

Parasites of the lake sturgeon, *Acipenser fulvescens*:

Systematics and Biogeography

BY

ANINDO CHOUDHURY

A Thesis

**Submitted to the Faculty of Graduate Studies
in Partial Fulfilment of the Requirements
for the Degree of**

DOCTOR OF PHILOSOPHY

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University of Manitoba
Winnipeg, Manitoba**

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**PARASITES OF THE LAKE STURGEON, Acipenser fulvescens:
SYSTEMATICS AND BIOGEOGRAPHY**

BY

ANINDO CHOUDHURY

**A Thesis/Practicum submitted to the Faculty of Graduate Studies of the University of Manitoba in partial
fulfilment of the requirements for the degree of**

DOCTOR OF PHILOSOPHY

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To

Mami

In loving memory

ABSTRACT

Sturgeons (Osteichthyes: Acipenseridae) are evolutionary relicts with a wide distribution in the northern hemisphere. As basal actinopterygian fishes with a basic diadromous life history and a markedly diverse assemblage of host specific parasites, sturgeons provides ideal opportunities for exploring the historical biogeography of host parasite relationships. However, the considerable database for sturgeon parasites in Eurasia has, in the past, contrasted with the lack of comparable data from North American sturgeons, a discrepancy which has also prevented any meaningful analyses of their biogeography and host associations. Consequently, a systematic and biogeographical study of the parasites of a major endemic North American species of sturgeon, *Acipenser fulvescens* Rafinesque, was undertaken. This study resulted in the description of *Diclybothrium atriatum* (Monogenea) and *Spinitectus acipenseri* (Nematoda), and synonymy of *Truttaedacnitis clitellarius* and *T. lebedevi* (Nematoda). The North American *Skrjabinopsolus manteri* (Digenea) is considered a subspecies of the European *S. semiarmatus*, based on a re-examination of both species. Morphological and systematic studies on the Diclybothriidae, Deropristiidae and the genera *Truttaedacnitis* and *Spinitectus* have established the monophyly of certain groups specific to sturgeons, identified phylogenetic relationships, and provided a basis for interpreting their coevolutionary history. The history of sturgeon parasites is one of colonization by host switching and subsequent variable periods of co-evolution, leading to the formation, through dispersal and vicariance, of small highly distinct

monophyletic assemblages whose species show strong associations with major discrete continental and oceanic formations. While the present association of lake sturgeon with two major drainage systems (Arctic and Atlantic) is reflected in the biogeography and systematic relationships of its parasites, the palaeontology, phylogeny and parasite relationships of sturgeons support the historical connection between North America and Northeast Asia and between *A. fulvescens* and *A. baeri*. It is hypothesized that a former contiguous distribution of Nearctic and Palaearctic (Siberian) sturgeons, was subsequently fragmented by orogeny, marine transgressions, and ultimately Pleistocene glaciations which caused major displacement of the lake sturgeon lineage and its association with the Gulf of Mexico drainages. This history follows the overall restriction of sturgeons in the freshwater Arctic drainages resulting in modification of a basic diadromous life history which has structured the parasite assemblage into one comprising freshwater species.

ACKNOWLEDGEMENTS

I would like to express my gratitude to the numerous people who have made the completion of this thesis possible.

I thank my supervisor, Terry Dick, for his perseverance in seeing through the successful completion of this thesis. He has often driven me beyond what I thought was possible and I am grateful for the ethic of hard work and the experience I have acquired in his laboratory and under his tutelage.

I thank members of my advisory committee, Drs. R. Brust, W.S. Evans and L.C. Graham for their constructive criticisms during my programme and while reading my thesis.

I thank my external examiner, Dr. D.I. Gibson, for his expert criticisms of my thesis.

I am grateful to Dr. E.V. Raikova, Academy of Science, St. Petersburg, for translating many Russian publications and sending me otherwise inaccessible Russian literature and specimens.

I acknowledge the following people and agencies for field work and sturgeon collections; Jim Beyette and staff of the Fisheries Branch, Manitoba Natural Resources, members of Ministry of Natural Resources Protection Branch and the Fisheries branch Saskatchewan Parks and Recreation, Walter Machbaur, Freshwater Fish Marketing Board (FFMB), Wawbowden, and numerous personnel at FFMB (receiving section), Winnipeg. I also thank Ron Bruch and personell of the Wisconsin

Department of Natural Resources for collecting and sending samples from Wisconsin.

I thank the following persons for arranging the loan of specimens or for correspondence regarding them: National Museum Moscow, Dr. J. Ralph Lichtenfels, U.S. National Museum; Dr. D.I. Gibson, British Museum of Natural History, Dr. G. Gibson and especially Ms. Judith Price, Canadian Museum of Nature; Dr. G. Hartwich, Alexander von Humboldt Museum Berlin; Dr. F. Moravec, Cezske Budejovice, Czech Republic; Dr. A. Petter, Museum National Histoire Naturelle, Paris; Ms. M.H. Pritchard, Dr. Scott Gardner and particularly Mr. Maurice (Skip) Sterner of the Harold W. Manter Laboratory, Nebraska; Ms. Luma Al-Banna, University of California, Davis. I am indebted to Professor Dr. Otto N. Bauer for sending the specimens of *T. lebedevi* and *T. sphaerocephala* and to Dr. Timofeeva for sending specimens of Diclybothriidae. I am indebted to Dr. Helmut Sattmann, Naturhistorisches Museum, Vienna for making available to me, all facilities at the museum during my visit there and allowing me access to old priceless material and original notes by the 'old masters'. It was at the Vienna museum that I rediscovered what is likely Leuckart's type specimens of *Diclybothrium armatum*. I also thank Helmut for his help in searching for specimens and literature, and for processing the specimens of *Diclybothrium* at the museum. I am also grateful to the staff at the III Abteilung Zoologie at Naturhistorisches Museum, Vienna, for their most gracious and cooperative attitude at all times.

I thank the Reference Librarians Mora Gregg and Marie Speare for their efforts on my behalf and for putting up with my idiosyncracies. I also thank the staff

of the Interlibrary Loans section, Dafoe Library, and particularly Mary-Ann and Barbara, for their help and efficiency.

I thank the following people for their help in various ways: Dr. E. Huebner for use of his microscope, drawing tube, and other facilities, Dr. Ross McGowan for free use of microscope facilities, Dr. Ken Stewart for sharing his knowledge of fishes, and material and facilities of his laboratory in true academic spirit, Gavin Hanke for sharing his knowledge of fishes, recent and fossil, and for his help whenever I needed it (it's a pleasure working with you, Gav), and Dr. Brenda Hann for the many hours of discussions on various aspects of science and academia.

Numerous people in the laboratory have provided various forms of support, academic and emotional, during the years spent in my PhD programme.

Kathleen Ma's compassion will be gratefully remembered. In the early years, Glenys Danell, Theo DeVos and particularly, Jean Tomkins, made the initial transition into a new lab atmosphere easier. Lu MingChuan and Theo DeVos continued to help me in various ways through the years and I am grateful to them for their patience, support and friendship. Xiuwei Yang always had a compassionate word for me and helped in various moments of crisis. Later, Joe Carney joined the lab and got me interested in cladistics, which has led to interesting applications in my work. I thank Mike Papst for his help in picking up samples. I also thank Chris Waterhouse for his friendship and help during his short stay here.

A number of people outside my immediate laboratory environs have helped me through their emotional support and friendship. Dianne Beattie, Kevin Campbell,

Darryl Chudobiak, Jason Duncan, Rene Harrison, and Patrick Nelson have been friends in need. Jason and Patrick played the role of punching bags over the years and I am grateful to them for putting up with me in many very trying situations and for their constant encouragement. This encouragement continued in no less measure through the indomitable spirit that is Kevin Campbell. I thank him for all his help during the final tiring stages of the writing of this thesis. I thank Dean Jeske for always making me smile; the sheer goodness of his nature never failed to cheer me up. Rene provided comfort during a most painful period of my life. Each of these people played a unique role in helping me maintain my sanity and emotional balance during what has been a long and at times stressful seven years. Irmie Wiebe was always a source of encouragement and her help in numerous ways is acknowledged. Ansari Khan has been everything a friend can be and more. I can only humbly and gratefully acknowledge his untiring and selfless help in various aspects of my work and my life in Winnipeg as well as the support and love his family, Bhabi, Linsa, Protiti and Shaila, has always extended me.

The Biswas family gave me a home and a second family. Nothing I write can ever adequately express my gratitude for everything they have done for me.

I am grateful to my family in India, particularly my aunt and uncle, whose blessings and teachings have made me strong.

Finally, my mother's tremendous personal sacrifices made it possible for me to pursue my academic career. This thesis is humbly dedicated to her memory.

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GENERAL INTRODUCTION

Sturgeons (Chondrostei: Acipenseridae) are evolutionary relicts with a wide distribution in the northern hemisphere (Gardiner, 1984; Findeis, 1993; Fig. 1). Their status as basal actinopterygian fishes (Lauder and Liem, 1983), their unique benthic specializations, and variation in their basic diadromous life history make sturgeons interesting biological and biogeographical subjects. Extensive studies on Eurasian sturgeons (Skrjabina, 1974) along with limited and scattered information from those in North America (Appy and Dadswell, 1978; Foley *et al.*, 1989; Hoffman, 1967; Margolis and McDonald, 1986) indicate that they are also unique among fish, in possessing a markedly diverse assemblage of host-specific parasites. Such an assemblage in a relict host group provides ideal opportunities for exploring the historical biogeography and coevolution of host-parasite associations (Brooks and Bandoni, 1988; Brooks and O'Grady, 1989). The rich database for sturgeon parasites in Eurasia (see Bauer, 1984-1987; Skrjabina, 1974) contrasts with the lack of comparable information from North American sturgeons. Such a discrepancy has prevented any meaningful analysis of their distribution and systematics, whose accurate evaluation is critical to any study on biogeography.

Of the sturgeons in North America, the lake sturgeon, *Acipenser fulvescens* Rafinesque occupies a central position on the continent (Lee *et al.*, 1980; Scott and Crossman, 1973) and has, among acipenserids, a freshwater range second only to the Siberian sturgeon, *A. baeri* Brandt (see Berg, 1948). In spite of its position as an

ancient and major component of the North American freshwater fauna, published surveys of lake sturgeon parasites have been rare, largely opportunistic, and based on a few individual fish from drainages predominantly belonging to only one (Laurentian Great Lakes) of the three major drainage basins in which this fish species occurs. Such studies are matched by equally scattered taxonomic accounts of a few of the parasites whose utility is limited by a paucity or, in certain instances, absence of deposited material as well as the lack of comparative studies with Eurasian taxa. Yet, by virtue of its biogeography, the lake sturgeon remains key to the information and material for any interpretations of historical biogeography of host-parasite relationships in this ancient group of fishes.

This thesis investigates the parasite fauna of the lake sturgeon with the objectives of:

1. establishing a database on lake sturgeon parasites, through survey studies and parasite collections, so as to make it comparable to studies on Eurasian sturgeon and useful for future comparative work.
2. examining the comparative morphology and systematics of parasites belonging to monophyletic groups with the intention of constructing testable phylogenetic hypotheses.
3. using the information from the systematic analyses to examine the historical biogeography of host parasite associations.
4. evaluating the position of lake sturgeon and the historical development of its parasite fauna in the context of the acipenserids and their parasites as a whole, by

combining systematic analyses of parasite taxa with evidence from palaeogeography, palaeontology, phylogenetic analyses and biogeography.

The thesis begins with the surveys conducted in this study and discusses the general characteristics of the parasite fauna recovered. Hypotheses regarding historical biogeography and coevolution must necessarily be based upon sound taxonomic assignment and systematic analyses. Consequently, sections in Chapter 2 examine the taxonomy and systematics of various parasite taxa. Systematic analyses of the various taxa are followed in each case by the implications of phylogenetic analyses on historical biogeography. In the final section (Chapter 3), phylogenetic analyses and biogeography of parasite taxa are combined with palaeogeography, palaeontology and host phylogeny to examine macro-evolutionary processes in the historical development of host-parasite associations.

Background Information

The Host

The lake sturgeon is endemic to North America. From all available records, it is a freshwater species although it has occasionally been taken from brackish waters of the St. Lawrence River (Scott and Crossman, 1979). The species inhabits larger rivers and lakes and is present from the Hudson Bay drainages and the St. Lawrence watershed in the North to the Mississippi river system and the Tennessee River in the

South, down to the state of Mississippi. The lake sturgeon reaches the western-most limit of its distribution in the North Saskatchewan and South Saskatchewan rivers in Alberta, and its northern most distribution in the Seal River in Manitoba, Canada (Hudson Bay drainage) (Fig. 2 a; Harkness and Dymond, 1961; Scott and Crossman, 1973). Populations of lake sturgeon in most states in the U.S.A. are either extirpated or endangered. In Canada, lake sturgeon were nearly extirpated from the Laurentian Great Lakes and other parts (e.g., Lake of the Woods, Ontario), and small populations in Saskatchewan, Manitoba, Quebec, and Ontario are all that remain of a once extensive range. The Hudson Bay drainages and the Laurentian Great Lakes drainages (including the Lake Winnebago system in Wisconsin, U.S.A.), harbour the only sizeable populations of lake sturgeon on the North American continent. At present, the lake sturgeon is sympatric in distribution with the Atlantic sturgeon *A. oxyrinchus* Mitchill only in a short segment of the St. Lawrence R. and possibly some of its tributaries (Scott and Crossman, 1973) although historically, it may have been sympatric also with freshwater migrants of *A. oxyrinchus desotoi* in the southern most part of its range (lower Mississippi and other Gulf of Mexico drainages). In the Mississippi R. system, the lake sturgeon occurs or used to occur sympatrically with the shovelnose sturgeons, *Scaphirhynchus platorynchus* (Rafinesque) and *S. albus* (Forbes and Richardson), and the paddlefish, *Polyodon spathula* (Walbaum).

The lake sturgeon is essentially a riverine species that has successfully utilized the extensive lake-river systems that typify the Hudson Bay and Laurentian Great Lakes drainage area (Scott and Crossman, 1973). The presence of a unique protrusible

ventral mouth constrains its feeding habit and, like most other acipenserines (see Findeis, 1993, for anatomical details of feeding mechanism), is predominantly benthivorous. Its diet generally consists of the most abundant (and dense) benthic macro-invertebrates in the feeding area (e.g. larval chironomids, nymphs of Ephemeroptera, gastropod and pelecypod molluscs, gammarids and malacostracans). Fish prey constitute a small part in the diet. Adults feed in deeper channels of rivers and in intrabasin lakes while little is known about the biology of juveniles (see Dick and Choudhury, 1992, for a bibliography on the biology of the species and Harkness and Dymond, 1961, for an exhaustive review of the older literature on this species).

The Parasite Surveys

The first report of parasites from lake sturgeon was by Linton (1898) who reported *Distomum auriculatum* Wedl (later to become *Crepidostomum auriculatum* after extensive taxonomic wrangling), collected from an unknown North American locality (possibly the Great Lakes). To this, Linton (1901) added *Echinorhynchus globulosus* Rudolphi (= *Tanaorhamphus ambiguus*). In 1903, Bean wrote about the parasitic lamprey *Petromyzon concolor* (= *P. marinus* L.) causing ulcerous sores on lake sturgeon. The following year, Stafford (1904) reported on the parasites of lake sturgeon obtained from Montreal fish markets; *Diplobothrium armatum* Leuckart, 1842 (= *Diclybothrium armatum*) was reported from the gills and for the first time from a North American acipenserid. Other species reported included *Acrodactyla petalosa* (= *C. auriculatum*) and *Deropristis hispidus* (Rudolphi, 1819) (= *D. hispida*). In 1915,

Cooper reported *A. petalosa* and *Diplobothrium armatum* from the St. Lawrence River and the following year, Wilson (1916) reported a crustacean parasite, *Argulus canadensis*, for the first time from lake sturgeon, in the Lake of the Woods, Ontario. A year later, Ward and Magath (1917) described the first nematode from lake sturgeon; *Cucullanus clitellarius* Ward and Magath, 1917 (= *Truttaedacnitis clitellarius*) from Lake St. Clair. Further reports on non-helminth parasites were made by Moore (1924; the leech *Macrobdella decora* (Say, 1824) and by Tidd (1931; the crustacean *Argulus stizostethi* Kellicott, 1880. Ward (1912) and Essex and Hunter (1926) reported on parasites of lake sturgeon but did not provide the identity of the parasites recovered. Meyer (1933, p.341) listed the lake sturgeon '*Acipenser rubicundus*' as a host of *Tanaorhamphus ambiguus* in Bronn's '*Klassen und Ordnungen des Tierreichs, Acanthocephala*'. Bangham and Hunter (1939) reported on what is possibly the first true survey of endohelminths from lake sturgeon; two specimens of *Acipenser fulvescens* were examined from pound nets near Pelee Isle, Lake Huron. Both were infected with small numbers of *Crepidostomum lintoni* and *Cucullanus clitellarius*, and one was infected with a species of *Allocreadium* Looss, 1899. This was followed by numerous surveys of lake sturgeon based on very small sample sizes (Fischthal, 1945 and Bangham, 1955, from waters of the Great Lakes drainage). Bangham (1955) reported "a species of *Spinitectus*" for the first time in lake sturgeon and also cited unpublished investigations of four rock sturgeons from Upper Lake Pepin and of one sturgeon from the Embarrass R. in Wisconsin which harboured "hundreds of *D. hamulatum*". The next report on lake sturgeon parasites was by

Dechtiar (1972a, b) who reported *Rhabdochona cascadilla* Wigdor, 1918 as a new record. Hoffman *et al.* (1974) added further to the list by reporting, for the first time in North America, the coelenterate egg parasite of acipenseriforms, *Polypodium hydriforme* Ussov 1885; the parasite was recovered from the eggs of the lake sturgeon from Black River, Michigan. The first major parasite survey of lake sturgeon was reported in abstract form in 1974 by Anthony from Lake Nipissing, Ontario. *Skrjabinopsolus manteri* (Cable, 1952) was reported for the first time from lake sturgeon (Anthony, 1974), although the site of infection (the stomach) was unusual. A monogenean species resembling *Paradiclybothrium* Bykhovskii and Gusev, 1950 and a variant of the typical '*Crepidostomum lintoni*' were also reported by Anthony (1974) but not elaborated upon. Beverley-Burton (1984) considered the presence of *Paradiclybothrium* in lake sturgeon from Lake Nipissing unlikely. Lampreys were observed on lake sturgeon by Vladykov (1985). A lake sturgeon from Saint-Pierre-les-Becquets (Quebec), weighing 16 kg. was found to have 61 parasitic silver lampreys (*Ichthyomyzon unicuspis*) attached to it. Dechtiar and co-workers (see Nepszy, 1988) reported on surveys of small numbers of lake sturgeon from the Great Lakes which yielded parasites that had been found before (Table 1). Eight species of parasites were reported in an abstract by Anthony (1989) from 294 lake sturgeon sampled between 1969 and 1989 from lakes and rivers of Ontario, all of which have been reported previously from lake sturgeon. Finally, Dick *et al.* (1991) extended the range of *Polypodium* in lake sturgeon to the Hudson Bay drainage.

Observations from this information reinforces previous comments about such

studies:

1. Reports were concentrated on the Great Lakes area.
2. Sample sizes of sturgeon hosts in published studies were small.
3. The Hudson Bay and Mississippi drainages were represented in only two studies.
4. The parasite community was remarkably consistent but species poor.
5. Three parasites specific for acipenserids, *Diclybothrium* Leuckart, 1835, *C. auriculatum* and *Truttaedacnitis clitellarius* were widely distributed and *Spinitectus* Fourment 1883 also appears to have been common.
6. A number of these parasites (*T. clitellarius*, *D. armatum* in North America, *Spinitectus* sp.) were not described in any detail and were not compared with other related species in North America or Eurasia.

All the parasitological surveys of lake sturgeon to date with locations and authorities and geographical locations are shown in Figure 3.

Biogeography, systematics and the study of host-parasite associations

The distribution of parasites and their hosts is essentially a study of biogeographical pattern and process. The study of this diversity in a spatial and temporal context (Cox and Moore, 1993) lies at the juxtaposition of several disciplines (ecology, evolution, systematics, geography and geology). In practice, however, biogeographical studies incorporate only few of these available disciplines. Two approaches, commonly used in this study of patterns of distribution, are derived from

two major schools of biogeographical thought. Of the two, *ecological biogeography* provides explanations of the distribution of extant species based on observed or inferred interactions between organisms and the environment as well as among themselves. As the name implies, the discipline is steeped in contemporary ecological theory (Myers and Giller, 1988). Most investigations under ecological biogeography are measured in 'human' time and involve relatively short term studies, occasionally spanning several decades or exceptionally extrapolated to several thousand years (Cox and Moore, 1993; Myers and Giller, 1988; Rosen, 1988). The alternative to this ecological approach is *historical biogeography* which attempts to explain observed patterns of distribution in the context of longer geological time and examines the influence of past dispersal and geological events (plate tectonics, orogeny, glaciation etc.) on the origin and fate of taxa (Briggs, 1987). As a result, the systematic relationships of taxa together with a knowledge of the geological history of the area occupied by extant taxa and fossils form a basis upon which inferences are made as to the causes of their observed patterns of distribution (Myers and Giller, 1988). As such, one of the important challenges facing biogeographers has been to distinguish between ecological and historical factors (Endler, 1982a). Although a distinction is made between ecological and historical biogeography, historical processes (such as dispersal, evolution and speciation) happen only in the context of ecology (Brooks, 1985; 1988) and recent years have seen the emergence of a historical ecology research programme which allows "communication between systematics and ecology to be re-established" (Brooks and McLennan, 1994). The persistence of a divide between ecological and

historical biogeography has also been attributed to scale, the biases of practitioners and the types of analyses and narratives presented by them (Rosen, 1988). It has been stressed that, for discussions of pure biogeography to be meaningful, a neutral position should be initially adopted and all possibilities examined since considerable overlap exists between the two areas (Rosen, 1988). Despite attempts at unification, Endler (1982b) was able to identify three main ideas in the biogeographical literature: *ecological determinism* (the basis for ecological biogeography) which holds that present day ecological factors are the major determinants of distribution, *vicariance*, which proposes that observed distributions of taxa are a result of fragmentation of a once continuous range of ancestral populations by geological processes, and *dispersal*, which postulates that distributions are due to long range dispersal among, often disjunct, geographical areas (Briggs, 1987; Endler, 1982b). Dispersal and vicariance form the major historical processes but discussions have been marred by increasing polarization of viewpoint in recent years (see for e.g., comments by Humphries, 1992) although there have been attempts to reduce this schism (Briggs, 1987; Endler, 1982 a,b).

The beginnings of parasite biogeography as an area of research are usually traced to the works of von Ihering (1891) and this tradition has been continued with the studies of Kellogg, Metcalf, Manter, Eichler, Szidat and, in more recent years, Brooks, Hoberg and others (see Brooks and McLennan, 1991; Brooks and McLennan, 1993; Klassen, 1992). This tradition can be characterized as being largely one belonging to historical biogeography since considerations of host and parasite

evolutionary history and systematic relationships have always been an important theme in such studies. As such, co-evolutionary studies play an increasingly integral part in understanding parasite biogeography. This can be distinguished from ecological biogeography of parasites where studies concentrate more on measures of diversity and their ecological interpretation (Rohde, 1982). Patterns are explained in the context of the biological properties of the parasites and their hosts and the nature of the environment (Esch and Fernandez, 1993). The study of parasite biogeography has been approached from various perspectives; some have described the characteristics of entire communities or subsets of such communities of certain host taxa on a zoogeographical scale (see discussion in Esch and Fernandez, 1993 of parasites of *Mugil* and *Merluccius*; in Rohde, 1982 on marine helminths; Dogiel *et al.*, 1958, and refs. therein). Others have focused on certain subsets of parasite communities in certain host taxa such as those of Brooks (1977), on plagiorchidiids of anurans, Brooks (1979), on the digeneans of crocodiles, Adamson and Richardson (1989) on certain nematodes in salamanders, Brooks (1992) on the helminths of potamotrygonid rays, Hoberg (1992) on the cestodes of seabirds and pinnipeds, and Platt (1992), on the spirorchiids of freshwater turtles, to name a few. Most of these studies have a strong phylogenetic and historical component to the analysis (see Brooks and MacLennan, 1991; 1993) and can be considered studies of historical biogeography.

An ecological-zoogeographical analysis of sturgeon parasites has been carried out by Shul'man (1954, not seen) and by Skrjabina (1974). Such primarily ecological analyses are handicapped by little or no knowledge of parasite life cycles. This

situation has not changed in two decades since Skrjabina's monograph. The transmission dynamics of some of the basic parasite fauna remain unknown and the effects of abiotic factors upon their distributions are largely unstudied [with few notable exceptions, e.g. studies by Bauer (see discussion by Skrjabina, 1974) on the effects of temperature and salinity on *Diclybothrium armatum*]. This lack of knowledge is more evident in North America, where only the study of one acipenserid parasite (*Skrjabinopsolus manteri*) has been able to identify some of the intermediate hosts involved with certainty (Peters, 1961; Seitner, 1951). Under these circumstances, it was felt advantageous to adopt a macro-evolutionary and historical approach in studying the biogeography of host-parasite associations in this relict group of fishes, since the materials required for such a study could be obtained from comprehensive surveys of at least one sturgeon species in North America, occupying a critical part of the holarctic/circumboreal distribution of its family.

The method of choice for systematic analyses, in this thesis, is cladistics (Harvey and Pagel, 1991; Hennig, 1966; Wiley, 1981) since it provides a method for producing an unambiguous statement of relationships which is testable by the addition of more data. Furthermore, the method allows a clear recognition of monophyletic groupings by identifying shared derived characters among taxa. However, the method cannot be applied to all taxa with equal effect, since morphological characters found in certain groups do not lend themselves to cladistic analysis. In such circumstances, a traditional approach of identifying key morphological characteristics as indicative of their systematic relationships, was used.

Several methods, including analytical ones (Morrone and Crisci, 1995) are available for biogeographical studies. Despite the schism between vicariance and dispersal biogeography, dispersal is the mechanism by which a taxon reaches proportions large enough to be affected by subsequent vicariant events and since every evolutionary lineage must have a relatively restricted place of origin. Strict adherence to either extreme stance is counterproductive (see comments by Nelson, 1994) and the involvement of both processes in biogeography is well illustrated by Lundberg's (1993) analysis of freshwater fishes showing South American-African connections. Consequently, the approach to analyzing biogeographical patterns in this thesis incorporates both vicariance and dispersal processes where indicated by the evidence.

Table 1. Parasitological surveys of lake sturgeon, *Acipenser fulvescens*, from waterways in N. America.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Surveyors.....	HBW	E&H	B&H	JF	RVB1	RVB2	RVB3	AOD1	AOD2	DA	D&L	D,C&R	D&C	DA2
Date.....	1912	1926	1939	1952	1955	1955	1955	1972a	1972b	1974	1988	1988	1988	1991
Sample size.....	(2)	(2)	(2)	(1)	(4)	(1)	(1)	(1)	(10)	(100)	(3)	(8)	(2)	(294)
Parasite Species														
MONOGENEA														
<i>Dicybothrium armatum</i>	?	?	-	-	-	-	-	P	P	P	P	P	P	P
<i>D. hamulatum</i>	?	?	-	-	P	P	P	-	-	-	-	-	-	P
DIGENEA														
<i>Allocreadium</i> sp.	?	?	P	P	-	-	-	-	-	-	-	-	-	-
<i>Crepidostomum auriculatum</i> *	?	?	P	P	P	P	P	P	P	P	P	P	P	P
<i>Diplostomum</i> (l)	?	?	-	-	-	-	P	P	-	-	P	-	P	P
<i>Skrjabinopsolus manteri</i>	?	?	-	-	-	-	-	-	-	P	P	P	P	P
CESTODA														
<i>Triaenophorus nodulosus</i>	-	-	-	-	-	-	-	-	-	-	-	-	P	-
NEMATODA														
<i>Rhabdochona cascadiella</i>	?	?	-	-	P	-	-	-	P	-	-	-	-	-
<i>Truetaedacnitis clitellarius</i> **	?	?	P	P	-	P	P	-	-	P	P	-	P	P
<i>Spinitectus carolini</i>	?	?	-	P	P	-	-	-	-	-	-	-	-	-
<i>S. gracilis</i>	?	?	-	-	-	P	-	-	-	-	P	P	P	-
<i>Spinitectus</i> sp.	?	?	-	-	P	-	-	-	-	P	-	-	-	P
ACANTHOCEPHALA														
<i>Echinorhynchus salmonis</i> ***	?	-	-	-	-	-	P	-	-	-	P	P	P	P
<i>E. lateralis</i>	?	-	-	-	-	-	-	-	-	-	P	-	-	-
<i>Neoechinorhynchus rutili</i>	?	-	-	-	-	-	-	-	-	-	-	-	P	-
HIRUDINEA														
<i>Piscicola punctata</i>	?	-	-	-	-	-	-	-	-	-	P	-	P	-

HBW: Ward (1912), Great Lakes?; E&H: Essex and Hunter (1926) watershed?, Illinois; B&H: Bangham and Hunter (1939) L. Erie; JF: Fischthal (1952), Ladysmith Flowage, N.W. Wisconsin; RVB1: Bangham (1955), L. Pepin; RVB2: Bangham (1955), South Bay, Manitoulin Island, L. Huron; RVB3: Bangham (1955), Embarrass R. Wisconsin; AOD1: Dechtiar (1972a), Lake of the Woods, Ontario; AOD2: Dechtiar (1972b), L. Erie; DA: Anthony (1974), L. Nipissing, Ontario; D&L: Dechtiar and Lawrie (1988), L. Superior; D,C&R: Dechtiar *et al.* (1988), L. Huron; D&C: Dechtiar and Christie (1988), L. Ontario; DA2: Anthony (1991), waterbodies of Ontario (unspecified).

*reported as *C. lintoni*, **reported as *Cucullianus clitellarius*, ***reported as *Metechinorhynchus salmonis*, P = Present.

Additional records from taxonomic studies: *Tanuorhamphus ambiguus* (Meyer, 1933), *Argulus canadensis* (Wilson, 1916) and *A. stizostethii* (Tidd, 1931).

Figure 1. Map of the world showing the distribution of the Acipenseriformes (sturgeons and paddlefishes). Small dots represent Acipenseridae while larger dots in the Yangtze and Mississippi-Missouri river systems represent Polyodontidae.

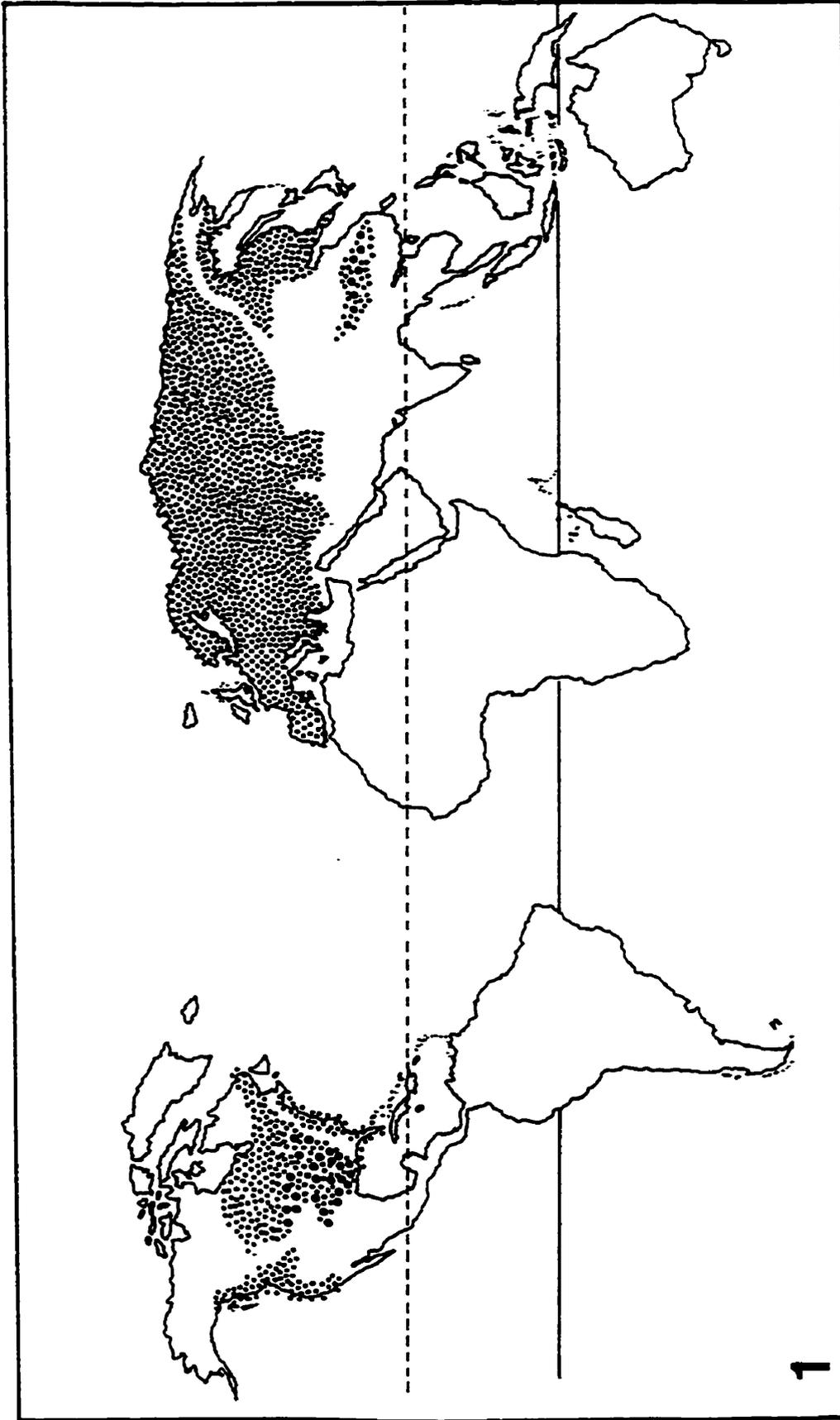


Fig. 1. Map of the world illustrating the distribution of Acipenseriformes: Acipenseridae (···) and Polyodontidae (●●).

Figure 2. a) Map of North America showing distribution of *Acipenser fulvescens* (A.f.) in the drainages of the central and eastern part of the continent. Atlantic coastal drainages are occupied by *A. oxyrinchus* (A.o.o) and its Gulf of Mexico subspecies *A. o. desotoi* (A.o.d.), and *A. brevirostrum* (A.b.). Pacific coastal drainages are occupied by *A. medirostris* (A.m.) and *A. transmontanus* (A. t.). b) Map of North America showing distribution of *Scaphirhynchus albus* (S.a.), *S. platyrhynchus* (S.p.), and *Polyodon spathula* (P.s.).

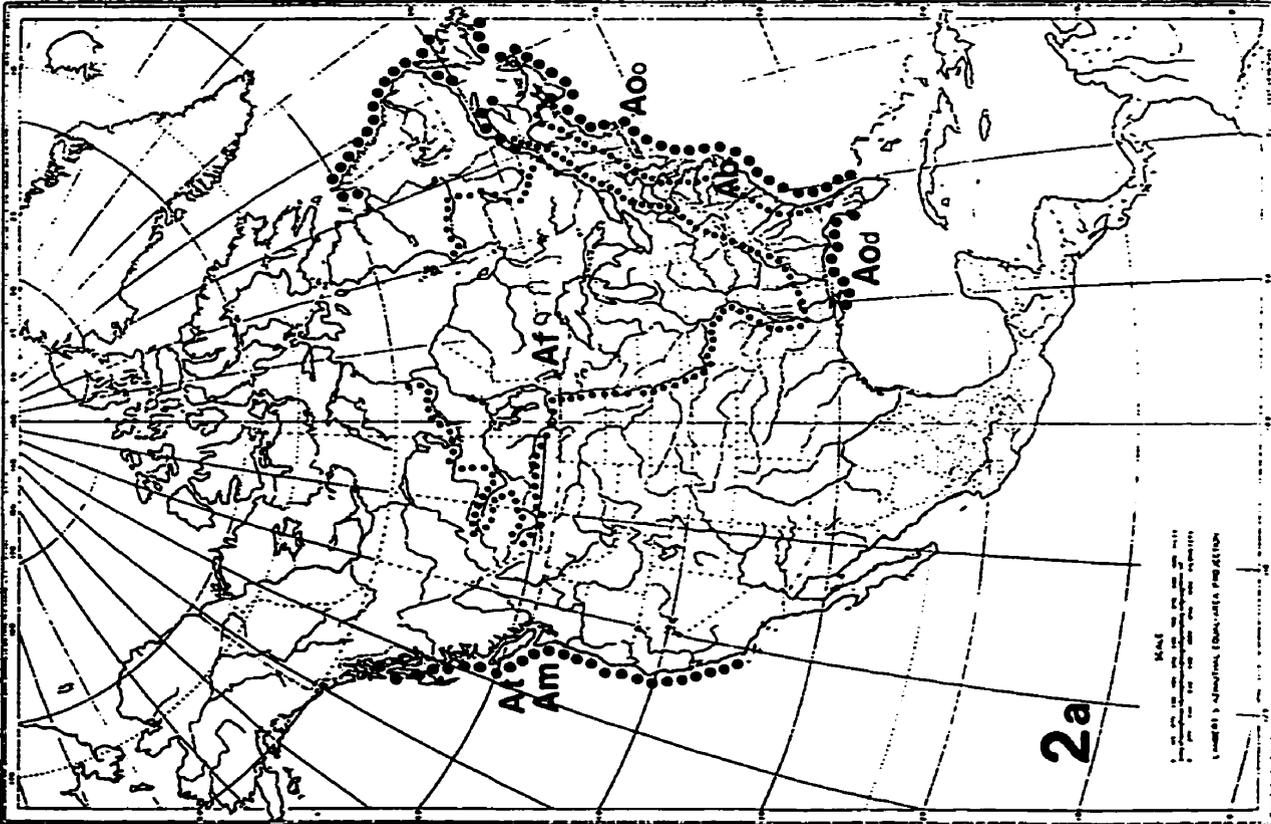
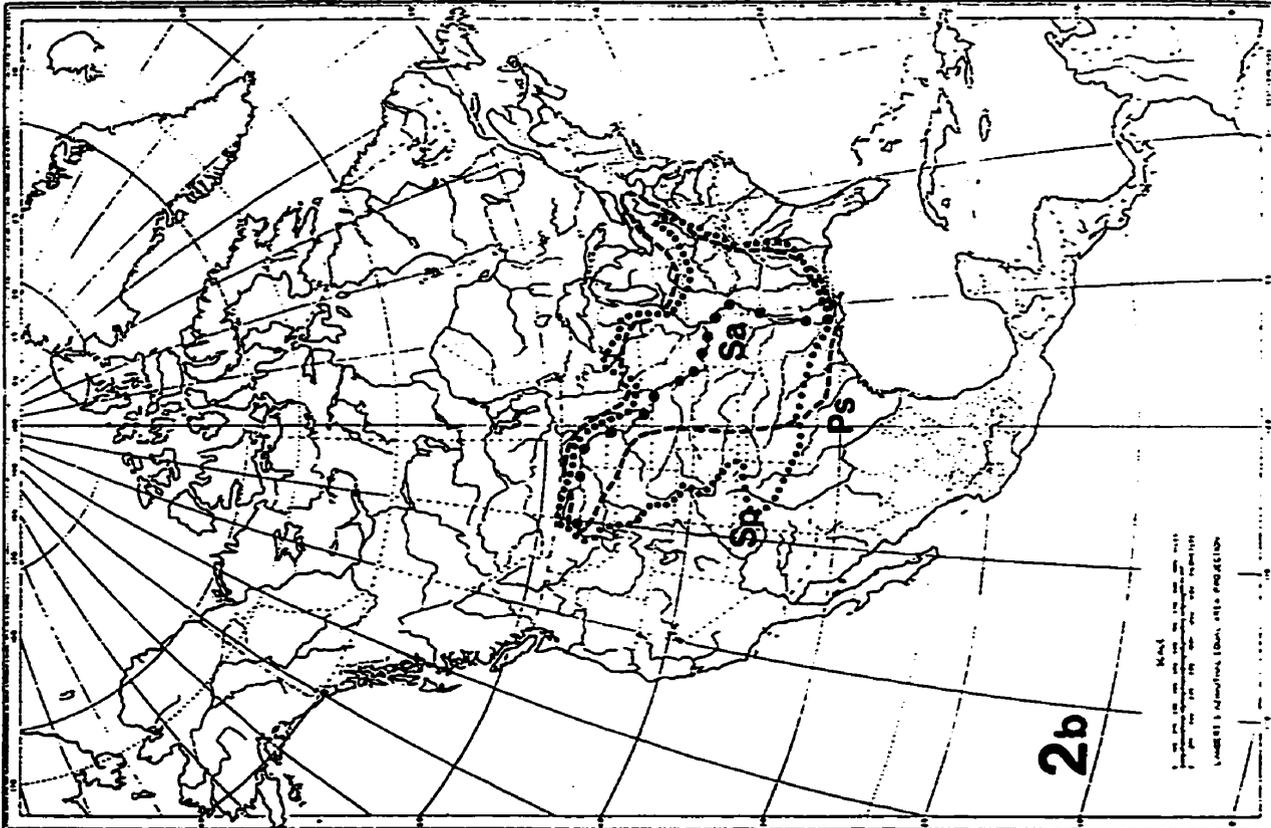
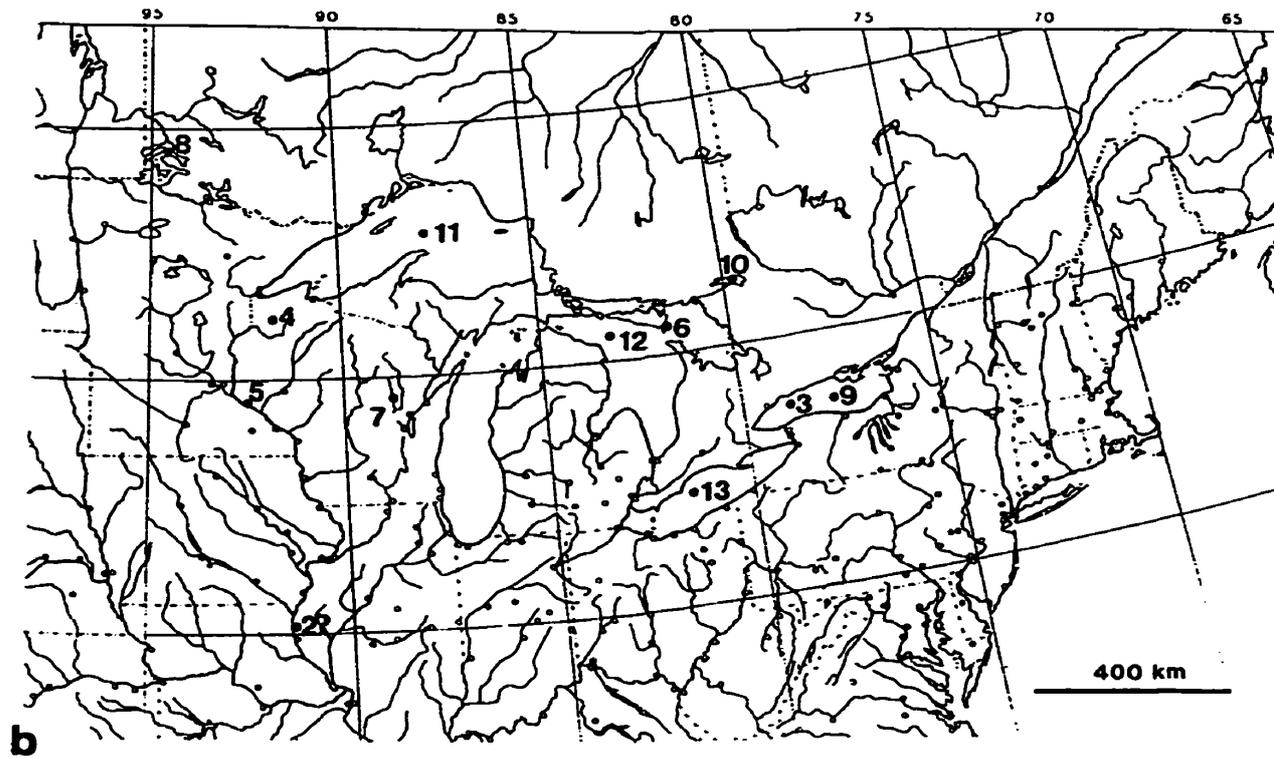


Figure 3. Map of North America and enlargement of boxed portion showing the locations of past surveys of lake sturgeon for parasites. Numbers on the lower enlarged map correspond to the numbers assigned to the surveys in Table 1.



3



CHAPTER 1. The Parasite Surveys: Hudson Bay drainage and Lake Winnebago system.

INTRODUCTION

Hypotheses regarding the biogeography of parasites in particular host species or groups depend to a large extent on information collected over as much of the geographical range of the host as is possible. As noted earlier (see General Introduction), the only study reporting sturgeon parasites from the Hudson Bay drainage is that of Dechtiar (1972a) from one sturgeon collected in the Lake of the Woods. One unpublished study on lake sturgeon parasites from Lake Nipissing (Anthony, 1974) remains the only survey study from a specified locality with a large sample size (100 sturgeon from the Great Lakes drainage). Consequently, a study was undertaken to examine the parasites of this host from four major river systems of the Hudson Bay drainage and from the western portion of the Great Lakes drainage, Lake Winnebago and the Wolf River in Wisconsin, U.S.A.

MATERIALS AND METHODS

Study Area

Hudson Bay drainage (Figs. 4, 5).

The Hudson Bay drainage system covers a topographically diverse land area of 3,884,000 sq km and consists of a network of 125 major rivers and innumerable lakes of different types and sizes (Crossman and McAllister, 1986). Although this system has been in existence at least since the Tertiary, old drainage patterns have been obscured by the singular most important climatic and geological event of the Cenozoic, the Pleistocene glaciations which reached their maximum extent during the

Wisconsin phase, and which is regarded to have covered the entire drainage area. This period of glaciation is also thought to have caused either extinction or, more commonly, widespread displacement of fish and other fauna to various refugia in the South. Following deglaciation, the drainage patterns were reorganized by large proglacial lakes and newly formed channels, beginning between 15,000 - 12,000 ya. New connections were established that linked watersheds and some old important connections were eventually severed. Consequently, most of the waterways and the communities of this drainage system are less than 11,000 years old although it is possible that drainages similar to the present day Saskatchewan River and Churchill River systems drained into the Hudson Bay in preglacial times (Crossman and McAllister, 1986). In any case, newly established watercourses provided an important pathway for the large scale dispersal of fish taxa that survived the glaciations in the various refugia (mainly south of the ice sheet) (Stewart and Lindsey, 1983). The present day fish fauna of the Hudson Bay drainage have gained access to this area over the last 11,000 years by colonization, a process that continues to this day. Consequently, and understandably, the fish fauna of the Hudson Bay system is depauperate (approx. 101 spp.) compared to some older and species rich drainage systems such as the Mississippi-Missouri and Ohio River systems, although most families of fish are represented. The overwhelming majority of the fish species present in the Hudson Bay drainage are due to colonization from the Mississippian and Missourian Pleistocene refugia (Crossman and McAllister, 1986; Stewart and Lindsey, 1983). The lake sturgeon is also believed to have colonized the various waterways of

this drainage from these two southern refugia (Crossman and McAllister, 1986) and remains the only acipenserid present in these waters. The Hudson Bay drainage also harbours the remaining sizeable lake sturgeon populations, distributed in the three major river systems of this basin, i.e., the Saskatchewan, Nelson and Winnipeg Rivers.

Saskatchewan River system (Reed, 1959, 1962; Wallace, 1991). (Figs. 4, 5a).

The Saskatchewan River is a 265 km long, broad, meandering river, formed by the merging of two of its main tributaries, the North Saskatchewan River and the South Saskatchewan River, which in turn are fed by numerous tributaries in Saskatchewan and Alberta. The headwaters of these rivers rise in the Rocky Mountains of Alberta. The Saskatchewan River flows uninterrupted by any natural lake basins until it reaches the vicinity of Cumberland Lake near the Manitoba border where the main channel divides into a southern Old Channel and multiple narrow channels which form a complex delta, before draining into Cumberland Lake. After emerging out of Cumberland Lake, the Saskatchewan River traverses a short distance eastward before draining into Cedar Lake and eventually Lake Winnipeg, in Manitoba. The Saskatchewan River and its two major tributaries drain a total land area of 147,850 sq. miles. The river bed is variable; areas of strong current have hard sand or gravel or small cobblestones as substrate while regions of slack current have soft sand or mud bottoms. The second half of the Saskatchewan River has considerable areas of sandy bottom. The benthic fauna has an uneven distribution; nymphs of Ephemeroptera, Trichoptera and Plecoptera dominate areas of strong current (riffles and rapids) while mud bottoms are characterized by oligochaetes and larvae of Chironomidae. The

extensive sandy bottoms are highly unproductive. At least 24 species of fish belonging to 9 major northern families are known from the Saskatchewan River system.

Approximately 80% of the flow of the Saskatchewan River is distributed through numerous anastomosing channels (total of 490 km) which form an extensive delta and eventually drain into Cumberland Lake. Approximately 20% of the flow bypasses Cumberland Lake to the south as the Old Channel (130 km long). This relatively shallow, warm, delta-lake system is a productive area with a notable standing crop of benthos (5.3 kg/ha) and supports most fish species found in the Saskatchewan River mainstem. It also supports the main population of lake sturgeon in the lower Saskatchewan River. This area is also the site of the commercial fishery on this river system.

Nelson River system (Green, 1988; Schlick, 1968; Swanson and Kansas, 1987). (Figs. 4, 5b).

The Nelson River serves as a major conduit for a considerable proportion of the waterflow from the eastern part of the Hudson Bay drainage. The river originates from the Northern end of Lake Winnipeg and for the first part of its course is essentially a river-lake system consisting of a riverine east channel and a modified west channel that broadens to form Playgreen Lake, both channels merging into Cross Lake. A short channel emerges out of Cross Lake and empties into Sipiwesk Lake, from where the Nelson River continues northwards as a single fast flowing riverine channel. It is further interrupted by two downstream lakes (Split and Stephens Lakes) before emptying into Hudson Bay. Sturgeon were obtained from 3 different sites on the

Nelson River system, Sipiwesk Lake, Sundance, and Angling Lake.

Sipiwesk Lake (55° 05' N., 97° 35' W) is a 48 mile long (approximate) mesotrophic lake with an area of 151.8 sq.miles. and a mean depth of 35.5 feet (max. 130 ft.). The lake is structured in part by an expansion of one of the channels of the Nelson River. A number of large and small islands are scattered throughout the lake which results in a number of relatively deep constricted channels with strong currents. The water is relatively turbid with a pH of 7.6 - 8.2. and the lake does not develop a thermocline. Sipiwesk Lake harbours a minimum of 23 species of fish belonging to 11 families (all major northern families are represented) including one introduced centrarchid *Pomoxis nigromaculatus* (black crappie) (Green, 1988; Schlick, 1968). Sipiwesk Lake also supported a small scale commercial fishery which was the source of the samples. Angling Lake (56°27'30''N, 93°53'30''W) is a small (689.6 ha) shallow (mean depth 2.64m, max. depth 9.5 m) midstream mesotrophic basin lake of the Angling River, a tributary of the Nelson (Swanson *et al.*, 1988; 1990). Angling Lake supports at least 9 species of fish belonging to 7 families. The collecting site at Sundance, on the mainstem of the Nelson River, is approximately midway between Stephens Lake and the Angling River inflow, and immediately downstream of the Limestone River inflow and the Limestone Generating Station. Surveys of the mainstem of the Nelson River (Swanson and Kansas, 1987; Swanson *et al.*, 1990) indicate varied habitat types and a fish fauna represented by all major families. Winnipeg River system (Crowe, 1972a, 1972b; Miller and Andrews, 1972). (Figs. 4, 5c).

The Winnipeg River originates in
headwaters lakes in the
between the river and
Park area in Manitoba
river system, below
intra-lake (lakes) and
Winnipeg at French
km and is character
rapids on its journey
constituting 1/3 of
du Esprit and main
small rapids on the
formed by widening
area of the Manitoba
of 117 km and a
Andrews (1972). In
strongly fluctuating
temperature of 15°C
water is so firmly
in winter. The lake
Chippewa and
Winnipeg River and

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The Winnipeg River is a classic example of a river-lake system. Originating in headwater lakes in Ontario (mainly Lake of the Woods), the Winnipeg River alternates between riverine channels and intra-basin lake systems, particularly in the Whiteshell Park area in Manitoba. The two main riverine stretches are in the second half of the river system, between Seven Sisters Falls and Lac Du Bonnet (the largest of the intrabasin lakes) and finally between McArthur falls and the inflow into Lake Winnipeg at Traverse Bay. The Winnipeg River covers a drainage basin of 125,504 sq. km and is characterized by a cumulative drop of 272 ft through a series of falls and rapids on its journey to Lake Winnipeg. Most of this energy has been harnessed by constructing hydroelectric dams. The river has a maximum depth of 40.5 m. near Point du Bois. The main sampling site on the Winnipeg River was at Nutimik Lake with a small sample collected at Slave Falls. Nutimik Lake is the first of a series of 5 lakes formed by widening of the Winnipeg River after Sturgeon falls in the Whiteshell Park area of Manitoba. Nutimik Lake has a surface area of 4058 sq km with a mean depth of 11.7 m and a maximum depth of 28.3 m (Crowe, 1972b) or 32.4 m (Miller and Andrews, 1972). Nutimik Lake can be classified as a temperate lake of the third order, strongly affected by current, with no thermocline and with a uniform mean summer temperature of 15.8°C (bottom) - 16.1°C (top). The euphotic zone extends 1.4 m, the water is uniformly oxygenated at all depths and little stagnation occurs under the ice in winter. The lake supports a diverse benthos with Gammaridae, Ephemeridae, Chironomidae and Sphaeriidae making up the bulk of the benthic standing crop. The Winnipeg River also harbours a diverse assemblage of 53 spp. of fish belonging to 16

families. Of these, *Pomoxis nigromaculatus*, *Micropterus dolomieu* (both Centrarchidae), *Salmo trutta* and *Salvelinus fontinalis* (both Salmonidae) are introduced sport fish. Lake sturgeon occur in this system mainly downstream from Slave Falls and the Nutimik Lake population has been continuously monitored for the past 15 years through tagging studies (Jim Beyette and T. A. Dick, pers. comm.).

Rainy River system (Holzkamm, *et al.* 1988; Mosindy, 1987). (Figs. 4, 5d).

The Rainy River is a short, relatively shallow, fast flowing river which emerges from Rainy Lake in Ontario and flows along the Minnesota (U.S.) - Ontario (Can.) border before draining into the Lake of the Woods. This river system constitutes the south-eastern fringe of the Hudson Bay drainage, its head waters extending to the vicinity of Lake Superior. Rainy River receives three tributaries and is characterized by two rapids which form the main spawning sites for sturgeon migrating upstream from the Lake of the Woods. Uncontrolled commercial exploitation at the turn of the century has depleted this sturgeon population. The Rainy River fish fauna is comprised of most of the common families of fish found in the Lake of the Woods and the Winnipeg River system.

Lake Winnebago drainage (Fig. 6).

The Lake Winnebago system, situated immediately west of Lake Michigan, is comprised of a 15,366 sq km watershed of interconnected lakes and rivers (Kempinger, 1988). The system includes two major rivers (Wolf and Fox) and four major lakes (Fig. 6, and Priegel and Wirth, 1975). Of these, Lake Winnebago is the

largest (45 km x 16 km), a shallow (mean depth 4.7 m, max. 6.4 m), eutrophic lake with an area of 557.52 sq km (Juday, 1914). The lake is connected to Green Bay of Lake Michigan by the Fox River. The lake bottom is an "extensive plain" (Priegel and Wirth, 1975) of mainly soft mud with reefs on the west shore and rock/gravel/sand shorelines and shoals (Juday, 1914; Priegel and Wirth, 1975). The 355 km long Wolf River, which drains into Lake Winnebago, is blocked upstream by the Shawano Dam, 201 km upstream of Lake Winnebago (Kempinger, 1988). The sampling area for young-of-the-year (YOY) sturgeon on the Wolf River (Fig. 6), downstream of the Shawano Dam, consists of an average river width of 80 m and a maximum depth of 7 m in pools, and an average depth of 1 m in the extensive riffle/run areas between pools. The river bed in this area is a mixture of rubble, sand and boulders.

Sampling

Hudson Bay drainage (Figs. 4, 5)

Lake sturgeon were collected during the summers (May-August) of 1989, 1990 and 1991 and these samples include whole fish, visceral samples and heads. Material examined consisted of 223 visceral samples, 218 pairs of gills and 224 pairs of eyes. As the collection of lake sturgeon for scientific studies is discouraged by provincial authorities in Canada in the areas covered in this survey, the majority of the samples were obtained from commercial fishermen. Samples of sturgeon heads and viscera were collected from the commercial fishery at Cumberland Lake and delta in 1989 (n=9) and in 1990 (n=44). Heads and viscera of two sturgeon were also obtained

further upstream, from near the forks of the North- and South Saskatchewan River merger. These were collected by the Fisheries Branch, Saskatchewan Department of Natural Resources. Two fish from the 1989 sample were examined fresh. All other samples were either frozen on arrival at Winnipeg or shipped in frozen condition. Heads and visceral samples (n=123) were obtained from the Sipiwesk Lake (Nelson River) commercial fishery during July, 1990. Sturgeon were fished by gill-netting and the samples bagged and sent to the laboratory in Winnipeg on ice within 36 hours of processing. Due to the large sizes of viscera and heads, and considerations of decomposition, only one or two samples could be examined fresh. Samples were deep frozen and examined at a later date. Two small samples of lake sturgeon viscera and heads were collected by the Manitoba Department of Natural Resources Fisheries Branch at Sundance (n=3) and in Angling Lake (n=3). Samples from Sundance were frozen on collection while samples from Angling Lake were transported on ice to Winnipeg within 36 hours of capture. One specimen from Angling Lake was examined fresh. All other samples were frozen and examined later. Sturgeon from the Winnipeg River system were obtained from two separate sites, Slave Falls (n=3) and from Nutimik Lake in 1989 (n=4) and in 1990 (n=17). These were obtained by gill netting. Blood smears were obtained from an additional 70 fish tagged and released on the Winnipeg River (blood was obtained from the caudal blood vessel) during 1990. Sturgeon (n=13) from Rainy River were gill netted immediately downstream from Manitou Rapids (subsistence fishery) in June 1991, and were examined for leeches and lampreys. The abdominal cavity of these fish were examined for the presence of

Amphilina during evisceration. The viscera and heads were packed into separate bags and transported back to the laboratory in Winnipeg, on ice. Two visceral and head samples were examined fresh upon reaching Winnipeg and the remaining samples were deep frozen and examined at a later date. All visceral organs were examined for parasites; sections of the spleen and liver were squashed and the major ducts in the liver were dissected and examined. Mucous from the pyloric stomach was scraped, removed, and examined between two glass plates for parasites. The mucous from the pyloric stomach forms a tough and elastic mass and is impossible to examine by standard methods of diluting with saline or water. The method of squashing between glass plates provides a guaranteed way to observe and count fine transparent nematodes such as species of Spirurida. Nematodes could be removed undamaged from the flattened sheets of mucous after removing one of the glass plates. Live trematodes and acanthocephalans were fixed after relaxation in dH₂O at 4°C for 1 hour followed by fixation in hot AFA (Acetic acid-Formalin-Ethyl alcohol). Live nematodes were fixed in hot 70% ethanol. Frozen specimens were thawed in H₂O and then fixed with AFA (trematodes and acanthocephalans) or alcohol (nematodes). All specimens fixed in AFA were stained with aqueous acetocarmine, dehydrated and mounted in permount or Canada balsam. Fixed nematodes were cleared in glycerine alcohol by allowing the alcohol to evaporate, or cleared in hot lactophenol (larger nematodes such as *Truttaedacnitis*). Nematodes were temporarily mounted in glycerine or lactophenol. Blood smears were stained with Wright's stain and gill smears were examined unstained, fresh or after drying.

Lake Winnebago system (Fig. 6).

Summer samples (N=45) were collected, between 19 June and 3 August 1992, from various locations in Lake Winnebago (Fig. 6) by trawling. Heads and viscera were available for fish older than 2 years. Whole fish were available for sturgeon younger than 2 years of age were. Winter samples (N=29) were collected by spear fishing on 13 and 14 February 1993, and one fish was collected on 25 February 1993. Summer samples were collected by Ron Bruch and presonnell of the Department of Natural Resources, Wisconsin, U.S.A., and winter samples were obtained from spear fishermen on Lake Winnebago. The viscera and gills of all these fish were removed and individually packed and sealed. Eyes were not available from the winter samples. All fish were weighed and their lengths measured before processing. Young-of-the-year (YOY) sturgeon (N=18) were collected from the Wolf River between the Shawano Dam and the county highway CCC bridge, 12.8 km downstream of the Shawano boat landing (Fig. 6) by electroshocking on 11 August 1992, and examined whole. Since hatching occurs in early May (Kempinger, 1988) these juveniles were approximately 3 months old. One additional adult male was caught on 5 May 1993, in the Wolf River at Shawano and the gills and viscera collected for examination. All samples were frozen following collection and examined after thawing. Necropsy procedures and processing of parasites were as before. Host specific parasite refers to a parasite specific to the acipenserids and not necessarily to the host species, *Acipenser fulvescens*.

Age determination of sturgeon

One pectoral finray was removed from each sturgeon, dried, and sectioned one inch from the basal articulation with a jewellers saw. These sections were generally examined after washing in alcohol but were occasionally mounted in glycerine, prior to reading with the aid of a microfiche reader. Ages were available from 215 individuals from the Hudson Bay drainage (fins processed and aged by me) and from all fish from Lake Winnebago (fins processed and aged by Ron Bruch and personnel at the Wisconsin Department of Natural Resources, Oshkosh).

Experimental Infection

Ten metacercariae from the lenses of two lake sturgeon were suspended in 0.9% saline and fed with the aid of a dropper to one ten-day old herring gull (*Larus argentatus*) chick. The bird was euthanised 48 hours later and dissected. One adult specimen of *Diplostomum spathaceum* (Rudolphi, 1819) was recovered from the duodenum, fixed, stained and processed as described previously. Measurements taken followed the protocol of Dick and Rosen (1981).

Analyses

Standard statistical computations (mean, standard deviation, range, prevalence) were calculated for samples grouped by geographical location. Terminology is that of Margolis *et al.*, (1982). Intensities of parasite species among the four waterways and between sexes were tested by the Kruskal Wallis (multiple comparisons) and the

Mann-Whitney U test (pairwise comparison). Correlations of age and sex of host and intensities of each parasite species were tested using Spearman's rank correlation (r_s). Results were considered significant at the 95% ($P < 0.05$) level. The lengths, weights and ages of sturgeon between the two samples were compared using the Mann-Whitney U test. Mean species richness was calculated as the mean number of parasite species per individual host. Sample sizes for this analysis excluded one fish from the winter sample ($N=28$) since its gills were not available. Jaccard's Index was used as an index of similarity in parasite community composition between the summer and winter samples and was calculated as:

$$100c/a+b-c,$$

where a = number of species in sample 1; b = number of species in sample 2 and c = number of species common to both samples.

In calculating Jaccard's index, *Diplostomum* sp. was not included as eyes were not available for examination from the winter sample.

Abundance is the mean number of parasites per host examined (includes infected and uninfected fish). Relative abundance of a parasite species 'A' was calculated as: abundance of parasite species 'A' / sum of the abundances of all parasite species.

Stomach contents of each sturgeon were examined and individual items were initially sorted by order. Samples were stored in 70% alcohol, identified to order or family and reported as frequency of occurrence.

RESULTS

Hudson Bay Drainage

Parasite survey

A total of 19 species of parasites was recovered from 223 lake sturgeon, 12 of which are new host records (indicated by asterisks, Table 2). The parasite fauna included the Monogenea (1 species, adult), Trematoda (3 species, including 2 adults), Nematoda (5 species, including 3 adults), Acanthocephala (4 species, including 1 adult), Cestoda (2 species, both larvae), Hirudinea (2 species, including 1 adult), Cnidaria (1 species, larva) and Vertebrata (1 species, possibly two, juvenile). All fish were infected with at least one parasite and the maximum number was seven species from an individual host. Two hitherto undescribed species of helminths were recovered from this study; *Diclybothrium atriatum* n. sp. and *Spinitectus acipenseri* n. sp. (See Chapter 2 for descriptions). Host-specific parasites *Crepidostomum auriculatum* (Wedl, 1857) (= *C. lintoni* Pratt in Linton, 1901), *Diclybothrium atriatum*, *Spintectus acipenseri* and *Truttaedacnitis clitellarius* (Ward and Magath, 1917) were recovered from all four river systems while *Polypodium* Ussov, 1885 was recovered from Stage IV lake sturgeon oocytes from three of the four waterways (Table 2).

Overall, host specific helminths showed the highest prevalences: *C. auriculatum* (96%), *S. acipenseri* (93.7%), *D. atriatum* (70.1%), and *T. clitellarius* (69.9%). *S. acipenseri* occurred with the highest mean abundance (292.07 ± 410.2 ; range 0-2684) followed by *C. auriculatum* (114.41 ± 220.2 ; range 0-2484).

Diplostomum sp. was the only host-generalist to be recovered from all sampling

locations. *Cystidicoloides* Skinker, 1931, *Pomphorhynchus bulbocolli* (Linkins, 1919), *Rhabdochona* Railliet, 1916 and *Raphidascaris* Railliet and Henry, 1915 were found in three of four waterways (the first three parasites were absent from the Rainy River samples, Tables 2, 3). *Echinorhynchus* Zoega in Mueller, 1776, *Neoechinorhynchus* Hamann, 1892 and *Azygia* Loos, 1899 were present in one sampling site only (Tables 2, 3). *E. leidy* Van Cleave, 1924 was the only acanthocephalan species found with eggs/shelled acanthors.

Pairwise comparison among river systems (Mann Whitney U test, $P < 0.05$) were carried out between seven species of parasites with a prevalence $>30\%$ and present in at least three of the four sampling sites (Table 4). Intensities of *Spinitectus* infections were significantly higher in the Nelson River samples ($X=383.9 \pm 447.1$, range 0-2684) than for sturgeon in other sampling sites. Intensities of *Diplostomum* were highest in the Saskatchewan River samples (mean 2.7 ± 3.5 , range 0-14), while differences in *Diclybothrium* infections varied among sampling sites (Table 4).

The endohelminths *Crepidostomum*, *Spinitectus* and *Truttaedacnitis* were highly correlated ($P < 0.05$). *Diplostomum* infections were negatively correlated with *Crepidostomum* and *Spinitectus* while *Diclybothrium* was positively correlated with these two helminths. *Pomphorhynchus* was negatively correlated with *Diclybothrium* infections while *Spinitectus* was highly correlated with the spirurids *Rhabdochona* and *Cystidicoloides*. The numbers of host specific endohelminths were significantly correlated with specific regions of the gut; *S. acipenseri* for the muscular stomach, *C. auriculatum* for the mid-gut and *T. clitellarius* for the hind-gut (Table 5). Host age and

sex were not significantly correlated with parasite intensities, except for *Pomphorhynchus* which was significantly ($P < 0.05$) correlated with female sturgeon. Ectoparasites such as glossiphoniid hirudineans were observed on sturgeon from Nutimik Lake (Winnipeg River) in 1990 and 1991. Although only six of 115 sturgeon were infected with a total of 9 leeches in the 1990 season, approximately 70% of fish had circular scars ranging from 2 mm to 1 cm in diameter on the ventral surface of the body accompanied by local inflammation. The smaller (2-5mm) diffuse areas of inflammation were confirmed from field observations to be lesions caused by leeches while the larger well defined circular lesions were due to lampreys. Eleven of 14 sturgeon examined at Nutimik lake during the 1991 field season (May-June) had lesions due to the leech, *Placobdella montifera* Moore, 1912.

Representative specimens of the following parasite species have been deposited at the U.S. National Museum Helminthological and Parasite Collection; *Azygia longa* (USNPC 82234), *Crepidostomum auriculatum* (USNPC 82235, 82236), *Diclybothrium atriatum* (USNPC 82237, 82238), *Diplostomum* sp. (metacercariae) (USNPC 82239), *Spinitectus acipenseri* (USNPC 82250), *Truttaedacnitis clitellarius* (USNPC 82249) *Raphidascaris acus* (larvae) (USNPC 82246), *Rhabdochona cascadilla* (USNPC 82247), *Cystidicoloides* sp. (larvae) (USNPC 82248), *Echinorhynchus leidy* (USNPC 82240); *Leptorhynchoides thecatus* (USNPC 82241), *Neoechinorhynchus tenellus* (USNPC 82242), *Pomphorhynchus bulbocolli* (USNPC 82243), *Placobdera montifera* (USNPC 82244) and *Polypodium* sp. (USNPC 82245). The only two specimens of larval cestodes recovered in this study, the adult *Diplostomum spathaceum* from the

experimental infection and the single specimen of *Ichthyomyzon unicuspis* are held in the collection of Dr. T.A. Dick, Department of Zoology, University of Manitoba, Winnipeg, Canada.

Experimental infection

One adult diplostomatid was recovered from the duodenum of the infected herring-gull chick and identified as *Diplostomum spathaceum*.

Host statistics

Overall, lake sturgeon (215 fish) averaged 24.08 years (\pm 6.95 yrs., range = 4-45 years) in age and 62.3% of the sample consisted of fish between 20 and 40 years of age. Two hundred fish were sexed (gonads of the remaining samples were either not available or were undeveloped); 102 females and 98 males. All stages of female gonad development were represented in the samples (Table 6) but only stage III oocytes (Nedoshivin's scale) were observed from Rainy River sturgeon. Nine of the females were spent indicating spawning either in the year of capture or the previous year; the majority of such spent females (eight) were from Sipiwesk Lake (Nelson River). Only one necropsied female was in Stage IV. The majority of the females (91) were between Stage Y/7 (immature juveniles or adults with regenerating gonads) and Stage III (Table 6).

The food items from sturgeon recovered in this study included larval insects belonging to Ephemeroptera (Ephemeridae, mainly *Hexagenia*, Ephemerellidae naiads), Trichoptera (Hydropsychidae, Brachycentridae, Polycentropodidae), Diptera (Chironomidae), Ceratopogonidae, Coryxidae, Dytiscidae, Nematoceridae (pupae),

Odonata (Gomphidae, other odonate pupae) and Megaloptera (Sialidae). Crustaceans in the diet were represented by *Hyaella* (Gammaridae), and *Orconectes* (Cambaridae). Other food items included Hirudinidae (leeches), Gastropoda (prosobranchs and other unidentifiable remains), Sphaeriidae and Unionidae (*Lampsilus*). Fish in the diet were identified as Cottidae (*Cottus ricei*) and Percidae (*Stizostedion vitreum*). Stomachs of two sturgeon from Sipiwesk lake were fully distended with fish eggs (probably of perch). Ephemeropteran naiads (predominantly Ephemeridae), chironomid larvae, gammaridean (*Hyaella*) and decapod (*Orconectes*) crustaceans were frequent components of consumed food items (Table 7).

Lake Winnebago drainage

Parasites

Eight different species of parasites (all helminths) were recovered; seven species were recovered from the summer samples and six species from the winter samples (Table 8). Five of these are host specific: *Diclybothrium* sp., *Crepidostomum auriculatum*, *Skrjabinopsolus manteri* (Cable, 1952), *Capillospirura pseudoargumentosa* (Appy and Dadswell, 1978) and *Triniaedacnitis clitellarius*, and were recovered from both sampling periods. Seven of the 29 winter fish and 10 of the 45 summer fish were uninfected. The maximum number of parasite species recovered from a single individual (viscera and gills) was 5 (all host specific helminths) from both sampling seasons. Up to nine nodules, 2-5 mm in diameter, were found on the posterior part of the spiral valve flap of one summer individual. A temporary squash

preparation of one nodule revealed a necrotic core containing the remains of an unidentified nematode-like body with adhering necrotic debris surrounded by concentric rings of typical connective tissue (fibroblast) proliferation. In the summer sample, intensities of *C. pseudoargumentosa*, *T. clitellarius* and *S. manteri* were significantly correlated with age ($r_s > 0.75$) but these were based on few observations (3-10). Community similarity between seasons was high (Jaccard's Index = 85); all the host specific helminth species were found in both samples. Relative abundance of *C. auriculatum* accounted for 87.8% and 56.3% of summer and winter samples, respectively. Relative abundances of the host specific helminths were, respectively, 97.5% and 99.5% in summer and winter samples. Mean helminth species richness was: 1.82 ± 1.1 / fish for the summer sample and 2.13 ± 1.3 / fish for the winter sample. None of the YOY sturgeon from the Wolf River was infected.

Voucher specimens of the following helminths were deposited in the U.S. National Museum, Bethesda, Maryland, with the accession numbers in parentheses: *Diclybothrium* sp. (USNPC 85720), *Crepidostomum auriculatum* (USNPC 85721), *Skrjabinopsolus manteri* (USNPC 85722), *Capillospirura pseudoargumentosa* (USNPC 85723) and *Truttaedacnitis clitellarius* (USNPC 85724).

Host statistics and food habits

The winter sample is made up of significantly older and larger fish (Table 9). Benthic macroinvertebrates occurred with the highest frequency, with chironomids dominating both samples (Table 9). Planktonic cladocerans (mainly *Daphnia* sp.

Mueller, some *Leptodora* sp. Lilljeborg) were also common in summer samples and were occasionally found in large quantities in the forestomachs of sturgeon.

Ephemeropteran nymphs (mainly Baetidae) were the predominant food items (Table 10) of YOY sturgeon; this insect order and Simuliidae were absent from the lake samples (summer and winter). The single sturgeon captured in the Wolf River at Shawano contained the only records of crayfish and unionid clams in the diet.

DISCUSSION

Hudson Bay drainage

As this is the first comprehensive survey of lake sturgeon parasites from several river systems covering a wide geographical range, it is not surprising that this study yielded 19 species of which 12 are new host records (Table 2). Sexually mature species recovered from all sample sites included *Crepidostomum auriculatum*, *Diclybothrium atriatum* (see Chapter 2-1), *Truttaedacnitis clitellarius* and *Spinitectus acipenseri* (Table 2,3). These species, along with *Polypodium*, are specific for lake sturgeon and form its core parasites, but some of these core species are also specific to other acipenserids (Skrjabina, 1974; Chapters 2, 3). Some of these core species were reported from previous surveys of small numbers (two-10) of lake sturgeon (Bangham and Hunter, 1939, from Peele Isle, Bangham, 1955 from South Bay and from Lake Pepin, Dechtiar, 1972a, 1972b, from Lake Erie and Lake of the Woods, and Anthony, 1974, from Lake Nipissing).

All other parasites recovered from this study were host generalists and showed

varied distribution patterns (Table 2). Although the sampling in this study was restricted by the commercial fishing season, gravid *Pomphorhynchus* were not recovered from infections of sturgeon through June (7 June - 23 June) in the Saskatchewan River, late June-early July (27 June - 10 July) in the Nelson River, and late July and early August from the Winnipeg River. Juvenile *Leptorhynchoides* Kostylew, 1924 were recovered from the Winnipeg River samples during late July and early August and from the Rainy River late in May. Previous studies (T.A. Dick, unpublished observations) found gravid *Pomphorhynchus* Monticelli, 1905 in catostomids during late July and August. While lake sturgeon may harbour heavy infections (see Tables 2, 3) of these acanthocephalans, they are probably not suitable hosts to produce gravid females, even though the acanthocephalans are firmly attached to the gut. This supports the contention of Amin (1987, 1988) that *L. thecatus* and *P. bulbocolli* show greater specificity for centrarchid and cypriniform (catostomids/cyprinids) fish respectively (i.e., they readily produce gravid females in these hosts) and consequently we consider lake sturgeon to be an "occasional" host of these two acanthocephalans, as defined by Amin (1987).

Based on distribution of the parasitofauna of lake sturgeon among our sampling areas, it is likely that benthic invertebrates in the diet of lake sturgeon (Table 7) are important in shaping the endohelminth communities. Although the specific intermediate hosts of *C. auriculatum*, *S. acipenseri*, and *T. clitellarius* are unknown, related congeneric species of *Crepidostomum* and *Spinitectus* develop in benthic arthropods such as gammarids and ephemeropteran naiads. The latter forms an

important constituent, in terms of prevalence in the gut and proportion by volume, of food items consumed by lake sturgeon (Table 7, T.A.Dick, unpublished). The use of similar food chains by these host specific parasites also explains the strong correlation between them. There was no evidence for histotropic development of *Truttaedacnitis* in lake sturgeon as has been reported for some cucullanids (see Anderson, 1992), and since piscivory is uncommon, the parasite may be transmitted by invertebrates in the diet (but see Appendix D). Khromova (1975) surveyed benthic invertebrates in an attempt to find the intermediate host of *Truttaedacnitis sphaerocephala* (Rudolphi, 1809), the cucullanid specific for European acipenserids, and found cucullanid type larvae in *Nereis diversicolor* which may act as an intermediate host. Diet also determines the distribution of non host-specific parasites. The relative abundance of *Pomphorhynchus* in the Cumberland House samples can be correlated to the abundance of gammarids in the gut of sturgeon (Table 7). In one gut sample, 6 of >200 gammarids were infected with *Pomphorhynchus* juveniles in the haemocoel, indicating that recruitment to the fish host was in progress (June 7-14). The presence of a tetraphyllidean plerocercoid in a Nelson River sturgeon may have resulted from scavenging on anadromous fish as proposed by Margolis and McDonald (1986) for freshwater inhabiting white sturgeon juveniles that were infected with marine helminths, although fish were not a major component of the lake sturgeon diet (Table 6). The correlation between female sturgeon and *Pomphorhynchus* is difficult to explain but it was noted for cystacanth infections in female white sturgeon by Margolis and McDonald (1986) and for *P. bulbocolli* in catostomids and cyprinids

(Amin, 1987). Perhaps it is an indication of differences in feeding behaviour between male and female fish. There was no correlation between parasite composition and lake sturgeon age but as our samples were comprised of older fish (see Results) this was expected. Similar results in juvenile and adult *A. ruthenus* and *A. baeri* were interpreted as similarities in diets among various stages of growth (Sokolov and Berdichevskii, 1989) and, as the following study on lake sturgeon from the Lake Winnebago system will show, juveniles change to an adult diet early in life (Dick and Choudhury, unpublished).

Larvae of *Diplostomum* are transmitted to fish via benthic gastropods but there is a negative correlation of *Diplostomum* infections with other parasite species with benthic life cycles (such as *Crepidostomum* and *Spinitectus*). This and the inverse correlation between *Diclybothrium* and *Diplostomum* may relate to the direct life cycle of the monogenean and chance infections by the larval digenean and the likelihood that neither are transmitted in the diet.

The range of *Polypodium* has been extended in North America [north to the Nelson River and west to the Saskatchewan River (see Dick *et al.*, 1991)] and in this study east to the Winnipeg River. From our reports and previous studies (Hoffman *et al.*, 1974; Dadswell, 1984, Dick *et al.*, 1991, Raikova, pers. comm.), *Polypodium* is well established among species of *Acipenser* in North America (Figure 7). While *Polypodium* is common in lake sturgeon from the waterways of central Canada, stolons were only apparent in Stage IV oocytes, as reported earlier (Dick *et al.*, 1991). Perhaps this explains the absence of reports of this parasite, despite the large scale

commercial fisheries in Canada for lake sturgeon meat and caviar (stage III oocytes preferred), in the late 1800s and early 1900s.

Lake Winnebago system

This is the first survey of lake sturgeon parasites from Lake Winnebago and the first to sample a range of age classes. The lake sturgeon constitutes a new host record for *Capillospirura pseudoargumentosa*, having been previously reported mainly from the shortnose sturgeon (Appy and Dadswell, 1978). Other host specific helminths found in this study were reported from lake sturgeon elsewhere (see species list compiled by MacDonald and Margolis, 1995). The helminth community is predominantly host specific with a low abundance of non-host specific parasites (Table 8). This contrasts with the high abundances of some non-host specific helminths reported from lake sturgeon of the Hudson Bay drainage.

The eutrophic nature of Lake Winnebago is reflected in the diet of lake sturgeon from winter and summer samples (e.g. tubificid oligochaetes and chironomid larvae which are abundant in Lake Winnebago (Hilsenhoff, 1966, Table 10). Data from this study corroborate previous records of sturgeon food habits from Lake Winnebago (Schneberger and Woodbury, 1944, Probst and Cooper, 1955; Table 10) and indicates that chironomids continue to be the predominant food item. Ephemerid nymphs (e.g. *Hexagenia* Walsh), crayfish, sphaeriid pelecypods and gammarids were scarce or absent from the diet of sturgeon and contrast with reports from less eutrophic systems such as the Hudson Bay drainage. The absence of nymphs of *Hexagenia* spp.

from Lake Winnebago is likely due to the highly eutrophic nature of the lake (sediment phosphorus loading) and resulting hypoxia (Rasmussen, 1988). Large cladoceran populations are also characteristic of Lake Winnebago (Marsh, 1903) and their presence in the diet of lake sturgeon indicate an opportunistic feeding behaviour. Interestingly, similar feeding behaviour was observed in another benthic species, the freshwater drum (*Aplodinotus grunniens* Rafinesque) in Lake Winnebago (Marsh, 1903).

