An Analysis of the Trematode Fauna of Two Intercontinental Migrants: Tringa Solitaria and Calidris Melanotos (Aves: Charadriiformes) (Ecuador, Louisiana, South Dakota, Canada).

Erika Jansic Tallman
Louisiana State University and Agricultural & Mechanical College

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AN ANALYSIS OF THE TREMATODE FAUNA OF TWO INTERCONTINENTAL MIGRANTS: TRINGA SOLITARIA AND CALIDRIS MELANOTOS (AVES: CHARADRIIFORMES)

The Louisiana State University and Agricultural and Mechanical Col. Ph.D. 1983

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TWO INTERCONTINENTAL MIGRANTS:
TRINGA SOLITARIA AND CALIDRIS MELANOTOS
(AMES: CHARADRIIFORMES)

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Zoology and Physiology

by

Erika Jansic Tallman
B.A., Antioch College, 1971
M.S., Louisiana State University, 1975
May, 1983
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ABSTRACT

One hundred ninety-seven Solitary Sandpipers, *Tringa solitaria*, and 213 Pectoral Sandpipers, *Calidris melanotos*, were examined for trematodes. Specimens were taken from the hosts' winter range in Ecuador, South America, during the fall and spring migrations from Louisiana and South Dakota in the United States, and from the breeding grounds of the Solitary Sandpiper in Ontario, Canada. The 13 species of trematodes recorded from the shorebirds included 5 that were common to both species of shorebirds: *Tanaisia fedtschenkoi*, *Cyclocoelum obscurum*, *Paramonostomum* sp., *Leucochloridium variae*, and *Zonorchis microrchis*. Of the remaining 8 species, *Cyclocoelum brasilianum*, *Plagiorchis maculosus*, *Stephanoprora denticulata*, and *Ervytrema lubens* occurred in Solitary Sandpipers while *Cyclocoelum tringae*, *Plagiorchis elegans*, *Echinoparyphium speotyto*, and *Echinoparyphium aconiatum* were found only in Pectoral Sandpipers. The overall prevalence of trematode infections in these hosts, regardless of season, was fairly constant, and ranged between 35 and 48 percent. The fauna of these long-distance intercontinental migrants was characterized by a high percentage (66%) of low prevalence parasite species. Although some of the trematode species from these migrants have been previously reported from both North and South America, this study includes several range extensions for
the parasites. The slight differences in species composition and prevalence of infections were not significant between spring and fall migrants. The fauna was found to be a composite of species acquired by the hosts at various localities throughout their migrations. The breeding grounds were no more significant a source of trematode infection for Solitary and Pectoral Sandpipers than other localities covered during the long migrations. Species from the digestive tract were usually of low prevalence and intensity. The most common species were ubiquitous in geographical distribution and were found within the hosts in sites other than the digestive system. The trematode fauna of the 2 sandpipers was found to be remarkably similar in spite of the hosts' very different breeding ecology.
INTRODUCTION

This study was conceived because of the statement in the text by Nobel and Nobel (1976, p.470):

"...Some birds spend their summers in Alaska and their winters in the South Pacific. Do these birds possess the same kinds and numbers of parasites at both locations? Probably not, but practically no studies of this nature have been made with birds..."

The authors' assessment of the accumulated knowledge on the subject was not altogether accurate. Parasitologists have been interested in the effects of avian host migration on parasite fauna since 1909 when Henry B. Ward published his preliminary impressions of the parasite fauna of ducks migrating through Nebraska. Many researchers since have used the same technique of examining migrants on their way to and from their breeding grounds (Dogiel and Bykhovskaia-Pavlovskai, 1955; DeJong, 1976; Broderson et al., 1977; Leveya et al., 1980). Conclusions concerning parasite faunas of the wintering and breeding birds were drawn from comparisons between the faunas of spring and fall migrants. Some Russian researchers have examined migrants on their breeding grounds (Dubinina, 1937), but according to Dogiel (1964) for birds nesting in the Soviet Union, the parasite fauna
of the tropical winter habitat is almost completely unknown. Generally, the Russians concentrated on short-distance migrants wintering within the Temperate Zone and examined large numbers of individuals of many species (Dogiel and Bykhovskai-Pavlovskai, 1955). Consequently, although they gained an overview of the general migration, they didn't conduct detailed analyses of the parasite fauna of individual host species. Most work in North America also has been with species that winter in the southern part of the Temperate Zone (Buscher, 1965; Hood and Welch, 1980). A recent investigation of intercontinental migrants involved hosts in their breeding grounds and during their migrations through the United States, but not birds wintering in the tropics (Schmidt and Frantz, 1972).

The present study is an attempt to compare the trematode faunas of long-distance, intercontinental avian migrants on their tropical wintering grounds, during their fall and spring migrations through the United States, and on their breeding grounds in Canada. For this purpose 2 species of shorebirds (family Scolopacidae) were chosen: the Solitary Sandpiper, *Tringa solitaria*, and the Pectoral Sandpiper, *Calidris melanotos*. 
MATERIALS AND METHODS

Solitary and Pectoral Sandpipers were collected in 1975 and 1976 from Ecuador, South America; 1977 through 1979 from Louisiana; 1980 and 1981 from South Dakota; and in the summer of 1980 from Ontario, Canada. In Ecuador the birds were collected from eastern, moist tropical lowland forest along the sandy banks of the Napo River and the wet cow pastures of the Summer Institute of Linguistics base, Limoncocha (0 24'S, 76 37'W; 300 m elev.) (Figures 1,3,4). In Louisiana, birds were collected from the Baton Rouge South Sewage Treatment Plant, the Louisiana State University Baton Rouge Agricultural Experiment Station, and the coastal marshes and mudflats in Cameron Parish of western Louisiana. Collecting areas in the plains of South Dakota were the muddy banks of Mocassin Creek and the mudflats of the sewage treatment plant, both in the town of Aberdeen. Baton Rouge, Louisiana and Aberdeen, South Dakota are indicated on the maps in Figures 3 and 4. Breeding Solitary Sandpipers were collected along roads in the taiga of Ontario Province, Canada (Figure 2). Dr. Dan Tallman, an ornithologist, collected all the birds with a double-barrelled 20 gauge shotgun using various small-sized shot. Voucher host specimens are housed at the Louisiana State University Museum of Zoology, Baton Rouge. Host specimens were examined for parasites as soon after being killed as possible;
none was frozen. The body cavity of each bird was searched carefully prior to placing the specimen's liver, gall bladder, lungs, digestive tract, and kidneys in separate water-filled petri dishes to be examined for trematodes under a dissecting scope. The host's sex, weight, molt, breeding condition, and subspecies identity were recorded. The trematode specimens were killed under slight coverslip pressure over a flame and then immediately fixed and stored in AFA (ethanol, formaldehyde, and acetic acid). Some specimens were stored in AFA for as long as 2 years before being stained with either Acetocarmine or Van Cleaves' Haematoxylin stain, cleared with methyl salicylate, and mounted on slides with permount. Host records and parasite species distributions were determined in part by a search of the Index-Catalogue of Medical and Veterinary Zoology. Trematode drawings were made with the aid of a camera lucida. Measurements are in millimeters unless otherwise stated. Mean measurements are given with ranges in parentheses. The ecological terms prevalence, intensity, site, and locality, that are used in the text, are defined according to the standardizations adopted by the American Society of Parasitologists (Margolis et al., 1982).
Figure 1. A map of Ecuador showing Limoncocha, the collecting locality for wintering Solitary and Pectoral Sandpipers.
Figure 2. A map of Ontario, Canada showing the collecting localities for breeding Solitary Sandpipers:

DAT 4745  S of Red Lake on Hwy. 105
4746      "      "      "      "      
4748  12 N Savant Lake
4749      "      "      "      
4750  3 mi S Savant Lake
4751  5 mi NW intersection of Hwy. 599 and 642 on Hwy. 642
4752  32 km N Savant Lake
4753  15 air km NE Jellicoe
4754  50 km N Geraldton
4755  30 km W Geraldton
Figure 3. A map of the breeding and wintering ranges of *Tringa solitaria*.

= breeding, late May through July
= wintering, August through April

A = Aberdeen, South Dakota
B = Baton Rouge, Louisiana
L = Limoncocha, Ecuador
Figure 4. A map of the breeding and wintering ranges of *Calidris melanotos*. Inset shows migration route of population nesting in eastern Siberia.

- breeding, late May through July
- wintering, August through April

A = Aberdeen, South Dakota

B = Baton Rouge, Louisiana

L = Limoncocha, Ecuador
RESULTS

One hundred ninety-seven Solitary Sandpipers and 213 Pectoral Sandpipers were examined for trematodes (Table 1). Of these totals, 85 were wintering birds (51 T. solitaria, 34 C. melanotos) from Ecuador; 157 were spring migrants (71 T. solitaria, 86 C. melanotos) from South Dakota and Louisiana; 10 were summer breeding Solitary Sandpipers from Ontario, Canada; and 158 were fall migrants (65 T. solitaria, 93 C. melanotos) from South Dakota and Louisiana. The prevalence of trematode infection for host species during each season from each locality is shown in Table 1. The prevalence of trematode infection during a season from localities with more than 10 host specimens ranged from 35.3% to 52.4% for Tringa solitaria and 35.3% to 50.1% for Calidris melanotos.

Thirteen species of trematodes were retrieved from the 2 species of shorebirds (Tables 2 and 3). Tanaisia fedtschenkoi, the most common species, was found in the kidney ducts of both Solitary and Pectoral Sandpipers from all collecting localities except Canada. Three species of the Cyclocoelum complex of avian air sac trematodes were encountered: C. obscurum, rare from Ecuador and Louisiana but in both host species; C. tringae, in all localities and from approximately 16% of all Pectoral Sandpipers; and C. brasilianum, also in all localities but found in approximately 24% of all Solitary Sandpipers. Two Solitary
Sandpipers and 1 Pectoral Sandpiper, from spring migrations through Louisiana, harbored *Zonorchis microrchis* in their livers or bile ducts. *Eurytrema lubens* was found in the gall bladders of 1 spring and 1 fall Solitary Sandpiper from Louisiana. *Leucochloridium variæ* occurred in the cloacae of a few spring and fall migrants of both shorebird species in the United States. The remaining 6 trematode species were found at low prevalence and low to moderate intensity from the hosts' intestines. *Paramonostomum* sp. was recorded from 1 Solitary Sandpiper in Canada and 3 fall migrant Pectoral Sandpipers from Louisiana. A Solitary Sandpiper from fall migration in Louisiana contained 1 specimen of *Stephanoprora denticulata*. Two species of *Echinoparyphium*, *E. aconiatum* and *E. speotyto*, were found in Louisiana specimens of Pectoral Sandpipers. *E. speotyto* was the only intestinal trematode species with more than 10 worms occurring in an individual host. The only specimen of *E. aconiatum* was found in a spring bird while *E. speotyto* was recorded from both spring and fall migrants. Two species of the genus *Plagiorchis* were in fall migrants; 1 specimen of *P. elegans* occurred in a Lousiana Pectoral Sandpiper and 1 specimen of *P. maculosus* was found in a South Dakota Solitary Sandpiper. A summary of the trematode species according to the host species from which they were recorded is given in Table 4.

