PHYLOGENETIC ANALYSIS OF THE NORTH AMERICAN SPECIES OF *TELORCHIS* LUEHE, 1899 (CERCOMERIA:DIGENEA:TELORCHIIDAE)

by

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Abstract

Telorchiids are plagiorchiform intestinal parasites inhabiting turtles, and occasionally snakes and salamanders. Previous taxonomic revisions of the group have been problematical due to a lack of information on intraspecific morphological variation. In the present study, ten of the thirty described North American species are considered valid. Phylogenetic analysis of 22 character states comprising 20 homologous series results in a single phylogenetic tree with a consistency index of 95%. Only one of the characters used in the analysis is homoplasious. In order to maintain a classification that reflects the phylogeny of the group, only one of four proposed genera is recognized. A biogeographical analysis is not feasible due to incomplete collecting records. The two most relatively plesiomorphic telorchiid species are found in salamanders. Five of the eight species from amniotes are considered to have co-speciated with their hosts. One of the secondarily evolved species is postulated to have evolved via a host-switch from turtles to snakes. The other two secondarily evolved species appear to have arisen via sympatric speciation, facilitated by mechanical pre-mating isolation due to a difference in genital pore position. As primarily coevolved telorchiids become more highly derived there is an increase in host specificity, which is consistent with the traditional view of host-parasite relationships.
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INTRODUCTION

Members of the genus *Telorchis* Luehe, 1899 are plagiorchiform intestinal parasites occurring worldwide. They are common inhabitants of North American freshwater turtles and, occasionally, snakes and salamanders. Telorchiids are characterized by having testes at the posterior end of the body, and by possessing an ovary that is pretesticular and separated from the testes by extensive uterine coiling (Brooks et al., 1985).

From a systematic standpoint, *Telorchis* is a problematical group. One point of contention is the nomenclature of the group. Luehe (1899) proposed *Telorchis*, with *T. clava* as type. One day later, Looss (1899) also proposed the genus *Telorchis*, but with *T. linstowi* as type. Luehe (1900) later divided *Telorchis* into two subgenera - *T. (Telorchis)* with *T. clava* as type and *T. (Cercorchis)* with *T. linstowi* as type. This division was based on the following characters: genital pore close to and in front of ventral sucker in *Cercorchis*, genital pore somewhat distant and to the left of the ventral sucker in *Telorchis*; testes in more or less strict tandem at the posterior end in *Cercorchis*, testes oblique or nearly tandem, midway between the genital aperture and the posterior end in *Telorchis* (Perkins, 1928; Wharton, 1940).

Subsequently, the genus *Cercorchis* has been recognized as an independent genus by some authors (Bennett, 1935; Bennett and Sharp, 1938; Bennett and Tobie, 1936; Byrd, 1937; Goldberger, 1911; McMullen, 1934; McMullen and Roudabush, 1936; Perkins,
1928; Zeliff, 1937) and rejected as superfluous by others (Stunkard, 1915; Dollfus, 1929; Wharton, 1940). However, these differences do not seem to be generic in nature because both morphologies can be observed within a single species. Considering the original separation to have been based on characters that have been shown to vary within a single species, recent workers (Yamaguti, 1958; Cable and Sanborn, 1970; Nasir, 1974) have tended to consider Cercorchis to be a junior synonym of Telorchis.

Other genera have also been proposed to accommodate single telorchiid species that possess unique characteristics. Barker and Covey (1911) erected Protenes for a species characterized by having a dorsolateral rather than medial genital pore. Stunkard and Franz (1977) proposed Paratelorchis, for P. auridistomi (synonym Telorchis auridistomi Byrd, 1937); they distinguished this species at the generic level because it has anterolateral lappets on the oral sucker. In both cases above, the diagnostic characteristics of the genera are autapomorphies, traits that are restricted to a single species. Autapomorphies can be used to characterize a species, but do not justify placement in a new genus when there are sufficient synapomorphies diagnosing the old genus (Hennig, 1966; Wiley, 1981). Yamaguti (1971) proposed Pseudotelorchis for P. compactus (synonym Telorchis compactus Cable and Sanborn, 1970). Due to its unusual morphology, the taxonomic status of this species is uncertain (I will discuss this species later).

The second problem is that the group is notorious for its
intraspecific morphological variation. This has led to some disagreement about the number of species in the genus. Extreme variability, coupled with a lack of experimental work to determine the extent of host-induced variation, has resulted in a tendency by some taxonomists to describe a new species for every specimen that exhibits the slightest variation, or for others to propose extensive synonymies.

Two previous extensive taxonomic revisions (Wharton, 1940; Nasir, 1974) have helped to dispel some of the problems associated with _Telorchis_, but have failed to resolve the taxonomy entirely. Neither author examined many of the type specimens and thus the studies lack the information that would have allowed them to produce a more inclusive list of synonymies. In addition, Watertor's (1967) study on host-induced variation has demonstrated the unsuitability of some characters previously used to distinguish species. These characters will be discussed more extensively in the results section.

In the present study, ten of the thirty described North American species of _Telorchis_ are considered valid. This assessment was based on the examination of all available type specimens, as well as voucher specimens deposited in the U.S. National Museum and H.W. Manter Lab Helminthological collections. Examination of these specimens made it possible to determine any previously reported features that were fixation artifacts and to find new characters of taxonomic use. In addition, the information on intraspecific morphological
variation among teloriichtids provided by Watertor (1967) was used to help determine species membership.

A taxonomic revision of Telorchis using phylogenetic systematics has never been attempted. The major purpose of a phylogenetic classification is to condense and summarize the inferred history of speciation as reflected by hypotheses of that history (Wiley, 1981). This type of analysis is useful not only as a means of formulating hypotheses about phylogenetic relationships, but also as a means of investigating evolutionary questions in developmental biology (Fink, 1982), biogeography (Nelson and Platnick, 1981), speciation (Wiley, 1981), coevolution, and evolutionary ecology (Brooks, 1985a).

Following a number of studies that concluded that coevolution is a prevailing pattern in parasite speciation (e.g. Dougherty, 1949; Harrison, 1914; Hopkins, 1942; Metcalf, 1929), the phenomenon of host-parasite coevolution has recently become topical (e.g. Futuyma and Slatkin, 1983; Wheeler and Blackwell, 1984). Two concepts of coevolution appeared independently and nearly simultaneously in systematics and ecology (Brooks, 1985b). One of these concepts defines coevolution in an adaptive sense by examining the reciprocal response between host and parasite. However, any explanation of the evolutionary significance of reciprocal response patterns requires an estimate of how long the host-parasite associations have existed.

Recent studies have defined coevolution in a phylogenetic sense by examining host-parasite relationships for patterns of
congruence; these patterns are believed to be the result of long-standing phylogenetic relationships between the host group and the parasite group. Congruence between host and parasite phylogeny is generally assumed to be the result of commonly experienced allopatric events. Conversely, the parasite may occur in a given host because it has colonized that host from another unrelated host (Brooks, 1981). By comparing the hypothesized host and parasite phylogenies, it is possible to estimate how much of the evolution of Telorchis can be attributed to coevolution, and how much to colonization.

MATERIALS AND METHODS

Whole mount specimens, most stained with haematoxylin and mounted in Canada balsam, were obtained from the U.S. National Museum Helminthological Collection, Beltsville, Maryland (USNM), and the H.W. Manter Laboratory, University of Nebraska (HWML). Specimens of all described North American species were available except Telorchis stenoura Ingles, 1930, which has been lost from the USNM collection (Ms. P. Pilitt, personal communication). The hosts and localities listed in the species diagnoses in the results section are only those that have been confirmed by the examination of specimens. Unconfirmed records are listed in the remarks section following each diagnosis.

Character data used for the phylogenetic analysis were obtained by both literature search and the examination of specimens. All specimens were examined with a light microscope. Measurements from those specimens that were immature, folded,
torn, contracted, or in otherwise poor condition were not included in the analyses. However, all specimens were examined to provide information on intraspecific variation. Measurements are given in micrometers unless otherwise noted. Drawings were prepared with the aid of a drawing tube.

The relative degree of plesiomorphy and apomorphy for the transformation series was determined by using the outgroup method of comparison (see Lundberg, 1972; Wiley, 1981). The outgroup used was the family Ochetosomatidae, a group of digeneans that are found in the digestive tract of reptiles, and have been considered to be closely related to Telorchis (Byrd and Denton, 1938). In addition, characters common to the Plagiorchiiformes were polarized using the phylogenetic analysis of the Digenea sensu Brooks et al. (1985).