The eutrophic nature of Lake Winnebago contributes to the helminth community of lake sturgeon since *Skrjabinopsolus manteri* and caryophyllaeids are both transmitted by oligochaetes (Peters, 1961; Hoffman, 1967). Infections with larval *Camallanus* sp. Railliet and Henry, can be related to opportunistic feeding on planktonic crustaceans (Anderson, 1992). However, the trophic status of the lake and the food items recovered from sturgeon do not satisfactorily explain the presence of other host-specific helminths. For example, helminth communities from lake sturgeon of Hudson Bay drainage were dominated by *Crepidostomum auriculatum* and *Spinitectus acipenseri*, while chironomids, ephemeropterans (mainly *Hexagenia* sp.), sphaeriid pelecypods and crayfish were the dominant food items. The absence of *Spinitectus* is likely due to the absence of ephemerid nymphs (e.g. *Hexagenia* spp.) in the diet since they are important intermediate hosts of other N. American *Spinitectus* spp. (Anderson, 1992). This indicates the possibility of a local extinction event, since this nematode has been reported from lake sturgeon of the Great Lakes drainage in the past (Bangham, 1955; Anthony, 1974, 1977).

Other host specific helminths reflect the riverine component of sturgeon habitat. The record of 2818 *Crepidostomum auriculatum* from an adult sturgeon caught in the Wolf River contrasts with the lower abundances of this helminth from both summer and winter fish in the lake. Food items consumed in large quantities in riverine areas include ephemerids, sphaeriid pelecypods and crayfish. Of these, ephemerid nymphs and crayfish are known to transmit *Crepidostomum* spp. (Hopkins, 1934; Caira, 1989). Transmission by ephemerids is difficult to reconcile with the absence of *Spinitectus* sp. which is also likely transmitted by these insects. Crayfish have been suggested as the intermediate host of *C. auriculatum* (Faust, 1918, 1919) although Hopkins (1934) doubted Faust's observations. Nevertheless, transmission by crayfish would explain the widespread presence of this parasite in lake sturgeon examined from all drainage systems to date.

The presence of *Capillospirura pseudoargumentosa* is enigmatic since the intermediate hosts, amphipods, (Appy and Dadswell, 1983) were not present as dietary items in either summer or winter fish. Information on the biology of *C. pseudoargumentosa* and related species from Eurasia (Skrjabina, 1974; Appy and Dadswell, 1978; Appy and Dadswell, 1983) indicates that transmission to sturgeon does occur in riverine areas. Of the amphipods present in the Lake Winnebago system, *Gammarus fasciatus* Say, is a known intermediate host of this nematode but we did not find it in benthic samples examined from the lake. Of the amphipods found in Lake Winnebago, *Hyalella azteca* Saussure is an unsuitable intermediate host (Appy and Dadswell, 1983) while the role of *Gammarus pseudolimnaeus* Bousfield remains

unknown. Thus, the transmission of *C. pseudoargumentosa* by gammarids such as *Gammarus fasciatus* possibly takes place in downstream riverine environments where this species is commonly found (Bousfield, 1958).

While the riverine environment appears to be a key area for the recruitment of some host specific helminths (this study), it is interesting that YOY sturgeon examined in this study were uninfected. This was unexpected since a benthic feeding habit is well established in these 3-month-old juveniles. However, their dietary items (Table 10) clearly reflect their preference for upstream lotic environments which are qualitatively different from those used by older sturgeon i.e., lakes and deeper riverine channels (Table 10). Interestingly, since nymphs of *Ephoron Williamson* dwell in burrows under stones in rapids and emerge to feed at night (Ide, 1935), their presence in the diet of juvenile sturgeon indicates that they are nocturnal feeders. This combined information of food habits and parasites has helped us understand how localized ecological conditions affect habitat utilization by increasingly fragmented lake sturgeon populations.

CONCLUSIONS

There are some notable differences between the parasite fauna of sturgeon from the Hudson Bay drainages and Lake Winnebago. Two host-specific parasites of acipenserids, *Capillospirura pseudoargumentosa* and *Skrjabinopsolus manteri* were not found in the Hudson Bay drainages. This absence may be related to the distribution of intermediate hosts. If *C. pseudoargumentosa* is host specific to the gammarid species

pair of *G. fasciatus*/*G. tigrinus* (see Appy and Dadswell, 1983), it would explain its absence in the Hudson Bay drainage since neither gammarid species is found in this system. Similarly, the distribution of *S. manteri* may be limited by the distribution of its putative intermediate mollusc host (Peters, 1961; Seitner, 1951) which does not occur in the Hudson Bay drainages sampled in this study. The absence of *Spinitectus acipenseri* from the Lake Winnebago system is also apparently due to the absence of an important intermediate host of *Spinitectus* spp. (ephmerids, particularly *Hexagenia*). Identifying likely causes for the limits in distribution for parasite taxa is also critical to the development of biogeographical hypotheses.

Other host specific parasites such as *D. atriatum*, *C. auriculatum*, *T. clitellarius* and *Polypodium* were found in both drainages and constitute the 'core' parasites of the lake sturgeon.

Non- host-specific parasites showed stochastic patterns of distribution that is dependent on associations with other host groups (catostomids, centrarchids) and, more importantly, feeding on intermediate hosts such as gammarids which transmitted most of the species of acanthocephalans (*L. thecatus*, *P. bulbocolli*, *E. leidyi*) found in this study. This study also shows how dietary habits may be modified by local conditions (Lake Winnebago) and this is reflected in accidental infections by certain parasites (e.g., larval *Camallanus*).

The parasite fauna of lake sturgeon shows similarities, to a limited extent, with that of the shortnose sturgeon, *A. brevirostrum*, and the shovelnose sturgeon, *Scaphirhynchus platorhynchus*, and less so with the North American Pacific sturgeons

(*A. medirostris* and *A. transmontanus*) or the Atlantic sturgeon (*A. oxyrinchus*) (Table 11). The overall parasite community of lake sturgeon from the Hudson Bay drainage is comparable to the predominantly freshwater acipenserids of Eurasia (*A. ruthenus* and *A. baeri*) (Skrjabina, 1974; Holcik, 1989). Similarities with these freshwater sturgeons is due to host specific helminths such as *Truttaedacnitis clitellarius* and *Crepidostomum auriculatum* as well as numerous non- host-specific helminths acquired through a common freshwater benthivorous feeding habit and association with dominant benthivores such as coregonids and cypriniforms in boreal and Arctic drainages (for a more detailed discussion, see Choudhury and Dick, submitted).

This survey yielded a sizeable collection of parasites belonging to diverse genera such as *Diclybothrium*, *Crepidostomum*, *Skrjabinopsolus*, *Capillospirura*, *Spinitectus* and *Truttaedacnitis*, most of which were collected over a considerable distributional range. This material formed the basis for the various taxonomic and systematic studies reported in subsequent sections.

Table 2. Mean intensities of infection, prevalence, range and distribution of parasites from lake sturgeon (N=223) from the Hudson Bay drainage.

PARASITE	SITE	PREV (%)	MEAN \pm S.D.	RANGE	LOCATION ⁴
MONOGENEA					
<i>Diclybothrium atriatum</i> * (N=218)	Gill	70.1	13.95 \pm 13.81	1-86	SR,NR,WR,RR
TREMATODA					
<i>Azygia longa</i> *	Gut	0.08	3 \pm 2.83	1-5	RR
<i>Crepidostomum auriculatum</i>	Gut	96.4	118.67 \pm 223.14	1-2484	SR,NR,WR,RR
<i>Diplostomum</i> sp.(larva)(N=224)	Eyes	30.3	3.13 \pm 2.96	1-14	SR,NR,WR,RR
CESTODA					
Proteocephalidea (l)* ¹	Gut				RR
Tetraphyllidea* ¹	Gut				NR
NEMATODA					
<i>Cystidicoloides</i> sp.(l)*	Gut	32.2	4.94 \pm 9.13	1-71	NR,SR,WR
<i>Raphidascaris</i> sp.(l)*	Gut	8.02	14.94 \pm 50.31	1-216	NR,SR,WR
<i>Rhabdochona cascadilla</i>	Gut	14.3	4.66 \pm 8.24	1-47	NR,RR,WR
<i>Spinitectus acipenser</i> *	Gut	93.7	311.64 \pm 416.47	1-2684	SR,NR,WR,RR
<i>Truttaedacnitis cliellarius</i>	Gut	69.9	5.24 \pm 6.07	1-40	SR,NR,WR,RR
ACANTHOCEPHALA					
<i>Echinorhynchus leidy</i> *	Gut	1.3	5 \pm 3.61	1-8	WR
<i>Leptorhynchoides thecatus</i> *	Gut	2.2	27.20 \pm 53.66	1-123	WR,RR
<i>Neoechinorhynchus tenellus</i> *	Gut	4.0	2 \pm 1.12	1-4	NR
<i>Pomphorhynchus bulbocolli</i> *	Gut	30.49	55.87 \pm 127.15	1-653	SR,NR,WR
CNIDARIA					
<i>Polypodium</i> sp.	Eggs.	100% infection of stage IV females.			SR,NR,WR
HIRUDINEA					
<i>Placobdella montifera</i> * ² .					NR,WR
Glossiphoniidae* ²					WR
VERTEBRATA					
<i>Ichthyomyzon unicuspis</i> ³ .					WR

* Indicates new host record. ¹One proteocephalid plerocercoid was recovered from the gut of a sturgeon from Rainy River and one tetraphyllid plerocercoid was recovered from a Nelson River (Sipiweski L.) gut sample. ²*Placobdella* were attached to the external body surface of lake sturgeon at Nutimik Lake, Manitoba. Six sturgeon of 115 that were examined, had *Placobdella* with a total of 9 specimens collected. In addition, one unidentified leech collected from Nutimik Lake in 1989 has been provisionally placed in the family Glossiphoniidae. ³Attached to one of 25 fish in May, 1991. One specimen was also observed on a sturgeon, of a total of 13 captured fish, from Rainy River, Ontario, and tentatively identified as *I. castaneus*. ⁴Indicates geographical location: SR=Saskatchewan River, NR=Nelson River, WR=Winnipeg River and RR=Rainy River.

Table 3. Mean intensities of infection and ranges of parasites of lake sturgeon from different geographical locations (Hudson Bay drainage).

PARASITE	Sask. R. (N=55)*	Nelson R. (N=131)*	Wpg. R. (N=24)*	Rainy R. (N=13)*
<i>Dicylbothrium airriatum</i> **	1 ± 0 (1)(N=45)	13.53 ± 12.7 (1-86)(N=141)	14.15 ± 13.4 (1-46)(N=19)	21.69 ± 21.62 (2-73)
<i>Crepidostomum auriculatum</i> **	63.98 ± 90.95 (1-370)	143.48 ± 275.55 (1-2484)	123.96 ± 84.37 (1-305)	67.38 ± 61.93 (3-208)
<i>Diplostomum</i> sp.(larva)	4.44 ± 3.51 (1-14)(N=45)	2.48 ± 2.44 (1-12)(N=147)	1.33 ± 0.71 (1-3)(N=18)	3.0 ± 1.73 (2-5)
<i>Azygia longa</i>	0	0	0	3.0 ± 2.83 (1-5)
<i>Spinitectus acipenseri</i> **	243.23 ± 395.64 (1-1706)	389.88 ± 447.97 (1-2684)	120.15 ± 187.45 (3-594)	77.15 ± 73.77 (8-244)
<i>Truttaedacnitis citellarius</i> **	7.43 ± 9.67 (1-40)	4.85 ± 4.42 (1-27)	3.25 ± 2.67 (1-9)	2.33 ± 1.63 (1-5)
<i>Raphidascaris</i> sp.	12.0 ± 0 (12)	2.56 ± 3.03 (1-12)	216.0 ± 0 (216 ¹)	0
<i>Rhabdochona cascadiilla</i>	0	4.69 ± 8.66 (1-47)	6 ± 0 (6)	3.5 ± 0.71 (3-4)
<i>Cystidicoides</i> sp (l).	1.5 ± 1.22 (1-4)	5.66 ± 10.04 (1-71)	2.37 ± 1.41 (1-4)	0
<i>Echinorhynchus leidy</i>	0	0	5 ± 3.61 (1-8)	0
<i>Leptorhynchoides thecatus</i>	0	0 (1-123)	31.75 ± 60.84 (9)	9.0 ± 0
<i>Neoechinorhynchus tenellus</i>	0	2.0 ± 1.12 (1-4)	0	0
<i>Pomphorhynchus bulbocolti</i>	89.2 ± 155.43 (1-653)	4.38 ± 8.24 (1-42)	28 ± 0 (28)	0

Abbreviations are as follows: MI = Mean intensity of infection ± standard deviation (values in brackets are ranges of infection for that particular parasite).
Sask. R.= Saskatchewan River; Wpg. R.= Winnipeg River.

* = N numbers except when stated otherwise. **= Host specific parasites.

¹Used as a minimum estimate from 216 cysts with a minimum of one nematode/cyst.

Table 4. Results of pairwise comparison, by ranking, of intensities of parasite infection among sturgeon from the four geographical locations (Mann Whitney U test).(Hudson Bay drainage).

Parasite species	Results
<i>Diplostomum sp.</i>	SR>NR, RR, WR
<i>Diclybothrium atriatum</i>	NR>SR; WR>SR; RR> SR, WR
<i>Crepidostomum auriculatum</i>	WR > SR; NR > SR, WR
<i>Spinitectus acipenseri</i>	NR > SR, WR, RR
<i>Truttaedacnitis clitellarius</i>	NR > WR, RR
<i>Pomphorhynchus bulbocolli</i>	SR> NR, WR

Abbreviations are as follows: NR, Nelson River; SR, Saskatchewan River; RR, Rainy River and WR, Winnipeg River. The symbol '>' indicates the relationship (at P < 0.05) among intensities of infection of a particular parasite among geographical locations.

Table 5. Distribution (mean abundance \pm S.D.) of the host specific helminths in the gut of lake sturgeon (Hudson Bay drainage).

Parasite	Forestomach	Stomach	Appendix	Midgut	Hindgut
<i>C. auriculatum</i>	2.0 \pm 8.5 (0-83)	1.0 \pm 4.3 (0-38)	4.9 \pm 15.1 (0-164)	98.9 \pm 209.3 (0-2393)	7.6 \pm 21.2 (0-191)
<i>S. acipenseri</i>	63.8 \pm 146.2 (0-1180)	220.9 \pm 314.3 (0-1693)	1.41 \pm 14.5 (0-205)	4.3 \pm 38.3 (0-557)	2.6 \pm 10.4 (0-121)
<i>T. clitellarius</i>	0	0.0 \pm 1.0 (0-1)	0.0 \pm 1.0 (0-1)	0.5 \pm 1.6 (0-16)	3.2 \pm 4.9 (0-36)

Values represented are : Mean abundances of infection \pm standard deviation (values within brackets represent ranges for the particular parasite)

Table 6. Stages of oocyte maturation (Nedoshivin's scale)¹ in sampled female sturgeon from the four different waterways.

	Total	Nelson R.	Saskatchewan R.	Winnipeg R.	Rainy R.
Stage 0	35	14	16	5	0
Stage I	12	8	3	1	0
Stage II	26	17	8	1	0
Stage III	18	12	4	1	1
Stage IV	1	0	1	0	0
Stage V	1	0	0	1 ²	0
Stage VI	9	8	0	1	0

¹Nedoshivin (1928).

²In addition, one running (Stage V) female was also observed at Nutimik Lake, Winnipeg River, and *Polypodium* was found amongst the running eggs.

Table 7. Frequency of occurrence (%) of food items in the gut of lake sturgeon from the different waterways (Hudson bay drainage).

	Eph	Chi	Tri	Gam	Cra	Biv	Lee	Fis
S.R.	23	17	1.9	18.9	26.4	13.2	11.3	3.8
N.R.	67.4	10.1	3.4	2.25	15.7	11.2	6.7	3.4
W.R.	41	45.4	9.1	4.5	22.7	13.6	0	0
R.R.	38.4	7.7	7.7	0	7.7	7.7	0	0

Abbreviations are as follows:

Eph=Ephemeroptera (naiads); Chi=Chironomidae (larvae); Tri=Trichoptera (larvae); Gam= Gammarids; Cra=Orconectes (crayfish); Biv= Bivalves; Lee= Hirudinidae; Fis= Fish.

S.R.= Saskatchewan River; N.R.= Nelson River; W.R.=Winnipeg River; R.R.=Rainy River.

Table 8. Abundance \pm S.D., % prevalence and range in intensity, of helminths of lake sturgeon from Lake Winnebago and the Wolf River.

Parasite	Summer sample (N = 45)	Winter sample (N = 29)	Wolf R. (N=1)
MONOGENEA			
<i>Dicybothrium</i> sp.	1.4 \pm 2* (53)(1-7)	2.4 \pm 2.8 (N=28) (71.4)(1-10)	7
DIGENEA			
<i>Crepidostomum auriculatum</i>	25 \pm 83.8 (20)(2-454)	11.7 \pm 39.7 (31)(1-177)	2818
<i>Diplostomum</i> sp.(1)	0.2 \pm 1.4 (6.6)(1-9)	NA	NA
<i>Skrjabinopsolus manteri</i>	1 \pm 4 (22.2)(1-26)	1 \pm 2.5 (24.1)(1-11)	2
CESTODA			
Caryophyllaeidae (1)	0.04 \pm 0.3 (6.8) 2	-	-
NEMATODA			
<i>Camallanus</i> sp.(1)	0.3 \pm 1.1 (11.1)(1-5)	0.1 \pm 0.6 (3.4)(3)	-
<i>Capillospirura pseudoargumentosa</i>	0.2 \pm 0.7 (6.6)(2-3)	4.5 \pm 14.9 (13.8)(1-67)	-
<i>Truttaedacnitis clitellarius</i>	0.2 \pm 0.7 (11.1)(1-4)	1.6 \pm 4.7 (20.7)(2-24)	13

*Abundance \pm S.D. (% Prevalence) (range). l=larval stage. NA =Not Available. - = Absent.

Table 9. Mean length, weight and age (\pm S.D.) over ranges for lake sturgeon from the Lake Winnebago system.

	Summer sample (N=45)	Winter sample (N=29)	Wolf R. YOY (N=18)	Wolf R. adult (N=1)
Length(cm)	88.5 \pm 21.1* (37-120.5)	146.1 \pm 16.5 (120.6-192.5)	17.3 \pm 1.7	146.05
Weight	4.3 \pm 2.6(kg) (0.2 - 10.8)	19.5 \pm 9(kg) (8.8 - 52.2)	21 \pm 5.1(g) (6.2 - 29)	19.9(kg)
Age(yr)	8.9 \pm 4.3 (2 - 21)	23.9 \pm 7.3 (13 - 51)	0.25	N.A.

*Mean \pm S.D. (range)

N.A. Not Available

Table 10. Frequency of occurrence of food items in lake sturgeon from the Lake Winnebago system.

Items	Summer sample (N=45)	Winter sample (N=29)	YOY (N=18)	Wolf R. (N=1)	S&W (N=11)	P&C (N=127)
Crustacea						
Cladocera						
<i>Daphnia</i>	17.7	6.8	-	-	-	-
<i>Leptodora</i>	4.4	-	-	-	-	-
Copepoda	4.4	-	-	-	-	-
Ostracoda	-	3.4	-	-	-	-
Decapoda (Cambaridae)	-	-	-	P	-	-
Isopoda	-	-	-	-	-	0.8
Insecta						
Diptera						
Chironomidae	80	86.7	83.3	-	100	86.6
Ceratopogonidae	-	6.8	-	-	-	1.6
Simuliidae	-	-	22.2	-	-	-
Ephemeroptera	-	-	100	-	-	1.6
Baetidae	-	-	88.8	-	-	nd
Polymitarcyidae	-	-	27.7	-	-	nd
Caenidae	-	-	5.5	-	-	nd
Megaloptera						
Sialidae	-	3.4	-	-	-	4.7
Trichoptera						
Hydropsychidae	-	-	5.5	-	-	-
Polycentropodidae(?)	2.2	-	-	-	-	-
Unidentified	4.4	-	-	-	-	-
Annelida						
Oligochaeta						
Tubificidae(?)	4.4	27.6	-	-	-	-

Table 10. continued.. Frequency of occurrence of food items in lake sturgeon from the Lake Winnebago system. continued..

Items	Summer sample (N=45)	Winter sample (N=29)	YOY (N=18) (N=1)	Wolf R. (N=11) (N=127)	S&W	P&C
Hirudinea	-	6.8	-	-	18	10.2
Mollusca						
Pelecypoda						
Sphaeriidae	24.4	6.8	-	P	9	2.4
Unionidae	-	-	-	P	-	nd
Gastropoda	2.2	-	-	-	9	-
Nematoda						
Tylenchida	28.8	-	-	-	-	-
Fish	-	-	-	-	-	1.6

?= tentative identification, P= present, - = Absent, nd = no data, S&W= Schneberger and Woodbury (1944), P&C= Probst and Cooper (1955).

Table 11. Host-specific parasites of Acipenseriformes in North America*.

	A. f.	A. b.	A. o.	A. m.	A. t.	S. p.	P. s.
Cnidaria							
<i>Polypodium hydriforme</i>	P	P	-	-	-	-	P
Monogenea							
<i>Dicybothrium atriatum</i> ¹	P**	P	-	-	-	-	-
<i>D. hamulatum</i>	P?	-	-	-	-	-	P
<i>Paradicybothrium pacificum</i>	-	-	-	P	-	-	-
<i>Nitzschia sturionis</i>	-	P	P	-	-	-	-
<i>N. quadriristes</i>	-	-	-	P	P	-	-
Cestoda							
<i>Amphilitina bipunctata</i>	-	-	-	-	P	-	-
<i>Bothrimonus sturionis</i>	-	-	P	-	-	-	-
<i>Marsipometra hastata</i>	-	-	-	-	-	-	P
<i>M. confusa</i>	-	-	-	-	-	-	P
<i>M. parva</i>	-	-	-	-	-	-	P
Digenea							
<i>Crepidostomum auriculatum</i>	P	-	-	-	P	P	-
<i>Cestrahelminis rivularis</i>	-	-	-	-	P	-	-
<i>Deropristis hispida</i>	-	-	P	-	-	-	-
<i>Skrjabinopsolus manieri</i>	P	-	-	-	-	P	-
Nematoda							
<i>Capillospirura</i>							
<i>pseudoargumentosa</i>	P	P	P	-	-	-	-
<i>Spinitectus acipenseri</i> ¹	P	-	-	-	-	P	-
<i>Truttaedacnitis clitellarius</i>	P	-	-	-	-	-	-
<i>T. sphaerocephala</i>	-	-	P	-	-	-	-
<i>Hysterothylacium dollfusi</i>	-	-	-	-	-	-	P

Table 11. continued.

	<i>A. f.</i>	<i>A. b.</i>	<i>A. o.</i>	<i>A. m.</i>	<i>A. t.</i>	<i>S. p.</i>	<i>P. s.</i>
Crustacea							
<i>Dichelesthium oblongum</i>	-	-	P	-	-	-	-

*Includes results from this study. **Bold character indicates new records from this study ¹See Chapter 2. Abbreviations are as follows: *A.f.*= *A. fulvescens* (lake sturgeon), *A.b.*= *A. brevirostrum* (shortnose sturgeon), *A.o.*= *A. oxyrhynchus* (North American Atlantic sturgeon), *A.m.*= *A. medirostris* (green sturgeon), *A.t.*= *A. transmontanus* (white sturgeon), *S.p.*= *Scaphirhynchus platyrhynchus* (shovelnose sturgeon), *P.s.*= *Polyodon spathula* (paddlefish). l= larva, P = present, *P* = New records from this study. '-' = no record.

Figure 4. Map of Central and Western Canada showing the different waterways with numbers of lake sturgeon samples obtained from each site () in this study.

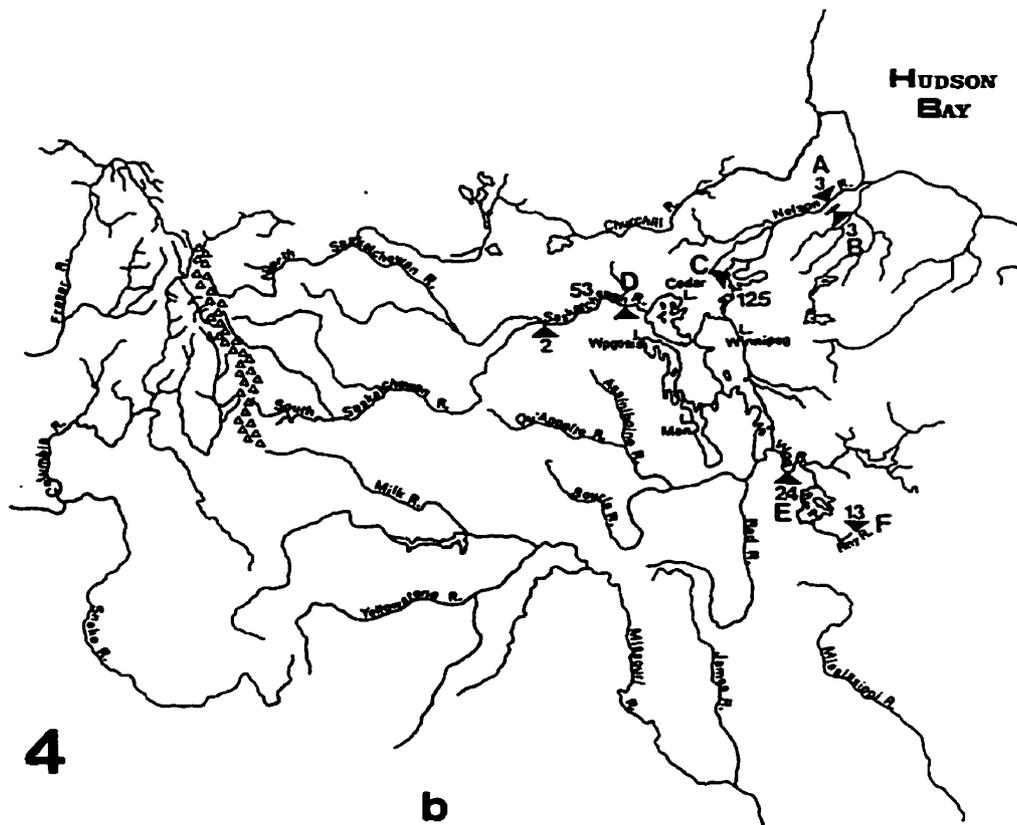


Figure 5. Enlarged maps of major locations sampled in the study. a) Saskatchewan River Delta and Cumberland Lake, b) Nelson River and Sipiwesk Lake, c) Winnipeg River, d) Rainy River. Solid arrows point to sampling locations, open arrows denote direction of flow.

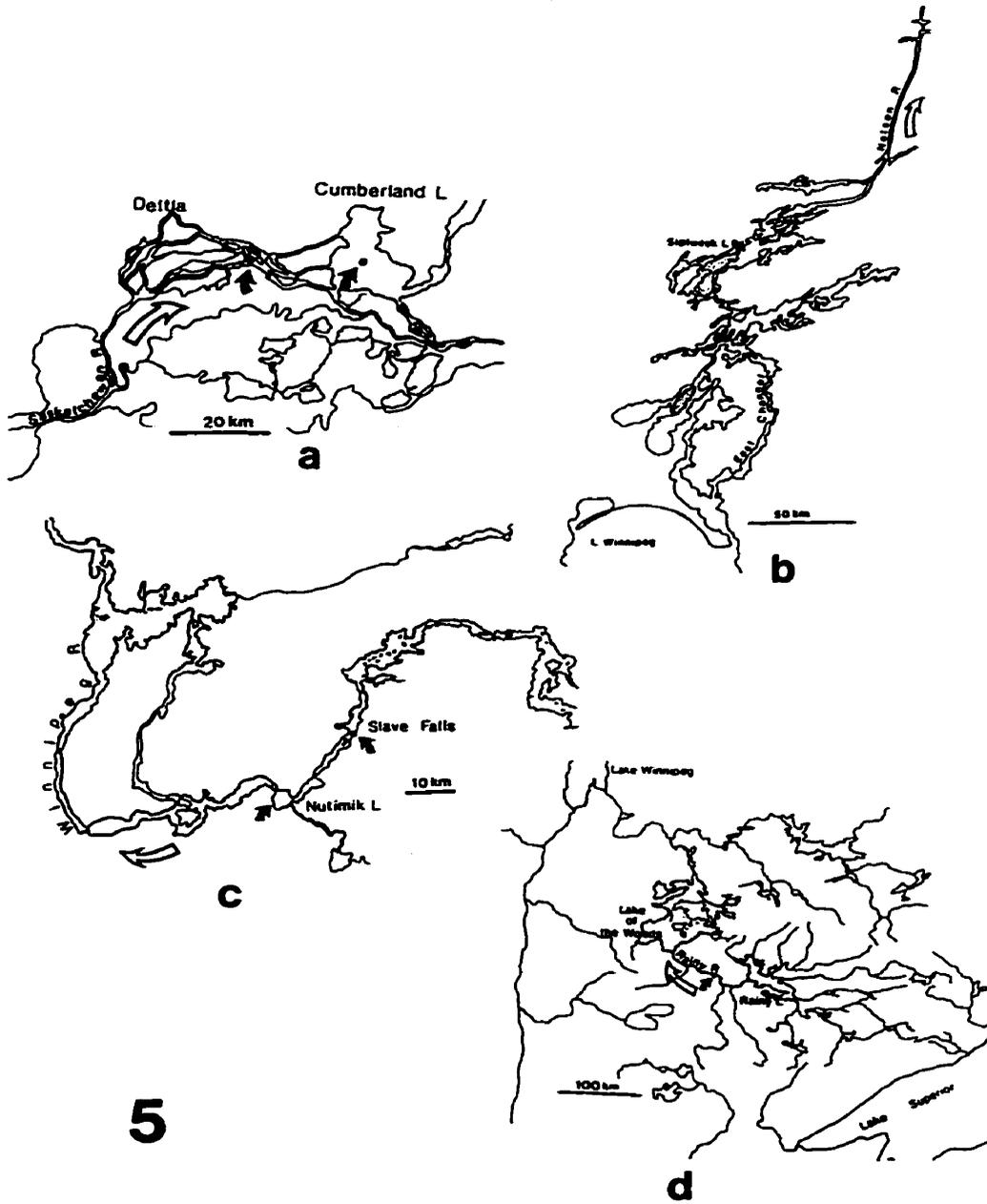


Figure 6. Map of the Lake Winnebago system showing sampling sites for summer samples and YOY fish. Numbers and stippled areas indicate the number of fish sampled from the system. YOY = Young-of-the-year sturgeon.

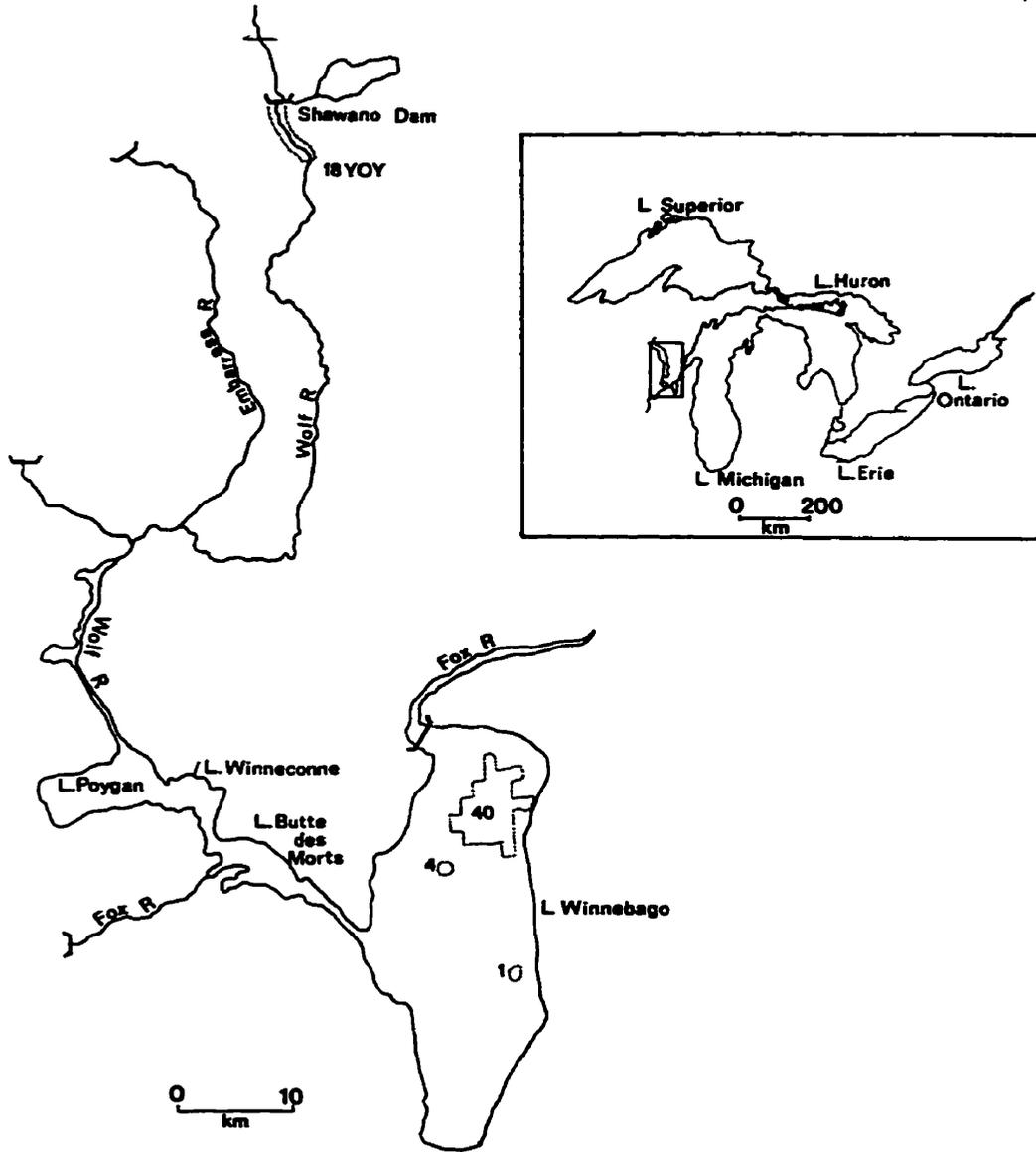


Figure 7. Map of North America showing areas where *Polypodium* has been found in species of *Acipenser* to date ; Ab indicates *Acipenser brevirostrum* from the St. John R. (Canada), Af indicates *Acipenser fulvescens* from the waterways of Central Canada and Lake Michigan, At denotes *Acipenser transmontanus* from the Davis River, California (U.S.A.), Ps denotes the paddlefish *Polyodon spathula*.



Chapter 2. The parasites: Systematics and Biogeography

Chapter 2-1.

Diclybothrium atriatum n. sp. (Monogenea: Diclybothriidae) from North American acipenserid fishes with observations on *D. armatum* and *D. hamulatum*.

INTRODUCTION

Species of Diclybothriidae Bykhovskii and Gusev, 1950 (Monogenea) are polyopisthocotylean gill parasites of acipenseriform fishes (Acipenseridae and Polyodontidae). Three nominal species have been recognized; *Diclybothrium armatum* Leuckart, 1835, from sturgeon in Eurasia and North America, *D. hamulatum* (Simer, 1929), originally described from the N. American paddlefish *Polyodon spathula* (Walbaum), and *Paradiclybothrium pacificum* Bykhovskii and Gusev, 1950, from the green sturgeon, *Acipenser medirostris* Ayres, of the Tartar Strait (Simer, 1929; Price, 1942; Bykhovskii and Gusev, 1950; Bykhovskii, 1957; Skrjabina, 1974; Beverley-Burton, 1984). During the parasite survey in this study (Chapter 1), numerous specimens of a species of *Diclybothrium* Leuckart, 1835 were recovered which was initially identified as *D. armatum*, based on available North American descriptions and reviews of species in this genus (Simer, 1929; Price, 1942; Beverley-Burton, 1984). However, subsequent examination revealed the presence of a glandular structure with a ventral opening leading into a deep crypt surrounded peripherally by deeply staining spherical bodies. This structure as well as the reproductive system was examined on whole mounts and in serial histological sections. The results of these investigations and comparison with Eurasian *D. armatum* and *D. hamulatum* have led me to establish *D. atriatum* as a separate species parasitizing North American acipenserids. Additional observations on the anatomy of the diclybothriids and a cladistic analysis of their phylogenetic relationships are also reported.

MATERIALS AND METHODS

Specimens of *Diclybothrium* were collected from the gills of lake sturgeon from Angling Lake (56°27'N 93°52'W), Sipiwesk Lake (55°27'N 97°35'W), and Nutimik Lake (50°09'N 95°41'W) (all in Manitoba), Manitou Rapids, Rainy River (48°39'N 93°55'W) (in Ontario) and Lake Winnebago (44°01'N 88°25'W) (Wisconsin, U.S.A.). Live specimens were fixed in hot AFA (alcohol-formalin-acetic acid) and previously frozen specimens were fixed in cold AFA after thawing. Specimens of *D. hamulatum* were obtained from the collection of the late Dr. G. Lubinsky, Department of Zoology, University of Manitoba. These had been recovered from the gills of the paddlefish, *Polyodon spathula*, from the Missouri River, North Dakota, U.S.A, and are henceforth referred to as the Lubinsky collection. The specimens had been fixed in formalin and were contracted. Specimens of *Diclybothrium* from lake sturgeon and those of *D. hamulatum* from the Lubinsky collection were stained with Semichon's acetocarmine or Ehrlich's haematoxylin, and cleared and mounted on slides. A total of 30 stained and permanently mounted specimens were used for the description, including 2 museum specimens (USNPC (= US National Parasite Collection) 35287/1509-18 and USNPC 73136/1257-18)]. Measurements of *D. hamulatum* (n=7) were taken from USNPC 50210 (5 specimens), USNPC 51577 and 2 specimens from the Lubinsky collection. Measurements of *D. armatum* were taken from 6 specimens [IZRAS (Institute of Zoology, Russian Academy of Sciences, St. Petersburg) Nos. 1, 2, 3). In addition, 40 specimens of *Diclybothrium* from lake sturgeon from Sipiwesk Lake, Nutimik Lake and Manitou

Rapids (Rainy River), and 4 specimens of *D. hamulatum* (Lubinsky collection) were cleared in hot lactophenol and the opisthaptor squashed prior to measuring haptor hooks/sclerites. The male terminal reproductive structures were dissected out intact as a unit, i.e., cirrus, seminal vesicle, sperm reservoir, and connecting sperm ducts, from 2 specimens of *Diclybothrium* from lake sturgeon to confirm the presence of paired sperm ducts. All measurements are in μm .

Specimens examined

Names of specimens examined and their hosts are from the original labels.

Thus, *Diplobothrium hamulatum* is now *Diclybothrium hamulatum*, *Polystoma armatum* (Leuckart, 1835) Dujardin, 1845 is *Diclybothrium armatum*, and *Acipenser rubicundus* LeSueur is *A. fulvescens* (lake sturgeon). HWML refers to the H.W.

Manter Laboratory, University of Nebraska State Museum, Lincoln, Nebraska, IZRAS refers to Institute of Zoology, Russian Academy of Sciences, St. Petersburg, NHMW refers to Naturhistorisches Museum Wien, Vienna, and USNPC refers to United States National Parasite Collection, Beltsville, Maryland.

Polystoma armatum: NHMW 4144 ex *Acipenser stellatus* (Pallas) (2 partial specimens in alcohol), (old label on bottle crossed out; *Hexacotyle elegans* von Nordmann, 1840).

NHMW 3423: Anterior portion of one worm from NHMW 4144 (above) subsequently stained and mounted on slide.

Diclybothrium armatum: USNPC 35287 ex *Acipenser rubicundus* LeSueur, New York Aquarium. Coll: 28.1.1912, (4 specimens). USNPC 35584 ex *A. rubicundus*, New York Aquarium. Coll: 1912. (10 specimens), USNPC 73136 ex *A. brevirostrum*

LeSueur, Washademoak Lake, St. John R. estuary, New Brunswick, Canada, Coll: 15.12.1977, from the study by Appy and Dadswell (1978), (1 specimen). IZRAS unnumbered ex *A. gueldenstaedti* Brandt, Caspian Sea, 17.8.1931 (det. B. Bykhovskii). (2 specimens). IZRAS unnumbered ex *A. gueldenstaedti*, Volga R., 15.6.1954 (det. A. Gusjew). (4 specimens). IZRAS 10756 ex *Huso dauricus* (Georgi), Amur R., 1.9.1978. (det. Yuchimenko). (3 specimens, immature).

Diplobothrium Leuckart, 1842: HWML 23634 ex sturgeon, Embarass R. Dated: 1/23/56. Deposited by Ralph Bangham. HWML redesignation: "*Diclybothrium armatum* ex *Scaphirhynchus platyrhynchus* (Rafinesque) ?, Embarass R., Illinois". (See Remarks section). (2 slides) (2 specimens).

Diplobothrium hamulatum: USNPC 50210 ex *P. spathula*, Money, Mississippi. Coll: 3/4-16/1927 (?) (4 specimens, vouchers). USNPC 51577 ex *P. spathula*, Money, Mississippi. Coll: 5.3.1927 - 14.8.1927. (1 specimen and 4 slides of serial sections).

Diclybothrium hamulatum: HWML 20494: ex *P. spathula*, Missouri R., Blair, Washington County, Nebraska. (10 specimens).

Paradiclybothrium pacificum: ex *A. medirostris*, Tartar Strait, (1 mounted specimen).

Histology: Specimens of *Diclybothrium* from lake sturgeon (from Angling Lake and Rainy River) were fixed in AFA, washed, dehydrated and embedded in Tissue Prep (Fisher Scientific, Fair Lawn, New Jersey) for sectioning. Embedded specimens were serially sectioned at 6-7 μm thickness in transverse, sagittal, and frontal planes, and stained with Ehrlich's haematoxylin and eosin (Humason, 1979). Histological serial sections are held in the collection of Terry A. Dick and are available for

examination on request. Observations on the histology of *D. hamulatum* are from serial transverse and sagittal sections under USNPC 51577. These were apparently stained with an iron-haematoxylin.

Phylogenetic analysis

A cladistic analysis of the species of Diclybothriidae was carried out. The outgroup is the family Hexabothriidae (Boeger and Kritsky, 1989; Boeger and Kritsky, 1993), a widely distributed, largely marine, family of polyopisthocotylean monogeneans of chondrichthyans, and closely related to the Diclybothriidae (Boeger and Kritsky, 1993; Bykhovskii, 1957). Character states for the hexabothriids were determined with reference to the literature and diagnoses of the family given in Beverley-Burton (1984), Boeger and Kritsky (1989; 1993), Bykhovskii (1957). Characters for the diclybothriids were taken from personal observations on all species and from published information on *P. pacificum* (Bykhovskii and Gusev, 1950)

The following characters and character states were used in the cladistic analysis and a character matrix was developed (Table 12):

1. Haptoral appendix. Two states occur. The appendix is either well developed or extremely reduced (less than half the size of a sucker). A well developed appendix (1-0) is considered plesiomorphic by outgroup comparison while a reduced (vestigial?) appendix is apomorphic (1-1).
2. Posterior extent of the confluent median caecum. Two states occur. The two caeca join medially and this median caecum either extends into the appendix or does not. An extension of the caecum into the appendix (2-0) is considered plesiomorphic by

outgroup comparison while the lack of such an extension is apomorphic (2-1).

3. Prohaptoral bothria. Two states occur. The musculature of the bothria is either weakly developed and the bothria are shallow depressions, or the musculature is very robust and encircles a deep depression. Since hexabothriids do not possess these bothria, the character states in the diclybothriids could not be polarized using the outgroup comparison. Consequently, the two states were assigned 3-1 (for weakly developed bothria) and 3-2 (for well developed bothria), and run unordered.

4. Apical organ. Two states occur. The apical organ is either made up of two weakly developed hemispherical halves or is a single conspicuous organ. Since hexabothriids do not possess such an apical organ, the character states could not be polarized using outgroup comparison. Consequently, two states were assigned 4-1 (for the apical organ with two halves) and 4-2 (for a single apical organ), and run unordered.

5. Position of the vaginal openings. Two states occur. The vaginal openings are either immediately anterior to the vitellaria or not. The position of the vaginal openings in many hexabothriids is at the same level or immediately anterior to the field of the vitellaria. Consequently, the position of vaginal openings in *Diclybothrium* spp. is considered plesiomorphic (5-0) by outgroup comparison while the position in *Paradiclybothrium* (displaced posteriorly) is considered apomorphic (5-1).

6. Body forming distinct 'shoulders' at vaginal openings. Two states occur. The body either widens immediately posterior to the vaginal openings so as to form 'shoulders' or the shape of the body does not change. The absence of such 'shoulders' is considered plesiomorphic (6-0) by outgroup comparison while the presence of

'shoulders' is considered apomorphic (6-1).

7. Ventral atrial organ. Two states occur. A ventral atrial organ is either present or absent. The absence of a ventral atrial organ is plesiomorphic (7-0) by outgroup comparison while the presence is considered apomorphic (7-1).

8. Musculature of the gonopore. Two states occur. The musculature is either simple or with a conspicuously developed concentric pattern. The simple gonopore is considered plesiomorphic (8-0) by outgroup comparison while the robust concentric rings of musculature is considered apomorphic (8-1).

9. Extent of bothrial margins. Two states occur. The musculature bordering the bothria are either along the ventrolateral margins of the body or the bothria are completely ventral. Since hexabothriids do not possess such bothria, the character states could not be polarized. Consequently, the two states were assigned 9-1 (for bothria with marginal musculature) and 9-2 (for completely ventral bothria), and run unordered.

10. Size of paired sperm ducts. Two states were recognized. The paired sperm ducts are either voluminous and occupy a considerable portion of the body anteriorly or not. Hexabothriids do not possess paired sperm ducts, hence the character states could not be polarized by outgroup comparison. Consequently two states were assigned, 10-1 (for unmodified sperm ducts) and 10-2 (for modified sperm ducts), and run unordered.

RESULTS**Diclybothrium atriatum n. sp.**

(Figs. 8-18), Tables 13 and 14.

Description (Based on 30 permanent whole mounts, measurements in μm , measurements of the holotype in parentheses).

Body 5400-18750 (14850) long, maximum width 491-1491 (1291), moderately flattened, consisting of less flattened narrower forebody 873-2127 (1818) long and 382-873 (764) wide (maximum width); body widening immediately posterior to the vaginal openings resulting in bilateral shoulders; body tapering posteriorly, terminating in haptor; haptor 654-1436 (1145) long bearing 6 pedunculate clamps (3 pairs) and terminal haptor appendix with 3 pairs of principal hooks and 1 pair of small hooks. Anterior end of worm with pair of apical organs and paired lateral bothria; left bothria 321-599 (511) long and right bothria 336-599 (540) long. Glandular *ventral atrial organ* (v.a.o) occupying body parenchyma between ovary and ootype, with median ventral opening 1327-3745 (3236) from anterior end; v.a.o possessing deep narrow crypt, widening internally; crypt wall thickened by acellular lining, crypt surrounded by tissue mass of scattered muscle fibres and apparently glandular cells; densely staining small spherical bodies bordering lumen of crypt with lightly staining nuclei of glandular cells extending deeper into parenchyma. Two pairs of dorsal eye spots at level of mouth. Oral opening ventral, medial, simple, between posterior parts of bothria. Gonopore ventral, medial, posterior to oral opening; oral opening leading to short stoma followed by muscular pharynx; pharynx 78-159 (142)

long and 67-133 (133) wide. Oesophagus medial, dividing at level of seminal vesicle to form 2 caeca extending bilaterally along sides of body, uniting posteriorly beyond vitellaria to form terminal median gut segment reaching into haptor; each cecum with smaller irregular lateral diverticula. Ovary consisting of proximal ovoid oogonial chamber (usually dextral); remaining portion of ovary tubular, somewhat convoluted (or folded), opening to oviduct; more distal portions of ovary containing progressively larger and more developed oocytes. Oviduct proximally narrow, widening to thick-walled and conspicuously dilated segment, apparently functioning as seminal receptacle; oviduct continuing forward, dorsolateral to v.a.o, connecting with genito-intestinal canal anterior to v.a.o. Genito-intestinal canal conspicuous. Seminal receptacle absent. Ootype lying medially, deep in body parenchyma, surrounded by loose/diffuse aggregation of gland cells; intensely staining aggregation of acidophilic mucous cells present at base of ootype. Uterus sinuous, medial, straightening immediately before 'shoulder' level of worm, continuing anteriorly along median axis of body, to genital pore. Two bilateral vaginal openings, situated dorso-laterally at posterior end of forebody, 873-2127 (1818) from anterior end. Vagina short and narrow distally, widening and receiving vitelline duct from vitellaria on either side, forming vitello-vaginal duct; conspicuous vitello-vaginal ducts on either side join medially to form common median vitello-vaginal canal. Vitellaria as broad lateral bands of follicles, beginning immediately posterior to vaginal openings and extending beyond testes, vitelline field narrowing posteriorly, occasionally, but sparsely, confluent posteriorly. Eggs ovoid, operculate, 70-217 (165,180) long, 55-136

(125,122) wide. Testes numerous (343), in 2 layers within body, total number increasing with size of worm, situated medially between lateral fields of vitellaria; field of testes beginning immediately behind ovary, occasionally up to 4 testes across single ventral plane, narrowing posteriorly (occasionally to single file); testes extending to short distance ahead of posterior limit of vitellaria. Male copulatory apparatus consisting of muscular cirrus, 261-460 (409) long and 64-131 (124) wide with small ovoid terminal bulb containing inverted spined terminal portion. Cirrus leading to looped duct connecting to posterior pyriform muscular seminal vesicle. Seminal vesicle 139-299 (248) long, 109-226 (204) wide. Lobed sperm reservoir present at posterior end of seminal vesicle. 2 lateral multichannelled sperm ducts, 1 on each side, merging into sperm reservoir ventro-laterally; sperm ducts narrower and deeper posteriorly, becoming larger (increasing number of channels), more ventral, anteriorly; sperm ducts becoming somewhat folded on themselves before emptying into sperm reservoir.

Taxonomic summary

Host: Type host: *Acipenser fulvescens* Rafinesque, 1817. Other host: *A. brevirostrum* Lesueur, 1818.

Site of infection: Gills

Specimens deposited: Total of 30 specimens. Type USNPC 85972 from *A. fulvescens* collected from Sipiwesk Lake, Nelson River system, Canada. Paratypes USNPC 85973 - 85978 from type host from Angling Lake, Sipiwesk Lake, Rainy River (all in Canada) and Lake Winnebago, U.S.A.

Additional designated paratypes: USNPC 35287(1509-18) from lake sturgeon, New York Aquarium, USNPC 73136(1257-18) from shortnose sturgeon, Washademoak Lake, New Brunswick, Canada.

Locality: Type locality: Sipiwesk Lake (Nelson River). Reported from Saskatchewan River, Sipiwesk Lake (Nelson River), Angling Lake, Nutimik Lake (Winnipeg R.), Rainy River, Lake Winnebago. Also from Washademoak Lake, New Brunswick.

Etymology: The specific name *atriatum* is after the diagnostic cavity opening on the ventral side of the body.

Synonyms: *D. armatum* of Stafford (1904), *D. armatum* of Cooper (1915), *D. armatum* of Price (1942), *D. armatum* of Beverley-Burton (1984).

Remarks: Whole mounts of *Diclybothrium* from lake sturgeon from all locations examined and from shortnose sturgeon (USNPC 73136) possess the characteristic ventral atrial organ and therefore belong to *D. atriatum*. The species is North American in distribution and, apparently, freshwater in habit. The original labels of slides with specimens of *Diclybothrium* under HWML 23634 only mention "sturgeon" as the host and do not specify the state in U.S.A. "*Scaphirhynchus platyrhynchus*" and "Illinois" were apparently curatorial additions at the HWML. Bangham (1955) reported "*Diplobothrium hamulatum*" from 1 lake sturgeon from the Embarrass River in Wisconsin. Bangham apparently did not conduct surveys in Illinois (references in Hoffman, 1967) and there are no reports of him having surveyed shovelnose sturgeon. Consequently, these specimens (HWML 23634) are probably

from the lake sturgeon of the Embarrass River in Wisconsin and not from *S. platyrhynchus* of the Embarrass River, Illinois. I was unable to locate any material from Bangham's survey (Bangham, 1955) reporting "*Diplobothrium hamulatum*" from lake sturgeon of Lake Huron. *Diclybothrium hamulatum* is apparently specific for paddlefish (*Polyodon spathula*) and it is likely that Bangham's (1955) report of this species on lake sturgeon actually refers to *D. atriatum*. Examination of NHMW 4144 (*Polystoma armatum*) showed they were *Diclybothrium armatum* (3 partial worms, 2 with posterior halves missing and 1 with anterior end in poor condition). The name on the bottle (*Hexacotyle elegans*) was von Nordmann's nomenclature whereas *Polystoma (Hexacotyle) armatum* on the label inside the bottle was the name given by Dujardin (1845). Although these labels could not be traced back to their sources, the specimens are possibly part of Leuckart's type series.

Observations on other *Diclybothrium* spp

D. hamulatum (Figs. 19-25): Stained whole mounts and serial transverse and sagittal sections of *D. hamulatum*, from the paddlefish (USNPC # 51577, this study) show no trace of the v.a.o. which we describe in *D. atriatum*. The terminal haptor appendix possesses 3 pairs of principal hooks and 1 pair of small hooks.

Histology (USNPC 51577) (Figs. 23-25):

Male reproductive system: Two conspicuous and voluminous multichannelled sperm ducts occupy the midventral field of the body and empty into the lobed sperm reservoir. Cells with densely staining nuclei are occasionally seen within the multichannelled sperm ducts, possibly part of the walls of the ducts. Sperm ducts

narrow posteriorly with concomitant decrease in channels.

Female reproductive system: The oviduct is convoluted and contains a muscular dilated segment (acting as seminal receptacle) and connects to the genito-intestinal canal. The ootype is situated deep in the body. Densely staining mucous cells open at the base of the ootype and sparsely distributed serous cells and possibly muscle tissue surround the ootype. Other structures are similar in arrangement to *D. atriatum*.

D. armatum (Figs. 26-29): A v.a.o. is absent in this species. The cirrus is broad with a broad dome shaped distal bulb. The vitellaria terminate as broad lateral bands beyond the testes. The vitellaria are confluent posteriorly in 2 of the 6 mature specimens, but separate in the other 4. Paired sperm ducts expand anteriorly and connect, laterally, to a reduced and flattened sperm reservoir present behind the seminal vesicle. In 1 specimen, the paired sperm ducts can be traced to the testes and contain sperm through their entire length.

Observations on *P. pacificum*

The morphology of the single specimen examined in this study agrees with the description of Bykhovskii and Gusev (1950) but I was unable to see the haptoral appendix due to the preparation, or the details of the reproductive organs. The anterior ventral bothria, apical organ, muscular gonopore, and distribution of the vitellaria were also as described by Bykhovskii and Gusev (1950).

Phylogenetic analysis

The cladistic analysis of the Diclybothriidae using the characters and states in

Table 12, resulted in a cladogram (Figure 30) which indicates that *Diclybothrium* forms a monophyletic group with *Paradiclybothrium* as sister taxon. The relationships among the *Diclybothrium* spp. could not be resolved cladistically. However, morphological characteristics of the three species (body size, anterior body shape, male reproductive system, robustness of the haptoral sclerites, anterior bothria) suggest that *D. atriatum* and *D. armatum* are more closely related. A combination of the cladogram with these additional characters provides a 'phenogram' (Fig. 31). Information on the distribution, hosts and habit have been added to the cladogram (Fig. 30) for discussion.

DISCUSSION

Early reports of "*Diclybothrium armatum*" from North America (Stafford, 1904; Cooper, 1915, from lake sturgeon) were followed by a redescription by Price (1942) who based his description on worms collected from lake sturgeon at the New York aquarium by MacCallum, and on Stafford's (1904) and Cooper's (1915) collections. His description and illustrations agree in general with our observations on *D. atriatum*, particularly the observation of the densely staining pre-ovarial glandular structure. However, it appears that Price (see Fig. 1M of Price, 1942) interpreted this structure as an ootype "surrounded by a dense mass of unicellular glands" and did not mention a ventral opening. It is clear from our observations that this pre-ovarial structure, which Price (1942) referred to, is not the ootype but the v.a.o (Figs. 8, 11, 12). Although it is not possible to ascribe a function to the organ at this time, the

presence of granular bodies along the periphery of the cavity and the arrangement of cells in the deeper parenchyma suggests a secretory function (Figs. 11, 12). It resembles, superficially, the independent prostatic vesicle found in some Turbellaria (Beauchamp, 1961). Price (1942) also illustrated (Fig. 1M of Price, 1942) the lobed sperm reservoir immediately posterior to the seminal vesicle but did not describe or illustrate the sperm duct(s). It seems certain that the species Price (1942) was 're-describing' was in fact *D. atriatum*. Wright and Dechtiar (1974) added SEM observations on the opisthaptor and the anterior (prohaptoral) region (using the name *D. armatum*) but did not mention nor show the smallest pair of hooks or vestigial clamps on the haptoral appendix (Fig. 11 of Wright and Dechtiar, 1974). Also, SEM photomicrographs (Figs. 1, 3 of Wright and Dechtiar, 1974) of the anterior portion of the parasite did not include the region of the ventral atrial organ. The illustration of *Diclybothrium* by Beverley-Burton (1984) was after Bykhovskii and Gusev (1950), with original observations. Although neither the v.a.o. nor the smallest pair of hooks on the terminal haptoral appendix were illustrated by Beverley-Burton (1984), both structures are present on *D. atriatum* from lake sturgeon (Figs. 8, 9, 10) and shortnose sturgeon (this study). Although we were unable to obtain specimens from Dechtiar's surveys (Dechtiar, 1972; Nepszy, 1988), it seems that all material of *Diclybothrium* from lake sturgeon may be assigned to *D. atriatum*.

Diclybothrium armatum has been described in some detail from Russian material by Skwortzoff (1928, as *D. circularis* (von Linstow, 1904)), and by Bykhovskii and Gusev 1950 (see also Bykhovskii 1957, Skrjabina, 1974, Slyusarev,

1983). Skwartzoff (1928) did not mention any structure resembling (the v.a.o.) and serial sagittal sections (Figs. 8, 9, 10 of Skwartzoff, 1928) do not show this structure. Skwartzoff's observation of the terminal position of the mouth opening is unusual in this family as is the description and illustration (Fig. 4 of Skwartzoff, 1928) of the 2 gut caeca originating immediately following the pharynx. In diclybothriids (including *D. armatum*), the oesophagus bifurcates at about the level of the seminal vesicle (Simer, 1929; Price, 1942; Bykhovskii and Gusev, 1950; this study), and the mouth opens mid-ventrally between the posterior margins of the bothria. Although *D. circularis* may represent a separate species, Skwartzoff (1928) may have mistaken the apical organ for a mouth opening. A similar error seems to have been made in the illustration of von Linstow (1904) and of Lavrov (1907). In addition, Skwartzoff's (1928) sagittal sections clearly show a more posterior bifurcation of the gut caeca. Bykhovskii and Gusev (1950) did not mention nor illustrate any v.a.o. in *D. armatum* (see also Bykhovskii, 1957) and specimens of *D. armatum* examined in this study also did not possess this structure (Fig. 27). A v.a.o. was not mentioned or illustrated in *D. hamulatum* by Simer (1929) or by Bykhovskii and Gusev (1950), and our observations of whole mounts and serial histological sections (USNPC 51577) confirm that such a structure does not exist in *D. hamulatum*.

The female reproductive system in all three species of *Diclybothrium* is basically similar (Figs. 8, 17, 19, 26, 28) and resembles that of the polystomes and some hexabothriids, particularly in the absence of a seminal receptacle and modification of the oviduct for sperm storage (Rohde and Ebrahimzadeh, 1969;

Boeger and Kritsky, 1989). In addition, the distribution of mucous glands at the base of the ootype and the possible serous glands is similar to that found in some polystomes (Kohlmann, 1961; Rohde and Ebrahimzadeh, 1969; Kearns, 1986). The shape of the eggs is variable in *D. atriatum* (sometimes even in the same individual) and in *D. hamulatum*, and is not a suitable character to distinguish the 2 species. Vitellaria were found to be confluent posteriorly in all specimens of *D. hamulatum* examined, but this condition is variable in *D. armatum* and *D. atriatum*. Confluent vitellaria are more common in *D. armatum* than in *D. atriatum*.

The male reproductive system deserves special mention because of the occurrence of paired sperm ducts in this family. Bykhovskii and Gusev (1950) illustrated a single median sperm duct (vas deferens) in their description of *D. armatum*, but we were unable to identify such a duct in specimens of this species examined in this study. Instead, paired sperm ducts were observed (Fig. 26) which appeared similar to those found in *D. atriatum*. *Paradicybothrium pacificum* was also described as possessing 2 sperm ducts (Bykhovskii and Gusev, 1950). The photomicrograph of a transverse section through *P. pacificum* (Fig. 10 of Bykhovskii and Gusev, 1950) shows the paired 'seminal ducts' which correspond in anatomical position to paired sperm ducts seen in transverse sections of *D. atriatum* and *D. hamulatum* (this study). Skwartzoff (1928) also observed paired tubular structures in cross-sections of *D. armatum*, corresponding in position to the paired sperm ducts seen in sections of *D. atriatum* and *D. hamulatum*. However, Skwartzoff (1928) also illustrated a conspicuous duct in cross-section, dorsal to the uterus (Skwartzoff,

1928), which he identified as the sperm duct, but which may have been a section through a part of the sinuous uterus (see Fig. 16, this study). Paired sperm ducts are apparently characteristic for the family Diclybothriidae. The sperm ducts in *D. hamulatum* are larger and apparently the most developed in the family. This character (paired sperm ducts) seems to be a persistent plesiomorphy since paired sperm ducts are common among Turbellaria with multiple testes (Beauchamp, 1961; Hyman, 1951). All 3 species of *Diclybothrium* possess the sperm reservoir immediately posterior to the seminal vesicle (first described and illustrated by Simer, 1929, in *D. hamulatum*) although it appears flattened and reduced in *D. armatum*. Judging from the description and illustrations of *D. circularis* (= *D. armatum*) by Skwartzoff (1928), it seems likely that Skwartzoff observed the sperm reservoir behind the seminal vesicle, but called it "Druesen?" (transl. = glands). The cirrus in *D. armatum* is more robust than in the other species (Figs. 18, 22, 29), whereas in *D. hamulatum* the cirrus is reduced as is the terminal spination. Additional observations on the haptoral appendix are also of diagnostic value at the genus and species level. The pair of smallest hooks previously reported from *D. armatum* (Bykhovskii and Gusev, 1950), are also present in *D. atriatum* and *D. hamulatum* (this study) and, therefore, are common to all *Diclybothrium* spp. The lateral pseudosuckers are more extensive, relative to the haptoral appendix, in *D. armatum* and *D. hamulatum* than in *D. atriatum* (Figs. 10, 21, 27). The haptoral sclerites of the haptoral appendix, particularly the outer and middle sclerites, are also more robust in *D. hamulatum*.

Phylogenetics and biogeography

The cladogram (Fig. 30) indicates the monophyletic nature of *Diclybothrium*. Relationships among the species of *Diclybothrium* could not be fully resolved since many of the synapomorphic character states could not be polarized (e.g., the morphology of the male reproductive structures). The 'phenogram' (Fig. 31) which was produced by combining this cladogram with other morphological characters not used in the cladistic analysis, suggests that *D. armatum* and *D. atriatum* are most similar to each other which may indicate sister-taxon relationships. *Paradiclybothrium* is unique among diclybothriids in its apparent specificity for the North Pacific green sturgeon (*A. medirostris*). This specificity and consequently a marine habit and restricted geographical range, combined with its unique morphology indicates a local speciation event associated with the evolution of the green sturgeon in the North Pacific basin.

The recognition of *D. atriatum* as a distinct species and its apparent specificity for *A. fulvescens* and *A. brevirostrum* in North America has significance concerning the evolution of the diclybothriids and suggests that speciation of *D. atriatum* occurred following the possible isolation of freshwater/estuarine *Acipenser* spp. in North America. These observations now enable us to develop hypotheses regarding the historical biogeography of host-parasite relationships between diclybothriids and their acipenserid hosts. Previous interpretations of the historical biogeography of the Diclybothriidae (Beverly-Burton, 1994) were based on the premise that only one species, *D. armatum*, was widely distributed in sturgeons throughout Eurasia and North America. Accordingly, Beverley-Burton (1994) hypothesized that *D. armatum*

was present in freshwater sturgeons across the holarctic regions during the Tertiary (time unspecified) and was subsequently isolated on the North American continent when the Palaearctic and Nearctic lineages of sturgeons separated. The presence of "*D. armatum*" on shortnose sturgeon was hypothesized to be a transfer "to a population of *A. brevirostrum* that was tied to a freshwater life cycle" (Beverley-Burton, 1994) and *D. hamulatum* was interpreted as a host switch from sympatric *Acipenser* spp. in the Mississippi and subsequent speciation on *Polyodon*. Although the cladistic analysis suggests the possibility of a 'host capture' in paddlefish, the association of *D. atriatum* with *A. fulvescens* and *A. brevirostrum* may have been a speciation event independent of the association of *D. hamulatum* with the paddlefish (see Chapter 3).

Table 12. Character matrix for the cladistic analysis of the Dicylbothriidae.

Characters Taxa	1	2	3	4	5	6	7	8	9	10
Hexabothriidae	0	0	-	-	0	0	0	0	-	-
<i>P. pacificum</i>	1	1	2	2	1	0	0	1	2	1
<i>D. armatum</i>	0	0	1	1	0	1	0	0	1	1
<i>D. hamulatum</i>	0	0	1	1	0	1	0	0	1	2
<i>D. atriatum</i>	0	0	1	1	0	1	1	0	1	1

- = Characters not found in the Hexabothriidae.

Table 13. Measurements of *Diclybothrium atriatum* and comparisons with *D. armatum* and *D. hamulatum*.*

	<i>D. atriatum</i> (n=30)	<i>D. hamulatum</i> (n=7)	<i>D. armatum</i> (n=6)
Length:	11946 ± 3178 (5400-18750)	4976 ± 768 (3950-6100)	7429 ± 1095 (6850-9375)
Width:	959 ± 253 (491-1491)	764 ± 141 (545-982)	1027 ± 231 (727-1273)
Forebody l	1533 ± 339 (873-2127)	849 ± 179 (545-1073)	963 ± 121 (836-1127)(n=4)
Forebody w	659 ± 151 (382-873)	512 ± 59 (436-582)(n=7)	782 ± 83 (691-891)(n=4)
Bothria (left)	450 ± 67 (321-599)	215 ± 19 (191-244)(n=6)	379 ± 30 (358-401)(n=2)
(right)	450 ± 70 (336-599)	213 ± 22 (180-235)(n=5)	387 ± 76 (299-438)(n=3)
Pharynx†	430 ± 80 (299-620)	215 ± 37 (180-277)(n=6)	294 ± 57 (219-358)(n=4)
Pharynx l	123 ± 23 (78-159)(n=28)	102 ± 10 (87-116)	104 ± 11 (93-119)(n=5)
Pharynx w	109 ± 20 (67-133)	86 ± 10 (72-104)	90 ± 18 (60-110)(n=5)
Cirrus l	381 ± 60 (261-460)(n=29)	203 ± 40 (136-232)(n=5)	350 ± 51 (277-416)
Cirrus w	113 ± 17 (64-131)(n=26)	94 ± 10.4 (84-107)(n=5)	195 ± 16 (175-212)
Sem vesicle l	228 ± 36 (139-299)(n=28)	210 ± 42 (154-277)	253 ± 63 (197-270)
Sem vesicle w	182 ± 27 (109-226)	170 ± 28 (130-194)	220 ± 38 (182-277)
Ventral atrial opening†	2505 ± 607 (1327-3745)	-	-
Haptor length:	1027 ± 174 (654-1436)(n=29)	600 ± 52 (545-709)	858 ± 92 (727-982)(n=5)
Eggs:			
l	168 ± 28 (70-217)(n=34)	140 ± 13 (119-154)(n=5)	(145-148)(n=2)
w	107 ± 17 (55-136)	83 ± 10 (72-99)	(107-110)

* Mean ± S.D. (range) in µm. Source of specimens are given in Materials and Methods.

†Distance from anterior end.

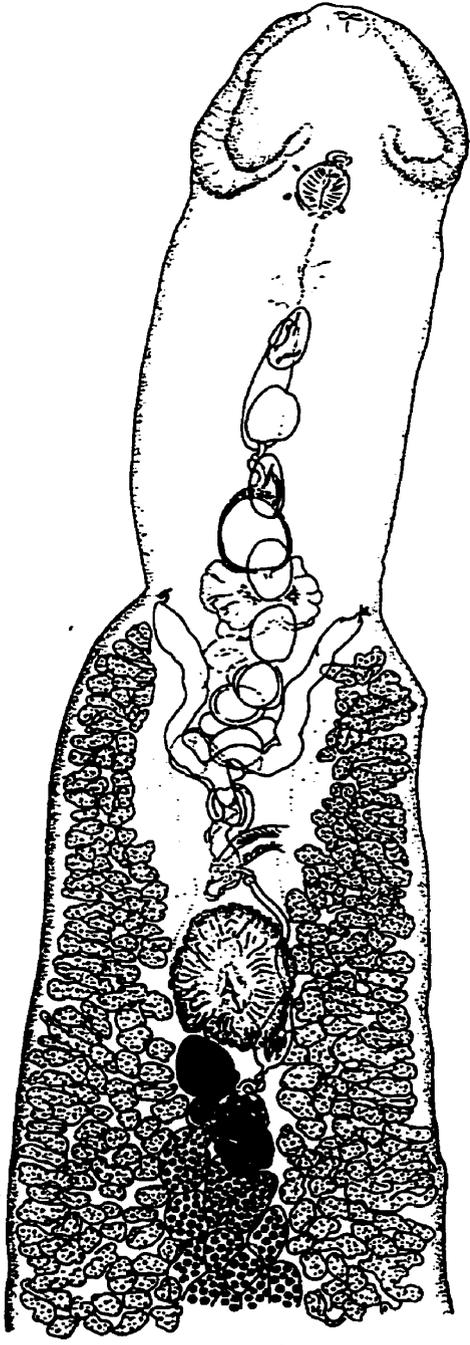
Table 14. Measurements of sucker and appendicular sclerites of the opisthaptor in *D. atriatum*, *D. hamulatum*, and *D. armatum*.*

	<i>D. atriatum</i> (n=40)	<i>D. hamulatum</i> (n=4)	<i>D. armatum</i> (B&G)
Body length	10435 \pm 4147 (5030-19225)	(4100-5500)†	(4000-23000)
Sucker sclerites:			
Anterior			(440-630)
left	565 \pm 111 (200-730)	412 \pm 17 (390-430)	
right	573 \pm 108 (400-780)	420 \pm 23 (400-450)	
Middle		(440-630)	
left	596 \pm 83 (450-740)	412 \pm 17 (390-430)	
right	604 \pm 92 (430-780)	441 \pm 31 (405-480)	
Posterior			(430-630)
left	604 \pm 92 (360-760)	424 \pm 35 (375-460)	
right	616 \pm 89 (460-800)	425 \pm 45 (360-460)	
Appendicular Sclerites:			
Outer			(200-360)
left	439 \pm 55 (320-540)	360 \pm 36 (330-400)	
right	442 \pm 53 (350-560)	345 \pm 26 (310-370)	
Middle			(260-440)
left	602 \pm 47 (510-700)	550 \pm 47 (510-600)	
right	609 \pm 54 (500-700)	555 \pm 34 (510-590)	
Inner			(80-100)
left	121 \pm 16 (100-150)	117 \pm 5 (110-120)	
right	122 \pm 16 (100-150)	125 \pm 6 (120-130)	

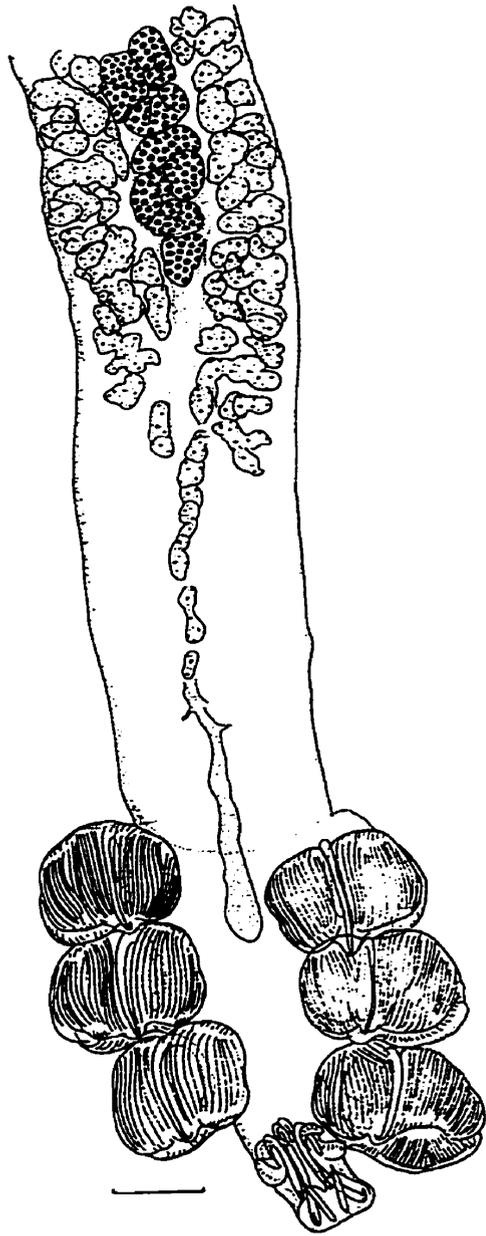
* Mean \pm S.D. (range) in μm . B&G = Data from Bykhovskii and Gusev (1950).

†Anterior ends of worms damaged. Approximate size range of post-vaginal distances.

- Figure 8. *Diclybothrium atriatum*. Holotype, Anterior portion showing bothria, ventral atrial organ, digestive and reproductive structures. Scale bar = 200 μm .
- Figure 9. *Diclybothrium atriatum*. Holotype, posterior portion showing testes, vitellaria and opisthaptor. Scale bar = 200 μm .

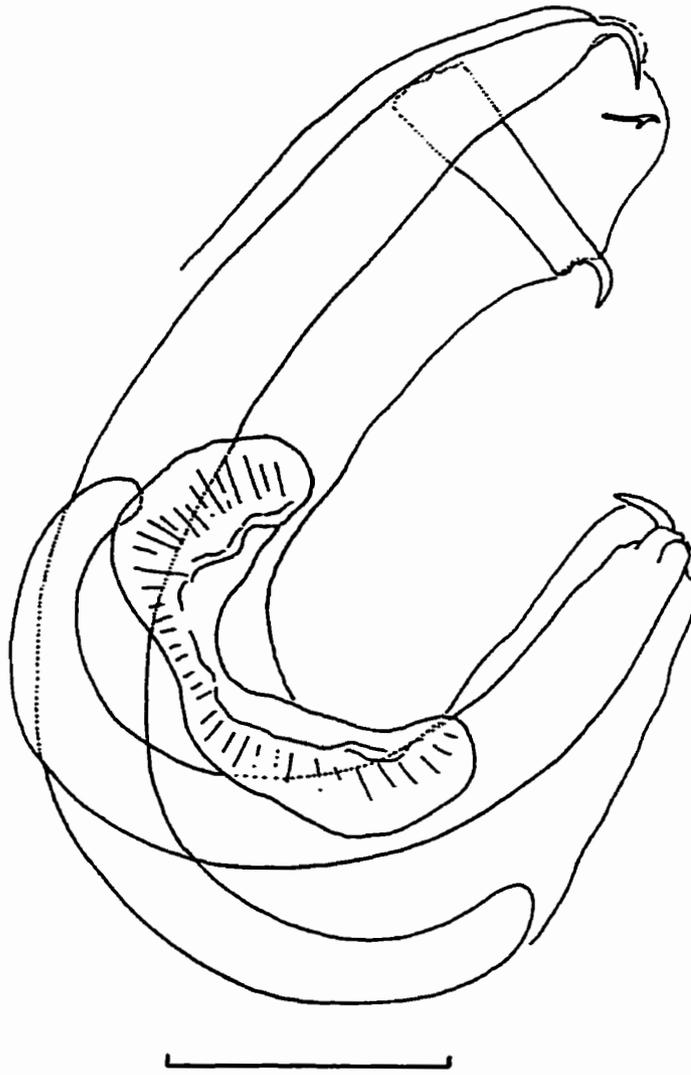


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Figure 10. *Diclybothrium atriatum*. One side of terminal appendix of opisthaptor showing hooks and lateral pseudosucker (lateral view) Scale bar = 100 μm .



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- Figure 11. *Diclybothrium atriatum*. Transverse section through the ventral atrial organ showing crypt (c) with thickened lining, dense granular bodies (small arrows) and deeper gland-like cells (large arrows). Note oviduct (od), vitellaria (v) and gut (g). Scale bar = 100 μm .
- Figure 12. *Diclybothrium atriatum*. Sagittal section through the ventral atrial organ showing laterally widened cavity at its base (arrow). Note ovary (o) and uterus (u). Scale bar = 100 μm .
- Figure 13. *Diclybothrium atriatum*. Sagittal section showing the positions of the ovary (o), ootype (ot), uterus (u), 2 layered testes (t) and ventral atrial organ (vao). (sectional plane passing through the edge of vao). Scale bar = 100 μm .
- Figure 14. *Diclybothrium atriatum*. Magnification of boxed area in Fig. 13 showing the distribution of mucous glands (large arrows) and serous glands (small arrows) around ootype (ot). Note uterus (u) with eggs (e). Scale bar = 100 μm .
- Figure 15. *Diclybothrium atriatum*. Cross section showing paired sperm ducts (s) merging (arrows) into sperm reservoir (r). Scale bar = 100 μm .
- Figure 16. *Diclybothrium atriatum*. Cross section through the anterior portion of the parasite showing paired multichannelled sperm ducts (arrows), uterus (u) with egg (e) and vitellovaginal ducts (v). Scale bar = 100 μm .

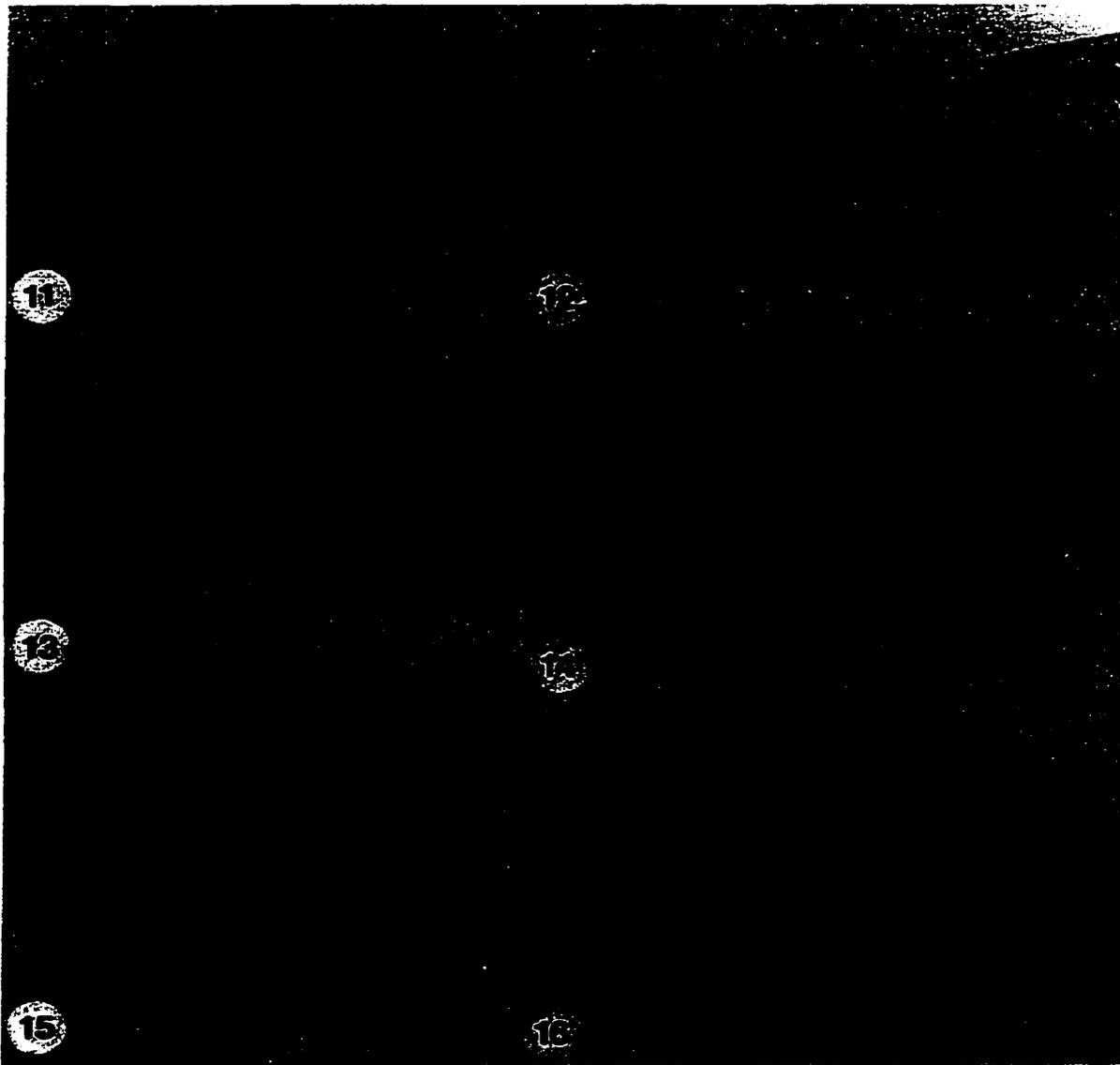
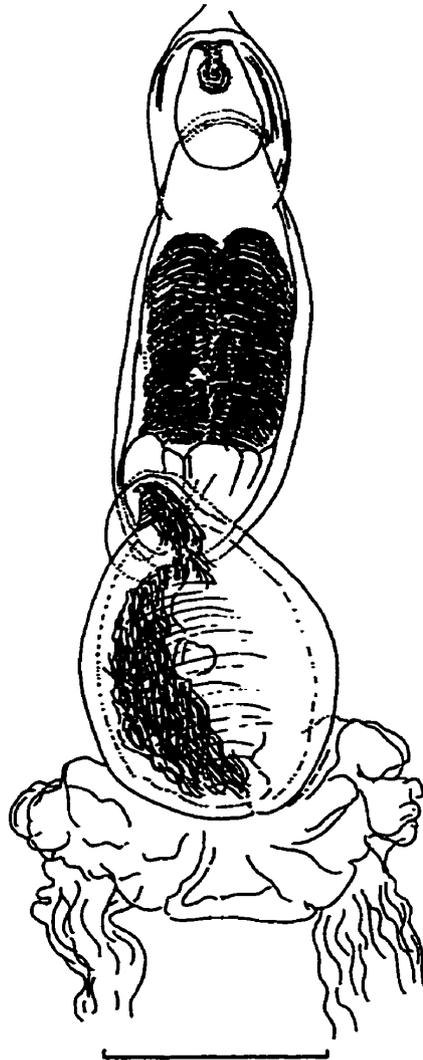


Figure 17. *Diclybothrium atriatum*. Reconstruction of female reproductive apparatus from whole mounts and serial histological sections.

