, so, instead of wholesale lumping, I am recognizing species about which there has been controversy on the grounds that this may provide more information. Pence (1975) provides useful keys and species, and host lists for North American forms.

**Rhinonyssus alberti* Strandtmann, 1956
From *Podiceps nigricollis,* type host, *Tachybaptus ruficollis, P. auritus* (Butenko 1984), *P. cristatus* (Domrow 1979). Eurasia, N. Amer., Austr. Grebe specialist (3).

**Rhinonyssus colymbicola* Fain & Bafort, 1963
From *Podiceps auritus,* type host, *Podiceps grisegena* (Butenko 1984). Eur. Grebe specialist (3).

**Rhinonyssus podicipedis* Feider & Mironescu, 1972
From *Podiceps cristatus,* type host. Euras. *Rhinonyssus tschomgae* Butenko, 1973, is a synonym (Butenko 1984). Known only from type host (4).

**Rhinonyssus podilymbi* Pence, 1972
From *Podilymbus podiceps.* N. Am. Known only from the original description (5).

**Rhinonyssus poliocephali* Fain, 1956
From *Tachybaptus ruficollis capensis,* type host, "*Podiceps rufficollis*" (=*T. novaehollandiae*) (Domrow 1969). Afr., Austr. Grebe specialist (3). Detailed description and figures in Fain (1957).

Order Acariformes
Suborder Trombidiformes
Superfamily Tydeoidea
Family Ereynetidae Nasal mites

**Neoboydaia colymbiformi* Clark, 1964
From *Podiceps nigricollis,* type host, *Podilymbus podiceps* (Pence 1973), *Tachybaptus novaehollandiae* (*as "Podiceps ruficollis,"* Domrow 1991). N. Amer., Austr. Grebe specialist (3).

Suborder Sarcoptiformes
Superfamily Pterolichoidea
Family Ptiloxenidae Feather mites

**Ptiloxenus colymbi* (Canestrini, 1878)
From *Tachybaptus ruficollis.* (*"Podiceps minor"* given as the type host is a synonym.) Eur. (Reports summarized by Dubinin 1956.) Report from *Gavia* needs confirmation. Otherwise known only from the type host (4). Genus confined to grebes.

**Ptiloxenus major* (Megnin & Trouessart, 1884)
From *Podiceps cristatus,* type host, *P. auritus, P. grisegena, P. nigricollis.* Eur. (Dubinin 1956). A report from *Corvus corone cornix* on the Volga Delta, where the mite was believed to have been acquired by feeding on the young of *Podiceps cristatus* (Dubinin *op. cit.*) is presumably erroneous (Atyeo *in litt.*). The name of this mite (spelled "maior" in older literature, Atyeo *in litt.*) also has appeared in the literature as *P.* "*maiory*," evidently a transliteration from Russian (B. OConnor, pers. comm.) Grebe specialist (3).

**Ptiloxenus* sp.
From *Aechmophorus* sp., (undescribed species Univ. Michigan Mus. Zool.).

**Schizurolichus elegans* Černy, 1969
From *Tachybaptus dominicus* type host, *Podilymbus podiceps* (W. T. Atyeo, pers. comm.). N. Amer. (Cuba), S. Amer. Grebe specialist (3).

Superfamily Analgoidea
[Family Psoroptoididae Feather mites]

[*Mesalgoides* (*"Mesalges"*) *oscinum* (Koch, 1840)
Report from *Tachybaptus ruficollis* (Gaud in Dolfuss 1961) is presumably an error, the type host of *Mesalgoides oscinum* is *Motacilla alba* and the genus *Mesalgoides* is characteristic of passerine birds. Members of the genus *Mesalges* are known only from the Bucerotidae.]

["*Colynisus* sp." reported from *T. ruficollis* by Gaud (in Dolfuss 1961) is a nomen nudum *fide* Atyeo *in litt.*]

Family Laminosioptidae Quill-wall mites

**Podicipedicoptes americanus* Lombert, Kethley & Lukoschus, 1979
From *Podilymbus podiceps,* type host. N. Am. Specimens also in Univ. Michigan Mus. Zool. Genus and species only known only from type host (4).

Family Xolalgidae Feather mites
Subfamily Ingrassiinae

Ingrassia colymbi Gaud, 1974
From *Tachybaptus ruficollis,* type host, *?Podiceps nigricollis.* Africa (Morocco, Transvaal, Cameroon). According to Gaud (1974), the mites from *P. nigricollis* in Morocco are very close to *I. colymbi* if not identical with it.

THE LICE (PHTHIRAPTERA) OF GREBES

The lice are external parasites of warm-blooded animals. Several chewing lice are pests of domestic birds and mammals. As a result of the economic importance of these animals, more is known about their parasites than those of wild birds.

The two suborders of chewing lice found on birds, the Amblycera and the Ischnocera, were long known by the collective name, Mallophaga. They are now believed to have been independently derived from primitive psocid-like ancestors and are thus classified as separate suborders of the order Phthiraptera, which also includes the sucking lice (suborder Anoplura).

The literature on the lice of grebes is sparse. The general account of these lice below is based on papers by Kellogg (1896) and, particularly, Calaby & Murray (1991). Hopkins & Clay (1952) is the most recent world check list of the genera and species of "Mallophaga" and their type hosts. Aside from the revisions of *Aquanirmus* by Edwards (1965) and of *Pseudomenopon* by Price (1974), most of the remaining references consist of species descriptions or regional lists.

The lice of grebes are very small insects, the largest reaching a length of ca. 10 mm. Their mouthparts are adapted for chewing. Some can run rapidly over the host's skin. A very flat body enables others to slip between feathers and the flat parts of feathers.

These insects tend to flee from light. Their sensory hairs apparently assist them in moving about in the narrow places they inhabit. They are sensitive to the odor of the host and to temperature. Optimal temperatures for feeding and breeding are slightly below that at the skin of the host, which in birds may approach the upper limits of tolerance for most animals. The production of heat by the hosts and the insulating coat of feathers or hair provide a constant, warm environment for these lice. Diving birds compress the feathers just before diving, presumably to decrease their specific gravity while under water, and expand the plumage upon surfacing. This bellows action may be likened to a lung in that it presumably aids in maintaining constant humidity and oxygen content in the air layer next to the skin. While lice can hardly make a significant change in oxygen content in the air surrounding them unless they are present in very large numbers, they are able to extract moisture from the surrounding air. However, excessively high humidities can inhibit egg laying and cause failure of development.

All the lice of birds feed to some extent on feathers. The Ischnocera tend to feed on the downy parts, whereas the Amblycera have a more varied diet, some feeding on the surface of the skin, and the eggs and nymphs of other lice. Some are known to secure blood by biting into developing feathers or through the skin, which presumably adapts them for being the intermediate host for the nematode, *Pelecitus fulicaeatrae*. They are rarely a pest on healthy wild birds, although they may become a problem on ailing ones.

Reproduction occurs throughout the year. The eggs or nits are attached to the feathers of the host and hatch into young resembling the adults in appearance.

Transmission of lice between hosts of the same species is probably largely by direct contact during brooding of the young or during mating or fighting. Transmission between host species probably is much rarer. At least in grebes, the most obvious method appears to be physical contact in the taking over of a nest of another species, although predation and fighting are possibilities.

Although many species of lice have been described from birds, many more remain to be. There are also questions about the validity of host records of some species. This may result from several causes. Birds collected at the same time may be kept together until they are prepared, allowing an opportunity for lice to move from one bird to another, and, especially in the early days, parasitologists working with external parasites may have made mistakes in the identification of the host or have forgotten which parasite came from which host.

In general, these insects inhabit specific areas of the hosts' bodies, but, in the case of those of grebes, I have found no such specific information on their distribution.

The lice of grebes are few in number of species. The reason for this is probably not that grebes are water birds, because petrels, gulls, auks, and most other waterbirds are infested with many species. Instead, the reason appears to be related to the nest platforms built by the birds themselves. Each nest is separated by water from the next one, is vigorously defended, and thus is readily accessible to few other birds.

The hosts are the principal enemies of the lice, which they remove in the course of preening, and, in some terrestrial birds, by dust-bathing. Predation by other bird lice has been reported.

Order Phthiraptera (Lice)
Suborder Amblycera (Antennae club-shaped, 4 segmented, often concealed beneath the head)
Family Menoponidae
Pseudomenopon dolium (Rudow, 1869)
On *Tachybaptus ruficollis, Podiceps auritus, P. grisegena* (Voucher in USNPC No. 079938.00), *P. cristatus, P. nigricollis, P. occipitalis, P. taczanowskii, Aechmophorus occidentalis* (Price 1974). *Pseudomenopon insolens frescai* Eichler, 1952, *P. tridens insolens* (Kellogg, 1896), *P. janiszewskae* Lucinska, 1969, *P. tridens par* (Kellogg, 1896), and *P. stuchlyi* Luscinska, 1969 are synonyms; the record of *P. dolium* from *Gavia immer* requires confirmation; and that of *P. scopulacorne* from *T. ruficollis* is incorrect (Price 1974). Formerly placed in the genera *Colpocephalum* and *Menopon.* Reports of *P. pilosum* (Scopoli, 1783) by Harrant *et al.* 1961 ex ICMVZ 17(7) and of *P. tridens* by Shcherbinina 1966 from *Tachybaptus ruficollis* refer to *P. dolium.* This species is presumably the intermediate host for the nematode *Pelecitus fulicaeatrae grisegenae* Bartlett & Anderson, 1989a, in grebes. Grebe specialist (3).
Family Laemobothriidae
Laemobothrion simile (Kellogg, 1896)
On *Podiceps nigricollis californicus* (type host), *Tachybaptus ruficollis*, Spain (Paz Martin *et al.* ex ICMVZ 19[7]) *Podiceps auritus*, ?*P. grisegena* (as *P. "rubricollis"*), *P. cristatus* (Kellogg 1896). Some of these records have been reported as *L. atrum* (Nitzsch, 1818), but Price (*in litt.*) considers all reports of this genus from grebes refer to *L. simile.* ?Generalist (?1).
Suborder Ischnocera (Antennae slender, 3 or 5 segmented, exposed)
Family Philopteridae
Aquanirmus emersoni group
Aquanirmus emersoni Edwards, 1965
On *Podiceps g. grisegena, P. g. holboellii,* type host. N. Amer., Eur. Known only from *P. grisegena* (4).
Aquanirmus occidentalis Edwards, 1965

On *Aechmophorus occidentalis,* type host. N. Amer. Known only from *A. occidentalis* and/or *A.clarkii* (4).

**Aquanirmus podilymbus* Edwards, 1965

On *Podilymbus p. podiceps,* type host, *P. p. antarcticus.* N. Amer., S. Amer. Known only from *P. podiceps* (4).

AQUANIRMUS BAHLI GROUP

**Aquanirmus bahli* Tandan, 1951

On *Tachybaptus ruficollis capensis.* India, Afr. Known only from type host (4).

**Aquanirmus chamberlini* Edwards, 1965

On *Tachybaptus d. dominicus,* type host. *T. d. brachypterus.* W. Indies, N. Amer. Known only from *T. dominicus* (4). Described as a subspecies of *A. bahli,* but considered a full species by Price (*in litt.*).

**Aquanirmus americanus* (Kellogg & Chapman, 1899)

On *Podiceps nigricollis californicus.* N. Amer. Known only from type host (4).

**Aquanirmus bucomfishi* Edwards, 1965

On *Podiceps auritus cornutus.* N. Amer. Known only from type host (4).

AQUANIRMUS COLYMBINUS GROUP

**Aquanirmus runcinatus* (Nitzsch, 1866)

On *Tachybaptus r. ruficollis,* type host. Eur. Specimens from *Podiceps cristatus* may belong to the similar but slightly larger *A. podicipis.* ?Known only from type host. (?4).

**Aquanirmus podicipis* (Denny, 1842)

On *Podiceps c. cristatus.* The record of this species from "*Colymbus*" [=*Tachybaptus*] *ruficollis capensis* by Shcherbinina (1966) presumably refers to *A. runcinatus.* ?Known only from type host (?4).

**Aquanirmus colymbinus* (Scopoli, 1763)

On *Podiceps a. auritus, P. n. nigricollis, P. n. gurneyi.* England, SW Afr. Specimens from *P. nigricollis* may belong to another species *fide* Edwards (1965). The report of this species from *T. ruficollis* (Dollfus 1961) presumably refers to *A. runcinatus.* Grebe specialist (3).

AQUANIRMUS GROUP ?

**Aquanirmus australis* Kettle, 1974

On *Poliocephalus rufopectus.* New Zealand. Known only from type host (4).

[*Incidifrons fulicae* (Linnaeus), 1758

On *Podiceps nigricollis.* Malcomson 1960, with no further information.]

[*Saemundssonia muelleri* Eichler, 1942

?On *Podiceps nigricollis californicus.* Record of Kellogg 1896 not listed as host in Hopkins & Clay (1952).]

The validity of some of the records of other lice reported from grebes has been questioned, most often on the basis of the known hosts of the genus. *Philopterus kansensis,* was described from *Podiceps nigricollis,* but this is considered an incorrect host, because the known hosts for this large genus are all passerine birds, with the possible exceptions of one motmot and two woodpeckers. Lice of the large genus *Saemundssonia* parasitize Charadriiform and Procellariiform birds plus cranes and tropicbirds while those of the genus *Incidifrons* are found only on rallids, including coots. In view of the association of coots with grebes (p. 60), the report of *Incidifrons* from a grebe seems more likely than that of *Saemundssonia.*

LIST OF PREY SPECIES TAKEN BY GREBES

The following list of the kinds of prey taken by each species (and in a few instances, subspecies) of grebes has been prepared in such a way that it can be used in computer searches for all the grebe species known to feed on a species, genus, family, or higher group of organisms; and the classification of prey species used is the same as that used for the intermediate and paratenic hosts of the parasites. (See Methods section p. 4)

No attempt has been made to indicate the relative importance of each prey species in the diet of each grebe species. Although several grebe species are specialists, all are opportunists and may take prey on which they do not specialize when such prey is particularly abundant or their speciality is rare or unavailable. (For information on specialization on different kinds of prey and character displacement, see the important paper by Fjeldså [1983a] and his other papers listed below.)

There are other reasons for listing all the prey species known for a grebe species. The chance of becoming infected by a parasite is determined by the number of individuals of an intermediate host consumed. If small like a cladoceran, this prey species may be taken by hundreds or even thousands and still make up a small percentage of the bulk of the total food intake; if large like a fish, larger larval parasites impossible to be carried by a small intermediate host may be taken, and, if the fish acts as a paratenic host, more individuals of a small intermediate host may be taken. Thus a large animal may also be a potential intermediate host for a greater number of parasite species as well as individuals. Furthermore, grebes are occasionally known to harbor parasites for which the intermediate hosts are terrestrial. These are presumably acquired from terrestrial intermediate hosts accidentally blown onto or washed into the water. Therefore, it is important to list such prey items.

As elsewhere in this paper, "FW" and "SW" stand for "fresh water" and "salt water" (including saline lakes), and "T" stands for "terrestrial arthropods" including land-based flying insects. As in the lists of intermediate and paratenic hosts the names of genera and species are in italics, those of families are in large and small capital letters, those of the next highest category used are in capital letters, and the highest category are in bold face. The sequence of grebe species follows that of Storer (1979).

In preparing this list, most of the references on food habits listed in the bibliography by Vlug & Fjeldså (1990) have been consulted, but many have not been included in the literature cited in this paper because they do not list prey species not found in other papers here cited. Thus, this list should include all species I have been able to find known as prey for each species of grebe but not all references to these species.

The total numbers of prey species taken by a grebe species must not be inferred from the relative lengths of these lists because much or most of the variation can be attributed to the relative amount of work done on the species.

Rollandia rolland (Quoy & Gaimard)
FW, SW. S. Am. Generalist.

FW. **Lake Junín. Bryozoans:** ("a few statoblasts"). **Annelids:** OLIGOCHAETE sp. **Crustaceans:** CLADOCERANS, DAPHNIIDAE (*Simocephalus* sp.); OSTRACODS, CYPRIDAE (*Candona*) FAMILY? (*Chlamydotheca*); AMPHIPODS, TALITRIDAE (*Hyalella simplex*). **Insects:** ODONATA Zygoptera sp.; HEMIPTERA, CORIXIDAE (*Trichocorixa* *reticulata*), Veliidae (sp.); COLEOPTERA, Dytiscidae (*Liodessus riveti, Lancetes theresae*), Elmidae ("Helmidae") (*Macrohelmis* sp.), Staphilinidae sp. [T]; DIPTERA, Chironomidae sp., Ephydridae sp. **Acarina:** HYDRACARINA sp. **Mollusks:** GASTROPODS Lymnaeidae (*Limnaea viator*), Planorbidae (*Taphius montanus*). **Fishes:** Cyprinodontidae (*Orestias.* sp.).

Lake Titicaca. Annelids: OLIGOCHAETES, Tubificidae sp.; LEECHES. (?*Helobdella*). **Crustaceans:** OSTRACODS sp.; AMPHIPODS, Talitridae (*Hyallela* spp.). **Insects:** ODONATA, Zygoptera nymphs spp., Coenagrionidae (*Amphiagrion titicacae*), Anisoptera nymphs spp., Aeschnidae (*Aeschna brevifrons*), Libellulidae (*Sympetrum illotum*); HEMIPTERA Corixidae spp., Notonectidae *(Buenoa* sp.), Saldidae sp.; COLEOPTERA Dytiscidae spp., Hydrophilidae spp., Elmidae (*Macrohelmis* sp.); DIPTERA Chironomidae spp., Ephydriidae spp. **Mollusks:** GASTROPODS, Planorbidae (*Taphius montanus*). **Fishes:** Cyprinodontidae (*Orestias* spp.). **Amphibians:** ANURANS, Leptodactylidae (*Pleurodema marmorata*).

Terrestrial arthropods. Spiders: (sp). **Insects:** COLEOPTERA, Staphilinidae sp.; DIPTERA, Brachycerous fly sp.; HYMENOPTERA, Psammocharidae (*Pepsis* sp.).

References: Fjeldså (1981a,b).

Rollandia microptera (Gould)

FW. S. Am. Generalist. Bill, fig. 6g.

FW. **Crustaceans:** CLADOCERANS sp.; OSTRACODS Family? (*Chlamydotheca* sp.); AMPHIPODS, Talitridae (*Hyallela*). **Insects:** ODONATA, Zygoptera Coenagrionidae (*Amphiagrion* sp.), Anisoptera Aeschnidae (*Aeschna* sp.); HEMIPERA, Corixidae spp., Notonectidae (*Buenoa* sp.); COLEOPTERA, Dytiscidae, Hydrophilidae, Elmidae ("Helmidae") (*Macrohelmis*); DIPTERA, Chironomidae spp. **Mollusks:** GASTROPODS, Planorbidae (*Taphius montanus*). **Fishes:** Cyprinodontidae (*Orestias* spp.), Atherinidae (*Odontesthes bonariensis* [introduced]). **Amphibians:** ANURANS, "Batrachians" Allen (1876).

Terrestrial insects: COLEOPTERA, Dermestidae, Meloidae; DIPTERA, flies spp.; HYMENOPTERA, Formicidae sp.

References: Allen (1876), Fjeldså (1981a).

Tachybaptus novaehollandiae (Stephens)

FW, SW. Austr. Arthropod or where sympatric with *P. poliocephalus* more of a fish specialist.

FW. **Crustaceans:** OSTRACODS, Daphniidae (*Daphnia*); AMPHIPODS, sp.; DECAPODS, Parastacidae (*Cherax albidus, Paratya australiensis*). **Insects**: EPHEMEROPTERA, Baetidae (*Cloeon "Chloeon"*); ODONATA, Zygoptera Coenagrionidae, Anisoptera Aeschnidae, Libellulidae; PLECOPTERA, sp.; TRICHOPTERA, "eruciform larvae"; HEMIPTERA, Anisopidae (*Anisops*), Belostomatidae, Corixidae (*Agraptocorixa, Sigara*), Gerridae (*Limnogonus*), Naucoridae (*Naucoris*), Nepidae (*Ranatra*), Notonectidae (*Notonecta*), Pleidae (*Plea*); COLEOPTERA, Dytiscidae (*Cybister tripunctatus, Eretes australis,* Hydroporinae sp., *Homeodytes scutellaris, Lancetes lanceolatus, Macroporus howitti, Necterosoma regulare*), Elmidae ("Helmidae") sp., Gyrinidae (*Dineutes neohollandicus*), Haliplidae (*Haliplus* sp.), Hydrobiidae sp., Hydrophilidae sp.; DIPTERA, Chironomidae (Brachycera sp., Nematocera sp.), Ephydridae sp. Stratiomyidae sp.; LEPIDOPTERA, Pyralidae, Nymphulinae (aquatic larvae). **Mites:** HYDRACARINA, Pionidae (*Piona*). **Mollusks:** GASTROPODS, Bullinidae (*Isidorella*), Costellariidae (*Vexillum "Tiara"*), Planorbidae (*Glyptophysa, Physastra*). PELECYPODS, fresh water mussels. **Amphibians:** ANURANS, frog. **Fishes:** Eleotridae (*Carassiops clunzinger, Philypnodon grandiceps*), Poeciliidae (*Gambusia affinis* [Introduced]).

Terrestrial insects. ORTHOPTERA, Blattoidea sp.; HOMOPTERA, cicada nymph; HEMIPTERA, Lygaeidae sp.; COLEOPTERA, Curculionidae sp., Staphylinidae sp.; DIPTERA, Blow fly (=Calliphoridae. sp.); HYMENOPTERA, Formicidae, *Iridomyrmex* sp.

References: Fjeldså (1988), Lea & Gray (1935), Marchant *et al.* (1990).

Tachybaptus ruficollis (Pallas)

FW, SW. Euras., Afr., Mad., Austr. Generalist.

FW. ?**Annelids** "worms." **Crustaceans:** CLADOCERANS, Daphniidae (*Daphnia*); AMPHIPODS, Asellidae (*Asellus*), Gammaridae (*Gammarus pulex*); DECAPODS, Palaemonidae (*Palaemonetes*). **Insects:** EPHEMEROPTERA; ODONATA, Zygoptera Agrionidae (*Agrion*); PLECOPTERA, Perlidae (*Perla*); TRICHOPTERA, Phryganeidae, Hydropschidae (*Hydropsche*), Rhyacophilidae (*Rhyacophila*); HEMIPTERA, Corixidae (*Corixa* [*"Corisa"*] *coleoptrata, C. geoffroyi, C. striata*), Gerridae (*Gerris*), Naucoridae (*Naucoris cimoides, N. maculatus*), Notonectidae (*Notonecta*), Pleidae (*Plea minutissima*); COLEOPTERA, Dytiscidae (*Agabis, Colymbetes, Dytiscus, Hydroporus, Hyphydrus*), Gyrinidae, Haliplidae (*Brychius elevatus, Cnemidotus caesus, Haliplus amoenus, H. fluviatilis, H. impressus, H. lineaticollis, H. ruficollis*), Hydraenidae (*Hydraena "Hydroena"*), Hydrophilidae (*Spercheus*); DIPTERA, Chironomidae (*Aphelocheirus aestivalis, Atherix, Cheironomus, Eristalis*). **Mites:** HYDRACARINA, sp. **Molluscs:** GASTROPODS, Bithyniidae (*Bithynia*), Epitoniidae (*Epitonium "Cyclostoma"* [SW]), Littorinidae (*Lacuna, Littorina*), Lymnaeidae (*Lymnaea*), Physidae (*Physa*), Planorbidae (*Planorbis*), Rissoidae (*Rissoa*), Valvatidae (*Valvata*), Viviparidae (*Viviparus "Paludina"*). **Fishes:** Anguillidae (*Anguilla anguilla* [FW, SW]), Cottidae (*Cottus gobio*), Cyprinidae (*Abramis brama, Alburnus lucidus, Cyprinus carpio, Gobio gobio, Leuciscus leuciscus, Phoxinus, Rutilus rutilus, Scardinius erythrophthalmus*), Gasterosteidae (*Gasterosteus, Pungitius pungitius* [FW, SW]), Mugilidae (*Mugil "Liza"* sp. [FW, SW]), Percidae (*Perca fluviatilis*). **Amphibians:** URODELES, Salamandridae (*Triturus alpestris*).

Terrestrial arthropods. Spiders: (spp.). **Insects:** ISOPTERA spp.; COLEOPTERA, Cantharidae (*Drilus*), Carabidae (*Amara, Calathus, Harpalus, Pterostichus*), Curculionidae (*Dorytomus, Phytonomus, Sitona*), Scarabaeidae (*Aphodius*); DIPTERA, Bibionidae (*Bibio*).

References: Bandorf (1970), Cramp (1977), Madon (1931), Madsen (1957 [Note: The prey species listed from SW in this reference are from waters around Denmark, many of which are brackish and may contain FW animals.]), Schmitz (1985), Steyn (1964), Sueur (1985), Witherby *et al.* (1940).

Tachybaptus rufolavatus (Delacour)

FW. Mad. Fish specialist.

FW. **Insects:** in 4 of 28 stomachs. **Fishes:** in 21 of 28 stomachs.

Reference: Voous & Payne (1965).

Tachybaptus pelzelnii (Hartlaub)

FW. Mad. ?Invertebrate specialist.

FW. Two stomachs contained **insects** (HEMIPTERA in 1), 1, **crustaceans**, and 2, **fishes**. (Bill shorter than than in *T. rufolavatus.*)

Reference: Voous & Payne (1965).

Tachybaptus dominicus (Linnaeus)

FW, SW? N. Am., S. Am. Invertebrate specialist. Bill, fig. 6a.

FW. **Crustaceans:** DECAPODS, crayfish and smaller crustaceans, including shrimp and crabs. **Insects:** ODONATA, Zygoptera and Anisoptera; HEMIPTERA, Belostomatidae (*Belostoma*), Corixidae, Naucoridae (*Pelocoris femoratus*), Nepidae (*Ranatra*), Notonectidae (*Buenoa striola*), Pleidae (*Plea*); COLEOPTERA, Dytiscidae, Hydrophilidae, Haliplidae. **Amphibians:** ANURANS, small tadpoles. **Fishes:** small fishes, Poeciliidae (?*"Limia"*) *Poecilia.*

Terrestrial arthropods. Spiders: (spp.). **Insects:** HEMIPTERA, Lygaeidae; HYMENOPTERA, Formicidae, (*Camponotus, Crematogaster, Pseudomyrmex*).

References: Palmer (1962), Storer (1992), and references therein.

Podilymbus podiceps (Linnaeus)

FW, SW. N. Am., S. Am. Decapod specialist. Bill, fig. 6b.

FW. **Annelids:** LEECHES, sp. **Crustaceans:** DECAPODS, crayfish Astacidae (*Cambarus, Potamobius*), shrimp Palaemonidae (*Palaemonetes* [FW, SW]). **Insects:** ODONATA, Zygoptera, Anisoptera Aeschnidae, Libellulidae; HEMIPTERA, Belostomatidae (*Belostoma*), Corixidae (*Pelocoris*), Hydrophilidae (*Berosus, Hydrophilus, Tropisternus*), Nepidae

(*Ranatra*), Notonectidae (*Notonecta*); COLEOPTERA, Donaciinae (*Donacia*), Dytiscidae (*Coelambus, Colymbetes, Cybister, Dytiscus, Rhantus*), Gyrinidae (*Dineutes*), Haliplidae (*Haliplus, Peltodytes*), Notaridae (*Colpius*); DIPTERA, Chironomidae, Stratiomyiidae. **Mollusks:** GASTROPODS, Lymnaeidae (*Limnaea*), Physidae (*Physa*), Planorbidae (*Helisoma, Planorbis*). **Fishes:** Anguillidae (*Anguilla* [FW,SW]), Atherinidae (*Membras* [*"Kirtlandia"*]), Catostomidae (*Catostomus*), Centrarchidae (*Lepomis gibbosus, Lepomis* sp.), Clupeidae (*Dorosoma* [FW, SW]), Cottidae (*Cottus asper* [FW, SW], *C. bairdi* [*"ictalops"*]), Cyprinidae, (*Cyprinus, Notemigonus*), Cyprinodontidae (*Fundulus* sp? [FW, SW]), Gasterosteidae (*Gasterosteus* [FW, SW]), Ictaluridae (*Ameiurus, Ictalurus*), Percidae, Poeciliidae [FW, SW], Salmonidae (*Onchorhynchus mykiss* [*"Salmo gairdneri"*] FW, SW]). **Amphibians:** ANURANS, Ranidae (*Rana clamitans, R. pipiens*), Hylidae (*Hyla regilla*) (M. J. Muller pers. comm.); URODELES Ambistomatidae (*Ambistoma gracile*) (M. J. Muller pers. comm.). **Reptiles:** SNAKES, Colubridae (*Liophis* sp.) (Sick, 1993).

SW. **Crustaceans:** PHYLLOPODS, Artemiidae (*Artemia*); DECAPODS, Cragonidae (*Crago*), Ocypodidae (*Uca*).

Terrestrial arthropods. Spiders: (spp). **Insects:** ORTHOPTERA, grasshoppers, Acrididae, Locustidae; HEMIPTERA, Pentatomidae; COLEOPTERA, Carabidae (*Pterostichus*), Curculionidae (*Balaninus, Sphenophorus*), Scarabaeidae (*Ligyrus*); DIPTERA, flies; LEPIDOPTERA, (larvae); HYMENOPTERA, Formicidae (ants), Chalcidoidea, Diapriidae (both parasitic wasps), bees.

