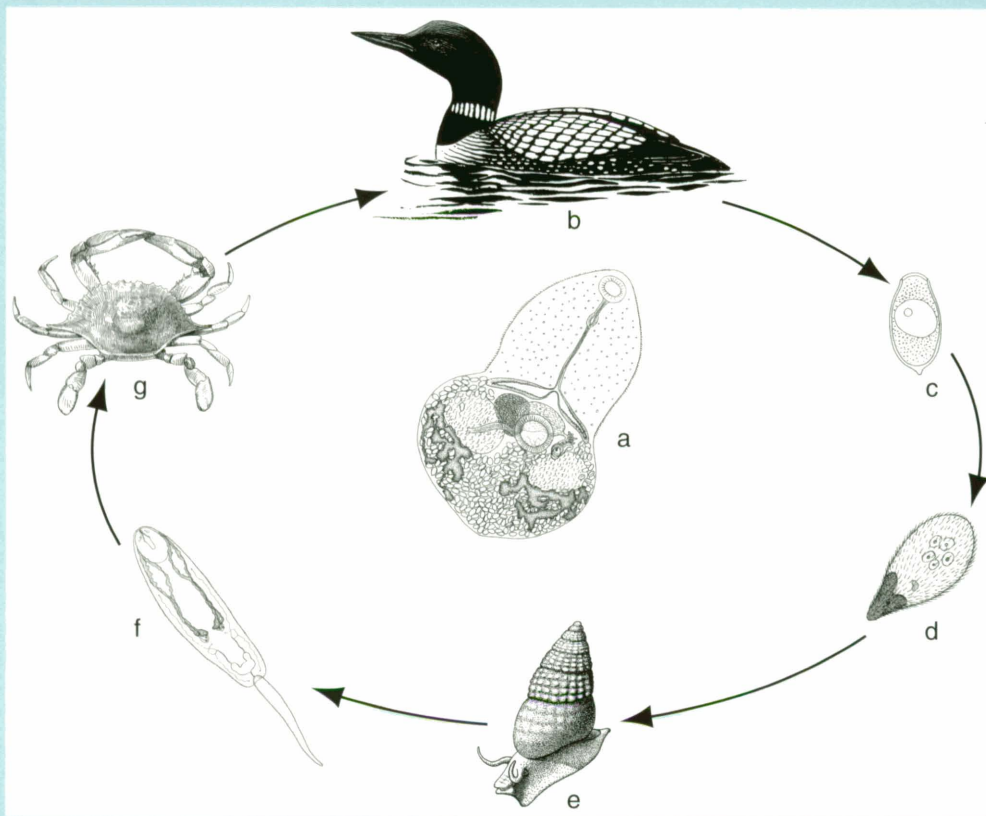# THE METAZOAN PARASITE FAUNA OF LOONS (AVES: GAVIIFORMES), ITS RELATIONSHIP TO THE BIRDS' EVOLUTIONARY HISTORY AND BIOLOGY, AND A COMPARISON WITH THE PARASITE FAUNA OF GREBES

BY

ROBERT W. STORER

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RECENT *MISCELLANEOUS PAPERS*

Albert, J.S. 2001. Species diversity and phylogenetic systematics of American knifefishes (Gymnotiformes, Teleostei). Misc. Publ. Mus. Zool. Univ. Michigan, 190:1-127, 50 figs.

Nussbaum, R.A. & C.J. Raxworthy. 2000. Systematic revision of the genus *Paroedura* Günther (Reptilia: Squamata: Gekkonidae), with the description of five new species. Misc. Publ. 189. 26 pp., 12 figs., 7 tables.

Storer, R. W. 2000. The metazoan parasite fauna of grebes (Aves: Podicipediformes) and its relationship to the birds' biology. Misc. Publ. 188. 90 pp., 9 figs., 7 tables.

Nussbaum, R.A. & M.E. Pfrender. 1998. Revision of the African caecilian genus *Schistometopum* Parker (Amphibia: Gymnophiona: Caeciliidae). Misc. Publ. 187. 35 pp., 15 figs., 15 tables, 2 color plates.

Nussbaum, R.A., C.J. Raxworthy & O. Pronk. 1998. The ghost geckos of Madagascar: a furthur revision of the Malagasy leaf-toed geckos (Reptilia, Squamata, Gekkonidae). Misc. Publ. 186. 26 pp., 25 figs., 5 tables.

RECENT *OCCASIONAL PAPERS*

Norris, S.M. 2001. Osteology of the southwestern darters, *Etheostoma* (*Oligocephalus*) (Teleostei, Percidae)-with comparison to other North American percid fishes. Occ. pap. 733. 44 pp., 18 figs.

Ng, H.H. & W.J. Rainboth. 2001. A review of the sisorid catfish genus *Oreoglanis* (Siluriformes: Sisoridae) with descriptions of four new species. Occ. Pap. 732. 34 pp., 13 figs., 3 tables.

Collette, B.B. 2001. *Opasanus dichrostomus*, a new toadfish (Teleostei: Batrachoididae) from the western Caribbean Sea and southern Gulf of Mexico. Occ. Pap. 731. 16 pp., 5 figs.

Fink, W. L. & A. Machado-Allison. 2001. *Serrasalmus hastatus*, a new species of piranha from Brazil, with comments on *Serrasalmus altuvei* and *Serrasalmus compressus* (Teleostei: Characiformes). Occ. Pap. 730. 18 pp., 16 figs.

Graf, D.L. 2000. The Etherioidea revisited: a phylogenetic analysis of hyriid relationships (Mollusca: Bivalvia: Paleoheterodonta: Unionoida). Occ. Pap. 729. 21 pp., 2 figs., 3 tables.

Ramanamanjato, J. B., R. A. Nussbaum & C. J. Raxworthy. 1999. A new species of *Mabuya* Fitzinger (Squamata: Scincidae: Lygosominae) from northern Madagascar. Occ. Pap. 728. 22 pp., 5 figs., 9 tables.

Sparks, J. S. & P. N. Reinthal. 1999. *Paretroplus maromandia*, a new cichlid fish from the northwest of Madagascar. Occ. Pap. 727. 18 pp., 5 figs., 3 tables.

The Metazoan Parasite Fauna of Loons (Aves: Gaviiformes), Its Relationship to the Birds' Evolutionary History and Biology, and a Comparison with the Parasite Fauna of Grebes

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COVER

The life cycle of the digenean, *Microphallus nicolli.* (a) The adult parasite, which reaches a mean length of 0.54 mm, inhabits the small intestine of the definitive host, a Common Loon, *Gavia immer* (b). The minute (0.02 mm) egg (c) is passed into the water where it hatches as a miricidium (d) which penetrates the first intermediate host a snail, *Bittium alternatum* (e) in which cercaria (f) are produced. These penetrate the second intermediate host, a blue crab, *Callinectes sapidus* (g). The definitive loon host becomes infected by eating by the crab. Infections of this parasite in the Common Loon occur most frequently when the birds are unable to catch their usual, faster-moving prey, fishes, and it has been commonly found in ailing loons on the wintering grounds off Florida.

Microphallids like this one show marked specificity in their two intermediate hosts (first a snail, and then a crustacean), but are generalists in their definitive hosts.

Original drawing by John Megahan from sources listed in the acknowledgments (p.32).

ABSTRACT

Storer, R. W. 2002. The metazoan parasite fauna of loons (Aves: Gaviiformes), its relatonship to the birds' evolutionary history and biology, and a comparison with the parasite fauna of grebes. Misc. Publ. Mus. Zool. Univ. Michigan, 191: iv+1- 44, 4 figs, 7 tables. The data base of this work parallels that of Storer (2000) on the grebes and contains lists of the multicellular parasites known to parasitize loons and a list of the known species of prey taken by each species of loon. The former includes information on where in the bird the parasites are found, the distribution of the parasite species by continents, the degree of host specificity, and life cycles (whether in 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 and their evolutionary histories.

The known species of helminths of loons include 47 digeneans, 22 cestodes, 14 acanthocephalans, and 15 nematodes, most of which have aquatic life cycles. No families or subfamilies and only 2 genera and 23 species of helminths are considered loon specialists.

Several factors appear to have contributed to the greater numbers of genera and species of parasites in grebes than loons. Most loons spend the breeding season on bodies of oligotrophic water, which have fewer species and numbers of potential prey than the eutrophic waters where most grebes nest. All species of loons winter on salt water, whereas many grebes are resident on fresh waters, although those nesting in regions where the fresh waters freeze in winter spend that season on salt waters. Much of the difference can also be attributed to the greater number of genera (7 versus 1) and species (21 versus 5) in the two groups of the birds, and the wider distribution (nearly cosmopolitan in the grebes *versus* holarctic in the loons). The difference is also consistent with the grebes' greater age and degree of parasite host specificity. Other factors affecting differences in the two helminth faunas are a presumed marine origin for the loons in contrast with a fresh-water one for the grebes, and the greater size and hence greater speed of loons underwater. The smaller size of grebes for which a greater number of prey species of optimal size is presumably available, the grebes' breeding on eutrophic bodies of water in which a greater variety of prey species (and hence greater number of species of hosts for parasites) is available, and grebes' greater diversity in bill form and foot proportions which are associated with specializations for taking a greater variety of prey, may all be involved. Adaptations for pursuit diving, include larger size, which makes possible a relatively larger mass of leg muscles, longer cnemial crests, which provide a larger area for the attachment of these muscles, and the possible affect of the coiled barbules on the outer part of grebe's contour feathers, which act as capillaries in absorbing water, which may decrease buoyancy and may also cause this part of the combined feathers to act like a flexible skin which cause movement of the water in the feathers to act like the skin of a cetacean in producing laminar flow of water across the surface of the birds. There is still much to be done before an adequate knowledge of the multicellular parasites of loons and grebes is known.

The larger number of species of external parasites found on grebes (12 mites and 13 lice *versus* 1 mite and 2 lice on loons) is believed to have resulted from the association of grebes with coots and subsequent speciation on the larger number of species of grebes than loons.

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INTRODUCTION

To date, there has been no general list of the multicellular parasites of loons comparable to that of grebes (Storer 2000). Because both are foot-propelled diving birds that feed on aquatic animals, comparisons between the parasites of the two groups, the species of prey taken, and the biology of the birds are of considerable interest. This paper is intended to fill the gap and follows the format of the grebe work. It also includes a comparison of the parasite faunas of the two groups and a discussion of the factors that might have accounted for the differenes in these faunas. I hope this will make possible future comparisons with the parasite faunas of other diving birds such as the alcids (Hoberg 1984).

Major sources. As with the grebes, major sources of information on helminths are the general studies of helminths, McDonald (1969); digeneans, Dubois (1968, 1970), Yamaguti (1958, 1971, 1975); cestodes, Dubinina (1966), Khalil *et al.* (1994), Ryzhikov *et al.* (1985), Yamaguti (1959); acanthocephalans, Crompton *et al.* (1985), Yamaguti (1963); nematodes, Anderson (2000), Barus *et al.* (1978), Yamaguti (1961). Basic synopses of the biology of loons include Barr *et al.* (2000), Cramp (1977), McIntyre (1988), McIntyre *et al.* (1997), North (1994) and Palmer (1962).

Some of the differences between loons and grebes that might affect differences in the birds' parasite faunas include their distribution (Holarctic for loons vs nearly cosmopolitan for grebes), the number of genera and species (1 genus and 5 species vs 7 genera and 21 species of grebes), the greater intergeneric and interspecific variation in bill form in grebes, the greater tendency for loons to spend the breeding season on oligotrophic bodies of water while grebes are usually found breeding on eutrophic waters, and the larger size of loons (ca 1,600 to 6,400 g vs ca 100 to 1,600 g for grebes). Because of this difference in size, loons take fewer individuals of larger prey and a smaller variety of prey species than grebes. Therefore, loons can be expected to have a more limited parasite fauna than grebes. On the other hand, loons would be capable of taking prey of a greater range of sizes, which might increase the number of species of intermediate hosts of parasites and through this a greater number of parasite species.

The evolution and relationships of the loons. The living loons (Order Gaviiformes, Family Gaviidae) consist of five species of foot-propelled diving birds. The fossil record of the loons goes back at least to the Upper Eocene and Lower Miocene (*Colymboides anglicus* and *Colymboides* sp., respectively) of Europe. A partial humerus and a partial carpometacarpus from the middle Miocene Pungo River Formation of North Carolina are tentatively assigned to *Colymboides* by Olson & Rasmussen (2001). Several fossil forms thought to have been loons are not now considered to belong to that order. These include *Enaliornis* from the lower Cretaceous of England thought by Elzanowski and Galton to have been an early Hesperornithiform bird (Feduccia 1999); *Neogaeornis* from the late Cretaceous of Chile, although considered a loon by Olson (1992), is probably Hesperornithiform (Feduccia 1999); *Eupterornis* from the Upper Paleocene of France described as a gull and placed in the loons by Lambrecht (1933) and Brodkorb (1963), is not a loon

(Mourer-Chauviré 1996) but is fragmentary and needs to be restudied; and *Gaviella*, the material of which is also fragmentary, which was tentatively placed in the loons by Brodkorb (1963), might be a plotopterid but requires further study (Olson 1985). In addition to the five living species, the genus *Gavia* is represented by several fossil species dating back to the Lower Miocene, where the early species *Gavia egeriana* of Czechoslovakia was found in the same deposit as *Colymboides minutus* (Svec 1982).

Long considered closely related to the grebes (Podicipedidae), the loons' similarities with birds of that group are generally considered the result of convergent evolution by Stolpe (1935) and subsequent authors. This has been disputed by Cracraft (1982), but see Boertmann (1990) and Feduccia (1999:162). Data from DNA-DNA hybridization (Sibley and Ahlquist 1990) indicate a closer relationship with the Sphenisciformes and the Procellariiformes, although loons lack the characteristic tubular nostrils and strong, musky odor of the latter group. Small downy young loons have "a diagnostic, small, separate, cornified, scute at the base of the upper mandible below the nostril" (Fjeldså 1977). This may be a vestige of the scutes on the bills of petrels and penguins. The downy young of the Little Blue Penguin *(Eudyptula minor)* are hatched with small tubular nostrils which "start to recede during the sixth week of age" and become slits like those of the adults by the time the young are 43 days old (Kinsky 1960). Adult loons share several morphological characters with the petrels and penguins (Sibley and Alquist 1990), but these authors consider that "These are all primitive characters shared with many other groups, hence of little value as evidence of relationship."

The classification of loons follows that of Storer (1978, 1979). Since then, a phylogenetic analysis of the living species of loons by Boertmann 1990 showed that *G. stellata* is the most highly specialized as a pursuit diver, has the lowest wing loading, both actually and proportionally of the genus, and is a sister group to the other species. He also considers that *G. arctica* (in which he apparently includes *G. pacifica*), is a sister group to *G. immer* and *G. adamsii.*

The nomenclature of loons. The nomenclature of loons used in this paper is that of The American Ornithologists' Union (1998). Because of the recent split of *G. pacifica* from *G. arctica* (American Ornithologists' Union, 1985), some records for the hosts of parasites reported under the name, *G. arctica*, may apply to *G. pacifica* or both. In instances in which it is not clear from which locality the host was found, nor which species (whether *arctica* or *pacifica*) was indicated, these are marked "*arctica* (and/or *pacifica*)." In addition, *Gavia adamsii* was formerly considered a subspecies of *G. immer* (*e.g.*, by Dementiev *et al.*, 1968), so some records of parasites from "*immer*," especially those taken in Siberia, presumably refer to *adamsii*. Many of the records from "*arctica*" (e.g. *Polymorphus gavii*) might be corrected if the precise localities from which the hosts were taken can be determined. (See also p. 10.) Synonyms of English names (especially in Europe) include Red-throated Diver for *Gavia stellata*, Black-throated Diver for *Gavia arctica*, Green-throated Diver for *Gavia arctica viridigularis*, Great Northern Diver for *Gavia immer*, and White-billed Diver for *Gavia adamsii*).

For purposes of some analyses, the five species of loons are combined into three superspecies: *1. arctica (arctica + pacifica), 2*

immer (immer + adamsii), and *3. stellata.* This also simplifies the cases in which *pacifica* was considered a subspecies of *arctica* and *adamsii* of *immer.*

Because loon hosts for parasites have been given under a variety of other names, which are now synonymized with current ones, the following list of synonyms is included. The generic name, *Colymbus,* was widely used for loons in the Old World and for grebes in the New World until it was placed on the Official Index of Rejected and Invalid Names in Zoology by the International Commission on Zoological Nomenclature (1972). Other synonyms of *Gavia* include *Eudytes* and *Urinator.* Synonyms of *Gavia immer* include *glacialis, imber, hyemalis,* and *torquatus.* The subspecies *G. i. elasson* is not currently recognized. Synonyms of *Gavia stellata* include *borealis, lumme, muelleri,* and *septentrionalis.* The subspecies, *G. stellata squamata,* is not currently recognized. The specific name *Podiceps arcticus* Boie, has also been used for *Podiceps auritus,* which has caused a problem in identifying the definitive hosts of *Confluaria capillaris* (Rudolphi, 1810) (Joyeux & Baer 1950; Vasileva *et al.* 1999a).

Purposes. The purposes of this paper are twofold. First, to prepare an account of the known multicellular parasites of loons, paralleling that of the grebes (Storer 2000) including the intermediate and definitive hosts, location in the loon host, broad geographic ranges, and the degree of host specificity; a list of the the known species of prey each loon species; and to present this in a form suitable for computer analysis, and second, to speculate on the possible causes of the differences. Because parasitologists and ornithologists are seldom familiar with the taxonomy and nomenclature of animals of other groups and because the names of all the groups change over time, I have attempted to list each species under the same name and in the same family.

Suggestions as to how the loons' parasite fauna might be related to the biology and evolutionary history of the birds, and a brief comparison with these aspects of parasite fauna of grebes are made. Other suggestions are made on what work should be done to improve basic knowledge of the faunas so that better documented theoretical studies can be attempted.

In speculating on possible causes of the differences between the parasite faunas of the loons and grebes, I have included a wide range of possibilities, including the ages, evolutionary histories, geographic distribution, and degree of morphological variation within the families that might lead to different foraging techniques and hence to taking different kinds of prey and different hosts of the parasites.

Methods. The methods used in preparing this paper are like those of the parallel paper on grebes (Storer 2000), and the format of the annotated list of parasites follows that of the similar list of grebe parasites. As in that list, references to original descriptions follow the convention in parasitology of placing a comma between the author's name and the date, whereas this is not done in the case of other references in the text. Citations for descriptions of species are not put into the Literature Cited unless other cited information on the species is given.

For geographic ranges, continents are used rather than zoogeographic regions for reasons explained in the previous work. "FW," "BW," and "SW" are used to define the habitat (fresh, brackish, or salt water, respectively) in which the final stage of the parasite is found. In the cases of parasites that require two intermediate hosts, the word **then** is placed between the lists for the first and second intermediate hosts.

Generic synonyms of parasites are not given except in instances in which references to loon hosts are concerned. One citation, not necessarily the first, for each definitive loon host is given. Page numbers in text references are usually omitted, except for those in McDonald 1969 (which is not indexed) and a few other long papers.

Brackets are used around entries in which either the specific name of the parasite or of the only definitive loon host is unknown, reports based on presumed errors in identifications, or for records of experiments, or other unnatural occurrences. These entries are not used in the analyses.

The categories of specificity for definitive hosts are: 1. Generalist. 2. Specialist in other group(s), rare or occasional in loons. 3. Specialist in loons, rare or unknown in other groups. 4. Known only from type (loon) host. 5. Known only from the original description. In the list of parasites, an asterisk opposite the name of the parasite indicates that it is a loon specialist (categories 3-5).

References to vouchers and other specimens from the Harold W. Manter Laboratory (HWML), University of Nebraska- Lincoln, and the United States National Parasite Collection (USNPC), Beltsville, Maryland, are given with accession numbers for each specimen.

As with the grebe parasite paper (Storer 2000), the basic data on each named parasite species has been put into a computer data base. These data include, where known, the class or subclass, 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 loon host, and intermediate, paratenic, and grebe hosts of each parasite species. A list of the known prey species of each loon species is also in the data base. Separate records for each species of parasite and loon have been created and manipulated using the program FileMaker Pro (Claris Corp. 1994). This makes it possible to add records of new parasites and prey species as they become available. This is available on the web at <http://www.ummz.lsa.umich.edu/curators/rwstorer/> CDs of the loon and grebe parasite databases are filed at the Manter Laboratory and USNPC.

THE INTERNAL PARASITIC HELMINTHS OF LOONS

The parasitic worms of loons, like those of grebes, belong to four major groups of invertebrates, the digenetic trematodes (or digeneans), tapeworms (Cestoda), spiny-headed worms (Acanthocephala), and the round worms (Nematoda).

Loons are not known to act as intermediate hosts for any parasites although they may harbor immature stages of some (*e.g. Corynosoma semerme* and *C. strumosum*).

THE DIGENEANS (FLUKES)

Subclass Trematoda, Infraclass Digenea
  Order Echinostomiformes
  Superfamily Psilostomoidea
    Family Psilostomidae
      Pseudopsilostoma varium (Linton, 1928)

In *Gavia immer* (Yamaguti 1958, 1971). Type in USNPC No. 007919.00. In intestine and proventriculus. SW? N. Amer. Intermed. hosts? Described in *Psilostomum*. Known only from type host (4).

Family Cathaemasiidae

Ribeiroia ondatrae (Price, 1931)

In *Gavia immer* (Conboy *et al.* in prep. voucher HWML No. 38121, Kinsella & Forrester 1999, voucher USNPC. No. 087046.00). 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 1939). Generalist (1), also in grebes. *Ribeiroia thomasi* (McMullen, 1938) is a synonym for the cercaria.

Superfamily Echinostomoidea

Family Echinostomidae

Echinochasmus coaxatus Dietz, 1909

In *Gavia arctica* (and/or *pacifica*) (McDonald 1969:149-150). Small intestine to cloaca. FW. Eurasia. Intermed. hosts, **mollusks:** GASTROPODS, then metacercaria encyst on FW mollusks (McDonald *loc. cit.*), which are eaten by FW **fishes:** Details in Storer (2000). Grebe specialist (2), also in ducks and *Ciconia*.

Echinochasmus skrjabini Oshmarin, 1946

In *Gavia immer* (Kinsella & Forrester 1999, voucher HWML No. 38130, and Conboy *et al.* in prep. voucher USNPC No. 087043.00), *G. arctica* (Kontrimovitschus & Bakhmet'eva 1960), *G. stellata*, type host. In duodenum, small intestine, gall bladder. FW? Eurasia, N. Amer. Intermed. hosts? Loon specialist (3), not in grebes. Has been placed in *Episthmium*.

Echinochasmus spinulosus (Rudolphi, 1809)

In *Gavia arctica, G. pacifica, G. immer, G. stellata* (McDonald 1969:158-159). Small intestine. FW? Eurasia, N. Amer. Intermed. hosts, snails? then? Generalist (1), also in grebes, *Alca*, and *Cepphus*, and occasionally ducks. Reports of this parasite from *Alca* and *Cepphus* suggests that anadromous fishes may act as second intermediate hosts. Sometimes placed in genera *Echinostoma* or *Monilifer* or considered a synonym of *Stephanoprora spinosa* (*e.g.*, by McDonald 1969:159). *Stephanoprora gilberti* Ward, 1917 (Voucher in USNPC No. 051842.00) is also a synonym *fide* McDonald (*loc. cit.*).

Echinoparyphium baculus (Diesing, 1850)

In *Gavia arctica* (and/or *pacifica*), *G. stellata* (McDonald 1969:165). Intestine. FW. Eurasia, N. Amer. First and second intermed. hosts, **mollusks:** GASTROPODS, Physidae (*Physa fontinalis*). Specialist in Anatidae, uncommon in loons, not in grebes (2).

Echinostoma revolutum (Froelich, 1902)

In *Gavia immer* (in Britain) Beverly-Burton (1961). Intestines, caecum. FW. Eurasia. Intermed. hosts, **mollusks:** GASTROPODS: Lymnaeidae, then various FW pulmonate and prosobranch snails, PELECYPODS: "mussels," AMPHIBIANS: "frogs," REPTILES: FW "tur-

tles." Life cycle in Kanev (1985, 1994), who considers American records to belong to *Echinostoma trivolvis* (Cort, 1914). The account of this species in Storer (2000) was based on the earlier, broader concept of *E. revolutum*.

Himasthla alincia Dietz, 1909

In *Gavia immer* (1 bird, Kinsella & Forester 1999, voucher HWML No. 38138). Small intestine. FW?, SW? N. Amer., S. Amer. Intermed. hosts ?**mollusks:** ?GASTROPODS, then? ?Generalist (?1), also in *"Tringa cinclus"* (= *Arenaria interpres*). Not in grebes.

Mesorchis denticulatus (Rudolphi, 1802)

In *Gavia arctica* (Bittner & Sprehn 1928), *G. immer* (Kinsella & Forrester 1999, voucher HWML No. 38113, and Conboy *et al.* in prep. voucher USNPC No. 087054.00, as *"Stephanoprora gilberti"* = *Stephanoprora "spinosa,"* voucher USNPC No. 051842), as *Stephanoprora pseudoechinata* USNPC Nos. 007932.00 and 007933.00), and as *Stephanoprora pseudodenticulata* [Kinsella *in litt.*]) also McDonald (1969: 156). Small intestine. FW. SW? Eurasia, N. Amer., S. Amer., Afr. Intermed. hosts, **mollusks:** GASTROPODS, Planorbidae, then encyst on gills of FW and SW **fishes:** Atherinidae, Cyprinidae, Cyprinodontidae, Gasterosteidae, and Gobiidae. Details in Storer (2000). Generalist (1), also in grebes. 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 (1969: 157) lists species of both *Podiceps* and *Gavia*, so Yamaguti's references might refer to either or both.

Mesorchis polycestus (Dietz, 1909)

In *Gavia* ("*Urinator*") *arctica* (and/or *pacifica*) (Yamaguti 1971). In intestines. FW? N. Amer., Eurasia. Generalist (1). Also in grebes, *Larus, Alca, Corvus*. Included in *S. denticulata* by Nasir *et al.* 1968, *contra* Beaver (1937).

Microparyphium facetum Dietz, 1909

In *Gavia immer* (1 bird, Kinsella & Forrester 1999, vouchers No. HWML No. 38123, and Conboy *et al.* in prep. voucher No. 087048.00). In cloaca. FW? N. and S. Amer. Intermed. hosts, ?snails, ?fishes. Described from *Cercibis ("Gerontias") oxycerca*. Generalist (1) in many ciconiiform birds (Kinsella pers. comm.), Osprey, and Bald Eagle, rare in loons, not known from grebes.

Petasiger coronatus Mendheim, 1940

In *G. stellata* (McDonald 1969:210). In duodenum, small intestine. FW. Europe. First Intermed. host, ?snails, then **annelids:** OLIGOCHAETES, Glossoscolecidae (*Criodrilus lacuum*). Known from *G.*

stellata, Podiceps cristatus, and *Anas platyrhynchos.*
?Generalist (?1).

Family Philophthalmidae

Parorchis acanthus (Nicoll, 1906)

In *Gavia immer* (Kinsella & Forrester 1999, 1 bird, voucher HWML No. 138114). In cloaca. SW. Eur., N. Amer., West Indies. Intermed. hosts **mollusks:** GAS-TROPODS, Muricidae *(Purpura lapillus),* then? Generalist (1) Not known from grebes.

Order Strigeiformes

Superfamily Clinostomoidea

Family Clinostomidae

Clinostomum complanatum (Rudolphi, 1814)

In *Gavia immer* (Conboy *et al.* in prep. voucher USNPC No. 087047.00). Buccal cavity and esophagus. FW. Cosmopolitan. Intermed hosts, **mollusks:** GASTROPODS, Lymnaeidae, then FW **fishes.** Details in Storer (2000). Rare in loons and grebes, heron specialist (2), also in other ciconiiforms, cormorants, pelicans, *Gallinula, Larus,* and man.

Superfamily Schistosomatoidea

Family Schistosomatidae

Austrobilharzia terrigalensis Johnston, 1917

In *Gavia immer* (Kinsella & Forrester 1999, voucher HWML No. 38132). In branches of mesenteric vein. SW. N. Amer., Austr. Intermed. hosts, **mollusks:** GASTROPODS, Potamidae *(Pyrazus australis, Velacumantus australis).* Life cycle in Appleton 1983a, b, Bearup 1956. ?Specialist in larids (?2), not known from grebes. For relationships with other forms of the genus, see Farley (1971).

Dendritobilharzia pulverulenta (Braun, 1901)

In *Gavia immer* (Kinsella & Forrester 1999, voucher HWML No.38131). Arterial system, most frequently in aorta and femoral arteries (Vande Vusse 1980). FW Cosmopolitan, except Austr. Life cycle unknown. FW snail may act as intermediate host. Specialist in anatids (2), also in grebes, pelicans, and coots. *D. anatinarum* is a synonym (Vande Vusse *op. cit.).*

[*Bilharziella polonica* (Kowalewski, 1895)

Not known from loons. Specialist on waterfowl (2), uncommon in grebes. (See Storer 2000.) Yamaguti (1971:479) lists *"Colymbus"* and *Podiceps* as definitive hosts. McDonald (1969:96) lists *Podiceps* but not *Gavia,* so Yamaguti's record for *"Colymbus"* presumably refers to *Podiceps.*]

Superfamily Strigeoidea

Family Cyathocotylidae

Mesostephanus appendiculatoides (Price, 1934)

In *Gavia immer* (Kinsella & Forrester 1999, voucher HWML No 38128). In small intestine. SW? West Indies, N. Amer. Intermed. hosts ?snails, then ?fishes. Described from *Pelecanus occidentalis.* ?Generalist (?1). Not known from grebes.