Figure 18. *Diclybothrium atriatum*. Male reproductive apparatus showing cirrus, seminal vesicle, sperm reservoir and paired sperm ducts. Scale bar = 100 μm .



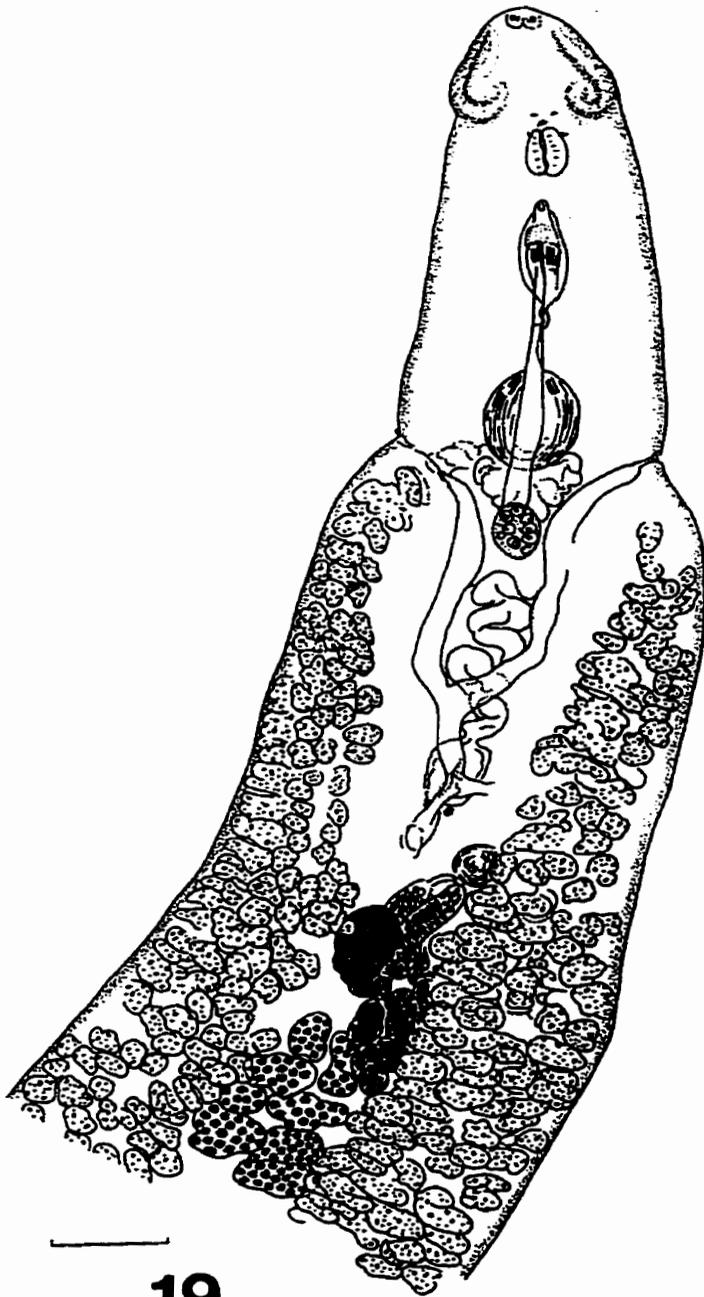
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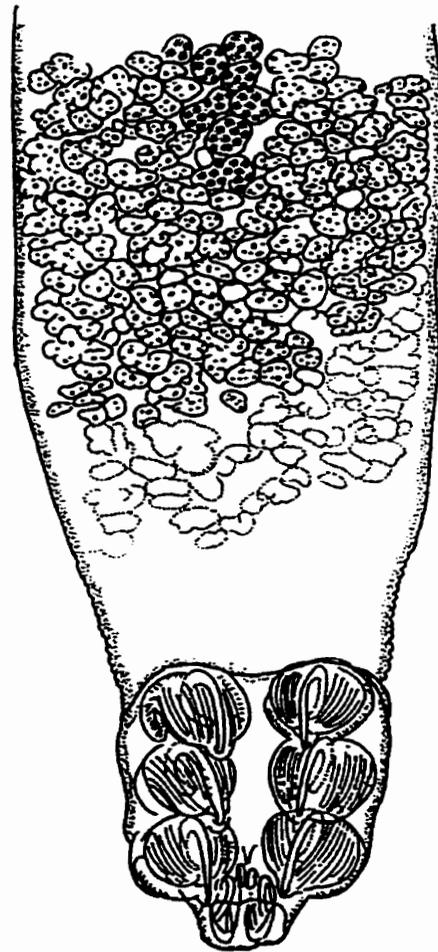
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Figure 19. *Diclybothrium hamulatum*. USNPC 50210. Anterior portion of worm showing bothria, digestive and reproductive structures. Scale bar = 200 μm .

Figure 20. *Diclybothrium hamulatum*. USNPC 50210. Posterior portion of worm showing confluent vitellaria and opisthaptor. Scale bar = 200 μm .

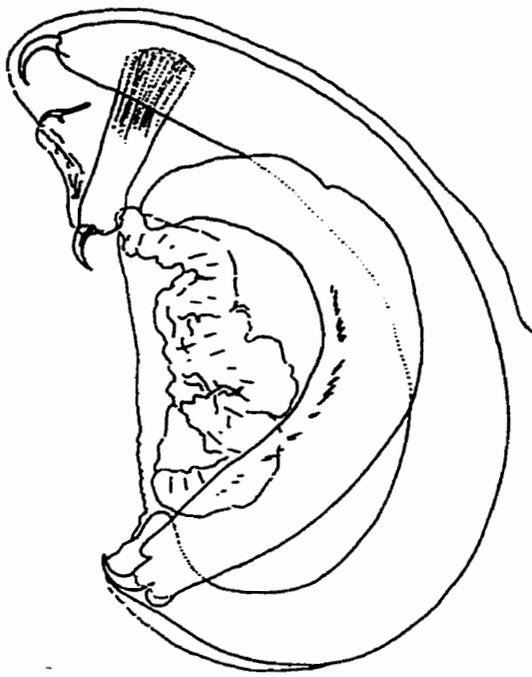


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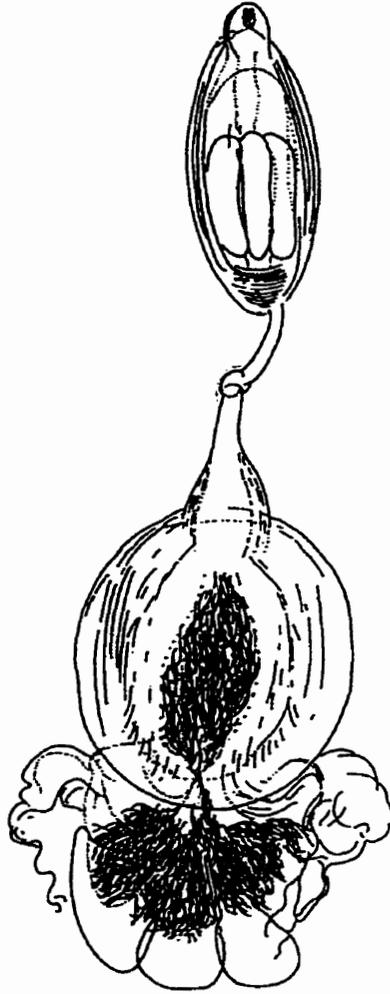


20

- Figure 21. *Diclybothrium hamulatum*. One side of terminal appendix of opisthaptor showing hooks/sclerites and lateral pseudosucker (lateral view). Scale bar = 100 μm .
- Figure 22. *Diclybothrium hamulatum*. Male reproductive apparatus showing cirrus, seminal vesicle and sperm reservoir. Scale bar = 100 μm .



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- Figure 23. *Dicybothrium hamulatum*. USNPC 51577. Transverse section through anterior region showing large paired sperm ducts (arrows), vitellovaginal ducts with vitelline cells (vc) and uterus (u) with collapsed egg (e). Note gut (g). Scale bar = 100 μm .
- Figure 24. *Dicybothrium hamulatum*. USNPC 51577. Transverse section through more posterior region of the sperm ducts (arrows) showing their smaller size and the vitello-vaginal ducts (v) prior to fusing. Note gut (g). Scale bar = 100 μm .
- Figure 25. *Dicybothrium hamulatum*. USNPC 51577. Sagittal section showing distribution of mucous glands (large arrows) and serous glands (small arrows) around ootype (ot). Note ovary (o) and uterus (u). Scale bar = 50 μm .

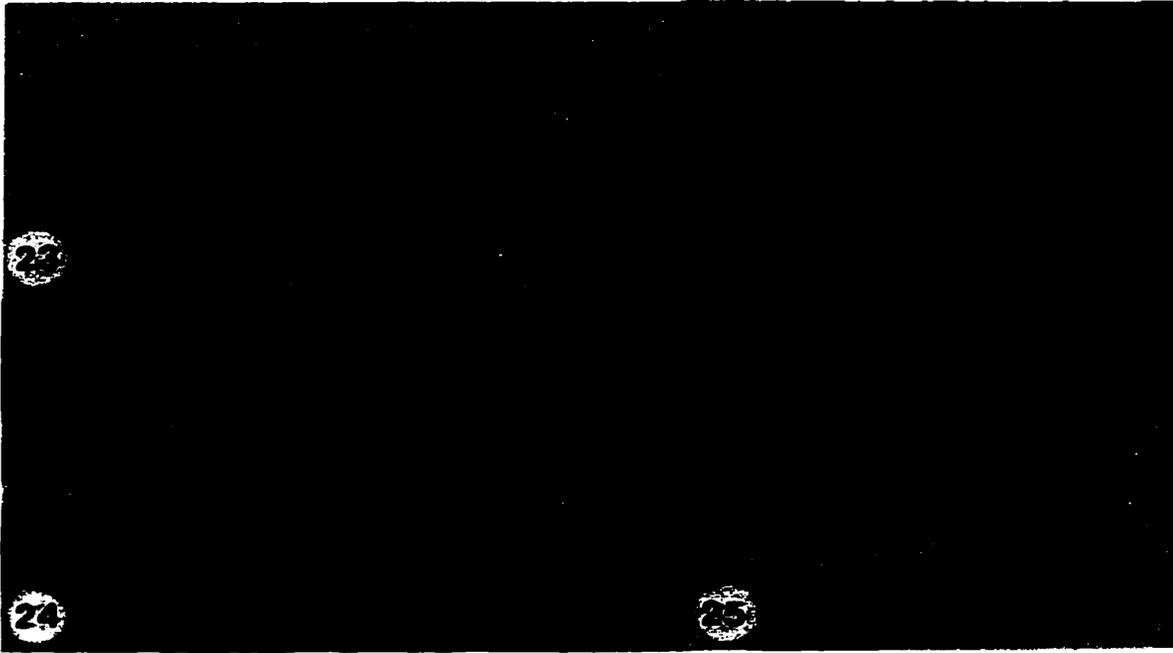
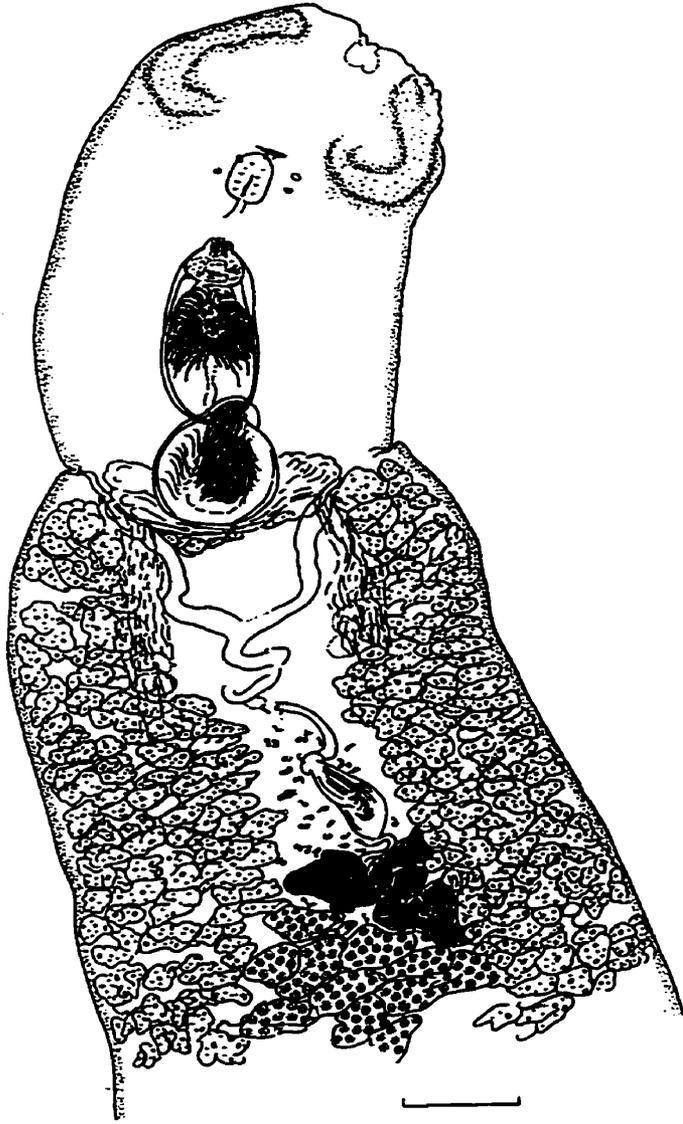
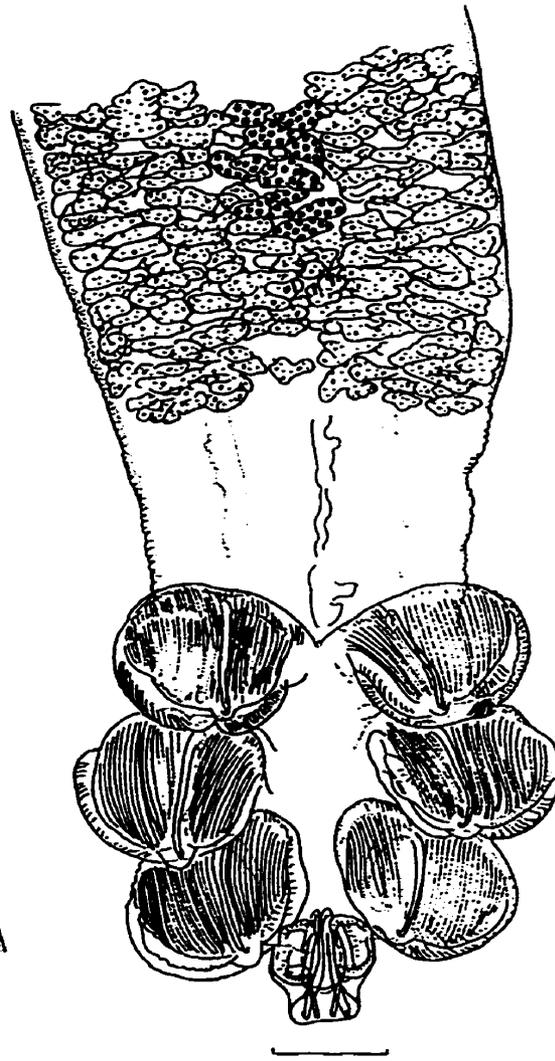


Figure 26. *Diclybothrium armatum*. IZRAS 2. Anterior portion of worm showing bothria, digestive and reproductive structures. Note absence of ventral atrial organ. Scale bar = 200 μm .

Figure 27. *Diclybothrium armatum*. IZRAS 2. Posterior portion of worm showing confluent vitellaria and opisthaptor. Scale bar = 200 μm .

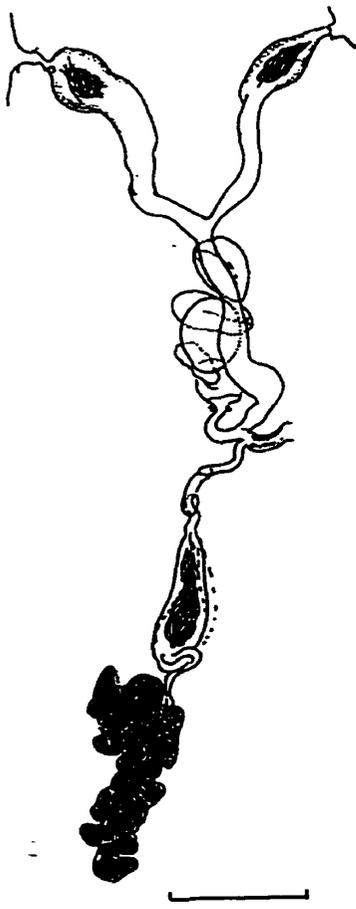


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- Figure 28. *Diclybothrium armatum*. IZRAS 1. Female reproductive system in a relaxed specimen. Scale bar = 100 μm .
- Figure 29. *Diclybothrium armatum*. IZRAS 1. Male terminal reproductive structures and paired multichannelled sperm ducts. Scale bar = 100 μm .



28



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Figure 30. Cladogram showing relationships among species of *Diclybothriidae*. Characters and states are defined in text and in Table 12.

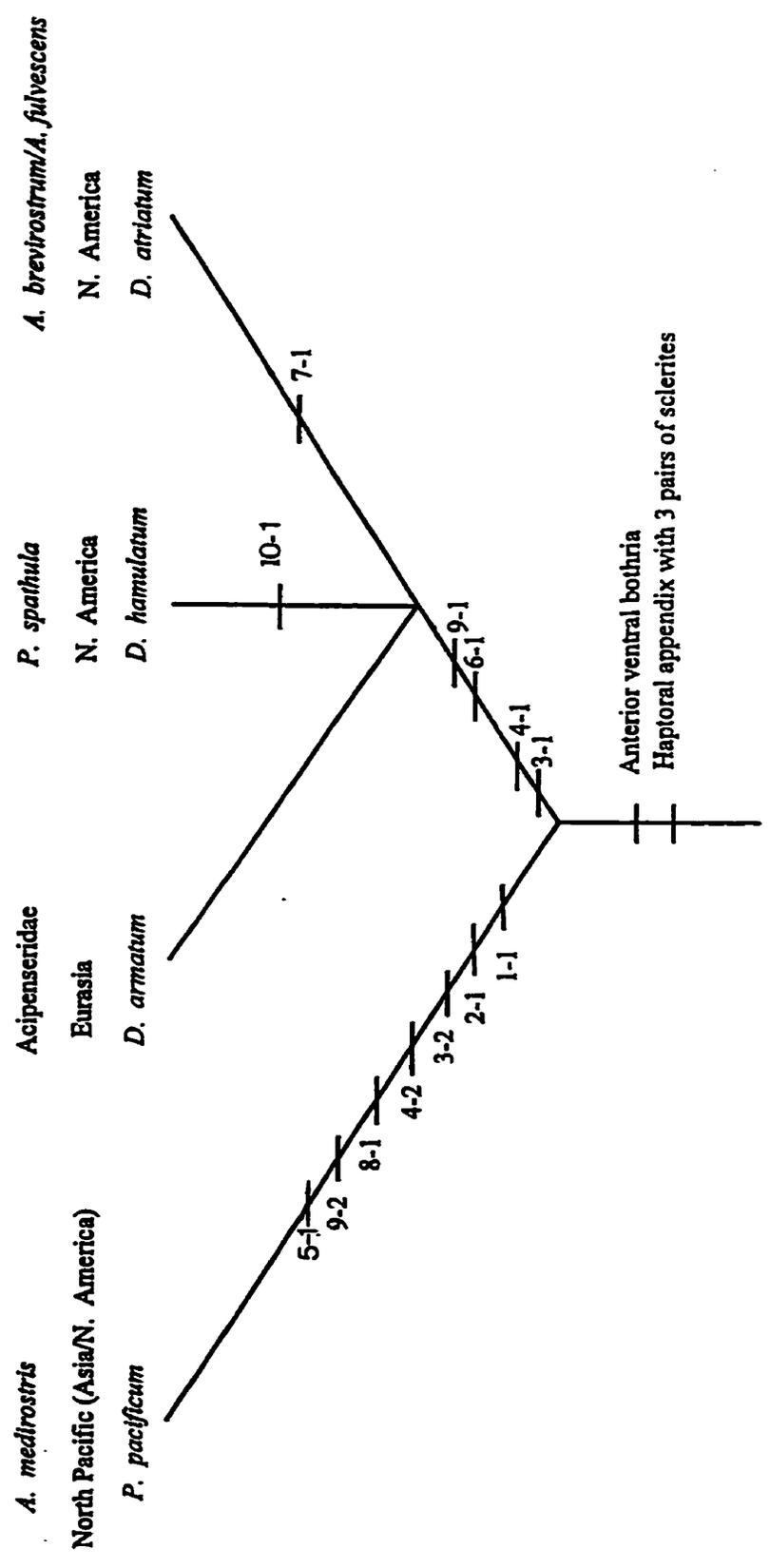


Figure 31. Phenogram of the species of *Diclybothriidae* based on the cladogram in Fig. 30.

Family: Diclybothriidae

N. Pacific

A. medirostris

P. pacificum

N. America

P. spathula

D. hamulatum

Eurasia

Huso spp.

Acipenser spp.

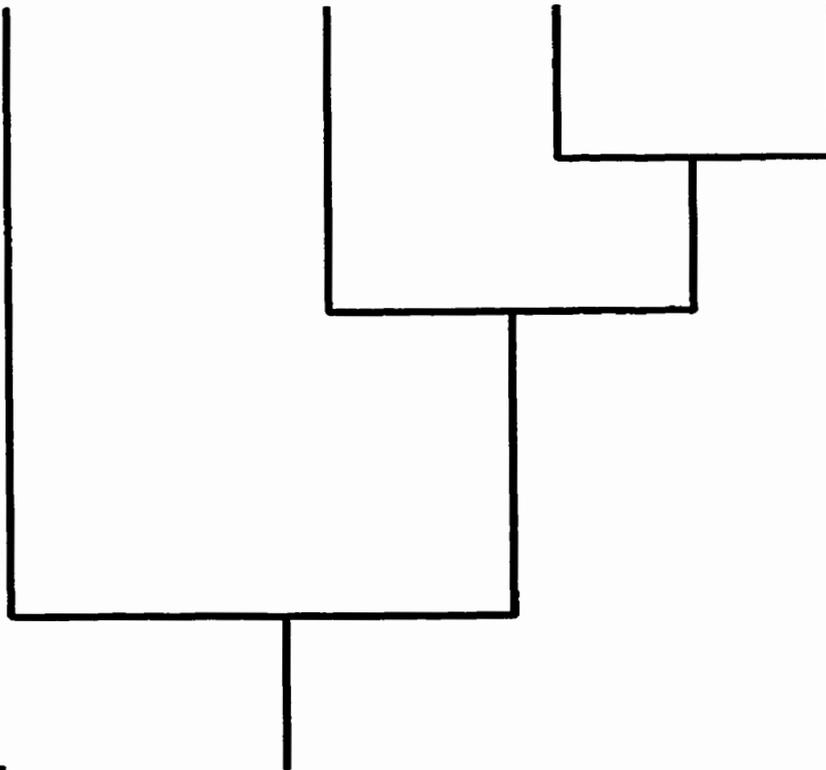
D. armatum

N. America

A. brevirostrum

A. fulvescens

D. atriatum



Chapter 2.2.

Systematics and biogeography of *Skrjabinopsolus manteri* (Digenea: Deropristiidae) and relationships within the Deropristiidae.

INTRODUCTION

The genus *Skrjabinopsolus* Ivanov 1934 (in Ivanov & Murygin 1937) has a wide distribution in acipenserids (sturgeons) of the basins and waterways of eastern Europe (mainly Mediterranean-Ponto-Caspian), and those of eastern North America. Two nominal species have been recognized; *S. semiarmatus* (Molin, 1858) parasitizes European freshwater and anadromous acipenserids (Bykhovskaya and Kulakova, 1987; Skrjabina, 1974) and *S. manteri* (Cable, 1952) occurs in North American freshwater acipenserids (Cable, 1952; McDonald and Margolis, 1995; Chapter 1). *S. manteri* has been distinguished from *S. semiarmatus* on the basis of a larger size of the body and widely separated testes (Skrjabina, 1974) as well as by the anterior position of the ovary (Peters, 1961). However, during the study of lake sturgeon parasites from lake Winnebago, U.S.A. (Chapter 1), I recovered numerous specimens of *Skrjabinopsolus* which showed variability in morphological characters considered diagnostic in the past. A re-examination of both species, from European sturgeons and from the type material of *S. manteri*, also revealed considerable variability in the position of the testes and ovary (Cable, 1952; Skrjabina, 1974). Consequently, diagnostic characters were compared across samples from different geographical locations in North America and Europe to evaluate the relationship and morphological divergence between *S. semiarmatus* and *S. manteri*. Although Cable (1952) and Cable and Hunnien (1942) considered the genus *Skrjabinopsolus* as having a basic 'bauplan' from which other related species (e.g., *Deropristis* spp. and *Pristicola sturionis* Little, 1930) could be derived, the deropristiids have not been subject to any phylogenetic analysis.

Furthermore, since Cable's (1952) account, the addition of *Cestrahelminis* to the Deropristiidae (Fischthal, 1957; Becker, 1971) has extended the range of the family to the Pacific coastal waterways. The specificity of most deropristiids for a geologically old and relict host group such as acipenserids (sturgeons) provides an opportunity to investigate their marine or freshwater origins and the effects of vicariance and dispersal on their evolution. Furthermore, the presence of two species of deropristiids in Atlantic eels and pike raises interesting questions concerning host switching in this group of digeneans. To address these questions, the evolutionary relationships of the various species of deropristiids were investigated using cladistics (Hennig, 1966; Wiley, 1981, Wiley et al., 1991). This forms the basis for evaluating further hypotheses regarding the historical biogeography of the Deropristiidae and their hosts.

MATERIALS AND METHODS

Specimens examined

The following museum specimens were examined:

Skrjabinopsolus semiarmatus. CSAV. No. Coll. D-113. ex sterlet, *Acipenser ruthenus*, R. Danube, Strevo, Slovakia, (n=14). NHMW 4256 [as *Distomum hispidum* (Abildgaard)] ex *Acipenser sturio*, unknown locality, (n=6). NHMW 1832, NHMW 1833, ex *Acipenser ruthenus*, R. Danube, Vienna, (n=4).

Skrjabinopsolus sp. ex lake sturgeon, *Acipenser fulvescens*, L. Winnebago, Wisconsin, U.S.A. (this study, see Chapter 1), (n=21).

S. manteri (Cable, 1952). HWML 1853. Paratype. ex *Scaphirhynchus platyrhynchus*,

Wabash R. Illinois, U.S.A. ; USNPC 37187 ex *S. platorynchus*, Wabash R. Illinois, U.S.A. (6 paratypes).

Deropristis hispida (Abildgaard). USNPC 8198 ex *Acipenser sturio* (actually *A. oxyrhynchus*), Woods Hole, Massachusetts, (n=2), USNPC 51976 ex *A. sturio* (actually *A. oxyrhynchus*) Woods Hole, Massachusetts, (n=5), USNPC 73137 ex *A. oxyrhynchus*, St. John Harbor, New Brunswick, Canada (n=2), USNPC 73859 ex *A. oxyrhynchus*, Raritan Bay, New Jersey, U.S.A.,(n=1).

Deropristis inflata (Molin): USNPC 51951 (as *Deropristis hispida*) ex American eel, *Anguilla rostrata*, Woods Hole, Massachusetts, (n=3), CSAV D-90 ex European eel, *Anguilla anguilla*, Nile River, Cairo, Egypt, (n=2). HWML 1851. ex. *Anguilla chrysopa* (= *A. rostrata*), Wood's Hole, Massachusetts. One voucher specimen. NHMW 1834 and 1835. (as *Distomum inflatum* Molin) ex *Anguilla vulgaris* (= *A. anguilla*), Triest, (n=14). *Cestrahelminis laruei* Fischthal, 1957. USNPC 55234. ex. *Esox masquinongy*, Teal Lake, Sawyer County, Wisconsin, U.S.A. (n=6, including 2 sectioned).

Cestrahelminis rivularis Becker, 1971. USNPC 71431 ex. *Acipenser transmontanus*, Central Columbia R., Washington State, U.S.A., (n=3).

Homalometron armatum (MacCallum, 1895). Specimens collected from *Aplodinotus grunniens* from the Red River, Manitoba, at Lockport (caught by angling), (n=12) stained and mounted as for other deropristiids in this study.

CSAV refers to Czech Academy of Sciences, Vermes Section, HWML refers to the Harold W. Manter Laboratory of the Nebraska State Museum, NHMW refers to the

Naturhistorisches Museum, Vienna, and USNPC refers to the United States National Parasite Collection, Bethesda, Maryland, U.S.A.

Phylogenetic Analysis

A hypothesis of the phylogenetic relationships within the Digenea by Brooks *et al.*, (1985, 1989) has been criticized by Gibson (1987), Pearson (1992) and Gibson and Bray (1994). Taking into account these criticisms, the phylogenetic tree of Brooks *et al.*, (1985) remains unchanged with respect to the relationships among the Deropristiidae, Lepocreadiidae and Homalometridae which form a monophyletic assemblage, the Lepocreadiiformes of Brooks *et al.*, (1985). Consequently, the Homalometridae and Lepocreadiidae are used as outgroups for a phylogenetic analysis of the Deropristiidae. Diagnostic characteristics of the outgroups were obtained by examination of *H. armatum* and by reference to Gibson (1996) (see also references therein) and Yamaguti (1971).

Characters and states used for phylogenetic analysis:

Outgroups are Homalometridae Mehra, 1962 and Lepocreadiidae Nicoll, 1934. The character matrix is provided in Table 15.

1. Body shape: Two states are recognized; forebody expanded in the cervical region or not. The presence of cervical expansions is considered apomorphic (1-1) by outgroup comparison while the absence of such modifications is plesiomorphic (1-0).
2. Morphology of cervical spines: Two states are recognized. Spines uniform in shape or dimorphism in spination with heavy spines along lateral margins of body. The first is considered plesiomorphic (2-0) while the second is apomorphic (2-1) by outgroup

comparison.

3. Oral spines: Two states are recognized. Oral sucker with heavy peg like spines or not. The first is considered apomorphic (3-1) while the second is considered plesiomorphic (3-0).

4. Hermaphroditic duct: Two states are recognized. The hermaphroditic duct is short (not extending beyond half of ventral sucker) or long (reaching beyond ventral sucker).

A hermaphroditic duct when present in the outgroups is short and the long hermaphroditic duct may be viewed as an evolutionary transformation; ductless --- short duct --- long duct. Thus the presence of a short hermaphroditic duct is considered plesiomorphic while a long duct is considered apomorphic (4-1).

RESULTS

Morphology and Taxonomy

Distomum hispidum NHMW # 4256: Lacking the anterior body expansions with heavy marginal and dorsal hump spination characteristic of *Deropristis hispida*, small worms (< 5 mm) with testes in tandem and close to each other at posterior end of the body (Fig. 32). Spination dense over major portion of body and other organ positions are as described for *Skrjabinopsolus semiarmatus*. These specimens are referred to that species (Table 16; Fig. 32).

Distomum hispidum NHMW # 1832 and 1833: Lacking the generic characters of *Deropristis*, possessing characteristics of *Skrjabinopsolus*. The testes show varying degrees of separation even in the few (4) specimens available, two specimens showing

considerable inter-testicular distances filled with uterine folds (Fig. 33). Based on the position of the ovary (Table 16); the diagnosis of *S. semiarmatus* is altered (see Discussion).

Skrjabinopsolus manteri (paratypes): Gravid worms were 3.6 mm - 12.5 mm in length, ovary in posterior half of body in 1 specimen, testes separated by less than half a testis length in 4 of 7 specimens (Fig. 34, Table 16).

Skrjabinopsolus from lake sturgeon: Mature specimens ranging from 4.6 mm to 15.0 mm in size, ovary more anterior in position with increasing size (Fig. 35). In addition, two of 21 specimens possessed closely situated testes. Comparisons with *S. semiarmatus* from the Danube sterlet and specimens of *S. manteri* (Table 16) indicates that the specimens share characters with both species (see Discussion).

S. semiarmatus. CSAV D-113. (13 specimens used): Testes tandem, situated close together and with ovary in posterior half of the body (Fig. 36, Table 16).

Cestrahelminis laruei: Forebody flat and widened, not swollen. Cirrus sac well developed containing broad well developed thick walled ejaculatory duct which possesses fine spine-like processes embedded in wall of duct, conspicuous rounded or pyriform pars prostatica surrounded by gland cells, and large unipartite seminal vesicle (Fig. 37). Metraterm saccular, thick wall consisting of rounded cells with luminal ends produced into minute spine-like processes. Metraterm receives tubular uterus side-ways, not terminally (Fig. 37). Terminal hermaphroditic duct well developed, aspinose. Genital pore submedian, postero-lateral to anterior margin of acetabulum.

C. rivularis: Body spines often with distal ends slightly recurved. Cirrus sac containing

spined ejaculatory duct which is narrow and thin walled proximally, surrounded by gland cells, and expanded distally, a conspicuous pars prostatica surrounded by gland cells followed by a large unipartite seminal vesicle (Figs. 38, 39). Metraterm tubular, thick walled with cells possibly bearing minute spines (not conclusive), receiving uterus terminally (?), hermaphroditic duct short and aspinose. Genital pore submedian, sinistral and preacetabular.

Phylogenetic Analysis

Only one character and character state (elongate hermaphroditic duct) was found that indicates *Deropristis* and *Pristicola* are sister taxa (Fig. 40). All three genera are very similar in their basic morphologies but readily distinguished by conspicuous autapomorphies, large circum-oral spines in *P. sturionis* and heavy marginal spination on the expanded cervical region of *Deropristis*.

DISCUSSION

Digeneans of the genus *Skrjabinopsolus* were first described by Molin (1858, 1861) as *Distomum semiarmatum* from the Adriatic sturgeon *Acipenser naccari*. The genus *Skrjabinopsolus* and the type species *S. acipenseris* was established for digeneans described by Ivanov and Murygin (1937) from sturgeon of the Black and Caspian Seas, although the authors recognized its resemblance to *Distoma semiarmatum* of Molin (1858). This was followed by descriptions of *S. skrjabini* from the Black Sea (Osmanov, 1940) and *S. minor* from *Acipenser gueldenstaedti* of the Azerbaijan part of the Caspian basin (Bykhovskaya-Pavlovskaya and Mikailov, 1969).

These were subsequently synonymised with *S. semiarmatus* as the type and only species in European sturgeon (Bykhovskaya and Kulakova, 1987; Bykhovskii and Dubinina, 1954; see Skrjabina, 1974). The only North American species of *Skrjabinopsolus*, *S. manteri*, was described by Cable (1952) from the shovelnose sturgeon *Scaphirhynchus platyrhynchus* as *Pristotrema manteri* but was not compared to any European forms as he was apparently unaware of either Molin's (1858) '*Distomum semiarmatum*' or of Ivanov's *Skrjabinopsolus* at the time. *Pristotrema* was later suppressed by Cable on becoming aware of this information (Cable, 1955).

The morphological characteristics used to distinguish the two species require re-evaluation, the first of which is body size. In her review of *Skrjabinopsolus* and key to the species, Skrjabina (1974) indicates a maximum size of 5.5 mm for *S. semiarmatus* which supposedly distinguished it from the larger *S. manteri*. The description of Bykhovskii and Dubinina (1954) was used as the basis for this comparison. However, Bykhovskaya-Pavloskaya and Mikailov (1969) described a length of 3.1 - 7.5 mm for *S. semiarmatus*. In comparison, the sizes of ovigerous *S. manteri* range between 3.44 and 12.38 mm (Cable, 1952). It is obvious that the sizes of ovigerous individuals of the two species overlap and, while maximum size attained may differ, size alone cannot distinguish the two species. The second difference is in the position of the testes (Skrjabina, 1974). In *S. semiarmatus*, the testes are stated to lie close together (e.g., less than one testis length) while in *S. manteri* the testes are well separated (Cable, 1952; Skrjabina, 1974). Cable (1952) did not mention any variability in position of the testes but my examination of 7 paratypes of *S. manteri*

(HWML 1853; USNM 37187) shows closely situated testes in 5 of the specimens, 4 of which were less than 4.5 mm. Closely situated testes were also noted in 2 of 21 individuals of *Skrjabinopsolus* from lake sturgeon (Lake Winnebago). Testes of young adult *S. manteri*, are also situated close together at the posterior end of the body (Peters, 1961), indicating that the testes become more widely separated during growth. This separation evidently occurs early in growth since specimens of *S. manteri*, from lake sturgeon, at the lower end of the size range (<5 mm) already showed widely separated testes. Peters (1961) distinguished *S. manteri* from Ivanov's *S. acipenseris* (= *S. semiarmatus*) based on the more anterior position of the ovary, and a smaller average size of eggs in *S. manteri*. Although the ovary in *S. semiarmatus* has always been described as being in the posterior half of the hind-body, its position seems highly variable within this region of the body (Skrjabin, 1954; Skrjabina, 1958). The extreme of this condition is seen in specimens from *A. sturio* (NHMW 4256, this study). Although this contrasts with the position of the ovary described for *S. manteri* (Cable, 1952; Peters, 1961), the position of the ovary in paratypes of *S. manteri* also varies (Table 16). My measurements of the position of the ovary in 21 specimens of *Skrjabinopsolus* from the lake sturgeon show a progressively anterior position of the ovary with increasing size of the worms (Fig. 34). This is likely due to allometric growth of the post-ovarian region of the body with increasing size. The position of the ovary in the hind-body (post-acetabular region) also overlaps considerably between specimens from the Danube sterlet (NHMW 1832, 1833 and CSAV D-113) and those from North American acipenserids (Table 16). In fact, specimens from *A. sturio*

(NHMW 4256, Fig. 32) show a greater posterior position of the ovary than the specimens of *Skrjabinopsolus* from the Danube sterlet or North American sturgeon. Since the dimensions of the eggs overlap considerably (Bykhovskaya-Pavlovskaya and Mikailov, 1969, Cable, 1952), it is not useful in distinguishing the two species. The differences lie in the trends towards a greater maximum size attained by *S. manteri* and the fact that closely situated testes and posterior ovaries are more common in *S. semiarmatus*. In view of these observations, there appears to be no discrete morphological criterion for separating the two species unequivocally.

The two species appear to differ in their life histories since *S. manteri* is a freshwater species while *S. semiarmatus* commonly parasitizes anadromous sturgeons and occurs with higher abundances in the marine phase of some of these hosts (Skrjabina, 1974). Skrjabina (1974) attributed infections of *S. semiarmatus* in the predominantly freshwater riverine sterlet (*A. ruthenus*) to feeding in downstream estuarine and brackish water environments and considered *S. semiarmatus* likely to be a marine species. However, it is evident from the museum collections (NHMW 1832, 1833) that, in the past, *Skrjabinopsolus* also occurred in upstream populations of the sterlet. Upstream (Bavarian and Austrian) populations of the sterlet, from which these specimens were collected in 1877-1878 (by Lorenz), have since been extirpated (Kinzelbach, 1994) but populations of sterlet still occur in Slovakian sections of the Danube, from which specimens were examined in this study (CSAV D-113). Since the sterlet is a resident riverine species and tagging studies have shown that downstream migrations are limited (Sokolov and Vasil'ev, 1989), it seems unlikely that infections

in the Austrian and Slovakian reaches of the Danube originated in the estuary and suggests the possibility of a freshwater life cycle.

On morphological grounds, *S. manteri* is relegated to a synonym of *S. semiarmatus*. However, since there may be differences in life history characteristics (freshwater vs. estuarine) and since there are identifiable trends in morphological differences, we consider it practical to use a sub-specific designation to differentiate the two populations (in accordance with the *International Code of Zoological Nomenclature*). Although "there is no refined sub-species concept" (Panchen, 1992, p. 333), it is a "convenient" sub-division (Panchen, 1992) which draws attention to the lack of defining morphological characters while acknowledging differences based on general trends in certain morphological features and possibly in their biology. Accordingly, *S. manteri* becomes *S. semiarmatus manteri*.

Odhner (1902) distinguished *Deropristis hispida* and *D. inflata* on the basis of a single row of heavy marginal cervical spines in *D. hispida* in contrast to multiple rows in *D. inflata*. Ward (1938) regarded it "unwise" to evaluate the taxonomic usefulness of this character (marginal spination) from the material available to him and suggested that the lesser size of the vitellaria in *D. inflata* as diagnostic. In all specimens of *D. hispida* examined in this study, the heavy marginal spines were arranged in a single row. In contrast, these posterior of these spines in *D. inflata* are more numerous and irregularly arranged. This difference in spination of the two species of *Deropristis* is reflected in the illustrations of *D. hispida* by Skrjabina (1974) and of *D. inflata* by Cable and Hunnien (1942). Consequently, these observations

support Odhner's (1902) view of the differences between the two species. *D. inflata* is also a much smaller species than *D. hispida*, on both sides of the Atlantic.

Hypotheses regarding the historical biogeography of host-parasite relationships depend on sound systematic analyses of taxa and on ensuring that the group in question is monophyletic. The systematics of the Deropristiidae, particularly the position of the genus *Cestrahelmins*, are controversial. Peters (1961) added *Cestrahelmins laruei* Fischthal 1957 to the family Deropristiidae Skrjabin, 1958 (Skrjabin, 1958) under a separate subfamily Cestrahelminae and placed the original genera *Deropristis* Odhner, 1905, *Pristicola* Cable 1952 and *Skrjabinopsolus* Ivanov in Ivanov and Murygin, 1937, under the subfamily Deropristiinae Cable and Hunnien 1942. To this, Becker (1971) added *C. rivularis*. Yamaguti (1971) placed *C. laruei* in the family Monorchiiidae, subfamily Lasiotocinae and Skrjabin's (1958) deropristiids in the subfamily Deropristiinae Cable and Hunnien 1942, within the family Acanthocolpidae. Life cycle studies have shown that both *Skrjabinopsolus* and *Deropristis* possess similar cercariae with a 'pseudostylet' and with setae on the tail (Cable and Hunnien, 1942; Peters, 1961; Seitner, 1951), the latter character defining the Lepocreadiiformes (Brooks *et al.*, 1989). The morphology of *Cestrahelmins* differs markedly from that of the Deropristiinae in the caecal length, morphology of the cirrus and metraterm and in the disposition of the vitellaria and gonads (Figs. 37, 38, 39 and Results section). *Pristicola*, *Deropristis* and *Skrjabinopsolus* possess a weakly developed prostatic complex, a thick conspicuously spined ejaculatory duct and a distinctly and unequally bipartite (septate) seminal vesicle. The metraterm in these

genera possesses similar spination and receives the uterus terminally (Cable, 1952; Cable and Hunnien, 1942; Little, 1930; Skrjabina, 1974). These and other characteristics defining the "Deropristiinae" (Cable, 1952) and their differences with *Cestrahelmins* are extensive enough to justify the removal of *Cestrahelmins* from the Deropristiidae as has been done by Yamaguti (1971). Consequently, the phylogenetic analysis of the Deropristiidae in this study does not include the genus *Cestrahelmins*. Until more information is available on the development of *Cestrahelmins* (e.g., morphology of the cercaria), this genus remains enigmatic and placing it in the Monorchiidae may be problematical since monorchiids are considered polyphyletic (Brooks *et al.*, 1989).

Results of the systematic analysis of the Deropristiidae indicate that *Deropristis* and *Pristicola* form a monophyletic group with *Skrjabinopsolus* as a sister taxon. All genera parasitize acipenserids but only in drainages associated with the Atlantic basin or immediately neighbouring it (Gulf of Mexico and Laurentian drainages). All three genera are absent from Siberian (including the Amur R.) and Pacific drainages (Bykhovskaya and Kulakova, 1987; Skrjabina, 1974; Margolis and McDonald, 1986). In contrast to *Skrjabinopsolus* and *Deropristis*, which are widely distributed (Skrjabina, 1974; Appy and Dadswell, 1978; Leidy, 1889), *Pristicola sturionis* has the most restricted distribution, having been reported, thus far, only from the anadromous European Atlantic sturgeon *A. sturio* from the Belgian coast and British waters (Little, 1930; Van Beneden, 1870). Extensive surveys of acipenserids in the Black and Caspian Sea basins have not reported *P. sturionis*. The record of *P. sturionis* from

Scaphirhynchus platyrhynchus in North America, attributed to Cable (1952, 1955) by Hoffman (1967) and repeated by Skrjabina (1974), is erroneous, as is the record of *P. sturionis* from the lake sturgeon attributed also to Cable (1952) by Yamaguti (1971). Cable (1952, 1955) made no such report in his studies.

The cladogram (Figure 40) indicates that a freshwater or marine ancestry are equally parsimonious possibilities. In view of the present day distribution of the deropristiids, post-drift dispersalist hypotheses involve long-range marine migrations of sturgeons from either landmass. It also implies that at least two of the three genera (*Deropristis* and *Skrjabinopsolus*) were translocated **after** they had originated. A marine origin also implies that the freshwater life history of *S. s. manteri* in North America is derived. In contrast, a drift-vicariance model would trace the origins of the deropristiids to Laurasia. Since fossil *Acipenser* are known from the late Cretaceous of both Europe and North America (Gardiner, 1984; Nesov and Kazmyshkin, 1983) and acipenserid fossils have been recently described from the mid-Jurassic (Nesov et al., 1990), vicariance hypotheses merit serious consideration and cause few chronological problems in this case. Under a strict vicariance mode, both marine and freshwater origins for the Deropristiidae involve the origin of *Skrjabinopsolus* and *Deropristis* **before** fragmentation of Laurasia. Consequently, the distributions of *S. semiarmatus* and *S. s. manteri* may be seen as the result of a vicariant separation of a once continuous population of *Skrjabinopsolus* in the freshwater systems of Laurasia by opening of the North Atlantic in late Cretaceous and early Tertiary (Rogers, 1993; Scotese et al., 1988). Additional evidence comes from outgroup distributions and the

distribution of the only deropristid in a non-sturgeon host, *D. inflata* in the Atlantic *Anguilla* species pair, *A. anguilla* (Europe) and *A. rostrata* (North America). Firstly, *Deropristis* is not found in Indo-Pacific *Anguilla* (Kennedy, 1994; Manter, 1955; Rid, 1973; Tesch, 1977) and its presence (as *D. inflata*) in Atlantic *Anguilla* likely represents a 'host switch' from acipenserids, following the colonization of the North Atlantic basin by *Anguilla* in the Cretaceous or later but probably before the closing off of the Mediterranean to the east by the northward moving African plate in the Tertiary. Surveys of upstream and resident freshwater eel populations (e.g., Nepszy, 1988) indicates that *D. inflata* is rare or absent in these populations and life cycle studies have shown that this species is transmitted in brackish water or coastal environments by polychaetes hosting the metacercaria (Cable and Hunnien, 1942; Vaes, 1978). The catadromous habits of *Anguilla* and the anadromous life history of acipenserid hosts of *D. hispida* interface in the brackish water of estuaries which are important feeding grounds for both hosts. Furthermore, polychaetes are also important food items for acipenserids (Skrjabina, 1974) and it is through this utilization of similar feeding areas and food items that the transfer to Atlantic *Anguilla* probably took place, historically, followed by speciation into *D. inflata*. This would strongly suggest that *Deropristis* is either marine or estuarine but not freshwater in origin. It is also curious that *S.s.manteri* utilize oligochaete annelids for their life cycle in freshwater North American acipenserids. Secondly, the outgroup families, Homalometridae and Lepocreadiidae, are marine, with a few notable exceptions. The homalometrids, *Homalometron armatum* and *Microcreadium parvum*, typically found

in the freshwater sciaenid *Aplodinotus grunniens* may be derived from marine ancestors since both parasite genera have marine species (Yamaguti, 1971) and since *A. grunniens* is the only freshwater representative (in North America) of the widely distributed marine family, Sciaenidae (Lee et al., 1980; Nelson, 1994). Phylogenetic analyses of the Sciaenidae indicates that *A. grunniens* is sister taxon to the marine genus *Pogonias* (see Burr and Mayden, 1992). The only other group with which *Skrjabinopsolus* has been aligned in the past (Acanthocolpidae) (Skrjabin, 1954) also has a wide marine distribution.

The available evidence allows us to develop the following scenario for the historical biogeography of the Deropristiidae involving both vicariance and dispersal processes. The family probably originated in ancestral acipenserids from a marine lepocreadiiform in estuarine or near coastal feeding areas associated with Laurasian drainages and basins of the newly formed Atlantic. The family was introduced into freshwater by sturgeon moving upstream, indicating that diadromy or at least, an estuarine habit, is old in this host group. *Skrjabinopsolus* originated early in the radiation of the Deropristiidae, possibly in the Cretaceous, and established freshwater populations along with their hosts (e.g., *A. ruthenus*, *A. fulvescens* or their ancestors) while retaining an estuarine transmission in other acipenserids. Further studies on acipenserids of the Atlantic coastal drainages (*A. brevirostrum* and *A. oxyrinchus*) may reveal the presence of estuarine populations of *Skrjabinopsolus* in North America. *Deropristis* attained its present day distribution by the distribution of its diadromous hosts (sturgeon, *Anguilla*) along newly developing North Atlantic margins (a process

of 'continental tracking') as the Laurasian landmass fragmented in the late Cretaceous and Tertiary. Thus, the overall hypothesis is one of co-accommodation and subsequent co-evolution with acipenserid hosts with one host switch to North Atlantic *Anguilla* spp.

Table 15. Character matrix for the cladistic analysis of Deropristiidae.

Characters and states Taxa/Species	1	2	3	4
Lepocreadiidae Homalometridae	0	0	0	0
<i>S. s. semiarmatus</i>	0	0	0	0
<i>S. s. manteri</i>	0	0	0	0
<i>D. hispida</i>	1	1	0	1
<i>D. inflata</i>	1	1	0	1
<i>P. sturionis</i>	0	0	1	1

Table 16. Measurements of *Skirjabinopsolus* spp. (in μm) from acipenserids in Europe and North America.

Host Location.. N	<i>A. ruthenus</i> R. Danube, Strevo (13)	<i>A. ruthenus</i> R. Danube, Vienna (4)	<i>A. sturio</i> Adriatic? (5)	<i>A. fulvescens</i> L. Winnebago (21)	<i>S. platyrinchus</i> Wabash R. (7)
Length ¹	3437 \pm 577 (2600-4600)	6919 \pm 1611 (5250-8850)	1640 \pm 288 (1450-2150)	8081 \pm 2373 (4600-15025)	6332 \pm 3310 (3600-12500)
Preovarian distance (Pd)	2046 \pm 196 (1300-2550)	3900 \pm 662 (3150-4725)	1035 \pm 235 (875-1450)	4269 \pm 974 (3000-6850)	3071 \pm 1411 (1900-5825)
Pd/length	0.59 \pm 0.05 (0.5-0.68)	0.54 \pm 0.04 (0.53-0.61)	0.63 \pm 0.03 (0.57-0.67)	0.54 \pm 0.05 (0.46-0.65)	0.50 \pm 0.04 (0.43-0.57)
Distance of ovary from acetabulum ² / post-acetabular body length	0.38 \pm 0.05 (0.28-0.46)	0.37 \pm 0.03 (0.35-0.42)	0.48 \pm 0.04 (0.42-0.54)	0.38 \pm 0.03 (0.33-0.48)	0.30 \pm 0.03 (0.26-0.34)

N= Number of specimens examined. ¹Distance in micrometres. ²Distance to anterior margin of ovary

Figure 32. *Skrjabinopsolus semiarmatus* (NHMW 4256) Outline drawings of specimens showing position of the ovary and testes. Scale bar = 200 μm .

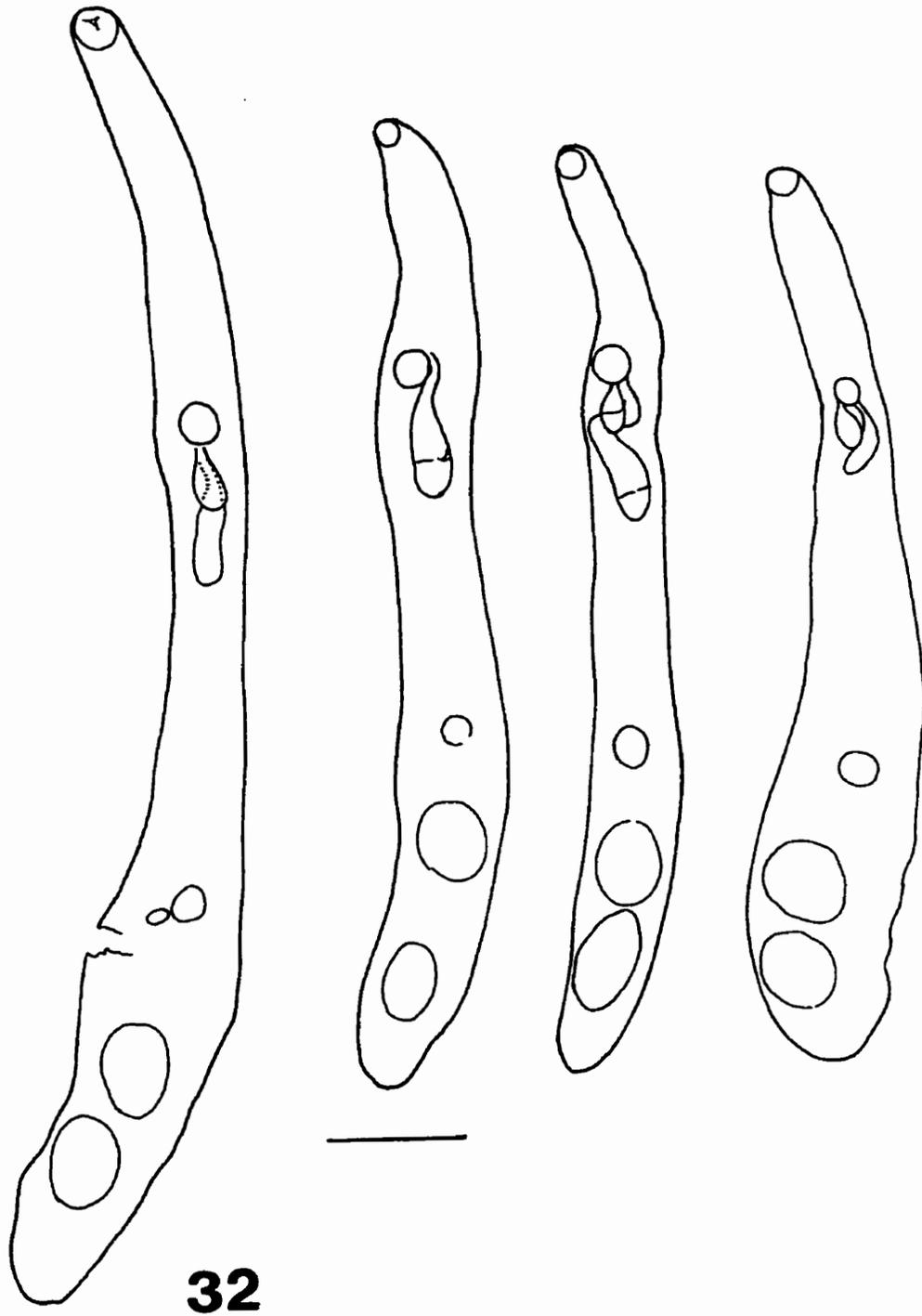
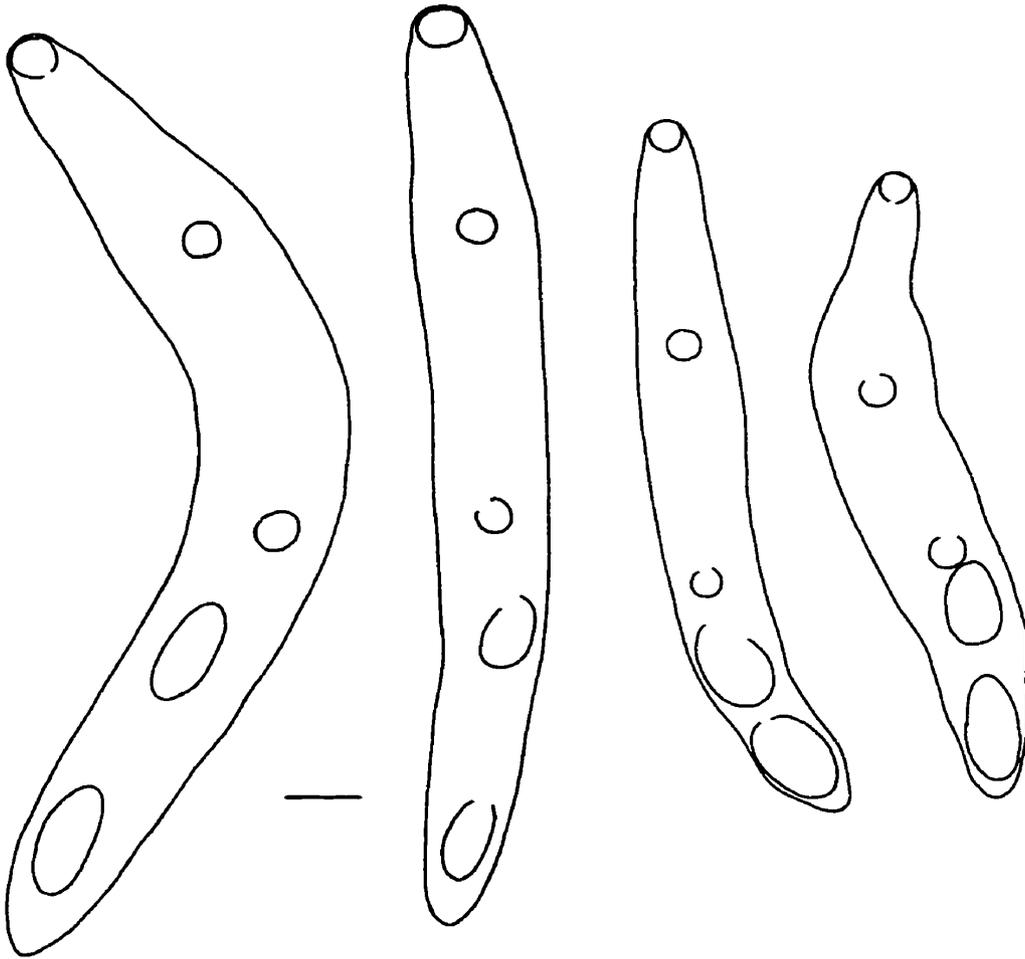


Figure 33. *Skrjabinopsolus semiarmatus* (NHMW 1832,1833). Outline drawings of specimens showing position of the ovary and testes. Scale bar = 400 μm .



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Figure 34. *Skrjabinopsolus manteri* paratypes. Outline drawings of specimens showing position of the ovary and testes. a) HWML 1853, b) USNM 37187. Scale bar a = 400 μm , b = 200 μm .

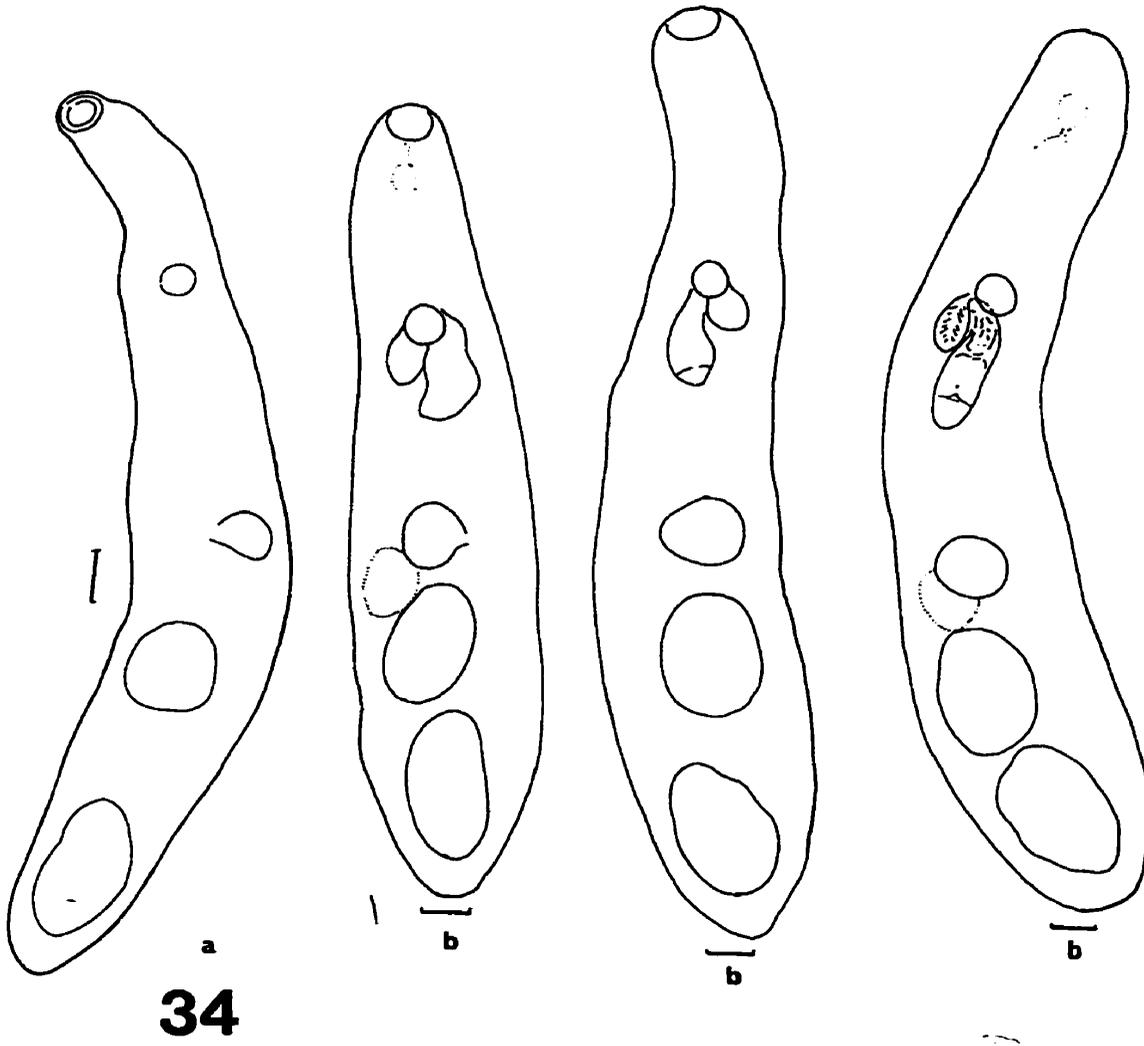
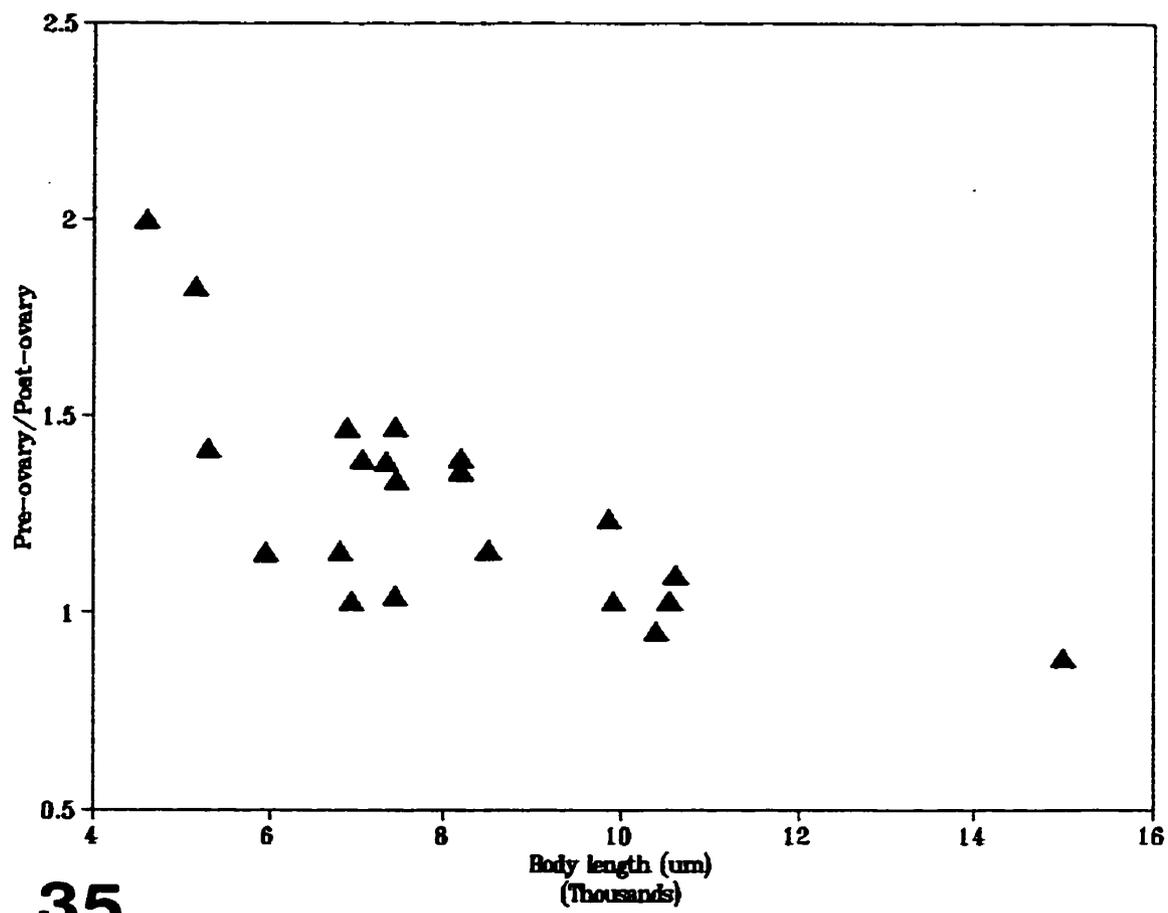


Figure 35. Plot of pre-ovarian distance over the length of the body of *Skrjabinopsolus* from lake sturgeon (L. Winnebago).

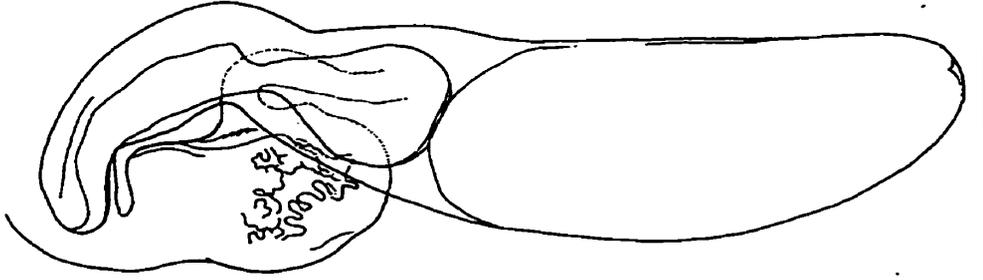


35

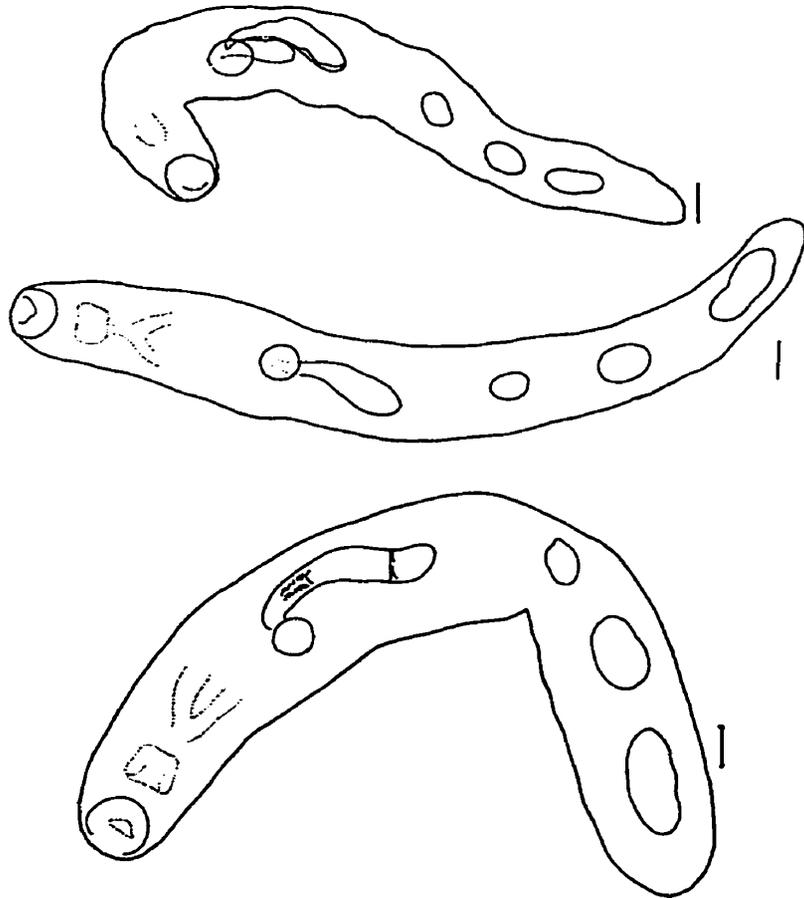
Figure 36. *Skrjabinopsolus semiarmatus* (CSAV D-113). Outline drawings of specimens showing position of the ovary and testes. Scale bar = 200 μm .

Figure 37. *Cestrahelminis laruei* (USNM 55234). Unipartite seminal vesicle, pars prostatica and saccate metraterm receiving the uterus sideways. Scale bar = 100 μm .

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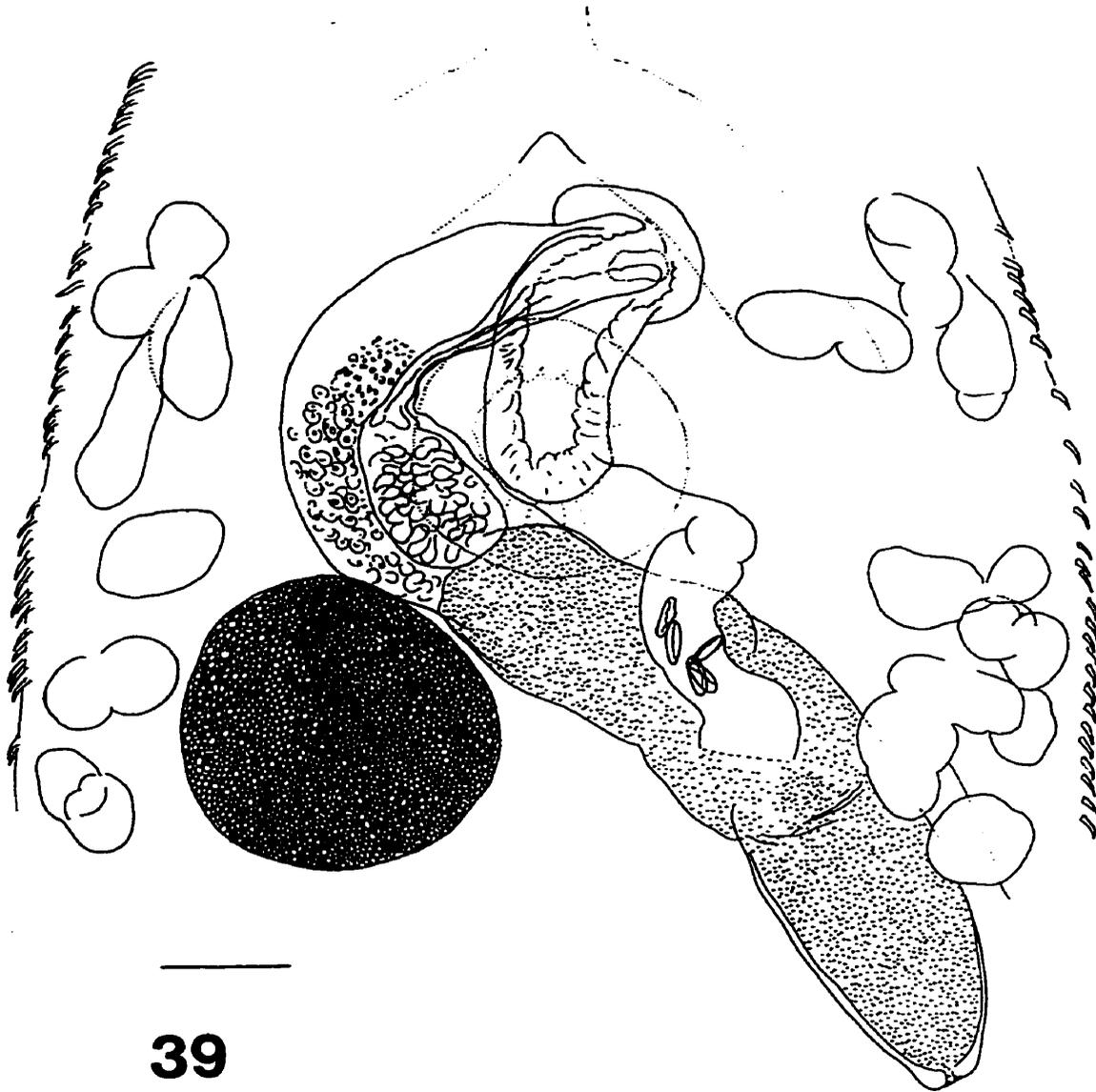
Figure 38. *Cestrahelmins rivularis* (USNM 71431). Whole specimen showing spination, disposition of vitellaria, reproductive structures and long oesophagus. Scale bar = 200 μm .

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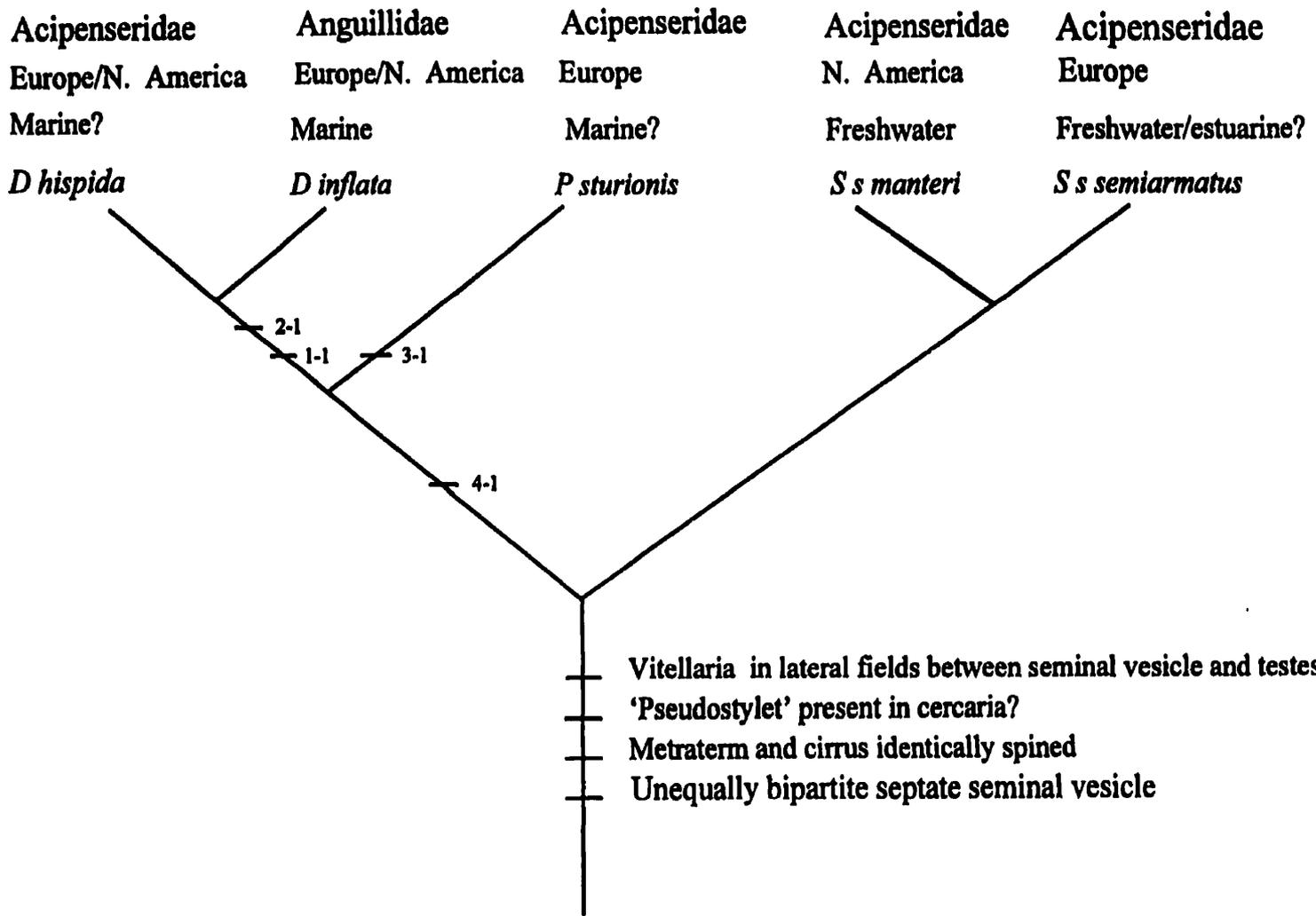
38

Figure 39. *Cestrahelmins rivularis* (USNM 71431). Details of terminal reproductive structures. Not lack of obvious spination in cirrus and metraterm and prominent pars prostatica. Scale bar = 100 μm .



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Figure 40. Cladogram showing the results of the phylogenetic analysis of the Deropristidae with host families and geographical ranges.



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Chapter 2-3. *Spinitectus acipenseri* n. sp. (Nematoda: Cystidicolidae): description and systematics.

INTRODUCTION

The genus *Spinitectus* is comprised of five nominal species in North America; three species, *S. gracilis* Ward and Magath, 1917, *S. carolini* Holl, 1928, and *S. micracanthus* Christian, 1972, are parasitic in freshwater hosts, while two, *S. beaveri* Overstreet, 1970, and *S. cristatus* Railliet and Henry, 1915, are marine. *S. gracilis* and *S. carolini* have been reported from a variety of freshwater fish (Hoffman, 1967; Pluto and Rothenbacher, 1978; Jilek and Crites, 1981; Williams, 1983), from amphibians (Holl, 1928; Jilek and Wolff, 1978) and *S. gracilis* has also been reported from a reptile (Camp, 1980).