Quantitative analyses were carried out using phylogenetic systematics (sensu Hennig, 1966) and the PHYSYS computer program developed by James S. Farris and Mary F. Mickevich. For characters which were difficult to polarize using the outgroups, polarities were determined by the functional outgroup method (Watrous and Wheeler, 1981). The fit of each transformation series was assessed with Farris optimization (Farris, 1970).

CHARACTER ANALYSIS

Character numbers in parentheses following each character name refer to columns in the data matrix in table I. The plesiomorphic, or primitive state is indicated by the code 0. For all characters, the outgroup possesses the plesiomorphic
condition. TBL=total body length; all measurements followed by this notation are given as a percentage of the total body length of the specimens.

1. BODY SHAPE (character 1). Telorchiids exhibit three body shapes; oval or linguiform, elongate, or filiform [see figure 1]. Body shape seems to have been a plastic character in digenean evolution. The interpretation which provides the best fit to the other data is that the plesiomorphic condition is oval/linguiform (0); the elongate body form is derived from that (1), with the filiform condition being the most highly derived (2).

2. BODY LENGTH (character 2). Telorchiids fall into two general categories of body length. Those species that are considered "short" never exceed 4.5 mm as ovigerous adults; the average body length is about 3.2 mm. The "long" species always exceed 4.8 mm as ovigerous adults. The average body length for these species is about 7.9 mm. The shorter body is considered plesiomorphic (0); the longer body is the apomorphic condition (1). Although body length may vary considerably with age, worm burden, or host, this conservative estimate is considered to be fairly representative of the average body length.

3. BODY PROPORTIONS (character 3). Most telorchiids have a ratio of body length to width greater than 4:1. Ochetosomatids and most other plagiorchiforms have ratios of less than 4:1. *Telorchis sirenis* also has a ratio of body length to body width of less than 4:1, and that is considered to be the plesiomorphic condition (0). A ratio of greater than 4:1
is the derived condition (1).

4. ORAL SUCKER LAPPETS (character 4). The oral sucker of most digeneans, including most telorchiids, is circular or subcircular without modifications (0). The presence of outgrowths of the sucker margins, such as the anterolateral lappets of *T. auridistomi* [see figure 10], is an autapomorphy (1).

5. PHARYNGEAL GLANDS (character 5). Small pharyngeal glands are present in all telorchiids (0). The enlarged, thickened glands characteristic of *Telorchis chelopi* [see figure 13] are considered autapomorphic (1).

6. ESOPHAGUS (character 6). The cecal bifurcation of *Telorchis robustus* is immediately postpharyngeal [see figure 14]; all other members of the genus possess at least a short esophagus, the plesiomorphic condition for digeneans (0). The lack of an esophagus appears to be autapomorphic (1).

7. CECAL BIFURCATION (character 7). For ochetosomatids and most plagiorchiforms the cecal bifurcation is more than 6% TBL from the anterior end of the body (0). Among telorchiids, when the cecal bifurcation is less than 6% TBL from the anterior end, it is considered to be an apomorphic trait (1).

8. CECAL EPITHELIUM (character 8). With one exception, the lining of the cecum has a uniform thickness; this is the condition for ochetosomatids and most other plagiorchiforms, and is considered plesiomorphic (0). *Telorchis chelopi* possesses noticeably thickened epithelium at the point of bifurcation [see figure 13], which is an autapomorphy for this species (1).
9. **SUCKER RATIO** (character 9). Most plagiorchiforms possess ventral suckers that are about the same width as the oral suckers. The range of ratios of oral sucker width to acetabular width for most telorchiids is 1:0.47-0.97, averaging about 1:0.75. In a few species, the range of sucker ratios is 0.86-1:1, with an average of 1:1. The latter condition is considered plesiomorphic (0), the former, apomorphic (1).

10. **POSITION OF TESTES** (character 10). Among plagiorchiiforms, the testes are primitively oblique or symmetrical and positioned in the mid-hindbody (0). Telorchiids have tandem testes positioned near the posterior end of the body, which is considered apomorphic (1).

11. **MUSCULARITY OF THE CIRRUS SAC** (character 11). Two cirrus sac morphologies are observed. Most telorchiids have long, thin cirrus sacs, the condition seen in most of the outgroups (0). The possession of a cirrus sac with markedly thickened muscular walls, seen in *T. chelopi* and *T. scabrae* [see figure 2], is apomorphic (1).

12. **CIRRUS SAC POSITION** (characters 12 and 13). Although the cirrus sac does not always end in exactly the same position in any one species, there are definite boundaries within which it is consistently found. These positions are specific to certain species of *Telorchis* [see figure 3]. One position is the area around the ovary. The cirrus sac may end anywhere from one ovarian length anterior to the ovary, to just posterior to the ovary. This position is the most common one among the outgroups and among telorchiids, and is considered to be the
plesiomorphic state (0,0). Two states are considered to be independently derived from the plesiomorphic state. One position is 1/2 to 2/3 of the distance from the acetabulum to the ovary (0,1). This particular state is found in *T. scabrae* and *T. attenuatus*. The other position is at the acetabular level. This is also a derived condition (1,0), and is found in *T. angustus*.

13. GENITAL PORE POSITION (characters 14 and 15). The plesiomorphic genital pore position for all digeneans is preacetabular and median or slightly left (0,0). This condition is present in most species of *Telorchis*. The genital pore may also be ventral to the left cecum or dorsolateral to the left cecum [see figure 4]. As there is no evidence to suggest that either of these other two character states evolved from the other, and the taxa they are found in are more closely related to other species than they are to each other, they are considered to have evolved independently from the primitive condition. *Telorchis scabrae* has a genital pore ventral to the left cecum (0,1); the genital pore of *T. angustus* is dorsolateral to the left cecum (1,0).

14. POSITION OF OVARY (character 16). The plesiomorphic condition is for the ovary to be closer to the acetabulum than to the testes (0). Two species, *Telorchis singularis* and *T. attenuatus*, have the ovary closer to the testes than the acetabulum; this is the apomorphic condition (1).

15. UTERINE CONFIGURATION (character 17). All species of *Telorchis* have a uterus with coiled ascending and descending
loops, separating the ovary from the testes [see figure 5]; this is a synapomorphy for the genus. The plesiomorphic trait, found in the outgroup, is an irregularly coiled sac (0); the former condition is apomorphic (1).

16. METRATERM BULB (character 18). The presence of a muscular bulb on the metraterm in *T. singularis* [see figure 15] is autapomorphic (1). Absence is plesiomorphic (0) for digeneans.

17. GENITAL ATRIUM (character 19). *Telorchis singularis* possesses a genital atrium [see figure 15], a chamber that receives the openings from the male and female reproductive ducts and opens on the body surface through a genital pore (Schell, 1970). The plesiomorphic condition, found in all other telorchiids, is for the metraterm and cirrus sac to meet at or near the genital pore (0); possession of a genital atrium is therefore a unique trait (1).

18. STRUCTURE OF VITELLINE FOLLICLES (character 20). Vitelline follicles are either in lateral, clustered groups, or in two continuous lateral bands [see figure 6]. The cluster conformation, commonly found in ochetosomatids, is considered plesiomorphic (0), the continuous rows apomorphic (1).

CHARACTERS NOT INCLUDED IN THE ANALYSIS

Watertor (1967) recognized that without knowing which characteristics are likely to exhibit intraspecific variation, it would be impossible to revise *Telorchis*. In order to identify these characters, she experimentally infected a number
of species of salamander and turtle hosts with *Telorchis bonnerensis* Waitz, 1960. Her experiments showed that many of the characters that had been used to differentiate between species were plastic, even among specimens taken from the same host species. Observations made during the course of this study confirm Watertor's suggestion that such variability was not restricted to a few species of *Telorchis*. A list of characteristics that are highly variable and unsuited for systematic analysis has been produced. This list of characters, along with justification for their exclusion, follows.

1. **ANTERIOR EXTENT OF VITELLARIA.** The vitelline follicles may extend anteriorly to anywhere between the ovary and acetabulum. They will also occasionally extend as far as the level of the anterior margin of the acetabulum.

2. **LOCATION OF OVARY.** Whether or not the ovary is closer to the acetabulum or testes does not vary within a species, but the exact location may vary considerably.

3. **SIZE OF SUCKERS.** Since the suckers frequently contract during fixation, this is not a reliable character.