Paracoenogonimus ovatus Katsurada, 1914

In *Gavia stellata* (J. Okulewicz 1984) Small intestine, FW. Eurasia. Intermed. hosts, see Storer (2000). Parasite of carnivores and birds of prey, rare in other birds, including loons. [Recorded from *Podiceps cristatus* in

Berlin Zoo, Odening 1963.]

[Cyathocotylidae gen.?, sp.?

In *Gavia stellata* (J. Okulewicz 1984)].

Family Diplostomidae

Diplostomum gavium (Guberlet, 1922)

In *Gavia adamsii* (as *D. colymbi,* Dubois & Rausch 1960), *G. immer* (Dubois and Rausch 1967), (vouchers Kinsella & Forrester 1999 HWML No. 38110, Conboy *et al.* in prep. vouchers (USNPC 087049.01 and 087049.02), *G. arctica, G. stellata,* (as *Diplostomum colymbi,* Kontrimovitschus & Bakhmet'eva 1960), *Gavia sp.* (voucher USNPC 060445,00). In stomach, duodenum, small intestine. FW. Eurasia, N. Amer. Intermed. hosts, snails? then fishes? Loon specialist (3), apparently uncommon in grebes. *Diplostomum colymbi* (Dubois, 1928) is a synonym. Has been placed in the genera *Hemistoma* and *Strigea.* Some records of this species may refer to *D. podicipinum.* Yamaguti (1971) lists *"Colymbus"* and *"Podiceps"* as definitive hosts but *"Colymbus [=Gavia] immer"* and *"Colymbus [=Podiceps] grisegena"* in his earlier (1958) work. Yamaguti's later reference to *Podiceps* probably comes from a report of the three other species of grebes reported by McDonald (1969:49).

Diplostomum pseudospathaceum Niewiadomska, 1984

In *Gavia stellata* (J. Okulewicz 1984). For distinction between this species and the next, see Niewiadomska (1984). (Separation of the life cycles has not been made.)

Diplostomum spathaceum (Rudolphi, 1819)

In *Gavia stellata* (J. Okulewicz 1984). Intestines. FW, BW. ?SW. Eurasia, N. Afr. Intermed. hosts, see Storer (2000). Commonest in larids, apparently rare in loons (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 *D. flexicaudum* (Cort & Brooks, 1928) and the Australian form *D. 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.

[*Diplostomum* sp.

In *Gavia stellata* (J. Okulewicz 1984).]

Posthodiplostomum minimum (Macallum, 1921)

In *Gavia immer* (Kinsella & Forrester 1999 in 1 bird, voucher HWML No 38126). In small intestine. FW. N. Amer. Intermed. hosts **mollusks:** GASTROPODS, Physidae *(Physa gyrina, P. heterostropha),* then fishes: Amiidae *(Amia),* Catostomidae *(Catostomus* sp.), Centrarchidae *(Ambloplites rupestris, Lepomis auritus, L. "Eupomotis" gibbosus, L. macrochirus "Helioperca incisor," L. "Xenotis" megalotis, Micropterus dolomieu, Pomoxis "Huro"* sp.), Cyprinidae *(Notropis anogenus, N. atherinoides, N. cornutus, Pimephales "Hyborhynchus" notatus, Rhinichthys* sp., *Richardsonius* sp., *Semotilis atromaculatus),* Cyprinodontidae *(Fundulus diaphanus),*

Ictaluridae *(Ameiurus* sp.), Percidae *(Etheostoma "Boleosoma" nigrum, Perca* sp., *Stizostedion* sp.), Salmonidae *(Salmo* sp.) (Yamaguti 1958). Heron specialist (2), rare in loons, not known from grebes.

Tylodelphys glossoides (Dubois, 1928)

In *Gavia arctica.* In ?intestine, ?FW. Europe. *"Colymbus asiaticus"* was listed in Yamaguti (1971) as definitive host of *Glossodiplostomum (=Tylodelphys) glossoides.* Because I cannot find *"asiaticus"* in the synonymy of species names for either *Gavia* or *Podiceps* in the twentieth century. I think it presumably 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 1800s in Europe, where the parasite was described. *Colymbus* was the generic name used for the loons at the time *glossoides* was described.) 4 known from the type host.

Tylodelphys immer (Dubois, 1961)

In *G. adamsii, G. immer* (Kinsella & Forrester 1999, Conboy *et al.* in prep., USNPC No. 087040.00 as *Diplostomum immer,* and voucher HWML No. 38111). Formerly listed as *Strigea* sp. Identified by J. M. Kinsella), *G. stellata* (Dubois & Rausch 1967). In small intestine. ?FW. N. Amer. Yamaguti (1971). Known only from loons (3).

[*"Tylodelphys* sp.

In *Gavia stellata* (J. Okulewicz 1984)].

Family Strigeidae

Cardiocephaloides brandesii (Szidat, 1928)

In *Gavia pacifica ("Colymbus arcticus")* (Yamaguti 1971). N. Amer. SW. Intermed. hosts: **mollusks: GASTRO-PODS,** ?Nassariidae *(Nassarius obsoletus);* then ventricles of brain and eyes of **fishes:** Atherinidae *(Menidia menidia),* Mugilidae *(Mugil cephalus).* Hunter & Vernberg (1960). Allocation to *pacifica* based on distribution of parasite. Formerly placed in *Cardiocephalus.* Also in *Larus* spp. and *Rynchops,* not in grebes. Generalist (1).

Ichthyocotylurus erraticus (Rudolphi, 1809)

In *Gavia adamsii* (Dubois & Rausch 1960), *G. immer* (1 bird Kinsella & Forrester 1999 voucher HWML No. 38112 and Conboy *et al.* in prep. voucher USNPC No. 087050.00), *G. stellata* (Dubois & Rausch 1967), *G. arcticus* (Kontrimovitschus & Bakhmet'eva 1960), and as *"Strigea aquavis"* from "loon" sp USNPC no. 060446.00) Small intestine. FW. Eurasia, N. Amer. Intermed. hosts **mollusks: GASTROPODS,** then **fishes:** Salmonidae. Details in Storer (2000). Infection in birds presumably may also be obtained from salmonids in salt-water habitats. Generalist (1). Also in Grebes, *Spheniscus, Larus, 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. *Cotylurus aquavis* (Guberlet, 1922) is here considered a synonym.

Ichthyocotylurus platycephalus (Creplin, 1825)

In *Gavia immer* (Kinsella & Forrester 1999, voucher

HWML No. 38124). *G. stellata* (McDonald 1969:84). *Bursa Fabricii* (most frequently, Gallimore 1964), intestines. FW? Eurasia, N. Amer. Intermed. hosts? Generalist (1), common in Lari, also in grebes, *Alca, Cepphus,* etc. (McDonald 1969:84). Dubois (1968) divided *Cotylurus platycephalus* into two subspecies, *"C." p. communis,* from *Larus argentatus* in N. Amer. and the nominate race from Eurasia.

Order Opisthorchiformes

Family Opisthorchidae

Amphimerus arcticus Kontrimovitschus & Bakhmet'eva, 1960

In *G. stellata* (type host), *G. immer* (Kinsella & Forrester 1999 voucher HWML No 38108) and Conboy *et al.* in prep. voucher USNPC No. 087041.00), formerly listed as *A. speciosus* is also this species *(fide* Kinsella *in litt.).* In liver, FW? SW? Asia, N. Amer. Intermed. hosts? Loon specialist (3). Not known from grebes.

Erschoviorchis lintoni (Gower, 1939)

In *G. immer* (McDonald 1969:345) and (Kinsella & Forrester, 1999 voucher HWML No. 38125), *G. stellata* (Kontrimovitschus & Bakhmet'eva 1960). Type and paratype of *lintoni* in USNPC Nos. 007916.02 and 007916.01, respectively. (Linton's material [No. 007916] formerly on one slide, has evidently been placed on two.) Cysts in pancreas. Eurasia, N. Amer. SW? Intermed hosts, ?snails, then ?fishes Not known from grebes. Generalist (1). In 1928, Linton described *"Haematotrephus fodiens* (Cyclocoelidae)." as having a free form in the intestine and an encysted form in the pancreas of *Gavia immer* from Woods Hole, MA. Gower examined Linton's material and placed the free form (the type of *H. fodiens)* in *Diasia* (now in *Plotnikovia)* and described the encysted form as a new species, *Amphimerus lintoni,* which has subsequently been placed in *Erschoviorchis.*

Euamphimerus sibiricus Kontrimovitschus & Bakhmet'eva, 1960

In *G. stellata* (Type host). In intestine? FW? Asia. Intermed. hosts? Known only from type host (4).

Metorchis intermedius Heinemann, 1937

In *G. stellata* (McDonald 1969:349). In gall bladder, bile ducts. FW. Eurasia. Intermed. hosts, **mollusks:** GAS-TROPODS, Bithyniidae *(Bithynia tentaculata),* then **fishes:** Cobitidae *(Cobitis taenia),* Cyprinidae *(Cyprinus carpio).* Generalist? (1?). Also in anatids, and pelecaniform birds, not known from grebes. Possibly a synonym of *Metorchis xanthosomus,* or, with that species, a synonym of *Metorchis bilis* (Braun, 1790) *fide* McDonald (1969:349).

Metorchis xanthosomus (Creplin, 1846)

In *G. stellata* (McDonald 1969:354). Gall bladder. FW? SW? Europe. Intermed. hosts, **mollusks:** GASTRO-PODS, Bithyniidae, then **fishes:** Balitoridae, Cobitidae, Gasterosteidae. Details in Storer (2000). Generalist (1), also in grebes, alcids, and other groups.

Plotnikovia fodiens (Linton, 1928)

In *Gavia immer,* type and only known definitive host (4). (Kinsella & Forrester 1999, voucher HWML No.

38107). Type in USNPC No. 007915. In intestine and liver, possibly a bile duct parasite (Kinsella *in litt*). SW? N. Amer. Intermed. hosts ?snails, then ?fishes. (See discussion of *Erschoviorchis lintoni* above.) This is the "free form" of Linton's description and has been placed in *Erschoviorchis, Haematotrephus,* and *Diasia.*

Family Heterophyidae

As far as known, members of this family use fishes as second intermediate hosts (Yamaguti, 1971).

Apophallus brevis Ransom, 1920

In *Gavia immer* (Kinsella & Forrester 1999, voucher HWML No. 38129), and (Conboy *et al.* in prep. voucher USNPC No. 087042.00). In small intestine. FW. N. Amer. Intermed hosts, almost exclusively in **mollusks:** GASTROPODS, <u>Amnicolidae</u> *(Amnicola limosa),* then **fishes:** <u>Percidae</u> *(Perca flavescens),* (Sinclair 1971b). Sometimes considered a synonym of *A. donicus,* (*e. g.* by McDonald 1969:326), but see Sinclair 1971a for discussion of specific status. *A. americanus* and *A. itascensis* are synonyms *fide* Sinclair *(loc. cit.).* Generalist (1). Also known from gulls but not from grebes.

Apophallus muehlingi (Jägerskiöld, 1889)

In *Gavia stellata, G. arctica* (Kontrimovitschus & Bakhmet'eva 1960). In intestine, caeca. Eurasia. FW. Intermed. hosts ?**mollusks:** GASTROPODS, then **fishes:** <u>Cyprinidae</u> *(Abramis "Blicca" bjoerkna, A. brama, Rhodeus sericeus, Rutilus rutilus, Scardinius erythrophthalmus, also Alburnoides bipunctatus, Alburnus alburnus, Leuciscus leuciscus* Zitnan 1966), <u>Percidae</u> *(Perca fluviatilis).*Yamaguti (1971:621) lists *"Colymbus"* as a definitive host. This presumably refers to his earlier (1958:702, 869) listing of *"Colymbus septentrionalis" (=Gavia stellata).* Generalist (1). Not known from grebes.

Cryptocotyle concava (Creplin, 1825)

In *Gavia immer* (Conboy *et al.* in prep., voucher USNPC No. 087038.00), *G. stellata* (McDonald 1969:332-333). Intestines. FW? SW? Eur., N. Amer. Intermed. hosts, **mollusks:** GASTROPODS, then **fishes**. Details in Storer (2000). Also in grebes, generalist (1).

Cryptocotyle cryptocotyloides (Isiaschikov, 1923)

In *G. arctica* (not *pacifica*) on basis of range (McDonald 1969:333-334). Small intestine. FW? Europe. Intermed. hosts, ?snails, then ?fishes. Generalist (1), most common in herons. Not known from grebes.

Cryptocotyle lingua (Creplin, 1825)

In *G. immer* (vouchers in USNPC. Nos. 007936.00 and Conboy *et al.* in prep. and 087052.00), *G. stellata* (McDonald 1969:335-336). Anterior half of small intestine. SW. Eurasia. N. Amer. Intermed. hosts, **mollusks:** GASTROPODS, <u>Hydrobiidae</u>, then **fishes** of many families. Details in Storer (2000). Common in Lari and Alcae; also found in canids (Rausch *et al.* 1990); rare in grebes and loons (2). Has been placed in the genus *Tocotrema.*

Heterophyopsis continua (Onji & Nishio, 1916)

In *Gavia pacifica* (as *Colymbus arcticus pacificus*)Yamaguti (1958:701). ?Intestine. SW, ?FW. Asia. Intermed. hosts ?**mollusks:** GASTROPODS, then **fishes:** <u>Atherinidae</u>

(Menidia menidia), <u>Clupeidae</u> *(Dorosoma thrissa),* <u>Cyprinidae</u> *(Cyprinus),* <u>Mugilidae</u> *(Mugil cephalus)* (Yamaguti 1975:288). Also *Larus,* and stray dogs. ?Generalist (?1). Not known from grebes. Has been placed in genera *Heterophyes* and *Pseudoheterophyes.* Two subspecies listed by Yamaguti (1958:701).

Phagicola longus Ransom, 1920

In *Gavia immer* (Kinsella & Forrester 1999, voucher HWML No. 38109). In small intestine. FW. Eurasia, N. Afr., N. Amer. Intermed. hosts, ?**mollusks:** ?GASTROPODS ?<u>Cerithiidae</u> *(?Cerithium),* <u>Potamidae</u> *(?Cerithidea),* then **fishes:** <u>Carangidae</u> *(Lichia),* <u>Cyprinidae</u> *(Barbus),* <u>Mugilidae</u> *(Mugil cephalus, M. curema, M. trichodon).* Generalist (1). Not known from grebes. Also in *Pelecanus, Milvus,* and carnivorous mammals in the wild, also a variety of other birds and mammals experimentally (Yamaguti 1975). (The specific name is sometimes incorrectly spelled *"longa."* The Latin root *-icola* 'inhabitant' is masculine.)

Pygidiopsis genata Looss, 1907

In *Gavia stellata* (J. Okulewicz 1984). In intestine. FW. Eurasia, N. Afr., N. Amer. Intermed hosts, see Storer (2000). Generalist (1), also in grebes. Common in fish-eating birds and mammals.

Pygidiopsis summa Onji & Nishio, 1916

In *Gavia pacifica* (as *"Colymbus arcticus pacificus"* Yamaguti 1958). Intestine. ?FW. Asia. Intermed. hosts: **mollusks:** GASTROPODS. <u>Potamidae</u> *(Tympanotomus microptera),* then **fishes,** <u>Gobiidae</u> *(Glossogobius brunneus),* <u>Mugilidae</u> *(Mugil cephalus).* Also in *Milvus, Nycticorax, Macacus rhesus,* and experimentally in cats, dogs, and rats. Generalist (1). Not known from grebes.

Stellantchasmus falcatus Onji & Nishio, 1915

In Gavia stellata (Uchida *et al.* 1991), *?G. pacifica* (as *Colymbus arcticus pacificus* Yamaguti 1958). Intestine. ?SW. Asia, Philippines, Hawaii, Austr. Intermed. hosts, **mollusks:** GASTROPODS, <u>Thiaridae</u> *(Tarebia ["Terebia"] granifera, Melania mauiensis, Stenomelania newcombi),* then fishes: <u>Gobiidae</u>: *(Acanthogobius flavimanus),* <u>Mugilidae</u> *(Mugil cephalus, M. ["Liza"] menada).* Also in cormorant. Generalist (1). Not known from grebes. Experimentally in cat. Other species in this genus found in mammals.

Stictodora lariformicola Sogandares-Bernal & Walton, 1965

In *Gavia immer* (In 1 bird, Kinsella & Forrester, 1999 voucher HWML No. 38582). In small intestine, ?SW. Intermed. hosts ?**mollusks:** GASTROPODS, then ?**fishes.** Common in larids (2), rare in loons. Not known from grebes.

Order Plagiorchiformes
Suborder Renicolata
Family Renicolidae

Renicola keimahuri Yamaguti, 1939

In *Gavia stellata* (Leonov *et al.* 1965). In kidney. SW? Asia. Intermed. hosts, snails, then ?fishes. Described from *Cepphus ("Uria") carbo.* Not known from grebes ?Generalist (?1).

Renicola pinguis (Mehlis, 1846)

In *Gavia stellata* (Yamaguti 1971). Kidney. SW? Eurasia. Intermed. hosts, ?snails, then ?fishes. Generalist (1), also in grebes.

Renicola pollaris Kontrimovitschus & Bakhmet'eva, 1960

In *Gavia stellata* (Type host), *G. immer* (Kinsella & Forrester 1999 voucher HWML No. 38122). In kidney. SW? Intermed. hosts, ?snails, then ?fishes. Eurasia (Russia), N. Amer. Loon specialist (3). Not known from grebes.

Suborder Plagiorchiata
Superfamily Microphalloidea
Family Microphallidae

As far as known, species of this family use crustaceans as second intermediate hosts and tend to be more specific to these hosts than to definitive ones. (*e.g.*, Yamaguti, 1971).

Levinseniella brachysoma (Creplin, 1837)

In *Gavia arctica* (and/or *pacifica*) (McDonald 1969:290-291). Small intestine, caeca. SW. Eurasia, N. Amer. Intermediate hosts ?**mollusks**, then **crustaceans:** AMPHIPODS, Corophiidae *(Corophium volulator),* Gammaridae *(Gammarus locusta),* ISOPODS Anthuridae *(Anthura gracilis),* Sphaeromidae *(Sphaeroma hookeri).* Not known from grebes. Generalist (1), commonest in Charadriiformes.

[*Maritrema* sp. of Harkema & Miller (1962)

In *Gavia immer* (Kinsella & Deblock 1997, Kinsella & Forrester 1999). Small intestine. SW. N. Amer. Intermed. hosts ?**mollusks:** ?GASTROPODS, then **Crustaceans:** DECAPODS Ocypodidae *(Uca* spp.). Generalist (1). Not known from grebes.]

[*Maritrema* sp. of the *Eroliae* group. Kinsella & Deblock (1997)

In *Gavia immer* (Kinsella & Deblock 1997, Kinsella & Forrester 1999). In small intestine. SW. N. Amer. Intermed. hosts, ?snails, then ?crustaceans. ?Generalist (?1) Not known from grebes.]

Microphallus forresteri Kinsella & Deblock, 1997

In *Gavia immer* (type host). (Type and paratype in USNPC No. 086795.00.) In small intestine. SW. N. Amer. Intermed. hosts ?snails, then ?crustaceans. Known only from type host (4).

Microphallus nicolli (Cable & Hunninen, 1938) Baer, 1944

In *Gavia immer* (Kinsella & Forrester 1999, *ex* Kinsella & Deblock 1997). In small intestine. SW. N. Amer. Intermed. hosts **mollusks:** GASTROPODS, Cerithiidae *(Bittium alternatum),* then **crustaceans:** DECAPODS, Portunidae *(Callinectes sapidus)* (Cable & Hunninen 1938). Life cycle in cover figure. ?Generalist (?1). Not known from grebes. This is presumably the microphallid mentioned by McIntyre (1988).

[*Microphallus* sp?

In *Gavia immer* (Conboy *et al.* in prep., voucher in USNPC No. 087055.00 from Nova Scotia). In *M. nicolli* complex *fide* Kinsella *in litt.*).]

Odhneria odhneri Travassos, 1921

In *Gavia immer* (Kinsella & Forrester 1999, voucher HWML No. 38117). In small intestine, SW. N. Amer. S. Amer. Intermed. hosts, ?**mollusks:** ?GASTROPODS, then **crustaceans:** DECAPODS, Palaemonidae *(Palaemonetes vulgaris)* and/or Crangonidae (sp.) (J. M. Kinsella *in litt.*) *Nyctanassa violacea* type host. ?Generalist (?1). Not known from grebes.

[Family Gymnophallidae

[*Parvatrema* sp?

In *Gavia immer* (1 bird, Kinsella & Forrester 1999, voucher HWML No. 38127). In small intestine. N. Amer. ?SW.]

Family Prosthogonimidae

Prosthogonimus ovatus (Rudolphi, 1803)

In *Gavia immer* (Kinsella & Forrester 1999, voucher HWML No. 38120. Generalist (1). Also in grebes. Usually in *Bursa Fabricii,* also in cloaca, large intestine, and oviduct. FW. Cosmopolitan. Intermed. hosts, **mollusks:** GASTROPODS, then **insects:** ODONATA (nymphs and adults). Details in Storer (2000).

Superfamily Teleorchioidea
Family Eucotylidae *(incertae sedis)*

Eucotyle cohni Skrjabin, 1924

In *G. arctica* (and/or *pacifica*) (McDonald 1969:270-271). Urinary tubules. FW? Eurasia, N. Amer. Intermed hosts? ?Generalist (?1). Also in grebes and ducks.

Eucotyle nephritica (Mehlis in Creplin, 1846)

In *G. arctica* (and/or *pacifica*) (McDonald 1969:271). Urinary tubules. ?FW. Eurasia. Otherwise known only from *Netta rufina* (Anatidae). ?Generalist (?1). Not known from grebes.

Tanaisia fedtschenkoi Skrjabin, 1924

In *Gavia immer* (1 bird, Kinsella & Forrester 1999). Urinary tubules. FW? Eurasia, N. Amer. Intermed. hosts, snails? Generalist (1), rare in loons and grebes.

THE CESTODES (TAPEWORMS)

Class Eucestoda
[Order Lecanicephalidea]
[Family Lecanicephalidae]
Polypocephalus sp. (ident. by E. P. Hoberg)

In *Gavia immer* (USNPC No. 035011.00) Intestine. SW. N. Amer. (MA, Woods Hole). If the host record is correct, this is a most remarkable record. The group is only known otherwise from elasmobranchs (skates and rays). Because the collector G. A. Macallum, worked on the parasites of skates as well as loons, there is a strong likelihood that the labels for this specimen were mixed with those of an elasmobranch (*fide* E. P. Hoberg *in litt.*)]

Order Pseudophyllidea
Family Diphyllobothriidae

Digramma interrupta (Rudolphi,1810)

In *Gavia arctica, G. stellata* (Yamaguti 1959). In intestine. FW. Eurasia. Intermed. hosts, **crustaceans:** COPEPODS, (Cyclopidae, Diaptomidae), then FW **fishes:** Cyprinidae. Details in Storer (2000). Generalist as adults (1), also in grebes. 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 *Gavia adamsii, G. immer,* (Ryzhikov *et al.* 1985), *G. arctica, G. stellata* (Kontrimovitschus & Bakhmet'eva 1960*)*. In small intestine. FW. Eurasia, N. Amer. Intermed. hosts, **crustaceans:** COPEPODS, (Cyclopidae, Diaptomidae), then **fishes:** especially Salmonidae, less often Lotidae and Osmeridae. Details in Storer (2000). Generalist as adults (1). Common in gulls and loons, uncommon in grebes.

Ligula colymbi Zeder, 1803

In *G. arctica* (?and/or *pacifica*. Malakhova 1985). FW. Eurasia, N. Amer. Intermed. hosts, experimentally in **crustaceans:** COPEPODS, (Cyclopidae, Diaptomidae), then FW **fishes:** especially Cobitidae, less often in Cyprinidae. Details in Storer (2000). Generalist (1), commonest 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 (1986) considers *Ligula* monotypic, with *L. intestinalis* the only species.

Ligula intestinalis (Linnaeus, 1758)

In *G. stellata* (Malakhova 1985). Large and small intestines, kidney (Shigin 1957). FW. Cosmopolitan. Intermed. hosts, **crustaceans:** COPEPODS, (Cyclopidae, Diaptomidae), then many genera of FW **fishes.** Details in Storer (2000). List of genera "not verified by recent classification" in McDonald (1969:367). Also in grebes. Generalist (1). *Ligula monogramma* Creplin, 1839 is considered a synonym by Dubinina (1966).

Schistocephalus solidus (Mueller, 1776)

In *Gavia arctica* (and/or *pacifica*), *G. immer* (Conboy *et al.* in prep., voucher USNPC. No. 087051.00.) *G. stellata* (McDonald 1969:371). Small and large intestines. FW. SW? Eurasia, Iceland, Greenland, Afr., N. Amer. Intermed. hosts, **crustaceans:** COPEPODS, (Cyclopidae, Diaptomidae), then **fishes:** Gasterosteidae, (specialist on *Gasterosteus,* also in *Culaea inconstans* Hoffman 1967) and possibly "Cottidae, *Cottus gobio, C. kaganowskii,* etc." Dubinina (1966). Details in Storer (2000). McDonald (1969:370) lists unverified reports from other genera. Some species of these (*e.g. Salmo)* may act as sources for hosts in marine environments. In definitive hosts a generalist (1). Also in grebes and a variety of other fish-eating birds, some marine (*e.g.* Procellariidae and Alcidae).

Order Tetrabothridea

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 *Gavia adamsii, G. arctica, G. immer* (vouchers USNPC No. 007863.00, Conboy *et al.* in prep. No.8739.00, and

Kinsella & Forrester 1999 HWML No. 3835, *G. stellata* (Ryzhikov *et al.* 1985 and voucher USNPC No. 66387.00. *G. pacifica* (Yamaguti 1959), and for *Gavia* sp., USNPC No. 049955.00). 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 *in litt.*). Ryzhikov *et al.* (1985) consider *T. immerinus* (Abildgaard, 1790*)* formerly used for this species, a *nomen oblitum* and *T. perfidus* Joyeux & Baer, 1934, a synonym. *Paratetrabothrius lobatus* (Linstow, 1905) and *P. orientalis* Yamaguti, 1959 are synonyms *fide* Schmidt (1986).

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

In *Gavia stellata.* 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 (*in litt.*) considers this identification to be incorrect.]

Order Cyclophyllidea

Family Dilepididae

Anomotaenia ciliata Fuhrmann, 1913

In *Gavia stellata* (McDonald 1969:381). Small intestine. FW. Eurasia, N. Amer. Intermed. hosts, **crustaceans:** CLADOCERANS, Daphniidae *(Simocephalus exspinosus).* Common in waterfowl (2), rare or accidental in loons. Not known from grebes. The presence of this cestode in a loon suggests that a paratenic host may have been involved.

[*Anomotaenia micracantha* (Krabbe, 1969)

In *Gavia arctica* "Chibichenko (1966)." Record of this parasite of gulls and terns considered "very doubtful" by Ryzhikov *et al.* 1985.]

Cyclustera ibisae (Schmidt & Bush, 1972)

In *Gavia immer* (Kinsella & Forrester 1999, voucher HWML No. 38137). Small intestine. ?FW. N. Amer. (Florida). Intermed. hosts? Common in the White Ibis (*Eudocimus albus*), also in Black Skimmer (*Rynchops niger*) immatures only, uncommon in loons, not known from grebes. ?Ibis specialist (?2).

Lateriporus skrjabini Matevossian, 1946

In *Gavia arctica* (and/or *pacifica*) (Ryzhikov *et al.* 1985). Small intestine. FW. SW? Eurasia, N. Amer. Intermed. hosts, **crustaceans:** AMPHIPODS, Gammaridae *(Gammarus lacustris)* (Ryzhikov *et al.* loc. cit.). Specialist in lari, also in anatids, occasional but not known to mature in grebes (Stock 1985). Rare or uncommon in loons (2).

Neovalipora parvispine (Linton, 1927)

In *Gavia arctica* (and/or *pacifica*), *G. immer, G. stellata* (Ryzhikov *et al.* 1985). (Type and paratype from *G. immer,* USNPC. No. 007889.00.) FW? SW? Eurasia, Iceland, N. Amer. Intermed hosts? Loon specialist, occasional in grebes and gulls (3).

Paradilepis urceus (Wedl, 1855)

In *Gavia arctica* (and/or *pacifica*) (Ryzhikov *et al.* 1985). Small intestine. FW? Eurasia, Afr. Intermed. hosts? Ciconiiform specialist, occasional in loons, grebes, and

several other groups (2).

Paricterotaenia ransomi (Linton, 1927)

In *Gavia immer* (Linton, 1927). Intestine. SW? Eurasia, N. Amer. Intermed. hosts? Specialist in Lari, uncommon in loons, not known from grebes (2). The type host is *Larus atricilla*, not *L. "crassirostris,"* contra Ryzhikov *et al.* (1985).

Family Hymenolepididae

Biglandatrium biglandatrium Spasskaya, 1961

In *Gavia arctica* (and/or *pacifica*) (Ryzhikov *et al.* 1985). Intestine. FW? Eurasia. Intermed. hosts? Monotypic genus. Loon specialist (3). Reports from grebes probably in error.

[Confluaria capillaris (Rudolphi, 1810)

In *Gavia arctica* (and/or *pacifica*) (Ryzhikov *et al.* 1985), *G. immer, G. stellata* (Schmidt 1986). Intestine. FW? Iceland, Eurasia, N. Amer. Intermed. hosts? Sometimes placed in genera *Hymenolepis, Variolepis,* or *Wardium.* Characteristic parasite of grebes. According to Vasileva *et al.* (1999a) reports from loons are erroneous or doubtful.]

