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The Helminth Fauna of Sympatric Anas Species
at Barberspan, Republic of South Africa.

Simon J. Alexander

A
Thesis
in the
Department
of
Biology

Presented in partial fulfilment
of the requirements for the degree
of Master of Science at
Concordia University
Montreal, Quebec, Canada

January, 1995

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ABSTRACT

The Helminth Fauna of Sympatric Anas Species
at Barberspan, Republic of South Africa

Simon J. Alexander

The examination of the helminth fauna of four waterfowl species; Anas undulata, Anas erythrorhyncha, Anas capensis and Anas smithii, collected at Barberspan, Republic of South Africa, revealed 34 species of helminths. Some of these species have been recorded from holarctic waterfowl, however, 10 of the 23 cestode species encountered appear to be new. Three cestode taxa, including new species in the genera Microsomacanthus and Echinocotyle, and a new genus of the Fimbriariinae, are described in this study.

The magnitude of helminth infections varied within the host community. Anas undulata and A. erythrorhyncha exhibited impoverished communities with relatively few species present, and their helminth communities were dominated by digeneans and nematodes. This differed from the fauna of Anas capensis and A. smithii which exhibited species - rich communities with large numbers of worms present, dominated by cestodes. A dichotomy also existed between the latter two species based upon cestode species composition in their helminth fauna.

The differences in the magnitude and diversity of the helminth fauna among host species are primarily due to diet.

Anas capensis and A. smithii are carnivorous and prey on entomostracan crustaceans that serve as intermediate hosts for the majority of the helminths encountered. As the diet and feeding zones of these species overlap, differences in their helminth communities presumably reflect high host specificity for particular helminths. Anas undulata and A. erythrorhyncha consume relatively few entomostracans resulting in lighter infections.

Analysis of the compound community suggests that A. capensis and A. smithii play an important role in maintaining the local infective pool, however, as A. undulata and A. erythrorhyncha have different diets and display limited overlap with foraging sites, their influence on the infective pool is limited.

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INTRODUCTION

The magnitude and diversity of the helminth (worm parasite) fauna that exists within a particular host community is influenced by evolutionary and ecological factors (Janovy et al., 1992). In general, "the presence of a parasite species, in a sample of host individuals, is considered to be an evolutionary phenomenon, but the parasite's population structure is considered to be an ecological one" (Janovy et al., 1992). Therefore, a group of parasite species may occur in sympatric hosts because these hosts share evolutionary histories, or share biochemical/physiological characteristics that may or may not reflect common ancestry, or simply occupy a common habitat as generalist parasites (Janovy et al., 1992).

In reviewing the community ecology of helminths, Bush et al. (1990) observed that the "habitat of the host is more important in determining community richness than is host phylogeny". Specific factors deemed essential for the production of diverse helminth communities included the complexity and physiology of the host alimentary canal, host vagility, broad host diet, selective feeding by the host on prey that serves as the intermediate host for a wide variety of helminths, and exposure of the host to helminths with direct life cycles which enter by penetration (Kennedy et al., 1986).

Aquatic hosts are, on average, infected with a greater number of parasite species than terrestrial hosts and aquatic birds harbour the richest gastrointestinal helminth communities of all (Bush et al., 1990). Waterfowl (Order Anseriformes) have a particularly diverse helminth fauna. They are hosts to some 1,041 species of helminths including 288 cestode, 524 digenean, 177 nematode and 52 acanthocephalan species worldwide (McDonald 1969; 1974; 1981; 1988). Many more species have been described since. The diversity and wide geographic distribution of helminth species found in waterfowl, along with their tendency to infect a range of host species, make them interesting from a scientific standpoint both in terms of their potential roles as pathogens and as models for the ecological study and analysis of parasitological systems.

Most of the work on waterfowl helminths has involved holarctic species (McDonald, 1969). Extensive studies in the former Soviet Union, Europe and North America have formed the basis of our understanding of the helminth fauna of waterfowl. Most studies have been of a survey nature examining the diversity of waterfowl helminths in specific geographic regions. A smaller number of studies have assessed seasonal dynamics, community structure and patterns of exchange of parasites among and between host species, that have contributed to an overall understanding of the dynamics of helminth infections in migratory birds.

In contrast, comparatively little information on waterfowl helminths from the rest of the world is available. The existing information is scattered in sporadic reports of waterfowl helminths encountered in small numbers of hosts in more general parasitological surveys.

This generalization is particularly true of Africa, home to some 15 indigenous waterfowl species that are found mostly in the Ethiopian region. Twenty - two other species with broader distributions (in Europe, Asia Minor, and the Indian subcontinent) either include Africa as part of their normal range, or more commonly, occur as winter migrants in North Africa and the upper Nile valley (Peters, 1979). Contact between the two host groups is therefore limited.

Excluding schistosomes, only 66 helminth species have been reported from African waterfowl (Appendix 1). Ten helminth species are known only from the Ethiopian region (Appendix 2).

The objectives of this study were twofold. The first was to obtain a preliminary understanding of waterfowl helminths in South Africa by examining the helminth fauna of some indigenous Anas species. The second was to examine and compare helminth communities in sympatric host species and to determine the importance of each species in maintaining the overall helminth community.

The thesis is presented in two sections. Section 1 involves the analysis of the helminth communities

encountered in sympatric Anas species examined at the Barberspan Ornithological Research Station, Republic of South Africa. Section 2 deals with the identification and description of three new species encountered in this study.

Section I

LITERATURE REVIEW

Helminths in holarctic waterfowl

This review is based primarily upon North American studies but is generally applicable to waterfowl and their helminth populations throughout the holarctic region. Season, age and social status all have an effect on helminth infections in a particular species.

Holarctic waterfowl exhibit distinct seasonal migration patterns. Adult birds migrate to northern breeding grounds each spring, reproduce in the summer, and migrate, along with the juvenile cohort, to southern wintering grounds in the fall.

Typically, adults arrive on breeding grounds with light parasite loads. Both the magnitude and the diversity of these loads increases throughout the spring and early summer (Buscher, 1965; Crichton and Welch, 1972; McLaughlin and Burt, 1973; Neraasen and Holmes, 1975; Dejong, 1976; Birova et al., 1989a, 1989b, 1990; Spakulova et al., 1989, 1991; and others). This is due to: (1) the presence of overwintering stages [e.g. acanthocephalan cystacanths in amphipods (Podesta and Holmes, 1970), cestode cysticercoids (Valkounova, 1983; Kiselene, 1982) and digenean metacercariae in snails] and (2) new pools of infective larvae established by arriving ducks. Infection levels

increase throughout the summer and, in both adults and juveniles, the heaviest loads occur in late summer (Buscher 1965; Kotecki 1970).

In fall, the magnitude and diversity of infection in most ducks declines. This is due mainly to dietary change which results in decreased recruitment. Birds continue to lose helminths during their migration and on the southern wintering grounds (Buscher, 1965; Neraasen, 1970; McLaughlin and Burt, 1973; Wallace and Pence, 1986). Lost parasites are not replaced (Wallace and Pence, 1986). Possible reasons for this decline include: (1) the absence or insufficient numbers of intermediate hosts necessary for transmission; (2) a change in diet that eliminates or restricts contact with intermediate hosts; or (3) the lack of other definitive hosts which are major hosts for particular species.

Age also influences the helminth fauna. Young ducks tend to have heavier parasite loads than adults (Cornwell and Cowan 1963; Buscher, 1966; Wallace and Pence, 1986). This is attributable to the fact that their diet includes larger amounts of animal matter than adults (Cornwell and Cowan, 1963). The crustaceans and snails that comprise the majority of the animal food items also serve as intermediate hosts for most of the helminths found in waterfowl (McDonald, 1969). It has also been suggested that young birds, lacking previous exposure to helminths, have no acquired resistance and are therefore more susceptible to

infection (Bush, 1990).

Social status may also affect parasite loads. Gray et al. (1989) found that paired male mallard ducks (Anas platyrhynchos) had lighter parasite loads than unpaired males. They hypothesized that males spent more time protecting their mates and nesting territory, and less time feeding than unpaired males. They suggested that the differences between paired and unpaired birds reflected reduced recruitment.

Exchange of helminths between species

Wetlands are shared by a variety of waterfowl species and both spatial and dietary overlaps occur. As a consequence, many helminth species occur in several host species. Neraasen and Holmes (1975) introduced the concept of the "infective pool" in a study of the intestinal helminth communities of sympatric species of geese nesting in the Anderson River Delta. They observed that in a particular wetland, a variety of waterfowl species may share feeding and nesting areas. This overlap facilitates the formation of a common pool of infective stages in the intermediate host community. In this pool, the larvae of common helminth species that are readily shared among a number of host species will predominate. Other species that are more host specific, and occur in fewer host species, will be less abundant and form a smaller proportion of the

infective pool. The contribution of a particular host species to this pool depends on its local density and on the relative abundance of other species in the host community. Dominant species (i.e. those that occur in the greatest abundance) will, therefore, have the greatest influence on the composition of the infective pool and ultimately on the infections that develop within the local host community.

From other studies, it is evident that closely related species sharing a wetland are likely to have similar helminth faunas. In a study of pintails (Anas acuta), gadwall (A. strepera) and shoveller (A. clypeata) at Delta, Manitoba, Buscher (1965) found 27 species of helminths, of which 10 were common to all three host species and 7 were shared by two host species. Only 10 helminths were restricted to a single host species. Eighteen of the 20 helminth species found in blue - winged teal (A. discors) at Delta (Buscher, 1966) occurred in one or more of the host species in his previous study. Crichton and Welch (1972) analyzed the helminth fauna of mallards (A. platyrhynchos) and pintails at Delta and found that they shared 20 of 21 helminth species. Eleven of these were common to the fauna of dabbling ducks previously reported by Buscher (1965, 1966).

While several host species may be susceptible to particular helminths, they may not all be responsible for the maintenance or dispersal of these parasites in the

community, due to differential levels of infection. Species with typically light infection levels would be less important in the establishment or maintenance of a particular helminth species than would a host species with consistent and high levels of infection.

The magnitude and diversity of the helminth fauna, that a given species, or individual, within a community will acquire, depends on factors operating at the physiological and ecological level.

Physiological mechanisms associated with excystment and establishment of parasites in the definitive host are important in determining host specificity (Chappell, 1980). Cues for excystment appear to be relatively specific and are closely tied with the physicochemical factors within the host alimentary canal. In the case of cestodes, for example, physical factors affecting establishment include partial pressures of CO₂, pH and temperature, while biochemical factors include diet and bile composition (Smyth and McManus, 1989). It is therefore likely that closely related host species with similar diets and feeding behaviours should provide similar cues to parasites entering the gut. Furthermore, the helminth fauna in these species should display greater similarities than they would to species with different diets.

Ecological factors, particularly diet, foraging sites or behaviour, are also important determinants of host

specificity. A species that does not forage in the same microenvironment as other species, or does not feed on particular invertebrates which act as intermediate hosts for specific parasites, will exhibit differences in both the helminth species and levels of infection it will acquire. This was demonstrated by Laberge and McLaughlin (1991) in a study on Streptocara crassicauda (Nematoda: Acuariidae) in gadwall. Gadwall were highly susceptible to S. crassicauda in the laboratory. Infections are rarely seen in nature due to the fact that gadwalls seldom eat amphipods, which act as the intermediate host, beyond the first few weeks of life (McLaughlin and McGurk, 1987).

Host Biology and Ecology of Waterfowl in the Ethiopian region of Africa

The ecology of waterfowl in Africa differs from that of holarctic species. In North America, for example, the seasonal migration of waterfowl is under the influence of photoperiod. Consequently, mass, synchronous movements of birds occur over large distances at predictable times of the year (Owen and Black, 1990). In the Ethiopian region of Africa, the seasonal availability of water appears to be the more important determinant of waterfowl dispersal (Owen and Black, 1990). During the dry seasons, many ephemeral wetlands dry up, forcing birds to seek refuge on larger permanent water bodies. Consequently, concentrations of

birds occur on large permanent wetlands during the winter months and during the dry seasons. Dispersal of waterfowl from these areas occurs with the onset of the wet season, which may vary from year to year (Skead, 1977).

Banding studies in southern Africa have revealed that, while a few species exhibit long range movements, most restrict their movements to the Ethiopian region. Some species, like the southern pochard (Netta erythrophthalma), migrate long distances (up to 3000 km, mainly along the Nile valley). Egyptian geese (Alopochen aegyptiacus) migrate up to about 1100 km and, while primarily restricted to the Ethiopian region, also occur along the Nile Valley. However, the movements of the more common duck species, including those studied here, are more limited. The redbilled teal (Anas erythrorhyncha), Cape teal (Anas capensis), whitefaced duck (Dendrocygna viduata) and the South African shelduck (Tadorna cana), are restricted to the Ethiopian region and generally exhibit relatively short movements (<1000km; Oatley and Prÿs- Jones, 1986). The yellowbilled duck (Anas undulata) and the Cape shoveller (Anas smithii) occur only in South Africa and Namibia and are apparently restricted within the 65°F isotherm (Figs. 1a,b) (Milstein, 1975; Oatley and Prÿs- Jones, 1986; Rowan, 1963; Siegfried, 1965).

THE STUDY AREA

Barberspan (26° 33' S; 25° 36' E) (Figs. 1,2), in the

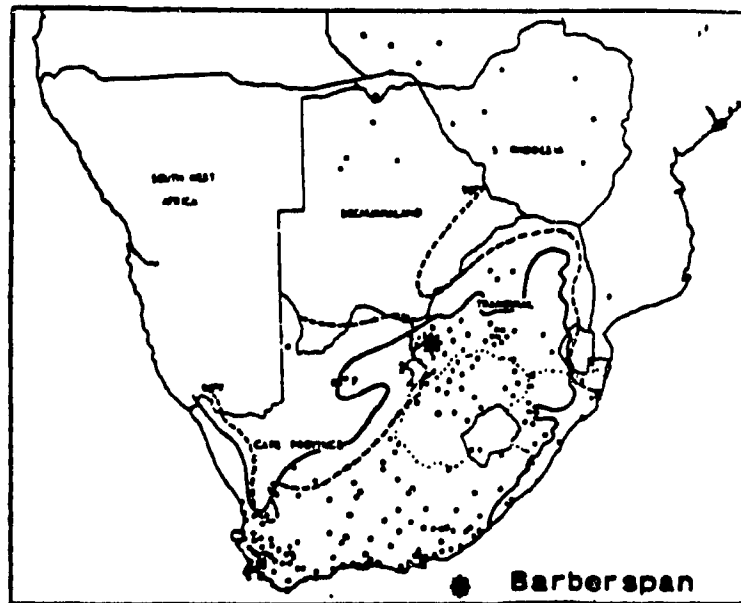


Figure 1a. Distribution of the yellowbilled duck (*Anas undulata*) in southern Africa (from Rowan, 1963); each dot represents a recorded locality. The heavy continuous line shows the 65°F isotherm; the broken line indicates those areas where mean monthly temperatures do not typically exceed 90°F.

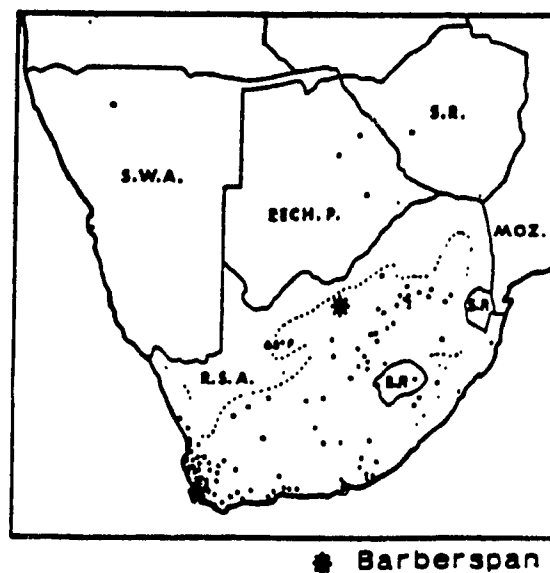


Figure 1b. Distribution of the Cape shoveller (*Anas smithii*) in southern Africa (from Siegfried, 1965); each dot represents a recorded locality; the broken line shows the 65°F isotherm.

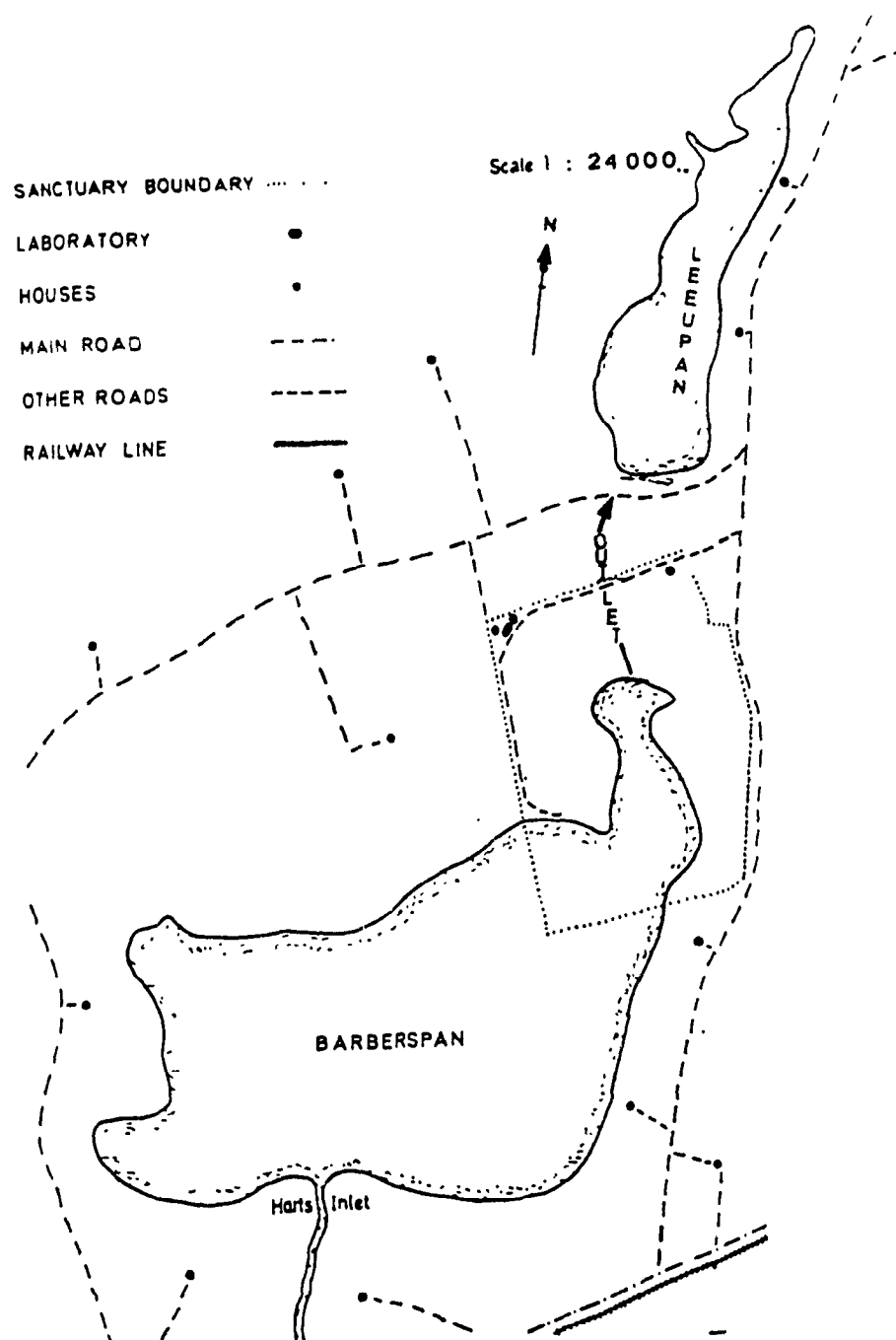


Figure 2. Diagrammatic Map of Barberspan (from Milstein, 1975)

western Transvaal of the Republic of South Africa, has been recognized as a wetland of international importance (Milstein, 1975). It is a large, shallow, alkaline lake which is one of only a few permanent natural water bodies in the region. While not pristine, it is regarded by limnologists as "potentially the least contaminated large body of water in the western Transvaal" (Milstein, 1975). Adjoining Barberspan is Leeupan (Fig. 2), a smaller, shallow, and more saline pan which is also used extensively by waterfowl. The surrounding area is characterized by shallow seasonally filled pans. Consequently, Barberspan functions as an important refuge for many waterfowl during the dry season. Barberspan has a rich zooplankton community (Milstein, 1975) as well as suitable vegetation making it attractive to a variety of waterfowl species (Mitchell, 1983; Skead and Mitchell, 1983).

Skead and Dean (1977b) studied the seasonal abundance of 15 anatid species and found that concentrations at Barberspan were greatest during the late winter and early spring. Spring populations were particularly high following very dry winters. With the onset of spring rains a large proportion of the birds (which varies among species) disperses to respective breeding areas. In years when spring rains arrive late, dispersal is delayed (Skead and Dean, 1977b). For some species [e.g. the yellowbilled duck (Anas undulata) and the spurwinged goose (Plectropterus

gambensis)] rain is a powerful dispersal cue, with dispersal from Barberspan coinciding very closely with the first heavy spring showers.

Although most waterfowl disperse in the spring, residual and, in some species, significant populations remain at Barberspan year round. Most of these species form breeding pairs at Barberspan throughout the year (Milstein, 1975). While breeding normally follows the onset of the rainy season, successful nesting of several species has been reported at Barberspan throughout the year (Milstein, 1975).

Four Anas species; the yellowbilled duck, (A. undulata), redbilled teal (A. erythrorhyncha), Cape shoveller (A. smithii) and Cape teal (A. capensis) are common residents and breed year round (Skead and Dean, 1977a; Milstein, 1975). The yellowbilled duck consistently appears to be the most common species at Barberspan, both in terms of overwintering numbers and year round breeding numbers. The redbilled teal, which is also abundant, usually occurs in lower numbers than the yellowbilled duck (Milstein, 1975; Skead and Dean, 1977b). Compared with the yellowbilled ducks and redbilled teal, populations of Cape teal and Cape shovellers remain relatively small at Barberspan year round.