4. **LENGTH OF ESOPHAGUS.** Although presence or absence of an esophagus is a reliable trait, the actual length will vary. Esophageal length is particularly affected by contraction of the worms during fixation.

5. **EGG SIZE.** Within a single species, eggs may vary by as much as 10 micrometers in length. They also seem to vary with the age of the worm.
6. BODY WIDTH. Body width can vary considerably with age of the parasite, and if there is contraction of the body.

7. TESTES CONTIGUOUS OR NOT. The posterior end of the specimens is frequently contracted or pushed outward during fixation and mounting, causing the position of the testes to vary.

8. PHARYNX SIZE. The pharynx, being muscular, may contract during fixation, causing a variation in size from specimen to specimen.

9. PERCENTAGE FOREBODY. The percentage forebody refers to the percentage of the total body length that is anterior to the acetabulum. The position of the acetabulum may vary by as much as 18% of the total body length in a single species. A variation of 2-5% TBL is therefore not a distinguishing characteristic.

10. POSTERIOR EXTENT OF CIRRUS SAC. There are three distinct areas to which the cirrus sac may extend: to the ovarian level, midway between acetabulum and ovary, and to the acetabular level. Within these areas, the exact location will vary. For example, at the ovarian level, the cirrus sac may end anywhere from one ovarian length anterior to the ovary to just posterior to the ovary.

11. RATIO OF SUCKER WIDTH TO PHARYNGEAL WIDTH. The ratio of the oral sucker to the pharynx, or the acetabulum to the pharynx, is often used to distinguish between species. However, the ranges of these ratios overlap to such an extent, that they could not be used to characterize species (see table II).
RESULTS

TAXONOMIC REVISION

Thirty species of Telorchis have been described from North American salamanders, snakes, and turtles. When the characteristics found to be intraspecifically variable are not used to distinguish between species, only ten of these thirty species can be considered to be valid. Diagnosis of these ten species follows.

Telorchis sirenis Zeliff, 1937

SYNONYMS: Cercorchis sirenis Zeliff, 1937.
HOSTS: Siren lacertina Linne, 1766, Greater siren; Amphiuma tridactylum Cuvier, 1827, three-toed Amphiuma.
LOCALITIES: type locality given as "southeastern U.S."; Reelfoot Lake, Tenn.
TAXONOMIC CHARACTERISTICS: Body linguiform, 2.2-3.1 mm long; ratio of length to width 2.6-3.8:1 (x=3.1:1). Oral sucker 184-216 in diameter. Pharynx 78-82 in diameter; ratio of oral sucker width to pharynx width 1:0.42-0.43 (x=1:0.43). Esophagus 8-67 long, 0.2-0.7% TBL. Cecal bifurcation 9-10% TBL from anterior end; ceca extend just posterior to testes, 5-6% TBL from posterior end. Acetabulum 192-216 in diameter. Forebody 15-21% TBL. Ratio of oral sucker width to acetabular width 0.87-1:1 (x=0.96:1).
Testes elliptical, tandem, contiguous, intercecal; posttesticular space 7-8% TBL. Cirrus sac ends partway down to posterior to ovary. Genital pore ventral, preacetabular, intercecal, slightly left of median.

Ovary 15-21% TBL from anterior end, intercecal, spherical to ovoid. Seminal receptacle and Laurer's canal not observed; Mehlis' gland present. Space occupied by uterus 56-57% TBL; metraterm 1/2 length of cirrus sac. Vitelline follicles separated into clusters; extend anteriorly from halfway down acetabulum to midway between acetabulum and ovary, posteriorly 9/10 distance ovary to testes to halfway down testes. Eggs 26-38 long by 15-18 wide.

Anterior extent of excretory vesicle not observed.

REMARKS: The specimens that were originally described by Zeliff (1937) were found to be immature. Wharton (1940) also noted this in his revision. Three mature specimens were collected at a later date (USNM Nos. 9396 and 9400). All information used in the description and phylogenetic analysis was obtained from those three specimens.

Telorchis stunkardi Chandler, 1923

SYNONYMS: Telorchis (Cercorchis) necturi (Perkins 1928) Wharton, 1940, new synonym; Telorchis (Cercorchis) cryptobranchi McMullen and Roudabush, 1936.

HOSTS: Amphiuma means Garden, 1821, two-toed Amphiuma; Necturus maculosus Rafinesque, 1818, Mudpuppy; Amphiuma tridactylum
Cuvier, 1827, three-toed Amphiuma.

LOCALITIES: Baton Rouge, La.; Wood's Hole, Mass.; Washington, D.C.


TAXONOMIC CHARACTERISTICS: Body elongate, 2.5-3.4 mm long; ratio of length to width 4-4.8:1 (x=4.4:1). Oral sucker 202-212 in diameter. Pharynx 67-78 in diameter; ratio of oral sucker width to pharynx width 1:0.32-0.37 (x=1:0.35). Esophagus 106-180 long, 3-7% TBL. Cecal bifurcation 12-18% TBL from anterior end; ceca extend just posterior to testes, 2-6% TBL from posterior end. Acetabulum 206-243 in diameter. Forebody 22-35% TBL. Ratio of oral sucker width to acetabular width 0.86-0.98:1 (x=0.9:1).

Testes spherical to elliptical, tandem, contiguous, intercecal; posttesticular space 4-7% TBL. Cirrus sac ends partway down to just posterior to ovary. Genital pore ventral, preacetabular, intercecal, slightly left of median.

Ovary 36-54% TBL from anterior end, intercecal, spherical to ovoid. Seminal receptacle and Laurer's canal nor observed; Mehlis' gland present. Space occupied by uterus 38-52% TBL; metraterm 2/3 length of cirrus sac. Vitelline follicles separated into clusters; extend anteriorly from just posterior to acetabulum to partway down ovary, posteriorly 3/4 distance from ovary to testes to immediately pretesticular. Eggs 41 long by 18 wide.

Anterior extent of excretory vesicle from ovarian level to
between acetabulum and ovary.

REMARKS: McMullen and Roudabush (1936) described *Cercorchis cryptobranchi* from *Cryptobranchus alleganiensis* Daudin, 1822 collected at Ames, Iowa. *Telorchis necturi* has been reported from *Graptemys pseudogeographica* Gray, 1831 from Nebraska, HWML #20213 (Brooks and Mayes, 1976). Additionally, *T. stunkardi* has been reported from *Siren lacertina* Linne, 1766 in the vicinity of Miami, Florida, HWML #20327 (Brooks and Buckner, 1976) and from *Amphiuma tridactylum* Cuvier, 1827 and *Amphiuma means* Garden, 1821 from Payne's Prairie, Florida and Ocean Springs, Mississippi (Brooks and Fusco, 1978).

Perkins (1928) claimed that although *Telorchis necturi* and *T. stunkardi* were similar in appearance, the two species were distinct from each other. However, he did not list any characters by which they differed, or provide any sort of justification for this statement. Examination of type specimens has shown that they differ only in anterior extent of vitelline follicles, egg size, sucker size, and body width, all characters which have been shown to have intraspecific variation.

*Telorchis corti* Stunkard, 1915

[figure 9]

SYNONYMS: *Telorchis* (Cercorchis) *linstowi* Goldberger, 1911; *Telorchis lobosus* Stunkard, 1915; *Telorchis guttati* MacCallum, 1919; *Telorchis insculpti* MacCallum, 1919; *Telorchis pallidus* MacCallum, 1919; *Telorchis angustus* MacCallum, 1921; *Telorchis stenoura* Ingles, 1930; *Telorchis* (Cercorchis) *texanus* Harwood,
1932; *Telorchis medi us* McMullen, 1934; *Telorchis bonnerensis* Waitz, 1960, new synonym.

HOSTS: *Chrysemys scripta elegans* Wied, 1839, red-eared turtle; *Ambystoma macrodactylum* Baird, 1849, long-toed salamander; *Chrysemys picta* Schneider, 1873, painted turtle; *Chelydra serpentina* Linne, 1758, snapping turtle; *Sternotherus carinatus* Gray, 1856, keel-backed musk turtle; *Sternotherus odoratus* Latreille, 1801, common musk turtle.

LOCALITIES: Havana, Ill.; Clark Fork, Bonner Co., Idaho; Lake Conway, Arkansas; Rosent on, Texas; Tuscaloosa, Ala.; Washington, D.C.; Arlington, Va.; Huntsville, Texas; Walker, Iowa; Raleigh, N.C.; Unknown (New York Aquarium).