Four of the 13 trematode species were found in hosts from
both North and South America: *Cyclocoelum obscurum*, *C. brasilianum*, *C. tringae*, and *Tanaisia fedtschenkoi*. No trematode species were recorded exclusively from South American hosts, but 9 species were found only in North America: *Plagiorchis elegans*, *P. maculosus*, *Echinoparyphium aconiatum*, *E. speotyto*, *Stephanoprora denticulata*, *Leucochloridium variae*, *Eurytrema lubens*, *Zonorchis microrchis*, and *Paramonostomum* sp. Approximately one-half of the species found were in both the spring and fall migrations through the United States: *E. speotyto*, *L. variae*, *E. lubens*, *C. brasilianum*, *C. tringae*, and *T. fedtschenkoi*. *Z. microrchis* and *E. aconiatum* were the only species recorded from spring but not fall migrants. The remaining 5 species (*P. elegans*, *P. maculosus*, *S. denticulata*, *C. obscurum*, and *Paramonostomum* sp.) occurred in fall migrants but were absent from spring birds. Summer breeding Solitary Sandpipers contained only *C. brasilianum* and *Paramonostomum* sp. Wintering shorebirds had 3 species of trematodes: *T. fedtschenkoi*, *C. tringae*, and *C. obscurum*. The 13 species accounts discuss in detail the taxonomic considerations and geographical distribution for each of the trematode species.
Table 1. Numbers of host specimens examined during each season from each collecting locality and the prevalence of trematode infection
<table>
<thead>
<tr>
<th>Locality/season</th>
<th>Number of</th>
<th>T. solitaria</th>
<th>Number of</th>
<th>C. melanotos</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>prevalence</td>
<td></td>
<td>prevalence</td>
</tr>
<tr>
<td>Ecuador/winter</td>
<td>51</td>
<td>18/51 = 35.3%</td>
<td>34</td>
<td>12/34 = 35.3%</td>
</tr>
<tr>
<td>Louisiana/spring</td>
<td>70</td>
<td>25/70 = 35.7%</td>
<td>65</td>
<td>33/65 = 50.1%</td>
</tr>
<tr>
<td>South Dakota/spring</td>
<td>1</td>
<td>1/1 = 100%</td>
<td>21</td>
<td>8/21 = 38.1%</td>
</tr>
<tr>
<td>Total/spring</td>
<td>71</td>
<td>26/71 = 36.6%</td>
<td>86</td>
<td>41/86 = 47.7%</td>
</tr>
<tr>
<td>Ontario, Canada/summer</td>
<td>10</td>
<td>4/10 = 40.0%</td>
<td>0</td>
<td></td>
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<tr>
<td>Louisiana/fall</td>
<td>44</td>
<td>19/44 = 43.2%</td>
<td>83</td>
<td>35/83 = 42.2%</td>
</tr>
<tr>
<td>South Dakota/fall</td>
<td>21</td>
<td>11/21 = 52.4%</td>
<td>10</td>
<td>9/10 = 90.0%</td>
</tr>
<tr>
<td>Total/fall</td>
<td>65</td>
<td>30/65 = 46.0%</td>
<td>93</td>
<td>44/93 = 47.3%</td>
</tr>
<tr>
<td>TOTAL SPECIMENS</td>
<td>197</td>
<td>78/197 = 39.6%</td>
<td>213</td>
<td>97/213 = 45.5%</td>
</tr>
</tbody>
</table>
DESCRIPTION OF THE TREMATODES

Family Plagiorchiidae Ward, 1917

Plagiorchis elegans (Rudolphi, 1802) Braun, 1902

Plate 1

host: Calidris melanotos

site: intestine

locality: Louisiana

1 specimen

A distomate worm 1.78 long by 0.37 wide. Tegument of anterior half minutely spined. Oral sucker subterminal, 0.19 long by 0.17 wide, followed immediately by pharynx 0.08 long by 0.09 wide. Esophagus absent. Narrow caeca extend to within 0.13 of end of worm. Acetabulum round, 0.08 in diameter. Ovary 0.16 long by 0.12 wide, displaced to one side midway between acetabulum and anterior testis. Uterus wide from level of mid-posterior testis, between testes and testes and ovary, but narrows at cirrus pouch. Uterus follows cirrus pouch to genital pore on median anterior border of acetabulum. Eggs numerous, 0.033 by 0.017. Globular vitellaria in lateral fields beginning midway between pharynx and acetabulum, extending to posterior. Vitellaria confluent anteriorly and fill entire body posterior to testes. Transverse vitelline ducts meet between ovary and anterior testis. Testes intercaecal, smooth margined, obliquely aligned with anterior testis on side opposite to ovary. Anterior
testis 0.17 long by 0.13 wide; posterior testis 0.20 long by 0.13 wide. Large crescent-shaped cirrus pouch from anterior border of acetabulum, curling around that organ to mid-ovary.

**Taxonomy:** The characteristics of this specimen are in general agreement with published descriptions of *Plagiorchis elegans* (Braun, 1902; Olsen, 1937; Styczynska-Jurewicz, 1962). Measurements given by Braun (1902) for oral sucker (177 x 156 μm), acetabulum (100 μm), and eggs (32 - 36 μm x 18 - 20 μm) are close to those for the worm from *C. melanotos*. However, body width, which according to Braun should be 0.66, is only 0.37 for this worm. Recent taxonomic investigations have shown *P. elegans* to be a maleable species with adult body widths ranging between 0.42 and 1.00 depending on the age of the specimen, the host from which it was taken, and the fixing techniques used to preserve the parasite (Styczynska-Jurewicz, 1962). Therefore, the discrepancy between the body width measurements is not considered to be taxonomically significant. Olsen (1937) differentiated between 2 species of *Plagiorchis*, *P. elegans* and *P. uhlwommi*, on the basis of pharynx to oral sucker ratio: 1:4 for *P. elegans* and 1:2 for *P. uhlwommi*. Other differences between the species cited by Olsen included *P. uhlwommi* having a shorter, straighter cirrus sac, vitellaria not confluent anteriorly, and an ovary in contact with the acetabulum. All of these differences have been shown to be within the range of
variation found in laboratory induced infections of *P. elegans* and therefore a synonomy of the 2 species has been proposed (Styczynska-Jurewicz, 1962). By having the pharynx to oral sucker ratio of *P. uhlwormi* but most other characteristics like *P. elegans*, the *Plagiorchis* specimen from *C. melanotos* lends credence to the proposed synonomy. Illustrations of the species in Braun (1902) and Styczynska-Jurewicz (1962) showed the uterus extending to the posterior of the worm, but the authors made no written mention of this characteristic. The present specimen differs from the aforementioned drawings by having a uterus that extends posteriorly only to the middle of the posterior testis. The abbreviated extent of the uterus cannot be explained by the immaturity of the worm since mature eggs are present near the genital pore. Because the specimen agrees in all other respects with the revised definition of *P. elegans*, the extent of the uterus must be considered insignificant until more material is obtained.

**Geographical Distribution:** *P. elegans* is primarily an Eurasian species that has been recorded from a wide variety of Old World avian hosts, including some in the genus *Calidris* (Styczynska-Jurewicz, 1962). The presence of this worm in *Calidris melanotos* represents a new host record and one of the few reports from North America. The only 2 previous North American records are from gulls in Colorado (Vermeer, 1969) and
Wyoming (Keppner, 1973). As shown in Figure 4, Pectoral Sandpipers breed in Siberia (Welty, 1982) and migrate through the United States on their way to South America, thus providing a biological linking of the 3 continents. Avian hosts with such a distribution could well provide the means to spread parasite populations. Birds could become infected in Asia and carry gravid adult trematodes to the U.S. and South America during their southward fall migration. Indeed, the Plagiorchis elegans life cycle must already be established in North America as evidenced by the parasite's presence in Ring-billed and California Gulls, 2 species that are known only from Canada south to Mexico (Vermeer, 1969; Bent, 1962b). Because the infective geographic range of P. elegans is now known to include North America, Pectoral Sandpipers could acquire this parasite either while breeding or during migration through Canada and the United States. The presence of the trematode in C. melanotos provides the potential for the eventual spread of the parasite to South America.
Plagiorchis maculosus (Rudolphi, 1802) Braun, 1901

Plate 2

host: Tringa solitaria

site: intestine

locality: South Dakota

1 specimen

A distomate worm 2.10 long by 0.27 wide. Tegument of anterior half minutely spined. Oral sucker subterminal, 0.20 long by 0.17 wide, followed immediately by pharynx 0.07 long by 0.08 wide. Esophagus absent. Intestinal caeca narrow, extending posterior to testes but exact extent obscured by uterus and vitellaria. Acetabulum 0.13 long by 0.12 wide, 0.27 posterior to intestinal bifurcation. Ovary 0.17 long by 0.11 wide, posterior to acetabulum and slightly displaced to one side. Mehlis' gland just posterior to ovary. Uterus fills posterior of body between vitelline fields, weaves between testes and ovary, crosses over acetabulum to genital pore on median, anterior margin of acetabulum. Eggs numerous, 0.03 by 0.02. Dense lateral vitelline fields from intestinal bifurcation to end of body. Testes, intercaecal, slightly oblique in alignment, smooth-margined, oval. Anterior testis 0.16 long by 0.12 wide; posterior testis 0.19 long by 0.13 wide. Slightly curved cirrus pouch crosses one side of acetabulum to anterior one-third of ovary. Cirrus split and narrow, 0.20 long by 0.03 wide, and
unornamented.

**Taxonomy:** This specimen is in agreement with the description and illustration provided in Olsen (1937). The *Plagiorchis* specimen from *T. solitaria* differs from the species in *C. melanotos* by having a larger acetabulum, a straighter cirrus pouch, uterus extending to the end of the body, and vitellaria that remain in lateral fields.

**Geographical Distribution:** *P. maculosus* is known from a variety of avian species in both Europe and North America (Yamaguti, 1958; McDonald, 1981). This specimen is the first record of *P. maculosus* from *Tringa solitaria.*
Family Echinostomatidae Poche, 1926

*Echinoparyphium aconiatum* Dietz, 1909

Plate 3

**host:** *Calidris melanotos*

**site:** intestine

**locality:** Louisiana

1 specimen

A distomate worm 2.75 long by 0.55 wide. Anterior tegument minutely spined. A 0.34 wide reniform spiny collar surrounds subterminal oral sucker, 0.16 long by 0.15 wide. Collar with 37 spines: 5 spines at each corner (3 oral, 2 aboral) connected by uninterrupted double row. Largest corner spine 0.053 by 0.014. Oral and aboral row spines approximately equal, largest being 0.050 by 0.012. Pharynx 0.12 long by 0.10 wide, 0.05 posterior to oral sucker. Esophagus narrow, 0.24 long. Intestinal bifurcation at anterior margin of acetabulum. Caeca extend posterior to testes. Acetabulum heavily muscled, 0.43 long by 0.42 wide. Ovary intercaecal, pretesticular, spherical, 0.14 in diameter, 0.56 posterior to acetabulum. Uterus short, intercaecal, anterior to testes, passing medially over acetabulum to genital pore at anterior margin of acetabulum. Eggs few, not measureable. Vitellaria in lateral fields from posterior limit of acetabulum to posterior of testes where vitellaria fill body. Testes medial, tandem, and smooth-margined. Anterior testis 0.16
long by 0.14 wide; posterior testis 0.20 long by 0.14 wide. Cirrus pouch 0.19 long by 0.10 wide, medial, just posterior to intestinal bifurcation.

**Taxonomy:** This specimen matches the descriptions of *E. aconiatum* found in Skrjabin (1964) and Buscher (1978).

**Geographical Distribution:** *E. aconiatum* is frequently recorded from waterfowl in Eurasia and North America (Yamaguti, 1958; McDonald, 1981). The species has also been found in Siberia (Buscher, 1978), a locality visited by some of the breeding Pectoral Sandpipers. Therefore, Pectoral Sandpipers could acquire this trematode from either Siberia or North America. The presence of *E. aconiatum* in *C. melanotos* represents a new host record.
**Echinoparyphium speotyto** Buscher, 1978

**Plate 4**

**host:** *Calidris melanotos*  
**site:** intestine  
**locality:** Louisiana  
17 specimens measured

Small, spinous, distomate trematodes 2.00 long (1.55 - 2.32) by 0.29 wide (0.16 - 0.37). Tegument anterior to acetabulum minutely spined. Oral sucker subterminal, 0.07 in diameter, surrounded by 0.19 wide reniform spiny collar. Collar with 41 spines; 5 spines at each corner (3 oral, 2 aboral) connected by uninterrupted double row of 31 smaller spines. Largest corner spine 0.04 by 0.01; spines of oral row 0.02 long; spines of aboral row 0.033 long. Pharynx 0.05 long by 0.04 wide. Esophagus narrow. Intestinal bifurcation just anterior to acetabulum. Posterior extent of caeca obscured by dense vitellaria. Acetabulum heavily muscled, 0.22 long (0.20 - 0.25) by 0.17 wide (0.13 - 0.20). Ovary medial, intercaecal, 0.11 long (0.10 - 0.15) by 0.10 wide (0.08 - 0.11), pretesticular, 0.31 (0.27 - 0.37) posterior to acetabulum. Ovary followed by Mehlis' gland and median vitelline reservoir on anterior margin of anterior testis. Short uterus extends from ovary medially over acetabulum to genital pore on anterior border of acetabulum. Eggs few, 0.080 by 0.045. Vitellaria in broad lateral fields from 0.11 posterior to
acetabulum to posterior of testes where vitellaria fill body.
Testes smooth-margined, intercaecal, tandem. Anterior testis 0.17 long (0.13 - 0.20) by 0.11 wide (0.07 - 0.13); posterior testis 0.19 long (0.13 - 0.23) by 0.11 wide (0.07 - 0.13). Cirrus pouch 0.18 long (0.17 - 0.19) by 0.07 wide (0.06 - 0.07), alongside and over acetabulum.