Drepanidotaenia lanceolata (Bloch, 1782)

In *Gavia immer* (McDonald 1969:482). Posterior half of small intestine. FW. Cosmopolitan. Intermed. hosts, **crustaceans:** COPEPODS (Cyclopidae, Diaptomidae), and OSTRACODS (rarely). Paratenic hosts **mollusks:** GASTROPODS, Lymnaeidae Details in Storer (2000). Specialist in anatids, occasional in grebes, loons, and other birds (2).

Dubininolepis fuhrmanni (Skrjabin & Matevossian, 1942)

In *Gavia adamsii, G. arctica* (and/or *pacifica*), *G. stellata* (Ryzhikov *et al.* 1985). In intestine. FW? SW? Eurasia, N. Amer. Intermed. hosts? Loon specialist, not known from grebes (3). Genus consists of loon specialists.

Dubininolepis pseudorostellatus (Joyeux and Baer, 1950)

In *Gavia immer* (Yamaguti 1959, Kinsella & Forrester 1999). In intestines. FW? Eur., N. Amer. Intermed hosts? Loon specialist (3), not known from grebes. Considered a synonym of *Dubininolepis rostellata* by Spasskaya 1966. Vasileva *et al.* (1999a) agree with Joyeux and Baer (1950) in considering that loons and grebes share no species of Hymenolepidids.

Dubininolepis rostellatus (Abildgaard, 1790)

In *Gavia arctica* (Kontrimovitschus & Bakhmet'eva 1960), *G. immer* (Vouchers USNPC. No. 007880.00 and as *Taenia globulus* No. 035918.00), *G. stellata* (Ryzhikov *et al.* 1985). Intestine. FW? Eurasia, N. Amer. Intermed. hosts? Loon specialist, rare in grebes (3). Formerly in genera *Armadoskrjabinia* and *Microsomacanthus. Taenia capitellata* Rudolphi, 1810 (voucher in USNPC No. 035933.00 from *G. immer*) and *Microsomacanthus pseudorostellatus* (Joyeux & Baer, 1950) are synonyms *fide* Spasskaya 1966, and Joyeux & Baer consider *Dubininolepis (Microsomacanthus) swiderskii* (Gasowska, 1932) a synonym of *rostellatus.*

Dubininolepis swiderskii (Gasowska, 1932)

In *Gavia arctica* (?and *pacifica*), *G. stellata* (Ryzhikov *et al.* 1985). Intestine. FW? Eurasia. Intermed. hosts?

Loon specialist, rare in grebes and gulls (3). Formerly placed in the genera *Microsomacanthus* and *Variolepis.* Described in *Hymenolepis.*

Microsomacanthus paracompressa (Czaplinski, 1956)

In *Gavia arctica* (Ryzhikov *et al.* 1985). Small intestine. FW. Iceland, Eurasia. Intermed. hosts, **crustaceans:** COPEPODS, Cyclopidae *(Acanthocyclops, Cyclops, Eucyclops, Macrocyclops, Mesocyclops, Paracyclops),* then, as paratenic hosts, **mollusks:** GASTROPODS, Acroloxidae (*Acroloxus*), Lymnaeidae *("Amphipepla" = Amphipeplea = Myxas, Lymnaea),* Planorbidae *(Planorbis),* Viviparidae, *(Viviparus)* (McDonald 1969:510-511). Common in anatids, rare in loons and *Larus,* not known from grebes (2).

Microsomacanthus paramicrosoma (Gasowska, 1931)

Gavia arctica (and/or *pacifica*) (Ryzhikov *et al.* 1985). Small intestine (anterior and midsections). FW. Eurasia, N. Amer. Intermed. hosts, **crustaceans:** COPEPODS, Cyclopidae *(Acanthocyclops, Eucyclops, Macrocyclops, Mesocyclops, Paracyclops),* Diaptomidae *(Diaptomus),* then, as paratenic hosts, **mollusks:** GASTROPODS. Lymnaeidae *(Lymnaea),* Planorbidae, *(Planorbis)* (McDonald 1969:511-512). Common in anatids, rare in loons, not known from grebes (2).

Microsomacanthus simulans (Joyeux & Baer, 1941)

In *Gavia arctica* (as *Colymbus arcticus*) Switzerland (Yamaguti 1959:311). Intestine. FW? Europe. Intermed. hosts? Known only from type host. Recognized by Schmidt 1986. ?Synonym of *Dubininolepis rostellatus.*

Nadjedolepis paranitidulans (Golikova, 1959)

In *Gavia stellata* (Ryzhikov *et al.* 1985). In intestine. FW? Eurasia. Common in charadriiformes (2), rare in loons not known from grebes.

THE ACANTHOCEPHALANS (SPINY-HEADED WORMS)

Phylum Acanthocephala

Class Palaeacanthocephala

Order Polymorphida

Family Polymorphidae

Andracantha gravida (Alegret, 1941)

In *Gavia immer* (Kinsella & Forrester 1999, voucher HWML No. 37465). In small intestine. SW? Intermed. hosts? N. Amer. Also in *Phalacrocorax auritus,* not in grebes. ?Generalist (?1).

Andracantha mergi (Lundström, 1941)

In *G. stellata* (vouchers USNPC. Nos. 073921.00 and 073922.00). Intestine. SW. Eurasia, N. Amer. Intermed. hosts? Paratenic hosts? Generalist (1), also in *Podiceps grisegena, P. cristatus, Mergus serrator,* and *Cepphus grylle.* Formerly placed in the genus *Hemiechinosoma.* Described in *Corynosoma* in which it is placed by McDonald (1969:661).

Andracantha phalacrocoracis (Yamaguti, 1939)

In *Gavia immer, G. stellata* (Ryzhikov *et al.* 1985). Small intestine. Asia. SW. Intermed. hosts? Cormorant specialist (2), also in *Rissa.* Not known from grebes. Described in *Corynosoma.*

Corynosoma anatarium Van Cleave, 1945

In *Gavia immer* (Ryzhikov *et al.* 1985.) Intestine. FW? SW? Eurasia, N. Amer. Intermed. hosts? Paratenic hosts? Also in grebes. Generalist (1).

Corynosoma clavatum Goss, 1940

In *Gavia stellata* (Rausch *et al.* 1990). In intestine. FW? SW? Australia, Antarctica, Alaska. Intermed. or paratenic hosts, **fishes:** Platycephalidae (*Platycephalus fuscus*). Specialist in cormorants (2), rare in loons, not known from grebes, also in seal *(Gypsophoca)* and fox *(Alopex lagopus)* (Rausch *et al.* 1990).

[*Corynosoma semerme* (Forssell, 1904)

In *Gavia immer, G. stellata* (Ryzhikov *et al.* 1985). Intestine, most often at anterior part of large intestine. SW. Eurasia, Atlantic and Pacific oceans, near Austr. Intermed. hosts, **crustaceans: AMPHIPODS** (Lysianassidae), then second intermediate and paratenic hosts, a wide variety of SW, and some anadromous and catadromous **fishes**. Details in Storer (2000) 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 *Gavia arctica* (and/or *pacifica), G. immer, G. stellata* (Ryzhikov *et al.* 1985). Small intestine. SW. Eurasia, N. Amer., S. Amer. Intermed. hosts, **crustaceans: AMPHIPODS** (Lysianassidae), second intermediate hosts, and, probably, paratenic hosts, marine and anadromous or catadromous **fishes** and **reptiles: SNAKES**. Details in Storer (2000). Juvenile forms have been found in mink *(Mustela vison),* blue fox *(Alopex),,* and "seal bear," (=? *Thalarctos).* 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, including loons and grebes, in which they are not known to mature; also reported from canids and man (Rausch *et al.* 1990).]

Polymorphus acutis Van Cleave & Starrett, 1940

In *Gavia arctica* (Kontrimovitschus & Bakhmet'eva 1960*), G. stellata* Ryzhikov *et al.* 1985). Intestine. FW? SW? Eurasia. N. Amer. Intermed. hosts? Paratenic hosts? Generalist (1), also in grebes, common in anatids.

Polymorphus brevis (Van Cleave, 1916)

In *Gavia immer* (Vouchers USNPC No. 038678.00, and Kinsella & Forrester 1999, HWML No. 38139). In intestines, SW? N. Amer. Intermed. hosts? Described in *Arhythmorhynchus.* Generalist (1), also in herons and *Pandion,* not known from grebes.

Polymorphus gavii Khokhlova, 1965

In *Gavia arctica* (and/or *pacifica), G. adamsii ("immer")* (Ryzhikov *et al.* 1985). Large and small intestines. FW? SW? Asia (Chutkhotsk). Intermed. hosts? Known only from loons (3). Because eastern Asia is outside the normal range of *G. immer* and because *G. adamsii* was

considered a subspecies of *immer* in the former USSR (Dement'ev *et al.* 1968, original publication in Russian, 1950), the above record of *"immer"* almost certainly refers to *adamsii.* Similarly, because *Gavia pacifica* was long considered a subspecies of *G. arctica,* in both the former USSR and North America, the report of *G. "arctica"* could apply to either species. If taken on the breeding grounds on the Arctic slope, it probably would be *pacifica,* otherwise it might be either. (This underscores the value of saving specimens of the hosts, especially of types.)

Polymorphus magnus Skrjabin, 1913

In *Gavia arctica* (and/or *pacifica), G. stellata* (McDonald 1969:676). Intestine. FW. Eurasia. Intermed. hosts, **crustaceans: AMPHIPODS** (Gammaridae). Details in Storer (2000). Paratenic hosts? Generalist (1), common in anatids and charadriiformes, also reported from grebes, other birds, and muskrats.

Polymorphus minutus (Goeze, 1782)

In *Gavia arctica* (and/or *pacifica)* (as *P. actuganensis,* Ryzhikov *et al.* 1985). Large and small intestines. FW, SW. Eurasia, N. Amer. Intermed. hosts, **crustaceans: AMPHIPODS** (Gammaridae) and **DECAPODS** (Astacidae). Details in Storer (2000). Paratenic hosts, **"fishes."** Generalist in birds (1), including grebes, alcids, and land birds. Commonest in Anatids and Charadriiformes (1). *P. boschadis* (Schrank, 1788) and *P. actuganensis* Petrochenko, 1949 are synonyms *fide* Amin in Crompton & Nickol (1985).

Polymorphus obtusus Van Cleave, 1918

In *Gavia arctica* (and/or *pacifica)* (Ryzhikov *et al.* 1985). In intestine. FW, SW. Eurasia, N. Amer. Intermed. hosts **crustaceans: AMPHIPODS,** Gammaridae *(Gammarus balcanensis, G. kischineffensis, G. lacustris,* and *G. mareoticus* in FW and *G. locusta* in SW. (Ryzhikov *et al.* 1985). Generalist (1), not known from grebes.

Polymorphus phippsi Kostylev, 1922

In *Gavia arctica* (Kontrimovitschus & Bakhmet'eva 1960*), G. stellata* (Ryzhikov *et al.* 1985). In small intestine. SW. Eurasian coast of Arctic Ocean. Intermed. hosts **crustaceans: AMPHIPODS,** Gammaridae *(Gammarus locusta).* Generalist (1). Not known from grebes. May be a synonym of *P. minutus.*

Southwellina hispida (Van Cleave, 1925)

In *Gavia immer* (Kinsella & Forrester 1999, voucher HWML No. 38140). 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 grebes and herons. Sometimes placed in the genus *Arhythmorhynchus*.

THE NEMATODES (ROUND WORMS)

Class Nematoda
Subclass Adenophorea
  Order Enoplida
    Superfamily Dioctophymatoidea
      Family Dioctophymatidae
        Eustrongylides tubifex (Nitzsch, 1819)
          In *Gavia stellata, G. arctica* (Kontrimovitschus & Bakhmet'eva 1960), *G. immer* (vouchers Kinsella & Forrester 1999, HWML 38150 and Conboy *et al.* in prep., USNPC No. 087045). In tumors in wall of proventriculus, muscular stomach. 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, also in grebes (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 hosts live (Measures 1988a, b, c).
        [Hystrichis sp.(Bouvier *et al.* 1962).]
    Superfamily Trichinelloidea
      Family Trichuridae
        Subfamily Capillariinae
          Baruscapillaria carbonis (Rudolphi, 1819)
            In *Gavia arctica* (and/or *pacifica)* (Barus *et al.* 1978:22). Small and large intestines. FW? Eurasia. Intermed. hosts, ?**annelids:** OLIGOCHAETES. Generalist (1), also in grebes.
          Baruscapillaria mergi (Madsen, 1945)
            In *Gavia stellata* (Barus *et al.* 1978:24), *G. arctica* (A. Okulewicz 1989), *G. immer* (Kinsella & Forrester 1999, voucher HWML No. 38146 as *Capillaria mergi).* Caeca, rectum, rarely small intestine. FW? Eurasia. Intermed. hosts ?**annelids:** OLIGOCHAETES. Specialist in anatids (especially mergansers), also in grebes and *Ardea* (2). The prevalence in fish-eating birds indicates that fishes may act as intermediate or paratenic hosts.
Subclass Secernentea
  Order Strongylida
    Suborder Strongylata
      Family Syngamidae
        Cyathostoma phenisci (Baudet, 1937)
          In *Gavia immer* (Kinsella & Forrester 1999, voucher HWML No. 38147). Nasal and orbital cavities. SW. N. Amer., S. Amer. Life cycle direct or ?with paratenic hosts, ?earthworms. Described in *Syngamus* from *Spheniscus humboldti.* ?Generalist (?1). Not known from grebes.
        Syngamus arcticus Ryzhikov, 1952
          In *Gavia stellata,* type host. In respiratory tract. NW. Eurasia (White Sea). Known only from original description (5). Life cycle unknown.
  Order Ascaridida

Family Anisakidae
  Contracaecum rudolphii Hartwich, 1964
    In *Gavia adamsii* (Barus *et al.* 1978), *G. arctica, G. stellata* (Kontrimovitschus & Bakhmet'eva 1960). In proventriculus, stomach. FW, SW. Cosmopolitan. Intermed. hosts, **crustaceans:** COPEPODS and AMPHIPODS, then, as intermediate and/or paratenic hosts, **insects:** ODONATA and DIPTERA and **fishes:.** Details in Storer (2000). Generalist in both FW and marine birds (1), including loons and grebes. (*Contracaecum spiculigerum* is a synonym *fide* Hartwich, 1964).
  Contracaecum variegatum (Rudolphi, 1809)
    In *Gavia immer, G. stellata* (type host) (Barus *et al.* 1978). In stomach, intestine. FW? SW? Nearly cosmopolitan. Intermed. hosts? Also in gulls and alcids, not known from grebes. ?Generalist (?1) Some records for *C. rudolphii* may belong to this species.
Order Spirurida
  Family Acuariidae
    Subfamily Acuariinae
      Cosmocephalus obvelatus (Creplin, 1825)
        In *Gavia arctica* (and/or *pacifica), G. immer* (Kinsella & Forrester 1999 voucher HWML No. 38143). Esophagus. FW, SW. Cosmopolitan, except S. Amer. (Reported from four genera of Alcids by Barus *et al.* 1978). Intermed. hosts, **crustaceans:** AMPHIPODS, Crangonyctidae, Gammaridae, Talitridae. Paratenic hosts, **fishes:** Cottidae, Cyprinidae, Gasterosteidae, Osmeridae. Details in Storer (2000). *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 & Anderson 1982b. Species redescribed by Anderson & Wong (1981), who consider *C. diesingi* and *C. firlottei* synonyms. Generalist, most common in gulls also in grebes, (1).
      Paracuaria adunca (Creplin, 1846)
        In *Gavia arctica, G. stellata* (as *P. macdonaldi [sic]* Kontrimovitschus & Bakhmet'eva 1960, and as *P. tridentata* A. Okulewicz 1989), *G. immer* (Kinsella & Forrester 1999, voucher HWML No. 38142). Most numerous near junction of proventriculus and gizzard. FW. Eurasia, N. Amer. Intermed. hosts, **crustaceans:** AMPHIPODS, Crangonyctidae, Gammaridae, Talitridae. Paratenic hosts, **fishes:** Cyprinidae, (and, experimentally, *Carassius auratus),* Gasterosteidae. Details in Storer (2000). Life cycle in gulls in Anderson & Wong (1982). Wong & Anderson (1982a) consider *adunca* type and only member of genus and *P. mcdonaldi* Rao, 1951, and *P. tridentata* (Linstow, 1877) synonyms. Report of infective larvae of *P.* "*tridentata*"found in **insects:** COLEOPTERA (larvae), Tenebrionidae *(Pimelia subglobosa, Tentiria taurica)* Barus *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. Common, widespread parasite of fish-eating birds including grebes, generalist (1).

Subfamily Seuratiinae

Ingliseria cirrohamata (Linstow, 1888)

In *Gavia arctica* (and/or *pacifica*) (Yamaguti 1961), *G. stellata* (Barus et al. 1978). In gizzard. FW? SW? Antarctic, E. Asia. Intermed. hosts? Formerly placed in genus *Streptocara.* Also in *Phalacrocorax, Clangula,* and *Larus,* not known from grebes. Generalist (1).

Stegophorus diomedeae (Johnston & Mawson, 1942)

In *Gavia immer* (1 bird, Kinsella & Forrester 1999, voucher HWML No. 38149). In kidneys and liver. SW. Oceanic. Intermediate hosts? Members of this genus specialize on procellariids and penguins, rare in *Gavia* and *Uria,* not known from grebes (2).

Stegophorus stellaepolaris (Parona, 1901)

In *Gavia stellata* (Barus et al.1978:205). Under cuticle of gizzard. SW. Holarctic. Generalist, not known from grebes (1).

Streptocara crassicauda (Creplin, 1829)

In *Gavia arctica* (and/or *pacifica*), *G. stellata* (Barus et al. 1978), *G. immer,* (as *S. c. longispiculata,* Gibson, 1968; vouchers Kinsella & Forrester 1999, HWML No. 38144. also USNPC Nos. 070945.00, 070946.00, and 070947.00, holotype, allotype, and paratype, resp.) (As *S. crassicauda charadrii,* vouchers USNPC No. 026774.02). Subspecies not widely recognized in this species. Under cuticle of gizzard. FW, SW. Eurasia, N. Amer., Austr. Intermed. hosts, [**annelids:** LEECHES, Erpobdellidae, This report, included in Storer (2000) is in error *fide* R. C. Anderson *in litt.*] **crustaceans:** AMPHIPODS, Gammaridae [FW, SW]), Talitridae [FW]). Paratenic hosts, **fishes:** Clupeidae, Cyprinidae, Gobiidae, Percidae. Details in Storer (2000). Life cycle in Denny 1969; Laberge et al. 1989. *S. pectinifera* (Neumann, 1900) is a synonym. For a revision of *Streptocara,* see Gibson (1968). Generalist (1). Also in grebes, widespread in waterfowl.

Streptocara formosensis Sugimoto, 1930

In *Gavia immer* (Kinsella & Forrester 1999, voucher HWML No. 38145). Under proventriculus or koilin lining of gizzard. FW? Asia (Taiwan), N. Amer. Intermed. hosts? Described from ducks. Rare in loons. (?2). Not known from grebes. The specific name is sometimes incorrectly spelled *formosus.*

[*Streptocara recta* (Linstow, 1879)

In *Gavia arctica, G. stellata* (Kontrimovitschus & Bakhmet'eva 1960). Gibson (1968) suggests that these records may refer to *S. c. crassicauda.*]

Family Ancyracanthidae

Sciadicara rugosa Schmidt & Kinsella, 1972

In *Gavia immer* (1 bird, Kinsella & Forrester 1999, voucher HWML No. 38148). Under koilin lining of gizzard. FW? Intermed. hosts? Described from Florida Duck (?2), not known from grebes.

Suborder Camallanina

Superfamily Dracunculoidea

Family Dracunculidae

Avioserpens galliardi Chabaud & Campana, 1949

In *Gavia stellata* (Barus et al. 1978:249). Hypodermal tissue, aponeurosis in upper part of esophagus. Eura-

sia, N. Amer. FW. Intermed. hosts, **crustaceans:** COPEPODS. Cyclopidae *(Cyclops).* Paratenic hosts? Heron specialist (2), also in *Mergus,* not known from grebes.

Avioserpens mosgovoyi Supryaga, 1965

In *Gavia arctica* (and/or *pacifica*) (Barus et al. 1978:250). 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).

Superfamily Filarioidea

Family Onchocercidae

Subfamily Splendidofilariinae

Splendidofilaria fallisensis (Anderson, 1954)

In *Gavia immer* (Anderson & Forrester 1974, voucher USNPC No. 072643.00). Adults in subcutaneous tissue, microfilaria in blood. Life cycle shown in Figure 1 and described in Anderson (1956). Vectors black flies (Simuliidae) (See, p. 14). Common in waterfowl (2), not known from grebes.

[THE PENTASTOMIDS (TONGUE-WORMS)

Two species of these parasitic crustaceans have been found in sea birds: *Reighardia lomviae* in alcids and *R. sternae* in gulls and terns. The life cycle of the latter has been described by Boeckeler (1984) and Thomas et al. (1999) as a one-host parasite in the respiratory system whereas the life cycles of most of the group involve one intermediate host. It is possible that one or more species of this group might be found in loons and/or grebes.]

THE EXTERNAL PARASITES OF LOONS

THE HIRUDINEA (LEECHES)

Class Hirudinea

Order Rhynchobdellida

Family Glossiphoniidae

Theromyzon "trizonare" Davies & Oosthuizen, 1993

In *Gavia pacifica* (reported by Bartonek & Trauger 1975 as *T. "rude"* from *Gavia "arctica,"* but almost certainly *pacifica* on the basis of range).

Canada, NWT. These authors also reported *Placobdella ornata* (Verrill, 1872) infesting waterfowl in the same area, but did not specify which was parasitizing the loon, but they commented that *P. ornata* "was infrequently encountered parasitizing waterfowl."

THE ACARINA (MITES)

Only a single species of mite *(Brephosceles forficiger)* has been found on loons. The family to which it belongs (Alloptidae) is found on most orders of water birds but is not known from grebes. Peterson, in his revision of *Brephosceles* (1971) pointed
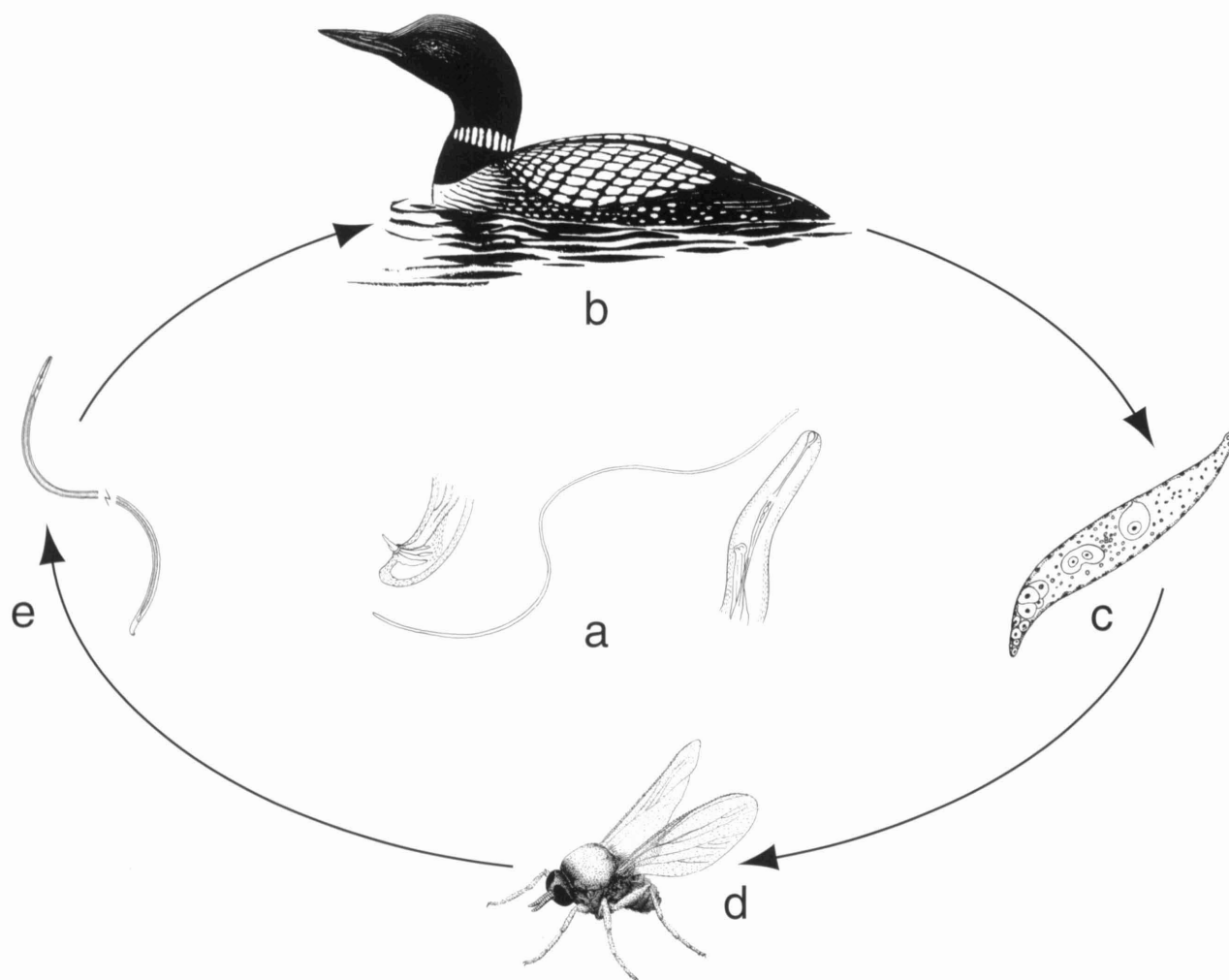
Figure 1. The life cycle of the filarioid nematode, *Splendidofilaria fallisensis.* (a) Adult from the subcutaneous tissue of the definitive host, (b), a Common Loon (*Gavia immer*), which becomes infected from bites of the black fly, *Simulium euryadminiculum* (d), which is attracted to the loon by a special substance found only on the bird. 70 microns-long microfilaria (c) from the blood of the loon are ingested by the fly vector where they develop in the insect's haemocoele, undergoing 2 molts before moving to the fly's head at a length of ca. 430 microns. From there, they, (e), are transmitted to another loon while it is bitten by the fly. (Details in Anderson, 1956.) Although the parasite is common in waterfowl in which other black flies are more common vectors, the attractant of the loon is a special situation. Original drawing by John Megahan from sources listed in the acknowledgments (p. 32).

out that the finding of members of this genus on plovers and oystercatchers (Charadriidae and Haematopodidae) supported my tentative conclusion (1956) that loons are related to charadriiform birds. It has since been shown that loons are closer to procellariiform birds by Prager & Wilson (1980) and Sibley & Ahlquist (1990) than to shorebirds, and Peterson's revision also shows that species *Brephosceles* are found on many procellariiform birds. Unfortunately, no phylogenetic analysis of *Brephosceles* has yet been made, so we cannot evaluate evidence of the relationships of the loons from the mites, although the presence of mites of this family in Procellariiform birds may be significant.

Order Acariformes
 Suborder Sarcoptiformes

Superfamily Analgoidea
 Family Alloptidae
  Brephosceles forficiger (Megnin & Trouessart, 1884)
   On *G. immer* (Type host), *Gavia arctica* (Peterson 1971).
   A rarely found mite, known from a few collections from northern Europe.

THE PHTHIRAPTERA (LICE)

Order Phthiraptera
 Suborder Ischnocera
  Family Philopteridae

Craspedonirmus colymbinus (Denny, 1842)

On *Gavia arctica, G. pacifica, G. stellata* (Emerson 1955). Emerson *(loc. cit.)* considers *Nirmus frontatus* Nitzsch, 1866, *Docophorus bisetosus,* Piaget, 1885, *D. graviceps,* Kellogg, 1896, and *D. atricolor,* Kellogg, 1896, synonyms of this species.

Craspedonirmus immer Emerson, 1955

On *Gavia immer* (type host).

THE DIPTERA (FLIES)

Although bloodsucking insects that fly freely from one host to another are not ordinarily included in this list, I believe that the close association of the following simuliid with the Common Loon is of sufficient interest to permit an exception.

Family Simuliidae Black flies

Simulium euryadminiculum Davies, 1949

On *Gavia immer.* N. Amer. An unidentified substance found on the Common Loon has been shown to be a specific attractant for this insect by Lowther & Wood (1964) and Fallis & Smith (1964), although the possibility that these insects might be attracted by other species of loons was not eliminated. While the principal host of this fly is the Common Loon, individuals occasionally feed on waterfowl and thus might have transmitted microfilariae of the nematode, *Splendidofilaria fallisensis,* from waterfowl to loons. It is perhaps more likely that one of the black flies that feed predominantly on ducks might have infected a loon with this nematode (Anderson *in litt.*).

Family Hippoboscidae Bird-flies

Pseudolfersia fumipennis (Sahlberg)

On *Gavia immer* Johnson (1922). Also known from the Osprey *(Pandion haliaetus)* and the Bald Eagle *(Haliaeetus leucocephalus).* N. Amer. The fact that both Common Loons and Ospreys (and probably Bald Eagles) smell strongly of fish suggests the possibility that these flies are attracted to this odor.

LIST OF PREY SPECIES TAKEN BY LOONS

The aim of this list is to include all the prey species known to be taken by each species of loon. As in Storer (2000), I have only listed the names of the known prey species. This is done to make possible determining if the birds are known to take a given species of final host of a parasite, and can be accomplished by comparing the lists of prey species with those of the final intermediate hosts on the web. (See p. 2) I have made no attempt to indicate the relative importance of the species taken or to list all of the references for each of these prey species.