Spinitectus has been found among the North American acipenserids only in lake sturgeon (see Chapter 1, Table 1). These were identified as *S. gracilis*, *S. carolini* or simply as *Spinitectus* sp. Anthony (1977) reported a new species of *Spinitectus* from lake sturgeon with a brief description, in an abstract, without giving a specific designation. A survey of lake sturgeon parasites in Saskatchewan and Manitoba found nematodes belonging to this genus in the mucous lining of the pyloric stomach with high intensities of infection in some areas. A preliminary examination of specimens from sturgeon showed similarities to *S. gracilis*, except in the character of the spines. Consequently, a more detailed description was made to determine their species status. The specimens from sturgeon were also compared to syntypes of *S. gracilis* from the USNM and existing descriptions of this latter species.

Although a phylogenetic analysis of *Spinitectus* has not been attempted so far (the genus contains over 40 species), there is one morphological characteristic which

initially suggested monophyly of the North American species: all species possess a terminal process at the distal end of the short spicule although the shape of this process in *S. gracilis* and in the species described here from lake sturgeon is different than in other North American *Spinitectus* spp. which possess a distinct ventral barb. A preliminary phylogenetic analysis of this group was carried out to evaluate the systematic relationships of the species described from the North American lake sturgeon. The North American species in this analysis includes what appears to be a previously undescribed species of *Spinitectus* from *Ictalurus punctatus* (channel cat, Ictaluridae) of the Red and Assiniboine rivers in Manitoba. I refer to this species as *Spinitectus* sp. and it will be described elsewhere (Choudhury and Dick, unpublished).

MATERIALS AND METHODS

Large numbers of live *Spinitectus* were collected from two lake sturgeon visceral samples from Cumberland House (Saskatchewan River), Saskatchewan. Fewer specimens of *Spinitectus* were also collected from three frozen visceral samples of lake sturgeon from Angling Lake, Northern Manitoba. Live worms were fixed in hot 70% alcohol, processed in glycerine alcohol and mounted in glycerine on slides. Specimens from frozen viscera were fixed in cold 70% alcohol and processed as above. All specimens were recovered from the mucous lining of the stomach. Temporary *en face* mounts were made in glycerine and studied. Microscopical examinations were made with Leitz and Zeiss Compound microscopes, and drawings and measurements were made with the aid of a drawing tube and an eye-piece micrometer. Measurements were

made on type male and female specimens and forty ovigerous females and forty males, as paratypes.

The following type material of *S. gracilis* Ward and Magath, 1917 was examined:

1. Cotypes, 2 females, USNM Cat # 50800, File No. M 907-D, from stomach of *Pomoxis sparoides*, Fairport Iowa, collected by R.H. Linkins on 7.7.1915, determined by Ward and Magath.

2. Cotypes, 4 immature specimens, USNM cat # 50801, File No. M 907-E, from stomach of *Roccus chrysops*, Fairport Iowa, collected by R.H. Linkins, determined by Ward and Magath.

In addition the following specimens of *Spinitectus* spp. were examined from the following fish in Manitoba (specimens were collected and processed by me unless otherwise mentioned):

Spinitectus gracilis: ex. rock bass (*Ambloplites rupestris*) from the Roseau R.; smallmouth bass (*Micropterus dolomieu*) from the Winnipeg R., whitefish (*Coregonus clupeaformis*) from the Winnipeg R., yellow perch (*Perca flavescens*) from Dauphin L. (material from Szalai, 1989) and Betula L. (material collected and prepared by Todd Schwarz), trout perch (*Percopsis omiscomaycus*) from Dauphin L., and northern pike (*Esox lucius*) from Winnipeg R.

Spinitectus carolini: ex. smallmouth bass (*Micropterus dolomieu*), Winnipeg R.

Spinitectus sp.: ex. *Ictalurus punctatus* (channel cat), Red R., Assiniboine R., Manitoba.

Phylogenetic analysis

A preliminary cladistic analysis of the species of *Spinitectus* was carried out (Hennig, 1966; Wiley, 1981; Wiley *et al.*, 1991).

Characters used in this preliminary analysis were those that were available from personal observations of North American species of *Spinitectus* and from the descriptions of Asian, African and South American forms (Bauer, 1987; Boomker, 1993; Boomker and Puvlaert, 1994; Campillo and Alvarez-Pellitero, 1976; De, 1988; Ogden, 1967; Overstreet, 1970; Petter, 1979; 1984, 1987; Petter and Morand, 1988; Skrjabin *et al.*, 1967; Sood, 1988; Vaucher and Durette-Dessett, 1980; Wang *et al.*, 1981; Yamaguti, 1935).

The following species of the outgroups were also examined (the literature consulted is also given):

Cystidicoloides tenuissima: ex. goldeye (*Hiodon alosoides*), Red and Assiniboine rivers. Literature: De and Moravec (1979), Maggenti and Paxman (1971), Moravec (1967; 1971; 1994), Rasheed (1965).

Ascarophis sp.: ex broad whitefish (*Coregonus nasus*), MacKenzie River delta. Literature: Appy (1981); Fagerholm and Berland (1988); Fusco and Overstreet (1978); Ko (1986); Lyaiman (1933); Machida (1981); Markowski (1938).

Capillospirura pseudoargumentosa: ex. lake sturgeon (*Acipenser fulvescens*), L. Winnebago, this study. Literature: Appy and Dadswell (1978); Appy and Anderson (1982); Skrjabina (1974).

Characters and character states in North American *Spinitectus*:

Outgroups are *Cystidicoloides (Sterliadochona) tenuissima*, *Capillospirura* and *Ascarophis*. All polarization of characters in this case is by outgroup comparison.

Table 17 provides the character matrix for this analysis.

1. Ventral barb.

Interpretation (i): The ventral barb is a simple backward directed barb or modified. A barbless short spicule may have given rise to a ventrally directed barb. The short spicule of *S. acipenseri* and *S. gracilis* is bent twice in the shape of a ram's horn. Such a modification may have also modified the position of the terminal barb resulting in the lateral process seen at the distal end of the short spicule. However, since the plesiomorphic condition is not known, I have assigned separate states to this character; a simple ventral barb is assigned (1-1) and the lateral process in *S. acipenseri* and *S. gracilis* is assigned (1-2). Note that the two are considered homologous in this interpretation.

Interpretation (ii): The lateral process of the short spicule in *S. acipenseri* and *S. gracilis* is not homologous to the distal ventral barb in the short spicule of the other North American *Spinitectus* spp. In this interpretation, the presence of a ventral barb is assigned the condition (1-1) (apomorphic by outgroup comparison) and the presence a lateral process in *S. acipenseri* and *S. gracilis* andis excluded from the analysis.

2. Short spicule form. The short spicule is either simple and arcuate or twisted. A simple arcuate spicule is considered plesiomorphic (2-0) while a twisted spicule is considered apomorphic (2-1).

3. Mucron on female tail: A terminal mucron is either lacking, simple when present or

of characteristic pyriform shape [see Christian's (1972) description of *S. micracanthus* for a description of this mucron]. I have also observed such a mucron in *Spinitectus* sp. from *I. punctatus*. Absence of such a pyriform mucron is considered plesiomorphic (3-0) while the presence is apomorphic (3-1).

4. Vagina. The vagina is either anteriorly or posteriorly directed. A posteriorly directed vagina is considered plesiomorphic (4-0) while an anteriorly directed vagina is apomorphic (4-1). A posteriorly directed vagina has been described in a number of South American species (e.g., *S. pachyuri*, *S. jamundensis*, *S. multipapillata*) (Petter, 1984, 1987, Petter and Morand, 1988). Most Eurasian and all African species of *Spinitectus* have anteriorly directed vaginae and it is also notable that the vulva is markedly displaced posteriorly in most of the Eurasian and African species. Such an anteriorly directed vagina is known from a South American species as well, *S. sternopygi* (Petter, 1984).

5. Extent of spination. Two states are recognized; spines are arranged in circlets and semicirclets along the entire length of the body upto the anal region or spines are so arranged only in the anterior third or half of the body with infrequently occurring scattered spines in the posterior fourth of the body. The presence of spines arranged in semi-circlets short of the anus is considered plesiomorphic since it is the widespread condition (5-0), the condition where spines become infrequent and scattered in the posterior third of the body is considered apomorphic (5-1).

RESULTS**Description**

Family Cystidicolidae Skrjabin, 1946.

Spinitectus acipenseri n. sp. (Figs. 41-51).

General: Spirurida, body cylindrical, anterior end blunt, body possessing transverse rows of spines, spines fairly long and pointed, radiating outwards at slight angle to surface, head region without spines. Spines single structures having low base, largest in anterior third of body, rows discontinuous over lateral lines appearing as two semicirclets of spines in same plane (Fig. 41), discontinuity progressively greater posteriorly with semicirclets losing their alignment and becoming staggered (Figures 42 a, b, c and d). Faults between semicirclets beginning to form as early as fourth row in some cases. First spine row with 20-22 spines (Fig. 41), spine numbers increasing posteriorly to as many as 30 by row 6. Spines further increasing in number but decreasing in size posteriorly. Intercirclet distance not constant, varying even throughout length of individual. First two spine rows always closest together, intercirclet distance 29.2-43.8 μm between rows three and four and 29.2-73 μm at the oesophagus-intestine junction. Mouth slit like, bordered by two pseudolabia with straight inner margins. Four cephalic papillae barely visible in *en face* view of the head, two behind each lip-base (Figs. 43a and b). Amphids not observed. Short buccal capsule. Oesophagus separated into anterior muscular and posterior glandular portions. Excretory gland short and narrow with basal excretory nucleus lying beside muscular oesophagus, excretory duct opening via excretory pore situated at base of fourth row

of spines, often between two spines and sometimes at base of individual spine (Fig. 44). Nerve ring present immediately posterior to second row of spines (Fig. 44).

Male: Anterior portion of body covered by 44-66 transverse rows of spines, posterior half of body devoid of spines. First 10-12 spine rows prominent, spines decreasing in size posteriorly to minute needle points on bulbous bases. Caudal end often spirally twisted in one to two turns. Prominent caudal alae extending to tip of tail (Fig. 45). Four pairs preanal and 6 pairs postanal papillae present (Fig. 45). Only five pairs postanal papillae visible in lateral view; sixth pair visible in ventral flattened view, often inconspicuous and situated on inside of and at same level as or slightly posterior to fifth pair. Papillae pedunculated, sixth pair with short stalks. Preanal papillae grouped in pairs; two pairs close to anus, two more anterior (Fig. 46). First and second pair of postanal papillae closer together immediately posterior to anus, next three pairs evenly spaced. Area rugosa composed of approximately 8 longitudinal rows of cuticular elevations or clefts starting near where tail coil starts, 800 - 1200 μm in front of anus ending at short distance anterior to anus (Fig. 47). Elevations 5-15 μm long and 5 μm high (maximum). Right short spicule helically bent like rams horn with prominent terminal barb, attached proximally to short thick muscle (Figs. 47, 48). Left, long spicule arcuate, broadening distally to scoop shape before narrowing to pointed tip (Figs. 47, 48). Some specimens with distal ends of either spicule or both extruded out through anus. Testis beginning some distance behind oesophageal-intestinal junction, running forward, flexing posteriorly forming a conspicuous loop $1628 \pm 253.83 \mu\text{m}$ (1175-2000 μm) from anterior end leading posteriorly to vas deferens.

Dimensions: (Holotype) followed by means, standard deviations and ranges (within parentheses) of 40 paratypes:

Length 4.85 mm [4.76 ± 0.59 mm (3.65-6.1)]; width 90.9 μm [89.97 ± 15.69 μm (80.3- 124.1)]; distance from anterior end to collar of first spine row (head) 103.53 μm [102.75 ± 12.68 μm (73-131.4)]; buccal capsule 32.13 μm [37.41 ± 3.72 μm (29.2-43.8)]; distance of nerve ring from anterior end 124.95 μm [146.36 ± 12.52 μm (102.2-160.6)]; muscular oesophagus 242.76 μm [261.85 ± 24.19 μm (226.3-335.8)]; glandular oesophagus 918.09 μm [867.97 ± 95.48 μm (700- 1065.8)]; muscular:glandular oesophagus ratio 1: 3.78 [1 : 3.32 ± 0.34 (1:2.74-1:4.08)]; oesophagus length: body length ratio 1:4.17 [1: 4.19 ± 0.44 (1: 3.46-1: 5.16)]; long spicule 315 μm [322.5 ± 22.44 μm (300-350)]; short spicule 99.96 μm [97.73 ± 2.78 μm (95.7-101.5)]; tail 127.26 μm [109.5 ± 8.03 μm (102.2-138.7)]; maximum spine size (anterior third of body) 11.65 μm [11.39 ± 0.80 (10.3-13)].

Female: Entire body covered by 130-175 transverse circlets and semicirclets of spines extending upto anus or short distance before it. First 8-10 spine rows prominent, spines noticeably smaller thereafter but similar throughout posterior half of body. Spine numbers increasing to 28 per semicirclet at posterior third of body, losing their arrangement in semicirclets after anus, becoming irregularly dispersed over tail (Fig. 49). Two folded ovaries present; one posterior near end of gut and extending to anus (Fig. 49) and the other anterior lying in region of glandular oesophagus. Two oppositely directed uteri (a bicornuate uterus) leading to vagina. Vagina fairly long, anteriorly directed, portion nearest vulva thick walled and strongly muscular, opening

to prominent vulva bearing bulbous lip protruding from body (Fig. 50). Whole length of vagina generally not discernible due to egg filled uteri. Anterior ovary rarely extending to muscular oesophagus (1 in 40). Terminal vaginal eggs elliptical, moderately thick shelled, without superficial formations, each egg containing coiled larva (Figure 51). Tail tapering and bearing simple terminal mucron (Fig. 49). Dimensions: Allotype followed by means, standard deviations and ranges (in parentheses) of 40 (unless N is different for a particular structure) paratypes. Length 7.25 mm [6.69 ± 1.42 mm (4.2-8.8)]; maximum width 135.66 μm [130.67 ± 25.3 μm (80.3-175.2)]; distance of anterior end to collar of first spine row (head) 124.95 μm [111.98 ± 16.79 μm (73-138.7) (N=35)]; buccal capsule 42.84 μm [38.9 ± 4.53 μm (29.2-43.8) (N=39)]; distance of nerve ring from anterior end 142.8 μm [154.87 ± 24.8 μm (138.7-197.1)]; muscular oesophagus 299.97 μm [301.12 ± 41.46 μm (226.3-416.1)]; glandular oesophagus 909.0 μm [1075.1 ± 153.8 μm (642.4-1335.9)]; muscular:glandular oesophagus ratio 1: 3.03 [1: 3.43 ± 0.55 (1: 2.6-1: 4.35)]; oesophagus: total body length ratio 1: 5.99 [1: 5 ± 0.72 (1: 3.87-1: 6.47)]; tail 67.83 μm [82.49 ± 10.58 μm (65.7-109.5)]; vagina, total length not followed in holotype [704.16 ± 224.07 μm (600-900)(N=12 only in which entire vagina could be followed, 5.62 ± 0.56 mm (4.2-7.1)long]; postvulva : prevulva ratio 1: 2.62 [1: 2.54 ± 0.39 (1.94-3.16)]; vaginal eggs 36.98 x 23.3 μm from 4 eggs [36.97 ± 1.50 μm (33.75-39.37) X 22.55 ± 0.88 μm (22.5-24.37) (from 86 eggs)]; maximum spine size (anterior third of body) 11.65 μm [12.96 ± 1.28 μm (10.31- 15)].

Type host: Acipenser fulvescens Rafinesque.

Site in host: Mucous of muscular (pyloric) stomach.

Type locality and date: Cumberland House, Saskatchewan River, Saskatchewan. July 1989.

Type material: Holotype (male): Canadian Museum of Nature, Ottawa, Parasite Collection (CMNP) 1991-0015 ; allotype (female): CMNP 1991-0016 ; paratypes: CMNP 1991-0017 and CMNP 1991-0018.

Etymology: The species name *acipenseri*, meaning from *Acipenser* (sturgeon), refers to the fact that it is the first species of the genus *Spinitectus* described from an acipenserid.

Phylogenetic analysis:

Two interpretations of Character 1 are provided which result in different cladograms and have different implications for biogeography. Interpretation (i) gives a cladogram (Fig. 52) which hypothesizes that North American species are monophyletic and that the condition of the anteriorly directed vagina (4-1) arose independently in several different lineages and species (African-Eurasian species, *S. gracilis* / *S. acipenseri* and in one South American species). Using interpretation (ii) of Character 1 produces a different hypothesis of relationships (fig. 53). Accordingly, the anteriorly directed vagina indicates the relationship of *S. gracilis* - *S. acipenseri* with species in Africa-Eurasia and South America. In either case, the monophyly of the *S. carolini* - *S. micracanthus* - *Spinitectus* sp. is supported as in the relationship of *S. gracilis* and *S. acipenseri*.

DISCUSSION

The specimens recovered from lake sturgeon resemble *Spinitectus gracilis* in the form and size of the spicules, and the direction and length of the vagina and therefore will be discussed in relation to the cotypes (USNM Cat.# 50800) and descriptions of *S. gracilis* from the literature (Table 18). The other North American species show significant differences; *S. carolini* Holl, 1928, has longer pointed spines, a posteriorly directed vagina and spicules of different length and shape; *S. micracanthus* Christian, 1972, possesses 56-72 fine spines per circlet and differs in spicule shape and apical structures; *S. beaveri* Overstreet, 1970, differs in apical structures and the spicules, and *S. cristatus* Railliet and Henry, 1915, differs in the shape and size of spicules and the number of rows of platelets in the area rugosa; the last two mentioned species are also exclusively marine (see Christian, 1972 for a comparison of the various North American freshwater species, Mueller and VanCleave, 1932, Overstreet, 1970 and Skrzabin *et al.* 1967).

There are four published descriptions of *S. gracilis*. *Spinitectus gracilis* was originally described by Ward and Magath (1917) from the black crappie (*Pomoxis nigromaculatus* = *P. sparoides*), white bass (*Morone chrysops* = *Roccus chrysops*) and sheepshead or freshwater drum (*Aplodinotus grunniens*), collected from Fairport, Iowa. Ward and Magath (1917) also reported the occurrence of "...some specimens 4 to 5mm long by 0.35 mm broad... " having "...spines extending even to the anal region". The "cotypes", from *R. chrysops*, (USNM Coll.# 50801) resembled the above description of Ward and Magath (1917) but were, judging from their state of maturity, fourth stage

larvae of *S. gracilis* (Jilek and Crites, 1982a). *S. gracilis* was redescribed in greater detail by Mueller and VanCleave (1932) from Oneida lake fishes and from original material of Ward and Magath. The smaller specimens with spines extending to the anal region, mentioned by Ward and Magath (1917), were not discussed by Mueller and VanCleave (1932) in their redescription and they do not list *R. chrysops* as a host of *S. gracilis*.

Christian (1972) reported measurements for *S. gracilis* (the data were reported as taken from Mueller and VanCleave, 1932) but requires clarification. Christian (1972, in his Table 1) stated the length of the long and short spicules to be 600 μm and 150 μm , respectively. Ali (1956), who is referred to by Christian (1972), also reported the length of the long and short spicules of *S. gracilis* to be 600 μm and 150 μm , respectively, and may be the source of these measurements. A description and illustration of the spicules presented by Jilek and Crites (1982a) are similar to the measurements reported by Ali (1956) and Christian (1972). The diagram (Plate 21, Fig. 36) from Mueller and VanCleave (1932) showed the long spicule of *S. gracilis* to be approximately 350 μm in length and the short spicule a little less than their accompanying scale bar of 100 μm . Moravec (1979) states for *Spinitectus inermis* that the length of the long spicule increases with increase in body size. This does not explain the discrepancy between Mueller and VanCleave's (1932) measurements and those of Jilek and Crites (1982a) since the reverse seems to be the case. Males of *Spinitectus gracilis* described by Mueller and VanCleave (1932) were 8 - 10 mm long with long spicules approximately 350 μm in length whereas males described by Jilek

and Crites (1982a) were 3.8 - 4.4 mm long with long spicules 600 μm in length. In addition, Jilek and Crites (1982a) illustrate five (not six) pairs of postanal papillae and other measurements reported by these authors also differ from the original description and from the ovigerous cotypes (USNM Cat.# 50800) (see Table 18). Since these female cotypes (male type specimens were unavailable) match the description of VanCleave and Mueller (1932) (see Table 18), it is considered the definitive description. The discrepancies noted in Ali (1956), Christian (1972) and Jilek and Crites (1982a) remain a mystery.

Jilek and Crites (1982b) described the external morphology of four North American species of *Spinitectus*, based on scanning electron microscopy, and reported 30-50 spines per row for *S. gracilis*, arranged as single structures as well as in doublets and triplets. These numbers as well as the grouping of spines were not observed in *S. acipenseri*. In the absence of internal morphometric measurements, this description is not included in Table 18.

Anthony's (1977) "...new species of *Spinitectus*..." from lake sturgeon, as reported in an abstract, differed from *S. gracilis* in the following characteristics: muscular: glandular oesophagus ratio = 1:3; total body length : oesophagus ratio = 6:1; 4 pairs preanal and 5 pairs postanal papillae, spiral portion of the male hind region and the distribution of spines all over the body in females and over one third of the male. Except for the number of postanal papillae, the few characters reported by Anthony (1977) agree with those of *S. acipenseri* described here. Anthony (1977) did not name this new form, and to my knowledge, there is no published description.

However, it is most likely that Anthony was describing the same species.

S. acipenseri differs from marine European species of *Spinitectus* such as *S. oviflagellis* Fourment, 1884 and *S. tamari* Naidenova, 1966 in lacking polar filaments on the eggs and from the freshwater European species, *S. gordonii* Cordero del Campillo et Alvarez-Pellitero, 1976 and *S. inermis* (Zeder, 1800), in possessing smooth surfaced eggs and fewer body spines/row in the anterior region of the body (see Moravec, 1979, 1994 for a key and account of the European species). *S. acipenseri* is distinguished from *S. gracilis* on the basis of a smaller length/width ratio, sexual dimorphism in spination, longer and fewer anterior spines, presence of conspicuous smaller spines arranged in semi-circlets over the body of females extending to the anus and a 1:4 -1:5 oesophagus: body length ratio. Similarities were noted in male and female reproductive structures of both species; shape and size of the spicules, form and direction of the vagina and egg size. Mueller and VanCleave (1932) and Jilek and Crites (1982b) did not report sexual dimorphism in spination of *S. gracilis*. However, based on this description of *S. acipenseri*, a comparison of descriptions in the literature and a reevaluation of cotypes, sexual dimorphism in spination appears to be taxonomically important.

Spinitectus acipenseri is the first *Spinitectus* to be described from sturgeon, although cystidicolids such as *Capillospirura* are commonly found in Eurasian and North American acipenserids (Appy and Anderson, 1982; Skrjabina, 1974). Since the completion of this study, I have also found *Spinitectus* from the stomachs of two shovelnose sturgeon, *Scaphirhynchus platorhynchus* from an unspecified locality

(likely Mississippi-Missouri drainage since shovel nose sturgeons do not occur in the Laurentian Great Lakes or Hudson Bay drainages). The specimens had been fixed in the guts of their host for over 20 years and were contracted but clearly resembled *S. acipenseri* and possessed the diagnostic semicriclets of spines reaching the anal region.

Phylogenetic analysis and biogeography

The monophyly of *S. carolini*, *S. micracanthus* and *Spinitectus* sp. (ex. *I. punctatus*) is hypothesized based on morphological synapomorphies. The short posteriad vagina can be considered a persistent plesiomorphy. It is possible that when more is known about the South American species, a revised systematic analysis may find some species more closely related to the North American species than previously considered. If the disposition of the vagina is any indication of relationships, then it implies that major lineages of *Spinitectus* were already established in freshwater fishes before the final separation of Africa and South America, 95 -100 million years ago (Goldblatt, 1993, Pitman *et al.* 1993). Certainly, the marked posterior displacement of the vulva in numerous African, Indian and far East Asian species, which by simple outgroup comparison, is a derived condition, seems compelling evidence for common ancestry.

The genus *Spinitectus* is distributed in phylogenetically diverse groups of hosts, in basal actinopterygians such as sturgeon, in basal teleosts such as mormyrids and anguillids as well as in the more derived Perciformes. In North America, results of surveys suggest that centrarchids are typical hosts of *S. carolini* and *S. micracanthus* while *S. gracilis* apparently has a long host list but is also common in centrarchids.

Mueller and Van Cleave (1932) pointed out that *S. gracilis* reaches its largest size and fecundity in centrarchids, a fact that is confirmed by my observations on *S. gracilis* in fish hosts in Manitoba (largest in *Ambloplites rupestris*). In the common hosts in Manitoba, *S. gracilis* is smallest in the trout-perch, *P. omiscomaycus* (personal observations). *Spinitectus gracilis* has not been reported from areas west of the Continental Divide in North America, nor from areas such as western Canada (i.e., Saskatchewan, Alberta or British Columbia and the genus has not been reported from the Arctic regions of North America or Eurasia (Bauer, 1984-1987; Hoffman, 1967; Margolis and Arthur, 1979; McDonald and Margolis, 1995). Consequently, the host-parasite relationships between *S. acipenseri* and North American sturgeons likely originated in the southern parts of North America, possibly in the Mississippi drainage. Since the original hosts of the *S. gracilis*-*S. acipenseri* clade cannot be easily identified, associations of these two closely related species with their fish hosts could have been independent colonization events from now extinct hosts. These aspects are discussed further in Chapter 3.

Table 17. Character matrix for North American *Spinitectus* spp.

Characters Species	1 (i)	1 (ii)	2	3	4	5
Outgroups	0	0	0	0	0	-
African/Eurasian <i>Spinitectus</i> spp.	0	0	0	0	1	0
<i>S. acipenseri</i>	2	-	1	0	1	0
<i>S. carolini</i>	1	1	0	1	0	1
<i>S. gracilis</i>	2	-	1	0	1	1
<i>S. micracanthus</i>	1	1	0	1	0	0
<i>Spinitectus</i> sp.	1	1	0	1	0	0
South American <i>Spinitectus</i> spp. (e.g. <i>S. pachyuri</i> , <i>S.</i> <i>jamundensis</i> , <i>S. multipapillata</i>)	0	0	0	0	0	0
South American spp. (<i>S.</i> <i>sternopygi</i>)	0	0	0	0	1	0

Table 18. Comparative morphometrics between *Spinitectus gracilis* and *Spinitectus acipenseri* from lake sturgeon.

	W&M	M&V	J&C(1)	<i>S. acipenseri</i>
Female				
length(mm):	11-19 [18, 18.5]	10-15	6.25 (5.6-7.4)	6.7 ± 1.4 (4.2-8.8)
width(µm):	66-140 [145, 155]	70-125	155 (147-163)	130.6 ± 25.3 (80-175)
Male				
length(mm):	12	8-10	4.15 (3.8-4.3)	4.76 ± 0.6 (3.6-6)
width(µm):	42-75		117 (102-130)	89.9 ± 15.7 (80-124)
Buccal capsule(µm):	25 [39, 35]			F:38.9 ± 4.5 (29-44) M:37.4 ± 3.7 (29-44)
Muscular oesophagus:	[296, 232]		F:229 (184-243) M:257 (203-303)	F:301.1 ± 41.46 (226-416) M:261.8 ± 24.19 (226-336)
Glandular oesophagus:	[854, 836]		F:1900 (1800-2000) M:1800 (1600-1900)	F:1075 ± 153.8 (642-1336) M:868 ± 95.5 (700-1066)
M:G	1:3 [1:3, 1:4]		F:1:8.3 M:1:7	F:1:3.3 ± 0.3 (1:2.7-1:4) M:1:3.4 ± 0.5 (1:2.6-1:4)
Oesophagus: body length	[1:16]		F:1:2.93 M:1:2.01	F:1:5 ± 0.72 (1:4-1:6.5) M:1:4.2 ± 0.44 (1:3.5-1:5)
Spine size(µm):	8(max) [7.5]			F:12.96 ± 1.28 (10.3-15) M:11.39 ± 0.80 (10.3-13)

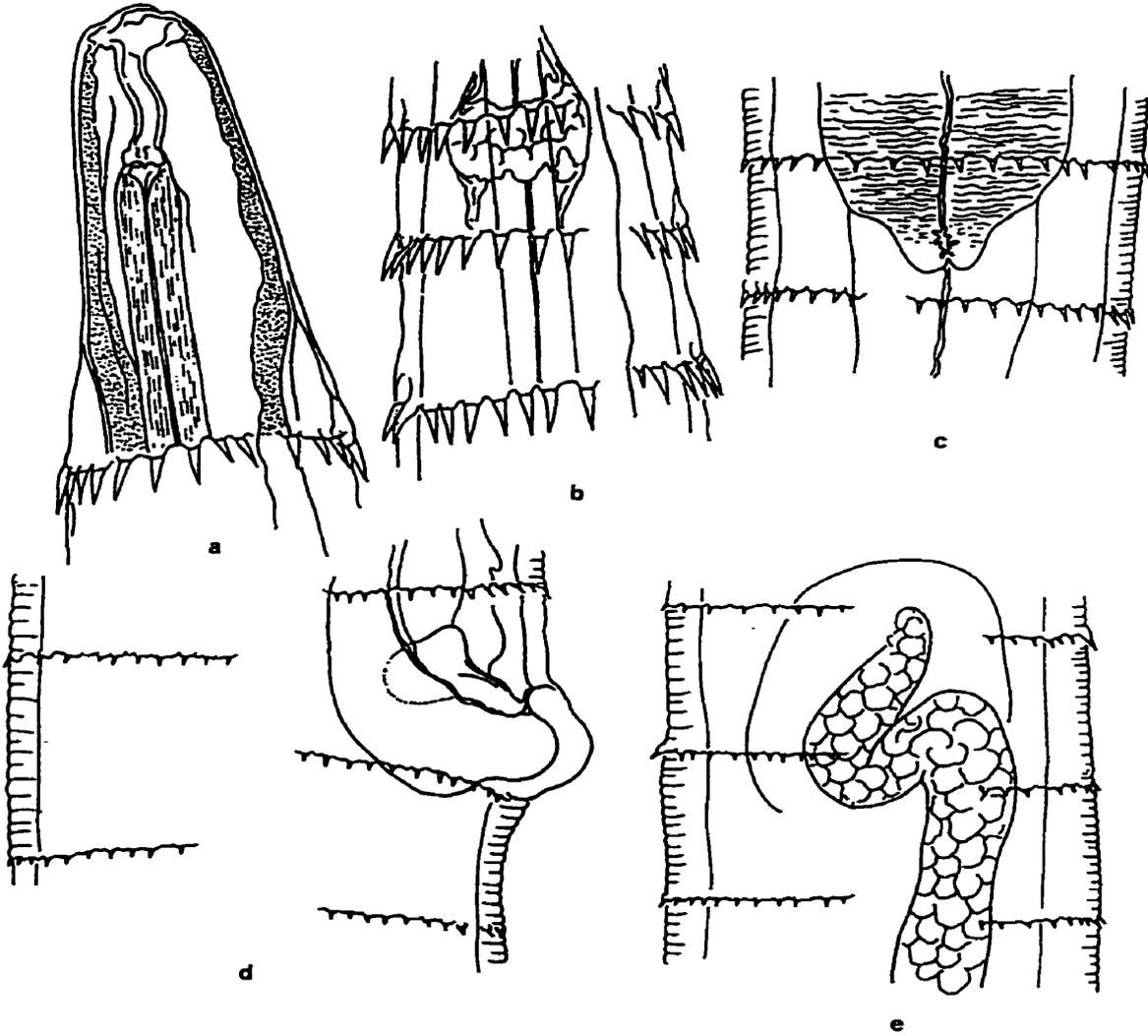
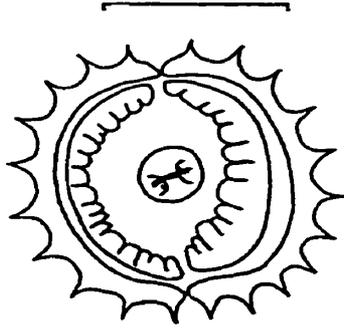
Table 18. continued.

	W&M	M&V	J&C(1)	<i>S. acipenseri</i>
Spines/cirlet:	28-30/40-50 [30-40]		35-50	20-22 anterior, upto 30 (row 6)
Postvulva: prevulva ratio	1:3 [1:3.6, 1:3.3]	1:3	Approx. 1:1	1:2.5 ± 0.39 (1:2-1:3.2)
Long spicule(µm):		Approx 350	600	322.5 ± 22.4 (300-350)
Short spicule(µm):		Approx 100	150	97.7 ± 2.7 (95.7-101.5)

Abbreviations are as follows: W&M: Ward and Magath, 1917; M&V: Mueller and VanCleave, 1932; J&C(1): Jilek and Crites, 1982a; M:G= Muscular: Glandular oesophagus; F: female; M: male. Measurements within third brackets ([]) under W&M are from USNM cotypes # 50800 of *S. gracilis* (N=2). Note: Numerals after the decimal point have been rounded off to the nearest integer.

- Figure 41. *Spinitectus acipenseri*. Apical view of the first row of spines showing their arrangement in semicirclets and the number (21) (scale bar represents 50 μm).
- Figure 42. *Spinitectus acipenseri*. Structure and arrangement of spines at various regions of the female body; a. first row of spines b. level of nerve ring; c. level of oesophagus-intestine junction, d. level of vulva and e. level of posterior ovary (scale bar represents 100 μm).

41



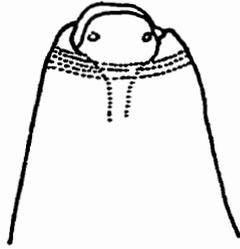
42

- Figure 43. *Spinitectus acipenseri*. Anterior end of female; a. *en face* view of head showing pseudolabia and papillae and b. side view of anterior end (scale bar represents 10 μm).
- Figure 44. *Spinitectus acipenseri*. Anterior end of female showing buccal capsule, muscular and glandular oesophagus, position of the nerve ring, excretory structures, and spination (scale bar represents 50 μm).

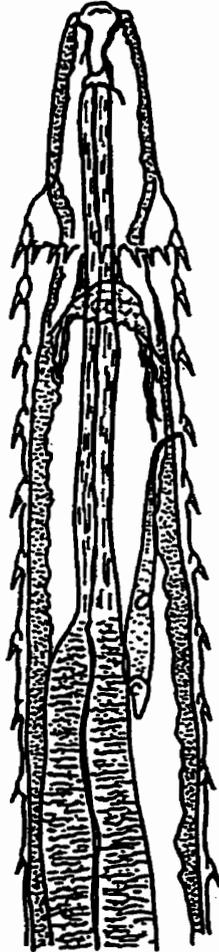
43



a



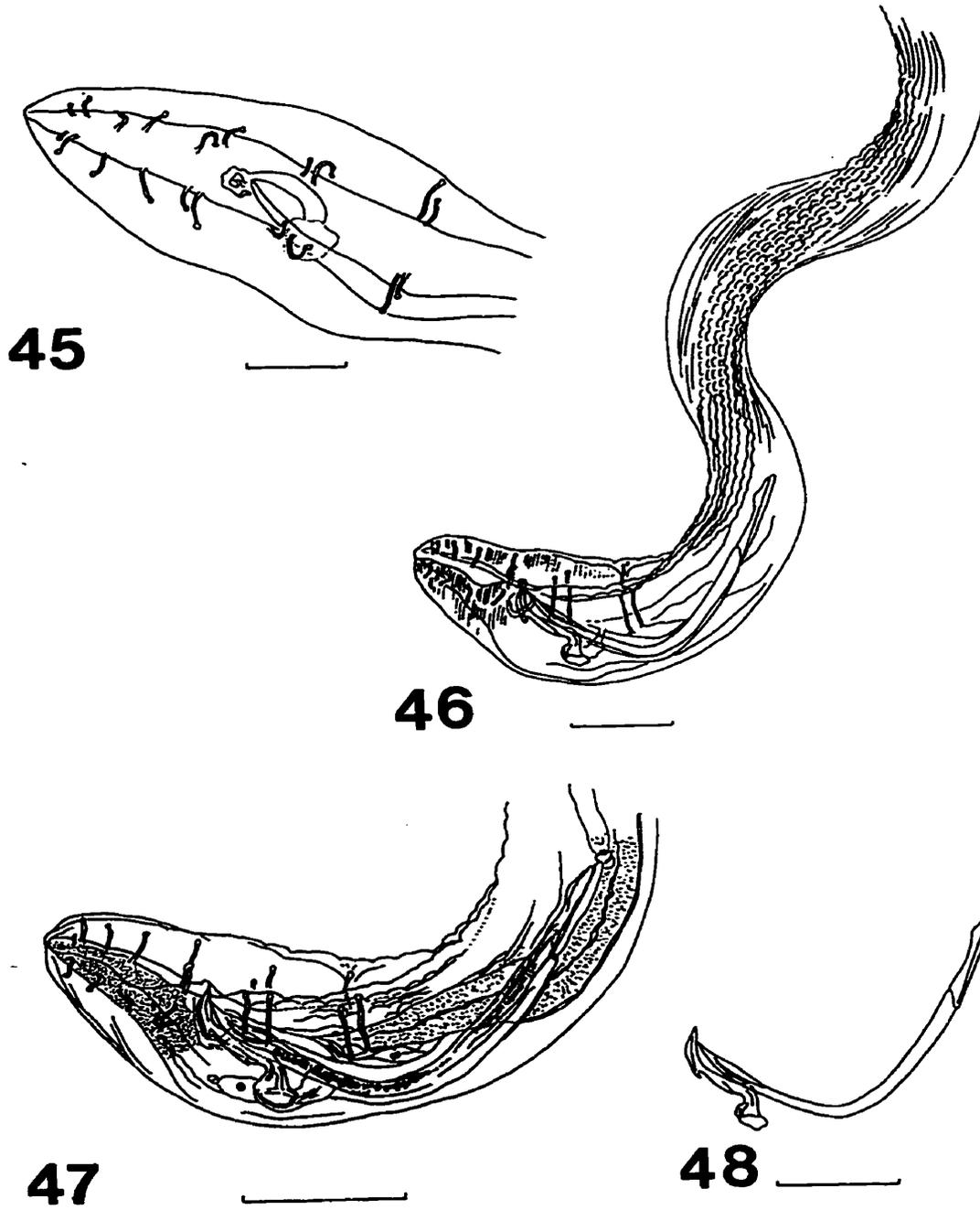
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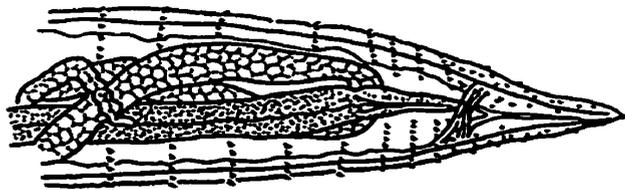
44



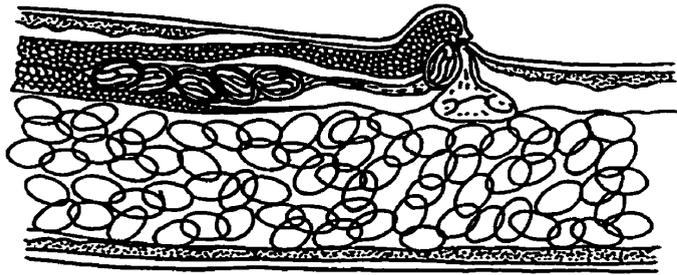
- Figure 45. *Spinitectus acipenseri*. Caudal region of male showing the caudal alae, pre- and postanal papillae (scale bar represents 50 μm).
- Figure 46. *Spinitectus acipenseri*. Caudal region of male showing cuticular clefts in the area rugosae and the position of the spicules (scale bar represents 100 μm).
- Figure 47. *Spinitectus acipenseri*. Caudal region of male showing details of the spicules and the distribution of the papillae (scale bar represents 100 μm).
- Figure 48. *Spinitectus acipenseri*. Spicules drawn in isolation to show the shape of the distal ends and the relationship between the shaft and the blade of the long spicule (scale bar represents 100 μm).



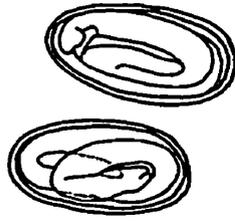
- Figure 49. *Spinitectus acipenseri*. Posterior end of female (ventral view) showing posterior ovary, spine arrangement, gut and a terminal mucron (scale bar represents 50 μm).
- Figure 50. *Spinitectus acipenseri*. Region of female showing protruding vulva, vagina with terminal eggs, and egg filled uterus (spines not drawn, scale bar represents 50 μm).
- Figure 51. *Spinitectus acipenseri*. Individual eggs showing absence of superficial structures and coiled larvae (scale bar represents 10 μm).



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Figure 52. Cladogram from the preliminary cladistic analysis of *Spinitectus* spp. with the first alternative assignment (i) to character 1 in Table 17.

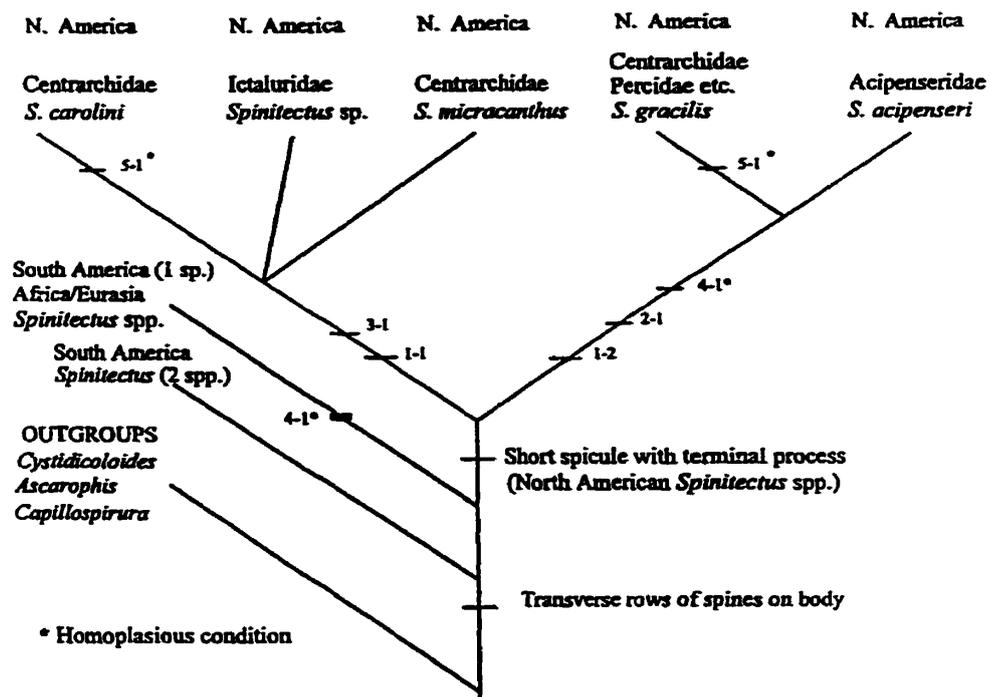
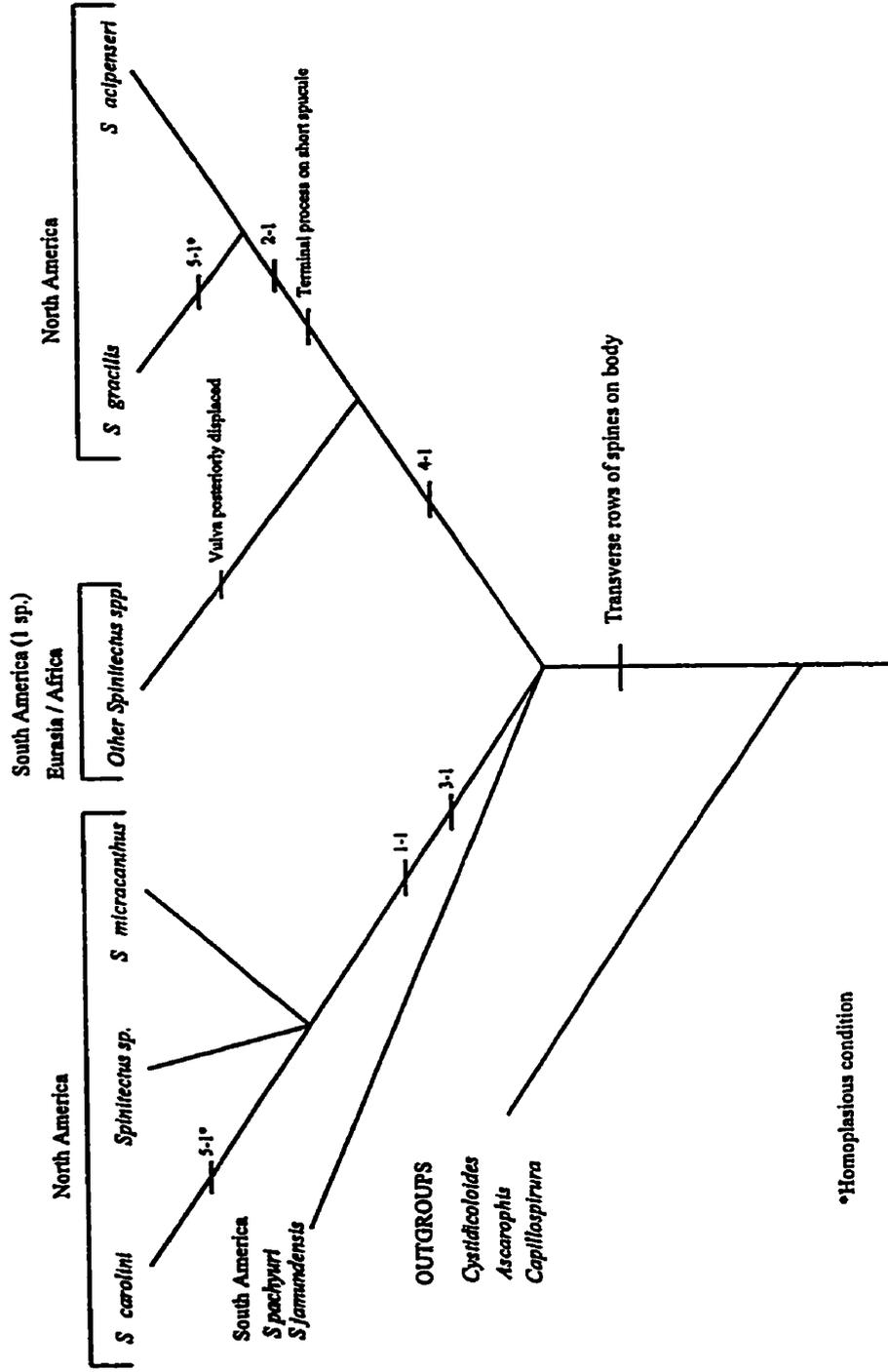


Figure 53. Cladogram from the preliminary cladistic analysis of *Spinitectus* spp. with the second alternative assignment (ii) to character 1 in Table 17.



*Homoplasious condition

Chapter 2-4.

Observations on the morphology of *Truttaedacnitis clitellarius* and *T. lebedevi*

(Nematoda: Cucullanidae) from acipenserids and synonymy of the two species.

INTRODUCTION

Three nominal species of *Truttaedacnitis* Petter, 1974, are recognized as being specific for acipenserids (sturgeon); *T. lebedevi* (Skrjabina, 1966) (= *T. sibiricus*, Finogenova, 1967; see Skrjabina, 1974) is specific for freshwater acipenserids in Siberia and the Amur R. drainage, *T. sphaerocephala* (Rudolphi, 1809) commonly parasitizes anadromous/estuarine sturgeons in Europe and North America (Skrjabina, 1974, Appy and Dadswell, 1978), and *T. clitellarius* has only been reported in lake sturgeon (N. America) (Hoffman, 1967; Margolis and Arthur, 1979; see General Introduction and Chapter 1). Of these three species, *T. lebedevi* and *T. sphaerocephala* have been fairly well described (Tomquist, 1931; Skrjabina, 1974). The survey conducted in this study (Chapter 1) yielded numerous specimens of *T. clitellarius*. However, an examination of the morphology of *T. clitellarius* and a re-examination of *T. lebedevi* indicated the two species are morphologically more similar than previously thought (Skrjabina, 1974). In view of the incomplete description of *T. clitellarius* by Ward and Magath (1917) and the close similarity with *T. lebedevi*, I redescribe *T. clitellarius*, add to the information on *T. lebedevi*, and re-evaluate the relationship between the two species.

MATERIALS AND METHODS

Specimens of *Truttaedacnitis clitellarius* were recovered from the intestines of lake sturgeon, *Acipenser fulvescens*, from Central Canada, i.e., Saskatchewan River (mostly Cumberland Lake), Nelson River (Angling Lake, Sipiwesk Lake), Winnipeg

River (Nutimik Lake and Slave Falls) and Rainy River (Manitou Rapids), and from L. Winnegbago, Wisconsin, U.S.A. (males only). Nematodes recovered from previously frozen viscera were washed briefly in water and stored in a mixture of 5% glycerine and 70% ethanol. Live nematodes from fresh gut samples were fixed in hot 70% ethanol and a few specimens were fixed in hot 10% formalin. All nematodes were cleared in hot lactophenol (65-70°C) and mounted in glycerine on slides. Some specimens were decapitated and the anterior end mounted en face to observe cephalic structures. Thirty five males and 35 females were examined and used for morphometrics of the various anatomical features (Table 19). Maximum widths of nematodes were measured only from those specimens that retained the normal cylindrical body shape at their widest points. Specimens of *T. lebedevi*, preserved in formalin, were donated by the Institute of Parasitology, Academy of Sciences of Russia and by Professor O.N. Bauer, St. Petersburg. These specimens were recovered from the Siberian sturgeon *Acipenser baeri* from the Lena and Ob River drainages. They were washed in water, transferred to 70% alcohol, and subsequently processed and measured as for *T. clitellarius*. Twenty-four males and 30 females were examined. Specimens were studied using bright field and phase contrast microscopy, on a Leitz microscope.

Histology: Two specimens of *T. clitellarius* and three specimens of *T. lebedevi*, fixed in formalin, were washed, dehydrated in ethanol, cleared in methyl salicylate, embedded in TissuePrep (Fisher Co., 56°C), and serially sectioned (7-10 um sections). Sections were stained with Ehrlich's and Delafield's haematoxylin and counterstained

with eosin (Humason, 1972).

Specimens of *T. clitellarius* and *T. lebedevi* are deposited in the U.S. National Museum, Maryland as follows; *T. clitellarius*: USNPC 84915 (Siberian material) and USNPC 84916 (North American material).

RESULTS

Description:

Truttaedacnitis clitellarius (Ward and Magath, 1917). Figs. 54-73

(Based on 35 males and 35 females. Measurements given in Table 19).

General: Body moderately robust, often with dorsally flexed anterior end, in rare cases, ventrally flexed. Cephalic end rounded. Posterior part of body often curved ventrally so as to give body overall sigmoid shape ; this shape, more pronounced in some specimens than in others. Maximum width in anterior third of body around oesophagus-intestine junction, becoming uniformly cylindrical posteriorly . Narrow lateral alae beginning in cervical region, narrowing posteriorly and terminating at anal region. Cuticle with transverse striations, more prominent in mid-body region. Mouth slit like, dorsally oblique to the longitudinal axis of the body (Fig. 54); oral opening spindle shaped, with three conspicuous papillae on either side of opening of which the central one is likely the amphid (Fig. 55); oral opening bordered by smooth transparent cuticular collar bearing weak longitudinal rib-like structures ('teeth') producing wavy margin (visible only under 400 X magnification) (Fig. 56). An inner circle of three small papillae present (Fig. 56). Two bud shaped deirids with bulbous bases, one on

either side of body, often asymmetrically situated, adjacent to lateral alae, posterior to nerve ring (Fig. 57). Additional pair of markedly asymmetrical deirids in posterior two-thirds of body (Fig. 58). Tail conical, gently tapering, bearing mucron (cuticular spine). Hemizonid posterior to nerve ring (Fig. 54). Oesophagus muscular, clavate, with triradiate lumen expanded anteriorly to form pseudobuccal capsule (oesophastome) with thickened cuticular lining (Figs. 54, 59). Bilaterally symmetrical cephalic plates present, separated by narrow sutures and attached to the thickened cuticular plates of pseudobuccal capsule (Fig. 60). Lumen of oesophagus lined by cuticle, each side of triradiate lumen thickened to give the appearance of 'longitudinal rods' embedded into musculature of oesophagus (Fig. 54). Oesophageal lumen widening anteriorly with concomitant widening and thickening of cuticular lining of pseudobuccal capsule (Fig. 54), these forming characteristic median ventral and lateral plates (Fig. 54). Outer edges of cuticular lining with sharp fine processes embedded into oesophageal musculature. Arrangement of fine cuticular processes changing at level of nerve ring. Cuticular thickenings ('longitudinal rods') not reaching base of oesophagus (Fig. 54), oesophageal lumen losing triradiate shape immediately anterior to junction. Junction of oesophagus and intestine guarded by cuticular folded valve (Fig. 54). Excretory pore at approximately mid-level of pseudobuccal capsule; posterior border of pore guarded by cuticular ridge appearing as tubercle like protuberance in lateral view (Figs. 54, 61), pronounced in some specimens. Excretory duct long, cuticular, extending posteriorly along ventral body wall past nerve ring to posterior half of oesophagus (Figs. 54, 61). Excretory duct merging into diffuse tissue

extending laterally on either side of oesophagus (lateral commissure) and becoming contiguous with lateral excretory bands (Fig. 61). Prominent nucleus present immediately posterior to base of the excretory duct (Fig. 61).

Males: Body often with marked curvature at posterior end. Posterior body deirids markedly asymmetrical. Minute deirid adjacent to left lateral ala, some distance anterior to preanal sucker. Deirid on right side post equatorial. Single testis originating posteriorly, extending anteriorly and looping back on itself, often braided for some distance (Fig. 62). Seminal vesicle opens posteriorly into vas deferens via valve like structure (Fig. 63). Sperm spherical. Posterior pre-anal sucker well developed (without cuticularized rim), bordered by radially situated muscle bands (Fig. 64). Spicules equal or slightly sub-equal, gouge shaped, proximal end often bifid and connected to muscle bands. Spicules broadening along mid-region and tapering to blunt (rounded) distal end (Fig. 65). Distal end of spicule occasionally bent. Median groove of spicules bordered by wavy serrations (Fig. 65). Gubernaculum with Y shaped sclerotized body (Fig. 66). Unsclerotized cuticular sheath like structures guarding the distal end of the spicules. Eleven pairs of sessile papillae present; four pairs pre-anal, one pair adanal, and six pairs post-anal of which one pair is phasmids (Figs. 64, 67). The relative positions of the last two pairs of papillae showing variation. Median papilla immediately above anterior edge of cloacal opening, prominent in lateral view (Figs. 64, 67).

Females: Body form often sigmoid, generally larger than males (Table 19). Left posterior body deirid posterior to vulva and right deirid anterior to vulva. Didelphic and amphidelphic. Ovaries coiled. Anterior ovary variable in position, at level of or

posterior to oesophagus-intestine junction, in anterior third of body. Posterior ovary in posterior fifth of body (Fig. 68), occasionally reaching the level of anus or further posterior. Oviducts running beyond vulvar region, turning back on themselves and giving rise to thin walled uteri containing eggs. Uteri fuse and open to thick walled vagina forming short curved final segment opening to vulva, this junction guarded by thick rounded projections of vaginal wall (Figs. 69, 70). Vagina occasionally looped. Vulvar opening a lateral slit, anterior and posterior margins guarded by cuticular thickenings (Fig. 70). Eggs ovoid, thin shelled, without surface ornamentation. Terminal uterine and vaginal eggs in early stages of embryonation (gastrula stage) (Fig. 69).

Truttaedacnitis lebedevi (Skrjabina, 1966)

Comments (based on 24 males and 30 females). Measurements are given in Table 19. The excretory pore opens at the level of the pseudobuccal capsule (Fig. 71). A hemizonid is present behind the nerve ring. (Fig. 71). The cephalic papillae and plates are arranged as in *T. clitellarius*. The caudal papillae (including the phasmids) total 11 pairs; 4 preanal, 1 adanal and 6 postanal (Figs. 72, 73). One median papilla situated immediately in front of the cloaca (Fig. 73). Spicules with serrated edges (Fig. 72). The gubernaculum is Y-shaped (Fig. 73). Anterior end with cephalic plates and posterior body deirids present on posterior two thirds of the body. Dentigerous ribs on the oral collarette are weakly developed or absent.

DISCUSSION

The genus *Truttaedacnitis* was erected by Petter (1974) based on the characters described in detail by Berland (1970) for his emended diagnosis of the genus *Dacnitis*. *T. clitellarius* and *T. lebedevi* can be easily distinguished from *T. sphaerocephala* by the presence of a ventral cephalic ridge in the latter and by the shape of the spicules: short, heavy and ending in a sharp point in *T. sphaerocephala* and elongate, tapering and terminating in a rounded end in the two other species. *T. clitellarius* and *T. lebedevi* can be distinguished from the other species of *Truttaedacnitis* [*T. truttae* (Fabricius, 1794) and *T. pybusae* Anderson, 1992] by the arrangement of the caudal papillae, position of the excretory pore, and morphology of the spicules (Tornquist, 1931; Berland, 1970; Mudry and McCart, 1974; Pybus *et al.*, 1978; Moravec, 1979; Anderson, 1992; this paper). Consequently, this discussion confines itself to the comparison between *T. clitellarius* and *T. lebedevi*.

Skrjabina (1974) distinguished *T. clitellarius* from *T. lebedevi* by the presence of 4 pairs of unequal sized post-cloacal papillae in *T. clitellarius* as opposed to 5 pairs of equal sized post-cloacal papillae in *T. lebedevi*. However, it is evident from this study that the papillar arrangements of the two species are identical, including the position of the phasmids which were not mentioned by Ward and Magath (1917) and apparently misplaced in the diagram of Skrjabina (Figure 48, page 84, of Skrjabina, 1974). The sizes of the caudal papillae (excluding the papilliform phasmids which are always the smallest) are frequently uniform in *T. lebedevi* while displaying much variability in *T. clitellarius*. This is particularly true of the last 2 pairs of papillae

where the outer pair is often larger than the inner pair. However, the anterior lateral pair of post-anal papillae appears more massive than all other papillae in both species. In view of this variability in papillar size, I am reluctant to assign it significant taxonomic value.

Skrjabina (1974) also considered the spicule size of *T. clitellarius* diagnostic and this is stated as being 1.6 mm as opposed to a smaller 1.1 mm for *T. lebedevi*. The data for *T. clitellarius* was apparently obtained from the original description of Ward and Magath (1917). Although I was unable to locate the type material (J.R. Lichtenfels, pers. comm.), such unusually long spicules were not found in any of the specimens examined by us over a considerable geographical range. It is clear from this study that there is overlap in spicule size between *T. clitellarius* and *T. lebedevi*, although the spicules in *T. lebedevi* are confined to the lower end of the size range and are often less robust than those of *T. clitellarius* (Table 19). Consequently, neither size nor morphology of the spicules can be used to differentiate the two species. The cephalic extremities of the two species are also similar, including an identical arrangement of 'cephalic plates' (terminology of Berland, 1970), and caudal papillae (this study). In *T. clitellarius*, the dentigerous rib-like structures characteristic of the cucullanids are variably developed and in some specimens only represented by a wavy margin. Using light microscopy, only a wavy margin could be identified in most specimens of *T. lebedevi*. The two species also share an identical anterior location of the excretory pore. The excretory pore in *T. lebedevi* was described as being posterior to the nerve ring (Skrjabina, 1974). However, specimens of *T. lebedevi* and serial

sections of the anterior portion show that the excretory pore is located anteriorly at the level of the pseudobuccal capsule as in *T. clitellarius*. This location of the excretory pore is the anteriormost among all *Truttaedacnitis* species and indeed among other cucullanids. The hemizonid which is posterior to the nerve ring may have been mistaken for the excretory pore.

In all other essential aspects of morphology and anatomical proportions, (Table 19), *T. lebedevi* and *T. clitellarius* show significant similarity. In my opinion, minor differences, such as more uniform papillar size, tendency towards smaller body size and less robust spicules in *T. lebedevi*, are geographical variations not consistent enough to be valid species characteristics, based on morphology. From a taxonomic standpoint, *T. lebedevi* may be relegated to a junior synonym of *T. clitellarius*. This reduces further the number of *Truttaedacnitis* species in primitive holarctic fish families (petromyzontids, acipenserids and salmonids) to four. *T. clitellarius* is apparently specific for freshwater acipenserids and its ancestral form was likely a freshwater parasite of acipenserids prior to continental separation. Furthermore, since morphological differences noted between Siberian and North American populations of this parasite (this study) are minor and largely related to size, there appears to have been a slow rate of evolution.

Table 19. Measurements of *T. clittellarius* and *T. lebedevi**. (Measurements are in micrometres unless otherwise stated)

	<i>T. clittellarius</i>		<i>T. lebedevi</i>	
	Male(N=35)	Female(N=35)	Male(N=24)	Female(N=30)
Length(mm)	13.5 ± 1.7 (9.6 - 16.9)	15.1 ± 1.9 (9.9 - 18.6)	12.4 ± 1.5 (9.4 - 14.8)	13.8 ± 1.6 (10.5-17.1)
Width(max)	402.4 ± 73.6 (N=21) (244 - 592)	431.8 ± 49 (N=19) (329 - 526)	389.9 ± 31.5 (N=20) (338 - 442)	438.9 ± 36 (N=27) (320 - 479)
Width 1	312.7 ± 48.6 (N=34) (198 - 404)	-	316.7 ± 27 (N=18) (273-376)	-
Width 2 (N=29)	-	354.9 ± 57.3 (263 - 461)	-	363.6 ± 37.2 (301 - 442)
Head width	307.2 ± 29.3 (244 - 348)	325.5 ± 26.1 (282 - 385)	264.7 ± 15.3 (235 - 301)	278.7 ± 19.9 (197 - 301)
Pseudobuccal capsule				
width	268 ± 19.3 (235 - 301)	294.8 ± 24.7 (263 - 385)	243.9 ± 17.9 (216 - 301)	256.2 ± 12.9 (226-282)
length	352.2 ± 18.5 (319 - 385)	372.2 ± 20.2 (273 - 395)	306.2 ± 23.5 (226 - 357)	322.8 ± 8.9 (301 - 338)
Nerve ring ¹	585 ± 28.4 (526 - 640)	613.4 ± 24.8 (564 - 677)	545.5 ± 35.7 (498 - 659)	567.1 ± 30.1 (489 - 639)
Left deirid ²	285.8 ± 33.7 (224 - 376)	293.9 ± 36.1 (226 - 385)	225.6 ± 27.8 (N=23) (168 - 273)	242.3 ± 25.2 (N=26) (187 - 310)
Right deirid ²	302.2 ± 46.9 (244 - 489)	301.9 ± 42 (235 - 385)	233.5 ± 24.4 (N=23) (187 - 277)	238.8 ± 28.1 (187 - 310)
Hemizonid ²	119 ± 23 (N=31) (67 - 187)	107.9 ± 29.3 (N=34) (37 - 168)	89.7 (0 - 187)	85.2 (0 - 188)
Oesophagus				
length	1351 ± 106.9 (1100 - 1550)	1419 ± 100.4 (1150 - 1600)	1275 ± 68.1 (1150 - 1400)	1330 ± 79.2 (1150 - 1450)
width(min)	126.5 ± 10.4 (103 - 150)	138.1 ± 11.8 (122 - 160)	139.1 ± 6.3 (132 - 150)	139.1 ± 8.7 (113 - 150)
width(max)	252.1 ± 31.5 (179 - 310)	276.4 ± 42 (207 - 367)	251 ± 18.6 (226 - 282)	256.8 ± 25.4 (197 - 291)
Tail length	428.2 ± 59.8 (301 - 564)	379.6 ± 52.2 (245 - 498)	439.7 ± 41.1 (357 - 508)	430.3 ± 44.5 (329 - 508)

Table 19. continued...

	<i>T. citreilarius</i>		<i>T. lebedevi</i>	
	Male(N=35)	Female(N=35)	Male(N=24)	Female(N=30)
Mucron	8.2 ± 1.6(N=28) (4.8 - 9.6)	8.05 ± 1.31(N=28) (4.8 - 9.6)	11.6 ± 2.27(N=23) (9.6 - 16.8)	11.6 ± 2.19(N=27) (7.5 - 17)
Phasmids ³	223.5 ± 37.5 (137 - 307)	197.8 ± 34(N=32) (108 - 273)	243.4 ± 22.4 (202 - 284)	219.3 ± 30.2 (142 - 269)
Testis ⁴	1458 ± 656.5(N=32) (122 - 2575)	-	850.6 ± 438.1 (150 - 1880)	-
Preanal sucker ³	1695.7 ± 188.5 (1250 - 2100)	-	1572.9 ± 151 (1300 - 1800)	-
Left spicule	1120 ± 81 (900 - 1300)	-	950 ± 54.5 (875 - 1100)	-
Right spicule	1135.7 ± 87.9 (875 - 1350)	-	954.1 ± 64.4 (850 - 1100)	-
Gubernaculum	138.7 ± 12.3 (101 - 172)	-	95.3 ± 10.3 (82 - 118)	-
Vulva ³	-	0.63 ± 0.02 (0.58 - 0.67)	-	0.62 ± 0.03 (0.55 - 0.69)
Anterior ovary ⁴	-	464.8 ± 357.8(N=29) (0 - 1269)	-	785.8 ± 681.1 (0 - 2820)
Posterior ovary ³	-	531.2 ± 167.4(N=32) (244 - 1051)	-	650.4 ± 194.1 (179 - 1051)
Vagina	-	762.8 ± 85.7 (N=15) (602 - 940)	-	565.5 ± 118.3(N=17) (376 - 808)
Egg	-	(67.3 x 41.4 - 78.5 x 48.6)	-	64.8 x 48.6 - 82.2 x 48.6
Oesophagus: body length	0.1 ± 0.01 (0.09 - 0.12)	0.09 ± 0.01 (0.08 - 0.13)	0.1 ± 0.01 (0.08 - 0.14)	0.09 ± 0.01 (0.08 - 0.11)

Table 19. continued...

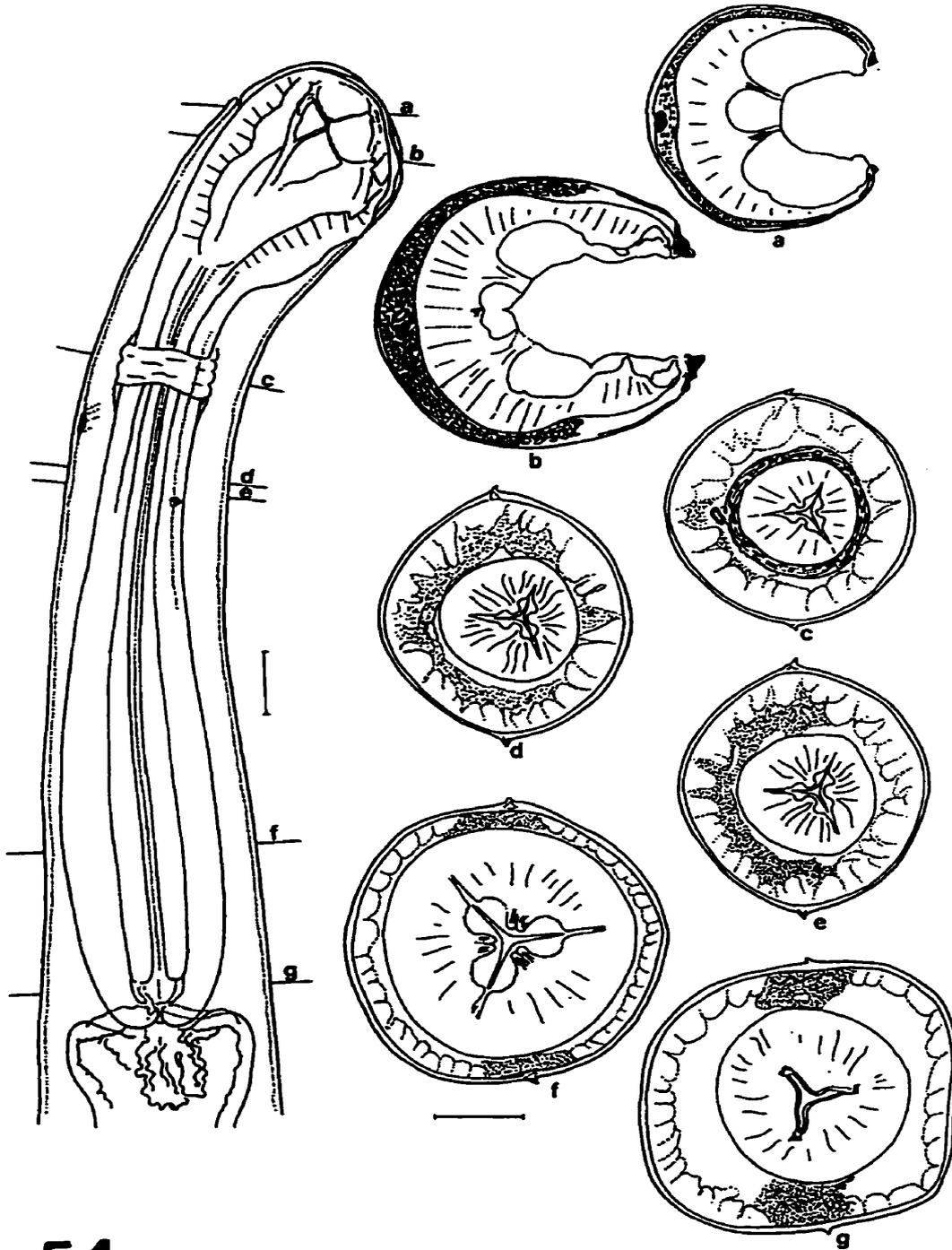
	<i>T. citellarius</i>		<i>T. lebedevi</i>	
	Male(N=35)	Female(N=35)	Male(N=24)	Female(N=30)
Left spicule: body length	0.08 ± 0.01 (0.07 - 0.11)	-	0.077 ± 0.01 (0.06 - 0.1)	-
Right spicule: body length	0.08 ± 0.01 (0.07 - 0.12)	-	0.077 ± 0.01 (0.06 - 0.1)	-
Preanal sucker ¹ : body length	0.125 ± 0.01 (0.11 - 0.15)	-	0.127 ± 0.01 (0.11-0.15)	-

*Means ±

S.D. (range) ¹Distance from anterior end, ²Distance from nerve ring, ³Distance from posterior end, ⁴Distance from oesophagus-intestine junction, ⁵Position (prevulva distance:total body length).

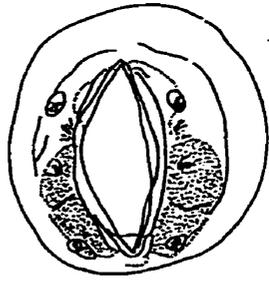
Width 1 = Width in posterior third of body where sides parallel. Width 2 = Width immediately anterior to vulva.

Figure 54. *T. clitellarius*. Anterior region with histological cross-sections from corresponding locations along the body. Note excretory duct. Scale bar = 100 μm .

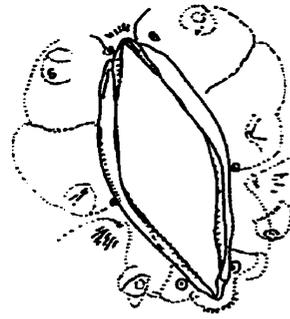


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- Figure 55. *T. clitellarius*. *En face* view of the cephalic region showing spindle shaped oral opening and outer cephalic papillae. Scale bar = 100 μm
- Figure 56. *T. clitellarius*. Closer view of oral opening showing ribbed oral collarette and inner papillae. Scale bar = 100 μm .
- Figure 57. *T. clitellarius*. Lateral view of right cervical deirid and prominent lateral ala. Scale bar = 100 μm
- Figure 58. *T. clitellarius*. Lateral view of right posterior body deirid and narrow lateral ala. Scale bar = 100 μm
- Figure 59. *T. clitellarius*. Male worm: Internal view of pseudobuccal capsule showing shape and musculature. Scale bar = 100 μm
- Figure 60. *T. clitellarius*. Superficial view of same region in '6' showing cephalic plates. Scale bar = 100 μm
- Figure 61. *T. clitellarius*. Anterior region of male showing excretory pore and duct and their relation to other anatomical structures. Scale bar = 100 μm .



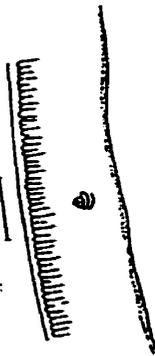
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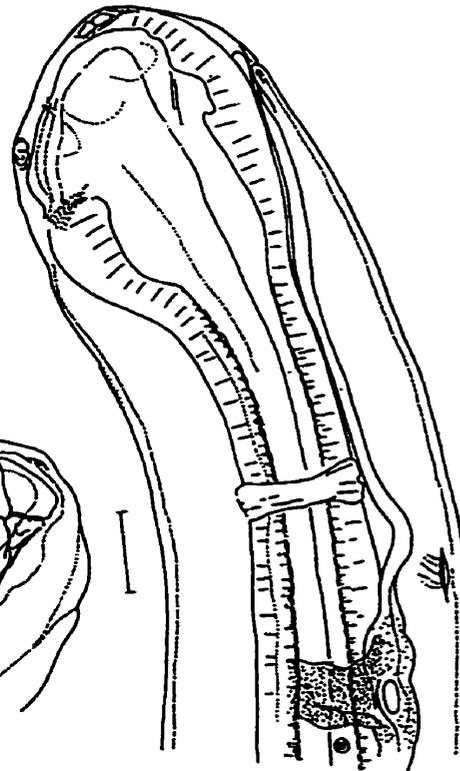
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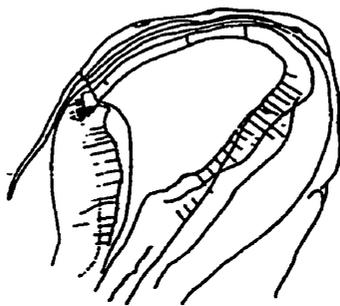
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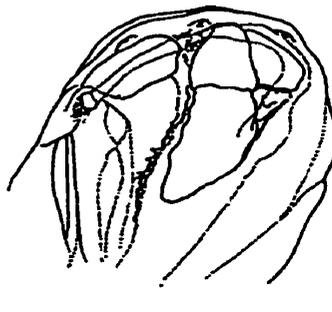
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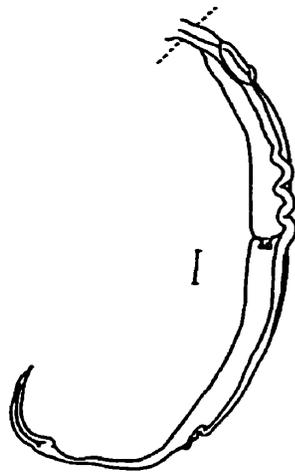


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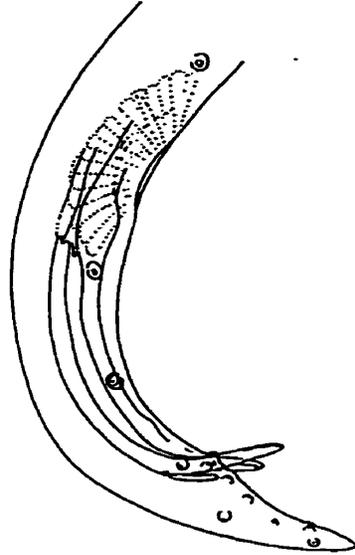
- Figure 62. *T. clitellarius*. Testis showing braiding and looping. Scale bar = 100 μm .
- Figure 63. *T. clitellarius*. Seminal vesicle, origin of the testis and ejaculatory duct. Scale bar = 100 μm .
- Figure 64. *T. clitellarius*. Posterior region of male showing pre-anal sucker, spicules and papillae. Scale bar = 100 μm .
- Figure 65. *T. clitellarius*. Distal portion of spicules showing gouge shape and median serrated margins. Scale bar = 100 μm .
- Figure 66. *T. clitellarius*. Gubernaculum. Scale bar = 100 μm .
- Figure 67. *T. clitellarius*. Ventral view of male caudal region. Scale bar = 100 μm .



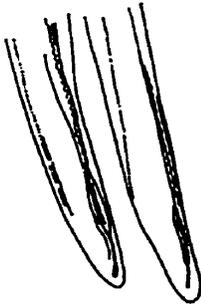
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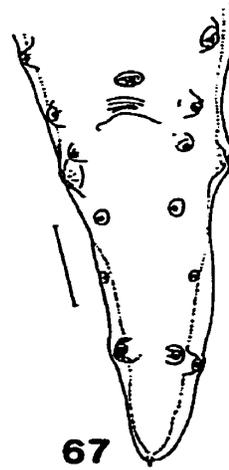
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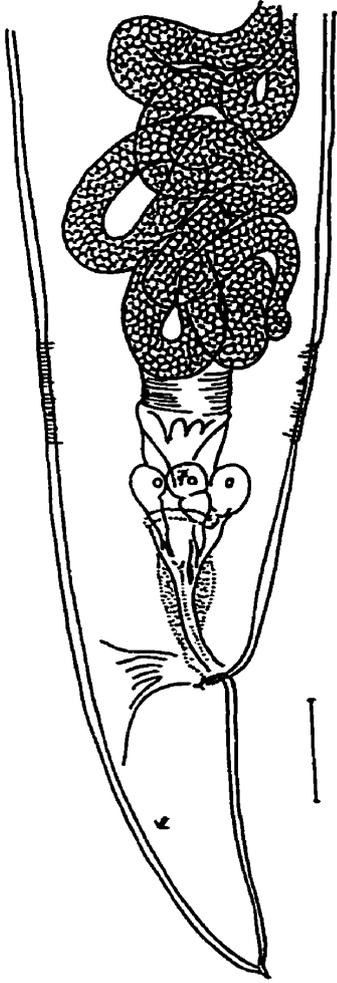


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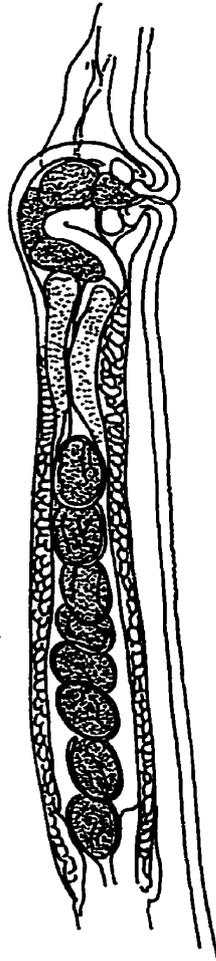


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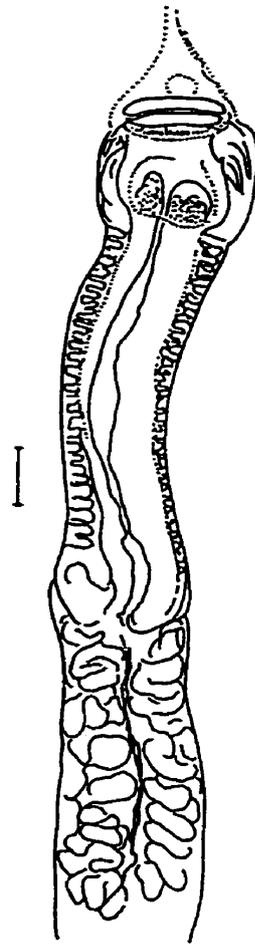
- Figure 68. *T. clitellarius*. Posterior portion of female showing posterior coiled ovary, rectal glands, phasmid and mucron. Scale bar = 100 μm .
- Figure 69. *T. clitellarius*. Lateral view of vagina with terminal eggs. Scale bar = 100 μm .
- Figure 70. *T. clitellarius*. Ventral view of vagina and vulva. Scale bar = 100 μm .



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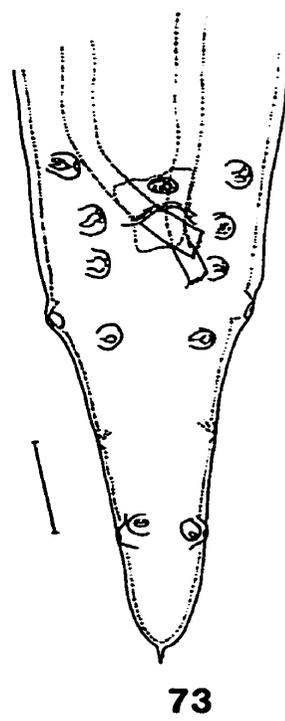
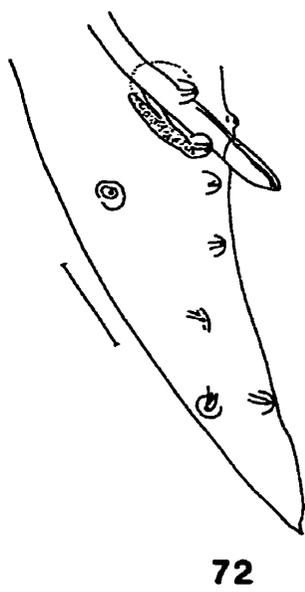
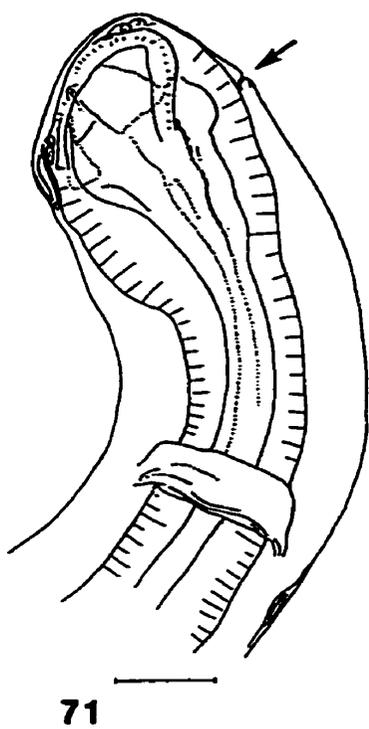


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- Figure 71. *T. lebedevi*. Anterior portion. Note excretory pore (indicated by arrow). Scale bar = 100 μm .
- Figure 72. *T. lebedevi*. Male caudal region. Note arrangement of caudal papillae and phasmids. Scale bar = 100 μm .
- Figure 73. *T. lebedevi*. Ventral view of male caudal region. Scale bar = 100 μm .