This creates an interesting situation with respect to parasite communities. Although anatids in the Holarctic region typically display smaller and less diverse helminth

loads on wintering grounds, the greatest concentrations of waterfowl species in South Africa, occur on large permanent waterbodies like Barberspan. The potential for the establishment of rich helminth pools exists here and it is possible that the exchange of helminths among host species could be facilitated at these refuges. This could have a profound influence on the diversity of helminth infections in these hosts.

The well - studied ecology of Barberspan, the availability of dietary data on the waterfowl species of interest, and the seasonal patterns of the four Anas species that concentrate there in the dry seasons afforded a unique opportunity to study a parasitic system in an area of the world which, to this point, has received little attention.

The overall objectives of this study were as follows: 1, to describe the helminth fauna of the four South African Anas species; 2, to compare the fauna with helminth species already recorded in Africa and to determine whether indeed any species are specific to the region itself; 3, to determine whether the Anas species maintain separate helminth communities; and if so then: 4, to determine the factors that contribute to the segregation of these helminth communities; and 5, to determine which helminth species are dispersed by what duck species during spring dispersal.

MATERIALS AND METHODS

Helminth collections

Field collections were made in November and early December, 1978 at the Barberspan Ornithological Research Station. The sample consisted of the gastrointestinal helminths of four Anas species (A. undulata, A. erythrorhyncha, A. smithii and A. capensis) which were collected, in relation to their respective abundances, at Barberspan and Leeupan (Fig. 2).

Ducks were either shot or trapped and were autopsied for gastrointestinal helminths within one hour of death. The proventriculus, gizzard, intestine and caecae were removed from the birds, separated, placed in separate Petri dishes and examined with the aid of a dissecting microscope. Gizzard worms were found following the removal of the gizzard lining. Both the lining and muscular surface were examined thoroughly for helminths.

Cestodes and digeneans from all host species were fixed in 5% formalin and stored in 70% ethanol. Due to time constraints during the collection period, representative helminths from individual Cape teal and Cape shoveller were removed and the remaining gut contents were fixed and stored in formalin. Cestodes and digeneans were stained in aceto-carmine or Ehrlich's haematoxylin. Those specimens stained in aceto-carmine were hydrated through decreasing concentrations of ethanol and placed in distilled water with

5 drops of stain /50 ml of water, for 24 hours. Specimens were then dehydrated, cleared in xylene and mounted in Permount or Canada balsam. Specimens stained in haematoxylin were first overstained, differentiated in 1% HCL in 70% ethanol then blued in 1% ammonium hydroxide in 70% ethanol. The helminths were dehydrated, cleared and mounted as above.

Nematodes were fixed in hot 70% ethanol, cleared in glycerine alcohol, and studied as temporary mounts in glycerine. Representative head collars of echinostome digeneans and copulatory bursae of nematodes were cut off and mounted in glycerine jelly to facilitate the counting and measurement of spines and the measurement of spicules, respectively.

Where necessary, specimens were embedded using standard paraffin techniques and sectioned at 10 microns. The sections were stained routinely in haematoxylin and eosin.

The identification of cestodes was carried out to the generic level following Schmidt (1986) while original descriptions were used to determine species. Digenean identifications were based on keys by Schell (1970), Dubois (1968) and McDonald (1981). Identifications of nematodes were based on keys by McDonald (1974).

In order to assess total numbers of small worms from the preserved gut contents of Cape teal and Cape shovellers, volumetric subsampling was applied. Following the removal of the larger cestode species, the initial volume of the

remaining contents (in 70 % ethanol) was measured, and three 1 - ml subsamples were taken. The helminths in each subsample were removed, identified and counted. Subsamples from each bird were compared in order to verify that the numbers of worms collected in each subsample were similar. Extrapolation of the mean number of helminths per 1 - ml sample was used to determine the total numbers in the original volume.

Definitions

Several terms commonly used by parasitological ecologists (Margolis et al., 1982) are employed in this thesis. Prevalence refers to the percentage of hosts infected with a particular parasite species; abundance refers to the mean number of individuals of a particular helminth species in the entire host sample (i.e. infected and uninfected hosts); intensity refers to the number of individuals of a particular helminth species in each infected host in the host sample; and mean intensity refers to the mean number of individuals of a particular helminth species per infected host.

The primary level of organization in helminth parasite communities is the infracommunity. Infracommunity refers to all populations of all helminths within a host individual (Esch et al., 1975). Two higher levels of community organization recognized are that of the component community,

which includes all of the infracommunities within a single host species, and the compound community which includes all of the helminth infrapopulations within a community of host species (Holmes and Price, 1986; Root, 1973).

Statistical analyses

Statistical analyses were performed using NCSS (Number Cruncher Statistical System; J. L. Hintze, Kaysville, Utah). Due to the fact that data were not normally distributed, non-parametric tests were employed. Specifically, the Kruskal - Wallis test was used to detect significant differences among both parasite species number and loads between the four host species, while the Mann - Whitney U test was used to detect significant differences among both parasite species numbers and loads between sexes within host species. For further analyses, rank transformations were performed on the dataset. Conover and Iman (1981) have demonstrated that by replacing the data with their ranks, the usual parametric tests (e.g. t - test, F - test etc) could then be applied. The rank transformation approach is also applicable in multivariate analyses. This technique has been used in a number of studies on parasites (Gray et al., 1989; Feduynich and Pence, 1994).

Comparisons of the helminth species diversity within the host sample were performed using Brillouin's index. This index takes into account both the richness (number of

species) as well as the evenness of helminth distributions within the host community. Measures of species diversity are based on information theory (introduced by MacArthur, 1955 and Margalef, 1958) and are related to the uncertainty of predicting the identity of a randomly picked individual in a community. Thus, in a highly diverse community, high diversity is associated with high uncertainty and low diversity, with low uncertainty. A high Brillouin's index indicates a relatively homogeneous distribution of a given number of helminth species within a host community. Therefore, the probability of being able to pick the identity of a species at random would be quite low. Brillouin's index is preferred over the more commonly used Shannon diversity index because the former is appropriate for communities with a complete census, while the latter is appropriate for a random sample of species from a larger population (Brower and Zar, 1984). Since Brillouin's index is determined, not estimated, the evenness index measures obtained using this index are unbiased (Zar, 1984). Unlike those obtained using the Shannon function, evenness measures of the different infracommunities can be compared with one another. The evenness index refers to how close a set of observed species abundances (from which Brillouin's index is calculated) are to those from an aggregation of species having maximal possible diversity for a given number of helminth species and individuals (Brower and Zar, 1984).

In order to examine the co - occurrence of helminth species within the compound community, Robson's variance test of species association was used (Schluter, 1984). This allows a test of the null hypothesis that helminth species do not covary among hosts. If the null hypothesis is true (i.e. negative covariance), it indicates that the presence of certain parasite(s) is excluding the establishment of other species.

Kendall's rank correlation was used to assess the relationship between parasite prevalence and intensity to test one of the assumptions of Hanski's (1982) core - satellite species hypothesis. The hypothesis assumes that frequent species are usually abundant. Kendall's tau is used to test for a positive association between prevalence and intensity. Assignments of particular helminths to core, satellite and secondary species classes were performed following the methods of Bush and Holmes (1986).

Patterns of helminth associations (in this case for individual ducks) were examined using recurrent group analysis (RGA) (Fager, 1957; Fager and McGowan, 1963), which identifies groups of helminth species that regularly co-occur. RGA is based on an index of affinity which is the geometric mean of the proportion of joint occurrences, corrected for sample size. Associations between helminth species pairs are dichotomized into those which are significantly positive and those that are not. Fager and

McGowan (1963) stated that recurrent species should be found together in more than half of their range (cutoff value = 0.5). The grouping procedure based on this dichotomy results in the formation of the largest possible group (known as the recurrent group) with which all possible pairs of species show affinity. Species forming significant positive associations with some but not all of the recurrent group species are known as associate species (Stock and Holmes, 1987). The procedure was employed for each individual host species and for the combined host community.

An initial analysis between the component communities was performed using Jaccard's coefficient of community similarity. This index, based solely on the presence or absence of parasite species, provides a simple and effective initial method for comparing the component communities of two hosts.

Hierarchical cluster analysis (HCA) is a technique used to search for relatively homogeneous groups of objects. In this case it was used to determine how the individual hosts within the compound and component communities compare to one another with respect to their helminth communities. Hierarchical cluster analysis provides a one dimensional scaling of the data set which results in homogeneous groups (in this instance host species) based on their similarities in a number of different variables (helminth species). This affords the opportunity to study the distinct relationships

between infracommunities as well as component communities within the compound community. HCA was performed on all helminths and ducks with the unweighted pair-group method using arithmetic averages (UPGMA). This is the most commonly employed and widely accepted method used in cluster analysis (Sokal and Sneath, 1963).

Principal components analysis (PCA) was employed in order to assess how parasites were shared in and among host communities. PCA is a technique used to reduce the dimensionality of a large number of potentially interrelated variables down to fewer components which account for most of the variation. It was used in this case to determine how the individual hosts within the compound and component communities relate to one another with respect to their helminth communities. PCA was conducted on the covariance matrix of all helminth species in all 63 hosts.

RESULTS

General

Sixty - three adult ducks including 25 yellowbilled ducks, 21 redbilled teal, 10 Cape teal and 7 Cape shoveller were examined. All were infected and harboured between two to 13052 helminths. A total of 34 helminth species was encountered. This included 23 cestode, five digenean, and six nematode species (Table 1).

A number of new helminth species have been discovered in this collection. Three, Echinocotyle capensis McLaughlin, 1989, Sobolevicanthus transvaalensis McLaughlin, 1984 and Microsomacanthus macrotesticulata Alexander and McLaughlin, 1993 have been described elsewhere. A new species of species of Echinocotyle and a new genus and species belonging to the Fimbriariinae are described in Section 2 along with M. macrotesticulata which was part of this study. For convenience the latter two will be referred to as Echinocotyle sp. (36) and "Fimbriariodes" sp. (30) respectively in the text. Fourteen cestode, two digenean and one nematode species represent new records from Anseriformes in Africa (Table 2).

Eight other cestode and one nematode species could only be identified to the generic level. The cestodes are designated by their rostellar hook length throughout this study. The cestodes do not correspond to any known species. However, the specimens were either immature or had deteriorated to the point where accurate description was not

Table 1. Frequency (prevalence), range, abundance (\pm sd) and mean intensity (\pm sd) of helminth infections in Anas species from Barberspan, Republic of South Africa.

Helminth species	Host species			
	<u>Anas undulata</u> n=25	<u>Anas erythrorhyncha</u> n=21	<u>Anas capensis</u> n=10	<u>Anas smithii</u> n=7
Cestoda				
<u>Platyscolex ciliata</u>	4 (16) ^a 1- 131 ^b 8.56 (30.1) ^c 53.5 (63.6) ^d	--	--	--
<u>Cloacotaenia megalops</u>	12 (48) 1- 8 1.7 (2.4) 3.6 (2.3)	14 (67) 1- 10 2.8 (2.6) 4.2 (2.0)	8 (80) 1- 26 7.7 (10.4) 9.6 (10.9)	7 (100) 1- 59 25.0 (22.8) 25.0 (25.0)
<u>Dicranotaenia coronula</u>	3 (12) 1- 3 0.25 (0.65) 1.7 (1.2)	--	3 (30) 1- 5 0.7 (1.6) 2.3 (2.3)	--
<u>Diorchis flavescens</u>	4 (16) 1- 3 0.3 (0.7) 1.8 (1.0)	--	9 (90) 3- 84 32.7 (29.2) 36.3 (28.4)	2 (29) 103- 245 49.7 (94.3) 174.0 (160.4)
<u>Diorchis</u> sp. (60) ^e	2 (8) 1 0.08 (0.3) 1 (ϕ)	1 (4.8) 1 0.05 (0.2) 1 (ϕ)	--	--

Table 1. cont'd
Helminth
species

	<u>Anas</u> <u>undulata</u>	<u>Anas</u> <u>erythrorhyncha</u>	<u>Anas</u> <u>capensis</u>	<u>Anas</u> <u>smithii</u>
<u>Cestoda</u>				
<u>Diorchis</u> sp. (68)	8 (32) 1.7 0.7 (1.6) 2.1 (2.2)	1 (5) 1 0.05 (0.2) 1 (φ)	--	--
<u>Diorchis</u> sp. (28)	--	--	10 (100) 1- 63 25.9 (20.7) 25.9 (20.7)	1 (14) 3 0.4 (1.1) 3 (φ)
<u>Diorchis</u> sp. (43)	--	--	1 (10) 2 0.2 (0.6) 2 (φ)	--
<u>Echinocotyle</u> <u>capensis</u>	--	--	10 (100) 4- 4103 1063.8 (1271.5) 1063.8 (1271.5)	7 (100) 1- 3003 1197.6 (1413.4) 1197.6 (1413.4)
<u>Echinocotyle</u> <u>clerci</u>	--	--	9 (90) 7- 801 119.6 (242.3) 132.9 (253.1)	7 (100) 2- 1151 315.1 (416.0) 315.1 (416.0)
<u>Echinocotyle</u> <u>rosseteri</u>	--	--	9 (90) 1- 2475 541.9 (774.7) 602.1 (796.5)	--

Table 1. cont'd

Helminth species	<u>Anas undulata</u>	<u>Anas erythrorhyncha</u>	<u>Anas capensis</u>	<u>Anas smithii</u>
<u>Cestoda</u>				
<u>Echinocotyle</u> sp. (36)	--	--	--	6 (86) 5- 3451 775.6 (1254.0) 904.8 (1321.6)
<u>Fimbriaria fasciolaris</u>	--	1 (5) 1 0.05 (0.2) 1 (φ)	--	--
" <u>Fimbriariodes</u> " sp. (30)	3 (12) 1 0.1 (0.3) 1 (φ)	1 (5) 2 1.0 (0.4) 2 (φ)	5 (50) 2- 1412 168.5 (443.5) 337 (609.5)	--
<u>Gastrotaenia cygni</u>	9 (36) 1- 8 1.0 (1.9) 2.7 (2.5)	12 (57) 1- 4 1.0 (1.1) 1.7 (1.0)	9 (90) 2- 15 6.7 (5.73) 7.4 (5.5)	7 (100) 7- 30 14.1 (8.6) 14.1 (8.6)
<u>Microsomacanthus macrotesticulata</u>	8 (32) 2- 31 3.1 (7.7) 9.8 (11.4)	2 (9.6) 1- 6 0.3 (1.3) 3.5 (3.5)	--	1 (14.3) 2 0.30 (0.75) 2 (φ)
<u>Microsomacanthus spiralicirrata</u>	9 (36) 1- 9 1.5 (2.9) 3.0 (2.8)	4 (19) 1- 4 0.5 (1.1) 2.5 (1.3)	10 (100) 277- 5903 2125.7 (1753.4) 2125.7 (1753.4)	6 (86) 38- 2147 488.7 (786.4) 570.2 (828.3)

Table 1. cont'd

Helminth species	<u>Anas undulata</u>	<u>Anas erythrorhyncha</u>	<u>Anas capensis</u>	<u>Anas smithii</u>
<u>Cestoda</u>				
<u>Microsomacanthus teresoides</u>	--	2 (9.6) 1 0.1 (0.3) 1 (φ)	--	--
<u>Microsomacanthus</u> sp. (25)	4 (16) 1- 3 0.3 (0.7) 1.8 (1.0)	--	--	--
<u>Skrjabinoparaxis tatianae</u>	--	1 (4.8) 1 0.05 (0.2) 1 (φ)	10 (100) 24- 275 98.9 (87.8) 98.9 (87.8)	7 (100) 11- 6366 1009.3 (2364.5) 1009.3 (2364.5)
<u>Sobolevicanthus gracilis</u>	9 (36) 1- 25 3 (6.1) 8.3 (7.9)	4 (19) 1- 9 0.9 (2.4) 4.5 (4.1)	--	--
<u>Sobolevicanthus transvaalensis</u>	--	--	10 (100) 13- 5108 963.5 (1614.8) 963.5 (1614.8)	--
<u>dilepidid</u> sp.	--	--	--	1 (14) 1 0.14 (.38) 1 (φ)

Table 1. cont'd

Helminth species	<u>Anas</u> <u>undulata</u>	<u>Anas</u> <u>erythrorhyncha</u>	<u>Anas</u> <u>capensis</u>	<u>Anas</u> <u>smithi</u>
<u>Digenea</u>				
<u>Apatemon</u> <u>minor</u>	15 (60) 1- 223 12.9 (44.7) 21.5 (56.8)	9 (43) 1- 68 5.4 (15.6) 12.6 (22.5)	--	--
<u>Echinoparyphium</u> <u>elegans</u>	4 (16) 1- 249 10.1 (49.8) 63.2 (123.8)	4 (19) 1- 3 0.3 (0.8) 1.8 (1.0)	1 (10) 1 0.1 (0.3) 1 (φ)	--
<u>Catantropis</u> <u>orientalis</u>	--	1 (5) 1 0.5 (0.2) 1 (φ)	1 (10) 1 0.1 (0.3) 1 (φ)	1 (14) 29 4.1 (11.0) 29 (φ)
<u>Hypoderaeum</u> <u>conoideum</u>	1 (4) 1 0.04 (0.9) 1 (φ)	--	--	--
<u>Zygocotyle</u> <u>lunata</u>	1 (4) 2 0.08 (0.4) 2 (φ)	--	--	--
<u>Nematoda</u> <u>Amidostomum</u> <u>acutum</u>	4 (16) 1- 4 0.3 (0.84) 1.8 (1.5)	--	--	--

Table 1. cont'd

Helminth species	<u>Anas</u> <u>undulata</u>	<u>Anas</u> <u>erythrorhyncha</u>	<u>Anas</u> <u>capensis</u>	<u>Anas</u> <u>smithii</u>
Nematoda				
<u>Epomidiostomum</u> <u>uncinatum</u>	13 (52) 1- 13 2.4 (4.0) 4.5 (4.5)	10 (48) 1- 2 0.6 (0.74) 1.2 (0.5)	1 (10) 1 0.1 (0.3) 1 (φ)	1 (14) 10 1.4 (3.8) 10 (φ)
<u>Tetrameres</u> <u>crami</u>	10 (40) 1- 98 7.0 (20.5) 17.4 (30.3)	--	--	--
<u>Tetrameres</u> <u>ryjikovi</u>	--	14 (67) 1- 41 6.0 (9.8) 9 (10.9)	6 (60) 2- 4 1.7 (1.6) 2.8 (0.8)	5 (71) 2- 23 7.6 (8.1) 10.6 (7.7)
<u>Tetrameres</u> sp.	2 (8) 8- 11 0.8 (2.7) 9.5 (2.1)	--	--	--
<u>Capillaria</u> <u>contorta</u>	--	2 (10) 2- 6 0.4 (1.4) 4 (2.8)	1 (10) 1 0.1 (0.3) 1 (φ)	--

a= number of hosts infected (Prevalence (%)); b= range of worm numbers detected; c= abundance (average number of helminths in total host sample); d= mean intensity (average number of helminths in infected hosts; e=length of rostellar hooks in micrometers; φ= null set.

Table 2. New African and host records for African Anseriformes

	New African Record	New Host Record			
	Y/N	Y*	R*	T*	S*
Cestoda					
<u>Platyscolex ciliata</u>	Y	X	X	X	X
<u>Cloacotaenia megalops</u>	N	X		X	X
<u>Dicranotaenia coronula</u>	Y	X	X		X
<u>Diorchis flavescens</u>	Y	X	X	X	X
<u>Echinocotyle capensis</u>	Y			X	X
<u>Echinocotyle clercki</u>	Y			X	X
<u>Echinocotyle rosseteri</u>	Y			X	
<u>Echinocotyle</u> (36)	Y				X
<u>Fimbriaria fasciolaris</u>	N	X	X	X	X
" <u>Fimbriariodes</u> " (30)	Y	X	X	X	X
<u>Gastrotaenia cygni</u>	Y	X	X	X	X
<u>Microsomacanthus macrotesticulata</u>	Y	X	X		X
<u>Microsomacanthus spiralicirrata</u>	Y	X	X	X	X
<u>Microsomacanthus teresoides</u>	Y		X		
<u>Skrjabinoparaxis tatianae</u>	Y		X	X	X
<u>Sobolevicanthus gracilis</u>	N	X	X		
<u>Sobolevicanthus transvaalensis</u>	Y			X	
Digenea					
<u>Apatemon minor</u>	Y	X	X		
<u>Catatropis orientalis</u>	Y		X	X	X
<u>Echinoparyphium elegans</u>	N	X	X	X	
<u>Zygocotyle lunata</u>	N	X			

Table 2 (Cont'd)

	New African Record	New Host Record			
	Y/N	Y	R	T	S
Nematoda					
<u>Amidostomum acutum</u>	N	X			
<u>Capillaria contorta</u>	Y		X	X	
<u>Epomidiostomum uncinatum</u>	N	X	X	X	X
<u>Tetrameres crami</u>	N	X			
<u>Tetrameres ryjikovi</u>	N		X	X	X

*- Y, Anas undulata; R, Anas erythrorhyncha; T, Anas capensis;
S, Anas smithii

possible. In the case of the nematode, males required for species identification were lacking.

No significant differences were detected between sexes in any of the four *Anas* species with respect to either the number of species or number of helminths present and, consequently, the data have been pooled. The prevalence, range, abundance and mean intensities of the helminths in each host are listed in Table 1.

New host and African records are listed in Table 2. Twenty- six species are new records for Africa. Seventeen species represent new host records for African waterfowl.

Description of component communities

Details of the helminth communities from each host species are presented in Table 3 and in Figures 3 and 4. Overall, redbilled teal had the most impoverished helminth fauna and the prevalence of most helminth species in this host was generally low (Table 1). Redbilled teal harboured, on average, the smallest number of species (3.9 ± 1.4) (Table 3; Fig. 3) and the lowest number of parasites (18.5 ± 18.3 per bird) of the four hosts examined (Table 3; Fig. 4). This is reflected in the low Brillouin's index (0.36 ± 0.11) and high evenness values (0.79 ± 0.19) obtained from this host.