Gavia stellata Red-throated Loon

FW. Annelids: LEECHES spp. **Crustaceans:** AMPHIPODS Gammaridae *(Gammarus* cf. *locusta).* **Insects:** DIPTERA Chironomidae *Chironomus islandicus, Tanytarsus gracilentus.* "Aquatic insects" spp. **Mollusks:** GASTROPODS Lymnaeidae *(Lymnaea),* Valvatidae *(Valvata).* **Fishes:** Cyprinidae *(Alburnus*

alburnus, Leuciscus leuciscus, Rutilus rutilus, Scardinius erythrophthalmus), Gasterosteidae *(Gasterosteus aculeatus* also SW). Percidae *(Perca flavescens* BW, *P. fluviatilis).* Salmonidae *(Coregonus albula, Salmo, Salvelinus alpinus, S. fontinalis, Thymallus* sp.). **Amphibians:** ANURANS frogs.

SW. Annelids: POLYCHAETES Nereidae sp. Polynoididae sp. **Crustaceans:** COPEPODS sp., ISOPODS Idotheidae *(Idothea* sp.), DECAPODS crabs, prawns, shrimps. **Mollusks:** PELECYPODS Cardiidae *(Cardium),* Mytilidae *(Mytilus).* CEPHALOPODS Loliginidae *(Loligo).* **Fishes:** Ammodytidae *(Ammodytes dubius, A.* sp.), Anguillidae *(Anguilla anguilla* also FW), Belonidae *(Belone belone),* Carangidae *(Caranx trachurus),* Clupeidae *(Clupea harengus, Sprattus sprattus),* Cottidae *(Cottus scorpius, Leptocottus armatus),* Gadidae *(Boreogadus saida, Gadus callarias, G. flavescens, G. minutus, G. morhua, Merlangius merlangus, Microgadus tomcod, Micromesistius poutassou, Pollachius virens),* Gasterosteidae *(Pungitius pungitius, Spinachia spinachia),* Gobiidae *(Chaparrudo flavescens, Pomatoschistus minutus),* Osmeridae *(Mallotus villosus),* Pholidae *(Pholis gunellus),* Pleuronectidae *(Hippoglossoides platessoides, Limanda limanda, Platichthys flesus, Pleuronectes platessa),* Scombridae *(Scomber scombrus),* Stichaeidae *(Lumpenus fabricii),* Zoarcidae *(Zoarces viviparus).*

References. Cramp (1977), Davis (1972), Durinck *et al.* (1994b), Eriksson *et al.,* (1990), Fjeldså *(in litt.),* Madsen (1957), Palmer (1962).

Gavia arctica Arctic Loon

FW. Crustaceans: DECAPODS Astacidae *(Astacus fluviatilis).* **Insects:** ODONATA Anisoptera nymphs. TRICHOPTERA larvae. HEMIPTERA Corixidae sp. COLEOPTERA sp. **Mollusks:** GASTROPODS aquatic snails. **Fishes:** Cyprinidae *(Alburnus alburnus, Cyprinus carpio, Leuciscus leuciscus, Rutilus rutilus),* Percidae *(Perca* sp.), Salmonidae *(Coregonus lavaretus, Salmo trutta, Salvelinus alpinus, Thymallus thymallus).* **Amphibians:** ANURANS Ranidae *(Rana temporaria).*

FW-SW. Fishes: Anguillidae *(Anguilla anguilla),*

SW. Annelids: POLYCHAETES Nereidae (sp.), *Polynoidae* (sp.), **Crustaceans:** MYSIDACEA Mysidae *(Mysis* sp.) ISOPODS Idotheidae *(Idothea* sp.), **Mollusks:** GASTROPODS Hydrobiidae *(Hydrobius* sp.), Littorinidae *(Littorina obtusata).* PELECYPODS Mytilidae *(Mytilus* sp.). **Fishes:** Ammodytidae *(Ammodytes* sp.), Atherinidae *(Atherina),* Carangidae *(Caranx trachurus),* Clupeidae *(Clupea harengus, Sprattus sprattus),* Cottidae *(Cottus scorpius),* Gadidae *(Gadus callarias, G. morhua),* Gasterosteidae *(Gasterosteus aculeatus [also FW],* Pungitius pungitius, Spinachia spinachia, Gobiidae *(Pomatoschistus minutus, Chaparrudo flavescens, Gobius niger),* Labridae *(Ctenolabrus rupestris),* Pholidae *(Pholis gunellus),* Pleuronectidae *(Pleuronectes flesus),* Scombridae *(Scomber scombrus),* Stromateidae *(Peprilus ["Rhombus"]* sp.), Zoarcidae *(Zoarces viviparus).*

References: Collinge (1927), Cramp (1977), Fjeldså *(in litt),* Madsen (1957), Merrie (1996).

Gavia pacifica Pacific Loon

FW. Crustaceans: ANOSTRACANS Family? NOTOSTRACANS. Family? **Insects:** ODONATA Anisoptera nymphs. TRICHOPTERA larvae. HEMIPTERA Corixidae spp.

Mollusks: GASTROPODS spp. **Fishes:** <u>Gasterosteidae</u> *(Gasterosteus aculeatus, Pungitius pungitius),* <u>Salmonidae</u> *(Thymallus thymallus).*

SW. **Crustaceans:** AMPHIPODS spp. **Mollusks:** CEPHALOPODA <u>Loliginidae</u> *(Loligo opalescens).* **Fishes:** <u>Batrachoididae</u> *(Porichthys notatus),* <u>Clupeidae</u> *(Clupea pallasi),* <u>Embiotocidae</u> *(Cymatogaster aggregatus),* <u>Engraulidae</u> *(Engraulus mordax),* <u>Stromateidae</u> *(Icichthys lockingtoni.).*

References: Baltz and Morejohn (1977), Davis (1972), Palmer (1962).

Gavia immer Common Loon

FW. Annelids: LEECHES, sp? **Crustaceans:** AMPHIPODS, <u>Gammaridae</u> *(Gammarus limnaeus),* DECAPODS, <u>Astacidae</u> *(Astacus leptodactylus, Cambarus* sp.), crabs sp? **Insects:** ODONATA, Anisoptera nymphs. TRICHOPTERA, "caddis flies." HEMIPTERA <u>Corixidae</u> *(Arctocorixa sutilis).* DIPTERA <u>Chironomidae</u> *(Chironomus islandicus, Tanytarsus gracilentus).* **Mollusks:** GASTROPODS <u>Planorbidae</u> *(Planorbis* sp.). **Fishes:** <u>Catostomidae</u> *(Catastomus catostomus, C. commersoni),* <u>Centrarchidae</u> *(Ambloplites rupestris, Lepomis gibbosus, L. macrochirus, Micropterus salmoides, Pomoxis annularis, P. nigromaculatus),* <u>Clupeidae</u> *(Alosa pseudoharengus, Dorosoma cepedianum),* <u>Cottidae</u> *(Cottus bairdi, Leptocottus armatus),* <u>Cyprinidae</u> *(Chrosomus eos, Hybopsis plumbeus, Notemogonus chrysoleucas, Notropis atherinoides, N. cornutus,* "Thickhead Minnow"= *Pimephales promelas, Rhinichthys sp., Semotilis atromaculatus),* <u>Cyprinodontidae</u> *(Fundulus heteroclitus),* <u>Esocidae</u> *(Esox lucius).* <u>Hiodontidae</u> *(Hiodon tergisus),* <u>Ictaluridae</u> *(Ameiurus nebulosus),* <u>Lotidae</u> *(Lota lota),* <u>Percidae</u> *(Perca flavescens, Stizostedion canadense, S. vitreum),* <u>Percopsidae</u> *(Percopsis omiscomaycus),* <u>Petromyzontidae</u> *(Petromyzon marinus),* ?<u>Pleuronectidae</u> "flounders," <u>Salmonidae</u> *(Coregonus artedi, C. clupeaformis, Salmo gairdnerii, S. trutta, Salvelinus fontinalis),* <u>Umbridae</u> *(Umbra limi).* **Amphibians:** URODELES "newts." ANURANS "frogs."

FW- SW. Fishes: <u>Anguillidae</u> *(Anguilla anguilla),* **Gasterosteidae** *(Gasterosteus aculeatus, Pungitus pungitus)* <u>Osmeridae</u> *(Osmerus mordax).*

SW. Annelids: POLYCHAETES <u>Maldanidae</u> sp. Mollusks: GASTROPODS <u>Marginellidae</u> sp. PELECYPODS sp. CEPHALOPODS sp. **Crustaceans:** STOMATOPODS <u>Squillidae</u> *(Squilla* sp.), DECAPODS <u>Calappidae</u> *(Calappa flammea),* <u>Homaridae</u> *(Homarus americanus),* <u>Leucosiidae</u> ["<u>Iliacanthidae</u>"] sp. <u>Peneidae</u> *(Peneus duorarum),* <u>Portunidae</u> *(Callinectes sapidus),* <u>Xanthidae</u> *(Menippe mercenaria).* **Fishes:** <u>Ammodytidae</u> *(Ammodytes americanus),* <u>Batrachoididae</u> *(Opsanus pardus),* <u>Clupeidae</u> *(Brevoortia tyrannus, Clupea harengus, Sprattus sprattus),* <u>Cottidae</u> *(Cottus scorpius, Hemilepidotus hemilepidotus, Myoxocephalus scorpius),* <u>Embiotocidae</u> *(Cymatogaster aggregata),* <u>Gadidae</u> *(Gadus callarias, G. morhua, Melanogrammus aeglefinus),* <u>Haemulidae</u> *(Orthopristis chrysoptera),* <u>Merlucciidae</u> *(Merlangus merlangus),* <u>Pleuronectidae</u> *(Pleuronectes flesus),* <u>Sciaenidae</u> *(Cynoscion regalus, Micropodonias undulatus),* <u>Syngnathidae</u> *(sp.),* <u>Tringlidae</u> *(Eutringla gurnardus),* <u>Zoarcidae</u> *(Zoarces viviparus).*

References: Bielsa and Forrester, unpublished data, Univ. Florida), Cramp (1977), Fjeldså *(in litt.),* Forbush (1925), Madsen (1957), McIntyre and Barr (1997), Palmer (1962).

Gavia adamsii Yellow-billed Loon

FW. North (1994) reports the following food species available to this loon on fresh water lakes on the Colville River Delta, Alaska:

Crustaceans: spp. **Mollusks:** GASTROPODS spp. **Insects:** aquatic spp. **Spiders:** spp. **Fishes:** <u>Cottidae</u> *(Myoxocephalus quadricornis),* <u>Gasterosteidae</u> *(Pungitius pungitius),* <u>Umbridae</u> *(Dallia pectoralis).*

SW. Annelids: POLYCHAETES, <u>Nereidae</u> *(Nereis* sp.). **Crustaceans:** AMPHIPODS, Family? *(Orchomonella* sp.), Family? *(Anonyx nirgax),* ISOPODS, <u>Idotheidae</u> *(Idothea* sp.), DECAPODS, <u>Hippolytidae</u> *(Spirontocharis ochotensis),* <u>Paguridae</u> *(Pagurus* sp.), <u>Pandalidae</u> *(Pandalus danae),* **Mollusks:** (sp.). **Fishes:** <u>Cottidae</u> *(Leptocottus armatus, Myoxocephalus joak?, M. scorpius),* <u>Gadidae</u> *(Gadus morhua, Microgadus proximus).* Cottam and Knappen (1939) found 11 % of the stomach contents to be gravel.

References. Cramp (1977), North (1994), Palmer (1962).

RESULTS AND CONCLUSIONS

In speculating on the possible causes of the differences between the parasite faunas of the loons and the grebes, I have included a wide range of possibilities, including the ages, geographic distributions, and the degrees of morphological variation within the two families that might lead to different foraging methods and hence to the taking of different kinds of prey containing different final hosts.

How good are the data? Several biases must be considered when analyzing the data. For the Common Loon, these have resulted from differences in focus of studies related to the food habits, parasitology, and threatened status of the species in parts of North America. Because loons feed predominantly on fishes, both sportsmen and fishery operators often consider them serious competitors. Early food-habits studies focused on the sport and food fishes and seldom included detailed identification of invertebrates. For similar reasons, studies on the parasites were often focused on the role of loons as definitive hosts whose intermediate hosts were these fishes.

Loons have great popular appeal, and the decline in the breeding populations of the Common Loon in parts of North America has caused concern among ornithologists and conservationists. In a study of die-offs of this species on the wintering grounds in Florida waters, Kinsella and Forrester (1999) found a greater variety of species and numbers of microphallid digenes whose final intermediate hosts are crustaceans in sick loons which they "thought to indicate a shift in the loons' diet due to low fish populations." They also pointed out the need for more studies on the loons' breeding grounds. At least in North America, the other species of loons breed at higher latitudes than most grebe species, and as a consequence, their parasites have been less thoroughly studied.

There have been very few reports of parasites of grebes taken on salt waters. The major studies of grebe parasites in North America (*e.g.* those of Gallimore [1964] and Stock [1985]) have been on birds taken on the freshwater breeding grounds.

THE BIOLOGY OF LOONS IN RELATION TO
THEIR PARASITE FAUNAS

Most loons require long stretches of water to permit taking off. So for breeding, they need rather large bodies of water. This need is greatest in the largest species, *Gavia adamsii* and *G. immer*. The exception is *G. stellata*, which has the least wing loading, both actually and proportionally, of all the species (Boertmann 1990), and is able to take off from land (Barr *et al.* 2000). While most members of other species of loons feed themselves and their young on the lakes by which they nest, Red-throated Loons normally nest by very small lakes and fly to larger bodies of water, often saline, for food (Barr *et al.* 2000). They therefore might be expected to harbor a higher proportion of parasites with salt-water life cycles than other loons.

Loons select oligotrophic lakes more often than eutrophic ones. They place their nests on islets or shores, usually within one meter of the water. The nest may start as a scrape or a mass of vegetation and is added to as incubation progresses. Because the nest material is usually damp, it seldom offers a suitable place for mites and insects that require dry land for at least one stage in their development. Oligotrophic lakes contain fewer individuals and species of potential prey than eutrophic ones, hence fewer individuals and species of potential intermediate hosts for parasites. Thus, parasite faunas from such lakes can be expected to contain fewer species than those that might be acquired from eutrophic lakes. Other fresh-water based parasites may be obtained from lakes visited by loons on migration.

Although all loons are highly territorial during the breeding season, they vary considerably in their degree of gregariousness in winter. Common Loons are most often found individually or in small groups, rarely as large as 20 birds, whereas Pacific Loons may forage in flocks of up to several thousands in areas of upwelling (Campbell *et al.* 1989).

Loons of all species winter on large bodies of water, most of them marine or estuarine, and may move offshore several miles, but they seldom venture beyond the continental shelves. They are thus subject to parasitism by a very different range of helminths from that acquired on the breeding grounds or on fresh-water lakes visited on migration.

Large flocks of small loons (Pacific and Red-throated Loon) winter off the West Coast of North America (Campbell *et al.*1989; Briggs *et al.* 1987), and Arctic and Red-throated loons in the Baltic and North seas (Durinck *et al.* 1994b; Skov *et al.* 1995), and often forage in mixed flocks with other seabirds where interfaces between types of sea water occur, such as those at upwellings and between the Jutland Coastal Current and the North Sea water off the German Bight (Skov and Prins 2001). In such places, abundant plankton attracts the small fishes on which the mixed avian flocks feed. These conditions presumably make possible parasite cycles in which parasite eggs excreted by the birds can be taken in by planktonic organisms, passed by these to the fishes, and finally to the birds. In such situations, the chances for a parasite's egg of reaching a definitive host and producing an adult parasite might be improved if the parasite were able to mature in a variety of definitive hosts.

The small species of loons are more gregarious and tend to occur further off shore than the larger Common and Yellow-billed loons. Many of the large, fish-eating, Great Crested, West-

ern, and Clark's grebes, and some of the smaller Horned and Eared grebes also winter at sea, but tend to stay close to shore (Durinck *et al.* 1994b; Briggs 1987).

Loons are very aggressive, frequently stabbing both loons and other birds with their bills from under water, therefore the opportunities for crossing over of external parasites from other species are negligible, and because loons' nests are near the water's edge, they spend virtually no time elsewhere on land where they might acquire external parasites through contact with other birds.

THE EVOLUTIONARY HISTORIES OF LOONS AND GREBES

Until 1935, when Stolpe demonstrated that the similarities among the loons, grebes, and *Hesperornis* resulted from convergent evolution, the birds of these groups were believed to be closely related. In spite of Stolpe's evidence, the convergence has been disputed by some (*e.g.* Cracraft 1982, but see Feduccia 1999). Molecular evidence (*e.g.* by Prager & Wilson, 1980; Sibley & Ahlquist 1990) has confirmed Stolpe's findings regarding the separation of the loons and grebes, and the many new findings about Cretaceous diving birds summarized in Feduccia (1999) have resulted in a better understanding of the Hesperornithiformes (including their former nearly world-wide distribution and radiation into two families, seven genera, and some twelve species) and the confirmation of their separate and much earlier evolution than that of the loons and grebes.

The last 40 years also have seen the rise and refinement of our ideas on plate tectonics and the conformation of the major land masses through the late Tertiary and the Quaternary periods. New fossil evidence and evolutionary studies based on molecular evidence also have become increasingly valuable in tracing and assessing the history and evolution of these groups.

It is now time to look at this information and to speculate on when, where, and how the loons and grebes originated. I do not hesitate to say "speculate" because speculation based on a solid base of information is the formulation of hypotheses which are the bases of science. Thus, they are important both in assessing what has gone before and especially in pointing out what can best be done in the future toward a better understanding of the evolutionary history of a group of organisms. I would emphasize that the best analyses of the evolution of any group of organisms are those based on the broadest range of supporting data.

When and where did the loons and grebes originate? On the basis of loon and grebe DNA-DNA hybridization studies, Sibley and Alquist (1990) give Delta $T_{50}H$ values of 10.0 and 14.9, respectively, for the time of separation of the loons and grebes from their parental stocks, but they did not assign a period of time for each unit of these values.

Recently Moum *et al.* (1994) gave a conversion figure of 3.0 million years for each delta $T_{50}H$ figure of 1.00. This conversion figure and the time scale of Harland *et al.* (1989), give the time of separation of the loons as 30 million years BP or the middle of the Oligocene and that of the grebes, 44.7 million years BP or the middle of the Eocene. That this timing is too short is apparent because the early loon, *Colymboides anglicus*, is known from the Upper Eocene. The latest figure for the origin of the grebes, calculated from *Colymboides anglicus* and Sibley

and Ahlquist's data must have been half again as early, or the early Eocene. Sibley and Ahlquist's estimates have not been generally accepted and assume a constant rate of evolution, which is not necessarily the case. We are left with the conclusion that fossil evidence is the only tangible means of evaluating the actual time of evolution.

The only reports of loons from the Southern Hemisphere or the Cretaceous are those of *Neogaeornis wetzeli* from the upper Cretaceous of Chile and *Polarornis* from the late Cretaceous of Seymour Island, Antarctica. The placement of the former in the Gaviiformes by Olson (1992) has been questioned by Martin (*in* Feduccia 1999) on the basis of its range, its age, the fragmentary nature of the material, and the hesperornithiform-like distal trochleae. Hence, it is best placed in the Hesperornithiformes, where it was included, as a member of the Baptornithidae by Martin and Tate (1976). It might be added that the tarsometatarsus, the only known skeletal element of *Neogaeornis*, is one of the elements most likely to show convergence in diving birds. The skull (*"Polarornis"* which has yet to be formally described) reported by Chatterjee (1997) to be a loon is definitely not that of a loon according to Feduccia (*in litt.*), and after comparing the figures in Chatterjee (1997) with skeletons of Recent loons, I agree with Feduccia, but just what *Polarornis* was remains to be determined.

Because all the other known reports of the Gaviidae are from the Northern Hemisphere, the loons probably arose in that hemisphere, and because to date, all the known records of the primitive subfamily, the Colymboidinae, with the possible exception of two partial bones from the middle Miocene (Pungo River Formation) of the Lee Creek Mine of North Carolina (Olson *et al.* 2001), it is likely that the loons arose in Eurasia.

Because Cooper & Penny (1997) used *Neogaeornis* as the only report of a bird of a modern order to have existed in the Cretaceous, its correct identification to order is crucial to their proposal that there was a mass survival of birds of modern orders across the Cretaceous-Tertiary Boundary.

The earliest known fossil grebes are those reported by Nessov (1992) from two Oligocene deposits in Eurasia. Unfortunately, this material has not been studied. The distal end of a femur from the John Day beds in northern Oregon was described by Shufeldt (1915) as "*Colymbus*" (=*Podiceps*) *oligocaenus*. These beds are now considered to be of lower Miocene age (Olson 1985). Because the genera of grebes were not worked out until more than 50 years after this fragment was described, its generic placement remains to be determined, but it is most unlikely that it will be included in *Podiceps*.

On the basis of the number of genera and species and of grebes now on each continent (Storer 2000), South America, with 5 genera (2 endemic) and 9 species (6 endemic), is the most likely area of origin of the grebes. However, except for a questionable fossil record from the Late Miocene of Florida for which no details of the structure are given (Becker 1985), the most "primitive" genus, *Rollandia*, is confined to South America.

That *Rollandia rolland* is the species probably nearest to the ancestral stock has been confirmed by a new cladistic analysis (Fjeldså ms). It and the genus *Poliocephalus* endemic to Australia and New Zealand share similar courtship ceremonies which, according to detailed analyses, are potential precursors of more elaborate behavior patterns of other grebes (Fjeldså 1983, 1985,

Storer 1967, 1971). The overall similarity of these ceremonies, which are unlike those of other grebes, and their occurrence in two "primitive" grebes which are largely, if not entirely, confined to the Southern Hemisphere, is consistent with a southern origin of the grebes.

Before the days when the concept of continental drift was accepted, it would have been thought either that *Rollandia*, or another South American ancestor of *Poliocephalus* spread north, then across the Bering Land Bridge, and finally south to Australia, or that *Poliocephalus* or, more likely, that the ancestor of both arose in the north and the ancestors of the two Southern Hemisphere forms spread south from there. Fossils of *Rollandia* have not been reported from South America and no fossils of *Poliocephalus* are known, but this is probably owing to a paucity of known lacustrine fossils in these regions at the crucial time period.

At the time estimated here for the separation of grebes from their relatives, South America, Antarctica, and Australia were connected as the continent, Gondwanaland. Up until the mid-Miocene, the climate of Antarctica was sufficiently warm to support populations of grebes. So, in spite of the tenuous evidence, I think it quite likely that the grebes arose either on Antarctica or South America, but probably not Australia, because of its much smaller grebe fauna (three species, one of which, *Podiceps cristatus*, was presumably a late arrival in Australia from the Palearctic via either Africa or southern Asia).

Fresh or Salt Water origins? The closest relatives of the loons are considered to be the petrels (Procellariiformes) and the penguins (Sphenisciformes). The considerable amount of morphological evidence for this is summarized in Feduccia (1999 and references therein) and is supported by molecular evidence (Prager & Wilson 1980, Sibley & Ahlquist 1990). Both the petrels and penguins are exclusively marine, as presumably were their common ancestors. According to Sibley and Ahlquist (*op. cit.*) the penguins split from the petrel-loon stock before the loons split from the petrel stock (by a difference in Delta $T_{50}H$ figures of 0.4). Therefore, it is highly probably that the loons arose in a marine environment. Modern loons still spend most of their lives on marine or estuarine waters and undergo the molt and regrowth of their flight feathers there.

The Red-throated Loon is a special case. Some populations breed on small moorland or montain ponds which are often too small and acidic to maintain sufficient food sources for the birds. Thus in many areas, Red-throated Loons continue to feed and obtain food for their young on coastal saline waters during the breeding season. This habit is made possible by low wing loading and structure of the legs, which are even more strongly adapted for pursuit diving than those of other loons (Boertmann 1990). These adaptations might be considered to represent a stage in the evolution of loons from petrel-like ancestors, but Boertmann presents evidence to show that they represent an advanced condition and that this species is the most specialized of the living loons.

In contrast to the loons, the grebes probably arose on bodies of fresh water. Grebes are unique in building floating nests usually anchored to the bottom, and this prevents their being moved by winds or currents. The fact that all members of all genera of grebes have this habit and rarely, if ever, build nests on land can be taken as evidence that the habit is an old one at least predat-

ing the division of the group into genera. Because these nests are anchored to the bottom, they cannot be used in tidal waters or other waters that fluctuate much in depth. For these reasons, I believe that floating nests have been a characteristic of grebes for much, if not all, of their evolutionary history since they first took to the water and therefore that the grebes had a fresh-water origin.

How did the loons originate? Like all the petrels and penguins, the loons have webs between the second and third and the third and fourth toes. This is a common pattern in web-footed birds and has probably evolved independently several times (*e.g.* in the waterfowl, the flamingos, and the gull-auk line as well as in the petrel-penguin-loon line). The fact that all members of the last line have similarly webbed feet suggests that the common ancestral forms of these birds also had such feet. The simplest type is that of the petrels, including the diving shearwaters like the Sooty Shearwater (*Puffinus griseus*) which show some adaptations for diving that approach those of the loons (*e.g.* an elongated cnemial crest and a flattened tarsometatarsus). The diving shearwaters are unusual in having both the feet and the wings modified for diving (Kuroda 1954). The penguins, having evolved as wing-propelled divers, have the feet modified for walking upright, as well as for swimming and for steering while the birds are under water, whereas the living loons' feet and legs' are probably the most modified for rapid foot-propelled pursuit-diving of all living birds, although the wings are also somewhat modified for underwater use (Olson 1985).

A major difference between the loons and the petrels and penguins is that most loons' habitat during the breeding season is freshwater lakes whereas the other two are exclusively marine. (In fact, all the groups of wing-propelled divers have been marine, probably because the aquatic vegetation in fresh waters would be a hinderance by either slowing down or preventing the pursuit of fast-moving prey.) Yet all wing-propelled divers have also had webbed feet for locomotion on the surface, therefore, in contrast with the grebes, the loons presumably evolved from web-footed ancestors like the petrels, and because all the petrels and penguins are marine, it is probable that the loons' ancestors inhabited salt waters.

How then, did loons come to nest on fresh-water lakes? The earliest known loons *(Colymboides)* were small, about the size of small grebes like *Tachybaptus* spp. and had reached approximately the same degree of adaptation for diving (Cheneval 1984). The better known species, *C. minutus*, is common in Aquitanian (Lower Miocene) deposits of Europe. According to Cheneval *(op. cit.)*, the best source of material of this species is from the deposits of a brackish lake unconnected to the sea at Saint-Gérand-Le-Puy near Alliers, France. Because none of the ca.150 bones of this species that Cheneval studied (nor the 110 that I examined [1956]) was that of a young bird, Cheneval opined that *C. minutus* did not nest at Saint-Gérand-Le-Puy. The avifauna at that locality indicates that the climate there was warm, perhaps subtropical or tropical. It is therefore likely that these birds were wintering from a more northern breeding ground.

Cheneval *(op. cit.)* also suggested that because the legs of *Colymboides* were less well adapted for diving than those of modern loons and were similar in this respect to those of the Little Grebe *(Tachybaptus ruficollis)* and that like that species *Colymboides*

minutus could stand and even run on land, it might also forage to some degree on land. I doubt that the last was true. I know of no report of any grebe actively foraging on land and believe that all these birds (and *Colymboides*) have or had reached a degree of adaptation for foraging in the water that made foraging on land ineffective.

If *Colymboides* represented an evolutinary stage through which the larger loons (*Gavia*) passed, it may well have been that foot-propelled diving began with small marine birds feeding on small invertebrates on bodies of salt water, then moving to eutrophic fresh waters for breeding, but returning to brackish waters like that at Saint-Gèrand-Le-Puy or marine ones, as indicated by Olson *et al.* (2001) on the basis of fragmentary material from the Lee Creek Mine. Then, some of the stock evolved into fish-eating pursuit divers much as the fish-eating grebes did, but moved to eutrophic waters to breed for reasons given below.

In his important paper on the phylogeny of the loons, Boertmann (1990), suggested that, because of features associated with the wings of wing-propelled diving birds, loons "might have arisen from wing-propelled ancestors, *e. g.*, from a primitive petrel/penguin stock, and subsequently abandoned this way of under-water locomotion." I believe that loons came to nest beside fresh-water lakes because these lakes provided a supply of fishes close at hand, whereas in the sea, shoals of fish may move long distances. Because the maximum size attainable by wing-propelled diving birds that can also fly appears to be limited to birds approximately the size of murres, *Uria,* (Storer 1960) and that wing-propelled diving appears to be less effective in fresh-water environments than marine ones, Boertmann suggested that the advantages of greater speed in catching fast-moving prey like salmonid fishes, resulted in a change in the loons to foot-propulsion as their major method of underwater foraging while retaining some ability for wing-propulsion for use in emergencies.

Greater size is advantageous in pursuit divers for several reasons. First, large birds are faster swimmers than smaller ones. For example, if two birds are the same shape and proportions, but one is twice the length of the other, the larger one will move twice as far as the smaller one with one stroke of the feet, and if the strokes are given at the same rate, which may not often be the case, the larger bird will move twice as fast as the smaller one. On the other hand, the force needed to move a bird through the water is related to the cross-sectional area of the bird (a function of the square of length), while the amount of muscle that may be available for this use is related to the bird's volume (a cubic function). Therefore, a larger bird with its relatively larger leg muscles, can, by moving faster, not only catch larger and faster-moving prey, but also will be better able to escape its potential predators. This may result in an evolutionary race in which smaller predators may compete with larger ones, and eventually may become their prey. An example of this might have been the extinction of the large wing-propelled divers, the Plotornithidae and the giant penguins, which died out concurrently with the rise of the still larger dolphins and the pinnipeds in the early Miocene (Feduccia 1999). Also, as Livezey (1988) pointed out, large size "reduces buoyancy and makes available a greater range of water depths for foraging," and because the surface-volume ratio decreases with increases in size, the rate of heat loss to the environment decreases with an increase in size.