Chapter 2-5.

Observations on the morphology, systematics and biogeography of the genus

Truttaedacnitis (Nematoda: Cucullanidae).

INTRODUCTION

The nematode family Cucullanidae Cobbold, 1864 contains several genera of parasites of marine, freshwater and diadromous fishes, with wide global distribution (Ivashkin and Khromova, 1976). Of those, the genus *Truttaedacnitis* Petter, 1974, contains four nominal species; *T. truttae* (Fabricius, 1794) in Eurasian and North American salmonids, *T. pybusae* Anderson, 1992, in North American lampreys, and *T. clitellarius* (Ward and Magath, 1917) and *T. sphaerocephala* (Rudolphi, 1809) in Eurasian and North American sturgeons (Acipenseridae) (Mudry and McCart, 1974; Skrjabina, 1974; Pybus, Anderson and Uhazy, 1978, Pybus, Uhazy and Anderson, 1978; Petter, 1985; Moravec, 1994; Chapter 2-4). *Truttaedacnitis heterodonti* (Johnston and Mawson, 1943) from *Heterodontus portusjacksoni* (Meyer) was transferred to *Cucullanus* Müller, 1777, by Petter (1985). Given the specificity of these nematodes for their host families, a phylogenetic analysis of the genus *Truttaedacnitis* was undertaken to gain insights into historical host-parasite associations. Consequently, *Truttaedacnitis* spp. were first examined for morphological characters suitable for analysis. Observations on the morphology of *T. truttae*, *T. sphaerocephala*, and *C. heterodonti*, helped clarify some ambiguities regarding certain anatomical features and are reported in this study. This is followed by a cladistic analysis of *Truttaedacnitis* spp. (Hennig, 1966; Wiley, 1981; Brooks and McLennan, 1991, 1993; Wiley *et al.*, 1991; Forey *et al.*, 1992) and a discussion of their historical biogeography.

MATERIALS AND METHODS

All species of *Truttaedacnitis* and several species of the two outgroups (*Cucullanus* Müller, 1777 and *Dichylene* Jaegerskiold, 1902) were examined from museum collections. Names of parasites and their hosts are according to the original museum labels. *Bulbodacnitis alpinus* Mudry and McCart, 1974, *B. ampullastoma* Maggenti, 1971, *B. scotti* Simon, 1935, *B. truttae* (Fabricius, 1794) and *Cucullanus truttae* Fabricius, 1794 and *T. stelmioides* (Vessichelli, 1910), are synonymous with *Truttaedacnitis truttae*. *Salmo gairdneri* Richardson (rainbow trout) is now *Oncorhynchus mykiss* (Walbaum) and *S. lewisi* Suckley (cutthroat trout) is *O. clarki* (Richardson). BMNH refers to the British Museum (Natural History), London, NMCP refers to the Canadian Museum of Nature, parasite collection, Ottawa, CSAV refers to the Czech Academy of Sciences Vermes collection, Ceske Budejovice, MNHN refers to the Museum National Histoire Naturelle, Paris, UCDNC refers to the University of California Davis nematode collection, and USNPC to the U.S. National Parasite Collection, U.S. National Museum, Beltsville, Maryland.

Specimens examined

Bulbodacnitis alpinus: USNPC 72533 Paratypes, ex *Salvelinus alpinus* (Linnaeus) (Arctic char), Babbage River, Yukon Territory, Canada. (5 females (f), 5 males (m)).

Bulbodacnitis ampullastoma: USNPC 72222 Paratypes, ex *Salmo gairdneri*, Hot Creek hatchery, California, U.S.A. (1 f, 1 m); UCDNC 189, 190 (2 m paratypes) and UCDNC 192 (1 f paratype), ex *Salmo gairdneri*, Hot Creek hatchery, California, U.S.A.

Bulbodacnitis scotti. USNPC 8816. Paratype (m) and allotype (f) ex *Salmo lewisi*, Wyoming. *Truttaedacnitis truttae*: USNPC 30702 ex *Salmo gairdneri*, Rogue River, Oregon. U.S.A. (5 f, 1 m); USNPC 46155 ex rainbow trout, hatchery near Logan, Utah, U.S.A. (3 f, 1 m; all immature); NMCP1984-8784 ex *Salmo gairdneri*, Arctic Lake, British Columbia, Canada; NMCP1986-0174 ex *Salvelinus fontinalis* (Mitchill) (brook char), Tabusintac River, New Brunswick, Canada. (5 f, 5 m); NMCP1984-6578 ex *Salvelinus malma* (Walbaum) (Dolly varden char), Southeast Arctic Lake, British Columbia, Canada. (1 immature); NMCP1984-6551. ex *Salvelinus namaycush* (Walbaum) (lake char), Southeast Arctic Lake, British Columbia, Canada. (1 m, 2 f).

Cucullanus truttae. BMNH 1931.3.9. 57-61 ex trout (species unspecified but possibly brown trout, *Salmo trutta*), River Test, Hampshire (1 f, 1 m); BMNH 1933.3.20. 79-81 ex trout, R. Test, Hampshire (2 m). CSAV No. N-66. ex *Salmo trutta m. fario* Linnaeus, Cernovsky brook, Czech Republic. (3 f, 3 m).

Bulbodacnitis truttae. BMNH 1973. 813-820 ex *Salmo trutta* L., Cornwall, England (2 f, 3 m).

Cucullanus heterodonti: MNHN 451 BB ex *Heterodontus portusjacksoni*. Australia. (7 f, 2 m, 1 immature).

Truttaedacnitis clitellarius: Specimens collected in this study from *Acipenser fulvescens*, Canada and U.S. (> 100 m, f), and from *A. baeri*, Ob and Lena Rivers, Siberia (formerly *T. lebedevi* (Skrjabina, 1966), see Chapter 2-4) (10 f, 10 m).

Truttaedacnitis sphaerocephala (Rudolphi, 1809): ex *Acipenser stellatus* Pallas, Kuban' River, Caucasia, Russia. (11 f, 8 m). Specimens donated by Dr. O.N. Bauer,

Institute of Zoology, St. Petersburg. Voucher specimens (3 f, 3 m) have been deposited to the U.S. National Parasite Collection, Beltsville, Maryland, (Accession number USNPC 86418).

Truttaedacnitis pybusae: USNPC 73130 ex *Lampetra lamottenii* (LeSueur), (brook lamprey) Ontario, Canada. (11 f, 9 m).

Truttaedacnitis stelmoides (Vessichelli, 1910). BMNH 1982.749-751 ex brook lamprey (species not given), Galway, Ireland (2 f).

The following species of the outgroups (*Cucullanus* and *Dichelyne*) were also examined:

Cucullanus dogieli Krotas, 1959. CSAV N-253 ex *Aspius aspius* (L.), River Latorica, Slovakia (2 f, 1 m).

Cucullanus himezi Yamaguti, 1941. CSAV N-253 ex *Parupaeneus indicus* (Shaw), Indian Ocean, near Somalia (3 f, 3 m).

Cucullanus sp. HWML 20746 ex *Platichthys stellatus* Pallas (starry flounder), Friday Harbour Laboratory, San Juan Islands, Washington (4 f, 4 m).

Dichelyne cotylophora (Ward and Magath, 1917). ex *Perca flavescens* (Mitchill) (yellow perch), Whiteshell, Manitoba, Canada (held in the collection of TAD) (3 f, 3 m).

Dichelyne lepisosteus Casto and McDaniel, 1967. USNPC 61491, 61492. ex *Lepisosteus spatula* (Lacepede) (alligator gar), Mathis Lake, Texas, U.S.A. (1 f, 1 m).

Histology: One specimen of *T. sphaerocephala*, fixed in formalin, was washed, dehydrated, cleared, embedded in paraffin (Tissue Prep, 56°C, Fisher Scientific, Fair

Lawn, New Jersey) and serially sectioned at 5-7 μm thickness. Sections were mounted on slides and stained with Ehrlich's haematoxylin and eosin (Humason, 1972).

Phylogenetic analysis

The outgroups are the genera *Cucullanus* and *Dichelyne* (both Cucullanidae). Both genera are well defined, contain most of the cucullanid species, and have a wide distribution in marine and freshwater fishes. Several species of *Cucullanus* have been described in detail (Berland, 1970; 1983) and these descriptions have also been used as a source of information. In this study, we follow the terminology of Pybus, Anderson and Uhazy (1978) for the cephalic plates [Berland's (1970) terminology is given in parentheses] as follows: ventral plate (transverse ventral plate), ventrolateral plates, vl_1 (postero-ventral triangle), vl_2 (ventrolateral crescent), vl_3 (intermediate area), vl_4 (anterior triangle) and vl_5 (ventral triangle), dorsal plates d_1 (dorsal median triangle) and d_2 (dorsal oval area) (Figs. 74 a, b, c, d).

Characters and states used in the cladistic analysis of *Truttaedacnitis* spp.

- (1). Longitudinal rib-like structures on oral collarette. Well developed, conspicuous, longitudinal rib-like structures on the oral collarette are considered plesiomorphic by outgroup comparison (1-0). Weakly developed rib-like structures are considered apomorphic (1-1).
- (2.) Excretory pore. The excretory pore is either posterior to nerve ring or well anterior near pseudobuccal capsule (see Chapter 2-4). A position posterior to the nerve ring level is considered plesiomorphic by outgroup comparison (2-0) and the anterior

position apomorphic (2-1).

(3.) Spicule shape. Two states are recognized. Simple tapering spicules and those with an angularly bent mid-region (Fig. 75). The first is the plesiomorphic condition (3-0) by outgroup comparison while a bent shape is considered apomorphic (3-1).

(4.) Dorsal cephalic ridge. Two states are recognized: absent or present. Absence is considered plesiomorphic by outgroup comparison (4-0) while presence is considered apomorphic (4-1).

(5.) Ventral cephalic ridge. Two states are recognized; absent or present. Absence is considered plesiomorphic (5-0) by outgroup comparison while presence is considered apomorphic (5-1).

(6.) Dorsal cephalic plates: Outgroups possess no plates (6-0). Two states are recognized in the ingroup; d_2 small (6-1) or very large (6-2). The posterior dorsal plate (d_1) could not be clearly discerned in whole mounts of *T. clitellarius* and *T. sphaerocephala* although serial sections indicate that thickenings exist (Fig. 81). Consequently, d_1 was not used in the analysis. While the morphology and arrangement of the dorsal plates in *T. pybusae*, *T. truttae*, *T. clitellarius* and *T. sphaerocephala* indicate homology, the arrangement in *T. heterodonti* is markedly different. However, we assume homology in this case. The character states were used unordered.

(7.) Ventral cephalic plate vl_3 : Outgroups lack this plate (7-0). Two states are recognized in the ingroup. This plate is either well developed (7-1) or small (7-2). It was not possible to determine the homology of the third ventrolateral plate in *T. heterodonti* (homologous to vl_1 or vl_3) and is consequently not used the analysis.

(8.) Ventral cephalic plate vl_2 : Two states are recognized. The plate is either present (8-1) or absent (8-0). Absence of the plate is the plesiomorphic condition. In the condition (8-1), vl_1 directly apposes vl_4 and vl_5 . Since it was not possible to determine the homology of the third ventrolateral cephalic plate in *T. heterodonti*, it was not included in the analysis.

RESULTS

Anatomical and taxonomic observations

Truttaedacnitis from North American salmonines: All specimens possessed a similar arrangement (Fig. 74 a) of three closely apposed cephalic plates. All specimens lacked a prominent or sharp caudal spike (mucron). A reduced button-shaped or dome-shaped mucron (Figs. 76, 77, 78) was present in all specimens examined. The phasmids were located close to the 9th pair of caudal papilla (Figs. 76) (terminology of Petter, 1974) in all specimens with the exception of the single male from rainbow trout of the Rogue R., Oregon (USNPC 30702) where the papilla was slightly more posterior in position (Fig. 77). Paratypes of *T. alpinus* (USNPC 72533) possessed a dorsal cephalic ridge and were similar in morphology to specimens from brook char (*S. fontinalis*) (NMCP 1986-0174).

Truttaedacnitis from European salmonines and lampreys: All male specimens from Cernovsky Brook (CSAV N-66) possessed a spike-shaped caudal mucron (Fig. 79) but such a mucron occurred in only 1 of 3 females (the others possessed rounded caudal ends). All specimens from *S. trutta* in Britain lacked a spike-shaped caudal

mucron but possessed a teat-shaped or button-shaped mucron. The specimens of *Truttaedacnitis* from brook lamprey (species unspecified) in Ireland were similar in morphology to *T. truttae* from *S. trutta* and possessed a rounded tail with a reduced button-shaped caudal mucron.

Truttaedacnitis sphaerocephala: These are moderately large worms (males: 11.9-16.2 mm; females: 15.9 - 18.8 mm in length), often with dorsally flexed anterior end and oral opening markedly oblique (dorsally) to axis of body (Fig. 80). The oral opening is bordered by a cuticular collarette bearing weakly developed inconspicuous longitudinal rib-like structures (discernible only under higher magnification, 400 X). A ridge traverses the ventral side of the body at the level of the pseudobuccal capsule and extends ventrolaterally on either side (Figs. 81, 82). Two broad closely apposed cephalic 'plates' are present, on either side of oral opening (Fig. 80). The pseudobuccal capsule possesses a thickened cuticular lining surrounded by musculature (Fig. 81 a-f) which becomes progressively thinner posteriorly. The triradiate lumen of the esophagus is also lined by cuticle with characteristic thickenings (Fig. 81 g-n). A hemizonid is present immediately posterior to the nerve ring (Fig. 81). The excretory pore is located between the 2 hemispheres of the ventral cephalic ridge (Figs. 81 g, 82). The cuticular excretory duct extends posteriorly between the body wall and esophagus (Fig. 81 h-l) and terminates in the lateral commissure immediately anterior to the level of the deirids (Fig. 81 m). The papillar arrangement (Fig. 75) is as in *T. clitellarius*, *T. pybusae* and *T. truttae* (Berland, 1970; Skrjabina, 1974; Pybus, Uhazy and Anderson, 1978; Choudhury and Dick, 1996).

Cucullanus heterodonti: (MNHN 451 BB). The oral opening is slightly inclined, dorsally. There are 3 closely apposed broad ventrolateral cephalic plates and one large dorsolateral cephalic plate on either side of the oral opening (Fig. 74 d). A peribuccal rim (Berland, 1970) could not be identified. Asymmetric posterior deirids are present as in other cucullanids. The species is hereby transferred back to the genus *Truttaedacnitis* (see also Discussion).

Phylogenetic analysis

The presence of cephalic plates establishes the monophyly of the species of *Truttaedacnitis*. Since the homology of some of the plates could not be determined, the total number of plates was not used in the analysis. The use of characters 6 and 7 (Table 20) as unordered multistate characters resulted in equally parsimonious trees of identical topology (Fig. 83). The character states in parentheses indicate the alternative positions. The unordered character state 6-1 suggests monophyly of *T. clitellarius*, *T. sphaerocephala*, *T. pybusae* and *T. truttae*. The anterior position of the excretory pore near the level of the pseudobuccal capsule in *T. clitellarius* (Chapter 2-4) and in *T. sphaerocephala* (this study) clearly establishes the monophyly of these 2 species. *T. truttae* and *T. pybusae* form a monophyletic group only if the cephalic plates are run unordered (7-1, 8-1). The geographical distributions and hosts of the species have been mapped onto the cladogram for purposes of discussion (Fig. 83).

DISCUSSION

Morphology and Systematics

The genus *Truttaedacnitis* Petter 1974, has been distinguished from *Cucullanus* Müller 1777, based mainly, on the presence of a markedly oblique oral opening, a dorsally flexed anterior end, cephalic 'plates', and absence/reduction of a peribuccal rim, in the former (Berland, 1970; Petter, 1974; Baker, 1984). However, *Truttaedacnitis* has not met with universal acceptance and has been considered synonymous with *Cucullanus* by some researchers (Moravec and Malmqvist, 1977; Moravec, 1979; Moravec et al., 1988). This is likely due to the presence of intermediate states of some of the morphological characters that have been used to differentiate the 2 genera. For example, detailed illustrations of the dorsal, ventral and lateral aspects of the heads of *C. heterochrous* Rudolphi, 1802, *C. cirratus* Müller, 1777 and *C. elongatus* Smedley, 1933 (Berland, 1970, 1983) clearly show the oral slits to be obliquely situated. The dorsally oblique oral opening (irrespective of the angle of inclination) is evidently a feature common to both *Cucullanus* and *Truttaedacnitis* (see also, reviews by Ivashkin and Khromova, 1976; Soota, 1983). The dorsal inclination of the anterior end is even more unreliable; this character differs among individuals of the same species (Berland, 1970; Pybus, Anderson and Uhazy, 1978) and *Cucullanus himezi* also exhibits it (Moravec et al., 1988; this study). The peribuccal rim has been demonstrated by SEM photographs of the anterior end of *C. elongatus* (Berland, 1983) and *C. cirratus* (Valovaya, 1984). SEM micrographs of *T. pybusae* (Pybus, Anderson and Uhazy, 1978; Appy and Anderson, 1981) also show a structure similar to the

peribuccal rim in *Cucullanus*. A similar structure can also be seen in other *Truttaedacnitis* spp. using light microscopy but is very narrow in *T. truttae*. The lining of the structure in the *Truttaedacnitis* spp. of sturgeon is smooth, unlike the rough margin of the rim in the *Cucullanus* spp. studied by Berland (1970). A closer study of this 'peribuccal rim' is necessary to prove its value as a generic character. The presence of conspicuous broad cephalic 'plates' separated by sutures in *Truttaedacnitis* is in contrast to smaller rough areas in *Cucullanus* and is useful in distinguishing the 2 genera. Although Baker (1984) states that discrete cephalic plates are actually differentiated parts of the continuous wall of the pseudobuccal capsule, we use the term here since it describes these structures aptly. Consequently, the presence of these plates establishes the validity of the genus *Truttaedacnitis*. Broad cephalic plates separated by narrow sutures are present in *T. heterodonti* (see also Fig.1, E of Petter, 1985) as in other *Truttaedacnitis* species (Berland, 1970; Moravec and Malmqvist, 1977; Pybus, Anderson and Uhazy, 1978; Moravec, 1979; Chapter 2-4), and do not resemble the "smaller rough areas" of *Cucullanus* spp. (Berland, 1970, 1983). However, the arrangement of the posterior ventrolateral cephalic plate in *T. heterodonti* makes it difficult to determine homology with corresponding plates in other species of *Truttaedacnitis*. *Truttaedacnitis pybusae* and *T. truttae* are similar in the arrangement of cephalic plates and caudal papillae, spicule shape, and position of the excretory pore (see Berland, 1970 and Pybus, Anderson and Uhazy, 1978). However, the 2 species are easily distinguished since *T. pybusae* possesses distinct lateral alae, a high oral collarette, and a prominent ampulla-like distal portion of the

excretory duct. It can also be distinguished from North American *T. truttae* in possessing a pointed caudal mucron (Pybus, Anderson and Uhazy, 1978).

The position of the excretory pore in *T. sphaerocephala* has been the subject of confusion in the past. Tornqvist (1931) described and illustrated it (Tafel 13, Fig. 2 of Tornqvist, 1931) immediately posterior to the pseudobuccal capsule, Agapova (1966) stated it to be anterior to the nerve ring and Ivashkin and Khromova (1976) described it close to the cephalic end. In contrast, Lomakin and Bauer (in Bauer, 1987) and Skrjabina (1974) described it posterior to the nerve ring near the level of the cervical papillae. Serial histological sections (Fig. 81, this study) show that the excretory pore opens near the pseudobuccal capsule, slightly more anteriorly than was originally illustrated by Tornqvist (1931). It is possible that the hemizonid may have been mistaken for the excretory pore in some descriptions. This anterior position of the excretory pore and the long excretory duct are similar to that found in *T. clitellarius* (Chapter 2-4).

A phylogenetic analysis of the cucullanids was previously presented by Petter (1974) based on 4 morphological characters namely intestinal caecum, thickness of cuticle, length:width ratio (stoutness), and migration of the 9th pair of caudal papillae (original papillar terminology of Chabaud and Petter, 1961). These characters were unsuitable for analysis in this study since these characters were either absent in the ingroup (intestinal caecum) or were found in similar states in outgroup and ingroup members (arrangement of caudal papillae). The migration of the 9th pair of caudal papillae towards the cloaca was considered an evolved condition in the cucullanids

(Figs. 2, 3, of Petter, 1974). In some species of *Truttaedacnitis*, the 9th pair of caudal papillae is anterior in position (Figs. 75-77, 79). According to Petter's (1974) scheme, this would indicate an evolved condition and not the basal primitive position assigned by her to the genus *Truttaedacnitis*. Consequently, the value of this character in the phylogeny of the cucullanids is questionable. Our phylogenetic analysis indicates that the relationships are resolved only if character states of the 'cephalic plates' are run unordered in the analysis (Fig. 83) although the precise plesiomorphic character states of the cephalic plates could not be determined for the genus *Truttaedacnitis* due to their absence from outgroups. The arrangement of the cephalic plates suggest the monophyly of the *Truttaedacnitis* spp. in diadromous holarctic host families (Petromyzontidae, Acipenseridae and Salmonidae). However, other similarities among these species, such as in the general arrangement of caudal papillae, can be viewed as persistent plesiomorphies, e.g., *C. cirratus* has a similar arrangement of caudal papillae (Tornqvist, 1931; Berland, 1970). Although *T. heterodonti*, *T. pybusae* and *T. truttae* possess 3 closely apposed ventrolateral cephalic plates, closer scrutiny reveals that the posterior ventrolateral plates (vl_1 , vl_2 and vl_3) of *T. truttae* and *T. pybusae* are markedly different from *T. heterodonti* and that homologues of vl_1 and vl_2 could not be identified with certainty in *T. heterodonti*. Furthermore, homologues of vl_1 and vl_3 can be identified in *T. clitellarius* and *T. sphaerocephala*. In view of the problems with determining true homology of the posterior ventrolateral cephalic plates (vl_1 , vl_2 and vl_3), states for these characters (7 and 8) were not assigned to *T. heterodonti* (Table 20). The shape and position of the cephalic plates (Fig. 74 a) may indicate a

monophyletic origin of *T. truttae* and *T. pybusae*. The presence of the excretory pore at the level of the pseudobuccal capsule as a synapomorphy for *T. clitellarius* and *T. spherocephala* (this study) establishes the monophyly of the two species and the character of the cephalic plates also consolidates the monophyletic origin of the two *Truttaedacnitis* spp. in sturgeon.

Biogeography

The phylogenetic analysis, using unordered character states, suggests a relationship among *Truttaedacnitis* spp. in acipenserids, salmonids and lampreys. Since the three host groups are circumboreal/holarctic families, the rivers of the holarctic region were likely a key area for the development of host-parasite relationships in these cucullanids. The presence of a species of *Truttaedacnitis* (*T. heterodonti*) in a heterodontid is enigmatic since heterodontids are native to the Pacific and western Indian Oceans (Castro, 1983; Nelson, 1984; Goodson, 1988). *T. heterodonti* is known only from the Port Jackson shark, *Heterodontus portusjacksoni* from Australian waters (Petter, 1985) and it is not known if the 2 heterodontid species of the North American Pacific coast (Goodson, 1988) are hosts of any species of *Truttaedacnitis*. Consequently, the evolutionary origins of this association are still unresolved.

Truttaedacnitis truttae has an apparently disjunct distribution on the North American continent, having been reported in eastern and western North America (both sides of the continental divide). The species has been commonly reported in the cutthroat trout (*O. clarki*) and rainbow trout (*O. mykiss*) from Pacific anadromous

forms and from more interior freshwater populations (Hoffman, 1967; Heckmann, 1971; Margolis and Arthur, 1979; MacDonald and Margolis, 1995). It reaches its most northwestern distribution in arctic char (*Salvelinus alpinus*). In eastern North America, it is found in the brook char, *S. fontinalis* (Frimeth, 1987a). All available accounts of the biology of *T. truttae* indicate it is predominantly a riverine species (Konovalov, 1971; Moravec, 1994). This may explain its absence or rare occurrence in lake char, *S. namaycush* (Margolis and Arthur, 1979; MacDonald and Margolis, 1995), which is also the only salmonine native to a vast range of oligotrophic freshwater lakes in the interior of northern North America (mainly Canada, Scott and Crossman, 1973). This, in turn, may account for the disjunct distribution of *T. truttae*. The absence of a spike-shaped caudal mucron in all North American *T. truttae* (Smedley, 1933; Simon, 1935; Maggenti, 1971; Mudry and McCart, 1974; this study) indicates a strong influence of the North American continental landmass in the distribution and possible genetic composition of this species. Many salmonines (most *Oncorhynchus* spp.) are common to both American and Asian North Pacific margins (Lee et al., 1980). Yet, *T. truttae* from *Hucho perryi* (Brevoort) of the Sarobetsu R. Japan (Moravec and Nagasawa, 1989) possesses a tail that ends in a sharp spike-like mucron, similar to that commonly reported in European *T. truttae* (Tornquist, 1931; Berland, 1970; Moravec, 1979; Moravec and Malmqvist, 1977), but unlike that found in specimens from western North America. The lack of a spike shaped mucron in specimens of *T. truttae* from the British Isles and in some from the European mainland raises at least two possibilities. First, it may represent a transition between spiked to reduced mucrons along the

eastern North American - European axis. Secondly, it may relate to stocking of North American salmonids into local sites in continental Europe and the British Isles. The consistent lack of a spike-shaped mucron in North American *T. truttae* can be considered evidence of divergence from populations in Eurasia. This is in keeping with the recent separation of the British Isles and northern Europe (Scandinavia) from the northeastern Canadian landmass (Hocutt and Wiley, 1986). Perhaps due to the wide circumboreal distribution of *T. truttae* (Bauer, 1987), riverine ancestral salmonines were parasitized by a cucullanid ancestral to, or even identical to *T. truttae*, and this host-parasite association may pre-date both the final dissociation of Europe and North America as well as speciation of, and within, the present day salmonid genera, particularly *Oncorhynchus* (Stearley, 1992). It is also possible that the extensive dispersal of salmonines following deglaciation, particularly by *Salvelinus* spp. and *O. clarki* (Black, 1983; Hocutt and Wiley, 1986; Trotter, 1987; Behnke, 1992; Stearley, 1992) in North America has resulted in widespread dissemination of the form of *T. truttae* that possess a reduced button-shaped caudal mucron.

Based on current knowledge, *T. pybusae* has a very restricted distribution in lampreys (*Lampetra lamottenii* and possibly *Petromyzon marinus* L.) of central Canada (McLain, 1951; Wilson and Ronald, 1967; Pybus, Anderson and Uhazy, 1978; Pybus, Uhazy and Anderson, 1978). In contrast, lampreys in Europe, Mongolia, and Kamchatka are infected only with *T. truttae* (Moravec, 1979, 1994; Butorina, 1988). Salmonids and lampreys are close ecological associates as indicated by the number of lamprey parasites that are typically found in salmonid hosts (Appy and Anderson,

1981) and the presence of *T. pybusae* in lampreys may be "... an outstanding example of a nematode parasite captured (from salmonids) by an intermediate host through the phenomenon of extreme precocity" (Anderson, 1992). However, the predator-prey relationship between salmonines and lampreys in Europe and Asia (Moravec, 1979; Butorina, 1988), which forms an integral part of the transmission dynamics of *T. truttae* in Eurasia, seems absent in the life history of *T. pybusae* (Pybus, Uhazy and Anderson, 1978). It is also not known whether lampreys play any role in the life cycle of *T. truttae* in North American salmonines (see discussion by Anderson, 1992). Consequently, the evolutionary history of host switching in *T. truttae* and *T. pybusae* remain elusive.

It is clear from the cladogram (Fig. 83) that *T. clitellarius* and *T. sphaerocephala* form a monophyletic group parasitic in acipenserids. Populations of *T. clitellarius* have a disjunct distribution in the freshwaters of Siberia, north-east Asia (Amur River drainage) and North America (Skrjabina, 1974; Chapter 2-4). This indicates a Siberian-North American connection and an association with acipenserids that pre-dates the final separation of sturgeon populations in the northern hemisphere, i.e., vicariance. More importantly, it indicates that lake sturgeon (or its ancestor) must have had a much wider distribution on the North American continent, perhaps contiguous with freshwater sturgeon populations in Siberia (see Chapter 3 for further discussion). In contrast, *T. sphaerocephala* is considered a marine species with a North Atlantic (European - North American) and Ponto-Caspian distribution, in predominantly anadromous sturgeon (Skrjabina, 1974; Appy and Dadswell, 1978). The

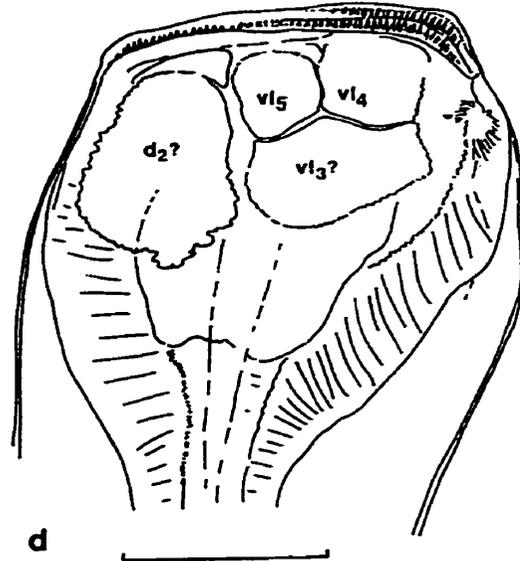
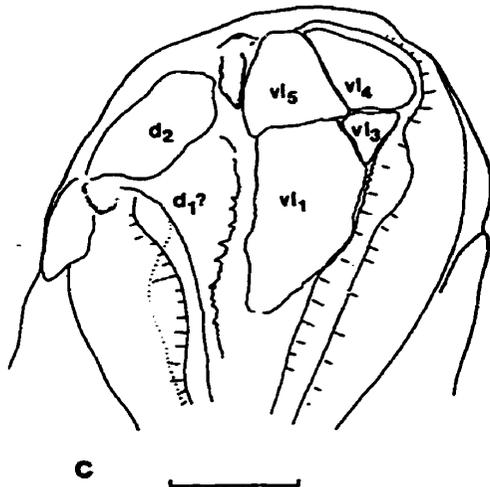
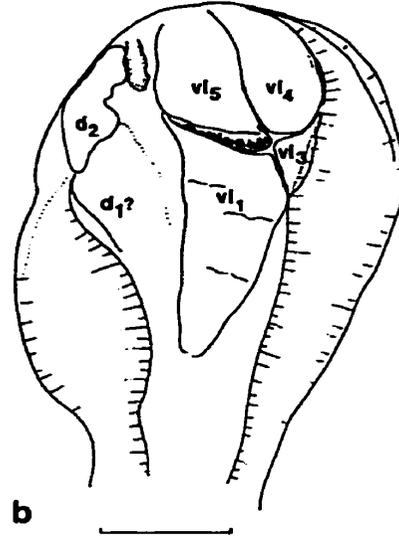
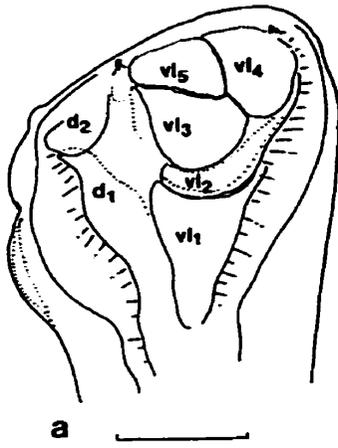
origin of *T. sphaerocephala* can be traced back at least to the Cenozoic since this cucullanid is associated with the geologically younger northern Atlantic basin (Rogers, 1993). This is supported by its presence in sister species of hosts (*A. oxyrhynchus* Mitchill and *A. sturio* L.) which (or whose ancestors) possibly attained their present distributions during that time.

Mapping of hosts on the cladogram (Fig. 83) indicates that the host-parasite associations are probably ancient, but co-speciation patterns are not evident. Instead, colonization events in ancient host clades and subsequent long co-association may explain the specificity of these cucullanids. The limited number of species of *Truttaedacnitis*, in contrast to the species rich *Cucullanus*, may also be due to the phylogenetically relictual, but widespread nature of some of their host families (petromyzontids, acipenserids, heterodontids). Finally, it appears that vicariant as well as host dispersal events, operating at different times and influenced by past oceanic and continental configurations, have produced the current distributions of *Truttaedacnitis* spp.

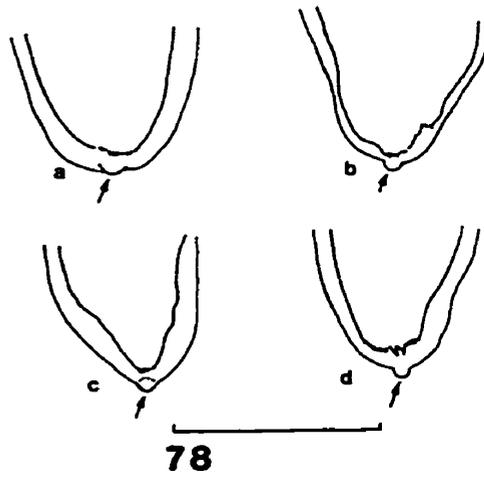
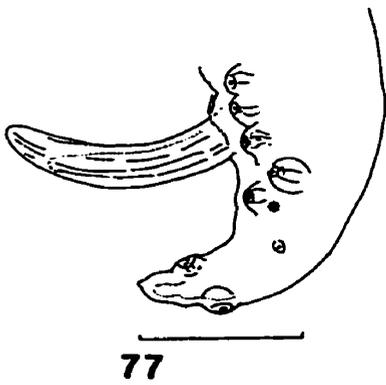
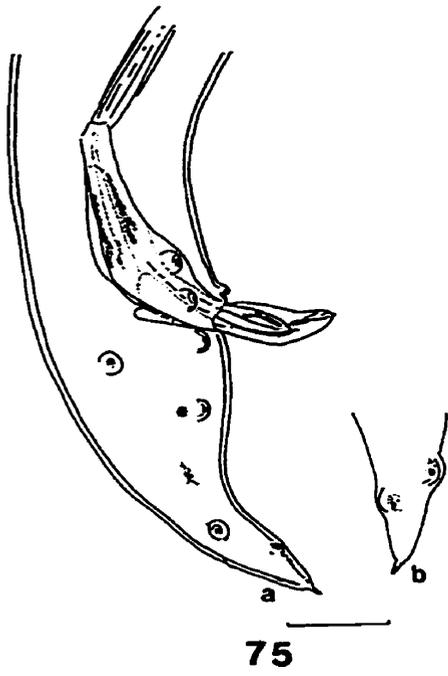
Table 20. Character matrix for the cladistic analysis of *Truttaedacnitis* spp.

	Characters and states							
	1	2	3	4	5	6	7	8
Taxa								
<i>Cucullanus</i> and <i>Dichelyne</i>	0	0	0	0	0	0	0	0
<i>T. heterodonti</i>	0	0	0	0	0	2	-	0
<i>T. truttae</i>	0	0	0	1	0	1	1	1
<i>T. pybusae</i>	0	0	0	0	0	1	1	1
<i>T. clitellarius</i>	1	1	0	0	0	1	2	0
<i>T. sphaerocephala</i>	1	1	1	0	1	1	2	0

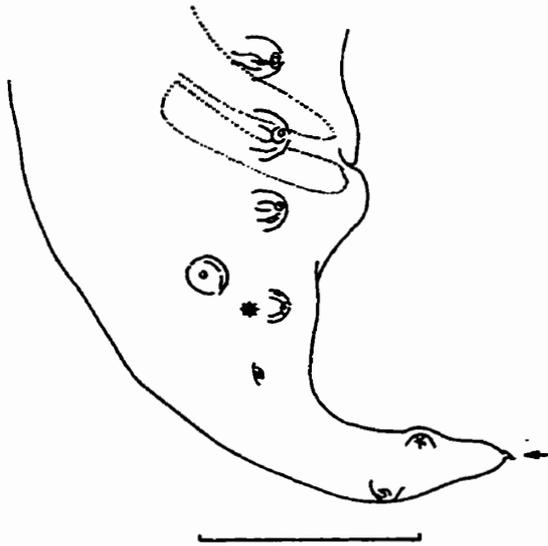
Figure 74. Anterior ends of different species of *Truttaedacnitis*. **a.** *T. truttae* (CSAV N66) ex *S. trutta*, Czech Republic, scale bar = 100 μm . **b.** *T. sphaerocephala* with cuticle and hypodermis removed to expose cephalic plates, ex *A. stellatus*, Kuban River, Russia, scale bar = 100 μm . **c.** *T. clitellarius* ex *A. fulvescens*, Cumberland Lake/Saskatchewan River, Canada, scale bar = 100 μm . **d.** *T. heterodonti* ex *H. portusjacksoni*, Australia. Scale bar = 150 μm . See text for abbreviations.



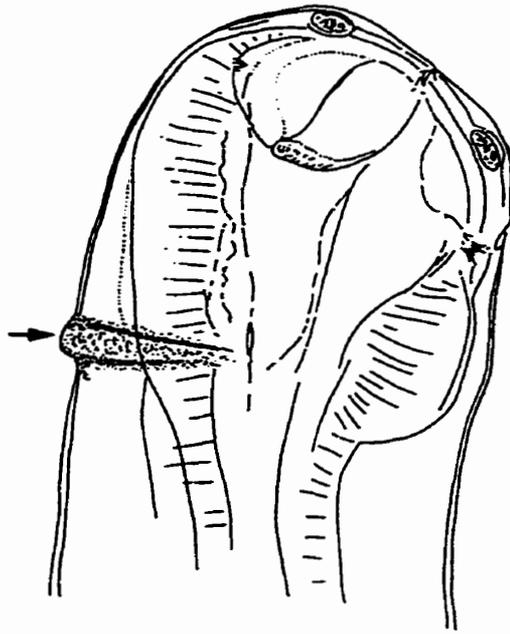
- Figure 75. Posterior end of male *T. sphaerocephala*. a. caudal region showing bent spicules and papillae. Asterisk is next to 9th papilla. b. Posterior most pair of papillae closer together in some specimens. Scale bar = 100 μm .
- Figure 76. Posterior end of *T. truttae* (USNPC 72533) ex *S. alpinus* Babbage R., Yukon, Canada, showing position of phasmid (arrow), papillae (asterisk next to 9th papilla), and reduced button shaped caudal mucron. Scale bar = 150 μm .
- Figure 77. Posterior end of male *T. truttae* (USNPC 30702) ex *O. mykiss*, Rogue R., Oregon, showing more posterior phasmid and dome shaped mucron. Asterisk marks the 9th papilla. Scale bar = 150 μm .
- Figure 78. Magnified views of posterior ends of North American specimens of *T. truttae* from different locations showing various forms of blunt or button shaped caudal mucrons; a. NMCP 1984-8784, b. USNPC 72533, c. USNPC 30702, d. USNPC 46155. Arrows point to the mucrons. Scale bar = 50 μm .



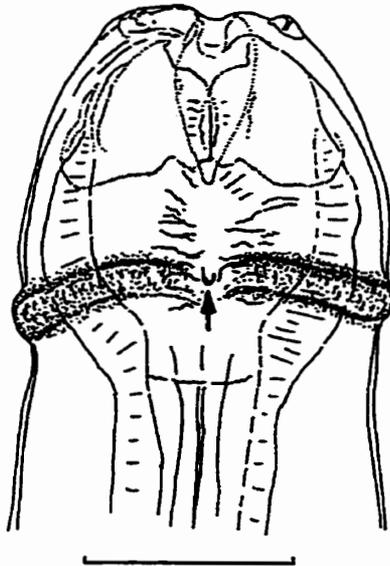
- Figure 79. **Posterior end of male (CSAV N-66) from Cernovsky Brook, Czech Republic, showing spike shaped caudal mucron (arrow). Asterisk marks the 9th papilla. Scale bar = 150 μ m.**
- Figure 80. ***T. sphaerocephala*. Anterior end showing closely apposed ventrolateral cephalic plates, papillae and ventral cephalic ridge (arrow). Scale bar = 150 μ m.**
- Figure 82. ***T. sphaerocephala*. Ventral view of anterior end showing ventral cephalic ridge and position of the excretory pore (see arrow). Scale bar = 150 μ m.**



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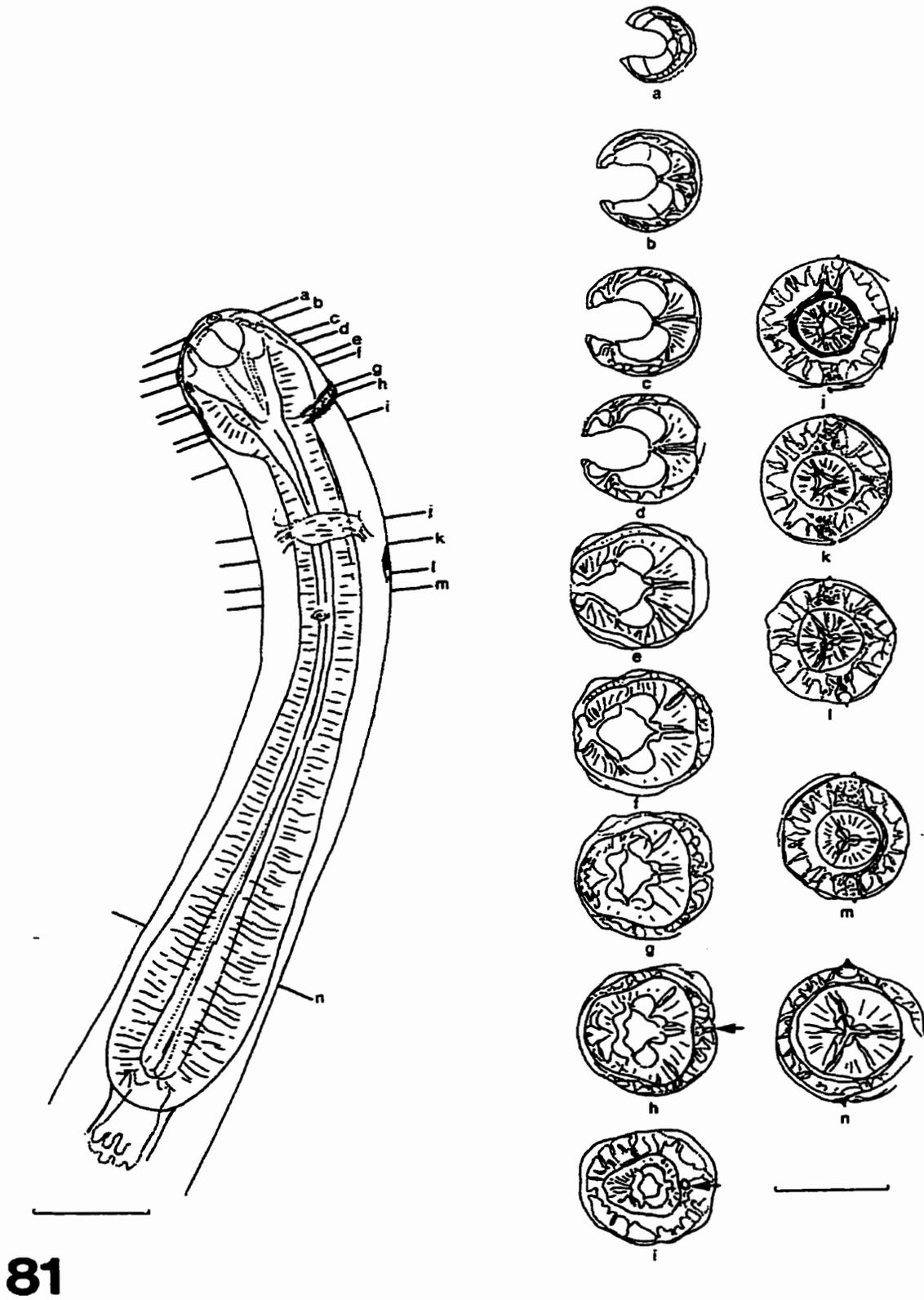


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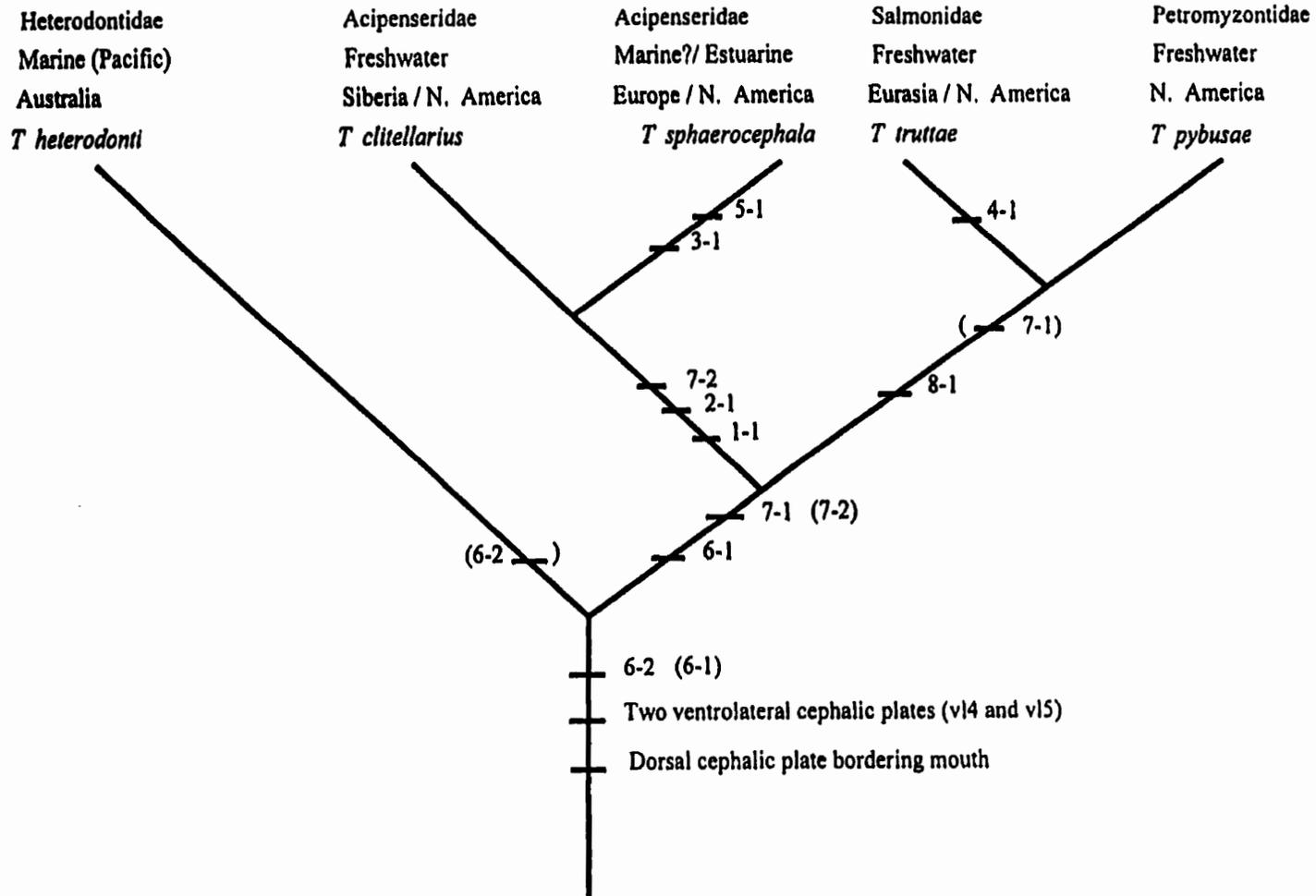
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Figure 81. *T. sphaerocephala*. Anterior region with corresponding histological sections showing the positions of the excretory pore and duct and morphology of the esophagus. Arrows point to the excretory duct. Scale bar = 200 μm .



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Figure 83. Cladogram showing the phylogenetic relationships of different species of *Truttaedacnitis* using character states from Table 20.



Chapter 2-6

Taxonomic and biogeographical notes on *Crepidostomum auriculatum* (Wedl, 1857)

(Digenea: Allocreadiidae) and *Capillospirura* Skrjabin, 1924 (Nematoda:

Cystidicolidae).

Crepidostomum auriculatum* (Wedl, 1857): Systematics and biogeography.*INTRODUCTION**

This species was first described as *Distoma auriculatum* by Wedl (1857) from the sterlet *Acipenser ruthenus*. Although Wedl (1857) did not specify the type locality, Skwartzoff (1928) stated that the worms were first recovered by Wedl in 1856 from the intestine of a sterlet in Austria (River Danube) and this type locality and host were also accepted by subsequent researchers (Hopkins, 1934; Wisniewski, 1933; Skryabina, 1974). Caira (1989, p.16) stated that "Wedl (1858) described *Distoma auriculatum* from *Acipenser rubicundus* in Lake Baikal, U.S.S.R." This is incorrect as *Acipenser rubicundus* is the North American lake sturgeon (= *Acipenser fulvescens*) and furthermore, the actual type host, the sterlet (*Acipenser ruthenus*), is not found in Lake Baikal.

A trematode under the name of "*Distomum auriculatum* Wedl" was first reported in North America by Linton (1897, publ.1898) with a brief description and illustrations. This report was based on specimens at the U.S. National museum, collected by J.W. Milner from the lake sturgeon, "*Acipenser rubicundus*" (= *A. fulvescens*) from an unknown North American locality. This information was repeated by Linton (1901) and should not be regarded as a bonafide report of this parasite (as in Caira, 1989) from the Woods Hole area. Incidentally, the lake sturgeon does not and did not occur in the Woods Hole area. Linton (1901, p.435) also mentioned that Pratt proposed the name *Bunodera lintoni* for this species. However, this name was

not used by Pratt in his first publication on the subject (Pratt, 1902), who used, instead, the name "*Crepidastomum auriculatum*". *Crepidastomum* is an obvious misspelling of *Crepidostomum* Braun (1900). Following Linton's report, the taxonomists of the time felt that the original description of *Distoma auriculatum* by Wedl (1857) indicated that the species was sufficiently different from the North American species of *Crepidostomum* in sturgeons, and a taxonomic wrangle ensued. Evidently, it began when C.H. Lander sent specimens labelled *Distomum petalosum* from North America (from lake sturgeon) to Looss in Germany who used this name (Looss, 1902). Looss (1902) distinguished between the European and North American forms, commenting that *D. petalosum* was the same as Linton's (1898) *D. auriculatum* but different from the species originally described by Wedl (1857) as *D. auriculatum*. Following up on this, Stafford (1904) erected the genus *Acrodactyla* with *A. petalosa* (= *D. petalosum*) as the type species for specimens recovered from lake sturgeon in the St. Lawrence drainage (Canada) which he (Stafford) considered identical to Linton's (1898) *D. auriculatum*. Odhner (1910, in Hopkins, 1934) considered *A. petalosa* a junior synonym of *Bunodera lintoni* (the name proposed by Pratt in Linton, 1901) since it had precedence over *A. petalosa*. The species was also reported by Cooper (1915) from lake sturgeon in the St. Lawrence drainage. The situation was further complicated when Ward (1917) stated that Lander's *petalosum* and Pratts *lintoni* were different, but presented no evidence in support. Ward (1917) also changed the genus name to *Acrolichanus* since *Acrodactyla* was preoccupied. In retrospect, such confusion seems to have been inevitable since the type description

(Wedl, 1857) was not detailed enough for an adequate comparison to be made and since none of these authors presented a careful comparison of specimens from European and North American sturgeon. The first detailed description of the North American form was by Faust (1918) although the inclusion of specimens from *Ambloplites rupestris* was in error (as pointed out by Hopkins, 1934). A detailed description of *C. auriculatum* from the Volga sterlet was given by Skwortzoff (1927, 1928) based on whole mounts and histological sections.

The prevailing taxonomic situation was resolved to a large extent by Hopkins (1933) who united all North American forms from sturgeon under *Crepidostomum lintoni*. Hopkins (1933, 1934) also recognized *C. auriculatum* (Wedl, 1857) from the sterlet as being a separate species, using the smaller sucker diameter and the posterior extent of the uterus in *C. lintoni* as diagnostic. Kaw (1944) was the first to propose that *C. auriculatum* and *C. lintoni* were synonymous, arguing that the characters used by Hopkins (1933, 1934) to distinguish them (extent of uterus and sucker ratio) could be attributed to variability. According to Skryabina (1974), Shulman (1954) provided additional details on *C. auriculatum* and showed that the North American *C. lintoni* was synonymous with it. This synonymy was accepted by Skrjabin and Koval' (1966) and Skryabina (1974). Caira (1989) also proposed synonymy of *C. lintoni* and *C. auriculatum*. Caira (1989) was apparently unaware of the work by Kaw (1944), Shulman (1954) or Skryabina (1974) since they are not cited. Interestingly, authors who have argued synonymy have reported only on examinations of specimens of either Eurasian or North American origin. Consequently, specimens were obtained

from different sources in Europe and North America and examined for potential differences. Since detailed descriptions and measurements exist for both the North American and Eurasian specimens of *C. auriculatum*, and since I was able to obtain very few Eurasian specimens from a very restricted geographical area (mainly western Europe), a detailed morphometric comparison could not be undertaken at this point (see comments by Gibson, 1996). However, the anatomy was studied and some additional details are reported here. This is followed by a discussion of the relationship of *C. auriculatum* with other *Crepidostomum* spp. and of its biogeography.

MATERIALS AND METHODS

Material examined: The names are from the original labels, modern synonyms are in parentheses, s.s.= sagittal sections, t.s. = transverse sections, numbers in parentheses are numbers of specimens examined.

North American specimens:

Material collected from lake sturgeon from the following river systems and locations:

Nelson River (Sundance, Sipiwesk L), Angling L., Saskatchewan River delta (Cumberland House), Winnipeg River (Nutimik L., Slave falls), Rainy River (Manitou rapids), and L. Winnebago. Stained (Acetocarmine and Ehrlich's haematoxylin) and mounted (Canada balsam) specimens from waterways of the Hudson Bay drainage (n=109) and from the Lake Winnebago system (n=248) (See Chapter 1) were examined.

The following museum specimens were also examined:

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CMNPA-1985-0115a, 0115b: ex. *Acipenser transmontanus*, Nicomen Slough (off Fraser River), B.C., Canada. (2).

USNPC 51543: ex *A. rubicundus* (= *A. fulvescens*), St. Lawrence River, Canada. (15 + s.s. , c.s).

USNPC 51544: ex *A. rubicundus* (= *A. fulvescens*), New Baltimore, Michigan, U.S.A. (5 + s.s., c.s).

USNPC 51545: ex *A. rubicundus*, near Detroit, Michigan, U.S.A. (5 + s.s., c.s).

HWML 18006: ex *Scaphirhynchus platorhynchus*, Lake Pepin, Wisconsin. (2 slides)

HWML 22983: ex. *A. transmontanus*, Nicomen Slough (off Fraser River), B.C., Canada (4).

European specimens:

NHMW Inv. Nr. 4279: (as *Acrolichasmus auriculata* Wedl). ex. 3 specimens received in alcohol, stained in acetocarmine and permanently mounted in balsam.

NHMW Inv. Nr. 4280: (as *Acrolichasmus auriculata* Wedl). ex.. 3 specimens received in alcohol, stained in acetocarmine and permanently mounted in balsam.

MNB 3247: ex *Acipenser ruthenus* (locality unspecified but possibly western Europe, fish dealer in Berlin). 16 specimens received in alcohol, stained in acetocarmine and permanently mounted in balsam.

BMNH 1971.6.4.24. ex *Acipenser ruthenus*, Tisa River, Hungary (1).

RESULTS AND DISCUSSION

Morphology

The morphology of the specimens from Europe and North America agree with each other in all essential details such as the shape of the body, shape and proportions of the muscular papillae, organization of the gut, position of the ovary and testes and other reproductive structures, arrangement of the vitellaria and the size relationships of the two suckers. However, a few differences in trends were noticed. In European specimens, the cirrus sac overlaps 1/2 of the acetabulum and in no case was the cirrus sac found to extend beyond the posterior border of the acetabulum. In contrast, the cirrus sac in many North American specimens, reaches the posterior margins of the acetabulum and occasionally extends beyond it, terminating beside the ovary. In 40 of the 109 specimens from the Hudson Bay drainages, the cirrus sac did not reach the posterior margin of the acetabulum (Fig. 84) and in 17 of those 40 specimens, the cirrus sac overlapped 1/2 of the acetabulum (the common condition of European specimens) (Fig. 85). In 33 of the specimens, the cirrus sac extended posteriorly beyond the posterior margin of the acetabulum. In contrast, all but 18 of the 248 specimens from Lake Winnebago possessed cirrus sacs that either reached (n=24) or extended beyond the posterior margin of the acetabulum. In one extreme case, the seminal vesicle was postacetabular. Most taxonomic keys (Amin, 1982; Gibson, 1996) state that the cirrus sac rarely extends beyond the acetabulum but this study shows that such a condition may in fact be common in some populations of *C. auriculatum*. Everted cirri were studied in specimens from both continents and were found to be

similar, unarmed and saccate with the intensely staining cells at the distal end clearly visible. The acetabulum in North American specimens (Fig. 84) and in all European specimens examined in this study (Figs. 85, 86) was found to be smaller in size than the oral sucker. In European specimens examined in other studies, this ratio is reportedly more variable (discussed by Hopkins, 1934; Caira, 1989).

In 1933, Wisniewski published a description of a new species, *Acrolichanus similis* Wisniewsky, 1933 from "*Salmo fario*" (= *Salmo trutta*) and *S. irideus* (= *Oncorhynchus mykiss*) from the Bosna River in Yugoslavia, which Hopkins (1934) regarded synonymous with *C. auriculatum*. This suggestion by Hopkins seems to have gone unnoticed. Slusarski (1958a,b in Yamaguti, 1971) considered it a bonafide species. Although Wisniewski (1933) appears in Caira's (1989) reference list, no reference to *A. similis* or Wisniewski (1933) was made in her discussion of *C. auriculatum*. Neither Skryabina (1974) nor Bykhovskaya and Kulakova (1987) list it as a synonym of *C. auriculatum*. The size and shape of the dorsal papillae (small and spaced far apart) and ventral papillae (small) are very different than in *C. auriculatum* and resemble closely those in *C. farionis*. The cirrus sac is superficially similar but the internal organization is very different. The deeply staining small cells that line the ejaculatory duct and the concentration of deeply staining cells at the distal end of this duct are missing in *A. similis* and the ejaculatory duct of this species is coiled (Figure 2 of Wisniewski, 1933). Furthermore, the ventral sucker is very large. Consequently, the proposed synonymy of *A. similis* with *C. auriculatum* cannot be accepted.

The arrangement of the ejaculatory duct, the cells surrounding it (particularly

concentrated at the anterior end) and the thick sausage shaped cirrus sac, are unlike those in any other species of *Crepidostomum*, a fact noted by previous workers (Hopkins, 1934; Skryabina, 1974) and used by some (Skryabina, 1974; Bykhovskaya and Kulakova, 1987) as support for the validity of the genus *Acrolichanus*. However, names such as *Acrolichanus* serve only to cloud the fact that it refers to a species of *Crepidostomum* with simply one or more unusual characteristics which may eventually turn out to be autapomorphies. Consequently, I find no justification for having *Acrolichanus* as a separate genus. The unusual characters of *C. auriculatum* places no burden upon the diagnosis of the genus *Crepidostomum* since the internal organization of the glands of the cirrus pouch is not a necessary part of its diagnosis (see Caira, 1989; Gibson, 1996). The sausage shaped cirrus pouch with the folded seminal vesicle in the posterior half of the pouch, the simple unmodified dorsolateral and dorsomedial anterior papillae (in contrast to modifications seen in many other species such as *C. illinoiense* Faust 1918, *C. brevivitellum* Hopkins 1934, *C. cornutum* (Osborne, 1903), *C. isostomum* Hopkins 1931), and possibly the distribution of the vitellaria (in contrast to *C. brevivitellum*, *C. cornutum*) may also be viewed as persistent plesiomorphies, some of which underwent modifications separate from the other *Crepidostomum* species.

Phylogeny and biogeography

The genus *Crepidostomum* Braun, 1900 is a monophyletic assemblage of freshwater allocradiids (Brooks and McLennan, 1993) characterized by six (three pairs of) muscular papillae at the anterior end and an essentially pretesticular uterus

(Caira, 1989). The genus is related to *Bunodera* Railliet, 1896, with which it forms a monophyletic clade. These papillose allocreadiids are arguably derived from an allocreadiid with certain characteristics of the genus *Allocreadium* Looss, 1902. Caira (1989) found *Crepidostomum* refractory to further analysis of species relationships but Brooks and McLennan (1993) were further able to resolve relationships among some terminal taxa. The monophyly of *C. auriculatum* and *C. sperpentimum* Talbott and Hutton, 1935, proposed by Caira (1989) and accepted by Brooks and McLennan (1993), based on the width of the dorso-medial papillae being $> 96 \mu\text{m}$, can be rejected because of the great variability of the size of these papillae and their dependence upon the size of the worm. *C. auriculatum* cannot be easily derived from any other *Crepidostomum* nor does it have obvious affinities with any other species. Given its rather basic morphology, it could be an early offshoot during the radiation of *Crepidostomum*. Biogeographical arguments presented below will attempt to show that this species, like its host group is of considerable geological age.

Both *Crepidostomum* and *Bunodera* have essentially Laurasian distributions with two notable exceptions. The two species, *C. platense* Szidat, 1954 and *C. macrorchis* Szidat, 1954 described from Argentina (Szidat, 1954, description and the original drawings seen in Skrjabin and Koval, 1966) do not resemble *Crepidostomum* (see Caira, 1989, for other digeneans with muscular 'oral papillae') and other features of the anatomy do not necessarily place them in *Crepidostomum*. Consequently, the genus can be considered to be Laurasian. *Crepidostomum* is not common from marine or estuarine environments (although *C. farionis* can survive in their salmonid hosts

during the sea phase, see Frimeth, 1987b) and its disjunct distribution on North American and Eurasian landmasses is largely through freshwater routes of dispersal and subsequent vicariance. The distribution of species of *Crepidostomum* also reflect the disparate rates of speciation on the two Laurasian landmasses. The North American continent is home to 12 species of *Crepidostomum*, 3 of which (*C. auriculatum*, *C. metoecus* and *C. farionis*) are shared with North America across northeastern Asia. The three Eurasian species appear to be highly endemic; *C. wikgreni* is restricted to certain drainages in Scandinavia and is closely related to *C. farionis* (see Gibson and Valtonen, 1988) while *C. latum* Pigulewsky, 1931 and *C. indicum*, Kaw 1944 are in need of redescription (or reappraisal?) since neither species has been reported since the original descriptions. The reasons for the greater species richness of *Crepidostomum* in North America is correlated to a large extent with the specificity of North American *Crepidostomum* spp. for their North American host groups.

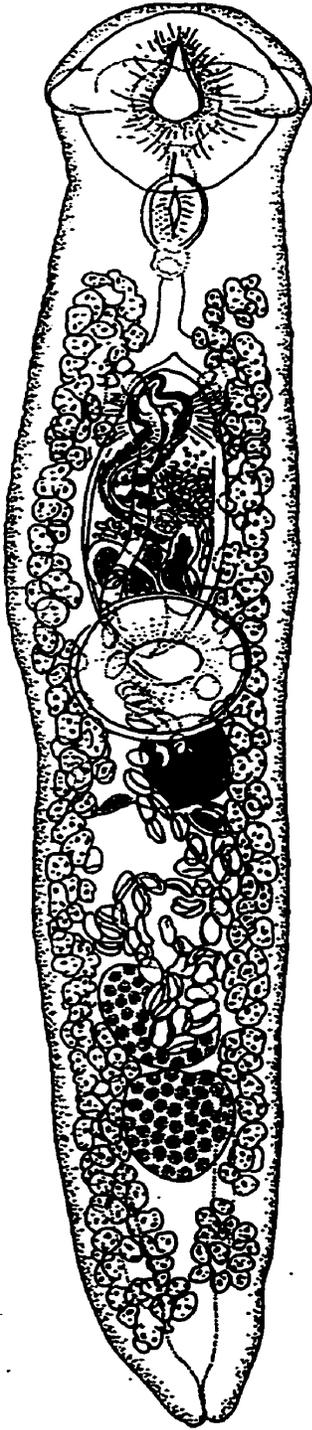
Most species of *Crepidostomum* are specific (some exceptional host records notwithstanding) for their host families or orders [e.g., *C. auriculatum* for acipenserids, *C. farionis* (Müller, 1784) for salmonids, *C. illinoiense* for hiodontids, *C. ictaluri* (Surber, 1928) for ictalurids, *C. auritum* (MacCallum, 1919) for the freshwater sciaenid, *Aplodinotus grunniens* etc.]. Even in species (*C. cooperi* Hopkins, 1931, and *C. cornutum* (Osborne, 1903)] with long host-lists, a closer scrutiny shows that these species are typically parasites of percids and centrarchids respectively where both host groups are sympatrically distributed. Many of the hosts

of *Crepidostomum* in North America (*Aplodinotus grunniens*, Centrarchidae, Hiodontidae, Ictaluridae, Percopsiformes) are endemic to North America and this fact undoubtedly contributes to the higher number of species of *Crepidostomum* in North America. It follows then that the radiation of *Crepidostomum* spp. in North America closely approximates the radiation of the various endemic host groups. The host relationships of *Crepidostomum* also seem to have been associated with a primarily macro-benthivore arthropod diet of the various host groups involved. The planktivore diet of paddlefish and the piscivorous food habits of groups such as gars (*Lepisosteidae*), bowfin (*Amiidae*) and pikes (*Esocidae*) perhaps explains why these groups were left out of this colonization/speciation process within *Crepidostomum*. An exception to this generalization is a major benthivorous North American endemic family, *Catostomidae*, which do not possess a specific *Crepidostomum* of their own (in fact *Crepidostomum* is rarely ever reported from them). However, the typical parasite fauna of catostomids contains some unique host specific elements (lissorchiid digeneans) and shows strong affinities with the *Cyprinidae* which is not surprising since catostomids are also cypriniforms, and the typical cypriniform helminth fauna is notable by the absence of *Crepidostomum* but by the presence of *Allocreadium* spp (Bauer, 1984-1987; Hoffman, 1967; Margolis and McDonald, 1979; McDonald and Margolis, 1995).

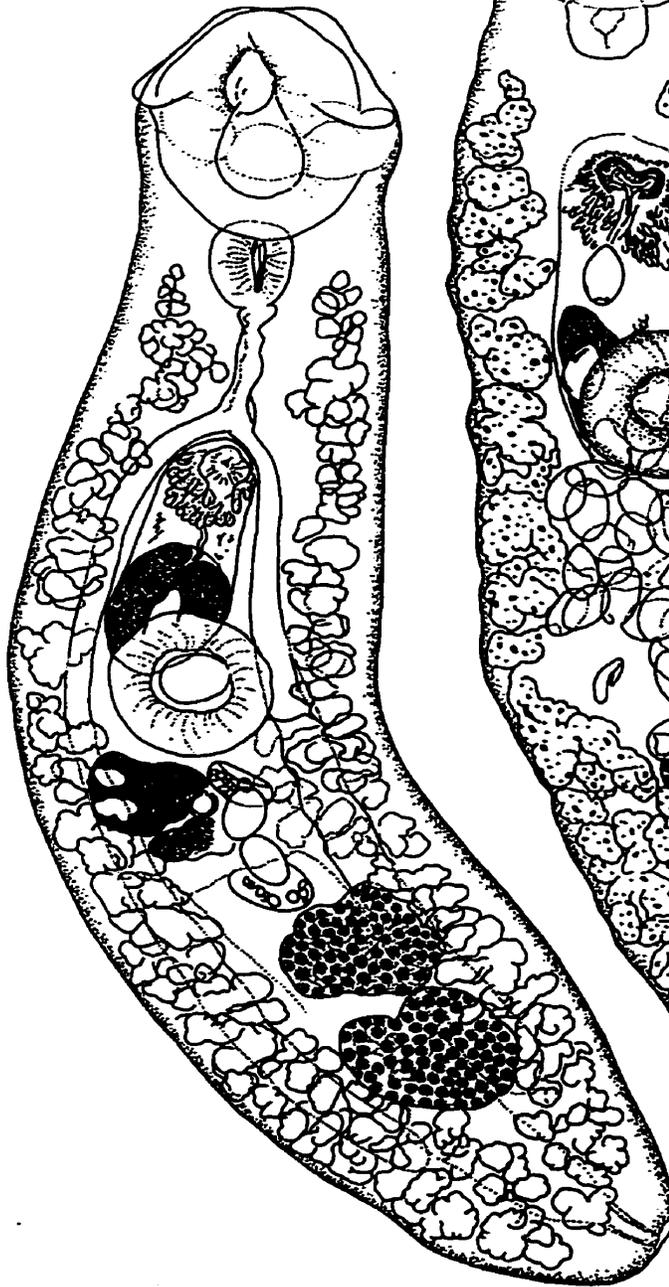
Crepidostomum auriculatum is evidently a strictly host specific parasite and exclusively freshwater in habit (Skryabina, 1974). Skryabina's (1974) statement that it is a parasite of freshwater sturgeons may be rephrased to reflect its distribution and

host relationships more accurately in that *C. auriculatum* is found in sturgeons in freshwater environments since some hosts of this digenean are basically anadromous or estuarine (*A. transmontanus*, *H. dauricus*). In the Ponto-Caspian drainages it is rare (Skryabina, 1974) and apparently only parasitizes the sterlet (*A. ruthenus*) (Skryabina, 1974; Bykhovskaya and Kulakova, 1987), usually in upstream locations of rivers in this region. In contrast, *C. auriculatum* is widely distributed in sturgeons of the Siberian, Pacific and North American drainages, reaching very high levels of infection in the lake sturgeon (see Chapter 1). The wide ranging distribution of both host and parasite coupled with the fact that acipenserids pre-date all the families that are hosts of *Crepidostomum* in Eurasia or North America, argues strongly against *C. auriculatum* being derived from any one of the species specific to endemic North American host taxa or being closely aligned to any one of these species. This is also supported by what could be regarded as a number of persistent plesiomorphies in *C. auriculatum*. The affinities of *C. auriculatum* to the holarctic/circumboreal *Crepidostomum* spp., *C. metoecus* (Braun, 1900) and *C. farionis*, are unclear, although *C. metoecus* has a similar rather simple morphology. The wide distribution of *C. auriculatum* in sturgeons of freshwater drainages of central and western North America, Europe, Siberia and North-east Asia (Amur River) suggests that this species may have existed during Laurasian times and consequently pre-dated both, the final separation of Eurasian and North American landmasses, and the formation of the Asian-American peninsula. These questions will be addressed in Chapter 3.

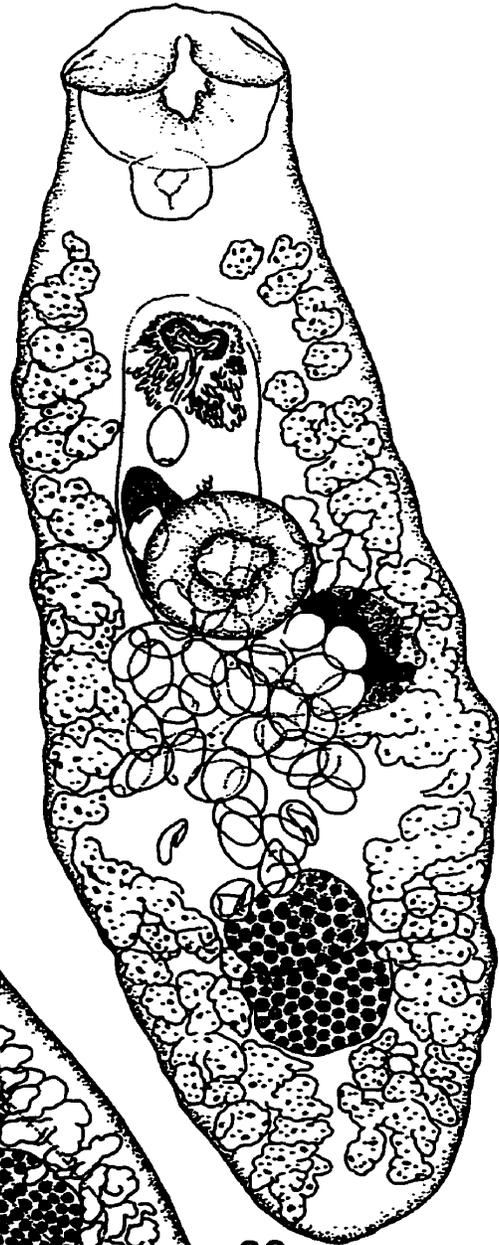
- Figure 84. *Crepidostomum auriculatum*. ex *Acipenser fulvescens*, Cumberland House, Saskatchewan River delta, Manitoba, Canada. Scale bar = 200 μm
- Figure 85. *Crepidostomum auriculatum*, MNB 3247. ex *Acipenser ruthenus*, Europe, unknown locality. Scale bar = 50 μm
- Figure 86. *Crepidostomum auriculatum*, NHMW Inv. 4279. ex *Acipenser ruthenus*, Europe, possibly Danube R. Scale bar = 100 μm .



84



85



86



**Observations on *Capillospirura pseudoargumentosa* (Appy and Dadswell, 1978)
and on the taxonomy and biogeography of *Capillospirura* spp.**

INTRODUCTION

The genus *Capillospirura* Skrjabin, 1924 was erected by Skryabin (1924) for *C. ovotrichuria* from *A. ruthenus* of the Volga River. This species was transferred to the genus *Ascarophis* van Beneden, 1871 by Polyanski (1952). Subsequently, Skryabina (1966) described *Ascarophis argumentosus* from the Siberian sturgeon, *Acipenser baeri* of the Lena River (Siberia). Appy and Dadswell (1978) described *Caballeronema pseudoargumentosa* from the shortnose sturgeon *Acipenser brevirostrum* of the St. John River estuary which was later transferred to *Capillospirura* (Appy and Anderson, 1982). Using SEM on the cephalic region, Appy and Anderson (1982), regarded the presence of bidentate plates under the pseudolabia in these spirurids from sturgeons as diagnostic and revalidated the genus *Capillospirura* for these three nominal species from sturgeons. This bidentate plate was also used by Appy and Anderson (1982) to distinguish *Capillospirura* from the genus *Ascarophis*. Species of *Capillospirura* were reviewed by Skryabina (1974) and Appy and Anderson (1982) but certain taxonomic, morphological and distributional observations pose problems for biogeographic analyses and these are discussed here.

MATERIALS AND METHODS

Specimens examined

The following specimens were examined from collections made during this study and from museum collections as follows:

Caballeronema pseudoargumentosa (= *Capillospirura pseudoargumentosa*): NMCP 1978 - 13a ex *Acipenser brevirostrum*, St. John River, New Brunswick, Canada (1 slide, 2 specimens), USNPC # 73133 ex *A. brevirostrum*, St. John River, New Brunswick, Canada (2 slides, 2 specimens), USNPC # 73134, ex. *A. brevirostrum*, St. John River, New Brunswick.

No Eurasian material was available for comparison but the Eurasian species were described and compared in considerable detail by Appy and Anderson (1983) using light microscopy and SEM. Their and other studies (Skryabina, 1974) were used for the discussion presented herein.

RESULTS AND DISCUSSION

Morphology

The morphology (Figs. 87, 88, 89, 90) of specimens of *C. pseudoargumentosa* collected in this study (Lake Winnebago system) are similar to those collected by Appy and Dadswell (1978) although the specimens from lake sturgeon are larger. The description of *C. pseudoargumentosa* (Appy and Dadswell, 1978; Appy and Anderson, 1982) shows a bend in the distal portion of the left spicule. Examinations of material from the type series, in museum collections (from *A. brevirostrum*) (Figs. 91, 92), and

from this study (from *A. fulvescens*) (Fig. 88) shows that the distal portion of the spicule possesses transparent unsclerotized alae which give it a boat shaped appearance when extruded (Figs. 91, 92). The apparent bent shape of this distal portion is an artifact caused by the folding in of the alae when the spicule is retracted into the spicule sheath.

Systematics and Biogeography

The genus *Capillospirura* is morphologically very similar to the genus *Ascarophis* and was distinguished by Appy and Anderson (1982) by the presence of bidentate plates (buccal teeth) below the pseudolabia in *Capillospirura* spp. *Ascarophis* is a widespread genus with species in a variety of anadromous and marine fish (mainly demersal) and this may have significance while considering the origins of *Capillospirura* (see Chapter 3).

There appears to be some controversy regarding the distribution of *Capillospirura* spp. in Eurasia. According to Skryabina's (1974) review, *C. ovotrichuria* is present in the Caspian drainages and in the Enisei River and possibly Lake Baikal. However, according to Vusmanus *et al.*, (1987), it is endemic to the Caspian Sea basin and its drainages. Regarding this controversy, I would like to draw attention to the description and distribution of *Ascarophis skrjabini* (Lyaiman, 1933) since this species is morphologically similar to *C. ovotrichuria* and the two species may have been confused in the past. *Ascarophis skrjabini* was described by Lyaiman (1933) as *Cystidicola skrjabini* from the gut of a variety of fish (mainly salmoniforms)

including the Baikal sturgeon (*Acipenser baeri baikalensis*). Zhukov (1960) stated that a close examination of Lyaiman's (1933) description of *Ascarophis skrjabini* indicated it was based on more than one species or even genus. However, no details were provided by Zhukov (1960) for this opinion. The discrepancies in Lyaiman's original figures accompanying his description are, on closer scrutiny, clearly due to a mix-up in the figure legends and the numbers of Figs. 29 and 33 (of Lyaiman, 1933) with *Cystidicola dispar* (= *C. farionis*) which Lyaiman also described in the same publication. However, Zhukov's (1960) view of *A. skrjabini* as 'species inquirenda' was shared by Appy and Anderson (1982) and also by Ko (1986), although Ko (1986) included it in his analyses. Nevertheless, *A. skrjabini* has been reported from benthivorous coregonids from the Enisei (Bauer, 1970) and it still appears as a nominal species in European and Russian works (Moravec, 1994; Vusmanus *et al*, 1987). It is possible that Zhukov (1960) was also influenced by the fact that Lyaiman (1933) described the species from a number of different hosts. As mentioned earlier, the species resembles *C. ovotrichuria* in a number of details (relative sizes of the spicules, papillar pattern, bipolar filamentous eggs) and this has likely resulted in taxonomic problems. The records of *C. ovotrichuria* in the Siberian sturgeon, *Acipenser baeri*, in the Enisei River and Lake Baikal coincide with the known distribution of *A. skrjabini* in Siberian waters. Consequently, there are two possibilities regarding the distribution of *C. ovotrichuria*:

1. *Capillospirura ovotrichuria* is distributed in the Enisei River and L. Baikal.

- a. Both *C. ovotrichuria* and *A. skrjabini* occur in the Siberian drainages, the

former being specific for acipenserids, the latter mainly parasitizing coregonids.

or,

b. *C. ovotrichuria* is the only species and is non-host specific; *A. skrjabini* is in fact this species.