**Taxonomy:** The genus *Echinoparyphium* has only 2 valid species with 41 collar spines, *E. westsibiricum* Isaichikov, 1925 described from domestic fowl in Russia and *E. speotyto* Buscher, 1978 described from Burrowing Owls (*Athene cunicularia*) in Oklahoma (Buscher, 1978). The specimens from *C. melanotos* agree with the description of *E. speotyto* published by Buscher (1978) and differ from *E. westsibiricum* by having smaller spines, vitellaria confluent posteriorly, and the acetabulum immediately posterior to the intestinal bifurcation. The measurements for the present specimens are quite close to the smaller limits in the range of variation given by Buscher (1978) in the original description of *E. speotyto*. The configuration of the collar spines with 4 larger medial and 1 smaller latero-oral corner spines and the double row of spines with the aboral spines larger than the oral ones is the same as reported for the specimens from Burrowing Owls. However, the spines themselves are slightly smaller in the specimens from *C. melanotos*. Buscher gave, as the low end of the range, 0.045 for the length of the largest corner
spine, 0.040 for the aboral row spines, and 0.028 for the oral row. The measurements, compared with the lengths from the worms from *C. melanotos*, 0.040, 0.033, and 0.020, are consistently larger. Because the relative sizes and positions of the spines and the measurements for other organs are close to the smaller dimensions reported in the species description, I feel justified in identifying these specimens as *E. speotyto*.

**Geographical Distribution:** These specimens represent a range extension for the trematode from Oklahoma to Louisiana and a new host record. The presence of *E. speotyto* in such seemingly diverse hosts as an owl and shorebird, at first glance, appears extraordinary. But an examination of the habitat preference and feeding behavior of the hosts reveals that ecologically the birds are not as dissimilar as one might suspect. Both hosts are present in the prairie of the midwest United States and both prefer open fields; Burrowing Owls inhabiting the dry higher ground while Pectoral Sandpipers are shorebirds that frequent wet grassy fields. However, Pectorals will feed on normally dry fields after heavy rains (Bull, 1974). More significantly, both Pectoral Sandpipers and Burrowing Owls are highly insectivorous (Bent, 1962a,c; Lohoefener, 1982). Several studies have revealed that a high percentage Burrowing Owls' diets consist of Coleoptera and Orthoptera (Bent, 1962a; Lohoefener, 1982). Furthermore, stomach contents surveys reporting the presence of fish, frogs,
and crayfish in Burrowing Owls indicate that, although these birds live in dry situations, they must occasionally feed near water (Bent, 1962a). Pectoral Sandpipers are also known to feed on a variety of insects, frogs, and small fish (Bent, 1962c). That these 2 hosts harbor the same species of trematode is understandable if the similarity of their diets and preference for non-woodland situations is considered.
**Stephanoprora denticulata** (Rudolphi, 1802) Odhner, 1910

**Plate 5**

host: *Tringa solitaria*

site: intestine

locality: Louisiana

1 specimen

A distomate worm 3.87 long by 0.28 wide. Tegument densely spined with largest spines anterior to acetabulum, spines smaller and more sporadic from acetabulum to posterior testis, lacking in posterior of body. Subterminal oral sucker surrounded by robust spiny collar. Collar with 22 spines approximately equal in size, in a single dorsally interrupted row. Spines 0.040 long by 0.013 wide. Acetabulum round, 0.20 in diameter. Ovary 0.11 long by 0.13 wide, medial, 0.21 posterior to acetabulum. Uterus preovarian, short, medial. Genital pore medial, just anterior to acetabulum. Eggs few, 0.08 by 0.04. Vitellaria begin at middle of anterior testis, are scattered around testes, and fill body posterior to testes. Testes medial, tandem, and smoothly oval. Anterior testis 0.26 long by 0.22 wide; posterior testis 0.32 long by 0.22 wide. Conspicuous cirrus pouch 0.20 long by 0.08 wide alongside and just anterior to acetabulum.

**Taxonomy:** This specimen is in agreement with the descriptions of *S. denticulata* in Weber (1968) and Nasir et al. (1970).
Geographical Distribution: *S. denticulata* has been recorded from North America (Weber, 1968), Panama (Yamaguti, 1958), and Venezuela, South America (Nasir et al., 1970). The species is known from Greater Yellowlegs, Willets, and Sanderlings from Louisiana (Weber, 1968) and Spotted Sandpipers from Venezuela (Nasir et al., 1970), all from the same family, Scolopacidae, as *Tringa solitaria*. Therefore, this first record of *S. denticulata* from a Solitary Sandpiper is not a surprising discovery.
Family Brachylaimidae Joyeux and Foley, 1930

*Leucochloridium variae* McIntosh, 1932

Plate 6

**host**: *Tringa solitaria* and *Calidris melanotos*

**site**: cloaca

**locality**: Louisiana; South Dakota

24 specimens measured (5 from *Tringa*, 19 from *Calidris*)

Robust, heavily muscled, oval trematodes 1.62 long (1.15 - 2.60) by 0.81 wide (0.60 - 1.20) at the equator. Tegument without spines or papillae. Both suckers well-developed. Oral sucker subterminal, 0.40 long (0.33 - 0.53) by 0.41 wide (0.31 - 0.58). Pharynx 0.11 long (0.08 - 0.16) by 0.16 wide (0.12 - 0.17), immediately posterior to oral sucker. Esophagus very short. Intestinal caeca fairly constant in width, straight, ending 0.13 from end of worm. Distance between caecal tips 0.18 (0.08 - 0.20). Acetabulum equatorial, equal to oral sucker, 0.39 long (0.30 - 0.53) by 0.41 wide (0.30 - 0.57). Genital complex intercaecal, in a triangular formation just posterior to acetabulum. Ovary intertesticular but displaced to left, 0.11 long (0.09 - 0.21) by 0.15 wide (0.10 - 0.27). Alongside and
slightly posterior to ovary is conspicuous fecundarium (see McIntosh, 1932), on a diagonal line between the testes. Uterus surrounds acetabulum without crossing it, weaves between ovary and anterior testis, and only occasionally extends into vitelline fields. Uterus extends from both sides of posterior portion of oral sucker to posterior of hindmost testis, descending along cirrus sac on side opposite from posterior testis. Genital pore near posterior of worm, subterminal, and medial. Eggs numerous, 0.023 by 0.017. Vitellaria in lateral fields not reaching interior margin of caeca from posterior one-third of oral sucker to just beyond caecal tips. Posterior extent of vitellaria variable. Transverse vitelline ducts join medially between ovary and testes forming vitelline reservoir 0.47 from end of worm. Right, anterior testis 0.13 long (0.08 - 0.18) by 0.15 wide (0.11 - 0.20). Posterior testis 0.13 long (0.09 - 0.23) by 0.14 wide (0.10 - 0.23). Cirrus pouch intercaecal, medial, 0.14 wide. Cirrus 0.08 long by 0.05 wide, without spines and unpustulated.

**Taxonomy:** Because the posterior extent of the vitellaria is variable in these specimens, they can be identified as either *L. melospizae* or *L. variae* according to the descriptions provided by Kagan (1952). However, comparison with the original species descriptions by McIntosh (1932) clearly shows these specimens to be *L. variae*. The gonad sizes for *L. melospizae*, anterior testis 70 um by 80 um, ovary 80 um by 100 um, are much smaller
than those for the specimens in the present study. All measurements of the specimens from *T. solitaria* and *C. melanotos* correspond to those of *L.* *variae* except for cirrus pouch size (larger for *L.* *variae*) and posterior extent of vitellaria (more posterior in *L.* *variae*). These 2 differences are minor and may well be caused by the obviously contracted nature of the specimens. Recent work on the life cycle of *L.* *variae* has revealed several variations in the adult anatomy (Lewis, 1974). Lewis found the cirrus pouch widths of adults grown in domestic chickens varied between 100 and 160 um, measurements that correspond well to cirrus pouch widths of the specimens in this study. Lewis found the young adult *L.* *variae* to have finely spined tegument and cirrus. Spinations were not reported by McIntosh in the original species description nor are they evident in the specimens from Solitary and Pectoral Sandpipers. One can only assume that the spination is variable and perhaps, as inferred by the Lewis article, lacking in older specimens.

**Geographical Distribution:** The reports herein are the first for *Leucochloridium variae* from Charadriid hosts. The species was previously recorded only in the northern United States from Michigan warblers (McIntosh, 1932), Ohio Red-winged Blackbirds (Cooper and Crites, 1974), Galliform birds in Alaska and New England (Lewis, 1974), and infected snails in Nebraska (Lewis, 1974). The records reported in this study extend the
known range of the trematode to Louisiana. Because Solitary and Pectoral Sandpipers from both spring and fall migrations through Louisiana harbor this parasite, a larger sampling of wintering hosts may reveal \textit{L. variae} in South America.
Family Dicrocoeliidae Odhner, 1911

Eurytrema lubens (Braun, 1901) Travassos, 1919

Plate 7

host: *Tringa solitaria*

site: gall bladder

locality: Louisiana

1 specimen measured

A heavily muscled, oval, distomate trematode 7.03 long by 2.10 wide at equator. Tegument without spines or papillae. Suckers well-developed, within anterior one-fifth of worm. Oral sucker subterminal, 0.40 long by 0.50 wide. Pharynx 0.17 long by 0.18 wide. Esophagus obscured. Intestinal caeca narrow in few areas where visible. Acetabulum 0.53 in diameter. Ratio of oral to ventral sucker 1:1.1. Ovary 0.67 posterior to left testis. Ovary 0.40 long by 0.43 wide, overlapped by Mehlis' gland 0.27 long by 0.23 wide. Uterus occupies majority of body to within 0.13 of hind end. Uterus passes between ovary and testes, one coil goes between testes and crosses center of acetabulum to genital pore at anterior edge of pharynx. Eggs numerous, 0.033 by 0.016. Globular vitellaria in lateral fields from mid-acetabular region to within 2.00 of end of worm. Testes opposite one another just posterior to acetabulum. Testes 0.32 long by 0.43 wide and 0.35 long by 0.32 wide. Conspicuous medial cirrus pouch between acetabulum and pharynx, 0.20 long by 0.12 wide.
**Taxonomy:** Most workers recognize *Lubens* as a subgenus (with only one species) in the genus *Eurytrema* (Travassos, 1944). The species appears to be variable, and the measurements of this specimen fall within the limits reported for *E. lubens* by Travassos (1944). The only discrepancy is the lack of tegumentary papillae in the specimen from *Tringa solitaria*.

**Geographical Distribution:** *E. lubens* is known from a wide variety of birds from both North and South America and has been reported from grackles on the United States Gulf Coast (Travassos, 1944; Denton and Byrd, 1951). The presence of this specimen in *T. solitaria* represents a new host record.
**Zonorchis microrchis** (Travassos, 1919) Travassos, 1944

**Plate 8**

**host:** *Tringa solitaria* and *Calidris melanotos*

**site:** liver and bile ducts

**locality:** Louisiana

2 specimens measured from *Tringa*.