Three young died from ingesting newts (*Taricha granulosa*) the skin glands of which produce a powerful toxin (Muller & Storer 1999).

References: Behrstock (1981), Munro (1941), Palmer (1962), Trautman (1940), Wetmore (1924).

Podilymbus gigas Griscom

FW. N. Am. ?Crab specialist.

FW. **Fishes:** Cichlidae (*Cichlasoma nigrofasciatum* [introduced]), Poeciliidae *Poecilia* [*"Mollienesia"*] *mexicana* or *P.* [*"M."*] *sphenops* [presumably introduced]). Believed to have evolved as a specialist on the crab, *Potamocarcinus guatemalensis.* (Potamocarcinidae).

Reference: Zusi & Storer (1969).

Poliocephalus poliocephalus (Jardine & Selby)

FW, SW. Austr. Arthropod specialist.

FW. **Bryozoans:** Plumatellidae (*Plumatella* sp.). **Annelids:** OLIGOCHAETES, sp. **Crustaceans:** CLADOCERANS, Daphniidae (*Daphnia*); OSTRACODS, Family? (*Mytilocypris henricae*); AMPHIPODS, sp.; DECAPODS, Parastacidae (*Cherax albidus, Paratya australiensis*). **Insects:** EPHEMEROPTERA, sp.; ODONATA, Zygoptera sp., Anisoptera Aeschnidae sp.; TRICHOPTERA, sp., Leptoceridae (?*Trianodes*); HEMIPTERA, Corixidae (*Agraptocorixa, Sigara*), Naucoridae (*Naucoris*), Notonectidae (*Anisops, Enithares, Notonecta*), Pleidae (*Plea*); COLEOPTERA, Dytiscidae (*Cybister tripunctatus, Homeodytes scutellaris, Hyphydrus australis, Macroporus howitti, Necterosoma penicillatum,* Hydroporiinae sp.), Haliplidae (*Haliplus testudo*), Helmidae sp., Hydrophilidae sp., Saldidae sp.; LEPIDOPTERA, Pyralidae, Nymphulinae (aquatic larvae); DIPTERA, Chironomidae (*Chironomus*), Ephydriidae sp., Tipulidae (*Eristalis*). **Mites:** HYDRACARINA, Arrenuridae (*Arrenurus*), Eylaidae (*Eylais*), Pionidae (*Piona*). **Mollusks:** GASTROPODS, Planorbidae (*Glyptophysa, Physastra*). **Fishes:** Poeciliidae (*Gambusia affinis* [introduced]). **Amphibians:** ANURANS, tadpole sp.

Terrestrial invertebrates. Spiders: Lycosidae? small spiders. **Insects:** THYSANOPTERA, sp.; ORTHOPTERA, short-horned grasshoppers, HEMIPTERA, Lygaeidae, Saldidae, Tingidae; COLEOPTERA, Carabidae sp., Curculionidae (*Bagous*), Scarabaeidae (*Heteronyx,* Melolonthinae sp.); DIPTERA, Stratiomyidae sp.; HYMENOPTERA, Formicoidea ants.

Feathers rarely eaten.

References: Fjeldså (1988), Lea & Gray (1935), Marchant *et al.* (1990).

Poliocephalus rufopectus Gray

FW, SW? NZ. ?Generalist.

Very little studied. "Consists largely of insects and fresh-water mollusca." (Oliver 1955). FW. **Annelids:** HIRUDINEA, "pale yellow leeches about 2.5 cm long." **Crustaceans:** DECAPODS, crayfish Family? *Paranephrops.* **Insects:** DIPTERA, Chironomidae?, "midges." **Fishes:** Eleotridae, *Gobiomorphus gobioides.* Eating feathers not recorded.

References: Oliver (1955), Marchant *et al.* (1990).

Podicephorus major (Boddaert)

FW, SW. S. Am. ?Fish specialist. Bill, fig. 6b.

SW. **Crustaceans:** DECAPODS, Brachyura "crabs."

FW. **Fishes:** Atherinidae (*"Atherinichthys"* =?*Basilichthys*). **Amphibians:** ANURANS, tadpole (?*Calyptocephalella gayi* [caught, manipulated, but not swallowed]). **Birds:** Rallidae ("chick of Coot" *Fulica* sp.) and young water birds.

References: Escalante (1980), Reed (1925), Storer (1963).

Podiceps auritus (Linnaeus)

FW, SW. N. Am., Euras. Generalist.

FW. **Bryozoans:** ECTOPROCTA, (*Plumatella fungosa*). **Annelids:** OLIGOCHAETES, Tubificidae (*Peloscolex ferox, Tubifex tubifex*), Lumbriculidae (*Lumbriculus variegatus, Stylodrilus herengianus*); LEECHES, (sp.). **Crustaceans:** PHYLLOPODS, Apodidae (*Lepidurus arcticus*); CLADOCERANS, Chydoridae (*Eurycercus lamellatus*), Daphniidae (*Daphnia longispina*); AMPHIPODS, Calliopidae [FW, SW], Gammaridae (*Gammarus lacustris*), "Metopidae" sp. [SW?], "Pontogeniidae" sp. [SW?]; ISOPODS, Asellidae (*Mancasellus*); DECAPODS, crayfish Astacidae (*Astacus, Cambarus, Potamobius*), Palaemonidae (*Palaemonetes* [FW, SW]). **Insects:** EPHEMEROPTERA, (*Ephemera vulgata, Caenis* sp.); ODONATA, Zygoptera Coenagrionidae (*Coenagrion* sp.), Anisoptera (nymphs and adults); NEUROPTERA, Sialidae, (*Sialis* sp.); PLECOPTERA, Nemouridae, (*Nemoura* sp.); TRICHOPTERA, Limnophilidae (*Limnophilus*), Rhyacophilidae (*Rhyacophila*); HEMIPTERA, Belostomidae (*Belostoma "Zaitha"*), Corixidae (*Arctocorisa carinata, Cenocorixa* (*"Arctocorixa"*) *bifida, Sigara* sp.), Gerridae (*Gerris thoracicus*), Notonectidae (*Notonecta*); COLEOPTERA, Donaciinae (*Donacia* sp., *Haemonia mutica, Plateumaris discolor*), Dytiscidae (*Agabus arcticus, A. bipustulatus, Coelambus, Colymbetes dolabratus, Hydroporus* spp., *Ilybius fuliginosus, Platambus maculatus, Ranthus bistriatus*), Gyrinidae, Haliplidae (*Haliplus fulvus, H. ruficollis, H. flavicornis, Peltodytes*), Hydrophilidae (*Berosus, Helophorus, Hydrobius, Hydrocharis, Tropisternus*); DIPTERA, Chironomidae (sp.), Ceratopogonidae (sp.), Psychodidae (sp.), Culicidae (sp.), Tipulidae (*Tipula oleracea* larvae), Nematocera (sp.), Brachycera (?*Clinocera stagnalis*). **Mites:** HYDRACARINA, sp. **Spiders:** small spiders. **Mollusks:** GASTROPODS, Lymnaeidae (*Lymnaea peregra*), Planorbidae (*Bathyomphalus contortus, Gyraulus acronicus, G. parvus, Helisoma anceps, Planorbis, Promenetus exacuous*); PELECYPODS, Pisidiidae (*Pisidium* sp.). **Fishes:** Anguillidae (*Anguilla anguilla*), Atherinidae (*Labidesthes sicculus, Menida*), Clupeidae (*Dorosoma* [FW, SW]), Cottidae (*Cottus*), Cyprinidae (*Cyprinus carpio, Ptychocheilus*), Gasterosteidae (*Culaea inconstans, Gasterosteus aculeata* [FW, SW]), Percidae (*Etheostoma "Boleosoma," Perca*), Salmonidae (*Onchorhynchus nerka* [roe], *Salmo trutta* fry [FW, SW]). **Amphibians:** URODELES, salamanders; ANURANS, small frogs, tadpoles.

SW. **Annelids:** POLYCHAETES, Nereidae (*Nereis*). **Crustaceans:** MYSIDACEA, Mysidae (*Michtheimysis*); EUPHAUSIACEA, Euphausiidae; DECAPODS, Cragonidae (*Crago*), Grapsidae (*Hemigrapsus*), Lysianassidae (*Anonyx "Chironesimus"*), Pandalidae (*Pandalus*), Penaeidae (*Penaeus*), Hippolytidae (*Spirontocharis*). **Mollusks:** GASTROPODS, Littorinidae (*Littorina*). **Fishes:** Cottidae (*Chitonotus, Leptocottus*), Clupeidae (*Clupea* roe), Embiotocidae (*Cymatogaster*), Engraulidae (*Anchoviella "Stolephorus"*), Gasterosteidae (*Spinachia spinachia*), Gobiidae. (*Gobius*)

Terrestrial arthropods: ORTHOPTERA, Grasshopper (indet.), Hemiptera, Pentatomidae (*Euchistus*), (Family? "Cicadina" (sp.), *Orthobezia urticae,* (Saldidae sp.); COLEOPTERA, Buprestidae, Carabidae (*Agonoderus, Amara, Anisodactylus, Otiorhynchus, Patrobius, Phyllodecta polaris*), Cerambycidae, Chrysomelidae, (except Donaciinae), Curculionidae, Elateridae, Geocoridae (*Myodocha, Reduviolus*), Histeridae (*Saprinus*), Nitidulidae, Scarabaeidae (*Aphodius fimetarius*), Scolytidae (*Tomicus*), Staphilinidae (*Stenus* sp.); DIPTERA, Bibionidae (*Bibio marci, B. pomonae*), Cecidomyidae (sp.), Empididae (*Empis* sp.), Syrphidae (sp.), Muscidae, Tabanidae (*Tabanus),* Tetanoceridae (indet.), Tipulidae, Brachycera (sp.); HYMENOPTERA, Agriotypidae, Apidae (*Bombus jonellus, Chloralictus*), Braconidae, Ceratinidae (*Ceratina*), Cynipidae, Formicidae (*Campanotus, Formica, Lasius*), Ichneumonidae (*Campoplex, Phaeogenes*), Ophionidae, Oryssidae. **Spiders:** spp.

References: Bayer (1980), Fjeldså (1973), Gallimore (1964), Madsen (1957), McAtee & Beal (1912), Munro (1941), Palmer (1962), RWS unpubl. data, Wetmore (1924), Witherby *et al.* (1940).

Podiceps grisegena grisegena (Boddaert)

FW, SW. Euras. Generalist (nominate race takes more invertebrates and New World form more fish).

FW. **Flatworms:** ?CESTODES [Simmons 1975]. **Crustaceans:** BRANCHIOPODS, Apodidae (*Apus*), Triopidae (*Triops*), Family? (*Est*[*h*]*eria*); OSTRACODS; DECAPODS, Palaemonidae (*Palaemon*), Family? (small crabs). **Insects:** ODONATA, (adults and nymphs of Zygoptera and Anisoptera); TRICHOPTERA, spp.; HEMIPTERA, Corixidae (*Corixa*), Naucoridae (*Naucoris cimicoides*), Nepidae (*Ranatra linearis*), Notonectidae (*Notonecta*); COLEOPTERA, Donaciinae (*Donacia, Haemonia*), Dytiscidae (*Agabus, Colymbetes, Dytiscus, Graphoderus, Hydroporus, Macrodytes, Noterus, Rhantus*), Gyrinidae, Hydrophilidae (*Helophorus, Hydrobius*); DIPTERA, Chironomidae, Culicidae, Stratiomyidae (larvae). **Mollusks:** GASTROPODS, Bithyniidae (*Bithynia*). **Fishes:** Anguillidae (*Anguilla*), Cyprinidae (*Abramis brama, Cyprinus carpio, Rutilus rutilus*), Gasterosteidae (*Gasterosteus aculeatus* [FW, SW], *Pungitius pungitius* [FW, SW]), Osmeridae (*Osmerus eperlanus*), Percidae (*Gymnocephalus cernuus, Stizostedion* [*"Lucioperca"*], *Perca fluviatilis*). **Amphibians:** ANURANS, tadpoles, frogs.

SW. **Coelenterates:** HYDROZOA, Family? (*Dynamena pumila* colony). **Annelids:** POLYCHAETES, Aphroditidae (*Lepidonotus squamatus*), Glyceridae (*Glycera* sp.), Nephthydidae (*Nephthys* sp.), Nereidae (*Nereis diversicolor, N. pelagica, N. virens*), Pectinariidae (*Pectinaria koreni*), Family? (*"Hyaloecia"* sp. = ?*Hyalinoecia*), Eunicidae. **Crustaceans:** CLADOCERA, Daphniidae (*Daphnia*); MYSIDACEA, Mysidae (*Mysis*); AMPHIPODS, Gammaridae (*Gammarus* sp.); ISOPODS, Idotheidae (*Idothea*), Janiridae (*Jaera*); DECAPODS, Cragonidae (*Crago* sp.), Palaemonidae (*Palaemon* [FW?, SW?]. **Mollusks:** GASTROPODS, Bucciniidae (*Buccinium undatum*), Littorinidae (*Littorina littorea*), Clausiidae (*Gibbularia* [*"Gibbula"*]); CEPHALOPODS, Squids Loliginidae (*Alloteuthis subulata*). **Echinoderms:** HOLOTHURIANS, Holothuriidae (*Holothuria apoda*), Synaptidae? (?*Leptosynapta inhaerens*). **Fishes:** Ammodytidae (*Ammodytes*), Clupeidae (*Clupea harengus*), Cottidae (*Cottus scorpius*), Gadidae (*Gadus callarias, Merluccius merluccius*), Gasterosteidae (*Gasterosteus aculeatus* [FW, SW], *Pungitius pungitius* [FW, SW], *Spinachia spinachia*), Gobiidae (*Gobius minutus*), Labridae (*Ctenolabrus rupestris*), Pholidae (*Pholis gunnellus*), Syngnathidae (*Nerophis, Syngnathus*), Zoarcidae (*Zoarces viviparus*).

Terrestrial arthropods. Insects: COLEOPTERA, Carabidae (*Amara, Harpalus*), Curculionidae (*Lixus*), Elateridae, Scarabaeidae (*Aphodius, Cetonia*), Staphylinidae (sp.); LEPIDOPTERA, (larvae); HYMENOPTERA, Formicidae. **Spiders:** (sp.). **Myriopods:** (sp.).

References: Cramp (1977), Fjeldså (1982b), Madsen (1957), Markuze (1965), Piersma (1988), Witherby *et al.* (1940).

Podiceps grisegena holboellii Reinhardt

FW, SW. E. Asia, N. Amer. Generalist.

FW. **Annelids:** HIRUDINEA, Family? **Crustaceans:** AMPHIPODS, Gammaridae (*Gammarus*); DECAPODS, Astacidae (*Cambarus* sp., *Potamobius klamathensis*). **Insects:** ODONATA, Zygoptera, Anisoptera (nymphs and adults); TRICHOPTERA, sp.; HEMIPTERA, Corixidae (*Corixa* sp.), Notonectidae (*Notonecta* sp.); COLEOPTERA, Dytiscidae (*Dytiscus* sp.), Gyrinidae (*Dineutes* sp.), Haliplidae (*Haliplus* sp.); DIPTERA, Chironomidae (adults). **Fishes:** Cottidae (small sculpins), Cyprinidae (*Richardsonius balteatus*), Gasterosteidae, (*Culaea inconstans*), Percidae (*Perca flavescens*).

SW. **Annelids:** POLYCHAETES, Nereidae, (*Nereis* sp.). **Crustaceans:** DECAPODS, Callinassidae (*Upogebia affinis*), Cragonidae (*Crago vulgaris*), Palaemonidae (*Palamonetes vulgaris* [FW, SW]). **Fishes:** Anguillidae (*Anguilla chrysypa*), Clupeidae (*Clupea pallasi, Sardinops caerulea*), Cottidae (*Myoxocephalus aeneus*), Cyprinodontidae (*Fundulus* sp. FW?, SW?), Gasterosteidae (*Gasterosteus aculeatus* [FW, SW]).

Terrestrial arthropods. Insects: ORTHOPTERA, Acrididae (Cyrtacanthacridinae sp.); HEMIPTERA, Pentatomidae sp.; COLEOPTERA, Carabidae, Curculionidae (Calandriinae), Elateridae (sp.), Scarabaeidae. (sp.); DIPTERA, Muscidae (sp.); HYMENOPTERA, Formicidae, "wasps."

References: Gallimore (1964), Munro (1941), Wetmore (1924).

Podiceps cristatus (Linnaeus)

FW, SW. Euras., Afr., Austr., NZ. Fish specialist.

FW. **Sponges:** FW sp. (gemmula). **Flatworms:** ?CESTODES, [Simmons 1975]. **Crustaceans:** BRANCHIOPODS, Apodidae (*Apus*); CLADOCERANS, Daphniidae (*Daphnia*); OSTRACODS; AMPHIPODS, Gammaridae (*Gammarus*); DECAPODS, Astacidae (*Astacus leptodactylus* [Traber 1991], *Cambarus affinis* [Rapin 1990]), Pandalidae (*Pandalus*). **Insects:** EPHEMEROPTERA; ODONATA, Zygoptera Agrionidae (*Agrion*), Anisoptera Aeschnidae (*Aeschna*), Libellulidae (*Libellula, Sympetrum*); PLECOPTERA; TRICHOPTERA, Phryganeidae (*Phryganea*), Rhyacophilidae (*Rhyacophila*); HEMIPTERA, Corixidae (*Corixa*), Gerridae (*Gerris*), Naucoridae (*Naucoris cimicoides*), Nepidae (*Ranatra linearis*), Notonectidae (*Notonecta*), Saldidae (*Salda*); COLEOPTERA, Donaciinae (*Donacia, Haemonia*), Dytiscidae (*Colymbetes, Dytiscus, Hydaticus, Hydroporus, Hyphydrus, Macrodytes, Rhantus*), Gyrinidae (*Gyrinus*), Haliplidae, Hydrophilidae (*Hydrobius, Hydrous,* Dynastinae); DIPTERA, Chironomidae, Culicidae, Simuliidae, Tipulidae. **Mollusks:** GASTROPODS, Lymnaeidae (*Lymnaea*), Valvatidae (*Valvata*). **Fishes:** Anguillidae (*Anguilla* [FW, SW]), Cobitidae (*Misgurnus fossilis, Nemacheilus barbatulus*), Cottidae (*Cottus gobio*), Cyprinidae (*Abramis brama, Alburnoides bipunctatus, Alburnus alburnus, Carassius, Cyprinus carpio, Gobio gobio, Leuciscus leuciscus, L. cephalus, Phoxinus phoxinus, Rutilus rutilus, Scardinius erythrophthalmus, Tinca tinca*), Eleotridae (*Philypnodon grandiceps*), Esocidae (*Esox*), Gasterosteidae (*Gasterosteus aculeatus* [FW, SW], *Pungitius pungitius* [FW, SW]), Lotidae (*Lota lota*), Osmeridae (*Osmerus* [FW, SW]), Percidae (*Gymnocephalus cernuus, Stizostedion* [*"Lucioperca"*] *lucioperca, Perca fluviatilis*), Retropinnidae sp., Salmonidae (*Oncorhynchus tschawytscha* [FW, SW], *O. mykiss, Salmo gairdneri* [FW, SW], *S. trutta* [FW, SW], *Salvelinus alpinus* [FW, SW]). **Amphibians:** ANURANS, tadpoles, Ranidae (*Rana esculenta*); URODELES, Salamandridae "newts." **Reptiles:** SNAKES, Colubridae (*Natrix natrix*).

SW. **Annelids:** POLYCHAETES, Aphroditidae (*Lepidonotus*), Glyceridae (*Glycera*), Nephthydidae (*Nephthys*), Nereidae (*Nereis*). Polynoidae. **Crustaceans:** ISOPODS, Idotheidae (*Idothea*); DECAPODS, Cragonidae, Palaemonidae. **Mollusks:** GASTROPODS, Littorinidae (*Littorina*); PELECYPODS, Mactridae (*Spissula*); CEPHALOPODS, Loliginidae (*Alloteuthis*). **Fishes:** Ammodytidae (*Ammodytes*), Clupeidae (*Clupea harengus*), Gadidae (*Gadus morhua, Micromesistius*), Gasterosteidae (*Gasterosteus aculeatus* [FW, SW], *Pungitius pungitius* [FW, SW], *Spinachia spinachia*), Gobiidae (*Gobius flavescens, G. minutus, G. niger*), Zoarcidae (*Zoarces viviparus*).

Terrestrial arthropods. Insects: ORTHOPTERA, Gryllidae (*Gryllus*), Family? *"short-horned grasshoppers";* COLEOPTERA, Carabidae (*Amara, Anchomenus, Calanthus, Feronica, Harpalus, Pterostichus*), Chrysomelidae (except Donaciinae), (*Cassida, Chrysomela, Clytra, Lema, Macroplea*), Coccinellidae, Curculionidae (*Alophus, Chlorophanus, Cleonus, Hylobius,* *Lixus, Otiorhynchus, Phyllobius, Sitona*), DERMESTIDAE (*Anthrenus*), ELATERIDAE, PTINIDAE, SCARABAEIDAE (*Anomala, Aphodius, Melolontha, Rhyzotrogus*), STAPHYLINIDAE; DIPTERA, MUSCIDAE; LEPIDOPTERA, (moths); HYMENOPTERA, APIDAE (*Anthophila*), FORMICIDAE (*Formica, Myrmica*), TIPHIIDAE (*Tiphia*). **Spiders:** (spp.).

References: Cramp (1977), Fjeldså (1982b), Madon (1931), Madsen (1957), Marchant *et al.* (1990), Markuze (1965), Mendheim (1937), O'Donnell (1982), Piersma *et al.* (1988), Rapin (1990), Traber (1991), Witherby *et al.* 1940).

Podiceps nigricollis Brehm

FW, SW. N. Am., S. Am., Euras., Afr. Invertebrate specialist.

FW. **Annelids:** LEECHES (including egg cases, sp.). **Crustaceans:** BRANCHIOPODS, APODIDAE (*Apus*); MYSIDACEA, MYSIDAE (*Mysis*); AMPHIPODS, ASELLIDAE (*Asellus*), GAMMARIDAE (*Gammarus limnaeus, G. pulex*). **Insects:** EPHEMEROPTERA, EPHEMERIDAE; ODONATA, Zygoptera sp., Anisoptera AESCHNIDAE (*Gomphus*), LIBELLULIDAE (*Libellula*); TRICHOPTERA, HYDROPSYCHIDAE (*Hydropsyche*), PHRYGANEIDAE (*Phryganea grandis*), RYACOPHILIDAE (*Ryacophila* sp.); HEMIPTERA, BELOSTOMATIDAE (*Belostoma* sp.), CORIXIDAE (*Corixa*), NAUCORIDAE (*Naucoris*), NEPIDAE (*Ranatra linearis*), NOTONECTIDAE (*Notonecta*), VELIIDAE (*Velia* sp.); COLEOPTERA, DONACIINAE (*Donacia, Haemonia*), DYTISCIDAE (*Dytiscus, Hydroporus, Noterus*), HALIPLIDAE (*Haliplus*), HYDROPHILIDAE (*Berosus, Helophorus*); DIPTERA, CHIRONOMIDAE (larvae and pupae), CULICIDAE, SIMULIIDAE, TIPULIDAE. **Mites:** HYDRACHNIDAE. **Mollusks:** PELECYPODS, PISIDIIDAE (*Pisidium*); GASTROPODS, PHYSIDAE (*Physa*), PLANORBIDAE (*Gyraulus parvus, Planorbis*). **Amphibians:** ANURANS, (small frogs and tadpoles). **Fishes:** GASTEROSTEIDAE (*Culaea inconstans*), GOBIIDAE (*Gobius* sp.), PERCIDAE (*Perca* sp.).

SW (including saline lakes). **Annelids:** POLYCHAETA, NEREIDAE (*Nereis* sp.). **Crustaceans:** PHYLLOPODS, ARTEMIIDAE (*Artemia monica, A. salina*); MYSIDACEA, MYSIDAE (*Mysis, Neomysis* sp.); AMPHIPODS; DECAPODS, CRAGONIDAE (*Crago*). **Insects:** DIPTERA, EPHYDRIDAE (*Ephydra hians*). **Fishes:** GOBIIDAE (*Gobius* sp.).

Terrestrial arthropods. Insects: DERMAPTERA, FORFICULIDAE (*Forficula*); ORTHOPTERA, grasshoppers sp.; HEMIPTERA, CICADELLIDAE (sp.); SALDIDAE (*Saldula* sp.); COLEOPTERA, CANTHARIDAE (*Drilus*), CARABIDAE (*Agonum, Amara, Badister, Harpalus, Notiophilus*), CERAMBICIDAE sp., CHRYSOMELIDAE, (except DONACIINAE), (*Cassida, Diabrotica, Myochrous*), CURCULIONIDAE (*Apion, Gymnetron, Hyperodes, Sitona, Sphenophorus*), ELATERIDAE sp., SCARABEIDAE (*Aphodius*), STAPHYLINIDAE (*Philonthus, Staphilinus*), TENEBRIONIDAE (*Phylan*); DIPTERA, CALLIPHORIDAE, CHIRONOMIDAE (adults), DROSOPHILIDAE, EMPIDIDAE, TABANIDAE; LEPIDOPTERA, PYRALIDAE (sp.); Nymphulinae?; HYMENOPTERA, FORMICIDAE. **Spiders:** (sp.). **Myriopods:** CHILOPODA, centipedes (sp).

References: Cramp (1977), Gallimore (1964), Jehl (1988), Madon (1931), Madsen (1957), Markuze (1965), Munro (1941), Palmer (1962), Wetmore (1924), Witherby *et al.* (1940).

Podiceps occipitalis occipitalis Garnot

FW, SW? S. Am. Invertebrate Specialist. Bill, fig. 6d.

FW. **Crustaceans:** CLADOCERANS, DAPHNIIDAE, (*Daphnia* sp.); AMPHIPODS, NIPHARGIDAE (*Niphargus*); COPEPODS, DIAPTOMIDAE (*Hemidiaptomus*). **Insects:** HEMIPTERA, CORIXIDAE (*Psectrocladius*); COLEOPTERA, DYTISCIDAE (*Lancetes*), HALIPLIDAE (*Haliplus*); DIPTERA, CHIRONOMIDAE. **Mollusks:** GASTROPODS, LYMNAEIDAE (*Lymnaea diaphana*).

SW. **Crustaceans:** PHYLLOPODS, ARTEMIIDAE (*Artemia* sp.) Thousands of this grebe on Lago Epiquen "in all probability attracted. . . by the abundant food available in the form of brine shrimp [*Artemia*, species]" Wetmore 1926).

References: Fjeldså (1986), Wetmore (1926).

Podiceps occipitalis juninensis Berlepsch & Stolzmann

FW. S. Am. Invertebrate specialist.

FW. **Annelids:** OLIGOCHAETES, NAIDIDAE (*Chaetogaster*); LEECHES, GLOSSIPHONIIDAE (*Helobdella* sp.). **Crustaceans:** CLADOCERANS, DAPHNIIDAE (*Simocephalus* sp.); OSTRACODS, CYPRIDAE (*Candona, Cypridopsis*), FAMILY? (*Chlamydotheca*); AMPHIPODS, TALITRIDAE (*Hyalella simplex*). **Insects:** ODONATA, Zygoptera COENAGRIONIDAE (*Amphagrion*), Anisoptera LIBELLULIDAE (*Sympetrum*); HEMIPTERA, CORIXIDAE (*Trichocorixa reticulata*), NOTONECTIDAE (*Buenoa*), SALDIDAE sp.; COLEOPTERA, DYTISCIDAE (*Lancetes theresae, Liodessus* sp.), ELMIDAE (*Macrohelmis*); DIPTERA, CHIRONOMIDAE sp., EPHYDRIIDAE sp. **Mollusks:** GASTROPODS, LYMNAEIDAE (*Taphius montanus*); PELECYPODS, PISIDIIDAE (*Pisidium titicacaense*). **Fishes:** CYPRINODONTIDAE (*Orestias* sp.), ATHERINIDAE (*Odontesthes* sp.).

Terrestrial arthropods. Insects: HYMENOPTERA, FORMICIDAE; DIPTERA, "limoniid" (sp.), "brachypterus fly."

Reference: Fjeldså (1981a).

Podiceps taczanowskii Berlepsch & Stolzmann

FW, S. Am. (Lake Junín only). Fish specialist. Bill, fig. 6c.

FW. **Crustaceans:** CLADOCERANS, DAPHNIIDAE (*Simocephalus* sp.); AMPHIPODS, TALITRIDAE (*Hyalella simplex*). **Mites:** HYDRACARINA sp. **Insects:** ODONATA, Zygoptera sp.; HEMIPTERA, CORIXIDAE (*Trichocorixa reticulata*); COLEOPTERA, DYTISCIDAE (*Lancetes*), ELMIDAE (*Macrohelmis*); DIPTERA, CHIRONOMIDAE sp., EPHYDRIIDAE sp. **Mollusks:** GASTROPODS, LIMNAEIDAE (*Taphius montanus*); PELECYPODS, PISIDIIDAE (*Pisidium*). **Fishes:** CYPRINODONTIDAE (*Orestias* sp).

Reference: Fjeldså (1981b).

Podiceps gallardoi Rumboll

FW, SW. S. Am. Snail specialist. Bill, fig. 6f.