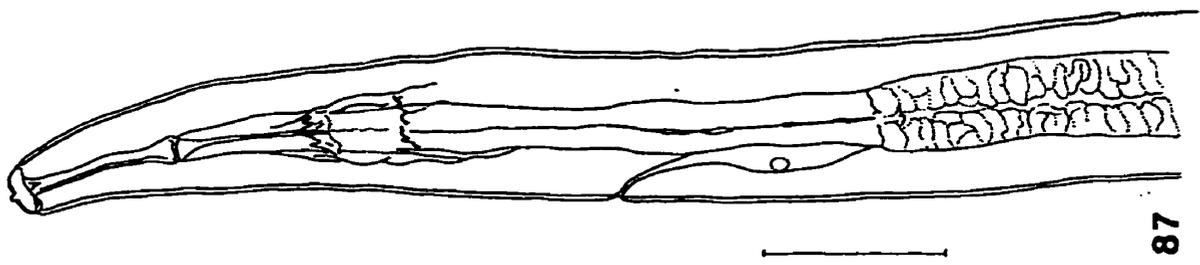
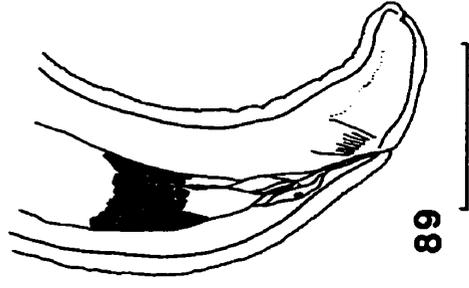
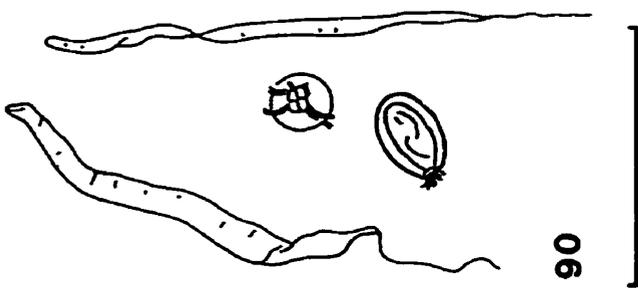
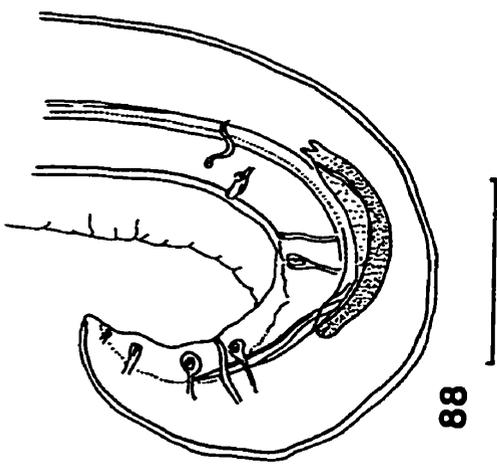
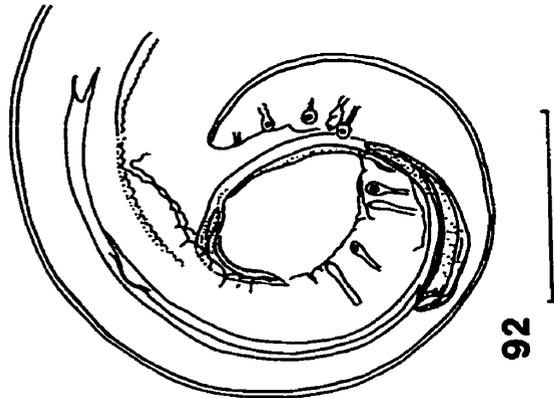
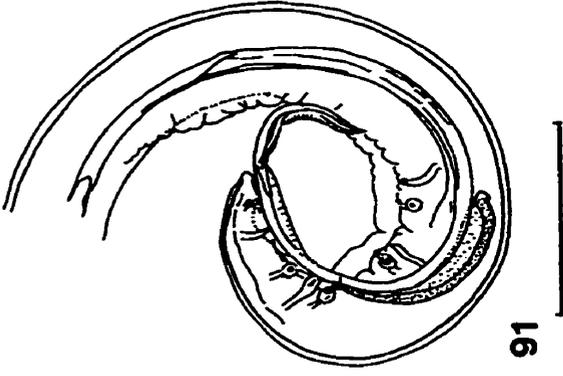
2. *Capillospirura ovotrichuria* is a mis-identification of the morphologically similar *Ascarophis skrjabini* which is a bonafide species in the Enisei River and L. Baikal.

A. skrjabini is the only species in the Enisei River and L. Baikal and infects a variety of freshwater fishes (mainly salmoniforms and *A. baeri*).

Only SEM studies on the cephalic extremity of *A. skrjabini* and *C. ovotrichuria* from Baikal and Enisei waters can resolve whether *C. ovotrichuria* really exists in Siberian waters.

In light of the above facts and possibilities, I follow Vusmanus *et al.*, (1987) in regarding the presence of *C. ovotrichuria* in Siberian drainages as uncertain pending future revisionary studies on these and closely related spirurids from that region. Consequently, *C. ovotrichuria* is regarded as endemic to the Ponto-Caspian region while *C. argumentosa* is the more widespread species on the Eurasian continent. The historical biogeography of this genus is further discussed in Chapter 3.

- Figure 87. *Capillospirura pseudoargumentosa*. ex *A. fulvescens*, Lake Winnebago. Anterior body of female specimen . Scale bar = 100 μm .
- Figure 88. *C. pseudoargumentosa*. ex *A. fulvescens*, Lake Winnebago. Caudal region of male showing distally tapering long spicule and gubernaculum. Scale bar = 100 μm .
- Figure 89. *C. pseudoargumentosa*. ex *A. fulvescens*, Lake Winnebago. Caudal region of female showing dorsally arched postanal region. Dark granular gut only partially drawn. Scale bar = 100 μm
- Figure 90. *C. pseudoargumentosa* ex *A. fulvescens*, Lake Winnebago. Eggs showing polar capsule and flattened distal ends of polar filaments. Scale bar = 100 μm
- Figure 91. *C. pseudoargumentosa* USNPC 73134. ex *A. brevirostrum*, St. John River, New Brunswick. Left view of extruded long spicule showing the alae along the spicule. Scale bar = 100 μm .
- Figure 92. *C. pseudoargumentosa* USNPC 73134. ex *A. brevirostrum*, St. John River, New Brunswick. Right view of Fig. 91 showing the alae on the opposite side. Scale bar = 100 μm .



Chapter 3.

Historical biogeography and coevolution

INTRODUCTION

It is clear from the preceding Chapters that the parasites of lake sturgeon represent a subset of the parasites of acipenseriforms in general. Of the parasites reported from lake sturgeon in this study, none is specific for lake sturgeon only and, with the exception of *Spinitectus*, all genera (*Polypodium*, *Diclybothrium*, *Crepidostomum*, *Truttaedacnitis*, *Capillospirura*, *Skrjabinopsolus*) and even some species (*P. hydriforme*, *C. auriculatum*, *T. clitellarius*) are found in/on sturgeons on both Eurasian and North American landmasses. Furthermore, the systematic and biogeographical analyses of parasites (Chapter 2) suggest that processes operating at larger geographical scales and acting at higher taxonomic levels (of the hosts) are important. Consequently, hypotheses regarding the origins of lake sturgeon parasites depend to a large extent on an understanding of the historical biogeography of sturgeon parasites as a whole.

Certain requirements have to be met before any discussion about historical biogeography can be attempted. The very basic of these is information on past geological and climatic processes which have affected the regions involved in the study. Such palaeogeographical information identifies historical associations of landmasses, possible dispersal routes, and vicariant events for taxa under consideration. Other historical evidence such as the fossil record of the host taxa being studied provides unequivocal evidence of past distributions as well as a method for refining the time frame used in historical reconstructions (Grande, 1985; Hoberg, 1992; Wilson and Williams, 1992). Phylogenetic analyses of the acipenserids (Artyukhin, 1995;

Grande and Bemis, 1991; Findeis, 1993; Mayden and Kuhajda, 1996) provide hypotheses of relationships which provide relative ages of lineages that can be compared with the fossil record to give even stronger evidence for geological age. It also allows the hypothesis of relationships to be mapped on to the present distributions. Such a method identifies area relationships, regions of diversification, as well as vicariant or dispersal events. The combined information from historical geology, palaeontology and phylogenetic studies serves as a basis for understanding the historical biogeography of sturgeons. Combined with parasite phylogenies (various sections of Chapter 2), such information allows a robust hypothesis of the co-evolutionary history of host-parasite relationships. Finally, evidence from the parasites is used to provide insight into the origins and diversifications of lake sturgeon and acipenserids as a whole.

MATERIALS AND METHODS

Several methods have been proposed to study historical biogeography (see Morrone and Crisci, 1995 for a succinct review) and co-evolution (Brooks and McLennan, 1991, 1993). Co-speciation models are not discussed here since sturgeon parasites show no evidence for such patterns. The method used here utilizes several types of evidence including cladistic methodology and traditional systematics and is an inductive method of inferring process from pattern.

Terminology: 'Vicariance' as used here refers to the fragmentation / disjunction of ancestral biota or ranges by geological and climatic processes, e.g., plate tectonics and

continental drift (in which case it is referred to as drift-vicariance, Lundberg, 1993), orogeny, marine transgressions, glaciation etc. 'Dispersal' refers to the active colonization of new areas by taxa. The acronym 'ya' following a number stands for 'years ago' while the suffix 'mya' stands for 'million years ago' and is used throughout the text to commonly refer to geological time.

Information from geological history and acipenserid biogeography and phylogeny.

Several independent sources of information have been used as the basis for studying the historical biogeography of host-parasite relationships in sturgeons. These include reviews of:

- a) important aspects of the palaeogeography which are relevant to the historical biogeography of sturgeons. Geological and climatic processes that could have acted as mediators of vicariance, as constraints on the distribution of the acipenserids, and as avenues for dispersal, were identified. A more detailed description of the major geological and climatological events in chronological order is provided in Appendix III. In view of the concentration of fossil acipenserids from the late Cretaceous onwards, emphasis is placed on events in the late Mesozoic and Cenozoic (Jurassic to Recent). Also, since the present day and fossil biogeography of acipenserids are restricted to what once comprised the Laurasian landmass, the discussion will concentrate on the palaeogeography of Laurasia and its derivatives.
- b) the fossil record of the acipenserids which is reviewed against the backdrop of Mesozoic and Cenozoic palaeogeography. Acipenserid fossil records have been

mapped upon palaeogeographic maps of the corresponding time frame (Appendix III, Figs. 1-6).

c) the current state of knowledge of the systematics and phylogenetics of sturgeons.

This provides some basis for postulating relationships of lake sturgeon with other acipenserids, the relative ages of certain lineages, and a basis for evaluating patterns of co-evolution.

d) the present day biogeography of the acipenserids since it is critical in understanding the biogeography of the parasites. This provides a basis for investigating the possibilities of acquisition and sharing of the parasite fauna and the history of separation, isolation and contact.

Information from parasite systematics and biogeography

Information on the distribution of sturgeon parasites has been compiled from the following sources: Appy and Dadswell (1978), Bauer (1984-1987), Bykhovskaya-Pavlovskaya *et al.* (1962), Carlson and Simpson (1987), Chen and Ye (1983), Dadswell *et al.* (1984), Dick *et al.* (1991), Hoffman (1967), Hoffman *et al.* (1974), Holcik (1989), Holloway *et al.* (1991), Foley *et al.* (1989), Lockard and Parsons (1971), Margolis and McDonald (1986), Markevich (1966), McCabe (1991), Moravec (1994), Moravec *et al.* (1989), Wang (1986), Yao (1989) and this study. Information on sister taxa have been compiled from the following sources: Bandoni and Brooks (1987), Boeger and Kritsky (1989, 1993), Brooks and McLennan (1993), Beverley-Burton (1984), Dubinina (1971), Gibson (1996), Kabata (1988), Wardle and McLeod

(1952) and Yamaguti (1971) and from various sections of Chapter 2. This information and the results of the systematic studies in various sections of Chapter 2 are represented as a series of maps and area cladograms where possible and are used to analyze the historical biogeography of host-parasite relationships.

RESULTS AND DISCUSSION

Information from geological history and acipenserid biogeography and phylogeny

a) Geological history (*palaeogeography and palaeoclimatology*)

Salient features of this palaeogeography of the Mesozoic and Caenozoic which are of special relevance to the biogeography of continental fishes may be summarized as follows:

1. Dissociation of Pangea began with the initial rifting between Africa and North America in the Jurassic and resulted in the formation of the early Atlantic. The central portion of this newly formed Atlantic was continuous between the North and South American continents until the Pliocene (Fig. 93). (Rogers, 1993; Smith *et al.*, 1994).
2. The Arctic Ocean region was a small bay of the vast Panthalassa Ocean (modern day Pacific) during the Jurassic but basin formation began in the Cretaceous and progressed as the North Atlantic continued spreading. (Fig. 94) (Lawver *et al.*, 1990; Rowley and Lottes, 1988).
2. Large parts of Laurasia (particularly continental Europe and western North America) were inundated by major marine transgressions in the Jurassic and Cretaceous (Fig. 95). Transgressive and regressive cycles led to the formation of large bodies of

brackish water and extensive fluvio-deltaic systems in North America and Eurasia (Howarth, 1981; Stanley, 1989; Imlay, 1984; Williams and Stelck, 1975).

3. North America progressively rotated away from Europe by sea-floor spreading in the north Atlantic. This movement coupled with the breaking away of the Kolyma plate and its joining with northeastern Siberia in the Cretaceous resulted in the formation of an Asian-American peninsula, via a Bering land-bridge, separated from eastern North America by the western interior seaway (Fig. 95c) (Biske and Baranova, 1976; Howarth, 1981). North America lost contact with Europe after the Eocene by development of the north Atlantic and Greenland Sea (Fig. 95 a, b). (Howarth, 1981; Smith *et al.*, 1994).

4. The Pacific margin of North America has a history of intense orogenic activity and accretion of allochthonous terranes in the north and northwest. A "series of mountain building episodes" (Patterson, 1981) mainly between the Late Jurassic and the Eocene produced the north-south Cordillera and 'basin and range province'. Erosion of the southern Rockies by the Late Eocene and before its renewed upliftment in the Miocene, temporarily reduced its effectiveness as an effective geographical barrier in the Oligocene (Grande, 1985).

5. The Paratethys was formed by trapping of the Tethys in the Miocene (23-5 mya) and gave rise to its modern derivatives (Black, Caspian, and Aral Seas) by subsequent fragmentation and desalinization of restricted basins in the late Miocene and Pliocene (5 mya). (Fig. 96, a,b,c.).

6. Climates throughout most of the Cretaceous and early Caenozoic were equable and

subtropical to cool temperate in the northern latitudes (Duellman and Trueb, 1994; Stanley, 1989). Drastic episodic cooling in the late Cenozoic and particularly in the Pliocene resulted ultimately in Arctic ice formation and subsequent Pleistocene glaciation (Adams, 1981; Dawson, 1992).

7. The emergence and submergence of the Bering land-bridge in the Pleistocene have been conventionally considered to be correlated with glacials and interglacials respectively and periods of glaciation are thought to have allowed movement of fauna across the emergent Bering landbridge. However, it has been recently argued that 'sea ice' formation formed a barrier to migration as did the Bering Sea during interglacial times (Hughes and Hughes, 1994). This implies that the similarities in fauna on either side of the Bering Sea (see Walters, 1955 for freshwater fishes) pre-date Pleistocene glaciations.

The geological and climatic history of the Laurasian landmasses also identifies potential routes of dispersal and important mediators of vicariance which are of importance to the distribution of freshwater and diadromous fishes. All possible routes of dispersal are theoretically possible for sturgeons, i.e., continental freshwater dispersal, coastal and brackish water dispersal and trans-oceanic marine dispersal, since all sturgeons seem to be able to withstand a certain amount of salinity and some (*A. oxyrinchus*, *A. sturio*, *A. medirostris*) are common in marine coastal waters. However, an open water trans-oceanic dispersal is the least likely. Consequently, a large body of seawater (e.g., Atlantic, Pacific or Arctic Ocean) forms a formidable barrier to their dispersal. Dispersal along coastal systems and establishment in large

lowland coastal plains rivers is a plausible mechanism and is in keeping with the requirements of this group of fishes. The basic preference of sturgeons for large lowland rivers and their middle and lower reaches suggests that the lack of coastal river systems of the appropriate physico-chemical characteristics may limit the distribution of this group of fishes. A freshwater route of dispersal is the most direct when continental landmasses are fused but also depends on waterbodies of appropriate characteristics. The Acipenseridae are also challenging since the distribution of the family, unlike that of many other groups, is not constrained by climate and temperature, and movements during the equable climates of the Mesozoic and Caenozoic would have been even less constrained.

Two freshwater and coastal avenues of dispersal are readily identifiable in the palaeogeography of the Laurasian landmass; the Northeast American-European route and the Bering land bridge (Asian-American peninsula) route. The northern European-North American connection is the original connection with the Eurasian landmass and dates to Pangean times. Maps of palaeocoastlines depict a narrow epicontinental seaway (Smith *et al.*, 1994) between Northeastern North America and Europe during the Mesozoic but its exact duration and continuous persistence is unknown. The North Atlantic is generally considered a major barrier to dispersal of terrestrial and freshwater organisms after the Eocene (Briggs, 1987; Cracraft, 1974) and cladistic hypotheses of fish families showing North American-European relationships (e.g., Percidae, see Wiley, 1992) implies that some of the major derived teleost genera (*Perca*, *Stizostedion*) existed prior to final separation of the continents. The North

American - European connection could have been important for sturgeons and their amphi-Atlantic distribution was likely established during the Tertiary as well; sturgeon fossils have been reported from Europe and the coastal plains of North America throughout the latter part of the Cenozoic (see Appendix IV, Figs 2-6) and sturgeons could have used both coastal and freshwater routes of dispersal between the continents and may have achieved wide distributions well before the Eocene separation of this region. The alternative is the Cretaceous Bering land-bridge which allowed the development of faunal relationships with Northeast Asia. A number of families of fossil (early and mid-Cenozoic) and Recent fishes show trans-Pacific relationships (Briggs, 1987; Patterson, 1981; Grande, 1994) including the sister taxon to the Acipenseridae, the Polyodontidae (paddlefishes, Grande and Bemis, 1991; Grande, 1994). In addition to allowing dispersal through freshwater routes, this North Pacific rim would have allowed the Pacific sturgeons to disperse along the northern and southern coasts of this Asian-American peninsula. This supports Artyukhin's (1995) suggestion that some of the Pacific rim sturgeons are related. A reconstruction of the Bering landbridge (Biske and Baranova, 1976) suggests that orogenic activity that accompanied the formation of the Bering land bridge has not allowed the formation of Arctic river systems, appropriate for sturgeon, in this transition area. While large Pacific river systems are shown on palaeogeographic maps (Walters, 1955; Biske and Baranova, 1976), Arctic drainages seem weakly developed. That is probably why *A. baeri* is not found east of the Kolyma. Similarly, the Arctic river systems of the Canadian eastern Arctic and Scandinavian regions are also likely unsuitable for

acipenserids which is also likely the reason Arctic sturgeons are restricted to the Siberian drainages (a similar distribution is also shown by a number of Arctic coregonids (see Lee *et al.*, 1980). Finally, the effects of the Pleistocene would have undoubtedly affected holarctic sturgeons, particularly in North America, since glaciation over land was unequal. This unequal glaciation left large parts of Siberia and N.E. Asia free of continuous ice cover and allowed sturgeons to survive in those drainages (an extensive Siberian ice cover would have likely caused the extirpation of the sturgeons since there were no major south flowing Pleistocene drainages in the Siberian Arctic). North American sturgeons did not survive glaciation in the Beringian refugium and the distribution of lake sturgeon (or its ancestor) in Pliocene times remains unknown. The position of the Cretaceous palaeopole over the Beringian region has been used as argument for a stronger filtering effect in faunal dispersal, particularly mammals (see McKenna, 1975) in comparison to the North American - European route which was characterized by equable climates. Such concepts are difficult to apply to sturgeons because they are represented in frigid Arctic as well as warmer southern Caspian waters, by species with anadromous and freshwater life histories. Consequently, dispersal is not as constrained as in other biota or even as in some other freshwater fishes (e.g., Amiidae, Lepisosteidae).

In summary, the distribution of sturgeons in the holarctic and circumboreal region via historical Pangean connections across the North Atlantic and via the Cretaceous American-Asian peninsula was probably facilitated by their ability to use freshwater as well as coastal routes for dispersal. This allowed the distribution of

sturgeons to reach circumboreal or holarctic proportions rather rapidly (with extensions along all the continental margins of the northern hemisphere), sometime during the Cretaceous. More robust statements about Mesozoic ranges cannot be made due to the absence of fossil acipenserids from the interior eastern part of North America.

Fossil record of the Acipenseridae

The chondrostean order Acipenseriformes is comprised of four families (Findeis, 1993). Chondrosteidae is represented by *Chondrosteus* and *Gyrosteus* from the marine Lower Jurassic (Lias) sediments of western Europe (England, Germany). Peipiaosteidae is represented by the Upper Jurassic freshwater *Peipiaosteus* and *Yanosteus* from China (Jin *et al.*, 1995; Zhou, 1992). Polyodontidae is represented by three extinct and two extant genera (Grande and Bemis, 1991). Extinct taxa are *Paleopsephurus* from the Late Cretaceous freshwater deposits of northeastern Montana, *Crossopholis* from early Eocene freshwater deposits of southwestern Wyoming (Grande and Bemis, 1991) and *Protopsephurus* from Upper Jurassic of northeast China (Lu, 1994). Fossil *Polyodon* include the extinct species *P. tuberculata* from the early Palaeocene of northeastern Montana (Grande and Bemis, 1991). According to Gardiner (1984), *Protoscaphirhynchus* from the Upper Cretaceous of Montana is not an acipenseriform although Findeis (1993) considered it related to scaphirhynchines. It is included here for the sake of completeness. The only other extant chondrostean order, Polypteriformes (see Nelson, 1994), is represented by Eocene and Recent fossil Polypteridae from Africa (Carroll, 1988) and by Maastrichtian and Palaeocene fossil

Polypteridae from Bolivia (Gayet and Meunier, 1991).

The following is a list of fossil Acipenseridae and their place of discovery according to chronological (geological age) order, beginning with the oldest. The locations of the fossils on palaeogeographical maps corresponding to the relevant time period are also provided (Appendix III, Figures 1-6).

Middle Jurassic (175 mya approx.) (no figure).

Asiacipenser kotelnikovi† Nesov and Kaznyshkin; Khirgystan, Estuarine/delta environment. (Nesov *et al.*, 1990).

Late Cretaceous (65 mya latest): (Appendix III, Fig. 1).

Acipenser shilini† Nesov and Kaznyshkin: Kazakhstan. (Nesov and Kaznyshkin, 1983).

Acipenser eruciferus† (Cope); Wyoming, Montana, Alberta (Campanian). (Estes, 1964; Gardiner, 1966, 1984).

Acipenser albertensis† Lambe; Alberta, Saskatchewan (Maastrichtian and Campanian). (Lambe, 1902; Gardiner, 1966, 1984).

Propenser hewletti† Applegate; Mooreville chalk, Selma formation, Alabama (Lower (early) Campanian). (Applegate, 1970; Cavender, 1986; Smith, 1981).

Protoscaphyrhynchus squamosus† Wilimovsky, Montana, Late Cretaceous. (Findeis, 1993).

Acipenser sp. Judith River formation, Alberta, Upper Cretaceous (Neumann *et al.*, 1988).

Late Palaeocene (55 mya latest). (Appendix III, Fig. 2).

Acipenser zhylgensis† Nesov and Kaznyshkin; Kazakhstan. (Nesov and Kaznyshkin, 1983).

Eocene (55-36 mya) (Appendix III, Fig. 3).

A. toliapicus† Agassiz, England (White, 1931; Woodward, 1889)

A. lemoinei† Priem, France (Gardiner, 1984)

Oligocene (36-23 mya) (Appendix III, Fig. 4).

A. parisiensis†, Paris basin, France. (Gardiner, 1984)

Acipenseridae, Isle of Wight, U.S.A. (Gardiner, 1984)

Acipenseridae, Western Siberia. (Obruchev, 1964).

Miocene (20-5 mya) (Appendix III, Fig. 5).

A. ornatus†, Virginia, U.S.A. (Gardiner, 1984; Woodward, 1889)

A. molassicus† Probst (Gardiner, 1984)

A. tuberculosus† Probst, Germany (Gardiner, 1984; Renz, 1939)

Acipenser sp. (Middle Miocene ?) Maryland and Virginia (Kimmel, 1983; 1985)

Acipenser sp. (Middle Miocene, Pungo Marl, North Carolina) (Cavender, 1986).

Acipenser sp. (Martha's Vineyard, Massachusetts) (Kimmel, 1986)

Pliocene (5-2 mya) (Appendix III, Fig 6).

Acipenser sp.†, Siberia, U.S., France, England and Rumania. (Gardiner, 1984; Woodward, 1889).

Pleistocene (2 mya - 10,000 ya) (no figure).

A. nudiventris, European Russia

A. stellatus, European Russia

A. ruthenus, European Russia

Huso huso, European Russia

Acipenser sp., Pennsylvania (Leidy, 1873 in Woodward, 1889; Smith, 1981)

Acipenser (transmontanus?), California (Casteel and Hutchison, 1973; Smith, 1981)

Holocene (10,000 ya - recent) (no figure).

Scaphirhynchus platyrhynchus, Texas, Toomey (1991)

Acipenser sp., Great Lakes region (Smith, 1981).

Nesov *et al.*, (1990) described what constitutes the oldest fossil Acipenseridae (*Asiacipenser kotelnikovi*) from the middle Jurassic of the Zindanskaya series of Ferghana (also Kyrgistan?) which they characterized as an estuarine basin or mouth of a river. The description has not been critically evaluated as yet by palaeontologists but is the first and only record of acipenserids earlier than the Cretaceous. The palaeontology of acipenserids was first reviewed by Woodward (1889) who listed the fossils (dermal scutes and other ossifications) from the following strata (mainly Britain); London Clay of Sheppey (Agassiz's *Acipenser toliapicus*), Upper Eocene of Hempstead, Upper Eocene of the Hampshire basin, Red Crag of Suffolk, and possibly Lower Pliocene of Montpellier (France). Woodward also referred

to fossil finds he made of pre-Eocene acipenseroids from the Upper Chalk of Kent and noted the similarity of the Eocene fossils with present day *Acipenser*. Lambe (1902) quotes Dawson in describing the Belly River Series (site of fossil *Acipenser albertensis*) as an "extensive fresh and brackish-water series" and characterized the period as a "prolonged interval in the Western Cretaceous area, during which the sea was more or less excluded from the region and its place occupied for long periods by lagoons or freshwater lakes". Estes (1964), in describing *Acipenser eruciferus* from the Upper Cretaceous Lance formation of eastern Wyoming interpreted the depositional environment as a "broad, lowland coastal plain". Gardiner (1967), in his review of palaeoniscoids and chondrosteans, stated early fossil *Acipenser* to be from marine deposits. This view seems echoed in Cavender's (1986) comment about North American acipenserid fossils that "sturgeons are extremely rare in freshwater deposits but more common in Gulf Coast sediments such as the Cretaceous Selma chalk (Applegate, 1970) and the Atlantic Coastal Plain deposits (for example, Middle Miocene Pungo Marl) of North Carolina". According to Nesov and Verzilin (1983), fossil sturgeon remains from the Late Cretaceous Jalovatsh formation (Lower Santonian) of western Ferghana indicate the "existence of a large non-dried river" which drained into the Ferghana brackish water bay and is regarded to have flowed from the northern mountainous region. Nesov and Kaznyshkin (1983) described *A. shilini* from the Santonian of the northeastern Aral region and remarked that it was probably estuarine. Nesov and Kaznyshkin (1983) also described *A. zhylgensis* from the Upper Palaeocene of Kazakhstan and characterized it as probably an Atlantic sturgeon.

Middle or late Pleistocene fossil sturgeon remains from the San Francisco Bay area (Casteel and Hutchison, 1973) were freshwater but apparently belonging to a coastal drainage. *Acipenser* fossils have also been discovered from the Upper Cretaceous Judith River formation of Alberta (Neuman *et al.*, 1988).

The implications of this fossil record for the historical biogeography of host-parasite associations can be summarized as follows:

1. There is no evidence that *Acipenseriformes* were part of a Gondwanan fauna. All fossil acipenserids are associated with the Laurasian landmass.
2. *Acipenser* was present both in Europe and North America during the Cretaceous, in drainages along the western interior seaway and in coastal drainages (estuaries) of the epicontinental marine Tethys.
3. The depositional character of the fossil acipenserids is equivocal in assigning a singular habitat type for the family. However, the fossil record indicates that a deep marine habitat is rare and most records are from fresh- and brackish water environments of coastal fluvial plains. This indicates that an estuarine habit is old in this group of fishes.
4. The oldest fossil *Acipenser* are found in late Cretaceous sediments of North America and western Asia. This rules out the Ponto-Caspian or Paratethys as the "centre of origin" for sturgeons since these Tethyan derivatives were not formed before the Miocene.

Acipenserid phylogenetics and the systematic status of the lake sturgeon.

The family Acipenseridae is a monophyletic assemblage of 24 extant species belonging to 4 genera; *Acipenser*, *Huso*, *Pseudoscaphirhynchus* and *Scaphirhynchus* (Findeis, 1994, Sokolov and Berdichevskii, 1989). The Acipenseridae is considered sister taxon to the Polyodontidae (paddlefishes, 2 extant species, *Polyodon spathula* and *Psephurus gladius*) (Findeis, 1994; Grande and Bemis, 1991; Figs. 3.6, 3.7) or alternatively to the Chondrosteidae (Gardiner, 1984; Schaeffer, 1973). Again, support for a closer relationship with the polyodontids appears to be better supported by the evidence (Grande and Bemis, 1991). The Acipenseridae and Polyodontidae comprise the extant Acipenseriformes and are related to the once flourishing Chondrosteiformes (Gardiner, 1984) and to the extant Polypteriformes of Africa (all belong to the Chondrostei, see Nelson, 1994; Lauder and Liem, 1983).

A cladistic analysis at the generic level by Findeis (1994) indicated that *Acipenser* is sister taxon to the monophyletic lineage of *Scaphirhynchus* and *Pseudoscaphirhynchus* combined. Together, these three genera comprise the subfamily Acipenserinae with *Huso* as its sister taxon (Findeis, 1993; Figure 97). However, a cladistic analysis by Mayden and Kuhajda (1996) indicated that *Acipenser* and *Huso* form a monophyletic clade separate from Scaphirhynchini. Findeis (1993) was unable to find a synapomorphy that defines the genus *Acipenser*, and consequently, regarded *Acipenser* as a potentially untenable assemblage. The phylogenetic analysis of Findeis (1993) is used as the basis of this discussion instead of the results of Mayden and Kuhajda (1996) in view of the more extensive database used by Findeis (1993) and

clearly argued characters. Furthermore, the use of certain characters and the assignment of some character states used by Mayden and Kuhajda (1996) may be contested.

The main points of difference between the cladograms of Findeis (1993) and Mayden and Kuhajda (1996) are the monophyly of *Huso* and *Acipenser*, and the status of *Acipenser*. Consequently, I will focus on 'node 3' on the cladogram of Mayden and Kuhajda (1996) and on the autapomorphies for *Acipenser*. Mayden and Kuhajda list 6 characters in support of the monophyly of *Acipenser* and *Huso*. Two of the characters (29 and 33) have states that require a subjective designation (very narrow, narrow and broad branchiostegal connections, and poorly, moderately, and well developed clavicle keels). One (character 29, branchiostegal connection) has identical conditions in *Acipenser* and one *Pseudoscaphirhynchus* but its potential homoplasious nature is not addressed. Character 4 (ventral scute counts) were assigned a state of 8-10 ventral scutes as compared to 7-8 (plesiomorphic) and 11-14 (the other apomorphic state). However, descriptions of species in Berg (1948) and Scott and Crossman (1973) indicate the following ventral scute counts for various species of *Acipenser* spp. and *Huso* spp.; *A. nudiventris* (12-16), *A. ruthenus* (11-18), *A. gueldenstaedti* (7-12), *A. persicus* (7-14), *A. baeri* (9-15), *A. stellatus* (9-14), *A. sturio* (8-12), *A. transmontanus* (9-12), *A. medirostris* (7-10), *A. fulvescens* (7-12), *H. huso* (9-11) and *H. dauricus* (8-12). Given this wide variability, the character appears inadmissible. Character 12 of Mayden and Kuhajda (1996), 'armature of caudal peduncle', also requires a subjective assignment for *Pseudoscaphirhynchus kaufmanni* (the state in *P. hermanni* was

unknown) which was described as "completely armed above, incomplete below" (Mayden and Kuhajda, 1996). However, *P. kaufmani* was not assigned the 'incompletely armed' state. Regarding *Pseudoscaphirhynchus*, Berg (1948) stated: "Rows of scutes extend to the end of the body, not coalescing or forming a carapace. Body between the rows of scutes covered with granules, not with plates". Findeis (1993 p. 410) referring to the peduncle scales of *Scaphirhynchus* stated: "similar peduncle and pre-anal scale rows are found in *Pseudoscaphirhynchus*, *Huso*, and many species of *Acipenser*, but they are not as organized and do not possess scales as numerous or large as those of *Scaphirhynchus*". Consequently, a conservative approach would be to regard the caudal peduncle armature of *Pseudoscaphirhynchus* as incomplete. The polarization of Character 36 (anadromy) of Mayden and Kuhajda (1996) is also problematical since the outgroup Polyodontidae is freshwater and not all *Acipenser* spp. are anadromous. Although anadromy may well be a basal trait, it is not a supported synapomorphy for *Acipenser* and *Huso*. Only the presence of a pseudobranch may be regarded as a synapomorphy for *Acipenser* and *Huso* based on outgroup comparison with Polyodontidae. The widespread presence of a pseudobranch in diverse unrelated lineages of actinopterygians supports it being a plesiomorphic trait for fishes, including *Acipenseriformes*, with independent losses in Polyodontidae and *Scaphirhynchini*. Consequently, this character remains suspect. In contrast, numerous synapomorphies support the monophyly of *Acipenser* and *Scaphirhynchini* (Findeis, 1993). Mayden and Kuhajda (1996) were able to identify one autapomorphy for *Acipenser* (the first time this has been done); the presence of parietal ridge like

elevations as opposed to spines in *Scaphirhynchus*. This hypothesis of the monophyly of *Acipenser* remains to be tested by future examinations of all *Acipenser* spp. Within the Scaphirhynchini, Gardiner (1984) felt that the distinction between *Scaphirhynchus* and *Pseudoscaphirhynchus* was based on "trivial" differences. However, Findeis (1993) has shown that species of both genera are distinct monophyletic assemblages (see also Mayden and Kuhajda, 1996). Consequently, I follow Findeis (1993), and convention (Berg, 1948), in recognizing the two genera as separate.

Only one species level phylogeny has been proposed for *Acipenser* (Artyukhin, 1995) and represents the first attempt at an argued phylogenetic hypothesis of all species in the genus. However, aspects of the proposed phylogeny have the following problems:

1. The outgroups are not clearly specified although they apparently include *Huso*, the polyodontids, scaphirhynchines and fossil genera such as *Moythomasia* and *Cheirolepis*. Accordingly, many of the character states cannot be or are not argued by either outgroup comparison or ontogenetic criteria (characters 3, 4, 5, 7, 8, 10, 11, 12, 14, 19 of Artyukhin, 1995).

2. Some of the argued character states cannot be used as presented. For example, in character 17, large oocytes are stated as being apomorphic when two species of the outgroup have large oocytes; in character 3 (heavily muscled or weakly-muscled stomach), both states are present in the outgroup (*Scaphirhynchus* has a conspicuous muscular pyloric stomach but *Huso* possesses a weakly muscled pyloric stomach).

3. Skin ossifications are addressed in Characters 4, 5, 6, 7 and 19 of Artyukhin (1995), in conjunction with other characters but characters 7 and 19 seem to be part of the same series.

4. The chromosome number of *A. schrencki* as given by Serebrakova (1979, in Findeis, 1993 and in Rab, 1986), Serebrakova (1969 in Birstein *et al.*, 1993) and Sokolov and Berdichevskii (1989) is approximately 240, not 120 as indicated by Artyukhin (1995). There is also no discussion of the view held by some Russian ichthyologists (see Skrjabina, 1974) that *A. schrencki* and *A. baeri* are closely related. Taken together, the chromosome count of $240 \pm$ for *A. schrencki* and Artyukhin's hypothesized sister taxon relationship with *A. nudiventris* indicate that *A. schrencki* arose from the ancestral stock by polyploidization. This and the fact that *A. schrencki* is endemic to the 'Amur R. zone' while *A. nudiventris* is not found outside 'Adriatic-Ponto-Caspian zone' implies that the ancestral diploid stock was widely distributed across Northern Asia (Siberia) or perhaps Central Asia prior to desertification (see discussions later on the disjunct distributions of *Huso* and *Acipenser* and some of their parasites within Eurasia).

6. I have examined the symplectic (=interhyal?) in *Acipenser fulvescens* (a 2 year old specimen and an older specimen of unknown age) and its morphology is similar to that of the white sturgeon, *A. transmontanus* (p.300, Findeis, 1993). The symplectic in these two species does not have the elongate narrow posterior portion as in *Huso*, nor is it elongate as in *A. stellatus* (Antoniou-Murgoci, 1936). Calculation of the ratio poses problems of its own since this element in these two species narrows

somewhat in the mid-region but has expanded ends for articulation. The width : length ratio of the symplectic in *A. fulvescens* ranges from 0.6 - 0.8 depending upon where the measurements are taken. Overall, the shape of the symplectic is stout, not narrow and elongate. A width : length ratio of 0.8 as given by Artyukhin (1994) for *A. schrencki* indicates a rectangular symplectic whereas the symplectic illustrated by Antoniu-Murgoci (1942) for *A. ruthenus* is even shorter. Given the variability of this character (see also comments by Findeis 1993, p. 298) and the presence of a small symplectic in some members of the outgroup (*Mimia* and *Moythomasia*, Findeis, 1993), a short and wide symplectic may be a persistent plesiomorphy.

7. No synapomorphy is presented in support of the monophyly of *A. medirostris* and *A. transmontanus*. However, published descriptions and personal observations on *A. transmontanus* (in the collection of Dr. T.A. Dick) reveal that these two species have an extra row of irregularly shaped and placed scutes on either side of and close to the dorsal row of scutes. This seems to be a unique character state and arguably synapomorphic for these two species.

8. It would appear that a dichotomy is indicated between the *A. medirostris* - *A. transmontanus* clade and the Chinese group.

9. The support for the monophyly of *Huso* and *Acipenser* seems rather weak. As discussed earlier, characters 1 and 2 are undermined by outgroup comparison while it seems that the first of the two character '3's (spines in centre of scutes) should be positioned with 1 and 2 as synapomorphies supporting the monophyly of *Acipenser* and *Huso*. The spines of the scutes in *S. platorynchus* have a strong elongated, antero-

posteriorly lengthened keel and is very difficult to compare to the spines of certain other acipenserids (such as the lake sturgeon, for example). It would appear rather tenuous to suggest a homology of scutes and caudal fulcra in fossil groups as has been done by Artyukhin (1995). The description of dermal ossifications in *Asiacipenser kotelnikovi* by Nesov *et al.* (1990) shows the spines arising centrally from a basal plate but directed backwards. This is particularly evident from ventral views of these dermal plates (Nesov *et al.*, 1990).

In spite of the problems associated with Artyukhin's (1995) proposed phylogeny, he (Artyukhin, 1995) was able to identify a synapomorphy (characteristic melanin blotches on the skin of juveniles) indicating that the lake sturgeon and shortnose sturgeon (*A. brevirostrum*) are sister species. This supports the long held view, by North American ichthyologists (see Hocutt and Wiley, 1986; Lee *et al.*, 1980), of these two species as sister taxa. This observation has considerable importance in the discussions to follow. Artyukhin (1994) further suggested that *A. baeri* is also closely related to the North American species pair based on morphology but did not provide any argued synapomorphy in support of this contention. Taking these considerations into account, I have modified the phylogeny of sturgeons as presented by Artyukhin to indicate where relationships seem strongly supported by synapomorphies and where relationships are supported by morphology (e.g. relationships of the *A. naccari* - *A. gueldenstaedti* - *A. persicus*).

A recent study of genetic relationships among four North American species of *Acipenser*, using sequence divergence in the mitochondrial DNA, Brown *et al.*, (1996),

revealed that the green sturgeon (*A. medirostris*) and the white sturgeon (*A. transmontanus*) are indeed sister taxa as the morphological data would indicate (both are Pacific coastal species) and that this group is related to *A. fulvescens*. Unfortunately, they did not include the shortnose sturgeon (*A. brevirostrum*) in their analysis. In keeping with the morphological and biogeographical data, the Atlantic sturgeon (*A. oxyrinchus*) was distantly related to these taxa. However, as recognized by Brown *et al.*, (1996), their postulated divergence times are problematical; the white sturgeon -green sturgeon species pair was postulated to have diverged from the lake sturgeon only 3.5 mya, a time frame which is not compatible with hypotheses, based on geological evidence, of vicariance of fish fauna by the continental divide in the Tertiary and perhaps earlier. Brown *et al.* (1996) pointed out that this discrepancy can be explained if one accepts a slower rate of nucleotide substitution in sturgeon since they were using a generalized rate of nucleotide substitution for mammalian mtDNAs (of 2.8% per million years) and they proposed a possible 2-4 fold slower rate based on a mid- Miocene separation (10 mya) of the continental faunas by the Rockies. The use of a time frame of 10 mya is problematical as well since according to the source (Smith, 1981) used by them, the "Rockies have been topographically dominant since before the Miocene" (p. 173 of Smith, 1981), pushing the time of separation possibly beyond 23 mya (the Miocene-Oligocene boundary according to Rogers, 1993). Perhaps the rate of nucleotide substitution is even slower for acipenserids. Martin *et al.* (1992) have shown that the rates of mtDNA evolution in sharks is seven- to eightfold slower than for mammals (carefully calibrated only in primates) and if such a rate is applied

to sturgeon, there is a closer fit with the geological time frame.

The above review of the phylogenetic studies on acipenserids can be summarized as follows:

1. All genera are demonstrably monophyletic.
2. *Acipenser* and *Scaphirhynchus* form a monophyletic assemblage, the Acipenserinae.
3. Several closely related species pairs of *Acipenser* can be recognized by clear synapomorphies. These include: *A. transmontanus* and *A. medirostris* (co-occurring in the Pacific North American drainages), *A. brevirostrum* and *A. fulvescens* (central and eastern North American), *A. oxyrhynchus* and *A. sturio* (North American and European Atlantic).
4. Several monophyletic groups within *Acipenser* have been suggested based on more equivocal cladistic evidence but on strong morphological grounds. These include *A. ruthenus*, *A. nudiventris* and *A. schrencki* (Trans-Eurasian group) and a second group: *A. gueldenstaedti*, *A. persicus* and *A. naccari* (Mediterranean-Ponto-Caspian group).
5. The phylogenetic position of the Yangtze sturgeons is unclear and may show trans-Pacific relationships with *A. medirostris* - *A. transmontanus* pair.
6. Considerable speciation (distinct from origin) of sturgeons is associated with the Ponto-Caspian basins but the North Pacific rim (and its drainages) harbours 6 species.
7. Polyploidy is widespread among acipenserids, most species are tetraploids or octoploids, and sister taxa sometimes differ in ploidy levels. Polyploidy is not an admissible character in the phylogenetic analysis. Polyploidy also allowed reproductive isolation without changes in external morphology.

Acipenserid biogeography:

(Main sources: Becker, 1983; Berg, 1948; Dadswell *et al.*, 1984; Dick and Choudhury, 1992; Holcik, 1989; Scott and Crossman, 1973; Lee *et al.*, 1980. Additional sources: Artyukhin and Andronov, 1990; Findeis, 1993).

The distribution of species in this family is restricted to north of 22°N Latitude, i.e. to what once comprised the Laurasian landmass (Figure 1). There are no sturgeon on any of the continental or subcontinental landmasses of the former Gondwanaland (Africa, South America, India, Australia, Antarctica), other than the spawning runs of *Acipenser persicus* and *Huso huso* in the Iranian rivers from the Caspian Sea. Fossils of acipenserids have also not been found on the derivatives of the Gondwana landmass.

The genus *Acipenser* is the most widespread with the highest number of species (17/18) and has an approximately holarctic or circumboreal distribution although some species have southern ranges; *A. oxyrinchus* is represented as far south as the Gulf of Mexico by the subspecies *A. o. desotoi* (historical records include Bermuda and the northeast coast of S. America) and the Chinese sturgeon *A. sinensis* has been reported from the China Sea. The three other genera are represented by *Huso* (2 spp.), *Scaphirhynchus* (2, possibly 3 spp.) and *Pseudoscaphirhynchus* (3 spp.).

Most species of sturgeons show restricted distributions on parts of continents or drainage basins as follows:

West Atlantic: Two species of *Acipenser* inhabit the North Atlantic coastal drainages and areas of North America. *A. oxyrinchus* is closely related to the European Atlantic

sturgeon, *A. sturio* and occupies the coastal zones along the Atlantic seaboard from Newfoundland to Florida. The species is also common in the lower St. Lawrence R. and its estuary and has been reported from Ungava Bay. It is not known whether the Gulf of St. Lawrence population is distinct from those of the Atlantic seaboard. A subspecies, *A. o. desotoi* inhabits the Gulf of Mexico and some of its drainages. The species is fully anadromous. In contrast, the shortnose sturgeon, *A. brevirostrum* is estuarine/riverine in habit and inhabits the coastal drainages from New Brunswick to Georgia. Like all acipenserids, both species utilize riverine freshwater areas to spawn.

East Atlantic: Only one species, the European Atlantic sturgeon, *A. sturio* inhabits the Atlantic and North Sea coasts of Europe (including the British Isles) and the range is said to extend to Greenland. *A. sturio*, like its North American counterpart, *A. oxyrinchus*, is fully anadromous and utilizes (or used to utilize) the coastal river systems (Thames, Rhine, Guadalquivir etc.) to spawn.

Mediterranean-Black-Caspian-Aral basin: This area contains the greatest number of acipenserid species. The Mediterranean harbours three (and possibly four) species; *A. sturio*, *A. naccari* which is apparently endemic to the Adriatic Sea, and *Huso huso* which is also found in the Adriatic Sea and its immediate vicinity. *A. naccari* is morphologically very similar, and arguably related, to the Russian sturgeon *A. gueldenstaedti* and is a predominantly estuarine species. *A. stellatus* also occurs but rarely in the Adriatic region. The Black Sea and its drainages also harbour *A. stellatus*, *H. huso* and 3 others; *A. nudiventris*, *A. gueldenstaedti*, and *A. ruthenus*. Of these, *A. ruthenus* is essentially a freshwater riverine species with possibly some estuarine

populations. The Caspian basin and its drainages has the greatest number of species. All the species in the Black Sea basin and drainages are represented in the Caspian. In addition, a species long recognized as a morph or subspecies of *A. gueldenstaedti* but now accorded full species status, *A. persicus*, is present in the southern Caspian Sea (mainly Iranian coast). Owing to this richness of acipenserids, the Ponto-Caspian basin has been traditionally recognized as the centre for evolution of the sturgeons by Russian ichthyologists. The Aral Sea contains only one species of *Acipenser*, *A. nudiventris*, but the Syr-Darya and Amu-Darya rivers are home to three freshwater species of the endemic shovelnose genus *Pseudoscaphirhynchus*. With the exception of *A. ruthenus*, all species of *Acipenser* occurring in this area and *H. huso* are anadromous in habit although some (e.g. *A. gueldenstaedti*) spend a considerable part of their juvenile phase in freshwater environments.

Northern Asia (Siberia): The Siberian sturgeon, *A. baeri* inhabits all the major river systems of Siberia; Ob, Enisei, Lena, Indigirka and Kolyma river systems and has the widest geographical range of all acipenserid species. It is absent from the rivers further east (e.g., Anadyr R.). The Ob and Enisei river systems are also inhabited by the Asian subspecies of *A. ruthenus*, *A. ruthenus marsiglii*. Both Siberian species are predominantly freshwater and riverine, but lacustrine (*A. baeri* in L. Baikal) and reservoir populations are also well known and some populations of *A. baeri* feed in the strongly freshened regions of the estuaries (Berg, 1948).

Northeast Asia (Amur River): The Amur river basin in north-east Asia is home to the endemic *A. schrencki* and *Huso dauricus*, both of which are considered to be an

estuarine/freshwater riverine species. However a recent record of *H. dauricus* from the Japan Sea (Honma and Itano, 1994) indicates the species may have anadromous populations as well. A third wide-ranging north Pacific anadromous species, *A. medirostris* may utilize the Amur R. for spawning.

East Asia (Chinese region): The Yangtze (Chang Jian) R. system is home to two poorly known species; the freshwater *A. dabryanus* and the anadromous *A. sinensis*. *A. dabryanus* is predominantly riverine although they are also known to occur in lakes. *A. sinensis* inhabits the estuaries and the coastal areas of the China Sea. It has also been caught near Hong Kong which indicates it may be wide ranging along the continental coast.

North Pacific: The seas of the eastern North Pacific (Okhotsk, Bering, Japan Seas, and Tartar strait) are home to the wide-ranging anadromous *A. medirostris* which presumably spawns in rivers along the Kamchatka and Chukchi peninsulas, Japanese coast, the Amur system and nearby drainages. The species ranges across the Bering Sea to the N. Pacific coast of N. America (Lee *et al.*, 1980; Scott and Crossman, 1973) and is reported from southern Alaska to northern California. The Japanese coastal river systems are home to two supposedly endemic but poorly known species, *A. multiscutatus* and *A. kikuchii*. The Pacific coast of North America and its drainages also harbours the anadromous white sturgeon, *A. transmontanus*.

Interior North America: The freshwaters of the greater part of N. America are inhabited by what is possibly the only exclusively freshwater species of *Acipenser* at present, the lake sturgeon, *A. fulvescens* (Figure 3). The Rocky mountain system in the

West and the Appalachian system along the Eastern seaboard form natural barriers that isolate the lake sturgeon in the central landmass of the continent from the four other coastal species. The distribution of *A. fulvescens* overlaps with *A. oxyrhynchus* in the St. Lawrence system but is limited. In addition, the Mississippi-Missouri system is inhabited by two (and possibly three) species of the shovelnose genus *Scaphirhynchus* and by the paddlefish *Polyodon spathula*.

The above information on the present day biogeography of sturgeons indicates that 1). Acipenseriforms show markedly disjunct distributions at various taxonomic levels.

2). The monophyletic group of shovelnose sturgeons (Scaphirhynchini) exhibit the most extreme case of such disjunction. The genus *Scaphirhynchus* with 2 (or 3) species is restricted to the Mississippi-Missouri and associated drainages of North America. The genus *Pseudoscaphirhynchus* with 3 species is endemic to the rivers of the Aral Sea. All species of shovelnose sturgeons are freshwater in habit.

3). The genus *Huso* also shows a markedly disjunct distribution, being widely separated by the vast Asian landmass. *Huso huso* (beluga) is native to the Mediterranean-Black-Caspian Sea basins and is an anadromous species while *Huso dauricus* is an estuarine (possibly anadromous) species inhabiting the Amur River basin.

4). Of the nominal species recognized, only the green sturgeon shows a disjunct distribution on either side of the North Pacific although *A. medirostris* may occur in the Bering Strait (Berg, 1948).

5). The other extant group of Acipenseriformes, the paddlefishes (Polyodontidae) also show a markedly disjunct distribution by being found in eastern Asia (Yangtze drainage) and North America (Mississippi-Missouri drainage) (Grande, 1994).

In conclusion, evidence from the fossil record, phylogenetics, and biogeography of acipenserids that identify a minimum age of sturgeon, are summarized as follows:

1. Fossil evidence: The fossil evidence dates back reliably to a minimum of late Cretaceous age in N. America and Eurasia. More acipenserid fossils (such as those of *A. kotelnikovi* but perhaps with more diagnosable features) from the Jurassic may firmly establish the minimum age of the family as mid-Jurassic. The presence of *Propenser hewletti* indicates the presence, during Cretaceous times, of an acipenserid with well developed tolerance for salt-water. The fact that phylogenetically more derived fish families (Lepisosteidae, Esocidae) have Cretaceous and Palaeocene fossils that resemble their modern relatives suggests that the sturgeon fossil record may be grossly underestimated. It might also suggest that certain lineages diversified within a similar narrow time frame and lapsed into a subsequently long period of morphological stasis. Consequently, while ancestral lineages may be old, a certain body plan (e.g. Acipenseridae) may have become established in a relatively short space of time.

2. Phylogeny and biogeography of the sturgeons. Relatively derived taxa such as Scaphirhynchini show a disjunct distribution on continents separated by the present day Atlantic Ocean. In North America, shovelnose sturgeon are associated with drainages and basins (Gulf of Mexico) that ultimately connect to the Atlantic and

palaeogeography indicates that areas now harbouring *Pseudoscaphirhynchus* in western Asia were drained by Tethyan drainages and eventually by a basin (Paratethys) that was also connected to the Atlantic. Scaphirhynchines are freshwater in habit with no evidence for anadromy. Consequently, a long range marine dispersal is not supported by the evidence at hand. A former continuous distribution or dispersal across the Bering land-bridge is less supported by present day distribution than is a European - Northeast North American connection. Vicariant hypotheses would put the date of separation at 100 mya (latest) if the vicariance is due to the opening of the north Atlantic between Iberia and North America or 50 mya (latest) if the vicariance is due to final separation across northern Euramerica. The disjunction of *Huso* seems enigmatic at first and owing to its basal position among acipenserids, it is tempting to attribute it to a geologically old vicariant event. However, similar patterns of disjunction are shown by at least two cyprinid subfamilies (Howes, 1984; 1991) and another potentially monophyletic group of *Acipenser* (see below) indicating that similar climatic and geological processes may have affected groups of varying phylogenetic age concurrently to produce concordant distributional patterns. Given the much younger age of cyprinids (Eocene) relative to sturgeons, it is possible that the terminal Eocene climatic changes, the drying up of central Asia (Travers, 1989), the Himalayan orogeny, and finally Pleistocene glaciations acted sequentially and resulted in modifications of the central and eastern Asian drainages causing in turn the vicariant distributions of *Huso* seen today. If there was a trans-Asian *Acipenser* group as hypothesized by Artyukhin (1994) (*A. nudiventris* - *A. ruthenus* - *A. schrenckii*),

similar effects upon this group may have produced the vicariant separation and eventual isolation of *A. schrencki* in the Amur R. drainage.

Historical biogeography of the host-parasite association

Host-parasite associations may be viewed at different geographical scales. Host taxa at various hierarchical levels (species, genus, family etc.) possess parasites with varying degrees of specificity (Dogiel *et al.*, 1958; Dogiel, 1961). At higher taxonomic levels of host, there appears to be a 'core' (not to be confused with the ecological 'core-satellite species' concept of Hanski, 1982) of parasites that are widely distributed and specific for the group of hosts in question (Dogiel, 1961; Esch and Fernandez, 1993) although the distribution of these parasites may be modified on a local scale (Aho and Bush, 1993; Dick and Choudhury, 1996; see also Chapter 1). In the North American freshwater fish fauna, it is possible to identify such 'core' groups of parasites that are associated with families or orders of fishes (Choudhury and Dick, submitted). Many of these core parasites in different host groups appear related at various taxonomic levels and potentially share a genealogical relationship influenced by processes of historical biogeography and co-evolution (Brooks and McLennan, 1991, 1993) that remain largely unanalyzed.

This discussion will address the historical biogeography of sturgeon-parasite associations by first comparing the parasite fauna of the Acipenseriformes with their closest phylogenetic relatives to determine the extent of host-sharing. This comparative approach will be extended to the parasite fauna in different monophyletic groups (e.g.,

Polyodontidae, Acipenseridae etc.) within the order to identify potential events of host capture or host switching. In the third section, I will discuss the biogeography, biology and phylogenetics of the parasites of sturgeons, which will be combined with information about palaeogeography and palaeontology reviewed in the previous section in an attempt to reconstruct hypotheses for the historical associations. This will be followed by an evaluation of the factors that have influenced the parasite composition in the widely distributed freshwater North American acipenserid, *Acipenser fulvescens* and how it fills a critical missing link in our overall understanding of acipenserid parasites. Finally I will address how this study compares with other studies on archaic hosts.

The only other extant chondrosteian group (hence related to the Acipenseriformes) is the Polypteridae, represented in the freshwaters of Africa by two genera *Polypterus* (bichirs) and *Callamoichthys* (reedfishes) (Nelson, 1994). A perusal of the surveys on polypterids (Khalil, 1969, 1971a; Shoter and Medaiyedu, 1977) and discussion on the zoogeographical affinities of the parasites of African freshwater fishes (Khalil, 1971b) indicate that parasites of polypterids have undeniable African affinities with no apparent relationships to parasites of Acipenseriformes. This is also understandable in view of the palaeontology and present-day distribution of the two groups since they appear to have been restricted to their respective landmasses (Gondwana and Laurasia) at least since the early Mesozoic.

Within the Acipenseriformes, the two families Acipenseridae and Polyodontidae are sympatric in North America, east of the Continental divide, and in the Yangtze

River system in China. Comparisons between these two families rely heavily on the parasite fauna of one of the two species in the family, i.e., the North American paddlefish *P. spathula*, since the parasite fauna of the Chinese (Yangtze) paddlefish, *P. gladius* (as well as of the 2 Yangtze sturgeons) is poorly known (only 3 parasites have been reported from *P. gladius*, viz. *Goezia* sp.(Nematoda), *Pseudotracheiastes soldatovi* (Crustacea) and an unidentified acanthocephalan). In contrast, the parasite fauna of *P. spathula* is well known (Hoffman, 1967; Lockard and Parsons, 1971; Schmidt *et al.* 1974; Raikova, 1994) but only two parasite taxa are shared with acipenserids, the genus *Diclybothrium* (specifically *Diclybothrium hamulatum*) and *Polypodium hydriforme*. *D. hamulatum* has a direct life-cycle and there is evidence that *Polypodium* is transmitted by an initial phase of ectoparasitism (Raikova, 1994). In contrast, none of the gastro-intestinal helminth taxa (4 species of host-specific parasites) is shared with other North American freshwater acipenserids despite the extensive historical and current overlap among their ranges. This is not surprising when one considers that *P. spathula* is exceptional among acipenseriforms in being a pelagic filter-feeder. This habit and the morphology of the branchial apparatus that allows this type of feeding are derived features (Grande and Bemis, 1991). Of the other related fossil and extant paddlefishes, the Miocene *Crossopholis* which historically occupied a range overlapping that of *Polyodon*, and the present day *P. gladius* of China, are piscivorous (Grande and Bemis, 1991), while the Late Cretaceous *Palaeopsephurus* of Montana was also not a filter feeder (from the evidence by Grande and Bemis, 1991). Of the enteric parasites of *P. spathula*,

Marsipometra Simer, 1929 (Cestoda) (3 spp.) and *Hysterothylacium dollfusi* Schmidt, Leiby and Kritsky, 1974 (Nematoda) belong to groups that are known to utilize copepods for transmission (Table 21). The life cycle of *H. dollfusi* has not been experimentally studied but larvae are found within the gut wall of paddlefish (Miyazaki *et al.*, 1988). This histotropic phase of larval development of *H. dollfusi* in the definitive host may indicate that the transmission of *H. dollfusi* is derived from an ancestral life cycle related to a plesiomorphic piscivorous habit for polyodontids. It is possible that this feeding innovation was correlated with the large lakes and other water bodies (see Grande, 1994) that formed in the Tertiary as a result of final withdrawal of the sea in the late Cretaceous. The phylogenetic relationships of species in the widespread marine and freshwater genus *Hysterothylacium* has not been analyzed but the morphologies of *H. dollfusi* and *H. bidentatum* (specific to European sturgeons) (Moravec, 1994; Skrjabina, 1974; Schmidt *et al.*, 1974) indicates that the two species are not closely related and therefore represent independent acquisitions in their respective endemic areas. In view of its restricted range, and specialized feeding habits, *Polyodon spathula* is unlikely to have had a major influence on the parasite fauna of acipenserids as a whole. The historical biogeography of *Diclybothrium* spp. and *Polypodium* will be discussed again later.

Within the Acipenseridae, it has been noted (Skrjabina, 1974) that there are no parasites that are specific for either *Huso* or *Acipenser* only. Species of parasites are shared between these two genera wherever they co-occur (Ponto-Caspian and Amur R.). If co-speciation events did occur in the past, they are now obscured by extensive

host sharing within the acipenserids. Instead, the distributions of the parasite fauna of sturgeons is characterized by associations with entire landmasses or portions thereof as well with certain oceanic basins. This has resulted in varying degrees of endemism at different taxonomic levels with only two exceptions (*Polypodium hydriforme* and *Crepidostomum auriculatum*). These two species occur in every major drainage basin where sturgeon occur (with a few notable exceptions, see for *Crepidostomum* below) and subsequent discussions will begin with these two widely distributed parasites.

Polypodium hydriforme, a widely distributed parasite (Fig. 100), was considered by Raikova (1994) to be an "ancient parasite" of acipenseriform fishes and is the only endoparasitic cnidarian known from vertebrates. The species is apparently more closely related to the marine Narcomedusae (marine Hydrozoa) than with any other group of cnidarians but is also characterized by a suite of unique characteristics (see Raikova, 1994). The historical association of sturgeons with estuarine and possibly marine environments (see section on fossil record) provided acipenserids with the necessary ecological conditions for the acquisition of this parasite. It will remain unknown whether this host-parasite association was a 'host-capture' from a pre-existing host-parasite relationship in now extinct hosts (e.g., contemporary Chondrosteidae?) or a direct acquisition from the marine or brackish water environments. The phylogenetic relationships of the Acipenseriformes does not support any one idea more strongly than another but if Polyodontidae were always confined to freshwater as the fossil record seems to indicate, then the presence of *Polypodium* in paddlefish could be regarded as an example of host-capture. The wide distribution of

Polypodium may be viewed as evidence for a very basic and therefore old host-parasite association in sturgeons (see also Raikova, 1994).

Crepidostomum auriculatum is an exclusively freshwater helminth and widely distributed (Fig. 100), but unlike *Polypodium*, allocreadiids as a group possess no obvious phylogenetic relationships with any marine taxa. The absence, in Europe, of *C. auriculatum* in acipenserids other than the sterlet, is enigmatic but could be due to a) the distribution of intermediate hosts and therefore reduced availability to other sturgeons, b) differing prey selectivity, c) resident riverine nature of the sterlet vs. early downstream movement of juveniles of other sturgeons, d) the paucity of studies on the juveniles and adults of the anadromous Ponto-Caspian sturgeons in upstream locations during the freshwater phase of the life history, most studies on Ponto-Caspian sturgeon having been carried out in the estuaries (Skrjabina, 1974), and e) the fact that European *C. auriculatum* represents a distinct species. Of these, e) is an unlikely possibility given the morphological studies on Eurasian *C. auriculatum* (see Skrjabina, 1974, and references therein). Historical reasons for this distribution include the origin and evolution of *C. auriculatum* in the Arctic-boreal drainages of northern Asia or in North America and subsequent wide distribution in drainages of the combined northern Asian-American region during the Tertiary. Consequently, the Ponto-Caspian drainages constitute the periphery of its distribution and may have been colonized by freshwater dispersant sturgeons during the proposed influx of freshwater from the Northern regions in the Pleistocene (Grossvald model of glaciation, see Appendix II) or earlier following the retreat of the Turgai strait and subsequent land

continuity between Europe and Asia in the Tertiary. It is unclear what role the northeastern North American - European connection had in the vicariance process (separation dated at mid-Eocene at the latest) since the parasite has not been found in Mediterranean drainages or in Atlantic coastal drainages of Europe and North America (Skrjabina, 1974, lists a historical record in the Rhine). Consequently, *C. auriculatum* may not have had a continuous holarctic distribution in the past. Of the *Crepidostomum* spp., only *C. farionis* (of salmonids) and possibly *C. metoecus* (also typically a salmonid parasite) have ranges that match or surpass that of *C. auriculatum*. Stearley (1992) considered it possible that vicariant separation of the salmonids and subsequent evolution of *Salmo* and *Oncorhynchus* occurred across northern Asia. Many coregonine species also have a northern Asian-North American distribution (see Lee *et al.*, 1980). This may have been also the site for the origin of their *Crepidostomum* spp. The potentially basal position among *Crepidostomum* spp. (see Chapter 2-5) indicates *C. auriculatum* may precede many of the species of the genus now found in North America which in turn would indicate its considerable geological age (assuming that all the other *Crepidostomum* species in North America did not arise simultaneously). The present day distribution of *C. auriculatum* is most satisfactorily explained by two vicariant events. The earlier of these is the final separation via Cordilleran orogeny between the central (e.g. lake sturgeon) and Pacific (e.g. white sturgeon) acipenserids during the late Tertiary (Miocene, see section on '*Acipenserid phylogenetics and systematic status of lake sturgeon*'). The second potential vicariant event was the Pleistocene glaciation and the subsequent

submergence of the Bering land bridge resulting in the disjunction between northeastern Asia and North America. However, since sturgeons were not part of a Beringian refugium (Hocutt and Wiley, 1986), it is likely that the vicariance between Siberian/Northeast Asian and American populations of *C. auriculatum* and their hosts occurred earlier due to orogeny of the Brooks and MacKenzie formations in the North and may have preceded the separation on either side of the Continental divide in North America. Consequently, Pleistocene glaciations only reinforced the vicariance by drastically modifying distributions of North American acipenserid hosts. Exact timing of such vicariant events is hindered by the lack of knowledge of pre-Pleistocene sturgeon distributions in the northern parts of North America since there are no freshwater sturgeon in the North American Arctic rivers (e.g., MacKenzie and Yukon Rivers).

At the higher taxonomic level of genus, 3 parasite taxa show wide holarctic/circumboreal distribution; *Capillospirura* (Fig. 101), *Truttaedacnitis* (Fig. 102) and *Diclybothrium* (Fig. 103). The relationship between *Capillospirura* and *Ascarophis* which is widely distributed in Arctic and north temperate marine, estuarine and anadromous hosts indicates a marine connection and it could be argued that *Capillospirura* is derived from an ancestral *Ascarophis* type, particularly since the presence of bidentate plates in *Capillospirura* (see Appy and Anderson, 1982) is derived within the Cystidicolidae. The euryhaline nature of *Capillospirura* spp. mirrors a widespread tolerance of all *Acipenser* and *Huso* for some level of salinity as a basic life history trait of the acipenserids. Although the three species of *Capillospirura* could

not be resolved cladistically, the presence of a number of autapomorphic characteristics in *C. ovotrichuria* (Appy and Anderson, 1982) and the plesiomorphic similarity between *C. argumentosa* and *C. pseudoargumentosa* argues for the derivation of *C. ovotrichuria* as an endemic species (Fig. 101) in the geologically young Caspian basin from a *C. argumentosa* - like ancestor. If the assessment of distributions is correct, then *C. ovotrichuria* has also replaced its hypothesized sister species *C. argumentosa*. Consequently, the basic holarctic distribution of *Capillospirura* has been modified with replacement by an endemic species in an area that formed after the origin of the genus in sturgeons. An essentially similar distribution, with some modification, is seen in the clade of *Truttaedacnitis* specific for sturgeons (Fig. 102). This clade is sister to the species in lampreys and trout (Chapter 2-5). The two species replace each other in space; *T. clitellarius*, a freshwater species with a basal morphology is widely distributed in northern and northeastern Asia, and central North America (and is possibly present in the North American Pacific drainages) while *T. sphaerocephala* is present in the Ponto-Caspian and Atlantic drainages and basins (see Chapters 2-4, 2-5). In western Siberia, the separation of the two species follows the line of the Ural orogen in Asia and the north-south axis of the topographically dominant Mesozoic and Cenozoic Turgai Sea. The Ural orogeny was not a vicariant event for sturgeons since its formation was by collision of continental blocks in the Palaeozoic (see Appendix II). Hypotheses of a Mesozoic separation of ancestral *Truttaedacnitis* involves the Turgai Sea which was an important vicarious feature during most of the Cretaceous and until the end of the Eocene (McKenna,

1975). However, this form of vicariance seems incongruent with patterns shown by *T. truttae* and other helminths of fishes, including those of sturgeon, in the region (e.g., *C. auriculatum*, *D. armatum*, *A. foliacea* etc.). A more recent origin for *T. sphaerocephala* involves isolation and speciation in the Paratethys or early Ponto-Caspian basins and drainages which indicates that the Atlantic distribution is even more recent and may be via dispersal of anadromous sturgeons to the Atlantic margins of North America in the late Miocene or thereafter. The freshwater life history of *T. clitellarius* and the common presence of *T. sphaerocephala* in marine and brackish water environments, combined with their present distributions, provide support for a third possibility. *T. sphaerocephala* may have evolved in predominantly estuarine or marine anadromous sturgeons in the European Tethyan drainages that underwent extensive transgressions and so had extensive periods of brackish water development. Subsequently, a combination of dispersal and vicariance produced the present amphiatlantic distribution whereby 'Atlantic' sturgeon (hypothetical ancestor of the *A. sturio*/*A. oxyrinchus* species pair) became distributed along newly developing continental margins as the North Atlantic gradually widened. This 'continental tracking' and subsequent isolation allowed the establishment and speciation of the hosts, by allopatry, in the Atlantic region but did not result in speciation of the parasite. At the same time, the parasite also became associated with the remnant of the Tethys (Mediterranean) and with the Paratethys and its products, i.e. the present day Ponto-Caspian basins. In any event, evidence from morphology, systematics and biogeography points to the northern Asian or North American origin of this clade of

parasites and subsequent speciation in the European (Ponto-Caspian) drainages.

The Diclybothriidae shows a basic circumboreal distribution (Fig. 103) and as in the previously discussed groups of parasites (e.g. *Truttaedacnitis* clade in sturgeon), is characterized by a replacement of species in acipenserids of disjunct geographical regions. *D. armatum* and *D. atriatum* replace each other in acipenserids on the Eurasian and North American landmasses respectively. Assessment of the historical development of diclybothriids is complicated by the uncertain relationships of the three species of *Diclybothrium* (see Chapter 2-1) and by the presence of *D. hamulatum* in North American paddlefish. Furthermore, the relationships of the taxa do not resolve whether vicariance was by dissociation across the North Atlantic or across the North Pacific. In the absence of an explicit statement of relationships among the species, plausible reconstruction of the coevolutionary history is based on evidence from morphology, palaeogeography and current distributions. The morphological evidence does not support a derivation of *D. hamulatum* from the current species of *Diclybothrium* in North American sturgeon (*D. atriatum*) or an ancestral form resembling it (i.e., with a ventral atrial organ). Rather, acquisition of *Diclybothrium* by paddlefish likely occurred before speciation of *D. atriatum* or concurrently with it by isolation of populations of the ancestral diclybothriid and its acipenserid and polyodontid hosts. If speciation followed isolation of acipenserids in the central and eastern parts of the continent, then the Cretaceous epicontinental seaway which bisected North America provides a powerful and extended historical mediator of such isolation. This implies however, that sturgeons had a holarctic distribution prior to the

development of the western interior seaway. Also, it does not address the nature of sturgeon-diclybothriid associations on the western margin of the seaway or the fate of such associations following the withdrawal of the inland sea. This speculation may be circumvented by hypothesizing that the Diclybothriidae are an ancient parasite of acipenseriforms and the *Diclybothrium* spp. on *Polyodon* (paddlefishes) and acipenserids (sturgeons) have been inherited from their acipenseriform ancestors. This would explain the morphological similarity between *D. armatum* of Eurasian sturgeons and *D. atriatum* of North American sturgeons.

A number of taxa specific for sturgeons show a distinct amphi-Atlantic distribution. These include families such as the Deropristiidae (Fig. 104) (see also Chapter 2-2), as well as a variety of unrelated taxa such as *Dichelesthium oblongum* (Crustacea), *Nitzschia* (Monogenea) (Fig. 103), *Bothrimonus* (Cestoda) (Fig. 105) and *Leptorhynchoides plagicephalus* (Acanthocephala) (Fig. 106), whose closest relatives belong to disparate and unrelated groups of fishes (Table 22). A redefinition of the Deropristiidae based on clearly defined synapomorphies and the systematic relationships of the various taxa within this family provide clear evidence for a trans-Atlantic connection. Adoption of a strict vicariance approach would date the separation as far back as the Cretaceous and the fossil evidence would support such a time frame. Adopting a vicariance approach and superimposing the cladogram on the geographical distribution of the taxa (Fig. 104) would indicate that separation of genera as well as speciation was complete by the final separation of North America from Europe in the Eocene. A combination of vicariance and dispersal through 'continental tracking' by

sturgeons and *Anguilla* would produce the present day distributions, similar to the mechanism proposed for the distribution of *Truttaedacnitis sphaerocephala* (see above). A similar trans-Atlantic disjunction is seen in the genus *Leptorhynchoides*, one of whose species, *Leptorhynchoides plagicephalus*, is restricted to sturgeons in the Mediterranean-Ponto Caspian basins and drainages. Like its sturgeon hosts, it is a euryhaline parasite with a freshwater life cycle (Skrjabina, 1974). In North America, the genus is represented by the well studied freshwater *L. thecatus*, a characteristic parasite of the Centrarchidae which can be considered its 'primary' host group (particularly *Micropterus* spp.). Support for the Centrarchidae as primary hosts of *L. thecatus* comes from the maturation and growth in these hosts (see Discussion in Chapter 1) and the fact that *L. thecatus* does not occur in freshwater fishes outside the range of the Centrarchidae. The third species, *L. aphredoderi* Buckner and Buckner, 1976 was originally described from another endemic North American family, the Aphredoderidae (pirate perches) and has been subsequently reported from other hosts but possesses a relatively restricted geographical range (Buckner, 1991). Its morphology indicates it is closely related to *L. thecatus*. The endemicity of *L. plagicephalus* for the Mediterranean-Ponto Caspian basins makes it unlikely that *L. thecatus* in Centrarchidae represents a 'host extension' or 'host capture' from sturgeons in North America although the lack of information about the parasites of the Gulf of Mexico sturgeons prevents a more definite statement. It is worth noting that *L. thecatus* parasitizes the lake sturgeon (in the southern parts of the Hudson Bay drainage) but does not mature in this host (see Chapter 1). The systematic position of

Leptorhynchoides as a rhadinorhynchid indicates a marine connection and a vicariant explanation of the disjunct distribution indicates a minimum separation of at least mid-Eocene across northern Europe and eastern North America. However, the concentration of fossil Centrarchidae in western and central North America (Cavender, 1986) and the present day biogeography of centrarchids indicate that the Gulf of Mexico region was important to the origin of this perciform family with dispersals across the southern part of the Continental divide, and that the northern American-European connection may not have been relevant in producing the current disjunct distribution. An older disjunction would date back to the early Cretaceous but causes chronological problems regarding the age of centrarchids (see also discussion by Lundberg, 1993 on similar problems with other fish taxa showing South American - African connections) while there is also the possibility of independent acquisition from now extinct host groups, neither of which is testable with the available information. It is also possible that *L. plagicephalus* and *L. thecatus* are not congeners and perhaps the species require a re-examination. The distribution of *Bothrimonus* (Fig. 105) and its recognition as a taxon distinct from *Diplocotyle* (see Appendix IV) also allows us to interpret the distribution of what are *de facto* sister species (*B. fallax* and *B. sturionis*) as a result of continental tracking and as products of allopatric speciation. The distribution of *Nitzschia*, while showing a similar trans-Atlantic connection of the above mentioned taxa, is complicated by the presence of *N. quadritestes* in the North American Pacific sturgeons, *A. medirostris* and *A. transmontanus* (Foley *et al.*, 1989; Pratt and Hermann, 1962). The distribution of *Nitzschia* is limited by its intolerance of

freshwaters which could explain its absence from the predominantly freshwater sturgeons of Siberia, the Amur R. and the North American continental interior (including lake sturgeon). Thus, *Nitzschia* may have been widespread at one time and subsequently lost in Asian and North American freshwater sturgeons. Alternatively, *Nitzschia* (Fig. 103) evolved in association with the developing North Atlantic basin and expanded its range laterally along the newly forming margins of the North Atlantic. The confluence of Atlantic and Pacific waters across the southern edge of the North American continent during most of the Tertiary provided ample opportunities for the spread of *Nitzschia* into anadromous Pacific sturgeons in the southern parts of their range. The isthmus of Panama could have provided the final vicariant separation as late as the Pliocene. Thus the hypothesis of an Atlantic origin and a single dispersal event into the Pacific is testable by surveys on the parasite fauna of estuarine and anadromous Chinese and western Pacific sturgeons combined with a phylogenetic analysis that identifies the sister taxon to *Nitzschia*.

Every case of trans-Atlantic relationships discussed above involves euryhaline / marine taxa, which indicates that a wholly marine dispersal is theoretically as possible as a strictly vicariant distribution. However, a process that combines the two (continental tracking) may more closely approximate reality. Such continental tracking is significant in historical biogeography since it allows the association of biota (particularly euryhaline and coastal fauna) with newly formed continental margins and drainages and eliminates the need for long range dispersal events to explain observed patterns of distribution.

Amphi-Pacific distributions involve marine and freshwater parasites in anadromous sturgeons inhabiting north Pacific coastal drainages. The most unambiguous example is *Paradiclybothrium pacificum* (Fig. 103) which is marine and evidently specific to *A. medirostris*. Distribution by coastal marine dispersal appears to be the most plausible mechanism. The formation of an Asian-American peninsula via the broad Bering landbridge during the Cretaceous and Tertiary provided a continuous coastline along the North Pacific rim which allowed distribution of coastal biota. The late Tertiary climatic deterioration and, eventually, glaciation acted as a vicariant event and interrupted this distribution and displaced the biota to the South. Consequently, a number of coastal and anadromous fishes, including *A. medirostris*, show the trans-Pacific pattern of distribution (eg. *Osmerus transpacificus*, *Hypomesus pretiosus*, *Lampetra tridentata*) (see Lee *et al.*, 1980), indicating that climate may have been influential in producing the observed patterns of trans-Pacific vicariance. Of the freshwater parasites present in the Pacific coastal drainages, the presence of *C. auriculatum* in *A. transmontanus* could be considered an extension of a basic holarctic/circumboreal distribution.

The distribution of *Amphilina* (Fig. 107) shows a trans-Pacific distribution since *A. bipunctata* and *A. japonica* appear to be closely related if not synonymous (Dubinina, 1982; 1987; Bandoni and Brooks, 1987; Margolis and McDonald, 1986). *Amphilina* has not been reported in any sturgeons east of the Continental Divide in North America. This evidence suggests a distribution basically centered around North Asia with extensions into Europe and western North America. With the exception of

Amphilina in acipenserids, the Amphilinidae are associated with derivatives of Gondwana (South America, Africa, India and Australasia) (Bandoni and Brooks, 1987; Gibson, 1994a). Studies by Bandoni and Brooks (1987) and Gibson *et al.*, (1987) indicate that the observed patterns of distribution in amphilinids are due to the fragmentation of Gondwanaland and subsequent separation of S. America and Africa. Furthermore, a cladistic analysis (Bandoni and Brooks, 1987) also indicates that speciation of *Schizochœrus* (including *Nesolecithus*, see Gibson, 1994a for alternative taxonomic arrangement) occurred before the final separation of South America and Africa. Although the area cladogram of Bandoni and Brooks (1987) provides a convincing argument for drift vicariance, the coevolutionary history is less clear. The genus *Amphilina* is present in acipenserids but not in the sister Polyodontidae (paddlefishes). *Schizochœrus* (sensu Bandoni and Brooks, 1987) infects osteoglossomorphs in Africa and S. America. Two species infect *Arapaima gigas* (Arapaimidae) in S. America and one species infects *Gymnarchus niloticus* in Africa. The Arapaimidae comprise two living species, *A. gigas* in S. America and *Heterotis niloticus* in Africa. I was unable to find a record of amphilinids from *Heterotis* (Khalil, 1971a,b; Helminthological Abstracts 1970-1992, Zoological Record 1970-1996). Similarly, it remains to be seen whether the sister families to the Arapaimidae, i.e., Osteoglossidae and Pantodontidae, host any amphilinids. The fourth species of *Schizochœrus* (after Bandoni and Brooks, 1987) is found in India, not in the well studied osteoglossomorph family Notopteridae, as one might expect, but in the unrelated ostariophysan order, Siluriformes. Also, the other major ostariophysan order,

the Cypriniformes, widely represented in Gondwana derivatives are not hosts of amphilinids. Finally, the only family of osteoglossomorphs in North America (Hiodontidae) are also not host to amphilinids. Host extinction with concomitant parasite extinction has been discussed as one explanation for patchy distribution and the extinct actinopterygians between the acipenserids and the osteoglossomorphs have been proposed as hosts of past (Bandoni and Brooks, 1987, Brooks and Bandoni, 1988). However, the problems in distribution in this case are not with extinct groups of fishes but lie rather in trying to explain 'absences' in extant host orders occupying positions between the osteoglossomorphs and perciforms, successful and basal teleost orders such as Salmoniformes, Clupeiformes, the speciose Cypriniformes, as well as other osteoglossomorphs. Since extinction cannot be invoked, one is led to conclude that they were never hosts of amphilinideans. Ecological explanations find little support since fish groups that are not hosts of amphilinids are found in every habitat and guild that the infected host groups occupy. A notable exception is *Polyodon spathula* which is planktivorous in contrast to the predominantly benthivorous Acipenseridae. The lack of a consistent presence of amphilinids within a clade of fish hosts supports a history of stochastic colonization events, possibly facilitated by past ecological associations (as intermediate hosts?) with now extinct host groups (see Gibson *et al.*, 1987, for discussion of extinct hosts). The apparent restriction of *Amphilina* to the Pacific coastal drainages in North America is also shown by *Cystoopsis acipenseris* which has not been reported from sturgeons east of the continental divide. The distribution of *Cystoopsis* does not appear to be restricted by

the distribution of intermediate hosts since the nematode is not specific for its intermediate gammarid hosts (*Dikerogammarus haemobaphes*, *Gammarus platycheir*, *G. pulex*) (Vusmanus *et al.*, 1987) and species of *Gammarus* occur throughout the range of acipenserids surveyed for parasites east of the Continental Divide.