The 2 specimens from *T. solitaria* are quite different in size so their measurements will be listed separately with those of the second specimen in parentheses. A specimen retrieved from *C. melanotos* was identifiable but too badly damaged to be measureable. Worms lanceolate, narrow at both ends, widest at level of testes, approximately one-fourth from anterior end. Body 3.38 long by 0.63 wide (5.15 x 1.48). Tegument smooth, lacking spines and conical papillae. Oral sucker subterminal, 0.23 (0.33) in diameter. Pharynx 0.08 long by 0.10 wide (0.13 x 0.13). Esophagus short, 0.08 long (0.15). Intestinal caeca narrow, extending nearly to hind end. Intestinal bifurcation just anterior to acetabulum. Acetabulum 0.47 (0.83) from anterior end, 0.37 long by 0.40 wide (0.45 x 0.53). Ratio of oral to ventral sucker 1:1.7 (1:1.6). Ovary intercaecal, directly posterior to right testis. Ovary 0.12 long by 0.19 wide; ovary of second worm damaged. Mehlis' gland 0.08 long by 0.12 wide (0.14 x 0.17), overlapping posterior of ovary. Uterus fills body from ovary to
within 0.12 (0.15) of hind end. Uterine coils pass between ovary and testis, between testes, around and across acetabulum, and to genital pore alongside pharynx. Vitellaria in lateral fields overlapping caeca from testes to within 1.15 (1.42) of hind end. Transverse vitelline ducts merge medially posterior to Mehlis' gland forming vitelline reservoir. Testes just posterior to acetabulum, one slightly more anterior than other. Testes equal, 0.13 long by 0.17 wide (0.25 x 0.27). Cirrus pouch between pharynx and intestinal bifurcation, 0.12 long by 0.05 wide (0.13 x 0.08).

**Taxonomy:** The measurements of both specimens fall within the limits for *Zonorchis microrchis* given by Travassos (1944). These specimens differ from *Z. delectans*, the only other species with which they might be confused, by having narrow caeca. The sucker ratio is closest to that reported for *Z. microrchis*. The only discrepancy from the species description is the lack of tegumentary papillae in the specimens from *T. solitaria* and *C. melanotos*. This absence is not considered significant because *Z. microrchis* from *Latteralis viridis* (the Russet-crowned Crake) also lack papillae (Travassos, 1944).

**Geographical Distribution:** Previous to this study, *Z. microrchis* was known only from avian hosts in Brazil. The records from the Louisiana shorebirds constitute the first North American reports for the parasite. Because the shorebirds winter in South
America and may therefore have acquired the trematodes while wintering, the range extension for *Z. microrchis* does not constitute a definite change in the species' known infective geographical distribution. The presence of the trematodes in only northward migrating shorebirds suggests that the hosts were transporting trematodes that had been acquired in South America. In fact, the parasite's South American range may be limited to the eastern portion of the continent; the Ecuadorian hosts did not harbor *Z. microrchis*. In any case, the presence of *Z. microrchis* in *T. solitaria* and *C. melanotos* indicates that there is the potential for the eventual spread of the trematode's infective range into North America if in fact that has not already occurred. *T. solitaria* and *C. melanotos* are new host records for *Z. microrchis*. 
Family Cyclocoelidae Kossack, 1911

*Cyclocoelum* (*Haematotrephus*) *brasilianum* Stossich, 1902

Plates 9, 10, 11

*host:* *Tringa solitaria*

*site:* air sacs

*locality:* Ecuador; Lousiana; South Dakota; Canada

90 specimens measured

Large, heavy-bodied, oblong trematodes, anterior half more tapered than posterior. Body length 10.84 (8.00 – 14.50); width 2.26 (1.47 – 3.40). Tegument spineless and slightly undulating. Mouth subterminal, oral sucker and acetabulum lacking. Strongly muscled pharynx 0.19 long (0.15 – 0.22) by 0.18 wide (0.15 – 0.22). Esophagus mostly narrow but swollen near bifurcation. Caeca wide, undulating in width, lacking diverticula, forming intestinal arch 0.25 (0.07 – 0.45) from end of worm. Genital complex in triangular configuration in posterior of body within caecal arch. Ovary oval, 0.33 long (0.23 – 0.43) by 0.28 wide (0.19 – 0.40), always smaller than testes, located anterior and opposite to anterior testis, and separated from testes by uterus. Ovary near midline, closest to anterior testis, averaging 0.20 distant (0.02 – 0.42). Mehlis' gland and seminal receptacle between ovary and posterior testis. Regularly arranged chevrons
of uterine coils fill body from ovary to intestinal bifurcation, extending laterally to edge of body. At bifurcation, uterus straightens and proceeds to genital pore on midline of posterior half of pharynx. Eggs near genital pore large, 0.13 (0.12 - 0.15) by 0.07 (0.06 - 0.08), embryonated, thick-shelled with apical operculum. Vitellaria in lateral fields midway between pharynx and intestinal bifurcation to end of intestinal arch. Anteriorly, one vitelline field extends farther forward than other, averaging 0.71 (0.38 - 1.02) from front. Posterior extent of vitellaria variable. Vitellaria do not reach inner caecal margin. Transverse vitelline ducts pass between testes to merge medially into a reservoir. Extension of duct passes from reservoir toward ovary. Testes obliquely aligned, smooth margined, variable in shape but approximately equal in size, never separated by uterus. Anterior testis 0.52 long (0.32 - 0.68) by 0.44 wide (0.29 - 0.67); posterior testis 0.52 long (0.30 - 0.73) by 0.49 wide (0.30 - 0.73). Cirrus pouch 0.54 long (0.35 - 0.77) lies along esophagus. Internal seminal vesicle 0.29 long (0.18 - 0.40) by 0.12 wide (0.10 - 0.17). Excretory bladder median, posterior to caecal arch.

**Taxonomy:** Many authors have noted that Cyclocoelid worms are maleable, their organs prone to changes in size and position due to the degree of fullness of the uterus and the diverse methods of killing and fixing employed by the researchers (Joyeux and Baer,
1927; Dubois, 1959). Other complicating factors include variations caused by specimen age and degree of muscle contraction. Dubois (1959) warned that no taxonomic decisions should be made without examining a large number of specimens. Further, taxonomies should be based on the characteristics least susceptible to distortion. After examining more than 100 specimens of C. brasilianum from Tringa solitaria, I concur that great variability is evident, even among worms taken from a single host. Among the most variable characteristics are the posterior extent of the vitellaria, cirrus pouch length, and the size and shape of the testes. Variations in the posterior body of the specimens in this study are shown in Plates 10 and 11 and in the measurements reported in the species description. These variations occur in worms from South America and both migrations in the United States, with no apparent correlation between the characteristics; worms with small testes have as wide a range of vitellaria distribution as do specimens having large testes. Of 100 worms, 18% have vitellaria confluent across the intestinal arch. The remaining 82% have vitelline fields separated by spaces 0.03 wide to as far apart as 0.47. The testes not only vary in size but also in shape, ranging from round, to oval, to asymmetrical. I suspect that some of the variation, such as testes size and perhaps development of the vitellaria, can be attributed to specimen age. But differences in testes shape,
cirrus pouch length, and vitellaria distribution are probably caused by a combination of the fullness of the uterus, the amount of pressure applied to the worm during killing and fixing processes, and contraction of the specimen. As can be seen from the measurements in the species description, the ovary is less susceptible to distortion.

Harrah (1922), in his keys to the genera and species of the Cyclocoelidae, relied heavily on organ size ratios and vitellaria distributions. He especially used relative testes sizes and testes/ovary ratios. These practices caused Harrah to recognize many species that other workers considered to be synonymous. Joyeux and Baer (1927) were some of the first to suggest a consolidation of species based on gonad configurations and pharynx and egg measurements. They grouped the genera Haematotrephus, Corpopyrum, and Uvitellina into the genus Cyclocoelum, because of gonad configuration. Dubois (1959) recognized 3 subgenera in Cyclocoelum, one of which, Haematotrephus, is characterized by a gonad triangle with contiguous testes not separated by uterus. Of importance to this discussion is Joyeux and Baer's proposal that Cyclocoelum halli Harrah and Corpopyrum brasiliananum (Stossich) be synonymized into Cyclocoelum brasiliananum. Dubois (1959) also combined these species, lumping with them a third, Haematotrephus nittanyense, which was described by Zeliff (1946) from 4 specimens found in Tringa solitaria from Pennsylvania. Zeliff had not
included *H. nittanyense* with the admittedly very similar *C. brasilianum* because of differences in egg size, cirrus pouch size, and the presence of equal (as opposed to unequal) testes in the 4 worms from *T. solitaria*. The measurements of the worms described by Zeliff fit within the variations found in more than 100 specimens in this study. Because Zeliff based his description on a small sample size using some characteristics shown by my data to be variable, I conclude that all of the worms represent 1 highly variable, wide-ranging species that should be most correctly named *Cyclocoelum (Haematotrephus) brasilianum* Stossich.

**Geographical Distribution:** The geographical distribution of the specimens from *T. solitaria* strengthens the taxonomic conclusions discussed above. Previously, *C. brasilianum* had been reported from *T. solitaria* in Brazil while *H. nittanyense* was recorded in *T. solitaria* in North America (Zeliff, 1946). Although *C. brasilianum* had not been reported from *T. solitaria* outside of Brasil, Taft (1971) had identified *C. brasilianum* in several other species of *Tringa* from the midwest U.S. The present study, having specimens from *T. solitaria* from both North and South America that agree with the description of *H. nittanyense* but that must be identified as *C. brasilianum* using Dubois' criteria, reinforces the conclusion that *H. nittanyense* should be considered synonymous with *C. brasilianum*. Therefore, *C. brasilianum* is a trematode characteristic of shorebirds and widely
distributed throughout North and South America.
Cyclocoelum (Haematotrephus) tringae Stossich, 1902

Plates 12,13,14

host: Calidris melanotos

site: air sacs

locality: Ecuador; Louisiana; South Dakota

35 specimens measured

Large, heavily muscled, oblong trematodes with anterior more tapered than posterior. Length 10.07 (7.50 - 13.00), width 2.61 (1.60 - 3.37). Tegument spineless and slightly undulating. Mouth subterminal, oral sucker and acetabulum lacking. Strongly muscled pharynx 0.22 in diameter (0.18 - 0.26). Esophagus narrow, 0.29 long (0.21 - 0.59). Caeca wide, undulating in width, lacking diverticula, forming an arch 0.26 (0.14 - 0.42) from end of worm. Genital complex in triangular configuration in posterior of body within caecal arch. Ovary slightly oval, 0.34 long (0.21 - 0.42) by 0.33 wide (0.21 - 0.43), almost always smaller than testes, and separated from them by uterus. Ovary lateral, 0.49 (0.26 - 0.71) from the anterior testis but only 0.30 (0.03 - 0.51) from posterior testis. Mehlis' gland and seminal receptacle between ovary and testes. Uterus fills intercaecal space from ovary to intestinal bifurcation. Uterus reaches only to inner caecal margins except in a few very gravid, well-flattened specimens whose coils slightly overlap caeca. At bifurcation uterus straightens and
proceeds to genital pore on midline at posterior one-half of pharynx. Eggs near genital pore 0.14 by 0.07, thick-shelled, embryonated, with apical operculum. Vitellaria in narrow lateral fields only slightly overlapping caeca, leaving space between vitellaria and uterus. One vitelline field usually farther forward than other, averaging 0.83 (0.56 - 1.49) from front. Posterior extent of vitellaria variable. Transverse vitelline ducts pass between testes to merge medially into reservoir. Testes vary in size and shape, posterior testis usually larger, smooth margined, obliquely aligned, and never separated by uterus. Anterior testis 0.43 long (0.25 - 0.69) by 0.43 wide (0.21 - 0.63) but rarely perfectly round; posterior testis 0.41 long (0.21 - 0.63) by 0.50 wide (0.28 - 0.65). Cirrus pouch 0.53 long (0.33 - 0.71) lies along esophagus. Internal seminal vesicle 0.30 long (0.14 - 0.45) by 0.14 wide (0.08 - 0.21). Medial excretory bladder posterior to caecal arch.
**Taxonomy:** These worms are similar to *C. brasilianum* in exhibiting great variation in posterior distribution of vitellaria, length of cirrus pouch, and size and shape of testes. Of 35 worms, 8% have vitellaria confluent across the intestinal arch. Worms showing this characteristic occur in all localities. The remaining 92% of the specimens have vitelline fields separated by spaces 0.10 wide to as far apart as 0.90. Testes vary greatly in size and shape but usually the posterior one is oval and slightly larger than the more rounded anterior one. The variations in the specimens' posterior region are shown in Plates 13 and 14 and in the measurements in the species description.