FW. **Annelids:** LEECHES, spp. **Crustaceans**: CLADOCERANS, DAPHNIIDAE (*Daphnia*); COPEPODS, DIAPTOMIDAE (*Hemidiaptomus*). **Insects:** HEMIPTERA, CORIXIDAE sp.; COLEOPTERA, DYTISCIDAE (*Lancetes*), HALIPLIDAE (*Haliplus*); DIPTERA, CHIRONOMIDAE (*Psectrocladius*). **Mollusks:** GASTROPODS, LYMNAEIDAE (*Lymnaea diaphana*) or SUCCINEIDAE (*Succinea burmeisteri*).

References: Fjeldså (1986), Storer (1982a).

Aechmophorus occidentalis (Lawrence)

FW, SW. N. Am. Fish specialist.

FW. **Crustaceans:** AMPHIPODS, GAMMARIDAE (*Gammarus* sp.). **Insects:** EPHEMEROPTERA, (larvae); ORTHOPTERA, spp.; ODONATA, Anisoptera (nymphs); HEMIPTERA, CORIXIDAE, (*Sigara*); COLEOPTERA, DRYOPIDAE, DYTISCIDAE, HYDROPHILIDAE; DIPTERA, CHIRONOMIDAE. **Fishes:** CATOSTOMIDAE (*Catostomus ardens*), CENTRARCHIDAE (*Archoplites interruptus, Lepomis gibbosus, L. macrochilus*), CYPRINIDAE (*Cyprinus carpio* [introduced], *Gila atraria* [*"Leuciscus lineatus"*], *Mylocheilus caurinus* [has limited tolerance for SW], *Notropis hudsonius*), ICTALURIDAE (*Ameiurus catus*), PERCIDAE (*Perca flavescens*), *Salmonidae* (*Onchorhynchus mykiss, O. clarki*). **Amphibians:** URODELES, AMBYSTOMIDAE (*Ambystoma tigrinum*).

SW. **Annelids:** POLYCHAETES sp. **Crustaceans:** DECAPODS, PANDALIDAE (*Pandalus*), HIPPOLYTIDAE (*Spirontocharis*). **Mollusks:** GASTROPODS, ACMAEIDAE (*Acmaea* sp.) [from grebe taken on FW but obviously from SW]). **Fishes:** BLENNIIDAE, CLUPEIDAE (*Clupea pallasii* and roe), COTTIDAE (*Leptocottus*), EMBIOTIDAE (*Cymatogaster*), GADIDAE (?*Microgadus*), OSMERIDAE (*Atherinops affinis, Atherinopsis californicus, Thaleichthys pacificus* [FW, SW], STICHAEIDAE; sculpins.

Terrestrial arthropods. Insects: COLEOPTERA, CARABIDAE, (*Bembidion*).

References: Bayer (1980), Forbes & Sealy (1988), Lawrence (1950), Modde, T., *et al.* (1996), Munro (1941), Palmer (1962), Phillips & Carter (1957), Wetmore (1924).

Aechmophorus clarkii (Lawrence)

FW., SW. N. Am. Fish specialist. Bill, fig. 6c.

Records in the literature not separated from those of *A. occidentalis.*

Table 2. The Diversity of Helminths in Grebes and Alcids. Data from Hoberg (1984) and this paper[1, 2].

	Families	Genera	Species
		DIGENES	
Grebes	20	55	113
Alcids	13	22	29
		CESTODES	
Grebes	6	34	86
Alcids	5	11	21
		NEMATODES	
Grebes	9	20	37
Alcids	6	13	17
		ACANTHOCEPHALANS	
Grebes	1	5	13
Alcids	1	2	5
		ALL GROUPS	
Grebes	36	114	249
Alcids	25	48	72

[1] Named species only.

[2] Does not include two species for which grebes act as intermediate or paratenic hosts.

RESULTS, CONCLUSIONS, AND SUGGESTIONS FOR FUTURE WORK

THE BIOLOGY OF GREBES IN RELATION TO THEIR PARASITE FAUNAS

Grebes are the only birds that may live their entire lives without going on shore. This is possible because they build floating nests of materials collected in or on the water. Unlike penguins, they are foot-propelled divers and are seldom found out of sight of land. Grebes feed on living animals, and what plant material is found in the stomach is generally considered to have been swallowed incidentally with the prey or to have come from the digestive tracts of the prey. Grebes typically spend much or all of the year on eutrophic ponds or lakes, which provide an abundance and variety of potential prey. Although most feeding is done by pursuing prey under water or by picking it off of submerged plants or the bottom, grebes frequently pick insects off the water surface or from emergent vegetation and occasionally will pursue or snap at flying insects. As a result, the diet of all species is varied and includes many kinds of aquatic animals that are the intermediate hosts for helminth parasites. On the other hand, the birds' opportunities for obtaining parasites from land-based intermediate hosts are limited to such hosts as may be taken from emergent vegetation, washed into the water, or blown over water and dropped onto it. The presence of the last type of prey in grebe's stomachs corroborates observations of these birds taking food from the surface of the water (Cramp 1977). Because grebes swallow much of their food whole, the feeding process tends to result in little or no damage to larval parasites in the prey.

Grebes not only use a variety of movements under water in obtaining their prey but also in aggressive behavior and courtship. It is clear that rapid pursuit of a fish requires a different shape of foot and kind of foot movement than that of picking up an object from the bottom or off a submerged plant. This can be seen in the differences in the silhouettes of the spread feet of a Horned Grebe and a Pied-billed Grebe (Storer 1960, Fig. 7). The former has narrower toes and the latter wider ones with more webbing between them. I believe these differences are related to differences in the way the feet are used, the former providing greater speed in pursuing prey than the latter. This parallels, but is less marked than the differences between the large-footed scoters (*Melanitta*) that feed on fixed or slow-moving prey, and the smaller-footed large species of merganser (*Mergus*) that are pursuit divers, which specialize on fishes. The wider bodies of *Podilymbus* and Old World species of *Tachybaptus* and the narrower, more streamlined bodies of species of *Podiceps* and *Aechmophorus* also parallel the similar, but more marked differences between *Melanitta* and *Mergus*. That the differences between the two groups of grebes are less than those between the two genera of diving ducks indicates that the grebes are less strongly adapted than the scoters for feeding on sessile or slow-moving prey, but that they are not so strongly modified as to prevent taking of faster-moving prey. That this is true is apparent from the large variety of kinds of prey taken by the grebes.

Another variant in the anatomy of grebes' legs is the presence or absence of M. flexor perforatus digiti II (Storer 1960), a muscle which, according to Hudson (1937), flexes the second toe. The tendon from this muscle passes through a separate

Table 3. Numbers of Named Species of Parasites Reported from each Grebe Species.

Species	No.	Range
Tachybaptus ruficollis	123	Eurasia, Africa
Podiceps grisegena	113	Eurasia, North America
Podiceps cristatus	110	Eurasia, Afr., Austral., N. Zealand
*Podiceps nigricollis**	101	Eurasia, Afr., N. and S. America
Podiceps auritus	81	Eurasia, North America
Aechmophorus occidentalis	33	North America
Podilymbus podiceps	30	North and South America
Tachybaptus dominicus	15	North and South America
Tachybaptus novaehollandiae	12	Australia
Poliocephalus poliocephalus	11	Australia
Rollandia rolland	4	South America
Podicephorus major	3	South America
Tachybaptus rufolavatus	1	Madagascar
Poliocephalus rufopectus	1	New Zealand
Podilymbus gigas	1	North America (Lake Atitlán)
Podiceps occipitalis	1	South America
Podiceps taczanowskii	1	South America (Lake Junín)
Rollandia microptera	0	South America (Lake Titicaca)
Podiceps gallardoi	0	South America
Tachybaptus pelzelnii	0	Madagascar

*Includes 3 helminths which occurred only as immatures

canal in the hypotarsus, making it easy to see from the skeleton whether this muscle is present or absent. It is present and well developed in *Podilymbus,* and the Old World species of *Tachybaptus,* small in *Rollandia,* small or absent in *Podicephorus,* and consistently absent in *Tachybaptus dominicus, Poliocephalus, Podiceps,* and *Aechmophorus.* Its function in moving a single toe and its presence in *Podilymbus* suggest that its function is related more to maneuverability than to rapid swimming.

Once lost in a phyletic line, this muscle has not been replaced. *Podiceps* probably evolved as a group of fish specialists, but in the Eared Grebe group (*P. gallardoi, P. nigricollis, P. occipitalis,* and *P. taczanowskii*), the first three have become specialists on small invertebrates, whereas *P. taczanowskii,* which, on the basis of close similarity of plumage and behavior probably was derived from *P. o. juninensis,* has become a fish eater – thus presumably having changed its feeding specialization three times in the course of its evolution.

The loss of this flexor muscle in *Tachybaptus dominicus* may have resulted from its almost complete sympatry with *Podilymbus,* which is larger and much heavier-billed and adapted for taking slow-moving, heavy-bodied prey. In this case, being smaller, being able to move more rapidly, and having a thinner bill, *T. dominicus* would have a competitive advantage over *Podilymbus* in being able to take faster-moving and smaller prey. Evidence for this can be seen from the large numbers of ants, presumably taken from emergent vegetation or the water surface and the habit of taking flying dragonflies (Storer 1976).

A comparative study of the functional anatomy of the legs and feet of grebes would be a valuable addition to the biology of these birds, especially if combined with analyses of motion pictures of the birds taken under water. This also would be important in assessing characters found in early fossil grebes, which are in need of a careful reassessment before they can be used in reconstructing the phylogeny of the group. Unfortunately, no one since has approached this problem, and Bocheński (1994), in his comparative analysis of the skeletons of grebes, did not mention the toe bones.

The aquatic existence of grebes is well reflected in their parasite fauna. To date, 249 named species of helminths (113 digenes, 86 cestodes, 13 acanthocephalans, and 37 nematodes) have been reported to parasitize birds of this family (Table 2). These figures for the digenes and cestodes combined are larger than those of any family of aquatic birds listed by Hoberg (1996, Table 2) except the Laridae, a family with approximately five times the number of species and with a wider geographic and ecologic range than grebes. Compared with the Alcidae, a group of comparable size and diversity, the figures for the number of species are approximately three and one half times as great (Table 2). Possible reasons for the large number of species of parasites in grebes include the birds' nesting on eutrophic lakes and ponds which provide a large number and variety of prey species, the grebes' wide geographic range, and, in many of the species, the move from fresh-water breeding grounds to salt-water wintering areas. This is particularly true in the comparison between the grebes and the alcids, which are marine and forage only in salt waters. Comparisons are also hampered by the virtual lack or paucity of information on the parasites of the Southern-Hemisphere grebes and on grebes on the salt-water wintering grounds.

The maximum number of parasite species reported for any grebe is 123 for the Little Grebe (*Tachybaptus ruficollis*), whereas none have been reported for two South American and one Madagascar endemics (Table 3). This is because few or none of these birds and those taken on salt water have been examined for parasites. It is thus probable that the total

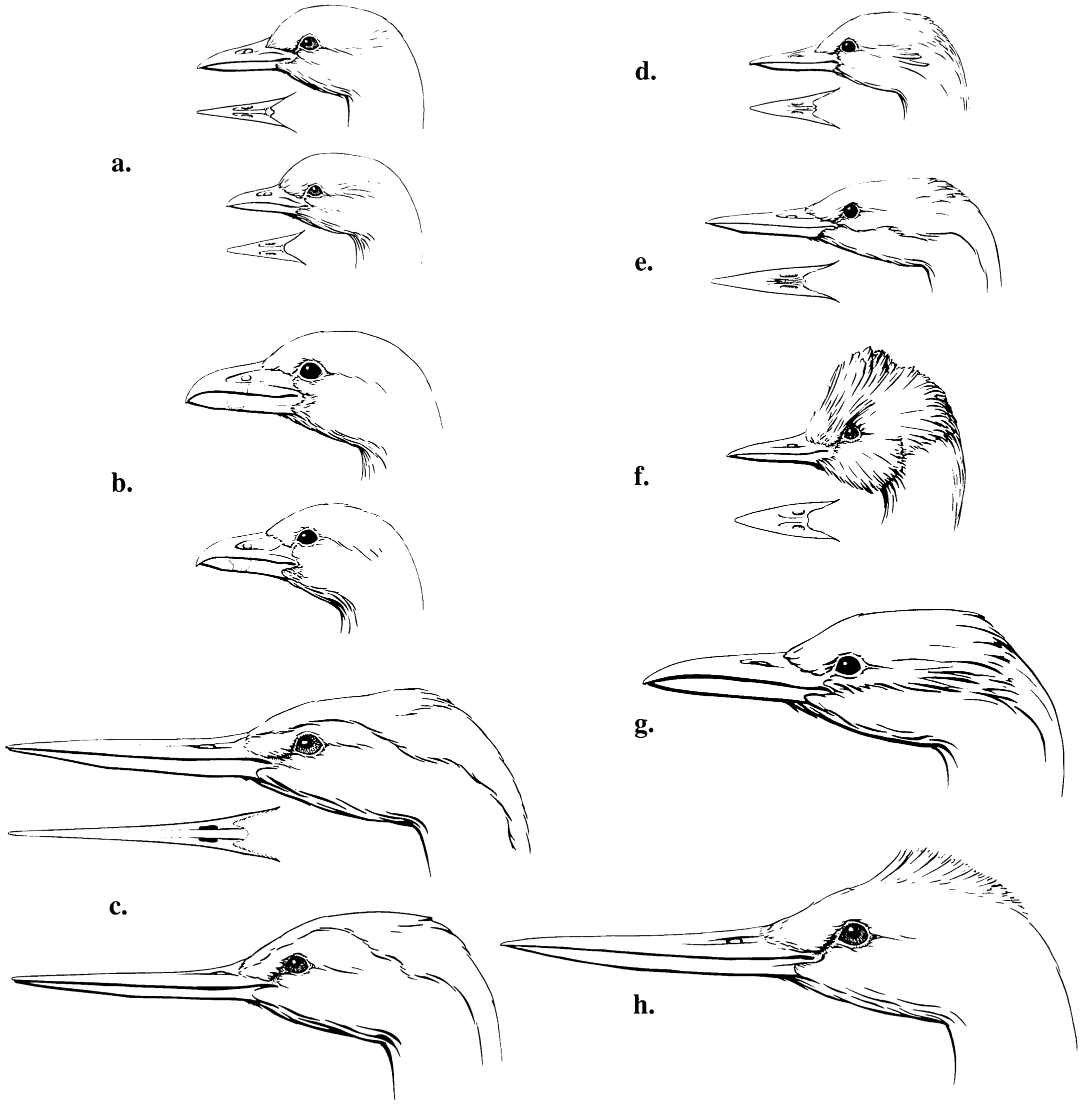

Figure 6. Adaptive radiation in the bill form of grebes. a. Generalized type. Least Grebe (*Tachybaptus dominicus*), male (UMMZ no. 90,758) above, female (no.100,639) below; b. Crushing type. Pied-billed Grebe (*Podilymbus podiceps*), male (no. 223,028) above, female (no. 223,031) below; c. Fish-spearing type, Clark's Grebe (*Aechmophorus clarkii*), male (no. 158,393) above, female (no. 158,392) below; d. Insect-picking type, Silvery Grebe (*Podiceps occipitalis*), male (no.157,233); e. Fish-eating type derived from above, Puna Grebe (*Podiceps taczanowskii*), female (no. 157,236); f. Snail specialist, Hooded Grebe (*Podiceps gallardoi*), male (no. 207,983); g. Large generalist, Short-winged Grebe (*Rollandia microptera*), male (no. 157,237); and h. Fish-eater, (*Podicephorus major*), male (no. 204,737). Original drawing by John Megahan.

number of species of parasitic helminths to be found in grebes will prove considerably higher, in spite of the likelihood that some of the little-known named species will be found to be synonymous with better-known ones.

Bill morphology and parasite faunas. With few exceptions, bill shape in grebes is basically similar, but within this general shape there are numerous variations in proportions (Figure 6). Longer, more slender bills are associated with catching and holding fishes, whereas shorter bills are associated with obtaining more slowly-moving prey (Fjeldså, 1982b). That many of these differences are results of ecological character displacement between sympatric populations of grebes has been shown convincingly in detail by Fjeldså (1983).

One extreme in bill form is found in the Pied-billed and Atitlán grebes (*Podilymbus*). In this genus the bill is very deep and is thought to be an adaptation for feeding on crayfish, crabs, and other hard-bodied animals (Zusi & Storer 1969). The opposite extreme is the sharply pointed bills of the Western and Clark's grebes (*Aechmophorus*), which presumably evolved in connection with the spearing mechanism that these birds use in obtaining fish (Storer & Nuechterlein 1992). Another variant is the broader bill with more upturned mandible found in the Eared Grebe and its South American relative, the Silvery Grebe (*P. occipitalis*), which specialize on small invertebrates. The swallowing mechanism of the latter species has been analyzed by Fjeldså (1981a), who found that in manipulating the prey, the birds press the the large, fleshy tongue against the roof of the mouth. Mahoney & Jehl (1985) suggest that in the similarly large-tongued Eared Grebe, this motion squeezes water from around the prey before it is swallowed. On Mono Lake and similar bodies of highly saline water to which these grebes move for molting and/or wintering, this must reduce the amount of salt ingested by feeding birds. The Hooded Grebe (*Podiceps gallardoi*) has a similar but broader and heavier bill and feeds to a large extent on snails (Storer 1982a; Fjeldså 1986). In spite of the considerable variation in proportions of the bill among grebes, the diet of all species consists of a wide variety of prey types (pp. 37-41). Sexual dimorphism in bill size is a characteristic of most, if not all, species of grebes, and a difference in bill shape is also found between the sexes of the Western and Clark's grebes. The first may extend the size range of prey for members of the species and the second, may increase the efficiency in the taking of different kinds of prey.

It should go without saying that the number and variety of helminth parasites found in an individual grebe host depend primarily on the number and variety of intermediate hosts the grebe consumes, but the establishment of the parasites can be altered by inherent resistance on the part of the host or interactions with other parasites in the bird's gut (*e.g.*, the apparent domination of the enteric helminth community of Red-necked Grebes by *Dioecocestus asper*, Stock & Holmes 1987a). Because differences in bill size may result in differences in the mean size and/or species of prey taken, they may affect at least the relative numbers of intermediate hosts of different species of helminth taken. This in turn may affect the relative numbers of the different intermediate hosts ingested, but because grebes take a wide variety of the available prey species, the relative numbers of different species of parasites may be expected to vary more than the numbers of species found in the birds. These ideas might be tested by comparisons of food habits with parasite loads on specific bodies of water.

While Fjeldså (1983a) demonstrated character displacement resulting in food specializations in sympatric grebes, he also pointed out that in isolated areas with a single species of grebe, the birds tend to have an "all-purpose" bill "which permits opportunistic fish-eating without loss of the ability to feed efficiently on tiny arthropods." Yet in spite of specializations, all grebes are opportunists and will take almost any animal food that is readily available. This increases the range of intermediate host species a grebe may consume and thus the range of helminth parasites it may acquire. Where more than one grebe species occur, this also increases the number of potential definitive hosts available to the parasites.

This general similarity in bill form and the varied diet of the grebes contrasts with the greater diversity of bill form (Bédard 1969) and more restricted diets found in some of the auks and their relatives (the family Alcidae). Several species of alcids feed in large numbers on specific kinds of swarming pelagic prey and thus may take few prey species. These alcids' prey swarm with their own prey, and presumably are intermediate hosts for cestodes of the genus, *Alcataenia*. The alcids are the definitive hosts and presumably excrete eggs of the parasite while feeding on the swarming prey. This is an ideal situation for the development of both host specificity in the parasite and specialized bill form in the host. The general similarity of bill form in most grebes, the varied diet of even grebes with bills modified for taking specific kinds of prey, and the fact that many of the grebes' parasites share several species of grebe hosts appear to negate likelihood that a similar situation occurs in any grebe species.

At least on the grebes' breeding grounds, one prey species may be abundant for a brief period while another becomes scarce. Such fluctuations necessitate the ability to switch from one kind of prey to another. For this, a generalized form of bill would be advantageous. The eutrophic bodies of fresh water on which grebes spend much of the year are rich in the amount and variety of prey. Here, again, unspecialized bills are presumably advantageous. Most temperate-zone grebes move from fresh to salt waters for wintering, and this presents the birds with a different set of potential prey. Some species may make seasonal switches from one kind of prey to another. For instance, Horned Grebes often breed on small potholes where there are no fish, but are known to feed on both fresh- and salt-water fishes (p. 39). These would be available where the birds breed on large bodies of water as well as during stopovers on migration and on the wintering grounds, respectively. Here, again, new kinds of prey may be available, and the generalized bill form is again presumably an advantage. The importance to parasites on stopovers by birds is illustrated by the case of the nematode *Eustrongyloides tubifex*, (p. 29) which relies on stopovers of migrating fish-eating birds to complete its life cycle (Measures 1988b, c, d).

After breeding, some species, like the Eared Grebe, make molt migrations to saline bodies of water where they congregate and remain during the molt and regrowth of the flight feathers before moving on to winter quarters (Storer & Jehl 1985). This may make them subject to parasitism by a new range of helminths whose intermediate hosts inhabit some of these waters.

Sympatry in grebes and its possible effect on parasites. The presence of several sympatric species of grebes with varied diets on the breeding grounds (or elsewhere) presumably increases the number of potential definitive hosts for a parasite. This sympatry in the hosts may have been a deterrent to the development of host specificity within the grebes. One feature of the grebe parasite specialists in general is that far more are found in more than one species of grebe host than in a single one. For example, among the 29 species of the family Amabiliidae, the largest family of grebe specialists, 17 are listed in category 3 (grebe specialists, except those known only from the type host), seven have been found in two species of grebes, five in three, and five in six species of grebe hosts. The figures for genera are two in one grebe genus, eleven in two genera, and four in three genera of grebes. Of the remaining amabiliid species, ten are, as far as I can find out, only known from the original description, the definitive host for one species is unknown, and two are known from a single host, and not very well known at that. The figures for the 12 named species of Hymenolepididae considered grebe specialists (category 3) are similar: three each are known from two, three, and five, and one each from four and six grebe species; and the figures for genera are three from one grebe genus, six from two, and two from three, and one from four grebe genera. Three other species of hymenolepidids are known only from the type host and probably only from the original description. While it is by no means certain that all of the species known only from the type host will eventually be known to parasitize one or more other grebe species, it is likely that some will, and it is also likely that some will turn out to be synonymous with better-known species. An exception to the general "rule" that most grebe specialists are known from more than one grebe host appears to be in the Dioecocestinae, one species of which, *Dioecocestus acotylus,* known only from *Tachybaptus dominicus,* is a common parasite of this grebe in southern Texas, and has also been found in that grebe in South America and the West Indies. As mentioned below (p. 54), the difference in the degree of host specificity between the American and Eurasian populations of *Dioecocestus asper,* suggests that two species may be involved. The paucity of cestode species specific to a single grebe species may be because restricting the number of possible host species would restrict the parasite's reproductive potential and therefore the chance of its offspring in reaching another host. If this is true, restriction to a single grebe host would need to be balanced or overweighed by some other factor, such as greater egg production, that might increase the parasite's fitness. Why the greater degree of specificity may be found in *Dioecocestus* than in other grebe parasites is unclear, but may be related to the facts that the species are dioecious, that it is usual for only a single pair of these large worms to be found in one definitive host, and that they may produce large numbers of eggs.

Although the parasite faunas of the species of grebes on Lake Junín and the Lake Titicaca basin have not been studied, Fjeldså (1981a) has reported on the diets of these grebes. On Lake Junín, he found that while, on the basis of mass, the diet of the Puna Grebe (*Podiceps taczanowskii*), an endemic fish specialist, consisted of an estimated 93-95 percent of fishes, only approximately 12 percent of the prey items were fishes, small aquatic invertebrates, especially midges (Chironomidae) and water boatmen (Corixidae), accounted for the rest. It is clear that the chance of ingesting a parasite larva from one of the last two groups would be greater than that from eating a fish. On the other hand, a fish, which is larger, might contain a larger number of infective larvae than a small invertebrate. In contrast, the related Silvery Grebe (*P. occipitalis*) took no fish, while the White-tufted Grebe (*Rollandia rolland*) took an even higher proportion of fish (by mass) than the Puna Grebe but ate more large and medium-sized fish than that species. In spite of this, it still ate large numbers of aquatic invertebrates. Although two species of fish inhabit Lake Junín, only one, a cyprinodontid, *Orestias,* was reported to be taken by grebes.

On Lake Titicaca, the Silvery and White-tufted grebes occur with the large, endemic Short-winged Grebe (*Rollandia microptera*). Both of the first two species differ morphologically from their counterparts on Lake Junín and the Short-winged Grebe is far more different from its congener than the Puna Grebe is from the Silvery. On Lake Titicaca, the Silvery Grebe takes a few fish, whereas the two others have predominantly fish diets, the large Short-winged Grebe taking both a larger proportion of fish and larger ones. Both of these fish eaters also take a considerable variety of invertebrates, most of them insects.

On the basis of Fjeldså's study, I think it worthwhile to speculate on the parasite faunas of these two lakes that can be expected to occur in grebes. The Lake Titicaca basin, which includes Lake Poopo and the river between the two lakes, is far larger than Lake Junín, has a greater variety of habitats and a larger fauna of fishes and invertebrates. Having a larger number of potential species of intermediate hosts for helminths, it can be expected to have a greater number of species of these parasites. The fact that all of the grebe species involved eat appreciable numbers of insects suggests that the helminths on these lakes having these invertebrates for intermediate hosts may well be found in all the grebe species on either of the lakes. With the possible exception of the Silvery Grebe on Lake Junín, all the grebe species can be expected to harbor the same species of parasites using fishes as intermediate or paratenic hosts. The grebes on these lakes are resident, and as indicated by the morphological differences between the populations of the Silvery and White-tufted grebes on the two lakes, there is no significant movement of these birds between the lakes. It is not unlikely that endemic species of parasites might occur on one or both of them. This is of particular interest because such endemism has yet to be demonstrated for any grebe helminth.

The rainbow trout (*Salmo gairdneri*) has been introduced on both lakes and an atherinid (*Odontesthes bonariensis*) (Fjeldså 1981a) and the lake trout (*Salvelinus namaycush*) on Lake Titicaca (R. R. Miller pers. comm.). The trout have evidently greatly reduced the populations of the native killifshes (*Orestias* spp.) on Lake Titicaca (R. R. Miller pers. comm.), but it is not known if parasites were introduced with these fishes or how the introductions have affected the diets of the grebes.

Feather-eating. It has been known for more than two hundred years that grebes swallow large numbers of their own feathers, and several hypotheses have been proposed to explain this unique habit. Piersma *et al.* (1989) have summarized the available information on the subject in their study of 407 Great Crested Grebes (*Podiceps cristatus*) accidentally drowned in gill nets in The Netherlands. After presenting evidence against other hypotheses, they proposed that the most likely explanation is that "ingested feathers, in the absence of other indigestible matter, contribute substance to the stomach content, enabling the formation of pellets that can be ejected," and that the "habit of regularly ejecting the stomach contents minimizes the chance that any serious population of gastric parasites will build up in the upper part of the alimentary tract." Observations of grebes drinking prior to pellet casting (*e.g.,* Storer 1961) also suggests that the stomach-cleaning hypothesis may be the correct one.

Although not often mentioned or differentiated from the mass of feathers free in the lumen of the stomach, a plug of several feathers is regularly found lodged in the stomach's small pyloric lobe from which the upper end of the small intestine opens. The plug, which is not cast at the same time as the pellets from the rest of the stomach (Wetmore 1924; Storer 1969), presumably acts as a filter preventing large indigestible objects such as fish bones and rough pieces of chitin from passing into the intestine. In this, it is very effective, because inspection of the intestinal contents reveals virtually no large indigestible food remains. This plug has an obvious advantage for grebes in preventing damage to the wall of the intestine, and when it is ejected, it may carry larval helminths with it. On the other hand, it may have an advantage for parasites that reach the intestines in reducing or eliminating the likelihood of their being dislodged. Still, the plug presents a barrier through or past which infective lar-

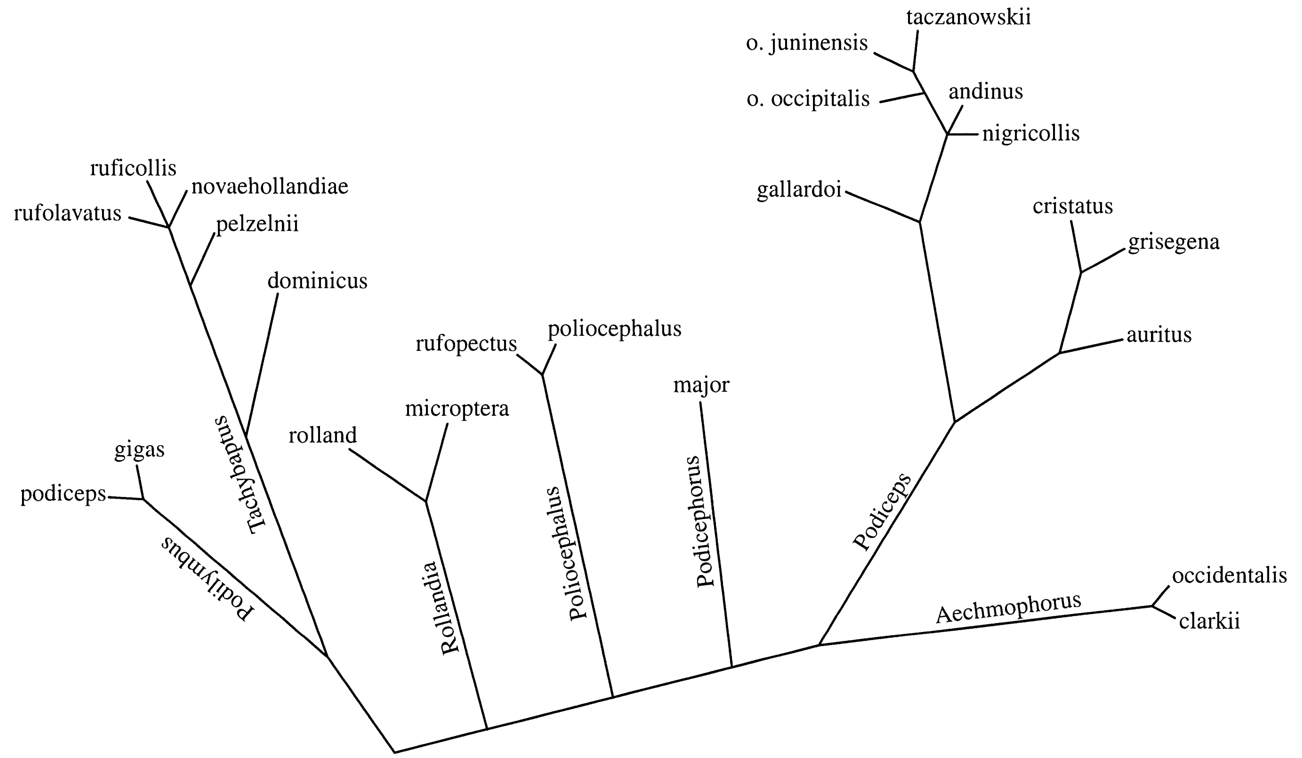

Figure 7. An unrooted tree showing the relationships among the genera and species of grebes, based primarily on courtship and mating behavior, patterns of the downy young, osteology and myology of the wing and pectoral girdle, and plumage. Drawing by John Megahan, modified from Fjeldså (1982a).

vae of parasites must pass.