The helminth community in yellowbilled ducks was similar to redbilled teal with generally low numbers of

Table 3. Comparison of helminth infections in Anas species from Barberspan, R.S.A.

	<u>Anas</u> <u>undulata</u>	<u>Anas</u> <u>erythro-</u> <u>rhyncha</u>	<u>Anas</u> <u>capensis</u>	<u>Anas</u> <u>smithii</u>
No. examined	25	21	10	7
Tot. # spp.	20	17	18	14
Mean # spp./ Bird (SD)	5.0 (3.0) ^a	3.9 (1.4) ^a	11.3 (1.4) ^b	8.4 (1.7) ^c
Range spp./ bird	1- 11	1- 6	9- 14	6- 11
ln Mean # worms/bird (SD)	4.0 (4.8) ^a	2.9 (2.9) ^a	8.5 (8.2) ^b	8.3 (8.5) ^b
Range worms/ bird	3- 581	2- 79	372- 10396	92- 13052
Brillouin's index (SD)	0.41 (.20)	0.36 (.11)	0.54 (.11)	0.60 (.07)
Eveness (SD)	0.78 (.23)	0.79 (.19)	0.52 (.081)	0.68 (.11)

note: values with different superscripts differ significantly

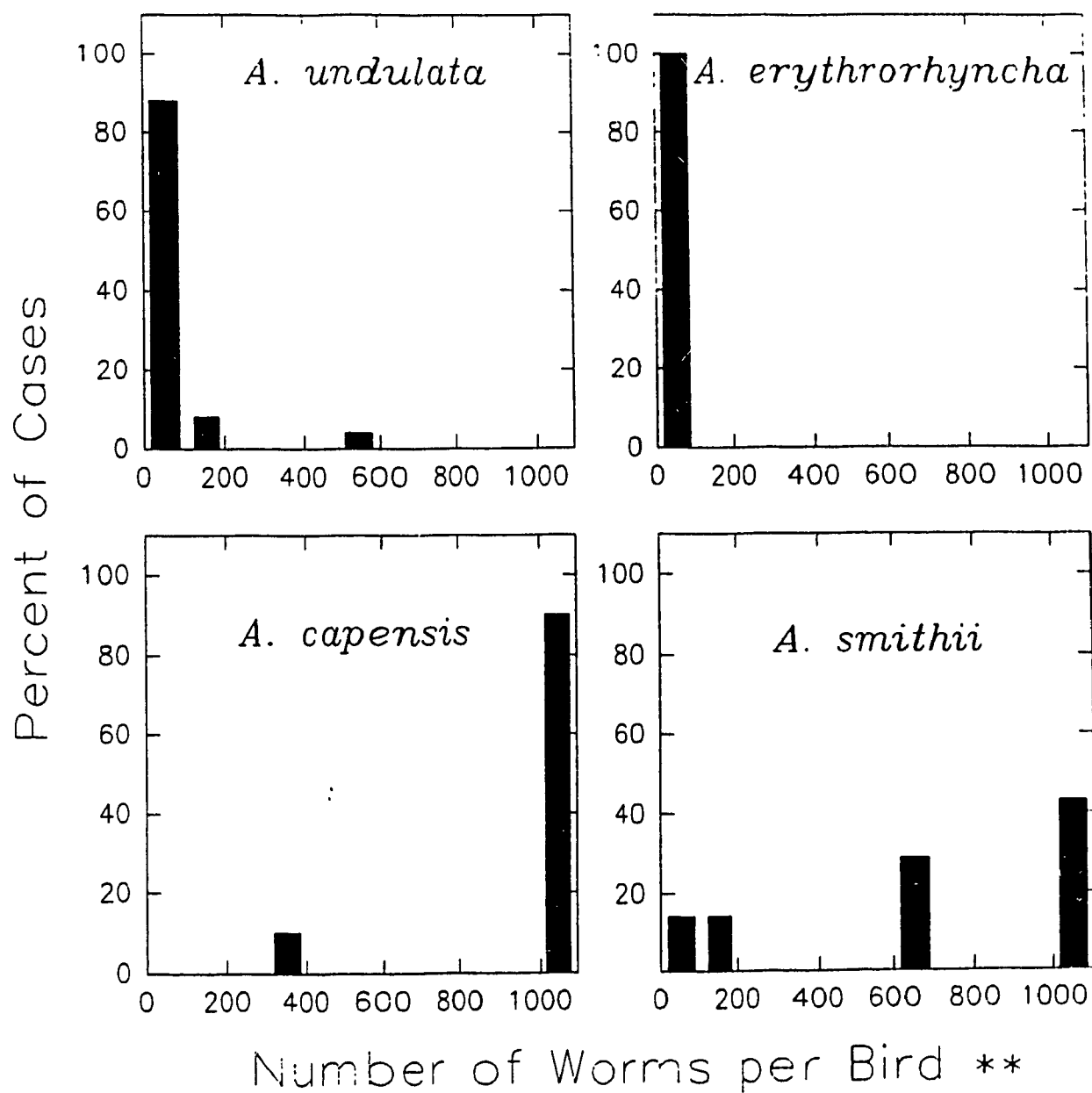


Figure 3. Distribution of total numbers of helminths in the *Anas* species.

** - *A.c.*, *A.s.* > *A.u.*, *A.e.* ($p < 0.05$).

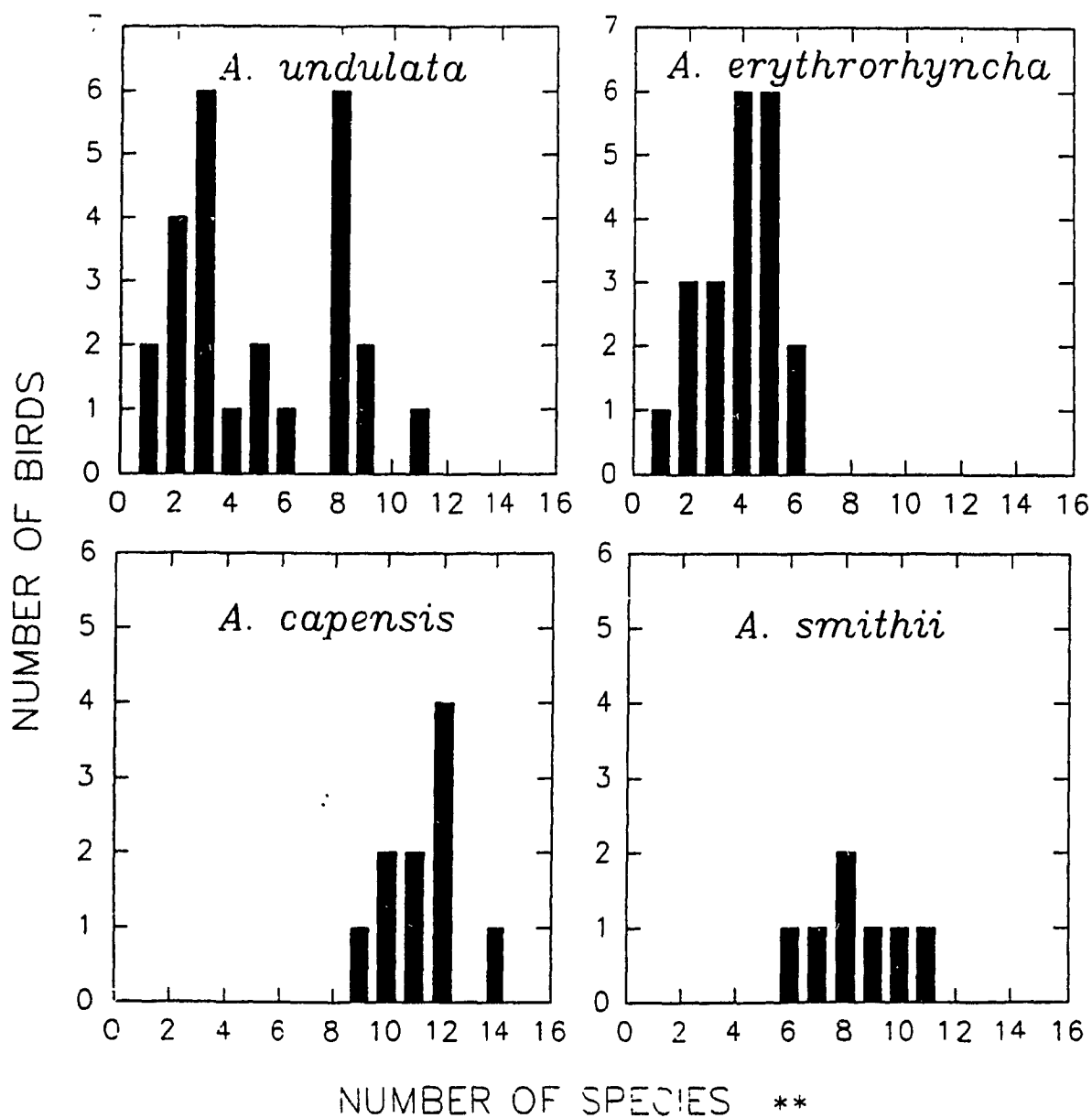


Figure 4. Distribution of the number of component helminth species in the *Anas* species.
 **- *A.c.* > *A.s.* ($p < 0.05$); *A.c.*, *A.s.* > *A.u.*, *A.e.* ($p < 0.05$).

parasites. Yellowbilled ducks displayed a greater mean number of helminth species (5.0 ± 3.0) (Table 3; Fig. 3) as well as a higher mean worm burden (53.8 ± 117) (Table 3; Fig. 4) but neither was significantly different from that in redbilled teal. Although yellowbilled ducks displayed a higher Brillouin's index (0.41 ± 0.20) indicating greater diversity of helminths, the evenness index was similar to that of the redbilled teal.

Cape shovellers harboured a significantly greater mean number of helminth species (8.4 ± 1.7) (Table 3; Fig. 3) ($P < 0.005$) and significantly greater mean worm burden (3889 ± 4966) (Table 3; Fig. 4) ($P < 0.005$) than the yellowbilled ducks or the redbilled teal. Cape shovellers had a Brillouin's index of $0.6 (\pm 0.07)$ and an evenness index of $0.68 (\pm 0.11)$. Prevalences of most helminth species were high (Table 1).

Cape teal displayed the most diverse helminth fauna. They harboured a mean of $11.3 (\pm 1.4)$ helminth species and had a mean worm burden of $5106.6 (\pm 3641.5)$ per bird. The mean number of species in Cape teal was greater ($P < 0.005$) (Table 3; Fig. 3) than in the other host species. The mean parasite load was significantly greater ($P < 0.005$) than in yellowbilled ducks and redbilled teal (Table 3; Fig. 4). Cape teal displayed a Brillouin's index of $0.54 (\pm 0.11)$ and an evenness index of $0.52 (\pm 0.08)$. As with the Cape shoveller, prevalence of most helminth species was

high (Table 1).

Dominance of helminth groups

Helminth communities in both the Cape teal and Cape shoveller were dominated by cestodes (Table 4). In both cases over 99% of the total number of helminths found consisted of cestodes. Digeneans and nematodes contributed little to the total numbers of helminths in these two species of duck. Cestodes made up 39% of the helminths found in yellowbilled ducks and 31% in redbilled teal. Digeneans and nematodes made up the greater proportion of the total numbers of helminths in these host species. Digeneans were the numerically dominant group in the yellowbilled ducks; nematodes were the dominant group in the redbilled teal.

Relative distributions of helminth species

The relative distributions of the various helminth species among the 4 Anas species differed. Four were common to all host species, seven occurred in three host species, nine occurred in two host species and the remaining 14 were found in only a single host species (Table 1). Of those that occurred in a single host species, four occurred commonly and in relatively high numbers (Echinocotyle rosseteri, Echinocotyle sp. (36), Sobolevicanthus transvaalensis and Tetrameres crami) in their respective hosts. The other 11

Table 4. Relative abundances of helminth groups with each *Anas* species from Barberspan, R. S. A.

	Host species			
	<u>Anas</u> <u>undulata</u>	<u>Anas</u> <u>erythrorhyncha</u>	<u>Anas</u> <u>capensis</u>	<u>Anas</u> <u>smithii</u>
Total worms	1345 ^a 100 ^b	389 100	51066 100	27222 100
Cestodes	521 38.7	121 31.1	51046 > 99.9	27140 99.7
Digeneans	579 43.1	121 31.1	2 < 0.01	29 0.11
Nematodes	245 18.2	147 37.8	18 < 0.01	53 0.19

a- total number in each species; b- relative percent (%)

were rare, occurring only once or twice (Platyscolex ciliata, Diorchis sp. (60), Diorchis sp. (43), Fimbriaria fasciolaris, Microsomacanthus teresoides, Microsomacanthus sp. (25), Zygocotyle lunata, Hypoderaeum conoideum, Amidostomum acutum, Tetrameres sp., and a dilepidid species).

Association patterns among parasites

Although helminth species within the compound community covaried positively (Robson's test of covariance: $P < 0.001$), there existed a dichotomy within the host communities. Cape teal and Cape shovellers had diverse helminth communities with large numbers of individuals. Over 97.8 % of the helminths found in this study were obtained from these species, even though only 10 and seven ducks were examined, respectively. Yellowbilled ducks and redbilled teal, had relatively fewer parasite species with many fewer individuals present than in the former group.

Hanski (1982) proposed the core - satellite hypothesis in order to relate the patterns of distribution of organisms to niche relations. This hypothesis makes two assumptions: 1) a positive correlation exists between prevalence and intensity; and 2) the frequency distribution of species within a population is bimodal. Core species occur frequently and are locally abundant, while satellite species are uncommon and therefore not abundant. Bush and Holmes

(1986) designated the former as species which would be found in $> 70\%$ of the hosts, while the latter would be found in $< 40\%$ of hosts. Bush and Holmes (1986) also noted that a third group, with prevalences intermediate between those characteristic of core and satellite species, may also occur. They designated these as secondary species.

The relationship between intensity and prevalence was positive and significant in each duck (Kendall's rank correlation; $P < 0.05$ for A. undulata; $P < 0.005$ for A. erythrorhyncha and A. smithii; and $P < 0.0005$ for A. capensis), thereby meeting the first assumption of the hypothesis. However, only Cape shovellers exhibited the predicted bimodal pattern of species frequency distribution (Fig. 5).

Cape shovellers had eight core and six satellite species (no secondary species were present); Cape teal had 10 core, two secondary and six satellite species. Yellowbilled ducks and redbilled teal had four and five secondary, and 16 and 12 satellite species respectively. No core species were present in either of these hosts (Fig. 5).

Six helminth species were shared as core species among Cape teal and Cape shovellers: C. megalops, E. capensis, E. clercki, G. cygni, M. spiralicirrata, and S. tatianae. Two of the other core species in Cape teal (D. flavescens and Diorchis (28) appeared as satellite species in the Cape shovellers, while one core species in Cape shoveller (T.

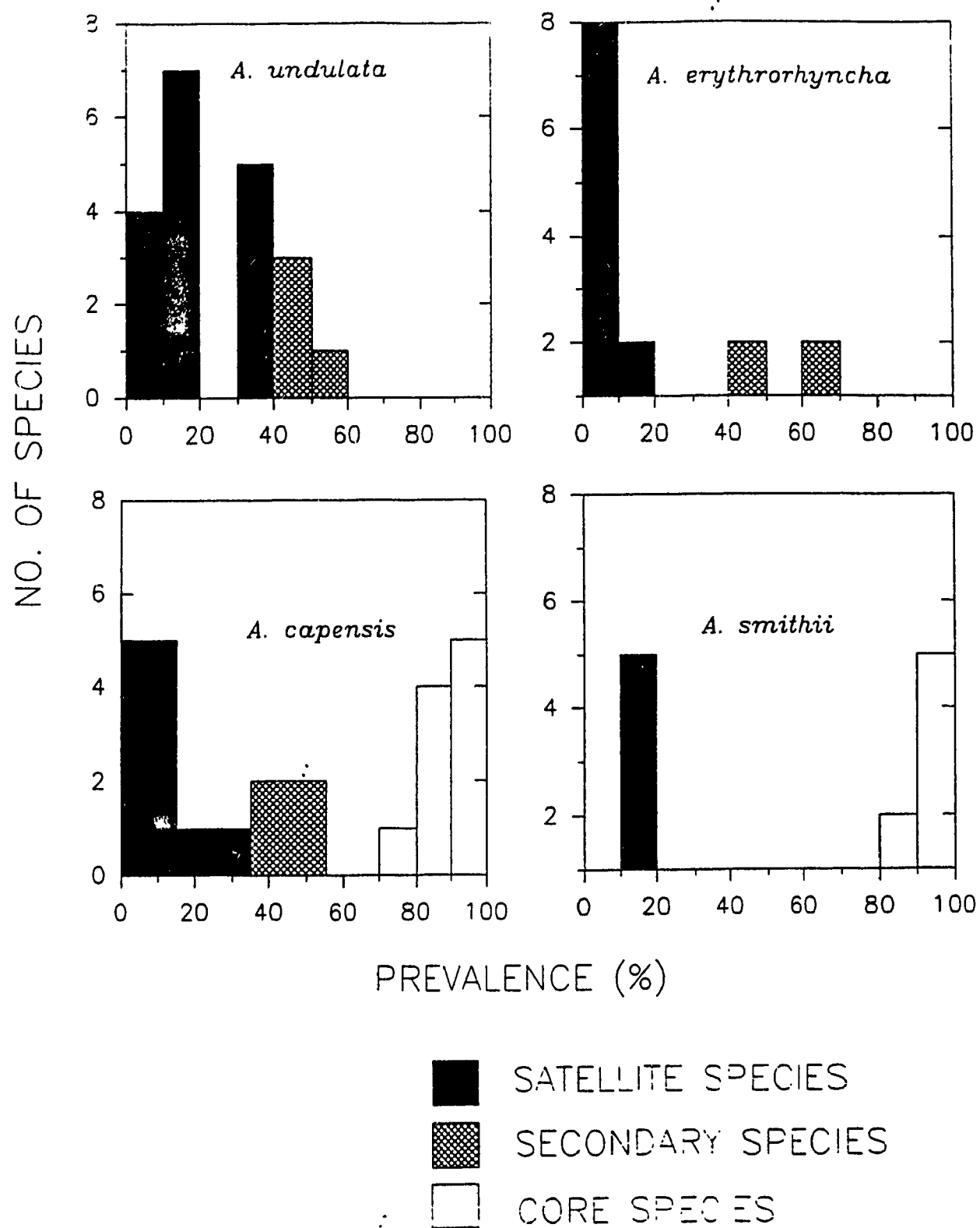


Figure 5. Frequency distributions of helminth prevalence in the *Anas* species.

ryjikovi) appeared as a secondary species in the Cape teal. A number of the core species from the Cape teal and Cape shovellers were also shared as secondary or satellite species by the yellowbilled ducks and redbilled teal (Table 5).

Recurrent group analysis (Fager, 1957) permitted the examination of the pattern in which individual helminth species associate in host species. The recurrent helminth groups from the component community in each host species are presented in Figures 6a-d. Figure 7 depicts the recurrent group from the compound community.

The Cape teal displayed the largest recurrent group (Fig. 6a). This consisted of 10 recurrent members, including nine core species and one secondary species. Three associate members which included one core species (C. megalops), one secondary species ("Fimbriariodes" sp. (30)), and one satellite species (Dicranotaenia coronula) were also present. The Cape shoveller had the next largest recurrent group (Fig. 6b) with seven members, all of which were core species in this host. Redbilled teal (Fig. 6c) displayed a recurrent group with only two members (C. megalops and T. ryjikovi). No associate members were found in the Cape shovellers or redbilled teal. Yellowbilled ducks (Fig. 6d) failed to display a recurrent group. Only five associate species (M. macrotesticulata, S. gracilis, M. spiralicirrata, E. uncinatum and A. minor) were found in this host.

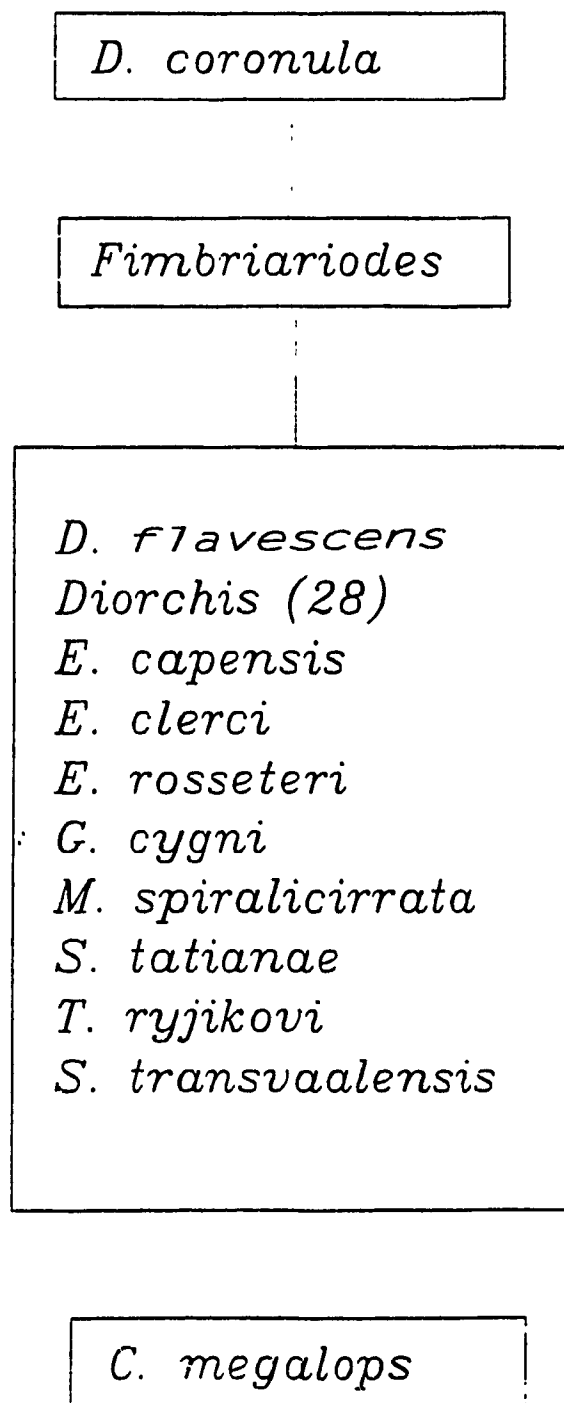
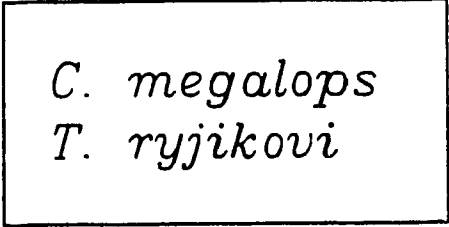


Figure 6a. Recurrent group analysis of helminths from Cape teal (*Anas capensis*). Note: species within boxes are recurrent species; lines joining boxes indicate associate species relationships.