Because the selective advantage of being able to move faster through the water may be great, I believe that a change from a small bird moving from a diet of slow-moving prey to a larger bird feeding on faster-moving prey could take place fairly rapidly, and this probably did take place in the evolution of of a *Colymboides*-like loon to *Gavia*. In such a case, remains of intermediates might be relatively rare.

In summary, it is probable that loons arose as small, wing-propelled marine relatives of the petrels. Ancestral loons first came to nest on fresh-water lakes because the supply of fishes remained in a circumscribed area, but the birds retained the power of flight because it was necessary to return to the sea before the lakes froze over in winter. Increase in size was advantageous because it made possible greater speed while wing-propelled diving was incompatible with foraging in fresh water. As a result the birds turned to foot-propelled diving.

How did the grebes originate? The information on many aspects of grebe biology is ably summarized in Vlug and Fjeldså (1990). As far as we know, the grebes have no close living relatives, nor do we know exactly how these birds evolved. On the basis of DNA-DNA hybridization, Sibley and Ahlquist (1990) concluded that the grebes "have no close living relatives" and "branched early from the common ancestor of the other groups in the Ciconiides and seems to be a sister group of the Phaethontida [tropicbirds], Sulida [boobies and cormorants], and the Ciconiida [a large group containing the Ciconiiformes (including the New World vultures), the frigatebirds, the penguins, the loons, and the petrels]." From their estimate, the time of evolution of the grebes was probably at least as early as the lower Eocene (see p. 16).

On the other hand, Zusi and Storer (1969) and Olson (1985) point out evidence for a possible connection with an early gruiform stock. This is consistent with a likely evolution from a marsh bird.

In a recent paper, Van Tuinen *et al.* (2001) proposed a close relationship between the grebes and the flamingos on the basis of molecular evidence. As yet, this is not supported by morphological or fossil evidence, although it might be supported by the fact that the cestode family, Amabiliidae, contains 29 species confined to grebes and one species confined to flamingos. However, the species in flamingos is considered to belong to a separate subfamily (Jones 1994) and might well have originated from an early crossover from grebes to flamingos.

To pursue the question of grebe origins, we may first ask how these birds are unique and how these unique characters might have been important in the birds' evolution.

In the evolution of the foot-propelled diving birds (including the loons, grebes, and Hesperornithiformes), the leg, changed from pointing downward like that of most birds, to lying in a plane parallel with the surface of the water. This was made possible by a shortening of the femur and the development of a process or crest anterior to the head of the tibia. The shortening of the femur is associated with a shift of a large part of the origin of M. gastrocnemius, the principal muscle involved in the power stroke in swimming, from the femur to this cnemial crest. As Stolpe (1935) pointed out, this crest is an extension of the tibia in the loons, a large patella in *Hesperornis*, and a combination of the two in the grebes. The combined nature of this structure is unique to grebes.

Patellas are sesamoids evolving from small bones within tendons connected with the knee. Loons have a small one imbedded in the patellar tendon (Wilcox 1952). From this, it seems apparent that the unique combination of a large patella and a crest on the tibiotarsus in grebes arose as part of the evolution of the leg for diving and therefore must be convergent with the large patella of *Hesperornis*, whose ancestors appeared far earlier in the fossil record (early Cretaceous) than the date Sibley and Ahlquist estimated for the appearance of grebes.

The feet of swimming and diving birds are usually divided into two categories: those with webs between the toes and those with lobed toes, each of which probably evolved independently more than once. Among the lobe-toed birds, there are three different types. The simplest type is like that of the coots, *(Fulica)* in which there are two series of nearly equal-sized lobes on each toe. In swimming, one folds down each side of the toe as the foot is brought forward on the recovery stroke and is spread on the power stroke. Coots use this type for swimming and simple dives from which the birds surface with the plant material which is their principal food. Coots' abdomens are enlarged to accommodate the large digestive apparatus needed for processing plant matter, and this may preclude any streamlining resulting in a decrease in the cross-sectional area of the body that would be advantageous in pursuit diving. The lobed toes of phalaropes are modified for bringing a water column containing food particles to the surface where the birds can pick this food up with their bills (Rubega *et al.* 2000). The structure of the toes of the Great Crested Grebe and presumably at least those of other fish-eating grebes is still different and involves a rotation of the toes between the power and recovery strokes (Johansson *et al.* 2000). The structure of the articulations of the phalanges for the fourth toe of *Hesperornis* indicates that these early divers had a similar but even more advanced type of this adaptation for pursuit diving.

In contrast to the feet of the piscivorous grebes, the outline of the foot of the Pied-billed Grebe (Storer 1960) shows shorter, much more widely lobed toes and much more webbing between them. This suggests an adaptation, like that of the large-footed scoters *(Melanitta)*, for feeding on slow-moving or sessile organisms. The feet of the dabchicks *(Tachybaptus)* are intermediate in shape between those of the Pied-billed Grebe and the pursuit divers (R.W.S. foot tracings), as might be expected in a generalist in feeding habits.

In the feet of grebes and *Hesperornis*, there is (or presumably was) a web between the basal parts of toes 2-4 and a single lobe on each side of the distal parts of the toes (Stolpe 1935). On each toe, the medial lobe is the larger, and both are stiffened and do not move in relation to the toe bones in swimming. Instead, the toes are rotated 90 degrees so that the side of the fourth toe and presumably that of the second and third toes are brought forward during the recovery stroke and the bottom of the toes backward in the power stroke. Stolpe *(op. cit.)* likened the folding of a grebe's foot during swimming to the motion of primary flight feathers during flying in that during the recovery stroke, the wider lobe (or vane) lies in the opposite direction from that of the movement but perpendicular to it in the power stroke. A hydrodynamic analysis of the Great Crested Grebes' toes in swimming is found in Johansson *et al.* (2000). This arrangement of the foot is not compatible with the idea that the

grebes' evolution as swimming birds might have been derived from any other swimming or diving birds. In other words, grebes' closest relatives will not prove to be found in these or any other known swimming birds. I believe that it is important to know how such adaptations arose to understand the evolution of the grebes.

Although Stolpe (op. cit.) suggested that Hesperornis arose from a marsh bird, I am not aware of any more detailed published explanation of how the rotation of the lobed toes in swimming might have evolved in these birds or in grebes. I suggest that the scenario for the evolution of the grebes' feet probably went somewhat as follows: grebes arose in marshes with dense, upright vegetation interspersed with areas of open, eutrophic water. In such land areas, fully webbed feet would be a disadvantage, whereas lobed feet would make it possible for a bird to let some of the irregularities on the ground, such as the stems of grasses or reeds, come between the toes, instead of being pressed down by the feet and possibly damaging the webs. (Coots and Phalaropes, which are also lobe-toed, spend much of their time in marshes with such vegetation.) Bringing forward the foot with the lobes of the toes parallel to the direction of the movement would make moving the foot through vegetation easier both on land and in the water, than bringing the width of the foot through it. In addition, the stiffer lobes would be more resistant than webs to damage from unevenness on land and would be stronger in swimming.

The nail-like distal phalanges on the toes are another unique feature of grebes. That of the fourth toe is especially large and, like the others, has a bony base. Presumably the nail on this toe adds an appreciable area to that of the foot in swimming. The function of the other distal phalanges is unclear.

Grebes' tail feathers are reduced to an almost hairlike tuft unlike those of any other flying bird. Although Olson (1995) makes no comment on the condition of these feathers in Thiornis sociata, as far as can be seen from his photographs of the specimen, the rectrices were similar to those of modern grebes. From this, it appears that the modern condition of these feathers had evolved by the Middle Miocene. Rectrices intermediate between the usual kind in grebes and that in other birds are found in at least some immature specimens of Rollandia rolland and suggest that this species has retained a primitive condition longer than other Recent grebes.

Because the most "primitive" grebes (Rollandia, Tachybaptus, and Poliocephalus) have relatively short cnemial crests and feed on a variety of small animals, most of them invertebrates (Storer 2000), I believe that the grebes arose from a group of marsh birds that also fed on small animals. These putative ancestors, attracted to insects with aquatic stages that came to the surface or climbed onto the stems of emergent vegetation to metamorphose, would move into the water to feed on them. Once this began, selection would favor the birds' developing morphology that favored swimming, until the birds became dependent on aquatic organisms for food and stopped foraging on land. The lobing and the rotation of the toes between the power and recovery strokes came with this evolution from a marshy habitat. Diving to glean underwater vegetation and then pursuit diving to capture swimming prey such as fishes would follow. What is known from the fossil record of grebes is consistent with this hypothesis.

The earliest well known fossil grebes, Thiornis and Miobaptus of the Miocene (Olson 1995, Svec 1982) were morphologically similar to Recent generalists like Tachybaptus. Pursuit divers, (Podiceps) appeared later in the record (in the late Miocene or early Pliocene) and the most advanced pursuit divers, (Aechmophorus), mid- to late Pliocene. The largest grebe, Podicephorus major, another piscivore, is unknown as a fossil.

The floating nests built by adult grebes are another of their unique features and has affected several aspects of these birds' biology. In the first place, it has made it possible, although not obligatory, for grebes to live their entire lives without going ashore.

The floating nests in turn have greatly reduced the possibilities for physical contact with birds of other species and thus the possibilities for the exchange of ectoparasites. As a result, but 25 species, 12 of mites and 13 of lice, are known from grebes (Storer 2000), and of these, one genus of lice (Aquanirmus) and three of the four genera of the family Ptiloxenidae, plus the mite genus Podicipedicoptes are known only from grebes. Two genera of mites (Rhinonyssus and Neoboydaia) and two of lice (Laemobothrion and Pseudomenopon) are shared with coots (Fulica). This is evidence that members of these genera in grebes resulted from colonization from coots, the birds with which grebes have the most frequent physical contacts (Storer 2000).

The grebes' habit of ingesting their own feathers has been known for more than two hundred years. In the course of preening, feathers may come out and are swallowed by the birds or fed to the small young. Most of these feathers come from the flanks and are not pulled out by the bird but come loose in the process of preening. Most of the swallowed feathers form a loose mass in the lumen of the stomach, while a smaller group forms a plug in the pyloric exit of that organ. The advantages of feather eating have been a source of much speculation and have been examined in detail by Piersma and van Eerden (1989) who favored the idea that the principal advantage of the large mass, which is regurgitated periodically as a pellet, is to remove indigestable material and parasites that live in the birds' stomachs feeding on the birds' ingested food. Another likely advantage is that the feathers may keep fish bones from injuring the stomach wall until they can be dissolved by the stomach acid. The feather-eating habit is made possible by a greatly extended period of molt and regrowth of the flank feathers, another unique feature of grebes.

Fjeldså (1983) found that Hoary-headed Grebes (Poliocephalus poliocephalus) very rarely swallow feathers. This might be a "primitive" character of this genus, and it would be interesting to find out whether or not these birds have an extended period of molt of the flank feathers.

The feathers that form a tight plug at the pyloric exit into the small intestine are not ejected with those from the lumen of the stomach (Storer 1969), but when they are ejected is not known. Feather-eating and such plugs are not known to occur in loons. This is probably because loons feed predominantly on fish, the bones of which are dissolved by stomach acid. Therefore the amount of indigestible material entering the small intestine is probably far less in these birds than it would be in grebes. In any event, large numbers of small microphallid digeneans can and do exist through the length of this organ in loons, much as large numbers of small amabiliid cestodes live in the anterior portion

of the intestine of grebes.

The pyloric plug in grebes presumably acts as a strainer preventing pieces of indigestible material, especially chitin, from entering the small intestine and results in an environment free from pieces of such material that might dislodge intestinal parasites. A relationship between the freedom from being dislodged and the helminth fauna of grebes has not been demonstrated, nor has how the larval parasites get past the plug been discovered, but both the number and variety of intestinal helminths in grebes are large. Stock and Holmes (1987) have reported a per-bird range of between 2 and 15 species and 231 and 33,169 individual helminths, most of them cestodes, from a sample of 31 Eared Grebes *(Podiceps nigricollis)*. The known helminth fauna of grebes is very large, *circa* 250 species, as is the number of these worms that occur entirely or with rare exceptions in these birds (Storer 2000). These grebe specialists include all but one of the 30 species of the Amabiliidae and one of the 7 species of the Dioecocestidae plus 6 genera and 13 species of the large family Hymenolepididae (details in Storer 2000). The evolution and radiation of a distinct family of the size of the Amabiliidae (7 genera and 30 species) probably took a very long time and is consistent with the grebes' early evolution. The life-cycle data of these cestodes involving insects (most frequently odonate nymphs) as intermediate hosts is evidence that the family is of fresh-water origin, therefore, the habitat of grebes during the period of evolution of this cestode family must have been at least in part fresh water also.

COMPARISONS BETWEEN THE PARASITE FAUNAS OF LOONS AND GREBES

Consequences of moving to a new habitat. As the grebes evolved from living in marshes to inhabiting eutrophic waters, the first new cestode parasites that they would encounter would be ones with intermediate hosts that lived in these waters for at least part of their lives. Of the 12 species of the Amabilidae for which the life-cycles are known, the intermediate hosts of ten are odonate nymphs (Storer 2000), and there is some evidence that these insects are also the intermediate hosts for the Dioecocestidae (Jögis 1978). One possible sequence in the evolution of this host-parasite relationship might have been for the marsh-dwelling ancestral grebes to take odonate nymphs coming out from the water onto reed stems to molt and remaining there until the teneral adults' wings became sufficiently dry and hard to permit flight. Later, as the grebes came to swim and dive, they might come to feed on these aquatic nymphs (as well as other aquatic animals). Host switching to corixid bugs (in the case of *Tatria biremis*) and mayflies (Ephemeroptera) in the case of *T. biuncinata* would then become possible. On the breeding grounds, grebes presumably also fed on intermediate hosts of diphyllobothriids, dilepidids, and hymenolepidids, but they only developed specificity for species and genera of the last family. Later in this radiation, when the breeding areas of some of the birds became cold enough in the winter to freeze over, some grebes moved to salt waters for that season. There they fed in part on intermediate hosts of tetrabothriids, whose degree of specificity tends to be at the ordinal level (Hoberg 1996).

The case of the loons is the reverse of this. These birds presumably arose on salt water from a petrel-penguin stock, many of whose cestode parasites were tetrabothriids. On moving to fresh water for the breeding season, the ancestral loons presumably brought with them no parasites with fresh-water life-cycles (with the possible exception of some whose final intermediate hosts moved from fresh water to salt water) and developed specificity for only a few hymenolepidids.

Helminths. The numbers of digenean and nematode species reported from loons is less than half that from grebes (Table 1), as is the maximum number of named parasite species is found in one host species (59 in *Gavia immer* [Table 2] *vs.* 123 in *Tachybaptus ruficollis* [Storer, 2000, Table 3]). On the other hand, the number of cestode specialists in grebes and the number of helminth specialists are *ca.* four times as great as that in loons (Table 3).

What factors might be responsible for the disparity in the number of species known to be found in the two groups? Loons are confined to the Holarctic region, nesting from the North Temperate to the high Arctic, whereas grebes are found on all continents except Antarctica and breed from the low Arctic through the tropics to the South Temperate zone and from sea level to high Andean lakes. Loons number 5 species in a single genus, whereas there are 21 Recent species and 7 genera of grebes. A very high percentage of the work done on grebe parasites has been in the Holarctic, especially in the former USSR and North America, whereas very little has been done in South America which has the largest and most complex grebe fauna, 9 species and 5 genera of which 6 species and 2 genera are endemic.

The parasite faunas may reflect a more recent, salt-water origin of the loons and an older, fresh-water one for the grebes. Although it must be admitted that the parasites of grebes taken on salt water have been very little studied compared with those of the loons from such waters, the numbers and percentages of parasite species acquired from salt-water final hosts is considerably higher in loons than in grebes, as are the percentages for parasites taken from final hosts like anadromous fishes and some sticklebacks (Gasterosteidae) that are found on both fresh and salt waters (Table 4).

The host specificity of the families Amabiliidae and Dioecocestidae may be related to the grebes early evolution and very long period during which they have inhabited fresh water and the shorter time the loons have been living there.

The younger age of the loons may be consistent with the smaller number and proportion of helminth parasites which are specific to loons (no families, two genera, and 23 species) as opposed to the two families, 15 genera, and 104 species specific to grebes (Table 5).

To avoid as much as possible regional differences in coverage and the effect of comparing a large group of hosts with a small one, we can compare the parasites of three Holarctic species of *Podiceps*, the Horned *(P. auritus)*, Red-necked *(P. grisegena)*, and Eared *(P. nigricollis)* grebes with the three superspecies of loons: Red-throated *(G. stellata)*, Common *(Gavia [immer] immer)* plus Yellow-billed *(G. [immer] adamsii)*, and Arctic *(G. [arctica] arctica)* plus Pacific *(G. [arctica] pacifica)* loons, members of each of the last two superspecies were long considered conspecific. Table 1 shows how well this sample of three species reflects the known diversity of grebe parasites in general. This arrangement also

Table 1. Diversity of Loon and Grebe Helminths[1]

	Digeneans	Cestodes	Acanths.	Nematodes	Totals
FAMILIES					
All Grebes	19 (56)	6 (18)	1 (3)	8 (23)	35 (100)
3 *Podiceps* spp.[2]	15 (50)	6 (20)	1 (3)	8 (27)	30 (100)
All Loons	7 (37)	4 (21)	1 (5)	7 (37)	19 (100)
GENERA					
All Grebes	55 (50)	32 (29)	5 (4)	19 (17)	111 (100)
3 *Podiceps* spp.[2]	24 (34)	25 (36)	4 (6)	17 (24)	70 (100)
All Loons	31 (50)	16 (26)	4 (6)	11 (18)	62 (100)
SPECIES					
All Grebes	112 (46)	84 (34)	12 (5)	36 (15)	244 (100)
3 *Podiceps* spp. [2]	49 (34)	57 (39)	10 (7)	29 (20)	145 (100)
All Loons	47 (47)	22 (23)	14 (14)	15 (15)	97(100)

[1]Expressed in numbers and (percentages).

[2] *Podiceps auritus, P. grisegena,* and *P. nigricollis* (Holarctic populations only.)

Table 2. Numbers of Named Parasite Species Reported from each Loon Species[1]

	Digeneans	Cestodes	Acanths.	Nemats.	Ectopara.	all
Gavia stellata	22	10	6	10	1	49
Gavia pacifica	5	1	0	0	0	6
Gavia arctica	8	6	2	4	2	22
Gavia arctica and/or pacifica	6	8	4	4	2	24
Gavia immer	32	9	5	11	2	59
Gavia adamsii	3	3	1	1	0	8

[1]For a comparable table of grebe species, see Storer (2000, p. 43).

takes advantage of the fact that the two groups have roughly overlapping ranges (Figure 2). (The parasites of the Eared Grebe populations outside of the Holarctic have not been studied.) This reduction of the grebe parasite fauna to those of the three Holarctic species of *Podiceps* has the additional advantage of eliminating 11 species of echinostomatid digeneans and 6 of amabilid cestodes known only from the original descriptions from *Tachybaptus ruficollis, Podilymbus podiceps,* or *Podiceps cristatus.*

The relative diversity of loon and grebe helminths is shown on Table 1. The two families (the Amabiliidae) and the Dioecocestidae), each with a single exception (not loons), being confined to grebes (Jones 1994) also increases the number of genera confined to grebes by 7 and the number of species by 35. In contrast, but two genera *(Biglandatrium* and *Dubininolepis)* and no higher groups are confined to loons, and the former genus is very poorly known.

The numbers of loon and grebe parasites with final stages in fresh-, brackish-, and salt-water habitats are shown in Table 4. The greater number and proportion of loon parasites with marine life cycles again is, at least in part, an artifact of the relative amount of work done on birds from the two habitat types.

The relative numbers of final hosts in animals of different

major groups are shown in Table 6. Many decapods reach larger sizes than insects and small crustaceans like copepods and amphipods and thus may be more subject to predation by loons than by grebes. The greater proportion of insects as final hosts for grebes than loons is probably real in part because most grebes are smaller and because the Eared and Silvery grebes, *Podiceps nigricollis* and *P. occipitalis,* are less well adapted for pursuit diving, but specially adapted for preying on small hosts. The greater proportion of fishes in loons' diets is probably a result of the loons' larger size and preference for feeding on these animals.

Ectoparasites. The numbers of genera and species of ectoparasites such as mites and lice on a group of birds are in large part dependent on the numbers of kinds of other birds with which these birds have had physical contact that permits host switching to occur and on the radiation of the birds after receiving the parasites. It is also dependent on the habitat in which the new hosts live and how this may affect the survival of the parasites.

Twelve species of mites and thirteen of lice are known from grebes but only a single mite and two lice from loons. The difference in the number of species of lice can be explained, at least in part, by the fact that unrelated genera of lice have speciated on each group, *Aquanirmus* on the grebes and *Craspedonirmus* on the loons, and this has resulted in eleven species on the former and two on the latter, a difference that can be explained by the larger number of species and wider geographic range of grebes.

The greater number of louse species on grebes is also accounted for by grebes' interactions with coots, which has resulted in several species of lice switching, more often, if not entirely, from coots to grebes than *vice versa.* For mites, the difference is less clear, but it might also be a matter of past host switching from birds of other groups. The presence of a hippoboscid fly is probably a result of the loons' nesting on land, which is necessary for the life history of the fly to be completed, but the single

Table 3. The Numbers and Percentages (in parentheses) of Helminth Generalists (?1, 1), Specialists in other groups, (?2, 2), and Specialists (?3-5) in Loons and Grebes

Specificity groups	?1+1	?2+2	?3 thru 5	Totals
Digeneans				
Loons	35 (58)	11 (18)	14 (23)	60
Grebes	43 (38)	26 (23)	44 (39)	113
Cestodes				
Loons	6 (27)	9 (41)	7 (32)	22
Grebes	7 (8)	27 (32)	52 (61)	86
Acanthocephalans				
Loons	10 (77)	2 (15)	1 (8)	13
Grebes	13 (100)	0 (0)	0 (0)	10
Nematodes				
Loons	12 (57)	8 (38)	1 (5)	21
Grebes	18 (49)	10 (27)	9 (24)	37
All Groups				
Loons	73(58)	31(24)	23(18)	127(100)
Grebes	81(33)	63(25)	105(42)	249(100)

record of this fly and the fact that it occurs on two fish-eating birds of prey suggests that the record may be based on an isolated occurrence. The association between the black fly, *Simulium euryadminiculum*, and the Common Loon, which is based a specific attractant found on the loon (Lowther *et al.* 1964), suggests that the association has been a long one. No comparable association with these flies on other loons or on grebes has been reported, although I see no obvious reason why this association in other loons might not exist if their breeding ranges occurred within the range of the fly.

The greater number and variety of mites and lice on grebes also may be attributable to the relative ages of the groups, but perhaps more so to the lesser amount of physical contact between loons and other species of birds which has presumably reduced the possibilities of host switching of these ectoparasites. The greater amount of time spent by loons on salt water, which is inimicable at least to mites, may also be a factor.

The reason for the apparent scarcity of the feather mite, *Brephosceles forficiger*, the only mite known from loons, is not clear, but it may be related to two aspects of loons' biology. Mites cannot survive immersion in salt water where loons winter, and loons molt their flight feathers simultaneously on these waters, the Red-throateds in the fall (Sept. to Dec.) and the Arctics in spring (Durinck *et al.*, 1994b), hence mites cannot move to adjacent flight feathers as they do in birds that have a serial remigeal molt (Dubinin, 1951). From this it is probable that these mites

Table 4. Loon and Grebe Helminths by Habitat of Definitive Host

Helminth	Taxon	FW[1]	?FW	BW[1]	SW[1]	?SW	FW& SW	?FW& SW	Total
All Grebes									
	Digeneans	39	57	4	3	2	0	4	109
	Cestodes	45	39	0	1	2	1	4	92
	Acanthoceph.	6	0	0	2	0	2	2	12
	Nematodes	15	17	0	0	0	3	1	36
	All 4 Groups	106	113	4	6	4	6	11	250
	%			87.6		4.0		6.8	
3 spp *Podiceps* [2]									
	Digeneans	19	24	0	3	1	0	1	48
	Cestodes	29	20	0	1	2	1	4	57
	Acanthoceph.	6	0	0	1	0	1	2	10
	Nematodes	9	14	0	0	0	3	1	27
	All 4 Groups	63	58	0	5	3	5	8	142
	%			83.5		5.6		9.2	
All Loons									
	Digeneans	15	16	0	6	5	0	3	45
	Cestodes	10	8	0	0	2	0	2	22
	Acanthoceph.	1	0	0	3	2	3	5	14
	Nematodes	4	2	0	2	2	3	2	15
	All 4 Groups	30	26	0	11	11	6	12	96
	%			50.0		22.7		18.6	

[1] FW = fresh water, BW = brackish water, SW = salt water.
[2] *Podiceps auritus, P. grisegena, and P. nigricollis.*

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

Taxa		Host Specificity Categories										
		Total Sp.	*1?*	*1*	*2?*	*2*	*3?*	*3*	*4?*	*4*	*5?*	*5*
Echinostomiformes	Cathaemasiidae	1	-	1	-	-	-	-	-	-	-	-
	Psilostomidae	4	-	-	-	-	-	-	-	4	-	-
	Philophthalmidae	1	-	-	1	-	-	-	-	-	-	-
	Echinostomidae	10	2	5	-	2	-	1	-	-	-	-
Strigeiformes	Clinostomidae	2	-	-	-	1	-	-	-	-	1	-
	Schistosomatidae	2	-	-	1	1	-	-	-	-	-	-
	Cyathocotylidae	2	-	-	1	1	-	-	-	-	-	-
	Diplostomidae	5	-	1	-	1	-	3	-	-	-	-
	Strigeidae	3	-	3	-	-	-	-	-	-	-	-
Opisthorchiformes	Opisthorchidae	6	1	2	-	-	-	1	-	1	-	1
	Heterophyidae	11	1	8	-	2	-	-	-	-	-	-
Plagiorchiiformes	Renicolidae	3	1	1	-	-	-	1	-	-	-	-
	Microphallidae	6	3	2	-	-	-	-	-	-	-	1
	Prosthogonomidae	1	-	1	-	-	-	-	-	-	-	-
	Eucotylidae	3	2	1	-	-	-	-	-	-	-	-
Digenea Totals		60	10	25	3	8	0	6	0	5	1	2

		Total Sp.	*1?*	*1*	*2?*	*2*	*3?*	*3*	*4?*	*4*	*5?*	*5*
Cestodes												
Pseudophyllidea	Diphyllobothriidae	5	-	5	-	-	-	-	-	-	-	-
Tetrabothriidea	Tetrabothriidae	1	-	1	-	-	-	-	-	-	-	-
Cyclophyllidea	Hymenolepididae	10	-	-	-	4	-	5	-	1	-	-
	Dilepididae	6	-	-	1	4	-	1	-	-	-	-
Cestode Totals		22	0	6	1	8	0	6	0	1		

		Total Sp.	*1?*	*1*	*2?*	*2*	*3?*	*3*	*4?*	*4*	*5?*	*5*
Acanthocephalans												
Polymorphida	Polymorphidae	13	1	9	-	2	-			1		

Nematoda												
Enoplida	Dioctophymatidae	1	-	1	-	-	-	-	-	-	-	-
	Trichuridae	2	-	1	-	1	-		-	-	-	-
Strongylida	Syngamidae	2	1	-	-	-	-	-	-	-	1	-
Ascaridida	Anisakidae	2	1	1	-	-	-	-	-	-	-	-
Spirurida	Dracunculidae	3	-	1	-	2	-	-	-	-	-	-
	Acuariidae	6	-	5	1		-					
	Ancyracanthidae	2	-	-	1	1	-	-	-	-	-	-
	Dracunclidae	2	-	1	-	1	-	-	-	-	-	-
	Onchocercidae	1	-		-	1	-	-	-	-	-	-
Nematode Totals		21	2	10	2	6	-	-	-	-	1	-

[1]Categories: 1 = Generalist. 2 = Specialist in other groups, rare or occasional in loons. 3 = Specialist in loons, rare or unknown in other groups. 4 = Known only from the type (loon) host. 5 = Known only from original description.
    For a comparable table of the host-specificity categories of grebe helminth parasites, see Storer (2000, p. 54).