Yamaguti (1958) recognized the genus *Corpopyrum* into which this species should be placed on the basis of intercaecal uterine coils. Other authors, however, proposed taxonomies emphasizing gonad configuration as generic and subgeneric criteria and therefore incorporated *Corpopyrum* into *Cyclocoelum* (Joyeux and Baer, 1927; Dubois, 1959). Dubois (1959) united *C. tringae* and *C. brasilianum* in the subgenus *Haematotrephus* by virtue of their contiguous testes not separated by uterus. The similarity of the gonad configurations of these 2 species is well demonstrated by Plates 10, 11, 13, and 14. The only consistent difference in the arrangement of the organs is the position of the ovary. The more lateral position of the ovary in *C. tringae* is closest to the posterior testis while the more medial ovary of *C. brasilianum* is
closest to the anterior one. Although the 2 species also differ in the lateral extent of the uterus and the angle of its coiling, all measurements for *C. tringae* and *C. brasilianum* are quite similar. Because of the great similarity between these 2 species, I am following the taxonomy proposed by Dubois (1959).

**Geographical Distribution:** *C. tringae*, as defined by Dubois (1959), is a wide-ranging species previously recorded mostly in the northern hemisphere. Dubois included in his synonymy the following species retrieved from shorebirds (Family Scolopacidae): *Corpopyrum tringae* (Brandes, 1892) from Sinai Peninsula; *Corpopyrum capellae* Yamaguti, 1933 from Formosa; *Cyclocoelum taxorchis* Johnston, 1916 from Australia; *Cyclocoelum wilsoni* and *Cyclocoelum triangularum* both described from Iowa birds by Harrah in 1922; and *Cyclocoelum tringae* Bych.-Pawl., 1953 from western Siberia. More recently, researchers following Dubois' taxonomy have recorded *C. tringae* from Dunlin (*Calidris alpina*) along the Louisiana coast (Weber, 1968) and Pectoral Sandpipers in Iowa (Taft, 1971). The specimens from the Pectoral Sandpipers of this study represent the first records for *C. tringae* from South America. Undoubtedly further research will reveal the parasite in other South American hosts because *C. tringae* has been recorded in the United States from Western Sandpipers (*Calidris mauri*), Semipalmated Sandpipers (*Calidris pusilla*), and Spotted Sandpipers (*Actitis macularia*), all
migrants that travel between North and South America (Weber, 1968).
Cyclocoelum (Cyclocoelum) obscurum (Leidy, 1887) Harrah, 1922

Plate 15

host: Tringa solitaria and Calidris melanotos

site: air sacs

locality: Ecuador; Louisiana

9 specimens measured from Calidris in Ecuador

Large, heavily muscled, oblong trematodes with anterior slightly more tapered than posterior. Length 11.61 (9.00 - 15.00); width 2.01 (1.47 - 2.60). Tegument spineless and slightly undulating. Mouth subterminal, oral sucker and acetabulum lacking. Strongly muscled pharynx 0.20 in diameter (0.18 - 0.22). Caeca wide, undulating in width, lacking diverticula, forming an arch 0.23 (0.13 - 0.31) from end of worm. Gonads spread apart but still in triangular configuration within caecal arch in posterior one-fourth of worm. Ovary intertesticular, 0.31 long (0.25 - 0.35) by 0.29 wide (0.24 - 0.32), separated from testes by uterus. Average distance between ovary and posterior testis 0.35 (0.28 - 0.42). Mehlis' gland overlaps posterior of ovary. Uterus fills intercaecal space from posterior testis to intestinal bifurcation where uterus straightens and proceeds to medial genital pore at posterior half of pharynx. Eggs embryonated, variable in size, largest 0.14 by 0.07. Vitellaria in prominent lateral fields
rarely reaching inner caecal margins. One vitelline field usually extends farther forward than other and averages 0.67 (0.49 - 0.80) from front. Posterior extent of vitellaria variable. Anterior testis surrounded by uterus, adjacent to caecum, 0.88 (0.49 - 1.74) from posterior testis. Posterior testis medial, just anterior to caecal arch, post-uterine, usually larger than anterior testis. Anterior testis 0.44 long (0.35 - 0.56) by 0.41 wide (0.28 - 0.50); posterior testis 0.48 long (0.40 - 0.59) by 0.47 wide (0.35 - 0.66). Cirrus pouch 0.43 long (0.31 - 0.49) lies along the esophagus. Internal seminal vesicle 0.25 long (0.22 - 0.29) by 0.12 wide (0.08 - 0.14). Medial excretory bladder just posterior to caecal arch.

**Taxonomy:** Insufficient material was obtained from the hosts in this study to permit observations on the variability of this species. The widely spaced testes separated by uterus place these specimens in the subgenus *Cyclocoelum* (Dubois, 1959). Lumsden and Zischke (1963) reported that 2 species of *C.* ( *Cyclocoelum*) are known from United States birds, *C.* _mutabile_ and *C.* _obscurum_. According to the pharynx size specifications cited by Dubois, 500 to 1270 um for *C.* _mutabile_ and 120 to 310 um for *C.* _obscurum_, the specimens in this study must be identified as *C.* _obscurum_. This identification is strengthened by Macko's (1965) observation that *C.* _obscurum_ is to be expected in Scolopacid hosts, whereas *C.* _mutabile_ is found in hosts of the family Rallidae.
Taft (1975) found life cycle and larval development of *C. obscurum* to be very similar to that of *C. brasilianum* and speculated that the 2 species might be synonymous. He attributed adult morphological differences to host induced variations. *T. solitaria* in this study harbor both forms, therefore the differences between the parasites are probably not host induced. I am considering the 2 forms to be separate species and am following the taxonomy proposed by Dubois (1959).

**Geographical Distribution:** *C. obscurum* has been recorded from shorebirds in Africa, the Phillipines, Asia, and North America (Yamaguti, 1958; Dubois, 1959). The specimens from *C. melanotos* in Ecuador represent the first records for *C. obscurum* from the South American continent. The presence of an air sac parasite in Pectoral Sandpipers from both North and South America is not surprising because parasites are not easily lost from such organs. There are no other records of *C. obscurum* from hosts that migrate between North and South America, but one would expect future research on wintering shorebirds to reveal the trematode in other South American hosts. Both Solitary and Pectoral Sandpipers are new host records for this trematode.
Family Eucotylidae Skrjabin, 1924

*Tanaisia* fedtschenkoi Skrjabin, 1924

Plate 16

host: *Tringa solitaria* and *Calidris melanotos*

site: kidney ducts

locality: Ecuador; Louisiana; South Dakota

73 specimens measured (43 from *Tringa*; 30 from *Calidris*)

Small to medium-sized, weakly muscled, monostomes with rounded ends and almost parallel sides, 2.54 long (1.86 - 3.28) by 0.52 wide (0.36 - 0.66). Tegument with regularly spaced minute spines throughout. Oral sucker subterminal, 0.18 long (0.14 - 0.23) by 0.20 wide (0.15 - 0.25). Pharynx 0.06 long (0.04 - 0.08) by 0.08 wide (0.06 - 0.12). In most specimens esophagus has bulge 0.03 to 0.17 wide. Intestinal bifurcation hidden by uterus, 0.12 to 0.15 from pharynx. Caeca narrow, unbranched, undulatory, and forming an arch approximately 0.28 from end of worm. Acetabulum lacking. Ovary deeply dendritic, irregular in shape, displaced from center, 0.22 long (0.15 - 0.30) by 0.20 wide (0.13 - 0.30). Uterus extends from mid-esophagus to within 0.05 of hind end. Uterine coils weave between ovary and testes so organs visible but margins obscured. Uterus never overlaps vitellaria. Genital pore
medial at anterior border of ovary. Eggs 0.03 by 0.01. Globular
vitellaria in extracaecal lateral fields from ovary to within 0.44
(0.12 - 0.83) of end of worm. Transverse vitelline ducts merge
medially to form reservoir posterior to ovary. Testes amorphously
shaped, obliquely aligned. Anterior testis 0.20 long (0.12 -
0.33) by 0.19 wide (0.10 - 0.30); posterior testis 0.20 long (0.12
- 0.40) by 0.19 wide (0.13 - 0.33).

**Taxonomy:** These specimens agree very well with the
description of *T. fedtschenkoi* provided in Byrd and Denton
(1950). All measurements of the specimens from *T. solitaria* and
*C. melanotos* closely match those of the species description (Byrd
and Denton, 1950). The only discrepancy is Byrd and Denton's
description of *T. fedtschenkoi* as a distomate worm: "Acetabulum
sometimes present in fully matured specimens." The statement was
based on the presence of a 54 μm by 84 μm acetabulum posterior to
the testes in only one specimen from a Common Snipe, *Gallinago
gallinago*. Of the more than 250 whole-mounted worms that were
examined in the present study, no acetabulum was found. Cross
sectioned preparations may reveal the presence of an acetabulum
not visible in whole mounted worms because the area posterior to
the testes is obscured by uterus. Because only 1 specimen is
known to have an acetabulum, I feel that the lack of acetabula in
whole mounted specimens from *T. solitaria* and *C. melanotos* is
not a significant deviation from the species diagnosis.
Geographical Distribution: *Tanaisia fedtschenkoi* has been found in aquatic and semi-aquatic North American birds and is characteristic of Charadriid hosts (Byrd and Denton, 1950). Previously, the species has been recorded from the United States, Russia, Turkestan, Macedonia, and Siberia, all northern hemisphere localities (Byrd and Denton, 1950). The presence of both adult and immature worms in Solitary and Pectoral Sandpipers wintering in Ecuador provide the first records for this trematode from South America. This range extension is not surprising because of the worms' occurrence in the kidney ducts of hosts migrating between the 2 continents. Parasites in the kidneys are less likely to be lost during migration than those found in the intestines. These records are the first reports for *T. fedtschenkoi* from Solitary and Pectoral Sandpipers.
Family Notocotylidae Luhe, 1909

Paramonostomum sp.

Plate 17

host: Tringa solitaria and Calidris melanotos

site: intestine

locality: Canada; Louisiana

5 specimens measured (1 from Tringa; 4 from Calidris)

Small, weakly muscled monostomate worms 3.00 long (2.90 - 3.13) by 0.65 wide (0.60 - 0.72). Worms rounded at ends, slightly more tapered anteriorly, with nearly parallel sides. Tegument minutely spined with most evident spination on anterior half. 8 rows of pores, 4 on each side of midline, visible on ventral surface, best seen at level of cirrus pouch and in area of ovary and testes. The 4 most prominent rows between caeca, 2 on each side of cirrus pouch. In these rows pores less numerous anteriorly and none visible at level of genital pore. Third row of pores along outer edge of each caecum. Fourth, and least discernible row, is lateral. Scattered pores occur lateral to the discernible rows. Ventral glands lacking. Oral sucker subterminal, 0.11 long (0.10 - 0.13) by 0.13 wide (0.12 - 0.13). Pharynx and acetabulum lacking. Esophagus narrow, 0.17 long. Intestinal caeca gradually diverge after bifurcation, spread
farther apart at level of uterine coils, and end 0.09 from end of worm. Genital complex in posterior one-fifth of body. Ovary medial, intercaecal, 0.20 long (0.18 - 0.22) by 0.16 wide (0.13 - 0.18). Mehlis' gland anterior to ovary and dorsal to vitelline reservoir. Uterus entirely anterior to ovary and testes with 23 regularly arranged uterine coils filling intercaecal space until mid-body where uterus straightens and proceeds medially to genital pore just posterior to intestinal bifurcation. Metraterm extends posteriad to point of transverse uterine coils. Polar filaments present on eggs. Eggs 0.02 long, excluding filaments. Vitellaria in lateral extracaecal fields confined to posterior half of body. Vitellaria begin just posterior to end of cirrus pouch, about 1.30 from hind end, and extend posteriad to anterior margin of testes. Transverse vitelline ducts merge medially forming reservoir between ovary and wide uterine coils. Testes lateral, overlapping caeca only slightly, and extending slightly posterior of caecal tips. Left testis 0.38 long (0.32 - 0.43) by 0.17 wide (0.13 - 0.20); right testis 0.35 long (0.30 - 0.40) by 0.16 wide (0.14 - 0.17). Cirrus pouch well-developed, extending posterior of point where uterus straightens. Cirrus finely spined 0.18 long by 0.03 wide.