E. capensis
E. clerici
Echinocotyle (36)
G. cygni
M. spiralicirrata
T. ryjikovi
C. megalops

Figure 6b Recurrent group analysis of helminths from Cape shoveller (*Anas smithii*).
Note: species within box are all recurrent species.



C. megalops
T. ryjikovi

Figure 6c. Recurrent group analysis of helminths from redbilled teal (*Anas erythrorhyncha*).
Note: species within box are recurrent species.

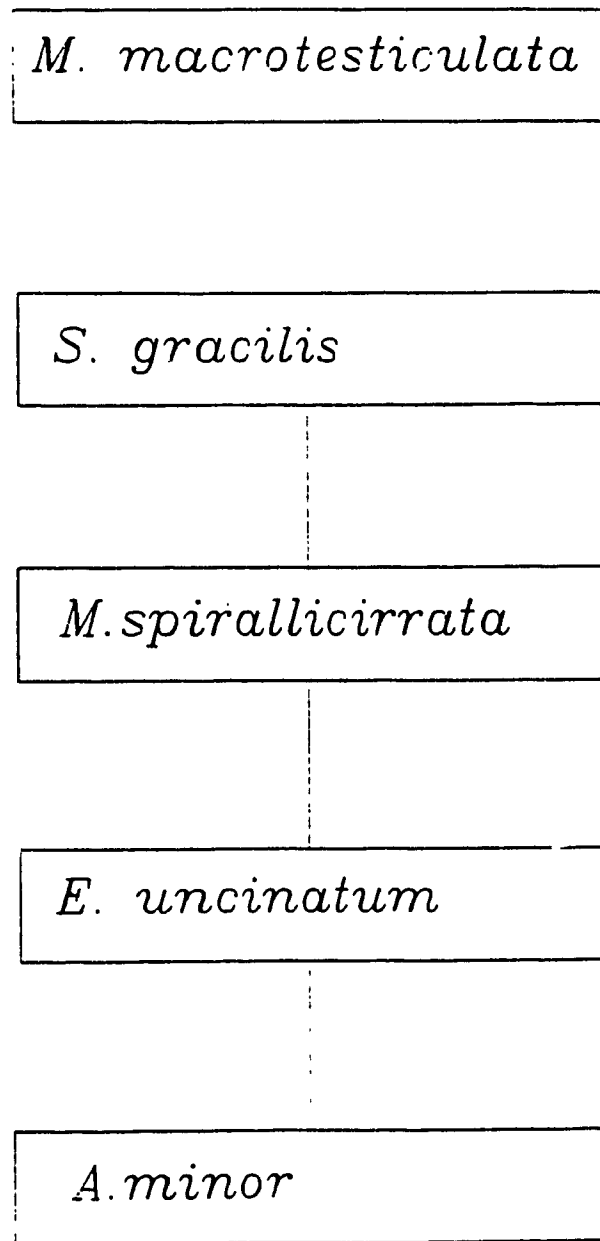


Figure 6d. Recurrent group analysis of helminths from yellowbilled ducks (*Anas undulata*). Note: all species are associate species as indicated by the lines.

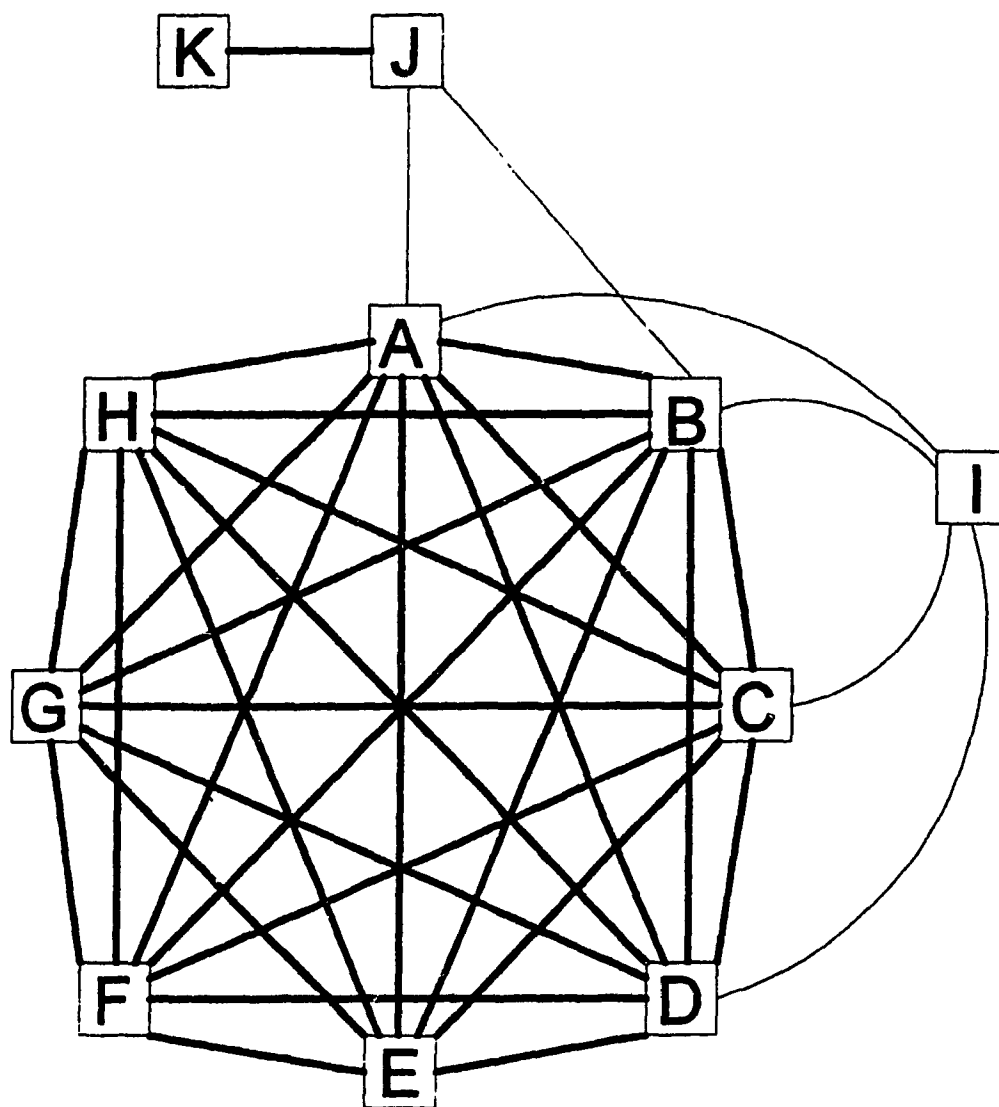


Figure 7. Recurrent groups from *Anas* species at Barberspan. A = *S. tatarianae*; B = *M. spiralicirrata*; C = *E. clerici*; D = *E. capensis*; E = *E. rosseteri*; F = *Diorchis* (28); G = *D. flavescens*; H = *S. transvaalensis*; I = *G. cygni*; J = *C. megalops*; K = *T. ryjikovi*.

Table 5. Summary of associations of helminths in the Anas species

	Recurrent Group	YBD	RBT	CT	CS
<u>Cestoda</u>					
<u>P. ciliata</u>		S			
<u>C. megalops</u>	a	2°	2° a	C a	C r
<u>D. coronula</u>		S		S a	
<u>D. flavescens</u>	X	S		C r	S
<u>Diorchis</u> (28)	X			C r	S
<u>Diorchis</u> (43)				S	
<u>Diorchis</u> (60)		S	S		
<u>Diorchis</u> (68)		S	S		
<u>E. capensis</u>	X			C r	C r
<u>E. clercki</u>	X			C r	C r
<u>E. rosseteri</u>	X			C r	
<u>Echinocotyle</u> (36)					C r
<u>F. fasciolaris</u>			S		
<u>"Fimbriariodes"</u> (30)		S	S	2°a	
<u>G. cygni</u>	a	S	2°	C r	C r
<u>M. macrotesticulata</u>		S a	S		S
<u>M. spiralicirrata</u>	X	S a	S	C r	C r
<u>M. teresoides</u>			S		
<u>Microsomacanthus</u> (25)		S			
<u>S. tatianae</u>	X		S	C r	C
<u>S. gracilis</u>		S a	S		
<u>S. transvaalensis</u>	X			C r	
dilepid sp.					S
<u>Digenea</u>					
<u>A. minor</u>		2°a	2°		
<u>E. elegans</u>		S	S	S	
<u>C. orientalis</u>			S	S	S
<u>H. conoideum</u>		S			
<u>Z. lunata</u>		S			
<u>Nematoda</u>					
<u>A. acutum</u>		S			
<u>C. contorta</u>			S	S	
<u>E. uncinatum</u>		2°a	2°	S	S
<u>T. crami</u>		2°			
<u>T. ryjickovi</u>	a		2°a	2°r	C r
<u>Tetrameres</u> sp		S			

YBD, yellowbilled duck; RBT, redbilled teal; CT, cape teal; CS, cape shoveller; X, member of the recurrent group of the compound community; r, recurrent group member in component community; a, associate species; C, core species; 2°, secondary species; S, satellite species.

The recurrent group from the combined data set of all host species is shown in Fig. 7. This group consisted of eight recurrent species, all of which were core species from the Cape teal. Four of the recurrent group species were also found as core species in the Cape Shoveller. The recurrent group also included three associate species. Two of these were core species in both the Cape teal and Cape shoveller. One was a core species in the Cape shoveller and a secondary species in the Cape teal. Only three of the eight recurrent group members occurred in the yellowbilled ducks and redbilled teal. These included S. tatianae and D. flavescens which both appeared as satellite species in the yellowbilled duck and redbilled teal respectively and M. spiralicirrata which appeared as a satellite species in both ducks.

Of the associate species, C. megalops and G. cygni occurred as core species in both the Cape teal and Cape shoveller and as secondary and satellite species in the redbills and yellowbills respectively. Tetrameres ryjikovi appeared as a core species in Cape shovellers, as a secondary species in both Cape teal and redbilled teal, and as a satellite species in yellowbilled ducks.

Patterns of similarity among host communities

The initial analysis of the infracommunities using the Jaccard coefficient of community similarity (Fig. 8) showed that the greatest amount of overlap in the species present

	YBD	RBT	CT	CS
YBD	1	0.42	0.27	0.21
RBT	-	1	0.40	0.35
CT	--	--	1	0.52
CS	--	--	--	1

Figure 8. Comparison of the component communities from the *Anas* species using the Jaccard coefficient of community similarity (CCj)*.

*- $CCj = C/(S1+S2-C)$; where S1 and S2 are the number of species in communities 1 and 2 respectively, and C is the number of species common to both communities.

in the component communities occurred between Cape teal and Cape shovellers (0.52). This was followed by the yellowbilled ducks and redbilled teal (0.42). The next highest degree of similarity was seen between the redbilled teal and the Cape teal (0.40), and Cape shoveller (0.29). The weakest associations occurred between the yellowbilled ducks and the Cape teal and Cape shovellers.

Hierarchical cluster analysis revealed segregations of component communities. Fig. 9 shows the cluster dendrogram (cophenetic correlation coefficient = 0.86) and Fig. 10 shows the rescaled cluster dendrogram. It is evident that fauna in Cape teal and the Cape shoveller cluster independently from those in yellowbilled ducks and redbilled teal and that the Cape teal and Cape shoveller also form clusters separate from one another. The fauna of yellowbilled ducks and redbilled teal display a strong overlap.

Principal components analysis (PCA) on the infracommunities in the four Anas species provided identical results to those in HCA. The first three PCA components accounted for a total of 54% of the total variation in the covariance matrix. Principal components 1, 2 and 3 accounted for 37, 9 and 8 % of the variation respectively. Principal component 3 failed to provide any further resolution of the groups and is therefore excluded. A plot of the factor scores of PC1 with PC2 (Fig. 11)

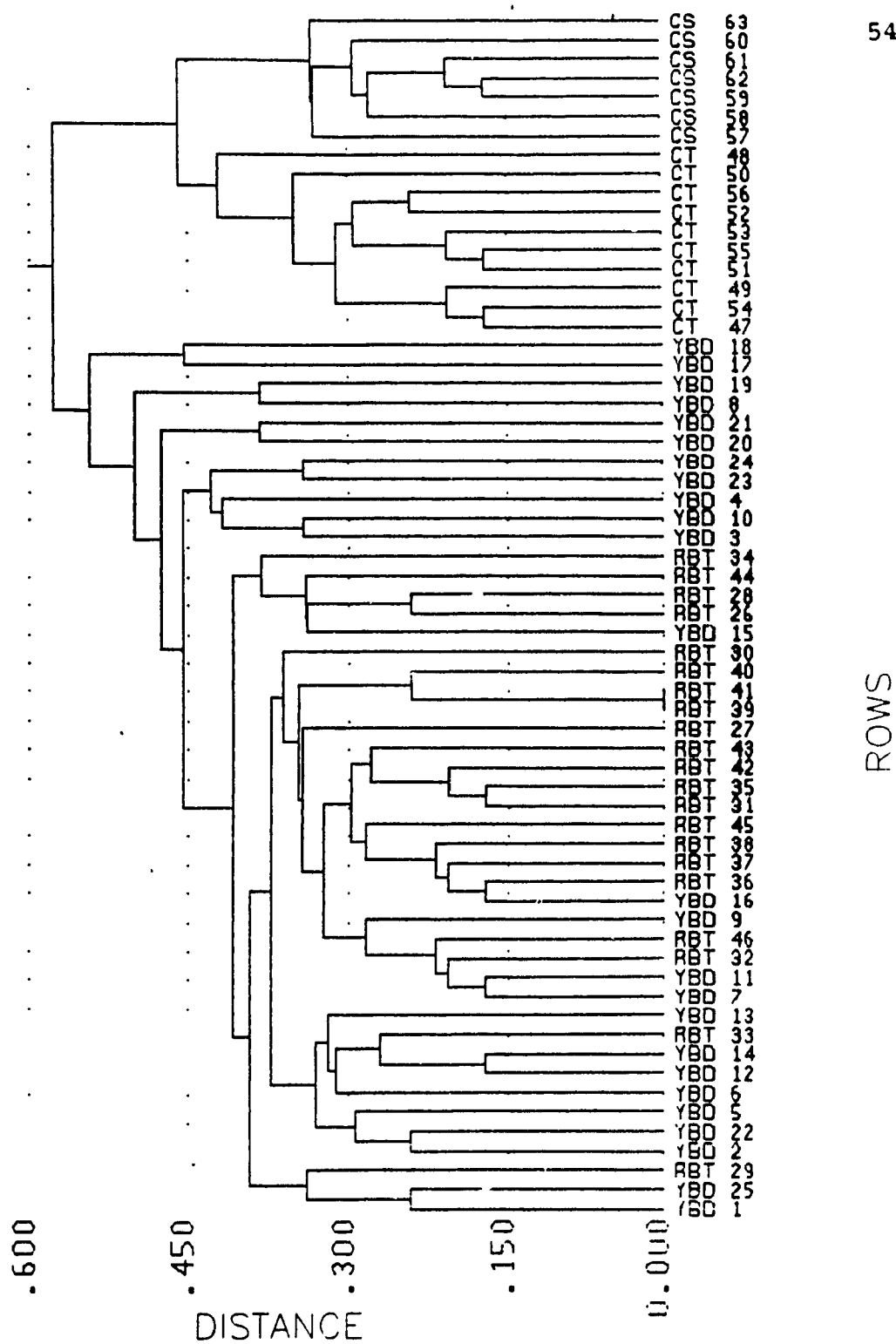


Figure 9. Hierarchical cluster analysis of helminths in the compound community of Barberspan anatids.

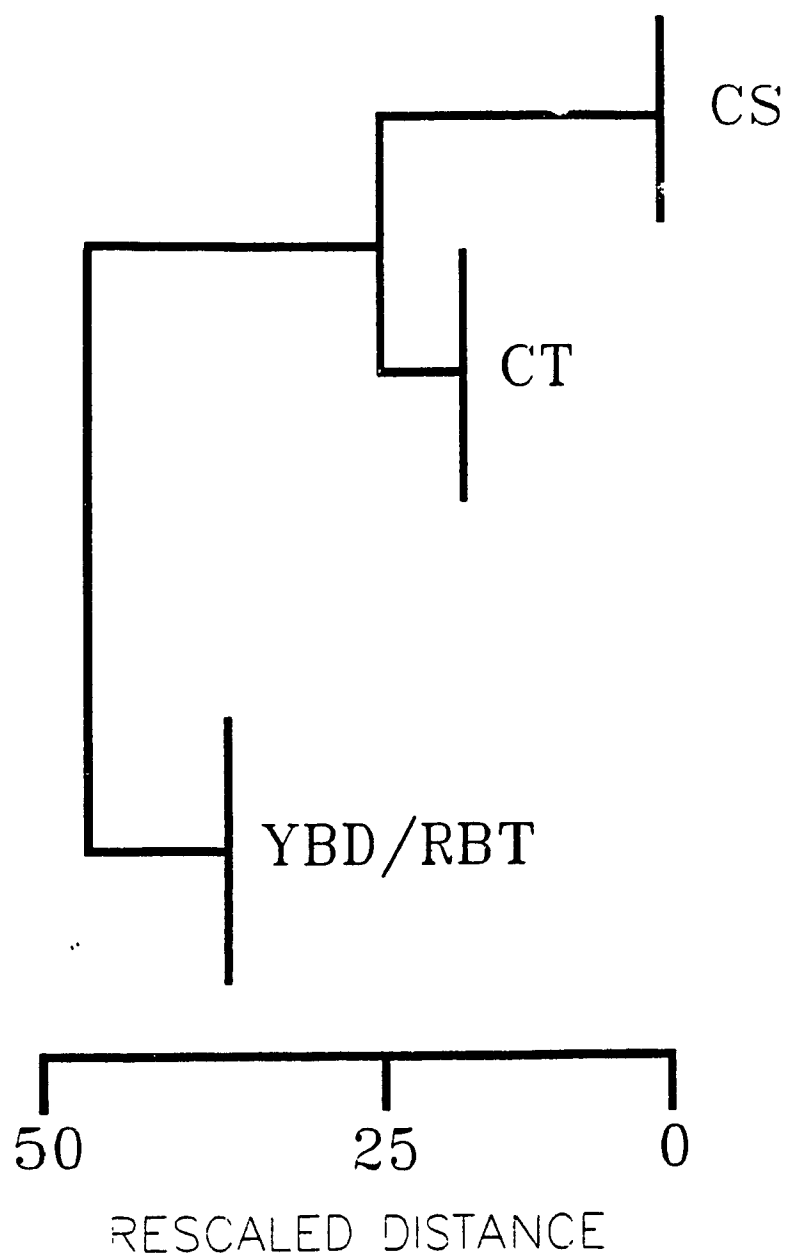


Figure 10. Summarized hierarchical cluster analysis of helminths in the compound community of Barberspan anatids.