In spite of this potential barrier, grebes usually contain very large numbers of intestinal parasites, especially cestodes. How the larval parasites get from the stomach into the intestine is not known. Those that do not excyst until they reach the intestine may well be caught in the plug and cast with it. Some that excyst before reaching the plug may well have evolved methods of getting past it, but it seems likely that unless large larvae can push past the plug, they may have to wait until a time when the plug is not in place. Not all infective larvae of cestodes are small. For example, a single larva of the grebe specialist, *Schistotaenia tenuicirrus*, is large enough (mean length of 20 mm) to fill a large part of the abdomen of a full-grown nymph of the large dragonfly, *Anax junius* (Boertje 1975). When the pyloric plug is replaced is unknown, but it might be when digestion is complete.

Although how infective larvae of parasites pass this barrier is unknown, it must be at a time (also unknown) when the plug is not in place. The lack of large pieces of indigestible material in the intestines indicates that this must be some time when the stomach is empty. I think it likely that these larvae may attach themselves temporarily to the wall of the digestive tract anterior to the plug, otherwise the loss of larvae ejected with pellets and/or the plug would be large, and this would provide a strong selective advantage for the retention of means of attachment that could be quickly released. Infective larvae must have attachment organs well developed and these are presumably like those of the adults. The digenes found in grebe intestines have two suckers and the Echinostomes also have a ring of hooks at the anterior end of the body. What the cestodes parasitizing grebes have in common is sucker-like organs on the scolex: two slit-like bothria in the Pseudophyllidea, four bothridia that are often sucker-like in the Tetrabothriidae, and four round suckers (in the Cyclophyllidea). In the last order, an eversible rostellum armed with one or more circles of hooks is usually present. It is possible that before the rostellum becomes permanently embedded in the lining of the gut, there may be some movement of the larva by the alternate attaching and detaching of the suckers and the rostellar hooks and extension and retraction of the rostellum. If this type of movement is used, I think it far more likely that it would be after the larvae reach the gut because the flow of liquids from the stomach to the small intestine would carry the larvae with them more rapidly and without effort on the part of the larvae. The acanthocephalans have a retractable, spine-covered proboscis.

We are left with the likelihood that infective larvae become attached temporarily by means of bothria or suckers (in at least the digenes and cestodes) to the wall of the stomach of the grebe until the pyloric plug is removed, presumably cast as a small pellet or with a pellet including the larger mass of feathers from the lumen of the stomach. The presence of attached larvae might be determined by careful examination of the stomach walls; finding out when the plug is lost would be more difficult but could be done by study of captive grebes.

Another aspect to the habit of feather eating might affect the presence of external parasites. Piersma *et al.* (1989) have shown that grebes show a preference for eating feathers from their own flanks. Because the feathers eaten are not plucked from the bird but come out naturally in the course of preening, one might expect that there would not be enough flank feathers available. But this is not the case; there is an almost constant molt in the tracts of flank feathers of grebes (Piersma 1988; Storer & Jehl 1985, and pers. observ.). This remarkable adaptation, which presumably coevolved with the habit of feather eating, results in a continuous growth of feathers that could provide a special habitat for external parasites such as quill-wall mites (Laminosioptidae), that feed in or on the follicles of growing feathers. To date, no such relationship has been reported.

Helminth-eating. The habit of eating their own helminths and feeding them to their young is another peculiar habit of grebes. In England, Simmons (1975) reported 28 instances of this or associated behavior by Great Crested Grebes (*Podiceps cristatus*) and one by a Red-necked Grebe (*P. grisegena*). The helminths were not identified, but were believed to be cestodes. In the 28 observations on the Great Crested Grebe 27 were by males. The birds were observed to pick the worms up from the water, take them from their own cloacas, indulge in "tail-chasing behavior" in apparent attempts to do the latter, feed them to young, and, in one instance, to their mate. I am unaware that similar observations have been reported since. This behavior should be looked for in other grebes.

The caeca and Bursa of Fabricius. In the digestive tract of grebes, the caeca are well developed and long (McLelland 1979) and thus can provide considerable space inhabitable by helminths, and the Bursa of Fabricius, which is connected to the rectum, is not resorbed until considerably later than that of most birds, up to 18 months (Storer & Jehl 1985). This considerably extends the length of time the Bursa can be inhabited by helminth parasites. Because the fluids in the caeca and Bursa probably differ little in salt concentration after the the grebe hosts move from fresh to salt water and *vice versa,* (see page 62), these organs may also act as refugia for parasites. Stock found (1985) two species of helminths with marine life cycles in the birds he examined on freshwater lakes in Alberta. One of these, *Pseudospelotrema japonicum,* is known to occur in the caecum, and its retention after the birds reached fresh water may be considered evidence for the refugium idea.

External parasites. Grebes' opportunities for exchanging external parasites through contact with other birds is largely limited to occasional physical contact with other water birds. The infrequency with which grebes are found on land and thus the rarity with which they come in contact with birds of other groups is reflected in the small number of species of their known external parasites (12 mites [one undescribed] and 13 lice). The maximum number of species of each group found on one species of grebe is four. Grebes' aquatic habits also save them from being parasitized by arthropods like ticks, bedbugs, flies, fleas, and some groups of mites that must leave their hosts for dry places at least once in the course of their life cycles.

Physical contact between members of different species of grebes is almost entirely limited to aggressive encounters in which actual fighting may occur. Hybrids between well-defined species of grebes are rare. I have seen only one such hybrid, a specimen of a hybrid between the Silvery and Hooded grebes (*Podiceps occipitalis* and *P. gallardoi*) (Storer 1982b) and, aside from Western and Clark's grebes which have barely passed the line by which species are defined, I have seen no mixed pairs. However, there is a report of a Horned Grebe and an Eared Grebe caring for the same chick (Dennis "*et al.*" 1973). More recently, Rogers *et al.* (1994) reported three young from a mating between a Pied-billed Grebe (*Podilymbus podiceps*) and a Little Grebe (*Tachybaptus ruficollis*). The rarity of hybrids is presumably the result of the elaborate pair-formation displays, combined with specific vocalizations, and distinctive differences in the plumage of the head and bill pattern by which species recognition is believed to take place. One can therefore assume that interspecific matings, which might permit an exchange of ectoparasites, must be exceedingly rare. Still, it takes only one mixed mating to enable an external parasite from one species of grebe to cross over to another.

Although there is one report of a group of Western Grebes nesting on a dry island (Nero *et al.* 1958) and I have seen one such nest elsewhere, grebes characteristically build floating nests on bodies of fresh water. These nests are wet and rarely, if ever, last for more than one breeding season. Hence they do not provide a place where external parasites such as certain kinds of mites can overwinter to infect a new generation of birds. On the other hand, grebe nests may be taken over temporarily, or for a breeding season, by other birds, especially coots (*Fulica*). Furthermore, mixed clutches of coot and grebe eggs have been found in the same nest (*e.g.*, Dittberner & Dittberner 1992; Daiz 1993). Grebes use their nests or similar structures as mating platforms and, if not defended, these may be used for this purpose by other pairs of the same, or even other species. (I once observed a pair of Horned Grebes and a pair of Eared Grebes mate on the same platform within a period of a few minutes.) Hence it is possible that ectoparasites that could survive for a short period on a nest or mating platform might cross over from one host to another, although if this does occur, it must be rare. In addition to actual fighting, another possible, although unlikely, source of crossovers of parasites from coots to grebes is predation. Great Grebes (*Podicephorus major*) have been reported to eat young coots (Reed 1925).

Opportunities for exchange of ectoparasites within a species may be greater in grebes than in many birds, not only because of rather frequent matings, but also by reverse mountings, which occur regularly early in the breeding cycle (Nuechterlein & Storer 1989). Young grebes are carried on their parents' backs both before and after the brood leaves the nest. In at the least the Western and Clark's grebes (*Aechmophorus*), back brooding may last until the young are between two and four weeks old (Storer & Nuechterlein 1992). By this time, at least the belly feathers are sufficiently grown to harbor feather mites and lice. The feeding of young by the parents probably results in the transfer of nasal mites from the parents to the young. This allows a long period during which the young can obtain external parasites from both parents or transfer them from one parent to the other. In the case of the nematode, *Pelecitus fulicaeatrae,* infection from parent to young, presumably occurs by transfer of the intermediate host, the louse, *Pseudomenopon dolium,* during the back-brooding period.

PROBLEMS RELATED TO PARASITES

Regional studies. How good are the data? In the former Soviet Union, there has been a long history of helminthological research aimed at documenting these parasites in all vertebrate groups across that enormous country. Begun by K. I.

Skrjabin in the 1920's, a series of All Union Helminthological Expeditions resulted in such important compilations as those of Baruš *et al.* (1978) and Ryzhikov *et al.* (1985). Outside the former Soviet Union the regional coverage has been extremely variable, being far more extensive in the Northern Hemisphere, especially in Eurasia, than in the Southern (Table 3). In North America, considerable important work has been done, but, as pointed out earlier (p. 7), funding for parasitological studies often has been roughly proportional to the importance of the parasites (and their hosts) to humans, and support for the study of general parasitology, never approaching that in the former Soviet Union, has been declining. Yet the number of helminth species is great and the number of helminthologists few in comparison with those of students of some other groups, such as birds.

This is particularly unfortunate because knowledge of parasites can lead to important interdisciplinary studies such as Hoberg's (1986, 1992) on the coevolution of parasites and hosts, zoogeography, and evolution of the Alcidae and Bartoli's study of the Yellow-legged Gull (*Larus cachinnans michahellis*) and its digene parasites in Corsica (1989), which clearly shows that the knowledge of the ecology and geographical distribution of parasites and their intermediate hosts can tell us much about the origin and choice of animal's prey, sexual differences in diet, the habitat in which the birds forage, and even in what regions the birds have wintered before reaching the breeding grounds. In addition, Hoberg (1996) points out the opportunities for the broad application of parasitological data to biodiversity studies.

The largest gap in our knowledge of grebe parasites is the virtual lack of information on those in South American species. That continent has not only had the greatest number of extant grebe species (nine), but also the greatest number of endemics (two genera and six species). It is most unfortunate that no cestodes, nematodes, or ectoparasites and only five digenes and one acanthocephalan (Table 4) have been reported from the two grebe genera endemic to South America. Of the six endemic species, no parasites have been reported from *Rollandia microptera* and *Podiceps gallardoi,* one louse from *P. occipitalis* and *P. taczanowskii,* three digenes and one acanthocephalan from *R. rolland,* and three digenes from *Podicephorus major,* a sharp contrast to the more than 100 parasite species known from each of the four best-studied grebes in the Northern Hemisphere (Table 3).

The group containing the greatest number of grebe specialists (the cestode family, Amabiliidae) has not been reported from Australia and is known in South America from two species found in *Tachybaptus dominicus.*

The mite genus *Rhinonyssus* and the louse genus *Aquanirmus,* which offer the best possibilities for comparative studies of the phylogenies of grebes and their ectoparasites, have yet to be reported from South America.

The endemic genus, *Rollandia,* is thought to be nearest the basal stock of grebes (Fjeldså 1985; Storer 1967a, b). Therefore, it is basic to studies in the phylogeny of the grebes. One of the two species, *R. rolland,* is widely distributed in the temperate parts of the continent. Some of its populations are confined to Andean lakes of varying sizes, others are found in the lowlands and winter on salt water, and one very large form is endemic to the Falkland Islands (Islas Malvinas). This offers an unusual opportunity to study parasite diversity and loads under different ecological conditions. The second species, *R. microptera,* is flightless and is confined to the Lake Titicaca basin. Even with the incomplete data available at present, a preliminary co-speciation analysis might lead to a prediction of what parasites might be expected to be found in *Rollandia* if co-speciation has occurred and/or if the fauna has resulted from colonizations (Hoberg 1992).

Australia, New Zealand, and Madagascar also have endemic species of grebes whose parasites need much further study. Work in subsaharan Africa, with a grebe fauna of three species all widely distributed in the Palearctic Region, might extend the known ranges of Palearctic parasites, might add parasites endemic to the Ethiopian region to the list of grebe parasites, and would form a base for understanding the virtually unknown parasite fauna of the Madagascar grebes, which are apparently the result of a triple invasion of *Tachybaptus* from the African mainland (Voous & Payne 1965).

Few studies of helminth parasites have been made of grebes taken on salt water, where populations of at least eight species, including members of the two South American endemic genera, are known to winter. As a result, the helminths with life cycles based on salt water are very poorly known. Another endemic, *Podiceps gallardoi,* has large nasal glands and hence was also believed to winter on salt water (Storer 1982a), and this has recently been found to be the case (Johnson & Serret 1994). Comparison of parasites obtained from these saline habitats with those obtained from similar ones by Northern Hemisphere grebes should prove interesting. *Podiceps gallardoi* has a high proportion of snails in its diet (Fjeldså 1986; Storer 1982a), which is unusual, if not unique, in grebes. It thus may have a distinctive parasite fauna, especially of digenes, some of whose infective (second intermediate hosts) stages are in or on snails.

Because cestodes and acanthocephalans are almost entirely confined to the digestive tract of their definitive hosts, this organ system is the one most frequently examined for helminths, which, in the case of the digenes and nematodes, must produce a bias in favor of members of these groups found in this part of the body. Furthermore, search for helminths inhabiting the circulatory system and the air sacs is difficult and is most often conducted by specialists who study the parasites inhabiting these parts of the body.

Systematic Studies. Although parasites of the gastrointestinal tract may be better known than those inhabiting other parts of the body, there is still much to be done on even the intestinal parasites, not only in investigating little-studied or unstudied species of grebes, but also in comparative ecological studies of the helminth communities. Bush *et al.* (1990) point out that "habitat of the host is more important in determining community richness than is host phylogeny" and that "aquatic birds harbour the richest helminth communities." The large number of species of parasites known from grebes would make them an excellent group in which to study this and other aspects of community ecology.

While the distribution of parasites in many grebe species is poorly known, there are also major problems to be attacked in the systematics of all the major groups of parasites, both helminths and arthropods. Knowledge of many of the parasites themselves is fragmentary. Many are known only from the original description and the type host, and some may be based on inadequate or improperly preserved material. Thus, some species may prove synonymous with others. It is also probable that when better known, many of these parasites will be found in other species of grebes, because, as has been pointed out earlier, there is a strong tendency for helminth parasites that specialize on grebes to be found in more than one species or genus of these birds.

While the distribution of the species of grebes is well known, the occurrence and distribution of their parasites, especially in the Southern Hemisphere is not, and tissue samples of both are badly needed for sound molecular phylogenetic studies. To fill these gaps, it is necessary to have adequate samples of high-quality, carefully collected specimens of both the parasites and their hosts. These must be accompanied by as complete data as possible, and it cannot be over-emphasized that vouchers for all tissue samples of both hosts and parasites must be preserved to insure that the source of the tissues can always be confirmed. It is only after this has been accomplished and comparisons of the results of molecular amd morphological information have been made that sound conclusions about the systematics of both parasites and hosts and parallel studies of the phylogeny and biogeography of both can proceed.

The extent of non-genetic variation within species is poorly known. Blankespoor (1974) demonstrated morphological differences in the trematode, *Plagiorchis noblei,* developed in different definitive hosts, and Korpaczewska (1963) found a relationship between intensity of infection and size of individual cestodes. More recently, Martorelli *et al.* (1996) have reported on host-induced and geographic variation in the digene *Levinseniella cruzi.* Knowledge of such variation is basic to understanding the morphology and systematics of helminth species.

It is especially important to base revisions of groups of parasites on actual specimens, particularly on types, which often may not be available on loan. It is also important that it be done in conjunction with new material from the type localities and type hosts.

Digenes are greatly in need of generic and family revisions. This is especially true of the Echinostomidae. As mentioned in the species accounts, Nasir *et al.* (1972) recommended synonymizing nine species of *Petasiger* found in grebes plus one described from a heron, one from a shelduck, and *Patagifer parvispinosus* with *Petasiger pungens.* The resulting enlarged species would be known from nine grebe species of five genera and would have a known distribution including North America, Eurasia, and Australia. While the conclusions of Nasir *et al.* may be correct, their brief study appears to have been based largely on the literature. Therefore, I recommend waiting until a thorough study based on examination of types and other material has been made before accepting their conclusions. Such a new study should include the species described since 1972. Seven species in the pertinent group are known from but one or two collections from single grebe hosts (four from *Tachybaptus ruficollis,* two from *Podilymbus podiceps,* and one from *Aechmophorus occidentalis*). It is clear that more material is needed to provide data for the thorough analysis of variation required for such a revision. Twelve species of the related genus, *Echinochasmus,* are known from grebes, and this genus is also a candidate for a revision. The method Blankespoor (1974) used in demonstrating non-genetic differences in morphology in *Plagiorchis noblei* would be useful in testing the validity of these species of *Petasiger* and *Echinochasmus.* Since the publication of Nasir *et al.* (1972), papers describing new species of *Petasiger* by Nassi (1980) and by Kostadinova & Gibson (1998) have not mentioned this earlier work, and their authors evidently did not accept the wholesale combining of species in this group.

Cestodes. There is also still much to be done on the systematics of the cestodes, particularly in the Cyclophyllidea, which include major groups in avian hosts and in which there remains much confusion at the familial, generic, and specific levels. Dubinina's study (1966) of the biology of the Ligulidae is excellent, and Ryzhikov & Tolkatcheva's revision of the suborder Acoleata (1981) is of special importance in covering the two major groups specializing on grebes, the Amabiliidae and the Dioecocestinae. Still, even these groups are in need of a more recent revisions because of the relatively large number of little-known species in them and the difficulty in assembling the scattered material. Such revisions of the Amabiliidae and the Dioecocestinae based on new material and reexaminations of material already available (especially types) would be particularly valuable additions to our knowledge of grebe parasites.

Nematodes. Although the work of R. C. Anderson and his students, especially Bartlett, Measures, and Wong (summarized in Anderson 1992), has greatly improved our understanding of the systematics and biology of some groups of nematodes, the systematics of many other groups of these worms, for example, the ascaridoids, particularly the genus *Contracaecum,* remains to be worked out, and the large and complex subfamily Capillariinae is especially in need of revisionary work.

The Biology of Parasites. One result of the all too limited support for parasitology is the lack of basic information on the biology of many parasite species. For example, the life cycles have been worked out for less than one half (ca. 47 percent) of the species of parasitic helminths reported from grebes. This percentage varies from 75 in the acanthocephalans, a small group with little host specificity, to 42, 44, and 54 in the digenes, cestodes, and nematodes, respectively. In addition, it should be noted again that the life cycles of grebe helminths with cycles in salt water are much less well known than those with fresh-water intermediate hosts.

The Amabiliidae and the Dioecocestinae, the two groups most closely associated with grebes, offer many opportunities for research. With the exception of one species in each, all are grebe specialists, and rarely, if ever, found in other definitive hosts. The two groups are believed to be related and are usually placed together in the Suborder Acoleata. Eleven of the 13 species of amabiliids for which the intermediate hosts are known have been found only in odonate (damselfly and dragonfly) nymphs, and these insects have been suggested as intermediate hosts for the Dioecocestinae as well (Jögis 1978a). It is thus possible that these groups evolved as parasites of grebes and odonata and that shifts to other hosts, both intermediate and definitive, occurred somewhat late in their evolution.

What makes the odonate nymphs good intermediate hosts? They occur commonly in fresh waters where grebes breed. They are large and much sought after by grebes. Analysis of the food habits data shows that they are known to be taken by 13 of the 20 grebe species. The prey of six of the remaining species are virtually unknown, and the seventh, *Aechmophorus occidentalis* (including *A. clarkii*), is certain to take odonate nymphs because it is known to be parasitized by *Tatria decacantha* which is known only to use odonate nymphs as intermediate hosts.

Boertje (1975) thought that "the rectal gills of the dragonfly naiads may very well be involved in the intake of viable eggs." However, because damselfly naiads, which have external gills, act as intermediate hosts for at least three species of *Schistotaenia*, I think that water brought into the cloaca for use in jet propulsion is a more likely mode of entry. Entering the naiads' bodies in this way would enable the eggs to avoid possible damage by the insects' mouthparts, but it has yet to be proved that infections occur by this means. Direct ingestion of the eggs or young larvae by the odonate nymph is still a possibility, as is the unlikely one that a small invertebrate might act as an intermediate host and the odonate nymph as a paratenic host.

The molt of many odonate nymphs to the adult stage takes place on emergent plants where they can be reached by swimming grebes. This is the most vulnerable stage in the life history of these insects, not only because of the time taken to molt, but also the period of time after the molt until the cuticle of the adult hardens sufficiently to permit flight. In addition, parasites may cause nymphs to become sluggish, not climb so far out of the water before molting, and be slower in molting, or not even to survive the molt. Finally, they are not intermediate hosts for many other helminths parasitizing grebes. Aside from acting as intermediate hosts for amabiliids and probably dioecocestids, odonate nymphs are only known as intermediate hosts for the digenes *Prosthogonimus cuneatus* and *P. ovatus* and the nematodes *Contracaecum microcephalum, C. micropapillatum, C. ovale* and *C. spiculigerum* and as paratenic hosts for the nematode *Avioserpens mosgovoyi*. None of these species is a grebe specialist, and fishes appear to be more frequent intermediate and paratenic hosts of *Contracaecum* spp. than do odonate nymphs.

The Amabiliidae and the Dioecocestidae as study groups. Radiation in a group of organisms makes possible the coexistence of a variety of related species through the evolution of different morphologies and other aspects of their biology. In the case of parasites, one obvious possibility is becoming established in a new species of intermediate or definitive host. As pointed out earlier (p. 45), there is little evidence of specialization of any species of amabiliid for a single grebe definitive host. While the known intermediate hosts of other species of amabiliids are all odonate nymphs, two species of amabiliids, *Tatria biremis* and *Tatria biuncinata*, have become established in other intermediate hosts, a corixid bug and a mayfly nymph, respectively, and as the life cycles of more amabiliid species become known, I think it possible that others also may be found to use insects other than odonates as intermediate hosts. Evolution of a new parasite might also occur when a species of intermediate or definitive host becomes geographically isolated and the accompanying population of the parasite with it.

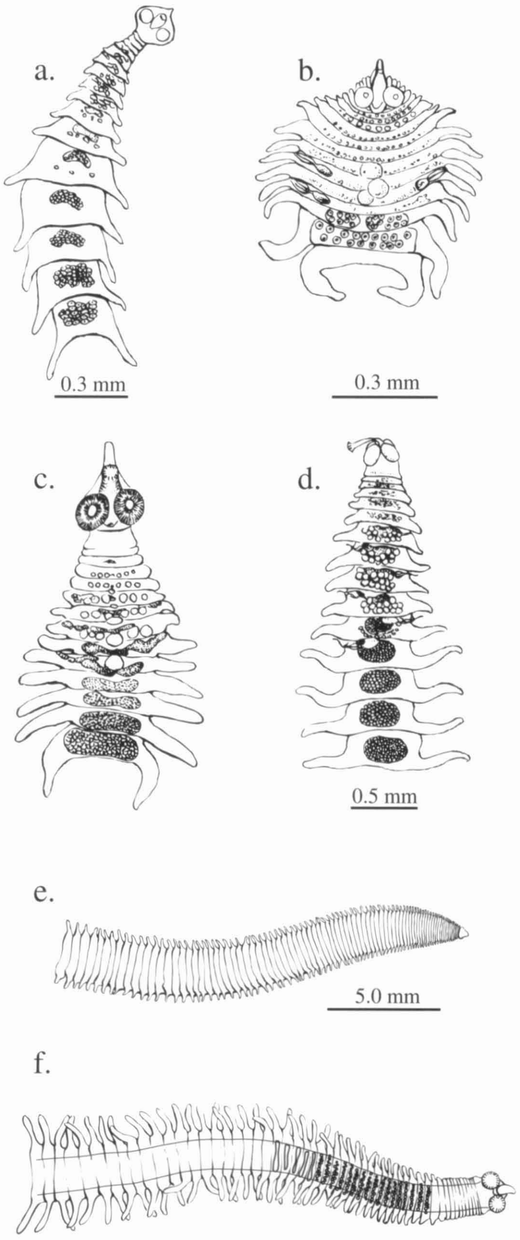

Figure 8. Some species of amabiliid cestodes showing variation in size, number of proglottids, number of eggs per proglottid, and the relative lengths of the lateral projections on the proglottids along the length of the worm. a. *Tatria appendiculata*. b. *T. fimbriata*. c. *T. decacantha*. (length to 7 mm) d. *T. biremis*. e. *Schistotaenia tenuicirrus*, f. *Ryjikovilepis dubininae*. (length 5.47- 6.76 mm). Redrawn from various sources by John Megahan.

The amabiliidae would be a fine group in which to study adaptations of different species to specific niches within the intestine. Stock (1985:142) has pointed out that there are two types of species within the absorber guild (cestodes and acanthocephalans): small species that are closely associated with the host's mucosal surface and can live among the villi and larger species that, although attached to the mucosal surface, keep most of their absorptive surface in the lumen. In the anterior part of the intestine, glucose and amino acids are relatively scarce in the lumen, so the larger species which absorb nutrients from the lumen tend to be found farther down than the small species, which, by living near the mucosal surface can absorb nutrients near the surface of the villi where digestion takes place. In the anterior third of the intestine, pulsations of the villi, sigmoidal contractions, strong peristalsis, and the influx of digesta, create a moderately severe habitat, to which the small species are adapted to avoid "by being small enough to hide among the well developed villi and complex folds of the mucosa, or to use extensively developed adaptations for attachment, or both" (Stock 1985). The availability of high-quality nutrients (glucose and amino acids) peaks approximately 30 percent of the way down the intestine and remains high to near the midpoint. Lumen-inhabiting cestodes in the second third of the intestine live in the area of maximum severity. Stock (1985, Fig. 21) found that in cestodes in general, the length of the hooks on the rostellum vary with where the worm is attached in the intestine. Among the amabiliids, the situation is more complex. The strength of the attachment must be assessed by both the length of the hooks and their number, and is probably determined at least in part by the size of the worm, which in turn determines the drag caused by motion of the contents of the gut on the attachment structures.

(The hymenolepidid grebe specialist *Pararetinometra lateralacantha* bears a row of 30-40 spines on a ridge on each posterolateral corner of the proglottids. These spines are believed to help the worm maintain its position within the intestine [Stock & Holmes, 1981]).

The Amabiliidae and the Dioecocestinae also would be an ideal group to study the evolution and adaptive radiation in life-cycle parameters, especially those those related to demography.

A major difference among species of amabiliids and dioecocestines is the length of the adult worms. What is probably the smallest species, *Tatria fimbriata,* reaches a length of 0.62 mm. (Ryzhikov *et al.* 1985), whereas females of *Dioecocestus asper* may reach a length of 350 mm. (Stock 1985). While this difference is actually small, the larger species is roughly 500 times as large as the smaller, a figure approximately that of the difference in body length between a Blue Whale (80 feet) and a small shrew (2 inches). Therefore, it presumably has considerable biological significance, especially considering the much smaller degree of difference in size among the grebe hosts.

There is little overlap in length of adults between pairs of genera. Those of *Tatria* range from 0.62 to ca. 16 mm, those of *Schistotaenia* from ca. 11 to nearly 100 mm (data from Ryzhikov *et al.* 1985), and those of *Dioecocestus* (*asper*) from 120 to 350 mm (Stock 1985). Size, in turn, can be related to the possible use of intermediate hosts. It is no coincidence that the only known amabiliid to use small corixid bugs as intermediate hosts is a small species of *Tatria* (*biremis*). Nor is it a coincidence that *Schistotaenia tenuicirrus,* the infective stage of whose larvae reaches a length of ca. 20 mm (Boertje 1975), uses nymphs of the very large dragonfly, *Anax junius.* I predict that when the life cycles of more species of these groups are known, more correlations between the relative sizes of parasite and intermediate host will be found.