TAXONOMIC CHARACTERISTICS: Body elongate, 2.2-4.5 mm long; ratio of length to width 5.1-11.7:1 (x=7.6:1). Oral sucker 94-160 in diameter. Pharynx 43-78 in diameter; ratio of oral sucker width to pharynx width 1:0.41-0.66 (x=1:0.51). Esophagus 39-216 long, 1-5% TBL. Cecal bifurcation 6-19% TBL from anterior end; ceca extend well past testes, 1-5% TBL from posterior end. Acetabulum 55-122 in diameter. Forebody 13-28% TBL. Ratio of oral sucker width to acetabular width 1:0.47-0.96 (x=1:0.78).

Testes spherical to ovoid, tandem, contiguous or not, intercecal; posttesticular space 5-10% TBL. Cirrus sac ends just anterior to partway down overy. Genital pore ventral, preacetabular, intercecal, median or slightly left of median.
Ovary 30-49% TBL from anterior end, intercecal, spherical to ovoid. Seminal receptacle small; Laurer's canal not observed; Mehlis' gland present. Space occupied by uterus 42-58% TBL; metraterm 1/2 to 2/3 length of cirrus sac. Vitelline follicles continuous, lateral bands; extend anteriorly from anterior border of acetabulum to anterior of ovary, posteriorly from 3/4 distance ovary to testes to partway down testes. Eggs 31-41 long by 14-20 wide.

Anterior extent of excretory vesicle midway between acetabulum and ovary.

REMARKS: This species has also been reported from the following hosts and localities: Deirochelys reticularia Latreille, 1801; Chrysemys marginata Agassiz, 1857; and Kinosternon subrubrum Lacepede, 1788, no locality given (Wharton, 1940); Chrysemys scripta elegans Wied, 1839 from Houston, Texas (Harwood, 1932); Thamnophis sirtalis Linne, 1766 from Clark Fork, Idaho (Waitz, 1960); Clemmys marmorata Baird and Girard, 1852 from Oakland, California (Ingles, 1930); Chelydra serpentina Linne, 1758, Graptemys pseudogeographica and Emydoidea blandingi Holbrook, 1838 from Nebraska (Brooks and Mayes, 1975); Chelydra serpentina, Chrysemys scripta elegans, and Terrapene carolina Linne, 1758 from southern Illinois (Martin, 1972); Ambystoma tigrinum Green, 1825 from Idaho (Watertor, 1967); and Sternotherus odoratus Latreille, 1801 from Louisiana (Bennett and Sharp, 1938); Kinosternon flavescens from Nebraska, HWML #20212 (Brooks and Mayes, 1976).

Telorchis corti, with ten synonyms, has been the most
problematical species. Part of the problem is that it is found in many different hosts, and exhibits extreme variability both in hosts of the same species and in hosts of different species. It also does not possess any autapomorphies that would make it immediately recognizable.

The characteristics used in the past to differentiate species are those that are now known to be plastic. These include such traits as the anterior and posterior extent of the vitelline follicles, position of ovary relative to cirrus sac, sucker size, pharynx size, esophagus length, body width, posterior extent of ceca, and whether the testes are contiguous or not. It is also interesting to note that in the description of each of these species, T. corti was always listed as the most similar species.

Examined specimens of T. diminutus and T. angustus (MacCallum, 1921) were found to be immature. Stunkard (1915) listed lobed testes as being one of the distinguishing characteristics for T. lobosus, but of the three specimens examined, only one was found to exhibit this trait. It appears to have been caused by distortion of the worm when it was fixed or mounted on the slide.

Telorchis bonnerensis has been considered most similar to T. corti, but was separated because it was found in salamanders, rather than turtles, and because it differed in the anterior extent of the vitelline follicles, distance of the ovary from the cirrus sac, and in egg size (Waitz, 1960). Watertor (1967) found that all of these characteristics are
highly variable, and that *T. bonnerensis* will mature in turtles. She concluded that the characteristics of *T. corti* overlapped the measurements of *T. bonnerensis* developing in the same hosts, in all criteria heretofore employed to differentiate these two species, but did not propose a synonymy. My study confirms Watertor's conclusions. I therefore designate *T. bonnerensis* a junior subjective synonym of *T. corti*.

**Telorchis auridistomi Byrd, 1937**

[figure 10]

SYNONYMS: *Cercorchis auridistomi* Byrd, 1937.

HOSTS: *Farancia abacura* Holbrook, 1836, the red-bellied mud snake.

LOCALITIES: Payne's Prairie, vicinity of Gainesville, Florida.

SPECIMENS MEASURED: 5, HWML No. 20896.

TAXONOMIC CHARACTERISTICS: Body elongate, 2.1-2.5 mm long; ratio of length to width 8-10.7:1 (x=9:1). Oral sucker with anterolateral lappets; 227-247 in diameter. Pharynx 67-78 in diameter; ratio of oral sucker width to pharynx width 1:0.29-0.32 (x=1:0.30). Esophagus 43-47 long, 2% TBL. Cecal bifurcation 11-17% TBL from anterior end; ceca extend well past testes, 0.7-1.5% TBL from posterior end. Acetabulum 122-129 in diameter. Forebody 22-27% TBL. Ratio of oral sucker width to acetabular width 1:0.5-0.57 (x=1:0.53).

Testes spherical to ovoid, tandem, contiguous, intercecal; posttesticular space 3-5% TBL. Cirrus sac ends partway down to just posterior to ovary. Genital pore ventral, preacetabular,
slightly left of median.

Ovary 37-43% TBL from anterior end, intercecal, spherical to ovoid. Seminal receptacle small; Laurer's canal not observed; Mehlis' gland present. Space occupied by uterus 48-51% TBL; metraterm 2/3 length of cirrus sac. Vitelline follicles continuous lateral bands; extend anteriorly from just anterior to just posterior to ovary, posteriorly from just anterior to partway down testes. Eggs 33-36 long by 15 wide.

Anterior extent of excretory vesicle at ovarian level.

REMARKS: The specimens from which this species was originally described were collected from *Farancia abacura* Holbrook, 1836 at Harvey, Louisiana.

Stunkard and Franz (1977) erected a new genus, *Paratelorchis*, to accommodate *T. auridistomi*. They justified this decision on the basis of the anterolateral lappets on the oral sucker, and vitelline follicles that overlap the ceca. Since the vitelline follicles of other telorchiids overlap the ceca, and the oral lappets are considered an autapomorphy for the species, a separate genus is considered to be unnecessary.

*Telorchis angustus* Stafford, 1905

[figure 11]

SYNONYMS: *Distomum angustum* Stafford, 1900; *Telorchis* (*Protenes*) *angustus* Barker and Covey, 1911; *Telorchis* (*Protenes*) *leptus* Barker and Covey, 1911; *Protenes angustus* Stunkard, 1915; *Protenes chapmani* Harwood, 1932; *Protenes vitelloidosus* Bennett, 1935.
HOSTS: *Chrysemys picta* Schneider, 1837, painted turtle; *Chrysemys scripta elegans* Wied, 1839, red-eared turtle; *Chrysemys picta marginata* Agassiz, 1857, midland painted turtle. LOCALITIES: Rosenberg, Texas; "Ohio"; Baton Rouge, La.; Unknown (New York Aquarium).


TAXONOMIC CHARACTERISTICS: Body elongate, 3.1-4.5 mm long; ratio of length to width 6-9.6:1 (x=7.6:1). Oral sucker 105-176 in diameter. Pharynx 61-96 in diameter; ratio of oral sucker width to pharynx width 1:0.5-0.75 (x=1:0.63). Esophagus 121-242 long, 4-6% TBL. Cecal bifurcation 11-14% TBL from anterior end; ceca extend well past testes, 1-6% TBL from posterior end. Acetabulum 61-165 in diameter. Forebody 22-25% TBL. Ratio of oral sucker width to acetabular width 1:0.58-0.94 (x=1:0.73).

Testes spherical to elliptical, tandem, contiguous, intercecal; posttesticular space 7-13% TBL. Cirrus sac ends just anterior to just posterior to acetabulum. Genital pore dorsal, lateral to left cecum, just posterior to cecal bifurcation.

Ovary 31-38% TBL from anterior end, intercecal, spherical to ovoid. Seminal receptacle small; Laurer's canal not observed; Mehlis' gland present. Space occupied by uterus 62-66% TBL; metraterm 1/2 to 3/4 length cirrus sac. Vitelline follicles continuous lateral bands; extend anteriorly midway between acetabulum and ovary to just posterior to ovary, posteriorly 3/4 distance acetabulum to ovary to partway down
testes. Eggs 31-41 long by 16-24 wide.