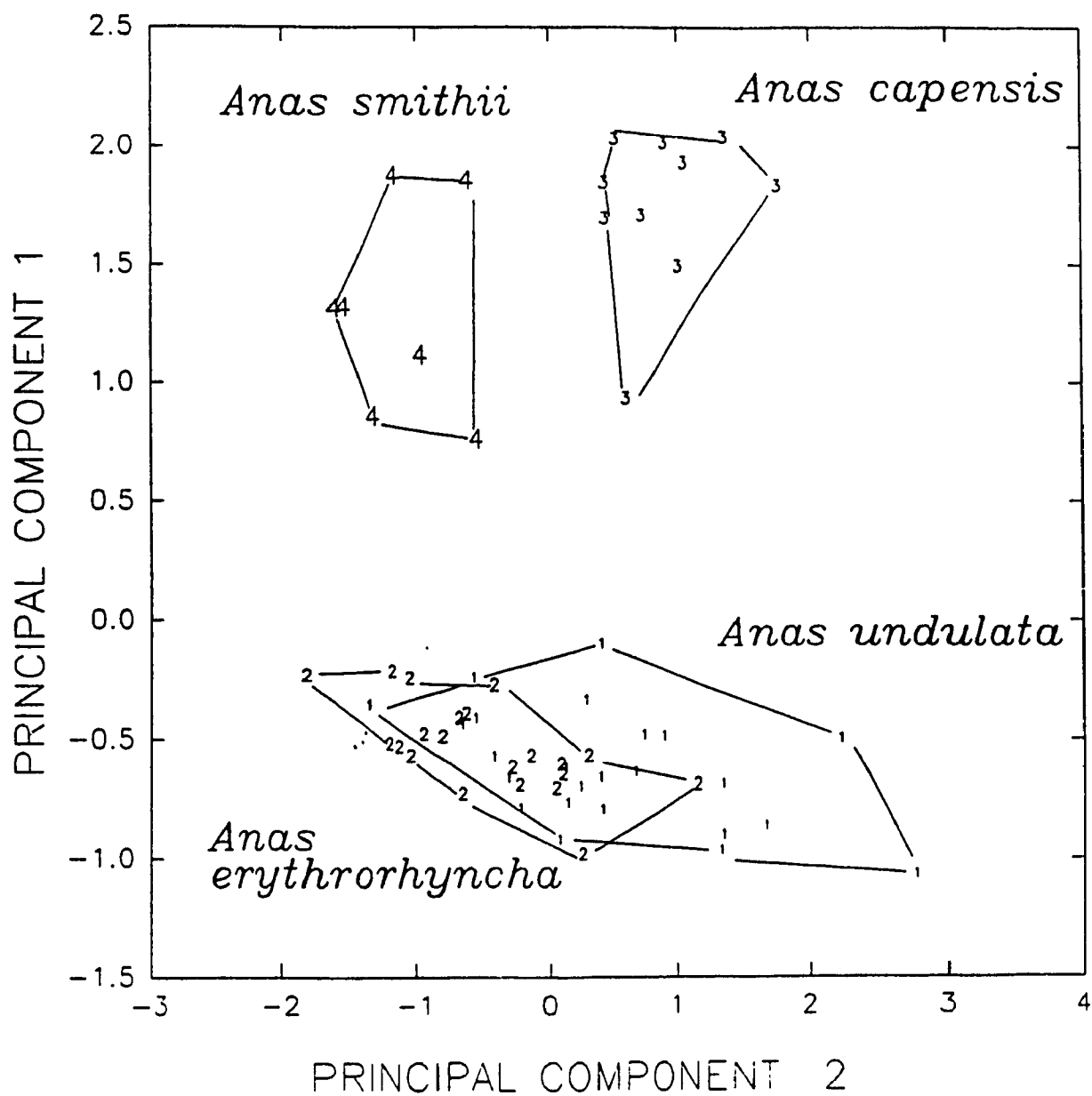


Figure 11. Principal components analysis of the compound community; principal components 1 and 2 accounting for 37% and 9.5% of the covariance matrix respectively.

revealed a separation of the infracommunities of yellowbilled ducks and redbilled teal from those of the Cape teal and Cape shoveller and between the latter two species as well. The loadings of each variable (helminth species) are presented in Table 6. Principal component 1 was loaded on most heavily by 17 variables (helminth species) (cutoff point 0.3). Seven species with heavy positive loadings (Diorchis (28), Echinocotyle capensis, E. clerici, E. rosseteri, Echinocotyle sp.(36), Skriabinoparaxis tatianae and Sobolevicanthus transvaalensis) occurred exclusively in Cape teal and/ or Cape shoveller (a single S. tatianae was also found in a redbilled teal). Three species with negative loadings (Apatemon minor, Sobolevicanthus gracilis and Tetrameres crami) occurred exclusively in yellowbilled ducks and redbilled teal. Other helminth species with positive loadings (e.g. C. megalops, G. cygni) were common (i.e. displayed prevalences of 20% or greater and relatively high mean intensities) in 3 or more host species.

Principal component 2 contributed to the separation of the Cape teal and Cape shoveller, but not the yellowbilled duck and redbilled teal communities. Seventeen helminth species loaded on PC2 (cutoff point 0.3). Three species with heavy positive loadings (E. rosseteri, S. transvaalensis and Fimbriariodes sp.(30)) occurred exclusively in the Cape teal and one species with a heavy negative loading (Echinocotyle sp. (36)) occurred exclusively in the Cape shoveller.

Table 6. Summary of Principal components analysis on the infracommunities of the host species from Barberspan, Republic of South Africa.

Species	Loadings* Factor 1	Loadings* Factor 2
<u>P. ciliata</u>	-.18	0.36
<u>C. megalops</u>	0.44	-.49
<u>D. coronula</u>	0.19	0.51
<u>D. flavescens</u>	0.72	0.30
<u>Diorchis</u> (60)	-.20	0.34
<u>Diorchis</u> (68)	-.26	0.20
<u>Diorchis</u> (28)	0.81	0.35
<u>Diorchis</u> (43)	0.11	0.07
<u>E. capensis</u>	0.97	0.04
<u>E. clerici</u>	0.94	0.01
<u>E. rosseteri</u>	0.76	0.36
<u>Echinocotyle</u> (36)	0.46	-.40
<u>F. fasciolaris</u>	-.07	0.04
<u>"Fimbriariodes"</u> (30)	0.40	0.31
<u>G. cygni</u>	0.72	-.13
<u>M. macrotesticulata</u>	-.16	0.32
<u>M. spiralicirrata</u>	0.79	0.33
<u>M. teresoides</u>	-.08	-.14
<u>Microsomacanthus</u> 25	-.18	0.31
<u>S. tatiana</u>	0.95	-.01
<u>S. gracilis</u>	-.35	0.43
<u>S. transvaalensis</u>	0.77	0.37
dilepid sp.	0.24	-.15
<u>A. minor</u>	-.52	0.40
<u>C. orientalis</u>	0.23	-.16

Table 6. (cont'd)

Species	Loadings* Factor 1	Loadings* Factor 2
<u>E. elegans</u>	-.18	0.29
<u>H. conoideum</u>	0.43	0.04
<u>Z. lunata</u>	-.08	0.08
<u>A. acutum</u>	-.19	0.37
<u>C. contorta</u>	0.08	-.15
<u>E. uncinatum</u>	-.35	0.41
<u>T. crami</u>	-.46	-.10
<u>T. ryjickovi</u>	0.70	-.01
<u>Tetrameres sp.</u>	-.15	0.22

DISCUSSION

BIOGEOGRAPHY AND SPECIATION

The distribution of most of the waterfowl species that occur at Barberspan, including the four Anas species in this study, is restricted to the Ethiopian region. Limited contact with waterfowl from other regions likely occurs along the Nile valley, however the number of waterfowl species involved is limited, due to the fact that only a small number of species (e.g. Sarkidiornis melanotos, Alopochen aegyptiacus, Plectropterus gambensis and Netta erythrophthalma) exhibit extensive movements. As a result, the opportunity for exchange of helminth species with European waterfowl wintering along the north coast of Africa is limited. Consequently, helminth groups here have evolved to an extent in isolation from those in European hosts.

The isolation of Ethiopian waterfowl species has resulted in extensive speciation, especially among cestodes. Ten of the 23 cestode species encountered here were previously undescribed. Three have subsequently been described: Sobolevicanthus transvaalensis (by McLaughlin, 1984), Echinocotyle capensis (by McLaughlin, 1989) and Microsomacanthus macrotesticulata (by Alexander and McLaughlin, 1993). Two others are described here for the first time: Echinocotyle sp. (36) and "Fimbriariodes" sp. (30) along with the description of M. macrotesticulata which represented part of this study. Five remaining species could

not be identified with any known members of their genera.

Cestodes

Among the cestode species which are not restricted to Africa, two groups emerge. The first includes C. megalops, D. coronula, E. fasciolaris, S. gracilis, P. ciliata, M. teresoides and E. rosseteri. These are cosmopolitan species and have been reported from a variety of waterfowl species throughout the Holarctic, and, in some cases from the Indian sub - continent (McDonald, 1969). Only C. megalops, E. fasciolaris and S. gracilis have been reported previously from Anseriformes in Africa. A fourth species, E. rosseteri, has been reported from Spermaspiza haematina (Passeriformes) in Zaire (Southwell and Lake, 1939), however this identification has been disputed (McLaughlin and Burt, 1979).

Among the remaining species, E. clerici, M. spirallidirrata and S. tatianae have limited distributions in Europe and the former Soviet Union; verifiable records of D. flavescens exist only for Australia and New Zealand (McDonald, 1969; Czaplinski and Aeschlimann, 1987).

Nematodes

Five of the six nematode species could be identified. Two, A. acutum and E. uncinatum, have been found previously in Anseriformes from Africa; both are cosmopolitan species that infect a wide range of anatid species in Europe, Asia, North America, Africa and Australia

(McDonald, 1969). The other three species, C. contorta, T. crami and T. ryjikovi are new records for Anseriformes from Africa. Capillaria contorta is a cosmopolitan species; T. crami and T. ryjikovi occur in anatids throughout the Holarctic (McDonald, 1969; Turner and Threlfall, 1975; Mahoney and Threlfall, 1978).

Digeneans

Of the five Digenean species encountered, two, H. conoideum and Z. lunata are cosmopolitan species in waterfowl, and have previously been detected in Africa on a number of occasions. Apatemon minor, E. elegans and C. orientalis are infrequent in waterfowl and are new African records for Anseriformes. Echinoparyphium elegans has been reported twice from Africa, once from an owl (Tyto alba) in Madagascar (Richard, 1965) and once from a stork (Phoenicopiterus antiquorum) in Egypt (Looss, 1899). Aside from the above, E. elegans has been detected only one other time, which was in North America from a Black duck (Anas rubripes) (Cannon, 1938). More recent studies by Mouahid and Moné (1988) suggest that E. bioccalerouxii and E. ralphaudyi, both of which were recorded originally from African material, are synonyms of E. elegans. If this is the case, E. elegans occurs more commonly and in a wider range of host species than the previous records suggest.

Presence of helminth groups among the compound and component communities

Four groups of helminths (Cestoda, Digenea, Nematoda and Acanthocephala) are common parasites of waterfowl in the Holarctic (McDonald, 1969). Cestodes, digeneans and nematodes were present in the four Anas species examined at Barberspan; no acanthocephalans were found.

A substantial amount of information has accumulated on the life cycles of most of the genera of helminths that infect waterfowl. Although details of the life cycles of many species in these genera are still unknown, the patterns for each genus are consistent enough to permit generalizations (see information summarized in McDonald, 1969).

The majority of cestodes that parasitize waterfowl are members of the the family Hymenolepididae. Typically, these utilize freshwater entomostracan Crustacea (principally ostracods and copepods) as intermediate hosts. A smaller number of species utilize malacostracans (amphipods) or aquatic annelids to complete their life cycles (McDonald, 1969). The genera encountered in this study, utilize ostracods and, to a lesser extent, copepods as intermediate hosts. Both occur at Barberspan (Milstein, 1975); ostracods are particularly abundant (Roode and van Eeden, 1970).

The life cycles of nematode genera encountered at Barberspan are of two types. Amidostomum, Epomidiostomum and

Capillaria have direct life cycles, although Capillaria can also be transmitted by Lumbricidae (McDonald, 1969).

Tetrameres species require an intermediate host. A wide variety of arthropods including entomostracans, malacostracans and insects, and some oligochaetes, serve as intermediate hosts for species in this genus (McDonald, 1969).

Digeneans are of special interest in this study because snails, which serve as the first intermediate host, are absent from Barberspan (Roode and van Eeden, 1970). However, snails do occur in surrounding river systems (Milstein, 1975) and have also been recovered from unfledged yellowbilled ducks at Barberspan (Skead, unpublished data). This confirms that snails also occur in nearby pans and are accessible to both the adult and juvenile ducks. While the transmission of digeneans at Barberspan apparently does not occur, foci exist nearby and the more vagile species like yellowbilled ducks and redbilled teal are likely to encounter them. The majority of digenean infections were detected in yellowbilled ducks and redbilled teal; only two Cape teal and one Cape shoveller, which are more sedentary, were infected.

Only a few species of acanthocephalans occur in ducks (McDonald, 1969) and none was detected at Barberspan. The genera that infect ducks require malacostracans, usually amphipods, as intermediate hosts. These are not present at

Barberspan (Roode and van Eeden, 1970) which accounts for their absence in this study. Only one verifiable record of an acanthocephalan infection in waterfowl exists from Africa (Appendix 1).

The intermediate hosts required for the transmission of cestodes and nematodes are abundant at Barberspan. Therefore, resident anatids should maintain infective pools in the local crustacean community. Further, these infective pools would be augmented by helminth eggs passed by other anatid species as well. Thus, transmission of cestode and nematode infections within host species, as well as exchange of these helminths between various species, in the host community should occur.

COMPONENT COMMUNITY STRUCTURES

Two distinct patterns were evident among the component communities in ducks at Barberspan. Component communities of yellowbilled ducks and redbilled teal were relatively impoverished and were characterized by infracommunities with low species diversity and high evenness. This was reflected by the low prevalence and low intensity of infections by most helminth species in these hosts. Due to the low diversity, the component communities were characterized by secondary and satellite species; no core species were found. The low prevalence also limited the size of the recurrent species groups in each host.

Cape teal and Cape shoveller had much richer component communities. Infracommunities displayed greater richness but lower evenness due to the greater number of species per host and greater disparity in the number of each species within each host. The component communities consisted mainly of core and satellite species. The high prevalence of a greater number of species resulted in larger recurrent groups of species than those seen in the yellowbilled ducks and redbilled teal.

The diversity and magnitude of helminth infections hosts acquire is strongly influenced by diet and by habitat. This is attributable to the fact that both diet and habitat determine the quantity and diversity of invertebrate hosts encountered and consumed.

Cape teal are exclusively carnivorous. Mitchell (1983) reported that the diet of the Cape teal at Barberspan consisted entirely of animal matter, the bulk of which was entomostacans (copepods and ostracods). Activity budgets show that the Cape teal are voracious feeders (Skead, 1977). Skead (1977) reported that Cape teal spent approximately 60% of their time feeding, most of which (93%) was spent with with the head and neck submerged indicating they were capturing prey at the mud water interface. The small size and low energetic value of the individual prey captured presumably forces the Cape teal to consume large numbers, thereby increasing their chances of acquiring heavy helminth

infections.

Cape shoveller are also carnivorous. Their diet at Barberspan was 98.5% animal matter, consisting mainly of copepods and ostacods (Mitchell, 1983). In other areas of South Africa their diet may include up to 30% plant matter (Siegfried, 1970). Cape shoveller spend about half of their feeding time billing along the surface (i.e. straining food from the water column with its specialized bill). The rest of the feeding time was spent with the head and neck submerged, suggesting benthic feeding (Skead, 1977).

Skead (unpublished) found that the diets of adult yellowbills at Barberspan consisted of approximately 84% vegetable matter along with small quantities of insect larvae and a few entomostracans. Yellowbilled ducks feed principally in perimeter areas near vegetation with their head and neck submerged (Skead, 1977).

Redbilled teal appear to be primarily carnivorous. However there appears to be some seasonal, and possibly, geographic plasticity in its feeding preferences. Douthwaite (1977), Woodall (1979) and Mitchell (1983) have all reported that redbilled teal consume varying proportions of plant and animal matter. However the animal matter that redbilled teal consume consists of larger invertebrates, primarily Chironomidae (Woodall, 1979; Mitchell, 1983), Corixidae (Mitchell, 1983) and oligochaete cocoons (Woodall, 1979), none of which is important as an intermediate host for

helminths. Redbilled teal at Barberspan feed along the perimeter next to windrows of sago pondweed debris (Mitchell, 1983).

The diet of both the Cape teal and Cape shoveller maximizes their contact with the invertebrates that act as intermediate hosts for a large number of helminth species. Consequently, these host species recruit new infections on a continuing basis and are therefore infected with a wide variety, and generally large numbers, of helminths at Barberspan. The continuous contact with the infective pool ensures that most individuals are not only exposed to the more common helminth species but also ensures contact with rare species. This results in the formation of the core - satellite species distribution which is characteristic of these hosts. Furthermore, many helminth species are transmitted by the same or similar species of intermediate hosts. Consumption of these would result in exposure to several helminth species and contribute to the formation of the larger recurrent groups detected in these hosts. This has previously been demonstrated in lesser scaup (Aythya affinis) a North American diving duck which preys extensively on amphipods (Bush and Holmes, 1986). Predictable groups of species were detected in this host due to its extensive use of amphipods as prey.

The pattern is quite different in the yellowbilled ducks and redbilled teal. Owing to their extensive use of

plants and insect larvae respectively, these species have limited contact with the infective pools. Chance encounters and the occasional active inclusion of certain invertebrates in their diets results in infection but the lack of the core - satellite patterns and the small or absent recurrent groups suggests that these species have had much less contact with the infective pool.

Studies on Holarctic anatids have revealed seasonal differences in magnitude and diversity of helminth infections in geese and various anatid species (Buscher, 1965; McLaughlin and Burt, 1973; Neraasen and Holmes, 1975; Spakulova et al., 1989, 1991). These differences are due to a number of factors which, individually or in combination, may affect recruitment of infections within the host community. These factors include: seasonal dietary changes; intermediate host availability and / or accessibility; and acquired resistance. Infection levels are typically lowest just prior to migration in late winter and early spring (Wallace and Pence, 1986).

Comparable data are not available from African anatids. The ecology of many species differs from those in the Holarctic region and the extent to which their helminth fauna varies seasonally is not known. The only study that seems comparable involves the Florida duck (Anas platyrhynchos fulvigula). This is a non migratory species, and the data available suggests that seasonal differences do

exist in the composition of its helminth fauna (Kinsella and Forrester, 1972). The diet of this species changes seasonally. Greater quantities of animal matter are consumed in spring and summer which results in increased recruitment (Kinsella and Forrester, 1972). Consequently, Anas species at Barberspan, particularly the redbilled teal which does show seasonal variation in its consumption of animal matter (Douthwaite, 1977), could also be expected to show some seasonal variation in their parasite fauna.

Temporally, the helminth communities studied at Barberspan correspond to spring communities of holarctic species. If seasonal variation does occur, these communities may not be representative of those present later in the summer. It is possible that the diversity of the helminth communities may increase thereby affecting the core - satellite relationship and the size of recurrent groups. This effect should be more pronounced among the generalist feeders (yellowbills and redbills) than in carnivorous species (Cape teal and Cape shoveller) which concentrate on specific types of prey year round. Studies made on the fauna of birds returning to Barberspan would be very informative.

Although many studies on the helminths of waterfowl exist, direct comparisons of communities are difficult owing to the fact that much of the data is presented in summary form and consequently impossible to analyze. Stock and Holmes (1987) summarized the available data on waterfowl

communities and ranked them on the basis of the number of parasite species present as well as the total numbers of worms present. Table 7 shows their ranking for 18 species of waterbirds, updated with data from the four Anas species examined in this study (shown in bold face). The Cape teal which ranked fourth in mean number of species and third in mean total number of parasites ranked third overall; Cape shovellers, which ranked twelfth and fourth in the same categories, ranked seventh overall. Yellowbilled ducks and redbilled teal ranked nineteenth and twenty-first in mean number of species and twentieth and twenty-second respectively in mean total number of parasites. Their overall ranking was twenty-first and twenty-second, respectively. The yellowbills and redbills therefore seem to be among species which harbour light parasite loads. Whether or not this is a seasonal artefact is unknown since no seasonal information is available on these species. However, the infection levels detected were consistent with the feeding data available on yellowbills and redbills at Barberspan. The Cape teal ranked among the most heavily infected hosts. Based on the diet of this host and that of the species it ranks with, the infection levels are consistent with hosts that specialize on a narrow range of prey items that serve as intermediate hosts for a variety of helminths.

Table 7. Comparison of the mean number of helminth species and mean total number of helminth species in African *Anas* species with other waterfowl species

Host	No. of species	Rank	No. of worms	Rank	Com- bined	Overall Rank
Shorebirds						
Bonaparte's gull ^a	5.5	17	51	21	38	20
Curlew ^a	4.2	20	263	15	35	18
Godwit ^a	3.4	22	509	12	34	17
Willet ^a	8.6	11	654	11	22	12
Ducks						
Blue-Winged Teal ^a	10.1	7	854	10	17	8
Lesser Scaup ^a	14.3	3	22 231	2	5	2
Bufflehead ^a	7.0	14	180	17	31	15.5
Canvasback ^a	17.3	2	917	9	11	4
Gadwall ^a	9.7	8	197	16	24	13
Mallard ^a	10.2	6	266	14	20	10
Ring-necked ^a	7.7	13	134	18	31	15.5
Ruddy ^a	8.7	10	1 680	8	18	9
Widgeon ^a	5.2	18	85	19	37	19
White-winged Scoter ^a	18.5	1	28 087	1	2	1
Yellowbilled duck ^b	5.0	19	54	20	39	21
Redbilled Teal ^b	3.9	21	19	22	43	22
Cape Teal ^b	11.3	4	5 107	3	7	3
Cape Shoveller ^b	8.4	12	3 889	4	16	7
Grebes						
Eared Grebe ^a	9.1	9	3 641	5	14	6
Horned Grebe ^a	6.7	15	1 808	6.5	21.5	11
Red-necked Grebe ^a	10.7	5	1 808	6.5	11.5	5
Western Grebe ^a	6.4	16	365	13	29	14

^aStock and Holmes 1987.

^bThis study

Gregory et al. (1991) conducted an extensive study on the relationships between various life history variables and parasite richness data from 158 species of birds. The only variable with a significant positive correlation with parasite richness was body weight. Similar results were reported by Guégan et al. (1992) who found that body size accounted for approximately 77% of the variability in species richness in the monogenean gill fauna of African cyprinids. Curiously, Cape teal, which had the the lowest mean body weight of the four species examined, had the greatest diversity and the largest number of parasites. While the above generalizations may hold for hosts that have comparable life history characteristics, smaller species, especially those that are highly carnivorous, may diverge from the general pattern.

COMPOUND COMMUNITY STRUCTURE

In addition to the quantitative differences noted in the component communities above, there were also differences in the species present.

Preliminary analysis using Jaccard's coefficient revealed two groupings within the compound community based on the species present. The fauna in yellowbills and redbills and in Cape teal and Cape shoveller displayed the greatest similarity to each other. Although useful for initial analysis, this coefficient is conservative and

treats all species equally regardless of their frequency of occurrence.

Multivariate procedures incorporate both frequency and abundance data, providing a more rigorous approach to the analysis.

Hierarchical cluster analysis confirmed the differences in the two communities suggested by the Jaccard analysis. Further, it revealed that while there was a broad overlap between infracommunities in the yellowbills and redbills, those in Cape teal and Cape shoveller formed distinct groups despite the fact that they shared many species.

The results obtained in PCA paralleled those obtained in HCA. However, in addition to identifying patterns in the data, it also provides some insight into factors that contribute to these patterns.