Table 6. Major Groups to which Final Intermediate Hosts of Loon and Grebe Helminths Belong

Expressed as Numbers:

Major Group	Digeneans		Cestodes		Acanths.		Nematodes		Totals	
	Loons	Grebes	Loons	Grebes	Loons	Grebes	Loons	Grebes	Loons	Grebes
Annelids	1	1	0	2	0	0	2	7	3	10
Mollusks	2	3	4	0	0	0	0	0	6	3
Decapods	1	2	0	0	2	2	0	0	2	3
Small Crust.	2	3	6	14	4	7	7	6	19	30
Insects	0	5	0	12	0	0	2	5	2	22
Fishes	17	15	5	6	2	1	6	8	31	30
Tetrapods	1	3	0	0	1	0	1	0	3	3

Expressed as Percentages:

Major Group	Digeneans		Cestodes		Acanths.		Nematodes		Totals	
	Loons	Grebes	Loons	Grebes	Loons	Grebes	Loons	Grebes	Loons	Grebes
Annelids	1.5	1	0	2	0	0	3	7	4.5	10
Mollusks	3	3	6	0	0	0	0	0	9	3
Decapods	0	1	0	0	3	2	0	0	3	3
Small Crust.	3	3	9	13.5	6	7	11	6	29	29.5
Insects	0	5	0	12	0	0	3	5	3	22
Fishes	27.5	14.5	7.5	6	3	1	9	8	47	29.5
Tetrapods	1.5	3	0	0	1.5	0	1.5	0	4.5	3
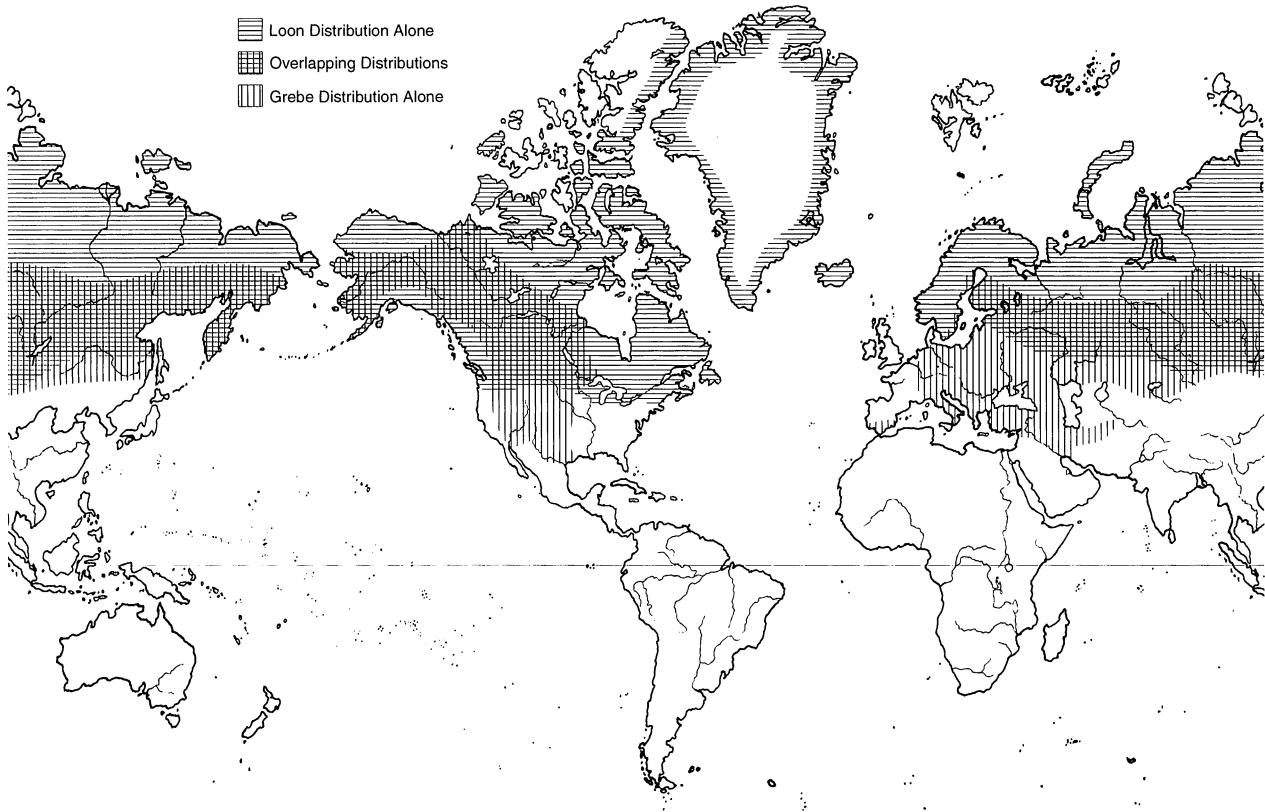
Figure 2. Map showing the World breeding distributions of the loons and of *Podiceps auritus*, *P. grisegena*, and the Holarctic breeding distribution of *P. nigricollis*, prepared by John Megahan from maps in Voous (1960) and Palmer (1962). (Breeding populations from Iceland, the British Isles and the Magdalen Islands in the Gulf of St. Lawrence are omitted.)

either live in a place such as the downy bases of feathers which remains dry or that they move to such a place before the molt takes place. Unfortunately, on what parts of which feathers these mites occur is not known. Grebes also have a simultaneous molt of the flight feathers, but in most species, this takes place while the birds are on fresh waters.

The grebes' floating nests are saturated with water and ordinarily do not last from one breeding season to the next. Thus, they do not provide a suitable environment for parasites like ticks, fleas, bedbugs, and other arthropods that have stages in their life cycles requiring a period on dry land. Loons often nest on dry land but keep adding wet material to their nests throughout the period of incubation. Both loons and grebes are highly aquatic and have little physical contact with birds of other groups. The major exception is that between grebes and coots (Fulica). In their frequent and often successful attempts to take over grebe nests for resting places or as bases for their own nests, coots will fight with grebes, and mixed clutches of grebe and coot eggs have been found in some nests. On the other hand, loons rarely nest near, or have physical contact with, other birds that might permit exchange of ectoparasites.

Single species of two other genera of lice (Pseudomenopon and Laemobothrion) are found on grebes and have close relatives on coots. Both genera contain several other species on coots and other rallids. This suggests that the lice on the grebes were derived from coots rather than vice versa. Two of the genera of mites (Rhinonyssus and Neoboydaia) found on grebes are also found on coots indicating a similar source for these parasites on grebes.

The overlap in parasite faunas. Accepting the current belief that loons and grebes are not closely related (pp. 1, 16), one can make several predictions about what helminth parasites they might share. First, that most of these parasites would be generalists in their definitive hosts, and, conversely, the frequency with which they are found would be reduced in parasites that specialize on other groups of birds; second, that their final hosts would be frequent prey to birds of both groups; and third, that there would be few, if any, parasites that would be specialists on birds of both groups, or if this occurs, it would be the result of similarity of diets. The data bear out these predictions.

Forty-eight species of helminths (22 digeneans, 12 cestodes, 6 acanthocephalans, and 8 nematodes) have been reported from both loons and grebes. Of these, 34 are generalists, 7 are specialists in other groups (3 in anatids and 2 each in Ciconiiformes and Lari), 4 are grebe specialists parasitizing loons, 2 are loon specialists parasitizing grebes. [One (Confluaria capillaris,) is said to be common in both groups, but Vasileva et al. (1999a) consider this species to be a grebe specialist and that reports of this species from other groups, including loons, to be "erroneous or doubtful."] Loons are not known to be parasitized by any of the 6 members of the Dioecocestidae or 29 members of the Amabiliidae, which specialize on grebes.

Fishes form the primary diet of loons, that of grebes is more varied, although all species for which there are sufficient data, are known to take fishes, and some, like the Great Crested Grebe (Podiceps cristatus), the Great Grebe (Podicephorus major), and the Western and Clark's grebes (Aechmophorus occidentalis and A. clarkii) are fish specialists. The final hosts for 21 of the 48 species known to parasitize both loons and grebes are unknown.

Of the other 27, 22 are known to be fishes, two, snails, and one each, oligochaete worms, odonate nymphs, and anurans.

The parasites of the five Palearctic species of grebes (Tachybaptus ruficollis, Podiceps auritus, P. grisegena, P. cristatus, and P. nigricollis) are the best known and the most frequently involved in the overlap. T. ruficollis, P. auritus, and P. nigricollis have been found to carry 22, P. cristatus, 28, and P. grisegena, 33 species also found in loons. Although all take fishes, P. cristatus and some populations of P. grisegena specialize in fishes, T. ruficollis is a generalist, and P. auritus takes more small invertebrates on the breeding grounds and more fishes in winter. The smaller number for P. cristatus than P. grisegena may be accounted for by the fact that the former is not found in the New World. On the surface, it may seem unlikely to find so many instances of grebes that are not fish specialists being parasitized by helminths whose final stages are carried by fishes. However, all grebes take whatever prey is easily available (Storer, 2000: 45), and some fishes may act sluggishly when carrying parasites. A known instance of this is that of the stickleback, Gasterosteus, which becomes slow-moving when infected by the large larvae of Schistocephalus solidus (Dolph Schluter, pers. comm.). This is but one of the many ways in which, directly or indirectly, parasites make intermediate hosts containing them conspicuous or easy to capture for potential definitive hosts.

As pointed out above, loons and grebes are not known to share any genera of external parasites. Loons are not known to have frequent physical contact with other kinds of birds or their nests comparable to that between grebes and coots which is thought to have resulted in exchanges of external parasites.

Host specificity. (Table 5). Digeneans. Members of 4 orders, 15 families, 41 genera, and 60 species of digenetic trematodes have been reported to parasitize loons. Of these, no genus is known only from these birds. Of the species found in loons, 14 or 22 percent are considered loon specialists, and 8 of these are known only from the loon host. Loon specialists are known from all four of the orders and 7 (47 percent) of the 15 families on the list.

Members of 3 orders, 4 families, 18 genera, and 22 species of cestodes have been reported to parasitize loons. Of these, 2 genera (Biglandatrium and Dubininolepis) consist of loon specialists. Of the species found on loons, 7 or 32 percent are considered loon specialists, 1 of them known only from the type host. Loon specialists are known from 1 order and 2 families (the Dilepididae and the Hymenolepididae) on the list.

Of the 4 genera and 13 species of acanthocephalans known from loons, 1 species (Polymorphus gavii) is considered a loon specialist.

Members of 4 orders, 9 families, 14 genera, and 21 species of nematodes have been reported from loons. Of these, no genera and but one species (Syngamus arcticus) is considered a loon specialist.

A single species of mite, the feather mite (Brephosceles forficiger), is found on and confined to loons. It comprises one of six groups of species in the genus (Peterson, 1971), but it is not clear to which of the other five groups it is most closely related.

A single genus of lice (Craspedonirmus) is known from loons. It is confined to loons and is not closely related to other genera of the Philopteridae.

The black fly, Simulium euryadminiculum, feeds primarily on

loons and is specially attracted to the Common Loon (Lowther *et al.* 1964), although it occasionally will land on waterfowl (Fallis *et al.* 1964). The hippoboscid, *Pseudolfersia fumipennis,* is not specific to loons and may be only an incidental parasite on them.

If we accept the hypotheses that parasites which are generalists as regards their definitive hosts indicate a similarity in diet but not necessarily an evolutionary relationship and that the higher the taxonomic level of a group of parasites specific to a group of definitive hosts, the longer the common evolutionary history shared by the parasite and host groups, we might be able to use information on host specificity of two groups of hosts to estimate the relative ages of the host groups.

Host switching from one group to another may have occurred in the past, but it may be detected if one species differs in its host group from that of the rest of the group. For example, the cestode family Amabiliidae contains 6 genera and 29 species specific to grebes and one monotypic genus *(Amabilia)* specific to flamingos, so it is probable that this family's history was shared with the grebes from its beginning, and the species on flamingos resulted from host switching. The case of the family Dioecocestidae is a little less clear. In it there is but a single genus of 7 or 8 species, one of which is known only from glossy ibises *(Plegadis)* in South America, whereas the other species, all of which are grebe specialists, are known from all continents except Africa and Antarctica. This indicates that it is most likely that this genus (and family) originated with grebes.

The paucity of genera and species of helminth parasites that are specific to loons (2 genera and 23 species) is in agreement with the relatively later appearance of the group compared with that of the grebes, in which the figures are two families or subfamilies, 15 genera, and 105 species (Storer 2000). The greater number of species of parasites specific to grebes may also be in part a result of the greater number of grebe species and the family's wider geographic distribution. The presence of two families or subfamilies specific to grebes as opposed to none in the loons is perhaps the greatest evidence from the parasite faunas of the greater age of the grebes.

WHAT MIGHT AFFECT THE NUMBER OF HELMINTH SPECIES IN LOONS AND GREBES?

The size and speed of the bird. Perhaps the most significant differences between loons and grebes with regard to their parasite faunas are the size of the birds and the relative numbers of invertebrates *(versus* fishes) in the diets.

Among predators with similar feeding habits, the optimal prey size will vary with the size of the predator (Storer 1966). The larger the prey species, the fewer species of optimal size will be available. The smaller number of prey species would mean the smaller number of species that could act as final stages for parasites. Therefore, the larger the predator the fewer species of parasites it might be expected to harbor. However, this effect might be offset by larger species of predators' being able to take prey of wider ranges of size.

Grebes range in mass from *ca* 100 to *ca* 1,600 g and loons from *ca* 1,600 to *ca* 6,400 g with virtually no overlap between the two groups. The grebes' smaller size makes it advantageous for them to take smaller prey, of which there are greater numbers and varieties of species. This in turn provides a greater number and variety of potential intermediate hosts for helminth parasites. Small prey are also taken in greater numbers, which may, in part, be responsible for the large number of individual helminths found in grebes (up to more than 33,000) found in a single Eared Grebe (Stock 1985), a species adapted for taking small prey.

Boertmann (1990) has shown that the Red-throated Loon differs from all other species of living loons in having the lowest wing-loading both relatively and actually, and most specialized legs for pursuit diving. The former is presumably an advantage to these birds for moving from the small, oligotrophic ponds where they nest to marine waters where they find the food needed for themselves and their young. The latter presumably makes it possible for these small loons to compete successfully with larger species and to take more pelagic than benthic fishes than the Arctic and Pacific loons.

In underwater locomotion, there are the two variable forces to be overcome: size, measured by the cross-sectional area, as mentioned earlier (p. 18), and the kind of flow (turbulent or laminar) of the water passing over the the body, measured by the surface area of the bird. Because both are areas, they vary in proportion to the square of linear measurements such as the length of the bird. On the other hand, the power, as represented by the volume of the muscles used to move the bird, varies with the cube of linear measurements. Therefore, in birds of the same shape, the amount of power available will be relatively greater in larger birds than the resistence or drag involved. Because turbulent flow caused by irregularities in the surface considerably increases drag, adaptations that decrease this can have considerable adaptive value in pursuit divers. In the case of dolphins and other cetaceans, turbulence is reduced in the skin by a layer of spongy tissue that holds water which can move as variations in pressure differentially compress various parts of the skin's surface. Thus by making the surface of the skin smoother, turbulent flow of the water passing over the skin can be damped and result in a laminar flow (Hertel, 1969). In turn, this greatly decreases the amount of energy needed to move the animal through the water and permits the energy saved for use in increasing its velocity.

A peculiarity of grebe feathers is the coiled barbules that lie parallel to the shaft of the barbs on the outer third of the contour feathers. Although this was figured by Chandler in his dissertation on the structure of feathers (1916), he made no comment about the possible significance of these barbules. Fifty-two years later, Maclean (1968) described how the males of some sandgrouse *(Pterocles)* use their belly feathers bearing similar coiled barbules, which act like capillaries, to carry water to their distant young.

In moving rapidly under water, grebes hold their folded wings against the body and cover them with their flank feathers. In this position, the stiff wing feathers are covered by more flexible feathers containing coiled barbules on their outer third, and other parts of the bird exposed to the water are covered with lax feathers, the outer third of which is similarly wetable. The barbs on each vane of the feather and the coiled barbules along each side of the barbs lie at an angle to the feather and the vane, respectively. Because this results in a "skin" of wet feathers with coiled barbules lying in many directions within the plane of the feather, the "skin," by movement in the water in and out of the

coils of the barbules, may produce an effect similar to the skin of cetaceans. I am not aware that a role for the coiled barbules in the damping process has been suggested and hope that it may be investigated.

Another effect of the water in the barbules may be to reduce the buoyancy of the bird, thereby increasing the depth to which it can forage, but this must be less effective than the rapid expulsion of much of the air trapped between the dry bases of the feathers and the skin as the bird submerges, and still more as the bird goes deeper.

Variation in bill form and specializations of the birds. The bills of loon species (Fig. 3) are basically of a generalized type, varying in size, depth, and shape, those of the Yellow-billed and Red-throated loons having a straight culmen and a more upturned line of the bottom of the lower mandible than the other species. The significance of this difference in foraging in unknown. At least in the Baltic and North seas, Red-throated and Arctic loons winter in large mixed feeding flocks, a situation in which the difference in bill shape might be related a difference in foraging places or prey taken.

In a reanalysis of Madsen's (1957) account of the stomach contents of the large series of Arctic and Red-throated loons taken in winter in Danish waters, Boertmann (Fjeldså *in litt.*) showed that the Red-throated Loons took a significantly larger proportion of pelagic and semipelagic fishes and the Arctic Loons a significantly larger proportion of benthic ones. This effectively showed that my earlier (1978) suggestion that the shape of the Red-throated Loon's bill might be an adaptation for bottom-feeding was incorrect.

The feeding on fast-moving, pelagic fishes is in agreement with Boertmann's demonstration (*op. cit.*) that the Red-throated Loon's legs are more strongly modified for pursuit diving than those of the other loons. I might add that, from his figures of the jaw musculature of these two species of loons, the heavier M. pseudotemporalis in the Red-throated Loon might be an adaptation for the rapid grasping of prey against the opposing force of the water during closing the bill, a force that increases with the speed of the bird.

If the straight line of the culmen is on a level with the eyes, it is possible that this is an adaptation for keeping the birds' eyes on the prey during the rapid chase and final capture. This is another possibility that might be investigated.

The Yellow-billed Loons' bills also have a straight culmen, but their diet is very little known (p. 15), and its skeleton does not appear to be more strongly modified for pursuit diving than that of the Common Loon. On the other hand, it is a larger species than this close relative, and this in itself can be an adaptation for more rapid pursuit diving. Salmonid fishes are common where it occurs and could well be a staple food.

On the other hand, grebes vary considerably in bill form (Storer 2000), and this increases their efficiency in taking a wide variety of prey, yet even the Western and Clark's grebes (*Aechmophorus occidentalis* and *A. clarkii*), the most highly adapted grebes for taking fishes, are known to take a variety of other kinds of prey, including aquatic insects, a fact evident not only from stomach analyses, but also from the birds' being infected by helminths whose final intermediate hosts are in insects. Loons show diversity in bill size but far less diversity in bill shape than grebes. Loons feed primarily on fishes but will take a variety of
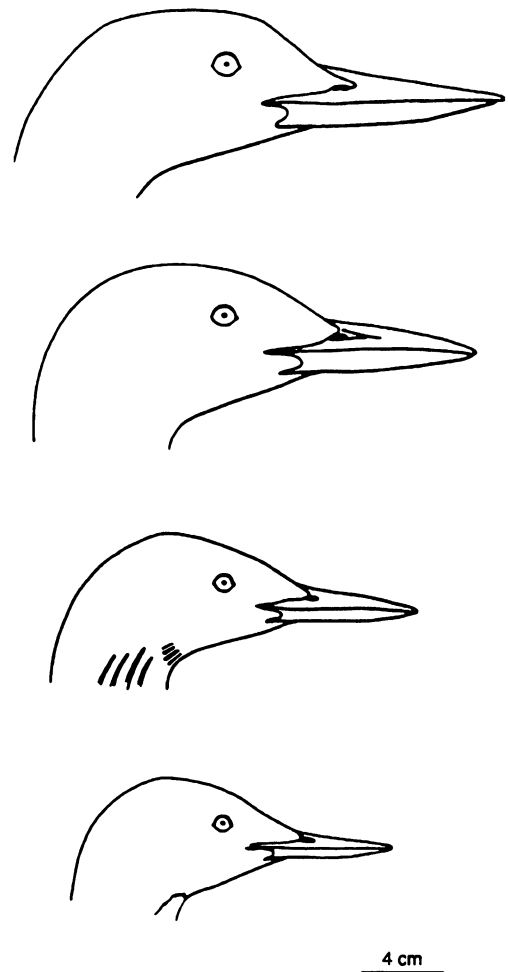
Figure 3. The bills of loons, from top to bottom; the Yellow-billed Loon (*Gavia adamsii*), the Common Loon (*G. immer*), the Pacific Loon (*G. pacifica*), and the Red-throated Loon (*G. stellata*), drawn by J. Megahan from specimens in the University of Michigan Museum of Zoology.

invertebrates as well. Therefore, it may be that the grebes' specializations for taking specific kinds of prey has a greater effect on the relative frequencies of infection by various species of parasites than the number of species of parasites involved.

Habitats. The habitats of loons and grebes are of primary significance to the helminth faunas of the birds through the numbers and variety of the intermediate hosts that can be transmitted to the birds.

Eutrophic lakes are rich in the number and variety of their animal life, especially small invertebrates whose numbers usually peak in the spring and summer when and where the birds are breeding. These provide abundant food for the slower-moving, small grebes, especially on small bodies of water that lack fish. Some species like the Pied-billed and Least grebes use such ponds throughout the year in areas where the waters remain free from ice in the winter. Horned Grebes may use fishless potholes during the breeding season but move off to larger lakes where they molt their flight feathers before moving to winter on coastal marine waters, where they feed on both fish and crustaceans (Stedman, 2000).

The smaller numbers and less variety of small invertebrates in oligotrophic lakes presumably make feeding on these organisms less efficient so birds can better survive and raise their young there by feeding on larger prey such as fish which require faster pursuit diving to catch. Thus, it can be expected that large predators like Common Loons use these lakes during the breeding season, and that these birds will require large feeding territories because of the sparser distribution of the available prey. This also may have been related to the smaller clutch size in loons (two) than in grebes (four or more).

As a result of these differences in habitat and the food resources in them, birds using eutrophic lakes will be subjected to a greater number and variety of intermediate hosts than birds on oligotrophic lakes.

Birds spending long periods on highly saline lakes like Great Salt and Mono lakes are a special case. These lakes differ from fresh-water lakes in having a very small number of prey species, most often brine shrimp *(Artemia)*, which may occur in vast numbers. However, they are available only to birds like the Eared and Silvery grebes that are adapted to survive the concentrations of salt (Mahoney & Jehl, 1985). Visits to Mono Lake, and probably Great Salt Lake, and swallowing the highly saline water, may be advantageous to the birds in purging them of intestinal helminths that may have been acquired on the breeding grounds. Jehl has examined many Eared Grebes taken on Mono Lake and but rarely has found intestinal parasties in them. (Jehl, 1988, and *in litt.*). On Kirgiz Lake in Kazakhstan, there is a population of the cestode, *Confluaria podicipina*, whose intermediate hosts there are brine shrimp (Maximova, 1981). Because the parasite cycle is found there, the salinity of this lake is presumably less than that of Great Salt and Mono lakes, but I have been unable to find a figure for this (Storer 2000).

The changeover of parasites grebes acquire on the breeding grounds to those acquired on the marine wintering grounds and *vice versa* has been discussed in Storer (2000) and presumably also occurs in loons, but proof that the degree of salinity causes this remains to be demonstrated.

Oceanic waters present different situations for pursuit divers. In pelagic waters, the prey is often scarce over large areas but clumped in certain predictable situations where schools of fish prey on shoals of invertebrates and/or smaller fishes. The birds may stay near these areas or, especially during the breeding season, may have to return to them between visits to their nests or young. If the concentrations of prey move, the returning birds may find the prey by seeing the feeding activities of other birds or large fishes. These feeding flocks often consist of different species of predators which have different host-parasite cycles with different components of the prey (Hoberg, 1996).

Other host-parasite systems can be expected to occur in coastal waters and estuaries with different types of bottoms. Such ecosystems are presumably more stable but provide smaller numbers of prey and thus are utilizable by individuals or small groups of predators. Because these ecosystems occur over long distances and often in isolated areas, I think it likely that relatively more of the parasites in them might be specific in their definitive hosts.

The differences in the numbers of digeneans, cestodes, and nematodes found in loons, grebes, and alcids (Table 7) agrees well with the habitats occupied by the birds of these families. Alcids are strictly marine and what helminths with fresh-water

Table 7. The Diversity of Helminths in Loons, Grebes, and Alcids. Data from Hoberg (1984), Storer (2000), and this paper[1,2].

	Families	Genera	Species
		DIGENEANS	
Loons	18	44	60
Grebes	20	53	111
Alcids	13	22	29
		CESTODES	
Loons	4	16	22
Grebes	6	35	85
Alcids	5	11	21
		NEMATODES	
Loons	10	12	21
Grebes	9	18	37
Alcids	6	13	17
		ACANTHOCEPHALANS	
Loons	1	4	13
Grebes	1	5	13
Alcids	1	2	5
		ALL GROUPS	
Loons	33	76	116
Grebes	36	111	246
Alcids	25	48	72

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

life cycles are found in them are those with intermediate hosts that move between fresh and marine waters. Most loons nest on oligotrophic fresh waters, spend more time in marine waters than grebes, and are intermediate in at least the number of digeneans.

The Condition of the Definitive Host. An ailing bird that is not able to take its usual prey will take any other prey that is easier to capture and thus may take prey carrying infective stages of parasites that would be rarely, if ever, taken by healthy birds. A striking example of this is documented in the paper by Kinsella and Forrester (1999) on the helminths of moribund or freshly dead Common Loons found during die-offs on the wintering grounds in Florida. This paper is notable both for the large number of species of helminths found, especially for the large numbers of microphallid digeneans for which crabs are the final intermediate hosts. This evidently resulted from loons having to rely on crabs rather than faster-moving fishes for food.

Physical contact with birds of other groups. Because of their aquatic habits neither loons nor grebes have much contact with other kinds of birds, and a result, they have far fewer kinds of ectoparasites than most birds. The major exception is that between grebes and coots, and, as mentioned earlier, this apparently has resulted in host switching of several kinds of mites and lice from coots to grebes. The possible sources of known species of mites (1) and lice (2) on loons are unknown.

PARASITE GENERA LOONS SHARE WITH PETRELS AND PENGUINS

If the loons were derived from the petrel-penguin line, some support might be found in a comparison of their parasite fau-

nas. Five species of helminths that have been found in loons have also been found in the petrels and/or the penguins: the digeneans *Diplostomum spathaceum* and *Ichthyocotylurus erraticus* (Yamaguti, 1971), the cestode *Schistocephalus solidus* (McDonald, 1969), and the nematodes, *Cyathostoma phenisci* and *Stegophorus diomedeae* (Yamaguti, 1961). The first three are generalists in their definitive hosts, *C. phenisci* is too little known to provide strong evidence, and *S. diomedeae*, a petrel-penguin specialist, is rarely found in loons and alcids, which may be only incidental hosts. Loons are known to share at least 12 species of helminths with alcids, as well as with birds of other groups, which is consistent with the idea that for parasites of gregarious fishes that attract mixed feeding flocks of birds, it would be advantageous to be generalists in their definitive hosts.

Only one species of mite, the feather mite, *Brephosceles forficiger*, has been found on loons. Members of the genus have been found on many procellariiform and charadriiform birds as well as birds of other groups, but as pointed out earlier (p. 13), a phylogenetic analysis of the genus has not been made so a closeness of relationship between the species on loons and petrels cannot be determined.

At this point, I see no strong evidence from the parasite faunas to support a relationship of the loons with any other group of birds.

PRIORITIES FOR FUTURE WORK

There is much valuable work is still to be done on the parasites of both the loons and the grebes. On the loons, this includes surveys of helminths, especially on the marine wintering grounds and the boreal breeding grounds in North America and on the life cycles of the parasites. (Life cycles are known for slightly less than one-half [ca. 48 per cent] of the helminth species known from the loons as well as the grebes.)

For parasites of both loons and grebes the major priorities for future studies in the Northern Hemisphere are survey work to find out what parasites are found in these birds and working out of life cycles of these parasites. In doing this, specimens of hosts taken should also be used to provide tissue samples and data on species of prey taken by the hosts. In grebes the first priorities are finding out what species of parasites are acquired from salt-water habitats and from the less well studied species, the Pied-billed *(Podilymbus podiceps)* and Least grebes *(Tachybaptus dominicus)*, in all habitats. For the loons, the major priorities are studies of the Red-throated, Pacific, and Yellow-billed loons on marine habitats and all four North American species on the breeding grounds. [I would emphatically not recommend taking Common Loons for this purpose on the southern parts of the range of the species where the birds are rare, but the total population is large enough so that taking a sample where the species is common on the northern breeding grounds should do no harm, especially if non-breeders and failed breeders were selected.] If such studies were conducted, the birds taken could also provide tissue samples for DNA analyses, seasonal changes in pectoral muscle and fat mass related to migration and the breeding cycle, and study specimens for which there are few for detailed analyses of geographic variation (Storer 1988). Valuable data on food habits could also be taken from the same specimens. Special effort also should be made to collect metazoan

parasites from freshly dead Common Loons elsewhere on the breeding grounds, where sampling of microbes and examination for other possible causes of death too often have been emphasized at the expense of metazoan parasites. (Methods for collecting and preserving avian helminths and protozoa can be found in Doster and Goater [1997] and references therein.)

Parasitology can be important in conservation. Knowledge of what parasites are found in a given species of host, what the life cycles of these parasites are, and the parasite load a given host can carry without damage to its well-being can be crucial to saving a threatened or endangered host species. Basic studies that provide information of this kind should be made while the host species have healthy populations from which a few individuals can be sacrificed for this purpose.

For the grebes, I believe that the Southern Hemisphere has the most to discover because of a probable Gondwanaland origin of the group and because no fossil grebes are as yet known from Australasia and no fossils of the endemic species in South America have been found. Although *Tachybaptus dominicus* and *Podilymbus podiceps* are known from the Pleistocene of Peru (Campbell 1943), I know of no reports of earlier grebe fossils from that continent.

The helminth parasites from the 6 endemic South American grebes are also little known, so far consisting only of 4 digenetic trematodes and one acanthocephalan. The numbers from the 3 endemic species of Australian grebes are not much higher: 9 trematodes, 2 cestodes, and 5 nematodes. The paucity of reports of cestodes is particularly unfortunate in view of the large number of species of this group found in grebes of the Northern Hemisphere (*e.g.*, by Stock 1985), and the likelihood that the Amabiliidae and the Dioecocestidae may have arisen in the Southern Hemisphere with the grebes.