Anterior extent of excretory vesicle 1/2 to 2/3 acetabulum to ovary.

REMARKS: This species has also been reported from Chrysemys marginata at St. Peter, Minnesota (Barker and Covey, 1911) and Chrysemys picta from Atkinson Lake, Nebraska (Brooks and Mayes, 1976).

The four putative species of Protenes have been differentiated on the basis of the ovary position, presence or absence of a Laurer's canal, size, length of cirrus sac, and extent of vitelline follicles. The presence or absence of a Laurer's canal is not a reliable characteristic, as it is extremely difficult to locate. The other characteristics are known to vary intraspecifically. Wharton (1940) concluded that there was probably only one valid species. The present analysis supports this conclusion.

Barker and Covey (1911) erected the genus Protenes to accommodate telorchiids possessing a genital pore that is dorsolateral to the left cecum, and a cirrus sac that extends only to the acetabular level. Since there is only one species, and these two unique traits can be considered autapomorphies for the species, placing this species in its own genus seems superfluous.

Telorchis scabrae Macdonald and Brooks, in press

[figure 12]

HOST: Chrysemys scripta scripta Schoepff, 1792, yellow-bellied
turtle.

LOCALITY: Unknown (New York Aquarium).


TAXONOMIC CHARACTERISTICS: Body elongate, 4.8-5.6 mm long; ratio of length to width 5.6-7.2:1 (x=6.5:1). Oral sucker 124-154 in diameter. Pharynx 66-77 in diameter; ratio of oral sucker width to pharynx width (1:0.46-0.55 (x=1:0.49). Esophagus 72-88 long, 2% TBL. Cecal bifurcation 6-7% TBL from anterior end; ceca extend well past testes, 3-5% TBL from posterior end. Acetabulum 121-150 in diameter. Forebody 11-14% TBL. Ratio of oral sucker width to acetabular width 1:0.85-0.97 (x=1:0.95).

Testes spherical to subcircular, tandem, not contiguous, intercecal; posttesticular space 6-9% TBL. Cirrus sac 578-825 long, extremely robust and muscular; extending posteriorly about 2/3 distance from acetabulum to ovary; containing slightly coiled seminal vesicle, elongate prostatic complex and eversible cirrus. Genital pore ventral to left cecum, equal or anterolateral to acetabulum.

Ovary 31-36% TBL from anterior end, intercecal, ovoid to elliptical. Seminal receptacle small; Laurer's canal not observed; Mehlis' gland present. Descending and ascending loops of uterus confined to area between ovary and testes; space occupied by uterus 45-48% TBL; metraterm equal to 1/2 length of cirrus sac. Vitelline follicles continuous lateral bands; extend from 2/3 to 4/5 ovary to testes to midway between acetabulum and ovary. Eggs 30-31 long by 14-17 wide.

Anterior extent of excretory vesicle not observed;
excretory pore terminal.

REMARKS: MacCallum (1919) gave these specimens a label name, but never formally described them. This species most closely resembles *T. chelopi* by possessing a robust, muscular cirrus sac, but lacks the prominent pharyngeal glands and thickened cecal epithelial lining of that species. It can be distinguished from all other telorchiids by the position of the genital pore, which is ventral to the left cecum.

No other specimens of *Telorchis scabrae* have ever been reported. The host occurs from southeastern Virginia to northern Florida (Conant, 1975), so this species of *Telorchis* probably occurs there.

*Telorchis chelopi* MacCallum, 1919

[figure 13]

SYNONYMS: *Telorchis gutturosi* Brooks and Mayes, 1976, new synonym.

HOSTS: *Clemmys insculpta* Le Conte, 1830, wood turtle; *Chrysemys scripta scripta* Schoepff, 1792, yellow-bellied turtle; *Chrysemys picta* Schneider, 1873, painted turtle.

LOCALITY: Unknown (New York Aquarium).

SPECIMENS MEASURED: 29, USNM Helm. Coll. Nos. 25265, 35265, 36174, 36176, 73522, 73523; HWML #20231.

TAXONOMIC CHARACTERISTICS: Body elongate, 4.8-7.1 mm long; ratio of length to width 4.6-8.8:1 (x=5.7:1). Oral sucker 209-314 in diameter. Pharynx with prominent pharyngeal glands, 94-209 in diameter; ratio of oral sucker width to pharynx width 1:0.41-
0.75 (x=1:0.59). Esophagus 11-116 long, 0.7-2.6% TBL. Cecal bifurcation 8-16% TBL from anterior end; ceca extend well past testes, 1.5-6% TBL from posterior end; cecal epithelium thickened at bifurcation. Acetabulum 132-220 in diameter. Forebody 15-29% TBL. Ratio of oral sucker width to acetabular width 1:0.55-0.9 (x=1:0.73).

Testes spherical to elliptical, tandem, contiguous, intercecal; posttesticular space 7-16% TBL. Cirrus sac extremely robust and muscular; ends partway down to just posterior to ovary. Genital pore ventral, preacetabular, intercecal; median or slightly left of median.

Ovary 26-41% TBL from anterior end, intercecal, spherical to ovoid. Seminal receptacle and Laurer's canal not observed; Mehlis' gland present. Space occupied by uterus 44-52% TBL; metraterm 2/3 length of cirrus sac. Vitelline follicles continuous lateral bands; extend anteriorly from posterior of ovary to just anterior to ovary, posteriorly 4/5 distance from ovary to testes to partway down anterior testis. Eggs 32-40 long by 12-20 wide.

Anterior extent of excretory vesicle from ovarian level to between acetabulum and ovary.

REMARKS: Wharton (1940) synonymized Telorchis chelopi with T. corti. However, not only is T. chelopi considerably larger, it possesses two autapomorphies, prominent pharyngeal glands and a thickened epithelium, that are quite distinctive. It also possesses a robust, muscular cirrus sac, which T. corti does not.
Brooks and Mayes (1976) described *T. gutturosi* from *Graptemys pseudogeographica* collected at Atkinson Lake in Nebraska. Type specimens of *T. gutturosi* appear to be less than fully mature *T. chelopi*.

**Telorchis robustus** Goldberger, 1911

[figure 14]

SYNONYMS: *Cercorchis robustus* Goldberger, 1911.

HOSTS: *Terrapene carolina* Linne, 1758, box turtle.

LOCALITIES: Great Falls, Md.; Wood's Hole, Mass.; Piscataway, Md.; Mount Vernon, Va.; "Louisiana".


TAXONOMIC CHARACTERISTICS: Body elongate, 6.6-15.1 mm long; ratio of length to width 5.1-9.5:1 (x=7.6:1). Oral sucker 209-407 in diameter. Pharynx 110-209 in diameter; ratio of oral sucker width to pharynx width 1:0.44-0.70 (x=1:0.55). Esophagus absent. Cecal bifurcation 3-6% TBL from anterior end; ceca extend well past testes, 0.7-2% TBL from posterior end. Acetabulum 132-319 in diameter. Forebody 14-32% TBL. Ratio of oral sucker width to acetabular width 1:0.63-0.91 (x=1:0.79).

Testes spherical to elliptical, tandem, not contiguous, intercecal; posttesticular space 3-7% TBL. Cirrus sac ends just anterior to partway down ovary. Genital pore ventral, preacetabular, intercecal, slightly left of median.

Ovary 45-58% TBL from anterior end, intercecal, spherical to elliptical. Seminal receptacle small; Laurer's canal not
observed; Mehlis' gland present. Space occupied by uterus 43-56% TBL; metraterm 1/2 to 2/3 length of cirrus sac. Vitelline follicles continuous lateral bands; extend anteriorly from just anterior to acetabulum to 4/5 distance acetabulum to ovary, posteriorly from midway between ovary and testes to just anterior to testes. Eggs 24-30 long by 11-16 wide.

Anterior extent of excretory vesicle at acetabular level.

REMARKS: Bennett and Sharp (1938) reported this species from *Sternotherus odoratus* in Louisiana. It was also reported by Brooks (1979b) from *Sternotherus carinatus* Gray, 1856 at Richland Parish, Louisiana.

**Telorchis singularis** Bennett, 1935

[figure 15]

SYNONYMS: *Cercorchis singularis* Bennett, 1935.

HOSTS: *Chrysemys scripta elegans* Wied, 1839, red-eared turtle; *Chrysemys scripta scripta* Schoepff, 1792, yellow-bellied turtle.