Principal component 1 effectively separated the infracommunities in the Cape teal and Cape shoveller group from those in the yellowbills and redbills. Seven species, Diorchis (28), Echinocotyle capensis, E. clerici, E. rosseteri, Echinocotyle sp. (36), Skrjabinoparaxis tatianae and Sobolevicanthus transvaalensis had strong positive loadings on PC1. These were maintained exclusively by the Cape teal and/ or Cape shoveller (a single S. tatianae was also found in one redbilled teal). These are all species which are, or are likely to be, transmitted by entomostracans and both Cape teal and Cape shoveller would

be highly susceptible to them.

Cape teal and Cape shoveller feed primarily at Leeupan (Skead, 1977) and consequently maintain localized infective pools there. Yellowbills and redbills feed mainly at Barberspan and also use Leeupan, but they do so less frequently and their contact with this pool is more limited. However, as some contact with the infective pool likely occurs, additional factors, such as accessibility of particular intermediate hosts or a greater degree of host specificity on the part of particular helminth species may be operating. These could contribute to the restriction of particular helminths to certain host species.

Three species, A. minor, T. crami and S. gracilis, which had strong negative loadings on PC1, occurred exclusively in yellowbilled ducks and redbilled teal. Apatemon minor requires a snail intermediate host. These are not available at Barberspan but do occur in peripheral wetlands. The presence of this species affirms the vagility of these hosts at Barberspan. Tetrameres crami is transmitted by a variety of aquatic arthropods and terrestrial insects. It is also common in land birds (McDonald, 1969). Because Yellowbilled ducks and redbilled teal feed in uplands (Skead and Dean, 1977b) as well as wetlands it is possible that infections are also acquired away from Barberspan. Cape teal and Cape shoveller are more sedentary and are less likely to acquire infections in

uplands or in peripheral wetlands.

Sobolevicanthus gracilis is a cosmopolitan cestode that occurs in many waterfowl species. It is transmitted by entomostracans. Why it should occur in yellowbilled ducks and redbilled teal and not in Cape teal and Cape shoveller is unclear. It is possible that the main hosts for this species were beyond the scope of this study. If these were restricted to Barberspan, any infective pools established would also be highly localized and not accessible to Cape teal or Cape shoveller.

Principal component 2 (PC2) resulted in the separation of the infracommunities in the Cape teal from those of the Cape shoveller. Three cestodes (E. rosseteri, S. transvaalensis and "Fimbriariodes" sp.(30)) with heavy positive loadings on PC2 occurred exclusively in the Cape teal, while Echinocotyle sp. (36), which loaded negatively, occurred exclusively in the Cape shoveller. As Cape teal and Cape shoveller share Leeupan in approximately the same numbers, have heavy infections of their respective helminths and feed on entomostracans, these differences were unexpected. Either the species in question are highly host specific or the intermediate hosts are inaccessible to the other definitive host. While some differences in feeding behaviour exist (Skead, 1977), the two species feed in the same area and, to a large degree, on the same prey. It seems likely therefore that each would encounter all of these

parasites. Restriction of these helminths to their particular hosts seems more likely due to host specificity than to accessibility.

While there is a broad overlap in the helminth fauna of yellowbills and redbills, a number of helminth species were restricted to a single host. For example, Tetrameres crami and Tetrameres sp , Platyscolex ciliata, Diorchis flavescens, and Dicranotaenia coronula were found in the yellowbills but are absent from the redbills. Conversely, Tetrameres ryjikovi, Capillaria contorta, Fimbriaria fasciolaris, Microsomacanthus teresoides and Skrjabinoparaxis tatianae are found in the redbills and not the yellowbills. Of these species, T. crami and T. ryjikovi were encountered frequently the others only rarely. With the exception of D. flavescens and S. tatianae, all of these helminths have been reported from a wide range of host species (McDonald, 1969). The rare occurrence of these helminths, resulting in their collection from a single host species, reflects irregular exposure to infective stages. This is due in part to the limited consumption of entomostracans by these hosts and, if the numbers found accurately reflect the abundance of these helminths, limited numbers of larval stages in the infective pool. In contrast with Cape teal and Cape shoveller, the low numbers of most species present in yellowbilled ducks and redbilled teal suggest that these species play a limited role in

maintaining infective pools at Barberspan, at least during the winter period.

The eight recurrent species in the compound community; (D. flavescens, Diorchis (28), E. capensis, E. clerici, E. rossetteri, M. spirallacirrata, S. tatiana and S. transvaalensis), were all core species in the Cape teal. Three, E. capensis, E. clerici and M. spirallacirrata, were core species in Cape shoveller. Microsomacanthus spirallacirrata and D. flavescens occurred as satellite species in the yellowbilled duck, while M. spirallacirrata and S. tatiana occur as satellite species in the redbilled teal. All of the species in Cape teal and Cape shoveller were recurrent members of their respective component communities; the species occurring in yellowbilled ducks and redbilled teal were associate species in their respective communities.

Cloacotaenia megalops, G. cygni and T. ryjikovi occurred as associate species in the compound community. Cloacotaenia megalops and G. cygni were core species in the Cape teal and Cape shoveller; Tetrameres ryjikovi was a core species in Cape shoveller. All were secondary species in redbilled teal and C. megalops and G. cygni were secondary and satellite species in yellowbilled ducks respectively. As defined by the recurrent group analysis, the most common species of the compound community are maintained by Cape teal and to a lesser extent by Cape shoveller.

Neraasen and Holmes (1975) demonstrated that the composition of the infective pool in a given habitat is most likely to be influenced by the numerically dominant host species. At first glance, this is counterintuitive to the situation at Barberspan, where the Cape teal and Cape shoveller, the least abundant hosts, harboured the richest and most diverse communities. However, given the differences in diet among the host species along with habitat preferences, this contradiction can be reconciled. Recent studies on salamanders (Goater et al., 1987) and grebes (Stock and Holmes, 1987) have demonstrated that differences in the component communities of various host species reflect differences in the diet and habitat preferences these hosts have evolved (Goater et al, 1987; Stock and Holmes, 1987) and on the degree of host specificity exhibited by parasite species (Stock and Holmes, 1987). These are also important determinants of the infective pool structure of the sympatric host species at Barberspan.

Although many helminth species were shared among the various hosts, the extent to which they were shared depended to a large degree on host diet and spatial distribution of the hosts. Cape teal and Cape shoveller shared a number of species and also harboured species found in yellowbilled ducks and redbilled teal. Infection levels of these latter

species are generally greater in Cape teal and Cape shoveller. As a consequence, infective pools of these species maintained by Cape teal and Cape shoveller could make Leeupan an important focus of infection for yellowbilled ducks and redbilled teal that move between the two wetlands.

SUMMARY

The overall objectives of this study were as follows: 1, to determine the helminth fauna of the four South African Anas species; 2, to compare the fauna with helminth species already detected in Africa and to determine if indeed any species are specific to the region itself; 3, to determine if the Anas species maintain separate helminth communities; and if so then: 4, to determine the factors that contribute to the segregation of these helminth communities; and 5, to determine which helminth species are dispersed by what duck species during spring dispersal.

The helminth fauna of anatids at Barberspan was dominated by cestodes but nematode and digenean species were also present. Conditions conducive to the development of infective pools of cestode and nematode larvae exist at Barberspan but infective pools and subsequent transmission of digenean larvae are apparently restricted to peripheral wetlands due to the absence of snails at Barberspan.

Many of the helminths found at Barberspan were cosmopolitan species. Others were previously only known from Europe, or in one instance, from Australia. However, of the 23 cestode species encountered at Barberspan, 10 were previously unknown, suggesting that extensive speciation has occurred within this group. Further studies would undoubtedly reveal the presence of more undescribed species as well as species previously unreported from Africa.

The helminth communities in the Anas species at Barberspan can be segregated quantitatively into two distinct groups. The first, characteristic of the yellowbilled ducks and redbilled teal, consisted of species - poor communities with parasites occurring in low numbers. The second, characteristic of those in Cape teal and Cape shoveller, consisted of species - rich communities with parasites occurring in large numbers.

The helminth communities can be separated in a similar manner based on species composition. Yellowbilled ducks and redbilled teal harbour similar species as do the Cape teal and Cape shoveller. While some species are shared, the fauna of both groups is distinct. Differences in the communities reflect differences in diet, spatial distribution, and apparently in host specificity of some cestodes.

Differences were also noted between the communities in the Cape teal and Cape shoveller. These were due to the presence or absence of particular cestode species in each host. The dietary and spatial overlap of these species suggests host specificity is the probable cause of these differences.

The carnivorous species (Cape teal and Cape shoveller) had the largest recurrent groups of parasites. These groups were largely composed of cestode species with similar life cycles, presumably transmitted by the same crustacean species. Specialization on these crustaceans as prey items

results in the acquisition of a predictable group of helminth species. A recurrent group with two members occurred in redbilled teal; no recurrent groups occurred in yellowbilled ducks.

Cape teal and Cape shoveller harboured several species of helminths that occur less frequently and in fewer numbers in yellowbilled ducks and redbilled teal. While the latter group likely establishes infective pools of many parasites at Barberspan it would also have access to pools established by species other than those examined in this study. The low numbers present in the birds examined, however, suggests that the pools are not extensive. This and the paucity of entomostracans in the diet of these hosts, likely limits infection levels in these species at Barberspan. Infective pools of species shared by both groups, established and maintained by the Cape teal and Cape shoveller at Leeupan, may be an important factor in the infection of yellowbilled ducks and redbilled teal.

Infection levels in yellowbilled ducks and redbilled teal resemble the levels seen in North American waterfowl in the spring. Adults disperse from Barberspan with light infections and relatively few species. Cape teal and Cape shoveller on the other hand, would disperse to breeding areas with heavy infections. In nesting areas, the infective pools produced by the eggs of helminths present in the local duck community would form with time. Species in the host

community would contribute to the infective pools in proportion to their abundance and infection levels. Infections resulting in the community would be influenced to some extent by diet, spatial overlap and specificity of particular helminths. Further studies in the nesting areas and on waterfowl returning to Barberspan are needed to determine what species are acquired, how the component and compound communities develop, and to assess the seasonal dynamics over the nesting season.

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SECTION 2

INTRODUCTION

This section contains the descriptions of 3 previously unknown species of cestodes found in anatids at Barberspan. Each is presented as a separate section, complete with references. The reason for this is that the references pertain to specific descriptions and those pertinent to one description are not pertinent to the others. The description of Microsomacanthus macrotesticulata has been published (Alexander and McLaughlin, 1993). The other two have not. As a thesis does not constitute publication, I have, in accordance with the International Commission for Zoological Nomenclature (Article 9, Section 6), refrained from naming the other species at this time. Specimens of these last two species will be submitted to museums when the descriptions are submitted for publication. Consequently, accession numbers are not available at this time.

Descriptions are presented in telegraphic style, consistent with current practice.

MATERIALS AND METHODS

Details of collection, staining and observational procedures have been published elsewhere (McLaughlin, 1984; 1989). Briefly, birds collected by shotgun or by trapping were examined within 1 hr. The helminths were removed, rinsed in clean tap water, fixed in 5 % buffered formalin

for 24 hours, then stored in 70 % ethanol. Specimens prepared as whole mounts were stained in acetocarmine and mounted in Canada balsam. Measurements and drawings were made using a Wild M - 20 microscope and drawing tube. All measurements are given in microns unless stated otherwise. The mean values \pm SD and sample sizes are given in parentheses following the range.

Microsomacanthus macrotesticulata

During study of a collection of anatid helminths from Barberspan, Republic of South Africa, small specimens of a cestode species belonging to the hymenolepidid genus Microsomacanthus were encountered in southern pochards (Netta erythrophthalma (Eyton)), yellowbilled ducks (Anas undulata Dubois), and redbilled teal (Anas erythrorhyncha Gmelin). The specimens belong to a group of microsomalcanthids characterized by rostellar hooks 29- 32 μ m long and a short cirrus sac that barely extends beyond the poral excretory vessels. The specimens represent a new species that is described herein.

DESCRIPTION

Microsomacanthus macrotesticulata

(Figs. 1 - 7)

Description based on seven specimens from Southern pochards. Five specimens were complete with scoleces, none had fully mature eggs.

General: Hymenolepididae; with characteristics of the genus. Small cestodes 6.2 - 9.5 mm long and 0.4 - 0.7 mm wide. Longest strobila with 134 proglottids. Scolex (Fig. 1) 236 - 252 long by 151 - 200 wide. Suckers round to oval, 91 - 113 X 70 - 108. Retractable rostellum, 196 - 240 long (everted) by 48 - 70 wide at tip, armed with 10 microsomalcanthid hooks 29 - 32 long (Fig. 2).

FIGURE CAPTIONS

Figures 1 - 7. Microsomaacanthus macrotesticulata.

1. Scolex, Holotype. 2. Rostellar hook, Holotype. 3.

Young proglottid, Holotype. 4. mature proglottid, Holotype.

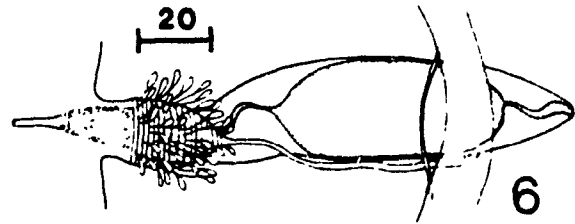
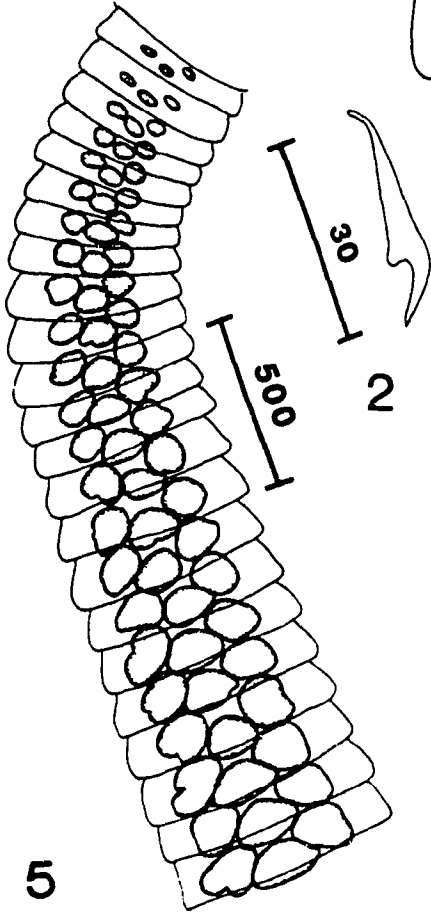
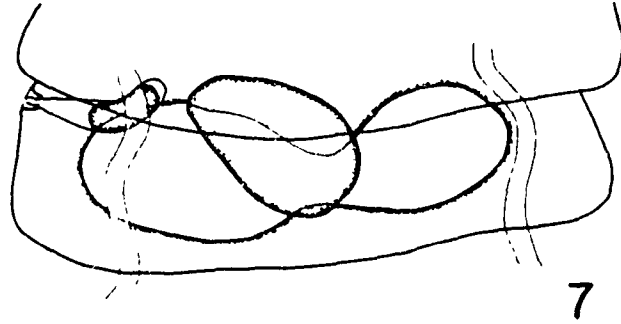
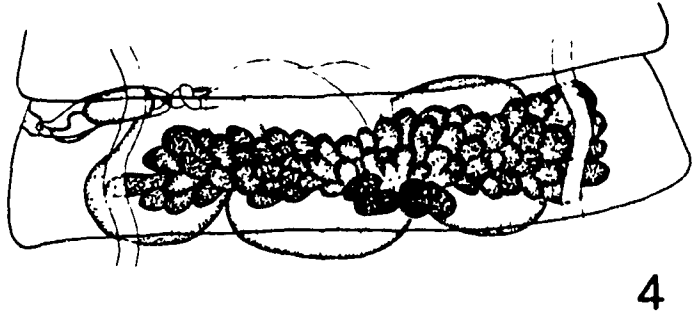
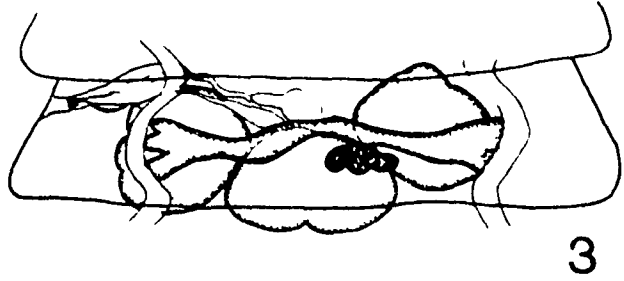
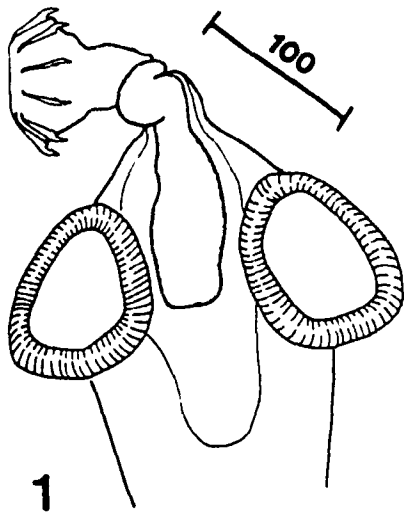
5. Strobila showing testis development, Holotype. 6.

Genital atrium, cirrus and copulatory portion of the vagina,

Paratype. 7. Proglottid showing developing uterus,

Holotype. All scales are in micrometers (μm). Figures 3,

4, and 7 are drawn to the same scale.



Neck 72 - 96 wide. Genital pores shallow, situated approximately $\frac{1}{4}$ of the distance along proglottid margin.

Male genitalia: Testes 3, arranged in a triangle with the median testis slightly posterior to the poral and antiporal testis (Figs. 3 - 4). Testes irregularly oval, slightly lobed (Figs. 3 - 5). Testes measure 106 - 192 in long diameter by 96 - 161 in short diameter in mature proglottids. Poral and antiporal testes overlap excretory canals slightly in mature proglottids (Fig. 4). Testes increase rapidly in size (Fig. 5). Cirrus sac short, 88 - 146 long by 20 - 34 wide. Antiporal end of cirrus sac extends just beyond poral excretory vessel (Figs. 3 - 4). Length of cirrus sac less than maximum testis diameter in mature proglottids. Internal seminal vesicle occupies the proximal half of cirrus sac when full. External seminal vesicle oval, up to 120 long by 62 wide, situated between the antiporal tip of the cirrus sac and midline of proglottid. Cirrus (Fig. 6) with conical spinous base and an aspinous, distal, tubular region. Longest cirrus 31 long; conical base 20 - 23 long by 9 - 11 wide; distal region 8 - 11 long by 2 at the tip.

Female genitalia: Ovary and vitelline gland situated ventral to median testis, slightly antiporal to midline, in posterior half of proglottid. Young ovary transversely elongated with lobulated distal ends (Fig. 3), becoming highly lobulated when mature (Fig. 4). Mature ovary 312 -

489 wide by 67 - 139 long in mature proglottids. Ovarian lobes extend beyond excretory canals when mature. Vitelline gland, lobated, postovarian, 24 - 55 long by 65 - 120 wide. Copulatory portion of vagina funnel - shaped (when not collapsed), 13 - 17 long, muscular, and surrounded by inconspicuous glandular cells (Fig. 6). Vagina dilates forming seminal receptacle shortly after crossing poral excretory vessels. Seminal receptacle oval and comparatively large, situated mainly in poral half of proglottid but crossing into antiporal half. Largest seminal vesicles occur in uterine proglottids. Maximum size of seminal receptacle 218 by 137. Uterus saccular (Fig. 7), first observed in proglottids 116-120. Young uterus extends beyond excretory canals. Mature eggs not observed.

Taxonomic summary

Type host: Netta erythrophthalma (Eyton), Southern Pochard.

Type locality: Barberspan, Transvaal Province, Republic of South Africa.

Other hosts: Anas undulata Dubois, Yellowbilled Duck; Anas erythrorhyncha Gmelin, Redbilled Teal.

Site: small intestine

Specimens deposited: National Parasite Collection, Canadian Museum of Nature (CMNP), Ottawa, Ontario, Canada, K1A 0M8.

Holotype: CMNP1993-0053, Paratypes: CMNP1993-0054 to 0059.

REMARKS

The length of rostellar hooks of hymenolepidid cestodes from avian hosts is relatively constant, varying less than 11% of the total length (Czaplinski, 1956). Subsequent experimental work however, has revealed that the variation in hook length in Sobolevicanthus gracilis and Diorchis stefanskii may be as great as 33% and 20% respectively, of the mean length (Misiura 1971, Czaplinski, et al., 1978). The variability is the result of crowding during development in the intermediate host. The discrepancy between the two studies is due to a single cysticercoïd, with rostellar hooks 10 μ m shorter than any other, reported by Misiura (1971). When this observation is disregarded, the variability in hook length is comparable in both studies. In comparing our material with other species, we examined those species whose rostellar hook range fell within 20% of the mean hook length of the new species i.e. $31 \pm 6 \mu$ m.

Despite efforts to subdivide the Hymenolepididae into more manageable groupings, some species currently defy assignment and are retained within Hymenolepis sensu lato (see Schmidt, 1986). Accordingly, we compared our material to species from avian hosts currently listed in Hymenolepis by Schmidt (1986) in addition to species in Microsomacanthus.

There are currently 19 species in Microsomacanthus with rostellar hooks that lie within the range of 25 - 37 μ m that

also possess cirrus sacs less than 200 μm long. Of these species, all but five have cirrus sacs that reach or extend beyond the midline in mature proglottids. These five include; Microsomacanthus styloides (Fuhrmann, 1906), Microsomacanthus macroovata (Fuhrmann, 1918), Microsomacanthus fulvicicola (Skrjabin and Mathevossian, 1942), Microsomacanthus formosa (Dubinina, 1953), Microsomacanthus spiralibursata (Czaplinski, 1956), and Microsomacanthus oidemae Spasski and Yurpalova, 1966. In addition, two unnamed Microsomacanthus species (Spasski and Yurpalova, 1966), Hymenolepis solowiowi of Beverley - Burton (1964) nec Skrjabin (1914) and Hymenolepis ibidis Johnston, 1913, also have cirrus sacs within this size range that extend just beyond the poral excretory vessels. The rostellar hooks of these latter four species were not present in the original material.