Acipenserid parasites with associations that have originated and been limited to their native landmasses include the disjunct *Pseudotracheliastes* which show close relationships with widespread taxa (eg. *Tracheliastes* spp.) in Eurasian ostariophysans (Markevich, 1966; Bauer, 1987), which suggests that parasitism of acipenserids may have been a 'host extension' with subsequent coevolution. These and other alternatives (e.g., 'host extension' from sturgeons into ostariophysans) are only testable through a phylogenetic analysis of the group. The disjunct distribution of the two species of *Pseudotracheliastes* in sturgeons may be related to the same vicariant event that produced the present day disjunct distribution of *Huso*. Endemism related to independent acquisition on discrete landmasses is also seen in North America. In this case, the acquisition of *Spinitectus* by freshwater acipenserids has resulted in an intracontinental host specific association (Chapter 2-3) but the 'donor' host group is not readily identifiable. *Spinitectus acipenseri* is closely related to *S. gracilis*, a nematode with a long host list although it is a common parasite of centrarchids. *S. acipenseri* is relatively plesiomorphic (arrangement of spines) and it is possible that the ancestral association originated with sturgeon by 'host extension' of the parasite from an unknown (or extinct) host group. Preliminary phylogenetic analysis of the North American *Spinitectus* suggest that although the *S. acipenseri* / *S. gracilis* clade

is endemic to North America, it is more closely related to the Eurasian/African group than to the '*S. carolini*' clade which is also endemic to North America. The plesiomorphic nature of the Central and South American species indicates that South America may be the place of origin of *Spinitectus* and that differentiation of the major groups of *Spinitectus* occurred before the final dissociation of the Pangean supercontinent.

The parasite fauna of sturgeons in the Ponto-Caspian basins and drainages is characterized by a high degree of endemism (Figs. 108 a, b). Seven species, belonging to disparate genera are found in this region; *Cyclozone acipenserina*, *Dogielina inexpectata* (considered a *species inquirenda* by Moravec, 1994), *Hysterothylacium bidentatum*, *Piscicapillaria tuberculata*, *Rhipidocotyle kovalae*, *Eubothrium acipenserinum* and *Proteocephalus skorikowi*. This pattern of endemism is in keeping with the general endemic nature of the Ponto-Caspian fauna (see also Zhadin, 1952) and also characterizes the acipenserid fauna inhabiting this area (see discussion on biogeography of acipenserids).

In summary, a number of generalizations may be made about evolutionary patterns of the various parasite groups in sturgeons, particularly those with wide distributions and consequently of interest in analyzing area relationships. The parasite fauna is characterized by a low level of speciation and species are generally widely distributed. Furthermore, parasite species within a clade specific for sturgeons tend to replace each other, in space, and this process is often associated with identifiable discrete geographical areas. This provides strong evidence for 'allopatric' speciation as

the dominant process of diversification. Co-speciation is not indicated but the 'sister taxon' relationships (Table 21) suggest that 'host capture' (i.e., 'host extension', 'host switch' etc.) from a variety of unrelated host taxa and a subsequent, arguably long period of association and speciation resulted in the formation of a number of markedly monophyletic but species-poor groups of parasites. In contrast to these widely distributed monophyletic groups are numerous unrelated species characteristic of isolated drainage systems (specific parasites in the Ponto-Caspian) or landmasses (*S. acipenseri* in North America). These are colonizers from other hosts, arguably acquired more recently.

Three main distributional patterns of sturgeons and their parasites emerge from the foregoing discussion. First, there exists a holarctic-circumboreal fauna which may include some of the earliest host-parasite associations. This pattern shows modifications as taxa 'spill over' into the north Pacific and Atlantic regions. Second, there exists a strong trans-Atlantic 'track' (sensu Croizat, 1964) for a number of euryhaline and marine parasite taxa. Finally, there appears to be a strong trans-Pacific 'track'. In addition, there is the pattern of endemism associated with the Ponto-Caspian basin which is not useful in resolving issues of area relationships and historical biogeography.

The above discussion allows us to assess host-parasite relationships in the centrally located freshwater lake sturgeon. It appears from this study that the lake sturgeon of the Hudson Bay drainage is not part of any trans-Atlantic connection and only shows Atlantic associations through the freshwater deropristiid *S. s. manteri* and

possibly *C. pseudoargumentosa* outside the Hudson Bay drainage area (Laurentian Great Lakes drainage). The lake sturgeon shows connections with the Pacific drainage only through *C. auriculatum* which parasitizes the related *A. transmontanus* in freshwater coastal systems although the wide distribution of *C. auriculatum* in the Northern Asian drainages suggests the primary connection may have been with Northeastern Asia and Siberia. The strongest evidence for a past Arctic continuity of *A. baeri* and *A. fulvescens* (or their ancestors), probably across the northern margins of the Tertiary Bering land bridge (North American - Asian peninsula), is the disjunct distribution of *T. clitellarius* (Chapter 2-4) in these and other Northeast Asian Pacific drainage freshwater acipenserids. Pleistocene glaciations, which were more severe over North America than over Siberia may have limited the northern distribution of the lake sturgeon while allowing *A. baeri* to retain much of its former distribution. However, holarctic Pleistocene glaciations must have affected North American and Siberian sturgeons with differences only in the degree of the effect. Glaciation would have been effective in eliminating any obligatory anadromous populations of Arctic sturgeons and severely curbing a basal tendency towards diadromy. This may be the reason why the species of *Acipenser* now present in Arctic drainages are predominantly freshwater. The presence of *Diclybothrium atriatum* in *A. fulvescens* and *A. brevirostrum* also indicates a former confluence of their ranges which is probable since they are demonstrably sister taxa and *A. brevirostrum* may be viewed as having been the coastal drainage population of the ancestral species. A number of marine/estuarine species such as *Nitzschia* and *Bothrimonus* may have been more widely distributed in

sturgeons in the past and their ranges may have included the Arctic (particularly since other closely related cyathocephalids are holarctic in distribution) but climatic deterioration in the late Tertiary and subsequent modification of the life histories of the Arctic sturgeons from a diadromous to predominantly freshwater one resulted in an elimination of such euryhaline parasites and the retention of freshwater taxa. Strong supporting evidence for a basic estuarine diadromous habit comes from experimental studies on juvenile lake sturgeon showing survival in brackish water for extended periods of time (T.A. Dick, unpublished data, pers. comm.). This evidence from what has been considered an exclusively freshwater species demonstrates that a diadromous life history is probably basal to the acipenserids. The ancestral life history strategy of anadromous fishes (e.g., Salmonidae) has traditionally been viewed as being either freshwater or marine. The importance of large bodies of brackish water and widespread estuarine conditions that have been a constant feature during repeated cycles of marine transgression and regression during much of the Mesozoic and early Cenozoic is generally underestimated. There is no reason why, as McDowall (1993) points out, the ancestor to the present day diadromous families could not have been estuarine or diadromous. This applies equally to the Acipenseridae. Such a hypothesis is also supported by the fossil record of sturgeons and is reflected in the high proportion of the host specific parasites showing recurring marine connections (Table 22). The lake sturgeon thus represents a stable lineage that has existed in North America at least since the late Cretaceous or early Tertiary whose ancestral range has been fragmented by Cordilleran orogeny and whose life history has been modified by

Tertiary climatic change and eventually Pleistocene glaciations. These palaeoclimatological and palaeogeographical effects are reflected in its present day host-parasite associations.

Comparisons of this study with similar studies on other archaic and potentially coevolved systems is limited by the paucity of such studies on monophyletic groups of freshwater fishes. Only one other study, on the freshwater stingrays (Potamotrygonidae), addresses the historical biogeography of host-parasite relationships in a freshwater fish family (Brooks, 1992; Brooks *et al.*, 1981; see also Brooks and McLennan, 1993). However, potamotrygonids are endemic to South America and its parasite fauna diversified through dispersal of hosts by "stream capture" (Brooks, 1992). This makes it difficult to compare with the results obtained in this study. Consequently, only a few studies on other vertebrate hosts can be used for a general discussion. These include the anurans and their plagiorchidiids (Brooks, 1977), crocodylians and their digeneans and ascaridoids (Brooks, 1979; Brooks and O'Grady, 1989), and turtles and their spirorchiids Platt (1992) and salamanders and their nematodes (Adamson and Richardson, 1989). These studies have demonstrated that the phylogenetic relationships of the various parasite taxa and their host-associations have resulted from pre- (and occasionally post-) drift dispersal or by vicariance due to the fragmentation of the ancestral Laurasian landmass. Although not apparent in the area cladograms provided in the original studies Brooks (1977, 1979; Brooks and O'Grady, 1989), the results of the cladistic analyses suggest a complex pattern of continental associations involving pre- and post- drift dispersal. This is clear when those

cladograms are superimposed in their original forms upon the present day distributions (Figs. 109, 110) of the parasites [from the data provided in Brooks (1977, 1979; Brooks and O'Grady, 1989)]. It is apparent that either there has been a considerable amount of pre-drift diversification, or extensive migrations. In the case of the crocodylians, the host-parasite associations are evidently determined to a large extent by pre-drift diversification and dispersal followed by drift-vicariance. This is in contrast to the situation in sturgeons where continental and drainage isolation of the various parasite taxa have resulted in varying degrees of morphological divergence. The relationships between the two Laurasian landmasses of Eurasia and North America are complex and fundamentally different from the fragmentation of Gondwana. The fission of the Laurasian landmass on one side (Atlantic) has been accompanied by fusion on the other (North Pacific) which has resulted in avenues for dispersal and a composite biota. In contrast, different fragments of Gondwana (South America, Africa, India, Australia etc.) were clearly separated from each other and some of the larger fragments (e.g., South America and Africa) have remained so. Consequently, the Laurasian fauna represents a more difficult challenge for biogeography and patterns of host-parasite associations of circumboreal or holarctic biota can be expected to be complex, involving both vicariant and dispersal elements. This mixed mechanism (dispersal and vicariance) is apparent in the association of a North-temperate group of nematodes (*Chabaudgolvania* spp.) and their salamander hosts (Adamson and Richardson, 1989) and also clearly reflected in the host-parasite associations of the sturgeons.

The use of parasites to provide clues about the historical biogeography of the host is a well established area of study (Klassen, 1992). Although there are numerous examples of such studies (reviewed by Brooks and McLennan, 1993; Esch and Fernandez, 1993; Williams *et al.*, 1991), none has dealt with a freshwater and diadromous group of Laurasian fishes. In the case of acipenserids, the recurring connection and relationship seems to be to a marine environment (Table 22). Of the parasites showing such connections, the Dicybothriidae are intriguing because of the hypothesized relationships with the Hexabothriidae, parasites of chondrichthyans (Boeger and Kritsky, 1993; Bykhovskii, 1957). However, the evolutionary history of the sturgeons and the concept of 'numerical relict' (see p. 70 of Brooks and McLennan, 1993), when applied to the Dicybothriidae, provide a plausible explanation for this relationship and present distributions. The chondrosteans are considered to have been derived from palaeonisciform ancestors, which were the dominant marine fish fauna along with the chondrichthyans in the Palaeozoic and Mesozoic, before the radiation of the teleosts. This ecological association may have allowed an ancestral monophyletic group of polyopisthocotyleans to diversify on the palaeonisciforms and chondrichthyans. With the widespread extinction of the palaeonisciforms in the Mesozoic, this once widespread and possibly speciose group of monogeneans (ancestral to the Dicybothriidae) was progressively reduced to a few parasites in a descendant relictual host group of chondrosteans that survived to the present time, the Acipenseriformes. In contrast, the diversity of the hexabothriids may have been maintained by the radiation of modern sharks and rays. Consequently, the

Diclybothriidae may represent an 'ancient' parasite inherited from its chondrosteian ancestors. The other potentially 'ancient' connection to the marine environment is the cnidarian *Polypodium* (see Discussion on *Polypodium*). The relationships of the *Truttaedacnitis* clade with diadromous families of the holarctic (Chapter 2-5) and the relationships of this nematode genus with the primarily marine genus *Cucullanus* also indicates a marine connection. However, in the case of *Truttaedacnitis*, the association is evidently related to the basic life history (diadromy) common to most of its holarctic host families and may represent an acquisition by estuarine interactions with ancestral host groups. Numerous other parasites indicate marine connections (*Leptorhynchoides*, *Nitzschia*, *Dichelesthium* etc., see Table 22) but are of a restricted and endemic nature. In contrast, purely freshwater connections are strongly represented only by *Crepidostomum* and some endemic forms in North America and Eurasia (*Pseudotracheliastes* ?, *Spinitectus acipenseri*, etc.), suggesting that an original diadromous (or estuarine) habit is probably a basal trait in this group of fishes.

The foregoing discussion on the biogeography of parasites of sturgeons as a whole, as well as the analysis of parasites in the exclusively freshwater lake sturgeon provide complementary and compelling evidence of the processes in which host-parasite associations, having their origins in various geological eras, have been structured and modified with changes in Earth history and with concomitant changes in the biology and life history patterns in this ancient and relictual group of hosts.

Table 21. Host-specific metazoan parasites of Acipenseriformes. Cnidaria and Digenea.

Parasite taxon	Hosts	Distribution	Habit
CNIDARIA <i>Polypodium hydriforme</i>	<i>Acipenser</i> spp., <i>Huso</i> spp., <i>P. spathula</i>	Eurasia (Ponto-Caspian-Aral drainages, Amur R.) North America (Mississippi-Missouri, Hudson Bay drainages)	FW
DIGENEA			
Bucephalidae <i>Rhipidocotyle kovalae</i>	<i>H. huso</i> , <i>A. gueldenstaedti</i>	Black Sea drainage (Volga R.), Caspian Sea	B
Allocreadiidae <i>Crepidostomum auriculatum</i>	<i>A. fulvescens</i> , <i>A. ruthenus</i> , <i>A. baeri</i> , <i>A. schrencki</i> , <i>H. dauricus</i> .	Drainages of the Black and Caspian Seas, of Siberia, Amur R., the Hudson Bay, of Laurentian Great Lakes	FW
Deropristidae <i>Skrjabinopsolus semiarmatus</i>	<i>A. ruthenus</i> , <i>A. gueldenstaedti</i> , <i>A. naccari</i> , <i>A.</i> <i>nudiventris</i> , <i>A. stellatus</i> , <i>A. sturio</i> , <i>H. huso</i> .	Basins and drainages of the Atlantic (European), of the Black and Caspian Seas	B/FW?
<i>S. manteri</i>	<i>A. fulvescens</i> , <i>S. platyrhynchus</i>	Mississippi drainage, Laurentian Great Lakes drainages	FW
<i>Deropristis hispida</i>	<i>A. ruthenus</i> , <i>A. gueldenstaedti</i> , <i>A. oxyrhynchus</i> , <i>A. nudiventris</i> , <i>A. stellatus</i> , <i>A. sturio</i> , <i>H. huso</i>	North Sea, Mediterranean Sea, Black Sea (also Azov Sea), North American Atlantic coast, estuaries of drainages of above basins.	B/M
<i>Pristicola sturionis</i>	<i>A. sturio</i>	North Atlantic (Belgian and British coasts).	
Monorchiidae? <i>Cestrahelminis rivularis</i>	<i>A. transmontanus</i>	Pacific North America (Columbia R.)	B?/M?
Zoogonidae <i>Parazoogonus acipenseri</i>	<i>A. sinensis</i>	Yangtze R. (Chang Jian)	FW?

Table 21. continued. Host-specific metazoan parasites of Acipenseriformes, Monogenea

Parasite taxon	Hosts	Distribution	Habit
MONOGENEA			
Capsalidae			
<i>Nitzschia sturionis</i>	<i>A. nudiventris</i> , <i>A. ruthenus</i> , <i>A. gueldenstaedti</i> , <i>A. sturio</i> , <i>A. stellatus</i> , <i>A. oxyrhynchus</i> , <i>H. huso</i>	North Atlantic (European & North American), Baltic, Mediterranean, Black, Azov, and Caspian seas, also estuaries and brackish waters associated with above basins	B/M?
<i>N. quadritestes</i>	<i>A. transmontanus</i> , <i>A. medirostris</i>	North American Pacific drainages (California, Oregon, Washington)	B/M?
Diclybothriidae			
<i>Diclybothrium armatum</i>	<i>H. dauricus</i> , <i>H. huso</i> , <i>A. nudiventris</i> , <i>A. ruthenus</i> , <i>A. gueldenstaedti</i> , <i>A. baeri</i> , <i>A. schrencki</i> , <i>A. stellatus</i> .	Black, Azov and Caspian Seas, and associated drainages; Siberian drainages, Amur R.	B/FW
<i>D. atriatum</i>	<i>A. brevirostrum</i> , <i>A. fulvescens</i>	Drainages of Mississippi, Hudson Bay, Laurentian Great Lakes, North American Atlantic (St. John R. system, Canada)	FW
<i>D. hamulatum</i>	<i>P. spathula</i> , (<i>A. fulvescens</i> ?)	Mississippi-Missouri drainages, (Laurentian Great lakes?)	FW
<i>Paradiclybothrium pacificum</i>	<i>A. medirostris</i>	Tartar Strait, North American Pacific (California, Washington)	M/B

Table 21. continued. Host-specific metazoan parasites of Acipenseriformes. Cestoda

Parasite taxon	Hosts	Distribution	Habit
CESTODA			
Amphilinidae <i>Amphilina foliacea</i>	<i>H. huso</i> , <i>A. nudiventris</i> , <i>A. ruthenus</i> , <i>A. gueldenstaedti</i> , <i>A. baeri</i> , <i>A. sturio</i> , <i>A. stellatus</i>	Basins and drainages of the Atlantic, of the Black and Caspian seas, Siberian rivers	FW/B
<i>A. bipuncata</i>	Unspecified <i>Acipenser</i> (<i>A. transmontanus</i> ?)	North American Pacific drainage/coast, Oregon	FW/M?
<i>A. japonica</i>	<i>H. dauricus</i> , <i>A. schrencki</i> , <i>A. medirostris</i>	Amur R. system, Okhotsk Sea	FW/M
Acrobothriidae <i>Bothrimonus sturionis</i>	<i>A. oxyrhynchus</i> ?	Unspecified Atlantic coastal drainage?, Wabash R.?	FW?
<i>B. fallax</i>	<i>H. huso</i> , <i>A. nudiventris</i> , <i>A. ruthenus</i> , <i>A. gueldenstaedti</i> , <i>A. sturio</i> , <i>A. stellatus</i>	Basins and estuaries of the Black and Caspian Seas	B
Trienophoridae <i>Eubothrium acipenserinum</i>	<i>H. huso</i> , <i>A. nudiventris</i> , <i>A. gueldenstaedti</i> , <i>A. stellatus</i> , <i>A. ruthenus</i> x <i>A. gueldenstaedti</i>	Black and Caspian Seas	B
Proteocephalidae <i>Proteocephalus skorikowi</i>	<i>A. stellatus</i> , <i>A. gueldenstaedti</i>	Caspian Sea	B
Marsipometridae <i>Marsipometra hastata</i>	<i>P. spathula</i>	Mississippi-Missouri system	FW
<i>M. confusa</i>	<i>P. spathula</i>	Mississippi-Missouri system	FW
<i>M. parva</i>	<i>P. spathula</i>	Mississippi-Missouri system	FW

Table 21. continued. Host-specific metazoan parasites of Acipenseriformes. Nematoda

Parasite taxon	Hosts	Distribution	Habit
Anisakidae <i>Hysterothylacium bidentatum</i>	<i>H. huso</i> , <i>A. ruthenus</i> , <i>A. gueldenstaedti</i> , <i>A. sturio</i> , <i>A. nudiventris</i> , <i>A. stellatus</i>	Basins and drainages of Black and Caspian Seas	B
<i>H. dollfusi</i>	<i>P. spathula</i>	Mississippi-Missouri drainage	FW
Cucullanidae <i>Truttaedacnitis sphaerocephala</i>	<i>H. huso</i> , <i>A. nudiventris</i> , <i>A. ruthenus</i> , <i>A. gueldenstaedti</i> , <i>A. stellatus</i> , <i>A. sturio</i> , <i>A. oxyrhynchus</i>	North Atlantic (European, North American), North Sea, Baltic, Mediterranean, Adriatic, Black, Caspian Seas and drainages	M/FW/B
<i>T. clitellarius</i>	<i>H. dauricus</i> , <i>A. ruthenus</i> , <i>A. fulvescens</i> , <i>A. baeri</i> , <i>A. schrencki</i>	Siberian rivers, Amur R., Hudson Bay drainages, Laurentian Great Lakes drainages	FW
Cystidicolidae <i>Capillospirura ovotrichuria</i>	<i>H. huso</i> , <i>A. nudiventris</i> , <i>A. ruthenus</i> , <i>A. gueldenstaedti</i> , <i>A. stellatus</i>	Black and Caspian Sea basin and drainages	FW/B
<i>C. argumentosa</i>	<i>H. huso</i> , <i>H. dauricus</i> , <i>A. gueldenstaedti</i> , <i>A. baeri</i> , <i>A. schrencki</i> , <i>A. ruthenus</i> , <i>A. stellatus</i> , <i>A. sturio</i>	Basins and drainages of Black and Azov Seas, Siberian rivers, Amur R.	FW/B?
<i>C. pseudoargumentosa</i>	<i>A. brevirostrum</i> , <i>A. fulvescens</i> , <i>A. oxyrhynchus</i>	North American Atlantic drainages, Laurentian Great lakes drainage	FW/B?
<i>Spinitectus acipenseri</i>	<i>A. fulvescens</i> , possibly <i>S. platorynchus</i>	Hudson Bay drainages, Laurentian Great Lakes drainage, possibly Mississippi-Missouri system	FW

Table 21. continued. Host-specific metazoan parasites of Acipenseriformes. Nematoda (continued) and Acanthocephala.

Parasite taxon	Hosts	Distribution	Habit
NEMATODA			
Cystidicolidae			
<i>Cyclozone acipenserina</i>	<i>H. huso</i> , <i>A. nudiventris</i> , <i>A. sturio</i> , <i>A. stellatus</i> , <i>A. gueldenstaedti</i> , <i>A. ruthenus</i> (exceptionally).	Black and Caspian Sea basins	B
<i>Dogielina inexpectata*</i>	<i>A. gueldenstaedti</i> , <i>A. stellatus</i>	Caspian Sea and R. Ural	B
Cystoosidae			
<i>Cystoopsis acipenseris</i>	<i>H. huso</i> , <i>A. nudiventris</i> , <i>A. gueldenstaedti</i> , <i>A. ruthenus</i> , <i>A. baeri</i> , <i>A. stellatus</i> , <i>A. transmontanus</i>	Basins and drainages of Caspian, Azov Seas, Aral Sea, Amur R., North American Pacific drainage (Columbia R.)	B
Capillariidae			
<i>Piscicapillaria tuberculata</i>	<i>H. huso</i> , <i>A. nudiventris</i> , <i>A. gueldenstaedti</i> , <i>A. ruthenus</i> , <i>A. stellatus</i>	Basins and drainages of Black and Caspian Seas	FW/B
ACANTHOCEPHALA			
Rhadinorhynchidae			
<i>Leptorhynchoides plagicephalus</i>	<i>H. huso</i> , <i>A. nudiventris</i> , <i>A. ruthenus</i> , <i>A. gueldenstaedti</i> , <i>A. naccari</i> , <i>A. sturio</i> , <i>A. stellatus</i> , <i>A. ruthenus</i> x <i>A. gueldenstaedti</i> , <i>H. huso</i> x <i>A. ruthenus</i>	Basins and drainages of Baltic, Mediterranean, Adriatic, Black and Caspian Seas	B/FW

*Considered species inquirenda by Moravec (1994).

Table 21. continued. Host-specific metazoan parasites of Acipenseriformes (Crustacea).

Parasite taxon	Hosts	Distribution	Habit
CRUSTACEA			
Dichelesthidae <i>Dichelesthium oblongum</i>	<i>H. huso</i> , diadromous <i>Acipenser</i> spp., <i>A. oxyrinchus</i>	Black Sea basin, North Atlantic coastal, estuaries (North America and Europe?).	B/M
Lernaeopodidae <i>Pseudotracheliastes stellatus</i>	<i>A. sturio</i> , <i>A. gueldenstaedti</i> , <i>A. stellatus</i>	Basins of Black, Azov and Caspian Seas	B/FW?
<i>P. soldatovi</i>	<i>H. dauricus</i> , <i>A. schrencki</i> , <i>A. sinensis</i> , <i>P. gladius</i>	Amur R., Yangtze R.	FW

Table 22. Relationships and affinities of metazoan parasites specific for Acipenseriformes.

Parasite taxon	Sister taxon ¹	Host (sister taxon)	Distribution (sister taxon) (Area/drainage/basin)	Habit
CNIDARIA				
<i>Polypodium</i>	Narcomedusae	Free-living, commensal	Worldwide	M
<i>P. hydriforme</i>	?			
PLATYHELMINTHES				
Digenea				
Bucephalidae	Brachylaemidae?	Birds/mammals	Worldwide	T
<i>Rhipidocoryle</i>	? (in Bucephalidae)			
<i>R. kovalae</i>	Other Ponto-Caspian species	Teleosts	Black Sea, Aral Sea	FW/B?
Allocreadiidae	? (in Plagiorchiiformes)	Vertebrates	Worldwide	T/FW/M
<i>Crepidostomum</i>	<i>Bunodera</i>	Fishes (invertebrates)	Eurasia/North America	FW
<i>C. auriculatum</i>	<i>C. serpentinum?</i>	Water snake	North America	FW
Deropristidae	Homalometridae/Lepocreadiidae	Teleosts	Atlantic/Pacific	M(FW)
<i>Skrjabinopsolus</i>	<i>Deropristis/Pristicola</i>	Sturgeons	North Atlantic	B/M
<i>Skrjabinopsolus manteri</i>	<i>S. semiarmatus</i>	Sturgeons	Ponto-Caspian	B/FW
<i>S. semiarmatus</i>	<i>S. manteri</i>	Sturgeons	North America	FW
<i>Deropristis</i>	<i>Pristicola</i>	<i>A. oxyrhynchus</i>	European Atlantic, coastal	M/B
<i>Deropristis hispida</i>	<i>P. sturionis</i>	<i>A. oxyrhynchus</i>	European Atlantic, coastal	M/B
<i>Pristicola</i>	<i>Deropristis</i>	Sturgeons/Atlantic eels	North Atlantic	M/B
<i>Pristicola sturionis</i>	<i>D. hispida</i>	Diadromous sturgeon	North Atlantic, Ponto-Caspian	M/B
Monorchiidae?	Uncertain	Teleosts	Atlantic, Pacific, Eurasia	M/FW
<i>Cestrahelmins</i>	?			
<i>C. rivularis</i>	<i>C. laruei?</i>	Esocidae (pike)	North America	FW
Zoogonidae	Lissorchiidae?	Catostomidae	North America	FW
<i>Parazoogonus</i>				
<i>P. acipenseri</i>	?	<i>A. sinensis</i>	Yangtze (ChangJian) R.	FW

Table 22. continued. Relationships and affinities of metazoan parasites specific for Acipenseriformes.

Parasite taxon	Sister taxon ¹	Host (sister taxon)	Distribution (sister taxon) (Area/drainage/basin)	Habit
Monogenea				
Capsalidae	Dionchiidae?	Marine fish	Worldwide	M
<i>Nitzschia</i>	?			
<i>Nitzschia sturionis</i>	<i>N. quadriestres</i>	<i>A. transmontanus</i>	North America, Pacific	M/B
<i>N. quadriestres</i>	<i>N. sturionis</i>	Diadromous sturgeons	North Atlantic, Ponto-Caspian	M/B
Dicylbothriidae	Hexabothriidae	Elasmobranchs	Worldwide	M(FW)
<i>Dicylbothrium</i>	<i>Paradicylbothrium</i>	Green sturgeon	North Pacific (Asia, N. America)	M
<i>D. armatum</i>	<i>D. atriatum</i>	<i>A. brevirostrum/A. fulvescens</i>	North America	FW
<i>D. atriatum</i>	<i>D. armatum</i>	Sturgeons	Europe, Ponto-Caspian	FW/B
<i>D. hamulatum</i>	<i>D. armatum/D. atriatum</i>	Sturgeons	Eurasia/North America	FW/B
<i>Paradicylbothrium</i>	<i>Dicylbothrium</i>	Sturgeons, <i>Polyodon</i>	Eurasia, N. America	FW/B
<i>P. pacificum</i>	<i>Dicylbothrium</i> spp.	Acipenseriformes	Eurasia/North America	FW/B
Cestoda				
Amphiliiniidae	Eucestoda	Vertebrates	Worldwide	T/M/FW
<i>Amphiliina</i>	<i>Gigantolima/Schizochœrus</i>	Turtles/fishes	Eurasia/Southern hemisphere	FW/M
<i>A. foliacea</i>	<i>A. bipunctata/A. japonica</i>	Pacific sturgeons	Pacific (Asia/North America)	FW/B?
<i>A. bipunctata</i>	<i>A. japonica</i>	Pacific sturgeons	Asian North Pacific	FW/B?
<i>A. japonica</i>	<i>A. bipunctata</i>	Pacific sturgeons	North American Pacific	FW/B?
Amphicotylidae	All other Pseudophyllidea	Vertebrates	Worldwide	T/FW/M
<i>Marsipometra</i>	?			
<i>Marsipometra hastata</i>	<i>M. confusa/M. parva</i>	<i>Polyodon spathula</i>	N. America	FW
<i>M. parva</i>	<i>M. hastata/M. confusa</i>	<i>P. spathula</i>	N. America	FW
<i>M. confusa</i>	<i>M. hastata/M. parva</i>	<i>P. spathula</i>	N. America	FW
<i>Eubothrium</i>	?	Teleosts	Northern hemisphere	FW?/B?
<i>E. acipenserinum</i>	Ponto-Caspian <i>Eubothrium</i> ?	Teleosts	Ponto-Caspian?	FW?/B?

Table 22. continued. Relationships and affinities of metazoan parasites specific for Acipenseriformes.

Parasite taxon	Sister taxon ¹	Host (sister taxon)	Distribution (sister taxon) (Area/drainage/basin)	Habit
Proteocephalidae	Other Proteocephalidea	Vertebrates	Worldwide	T/FW
<i>Proteocephalus</i>	?	Fish?	Worldwide?	FW?
<i>P. skorikowi</i>	Other <i>Proteocephalus</i> spp.	Fish	Ponto-Caspian	FW
Bothrimonidae	Other Spathebothridea	Fish	Northern hemisphere	FW?/M?
<i>Bothrimonus</i>	<i>Diplocotyle?</i>	Marine, estuarine teleosts	Holarctic	M/B
<i>B. sturionis</i>	<i>B. fallax</i>	Anadromous sturgeon	Ponto-Caspian	B
<i>B. fallax</i>	<i>B. sturionis</i>	Anadromous sturgeon	North American Atlantic?	B
Nematoda				
Capillariidae				
<i>Piscicapillaria</i>	Other Capillariidae	Fishes	Northern hemisphere	M/FW/B
<i>P. tuberculata</i>	Other <i>Piscicapillaria</i>	Chondrichthyans	Northern hemisphere	M
Cystoosidae	?			
<i>Cystoopsis</i>	?			
<i>C. acipenseris</i>	?			
Anisakidae	?			
<i>Hysterothylacium</i>	Raphidacaridinae	Teleost	Northern hemisphere	M?
<i>H. bidentatum</i>	<i>Hysterothylacium</i> (Eurasian?)	Teleost	Northern hemisphere	?
<i>H. dollfusi</i>	<i>Hysterothylacium</i> (N. American)	Teleost	N. America?	?
<i>A. scaphirhynchi?</i>	?			
Cucullanidae	Other Seuratoidea	Fish?	Worldwide	?
<i>Truttaedacnitis</i>	<i>Cucullanus?</i>	Fish	Worldwide	M
<i>T. clitellarius</i>	<i>T. sphaerocephala</i>	Sturgeons	North Atlantic, Ponto-Caspian	B/M
<i>T. sphaerocephala</i>	<i>T. clitellarius</i>	Sturgeons	North America, Northern Asia	FW

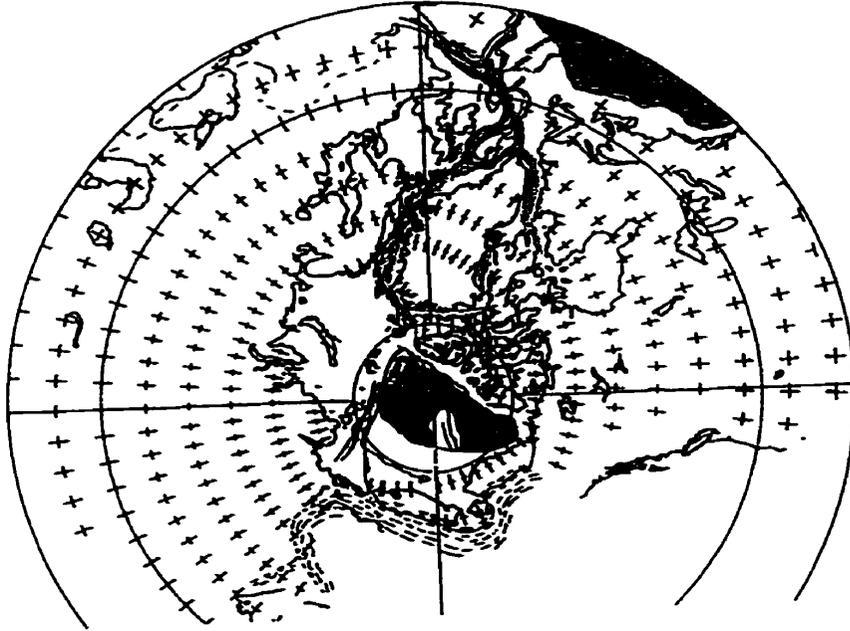
Table 22. continued. Relationships and affinities of metazoan parasites specific for Acipenseriformes.

Parasite taxon	Sister taxon ¹	Host (sister taxon)	Distribution (sister taxon) (Area/drainage/basin)	Habit
Cystidicolidae	Rhabdochonidae?	Fish	N. America, Eurasia	FW
<i>Capillospirura</i>	<i>Ascarophis</i>	Teleosts	Worldwide	M/B
<i>C. ovotrichuria</i>	Other <i>Capillospirura</i>	Sturgeons	N. America, Eurasia	FW
<i>C. argumentosa</i>	Other <i>Capillospirura</i>	Sturgeons	N. America, Europe	FW/B
<i>C. pseudoargumentosa</i>	Other <i>Capillospirura</i>	Sturgeons	Eurasia	FW/B
<i>Cyclozone</i>	Other Cystidicolidae	Fish	Eurasia?	FW?/B?
<i>C. acipenserina</i>	?			
<i>Spinitectus</i>	Other Cystidicolidae	Fish	?	FW?/M?
<i>S. acipenseri</i>	<i>S. gracilis</i>	Teleosts	N. America	FW
Acanthocephala				
Rhadinorhynchidae	?			
<i>Leptorhynchoides</i>	<i>Rhadinorhynchus?</i>	Teleost	Europe?	M
<i>L. plagicephalus</i>	<i>L. thecatus</i>	Centrarchidae	N. America	FW
Crustacea				
Dichelesthidae	Other Siphonostomatoidea	Fish	Northern hemisphere	M
<i>Dichelesthium</i>	<i>Anthosoma?</i>	Chondrichthyans	Atlantic/Pacific	M
	<i>Lamproglena?</i>	Cyprinidae	Eurasia	FW
<i>D. oblongum</i>	?			
Lernaeopodidae				
<i>Pseudotracheliastes</i>	<i>Tracheliastes?</i>	Ostariophysi	Eurasia	FW
<i>P. stellatus</i>	<i>P. soldatovi?</i>	Sturgeons	Amur R., Yangtze R.	FW
<i>P. soldatovi</i>	<i>P. stellatus</i>	Sturgeons	Europe	FW

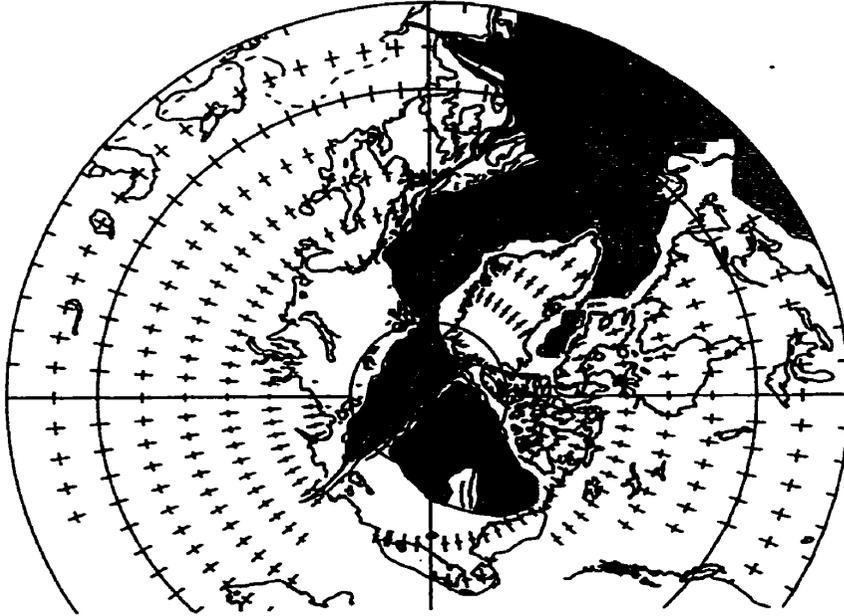
¹See Materials and Methods, Chapter 3, for sources. () (parentheses) indicate secondary condition. ? = unknown or uncertain designation, B= brackish water, FW = freshwater, M= marine.

Figure 93 a. Early Jurassic (Pliensbachian, 190 mya) palaeogeography showing the configuration of Pangea prior to dissociation. Note the central Tethys Sea, Laurasia, Gondwana, and the marine transgression across western North America. b. Late Jurassic (Callovian, 160 mya) palaeogeography showing continuous seaway between North America and Gondwanaland. Note the marine transgressions over Europe and western North America. c. Opening of the various segments of the Atlantic Ocean. Hatched lines are spreading ridges with their initial age of separation denoted in mya, bold lines are fracture zones with their names. Figs. a and b are from Smith *et al.*, 1994, c is from Rogers, 1993).

Figure 94. Sea floor spreading and Arctic Ocean basin formation. a. Reconstruction of polar region plates during Cretaceous Aptian times (approx. 118 mya) prior to sea floor spreading between North America, Greenland and Eurasia. Hatched regions within the Arctic basin denote early basin formation. b. Present day Arctic Ocean and North Atlantic basins and tectonic plates. Vertical hatching denotes Eurasian plate and horizontal hatching denotes North American plate. From Rowley and Lottes (1988).



a



b

Figure 95. Polar view of the world palaeogeography during the late Mesozoic. a. Late Jurassic, b. Early Cretaceous c. Late Cretaceous. Note the extensive marine transgressions over Europe in a, b and c. Note the formation of the Asian-western American peninsula and the western interior seaway (North American) in c. All from Howarth (1981).

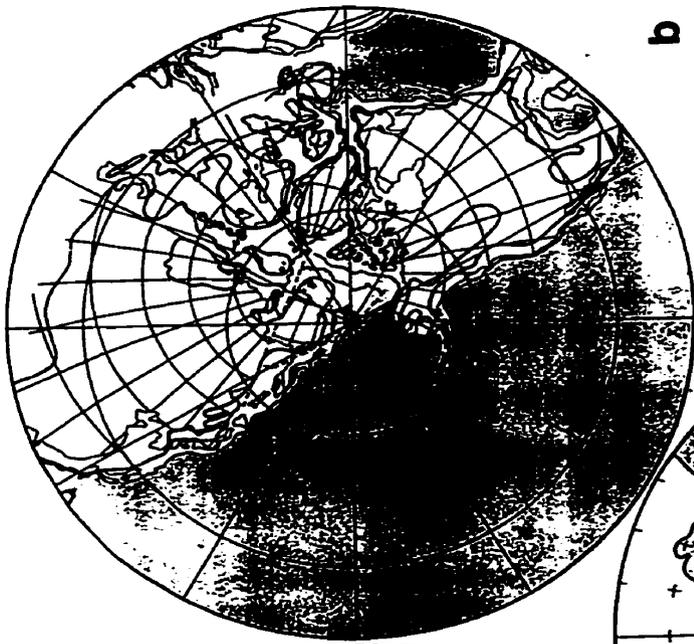
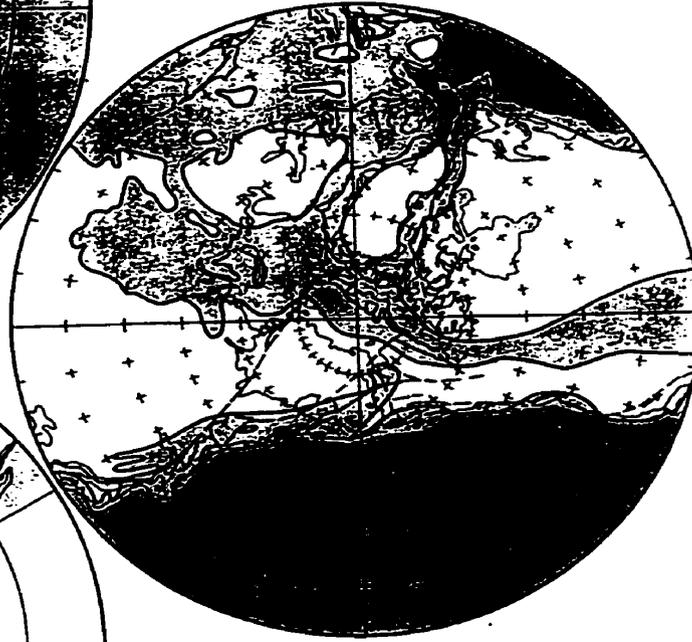
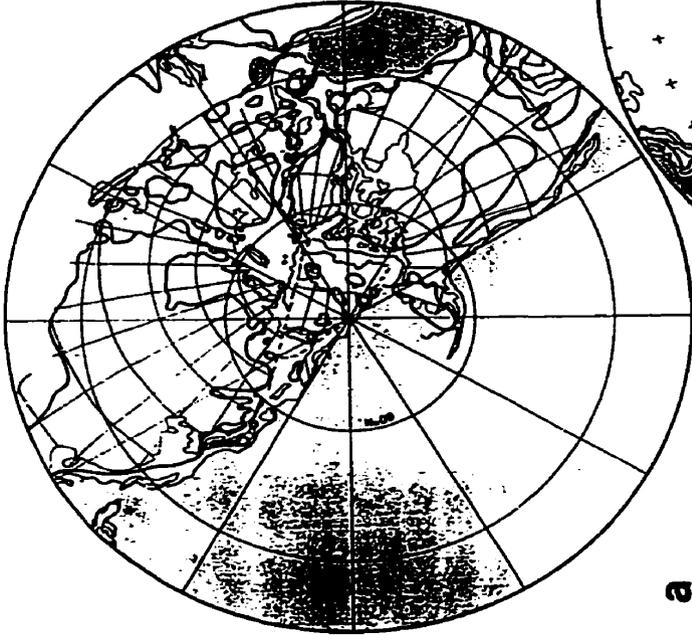
**b****c****a**

Figure 96. Sequence of palaeogeographic maps showing the formation of the Paratethys and the precursor to the Ponto-Caspian basins. a. Oligocene (approx. 30 mya) showing the reduction of the Tethys by the northward moving African-Arabian plate. b. early Miocene (20 mya) showing the formation of the Mediterranean and the Paratethys to the North. c. Pliocene (5 mya) showing the extent of the Ponto-Aralo-Caspian Sea and its greater isolation from the Mediterranean. Also, note the absence of the Panamanian isthmus until the Pliocene (c.). All from Smith *et al.*, 1994.

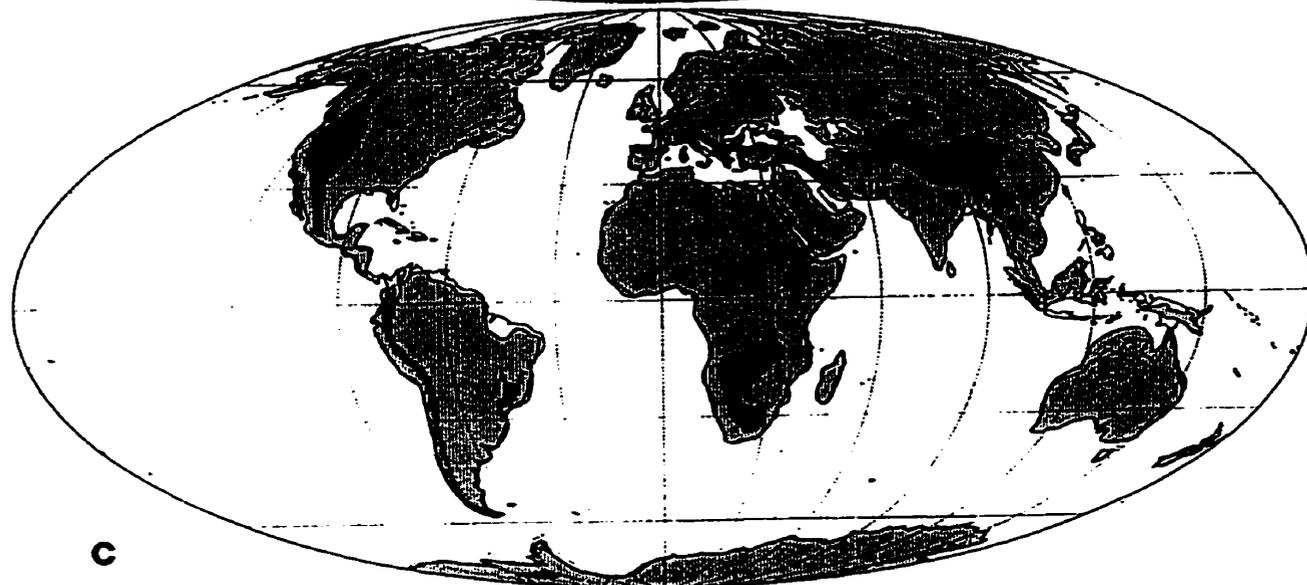
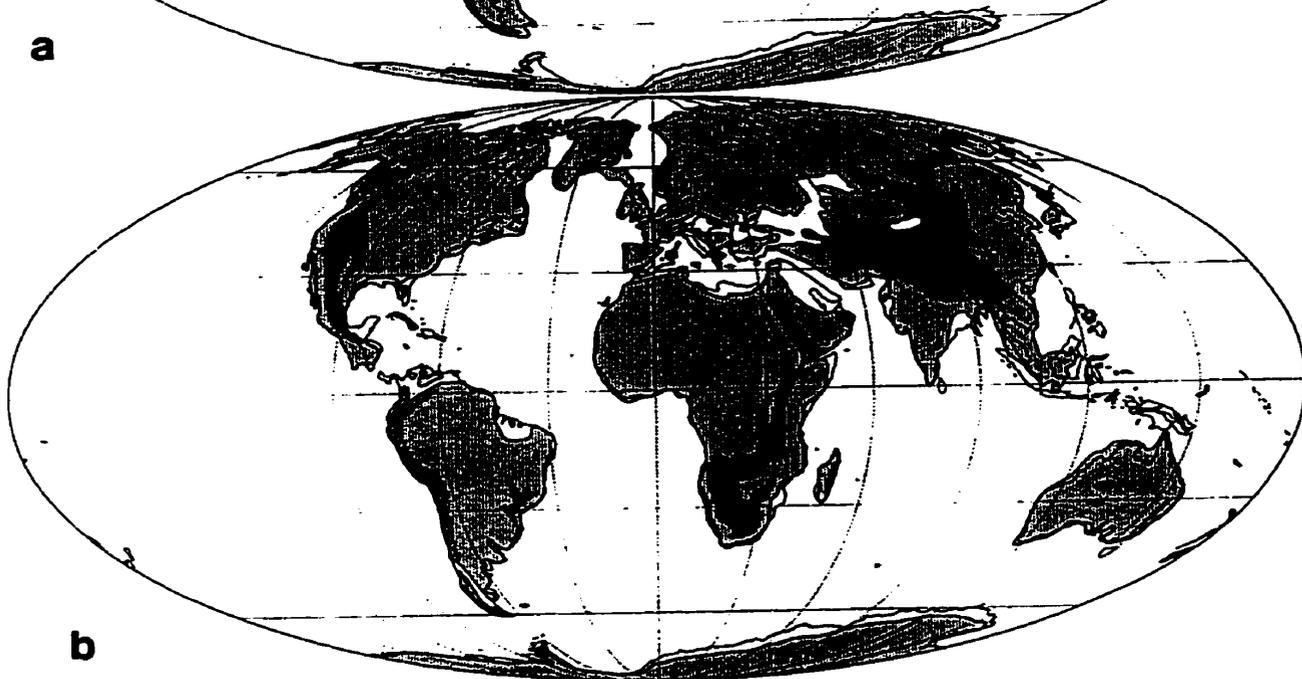
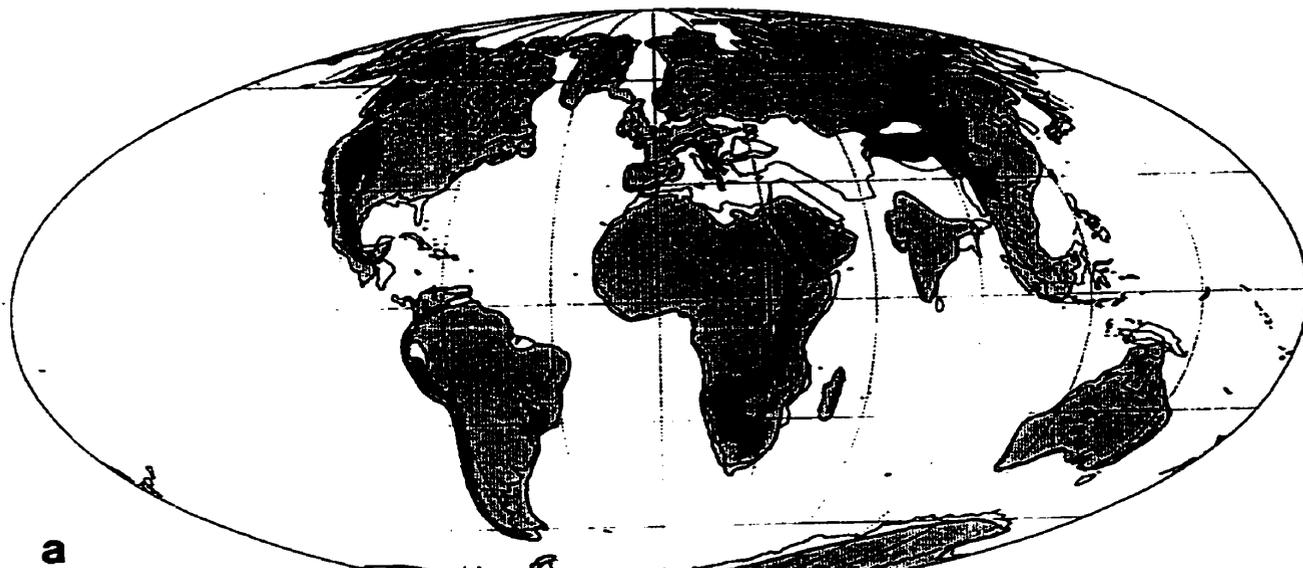
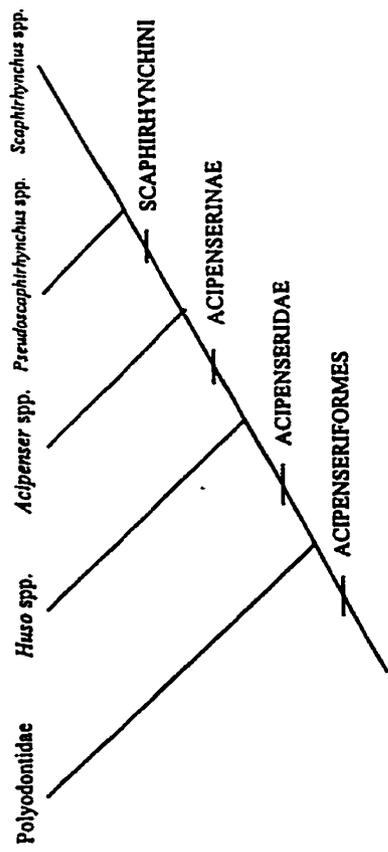


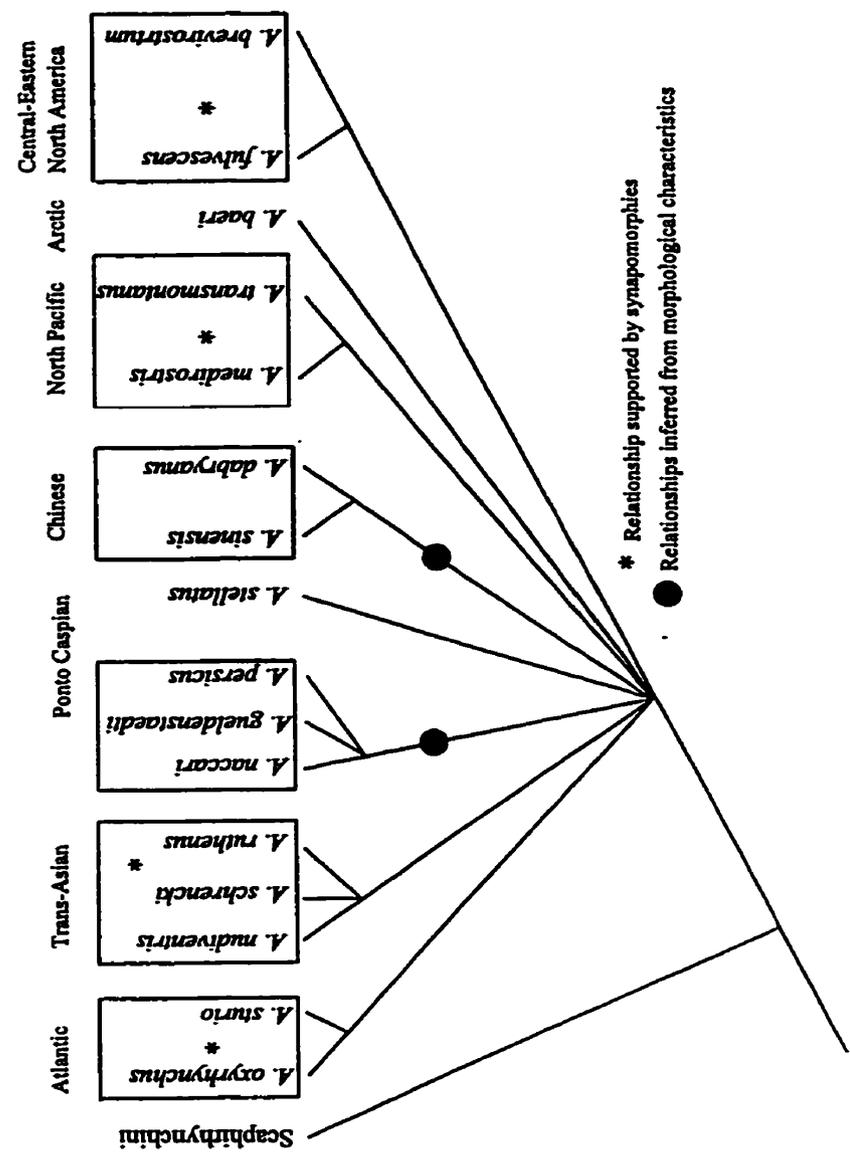
Figure 97. Cladogram showing the hypothesized relationships of the Acipenseriformes.

Figure 98. Cladogram showing the hypothesized relationships among *Acipenser* spp.



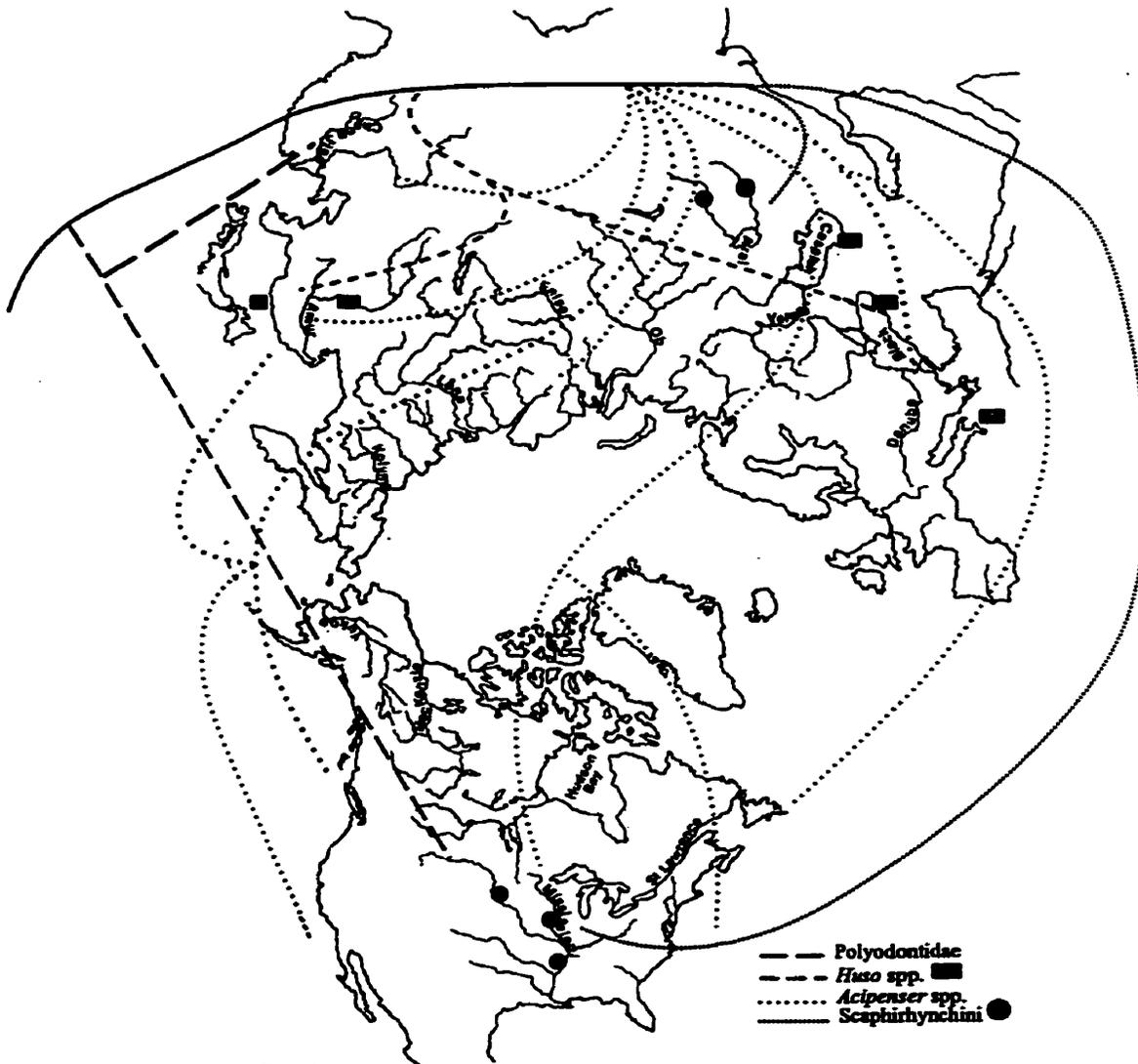
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Figure 99. Cladogram superimposed upon the present day distributions of acipenseriforms.



- Figure 100. Distribution of two of the most widely distributed freshwater host-specific parasites of acipenserids; *Polypodium hydriforme* and *Crepidostomum auriculatum*.
- Figure 101. Disjunct distribution of *Capillospirura* spp. Solid lines indicate relationships among morphologically similar species. Broken lines encompass approximate ranges of the species. the distribution of *C. argumentosa* is disjunct across Europe and Northern Asia.

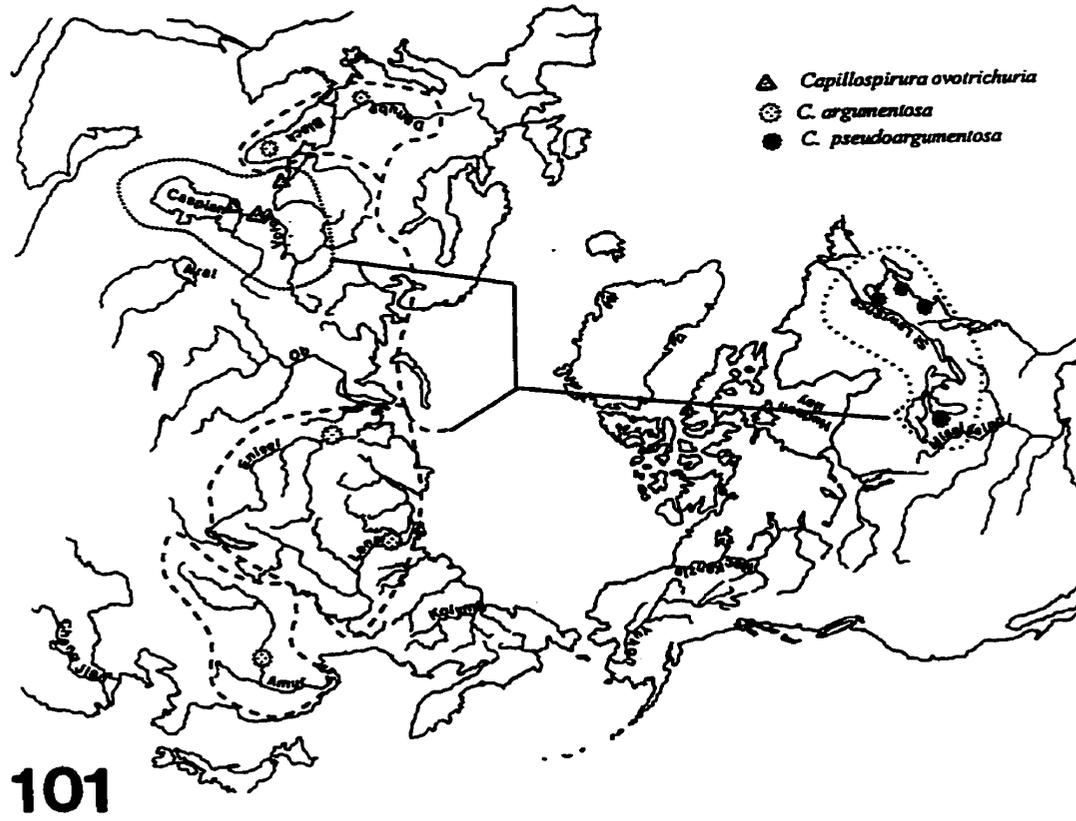
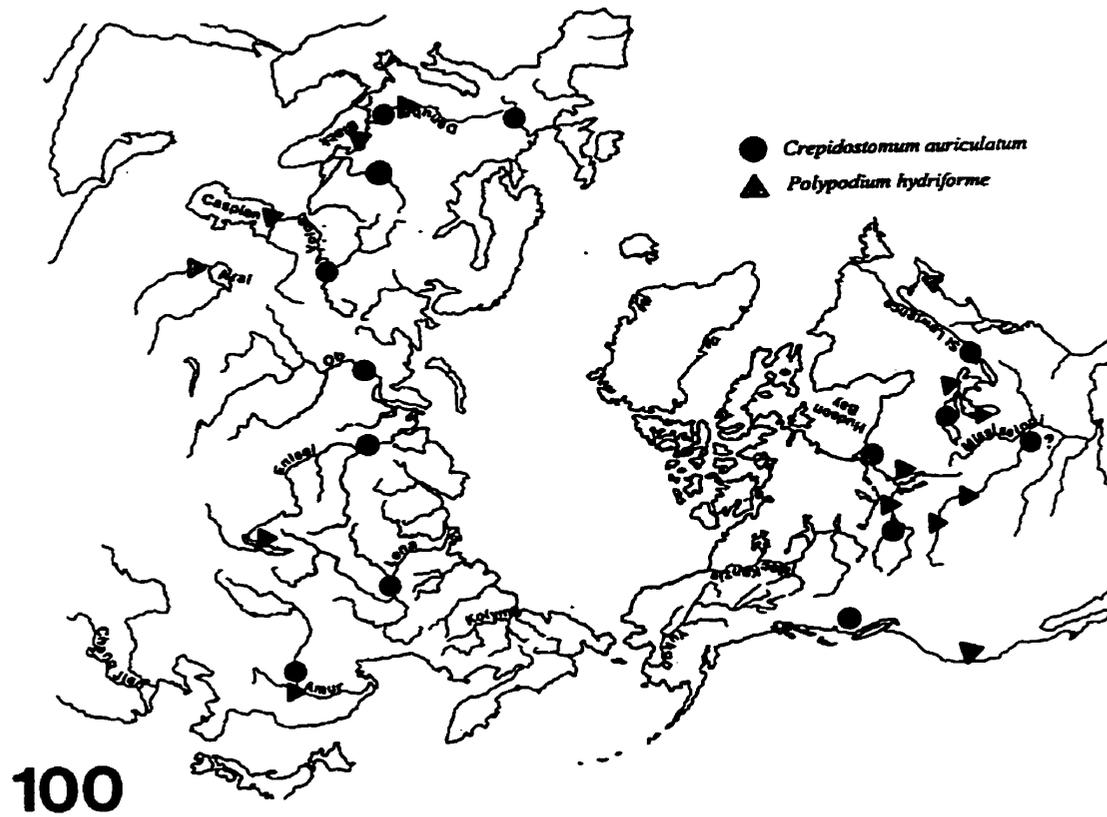


Figure 102. a. Distribution of *Truttaedacnitis* spp. specific to sturgeons. Broken lines encompass general ranges for the species. b. Cladogram with terminal taxa replaced by their areas of occurrence. Boxed species indicate the clade specific to sturgeons. Atl. = Atlantic Ocean.

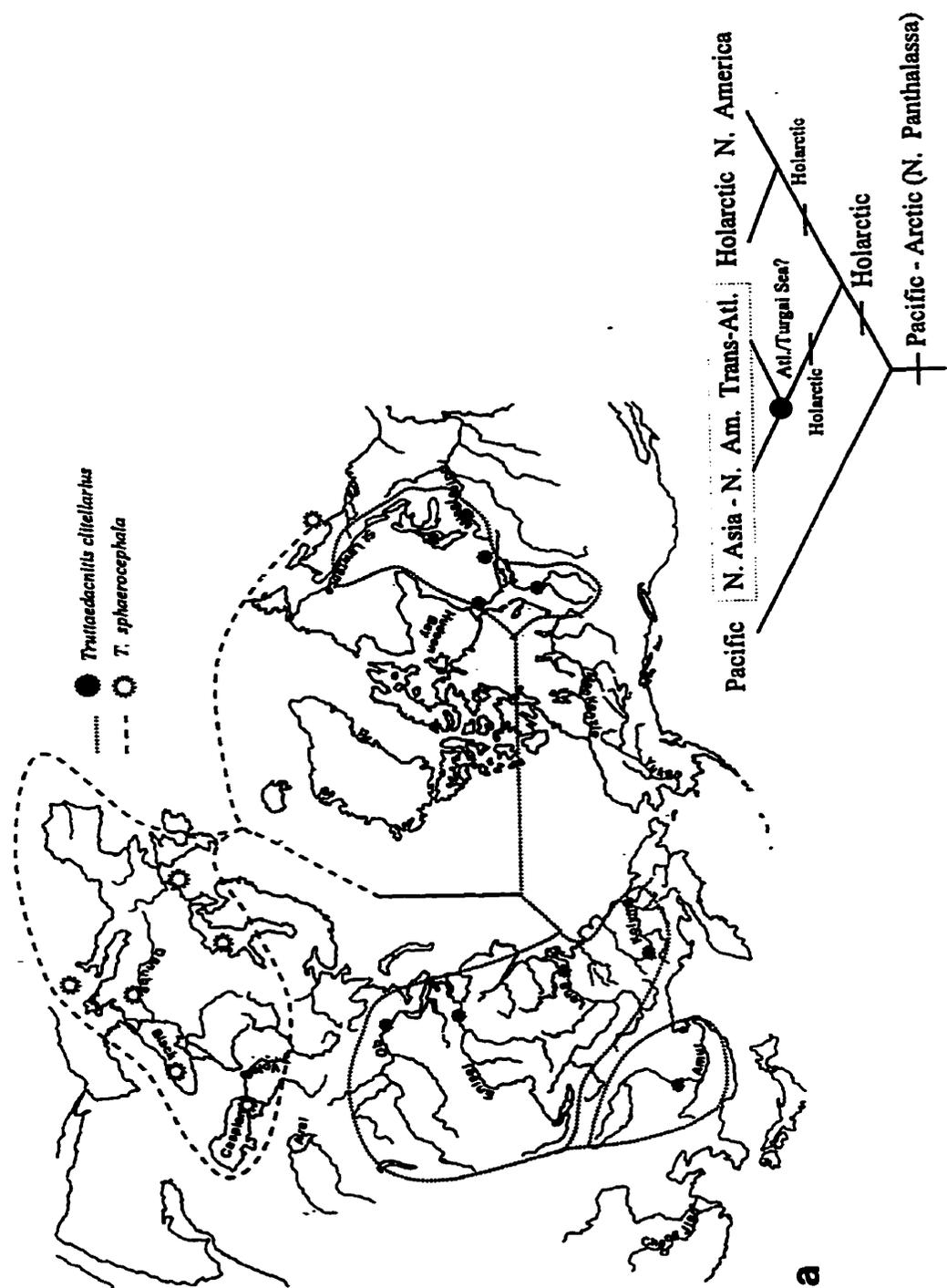
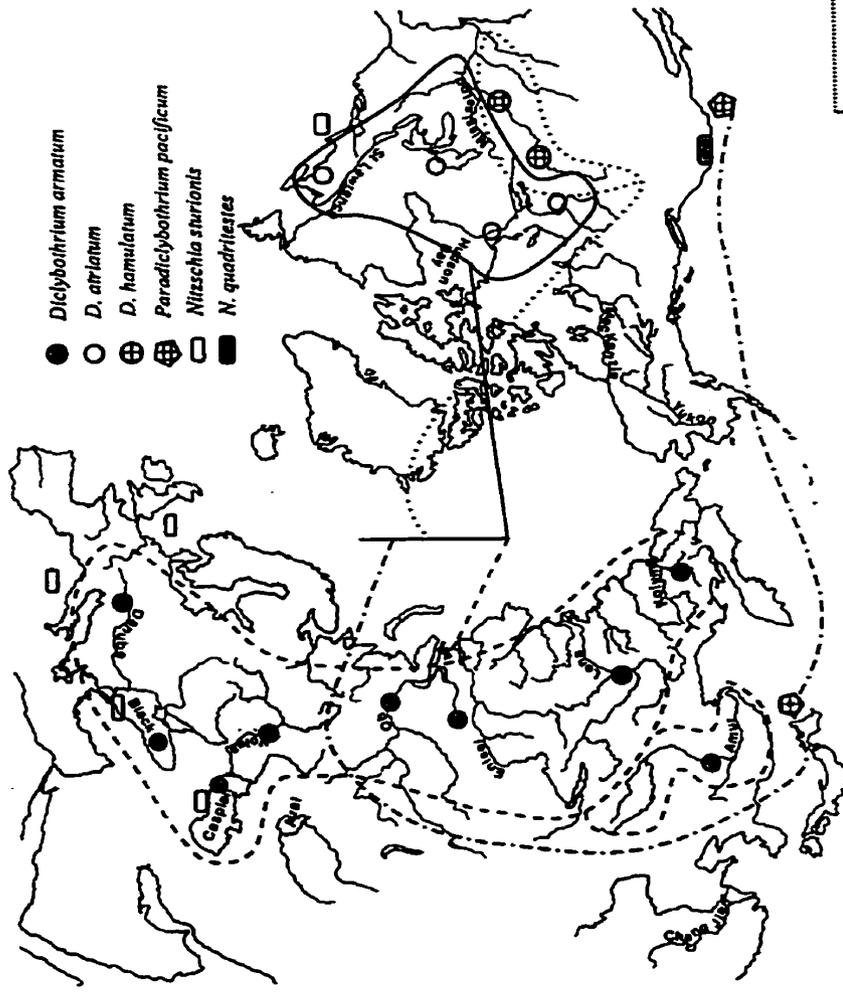
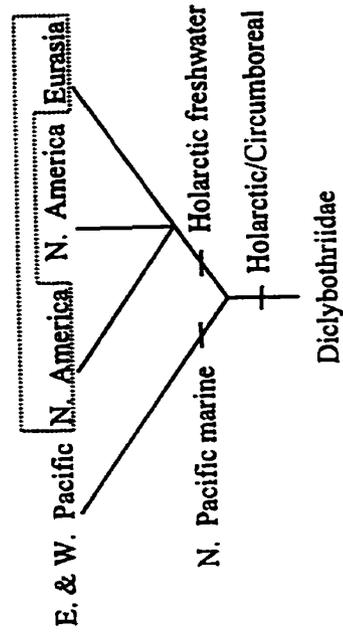


Figure 103 a. Distribution of Diclybothriidae based on their hypothesized relationships. Broken lines indicate general ranges of taxa. b. Cladogram with terminal taxa replaced by their areas of occurrence. Boxed species indicate morphological similarity. The distribution of *Nitzschia* has also been added.

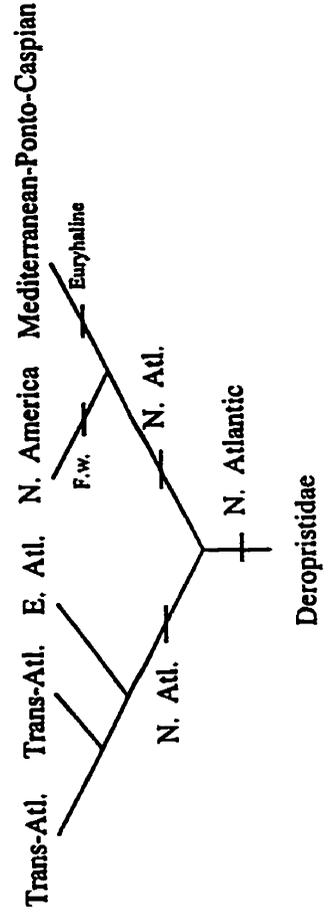
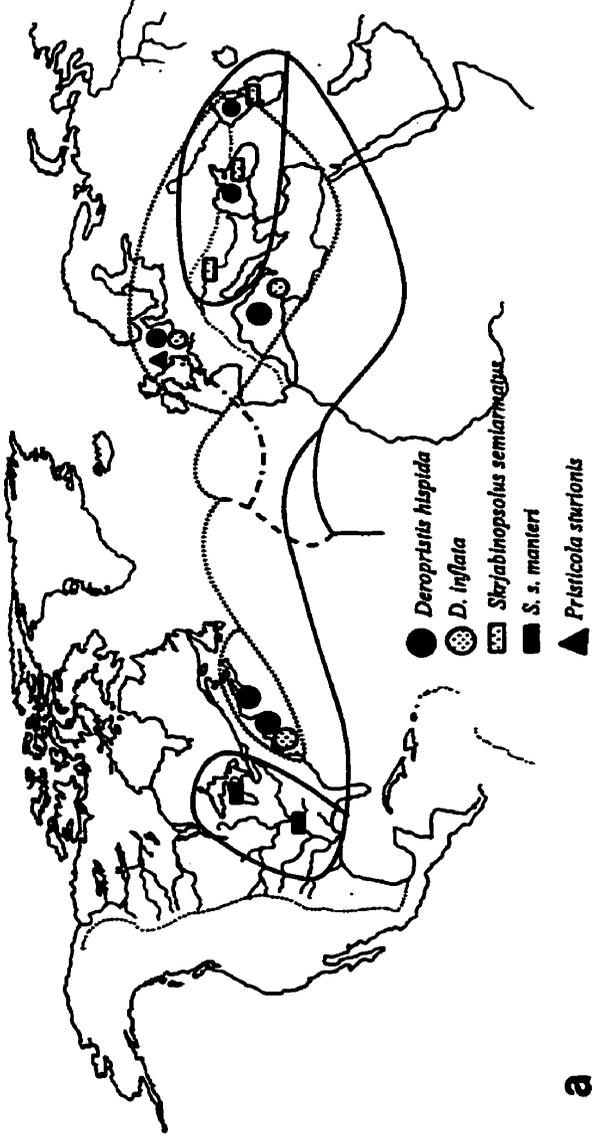


a

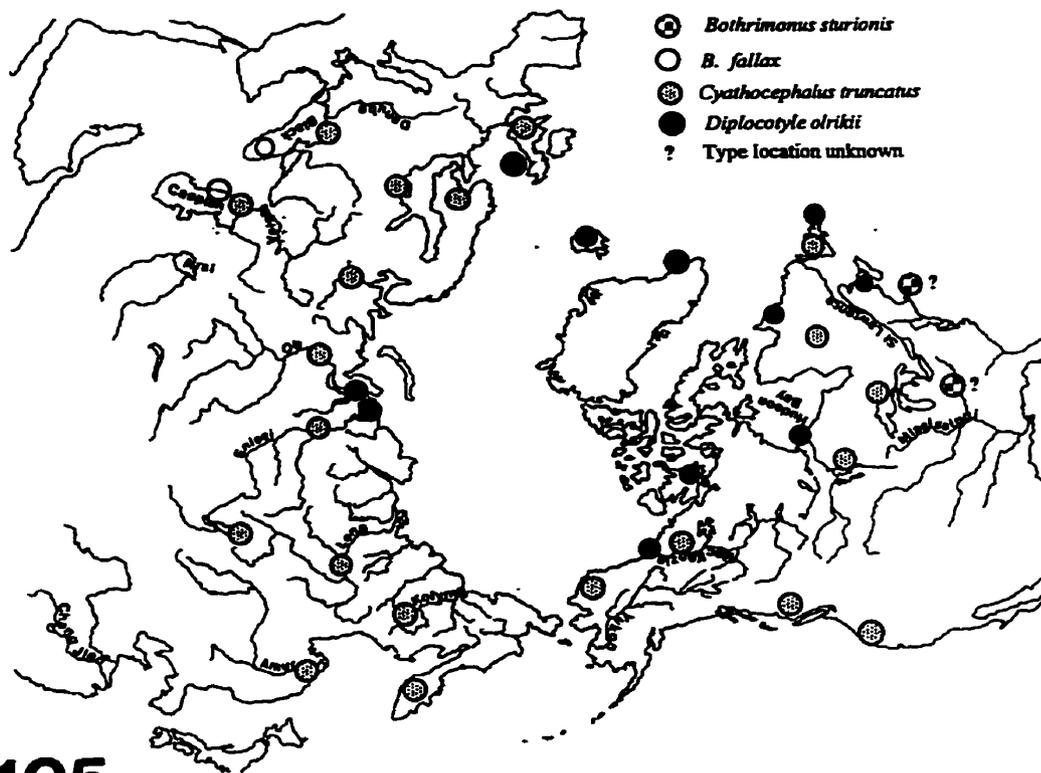


b

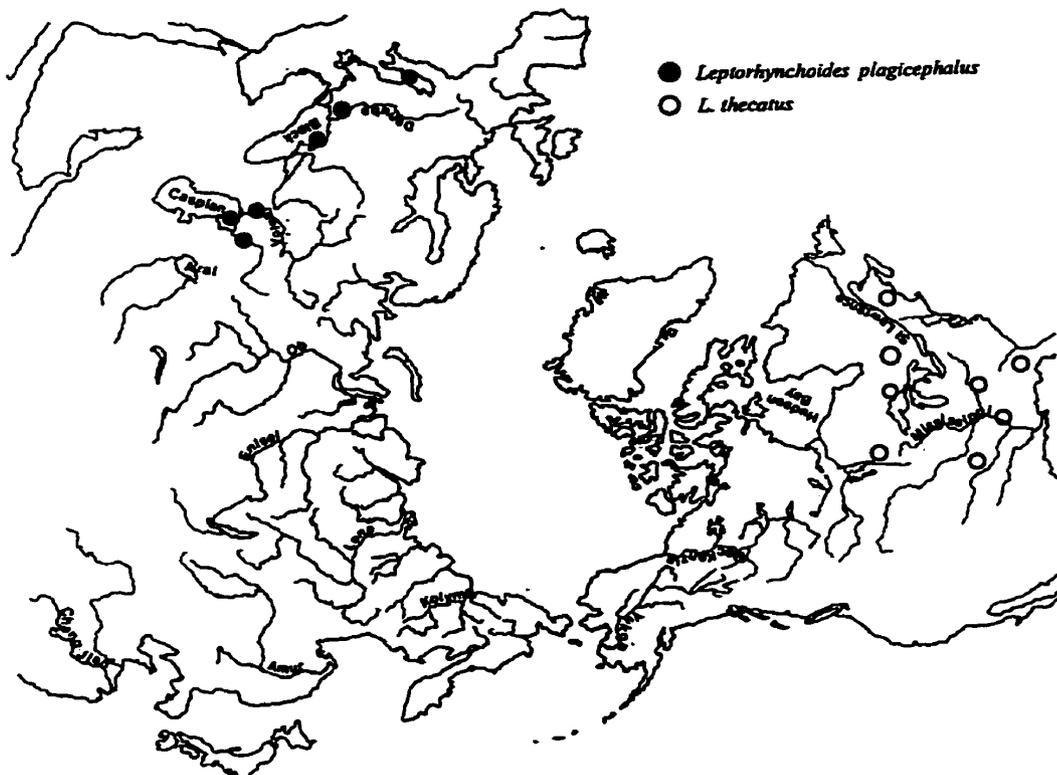
Figure 104 a. Cladogram for the Deropristiidae superimposed upon the distribution of the taxa. b. The original cladogram with terminal taxa replaced by their areas of occurrence.