LOCALITIES: Baton Rouge, La.; Lake Conway, Arkansas.


TAXONOMIC CHARACTERISTICS: Body filiform, 8.7-9.8 mm long; ratio of length to width 8.7-9.8:1 (x=7.8:1). Oral sucker 154-220 in diameter. Pharynx 110-143 in diameter; ratio of oral sucker width to pharynx width 1:0.65-0.86 (x=1:0.74). Esophagus 77 long, 1% TBL. Cecal bifurcation 6% TBL from anterior end; ceca extend well past testes, 1% TBL from posterior end. Acetabulum 143-198 in diameter. Forebody 18-28% TBL. Ratio of oral sucker width to acetabular width 1:0.9-0.93 (x=1:0.91).
Testes ovoid to elliptical, tandem, not contiguous, intercecal; posttesticular space 2-5% TBL. Cirrus sac ends just anterior to partway down ovary. Genital pore ventral, preacetabular, intercecal, median or slightly left of median. Common genital atrium present.

Ovary 57-59% TBL from anterior end, intercecal, spherical to elliptical. Seminal receptacle and Laurer's canal not observed; Mehlis' gland present. Space occupied by uterus 43-48% TBL; metraterm 1/2 length of cirrus sac; possessing a muscular bulb. Vitelline follicles continuous lateral bands; extend anteriorly 1/3 to 1/2 distance acetabulum to ovary, posteriorly just anterior to partway down testes. Eggs 24 long by 16 wide.

Anterior extent of excretory vesicle to Mehlis' gland.

Telorchis attenuatus Goldberger, 1911

SYNONYMS: Cercorchis attenuatus Goldberger, 1911.

HOSTS: Chrysemys picta Schneider, 1873, painted turtle.

LOCALITIES: Lake Maxinkuckee, Indiana; Atkinson Lake, Nebraska.


TAXONOMIC CHARACTERISTICS: Body filiform, 10.2-11.6 mm long; ratio of length to width 11.4-17.2:1 (x=15.8:1). Oral sucker 143-185 in diameter. Pharynx 88-102 in diameter; ratio of oral sucker width to pharynx width 1:0.49-0.62 (x=1:0.56). Esophagus 90-123 long, 0.8-1.2% TBL. Cecal bifurcation 4% TBL from
anterior end; ceca extend well past testes, 0.34-1.4% TBL from posterior end. Acetabulum 118-165 in diameter. Forebody 14-19% TBL. Ratio of oral sucker width to acetabular width 1:0.66-0.88 (x=1:0.75).

Testes spherical to ovoid, tandem, not contiguous, intercecal; posttesticular space 3-5% TBL. Cirrus sac ends 1/2 to 2/3 distance acetabulum to ovary. Genital pore ventral, preacetabular, intercecal, slightly left of median.

Ovary 50-55% TBL from anterior end, intercecal, spherical to ovoid. Seminal receptacle present; Laurer's canal not observed; Mehlis' gland present. Space occupied by uterus 63-66% TBL; metraterm 2/5 to 1/2 length of cirrus sac. Vitelline follicles continuous lateral bands; extend anteriorly 1/3 to 4/5 distance acetabulum to ovary, posteriorly 3/4 to 5/6 distance ovary to testes.

Anterior extent of excretory vesicle to 1/3 distance acetabulum to ovary.

**SPECIES INQUIRENDA**

*Telorchis compactus* Cable and Sanborn, 1970 [figure 17], described from *Emydoidea blandingi*, is of uncertain status at this time. Five morphological features that are partially diagnostic of the genus *Telorchis* are the uterine configuration, the shape of the ovary, the position of the ovary relative to the acetabulum, the shape of the testes, and the position of the testes. *Telorchis compactus* does not conform to the diagnosis of *Telorchis* in any of these character traits; furthermore, it
differs by living in the oviducts rather than the intestine of the turtle host.

What needs to be determined, then, is whether T. compactus could be an aberrant telorchiid (as suggested by Cable and Sanborn, 1970), or if it belongs in a separate genus. One way to decide will be to look for evidence of relationship from life history studies, which is beyond the scope of this study.

KEY TO THE SPECIES OF TELORCHIS

1a. Vitelline follicles clustered in groups; acetabulum larger than oral sucker............................................. 2
1b. Vitelline follicles in continuous lateral bands; acetabulum smaller than or equal to oral sucker......... 3
2a. Ratio of body length to body width less than 4:1................................................................. T. sirenis
2b. Ratio of body length to body width greater than 4:1............................................................. T. stunkardi
3a. Ovary closer to acetabulum than testes...................... 4
3b. Ovary closer to testes than acetabulum......................... 9
4a. Oral sucker lacking anterolateral lappets...................... 5
4b. Oral sucker with anterolateral lappets...... T. auridistomi
5a. Genital pore preacetabular, median or slightly left..... 6
5b. Genital pore ventral or dorsolateral to left cecum...... 7
6a. Ovigerous specimens 4.8 mm or more in body length...... 8
6b. Ovigerous specimens 4.5 mm or less in body length......

................................................................. T. corti
7a. Genital pore dorsal, lateral to left cecum............. T. angustus
7b. Genital pore ventral to left cecum.................. T. scabrae
8a. Esophagus present................................. T. chelopi
8b. Esophagus lacking................................. T. robustus
9a. Metraterm with muscular bulb..................... T. singularis
9b. Metraterm lacking muscular bulb.................. T. attenuatus

PHYLOGENETIC ANALYSIS

A phylogenetic analysis based on 22 character states comprising 20 homologous series produced a single tree [figure 18]. This phylogenetic tree represents the most parsimonious hypothesis of the phylogenetic relationships among North American telorchiids. The consistency index (Kluge and Farris, 1969), a goodness of fit measure, is 95%, indicating a low level of parallel and convergent evolution among the characters used. There is only one homoplasic characteristic in the analysis, a parallelism in characters 12 and 13.

The occurrence of T. angustus and T. auridistomi in a polytomy with T. corti is a further indication that they are telorchiids, and should therefore not be placed in separate genera. It is desirable for the classification of a group to reflect the phylogenetic relationships, or history of descent, of that group. The phylogenetic tree indicates that these two species and the rest of the telorchiids evolved from a common ancestor. If T. angustus and T. auridistomi are placed in separate genera, the genus Telorchis will be rendered paraphyletic, and thus not contain all of the descendents of the
common telorchiid ancestor. In order for the classification to reflect the phylogeny, the genera Protenes and Paratelorchis must not be used.

DISCUSSION

CLASSIFICATION

The results of this study support the placement of the North American telorchiid species in the single genus Telorchis. Characters previously used to divide the group into two separate genera, Telorchis and Cercorchis, have been shown to exhibit pronounced morphological variation. Since individuals from a single species may possess the "Telorchis" morphology for one characteristic, and the "Cercorchis" morphology for another, there is no justification for separate genera.

There is also no support for the monotypic genera Protenes, for Protenes angustus, and Paratelorchis, for Paratelorchis auridistomi. Although these species possess characteristics that are distinctive and unique, they also possess all of the characteristics that are diagnostic of the genus Telorchis. Their possession of autapomorphies does not require them to be placed in a separate genus. Furthermore, their placement in the middle of the phylogenetic tree supports their membership in Telorchis. If they are given generic status, Telorchis would have to be broken down into many small genera.
EVOLUTIONARY HISTORY

There are three main aspects of the evolutionary history of parasites that can be examined once a phylogenetic study has been done. These questions are: (a) "Where do the parasites occur?", which is a study of the biogeography of the organisms; (b) "In what hosts are they found?", which examines host-parasite relationships and coevolution; and (c) "What functional and/or structural attributes are relevant to the host-parasite relationship?", which may help to explain unique or unusual relationships.

A. BIOGEOGRAPHY

The biological history of organisms and the geological history of the areas in which they occur can be examined for congruence in their evolutionary trees. This type of analysis, called vicariance biogeography (see Croizat et al., 1974; Nelson and Platnick, 1981; Cracraft, 1983), has been utilized for a number of helminth groups (see Brooks, 1985a for a review; also Bandoni and Brooks, in press).

A biogeographic analysis of Telorchis is not feasible at this time. Incomplete collecting and a lack of voucher specimens make this type of analysis difficult. For example, a map of confirmed localities for T. corti is shown in figure 19. All reported localities, many of which cannot be confirmed, are shown in figure 20. In addition, about half of the specimens examined were taken from turtles at the New York Aquarium; the
exact localities for these specimens are unknown. Until more extensive, carefully documented collecting is carried out, there is not enough information to conduct vicariance studies.