The rostellar hooks of M. styloides (from Charadriiformes) and M. magniovata (from Passeriformes) have short blades (Fuhrmann, 1906, 1918, respectively) and are of a distinctly different shape than those of M. macrotesticulata.

Microsomacanthus fulvicicola (= Hymenolepis sp. from Fulica americana (Gruiformes) of Linton, 1927), M. formosa (from Anseriformes) and H. ibidis (from Ardeiformes) all possess small testes (M. fulvicicola; 21 μm , M. formosa; 32 x 22 μm) (Linton, 1927, Dubinina, 1953, Spasskaya and Spasski

1961, Johnston, 1913). Testis measurements were not given for H. ibisi, however, based on the illustration provided, the testis diameter in this species like those of the other two, is only 1/4 to 1/3 of the cirrus sac length (Johnstone, 1913). In M. macrotesticulata, the diameter of testes in mature proglottids is as great or greater than the length of the cirrus sac.

Skrjabin (1914) described H. solowiowi from specimens lacking scoleces. The species resembles Microsomacanthus compressa (Linton) and several authors regard it as a synonym. Beverley - Burton (1964) described specimens identified as H. solowiowi with hooks 28 - 29 μ m long. Hymenolepis solowiowi sensu Beverley - Burton (1964) differs from M. macrotesticulata on the basis of hook shape, the presence of a muscular cirrus sac, and a differently shaped cirrus that is armed with conspicuous spines along its length.

The cirrus sac in Microsomacanthus spiralibursata (150 - 318 μ m long) is longer than that of M. macrotesticulata. It extends to the middle of the proglottid in small specimens but only to the poral excretory vessels in larger ones (Czaplinski, 1956). This feature and differences in cirrus structure are sufficient to separate M. spiralibursata from the new species.

Microsomacanthus II (Spasski and Yurpalova, 1966) differs from the new species in that the poral testis lies

almost entirely between the poral excretory canals and the proglottid margin.

The species that show the greatest similarity to M. macrotesticulata are M. oidemae and Microsomacanthus I of Spasski and Yurpalova (1966). All three species possess short cirrus sacs that extend slightly beyond the poral excretory vessels and comparatively large testes arranged in a similar manner within the proglottid.

While the size of many structures in M. macrotesticulata overlap those of M. oidemae, the maximum dimensions of external seminal vesicle and the seminal receptacle differ greatly between the two species. The cirrus structure is also different. In M. oidemae the cirrus is tubular, tapers along its length and is covered along its length with fine spines (Spasskii and Yurpalova, 1966). The cirrus in M. macrotesticulata has a distinct conical base covered with coarser spines and a narrow, tubular, distal portion that lacks spines.

Comparison of Microsomacanthus I with M. macrotesticulata is tenuous because the rostellar hooks are unknown. The cirrus structure is similar in both species, however sufficient differences in proglottid morphology and morphometrics exist to separate the two species. Measurements of the cirrus in Microsomacanthus I (from the figure) indicate that it is approximately twice as large as that in M. macrotesticulata. The cirrus sac in

Microsomacanthus I is slightly longer than that in the new species, the testes are smaller, and their maximum diameter is only half the length of the cirrus sac. The ovary in this species is trilobed rather than multilobed as in M. macrotesticulata.

DISCUSSION

Additional specimens were encountered in eight of 25 Yellowbilled Ducks (range 2 - 31 specimens) and one of 21 Redbilled Teal (5 specimens). Most specimens had intact scoleces and, as the testes and cirrus sacs had developed, they can be assigned with confidence to this species. The only difference noted was the tendency for the cirrus sac lengths to cluster in the lower half of the range.

The ovaries and vitelline glands in these specimens were only in the earliest stages of development and no uterine development was seen. The relatively large number of specimens at the same stage of development in Yellowbilled Ducks and Redbilled Teal collected over a five week period, raises the question of whether this cestode can attain maturity in these hosts.

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Echinocotyle n. sp.

During study of a collection of anatid helminths from Barberspan, Republic of South Africa, small specimens of a cestode species belonging to the hymenolepidid genus Echinocotyle were encountered in Cape shoveller (Anas smithii, Gmelin). The specimens belong to a group of small cestodes within the genus Echinocotyle which typically have overall body lengths of less than 2 mm and rostellar hooks 30 - 40 μ long. The specimens represent a new species that is described herein.

DESCRIPTION

Echinocotyle n. sp.

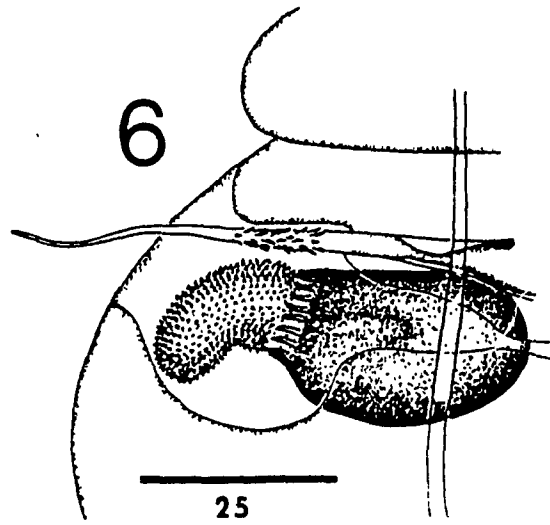
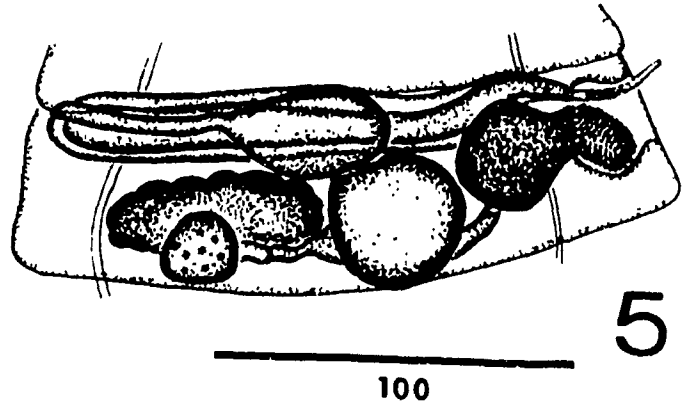
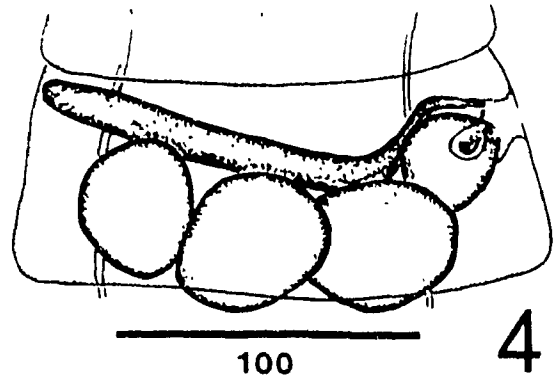
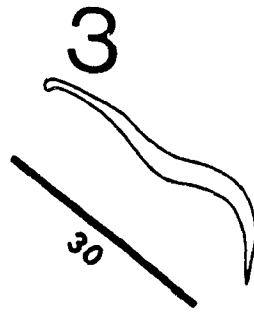
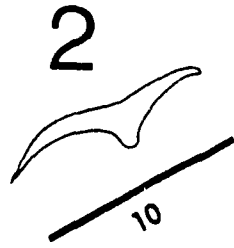
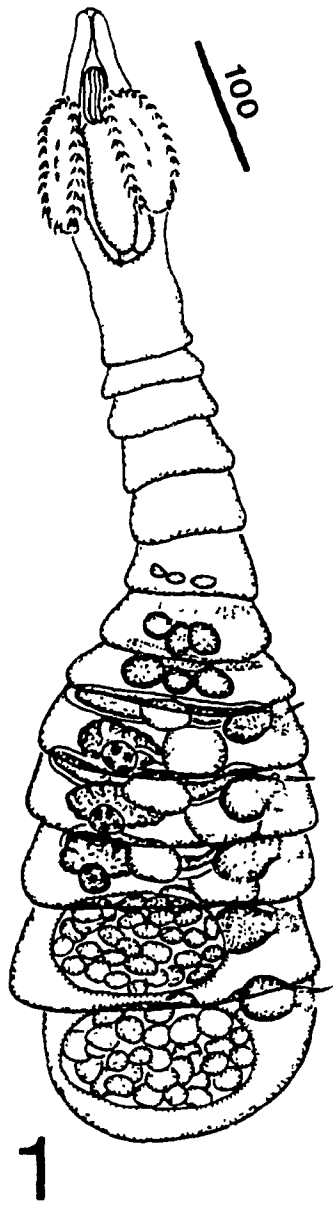
(Figs. 1 - 6)

Description based on eight specimens from Cape shoveller. All eight specimens were complete with scoleces, all specimens were mature, however, none was fully gravid. All measurements are in micrometers (μ m).

General: Hymenolepididae; with characteristics of the genus. Small cestodes 622 - 870 (725 ± 65 , $n=8$) long and 138 - 192 (166 ± 17 , $n=7$) wide. Longest strobila with 14 proglottids (12 ± 1 , $n=8$). Scolex (Fig. 1) 168 - 216 (189 ± 14.0 , $n=8$) long by 96 - 132 (106 ± 9.5 , $n=8$) wide. Suckers oval, 66 - 95 (78.1 ± 8.0 , $n=8$) long by 30-44 (37.9 ± 4.5 , $n=8$) wide, armed with three to four rows of small hooklets 9 - 10 (9.3 ± 0.5 , $n=6$) long along all but the bottom of the sucker margins (Fig. 2).

FIGURE CAPTIONS

Figures 1 - 5. Echinocotyle n. sp. I. 1. Complete specimen. 2. Sucker hook. 3. Rostellar hook. 4. Young proglottid, dorsal view. 5. Mature proglottid, dorsal view. 6. Genital atrium, cirrus and accessory sac, ventral view. All scales are in micrometers (μm).



One to two incomplete rows of hooklets found in the medial aspect of suckers. Retractable rostellum, 228 - 235 long (everted) by 24 - 40 (31.5 ± 5.0 , $n=8$) wide at tip. Rostellum armed with 10 hooks of the nitidoid type 35 - 37 (36 ± 0.5 , $n=8$) long with a reduced guard (Fig. 3). Rostellar sac extends past the posterior sucker margin. Neck 46 - 60 (53.5 ± 5.0 , $n=8$) wide. Genital pores shallow, situated in the anterior portion of proglottid margin.

Male genitalia: Testes 3, arranged transversely (Figs. 1, 4). Testes oval measuring 25 - 48 (34.3 ± 3.3 , $n=16$) in long diameter by 23 - 38 (28.0 ± 2.5 , $n=15$) in short diameter, generally absent by the time the ovary is mature (Fig. 5). Cirrus sac elongate, 102 - 156 (129 ± 7.5 , $n=16$) long by 12 - 20 (16.5 ± 1.5 , $n=16$) wide, extending to the antiporal margin in mature specimens (Fig. 5). Internal seminal vesicle present, filling most of cirrus pouch in mature proglottids. External seminal vesicle oval, up to 48 long by 40 wide, situated slightly antiporal to the proglottid midline, lying dorsal to the cirrus pouch in mature proglottids. Cirrus (Fig. 6) very slender, tubular and heavily armed with fine spines at its base, spines become less numerous approaching the distal half of the cirrus, unarmed at its tip. Longest cirrus 36; base approximately 2 wide; less than 1 wide at tip. Accessory sac situated dorsal to cirrus sac, oval 28 - 43 (32.7 ± 2.5 , $n=14$) long by 19 - 30 (24.5 ± 2.0 , $n=13$) wide, and

armed with small spines around its opening. Everted portion 15 - 16 (15.5 ± 1.5 , $n=4$) long by 10 - 13 (11 ± 2.0 , $n=4$) wide, heavily armed with spines.

Female genitalia: Ovary and vitelline gland situated in lateral antiporal region of proglottid. Mature ovary elongate 35 - 66 (47.5 ± 7.0 , $N=9$) wide by 15 - 26 (21.0 ± 2.7 , $n=9$) long in mature proglottids. Vitelline gland postovarian, round to oval, smooth, 18 - 26 (21.0 ± 2.5 , $n=6$) long by 13 - 23.5 (18.5 ± 3.3 , $n=6$) wide. Vagina dilates forming seminal receptacle. Seminal receptacle round to oval, situated in poral half of proglottid. Largest seminal vesicles occur in mature proglottids. Maximum size of seminal receptacle 38 long by 35 wide. Uterus saccular (Fig. 1), first observed in proglottids 11 - 12. No gravid proglottids were encountered.

Taxonomic summary

Type host: Anas smithii Gmelin, Cape teal.

Type locality: Barberspan, Transvaal Province, Republic of South Africa.

Site: small intestine

REMARKS

There are currently six species within the genus Echinocotyle that possess rostellar hooks measuring 28 - 42 μm ($36 \mu\text{m} \pm 20\%$) and have strobilae of less than 5 mm. Two species, Echinocotyle vojteki Koubek, 1982, (3.7 - 4.7 mm)

from Lariformes and Echinocotyle anadryensis Yurpalova and Spasskii, 1970 (4.5 mm) from Charadriiformes are several times longer than the new species. In addition, the arrangement of the sucker armature differs. The spines on the sucker margins are arranged in two rows in E. vojteki (Koubek, 1982) rather than three or more as occurs in the new species and there are apparently no spines present in the sucker cavity. The sucker spines in E. anadryensis are arranged in rows of 5 spines around the margins and the sucker cavity is armed with 4 - 5 rows as well (Yurpalova and Spasskii 1970) . Neither condition occurs in the new species.

The remaining four species all occur in Anseriformes. All are minute cestodes, generally less than a millimetre long. As can be seen in Table 1, the measurements of most of the organs of these species as well as those of the new species overlap. The primary differences between these species and the new species concern the shape of the rostellar hooks and the size and morphology of the accessory sacs.

The new species differs from Echinocotyle rosseteri (Blanchard, 1891) in the shape of the rostellar hook, details of proglottid morphology and in the size of the accessory sac. The hooks of E. rosseteri, as described by Czaplinski (1956), possess a conspicuous guard not present on those of the new species. The cirrus sac in E. rosseteri

Table 1: Comparison of the measurements of *Echinocoryle rosseteri* (Blanchard, 1891), *Echinocoryle skrabini* (Mathevosian and Kirov, 1949), *Echinocoryle ryzhikov* (Jogis, 1963) and *Echinocoryle singhi* (Srivastava and Pandey, 1980) with specimens from *Anas singhi* from South Africa. All measurements are in micrometers (µm) unless designated otherwise

Species:	<i>E. rosseteri</i>		<i>E. skrabini</i>		<i>E. ryzhikov</i>		<i>E. singhi</i>		<i>Echinocoryle</i> n.s.p.	
	Blanchard (1891), Czaplinski (1956)		Mathevosian and Kirov (1949)		Jogis (1963), Ryzhikov (1956)		Srivastava and Pandey (1980)			
Strobila	L (mm)	0.76 - 1.5 (1.15) ¹		0.48 - 0.36		0.53 - 0.97 (0.53 - 0.74) ²		0.64 - 0.87		0.62 - 0.87
	W (mm)	0.24 - 0.3 (0.18)		0.18 - 0.19		0.16 - 0.24		0.21		0.13 - 0.19
Number of Proglotids		18 - 28 (26)		14 - 20		9 - 12		9 - 15		10 - 14
Scolex	L	105 - 118 (85 - 105)		--		-- (234)		185 - 227		168 - 216
	W	110 - 126 (75 - 105)		129 - 153		100 - 110 (105)		87 - 100		96 - 132
Suckers	L	85 - 103 (67 - 90)		90 - 112		62 - 80 (62)		75 - 94		66 - 95
	W	45 - 55 (27 - 32)		45 - 54		30 - 40		24		30 - 44
Rows of Spines		3 - 5		3 - 5		3 - 4		3 - 5		3
Rostellum	L	150 - 160		--		--		77 - 87		228 - 235
	W	28 - 33 (tip)		45		--		45 - 52		24 - 40
Rostellar Hook	L	36 - 39 (35 - 38)		36		42		38 - 49 (sic)		35 - 37
Testes	L	23 - 55		15 - 16		36 - 40*		17 - 28		25 - 48
	W	23 - 55		15 - 16		--		24 - 28		23 - 38
Cirrus Sac	L	135 - 160 (140)		162 - 170		102 - 144 (144)		143 - 157		102 - 156
	W	16 - 23 (14)		--		(46)*		20 - 30		12 - 20
Cirrus	L	43 - 46		--		38*		22		36
	W (base)	3.7 - 4.5 (5)		--		(2 - 3)*		4		2
	W (tip)	--		--		--		--		1
Accessory Sac	L	30		present and		(56)*		20 - 32		28 - 43
	W	10		conspicuous		(54)*		11 - 20		19 - 30
Ovary	L	24		--		25*		35 - 45		35 - 66
	W	100		--		54*		38 - 77		15 - 26
Viteline Gland	L	23		--		--		24		18 - 25
	W	48		--		--		28 - 31		13 - 23

Footnotes

- 1 Data in brackets from Blanchard (1891)
- 2 Data in brackets from Ryzhikov (1956)
- Direct measurement from figure in Ryzhikov (1956)

extends to, or slightly beyond the midline of the proglottid whereas it extends almost to the antiporal margin in the new species. The accessory sac is larger and more prominent than in E. rosseteri.

The rostellar hooks of E. skrjabini possess a prominent guard and a comparatively short blade (Mathevossian and Krotov, 1949) and are readily distinguishable from those of the new species on this basis. The margins in the posterior half of the suckers have five hooklets per row compared to three or four in the new species.

Several features distinguish E. singhi from the new species. In E. singhi, the ovary is round rather than elongate, the vitelline gland lies to the poral side of the ovary rather than posterior to it and a conspicuous vaginal sphincter is present (Srivastava and Pandey, 1982). The wide range in rostellar hook length is highly unusual and requires verification. Studies by Czaplinski (1956), supported by our own observations, indicate that the normal variation in hook length of a particular hymenolepidid species seldom varies by more than 11%.

Echinocotyle ryjikovi, which includes specimens described as Echinocotyle sp. by Ryzhikov (1956), resembles the new species closely in general morphology, and in the size of most of the organs (Ryzhikov, 1956; Jogis, 1963). The rostellar hooks are of similar size and shape to those

of the new species, but are nearly 20% longer. Differences also exist in the size and morphology of the accessory sacs. The accessory sacs are smaller in the new species (Table 1) and differ in shape and internal detail from those described by Ryzhikov (1956). Further, the cirrus sac, as described by Ryzhikov (1956), has muscular walls that are not evident in the new species.

In view of the foregoing, the material from A. smithii can be reliably distinguished from other small Echinocotyle species in anatids and erection of a new species is justified.

DISCUSSION

In a recent review of Echinocotyle, Korniyushin (1983) subdivided the genus into five subgenera. The subgenus Echinocotyle was erected for those small species with few proglottids, an armed cirrus and an accessory sac with a row of spines around its aperture. The four species listed in Table 1, E. clerici Mathevossian and Krotov, 1949 and E. minutissima Singh, 1952 were included in it. Echinocotyle capensis McLaughlin, 1989 would also be included in this group. All members are parasites of Anseriformes.

The new species was a common parasite of Cape shovellers at Barberspan. Due to time constraints during collection, it was necessary to preserve, en masse, the gut contents of the shovellers examined and unfortunately few

specimens were preserved well enough for critical study. All 7 shovellers examined were infected with this species; most had in excess of several hundred specimens.

Although large numbers of this species, *E. rosseteri*, *E. clerici*, and *E. capensis* were encountered in anatids at Barberspan, few individuals of any species were encountered with mature oncospheres in the uterus. Examination of original descriptions indicates that while all of these species had uteri with developing eggs, there was no indication that mature eggs were present. Both Singh (1952) and Srivastava and Pandey (1980) present measurements of eggs in the 10 - 14 μ m range, suggestive of maturing eggs. No oncospherical hooks were reported in either study. As observed first by Blanchard (1891) and later by Czaplinski (1956) for *E. rosseteri*, it appears that for these species of *Echinocotyle* at least, maturation of the eggs occurs following apolysis.

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Fimbriariinae n. gen, n.sp.

During study of a collection of anatid helminths from Barberspan, Republic of South Africa, small specimens of a cestode species belonging to the hymenolepidid subfamily Fimbriariinae were encountered in Cape teal (Anas capensis, Gmelin). The specimens do not belong to any of the known genera within the Fimbriariinae. They resemble the genus Fimbriariodes most closely. However, the specimens differ based on the presence of a large spinose accessory sac associated with the genital atrium, not found in Fimbriariodes, and in the presence of only two testes per proglottid. The presence or absence of an accessory sac and the number of testes per segment are generic characteristics in the hymenolepididae. The specimens represent a new genus and species that are described below.

DESCRIPTION

Fimbriariinae n.gen., n. sp.

Generic diagnosis: Hymenolepididae: Fimbriariinae. Rostellum invaginable, armed with a single circle of ten hooks. Pseudoscolex poorly developed. Genital primordia present in last few segments of pseudoscolex. External segmentation absent, internal segmentation evident. Single layer of longitudinal muscular bundles present. Six osmoregulatory canals. Genital pores unilateral. Testes two, arranged obliquely. Cirrus sac opens into spinose invagination of genital atrium. Internal and external

seminal vesicles present. Armed accessory sac associated with genital atrium. Vitelline gland smooth, median, preovarian. Mature ovary four lobed, metameric. Uterus reticulate, continuous in gravid proglottids.