This is not the only effect of size on the relationships between these parasites and their hosts. Small intermediate hosts usually occur in larger numbers than large ones, but they also tend to have lower infection rates. So, although they tend to be eaten in larger numbers than the larger ones, this may not increase the likelihood of an infected intermediate host being taken. Given that the infective stages are of similar size (which is by no means always true), a larger intermediate host may carry greater numbers of parasites and paratenic hosts even more. I also think it fairly obvious that larger infective stages may either result in larger adult parasites or may reduce the time needed to reach maturity, or both.

Egg size also varies. Those of species of *Tatria* range from roughly 0.02 to 0.035 mm in diameter and those of *Schistotaenia* from 0.04 to 0.09 mm. Although the data in Ryzhikov *et al.* (1985) are limited, it is significant that eggs of *T. biremis* are the smallest (0.02 mm) and presumable the easiest taken in by corixid bugs which feed by sweeping small particles into their mouths with their forelegs.

Small parasites can occur in greater numbers in a host than larger ones. For example, Stock & Holmes (1987b) reported a mean of 2,794 *Tatria biremis* from 31 *Podiceps nigricollis* while a mean of two (usually a pair) of *Dioecocestus asper* was found in the 33 examples of *Podiceps grisegena* examined. It would be interesting to study the possible crowding effect of high population densities on the maturation and size of different cestode species like those reported by Korpaczewska (1963) in *Ligula intestinalis* and *Confluaria* (*"Dubininolepis"*) *furcifera.*

The number of proglottids and the number of eggs per proglottid vary greatly, as can be seen in Figure 8 and by comparing other figures in Ryzhikov & Tolkatcheva (1981). While the number of proglottids in an adult worm can easily be determined, in most cyclophyllideans, the mature proglottids drop off and new ones are constantly produced throughout the life of the parasite, so in these cestodes, it is difficult to determine the total number of proglottids (and eggs) produced in the lifetime of an individual.

Variation in characters related to demography is evident in comparing *Tatria biremis* with *Schistotaenia tenuicirrus.* The intermediate host of the former, a corixid (*Sigara*), is small, as are the infective stage and the adult. The former has few proglottids and, presumably, few eggs per proglottid, but, as noted above, occurs in large numbers in the definitive host. On the other hand, the intermediate hosts of *S. tenuicirrus* are nymphs of large dragonflies (*Anax*). The infective stage and adult of the parasite are considerably larger than those of *T. biremis,* the number of proglottids and, presumably, the number of eggs per proglottid are also larger, but the adults are found in smaller numbers per infected host (a mean of 6.4 and maximum of 36 in a sample of *Podilymbus podiceps* from Iowa [Boertje 1974]). Members of the genus *Dioecocestus* are even more extreme in some of these parameters, being dioecious and usually occurring in single pairs in a definitive host. The presence of *D. asper* appears not only to prevent or greatly reduce the likelihood of other individuals of the same species from maturing in the host, but also to affects "the species richness and distributions of smaller enteric helminths" in the host (Stock & Holmes 1987a). The infective stage of *D. asper* is large and is believed to develop in dragonfly nymphs (Jögis 1978a). The mechanism(s) resulting in these effects would be especially interesting (and difficult) to determine.

The whole matter of demographic "strategies" (an unfortunate term I use for want of a better one) is of special interest because of the likelihood of one parasite egg reaching the adult stage is often minute, and in the case of this group of families, the wide ranges in the variables involved makes this a prime subject for study.

Another way in which species of cestodes differ is where they are attached in the digestive tract. A few are rarely or never found outside of the caeca or cloaca. Within the small intestine, mean differences in location along the intestines between two pairs of congeneric helminths have been documented by Stock (1985). These include *Tatria biremis,* which, on the average, is found more anteriorly than is *T. decacantha.* On the other hand, the differences between *Schistotaenia colymba* and *S. srivastavai* are slight, perhaps because these species were found in much smaller numbers.

While the effect of the above adaptations on other species of parasites is indirect, the large species, *Dioecocestus asper,* appears to affect more directly the distribution and number of species of smaller helminths in the hosts' gut. It may dominate the community interactively and/or by damaging part of the lining of the intestine. The effect is greater on the scarcer helminth species than those occurring regularly in large numbers (Stock & Holmes 1987a).

As has been pointed out earlier (Results p. 50), odonate nymphs are, with two exceptions, the only known intermediate hosts for amabiliids and the probable ones for the Dioecocestinae. Intensive surveys of odonate nymphs for larval stages of these and other groups of helminths should prove useful in elucidating these life cycles and might indicate seasonality in some species.

A striking feature of most amabiliids is the pair of lateral projections on each proglottid. Although I have seen no reference in the literature to their adaptive value, it is clear, as Stock & Holmes (1987a) have pointed out, that in parasites that absorb nutrients through the integument, "the ability to absorb nutrients should be a function of the surface area of the worm, whereas the requirement for nutrients should be a function of the biomass, which is related to tissue volume." Therefore I believe, that by increasing the surface area of the worm, these projections probably increase the amount of nutrients that can be absorbed from the host in a given time. Because these projections are lined with muscle tissue (Boertje 1974), their movements may stir the contents of the host's gut, especially among the villi, making more molecules of nutrients available for absorption and also aid in circulating nutrient-rich fluid throughout the proglottid more rapidly than would occur by diffusion. This in turn may increase the growth rate of the animal and thus reduce the time taken to reach maturity. That this is so is suggested by the maximum enlargement of the processes in proglottids in which eggs are developing, as can be seen in illustrations of species of *Tatria* (*e.g.,* Fig. 8). This seems to be true especially in the case of the small species with few proglottids and may be a means of increasing the rate of development of the eggs, as well as improving the parasites' competitive advantage. The processes also may permit the parasite to live in parts of the

Table 4. Numbers of Named Species of Parasites in each Major Parasite Group Reported from each Grebe Species[1].

Species	Trem.	Cest.	Acan.	Nema.	Leech.	Mites	Lice	Total
Rollandia								
rolland	3	0	1	0	0	0	0	4
microptera	0	0	0	0	0	0	0	0
Tachybaptus								
novaehollandiae	4	2	0	4	0	2	0	12
ruficollis	45	39	3	27	1	4	4	123
rufolavatus	0	0	0	1	0	0	0	1
pelzelnii	0	0	0	0	0	0	0	0
dominicus	4	7	0	2	0	1	1	15
Podilymbus								
podiceps	10	10	1	2	2	4	1	30
gigas	0	1	0	0	0	0	0	1
Poliocephalus								
poliocephalus	8	0	0	3	0	0	0	11
rufopectus	0	0	0	0	0	0	1	1
Podicephorus								
major	3	0	0	0	0	0	0	3
Podiceps								
auritus	25	28	3	16	2	3	4	81
grisegena	36	41	9	21	1	2	3	113
cristatus	46	31	2	23	1	3	3	109
nigricollis	29	38	4	21	1	4	4	101
occipitalis	0	0	0	0	0	0	1	1
taczanowskii	0	0	0	0	0	0	1	1
gallardoi	0	0	0	0	0	0	0	0
Aechmophorus								
occidentalis[2]	11	10	2	6	1	1	2	33

[1] Includes those that act as intermediate or paratenic hosts.

[2] Presumably includes *A. clarkii.*

Table 5. The Numbers of Grebe Helminth Species in each Host-Specificity Category[1] by Family.[2]

Taxa		Host Specificity Categories										
		Total Sp.	?1	1	?2	2	?3	3	?4	4	?5	5
Digenes												
Paramphistomiformes	Notocotylidae	4	1	2	-	1	-	-	-	-	-	-
Echinostomatiformes	Cyclocoelidae	4	-	-	-	3	-	1	-	-	-	-
	Psilostomidae	1	-	-	-	1	-	-	-	-	-	-
	Cathaemasiidae	1	-	1	-	-	-	-	-	-	-	-
	Philophthalmidae	1	-	1	-	-	-	-	-	-	-	-
	Echinostomidae	47	2	11	1	3	1	13	-	1	14	1
Strigeiformes	Clinostomidae	2	-	-	-	1	-	-	-	-	1	-
	Schistosomatidae	4	-	1	-	2	-	-	1	-	-	-
	Cyathocotylidae	2	-	-	-	1	-	1	-	-	-	-
	Diplostomidae	10	-	2	-	4	1	2	-	1	-	-
	Strigeidae	9	-	3	-	5	-	-	-	-	1	-
Opisthorchiformes	Opisthorchidae	3	-	2	-	-	-	-	-	-	1	-
	Heterophyidae	5	-	3	-	1	-	-	-	-	1	-
	Pachytrematidae	1	-	-	-	1	-	-	-	-	-	-
Plagiorchiformes	Renicolidae	1	-	1	-	-	-	-	-	-	-	-
	Plagiorchiidae	2	-	2	-	-	-	-	-	-	-	-
	Microphallidae	6	-	6	-	-	-	-	-	-	-	-
	Prosthogonimidae	2	-	2	-	-	-	-	-	-	-	-
	Ochetosomatidae	3	-	1	-	-	-	-	-	-	1	1
	Eucotylidae	5	1	1	1	1	-	-	-	-	1	-
Digenes Totals		113	4	39	2	24	2	17	1	2	20	2
Cestodes												
Pseudophyllidea	Diphyllobothriidae	8	-	6	-	-	-	-	-	-	1	1
Tetraphyllidea	Tetrabothriidae	1	-	1	-	-	-	-	-	-	-	-
Cyclophyllidea	Dioecocestidae	6	-	-	-	-	-	2	-	1	2	1
	Amabiliidae	29	-	-	-	-	-	17	-	2	8	2
	Dilepididae	6	-	-	-	6	-	-	-	-	-	-
	Hymenolepididae	36	-	-	-	21	-	12	-	1	2	0
Cestode Totals		86	0	7	0	27	0	31	0	4	13	4
Acanthocephalans												
Polymorphida	Polymorphidae	13	-	13	-	-	-	-	-	-	-	-
Nematoda												
Enoplida	Dioctophymatidae	2	-	2	-	-	-	-	-	-	-	-
	Trichuridae	7	-	5	-	1	-	1	-	-	-	-
Strongylida	Amidostomatidae	3	-	-	-	3	-	-	-	-	-	-
Ascaridida	Anisakidae	10	-	5	1	2	-	1	-	-	-	1
Spirurida	Dracunculidae	1	-	1	-	-	-	-	-	-	-	-
	Tetrameridae	2	-	1	-	-	-	1	-	-	-	-
	Acuariidae	10	-	4	0	2	-	3	-	-	1	-
	Onchocercidae	2	-	0	-	1	-	-	-	-	-	1
Nematode Totals		37	0	18	1	9	0	6	0	0	1	2

[1] Categories: 1 = Generalist. 2 = Specialist in other groups, rare or occasional in grebes. 3 = Specialist in grebes, rare or unknown in other groups. 4 = Known only from the type (grebe) host. 5 = Known only from original description.

[2] Does not include two species, the digene, *Strigea falconis,* and the nematode, *Gnathostoma spinigerum,* for which grebes act as intermediate or paratenic hosts.

intestine where the concentration of nutrients is low or in areas with dense helminth populations. A relatively low concentration of nutrients in the anterior portion of the small intestine could explain Stock's (1985) finding that *T. biremis,* which is small and thus has a high surface-to-volume ratio, occurs in great numbers in approximately the anterior one-fifth of the small intestine whereas the larger *T. decacantha,* which was found in much smaller numbers, is found near the midpoint.

Another possibility is that the contractile projections may make a proglottid attractive to a potential intermediate host. This is unlikely because Boertje (1975) reported that when gravid proglottids were fed to *Anax* nymphs, the nymphs did not become infected.

The dioecy in *Dioecocestus* has been studied by Coil (1970, 1984) and others, but remains of considerable interest with possibilities for still further research.

Several questions regarding *Dioecocestus acotylus* and *D. asper* in North America need to be addressed. Gallimore (1964) & Stock (1985) found *D. asper* in only *Podiceps grisegena* in Alberta, although it has been recorded from all the five Eurasian grebes, including *P. auritus* and *P. nigricollis,* in which Gallimore and Stock failed to find it. Why is this so? Is it possible that the Old World and New World populations referred to this cestode belong to different species, and if so, what in the North American form prevents it from becoming established in any grebe but *P. grisegena?*

No species of *Dioecocestus* is known from the Pied-billed Grebe (*Podilymbus podiceps*). Again, why? The bird has a heavy bill and jaw muscles (Zusi & Storer 1969) and pinches large prey before swallowing it. This processing might kill larval parasites, but evidently it does not kill the large larvae of *Schistotaenia tenuicirrus,* which are fed in large dragonfly nymphs to young as small as 36 grams without apparent damage (RWS data). In addition, they may be processed more for the young than for the adults themselves. It might be that the stout bodies of the intermediate host of this parasite (*Anax junius*) in some way protect the cestode larvae or that the grebes concentrate their pinching on the head and thorax of the nymphs leaving the abdomen, in which the larvae are found, undamaged, whereas larvae in weaker odonate nymphs would not be protected from crushing by the grebes.

Dioecocestus acotylus is one of the few cestodes that has been found several times in several localities, but in only a single definitive host, in this case, the Least Grebe (*Tachybaptus dominicus*). It may be specific to this grebe, but the Pied-billed Grebe is widely sympatric with the Least Grebe and is frequently found on the same waters. It therefore should be examined thoroughly for the presence of *D. acotylus* before a firm statement can be made concerning host specificity of this parasite. The Pied-billed Grebe has not been studied as intensively as the species of grebes examined by Stock, and if, after a comparable study, a species of *Dioecocestus* is not found in this grebe, it would be interesting to find out why.

Although intermediate hosts for no species of the tapeworm subfamily Dioecocestinae is known, odonate nymphs have been suggested as the most likely candidates (Jõgis 1978a, b). *Dioecocestus acotylus* has been found in 100% of *Tachybaptus dominicus* in southern Texas (Coil *in litt.*) and in six of nine of these birds examined in Cuba (Ryšavy & Macko 1971). It is thus common where it occurs. Although the two grebe species may be found on the same bodies of water, they have different habitat preferences, Least Grebes being found more often on temporary ponds with trees or shrubs growing in the water whereas Pied-billed Grebes prefer more open permanent ponds with cattails. To find the intermediate host for this cestode, one might look for a species or genus of dragon- or damselfly that breeds in temporary ponds and/or ponds with emergent shrubs and is found in the Greater Antilles and from southern Texas south to at least Brazil. If the intermediate host were confined to breeding in the sort of habitat favored by the Least Grebe, it might seldom be taken by a Pied-billed Grebe, and if it were, any larvae in it might be crushed.

Still another possibility is that there may be something in the Pied-billed Grebe's digestive tract that prevents the young larvae from developing, or even remaining. This is not likely because *Dioecocestus asper* has been found in two genera and five species of grebes in the Old World.

Gallimore (1964) only examined six Pied-billed Grebes (all immature) for parasites. Therefore, more of these grebes should be examined for *Dioecocestus* on lakes where Red-necked Grebes were found infected and odonate nymphs should be checked for larvae on the same lakes. As a bonus, the larvae of amabiliids might also be found.

HOST SPECIFICITY

The categories that I have established for use in this paper are explained on p. 5. Host specificity is a complex phenomenon of which time for evolution is an important determinant. The early separation of grebes from other birds is reflected in the many helminth species that are found largely or exclusively in these birds. Yet few, if any, are known to be specific to any one species of grebe. Other determinants include the potential for the acquisition of helminths, the development of specificity, and the potential for co-speciation.

Digenes. Members of five orders, 20 families, 55 genera, and 113 species of digenes have been reported to parasitize grebes (Table 2). Of these, one genus, *Taphrogonimus,* is known only from grebes. It is of uncertain taxonomic position and known only from the original description. Of the species found in grebes, 44, or 39 percent, are grebe specialists, 25 of these are only known from the type host (Table 5). Grebe specialists are found in four of the five orders and nine of the 20 families on the list. By far the largest number (30) is found in the Echinostomidae, but this figure is probably too high. (See p. 50).

Of the 23 trematode species known only from the type host, ten were found in *Tachybaptus ruficollis,* four in *Podilymbus podiceps,* three in *T. dominicus,* and two in *Podiceps cristatus,* all of them widespread species that are resident in many parts of their ranges. One each was found in *Rollandia rolland, Podiceps auritus, P. grisegena,* and *Aechmophorus occidentalis.* Some of these parasite species will probably prove invalid, but further collecting will probably result in finding some of the remaining species in other species of grebes. It is therefore uncertain how many trematode species may prove specific to a single grebe host. Of the 19 grebe specialists known from two or more grebe species, 12 have been found in three or more grebe hosts and all but three in two or three grebe genera. Although Kostadinova & Gibson (1998) suggest that "the four morphologically similar species of *Petasiger* [*caribbensis, grandivesicularis, pseudoneocomensis,* and *oschmarini*] exhibit a certain degree of host-specificity," I see no evidence for a strong pattern of specificity to single definitive host species or genus and think it more likely that the fact that these parasites are known from but one or two species of grebe has more to do with sampling and/or geographic isolation than with any inherent factors in the grebes that might prevent successful infection by these parasites.

Grebes are known to be parasitized by more species of digenes (113) than any other major group of parasites, but in only two well-studied grebe species have more species of these digenes than of cestodes been found: (*Tachybaptus ruficollis,* 45 digenes, 40 cestodes; *Podiceps cristatus,* 46 digenes, 32 cestodes [Table 4]). Stock & Holmes (1987b) found fewer individuals and species of intestinal digenes than cestodes in the four species of grebes they studied in Alberta. Although the mean number of one digene (*Petasiger nitidus*) per bird was 1,025 in *Podiceps grisegena,* this figure was less than half the highest mean number of 2,790 individuals of the cestode (*Tatria biremis*) found in a species of grebe (*Podiceps nigricollis*).

Because the species of the Echinostomidae reported from grebes may have been oversplit (Nasir *et al.* 1972), it is possible that the number of species of echinostomids in the above analysis is too large. On the other hand, a bias in favor of collecting intestinal parasites may indicate that relatively more species of digenes are yet to be found in other parts of grebe bodies, and judging from a study of the Common Loon (*Gavia immer*) in Florida Forrester *et al.* (1997), the needed surveys of grebes on salt-water wintering grounds should increase considerably the number of species of microphallids and heterophyids known from grebes.

Cestodes. Cestodes show the greatest degree of host specificity of grebe helminth parasites. Members of three orders, six families, 34 genera, and 85 species of cestodes are reported to parasitize grebes. Of these, one family, the Amabiliidae (with the exception of the monotypic type genus, which is of uncertain taxonomic position), and one subfamily, the Dioecocestinae (again with the exception of one species) are grebe specialists. In all, 14 (40 percent) of the genera and 51 (60 percent) of the species reported from grebes are considered grebe specialists. Of the latter, 21 are known only from the type host (Table 5). That all of these 21 species may be confined to a single species of grebe host seems highly unlikely. The known host for ten of these species is *Tachybaptus ruficollis,* the most widespread and most easily collected grebe in Eurasia. On the other hand, this grebe is resident in many parts of its range and occupies a considerable variety of bodies of water, hence is perhaps most likely to be host to parasites whose intermediate hosts may be restricted to small geographic areas or special habitats. Eleven of these 21 species belong to the family Amabiliidae, which is in need of a revision for which additional material must be obtained. The hymenolepidid cestode *Lobatolepis lobulata* is a common parasite of *Podilymbus podiceps* and also has been found in *P. gigas.* It is probably a specialist on grebes of this genus (*fide* J. M. Kinsella, *in litt.*).

The Diphyllobothriidae is the only family of the order Pseudophyllidea known to include grebe parasites. The first intermediate hosts in those that parasitize grebes are copepods (especially cyclopids and diaptomids). The second intermediate hosts are fishes, and in these, there is a range of host specificity from specialists on single genera or species of fishes (*e.g., Schistocephalus* spp.) to generalists in both intermediate and definitive hosts like the other Pseudophyllidea found in grebes.

The life cycles of the Tetrabothriidae are unknown, but according to E. P. Hoberg (*in litt.*), the "cycles appear to involve 1) crustacean intermediates: 2) piscine or cephalopod paratenic hosts" and "there . . . is no evidence for FW life cycles in this group." Hoberg (1987) has found larvae in the intestine of the Greater Shearwater (*Puffinus gravis*). The species found in grebes is a generalist as regards definitive hosts.

The Amabiliidae consist of seven genera. The monotypic type genus is confined to flamingos (Phoenicopteridae), and the other six consist of grebe specialists. Of the 30 species of the latter, intermediate hosts are unknown for 18. Larvae of ten of the remaining species are only known from odonate nymphs (six from Zygoptera, three from Anisoptera and one from both), and the last two only from a Corixid bug (*Sigara concinna*) and an unidentified mayfly (Ephemerid) nymph. Amabiliids specializing on grebes thus appear to be specialists in both their intermediate and definitive hosts.

The intermediate hosts for members of the Dioecocestinae have not been found, but as suggested elsewhere (Cestodes p. 20), are thought to be odonate nymphs as well.

There is no strong evidence that any amabiliid is specific to one species of grebe. Although 12 of the 29 species for which a definitive host is known in the family are known from but one grebe species, 11 of these are known only from the original description, and none of these has been well studied. Furthermore, when the family is better known, some species may turn out to be synonymous with others.

The systematics of the Dioecocestidae is even more poorly known than that of the Amabiliidae. Of the six species known from grebes, four are known from a single grebe species. Of these, at least one (*Dioecocestus novaehollandiae*) has been synonymized with *D. asper* by Ryzhikov *et al.* (1981). The Australian material needs checking. Little material of the genus has been found because, at least in *D. acotylus* (Coil 1970) and *D. asper* (Stock & Holmes 1987a), only a one pair is usually found in a single host. *Dioecocestus acotylus* is only known from *Tachybaptus dominicus* but from Jamaica, Cuba, Brazil, and southern Texas, where it is common. As pointed out earlier (p. 55) it may well be specific to that grebe, as suggested by Coil (1970), although it should be looked for in *Podilymbus podiceps,* which is widely sympatric with *T. dominicus.*

None of the six species of dilepidids found in grebes is a grebe specialist; all are specialists in other groups (four in larids, one in loons, and one in storks) and are rare or uncommon in grebes.

The work of Vasileva, Georgiev & Genov (See refs. in lit. cit.) has greatly improved our understanding of the systematics and host specificity of the Hymenolepididae that parasitize grebes. These authors consider 15 of the 36 species of this family known from grebes to be grebe specialists and place them in nine genera, seven of which consist entirely of grebe specialists. Two of these specialists are known only from the original description while the remaining 13 are known from two to six (mean 3.5) species and one to three (mean 1.7) genera of grebe hosts. These findings are in agreement with the findings that parasites specializing on grebes are more often than not found in more than one grebe species or genus.

The remaining 21 species of hymenolepidids reported from grebes are considered specialists on other groups of birds: 13 on anatids, three each on Charadrii and Lari, and two on loons. That most are specialists on anatids is probably a result of the high frequency with which ducks and grebes share common breeding grounds, and therefore the grebes may more frequently ingest the intermediate hosts of anatid helminth parasites than those of other avian groups.

At least two factors can affect the numbers of species and individual parasites found in a given host: the degree of specialization in feeding habits of the grebe and the preferred range of prey size. In the case of the first, it is clear that a bird like the Western Grebe, feeding largely on fish, will have the opportunity of becoming infected by relatively few species of parasites, whereas the Red-necked and Horned grebes, which are generalists, can be expected to be host to more species. The preferred size of prey has the opposite effect.

The smaller the prey size, the greater the number of species is available, and, presumably the greater number of parasite species would be available in them, and also the larger number of individuals would be needed to sustain a grebe. Stock's data from Alberta (1985) support these ideas. The fish-eating Western Grebe (*Aechmophorus occidentalis*) was host to four to ten species of intestinal helminth per bird (mean, 6.4) with a total of 16 species and a range of 112 to 1,800 parasites per bird. In contrast, the Eared Grebe (*Podiceps nigricollis*), which feeds primarily on small aquatic invertebrates, had two to 15 species of helminths per bird (mean, 9.1), a total of 26 species and from 231 to 33,169 individuals per bird. The Red-necked Grebe (*P. grisegena*) had four to 14 species (mean, 10.7), a total of 23 species and 326 to 10,459 individuals per bird. The sample of Horned Grebes (*P. auritus*) was too small for a meaningful comparison.

Although as a group, more species of digenes than of any other helminth group have been found in grebes (Table 5), in the intestines of individual birds, tapeworms tend to outnumber them both in terms if species and individuals (Stock & Holmes 1987b p. 670). Means of 2,794 individuals of *Tatria biremis*, 1,635 of *Diorchis* sp. "P," and 1,183 of *Dicranotaenia paraporale* were reported from 31 individuals of *Podiceps nigricollis*. These three species of cestodes are all considered grebe specialists by the authors, and the numbers attest to the success of specificity to grebe hosts in these cestodes.

Acanthocephalans. Members of one family, five genera, and 13 species of this group have been found in grebes as definitive hosts in nature. None is specific to grebes. Two others, *Corynosoma semerme* and *C. strumosum*, whose definitive hosts are mammals, primarily pinnipeds, are not known to mature in grebes or to use them as paratenic hosts, and one, *Polymorphus formosus*, has only been infected experimentally in a grebe. Acanthocephalans are not common in grebes. In their study of intestinal parasites of 91 grebes of four species in Alberta, Stock & Holmes (1987b) reported a maximum of 12 percent of the individuals of any species (*Podiceps grisegena*) infected by a species of acanthocephalan (*Corynosoma constrictum*) and the highest mean number of individuals per parasitized bird was ten (immature) *Polymorphus marilis* in *Podiceps nigricollis*. Gallimore (1964) reported a higher rate of infection by *P. paradoxus* in smaller samples and a maximum of 112 individuals of this parasite in a single grebe. According to Holmes (*in litt.*), Gallimore's samples included many immature individuals, including examples of *P. marilis*. Gallimore sampled a wider variety of habitats than Stock, and it is not unlikely that in some the grebes fed to a larger extent on gammarids, which are the intermediate hosts of *P. marilis*.

The intermediate hosts for nine of the 13 species known to mature in grebes are known. All are crustaceans, either amphipods or decapods or both. The number of species of intermediate hosts appears to be directly related to the number of studies of the life cycles. The same applies to the paratenic hosts. In one of the best-studied species, *Corynosoma strumosum*, 39 species of fishes of 19 families plus one snake have been reported in this category, and juvenile forms have also been found in members of three families of carnivorous mammals, but are known only to mature in pinnipeds.

Acanthocephalans have been reported from eight species of grebes: nine species from *Podiceps grisegena*, four from *P. nigricollis*, three each from *Tachybaptus ruficollis* and *Podiceps auritus*, two each from *P. cristatus* and *Aechmophorus occidentalis*, and one each from *Rollandia rolland* and *Podilymbus podiceps*. (These figures do not include species not known to mature in grebes.) As a group, acanthocephalans show little specificity to host groups, and as yet there is no evidence that any acanthocephalan is a grebe specialist. All of those reported from grebes are also known from at least one other order of birds, and most are found in waterfowl, which commonly occur on the same bodies of water as grebes and in most species of these acanthocephalans, anatids are the most frequently reported hosts. Why so many have been reported from *P. grisegena* is unclear but is probably diet-related. These grebes are known to take both groups of intermediate hosts as well as fishes that act as paratenic hosts. This reason for the greater numbers of reports of acanthocephalans from *P. grisegena* appears to be borne out by Gallimore's data (1964) on *Polymorphus paradoxus*, which show both a higher infection rate and greater mean number of worms per infected bird in *P. grisegena* than in the other three species he examined. The fact that eight of the 13 species acanthocephalans known to mature in grebes are known from one species of these birds (in four instances *P. grisegena*) may similarly be explained by the infrequency of occurrence in grebes and the diet of the birds. Diet may also explain why but one or two species of acanthocephalan have been reported from the two large, fish specialists, *Podiceps cristatus* and *Aechmophorus occidentalis*.