Taxonomy: Cross-sections of one specimen show that ventral glands are lacking in these worms and therefore they must be classified as Paramonostomum (Skrjabin, 1964). Lal (1936) divided
the known species of *Paramonostomum* into 2 genera based on the position of the genital pore, those with the pore posterior to the intestinal bifurcation being renamed *Neoparamonostomum*. Lal's taxonomy is not being followed here because more recent researchers have advocated the rejection of his classification (Yamaguti, 1958; Skrjabin, 1964). The specimens from Solitary and Pectoral Sandpipers have the genital pore just posterior to the intestinal bifurcation and are therefore distinguishable from *P. alveatum*, *P. pseudalveatum*, *P. casarcum*, *P. nettoni*, and *P. querquedulum*, all of which have more anterior genital pores. The known species of *Paramonostomum* exhibit 2 general body types, those that are oval with body lengths not more than twice their body widths and elongate species that are considerably longer than they are wide. Ching (1961) listed the following species with elongated bodies: *P. actitidis*, *P. bucephalae*, *P. echinum*, *P. elongatum*, *P. histrionici*, and *P. malerischi*. Species that also should be included in this group are *P. signiensis* and *P. ionorne* (Jones and Williams, 1969) and *P. alveoelongatum*, *P. chabaudi*, *P. harwoodi*, and *P. nettoni* (McDonald, 1981). Of this group, *P. nettoni* has already been separated from the specimens in the present study by the location of its genital pore. The specimens from *Tringa* and *Calidris* are elongate in body form but cannot be assigned to any of the above species. *P. actitidis*, *P. alveoelongatum*, *P. bucephali*, *P. malerischi*. 
and *P. signiensis* all have fewer than 20 transverse uterine loops whereas each of the 5 specimens in this study has 23 loops. *P. chabaudi* differs from the present specimens in its length, 0.50 - 0.80. *P. elongatum* can be eliminated because it lacks spines on the tegument and cirrus and has vitellaria that never reach the base of the cirrus pouch (Lai, 1936). *P. histrionici* reaches a total length of only 1.90 yet is 0.60 wide, has an unarmed, club-shaped cirrus, and only 16 to 18 uterine loops (Ching, 1961). A few of the worms in the present study have irregularly sized and shaped caecal diverticula similar to those described for *P. echinum* (Harrah, 1922). But, the presence of the diverticula in the present specimens is variable; most obvious in contracted worms and nearly lacking in more relaxed individuals. This trend leads one to suspect that the diverticula may be artifacts of the worms' contraction. The specimens are different from *P. echinum* by not being cup-shaped, having smaller tegumentary spines, having a spined cirrus, and a subterminal mouth (Harrah, 1922). The worms from *Tringa* and *Calidris* most closely resemble *P. ionorne*, a species reported to have a genital pore posterior to the intestinal bifurcation, a body much longer than wide (the body length averaging 3.00), no intestinal diverticula, and vitellaria reaching the posterior limit of the cirrus pouch (Skrjabin, 1964). Jones and Williams (1969) remarked, in comparing *P. signiensis* and *P. ionorne*, that *P. ionorne* lacks tegumentary spines. This
characteristic is not mentioned in the original description by Travassos (1921). However, Travassos did specify that P. ionorne lacks an esophagus, has an oral sucker 0.21 in diameter, testes approximately 0.52 by 0.21, an ovary 0.33 by 0.35, and a body 3.20 long by 1.50 wide. Clearly the specimens from Solitary and Pectoral Sandpipers do not fit this description. One must therefore conclude that the present specimens represent an undescribed species of Paramonostomum, but because only 5 specimens have been found, further research is needed before an adequate description of the species can be accomplished.

**Geographical distribution:** Paramonostomum sp. were retrieved from breeding Solitary Sandpipers in Canada and from southward migrating Pectoral Sandpipers in Louisiana. This distribution suggests that the species is a northern one. However, the genus is world-wide and includes species from both North and South America (Yamaguti, 1958), therefore more data are required before speculation on the parasite's infective geographical range can be made.
Table 2. Trematode species recorded from *Tringa solitaria* and their prevalence from each locality and season.
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<thead>
<tr>
<th>trematode species</th>
<th>total % in host (197)</th>
<th>Ecuador spring (70)</th>
<th>LA spring (1)</th>
<th>SD total spring (71)</th>
<th>Canada fall (10)</th>
<th>SD fall (21)</th>
<th>LA fall (44)</th>
<th>total fall (65)</th>
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<tbody>
<tr>
<td><strong>Tanaisia fedtschenkoi</strong></td>
<td>37 (18.78%)</td>
<td>12 (23.53%)</td>
<td>10 (14.29%)</td>
<td>11 (15.49%)</td>
<td>0 (23.81%)</td>
<td>5 (20.45%)</td>
<td>9 (21.54%)</td>
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<td>47 (23.86%)</td>
<td>11 (21.57%)</td>
<td>16 (22.86%)</td>
<td>16 (22.53%)</td>
<td>3 (38.09%)</td>
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<td>9 (26.15%)</td>
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<td><strong>Cyclocoelum obscurum</strong></td>
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<td>0 (0%)</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
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<tr>
<td><strong>Paramonostomum sp.</strong></td>
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<td>0 (0%)</td>
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<td><strong>Leucochloridium variae</strong></td>
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<td>1 (1.43%)</td>
<td>1 (1.41%)</td>
<td>0 (9.52%)</td>
<td>2 (4.55%)</td>
<td>2 (6.15%)</td>
<td>4 (6.15%)</td>
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<td><strong>Stephanoprora denticulata</strong></td>
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<td>0 (0%)</td>
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(Percentages in parentheses)
Table 3. Trematode species recorded from *Calidris melanotos* and their prevalence from each locality and season.
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<tr>
<th>Trematode Species</th>
<th>Total % in Host</th>
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<th>LA</th>
<th>SD</th>
<th>Total</th>
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<td>(0.47%)</td>
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Table 4. Comparison of the trematode fauna of 

*Tringa solitaria* and *Calidris melanotos*. 
<table>
<thead>
<tr>
<th>Species in common</th>
<th>Found only in Tringa</th>
<th>Found only in Calidris</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tanaisia fedtschenkoi</td>
<td>Cyclocoelum brasillianum</td>
<td>Cyclocoelum tringae</td>
</tr>
<tr>
<td>Cyclocoelum obscurum</td>
<td>Plagiorchis maculosus</td>
<td>Plagiorchis elegans</td>
</tr>
<tr>
<td>Paramonostomum sp.</td>
<td>Stephanoprora denticulata</td>
<td>Echinoparyphium speotyto</td>
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<td>Leucochloridium variae</td>
<td>Eurytrema lubens</td>
<td>Echinoparyphium aconiatum</td>
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<td>Zonorchis microrchis</td>
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</tbody>
</table>
DISCUSSION

Biology of the Hosts

Solitary and Pectoral Sandpipers were chosen for this study because of their long-distance intercontinental migrations, their availability in Ecuador, Louisiana, South Dakota, and Canada, and their habit of feeding on a wide variety of animal material throughout the year. Comparison of the trematode faunas of these 2 species is of interest because of the hosts' diverse feeding and nesting ecology. In the South American tropics, both species were found in wet situations along small streams, ponds, and flooded pastures. However, Solitary Sandpipers preferred the muddy, manure-filled puddles of cow pastures while Pectorals were most easily located on the sand bars of the Napo River. Indeed, Solitary Sandpipers are notorious for their fondness of liquid manure (Bent, 1962c) and, during migration through the United States, were found at such unsavory locations as muddy banks of polluted streams and the shallow ponds of sewage treatment plants. During migration Pectorals were more commonly found in wet grassy fields and coastal mudflats. Solitary Sandpipers, as the name suggests, feed singly or in pairs while Pectorals feed in small to large flocks, often in association with other species of shorebirds.

The literature and a cursory stomach content survey in this study indicate that these 2 species are widely omnivorous and
include in their diets a wide variety of aquatic and terrestrial adult and larval insects, worms, small molluscs, crustaceans, frogs, and fishes (Bent, 1962c). The shorebirds remain omnivorous throughout migration and breeding (Bent, 1962c). It is highly likely, therefore, that while migrating these 2 species encounter many helminth infective stages. Variety in the birds' diets is augmented because long distance migrants pass through many ecologically diverse areas. Especially during the fall and spring migrations, these 2 species have broad feeding niches (Brooks, 1967). A notable difference between the feeding behavior of Solitary and Pectoral Sandpipers is evident in pond and coastal mudflat situations where Pectorals feed on or near the shore or in algal mats while the long-legged Solitary Sandpipers feed in water up to belly deep (Brooks, 1967).

Male and female Pectoral Sandpipers differ significantly in size; males average 73 gms (35 - 120) and females weigh 51 grams (32 - 93). While this size disparity may result in dietary differences, no significant difference in trematode fauna was noted between the sexes in this study.

The 2 recognizable subspecies of Solitary Sandpipers are the eastern race T. s. solitaria identified by unmarked dark inner webs to the primaries and the western race T. s. cinnamomea having inner primary webs mottled with white (Chapman, 1926). The winter distribution of these 2 forms is not well understood (Bent
1962c), but in this study both races were found in Ecuador in a ratio of 4 T. s. solitaria to every T. s. cinnamomea. Of the 114 Solitary Sandpipers collected in Louisiana, only 21 were western-race birds. All specimens from South Dakota and Ontario, Canada were T. s. solitaria. Insufficient numbers of T. s. cinnamomea were collected in this study to allow a valid comparison between the trematode faunas of the 2 forms.

Breeding strategy is the greatest ecological difference between these 2 species of shorebirds. Solitary Sandpipers breed in the Canadian taiga, a boreal forest of spruce, fir, popular, and birch. Tringa solitaria is one of the few Scolopacids to nest in trees, selecting nests abandoned by American Robins, waxwings, Canada Jays, or Rusty Blackbirds (Bent, 1962c). Nests are usually 4 to 40 feet from the ground near small woodland ponds. In their breeding grounds, Solitary Sandpipers are widely dispersed and difficult to locate. Pectorals, on the other hand, breed in the grassy meadows of the Arctic tundra, primarily along the coasts of Alaska, Mackenzie, and into eastern Siberia. Pectorals prefer high, dry locations where their nests are grass-lined depressions in the ground. Because of time and expense limitations, no attempt was made to survey nesting Pectoral Sandpipers.

Solitary and Pectoral Sandpipers arrive in South America in August, spend the winter there, and the last birds leave for the
northward spring migration by late April. The earliest arrivals reach the United States in March, pass through South Dakota in late April and May, breed in Canada and Alaska during late May through July, and begin to head southward through South Dakota and Louisiana in late July. The last southward migrants can be seen in the United States through the first 2 weeks of October.

Shorebirds collected in Ecuador may have been heading farther south, but both species were found in Ecuador throughout the winter months.
Analysis of Trematode Fauna According to Dogiel's Classification of Parasites

Recent workers (Threlfall, 1968; Hood and Welch, 1979) investigating the parasite fauna of migrating hosts have interpreted their data according to the categories erected by Dogiel (1964) based on his pioneering research with Russian birds. He distinguished 4 groups of parasites from birds breeding in the northern hemisphere: 1) ubiquitous species that occur in hosts throughout the year and can complete their life cycles on all parts of the hosts' range, 2) southern forms that can only infect their hosts on the wintering grounds, 3) northern forms that infect hosts only on the breeding grounds, and 4) species that infect the hosts only during the fall and spring migrations. Southern forms theoretically would be gradually lost from the migrating populations, become least prevalent in fall migrants, and disappear completely from southward migrating young of the year. Northern forms would be present in hatchlings and breeding adults, lost from the population before or during fall migration, and thus least prevalent in spring migrants. Determining the affinities of the complex of species comprising a host's parasite fauna is accomplished by comparing the parasites of fall and spring migrants, determining the fauna of nestlings, sampling hosts in their breeding and wintering ranges, and studying the zoogeography of the parasite species (Dogiel, 1964).
Of the trematodes found in this study, 3 species are definitely ubiquitous: *Tanaisia fedtschenkoi*, common to both hosts, *Cyclocoelum brasilianum* from Solitary Sandpipers, and *C. tringae* from Pectoral Sandpipers. All 3 species were of approximately equal prevalence in wintering birds and fall and spring migrants. The designation of the *Cyclocoelum* species as ubiquitous is supported by their extensive zoogeographical range (see geographical distribution sections of the species descriptions).