REMARKS

The Fimbriariinae contain 4 genera (Schmidt, 1986). Of these, only two, Fimbriariodes and Fimbriaria, possess pseudoscolices. The new genus most closely resembles the genus Fimbriariodes in general size, structure of the pseudoscolex, proglottid characteristics and arrangement of internal organ systems.

The new genus differs from Fimbriariodes in a number of important characteristics. The new genus has an accessory sac, which is absent in Fimbriariodes. The new genus possesses two testes per proglottid arranged obliquely, rather than three as occurs in Fimbriariodes. The vitelline gland in the new genus is smooth and preovarian; it is lobate and postovarian in Fimbriariodes. The new genus possesses a 4 - lobed ovary; the ovary is reticulate in Fimbriariodes. Finally, the new genus possesses 6 osmoregulatory canals, compared with 9 - 11 in Fimbriariodes.

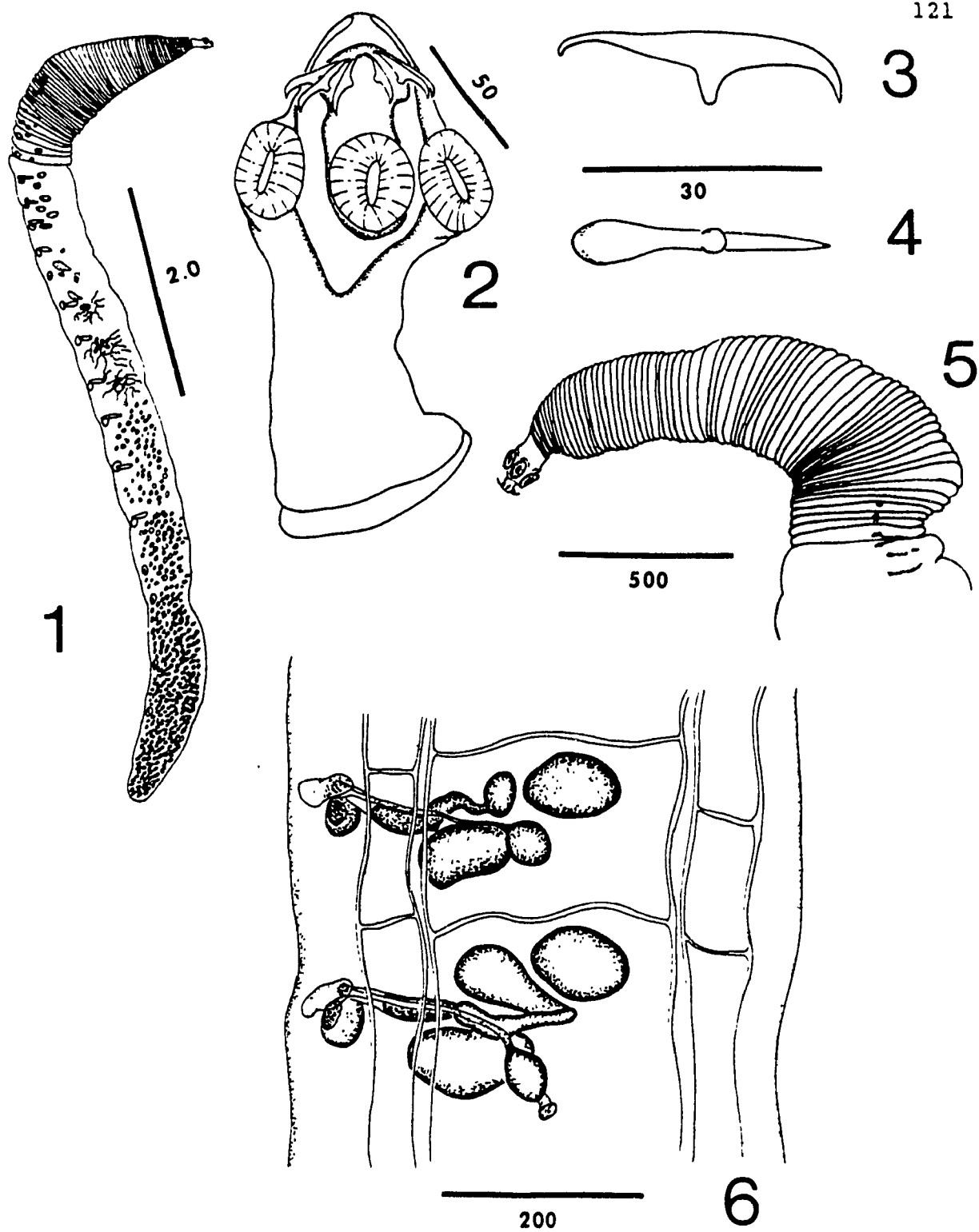
Fimbriariinae n.gen., n. sp.

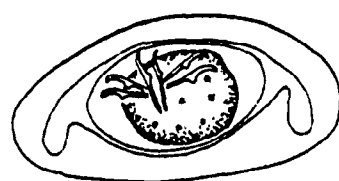
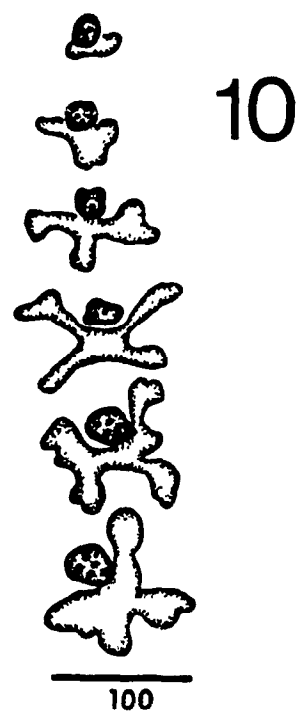
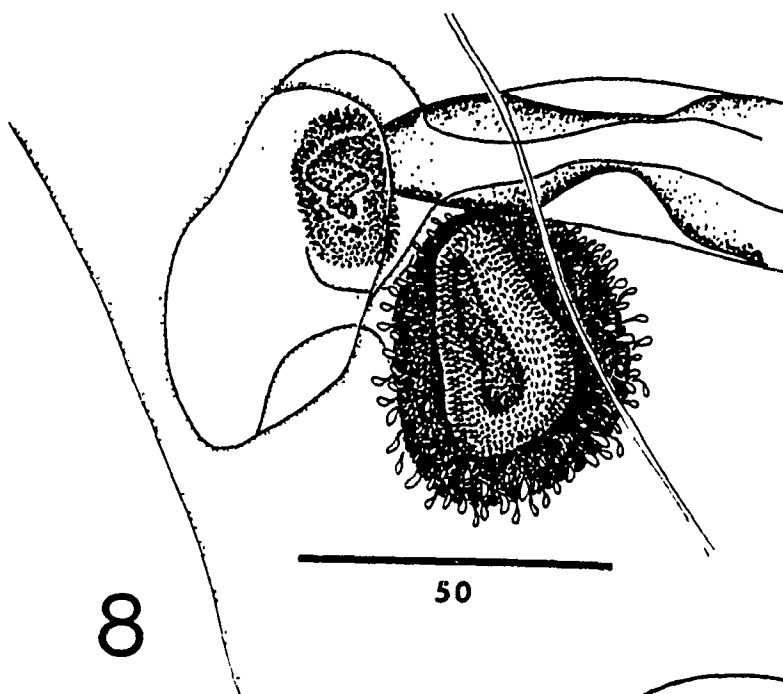
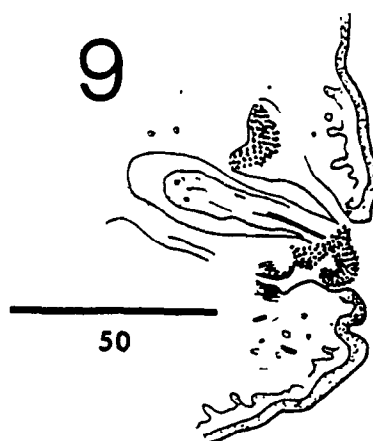
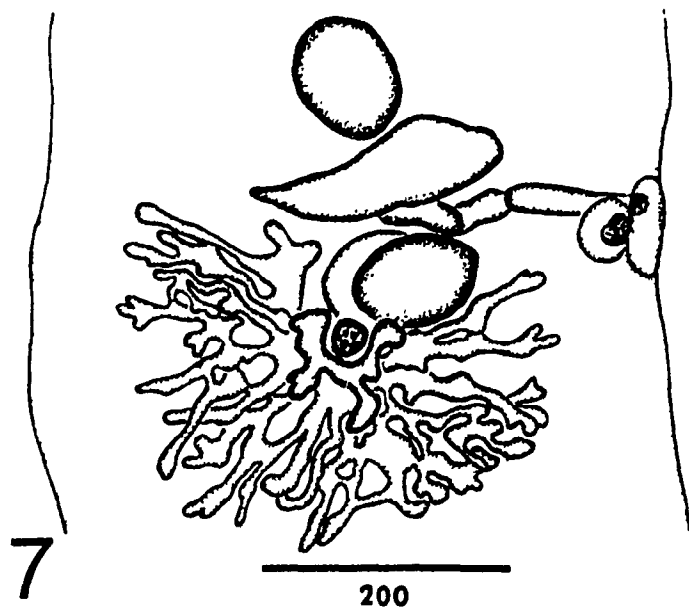
(Figs. 1 - 11)

Description based on seven specimens from Cape Teal. Five had scoleces, several specimens were fully gravid.

FIGURE CAPTIONS

Figures 1 - 11. *Fimbriariinae* n. gen., n. sp. All scales are in micrometers (μm) unless otherwise noted. 1. Complete specimen (scale in mm). 2. Scolex. 3. Rostellar hook, lateral view. 4. Rostellar hook, inferior aspect. 5. Pseudoscolex. 6. Young proglottids. 7. Mature proglottid. 8. Genital atrium, cirrus and accesory sac. 9. Section through genital atrium showing the position of the accessory sac, cirrus pouch and vagina relative to the genital atrium. 10. Development of ovary and vitelline gland in successive proglottids. 11. Internal envelope, embryophore and oncosphere.





General: Small cestodes 5.0 - 10.0 mm ($7.6 \text{ mm} \pm 1.9 \text{ mm}$, $n=7$) long and 0.5 - 0.6 mm (0.53 ± 0.03 , $n=7$) wide (Fig. 1). Longest strobila with 27 proglottids. Scolex (Fig. 2) 120 - 180 (145.3 ± 18.5 , $n=5$) long by 86 - 141 (113.2 ± 21.5 , $n=5$) wide. Suckers round to oval, 42 - 60 (47.3 ± 7.1 , $n=5$) long by 37 - 54 (45.0 ± 6.9 , $n=5$). Retractable rostellum, 90 long (everted) by 32 - 39 (36.3 ± 3.1 , $n=4$) wide at tip, armed with 10 hooks 34 - 36 (35.0 ± 0.6 , $n=8$) long (Fig. 3). Handle and blade of approximately equal length; guard prominent. Proximal end of handle spatulate in dorsal or ventral view (Fig. 4). Pseudoscolex triangular 1.7 - 2.6 mm ($2.1 \text{ mm} \pm 0.3 \text{ mm}$, $n=7$) long by 435 - 615 (528 ± 67.0 , $n=7$) wide at widest point (Fig. 5). Genital pores shallow, situated approximately $1/2$ of the distance along proglottid margin. Largest proglottid 562 wide by 312 long. Six, branched, osmoregulatory canals present; one pair situated close to lateral margins, and two pairs situated about $1/3$ of the proglottid width in from margins (Fig. 6). Cirrus pouch and vagina pass dorsally to osmoregulatory canals. Single row of 38 - 48 muscular bundles visible in transverse section.

Male genitalia: Testes 2, arranged obliquely with the anterior testis situated antiporal to the posterior testis (Figs. 6 - 7). Testes oval measuring 65 - 115 (87.2 ± 12.8 , $n=25$) in long diameter by 45 - 76 (63.2 ± 8.7 , $n=24$) in short diameter in mature proglottids (Figs. 6 - 7). Cirrus

sac short, 96 - 144 (117 ± 12.4 , $n=26$) long by 19 - 25 (22.3 ± 2.0 , $n=26$) wide. Internal seminal vesicle occupies the proximal two - thirds of cirrus sac when full. External seminal vesicle oval, up to 216 long by 113 wide, situated between the midline of proglottid and the poral excretory vessels anterior to cirrus pouch. Cirrus (Figs. 8 - 9) tubular and spinous throughout its length coiled within the genital atrium, 3.5 - 4.5 wide at its base. Accessory sac round to oval, located posterior and dorsal to cirrus sac, 34 - 60 (47.0 ± 8.8 , $n=22$) long by 24 - 46 (36.6 ± 7.1 , $n=22$) wide and surrounded by a layer of glandular cells.

Female genitalia: Ovary and vitelline gland situated medially, posterior and ventral to poral testis, near midline of proglottid. Young ovary compact (Fig. 6), becoming lobulated, with four distinct lobes when mature (Fig. 7, 10). Mature ovary 84 - 140 (117 ± 20.5 , $n=11$) wide by 65 - 110 (87.3 ± 16.2 , $n=11$) long in mature proglottids. Vitelline gland preovarian, round to oval, smooth, 26 - 38 (33.0 ± 4.7 , $n=12$) long by 21 - 36 (27.5 ± 4.8 , $n=12$) wide. Vagina dilates forming seminal receptacle slightly antiporal to midline. Seminal receptacle oval and comparatively large, situated mainly in poral half of proglottid but crossing into antiporal half. Largest seminal vesicles occur in mature proglottids. Maximum size of seminal receptacle 120 by 103. Uterus reticulate (Fig. 7), first

observed in proglottids 15 - 22, filling entire proglottid and becoming confluent between adjacent proglottids when fully gravid. Internal envelope oval. Embryophore oval with small apical extensions. Oncospheres 38 - 50 (43.8 ± 5.6 , $n=20$) long by 14 - 20 (17 ± 2.9 , $n=20$) wide with three pairs of hooklets approximately 10 long (Fig. 11)

Taxonomic summary

Type host: Anas capensis Gmelin, Cape teal.

Type locality: Barberspan, Transvaal Province, Republic of South Africa.

Other hosts: Anas undulata Dubois, Yellowbilled Duck; Anas erythrorhyncha Gmelin, Redbilled Teal.

Site: small intestine

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APPENDIX 1

Host Parasite List of Helminths Reported From
Anseriformes In Africa or From Indigenous
African Species Held in Captivity Elsewhere

Anas acuta acuta¹ L., Northern pintail

Sobolevicanthus octacantha² (Egypt)

Anas boschas L.

Catatropis verrucosa (Egypt)

Opisthorchis geminus (Egypt)

Cloacotaenia megalops (Egypt)

Hymenolepis sp. (Egypt)

Microsomacanthus abortiva (Egypt, Nigeria)

Anas capensis Gmelin, Cape Teal

- * Dicranotaenia coronula (zoo- England)
- Echinocotyle capensis (South Africa)
- Sobolevicanthus transvaalensis (South Africa)
- * Capillaria anatis (zoo- England)
- *§ C. obsignata (zoo- England)
- *§ Echinuria uncinata (zoo- England)
- * Streptocara crassicauda (zoo- England)
- * Fillicolis anatis (zoo- England)

Anas clypeata L., Common Shoveller

Catatropis verrucosa (Egypt)

Hypoderaeum conoideum (Egypt)

Cloacotaenia megalops (Egypt)

Echinocotyle birmanica (Egypt)

Hymenolepis fructicosa (Egypt)

H. fructifera (Egypt)

Hymenolepis sp. (Egypt)

Microsomacanthus abortiva (Egypt)

M. collaris (Egypt)

M. pauciannulata (Egypt)

M. pauciovata (Egypt)

1= host species; 2= helminth species; *- records reported from captive waterfowl outside continental Africa; §- indicates species above (*) which have also been reported from other Anseriformes within continental Africa.

Anas crecca crecca L., European green-winged teal

Hypoderaeum conoideum (Egypt)
Diorchis longicirrosa (Egypt)
Amidostomum anseris (Egypt)
Epomidiostomum querquedulae (Egypt)

Anas erythrorhyncha Gmelin, Redbilled teal

Zygocotyle lunata (Madagascar)
Cloacotaenia megalops (Zimbabwe)
Diploposthe laevis (Zaire)
Microsomacanthus macrotesticulata (South Africa)

Anas penelope L., European wigeon

Opisthorchis simulans (Egypt)
Echinuria uncinata (Algeria)

Anas platyrhynchos platyrhynchos L., Mallard

Apatemon gracilis (Madagascar)
Stictodora sawakinensis (Tunisia)

Anas platyrhynchos platyrhynchos dom., Domestic Duck

Echinoparyphium bioccalerouxii (Egypt)
E. ralphaudyi (Egypt, Ethiopia)
Echinostoma fulicae (South Africa)
E. liei (Egypt)
E. revolutum (Zambia, Egypt)
Maritrema subdolum (Chad)
Microphallus claviformis (Chad)
Notocotylus aegyptiacus (Egypt)
Paramonostomum anatis (Chad)
P. aegyptiacum (Egypt)
Pygdiopsis genata (Egypt)
Zygocotyle lunata (Zimbabwe)

Anas querquedula L., Garganey

Hypoderaeum conoideum (Ethiopia)
Microsomacanthus pauciannulata (Egypt)
Tetrabothrius sp. (Egypt)

Anas smithii (Hartet), Cape shoveller

Echinocotyle capensis (South Africa)
 * Epomidiostomum sp. (zoo- England)

Anas sparsa leucostigma Rüppel, Abyssinian black duck

- Hymenolepis sp. (Ethiopia)
 *\$ Amidostomum anseris (zoo- England)
Porrocaecum crassum (Kenya)

Anas undulata DuBois, African yellowbill

- Hypoderaeum conoideum (Ethiopia)
Diorchis longiovum var. aethiopicus (Ethiopia)
Lateriporus biuterinus (Ethiopia)
Microsomacanthus macrotesticulata (South Africa)
Retinometra longicirrosa (Ethiopia)
 *\$ Echinuria uncinata (zoo- England)

Anas sp.

Polymorphus minutus (Egypt)

'Wild duck'

- Mesostephanus sp. (Madagascar)
Notocotylus aegyptiacus (Egypt)
Zygocotyle lunata (Zaire)
Contracaecum microcephalum (Zaire)

Aythya fuligula (L.), Tufted duck

- Opisthorchis simulans (Egypt)
Psilochasmus oxyurus (Egypt)
Diploposthe laevis (Egypt)
Fimbriaria fasciolaris (Egypt)

Aythya ferina (L.), European pochard

Capillaria obsignata (Egypt)

Netta erythrophthalma brunnea (Eyton), Southern pochard

- Cloacotaenia megalops (Kenya)
 * Diorchis nyrocae (zoo- England)
 *\$ Diploposthe laevis (Ethiopia, Kenya, zoo- England)
Fimbriaria fasciolaris (Kenya)
Microsomacanthus macrotesticulata (South Africa)
 * Sobolevicanthus gracilis (zoo- England)

Cairina moschata dom. Barbary domestic duck

- Ascaridia galli (Zambia)
Gongylonema congolense (Zaire)
Heterakis gallinarum (Zambia)

Plectropterus gambensis gambensis (L.) Spur - winged goose

- Hypoderaeum conoideum (Zaire)
- Opisthorchis geminus (Zimbabwe)
- Opthalmophagus magahaesi (South Africa)
- Typhlocoelom cucumerinum (South Africa)
- Sobolevicanthus octacantha (Zaire)
- * Cyathostoma coscorobae (zoo- Philadelphia)
- Epomidiostomum uncinatum (Senegal)
- Tetrameres plectropteri (Nigeria)

Sarkidiornis melanotos melanotos (Pennant), Comb duck

- Typhlocoelom cucumerinum (Madagascar)
- Contracaecum spiculigerum (Senegal)
- * Cyathostoma sarkidiornis (zoo- Berlin)
- Echinuria minor (Zaire)
- * Streptocara crassicauda (zoo- England)

Alopochen aegyptiacus (L.) Egyptian goose

- Notocotylus aegyptiacus (Egypt)
- Amphipetrovia biaculeata (South Africa, Sudan)
- *§ Cloacotaenia megalops (zoo- Warsaw)
- Fimbriaria fasciolaris (Somalia)
- Capillaria retusa (Senegal)
- * Hystrichis tricolor (zoo- England)
- Polymorphus minutus (unknown)

Cyanochen cyanopterus (Rüppel), Abyssinian Blue - winged goose

- *§ Fimbriaria fasciolaris (zoo- England)
- * Dicranotaenia coronula (zoo- England)
- * Diorchis stefanskii (zoo- England)
- * Sobolevicanthus gracilis (zoo- England)

Dendrocygna fulva (Gmelin), Fulvous Whistling Duck

- Typhlocoelom cucumerinum (Zimbabwe)
- Diorchis sp. (Zaire)
- Hymenolepis sp. A (Zaire)
- Hymenolepis sp. B (Zaire)
- Hymenolepis sp. (Ethiopia)

Dendrocygna viduata (L.) White Faced Whistling Duck

- Echinostoma revolutum (Zambia)
- Opisthorchis geminus (Zimbabwe)
- Hymenolepis sp. (Senegal)
- *§ Echinuria uncinata (zoo- England)
- Paracamallanus sp. (Senegal)
- Subulura brumpti (Senegal)

Thalassornis leuconotos leuconotos Eyton, Whitebacked Duck

Apatemon gracilis congolense (Zaire)

Anser cinereus Meyer, Domestic Goose

Galactosomum baylisi (Egypt)

Hymenolepis sp. (Kenya)

Anser albifrons albifrons (Scopoli), European White- Fronted Goose

Amidostomum acutum (Egypt)

Cygnus olor (Gmelin), Mute Swan

Amidostomum anseris (Zoo- Sudan)

List of helminths known only from the Ethiopian region of
Africa.

Helminth Species

Cestoda

Diorchis longiovum var aethiopicum

Echinocotyle birmanica

E. capensis

Microsomacanthus macrotesticulata

Sobolevicanthus transvaalensis

Nematoda

Gongylonema congolense

Echinuria minor

Tertameres plectropteri

Digenea

Apatemon gracilis congolense

Opthalmophagus magalhaesi