While we have a fairly good understanding of the relationships among the species and genera of grebes based on cladistic analyses by Bochenski (1994) and Fjeldså (ms.) of morphological data, as well as many behavioral studies by Fjeldså and others, we now need parallel molecular studies of both the grebes and the parasites (especially those which specialize on these birds). A comparative study of the Miocene grebes, *Miobaptus walteri* and *Thiornis sociata*, and the scattered Oligocene material reported by Nessov (1992) would be valuable in placing the early European genera within the framework of what we know about the relationships of the Recent genera. In addition, the behavior of *Tachybaptus dominicus, T. novaehollandiae, T. pelzelni,* and *Podicephorus major* needs much more study.

I think the parasite groups that show the greatest potential for future studies are the Amabiliidae and the Dioecocestidae with their nearly complete specificity for their grebe hosts; and, as Hoberg *et al.* (1999) pointed out, this information could "be used for estimating a minimum age for the radiation of the cyclophyllideans." The largest gaps in our knowledge of the Amabiliidae are the lack of material from the South America and Australasia, to which most of the "primitive" genera of grebes are confined, and information on the life-cycle of *Amabilia lamelligera*. This species is confined to flamingos and such information might provide evidence as to whether the grebes or the flamingos were the original hosts for the Amabiliidae.

I urge that the Amabiliidae be the basis for a multi-pronged attack. First, the endemic South American and Australasian

grebes should be examined for these parasites and the life cycles of those found worked out. Then, a cladistic analysis of the Amabiliidae should be made and compared with that of the grebes. Specificity for species of grebes and geographic ranges of the parasites should be determined. Finally, lacustrine fossil localities from the late Cretaceous through the Miocene (but especially the Paleocene and Eocene) in southern South America, Antarctica, and Australasia should be carefully examined for fossil grebes. Such fossils, if found, might provide evidence regarding the proposed Gondwanaland origin for the grebes and when this occurred.

For comparison with the Amabiliidae, similar studies of the Dioecocestidae would be useful in attempting to date the origin of the latter family. Although the life-cycle on no species of *Dioecocestus* has been worked out, Jögis (1978) found evidence that odonate nymphs are probably the intermediate hosts for *D. asper* in Europe. Two good places in North America to work out the life cycles of species in this genus would be southern Texas, where a high proportion of *Tachybaptus dominicus* is known to be parasitized by *D. acotylus*, and Alberta, where Stock found *D. asper* in several specimens of *Podiceps grisegena* (1985). The life cycle of *D. paranoi* from the glossy ibises in South America would be especially valuable to compare with those of the species of *Dioecocestus* from grebes and might provide evidence for whether this species or one from grebes was basal to the origin of the family. (The likelihood that odonate nymphs are the intermediate hosts of members of this family suggests the possibility that *Dioecocestus* split off from the Amabiliidae.)

Then, molecular analyses of both the parasites and the birds should be made for comparison with those of the cladistic ones. In 1985, Stock included a preliminary coevolutionary analysis of the grebes and the Amabiliidae in his thesis. The accumulation of all the above information would make possible a coevolutionary study similar to, but even more complete, that of Hoberg's on the Alcidae and *Alcataenia* (1985).

The diversity in the structure of the feet in diving birds offers excellent possibilities for functional anatomical studies, for instance, a comparison of those of the less specialized grebes like *Rollandia* and *Tachybaptus* spp. with the Great Crested Grebe or the last with the even more specialized Western and Clark's grebes. Such studies should provide evidence on how the grebes' foot structure (and that of *Hesperornis* and its relatives) evolved and became diversified, as well as how the patella became involved with these mechanisms.

The decline in support for parasitology in this country is deplorable, especially in an age when biodiversity is being emphasized. When a species of animal or plant becomes extinct, all the species dependent on it are also lost. Yet too many administrators judge research more by the amount of overhead grants brought to their institutions than on the new ideas and information the resulting research will provide. It is of course important for researchers to raise the funds needed to conduct their work, but the amount raised should be determined by the needs of the project itself and should be judged by the value of the data and ideas resulting from it.

In evolutionary biology, all aspects of the biology of an organism are potentially important in tracing its evolutionary history, and conversely, the more different kinds of evidence are in agreement, the sounder the conclusions will be. It should be emphasized that the more one knows about the biology of a group of organisms, the sounder the results of cladistic and molecular analyses, and even ecological studies, will be. There is no substitute for knowing whole organisms in the field and laboratory.

Documentation. In studies involving more than one group of organisms, documentation of the materials used is particularly important. It is encouraging to find that voucher specimens of parasites used in recent studies are being preserved in parasite collections and are available for the use of future workers. But it is disappointing to find that comparable material of definitive and intermediate hosts is not. It is especially unfortunate that documentation of the sources of material for molecular studies is not provided when the identification of the source of this material is crucial. Even in such well studied groups as birds, this needs to be done. Taxonomic levels between species may change, as in the case of the loons parasitized by *Polymorphus gavii* (p. 10). Cryptic species are being discovered, and considerable molecular differences are being found between populations within species. Nor can we be confident that all voucher specimens are correctly identified, even in the best-curated collections. Therefore, I urge that editors require documentation of all the material used.

In these days, coauthored papers are the rule, so I would go even further in requiring that in these papers, there be some documentation of which author was responsible for which part(s) of the study. This is something the reader needs and has the right to know in order to evaluate the work.

> "A little learning is a dangerous thing;
> Drink deep or taste not the Pierian spring."

This advice is no less cogent now than it was when Pope penned it nearly three hundred years ago. Students now can learn the jargon of cladistic analysis before they learn (if ever) how to write simple, direct, precise English. Similarly, they can learn how to make cladistic analyses before they know the basic biology of the organisms they are analyzing. Cladistic analysis is an important methodology for constructing hypotheses about the phylogenetic relationships within groups of organisms. It is based primarily on two principles that systematists have been using, consciously or unconsciously, for a long time. These are that in comparing the characters of different organisms one must polarize the states of each character (that is, which is the more "primitive" and which is the most advanced evolutionarily), and that characters which are believed to have resulted from convergent evolution should not be used. From this, it should be clear that the best analyses are those made by those biologists who have the best basic knowledge of the group being analyzed. Not correctly polarizing the states of the characters or recognizing convergent evolution can lead to erroneous conclusions. If the premises are untenable, even the best logic cannot produce viable results. Similarly, because fossils are the only tangible evidence for checking the results of time of evolution of organisms, it is advisable that molecular biologists engaged in this work should know enough about the osteology of the organisms they are studying to enable them to evaluate the fossil evidence. Here again, polarizing character states and awareness of convergent evolution are critical factors. For example, Cooper and Penny's (1997) use of *Neogaeornis* (known only from poorly preserved

material of a single skeletal element which is known to show convergence among diving birds) as their only example of a living order of birds that they cite as having existed in the Cretaceous, is questionable no matter how positively some paleontologists have stated their case.

I see no reason to argue that the time since the Cretaceous-Tertiary Boundary was too short for the rapid divergence of the orders of Recent birds when fossil evidence has shown, for example, that whales evolved from marsh-dwelling, semiaquatic quadrupeds to their present, highly specialized form of locomotion in a span of about 12 million years between the early and late Eocene (Gingerich, 1998). Such rapid evolution is characteristic of newly-formed land masses, and a major catastrophic event would leave many ecological niches open, thus making the world ripe for rapid adaptive radiation on an even greater scale than that on newly formed volcanic islands like the Galapagos and the Hawaiian islands.

Much of the basic information on the biology of birds can be found in research museums where not only tissues available for molecular analysis are stored, but also the specimens from which the tissues were taken are saved as voucher specimens that permit certain identification of the source of the tissue. A single misidentified tissue can severely damage or invalidate a molecular study.

In addition to these specimens (skeletons and fluid-preserved material [world lists of which can be found in Wood and Schnell 1986, and Wood et al. 1982), respectively], study skins, films of behavior (much of it believed to be genetically based), tapes of vocalizatons, and field notes with ecological and a variety of other information can be found.

The need for collecting more specimens of birds for museums and the rationale for doing this have been ably documented by Remsen (1995), and the need for more surveys of parasite faunas and their importance for faunistic, coevolutionary, and biogeographic studies by Hoberg (1996) and by Brooks and Hoberg (2000). A concerted effort to combine the two objectives should be an important goal for biodiversity studies and an urgent reason for universities and museums to teach basic whole-animal biology and to develop training and research programs for this purpose.

Although it is tempting only to taste the Pierian spring, we should also remember that the proverbial turtle must stick its neck out in order to get anywhere.

ACKNOWLEDGMENTS

LITERATURE CITED

American Ornithologists' Union. 1985. Thirty-fifth supplement to the American Ornithologists' Union Check-list of North American Birds. Auk 102:680-686.

American Ornithologists' Union.1998. *Check-list of North American Birds*. 7th edition. American Ornithologists' Union. Washington, D. C.

Anderson, R.C. 1956. The life cycle and seasonal transmission of *Ornithofilaria fallisensis* Anderson, a parasite of domestic and wild ducks. Canad. J. Zool. 34:485-525.

Anderson, R.C. 1992. Nematode parasites of vertebrates: their development and transmission. xiii+578 pp. C.A.B. International. Wallingford, Oxon. U. K.

Anderson, R.C. 2000 Nematode parasites of vertebrates; their development and transmission. 2nd. edition. xx+650 pp. C. A. B. International. Wallingford, Oxon. U. K.

Anderson, R.C., & D.J. Forrester. 1974. *Splendidofilaria fallisensis* (Nematoda) in the common loon, *Gavia immer* (Brünnich). Canad. J. Zool. 52:547-548.

Anderson, R.C., & P.L. Wong. 1981. Redescription of *Cosmocephalus obvelatus* (Creplin, 1825) (Nematoda: Acuarioidea) from *Larus delawarensis* Ord (Laridae). ibid. 59:1897-1902.

Anderson, R.C., & P.L. Wong. 1982. The transmission and development of *Paracuaria adunca* (Creplin, 1846) (Nematoda: Acuarioidea) of gulls (Laridae). ibid. 60:3092-3104.

Appleton, C.C. 1983a. Studies on *Austrobilharzia terrigalensis* (Trematoda: Schistosomatidae) in the Swan Estuary, Western Australia: Observations on the biology of the cercaria. Internat. J. Parasitol. 13:239-247.

Appleton, C.C. 1983b. Studies on *Austrobilharzia terrigalensis* (Trematoda: Schistosomatidae) in the Swan Estuary, Western Australia: Infection in the Definitive host, *Larus novaehollandiae*. ibid: 13:249-259.

Baltz, D.M., & G.V. Morejohn. 1977. Food habits and niche overlap of

seabirds wintering on Monterey Bay, California. Auk 94:526-543.

Barr, J.F, C. Eberl, & J.W. McIntyre. 2000. Red-throated Loon *(Gavia stellata). In* The Birds of North America. No. 513 (A. Poole and F. Gill. eds). The Birds of North America, Inc. Philadelphia PA.

Bartonek, J.C., & D.L. Trauger. 1975. Leech (Hirudinea) infestations among waterfowl near Yellowknife, Northwest Territories. Can. Field-Nat. 89:234-243.

Barus, V., T. P. Serge[j]eva, M. D. Sonin, & K. M. Ryzhikov 1978. Helminths of fish-eating birds of the Palearctic Region I. Nematoda. 318 pp. B. Rysavy. and K.M. Ryzhikov Eds. Dr. W. Junk, b. v. Publ., The Hague.

Bearup, A.J. 1956. Life cycle of *Austrobilharzia terrigalensis* Johnston, 1917. Parasitol. 46: 470-479.

Beaver, P.C. 1937. Experimental studies on *Echinostoma revolutum* (Froelich), a fluke of birds and mammals. Illinois Biol. Monogr. 15:1-96.

Beaver, P.C. 1939. The morphology and life history of *Psilostomum ondatrae* Price, 1931 (Trematoda: Psilostomidae). J. Parasitol. 25:383-393.

Becker, J.J. 1985. The fossil birds of the late Miocene and early Pliocene of Florida. Ph. D. Diss., Univ. Florida

Beverley-Burton, M. 1961. Studies on the Trematoda of British freshwater birds. Proc. Zool. Soc. London 137:13-39.

Bittner, H., & C. Sprehn. 1928. Trematodes. Saugwürmer, Lieferung 27, Teil 5. Pp. 5.1-5.133. In P. Schulze ed. Biologie der Tiere Deutschlands. Borntraeger Bros. Berlin.

Bochenski, Z.M. 1994. The comparative osteology of grebes (Aves: Podicipediformes) and its systematic implications. Acta zool. cracov. 37(1):191-346.

Boeckeler, W. 1984. The life-cycle of *Reighardia sternae* Pentastomida after investigations of naturally and experimentally infected sea gulls. Zool. Anzeiger 213(5-6): 374-394.

Boertmann, D. 1990. Phylogeny of the divers, family Gaviidae (Aves). Steenstrupia 16:21-36.

Bouvier, G., H. Burgisser, & P.A. Schneider. 1962. Observations sur les maladies du gibier et des animaux sauvages faites en 1959 et 1960. schwweiz. Arch. Tierh. 104(7):440-445.

Briggs, K.T., W.B. Tyler, D.B. Lewis, & D.R. Carlson. 1987. Bird communities at sea off California: 1975-1983. Studies Avian Biol. No. 11. iv +74 pp.

Brooks, D. R. & E. P. Hoberg. 2000. Triage for the biosphere: the need and rationale for taxonomic inventories and phylogenetic studies of parasites. Comp. Parasitol. 67: 1-25.

Brodkorb, P. 1963. Catalogue of fossil birds. Part 1 (Archaeopterygiformes through Ardeiformes). Bull. Florida State Mus. 7:179-293

Cable, R.M. & A.V. Hunninen. 1938. Studies on the life history of *Spelotrema nicolli* (Trematoda: Microphallidae) with the description of a new microphallid cercaria. Biol. Bull. 78:136-157.

Campbell, K. E., Jr. 1943. The non-passerine Pleistocene avifauna of the Talara Tar Seeps, northwestern Peru. Life Sci. Contrib. Royal Ontario Mus 118 203 pp.

Campbell, R.W., N.K. Dawe, I. McTaggart-Cowan, J.M. Cooper, G.W. Kaiser, & M.C.E. McNall. 1989. The Birds of British Columbia. Vol. 1. Royal British Columbian Museum and Canadian Wildlife Service.

Chandler, A.C. 1916. A study of the structure of feathers, with reference to their taxonomic significance. Univ. Calif. Publ. Zool. 13:243-446.

Chatterjee, S. 1997. The Rise of Birds: 225 million years of evolution. Johns Hopkins Univ. Press, Baltimore and London.

Cheneval, J. 1984. Les oiseaux aquatiques (Gaviiformes à Ansériformes) du Gisement Aquitanien de Saint-Gérand-le Puy (Allier, France): Révision Systématique. Palaeovertebrata, Montpellier, 14 (2): 33-115.

Claris Corp. 1994. FileMaker Pro for the Macintosh, 2.1v3. Claris Corporation, Santa Clara, CA.

Collinge, W.E. 1927. The food of some British wild birds: a study in economic ornithology. Ed. 2. Publ. by author, York.

Cooper, A., and D. Penny. 1997. Mass survival of birds across the Cretaceous-Tertiary boundary: Molecular evidence. Science:275:1109-1113.

Cottam, C., and P. Knappen. 1939. Food of some uncommon North American birds. Auk, 56: 138-169.

Cracraft, J. 1982. Phylogenetic relationships and monophyly of loons, grebes, and hesperornithiform birds, with comments on the early history of birds. Syst. Zool. 31:35-56.

Cramp, S. (Chief Ed.). (1977). Handbook of the birds of Europe, the Middle East and North Africa. The birds of the western Palearctic. Vol. 1. Ostrich to ducks. Oxford Univ. Press; Oxford, London, New York.

Crompton, D. W.T., & B.B. Nickol, eds. 1985. Biology of the Acanthocephala. xi + 519 pp. Cambridge Univ. Press, Cambridge, London, New York, etc.

Davis, R. A. 1972. A comparative study of the use of habitat by Arctic Loons and Red-throated Loons. Ph.D. Thesis Univ. Western Ontario.

Dementiev, G. P., & N. A. Gladkov. Eds. 1968. Birds of the Soviet Union, vol. 2. Israel Program for Scientific Translations, Jerusalem. Original publication (in Russian) dated 1950.

Denny, M. 1969. Life-cycles of helminth parasites using *Gammarus lacustris* as an intermediate host in a Canadian lake. Parasitol. 59:795-827.

Doster, G.L., & C.P. Goater. 1997. Collection and quantification of avian helminths and protozoa. Pp. 396-418 in D. H. Clayton and J. Moore Eds. Host-parasite evolution: general principles and avian models. Oxford Univ. Press, Oxford, New York, and Tokyo.

Dubinin, V.B. 1951. Fauna of the USSR. Arachnida, Vol. 6, No. 5. Feather MItes Analgoidea. 363 pp. (In Russian).

Dubinina, M.N. 1966. Tapeworms (Cestoda, Ligulidae) of the fauna of the USSR. Translated from Russian. 1980. vii + 320 pp.Amerind Publ. Co. Pvt. Ltd. New Delhi.

Dubois, G. 1968. Synopsis des Strigeidae et des Diplostomatidae (Trematoda). Mém. Soc. Neuchateloise Sci. Nat. 10:1-258.

Dubois, G. 1970. Synopsis des Strigeidae et des Diplostomatidae (Trematoda). ibid. 10:259-727.

Dubois, G., & R. Rausch. 1960. Quatrième contribution a l'étude des *Strigeides (Trematoda)* nord-américains. Bull. Soc. neuchâteloise Sci. nat. 83:79-92.

Dubois, G., & R.L. Rausch. 1967. Les *Strigeata (Trematoda)* des Gaviidés nord-américains. Rev. Suisse Zool. 74: 399-407.

Durinck, J., H. Skov, F. Danielsen, & K. D. Christensen, 1994a. Vinterføden hos Rødstrubet Lom *Gavia stellata* i Skagerrak. Dansk Orn. Foren. Tidsskr. 88:39-41.

Durinck, J., H. Skov, F.P. Jensen, & S. Pihl. 1994b. Important marine areas for wintering birds in the Baltic Sea. EU DG XI research contract no. 2242/90-09-01. Ornis Consult report 1994, 110 pp.

Emerson, K.C. 1955. A new mallophaga from a loon. Ann. Mag. Nat. Hist. Ser. 12, no. 8:718-720.

Eriksson, M.O.G., D. Blomqvist, M. Hake & O.C.O. Johansson. 1990. Parental feeding in the Red-throated Diiver *Gavia stellata.* Ibis 132:1-13.

Fallis, A.M. & S.M. Smith. 1964. Ether extracts from birds and CO_2, as attractants for some ornithophilic simuliids. Canad. J. Zool. 42:723-730.

Farley ????? 1971. A Review of the Family Schistosomatidae: excluding the Genus *Schistosoma* from Mammals. J. Helminthol. 45:289-320.

Feduccia, A. 1999. The Origin and Evolution of Birds. Ed. 2. Yale Univ. Press. New Haven and London.

Fjeldså, J. 1977. Guide to the Young of European Precocial Birds. Skarv Nature Publ. Tisvildeleje, Denmark.

Fjeldså, J. 1983. Social behaviour and displays of the Hoary-headed Grebe *Poliocephalus poliocephalus.* Emu 83: 129-140.

Fleldså, J. 1985. Displays of the two primitive grebes *Rollandia rolland* and *R. microptera* and the origin of the complex courtship behaviour of the *Podiceps* species (Podicipedidae). Steenstrupia 11:133-155.

Forbush, E.H. 1925. Birds of Massachusets and other New England states. Vol. 1.Commonwealth of Massachusetts.

Gallimore, J.R. 1964. Taxonomy and ecology of helminths of grebes in Alberta. M. Sc. thesis, Univ. Alberta, 167 pp. +14 pls.

Gibson, G.G. 1968. Species composition of the genus *Streptocara* Railliet *et al.,* 1912 and the occurrence of these avian nematodes (Actuariidae) on the Canadian Pacific coast. Can. J. Zool. 46: 629-645.

Gingerich, P.D. 1998: Paleobiological perspecitves on Mesonychia, Archaeoceti, and the origin of whales. Chapter 15 in The Emergence of Whales, J.G.M. Thewissen Ed., Plemum Press, New York.

Gower, W.C. 1939. A new trematode from the loon, *Gavia immer*, and its relationship to *Haematotrephus fodiens* Linton, 1928. Proc. U. S. Natl. Mus. 87, no. 3071, pp. 139-143.

Harland, W.B., R.L. Armstrong, A.V. Cox, L.E. Craig, A.G. Smith, & D. G. Smith. 1989. A geologic time scale 1989. Cambridge Univ. Press. Cambridge, New York, Port Chester, Melbourne, and Sydney.

Hertel, H. 1969. Hydrodynamics of Swimming and Wave-riding Dolphins. Pp. 31-63 *in* The Biology of Marine Mammals, H.T. Andersen ed. Academic Press. New York and London

Hoberg, E.P. 1984. Systematics, zoogeography and ecology of platyhelminth parasites of the seabird family Alcidae (Charadriiformes: Suborder Alcae). Ph. D. Dissertation, Univ. Washington. 324 pp.

Hoberg, E. P. 1987. Recognition of larvae of the Tetrabothriidae (Eucestoda): implications for the origin of tapeworms in marine homeotherms. ibid. 65:997-1000.

Hoberg, E.P. 1996. Faunal diversity among avian parasite assemblages: the interaction of history, ecology, and biogeography in marine systems. Bull. Scand. Soc. Parasitol. 6(2); 65-89

Hoberg, E.P., A. Jones, & R.A. Bray. 1999. Phylogenetic analysis among the families of the Cyclophyllidea (Eucestoda) based on comparative morphology, with new hypotheses for co-evolution in vertebrates. Systematic Parasitol. 42:51:73.

Hoffman, G.L. 1967. Parasites of North American freshwater fishes. Univ. Calif. Press, Berkeley and Los Angeles. ix + 486 pp.

Hunter, W.S., & W.B. Vernberg. 1960. Preliminary studies on the life history of *Cardiocephalus brandesi* Szidat, 1928 (Trematoda: Strigeidae). J. Parasitol. 46:797-799.

International Commission on Zoological Nomenclature.1972. Extract from Opinion 981 in Bull. Zool. Nomencl. 29(1) 1972: 152. Bull. Brit. Ornithol. Club 92: 172.

Jehl, J.R., Jr. 1988. Biology of the Eared Grebe and Wilson's Phalarope in the nonbreeding season: a study of adaptations to saline lakes. Studies in Avian Biol. No. 12. iv + 74 pp.

Jögis, V.A. 1978. [An unusual type of cestode development in the dioecious species *Dioecocestus asper* (Cyclophyllidea: Acoleidae)] (In Estonian with English summary.) Izv. Akad, Nauk Estonskoi CCR, ser. Biol. 27:31-37.

Johansson, L.C., & U.M.L. Norberg. 2000. Asymmetric toes aid underwater swimming. Nature 407:582-583.

Johnson, C.W. 1922. Notes on distribution and habits of some of the bird-flies, Hippoboscidae. Psyche 29:79-85.

Johnston, T.H. & L.M. Angel. 1941. Life history of the trematode, *Petasiger australis* n. sp. Trans. Roy. Soc. S. Austr. 65:285-291.

Jones, A. 1994. Family Dioecocestidae Southwell, 1930. Pp. 391-398, and the Family Amabiliidae Braun, 1900. Pp. 400-405, *in* Khalil, L. F., A. Jones, and R. A. Bray. eds. Keys to the cestode parasites of vertebrates. CAB International. Wallingford, Oxon. U.K.

Joyeux, Ch., & J. G. Baer.1950. Sur quelques espèces nouvelles ou peu connues du genre *Hymenolepis* Weinland, 1858. Bull. Soc. Neuchateloise Sci. Nat. 73 (ser. 3):51-70.

Kanev, I. 1985. On the morphology, biology, ecology and taxonomy of the *Echinostoma revolutum* group (Trematoda: Echinostomatidae: *Echinostoma*). DSc Thesis, Bulgarian Academy of Sciences, Sofia, 467 pp. (In Bulgarian with English summary). Not seen.

Kanev, I. 1994. Life-cycle, delimitation and redescription of *Echinostoma revolutum* (Froelich, 1802) (Trematoda: Echinostomatidae). Syst. Parasitol. 28: 125-144.

Khalil, L. F., A. Jones, & R. A. Bray. 1994. Keys to the cestode parasites of vertebrates. CAB International. Wallingford, Oxon., U.K.

Kinsella, M., & S. Deblock. 1997. Contribution à l'étude des Microphallidae (Trematoda). LI. De cinc espèces du plongeon imbrin *Gavia immer* (Aves) des Etats Unis, dont *Microphallus forresteri* n. sp. Pluralité vraisemblable de l'éspèce *Microphallus nicolli* (Cable & Hunninen, 1938). Syst. Parasitol. 37:139-148.

Kinsella, M., & D. J. Forrester. 1999. Parasitic helminths of the Common Loon, *Gavia immer*, on its wintering grounds in Florida. J. Helminthol. Soc. Wash. 66(1): 1-6.

Kinsky, F. C. 1960. The yearly cycle of the Northern Blue Penguin, *Eudyptula minor novaehollandiae*) in the Wellington Harbour area. Dominion Mus. Rec (New Zealand): 3:145-218.

Køie, M. 1986. The life-history of *Mesorchis denticulatus* (Rudolphi, 1802) Dietz, 1909 (Trematoda, Echinostomatidae). Zeitschr. f. Parasitenk. 72:335-343.

Kontrimovitschus, V. L., & T. L. Bakhmet'eva. 1960. [Helminths occurring in *Gavia* in the lowlands of the River Lena] Trudy gelmint. Lab. 10:124-133. In Russian).

Kuroda, N. 1954. On the classification and phylogeny of the order Tubinares, particularly the shearwaters *(Puffinus)*, with special considerations on their osteology and habit differentiation (Aves). Herald Co., Ltd., Tokyo, Japan.

Laberge, R. J. A. & J. D. McLaughlin. 1989. *Hyalella azteca* (Amphipoda) as an intermediate host of the nematode *Streptocara crassicauda*. Can. J. Zool. 67:2335-2340.

Lambrecht, K. 1933. Handbuch der Palaeornithologie. Berlin: Gebrüder Borntraeger.

Leonov, V. A., O. I. Belogurov, N. M. Shagvaleeva, and S. K. Bondarenko. 1965. [On the trematode fauna of piscivorous birds in Kamtchatka.] (In Russian.) pp. 130-158, plus addendum following p. 349. In Leonov, V. A. [Papers on helminthology presented to Prof. A. A. Sobolev on the 40th anniversary of his scientific and teaching activities.] (In Russian.) Vladivostok. Not seen.

Linton, E. 1928. Notes on the trematodes of birds. Proc. U. S. Natl. Mus. 73: 1-36.

Livezey, B. C. 1988. Morphometrics of flightlessness in the Alcidae. Auk 105:681-698.

Lowther, J. K., & D. M. Wood. 1964. Specificity of a Black Fly, *Simulium euryadminiculum* Davies, toward its host, the Common Loon. Canad. Ent.   96:911-913.

Madsen, F. J. 1957. On the food habits of some fish-eating birds of Denmark.   Divers, grebes, mergansers, and auks. Danish Rev. Game Biol. 3(2):19-83

Mahoney, S. A., and J. R. Jehl, Jr. 1985. Avoidance of salt-loading by a diving bird at a hypersaline and alkaline lake: Eared Grebe. Condor 87:389-397.

Malakhova, R. P. 1985. On the cestode fauna of certain lamellirostral birds of Karelia. p. 92-104. In: Shulman, S. S. , and R. P. Malakhova (Eds.) (in Russian). Ekologiya Paraziticheskikh organizunov Acad. Sci. Karelian Branch, Petrozavodsk.

Martin, L.D. & J. Tate, Jr. 1976. The skeleton of *Baptornis advenus* (Aves: Hesperornithiformes. Smiths. Contrib. Paleobiol. No. 27: 35-66.

Maximova, A. P. 1981. [Morphology and developmental cycle of the cestode *Confluaria podicipina* (Szymanski, 1905) (Cestoda: Hymenolepididae).] (In Russian with English summary.) Parazitologiya (Leningr.)15:325-331.

McDonald, M. E. 1969. Catalogue of helminths of waterfowl (Anatidae). U.S. Dept. Interior, Bureau Sport Fisheries and WIldlife.Spec. Sci. Rept. — WIldlife no. 126. Washington, D.C. viii+692 pp.

McIntyre, J.W. 1988. The Common Loon, spitrit of northern lakes. Univ. Minnesota Press, Minneapolis. xii + 229 pp.

McIntyre, J.W. & J.F. Barr. 1997. Common Loon *(Gavia immer)*. *In* The Birds of North America, No. 313 (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, PA and The American Ornithologists' Union, Washington, D.C.

Measures, L.N. 1988a. The development of *Eustrongylides tubifex* (Nematoda: Dioctophymatoidea) in oligochaetes. J. Parasitol. 74:294-304.

Measures, L.N. 1988b, Epizootiology, pathology, and description of *Eustrongylides tubifex* (Nematoda: Dioctophymatoidea) in fish. Can. J. Zool. 66:2212-2222.

Measures, L.N. 1988c. The development and pathogenesis of *Eustrongylides tubifex* (Nematoda: Dioctophymatoidea) in piscivorous birds. Can. J. Zool. 66:2223-2232.

Merrie, T.D.H. 1996. Black-throated Diver feeding on Common Frogs. Scottish Birds 18:253.

Moum, T, S. Johansen, K.E. Erikstad, & J.F. Piatt. 1994. Phylogeny and evolution of the auks (subfamily Alcinae) based on mitochondrial DNA sequences. Proc. Natl. Acad. Sci. USA. 91:7912-7916.

Mourer-Chauviré, C. 1996. Paleogene Avian Localities of France. In J. Mlikovsky (Ed.) Tertiary Avian Localities of Europe. Acta Univ. Carolinae, Praha. 39 (1995): 567-598.