Nematodes. Members of four orders, nine families, 20 genera, and 38 species of nematodes are known to parasitize grebes. Of these, nine species (22 percent) and no genera

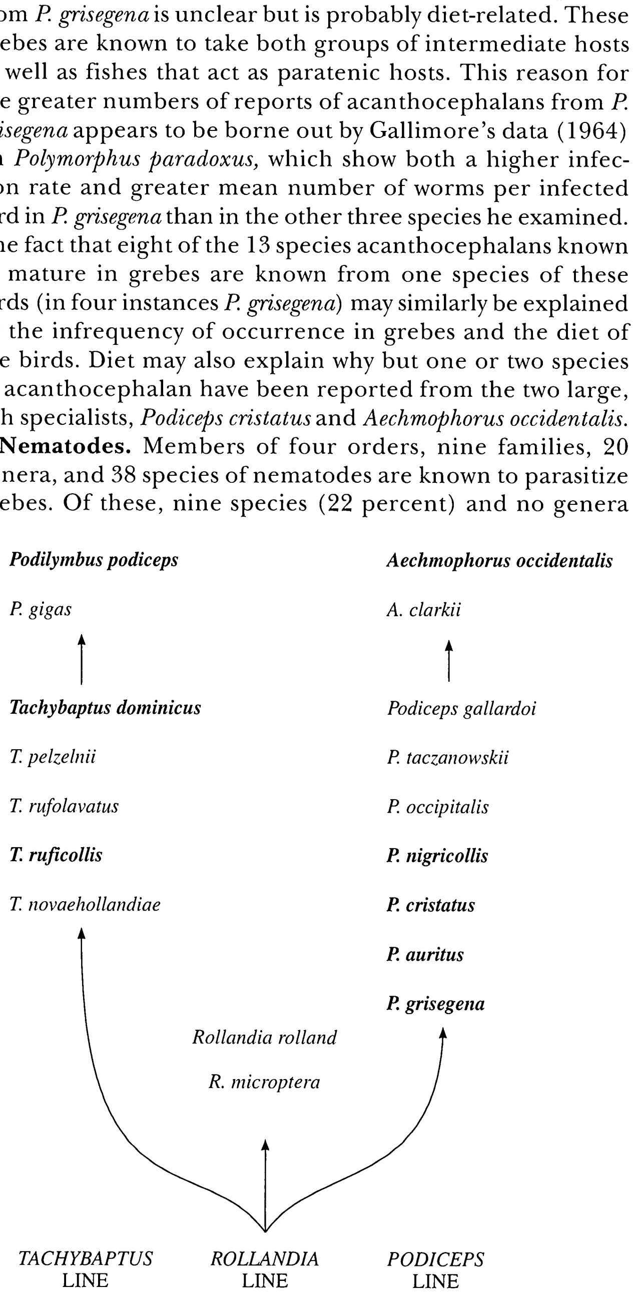

Figure 9. Three lines of grebes for comparison with the groups of *Aquanirmus* (Table 7). The species in bold face are those harboring the species of *Aquanirmus* discussed by Edwards (1965).

Table 6. The Distribution of Mite Species on Grebes.

		Tachybaptus Line				Podiceps Line				
Mite	Taxa	*T. novae.*	*T. rufic.*	*T. dom.*	*P. podil.*	*P. aur.*	*P. gris.*	*P. crist.*	*P. nigri.*	*Ae.* sp.
Dermanyssoidea										
Rhinonyssidae	*Rhynonissus alberti*		+			+		+	+	
	Rhynonissus colymbicola					+	+			
	Rhynonissus podicipedis							+		
	Rhynonissus podilymbi				+					
	Rhynonissus poliocephali	+	+							
Tydeoidea										
Ereynetidae	*Neoboydaia colymbiformi*	+			+				+	
Pterolichoidea										
Ptiloxenidae	*Ptiloxenus colymbi*		+							
	Ptiloxenus major					+	+	+	+	
	Ptiloxenus sp.									+
	Schizurolichus elegans			+	+					
Analgoidea										
Laminosioptidae	*Podicipedicoptes americanus*				+					
Xolalgidae	*Ingrassia colymbi*		+						+[1]	

[1] According to Gaud (1974), the mites from *P. nigricollis* in Morocco are very close to *I. colymbi*, if not identical with it.

are considered grebe specialists. Three of the nine species of specialists are known only from the original descriptions, and two of these are placed in genera with other species known to parasitize grebes. The six other species of grebe specialists are known from three to six species and two or four genera of grebes. There is no strong evidence that any species of nematode is a specialist on a single species of grebe.

The species of nematode grebe specialists belong to three of the four orders and five of the eight families found in grebes (Table 5).

Why is it that while many intestinal helminths are grebe specialists, few, if any, will prove to specialize on a single species of grebe? In general, grebes spend the breeding season on eutrophic bodies of water with a wide variety of potential prey species, and as pointed out earlier (Results p. 43), although a grebe may take a large mass of the prey on which it specializes, it usually takes smaller masses of a considerable variety of other kinds of prey. Furthermore, it is common for two or more species to nest on the same body of water, hence, it might well be disadvantageous for a parasite to be restricted to one species of grebe as its definitive host because that would reduce the number of potential hosts available to it and thus reduce the potential number of offspring it might produce. (A similar situation presumably obtains on the many wintering grounds where more than one species of grebe occur.) This may have or have had a damping effect on the evolution of specificity of helminths for single species of grebes.

Some members of the genus *Dioecocestus* may be exceptions to the general rule that few or no species of cestodes are specific to single species of grebes. Why this should be true is a question that might be worth investigating.

POSSIBLE COEVOLUTION OF GREBES AND THEIR PARASITES

For summaries of the methods used in making studies of host-parasite co-speciation and their importance in various branches of biology, see Hoberg *et al.* 1997.

Helminths. To date, there has been only one attempt to relate co-speciation of grebes with their helminth parasites. Stock (1985) compared a phylogeny of the grebes with those of two genera of amabiliid cestodes, *Schistotaenia* and *Tatria*. While his phylogeny of modern grebes is in general agreement with that of Fjeldså (1982a) and Figure 7, these phylogenies are not cladograms and include no molecular information with which to compare them. Stock took the fossil record of grebes back into the Cretaceous on the basis of Rich (1983, Fig. 9-17), who shows five unspecified genera of Cretaceous birds as possibly belonging to the grebe line. It is now believed (Feduccia 1996) that these Cretaceous diving birds resulted from a much earlier radiation than that which produced the grebes. On the basis of a presumed earlier Cretaceous origin for the grebes, Stock based his zoogeography of the grebes on the breakup of Gondwanaland, which probably took place too early to account for the distribution of Recent grebes.

Isolated tarsometatarsi of diving birds are often found as fossils, and it should be noted that there is much convergence, as well as divergence, in this element of diving birds. This makes identifying these bones to order difficult without material of other parts of the skeleton. The earliest fossil known certainly to have been a grebe, is of Oligocene age (Nessov 1992), and because this fossil is very similar to Recent grebes, the grebe line probably diverged from other lines of modern water birds much earlier.

There is considerable debate on when the major radiation of modern birds took place. Cooper & Penny (1997) present a combination of molecular and fossil evidence suggesting that there was a Cretaceous diversification of birds and mammals rather than an explosive radiation of them in the Early Tertiary, but while there is fossil evidence for this in several other groups, Cooper & Penny cite none for the grebes. On the other hand, Feduccia believes that there were two radiations of birds in the Cretaceous, neither of which included birds of modern orders and that the orders of Recent birds arose in the five million or so years following the major extinctions at the Cretaceous-Tertiary boundary. Therefore, in the lack of good fossil evidence, the time of origin of the grebes is moot.

While a co-speciation analysis might provide speculation about the parasite faunas of the grebe genera (*Rollandia, Poliocephalus* and *Podicephorus*) from which amabiliid parasites are not known, I believe that far better comparisons of the phylogenies of grebes and these parasites could be made with samples from these genera, the first of which is believed nearest to the ancestral stock of the grebes and the last two are of uncertain position with respect to the two principal lines resulting in the genera *Tachybaptus* and *Podilymbus* on the one hand and *Podiceps* and *Aechmophorus* on the other. In addition, I am by no means convinced that Stock's association of grebe species with parasite species in a coevolutionary sense is entirely correct. Similarly detailed data from other communities than those he studied are lacking. It is entirely possible that what may be the principal host in one area may not be in another. Four of the amabiliid species appear to be known only from the original description (three from *Tachybaptus ruficollis,* and one from *Podilymbus podiceps,* both common, widespread, and easily collected species), so assigning a core species for these is by no means certain. The definitive host of one species (*Tatria fuhrmanni*) is unknown, so its core species as yet cannot be determined. Four species of *Tatria* have been described since Stock completed his dissertation (1985), and descriptions of several of the earlier species lacked sufficient morphological data to be included in his analysis. Therefore, there will be an excellent opportunity to make a more complete analysis when more basic information is available. Because of the community-based nature of the analysis, information on intermediate hosts must also be included. Perhaps the most significant crossovers in the communities have been those of intermediate hosts, odonate nymphs to a corixid bug in the case of *Tatria biremis* and to a mayfly nymph in that of *T. biuncinata.* This suggests a parallel with two species of *Schistocephalus,* each of which is specific to a different genus of sticklebacks (Gasterosteidae) as an intermediate host yet is found in a great variety of definitive hosts.

Molecular studies on both the grebes and their helminth parasites would be particularly valuable for comparisons with the morphological data in co-speciation studies.

The other family of cestodes known to contain several species that are grebe specialists is the Hymenolepididae. Although Vasileva *et al.* have made considerable progress in sorting out the relationships of the Palearctic species, more work with those from other regions waits to be done, hence it is not yet a likely one in which to evaluate co-speciation. The digene family Echinostomidae is another family containing numerous grebe specialists, but it is also in need of a careful revision before co-speciation with grebes can be attempted. I see no other helminth family as a likely one for such studies.

External parasites. Because the mites and lice parasitizing grebes spend all their lives on their hosts, they might be likely to speciate more rapidly with their hosts than grebes' helminths. If this has occurred, it should become apparent through comparison of the phylogenies of the parasite and host groups. For making preliminary comparisons, I have divided the species of grebes into three groups or lines (Figure 9): a basal *Rollandia* line and the *Tachybaptus-Podilymbus* line and the *Podiceps-Aechmophorus* line which form major branches of the similar phylogenies of grebes by Fjeldså (1977, 1985) and Storer (1967a and Figure 7). *Poliocephalus* and *Podicephorus,* whose relationships to the others are less well

Table 7. Distribution and Hosts of Lice of the Genus *Aquanirmus.*

Aquanirmus species	Grebe host	Grebe Group	Hemisphere
	A. emersoni group		
A. emersoni	*Podiceps g. grisegena*	P	E
	P. g. holboellii	P	W
A. occidentalis	*Aechmophorus occidentalis*	P	W
A. podilymbus	*Podilymbus podiceps*	T	W
	A. emersoni group?		
A. australis	*Poliocephalus rufopectus*	?	E
	A. colymbinus group		
A. runcinatus	*Tachybaptus ruficollis*	T	E
A. podicipis	*Podiceps cristatus*	P	E
A. colymbinus	*Podiceps a. auritus*	P	E
	Podiceps n. nigricollis	P	E
	Podiceps n. gurneyi	P	E
	A. bahli group		
A. bahli	*Tachybaptus ruficollis*	T	E
A. chamberlini	*Tachybaptus dominicus*	T	W
A. americanus	*Podiceps n. californicus*	P	W
A. bucomfishi	*Podiceps a. cornutus*	P	W

established, are omitted.

Coots (*Fulica*) are common in habitats where most species of grebes nest, and this association has probably been a long one. Assuming that the region with the greatest numbers of species of a group is likely to be the place of origin of the group, the coots, like the grebes, probably arose in South America, where six species occur (Blake 1977), while no more than two species of coots are found on any other continent (Peters 1934). Because, as mentioned before, coots are common throughout much of the ranges and habitats of grebes, have aggressive interactions involving physical contact with grebes, get up onto, and even take over, grebe nests or mating platforms, and mixed clutches of coot and grebe eggs have been found, they are the most likely birds with which grebes can exchange ectoparasites. The fact that coots and grebes belong to two different, unrelated orders of birds is strong evidence that the sharing of groups of external parasites is not the result of common ancestry but of crossing over from one host to another.

All of the 12 species of mites found on grebes are known only from these birds. Five species of the rhinonyssid nasal mite genus *Rhinonyssus* have been reported from grebes. The reported degrees of host specificity of a single species of these mites range from four species and two genera of grebes to one species of mite to a single species of grebe and of geographic ranges from Eurasia, Australia, and North America to a single continent. From this, there appears to be no pattern of specificity. The suggestion by Pence (1972) that each species of *Rhinonyssus* found on grebes will prove to be specific to a single species of grebe remains to be demonstrated.

The single species of the ereynetid nasal mite of the genus *Neoboydaia* reported from grebes shows no specificity to a single grebe species, having been reported from three species all in different genera and in two of the three lines of grebes.

Three species of the feather mite genus *Ptiloxenus* are known from grebes. Each is confined to a single genus of grebe, with a maximum of four species in the case of *Ptiloxenus major* on the genus *Podiceps.* While this fact suggests a possible example of coevolution, information from this group of mites from the four remaining genera of grebes, especially *Rollandia,* would be important in providing corroborative evidence.

Feather mites of three other genera are known from grebes: *Schizurolichus elegans* is reported from two species and genera of the *Tachybaptus* line in the New World, the monotypic genus *Podicipedicoptes* is only known from *Podilymbus podiceps* in North America, and the genus *Ingrassia* is reported from two species of grebe in two genera in different lines, in North Africa. All these three genera of feather mites belong to different families, and the fact that all have been reported from the *Tachybaptus* line of grebes and only one from another line (Table 6) may be a matter of sampling because the species on which these mites have been found are both widespread and easily collected.

Mites of the genera *Rhinonyssus* and *Neoboydaia* have been reported from coots (*Fulica*) by Pence (1972, 1975), which suggests a possible source of mites of these genera on grebes. Members of the subfamily Ingrassiinae are found on birds of 16 orders including the Gruiformes (Gaud & Atyeo 1996), so coots might well be a source of these mites on grebes (or *vice versa*).

Two species of the louse suborder Amblycera are known from grebes. The first, *Pseudomenopon dolium,* is confined to grebes, with one questionable record from a loon. It belongs to a genus of 17 species of which 12 of the remaining 16 are found on rallids including one, *P. pilosum,* which has been found on six species of coots, two on other gruiform birds, and two on charadriiform birds (Price 1974). The similarity of *P. pilosum* to *P. dolium* (Price *op. cit.*), the fact that these two species are the only known intermediate hosts of the nematode, *Pelecitus fulicaeatrae,* which has been found on both coots and grebes, and the relatively frequent contact of grebes with coots strongly suggest that grebes obtained the ancestor of *P. dolium,* and hence *Pelecitus fulicaeatrae,* from these birds. This supports Clay's idea (1957) that *Pseudomenopon* "has possibly become secondarily established on certain water and marsh birds." The second species, *Laemobothrion simile,* to which Price (*in litt.*) believes all reports of this genus from grebes belong, is very similar to *L. atrum,* which was described from a coot. Most (24) other members of this large genus are found on falconiformes, with lesser numbers of species (five, including the one on coots) on gruiformes, and members of several other groups Hopkins & Clay (1952). These authors believed that the species of *Laemobothrion* not found on falconiform birds might be considered to belong to a separate subgenus. Because more species of both *Pseudomenopon* and *Laemobothrion* are found on rallids (including coots) than on grebes, I think it more likely that in both instances crossovers occurred from coots to grebes than *vice versa.* It is also likely that the crossover from coots occurred fairly recently because the single species each of *Pseudomenopon* and *Laemobothrion* known from grebes parasitizes several species of grebes without significant reported differentiation.

In contrast, the only genus of the louse suborder Ischnocera (*Aquanirmus*) known with certainty from grebes has been found only from these birds. According to Clay (1957), this genus "has no obvious relationship to any other and throws no light on the relationship of its hosts." With the exception of the mite genus, *Rhinonyssus,* this is the only genus of ectoparasites which appears to have speciated on grebes. *Aquanirmus* has the most described forms (11 species, one of which was described as a subspecies) of any genus of ectoparasites known from grebes and has been divided into three species groups by Edwards (1965). This degree of differentiation indicates that it has probably been on grebes for a long time and, therefore, is the most suitable group of external parasites for comparing its phylogeny with that of the grebes.

With one exception, each of these forms of *Aquanirmus* is known from a single grebe species. The exception is *A. colymbinus* reported from both *Podiceps auritus* and *P. nigricollis.* However, in his revision of the genus, Edwards (1965) suggests that specimens from the latter grebe may represent a different species.

Edwards' division of the forms of *Aquanirmus* into three groups was based on unspecified "morphological grounds" (*op. cit.,* p. 932). They are shown on his table (p. 933) with their grebe hosts and the hemispheres from which the species of lice are known. Edwards' classification of the grebes is out of date, and his figure contains several errors, which I have corrected on Table 7, and to which I have added the groups to which the grebe species belong. I have also brought the grebe classification which Edwards used up to date and added the species *Aquanirmus australis* described by Kettle (1974). Assuming that the phylogenetic relationships among both groups are correct, one might expect a large degree of congruence between the relationships of the grebes and those of the parasites if co-speciation had occurred. As Edwards has pointed out, this is clearly not the case. The relationships appear to be geographic rather than phylogenetic.

The hosts of each of the three groups of *Aquanirmus* include at least one member of the *Tachybaptus* and *Podiceps* lines. (No species of *Aquanirmus* has yet been reported from *Rollandia*.) On the other hand, as far as known, members of the *emersoni* group are confined to grebes in the New World, except that *A. emersoni* is found on the European race of *P. grisegena* (as well as on the New World race of the same host species); the *bahli* group is confined to the New World except for the Indian-African race of *T. ruficollis,* and the *A. colymbinus* group is confined to the Old World.

If the reports of both *Podiceps auritus* and *P. nigricollis* apply to the same species of the *colymbinus* group, the crossover from one of these hosts to the other was presumably a recent one. A likely mechanism for such a crossover is indicated by the report of a mixed pair of these two species back-brooding and feeding the same chick (Dennis "*et al.*" 1973).

Tachybaptus ruficollis, Podiceps auritus, and *P. nigricollis* all have mallophaga of both the *bahli* and *colymbinus* groups. In the case of the first, the European race hosts a member of the *colymbinus* group and the Indian-African race one of the *bahli* group, whereas in the other two grebes, the split between parasite groups is between the New and Old Worlds.

This lack of congruence between the phylogenies of the grebes and *Aquanirmus* suggests either that the parasite became established on grebes rather late in their radiation, or that crossing over between species of grebes occurred rather frequently, or both.

Clay (1957) pointed out that there is a tendency for some lice to be larger on larger hosts. The species of grebes vary greatly in size, the smallest weighs ca. 100 g and has a wing length of ca. 100 mm, whereas the largest weighs ca. 1600 g. and has a wing length of ca 200 mm. To test whether size of parasite is related to size of host, I compared Edwards' (1965) measurements of head length and width of the species of *Aquanirmus* with size of the host. The results were inconclusive. The three largest grebes known to be parasitized by *Aquanirmus, Podiceps grisegena, P. cristatus,* and *A. occidentalis,* all are hosts of large species of *Aquanirmus,* but so is the smallest grebe (*Tachybaptus dominicus*). At this stage in our knowledge, such a comparison may be futile because we do not know what parts of the bodies of the hosts these lice inhabit, and the variation in size and texture of feathers on a single grebe is considerable.

The exceptions to the rule that each of the groups of *Aquanirmus* is confined to one hemisphere pose interesting questions, but I doubt that we have enough information or specimens to speculate on their origins. The description of *A. b. chamberlini* is based on only three females so the male genitalic characters are unknown, and Edwards' suggestion that both *Podiceps auritus* and *P. nigricollis* are host to the same species of *Aquanirmus* in the Old World is weakened by his comment that the parasite populations on these two species "may not be conspecific."

Reproductive isolation between species of lice has not been studied, and subspecies in that group appear to be defined purely on the basis of slight differences in morphology. The finding of subspecies of the same species of louse on the Old World Little Grebe (*Tachybaptus ruficollis*) and the New World Least Grebe (*T. dominicus*) is odd, because these species differ considerably in morphology and may belong to different subgenera, or according to some (*e.g,*. Oberholser 1974, K.E.L. Simmons *in litt.*), even different genera. In Edwards' figure, they are placed in the same species! If their *Aquanirmus* parasites are as similar as Edwards indicates, there presumably was a transoceanic spread of one to the other. At present, the shortest distance between the ranges of the two grebe species is between South America and Africa. Another possibility is that contact across the Bering Land Bridge may have been made during a warm interglacial period.

No species of *Aquanirmus* has yet been described from the six species of grebes endemic to South America and but one of the three endemic to the Australian region. Mallophaga from the South American grebes would be especially valuable in comparing relationships between the parasites and their hosts because the greatest diversity of grebes (five genera and nine species) is found on that continent. Furthermore, the endemic genus, *Rollandia*, is intermediate between the two lines of grebes and may be considered nearest the ancestral form of the family.

The genera to which the other five species of lice found on grebes belong, *Pseudomenopon, Laemobothrion,* and *Incidifrons,* (the last listed by Malcomson [1960] from *Podiceps nigricollis*) all are known from coots (*Fulica*), as are two of the genera of mites (*Rhinonyssus* and *Neoboydaia*) found in grebes (p. 60).

In summary, there is as yet little evidence of congruence in the phylogenies grebes and their external parasites. The three species of the mite genus *Ptiloxenus* known from grebes are each known only from a single genus of grebe and each of species of the genus *Rhinonyssus* may turn out to be confined to a single species of grebe. On the other hand, the evolution in the louse genus *Aquanirmus* is better explained on geographic than on phylogenetic terms. What does seem apparent is that coots are the most likely source of several of the ectoparasitic genera infecting grebes.

Again, it is clear that more collecting, especially in South America and Australia, is needed. When this is done and when we know more about where on the birds' bodies the lice occur, further research on the evolutionary relationships between these external parasites and their grebe hosts should yield interesting results.

Future coevolutionary studies. Studies comparable to that of Hoberg (1986, 1997; Hoberg *et al.* 1997) on *Alcataenia* and its alcid hosts have not been made on grebes and their parasites. At present, opportunities for this seem limited. In the case of helminths that are grebe specialists, most species that are well studied are known to parasitize more than one species and often, more than one genus of grebes. As pointed out earlier, this is probably related to grebes' breeding on eutrophic bodies of water in which a wide variety of potential prey (and thus of infective stages of parasites) occur and the grebes' habit of taking almost any kind of prey that they they encounter (p. 45). Thus, they acquire a wide variety of parasites. As a group, grebes tend to forage near their nests and usually swim to where they forage. This contrasts with the situation in some alcids that feed intensively on prey which tends to occur in vast shoals to which the birds usually must fly. Individuals in these shoals of prey may also act as intermediate hosts of the specific alcid parasites. Such a host-parasite system would be ideal for studying the evolution of host specificity, whereas host specificity may be likely to develop more slowly in situations where more than one species of definitive host live and feed on the same variety of prey (although in different proportions). In such a situation, it might be disadvantageous for the parasite to be limited in the number of its possible definitive hosts because this might reduce the number of offspring it could produce. If this is so, speciation of the parasite would be more likely to occur when the host-parasite communities are isolated geographically.

One might think that because external parasites live their entire lives on their hosts, coevolutionary studies of these parasites would offer more promise, but this is not necessarily the case. In the louse genus *Aquanirmus*, the relationships between hosts and these parasites appear to have resulted from speciation and later geographic isolation of the grebe hosts and subsequent speciation of the lice. However, no species of *Aquanirmus* is known from the South American endemics, and in the revision of the genus (Edwards 1965), phylogenetic conclusions are limited to the arrangement of the species into three groups which seem unrelated to the phylogeny of the grebes. The mite genera *Rhinonyssus* and *Ptiloxenus*, which may prove useful groups for comparing phylogenies with those of the grebes, are in need of a revisions based on more material, especially from the Southern Hemisphere, than is now available.

Fresh-water/salt-water changeovers of parasites. Grebes are normally hosts to many individuals and species of intestinal helminths. One group of these is derived from intermediate hosts living in fresh water and another from intermediate hosts living in salt water. Like some other waterbirds, grebes presumably have a changeover of intestinal parasites after moving from salt-water wintering grounds to fresh-water breeding grounds and another after the return trip to the wintering areas. Some of the changes may be based on a short life span of the parasites, but other factors also may be involved. If so, the mechanism(s) responsible for these changeovers needs to be determined. A likely possibility is that different salt concentrations in the gut are responsible.

On fresh water, birds presumably only obtain salt from their food, and salt is diluted in the intestines by the intake of fresh water. On salt water, the water ingested with food or otherwise would have a salt concentration greater than that in the intestines.

Because excess salt (or water) is presumably removed along the course of the small intestine, salt concentrations of birds living on marine or fresh waters may be expected to be most similar in the large intestine, caeca, and Bursa of Fabricius. This means that parasites living in these areas would be little or not at all affected by the change of the birds' habitats. This idea is supported by Gallimore (1964) and Stock (1985), who in grebes taken on the breeding grounds in Alberta, found specimens of only two species of helminths known to have saltwater life cycles, *Pseudospelotrema japonicum* and *Tetrabothrius macrocephalus*. The adults of the former inhabit the caeca, and Stock (1985) found the latter only in the posterior part of the intestine.

Some birds that winter on salt water near the coast may move freely between that habitat and fresh waters near the coast, and acquire parasites from both sources (J. C. Holmes *in litt.*). It would be interesting to find out what intestinal parasites such birds carry.

Aside from a sense of touch, sensory perception in cestodes must be largely or entirely restricted to chemical stimuli received through the integument. Electrolyte concentration, the presence of certain ions, and pH are three obvious things that might be sensed and to which the parasites might react by loosening their hold on the wall of the birds' intestines.

From the lists of helminths, it seems clear that birds confined to marine habitats must obtain some parasites with fresh-water life cycles by feeding on anadromous or catadromous fishes. This would appear to be a dead end for the parasites. But is it? Might not a smelt which obtained larval parasites before it moved from its natal fresh-water habitat to its marine one carry these back to its breeding grounds and be eaten by a bird there, thereby completing its life cycle? *Diphyllobothrium ursi* has such a cycle, in salmon and brown bears (Rausch 1954).

Unlike cestodes, nematodes and digenetic trematodes have digestive tracts and feed actively. They are thus not confined to the digestive tracts of their hosts. It would be worthwhile to compare how long these parasites living outside the digestive tract survive the hosts' moves from fresh water to salt water and *vice versa* with the survival of nematodes that are confined to the gastrointestinal tract.

We need to find out much more about the longevity of adults of different species of parasites. This may be brief, as in the case of *Eustrongylides tubifex,* which develops and breeds in the definitive hosts (mergansers) in the brief period (3-4 weeks) spent on the birds' stop-overs on migration (Measures 1988d), or it may be much longer, as in the nematode, *Pelecitus fulicaeatrae,* which, after a short reproductive period, becomes senescent and lives on in the definitive host (Anderson & Bartlett 1994).

What is known about the changeover of parasites in other groups of birds such as ducks would be important for comparison with that in grebes, but is outside the scope of this paper.

Parasites and the Eared Grebes' molt migrations to saline lakes. Every year after the breeding season, as many as 1,845,000 North American Eared Grebes (*Podiceps nigricollis californicus*) gather on Mono Lake, California (Boyd & Jehl 1998). There the adults undergo a complete molt and replacement of their plumage and the young of the year molt and replace all but their remiges (Storer & Jehl 1985). In other parts of western North America and elsewhere in the world, Eared Grebes have similar molt migrations to salt lakes.

Although several advantages to using saline lakes for this purpose are possible, a connection with parasite load does not appear to have been suggested. These molt migrations may have an advantage in reducing the food intake needed for molting and building of premigratory fat deposits by eliminating loss of nutrients through the parasites. Reducing the amount of food needed for these processes would also reduce the amount of hypersaline water taken in with the food and hence the amount of energy needed to excrete the excess salt. These lakes may also have the advantage of containing large supplies of food to which access is limited to the few species of birds that can tolerate the concentration of salt.

Grebes, especially Eared Grebes, carry unusually large numbers of helminth parasites in the small intestine. In his study of four grebe species in Alberta, Canada, Stock (1964) found a range of from 231 to 33,169 such parasites in the 31 Eared Grebes he examined. He did not give a figure for the mean number of helminths per bird, so I calculated a rough estimate of this by summing the mean number per bird of each of the 26 species of parasite found and dividing this by the number of birds examined. The resulting figure was 7,407, more than twice that for the Red-necked Grebe (3,116 for 23 species of helminths). Figures for the Horned and Western grebes were even smaller.

Large numbers of small invertebrates make up the bulk of the Eared Grebes' diet. This includes intermediate hosts of many helminths. Thus, the birds are subject to higher infection rates and larger numbers of individuals of these parasites than grebes that feed on smaller numbers of larger prey.

Jehl (1988) found few or no intestinal parasites in the many Eared Grebes taken on Mono Lake, where the salinity is approximately 2.5 times that of sea water and the water is also highly alkaline (Mahoney & Jehl 1985). The cestode, *Confluaria podicipina,* which is a core species of helminth in Eared Grebes from fresh-water lakes in Alberta (as *"Dubininolepis podicipina,"* Stock & Holmes 1987b) is known to have a life cycle with *Artemia* and these grebes on Tengiz Lake, a saline lake in Kazakhstan (Maximova 1981). The virtual lack of cestodes in grebes on Mono Lake suggests that Mono Lake is too saline to support a cycle of *C. podicipina* (or any intestinal helminth) either in *Artemia,* which is the principal food source for the grebes on the lake, or in the grebes. Assuming that parasite species vary in ranges of tolerance for or have different preferences regarding salinity, this, in turn, might well account for their dying or leaving the host in response to a change in the salt concentration in the intestines when the birds move from fresh to salt water, and *vice versa.*

Jehl (1997) showed that prior to their migratory flight from Mono Lake to their wintering grounds on the Salton Sea or the Gulf of California, Eared Grebes decrease the mass of their digestive organs, which in turn decreases their wing loading. This is especially important for birds like grebes for which this figure is extremely high. The loss of several thousand parasites, even though small, would decrease the wing loading even more.

On Mono Lake, the salt content of water entering the stomach (and the intestine) would be even greater than when the birds are on sea water. This greater salinity might result in the birds' losing the parasites faster than on marine environments. Although Eared Grebes greatly reduce the intake of water with the food by pressing food items against the roof of the mouth with their fleshy tongue (Mahoney & Jehl 1985), an appreciable amount must be taken in, because a considerable amount of water must be held among the many appendages of these crustaceans.