The 10 breeding Solitary Sandpipers harbored *C. brasilianum* but lacked *Tanaisia*. This deficiency is most probably due to insufficient sampling of the breeding populations since the South Dakota fall migrants that had just left the breeding grounds had about a 24% infection of viable, gravid worms. Viable, gravid specimens of *T. fedtschenkoi* from both Solitary and Pectoral Sandpipers in Ecuador extend the parasite's known range and confirm it as a ubiquitous species at least for these 2 hosts. Further evidence that the *Tanaisia fedtschenkoi* life cycle can be completed in South America is provided by the presence of very immature worms in the Ecuadorian hosts.

*T. fedtschenkoi* is found here to be a ubiquitous parasite in contrast to Dogiel's classification of the same species in Glossy Ibis (*Plagadis falcinellas*) along the Volga as a southern form that was gradually lost, the parasite either lacking from fall
migrants or present as moribund individuals (Dogiel, 1964). Previously, *T. fedtschenkoi* was known from the United States, Russia, and Europe, all northern latitudes (Byrd and Denton, 1950). This distribution would tend to rule out *T. fedtschenkoi* as a southern form for intercontinental migrants. Hood and Welch (1979) classified this species as a ubiquitous form present in Red-winged Blackbirds breeding in Manitoba, Canada, in fall and spring migrants, and in birds wintering in the southern United States. Dogiel maintained that a parasite species need not have the same classification for all hosts as the dynamics, range, and timing of migrations differ for each host species. Differences in feeding behavior during migration or variations in departure time in relation to intermediate host development affect the host's susceptibility to infection. For these reasons, Dogiel cautioned that each parasite species must be categorized separately according to each host species.

As might be expected, the ubiquitous species of these long-distance migrants are from locations in the body other than the intestines and are therefore less susceptible to elimination resulting from the stresses of migration. Residence in the abdominal air sacs (*Cyclocoelum*) and kidney ducts (*Tanaisia*) make these species less likely to be expelled.
Dogiel (1964) observed that the greatest percentage of ubiquitous parasites were found in birds that had short migrations, within the Temperate Zone for example, and did not change their type of feeding during migration. In such a host, as the Starling (Sturnus vulgaris) in Russia, 55% of the fauna was found to be ubiquitous (Dogiel, 1964). Ginetsinskaya (in Dogiel, 1964), studying Russian ducks with short migration routes, found ubiquitous species to be the main component of the ducks' parasite fauna. Long-distance migrants, such as those in the present study, experience greater stress because of the tremendous distances travelled and the substantial dietary changes resulting from the diversity of prey species encountered across a variety of ecological habitats. For both Solitary and Pectoral Sandpipers, only 2 of 9 trematode species (22%) can be classified as ubiquitous, a result in agreement with Dogiel's hypothesis.

Paramonostomum sp. can be classified as a northern form based on the seasons during which the worms were recovered. One specimen was retrieved from a breeding Solitary Sandpiper in Ontario and the remaining specimens were in fall, southward migrating Pectoral Sandpipers from Louisiana. This evidence suggests the parasite is acquired in the breeding grounds but is lost before or during fall migration. Evidently, the worms are easily shed during the stresses of migration when the hosts' feeding schedules and diets are altered. Interestingly, this
species is common to 2 hosts with very different breeding ecology. For this reason and because so little is known about the species' biology and zoogeography, the designation of *Paramonostomum* sp. as a northern form must be tentative.

The other species common to both hosts that seems likely to be a northern form is *Leucochloridium variæ*. This conclusion is based on the higher prevalence in the fall migrants of both hosts and the parasite's presence in only one specimen of each host species in the spring (see Tables 2 and 3). As previously mentioned, all records to date for *L. variæ* are from birds in the United States and Canada, a geographic distribution that suggests a northern nidus. If this species is indeed a northern form, some individuals are able to maintain themselves in the host's intestine throughout the host's arduous migration as evidenced by the spring records in this study. For reasons that will be discussed later, this species is tentatively classified as a northern form.

One species, *Cyclocoelum obscurum*, can be justifiably classified as a winter, or southern, form in Pectoral Sandpipers because it occurred in 2 of 34 Ecuadorian specimens but was lacking from 179 Pectorals collected in the United States. This finding is bizarre since the species was previously recorded in other shorebirds only from Africa, Philippines, Asia, and North America (Yamaguti, 1958; Dubois, 1959). The records here
represent a range extension for *C. obscurum* to South America. Why Pectorals would not become infected with this species in Louisiana where it has been recorded from other shorebirds such as Marbled Godwit, (*Limosa fedoa*) and Willet, (*Catoptrophorus semipalmatus*) (Weber, 1968) is difficult to understand, but may be explained by feeding habits. Pectorals are not usually seen feeding with godwits and Willets during migration (Dan Tallman, pers. comm.). The presence of an immature *C. obscurum* in a Louisiana Solitary Sandpiper probably can be viewed as an accidental infection. The possibility that such a large, conspicuous species was overlooked in any of the host specimens is unlikely.

The only remaining trematode species of greater than a 2% prevalence is *Echinoparyphium speotyto* from fall and spring Louisiana Pectoral Sandpipers. The species was equally common in both Louisiana migrations but was absent from South Dakota hosts. This distribution suggests that the species may be of local occurrence and easily lost from the host. Previously, *E. speotyto* was known only from Burrowing Owls in Oklahoma (Buscher, 1978). The fact that the species has been recorded from such a limited number of hosts from such a small geographic area supports the conclusion that the parasite is acquired only during migration through the south-central United States. However, the sample size of Pectorals from the other localities is small, so further study
may show *E. speotyto* to have a wider infective geographic range.

The remaining 6 species, *Eurytrema lubens*, *Zonorchis microrchis*, *Stephanoprora denticulata*, *Echinoparyphilum aconiatum*, *Plagiorchis elegans*, and *Plagiorchis maculosus*, were so infrequently encountered in Solitary and Pectoral Sandpipers that their affinities are difficult to discern. All are digestive tract worms and therefore the most susceptible to the stresses of host migration.

*Zonorchis microrchis* was found in both host species but only from spring migrants. *Z. microrchis* is known as a Brazilian species (Travassos, 1944) so the specimens retrieved from the Louisiana hosts probably were transported to the United States from South America where the infection was acquired. The species' absence from the Ecuadorian birds is surprising but can be attributed to either the smaller sampling of wintering birds or to the parasite's South American range being limited to Brazil and areas other than Ecuador with only those sandpipers wintering there becoming infected.

The specimens of *Plagiorchis*, 1 individual of *P. maculosus* from a Solitary Sandpiper and 1 *P. elegans* from a Pectoral, were both from fall migration. These records are as would be expected since the genus is a northern one (Dogiel, 1964). In fact, Dogiel and Bykhovskaia-Pavlovskaja (1955) found no species of *Plagiorchis* in wintering Passerines but found the genus to be typical in the
northern part of the birds' range. Therefore, the present specimens are probably breeding grounds parasites that had not yet been purged from the hosts' intestines. As mentioned earlier, *P. elegans*, a primarily Eurasian species, has an infective geographic range that includes North America as demonstrated by the parasite's presence in 2 species of gulls that are not found outside of the North American continent (Bent, 1962b; Vermeer, 1969). The presence of *P. maculosus* in *Tringa solitaria*, an exclusively New World shorebird, proves that the infective geographic range of *P. maculosus* also must include North America.

The affinities of *Eurytrema lubens*, *Stephanoprora denticulata*, and *Echinoparyphium aconiatum* cannot be ascertained from the meager data available. *E. lubens* was found in Louisiana from 1 spring and 1 fall Solitary Sandpiper. The trematode species is common to both North and South America so its distribution offers no clue to its role in the parasite fauna of the sandpiper. Similarly, *S. denticulata* and *E. aconiatum* were both single records of trematode species whose large geographic ranges do not help to decipher the origin of infection.

Table 5 summarizes the designations made for each trematode species.
Table 5. Classification of the trematodes found in *Tringa solitaria* and *Calidris melanotos* according to where the hosts probably became infected.

\[ T = \text{Tringa solitaria} \]
\[ C = \text{Calidris melanotos} \]
\[ * = \text{tentative designation} \]
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<td>C</td>
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<tr>
<td>Echinoparyphium acroniatum</td>
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<td>C</td>
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General Analysis

The parasite fauna of winter hosts has generally been found to be depauparate, reduced both in numbers of species and intensity of infection, in comparison to the fauna of specimens from other parts of the birds' range (Dogiel and Bykhovskaia-Pavlovskiaia, 1955; Kinsella, 1973). This phenomenon has been partially explained, for migrants that winter within the Temperate Zone, by the decline during the colder months in populations of intermediate host species and the resulting decline in the opportunity for reinfection. This explanation is not sufficient, however, for intercontinental migrants that winter in the austral summer. The data from the present study indicate that even migrants wintering in the tropics have a depauparate fauna; only 3 of the 13 trematode species recorded from the sandpipers were found in hosts wintering in Ecuador.

The contrast between the variety of trematodes found in wintering and migrating birds may be due to a wider feeding niche for the birds during migration. Because of the habitat changes encountered by the migrants over a number of weeks and thousands of miles, the variety of species of invertebrates and small vertebrates consumed during migration probably is greater than the number of prey species eaten while either wintering or breeding. In addition, the fauna of migrating individuals will be a composite of species "holding on" after having been acquired in
the breeding or wintering areas plus those species picked up during migration.

The larger number of species recorded from migrating birds may also indicate that metacercariae picked up during migration mature very quickly, deposit eggs at the interim locality, are quickly shed from the host, and are thus absent from wintering birds. The intermediate, molluscan hosts would in such instances provide the predominant stage for the trematode species. If the trematode adults of migrating birds are indeed short-lived, one would suspect that surveys of the avian hosts would yield data composed of trematode species with low prevalence as well as low intensity of infection. This is the case with many species in the present study. *Plagiorchis elegans*, *Plagiorchis maculosus*, *Echinoparyphium aconiatum*, and *Stephanoprora denticulata* are 1 worm records and *Eurytrema lubens* and *Zonorchis microrchis* are each represented by 1 worm infections from 2 and 3 hosts respectively. In fact, the host species in this study have a high incidence (66%) of trematode species that occur in 2% or less of the overall host population. All of the low prevalence species are digestive tract inhabitants and are probably quite susceptible to the stresses of host migration. Certainly, rapid maturation and early egg shedding would be successful strategies to survive in an environment as precarious as an intestine of a migrating host whose feeding schedules and diet are in constant flux.
Examination of 15 to 20 hosts is believed by some authorities (Ginetsinskaya, 1966 in Hood and Welch, 1980) to be sufficient to characterize the parasite fauna of a given host species from one location. But such small samples are probably insufficient to reveal the occurrence of very low prevalence species. Certainly, when dealing with long-distance migrants that apparently have a parasite fauna characterized by a large number of low prevalence species, large samples should be examined and great care must be taken when analyzing data. The present study cannot rule out the possibility that long-distance migrants may have several low prevalence species during the summer and winter because of the relatively small samples taken from those seasons. Russian research that employed the procedure of collecting small numbers of many species must be considered inadequate to reveal any but the most common parasites of each host.

Most researchers have found more parasites in breeding birds than in birds during other seasons and have concluded that most parasite acquisition occurs while birds are nesting. Work showing the breeding grounds to be of primary importance in parasite infection has been done with relatively short-distance migrants or using small samples of long-distance migrants that were not examined outside of the Temperate Zone (Dogiel and Bykhovskaia-Pavlovskaia, 1955). Schmidt and Frantz (1972) conducted one of the few North American studies of a long-distance
migrant. They examined 90 Wilson's Phalaropes, Steganopus tricolor, a species that breeds in north-central United States and winters in Chile and Argentina. Because Colorado birds migrating north lacked trematodes whereas the breeding Montana birds were infected with 3 trematode species, the researchers concluded the summer habitat was the primary source for helminth infections for long-distance migrants. The Schmidt and Frantz study and the present one agree that long-distance migrants harbor few trematodes, but the studies differ in their assessment of the importance of the breeding grounds as a source for trematode infections.