B. HOST-PARASITE RELATIONSHIPS

Using phylogenetic systematics, it is possible to determine the degree to which contemporaneous host-parasite relationships reflect long-standing associations between the host group and the parasite group. This methodology has been employed for a number of coevolution studies (for a review see Brooks, 1985a).

The term coevolution encompasses two phenomena, co-speciation and co-accommodation. Co-speciation refers to the existence of congruence between host and parasite phylogenies as a result of concomitant speciation (Brooks, 1979a). This implies that cladogenesis of the parasite species occurred as a result of, or concomitant with, host cladogenesis. What you would expect to find, then, if co-speciation plays a major role in these relationships, is congruence between host phylogeny and parasite phylogeny. Co-accommodation refers to the relationship between a parasite species and its host during the period in which the parasite exhibits no cladogenesis (Brooks, 1979a). Both co-speciation and co-accommodation will be addressed with respect to Telorchis phylogeny.

A parasite may occur in a particular host as a result of one of two processes: colonization, which would indicate a recent association, or coevolution, which is indicative of an ancient association (Brooks, 1980). In colonization, or host-
switching, associations arise by chance. Such a pattern is inconsistent with the non-random associations that are generally observed (Brooks, 1981). This is not to say that colonization does not occur; indeed, many contemporaneous host-parasite associations can only be explained in terms of a host-switch. Also, any instance of host-parasite coevolution must have begun with a colonization of the host's ancestor by the parasite's ancestor. Nevertheless, the congruence between host and parasite phylogenies provides evidence that hosts and their parasites have evolved together (Brooks, 1979a, 1980, 1981).

The two most plesiomorphic North American telorchiid species are *Telorchis sirenis* and *T. stunkardi*. These species usually utilize salamanders rather than turtles as hosts, although *T. stunkardi* has been reported from turtles. Even though telorchiids are generally considered to be turtle parasites, the occurrence of the most plesiomorphic species in amphibians is not inconsistent with a coevolutionary hypothesis.

A partial phylogenetic tree of North American freshwater turtles, including only those taxa from which telorchiids have been reported, is shown in figure 21. When the parasite species are mapped onto this host phylogeny, five of the eight species found in amniotes show phylogenetic congruence [figure 22]. These species are considered to have co-speciated.

The consistency index for the tree in figure 22a is only 83% (5/6). The reason that the consistency index is not 100%, as might be expected, is that *Telorchis robustus* [C in figure 22a] appears to have evolved by co-speciation, and then
colonized another host. Although *Telorchis robustus* is usually found in *Terrapene carolina*, it has been reported from *Sternotherus carinatus* (Brooks, 1979b) and *S. odoratus* (Bennett and Sharp, 1938) [II in figure 22a]; these hosts are inconsistent with the co-speciation hypothesis. However, considering that all three host species exhibit habitat overlap, the most likely explanation for this phenomenon is that *T. robustus* coevolved with *Terrapene carolina*, and has since colonized *Sternotherus carinatus* and *S. odoratus*.

The other three species are not congruent with an hypothesis of co-speciation [see figure 23]. One of these species, *T. auridistomi*, is postulated to have arisen via a host-switch from turtles to snakes. *T. scabrae* and *T. angustus* are postulated to have evolved via sympatric speciation. The hypotheses of evolution for these species will be discussed in more detail later.

Brooks (1979a) defined co-accommodation as the relationship between a parasite species and its host during the period in which the parasite lineage exhibits no cladogenesis. This involves primarily the phenomenon of host specificity. Price (1980) and Rohde (1982) divide host specificity into two distinct areas, the host range of a parasite, and the specificity of a parasite.

Host range is defined as the number of host species for a certain parasite species irrespective of the frequency or intensity of infection (Rohde, 1982). Many parasites exhibit rather general host requirements, and may become established in
a wide variety of hosts without undergoing speciation (broad co-accommodation or broad host range). Alternatively, other parasites have very specific host requirements, and can survive only in the hosts with which they have co-speciated (narrow co-accommodation or narrow host range) (Brooks, 1979a).

Specificity is defined as the frequency with which a particular host species is infected (Rohde, 1982). Even parasites found in many host species usually infect one or a few species more heavily than others. For example, even though Telorchis corti has been reported from turtles, snakes, and salamanders, it is collected most frequently from, and is considered to be primarily a parasite of, turtles.

There are three predictions that can be made about the relationship between host specificity and evolutionary history. The traditional view predicts that as primarily coevolved parasites become more highly derived, their host specificity will become more pronounced (Brooks, 1979a, 1985b). When host specificity is said to be pronounced, specificity increases as the host range narrows. This does not necessarily mean that host range and specificity are always inversely proportional [see figure 25], although this does seem to be the predominant observation. There is also the possibility that as parasites become more highly derived, specificity becomes less pronounced; this particular situation does not seem to have ever been observed. The third prediction is that host specificity has no correlation with history.

The present analysis supports the traditional view of host
specificity; as primarily coevolved telorchiids become more highly derived, host specificity becomes more pronounced [see figure 26]. *Telorchis corti*, which is considered to be the relatively most plesiomorphic species among those inhabiting amniotes, has the greatest host range. It has been reported from 15 different host species, including two species of salamander and one species of snake. This particular species also exhibits low specificity; even though it seems to occur most frequently in turtle hosts, there does not seem to be one particular species of turtle that is preferentially infected.

Elsewhere on the tree, *Telorchis attenuatus*, one of the relatively most derived species, exhibits the most pronounced host specificity, occurring in only one host species, *Chrysemys picta*. In this case, the host range is very narrow and the specificity is very pronounced. The general trend in the telorchiids, then, has been an increase in specificity as the parasites become more highly derived, with a subsequent decrease in host range. *T. auridistomi*, *T. angustus*, and *T. scabrae*, because they did not coevolve with their hosts, do not follow this pattern.

C. FUNCTIONAL/STRUCTURAL ATTRIBUTES

*Telorchis auridistomi* is geographically sympatric with other telorchiids, but is not found in any turtle hosts (i.e. it is *allohospitalic* with other telorchiids). This species has been collected exclusively from *Farancia abacura*, the mud snake, yet it is closely related to telorchiid species found in
turtles. The presence of *T. auridistomi* in a snake host cannot be explained in terms of coevolution. It is therefore postulated to have arisen via a host-switch from turtles to snakes.

The closest relatives of *T. auridistomi* are *T. corti* and *T. angustus*. Although *T. corti* is predominantly a turtle parasite, it has been collected in *Thamnophis sirtalis*, the common garter snake (Waitz, 1960). In addition, the geographical ranges of *Farancia abacura*, *Thamnophis sirtalis*, and some of the turtle hosts overlap to some extent (Conant, 1975).

Since the geographical ranges of the various host species overlap to some extent, they would most certainly come in contact with one another. It seems likely, then, that at some time in the past, the ancestor of *T. auridistomi* was able to colonize snakes from turtles, via a host-switch. Whether or not this ancestor is *T. corti* is unknown. The contemporary morphology of *T. auridistomi* is a result of subsequent speciation with the colonized host.

Both *Telorchis scabrae* and *T. angustus* occur in hosts that are also inhabited by their closest relatives. *T. scabrae* is most closely related to *T. chelopi*; both are found in *Chrysemys scripta scripta*. *T. angustus* is a sister species of *T. corti*; these species have two common hosts, *Chrysemys picta* and *Chrysemys scripta elegans*. Parasites that exhibit this type of relationship are said to be synhospitalic.

When a host species is infected by two or more sister-
species of parasites, it is possible that the co-occurrence of the parasite species is the result of sympatric speciation from some ancestral species, unless allopatry and vicariance can be shown (Brooks, 1979a). In this case, the sister-species are sympatric and synhospitalic. This implies that the parasite has speciated but the host has not.

The major difference between T. scabrae and T. angustus and their sister-species is their genital pore morphology. Hermaphroditic digeneans mate by aligning their genital pores and exchanging gametes. Most telorchiids possess a genital pore that is preacetabular and median or slightly left of median. The genital pore of T. scabrae is ventral to the left cecum, while that of T. angustus is dorsolateral to the left cecum. These changes in genital pore position make it difficult to align genital pores with other telorchiids and could lead to mechanical pre-mating isolation. Subsequently, T. scabrae and T. angustus could have evolved independently from their closest relatives while inhabiting the same host.