Alkalinity might also be a problem for helminths in grebes on Mono Lake. However, the alkalinity would presumably be neutralized by stomach acid so that by the time the stomach contents reached the intestine, the pH presumably might be nearly similar in birds on both sea water and fresh water. The presence of other ions in the water might also cause the helminths to be killed or to leave. In any case, it is probable that high levels of dissolved salt and other minerals, pH, or a combination of these, would be responsible for ridding the birds of intestinal parasites shortly after their arrival on the lake.

How might the loss of parasites be important to the birds? Most of the commonly found parasites in these birds are small. *Tatria biremis* range from 1.5 to 3.3 and *T. decacantha* from 1.0 to 7.0 mm in length, and the fluke, *Petasiger nitidus,* is in the same size range. Other cestodes like *Diorchis* and several other hymenolepidids, are long but narrow, with widths of roughly 1 to 2 mm. This means that the surface area of the enormous numbers of these small animals must be very large in proportion to their mass and must have the capacity to absorb large amounts of nutrients. In addition, the damage caused by the implanting of thousands of attachment organs in the lining of the intestine must decrease the birds' ability to absorb nutrients. This decreased absorption of nutrients by the birds must be added to the energetic cost of removing excess salt from the digestive tract through the salt glands, and the energetic needs for the development of new feathers.

The invertebrate faunas of saline lakes are few in species, but brine shrimp (*Artemia*) are common in many such lakes, including Mono Lake, where they are abundant and form the principal food of Eared Grebes. The fleshy tongue and, presumably, the habit of pressing food against the roof of the mouth are shared by the Eared Grebe's South American relative, the Silvery Grebe (*Podiceps occipitalis*), which Wetmore (1926) found in Lake Epiquen, Argentina, a saline lake in which *Artemia* were abundant. The time was December and the grebes were courting, so they were presumably not molting, but it is likely that after breeding, they would return there on a molt migration or for both molting and wintering.

Mono Lake may be unique or atypical in its extreme salinity and alkalinity, the superabundance of food, and the presumed lack of infective hosts for parasites. Although I have been unable to find data on the salinity or alkalinity of Tengiz Lake, in Kazakhstan where a population of the cestode (*Confluaria podicipina*) is able to survive (p. 24), it presumably has a considerably lower salinity and alkalinity than Mono Lake. Comparisons between situations regarding salinity, food abundance, and presence of intermediate hosts for grebe parasites on other saline lakes to which Eared Grebes move might shed some light on why the grebes move to these lakes and also might offer clues to how this habit may have evolved.

The ecology of intestinal helminths in grebes. In their broad study of the determinants of community richness in the major groups of vertebrates, Bush *et al.* (1990) found that aquatic birds tend to have more parasites than any other major group and describe them as "the 'tropics' of the parasite world." This is particularly true of those found of fresh water, and of these, grebes may well prove to have the most. Bush *et al.* also introduce the term "component species" for parasites which are found in ten or more percent of the hosts in a study, a term which is valuable in eliminating from comparative studies species of only incidental or accidental occurrence.

Stock (1985) determined the size and distribution of intestinal helminth faunas of four species of grebes on the breeding grounds in Alberta, Canada, by quick freezing, tying off the length of the small intestine into twenty equal sections, and counting the number of each helminth species in each section. This resulted in much new information on the abundance and distribution of these parasites within grebes. In the 91 individuals of four species of grebes that Stock examined, he found each bird infected by from two to 15 species of helminths. This is a greater percentage than those reported from elsewhere by Rausch (1983) but is consistent with Rausch's statement that "high rates of infection are typical of birds that feed on freshwater organisms during the warmer months of the year." Stock also found high infection rates of several species of helminths: 90 of 91 of all his grebes were infected by *Dicranotaenia paraporale,* 50 of 53 Western and Red-necked grebes by *Confluaria furcifera,* and 59 of 64 Red-necked and Eared grebes by *Tatria biremis.*

The functional relationships and microhabitat distributions of the helminths Stock found were reported in Stock and Holmes (1988). From these studies in Alberta, they concluded (1987a) that these helminths formed interacting communities. They argued that such communities "would be expected in species-rich assemblages of parasites with relatively high transmission rates, leading to regular co-occurrence of large populations of many species" and that "in such a system, interspecific interactions would be expected to produce communities of species adapted not only to their host but also to other frequently encountered parasites." A likely result of such interactions was the predictable occurrence of the parasite species in various sections of the intestine. A conspicuous interaction was the effect of the large dioecious cestode, *Dioecocestus asper,* on the presence and distribution of other members of the helminth community in *Podiceps grisegena.*

In describing these communities, Stock classified the helminth species found in each species of grebe in three categories: core species - those occurring in more than 70 percent of the birds examined, satellite species - those occurring in less than 40 percent, and secondary species - those in between 40 and 70 percent of the birds.

Because the presence of the intestinal parasites in the birds depends directly on ingesting the intermediate hosts of the parasites by the birds, the relative importance of this and of interactions with other parasites after the larval parasites arrive in the bird remain to be determined.

Stock sampled nine lakes of varied sizes and depths but from only one were all four species of grebe taken and from six, only a single grebe species was taken. As might be expected, the number of parasite species found in each grebe species was related to the number of lakes sampled, as was the size of the sample of each grebe species. Comparisons between lakes were not made, presumably because time did not permit sufficient samples to be taken and analyzed.

In spite of the fact that all but one of the 12 named core species and two of the six secondary species listed by Stock (1985) are known to occur in Eurasia as well as North America, it is likely that regional differences occur in the make-up of parasite faunas. This is supported by the fact that of the 51 named species of cestodes and acanthocephalans reported from the Red-necked Grebe, only 15 (plus two species not identified with named species) were found by Stock, and the comparable figures for the Eared Grebe were 40, 20, and seven. The data for the Horned Grebe are too small for meaningful comparison. All three of these species of *Podiceps* are widely distributed in Eurasia where they are sympatric with the large, fish-eating Great Crested Grebe (*P. cristatus*). In areas where this species occurs with the Red-necked Grebe, the latter is smaller and shorter billed than in North America and, at least before the rapid recent northward expansion of the range of the Great Crested Grebe in Eurasia north of the breeding range of the Great Crested. This difference was reflected in the higher proportion of fish in the diet of the northern than the southern Eurasian populations of the Red-necked Grebe, even on the wintering grounds where these two forms occur together (Fjeldså 1982b). These dietary differences presumably affected at least the proportions of different species in the helminth communities of these two populations and between them and that of the North American Red-necked Grebes. It is also clear that helminth communities of grebes on salt-water wintering grounds must differ from those on the fresh-water breeding grounds. Parasites acquired from fresh waters in the course of migration may also affect helminth communities after arrival at the breeding grounds. It would be interesting to find out how ecological character displacement and character release in these and other species pairs of grebes (Fjeldså, 1983a) may have affected parasite faunas in closely related species of grebe hosts.

Bush (1990) discusses some of the major conceptual issues in the study of avian helminth communities and presents results from a study of helminths of the Willet (*Catoptrophorus semipalmatus*) which contrast the communities found in the birds on the breeding grounds in Alberta, with those in birds on the coastal wintering grounds. This study provides a model for continuing the work of Stock (1985) by obtaining material of parasites on the salt-water wintering grounds of the species of grebes that Stock studied on the breeding grounds in Alberta and comparing it with Stock's results.

Other species of grebes which are likely to have very different helminth communities are the Pied-billed Grebe, whose breeding range extends from central Canada through the tropics well into temperate South America, and the Little Grebe (*Tachybaptus ruficollis*), which occurs widely in Eurasia and Africa and has the greatest number of digene plus cestode species (84) and total number of parasite species (123) reported from any grebe (Table 4). Because grebes exhibit sexual dimorphism in bill size, and several in shape as well (Figure 6), it is likely that these differences may be reflected in the diet, and hence in the intestinal parasite faunas.

Stock's method of collecting and gathering data would be particularly valuable in future studies of grebe helminths to determine how much the faunas of the same grebe species vary with sex and age and both locally and regionally. Although extremely time-consuming, such studies would be basic to interpretations of possible coevolution of parasite faunas with the hosts.

In order to make meaningful comparisons between the parasite faunas of widespread grebe species inhabiting different continents or even smaller areas, more basic systematic work still needs to be done. For example, Gallimore's (1964) and Stock's (1985) finding the apparent difference in degree of host specificity between the North American and European populations of *Dioecocestus asper* suggests that different species may be involved. In addition, ten of the species found by Stock were not identified to named species. Eight of these were hymenolepidids, a group in need of a revision. While this detracts but little from Stock's study, it makes detailed comparisons with similar studies in other parts of the world difficult or impossible until the proper names can be provided. As Rausch (1983) pointed out, "taxonomy, systematics, and knowledge of cycles remain basic to investigations involving helminths."

The paucity of known species of ectoparasites on grebes does not make the study of their communities worthwhile, at the present time.

In summary, the need for new material of parasites of most species of birds is great. With the increasing difficulties in obtaining collecting permits and the fact that when a host species becomes extinct, the parasites that depend on it for their existence do also, a concerted effort to link avifaunal surveys with those of the birds' parasite faunas is sorely needed. Thus, it is important that ways be found for someone versed in the collection and preservation of parasites, to be part of regional surveys of vertebrates. (Clayton & Moore [1997 appendices A, B, and C] and references therein provide basic and detailed "how to" information for this.) It is also important that at least vouchers of the species of parasites found be deposited in reputable long-term collections such as the U. S. National Parasite Collection (Lichtenfels *et al.* 1992).

I do not think it an exaggeration to say that a profitable lifetime of research could be spent studying the parasites of just the grebes.

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The fine original drawings of parasite life cycles were prepared by John Megahan after illustrations in the following sources: Cover. *Tatria biremis* Adult worm redrawn from figure in Gulyaev (1990a). Eared Grebe Farrand (1983). *Sigara* from specimen in UMMZ. (No figure of the structure of the egg was found.) Figure 1. *Petasiger nitidus.* a. adult worm Beaver (1939a) and Schell (1985), b. Pied-billed Grebe Farrand (1983), c. egg Beaver (1939a), d. miracidium, e. planorbid snail UMMZ specimen, f. cercaria Beaver (1939a), g. bullhead (*Ictalurus*) from life. Figure 2. *Strigea falconis.* a adult worm, Schell (1985), b. Peregrine Falcon paintings in Brown & Amadon (1968), c. egg and d. miracidium (of *Cotylurus*) Olson (1974), e. planorbid snail UMMZ specimen, f. cercaria, Schell (1985). Both Great Crested Grebes and Peregrine Falcons are known to harbor this parasite and Peregrines are known to take this grebe (Uttendörfer 1939). Figure 3. *Schistocephalus solidus.* a. adult worm, b. Red-necked Grebe Farrand (1983), c. egg, and d. coracidium, Dubinina (1980), Copepod (*Cyclops*), (T. I. Storer 1943), Stickleback (*Gasterosteus*), Scott & Crossman (1973). Figure 4. *Schistotaenia tenuicirrus.* a. adult worm, Chandler (1948), Pied-billed Grebe Farrand (1983), c. egg and d. dragonfly nymph (*Anax junius*) with strobilocercoid larva of parasite, Boertje (1975). Figure 5. *Corynosoma strumosum.* a. adult worm and c. egg, Ryzhikov *et al.* (1985), b. Red-necked Grebe Farrand (1983), d. amphipod (*Pontoporeia*), Bousfield (1973), California Sealion Peterson and Bartholomew (1967), and adult and young Steelhead Trout (*Salmo gairdneri*), Scott & Crossman (1973).

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APPENDIX. LIST OF GREBES AND THEIR PARASITES

Parasites of ***Rollandia rolland***

DIGENES

Echinostomidae

- *Episthmium wernickii* (Marco del Pont, 1926)
- *Mesorchis argentinensis* (Sutton, Lunaschi & Topa, 1982)

Microphallidae

- *Levinseniella cruzi* Travassos, 1921

ACANTHOCEPHALANS

Polymorphidae

- *Polymorphus chasmagnathi* (Holcman Spector, Mane Garzon & Dei Cas, 1977)

Parasites of ***Tachybaptus novaehollandiae***

DIGENES

Cyclocoelidae

- *Corpopyrum jaenschi* (Johnston & Simpson, 1940)

Echinostomidae

- *Petasiger australis* Johnston & Angel, 1941

Strigeidae

- *Schwartzitrema pandubi* (Pande, 1939)

Microphallidae

- *Maritrema oocystum* (Lebour, 1907)

CESTODES

Dioecocestidae

- *Dioecocestus novaeguineae* Fuhrmann, 1914
- *Dioecocestus novaehollandiae* (Krefft, 1873)

NEMATODES

Anisakidae

- *Contracaecum ovale* (Linstow, 1907)

Tetrameridae

- *Tetrameres gubanovi* Shigin, 1957

Acuariidae

- *Streptocara crassicauda* (Creplin, 1829)
- *Streptocara recta* (Linstow, 1879)

MITES

Rhinonyssidae

- *Rhinonyssus poliocephali* Fain, 1956

Ereynetidae

- *Neoboydaia colymbiformi* Clark, 1964

Parasites of ***Tachybaptus ruficollis***

DIGENES

Notocotylidae

- *Paramonostomum elongatum* Yamaguti, 1934

Echinostomidae

- *Echinochasmus coaxatus* Dietz, 1909
- *Echinochasmus colymbi* Oshmarin, 1950
- *Echinochasmus dietzevi* Issaitschikoff, 1927
- *Echinochasmus fotedari* Chisti & Mir, 1989
- *Echinochasmus japonicus* Tanabe, 1926
- *Echinochasmus podicepensis* (Bhardwaj, 1962)
- *Echinochasmus ruficapensis* Verma, 1935
- *Echinochasmus spinulosus* (Rudolphi, 1809)
- *Echinostoma echiniferum* (La Valette, 1855)
- *Echinostoma revolutum* (Froelich, 1802)
- *Euparyphium pindchi* Khan & Chishti, 1984
- *Hypoderaeum conoideum* (Bloch, 1782)
- *Hypoderaeum gnedini* Bashkirova, 1941
- *Microparyphium ruficollis* (Ishii, 1935)
- *Patagifer bilobus* (Rudolphi, 1819)
- *Patagifer parvispinosus* Yamaguti, 1933
- *Petasiger grandivesicularis* (Ishii, 1935)
- *Petasiger lobatus* Yamaguti, 1933
- *Petasiger megacanthus* Kotlán, 1922
- *Petasiger neocomensis* Fuhrmann, 1928
- *Petasiger pungens* (Linstow, 1894)
- *Petasiger soochowensis* Ku, Chiu, Li & Chu, 1977
- *Petasiger tientsinensis* Ku, Chiu, Li & Chu, 1977

Cyathocotylidae

- *Cyathocotyle prussica* Muehling, 1896
- *Cyathocotyle teganuma* Ishii, 1935

Diplostomidae

- *Diplostomum gavium* (Guberlet, 1922) of Hughes, 1929
- *Histeromorpha triloba* (Rudolphi, 1819)
- *Posthodiplostomum podicipitis* (Yamaguti, 1939)
- *Tylodelphys conifera* (Mehlis, 1846)
- *Tylodelphys excavata* (Rudolphi, 1803)

Strigeidae

- *Apatemon gracilis* (Rudolphi, 1819)
- *Cotylurus cornutus* (Rudolphi, 1808)
- *Ichthyocotylurus platycephalus* (Creplin, 1825) Szidat, 1928
- *Parastrigea robusta* Szidat, 1928
- *Strigea falconis* Szidat, 1928

Opisthorchidae

- *Metorchis orientalis* Tanabe, 1920
- *Metorchis xanthosomus* (Creplin, 1846)

Heterophyidae

- *Metagonimus takahachii* Suzuki, in Takahashi, 1929

Prosthogonimidae

- *Prosthogonimus cuneatus* (Rudolphi, 1809)
- *Prosthogonimus ovatus* (Rudolphi, 1803)

Ochetosomatidae

- *Stomylotrema grebei* Mathur, 1950

Eucotylidae

- *Eucotyle cohni* Skrjabin, 1924
- *Tanaisia fedtschenkoi* Skrjabin, 1924
- *Tanaisia integerriorcha* Saidov, 1954

CESTODES

Diphyllobothriidae

- *Diphyllobothrium podicipedis* (Diesing, 1854)
- *Ligula colymbi* Zeder, 1803
- *Ligula intestinalis* (Linnaeus, 1758)
- *Schistocephalus solidus* (Mueller, 1776)

Tetrabothriidae

- *Tetrabothrius macrocephalus* (Rudolphi, 1810)

Dioecocestidae

- *Dioecocestus asper* (Mehlis, 1831)
- *Dioecocestus cablei* (Siddiqi, 1960)
- *Dioecocestus fevita* Meggitt, 1933
- *Dioecocestus novaeguineae* Fuhrmann, 1914

Amabiliidae

- *Diporotaenia colymbi* Spasskaya, Spassky & Borgarenko, 1971
- *Pseudoschistotaenia indica* Fotedar & Chisti, 1976
- *Pseudoschistotaenia pindchii* Fotedar & Chisti, 1977
- *Schistotaenia colymba* Schell, 1955
- *Schistotaenia indica* Johri, 1959
- *Schistotaenia macrorhyncha* (Rudolphi, 1810)
- *Schistotaenia mathevossianae* Okorokov, 1956
- *Schistotaenia rufi* Sulgostowska & Korpaczewska, 1969
- *Tatria acanthorhyncha* (Wedl, 1855)
- *Tatria biremis* Kowalewski, 1904
- *Tatria biuncinata* (Joyeux & Baer, 1943)
- *Tatria decacantha* Fuhrmann, 1913

Tatria decacanthoides (Borgarenko & Gulyaev, 1991)
Tatria iunii Korpaczewska & Sulgostowska, 1974
Tatria jubilaea Okorokov & Tkachev, 1973
Tatria octacantha Rees, 1973
Tatria pilatus (Borgarenko & Gulyaev, 1991)
Tatria skrjabini Tretyakova, 1948
Dilepididae
Liga lencoranica Sailov, 1962
Hymenolepididae
Aploparaksis crassirostris (Krabbe, 1869)
Aploparaksis furcigera (Nitzsch in Rudolphi, 1819)
Confluaria japonica (Yamaguti, 1935)
Confluaria multistriata (Rudolphi, 1810)
Confluaria podicipina (Szymanski, 1905)
Diorchis spinata Mayhew, 1929
Diploposthe laevis (Bloch, 1782)
Drepanidotaenia lanceolata (Bloch, 1782)
Mackoja podirufi (Macko, 1962)
Microsomacanthus compressus (Linton, 1892)
Podicipitilepis laticauda (Yamaguti, 1956)
ACANTHOCEPHALANS
Polymorphidae
Filicollis anatis (Schrank, 1788)
Polymorphus minutus (Goeze, 1782)
Southwellina hispida (Van Cleave, 1925)
NEMATODES
Dioctophymatidae
Eustrongylides mergorum (Rudolphi, 1809)
Eustrongylides tubifex (Nitzsch, 1819)
Trichuridae
Baruscapillaria mergi (Madsen, 1945)
Baruscapillaria podicipitis (Yamaguti, 1941)
Baruscapillaria ryjikovi (Daiya, 1972)
Eucoleus contortus (Creplin, 1839)
Amidostomatidae
Amidostomum anseris (Zeder, 1800)
Amidostomum fulicae (Rudolphi, 1819)
Epomidiostomum uncinatum (Lundahl, 1848)
Anisakidae
Contracaecum andersoni Vevers, 1923
Contracaecum micropapillatum (Stossich, 1890)
Contracaecum ovale (Linstow, 1907)
Contracaecum praestriatum Moennig, 1923
Contracaecum spiculigerum (Rudolphi, 1809)
Dracunculidae
Avioserpens mosgovoyi Supryaga, 1965
Gnathostomatidae
Gnathostoma spinigerum Owen, 1836
Tetrameridae
Tetrameres fissispina (Diesing, 1861)
Tetrameres gubanovi Shigin, 1957
Acuariidae
Echinuria uncinata (Rudolphi, 1819)
Paracuaria adunca (Creplin, 1846)
Rusguniella wedli Williams, 1929
Streptocara crassicauda (Creplin, 1829)
Streptocara recta (Linstow, 1879)
Syncuaria decorata (Cram, 1927)
Syncuaria squamata (Linstow, 1883)
Onchocercidae
Carinema bilqueesae Gupta & Jaiswal, 1989
Pelecitus fulicaeatrae (Diesing, 1861)
LEECHES
Glossiphoniidae
Theromyzon cooperi (Harding, 1932)
MITES
Xolalgidae
Ingrassia colymbi Gaud, 1974
Ptiloxenidae
Ptiloxenus colymbi (Canestrini, 1878)
Rhinonyssidae
Rhinonyssus alberti Strandtmann, 1956
Rhinonyssus poliocephali Fain, 1956
LICE
Menoponidae
Pseudomenopon dolium (Rudow, 1869)
Laemobothriidae
Laemobothrion simile Kellogg, 1896
Philopteridae
Aquanirmus bahli Tandan, 1951
Aquanirmus runcinatus (Nitzsch, 1866)

Parasites of ***Tachybaptus rufolavatus***

NEMATODES
Anisakidae
Contracaecum sp. (only immature stages found—Vassiliades, 1970)

Parasites of ***Tachybaptus dominicus***

DIGENES
Echinostomidae
Nephrostomum robustum Pérez Vigueras, 1944
Petasiger novemdecim Lutz, 1928
Clinostomidae
Clinostomum pusillum Lutz, 1928
Diplostomidae
Tylodelphys elongata (Lutz, 1928)
CESTODES
Dioecocestidae
Dioecocestus acotylus Fuhrmann, 1904
Amabiliidae
Laterorchites bilateralis (Fuhrmann, 1908)
Schistotaenia macrorhyncha (Rudolphi, 1810)
Schistotaenia scolopendra (Diesing, 1856)
Tatria acanthorhyncha (Wedl, 1855)
Tatria appendiculata Fuhrmann, 1908
Hymenolepididae
Variolepis capillaris (Rudolphi, 1810)
NEMATODES
Anisakidae
Contracaecum quincuspis Lucker, 1941
Contracaecum spiculigerum (Rudolphi, 1809)
MITES
Ptiloxenidae
Schizurolichus elegans Černy, 1969
LICE
Philopteridae
Aquanirmus chamberlini Edwards, 1965

Parasites of ***Podilymbus podiceps***

DIGENES
Cyclocoelidae
Tracheophilus cymbium (Diesing, 1850)

Cathaemasiidae
- *Ribeiroia ondatrae* (Price, 1931)

Echinostomidae
- *Echinochasmus donaldsoni* Beaver, 1941
- *Petasiger chandleri* Abdel-Malek, 1952
- *Petasiger floridus* Premvati, 1968
- *Petasiger nitidus* Linton, 1928

Schistosomatidae
- *Gigantobilharzia elongata* (Brackett, 1940)

Diplostomidae
- *Tylodelphys elongata* (Lutz, 1928)

Opisthorchiidae
- *Plotnikovia podilymbae* (Olsen, 1938)

Plagiorchiidae
- *Plagiorchis maculosus* (Rudolphi, 1802)

CESTODES

Diphyllobothriidae
- *Ligula colymbi* Zeder, 1803
- *Ligula intestinalis* (Linnaeus, 1758)
- *Schistocephalus solidus* (Mueller, 1776)

Amabiliidae
- *Schistotaenia colymba* Schell, 1955
- *Schistotaenia macrocirrus* Chandler, 1948
- *Schistotaenia scolopendra* (Diesing, 1856)
- *Schistotaenia tenuicirrus* Chandler, 1948
- *Tatria duodecacantha* Olsen, 1939

Hymenolepididae
- *Confluaria furcifera* (Krabbe, 1869)
- *Lobatolepis lobulata* (Mayhew, 1925)

ACANTHOCEPHALANS

Polymorphidae
- *Polymorphus meyeri* Lundström, 1942

NEMATODES

Anisakidae
- *Contracaecum ovale* (Linstow, 1907)
- *Contracaecum spiculigerum* (Rudolphi, 1809)

LEECHES

Glossiphoniidae
- *Theromyzon "occidentalis"* (Verrill, 1874)
- *Theromyzon "trizonare"* Davies & Ooshuizen, 1993

MITES

Laminosioptidae
- *Podicipedicoptes americanus* Lombert, Kethley & Lukoschus, 1979

Ptiloxenidae
- *Schizurolichus elegans* Černy, 1969

Ereynetidae
- *Neoboydaia colymbiformi* Clark, 1964

Rhinonyssidae
- *Rhinonyssus podilymbi* Pence, 1972

LICE

Philopteridae
- *Aquanirmus podilymbus* Edwards, 1965

Parasites of ***Podilymbus gigas***

CESTODES

Hymenolepididae
- *Labatolepis lobulata* (Mayhew, 1925)

Parasites of ***Poliocephalus poliocephalus***

DIGENES

Notocotylidae
- *Paramonostomum caeci* Smith & Hickman, 1983

Cyclocoelidae
- *Corpopyrum jaenschi* (Johnston & Simpson, 1940)

Psilostomidae
- *Psilochasmus oxyurus* (Creplin, 1825)

Echinostomidae
- *Petasiger australis* Johnston & Angel, 1941

Strigeidae
- *Schwartzitrema pandubi* (Pande, 1939)

Microphallidae
- *Atriophallophorus coxiellae* S. J. Smith, 1974
- *Levinseniella tasmaniae* (S. J. Smith, 1974)
- *Maritrema calvertense* S. J. Smith, 1974

NEMATODES

Anisakidae
- *Contracaecum praestriatum* Moennig, 1923

Acuariidae
- *Streptocara crassicauda* (Creplin, 1829)
- *Streptocara recta* (Linstow, 1879)

Parasites of ***Poliocephalus rufopectus***

LICE

Philopteridae
- *Aquanirmus australis* Kettle, 1974

Parasites of ***Podicephorus major***

DIGENES

Echinostomidae
- *Mesorchis argentinensis* (Sutton, Lunaschi & Topa, 1982)
- *Mesorchis denticulatus* (Rudolphi, 1802)
- *Mesorchis podicipei* (Etchegoin & Martorelli, 1997)

Parasites of ***Podiceps auritus***

DIGENES

Notocotylidae
- *Notocotylus attenuatus* (Rudolphi, 1809)

Cathaemasiidae
- *Ribeiroia ondatrae* (Price, 1931)

Echinostomidae
- *Echinochasmus donaldsoni* Beaver, 1941
- *Echinochasmus mordax* (Loos, 1899)
- *Echinochasmus spinulosus* (Rudolphi, 1809)
- *Echinoparyphium aconiatum* Dietz, 1909
- *Echinostoma revolutum* (Froelich, 1802)
- *Mesorchis denticulatus* (Rudolphi, 1802)
- *Petasiger megacanthus* Kotlán, 1922
- *Petasiger neocomensis* Fuhrmann, 1928
- *Petasiger nitidus* Linton, 1928
- *Petasiger oschmarini* Kostadinova & Gibson, 1998
- *Petasiger pungens* (Linstow, 1894)

Diplostomidae
- *Diplostomum capsulare* (Diesing, 1858) Bittner & Sprehn, 1928
- *Diplostomum gavium* (Guberlet, 1922) of Hughes, 1929
- *Tylodelphys conifera* (Mehlis, 1846)
- *Tylodelphys podicipina* Kozicka & Niewiadomska, 1960

Strigeidae
- *Apatemon gracilis* (Rudolphi, 1819)
- *Ichthyocotylurus erraticus* (Rudolphi, 1809)
- *Ichthyocotylurus platycephalus* (Creplin, 1825) Szidat, 1928

- Heterophyidae
  - *Cryptocotyle lingua* (Creplin, 1825)
- Renicolidae
  - *Renicola pinguis* (Mehlis in Creplin, 1846)
- Prosthogonimidae
  - *Prosthogonimus cuneatus* (Rudolphi, 1809)
- Eucotylidae
  - *Eucotyle cohni* Skrjabin, 1924
  - *Eucotyle hassalli* Price, 1930

CESTODES

- Diphyllobothriidae
  - *Digramma interrupta* (Rudolphi, 1810)
  - *Ligula colymbi* Zeder, 1803
  - *Ligula intestinalis* (Linnaeus, 1758)
  - *Schistocephalus pungitii* Dubinina, 1959
  - *Schistocephalus solidus* (Mueller, 1776)
- Tetrabothriidae
  - *Tetrabothrius macrocephalus* (Rudolphi, 1810)
- Dioecocestidae
  - *Dioecocestus asper* (Mehlis, 1831)
- Amabiliidae
  - *Schistotaenia colymba* Schell, 1955
  - *Schistotaenia indica* Johri, 1959
  - *Schistotaenia macrorhyncha* (Rudolphi, 1810)
  - *Schistotaenia mathevossianae* Okorokov, 1956
  - *Schistotaenia srivastavai* Rausch, 1970
  - *Schistotaenia tenuicirrus* Chandler, 1948
  - *Tatria acanthorhyncha* (Wedl, 1855)
  - *Tatria biremis* Kowalewski, 1904
  - *Tatria biuncinata* (Joyeux & Baer, 1943)
  - *Tatria decacantha* Fuhrmann, 1913
  - *Tatria jubilaea* Okorokov & Tkachev, 1973
  - *Tatria pilatus* (Borgarenko & Gulyaev, 1991)
- Hymenolepididae
  - *Confluaria capillaris* (Rudolphi, 1810)
  - *Confluaria furcifera* (Krabbe, 1869)
  - *Confluaria multistriata* (Rudolphi, 1810)
  - *Confluaria podicipina* (Szymanski, 1905)
  - *Dicranotaenia paraporale* (Podesta & Holmes, 1970)
  - *Dubininolepis swiderskii* (Gasowska, 1932)
  - *Dubininolepis rostellatus* (Abildgaard, 1790)
  - *Parafimbriaria websteri* Voge & Read, 1954
  - *Wardium cirrosum* (Krabbe, 1869)