Another study that found the breeding grounds to be a significant source for helminth infections involved birds that radically alter their diet while breeding (Hood and Welch, 1980). The high incidence of endoparasitism in breeding Red-winged Blackbirds, a species that is primarily vegetarian until nesting when it becomes omnivorous, revealed more about the effects of diet on parasite fauna than about the effects of host migration.

If the breeding grounds were of primary importance as a source of trematode infections for Tringa solitaria and Calidris melanotos one would expect the following patterns: 1) more trematodes in South Dakota fall migrants than in Louisiana fall migrants, 2) the greatest contrast in parasite variety and prevalence of infection between fall and spring South Dakota
birds, 3) a high degree of parasitism in the 10 breeding Solitary Sandpipers from Ontario, 4) more trematode species and higher prevalence of infection in Louisiana fall migrants than in Louisiana spring birds, and 5) a marked difference between the trematode faunas of Solitary and Pectoral Sandpipers because of the hosts' very different breeding ecology.

The sample sizes from South Dakota were too small to allow for reliable comparisons with the large samples from Louisiana, especially in light of the number of low prevalence parasite species. However, of the migration route localities studied, South Dakota was the closest to the hosts' breeding territory yet, only 1 species of trematode, *Plagiorchis maculosus*, was recorded exclusively from South Dakota fall birds. The Ontario sample of *T. solitaria* also was small but, because of the high incidence of infection reported in the literature for breeding birds (90% trematode infection for Mallards, DeJong, 1976; 81% trematode infection for Blue-winged Teal, Buscher, 1966), the depauparate fauna found in the breeding birds of this study is surprising. Only 2 species of trematodes, *Cyclocoelum brasilienum* and *Paramonostomum* sp. were recorded in Ontario and the prevalence of trematode infection was 40%, no greater than would be expected at any point along the migration route (see Table 1). Further, no species was found in the breeding hosts that was not recorded from other localities.
For Tringa solitaria, the Louisiana fall birds had a slightly higher incidence of infection (43.2%) than the spring migrants (35.7%). However, fall Calidris melanotos from Louisiana had only 42.2% prevalence of trematode infections as compared to 50.1% for the northward spring migrants in the state. Solitary Sandpipers harbored 1 more species of trematode during fall migration than during spring while Pectorals had 6 species from each migration.

When comparing the trematode faunas of the 2 host species, one finds 5/9 (55%) of the species to be the same (see Table 4). Of the remaining 45% of the faunas unique to one host species or the other, 1 subgenus (Haematotrephus), 1 genus (Plagiorchis), and 1 family (Echinostomatidae), are common to both hosts. These faunas are remarkably similar despite the extreme difference in the hosts' breeding ecology.

Considering all the above points, one must conclude that although undoubtedly some part of the trematode fauna is derived from the breeding grounds, this location is not the major source for trematode infection. The complex of species recorded from these 2 long-distance migrants is a more balanced mixture than has been reported from studies of shorter distance migrants within the Temperate Zone or of small samples of long-distance migrants examined only in the Temperate Zone (Dogiel and Bykhovskaja-Pavlovskaja, 1955; Schmidt and Frantz, 1972).
Much significance has been placed on the pattern showing greater variety of parasites in fall migrants and the comparatively less varied fauna of spring migrants (Ward, 1909; Dogiel, 1964; Buscher, 1965). The conclusion from such data has been that parasites, mostly acquired by the hosts while breeding, were gradually lost during migration. Data from Solitary Sandpipers in Louisiana have revealed a weakness in this research method. Of the hosts collected within 5 miles of Louisiana State University at Baton Rouge, 4 of 48 spring migrants (8.33%) and 15 of the 44 fall migrants (34.09%) were the western race T. s. cinnamomea. When specimens collected in the more western areas of Louisiana are included, the difference between the spring and fall migrants is approximately the same, 8.57% for spring and 34.09% for fall. This finding demonstrates that, although researchers are studying migrants through one locality, they may not be sampling from the same breeding populations at different seasons, but from 2 different composite populations. Comparison of the parasite faunas of 2 such populations will not necessarily illustrate gradual loss of parasites but may merely reflect different prevalence of trematode infections for different parts of the hosts' breeding range. For instance, Threlfall (1968) took Common Snipe from 2 localities within the species' breeding range. In 1965, none of the 19 birds collected in Ontario had trematodes while 17 specimens from Newfoundland harbored 5 trematode species.
Other studies showed differences between parasite faunas of wintering birds from separate localities within the winter range. December and January Shovelers, *Anas clypeata*, from southwest Texas in 1974 through 1975 harbored *Echinoparyphium recurvatum* (Broderson et al., 1977) while the same species of duck from southeast Texas in 1963 through 1964 had *Echinoparyphium flexum* (Buscher, 1965). Results such as these must cause researchers to compare parasite faunas of fall and spring migrants with caution. Certainly, conclusions about parasites' affinities must not be based solely on infection percentage differences between fall and spring hosts.

Furthermore, research with European passerine birds has demonstrated seasonal variation in the speed of avian migrations (Stresemann, 1955). Spring migrants, under the influence of high concentrations of reproductive hormones, travelled more rapidly and directly than the more leisurely flying post-breeding birds in the fall. One might suspect that the fall migrants might feed more during their leisurely southward migration than the rapidly migrating spring birds and therefore be more likely to acquire migration route parasites. This difference alone could conceivably result in disparate trematode prevalences between the 2 migrating populations. Unless fall and spring migrations for a particular species are shown to be of equal duration and stress one should not assume they can be compared as equal.
For the above reasons, *Leucochloridium variae* is only tentatively classified as a northern form in this study. Further investigations may reveal it to be a low incidence ubiquitous species of both Solitary and Pectoral Sandpipers.

People have long realized that avian migrants are agents for the geographic spread of diseases and parasites; this realization provides the incentive for many studies of bird parasites. Long-distance migrants are especially likely to introduce foreign organisms to an area. Although one cannot possibly know if *T. solitaria* or *C. melanotos* was responsible for the initial spread of some species of trematodes between North and South America, the range extensions for trematode species in this study are noteworthy.

Three northern hemisphere species are recorded for the first time from South America, *Cyclocoelum obscurum*, *Cyclocoelum tringae*, and *Tanaisia fedtschenkoi*. The South American species, *Zonorchis microrchis*, previously known only from Brazil, is reported for the first time from North America. The presence of *Plagiorchis elegans* in *C. melanotos* in Louisiana provides one of the few North American records for this Eurasian trematode and thereby demonstrates a link between the faunas of the Eurasian and North American continents. A range extension within the United States is shown by the discovery of a northern U.S. species, *Leucochloridium variae*, in both sandpiper hosts in Louisiana.
With many avian species travelling between North and South America, one would expect numerous avian parasites to be known from both continents. Of the 9 trematode species recorded from *T. solitaria* in this study, 7 (78%) are known from both continents: *T. fedtschenkoi, C. brasilianum, C. obscurum, E. lubens, Z. microrchis, S. denticulata, and P. maculosus*. Fewer species from *C. melanotos*, 4 of 9 (44%), have been recorded from both North and South America: *T. fedtschenkoi, C. tringae, C. obscurum, and Z. microrchis*. This difference in the character of the trematode faunas of the 2 host species may be explained by the differences in the geographic distributions of the birds. Far less territory is covered by the breeding and wintering ranges of Pectoral Sandpipers than Solitary Sandpipers (see Fig. 3 and 4). Solitary Sandpipers' wider range in South America, for example, may facilitate the birds' increased encounters with greater numbers of neotropical helminth species. The host species known from the greatest area in the 2 continents probably would have the fauna with the largest number of trematode species known from both continents. Also, birds wintering in the northern parts of South America, as do the Solitary Sandpipers, would be more likely to transport their winter parasites to North America than birds wintering in the southern areas of the continent. A similar situation occurs in the breeding ranges with Solitary Sandpipers breeding farther south than Pectorals.
SUMMARY

Examination of Solitary and Pectoral Sandpipers from Ecuador, Louisiana, South Dakota, and Canada demonstrates that the overall prevalence of trematode infections, regardless of season, is fairly constant and ranges between 35 and 48%. In any given host carrying trematodes, one is likely to find only 1 to 3 trematode species, rarely more. Thirteen trematode species are recorded from the shorebirds, 9 from each host species. Two-thirds of the trematode fauna from each shorebird species consists of low prevalence (2% or less infection rate) parasites. A high percentage of the trematode species from Solitary and Pectoral Sandpipers are known from avian hosts in both North and South America. The trematode faunas of the spring and fall migrants differ slightly in species composition and prevalence of trematode infections but these differences are not considered significant, especially in light of the differences in subspecies composition between fall and spring Louisiana Solitary Sandpiper populations. Forms that are found in the digestive tract are usually of low prevalence and intensity. The most common trematode species are ubiquitous in geographical distribution and occur within the hosts in sites other than the digestive system. The fauna of these 2 species of long-distance migrants is more of a composite of parasites in origin of infection than the fauna of birds in previously reported studies. The breeding grounds are no more
significant a source for trematode infection for *Tringa solitaria* and *Calidris melanotos* than other localities covered during the long migration. The trematode fauna of the Solitary Sandpiper is remarkably similar to that of the Pectoral Sandpiper in spite of the hosts' very different breeding ecology.
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EXPLANATION OF PLATES

All drawings were made with the aid of a camera lucida. The scale used is indicated on each plate. All worms are shown in a ventral view.

Plate 1. Plagiorchis elegans
Plate 2. Plagiorchis maculosus
Plate 3. Echinoparyphium aconiatum
Plate 4. Echinoparyphium speotyto
Plate 5. Stephanopora denticulata
Plate 6. Leucochloridium variae
Plate 7. Eurytrema lubens
Plate 8. Zonorchis microrchis
Plate 9. Cyclocoelum brasilianum
Plate 10. C. brasilianum, range of variation
Plate 11. C. brasilianum, range of variation
Plate 12. Cyclocoelum tringae
Plate 13. C. tringae, range of variation
Plate 14. C. tringae, range of variation
Plate 15. Cyclocoelum obscurum
Plate 16. Tanaisia fedtschenkoi
Plate 17. Paramonostomum sp.
Plate 2

Plagorchis maculosus
Plate 3

Echinoparyphium aconiatum
Plate 4

Echinoparyphium speotyto
Plate 5

Stephanoprora denticulata
Plate 6

Leucochloridium variae
Plate 7

Eurytrema lubens
Plate 8

Zonorchis microrchis
Plate 9

*Cyclocoelum brasilianum*
Plate 10

*Cyclocoelum brasilianum*
Plate 11

Cyclocoelum brasilianum
Plate 12

Cyclocoelum tringae
Plate 13

*Cyclocoelum tringae*
Plate 14

*Cyclocoelum tringae*
Plate 16

Tanaisia fedtschenkoi
Plate 17

*Paramonostomum* sp.
VITA

Erika Tallman, nee Jansic, was born in Cleveland, Ohio on 19 January 1949. Having spent most of her childhood in Westchester County, New York, she was graduated from Yorktown High School in 1967. She earned a B.A. in biology from Antioch College, Yellow Springs, Ohio in 1971, the same year she married Dan Allen Tallman. The Tallmans moved to Baton Rouge, Louisiana where Erika entered the Masters program in zoology at Louisiana State University in 1972. She earned her Master's in vertebrate zoology under Dr. George H. Lowery, Jr. in 1975. After completing several expeditions to Peru and Ecuador, South America, Dan and Erika returned to Baton Rouge in 1977 to complete their coursework and give birth to their first son, David Alan, born on 26 September 1977. After passing her doctoral exams, Erika accompanied her family to Aberdeen, South Dakota where Dan obtained a teaching position at Northern State College. While in South Dakota, Erika completed her dissertation and gave birth to her second son, Jon Anthony, born 18 June 1981. Erika is a candidate for the degree of Doctor of Philosophy in May 1983. She is presently an adjunct professor at Northern State College.
EXAMINATION AND THESIS REPORT

Candidate: Erika J. Tallman

Major Field: Zoology

Title of Thesis: An Analysis of the Trematode Fauna of Two Intercontinental Migrants: *Tringa solitaria* and *Calidris melanotos* (Aves: Charadriiformes)

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Date of Examination:

March 8, 1983