Nasir, P, & J.V. Scorza. 1968. Studies on freshwater larval trematodes. XVIII. The life cycle of Stephanoprora denticulata (Rudolphi, 1802) Odhner, 1910. Zeitschr. f. Parasitenk.30: 134-148.

Nessov, L.A. 1992. Mesozoic and Paleogene birds of the USSR and their paleoenvironments. Papers in Avian Paleontol. honoring Pierce Brodkorb. Sci Ser. 36, Nat. Hist. Mus. Los Angeles Co.:465-478.

Niewiadomska, K. 1984. Present status of Diplostomum spathaceum (Rudolphi, 1819) and differentiation of Diplostomum pseudospathaceum nom. nov. Trematoda: Diplostomidae). Syst. Parasitol. 6: 81-86.

North, M.R. 1994. Yellow-billed Loon (Gavia adamsii). In The Birds of North America, No. 121 (A. Poole and F. Gill, Eds.). Philadelphia: Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Odening, K. 1963. Strigeida aus Vögeln des Berliner Tierparks. Angew. Parasitol. 4(3):171-182.

Ogilvie-Grant, W.R. 1898. Catalogue of the birds in the British Museum, 26 (part) Order XVIII Pygopodes. Pp 485-558.

Okulewicz, A. 1989. [Gastrointestinal nematodes of Gavia stellata and Gavia arctica (Gaviidae)] (in Polish with English summary.). Wiadomosci Parazytologiczne 35(1): 35-42.

Okulewicz, J. 1984. [Bird trematodes of Lower SIlesia. II. Intestinal trematodes of Red-throated Diver (Gavia stellata (Pont.). Wiadomosci Parazytologiczne 30(4): 503-519.

Olson, S.L. 1985. The fossil record of birds. Pp. 79-238, in Farner, D.S., J.R. King, and K.C. Parkes. Avian Biology. Vol. 8. Academic Press, New York, London, etc.

Olson, S.L. 1992. Neogaeornis wetzeli Lambrecht, a Cretaceous loon from Chile (Aves: Gaviidae). J. Vert. Paleontol. 12:122-124.

Olson, S.L. 1995. Thiornis sociata Navás, a nearly complete miocene grebe (Aves Podicipedidae). Courier Forschungsinst. Senkenberg 181:131-140.

Olson, S.L., & P.C. Rasmussen. 2001. Miocene and Pliocene birds from the Lee Creek Mine, North Carolina. Pp. 233-365. In C.F. Ray and D.J. Bohaska, eds. Geology and Paleontology of the Lee Creek Mine, North Carolina III. Smiths. Contrib. Paleobio. No. 90.

Palmer, R.S. (Ed.) 1962. Handbook of North American Birds. Vol. 1. Loons through Flamingos. Yale Univ. Press, New Haven and London.

Pearse, V., J. Pearse, M. Buchsbaum, & R. Buchsbaum. 1987. Living Invertebrates. Blackwell Scientific Publs., Palo Alto, Ca, and The Boxwood Press, Pacific Grove, CA.

Peterson, P.C. 1971. A revision of the feather mite genus Brephosceles (Proctophyllodidae: Alloptinae). Bull. Univ. Nebraska State Mus. 9(4):88-172.

Piersma, T., & M.R. Van Eerden. 1989. Feather eating in Great Crested Grebes Podiceps cristatus: a unique solution to the problems of debris and gastric parasites in fish-eating birds. Ibis 131:477-486.

Prager, E.M. & A.C. WIlson. 1980. Phylogenetic relationships and rates of evolution in birds. Acta XVII Congr. Internatl. Ornithol. Pp. 1209-1214.

Rausch, R.L., F.H. Fay, & F.S.L. Williamson. 1990. The ecology of Echinococcus multilocularis (Cestoda: Taeniidae) on St. Lawrence Island, Alaska. II. Helminth populations in the definitive host. Ann. Parasitol. Hum. Comp., 65: 131-140.

Remsen, J.V., Jr. 1995. The importance of continued collecting of bird specimens to ornithology and bird conservation. Bird Conservation Internatl. (1995) 5:1455-180.

Rubega, M. A., D. Schamel, & D. M. Tracy. 2000. Red-necked Phalarope (Phalaropus lobatus) In The Birds of North America, No. 538 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Ryzhikov, K. M., B. Rysavy, I.G. Khokhlova, L.M. Tolkatcheva, & V.V. Kornyuchin. 1985. Helminths of fish-eating birds of the Palaearctic region. 2. Cestoda and Acanthocephala. Akademiya Nauk USSR and Czechoslovak Acad. Sci., Moscow and Prague.

Schmidt, G.D. 1986. CRC Handbook of tapeworm identification. CRC Press, Inc., Boca Raton, Fla. 675 pp.

Shigin, A.A. 1957. [Parasitic worms of heron and grebe of the Rybinsk Reservoir.] (In Russian.) Trudy Darvinsk. Gosudarstv. Zapovedn. (4):245-289.

Shufeldt, R.W. 1915. Fossil birds in the Marsh collection of Yale Univ. Trans. Conn. Acad. Arts Sci. 19-110.

Sibley, C.G., & J.E. Ahlquist. 1990. Phylogeny and classification of birds. xxiii + 976 pp. Yale Univ. Press, New Haven and London.

Sinclair, N.R. 1971a. Studies on the heterophyid trematode Apophallus brevis, the "sand-grain grub" of yellow perch (Perca flavescens). 1. Redescription and resolution of synomyic conflict with Apophallus imperator Lyster, 1940 and other designations. Can. J. Zool. 50(3): 357-364. (Get.)

Sinclair, N.R. 1971b. Studies on the heterophyid trematode Apophallus brevis, the "sand-grain grub" of yellow perch (Perca flavescens). 2. The metacercaria: position, structure, and composition of the cyst: hosts; geographical distribution and variation. ibid. 50(5):577-584.

Sinclair, N.R. 1971c. A reviewal of Odhneria odhneri Travassos, 1921 (Trematoda: Microphallidae). J. Parasitol. 57:980-982.

Skov, H., J. Durinck, M.F. Leopold, & M.L. Tasker. 1995. Inportant bird areas for seabirds in the North Sea. BirdLife International, Cambridge, UK.

Skov, H., & E. Prins. 2001. The impact of estuarine fronts on the dispersal of piscivorous birds in the German Bight. Marine Ecol. Progress Ser. 214: 279-287.

Spasskaya, L.P., & E.M. Ivakina. 1973. [Cestodes of Gaviiformes, Colymbiformes, and Procellariiformes from Koryaksk national district.] pp. 79-92. In Spasskii, A. A. [Ed.] [Parasites of animals and plants.] Shtüntza, Kishinov. Vol. 9. 1-304. In Russian.

Stedman, S.J. 2000. Horned Grebe (Podiceps auritus). In The Birds of North America, No. 505 (A. Poole and F. Gill, eds.). The Birds of North America, Inc. Philadelphia, PA.

Stock, T.M. 1985. Patterns of community ecology and coevolution of intestinal helminths of grebes. Ph. D. Thesis, Univ. Alberta. xvi +213 pp.

Stock, T.M., & J.C. Holmes. 1987. Host specificity and exchange of intestinal helminths among four species of grebes (Podicipedidae). Can. J. Zool. 65:669-676.

Stolpe, M. 1935. Colymbus, Hesperornis, Podiceps: ein Vergleich ihrer hinteren extremität. J, f. Ornithol 83: 115-128.

Storer, R.W. 1956. The fossil loon, Colymboides minutus. Condor 58:413-426.

Storer, R.W. 1960. Evolution in the diving birds. Proc. XII Internat. Ornithol. Congr., Helsinki. Pp. 694-707.

Storer, R.W. 1966. Sexual dimorphism and food habits in three North American accipiters. Auk 83: 423-436.

Storer, R.W. 1967. Observations on Rolland's Grebe. Hornero 10:339-350.

Storer, R.W. 1969. The behavior of the Horned Grebe in spring. Condor 71:180-205.

Storer, R.W. 1971. The behaviour of the New Zealand Dabchick. Notornis 18: 175-186.

Storer, R.W. 1978. Systematic Notes on the Loons (Gaviidae: Aves). Breviora. Mus. Comp. Zool. No. 448, pp. 1-8.

Storer, R.W. 1979. Order Gaviiformes In Check-list of birds of the world Vol. 1, 2nd. Ed. pp. 135-139. (E. Mayr and G. W. Cottrell eds.) Mus. Comp. Zool.; Cambridge, MS.

Storer, R.W. 1988. Variation in the Common Loon (Gavia immer). Pap. 1987 Confer. Common Loon Res. and Management. Pp 54-65.

Storer, R.W. 2000. The metazoan parasite fauna of grebes (Podicipediformes) and its relationship to the birds' biology. Misc. Publs. Mus. Zool. Univ. Mich. No 188. iv + 90 pp.

Svec, P. 1982. Two new species of diving birds from the Lower Miocene of Czechoslovakia. Casopis mineral. geol. 27: 243-260.

Thomas, G., S.S. Seidel, & W. Boeckeler. 1999. Considerations about

the ontogenesis of *Reighardia sternae* in comparison with *Raillietiella* sp. (Pentastomida: Cephalobaenida). Parasitol. Res. 85(4): 280-283.

Uchida, A., K. Uchida, H. Itagaki, & S. Kamegai. 1991. Check list of helminth parasites of Japanese birds. Japan J. Parasitol. 40(1):7-85.

Vande Vusse, F. J. 1980. A review of the genus *Dentritobilharzia* Skrjabin & Zakharow 1920 (Trematoda: Schistosomatidae). J. Parasitol. 66:814-819.

Van Tuinen, M., D.B. Butvill, J.A.W. Kirsch, & S.B. Hedges. 2001. Convergence and divergence in the evolution of aquatic birds. Proc. Roy. Soc. London. 268: 1345-1350.

Vasileva, G.P., B.B. Georgiev, & T. Genov. 1999a. Palaearctic species of the genus *Confluaria* Ablasov (Cestoda, Hymenolepididae): a redescription and synonymy of *C. capillaris* (Rudolphi). Systematic Parasitol. 43: 49-57.

Vasileva, G.P., B.B. Georgiev, & T. Genov. 1999b. Palaearctic species of the genus *Confluaria* Ablasov (Cestoda, Hymenolepididae): redescriptions of *C. multistriata* (Rudolphi, 1810) and *C. japonica* (Yamaguti, 1935), and a description of *Confluaria* sp. Systematic Parasitol. 44:87-103.

Vasileva, G.P., B.B. Georgiev, & T. Genov. 2000. Palaearctic species of the genus *Confluaria* Ablasov (Cestoda, Hymenolepididae): redescriptions of *C. podicipina* (Szymanski, 1905) and *C. furcifera* (Krabbe, 1869), and description of *C. pseudofurcifera* n. sp., a key and final comments. Systematic Parasitol. 45: 109-130.

Vlug, J.J., & J. Fjeldså. 1990. Working bibliography of grebes of the world with summaries of current taxonomy and of distributional status. Zool. Mus. Univ. Copenhagen. 210 pp.

Voous, K.H. 1960. Atlas of European BIrds. Thos. Nelson & Sons, Ltd., London.

Warren, B.H. 1953. A new type of metacercarial cyst of the genus *Apophallus,* from the perch, *Perca flavescens,* in Minnesota. Amer. Midland Nat. 50:397-401.

Wilcox, H.H. 1952. The Pelvic Musculature of the Loon, *Gavia immer.* Amer Midland Nat. 48:513-573.

Wong, P.L. & R.C. Anderson. 1982a. Redescription of *Paracuaria adunca* (Creplin, 1846) (Nematoda: Acuarioidea) from *Larus delawarensis* Ord (Laridae). Canad. J. Zool. 60: 175-179.

Wong, P.L. & R.C. Anderson. 1982b. The transmission and development of *Cosmocephalus obvelatus* (Nematoda: Acuarioidea) of gulls (Laridae). Canad. J. Zool. 60: 1426-1440.

Wood, D. S., & G. D. Schnell. 1986. Revised World Inventory of Avian Skeletal Specimens. 1986. 296 pp. Amer. Ornithol. Union and Okla. Biol. Survey, Norman, Okla.

Wood, D.S., R.L. Zusi, & M.A. Jenkinson. 1982. World Inventory of Avian Spirit Specimens. 1982. xxix + 181 pp. Amer. Ornithol. Union and Okla. Biol Survey, Norman, Okla.

Yamaguti, S. 1958. Systema Helminthum, vol. 1. The digenetic trematodes of vertebrates. Pts. 1 & 2. xi + 1575 pp. Interscience Publ. Inc. New York, London.

Yamaguti, S. 1959. Systema Helminthum, vol.2. vii + 860 pp. The cestodes of vertebrates. Interscience Publ. Inc. New York, London.

Yamaguti, S. 1961. Systema Helminthum, vol. 3. Pts. 1 & 2, 1261 pp. The nematodes of vertebrates. Interscience Publ. Inc. New York, London.

Yamaguti, S. 1963. Systema Helminthum, vol. 5. Acanthocephala. vii + 423 pp. Interscience Puble. inc. J. Wiley & Sons. New York.

Yamaguti, S. 1971. Synopsis of Digenetic Trematodes of Vertebrates. Vol. 1. 1074 pp. Keigaku Publ. Co. Tokyo.

Yamaguti, S. 1975. A Synoptical Review of Life Histories of Digenetic Trematodes of Vetebrates with Special Reference to the Morphology of their Larval Forms. 590 pp. + 219 pls. Keigaku Publ. Co. Tokyo.

Zitnan, R. 1966. Die Trematoden des Flusses Hron. Helminthologia 7(3/4): 201-220.

Zusi, R.L. & R.W. Storer. 1969. Osteology and myology of the head and neck of the pied-billed grebes (*Podilymbus*). Misc. Publ. Mus. Zool. Univ. Michigan No. 139, pp. 1-49.

APPENDIX A

LIST OF LOONS AND THEIR MULTICELLULAR PARASITES

Parasites of *Gavia stellata*

DIGENEANS
Echinostomidae
  Echinochasmus skrjabini Oshmarin, 1946
  Echinochasmus spinulosus (Rudolphi, 1809)
  Echinoparyphium baculus (Diesing, 1850)
  Petasiger coronatus Mendheim, 1940
Cyathocotylidae
  Paracoenogonimus ovatus Katsurada, 1914
Diplostomidae
  Diplostomum gavium (Guberlet, 1922)
  Diplostomum pseudospathaceum Niewiadomska, 1984
  Diplostomum spathaceum (Rudolphi, 1819)
  Tylodelphys immer (Dubois, 1961)
Strigeidae
  Ichthyocotylurus erraticus (Rudolphi, 1809)
  Ichthyootylurus platycephalus (Creplin, 1825)
Opisthorchidae
  Amphimerus arcticus Kontrimovitschus & Bakhmet'eva, 1960
  Erschoviorchis lintoni (Gower, 1939)
  Euamphimerus sibiricus Kontrimovitschus & Bakhmet'eva. 1960
  Metorchis intermedius Heinemann, 1937
  Metorchis xanthosomus (Creplin, 1846)
Heterophyidae
  Apophallus muehlingi (Jägerskiöld, 1889)
  Cryptocotyle concava (Creplin, 1825)
  Cryptocotyle lingua (Creplin, 1825)
  Pygidiopsis genata Looss, 1907
  Stellantchasmus falcatus Onji & Nishio, 1915
Renicolidae
  Renicola keimahuri Yamaguti 1939
  Renicola pinguis (Mehlis, 1846)
  Renicola pollaris Kontrimovitschus & Bakhmet'eva, 1960

CESTODES
Diphyllobothriidae
  Digramma interrupta (Rudolphi, 1810)
  Diphyllobothrium ditremum (Creplin, 1825)
  Ligula intestinalis (Linnaeus, 1758)
  Schistocephalus solidus (Mueller, 1776)
Tetrabothriidae
  Tetrabothrius macrocephalus ((Rudolphi, 1810)
Dilepididae
  Anomotaenia ciliata Fuhrmann, 1913
  Neovalipora parvispine (Linton, 1927)
Hymenolepididae
  Dubininolepis fuhrmanni (Skrjabin & Matevossian, 1942)
  Dubininolepis rostellatus (Abildgaard, 1790)
  Dubininolepis swiderskii (Gasowska, 1932)
  Nadjedolepis paranitidulans (Golikova, 1959)

ACANTHOCEPHALANS
Polymorphidae
  Andracantha mergi (Lundström, 1941)
  Andracantha phalacrocoracis (Yamaguti, 1939)
  Corynosoma clavatum Goss, 1940
  Polymorphus acutis Van Cleave & Starrett, 1940
  Polymorphus magnus Skrjabin, 1913
  Polymorphus phippsi Kostylev, 1922

NEMATODES
Dioctophymatidae
  Eustrongylides tubifex (Nitzsch, 1819)
Trichuridae
  Baruscapillaria mergi (Madsen, 1945)
Syngamidae
  Syngamus arcticus Ryzhikov, 1952
Anisakidae
  Contracaecum rudolphii Hartwich, 1964
  Contracaecum variegatum (Rudolphi (1809)
Acuariidae
  Paracuaria adunca (Creplin, 1846)
  Ingliseria cirrohamata (Linstow, 1888)
  Stegophorus stellaepolaris (Parona, 1901)
  Streptocara crassicauda (Creplin, 1829)
Dracunculidae
  Avioserpens galliardi Chabaud & Campana, 1949

LICE
Philopteridae
  Craspedonirmus colymbinus (Denny, 1842)

Parasites of *Gavia pacifica*

DIGENEANS
Echinostomidae
  Echinochasmus coaxatus Dietz, 1908
  Echinochasmus skrjabini Oshmarin, 1946
  Echinochasmus spinulosus (Rudolphi, 1809)
Strigeidae
  Cardiocephaloides brandesii (Szidat, 1928)
Heterophyidae
  Heterophyopsis continua (Onji & Nishio, 1916)
  Pygidiopsis summa Onji & Nishio, 1916

CESTODES
Tetrabothridae
  Tetrabothrius macrocephalus (Rudolphi, 1810)

LEECHES
Glossiphoniidae
  Theromyzon trizonare Davies & Oosthuizen, 1993

LICE
Philopteridae
  Craspedonirmus colymbinus (Denny, 1842)

Parasites of *Gavia arctica*

DIGENEANS
Echinostomidae
  Echinochasmus spinulosus (Rudolphi, 1809)
  Mesorchis denticulatus (Rudolphi, 1802)
Diplostomidae
  Diplostomum gavium (Guberlet, 1922)
  Tylodelphys glossoides (Dubois, 1928)
Strigeidae
  Ichthyocotylurus erraticus (Rudolphi, 1809)
Heterophyidae
  Apophallus muehlingi (Jägerskjöld, 1889)
  Cryptocotyle cryptocotyloides (Isiaschikov, 1923)

CESTODES
Diphyllobothriidae

Digramma interrupta (Rudolphi, 1810)
Diphyllobothrium ditremum (Creplin, 1825)
Tetrabothriidae
    Tetrabothrius macrocephalus (Rudolphi, 1810)
Hymenolepididae
    Dubininolepis rostellatus (Abildgaard, 1790)
    Microsomacanthus paracompressa (Czaplinski, 1956)
    Microsomacanthus simulans (Joyeux & Baer, 1941)

ACANTHOCEPHALANS
Polymorphidae
    Pollymorphus acutis Van Cleave & Starrett, 1940
    Polymorphus phippsi Kostylev, 1922
NEMATODES
Dioctophymatidae
    Eustrongylides tubifex (Nitzsch, 1819)
Trichuridae
    Baruscapillaria mergi (Madsen, 1945)
Anisakidae
    Contracaecum rudolphii Hartwich, 1964
Acuariidae
    Paracuaria adunca (Creplin, 1846)

MITES
Alloptidae
    Brephosceles forficiger (Megnin & Trouessart, 1884)

LICE
Philopteridae
    Craspedonirmus colymbinus (Denny, 1842)

Parasites of *Gavia pacifica* and/or *arctica*

DIGENEANS
Echinostomidae
    Echinochasmus coaxatus Dietz, 1909
    Echinoparyphium baculus (Diesing, 1850)
    Mesorchis polycestus (Dietz, 1909)
Microphallidae
    Levinseniella brachysoma (Creplin, 1837)
Eucotylidae
    Eucotyle cohni Skrjabin, 1924
    Eucotlye nephritica (Mehlis in Creplin, 1846)

CESTODES
Diphyllobothriidae
    Schistocephalus solidus (Mueller, 1776)
Dilepididae
    Lateriporus skrjabini Matevossian, 1946
    Neovalipora parvispine (Linton, 1927)
    Paradilepis urceus (Wedl, 1855)
Hymenolepididae
    Biglandatrium biglandatrium Spasskya, 1961
    Dubininolepis fuhrmanni (Skrjabin & Matevossian, 1942)
    Dubininolepis swiderskii (Gasowska, 1932)
    Microsomacanthus paramicrosoma (Gasowska, 1931)

ACANTHOCEPHALANS
Polymorphidae
    Polymorphus gavii Khokhlova, 1965
    Polymorphus magnus Skrjabin, 1913
    Polymorphus minutus (Goeze, 1782)
    Polymorphus obtusus Van Cleave, 1918

NEMATODES
Trichuridae
    Baruscapillaria carbonis (Rudolphi, 1819)
Acuariidae

Cosmocephalus obvelatus (Creplin, 1825)
Ingliseria cirrohamata (Linstow, 1888)
Streptocara crassicauda (Creplin, 1829)
Dracunculidae
    Avioserpens mosgovoyi Supryaga, 1965

Parasites of *Gavia immer*

DIGENEANS
Psilostomidae
    Pseudopsilostoma varium (Linton, 1928)
Cathaemasiidae
    Ribeiroia ondatrae (Price, 1931)
Echinostomidae
    Echinochasmus skrjabini Oshmarin 1946
    Echinochasmus spinulosus (Rudolphi, 1809)
    Echinostoma revolutum (Froelich, 1802)
    Himasthla alincia Dietz, 1909
    Mesorchis denticulatus (Rudolphi, (1802)
    Microparyphium facetum Dietz, 1909
Philophthalmidae
    Parorchis acanthus (Nicoll, 1906)
Clinostomidae
    Clinostomum complanatum (Rudolphi, 1814)
Schistosomatidae
    Austrobilharzia terrigalensis Johnston, 1917
    Dendritobilharzia pulverulenta (Braun, 1901)
Cyathocotylidae
    Mesostephanus appendiculatoides (Price, 1934)
Diploostomidae
    Diplostomum gavium (Guberlet, 1922)
    Posthodiplostomum minimum (Macallum, 1921)
    Tylodelphys immer (Dubois 1961)
Strigeidae
    Ichthyocotylurus erraticus (Rudolphi, 1809)
    Ichthyocotylurus platycephalus (Creplin, 1825)
Opisthorchidae
    Amphimerus arcticus Kontrimovitschus & Bakhme'teva
    Erschoviorchus lintoni (Gower, 1939)
    Plotnikovia fodiens (Linton, 1928)
Heterophyidae
    Apophallus brevis Ransom, 1920
    Cryptocotyle concava (Creplin, 1825)
    Cryptocotyle lingua (Creplin, 1825)
    Phagicola longus Ransom, 1920
    Stictodora lariformicola Sogandares-Bernal & Walton, 1965
Renicolidae
    Renicola pollaris Kontrimovitschus & Bakhmet'eva, 1960
Microphallidae
    Microphallus forresteri Kinsella & Deblock, 1997
    Microphallus nicolli (Cable & Hunninen, 1938) Baer, 1944
    Odhneria odhneri Travassos,1921
Prosthogonimidae
    Prosthogonimus ovatus (Rudolphi, 1803)
Eucotylidae
    Tanaisia fedtschenkoi Skrjabin, 1924

CESTODES
Diphyllobothriidae
    Diphyllobothrium ditremum (Creplin, 1825)
    Schistocephalus solidus (Mueller, 1776)
Tetrabothriidae
    Tetrabothrius macrocephalus (Rudolphi, 1810)
Dilepididae
    Cyclustera ibisae (Schmidt & Bush, 1972)
    Neovalipora parvispine (Linton, 1927)
    Paricterotaenia ransomi (Linton, 1927)
Hymenolepididae

Drepanidotaenia lanceolata (Bloch, 1782)
Dubininolepis pseudorostellatus (Joyeux & Baer,1950)
Dubininolepis rostellatus (Abildgaard, 1790)

ACANTHOCEPHALANS
Polymorphidae
Andracantha gravida (Alegret, 1941)
Andracantha phalacrocoracis (Yamaguti, 1939)
Corynosoma anatarium Van Cleave, 1945
Polymorphus brevis (Van Cleave, 1916)
Southwellina hispida (Van Cleave, 1925)

NEMATODES
Dioctophymatidae
Eustrongylides tubifex (Nitzsch, 1819)
Trichuridae
Baruscapillaria mergi (Madsen, 1945)
Syngamidae
Cyathostoma phenisci (Baudet, 1937)
Anisakidae
Contracaecum variegatum (Rudolphi, 1809)
Acuariidae
Cosmocephalus obvelatus (Creplin, 1825)
Paracuaria adunca (Creplin, 1846)
Stegophorus diomedeae (Johnston & Mawson, 1942)
Streptocara crassicauda (Creplin, 1829)
Streptocara formosensis Sugimoto, 1930
Ancyracanthidae
Sciadocara rugosa Schmidt & Kinsella, 1972
Onchocercidae
Splendidofilaria faillisensis (Anderson, 1954)

MITES
Alloptidae
Brephosceles forficiger (Megnin & Trouessart, 1884)

LICE
Philopteridae
Craspedonirmus immer Emerson, 1955

FLIES
Simuliidae
Simulium euryadminiculum Davies, 1949
Hippoboscidae
Pseudolfersia fumipennis (Sahlberg)

Parasites of *Gavia adamsii*

DIGENEANS
Diplostomidae
Diplostomum gavium (Guberlet, 1922)
Tylodelphys immer (Dubois, 1961)
Strigeidae
Ichthyocotylurus erraticus (Rudolphi, 1809)

CESTODES
Diphyllobothriidae
Diphyllobothrium ditremum (Creplin, 1825)
Tetrabothriidae
Tetrabothrius macrocephalus (Rudolphi, 1810)
Hymenolepididae
Dubininolepis fuhrmanni (Skrjabin & Matevossian, 1942)

ACANTHOCEPHALANS
Polymorphidae
Polymorphus gavii Khokhlova, 1965

NEMATODES
Anisakidae
Contracaecum rudolphi Hartwich, 1964

APPENDIX B

ADDENDA TO THE PARASITES OF GREBES STORER (2000)

New species described. (These were not included in the numbers of species used in the analyses in Storer 2000 or this paper).

Hymenolepididae
Confluaria krabbei Vasileva, Kornyushin, and Genov. 2001b. In *Tachybaptus ruficollis*, type host. This is the *Confluaria* sp. in Vasileva, Georgiev, and Genov, 1999. Small intestine. FW. Eurasia. Intermed. hosts?
Confluaria pseudofurcifera Vasileva, Georgiev, and Genov. 2000. In *Podiceps* (=*Tachybaptus*) *ruficollis*. Type host. In small intestine. FW. Eurasia. Intermed. hosts?
Dollfusilepis grisegenicus Vasileva, Kornyushin, and Genov. 2001a. In *Podiceps grisgena*, type and only known host. Known only from original description (5). Small intestine. FW. Eurasia. Intermed. hosts?

These add three species to the list of known parasites of grebes, including two in the list known to parasitize *T. ruficollis* and one to the list for *P. grisegena*.

NEW AND AMENDED REFERENCES

Vasileva, G. P. & B. B. Georgiev. 1999. Cestode communities in non-breeding populations of four grebe species (Aves: Podicipedidae) from the Bulgarian Black Sea Coast. Parasite 6:249-258.

Vasileva, G.P., B.B. Georgiev, & T. Genov. 1999. Palaearctic species of the genus *Confluaria* Ablasov (Cestoda, Hymenolepididae): redescriptions of *Confluaria multistriata* (Rudolphi, 1810) and *Confluaria japonica* (Yamaguti, 1935), and a description of *Confluaria* sp. Systematic Parasitol. 44: 87-103.

Vasileva, G.P., B.B. Georgiev, & T. Genov. 2000. Palaearctic species of the genus *Confluaria* Ablasov (Cestoda, Hymenolepididae): redescriptions of *Confluaria podicipina* (Szymanski, 1905) and *Confluaria furcifera* (Krabbe, 1869), and description of *Confluaria pseudofurcifera* n. sp., a key and final comments. Systematic Parasitol. 45: 109-130.

Vasileva, G.P., V.V. Kornyushin, & T. Genov. 2001a. Hymenolepidid cestodes from grebes (Aves: Podicipedidae) in Ukraine: the genera *Dollfusilepis* and *Parafimbriaria*. Vestnik zoologii. 35(2): 3-14.

Vasileva, G.P., V.V. Kornyushin, & T. Genov. 2001b. Hymenolepidid cestodes in grebes (Aves: Podicipedidae) in Ukraine: the genus *Confluaria* Ablasov in Spasskaya, 1966. Vestnik zoologii. 35(6): 13-31. [This reference includes redescriptions of *Confluaria capillaris*, *Confluaria flurcifera*, *Confluaria multistriata*, *Confluaria podicipina*, and *Confluaria pseudofurcifera* and the description of *Confluaria krabbei* sp. n. (syn. *Confluaria* sp. from Vasileva, Georgiev, & Genov, 1999b) from *Tachybaptus ruficollis*].

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For ease in finding species in the general accounts of parasites and of loons in the the lists of 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 list of parasites of the loon species. Other entries are in plain text. Subjects in the table of contents, the 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. 2)