ACANTHOCEPHALANS

- Polymorphidae
  - *Filicollis anatis* (Schrank, 1788)
  - *Polymorphus acutis* Van Cleave & Starrett, 1940
  - *Polymorphus paradoxus* Connell & Corner, 1957

NEMATODES

- Dioctophymatidae
  - *Eustrongylides mergorum* (Rudolphi, 1809)
- Trichuridae
  - *Baruscapillaria obsignata* (Madsen, 1945)
  - *Baruscapillaria podicipitis* (Yamaguti, 1941)
  - *Eucoleus contortus* (Creplin, 1839)
- Anisakidae
  - *Contracaecum microcephalum* (Rudolphi, 1809)
  - *Contracaecum ovale* (Linstow, 1907)
  - *Contracaecum spiculigerum* (Rudolphi, 1809)
  - *Porrocaecum praelongum* (Dujardin, 1845)
- Tetrameridae
  - *Tetrameres fissispina* (Diesing, 1861)
- Acuariidae
  - *Cosmocephalus obvelatus* (Creplin, 1825)
  - *Echinuria uncinata* (Rudolphi, 1819)
  - *Paracuaria adunca* (Creplin, 1846)
  - *Streptocara crassicauda* (Creplin, 1829)
  - *Streptocara recta* (Linstow, 1879)
  - *Syncuaria decorata* (Cram, 1927)
- Onchocercidae
  - *Pelecitus fulicaeatrae* (Diesing, 1861)

LEECHES

- Glossiphoniidae
  - *Placobdella ornata* (Verrill, 1872)
  - *Theromyzon "trizonare"* Davies & Oosthuizen, 1993

MITES

- Ptiloxenidae
  - *Ptiloxenus major* (Megnin & Trouessart, 1884)
- Rhinonyssidae
  - *Rhinonyssus alberti* Strandtmann, 1956
  - *Rhinonyssus colymbicola* Fain & Bafort, 1963

LICE

- Menoponidae
  - *Pseudomenopon dolium* (Rudow, 1869)
- Laemobothriidae
  - *Laemobothrion simile* Kellogg, 1896
- Philopteridae
  - *Aquanirmus bucomfishi* Edwards, 1965
  - *Aquanirmus colymbinus* (Scopoli, 1763)

Parasites of ***Podiceps grisegena***

DIGENES

- Notocotylidae
  - *Notocotylus attenuatus* (Rudolphi, 1809)
  - *Paramonostomum bucephalae* Yamaguti, 1935
- Cathaemasiidae
  - *Ribeiroia ondatrae* (Price, 1931)
- Echinostomidae
  - *Echinochasmus amphibolus* Kotlán, 1922
  - *Echinochasmus coaxatus* Dietz, 1909
  - *Echinochasmus colymbi* Oshmarin, 1950
  - *Echinochasmus dietzevi* Issaitschikoff, 1927
  - *Echinochasmus spinulosus* (Rudolphi, 1809)
  - *Echinostoma intermedium* (Mehlis in Creplin, 1846)
  - *Echinostoma revolutum* (Froelich, 1802)
  - *Mesorchis denticulatus* (Rudolphi, 1802)
  - *Petasiger lobatus* Yamaguti, 1933
  - *Petasiger megacanthum* Kotlán, 1922
  - *Petasiger neocomensis* Fuhrmann, 1928
  - *Petasiger nitidus* Linton, 1928
  - *Petasiger oschmarini* Kostadinova & Gibson, 1998
  - *Petasiger skrjabini* Bashkirova, 1941
- Schistosomatidae
  - *Bilharzia polonica* (Kowalewski, 1895)
- Cyathocotylidae
  - *Cyathocotyle teganuma* Ishii, 1935
- Diplostomidae
  - *Diplostomum gavium* (Guberlet, 1922) of Hughes, 1929
  - *Diplostomum mergi* Dubois, 1932
  - *Diplostomum spathaceum* (Rudolphi, 1819)
  - *Tylodelphys conifera* (Mehlis, 1846)
  - *Tylodelphys podicipina* Kozicka & Niewiadomska, 1960

- Strigeidae
  - *Apatemon gracilis* (Rudolphi, 1819)
  - *Ichthyocotylurus erraticus* (Rudolphi, 1809)
  - *Strigea falconis* Szidat, 1928
- Heterophyidae
  - *Cercarioides humbargari* (Park, 1936)
  - *Cryptocotyle concava* (Creplin, 1825)
- Renicolidae
  - *Renicola pinguis* (Mehlis in Creplin, 1846)
- Microphallidae
  - *Pseudospelotrema japonicum* Yamaguti, 1939
- Prosthogonimidae
  - *Prosthogonimus ovatus* (Rudolphi, 1803)
- Plagiorchiidae
  - *Plagiorchis laricola* Skrjabin, 1924
  - *Plagiorchis maculosus* (Rudolphi, 1802)
- Ochetosomatidae
  - *Lobogonimus skrjabini* Filimonova, 1973
- Eucotylidae
  - *Eucotyle cohni* Skrjabin, 1924

CESTODES

- Diphyllobothriidae
  - *Digramma interrupta* (Rudolphi, 1810)
  - *Diphyllobothrium ditremum* (Creplin, 1825)
  - *Ligula colymbi* Zeder, 1803
  - *Ligula intestinalis* (Linnaeus, 1758)
  - *Schistocephalus pungitii* Dubinina, 1959
  - *Schistocephalus solidus* (Mueller, 1776)
- Tetrabothriidae
  - *Tetrabothrius macrocephalus* (Rudolphi, 1810)
- Dioecocestidae
  - *Dioecocestus asper* (Mehlis, 1831)
- Amabiliidae
  - *Ryjikovilepis dubininae* (Ryzhikov & Tolkatcheva, 1981)
  - *Schistotaenia colymba* Schell, 1955
  - *Schistotaenia macrorhyncha* (Rudolphi, 1810)
  - *Schistotaenia mathevossianae* Okorokov, 1956
  - *Schistotaenia srivastavai* Rausch, 1970
  - *Schistotaenia tenuicirrus* Chandler, 1948
  - *Tatria acanthorhyncha* (Wedl, 1855)
  - *Tatria biremis* Kowalewski, 1904
  - *Tatria decacantha* Fuhrmann, 1913
  - *Tatria fimbriata* (Borgarenko, Spasskaja & Spassky, 1972)
- Dilepididae
  - *Lateriporus clerci* (Johnston, 1912)
  - *Lateriporus skrjabini* Mathevossian, 1946
  - *Neovalipora parvispine* (Linton, 1927)
- Hymenolepididae
  - *Aploparaksis filiformis* Spassky, 1963
  - *Confluaria capillaris* (Rudolphi, 1810)
  - *Confluaria furcifera* (Krabbe, 1869)
  - *Confluaria japonica* (Yamaguti, 1935)
  - *Confluaria multistriata* (Rudolphi, 1810)
  - *Confluaria podicipina* (Szymanski, 1905)
  - *Dicranotaenia coronula* (Dujardin, 1845)
  - *Dicranotaenia paraporale* (Podesta & Holmes, 1970)
  - *Diorchis skarbilowitschi* Shakhtakhtinskaya, 1952
  - *Diploposthe laevis* (Bloch, 1782)
  - *Dubininolepis rostellatus* (Abildgaard, 1790)
  - *Fimbriaria fasciolaris* (Pallas, 1781)
  - *Microsomacanthus compressus* (Linton, 1892)
  - *Microsomacanthus microskrjabini* Spassky & Yurpalova, 1965
  - *Microsomacanthus pachycephalus* (Linstow, 1872)
  - *Parafimbriaria micrantha* Gulyaev, 1990
  - *Parafimbriaria websteri* Voge & Read, 1954
  - *Pararetinometra lateralacantha* Stock & Holmes, 1981
  - *Wardium amphitricum* (Rudolphi, 1819)
  - *Wardium fusum* (Krabbe, 1869)

ACANTHOCEPHALANS

- Polymorphidae
  - *Andracantha mergi* (Lundström, 1941)
  - *Corynosoma anatarium* Van Cleave, 1945
  - *Corynosoma constrictum* Van Cleave, 1918
  - *Polymorphus acutis* Van Cleave & Starrett, 1940
  - *Polymorphus contortus* (Bremser in Westrumb, 1821)
  - *Polymorphus magnus* Skrjabin, 1913
  - *Polymorphus marilis* Van Cleave, 1939
  - *Polymorphus minutus* (Goeze, 1782)
  - *Polymorphus paradoxus* Connell & Corner, 1957

NEMATODES

- Trichuridae
  - *Baruscapillaria carbonis* (Rudolphi, 1819)
  - *Baruscapillaria obsignata* (Madsen, 1945)
  - *Baruscapillaria podicipitis* (Yamaguti, 1941)
  - *Baruscapillaria ryjikovi* (Daiya, 1972)
  - *Capillaria anatis* (Schrank, 1790)
  - *Eucoleus contortus* (Creplin, 1839)
- Amidostomatidae
  - *Epomidiostomum uncinatum* (Lundahl, 1848)
- Anisakidae
  - *Contracaecum microcephalum* (Rudolphi, 1809)
  - *Contracaecum ovale* (Linstow, 1907)
  - *Contracaecum spiculigerum* (Rudolphi, 1809)
  - *Porrocaecum crassum* (Deslongchamps, 1824)
- Dracunculidae
  - *Avioserpens mosgovoyi* Supryaga, 1965
- Tetrameridae
  - *Tetrameres fissispina* (Diesing, 1861)
  - *Tetrameres gubanovi* Shigin, 1957
- Acuariidae
  - *Cosmocephalus obvelatus* (Creplin, 1825)
  - *Echinuria uncinata* (Rudolphi, 1819)
  - *Paracuaria adunca* (Creplin, 1846)
  - *Rusguniella elongata* (Rudolphi, 1819)
  - *Streptocara crassicauda* (Creplin, 1829)
  - *Syncuaria decorata* (Cram, 1927)
- Onchocercidae
  - *Pelecitus fulicaeatrae* (Diesing, 1861)

LEECHES

- Glossiphoniidae
  - *Theromyzon "trizonare"* Davies & Oosthuizen, 1993

MITES

- Rhinonyssidae
  - *Rhinonyssus colymbicola* Fain & Bafort, 1963
- Ptiloxenidae
  - *Ptiloxenus major* (Megnin & Trouessart, 1884)

LICE

- Menoponidae
  - *Pseudomenopon dolium* (Rudow, 1869)
- Laemobothriidae
  - ?*Laemobothrion simile* Kellogg, 1896
- Philopteridae
  - *Aquanirmus emersoni* Edwards, 1965

Parasites of *Podiceps cristatus* (Linnaeus)

DIGENES

- Notocotylidae
  - *Notocotylus attenuatus* (Rudolphi, 1809)
- Cyclocoelidae
  - *Transcoelum oculeum* (Kossack, 1911)
  - *Typhlocoelum cucumerinum* (Rudolphi, 1809)
- Philophthalmidae
  - *Philophthalmus lucipetus* Rudolphi, 1819; Braun, 1902
- Echinostomidae
  - *Echinochasmus coaxatus* Dietz, 1909
  - *Echinochasmus colymbi* Oshmarin, 1950
  - *Echinochasmus dietzevi* Issaitschikoff, 1927
  - *Echinochasmus mordax* (Loos, 1899)
  - *Echinochasmus spinulosus* (Rudolphi, 1809)
  - *Echinochasmus squamatus* Mendheim, 1940
  - *Echinostoma intermedium* (Mehlis in Creplin, 1846)
  - *Echinostoma revolutum* (Froelich, 1802)
  - *Hypoderaeum gnedini* Bashkirova, 1941
  - *Mesorchis denticulatus* (Rudolphi, 1802)
  - *Mesorchis spinosus* (Odhner, 1910)
  - *Paryphostomum radiatum* (Dujardin, 1845)
  - *Petasiger australis* Johnston & Angel, 1941
  - *Petasiger coronatus* Mendheim, 1940
  - *Petasiger megacanthus* Kotlán, 1922
  - *Petasiger neocomensis* Fuhrmann, 1928
  - *Petasiger nitidus* Linton, 1928
  - *Petasiger pungens* (Linstow, 1894)
  - *Petasiger skrjabini* Bashkirova, 1941
  - *Petasiger variospinosus* (Odhner, 1910) Yamaguti, 1933
- Clinostomidae
  - *Clinostomum complanatum* (Rudolphi, 1814)
- Schistosomatidae
  - *Bilharziella polonica* (Kowalewski, 1895)
  - *Gigantobilharzia monocotylea* Szidat, 1930
- Cyathocotylidae
  - *Cyathocotyle prussica* Muehling, 1896
  - *Cyathocotyle teganuma* Ishii, 1935
- Diplostomidae
  - *Diplostomum gavium* (Guberlet, 1922) of Hughes, 1929
  - *Diplostomum mergi* Dubois, 1932
  - *Diplostomum spathaceum* (Rudolphi, 1819)
  - *Tylodelphys conifera* (Mehlis, 1846)
  - *Tylodelphys excavata* (Rudolphi, 1803)
  - *Tylodelphys podicipina* Kozicka & Niewiadomska, 1960
- Strigeidae
  - *Apharyngostrigea cornu* (Zeder, 1800)
  - *Ichthyocotylurus pileatus* (Rudolphi, 1802)
  - *Ichthyocotylurus platycephalus* (Creplin, 1825) Szidat, 1928
  - *Schwartzitrema pandubi* (Pande, 1939)
  - *Strigea falconis* Szidat, 1928
- Heterophyidae
  - *Cryptocotyle concava* (Creplin, 1825)
  - *Taphrogonimus holostomoides* (Mehlis in Creplin, 1846)
- Pachytrematidae
  - *Pachytrema paniceum* Brinkmann, 1942
- Renicolidae
  - *Renicola pinguis* (Mehlis in Creplin, 1846)
- Prosthogonimidae
  - *Prosthogonimus cuneatus* (Rudolphi, 1809)
- Ochetosomatidae
  - *Pygidiopsis genata* Looss, 1907
- Eucotylidae
  - *Eucotyle popowi* Skrjabin & Evranova, 1942

CESTODES

- Diphyllobothriidae
  - *Digramma interrupta* (Rudolphi, 1810)
  - *Ligula colymbi* Zeder, 1803
  - *Ligula intestinalis* (Linnaeus, 1758)
  - *Schistocephalus pungitii* Dubinina, 1959
  - *Schistocephalus solidus* (Mueller, 1776)
- Tetrabothriidae
  - *Tetrabothrius macrocephalus* (Rudolphi, 1810)
- Dioecocestidae
  - *Dioecocestus asper* (Mehlis, 1831)
- Amabiliidae
  - *Ryjikovilepis dubininae* (Ryzhikov & Tolkatcheva, 1981)
  - *Schistotaenia colymba* Schell, 1955
  - *Schistotaenia macrocirrus* Chandler, 1948
  - *Schistotaenia macrorhyncha* (Rudolphi, 1810)
  - *Schistotaenia scolopendra* (Diesing, 1856)
  - *Tatria acanthorhyncha* (Wedl, 1855)
  - *Tatria biremis* Kowalewski, 1904
  - *Tatria decacantha* Fuhrmann, 1913
- Dilepididae
  - *Liga lencoranica* Sailov, 1962
  - *Paradilepis urceus* (Wedl, 1855)
- Hymenolepididae
  - *Aploparaksis filiformis* Spassky, 1963
  - *Aploparaksis furcigera* (Nitzsch in Rudolphi, 1819)
  - *Cloacotaenia megalops* (Nitzsch in Creplin, 1829)
  - *Confluaria capillaris* (Rudolphi, 1810)
  - *Confluaria multistriata* (Rudolphi, 1810)
  - *Confluaria podicipina* (Szymanski, 1905)
  - *Confluaria*, n.sp. Vasileva, Georgiev & Genov (in press a)
  - *Dicranotaenia coronula* (Dujardin, 1845)
  - *Diorchis inflata* (Rudolphi, 1819)
  - *Diploposthe laevis* (Bloch, 1782)
  - *Dollfusilepis hoploporus* (Dollfus, 1951)
  - *Drepanidotaenia lanceolata* (Bloch, 1782)
  - *Fimbriaria fasciolaris* (Pallas, 1781)
  - *Retinometra macracanthos* (Linstow, 1877)

ACANTHOCEPHALANS

- Polymorphidae
  - *Andracantha mergi* (Lundström, 1941)
  - *Filicollis anatis* (Schrank, 1788)

NEMATODES

- Dioctophymatidae
  - *Eustrongylides mergorum* (Rudolphi, 1809)
  - *Eustrongylides tubifex* (Nitzsch, 1819)
- Trichuridae
  - *Baruscapillaria obsignata* (Madsen, 1945)
  - *Baruscapillaria podicipitis* (Yamaguti, 1941)
  - *Eucoleus contortus* (Creplin, 1839)
- Amidostomatidae
  - *Amidostomum fulicae* (Rudolphi, 1819)
  - *Epomidiostomum uncinatum* (Lundahl, 1848)
- Anisakidae
  - *Contracaecum microcephalum* (Rudolphi, 1809)
  - *Contracaecum ovale* (Linstow, 1907)
  - *Contracaecum spiculigerum* (Rudolphi, 1809)

- *Porrocaecum reticulatum* (Linstow, 1899)

Dracunculidae

- *Avioserpens mosgovoyi* Supryaga, 1965

Tetrameridae

- *Tetrameres fissispina* (Diesing, 1861)
- *Tetrameres gubanovi* Shigin, 1957

Acuariidae

- *Cosmocephalus obvelatus* (Creplin, 1825)
- *Echinuria uncinata* (Rudolphi, 1819)
- *Paracuaria adunca* (Creplin, 1846)
- *Rusguniella elongata* (Rudolphi, 1819)
- *Rusguniella wedli* Williams, 1929
- *Streptocara crassicauda* (Creplin, 1829)
- *Streptocara recta* (Linstow, 1879)
- *Syncuaria decorata* (Cram, 1927)

Onchocercidae

- *Pelecitus fulicaeatrae* (Diesing, 1861)

LEECHES

Glossiphoniidae

- *Theromyzon tessulatum* (O.F. Müller, 1714)

MITES

Ptiloxenidae

- *Ptiloxenus major* (Megnin & Trouessart, 1884)

Rhinonyssidae

- *Rhinonyssus alberti* Strandtmann, 1956
- *Rhinonyssus podicipedis* Feider & Mironescu, 1972

LICE

Menoponidae

- *Pseudomenopon dolium* (Rudow, 1869)

Laemobothriidae

- *Laemobothrion simile* Kellogg, 1896

Philopteridae

- *Aquanirmus podicipis* (Denny, 1842)

Parasites of ***Podiceps nigricollis***

DIGENES

Notocotylidae

- *Paramonostomum bucephalae* Yamaguti, 1935

Echinostomidae

- *Echinochasmus amphibolus* Kotlán, 1922
- *Echinochasmus coaxatus* Dietz, 1909
- *Echinochasmus colymbi* Oshmarin, 1950
- *Echinochasmus dietzevi* Issaitschikoff, 1927
- *Echinochasmus donaldsoni* Beaver, 1941
- *Echinochasmus spinulosus* (Rudolphi, 1809)
- *Echinostoma revolutum* (Froelich, 1802)
- *Mesorchis denticulatus* (Rudolphi, 1802)
- *Petasiger lobatus* Yamaguti, 1933
- *Petasiger megacanthus* Kotlán, 1922
- *Petasiger neocomensis* Fuhrmann, 1928
- *Petasiger nitidus* Linton, 1928

Schistosomatidae

- *Dendritobilharzia pulverulenta* (Braun, 1901)

Diplostomidae

- *Diplostomum capsulare* (Diesing 1858) Bittner & Sprehn, 1928
- *Diplostomum gavium* (Guberlet, 1922) of Hughes, 1929
- *Tylodelphys conifera* (Mehlis, 1846)
- *Tylodelphys excavata* (Rudolphi, 1803)
- *Tylodelphys podicipina* Kozicka & Niewiadomska, 1960

Strigeidae

- *Apatemon gracilis* (Rudolphi, 1819)
- *Ichthyocotylurus erraticus* (Rudolphi, 1809)
- *Ichthyocotylurus platycephalus* (Creplin, 1825) Szidat, 1928
- *Strigea falconis* Szidat, 1928

Heterophyidae

- *Cryptocotyle concava* (Creplin, 1825)

Microphallidae

- *Pseudospelotrema japonicum* Yamaguti, 1939

Prosthogonimidae

- *Prosthogonimus cuneatus* (Rudolphi, 1809)
- *Prosthogonimus ovatus* (Rudolphi, 1803)

Plagiorchiidae

- *Plagiorchis laricola* Skrjabin, 1924

Eucotylidae

- *Eucotyle cohni* Skrjabin, 1924

CESTODES

Diphyllobothriidae

- [*Digramma interrupta* (Rudolphi, 1810)]
- *Ligula colymbi* Zeder, 1803
- *Ligula intestinalis* (Linnaeus, 1758)
- *Schistocephalus solidus* (Mueller, 1776)

Tetrabothriidae

- *Tetrabothrius macrocephalus* (Rudolphi, 1810)

Dioecocestidae

- *Dioecocestus asper* (Mehlis, 1831)

Amabiliidae

- *Ryjikovilepis dubininae* (Ryzhikov & Tolkatcheva, 1981)
- *Schistotaenia colymba* Schell, 1955
- *Schistotaenia macrorhyncha* (Rudolphi, 1810)
- *Schistotaenia srivastavai* Rausch, 1970
- *Tatria acanthorhyncha* (Wedl, 1855)
- *Tatria biremis* Kowalewski, 1904
- *Tatria decacantha* Fuhrmann, 1913
- *Tatria duodecacantha* Olsen, 1939
- *Tatria iunii* Korpaczewska & Sulgostowska, 1974
- *Tatria mircia* Gulyaev, 1990

Dilepididae

- *Paricterotaenia porosa* (Rudolphi, 1810)
- *Lateriporus skrjabini* Mathevossian, 1946

Hymenolepididae

- *Aploparaksis filiformis* Spassky, 1963
- *Aploparaksis furcigera* (Nitzsch in Rudolphi, 1819)
- *Aploparaksis larina* (Fuhrmann, 1921)
- *Confluaria capillaris* (Rudolphi, 1810)
- *Confluaria furcifera* (Krabbe, 1869)
- *Confluaria multistriata* (Rudolphi, 1810)
- *Confluaria podicipina* (Szymanski, 1905)
- *Dicranotaenia coronula* (Dujardin, 1845)
- *Dicranotaenia paraporale* (Podesta & Holmes, 1970)
- *Diorchis elisae* (Skrjabin, 1914)
- *Diploposthe laevis* (Bloch, 1782)
- *Drepanidotaenia lanceolata* (Bloch, 1782)
- *Fimbriaria fasciolaris* (Pallas, 1781)
- *Mackoja podirufi* (Macko, 1962)
- *Microsomacanthus compressus* (Linton, 1892)
- *Parafimbriaria micrantha* Gulyaev, 1990
- *Parafimbriaria websteri* Voge & Read, 1954
- *Pararetinometra lateralacantha* Stock & Holmes, 1981
- *Wardium cirrosum* (Krabbe, 1869)
- *Wardium fusum* (Krabbe, 1869)

ACANTHOCEPHALANS

POLYMORPHIDAE
- *Filicollis anatis* (Schrank, 1788)
- *Polymorphus acutis* Van Cleave & Starrett, 1940
- *Polymorphus marilis* Van Cleave, 1939
- *Polymorphus paradoxus* Connell & Corner, 1957

NEMATODES

TRICHURIDAE
- *Baruscapillaria carbonis* (Rudolphi, 1819)
- *Baruscapillaria obsignata* (Madsen, 1945)
- *Baruscapillaria podicipitis* (Yamaguti, 1941)
- *Baruscapillaria ryjikovi* (Daiya, 1972)
- *Eucoleus contortus* (Creplin, 1839)

AMIDOSTOMATIDAE
- *Amidostomum fulicae* (Rudolphi, 1819)

ANISAKIDAE
- *Contracaecum ovale* (Linstow, 1907)
- *Contracaecum praestriatum* Moennig, 1923
- *Contracaecum spiculigerum* (Rudolphi, 1809)

TETRAMERIDAE
- *Tetrameres fissispina* (Diesing, 1861)
- *Tetrameres gubanovi* Shigin, 1957

ACUARIIDAE
- *Cosmocephalus obvelatus* (Creplin, 1825)
- *Echinuria uncinata* (Rudolphi, 1819)
- *Paracuaria adunca* (Creplin, 1846)
- *Rusguniella elongata* (Rudolphi, 1819)
- *Rusguniella wedli* Williams, 1929
- *Streptocara crassicauda* (Creplin, 1829)
- *Streptocara recta* (Linstow, 1879)
- *Syncuaria decorata* (Cram, 1927)
- *Syncuaria longialula* Wang, 1976

ONCHOCERCIDAE
- *Pelecitus fulicaeatrae* (Diesing, 1861)

LEECHES

GLOSSIPHONIIDAE
- *Theromyzon "trizonare"* Davies & Oosthuizen, 1993

MITES

RHINONYSSIDAE
- *Rhinonyssus alberti* Strandtmann, 1956

EREYNETIDAE
- *Neoboydaia colymbiformi* Clark, 1964

PTILOXENIDAE
- *Ptiloxenus major* (Megnin & Trouessart, 1884)

XOLALGIDAE
- *Ingrassia colymbi* Gaud, 1974

LICE

MENOPONIDAE
- *Pseudomenopon dolium* (Rudow, 1869)

LAEMOBOTHRIIDAE
- *Laemobothrion simile* Kellogg, 1896

PHILOPTERIDAE
- *Aquanirmus americanus* (Kellogg & Chapman, 1899)
- *Aquanirmus colymbinus* (Scopoli, 1763)

Parasites of *Podiceps occipitalis*

LICE

MENOPONIDAE
- *Pseudomenopon dolium* (Rudow, 1869)

Parasites of *Podiceps taczanowskii*

LICE

MENOPONIDAE
- *Pseudomenopon dolium* (Rudow, 1869)

Parasites of *Aechmophorus occidentalis* (Lawrence) (includes those of *A. clarkii*)

DIGENES

CATHAEMASIIDAE
- *Ribeiroia ondatrae* (Price, 1931)

ECHINOSTOMIDAE
- *Echinochasmus donaldsoni* Beaver, 1941
- *Mesorchis polycestus* (Dietz, 1909)
- *Petasiger nitidus* Linton, 1928
- *Petasiger pseudoneocomensis* Bravo-Hollis, 1971

DIPLOSTOMIDAE
- *Tylodelphys podicipina* Kozicka & Niewiadomska, 1960

STRIGEIDAE
- *Apatemon gracilis* (Rudolphi, 1819)
- *Ichthyocotylurus erraticus* (Rudolphi, 1809)
- *Ichthyocotylurus pileatus* (Rudolphi, 1802)
- *Ichthyocotylurus platycephalus* (Creplin, 1825) Szidat, 1928

HETEROPHYIDAE
- *Cercarioides humbargari* (Park, 1936)

CESTODES

DIPHYLLOBOTHRIIDAE
- *Ligula intestinalis* (Linnaeus, 1758)
- *Schistocephalus solidus* (Mueller, 1776)

TETRABOTHRIIDAE
- *Tetrabothrius macrocephalus* (Rudolphi, 1810)

AMABILIIDAE
- *Tatria biremis* Kowalewski, 1904
- *Tatria decacantha* Fuhrmann, 1913

HYMENOLEPIDIDAE
- *Confluaria furcifera* (Krabbe, 1869)
- *Confluaria podicipina* (Szymanski, 1905)
- *Dicranotaenia paraporale* (Podesta & Holmes, 1970)
- *Microsomacanthus microskrjabini* Spassky & Yurpalova, 1965
- *Pararetinometra lateralacantha* Stock & Holmes, 1981

ACANTHOCEPHALANS

POLYMORPHIDAE
- *Polymorphus marilis* Van Cleave, 1939
- *Polymorphus paradoxus* Connell & Corner, 1957

NEMATODES

TRICHURIDAE
- *Baruscapillaria obsignata* (Madsen, 1945)

ANISAKIDAE
- *Contracaecum ovale* (Linstow, 1907)

ACUARIIDAE
- *Cosmocephalus obvelatus* (Creplin, 1825)
- *Streptocara crassicauda* (Creplin, 1829)
- *Syncuaria decorata* (Cram, 1927)

TETRAMERIDAE
- *Tetrameres fissispina* (Diesing, 1861)

LEECHES

GLOSSIPHONIIDAE
- *Theromyzon "trizonare"* Davies & Oosthuizen, 1993

MITES

PTILOXENIDAE
- *Ptiloxenus* sp. nov.

LICE

MENOPONIDAE
- *Pseudomenopon dolium* (Rudow, 1869)

PHILOPTERIDAE
- *Aquanirmus occidentalis* Edwards, 1965

INDEX

For ease in finding species in the general accounts of parasites and of grebes in the lists of their prey species and parasites, page numbers for these are in italics. For the last two, the lower number is for the list of prey species and the higher number is for the list of parasites of the grebe species. The first page of each species account for each family of parasites is also given in italics. Page numbers for other entries are in plain text. Subjects in the table of contents, and names of species of prey and of intermediate hosts are not indexed. The data on the last two are in analyzable form on the web (see p. 6). def. = definition, fig. = figure.