- Figure 105. Disjunct distribution of *Bothrimonus* spp. in relation to the holarctic freshwater and marine/estuarine distribution of *Cyathocephalus truncatus* and *Diplocotyle olrikii* respectively.
- Figure 106. Distribution of *Leptorhynchoides* spp. (*L. aphredoderi* not shown) showing trans-Atlantic pattern of disjunction.

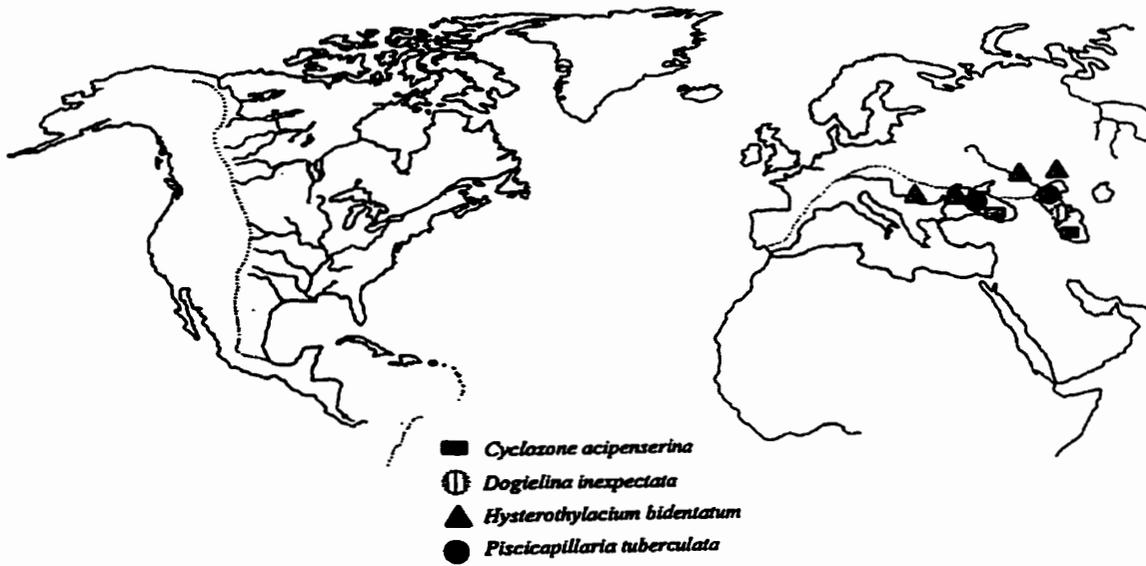


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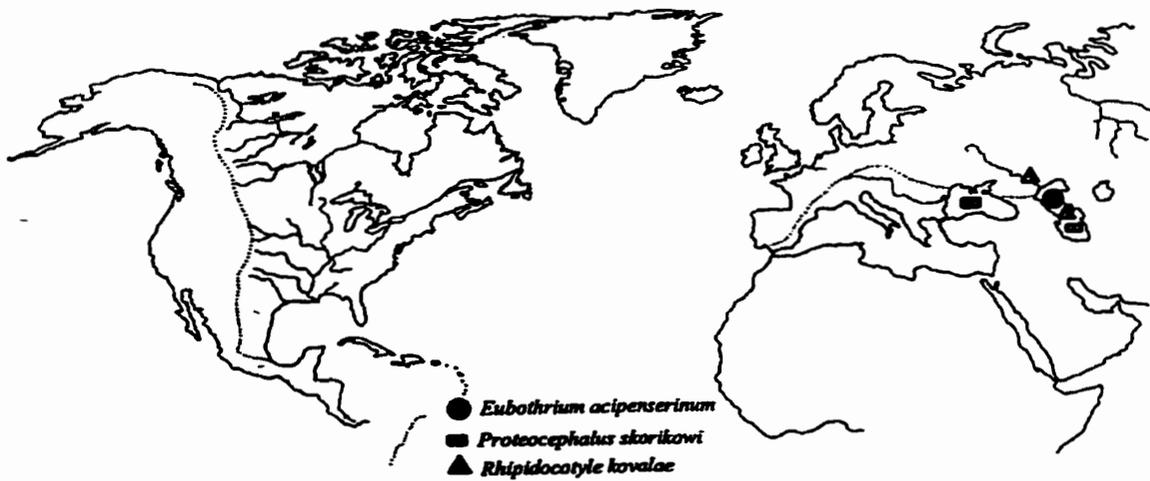


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Figure 107. a. Distribution of *Amphilina* spp. based on their hypothesized relationships. Also shows the disjunct amphi-Pacific distribution of *Cystoopsis acipenseris*. Broken lines encompass general ranges of taxa. b. Cladogram with terminal taxa replaced by the areas in which they occur.



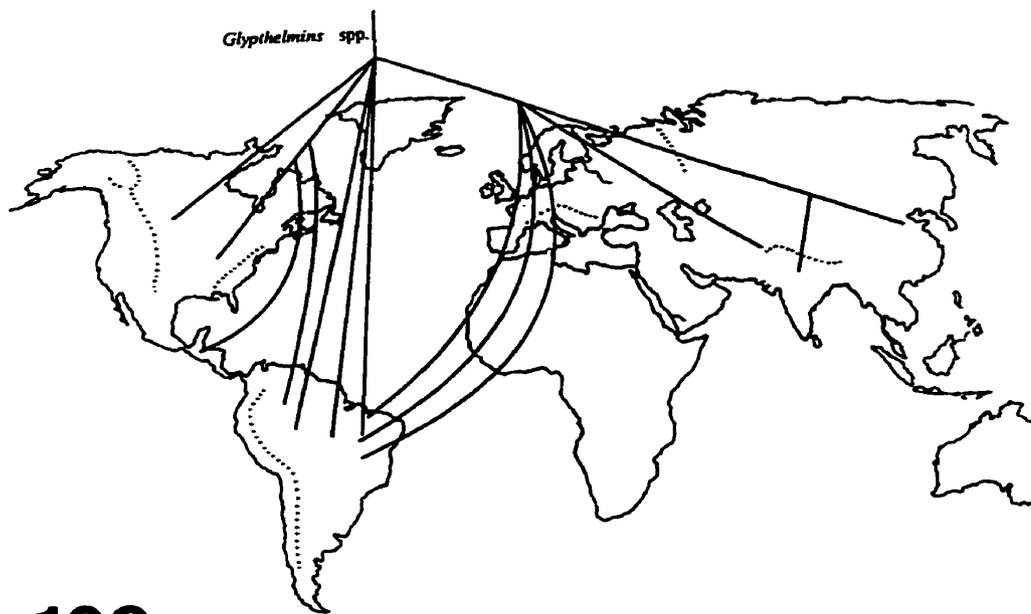
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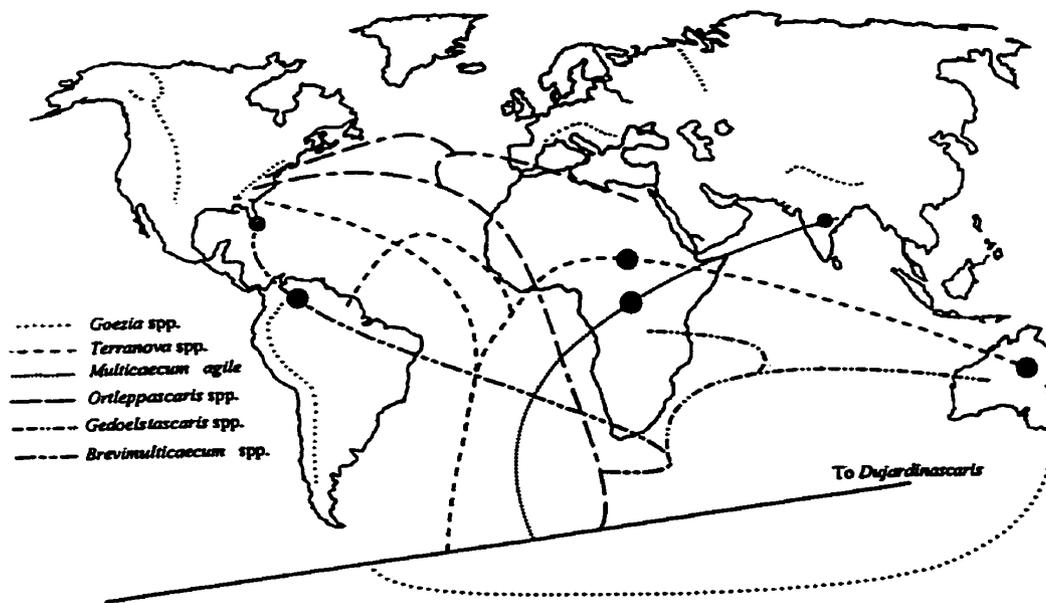
b

108 Figure 108. a &b. Endemic Ponto-Caspian species of helminths specific for sturgeons. . .

- Figure 109. Area cladogram of the species of *Glythelmins* spp. reconstructed from the cladogram of relationships among *Glythelmins* spp. in anurans presented by Brooks (1977). Note pre-drift differentiation of different lineages and the apparent absence of any congruent biogeographical patterns.
- Figure 110. Area cladogram of the ascaridoids of crocodylians, reconstructed from the cladogram of the ascaridoid genera provided by Brooks and O'Grady (1989) and the distribution of the genera from references of Sprent (1977, 1978a, 1978b, 1979a, 1979b) in Brooks and O'Grady (1989).



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SUMMARY

The main findings in this thesis are summarized as follows:

1. In total, 23 species of parasites were recovered, 17 of which are new host records.
2. Two species new to Science have been described: *Diclybothrium atriatum* (Monogenea: Diclybothriidae) and *Spinitectus acipenseri* (Nematoda: Cystidicolidae).
3. *Truttaedacnitis clitellarius* and *T. lebedevi* (Nematoda: Cucullanidae) are synonymized.
4. Morphological studies on the two *Truttaedacnitis* spp. from sturgeons, *T. clitellarius* (= *T. lebedevi*) and *T. sphaerocephala* have identified similar positions of the excretory pore and similar arrangement of cephalic plates. These serve as synapomorphies, based upon which one may hypothesize that they are monophyletic.
5. Systematic analysis of Deropristiidae (Digenea: Lepocreadiiformes) demonstrates strong trans-Atlantic (or amphi-Atlantic) patterns. Morphological variability reported for the first time from both *Skrjabinopsolus* spp. indicate that *S. manteri* should be assigned subspecific rank.
6. Biogeographical analyses of the various parasite taxa indicate three major tracks,

joining disjunct areas, viz. 1) a strong amphi-Atlantic track involving mainly the *A. oxyrhynchus* / *A. sturio* species pair, 2) an amphi-Pacific track involving *A. medirostris*, and 3) an Arctic-North Pacific track involving *A. baeri*, *A. fulvescens* and the north Pacific sturgeons.

7. This core holarctic fauna contains freshwater species of parasites and is identifiable as being Siberian-Northeast Asian and North American Arctic in character.

8. Endemism of at least 8 species of host specific sturgeon parasites in the Ponto-Caspian basin is in keeping with the general characteristics of the Mediterranean-Ponto-Caspian fauna and has little bearing upon the more widely distributed "core" parasite fauna of Acipenseridae.

9. There is no unequivocal evidence for co-speciation events except possibly the presence of *Paradiclybothrium pacificum* on *Acipenser medirostris*.

10. Based on the evidence from the systematics and biogeography of the parasites, a hypothesis was developed for the historical biogeography of host-parasite relationships in the lake sturgeon, *A. fulvescens* as follows:

(i) Ancestral *A. fulvescens* was widely distributed in the North American Arctic drainages (including the MacKenzie River system).

(ii) This ancestral Nearctic 'lake sturgeon' population was in close proximity or in contact

with (ancestral?) the Palearctic *A. baeri* populations in the Siberian Arctic during the early Tertiary.

(iii) The species became increasingly separated by intensifying orogenic activity in the MacKenzie mountains and Brooks Range, as well as in the Chukotka peninsula.

(iv) This isolation in the northern drainages allowed the development of *Diclybothrium atriatum* in ancestral lake sturgeon, separate from paddlefish populations to the southwest.

(v) Pliocene cooling and Pleistocene glaciation destroyed lake sturgeon habitat in the northern regions and unequal glaciation in the holarctic region forced the remaining populations of the lake sturgeon lineage further South than the Siberian sturgeon. Lake sturgeon did not survive glaciation in the Beringian refugium (fact).

(vi) Reduction of diadromy in Siberian and lake sturgeon perhaps concomitant with long periods of restriction in the freshwaters of the Arctic and boreal drainages during the Pleistocene.

(vii) Displacement south of the ice sheet caused widespread dispersal throughout the Mississippi drainage. Alternatively, southern populations could have existed prior to glaciation.

(viii) Glaciation isolated shortnose sturgeon along the Atlantic coastal refugium; this species can be seen as the original eastern arm of the ancestral 'lake sturgeon' population in North America. Relationships between the two species are supported by the parasite fauna.

(ix) The lake sturgeon has retained the freshwater Arctic component of its parasite fauna; *Truttaedacnitis clitellarius*, *Crepidostomum auriculatum*, *Diclybothrium atriatum*, and

possibly *Capillospirura pseudoargumentosa*.

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APPENDIX I

Observations on the early development of *Truttaedacnitis clitellarius* (Nematoda: Cucullanidae).

INTRODUCTION

Information on the life cycles of *Truttaedacnitis* spp. parasitizing sturgeon remains scarce. Khromova (1975) found natural infections of *Truttaedacnitis* larvae in marine polychaetes and argued that they may represent *T. sphaerocephala*. There is no information on the life cycle of *T. clitellarius*, a freshwater cucullanid of North American, Siberian and north-east Asian (Amur River) sturgeons. During work on the biology of sturgeon from the Saskatchewan River delta (Dick, unpublished), fresh sturgeon viscera were made available by commercial fishermen. Live *T. clitellarius* were collected from the spiral-valved intestines and served as a source of material for this preliminary study.

MATERIALS AND METHODS

Live female *T. clitellarius* were recovered from the spiral valved intestine of 2 lake sturgeon caught at the Saskatchewan River delta at Cumberland Lake, Saskatchewan. The viscera were transported overnight on ice to the laboratory at the University of Manitoba in Winnipeg. The nematodes were washed in 0.6% saline and put in fresh saline or well water, following which they released eggs. Few eggs were

obtained and the nematodes were not dissected for additional eggs since the adult worms were to be used for other morphological studies. The number of eggs were estimated to be less than 50. Eggs were incubated at 12-15° C and at room temperature. Given the few eggs available, they were only examined under a dissecting microscope (40X) to monitor development. Four *Helisoma trivolvis* and 2 *Physa jenessi* (both Mollusca: Gastropoda) were obtained from established (3 year) laboratory cultures of these snails and exposed to larvated eggs of *T. clittellarius* (<50) in a petri dish. Feeding of these snails was observed under a dissecting microscope. After 10 minutes of exposure, snails were transferred to clean culture dishes and maintained on algal fronds and *Artemia* nauplii at room temperature. Ten days later 1 *Physa* was dissected and the viscera squashed under a cover slip on a slide and examined under a compound microscope at 400X magnification. Eight days later, 2 lake sturgeon juveniles (1 year old, cultured by T.A. Dick) were each given 1 *Physa* and 1 *Helisoma* (viscera only, dissected out of shell) by stomach intubation. Sturgeon juveniles were maintained on a diet of frozen plankton.

RESULTS

Eggs: The eggs were ovoid and thin shelled. Released eggs were found in the following conditions; uncleaved, 2 celled stage or morula stage. No eggs were embryonated beyond the morula stage. Eggs in the 2 cell stage and the morula stage developed into transparent moving larvae. It was not determined whether uncleaved eggs developed further but all eggs that had not undergone development were of the

uncleaved type. Moving larvae were observed 5 days after incubation at room temperature and 10 days after incubation at 12-15° C. Eggs containing moving larvae were examined under a compound microscope in water. Larvae could be seen inside the egg but no moult or sheath was observed. Attempts were made to press the larvae out of the egg. This resulted in considerable flattening of the egg but no rupturing. Continued efforts resulted in rupturing of the egg with disintegration of the larvae and such attempts were abandoned. Larvae became progressively transparent and only one hatched and dead larva was found after 14 days of incubation

Infection of snails: Snails were observed to feed by scraping off the bottom and appeared to ingest the nematode eggs. A total of 9 larvae were found associated with the viscera of one squashed *Physa* 10 days after exposure. One nematode began coiling and uncoiling vigorously when freed out of surrounding visceral tissue. There appeared to be no haemocytic host response to the larvae or encapsulation. Six larvae were recovered in one dissected and squashed *Helisoma* 12 days after exposure.

Worms from *Helisoma* were found in the hepatopancreas. The two remaining *Helisoma* were also dissected and one squashed on a slide 20 days after exposure and examined under a compound microscope. Five larvae were observed moving slowly in the visceral tissue. It was noteworthy that the larvae had undergone little or no development since last examination. Some of these larvae were heat killed and examined fresh in 0.6% saline or fixed in hot 5% buffered neutral formalin and examined in water. Larvae that could be extracted from the visceral tissue were fixed with hot neutral buffered 5% formalin, washed in water, and cleared in a solution of

5% glycerine in 70% alcohol by allowing the alcohol to evaporate. Worms were mounted and examined in glycerine. Two control *Physa* and 2 *Helisoma* were dissected and found uninfected.

Infection of lake sturgeon juveniles: The 2 sturgeon juveniles were necropsied 45 and 62 days post intubation. No larvae were recovered from the gut lumen, the body cavity nor the liver, and there was no evidence for encapsulation in any of the organs (a histotrophic phase is known for some cucullanids).

Morphology of the larvae: The morphology of the larvae recovered from the snails bears close resemblance to hatched L2 larvae of *T. pybusae*. Based on this comparison, the larvae recovered from the visceral tissues of *Physa* and *Helisoma* are likely L2 larvae.

Description (measurements are based on 6 larvae cleared in glycerine and are reported in μm as mean \pm S.D., followed by range in parentheses: Body 586.6 ± 38 (520 - 620) long, anterior end blunt; tail 66.6 ± 6 (55 - 70) long and tapering with a peculiar posterior end (see Discussion); prominent alae from cervical to anal region; deirids posterior to nerve ring; ventral excretory pore well anterior to nerve ring, excretory duct long and conspicuous (particularly in freshly killed worms); nerve ring inconspicuous in fixed cleared specimens; prominent dorsal oesophageal gland nucleus at base of oesophagus, granular dorsal portion of distal oesophagus possibly duct of dorsal oesophageal gland; oesophagus 193 ± 10 (185 - 210) long without anterior buccal expansion but slightly enlarged posteriorly; cuticular valve at the oesophagus-intestine junction inconspicuous; structure resembling the hemizonid visible in two

specimens.

DISCUSSION

Morphology of the larvae: It is likely that other species of *Truttaedacnitis* also possess the features reported here for *T. clitellarius* (with the notable exception of the details of the excretory pore and duct) but only the L2 larva of *T. pybusae* has been illustrated and described in detail to permit comparisons. A granular dorsal portion of the anterior oesophagus was described by Pybus, Uhazy and Anderson (1978) from L2 larvae while a similar structure was described by Moravec (1979) from L3 larvae of *T. truttae* and by Moravec and Rahemo (1993) in unidentified *Cucullanus* larvae from the pericardium of the cyprinid, *Garra rufa*. The peculiar terminal region of the tail is similar to that shown in L2 larvae of *T. pybusae* (Pybus, Uhazy and Anderson, 1978). Several features are present in this early larval stage that persists throughout development to the adult stage. These include lateral alae, deirids and a prominent dorsal oesophageal nucleus. The anterior end of *Truttaedacnitis* spp. must undergo marked restructuring and from the position of the excretory pore in these larvae and in adult *T. clitellarius*, there is evidently a shortening of the region anterior to the excretory pore relative to the total length of the body during subsequent development, by allometric growth.

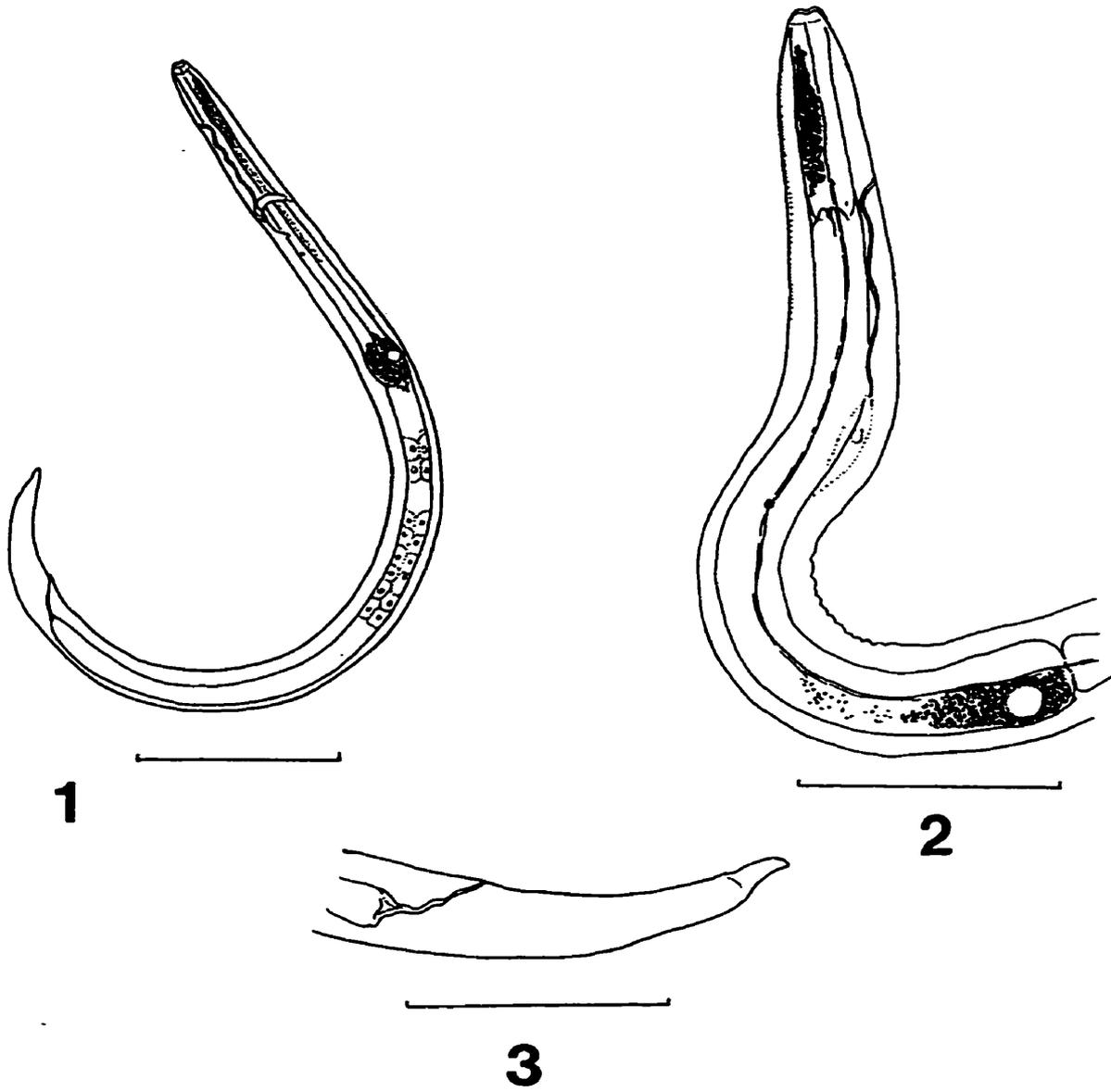
Life cycle: Little is known about the life cycle or larval development of *Truttaedacnitis* sp. parasitizing sturgeons. Khromova (1975) and Ivashkin and Khromova (1976) suggested polychaetes as intermediate hosts of *T. sphaerocephala* based on cucullanid

like larvae recovered in natural infections of *Nereis diversicolor* in the Caspian Sea and comparisons with larval worms recovered from the intestines of naturally infected sturgeons. Moravec (1994) feels that Khromova's (1975) suggestion requires confirmation through experimental infections. Gibson (1972) suggested a number of possibilities in the life cycles of cucullanids including 1) a free living phase of growth of the hatched larvae, 2) earlier site of infection in the definitive host and 3) presence of an intermediate host. Of these, a free living growth phase can be ruled out in *T. clitellarius* since hatching was rare and a hatched larva was found dead soon after hatching. An earlier site of infection of the definitive host was considered and the livers and gut of the sturgeon were examined by squashing but no larvae were observed. The sturgeon gut is thick walled and it is possible that nematodes deep within the tissue could have been overlooked, particularly if they were small. This study shows that larvae are infective to gastropods and that gastropods may act as paratenic hosts in transmitting this larvae to other intermediate hosts. It is also possible that fish act as intermediate hosts where development to the infective stage takes place since fish form an important part of the diet of some acipenserids (*Huso* spp., *A. stellatus*, *A. gueldenstaedti*, *A. transmontanus*) and a small but constant part of the diet of most acipenserids (Holcik, 1989; Scott and Crossman, 1973). Interestingly, only relatively large adult worms were ever found during surveys of lake sturgeon from the Hudson Bay drainage and the Lake Winnebago system (See Chapter 1).

Life cycle studies on two other species of *Truttaedacnitis* do not allow any generalizations since *T. truttiae* is transmitted to salmonids in Eurasia by lampreys

harbouring L3 larvae (Moravec, 1979; Buttorina, 1988) while *T. pybusae* has a monoxenous life cycle in N. American lampreys with a histotropic phase of development. However, Pybus, Uhazy and Anderson (1978) suggested that the life cycle of *T. pybusae* was essentially heteroxenous because the definitive host (brook lamprey) acts as an intermediate host. Studies on other species of cucullanids indicate that the life cycle may involve intermediate hosts (*Dichelyne cotylophora*, *Cucullanus* sp.) (Baker, 1984b; Moravec and Rahemo, 1993) or may be direct with a histotropic phase (*Cucullanus chabaudi*, *C. cirratus*) (Gibson, 1972; Le-Van-Hoa and Pham-Ngoc-Khue, 1967; Valovaya, 1979). The problems with the life cycle patterns in the cucullanids parallels the situation in the aquatic ascaridoids (see Anderson, 1992) where transmission varies within genera and among species and larval development is occasionally controversial.

- Figure 1.** Whole larva recovered from the visceral tissue of *Physa*. Scale bar = 100 μm .
- Figure 2.** Anterior end of an unfixed freshly killed (heat killed) larva mounted in saline showing the granular anterior dorsal region of the oesophagus, dorsal oesophageal nucleus, excretory pore, deirids and lateral alae. (Oil immersion). Scale bar = 50 μm .
- Figure 3.** Posterior end of the worm in Figure 2 showing peculiar terminal portion of the tail region and distinct rectum. Scale bar = 50 μm .



APPENDIX II

Geological history (palaeogeography and palaeoclimatology): a brief review.

The early Mesozoic (Triassic) was characterized by the earliest fragmentation of the Permian supercontinent Pangea (Rogers, 1993). A dominant feature of Pangea relevant to biogeography was the Ouachita-Appalachian orogen that formed during the assembly of Pangea in the late Carboniferous and Permian (300-245 mya) and remained topographically dominant throughout the late Palaeozoic and early Mesozoic (Rogers, 1993; Stanley, 1989). The other major orogenic system of the Palaeozoic was the Ural orogeny caused by the collision of the Baltica terrane with the 'Kazakhstan stable block' (Rogers, 1993) during the assembly of Eurasia. Another major feature of Pangean plate reconstructions is the placement of the broad present off-shore shelf of the northern margin of North America against the Siberian shelf (Rogers, 1993). The final configuration of Pangea during the Triassic indicates that the Tethys had spread westward driving a narrow wedge of ocean that separated North Africa from southern Europe (Stanley, 1989). The dissociation of Pangea began in the middle Jurassic (approx. 180 mya) by initial rifting between Africa and North America along the original Hercynian suture (Rogers, 1993; Stanley, 1989). By the late Jurassic, the rift had also extended westward between North and South America to produce the earliest precursor of the modern day Gulf of Mexico. Jurassic Callovian (160 mya) palaeomaps (Smith *et al.*, 1994) show a continuous oceanic passage between North

America-Eurasia (loosely termed Laurasia) and the combined southern continents (Gondwana) although spreading was slow enough that tenuous connections between southern Europe and north-west Africa may have persisted, even intermittently, until the late Jurassic (approx. 160 mya) (Morell, 1994). Furthermore, the presence of abundant evaporite depositions in these early rifts indicate cycles of relatively shallow spill-over from the Tethys and the Pacific and subsequent drying (Stanley, 1989).

The Jurassic, particularly the middle and late Jurassic (approx. 175 mya - 150 mya) was characterized by several major episodes of worldwide marine transgression (Howarth, 1981) with more rapid oscillations during the later Jurassic against a relatively high sea level (Stanley, 1989). This resulted in several important transgressive features. The early Jurassic (Pliensbachian, approx. 180 mya) saw the greater portion of central, western and southern Europe inundated by a vast marine transgression which reduced Europe to a "complicated pattern of islands and sea-shelves" (Howarth, 1981). A major north-south epicontinental seaway separated an eastern Siberian-Asian landmass from landmasses to the west of it (Europe, and North America and Greenland combined). This vast seaway, later to become the Turgai Strait, remained topographically dominant and a biogeographically critical vicarious feature until the Oligocene (35-23 mya) or early Miocene (approx. 20 mya), a period of at least 120 million years. Consequently, throughout the Jurassic, large portions of Europe and western Siberia were covered by epicontinental seas and there was broad mixing of Arctic and Tethyan waters. Middle Jurassic palaeogeographic reconstructions of northern Europe show rivers draining northern uplands into the

Jurassic seas and brackish waters of the Tethyan region, forming extensive deltas and sedimentary deposits (Stanley, 1989). In western North America, the continental margins were flooded by several cycles of marine transgressions, some of which (mainly between Bajocian and middle Oxfordian of the middle and late Jurassic (approx. 175 - 140 mya) extended deep into the western North American landmass (Imlay, 1984). Major marine transgressions also inundated north-east Siberia but retreated since the Kimmeridgian (approx. 150 mya) in the latest Jurassic. Thus it appears that epicontinental marine transgression affected areas independent of actual fragmentation of the crust or the formation of new oceanic crust which progressed by rifting in the middle Jurassic, a process that continued as North America began its clockwise rotation away from Africa while remaining joined via Greenland and Scandinavia to Eurasia (hence the northern landmass of Laurasia). Plate tectonic reconstructions (Scotese *et al.*, 1988) show the formation of early oceanic lithosphere as precursors of the modern day Atlantic Ocean and the Gulf of Mexico, at the close of the Jurassic and the beginning of the Cretaceous. In contrast to this process of fragmentation in central Pangea in the Jurassic, the tectonic history of eastern Asia during the Jurassic was marked by the gradual narrowing of the wide Mongol-Okhotsk Sea that separated the southeastern margins of Siberia from the northern margins of the composite "Chinese block" (Enkin *et al.*, 1992) which simultaneously underwent consolidation by fusion of various smaller blocks. The composite Chinese block had a narrow and tenuous connection with the Eurasian landmass via eastern Kazakhstan (Enkin *et al.*, 1992; Upchurch, 1995).

The Cretaceous (143/146 mya - 65 mya) was characterized by continued fragmentation of both Laurasia and Gondwana due to tectonic movements (Rogers, 1993; Scotese *et al.*, 1988) and by drastic reorganization of the interior of continental landmasses and their margins by widespread epihercynian marine transgressions and orogenesis (Rogers, 1993; Stanley, 1989). The North Atlantic rift between North America and Africa which produced the North Atlantic oceanic crust continued to widen as did the rift in central America (modern Gulf of Mexico and isthmus of Panama), and another rift was initiated at approximately 110 mya (Rogers, 1993) opening the northern portions of the North Atlantic and resulting in the movement of Iberia away from North America (Rogers, 1993; Scotese *et al.*, 1988; Sclater *et al.*, 1977). This initiated the beginning of the final break-up of Laurasia. The relationship between north-western Alaska and north-eastern Siberia, in terms of the exact location of the plate boundary and the geological time frame for their joining in the Cretaceous, is controversial (Howarth, 1981; Rogers, 1993). The continued rifting of North America from Europe and the tectonics of the Arctic basin resulted in a complex interaction of the various continental blocks and smaller mobile units (Jackson and Gunnarsson, 1990; Rogers, 1993). This ultimately resulted in the fusion of Alaska and north-east Asia sometime in the mid-late Cretaceous, a process characterized by intrusions, compression, uplift and erosion (Parrish, 1987). Consequently, an emergent Bering land-bridge joined the relatively narrow western portion of North America with Asia by the late Cretaceous (Howarth, 1981; Parrish, 1987). During the late Cretaceous but prior to the late Maastrichtian time, this

emergent part of western North America has been considered "essentially a peninsula connected to northeast Asia" (Lehman, 1987). An important and controversial feature of the Cretaceous was the development of oceanic lithosphere in the Arctic by spreading ridges, strike-slip faults and subduction zones (Rogers, 1993).

The Cretaceous was also marked by a progressive increase in sea levels which together with continued Cordilleran orogeny in western North America resulted in a foredeep (Stanley, 1989) being flooded by the gradual development of the 'western interior seaway' in at least "five major transgressive-regressive pulses" (Rogers, 1993). During the earliest Cretaceous (Neocomian epoch, 140-130 mya), the continental landmass of North America was bound on the east by the Appalachian and Acadian orogenic belts and on the west and northwest by the on-going Cordilleran orogeny (Williams and Stelck, 1975). The continental landmass was bordered in the north by the Arctic and in the south by the continuous east-west ocean passage. A small scale Pacific transgression covered the lower reaches of a Mesozoic river system that drained the late Jurassic swamps of Montana, Wyoming and the Williston basin, resulting in the formation of a marine 'Peace River embayment' in north-western North America (also shown in palaeomaps of Smith *et al.*, 1994). This flow to the Pacific lasted through a proposed canyon until the Aptian (120 mya) at which time continued orogeny cut off the Pacific from the interior continent and a continuous Cordillera was thought to have been present since the Aptian. Rivers from Arizona, north Texas and New Mexico, which initially flowed into the Peace River embayment subsequently drained north into the Arctic along a route parallel to the present MacKenzie system

(Williams and Stelck, 1975). Marine transgressions to the north were "marginal to the actual interior craton" (Williams and Stelck, 1975). Deep marine transgressions into the western interior of North America by a broad gulf of the Arctic Ocean inundated old drainage basins and progressed southward. This deep marine transgression was thought to have made contact with northward transgressions by the Gulf of Mexico at various times during the Albian resulting in early mid-continental seaways (Williams and Stelck, 1975). However, the late Albian saw the regression of this sea northward and a narrowing of the northern opening to the Arctic, giving rise to an inland sea of sorts, the Mowry Sea (Williams and Stelck, 1975). By the late Turonian (approx. 88 mya), rising sea levels once again formed a continuous north-south interior seaway, extending from the Arctic to the Gulf of Mexico (where the connection was broad) and bisecting the North American continent (Williams and Stelck, 1975). The major portion of this seaway occupied the "tectonically generated foreland basin" (Kaufmann, 1984), and at its maximum extent (approx. 90 mya), was 4800 km long, 1620 km wide, and 500 m deep. Marine fossil evidence suggests strongly that an arm of this seaway, whose exact boundary is uncertain, is thought to have extended over the transcontinental arch across the Hudson Bay area and Ungava Strait and occurred intermittently during a major portion of the late Cretaceous [early Turonian (approx. 88 mya) until the Maastrichtian (approx. 68 mya)] (Williams and Stelck, 1975; Smith *et al.*, 1994). These transgressive-regressive cycles were apparently due to repeated orogenic pulses. One such orogenic belt, the Sevier orogeny, is thought to have caused great influxes of freshwater into this interior seaway resulting in extensive areas of

brackish water (Rogers, 1993). Fossil evidence indicates a strong Arctic influence on the northern biota of the interior seaway with a tethyan fauna in the region of the Gulf of Mexico, and relatively little Pacific incursion (Williams and Stelck, 1975). This was apparently primarily due to the tectonics of northwestern North America and the exclusion of the Pacific by a continuous land connection with north-east Asia during the Cretaceous (see above). The vertebrate and invertebrate fossil evidence (Kaufmann, 1984; Nicholls and Russell, 1990) indicates the presence of northern cool temperate (17° - 27° C) and southern warm temperate (21° - 33° C) zones in this interior seaway. Throughout the Cretaceous, the Cordillera of western North America underwent intense orogeny and the period was characterized by plutonism and accretion of several allochthonous terranes along the northwestern margin (Lehman, 1987; Rogers, 1993; Stanley, 1989). Consequently, the Cretaceous topography of North America was dominated by the "great Cordilleran thrust belt" (Kaufmann, 1984) to the west of the interior seaway and "a broad planed, stable craton" (Kaufmann, 1984) to its east. The flood of detritus from the rising Cordillera produced "extensive delta complexes" in the Northwest Territories, in Alberta, Saskatchewan, Montana, Wyoming and New Mexico, along the western margin of the interior seaway (Williams and Stelck, 1975). Although the interior seaway was topographically dominant until the early Maastrichtian (approx. 68 mya), it rapidly diminished and by the late Maastrichtian (65 mya), it had completely retreated, leaving behind lacustrine and fluvial drainage systems. This rapid retreat is indicated by the absence of middle and late Maastrichtian marine sediments from the interior region of North America (Lehman, 1987). This

rapid retreat was due mainly to the sedimentary filling of the basin from the west and the rising MacKenzie mountains.

Reconstructions of European Cretaceous shorelines (Tyson and Funnell, 1987) show several episodes of marine transgression and regression during the early Cretaceous and progressive flooding by epicontinental seas in the late Cretaceous. In the early Cretaceous, following the retreat of the late Jurassic seas, a the major portion of Europe became emergent and contained "constricted hyposaline or hypersaline lagoons" (Tyson and Funnell, 1987). Throughout the early Cretaceous, regressive stages were followed by the development of extensive deltaic and fluvio-lacustrine features. During the Aptian times, a renewed phase of transgression affected Europe, progressively flooding large portions of Europe during the late Cretaceous. The Campanian-Maastrichtian boundary marked the maximum high stand of Cretaceous shelf seas in Europe leaving only a small portion of Europe emergent. As in North America, the late Maastrichtian saw a progressive retreat of the seas and a large portion of northern and western Europe became emergent by the early Cenozoic. The topography of Europe following this emergence included large deltaic and fluvio-lacustrine deposits. The Russian/Siberian platform was covered by two major marine transgressions. An extensive north-south "Russian Sea" passage (Vakhrameev, 1987, but also known later as the Turgai Sea) covered western Russia that connected the Arctic and Tethyan waters. Adjacent to it to the east lay a deep marine incursion, the West Siberian Sea, over the present day Ob' basin which extended from the Arctic south to about 53°N (Vakhrameev, 1987). The Russian Sea and west Siberian Sea

were separated by the Ural mountainous region. The Siberian landmass to the east of the West Siberian Sea remained more or less unaffected by marine transgressions throughout the Cretaceous (Vakhrameev, 1987). Numerous marginal and other islands characterized the northeastern edge of the Siberian landmass and the Anuyi Strait connected the Arctic to the Pacific. Following a slight desalinization and shrinking of the West Siberian Sea in the Albian, renewed marine transgressions in the late Cretaceous resulted in southern extensions of this West Siberian Sea and its narrow connection with the Tethys throughout the late Cretaceous (Vakhrameev, 1987) (note the parallel with the Mowry Sea and the development of the western interior seaway of North America). By the early Cretaceous, the Mongol-Okhotsk Sea had closed and the Chinese block was firmly accreted to the Siberian-Kazakhstan blocks, giving Eurasia its bulky shape throughout the later Mesozoic until deformed by the Himalayan orogeny in the mid-Tertiary. The continental interior of China during the Cretaceous contained large lake systems (particularly in the southwestern portion) and intermontane basins, in tectonic depressions, which changed in shape, size and duration in response to "regional and plate-margin tectonic episodes" (Pei-Ji, 1987). These lakes persisted for more than 100 my during the Jurassic and Cretaceous and were "continuously linked by the ancient Yangtze River, flowing east to west into the Tethys Sea" (Pei-Ji, 1987). Marine transgressions (Tethyan) were restricted to eastern and western margins and filled tectonic troughs of the Tibet plateau (Pei-Ji, 1987). The late Cretaceous (Cenomanian - Santonian) palaeogeography of China was characterized by the development of brackish or salt lakes in the southern part related to the warm

dry climates of this region. The climate throughout the Cretaceous was warm and equable with discontinuous temperate humid zones in high latitudes and regions of high rainfall (Parrish *et al.*, 1982). Tropical and subtropical climates dominated most continents with small discontinuous arid zones (Duellman and Trueb, 1994). An important feature of central Asia in the mid-Cretaceous was the existence of a vast inland lake in Mongolia that extended from "what is now the Pacific eastern seaboard across Manchuria and Central Asia into the western Gobi basin of Mongolia" (Travers, 1989). This Asian freshwater system existed in late Cretaceous times following which it fragmented (Travers, 1989). The modern topography was shaped by orogenesis in the Pleistocene (Travers, 1989).

The Cenozoic (65 mya - present) was a period of major geological, climatic and biological change. Sea-floor spreading continued to cause the dissociation of North America, Greenland and the rest of Europe. The Greenland Sea began to open during the Cretaceous-Tertiary boundary (65 mya) and this was followed by the initial opening of sea between Britain and southern Greenland (55 mya) and between Scandinavia and Greenland (50 mya) (Rogers, 1993). Although the spreading of the Greenland Sea stopped in the mid-Palaeogene rifting continued between Greenland and Eurasia (Stanley, 1989), allowing broad mixing of Arctic and North Atlantic waters and producing the current geography of the region. The palaeogeography of the Palaeocene shows Africa still well separated from the southern margins of Eurasia by a broad Tethys connection with the Atlantic in the future Mediterranean Sea region (Adams, 1981). The Obik Sea continued to be a dominant feature of western Siberia

and persisted until the end of the Eocene (57-35 mya). Marine transgressions resulted in epicontinental flooding of Europe during various times in the Palaeocene, Eocene and Oligocene (Adams, 1981). A narrow arm of the Arctic extended into central plains east of the North American Cordillera in the early Palaeocene (Proto-Cannonball Sea) (Lehman, 1987) which retreated by the end of the Palaeocene. The lower Mississippi was flooded for the last time by another marine incursion that extended to Missouri and lasted for a short period in the early Tertiary. Since the Palaeocene, the Cenozoic shorelines of North America have had a rather modern aspect, some transgressive-regressive episodes along the margins notwithstanding. The K/T boundary was marked by extinction of several lineages of biota, particularly of dinosaurs, fusulinid? nannoplankton, brachiopods etc. This boundary is also marked by the possible impact of a large bolide (Stanley, 1989; Rogers, 1993). The Bering land bridge formed an intermittent connection between North America and Asia in the west throughout most of the Cenozoic until the Pliocene (approx. 3-5 mya) (Adams, 1981; Duellman and Trueb, 1994). It is generally held that intermittent land-bridges connected eastern North America to Europe via northern Greenland (DeGeer passage) and southern Greenland (Thulean route) until the late Eocene (Briggs, 1987; McKenna, 1971; 1972; 1975). This trans-Atlantic connection is supported by similarity of biota, particularly the early Eocene mammalian fauna of eastern North America and Europe (Briggs, 1987; McKenna, 1975). The Turgai Sea persisted until the mid-Cenozoic but by the beginning of the Oligocene (35 mya), this seaway had retreated and Europe and Asia had substantial dry land connections for the first time since the Jurassic. Continuous

land connection between North and South America (Isthmus of Panama) was not present until the mid-Pliocene (Adams, 1981) allowing direct communication between Pacific and Atlantic waters. The western North American Cordillera experienced a major phase of mountain building (Laramide orogeny) which re-enforced the north-south Continental divide and influenced the modern day 'basin and range province'. However, temporary erosion of the southern Cordillera in the Cenozoic apparently reduced its effectiveness as a major geographic barrier in the Late Eocene (Grande, 1985).

The southern margin of Europe and the Tethys were drastically modified by the Alpine orogenic belt due to the northward moving African-Arabian plate (Rogers, 1993). This tectonic event resulted in the gradual shrinking of the western Tethys and the formation of two biogeographically important basins; the Mediterranean and the Paratethys. At the end of the Oligocene, emergent land in Europe and western Asia caused the Tethys to lose its connections with the North Sea and the Ural Sea. Alpine orogeny in the South resulted in the upliftment of the Dinarides and Balkans which isolated a large portion of the Tethys to a considerable extent from the Tethys proper (future Mediterranean) to the South. This Paratethys basin occupied central and eastern Europe and extended "from Vienna across the Caucasus to the Aral Sea" (Pomeroy, 1982). In the Middle Miocene, the Paratethys was composed of four major interconnected basins; (from west to east) '*Pannonian*', surrounded by the Alps, Dinarides and Carpathian orogenic formations (present day remnant: Lake Balaton, Hungary), '*Dacic*' between the Carpathians and the Balkans in the east (present day:

entirely continental), '*Euxinic/Pontic*' bound by the Russian platform, Balkans, Caucasus and Taurus highlands (present day Black and Azov Seas) and the '*Aral-Caspian*' basin bound by the Eurasian and Russian landmasses and the northern mountain chains of Iran (Pomerol, 1982). The extent of the Paratethys is supported by Oligocene sediments (Veto, 1987). During early Miocene times, the Paratethys was a sea of normal salinity. With progressive upliftment of Southern Europe by Alpine orogeny, the Paratethys became isolated from the Mediterranean in mid-late Miocene times and developed a typical inland sea fauna (Adams, 1981). Since the mid-Miocene, the western and central basins underwent desalinization and eventually contained a freshwater lacustrine fauna (Adams, 1981). In the Pliocene, the Paratethys was reduced in size due to shrinking of the Pannonian, Transylvanian and Dacic basins. The progressive desalinization allowed the development of the Caspian brackish fauna which was apparently destroyed (Adams, 1982) as the Pontic (Black Sea) basin re-established its connection with the Mediterranean via the Bosphorus in the Quarternary (Adams, 1981). This once extensive inland Paratethys is represented today by brackish inland seas; Black Sea (18 ppt salinity), Caspian Sea (12 ppt salinity) and Aral Sea (10 ppt salinity before its present-day crisis). The history of the Mediterranean Sea is characterized by several episodes of drying out (desertification) and refilling from the Atlantic across the Straits of Gibraltar (Adams, 1981; Hsu, 1983; Rogers, 1993). The connection between the Mediterranean and the Indo-Pacific was terminated in the early Miocene (Burdigalian) (Adams, 1981) by the docking of the Arabian plate against Eurasia. The early Tertiary (until mid Eocene times) was

characterized by warm subtropical climates in the northern hemisphere and equable climates in the northern latitudes (Duellman and Trueb, 1994). Climatic deterioration was especially marked in the late Eocene when global climates cooled by 10°C. This 'terminal Eocene event' marked the first phase of Cenozoic extinctions and progressive cooling in the late Tertiary resulted in marked seasonality and eventually Arctic ice formation in the Pliocene (Adams, 1981). This was followed by the Pleistocene glaciation cycles which had a drastic effect on the biota of the northern hemisphere. The best studied of these glaciation phases is the last of them (Wisconsinian of North America and Valdai of Eurasia) (Dawson, 1992). At its maximum extent, the ice sheet covered the major portion of northern North America. In North America, at least some of the biota of the affected regions survived in 6 major 'refugia' (and possibly some minor ones), one to the northwest of the ice sheet termed *Beringia* which comprised parts of Alaska and the emergent Bering land bridge with northeastern Asia, one (*Banff-Jasper*) between the Cordilleran and Laurentide ice sheets, three (*Columbian*, *Missourian* and *Mississippian*) to the south of the ice sheet, and one (*Atlantic*) east of the Appalachians (Crossman and McAllister, 1986). Approximately 12000 ya, the ice sheet began melting, forming extensive glacial lakes along its margins which changed shape and altered their connections as the glaciers retreated over a period of 10,000 years (Dawson, 1992). The large lakes of the northern regions of North America (Great Slave and Great Bear lakes, the Winnipeg-Manitoba-Winnipegosis lakes complex and the Laurentian Great lakes complex are the present day remnants of those large proglacial lakes. The connections of glacial Lake

Agassiz with the upper Mississippi to the south via the Minnesota spillway and with the nascent Great Lakes complex to the east via the Lake Superior outflow allowed multiple colonization routes for many fish species, including lake sturgeon, from southern refugia (Crossman and McAllister, 1986). The maximum extent of the late Valdai glaciation over Europe and Russia is controversial (Dawson, 1992). The "Grosswald model" (Dawson, 1992) indicates that there was a large Eurasian ice sheet that extended from the western Siberian lowlands to Britain whose southern margins extended across northern Poland, Germany and Denmark. This model holds that there were large marginal lakes with large amounts of fluvial discharge into the Aral, Caspian and Black Sea basins. In contrast the "Velichko *et al.* model" of glaciation (Dawson, 1992) shows a restricted ice cover and argues against large ice-dammed lakes and the extensive fluvioglacial discharge into the Aral and Caspian basins.

Readers are also referred to the accounts of Barron (1987), Barron *et al.*, (1981) for global palaeogeography and Crame (1992) for perspectives on the evolutionary history of the polar regions.

Mesozoic and Cenozoic time scales (after Rogers, 1993 and Smith *et al.*, 1994).

Era & Boundary Ages	Period and duration in mya.	Epoch and duration in mya.	Stage & approximate age (mya)
0 Cenozoic 65	Quaternary (0-1.5) Tertiary (65 - 1.5)	Holocene Pleistocene Pliocene (1.5 - 5) Miocene (5 - 23) Oligocene (23 - 35) Eocene (35 - 57) Palaeocene (57 -65)	
65 Mesozoic (Jurassic onwards) 208	Cretaceous Jurassic	Senonian Neocomian Malm Dogger Lias	Maastrichtian (70) Campanian (80) Santonian (85) Coniacian (88) Turonian (90) Cenomanian (95) Albian (105) Aptian (115) Barremian-Hauterivian (125) Valanginian-Berriasian (138) Tithonian (148) Kimmeridgian (153) Oxfordian (155) Callovian (160) Bathonian (165) Bajoician (170) Aalenian (175) Toarcian (180) Pliensbachian (190) Sinemurian (200) Hettangian (205)

APPENDIX III

The following figures show the location of the fossil Acipenseridae on corresponding palaeogeographical maps. Base maps are from Howarth (1981) for Fig. 1 and from Smith *et al.*, 1994, for Figs. 2-6. Dark shading on continents in Figs. 2-6 indicates highlands.

Figure 1. Upper Cretaceous world palaeogeography showing locations of fossil acipenserids along the western coasts of the western interior seaway and in western Asia. Heavy outlines indicate exposed land (superimposed upon finer present day continental outlines).

Figure 2. Late Palaeocene world palaeogeography showing location of fossil acipenserids in western Asia.

Figure 3. Eocene world palaeogeography showing location of fossil acipenserids in western Europe.

Figure 4. Oligocene world palaeogeography showing location of fossil acipenserids in western Europe, western Siberia and North America.

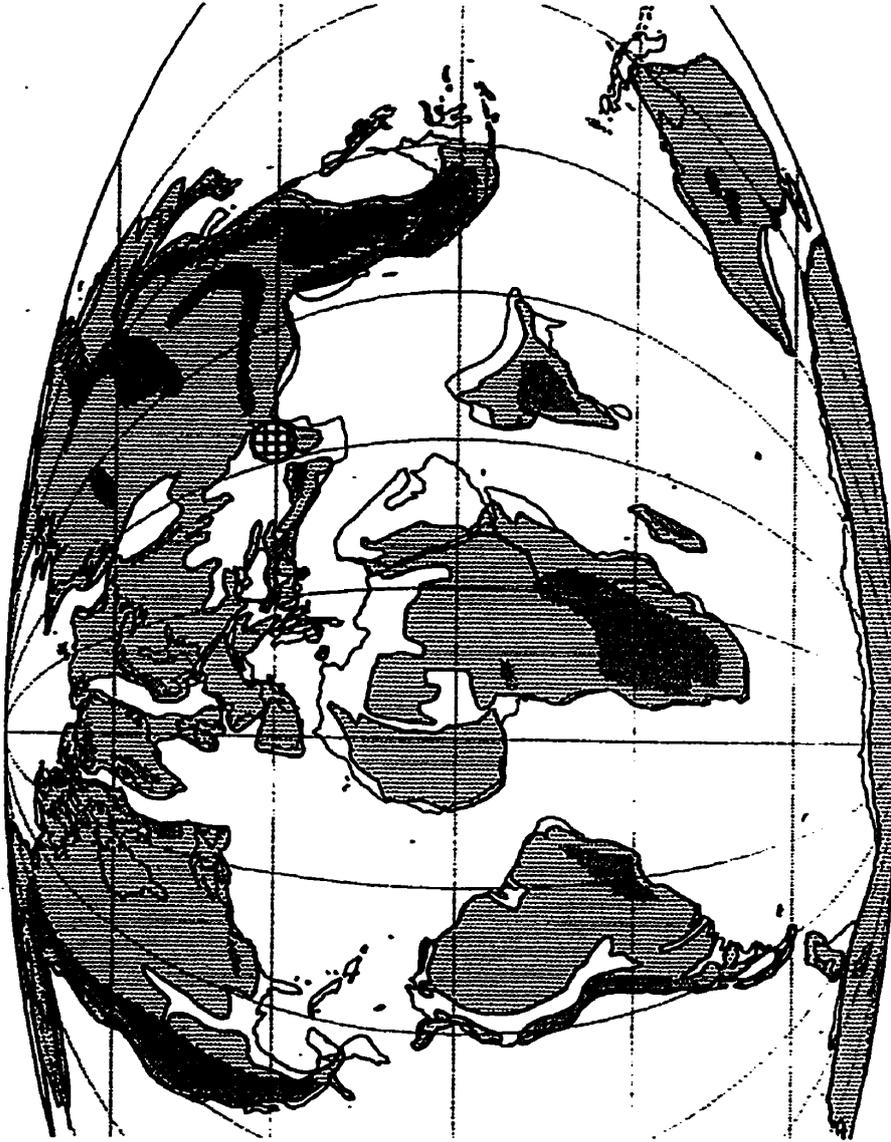
Figure 5. Miocene world palaeogeography showing location of fossil acipenserids in Europe and North America. Note the closing off of the Tethys and the formation of the Paratethys.

Figure 6. Pliocene world palaeogeography showing location of fossil acipenserids in Siberia, Europe and an undetermined locality in North America. Note the extensive Ponto-Aralo-Caspian basin.

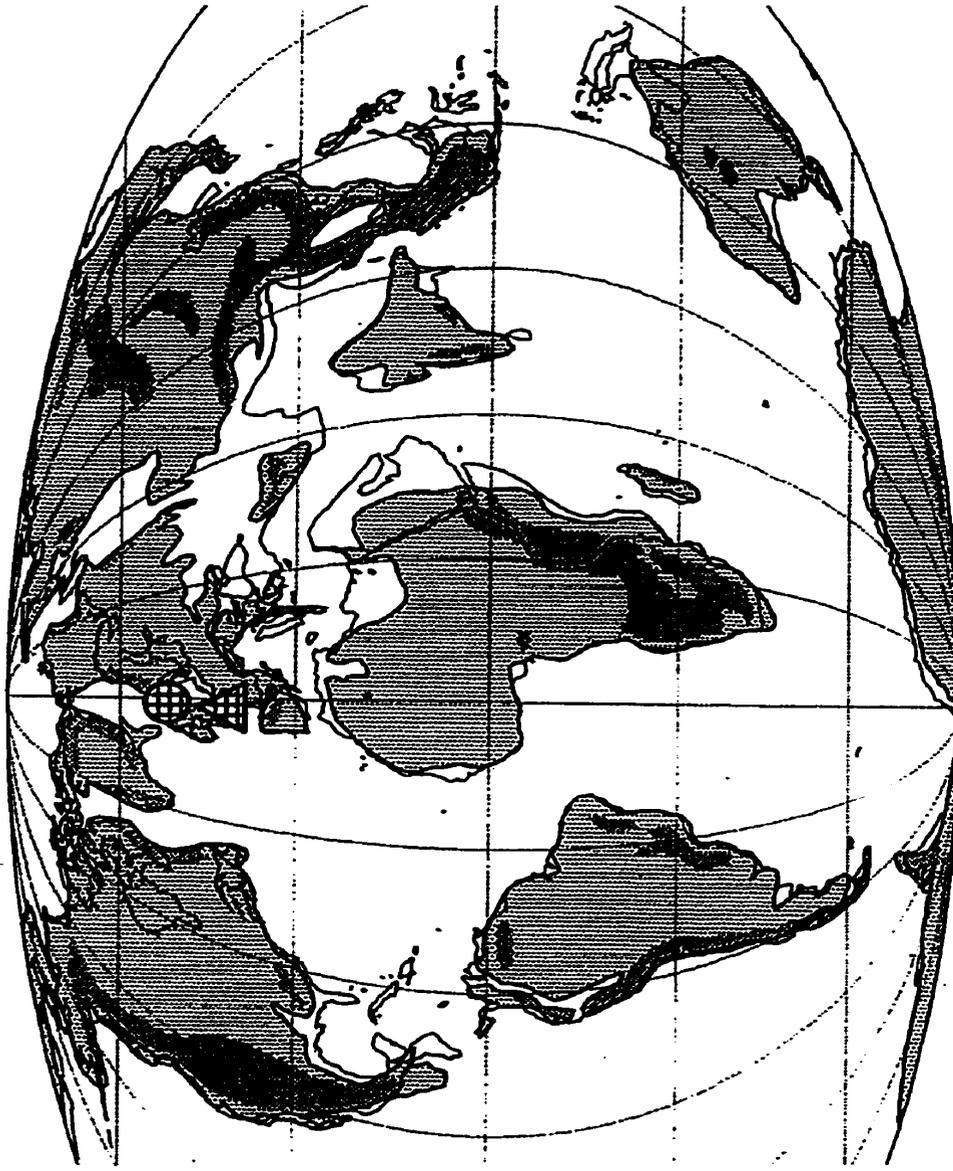
Late Cretaceous palaeogeography (after Howarth, 1981)

▲ *Acipenser albertensis*△ *Acipenser eruciferus*■ *Acipenser shilini*○ *Protoscapirhynchus squamosus*● *Propenser hewletti*□ *Acipenser* sp.

Late Palaeocene palaeogeography (after Smith *et al.* 1994)



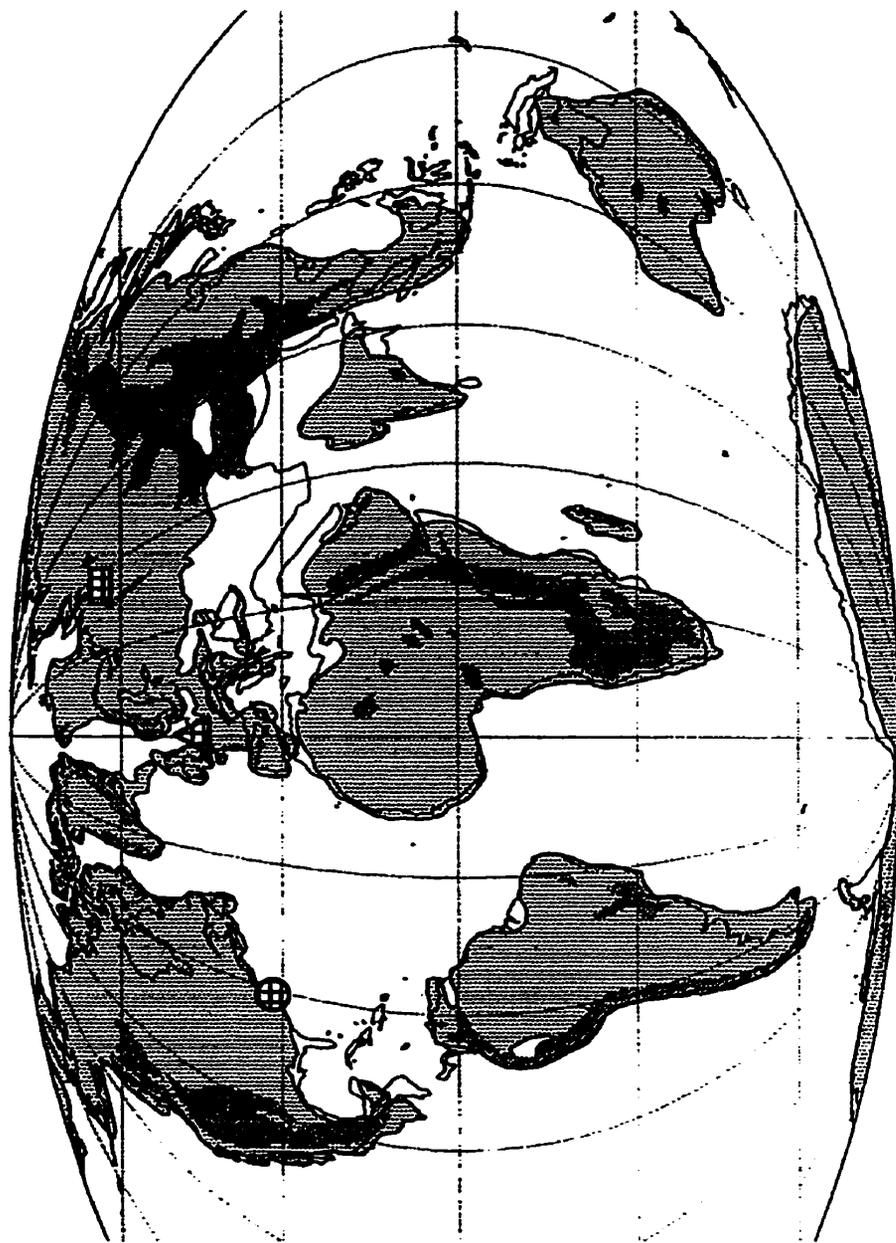
 *Acipenser zhylgensis*

Eocene palaeogeography (after Smith *et al.* 1994)

● *Acipenser toliapicus*

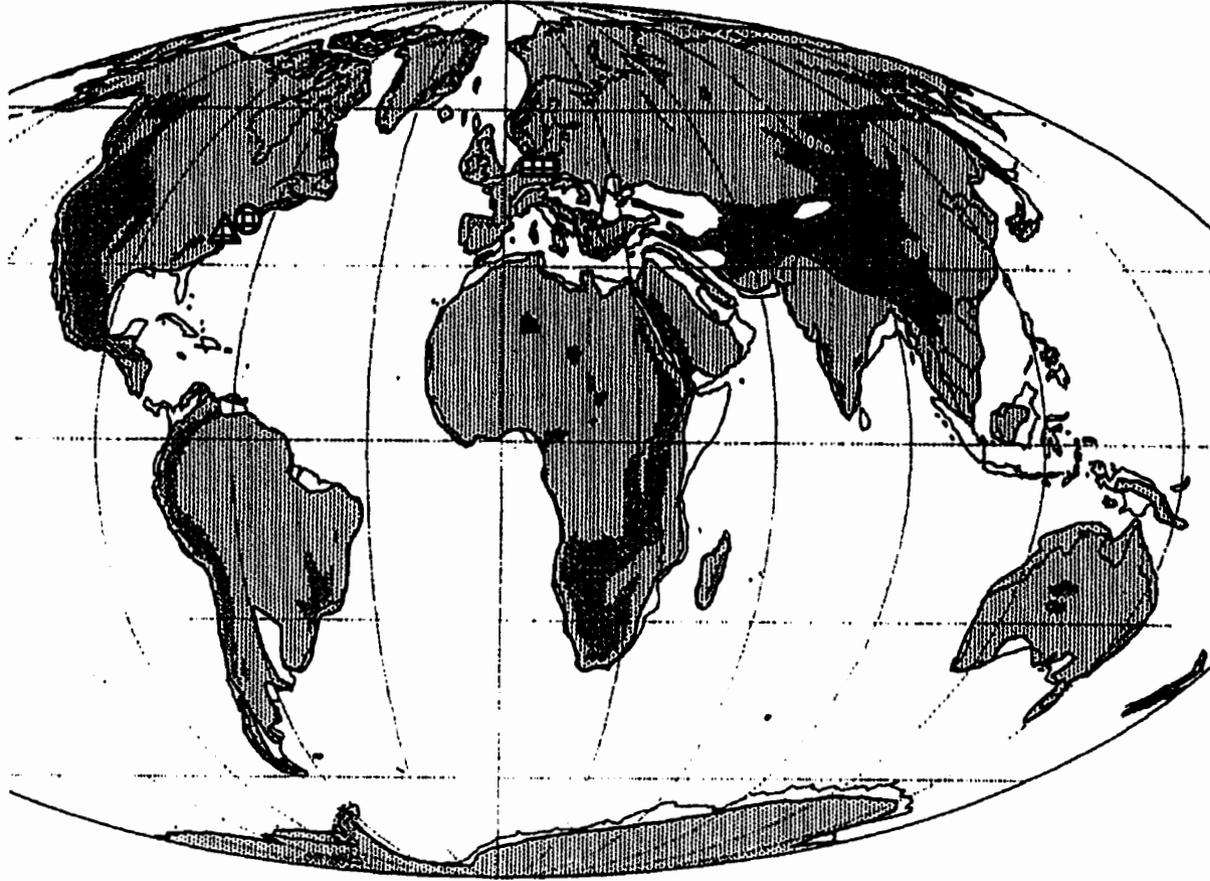


Acipenser leimonei

Oligocene palaeogeography (after Smith *et al.* 1994)

▲ *Acipenser paristensis* ⊕ Acipenseridae ⊞ Acipenseridae

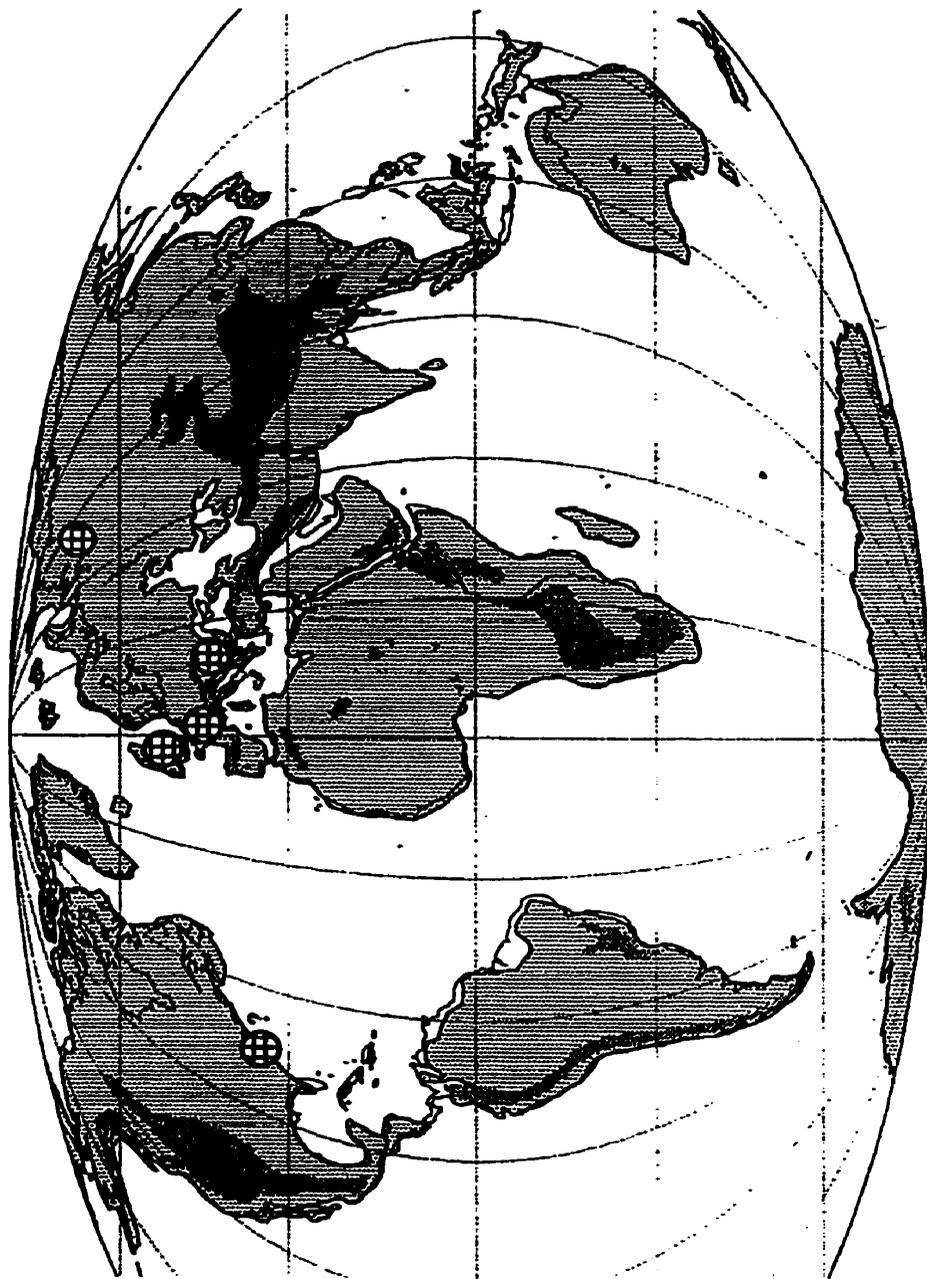
Miocene palaeogeography (after Smith *et al.* 1994)



5  *Acipenser ornatus*

 *Acipenser sp.*

 *Acipenser tuberculosus*
Acipenser molassicus

Pliocene palaeogeography (after Smith *et al.* 1994)

6

 *Acipenser* sp.

APPENDIX IV

Rationale for regarding *Bothrimonus sturionis* Duvernoy, 1842 and *Diplocotyle olrikii* Krabbe, 1874 as separate species.

Diplocotyle olrikii (a species commonly found in salmonids in the holarctic estuarine and coastal environments) and *Bothrimonus sturionis* (described from a North American sturgeon by Duvernoy in 1842 but not found again) were synonymized by Burt and Sandeman (1969) and this has been followed by North American workers (see Margolis and Arthur, 1979; McDonald and Margolis, 1995; Schmidt, 1985). Russian and European workers have apparently not accepted this synonymy and have retained *D. olrikii*, *B. sturionis* and *B. fallax* as separate species (Dubinina, 1987; Gibson, 1994; Skrjabina, 1974). Prior to Burt and Sandeman (1969), some North American parasitologists also preferred to keep the two species distinct (Wardle and McLeod, 1952). In this thesis, I follow Wardle and McLeod (1952) and the European/Russian workers in regarding the two species as distinct for reasons outlined below.

Bothrimonus sturionis was described by Duvernoy (1842) based on worms that were collected in 1835 by LeSueur from "le canal intestinal d'un Esturgeon (l'*Acipenser oxyrinchus* Mitschil), pris non loin de l'embouchure, dans l'Ohio, de la rivière de Wabasch, qui arrose l'Indiana, l'un de Etats-Uni de l'Amérique du Nord" (Duvernoy, 1842). This statement introduces uncertainty about the type host and the

type locality. *Acipenser oxyrinchus* (the Atlantic sturgeon) does not (and did not) occur in the Wabash River. The only sturgeons native to the Wabash R. are the shovelnose sturgeon (*S. platorhynchus*) and the lake sturgeon (*A. fulvescens*). However, if the type host is correct, then it must have been collected from either somewhere along the North American Atlantic seaboard, the Gulf of Mexico or the Gulf of St. Lawrence. It is ironic that such confusion should prevail given LeSueur's extensive research and expertise on sturgeons (he provided the first detailed description of the lake sturgeon under the name *Acipenser rubicundus* in 1818). It is also noteworthy that Duvernoy described the type locality in considerable detail and since he did not work in North America his information may have come from LeSueur himself. In any case, researchers since have accepted the Atlantic sturgeon as the type host and have preferred to regard the type locality as uncertain. For the moment, the specific identity of the type host and location have little bearing upon the taxonomic status of *B. sturionis*. What is relevant is that it was described from a sturgeon somewhere in eastern North America. Duvernoy (1842) devoted a considerable part of the description of *B. sturionis* (including 4 of 8 figures) to "L'extrémité céphalique" stating that the "ventouse" (= sucker, referring to the scolex/holdfast) was made up of two hemispheres, each corresponding to one side of the worm and that the orifice of the "ventouse" was oblong and enlarged towards the commissures and "retraced in the middle part by two semi-cylindrical "sailles" which project in the depth of the cavity of the ventouse and seems to share it **incompletely** with the two hemispheres of the "ventouse". Duvernoy's only comment about variation was "for the rest, the look of

the ventouse and of its orifice varies a little proportional to its degree of contraction". All of Duvernoy's figures indicate a single oblong opening as he had described and his comment about variation is not illustrated by any figure.

In 1874, Krabbe described a cestode from northern European salmonids under the name *Diplocotyle olrikii*. Krabbe (1874) was apparently unaware of Duvernoy's description of *Bothrimonus sturionis* since Krabbe did not refer to it (Burt and Sandeman, 1969). *Diplocotyle olrikii* was described as possessing two hemispheres completely divided by a septum (Wardle and McLeod, 1952).

In 1899, Lühe, described *Bothrimonus fallax* from *Acipenser ruthenus* (the sterlet) based on worms collected by Jacquet from the Rumanian section of the Danube (Burt and Sandeman, 1969). Although Lühe (1899) also synonymized the genera *Diplocotyle* and *Bothrimonus*, he re-established the two genera in 1900 (Lühe, 1900) and distinguished the two on the basis of the complete (in *Diplocotyle*) or partial (in *Bothrimonus*) fusing of the two suckers.

Schneider (1902) combined *Bothrimonus* and *Diplocotyle* based on observations of the motility of the suckers in living worms and Cooper (1918) agreed with this decision.

In 1922, Nybelin re-described *Bothrimonus fallax* from the Caspian sturgeon and described and illustrated it as possessing a 'scolex' with two hemispherical cavities incompletely divided by a septum that is illustrated as approximately half the height of the cavity or less (diagram reproduced in Skrjabina, 1974 and Wardle and McLeod, 1952). Nybelin also recognized *B. sturionis* and *Diplocotyle olrikii*. *B. fallax*

and *B. sturionis* are distinguished by rounded suckers in *B. fallax* and "obal'naya" (Skrjabina, 1974) (meaning collapsed, narrow?) suckers in *B. sturionis* (Skrjabina, 1974).

Wardle and McLeod (1952) stated that "An examination of a large number of specimens of *Diplocotyle* from salmonoid fishes of northern Canada by one of the present writers gave no indication that contracted specimens may show a single holdfast aperture as Cooper and Schneider suggested; **and until an opportunity occurs for examining material from Canadian sturgeon species, we retain the generic term *Bothrimonus* for the species *sturionis* and *fallax*, while retaining the term *Diplocotyle* for the species *olrikii*".**

Burt and Sandeman (1969) examined material from the North Atlantic and observed and illustrated the various shapes assumed by the suckers (Figs. 1-3 of Burt and Sandeman, 1969) of living worms. They remarked that some large live specimens showed a single opening when the suckers contracted. Like Schneider (1902) and Cooper (1918), they decided the sucker shape to be a variable and apparently unreliable character to distinguish between *D. olrikii* and *Bothrimonus*. However, the following comments can be made regarding the review by Burt and Sandeman (1969):

1. While the morphology of the scolex in living worms were reportedly variable, they did not mention what percentage of the "large" live worms showed a single opening nor do they indicate whether a single opening was ever seen in any fixed material. Contrary to Burt and Sandeman's statement, Duvernoy (1842) made no observations on the variation and motility of the suckers in living worms of *B.*

sturionis (his material consisted of worms that had been sent from North America by LeSueur, a good proportion of which Duvernoy lamented was detained by customs!), nor did he discuss the variations in the opening of the sucker. Also, contrary to Burt and Sandeman's statement, Duvernoy's figures do not show both arrangements of the suckers!

2. In Table 2, where they list the measurements and morphologies of the scolex from the various descriptions, Duvernoy (1842) is listed but no mention is made of his description of the scolex opening, despite the fact that Duvernoy took pains to describe it as precisely as he could (see discussion of Duvernoy's description above).

3. By their own admission, no *Bothrimonus* from sturgeon were examined (only *B. fallax* from sturgeons of the Ponto-Caspian basins would have been available). Given that much of their argument is based on the variation of the suckers, it seems critical that the variability of the sucker morphology in *B. fallax* be evaluated; *B. fallax* has always been described as having one opening and partially fused hemispherical cavities. Given that *B. sturionis* and *B. fallax* have both been described as having single openings of the scolex (Duvernoy, 1842; Nybelin, 1922), Burt and Sandeman's synonymy would suggest that *D. olrikii* and *B. fallax* are also synonymous (although they do not go as far as to suggest it!).

4. Wardle and McLeod (1932) indicated that the shallow vagino-uterine atrium in *Bothrimonus* (as seen in sections of *B. fallax*) distinguishes it from *D. olrikii*. Although Burt and Sandeman do not explicitly address this reported difference, their sections of *D. olrikii* indicate a very shallow atrium, whereas the atrium in *B. fallax*

seems slightly deeper. Again, this difference is difficult to evaluate in the absence of material from sturgeons.

The central question then concerns the extent of the median ridge or septum separating the two hemispherical suckers of the scolex. Cooper (1918, p. 63) stated regarding this: "While in **none** of the few specimens of the species described below (*referring to Bothrimonus intermedius*) were the openings fused, various stages in the formation of a single terminal and almost circular opening from the two otherwise separate openings were observed in some material from *Microgadus tomcod* which was, however, too young to be determined with certainty specifically". Cooper goes on to say under his description of *Bothrimonus intermedius* (Cooper, 1918, p. 63) "Bothria hemispherical, their apertures **ordinarily not fused** to form a single opening". Cooper's use of the word "ordinarily" is misleading since he already stated that the apertures were not fused in **any** specimens of *B. intermedius*. Cooper (1918, p. 63) also discussed the observations of Schneider (1902) regarding the suckers in *B. nylandicus*. Schneider (1902) did mention the retraction of the median ridge of the scolex of live worms which gave the appearance of a common terminal opening in *B. nylandicus* as did Burt and Sandeman (1969) for *D. olrikii* but again, it is unclear what proportion of fixed worms, if any, showed a low median ridge and a single opening.

It seems from the above discussion that the ability of the median ridge of the scolex to change form by muscular movement in live worms has been confused with the actual morphology of the ridge in the various species when the worms have been relaxed and fixed. The argument that because a structure is variable in life, it has little

value taxonomically, is a fallacious one because very often the shape of muscular structures and that of the body of worms in the living condition bear little resemblance to conditions of those structures or of the body in a properly relaxed and fixed specimen. This is true for the heads, bothria and strobilae of a variety of cestodes which I have observed in the living and subsequently relaxed and fixed condition, e.g., *Proteocephalus*, *Eubothrium*, *Bothriocephalus*, *Corallobothrium* and for muscular structures (oral papillae, suckers) and bodies of a variety of digeneans; *Crepidostomum* spp., *Phyllodistomum* spp. etc. Observations of living worms are undoubtedly useful since many parasites belonging to the same genus have unique characteristic movements (personal observation) but taxonomic and systematic work relies ultimately on properly fixed and processed material. Unless it can be demonstrated unequivocally that relaxed and fixed specimens of *Diplocotyle olrikii* and *Bothrimonus* (e.g., *B. fallax*) randomly exhibit a full range of variation of the fusion/separation of the hemispheres of the scolex, there seems little justification for synonymizing *D. olrikii* with *B. sturionis*, has been done by Burt and Sandeman (1969).

Finally, there is biological and biogeographical information that can be brought to bear upon the problem. *Diplocotyle olrikii* commonly parasitizes salmonids in the estuarine environment of the holarctic region but has not been reported in sturgeon (*A. baeri*, *A. ruthenus*) from the Arctic regions, possibly because these sturgeons are predominantly freshwater in habit. *D. olrikii* is also not found in salmonid hosts (*S. trutta*) in the Ponto-Caspian region or in the Mediterranean trouts (*Acantholingua*, *Platysalmo* and *Salmothymus*). (The absence in freshwater populations of *S. trutta* and

in the Mediterranean trouts which are also freshwater species is understandable given the predilection of *Diplocotyle* for saline environments, but noteworthy for anadromous Caspian populations of the brown trout. In contrast, *B. fallax* is found in the Ponto-Caspian basins and drainages but in sturgeons only. This further argues for the validity of *B. fallax* in sturgeons.

Based on the information at hand, I follow Wardle and McLeod (1952), the Russian workers and Gibson (1994b) in recognizing *B. sturionis* as distinct from *D. olrikii* and provisionally accept *B. fallax* as a species distinct from *B. sturionis* pending the rediscovery of *Bothrimonus* in North American sturgeons.