CONCLUSIONS

The hypothesis of the evolutionary history of the North American species of Telorchis is summarized in figure 27. T. sirenis and T. stunkardi, the two most relatively plesiomorphic species, are found in salamanders. T. corti, T. chelopi, T. robustus, T. singularis, and T. attenuatus are believed to have co-speciated with North American freshwater chelonians. The more highly derived a species is in this group, the more
pronounced the host specificity. *T. auridistomi* is postulated to have evolved via sympatric speciation due to a host-switch from turtles to snakes. *T. scabrae* and *T. angustus* appear to be the result of sympatric speciation due to the evolution of autapomorphies causing mechanical pre-mating isolation.

There is a need for additional taxonomic and experimental studies of telorchiids. Further experimental work on host-induced variation and host-specificity would enhance the present analysis. Hybridization experiments might provide some additional information on the sympatric species. Finally, more thorough collecting of North American and worldwide *Telorchis* species would supply the information on distribution patterns that would make vicariance studies possible, thus providing a further test of the relationship between telorchiids and their hosts.
REFERENCES CITED


APPENDIX A

Table I - Character data for Telorchis species

Codes 0, 1, and 2 identify particular characters. Code 0 indicates the plesiomorphic, or primitive state. Code 1 indicates a trait derived from 0; code 2 indicates a trait derived from 1.

<table>
<thead>
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<td>21100010110000001111</td>
<td>21100010110010011001</td>
</tr>
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</table>
Table II - Ranges of sucker to pharynx ratio for *Telorchis* species

**LEGEND:** Os=Oral sucker; Vs=Ventral sucker; Ph=Pharynx.

<table>
<thead>
<tr>
<th>Species</th>
<th>Os:Ph</th>
<th>Vs=Ph</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>T. sirenis</em></td>
<td>1:0.42-0.43</td>
<td>1:0.37-0.43</td>
</tr>
<tr>
<td><em>T. stunkardi</em></td>
<td>1:0.32-0.37</td>
<td>1:0.28-0.52</td>
</tr>
<tr>
<td><em>T. corti</em></td>
<td>1:0.41-0.66</td>
<td>1:0.48-0.88</td>
</tr>
<tr>
<td><em>T. auridistomi</em></td>
<td>1:0.29-0.32</td>
<td>1:0.52-0.64</td>
</tr>
<tr>
<td><em>T. angustus</em></td>
<td>1:0.50-0.75</td>
<td>1:0.53-1.00</td>
</tr>
<tr>
<td><em>T. scabrae</em></td>
<td>1:0.46-0.55</td>
<td>1:0.48-0.56</td>
</tr>
<tr>
<td><em>T. chelopi</em></td>
<td>1:0.41-0.75</td>
<td>1:0.49-0.92</td>
</tr>
<tr>
<td><em>T. robustus</em></td>
<td>1:0.44-0.70</td>
<td>1:0.46-1.00</td>
</tr>
<tr>
<td><em>T. singularis</em></td>
<td>1:0.65-0.86</td>
<td>1:0.70-0.77</td>
</tr>
<tr>
<td><em>T. attenuatus</em></td>
<td>1:0.49-0.62</td>
<td>1:0.53-0.84</td>
</tr>
</tbody>
</table>
Figure 1 - Body shapes of telorchiids

(a) oval body; (b) linguiform body; (c) elongate body; (d) filiform body (redrawn from Schell, 1970).
Figure 2 - Muscularity of cirrus sac

(a) muscular, robust cirrus sac; (b) long, thin cirrus sac.
Figure 3 - Position of cirrus sac

(a) at ovarian level; (b) midway between acetabulum and ovary; (c) at acetabular level.
Figure 4 - Position of genital pore

(a) preacetabular, slightly left of median; (b) ventral to left cecum; (c) dorsolateral to left cecum.
Figure 5 - Uterine configuration

(a) irregularly coiled; (b) coiled ascending and descending loops.
Figure 6 - Structure of vitelline follicles

(a) lateral, clustered groups; (b) continuous lateral bands.
Figure 7 - *Telorchis sirenis*, ventral view

Figure 8 - *Telorchis stunkardi*, ventral view
Figure 9 - Telorchis corti, ventral view
Figure 10 - Telorchis auridistomi, ventral view
Figure 11 - Telorchis angustus, ventral view
Figure 12 - *Telorchis scabrae*, ventral view

Figure 13 - *Telorchis chelopi*, ventral view

Figure 14 - *Telorchis robustus*, ventral view
Figure 15 - Telorchis singularis, ventral view
Figure 16 - Telorchis attenuatus, ventral view
Figure 17 - *Telorchis compactus*, ventral view
Figure 18 - Phylogenetic tree of North American Telorchis

LEGEND: (1) testes at posterior of body, tandem; (2) uterus coiled ascending and descending loops; (3) body elongate; (4) ratio of body length to body width greater than 4:1; (5) acetabular width less than oral sucker width; (6) vitelline follicles in continuous lateral bands; (7) oral sucker with anterolateral lappets; (8) cirrus sac ends at acetabular level; (9) genital pore dorsolateral to left cecum; (10) body length greater than 4.8 mm; (11) cirrus sac thick, muscular; (12) cirrus sac ends midway between acetabulum and ovary; (13) genital pore ventral to left cecum; (14) prominent pharyngeal glands; (15) thickened cecal epithelium at point of bifurcation; (16) cecal bifurcation less than 6% TBL from anterior end; (17) esophagus lacking; (18) body filiform; (19) ovary closer to testes than acetabulum; (20) metraterm with muscular bulb; (21) genital atrium present; (22) cirrus sac ends midway between acetabulum and ovary (the asterisk [*] indicates that this is a homoplasious character).
T. sirenis
T. stunkardi
T. corti
T. auridistomi
T. angustus
T. scabrae
T. chelopi
T. robustus
T. singularis
T. attenuatus
Figure 19 - Map of confirmed localities for *Telorchis corti*
Figure 20 - Map of reported localities for Telorchis corti
Figure 21 - Partial phylogenetic tree of turtle taxa

(Used with permission from Linda Dryden, Univ. of Kansas).
Figure 22 - Hypothesis of host-parasite coevolution

(a) Partial phylogenetic tree of turtle taxa, with the congruent (100% fit) parasite species mapped on. LEGEND: I = Kinosternon; II = Sternotherus; III = Chelydra; IV = Clemmys; V = Terrapene; VI = Deirochelys; VII = Emydoidea; VIII = Graptemys; IX = Chrysemys scripta scripta; X = Chrysemys scripta elegans; XI = Chrysemys picta.

(b) Phylogenetic tree of congruent parasite species.
Figure 23 - Partial phylogenetic tree of host taxa with secondarily evolved parasite species mapped on

LEGEND: I = Kinosternon; II = Sternotherus; III = Chelydra; IV = Clemmys; V = Terrapene; VI = Deirochelys; VII = Emydoidea; VIII = Graptemys; IX = Chrysemys scripta scripta; X = Chrysemys scripta elegans; XI = Chrysemys picta; XII = Farancia abacura.
Figure 24 - Phylogenetic tree of *Telorchis* species in amniotes

The broken lines indicate secondarily evolved species.
Figure 25 - Possible combinations of host range and specificity

Each box represents a different type of host; each dot is a parasite of the same species.
broad host range
low specificity

broad host range
high specificity

narrow host range
low specificity

narrow host range
high specificity
Figure 26 - Host specificity of *Telorchis* species in amniotes

Numbers in parentheses indicate the number of hosts that each species has been reported from. Note increasing host specificity among primarily coevolved species (I, V-VIII).

LEGEND: I= *Telorchis corti*; II= *Telorchis auridistomi*; III= *Telorchis angustus*; IV= *Telorchis scabrae*; V= *Telorchis chelopi*; VI= *Telorchis robustus*; VII= *Telorchis singularis*; VIII= *Telorchis attenuatus.*
[Diagram]

- (1) II
- (2) III
- (1) IV
- (4) V
- (3) VI
- (2) VII
- (1) VIII

\[\boxed{\text{secondarily evolved species}}\]
Figure 27 - Summary cladogram of the hypothesized evolutionary history of the North American species of Telorchis
T. sirenis (2)
T. stunkardi (6)
T. corti (15)
T. auridistomi (1)
T. angustus (2)
T. scabre (1)
T. chelopi (4)
T. robustus (3)
T. singularis (2)
T. attenuatus (1)