A New Species of Fluke, *Ascocotyle howei*, in the Context of Sibling Speciation

Richard D. Lumsden[+] and Mark H. Armitage[*]

Abstract

Ascocotyle (L.) howei, n. sp., is described from adults found in the intestines of naturally infected Colombian opossums, *Didelphis marsupialis* L. The new species is characterized by a distinctive flagon-shaped body, and 24-28 scalpel-shaped spines per row, arranged in two complete circumoral rows around a massive oral sucker. This new species most closely resembles A. *(L.) megalocephala* by way of a large oral sucker, a reduced pre-oral lip, a short ceca, and vitellaria which extend anteriorly to the level of the pharynx and posteriorly to the upper margin of the testes. Some characters, however, would place it in subgenus *Ascocotyle* or even *Phagicola*. In an introduction, the typical life histories and anatomical designations are reviewed for *Ascocotyle* trematodes, commonly referred to as flukes. Remarks concerning sibling speciation and its relevance to creation are summarized in the appendix.

Introduction

Parasitic trematodes such as the worm described in this study are classified as follows:

Kingdom:	Animalia
Phylum:	Platyhelminthes
Class:	Trematoda
Order:	Digenea
Family:	Heterophyidae Odhner 1914
Subfamily:	Centrocestinae Looss 1899
Genus:	*Ascocotyle* Looss 1899
Subgenus:	*Leighia* Sogandares-Bernal and Lumsden 1963
Species:	*howei* Lumsden and Armitage 1998 (this paper)

Typically, parasitic trematodes, or flukes mature as adults in birds, but prior to this they complete part of their life cycle in other organisms, such as snails and fish. There are many differing life cycles for trematodes, and a full discussion of these exceeds the present purpose. The life cycle for *Ascocotyle*, such as described in this study, however, requires a snail within the marsh or estuary as the first intermediate host, and a fish in the marsh as the second intermediate host. Fish eating birds and mammals which come to the marsh to feed, can serve as final or definitive hosts if they consume infected fish, and if they have the appropriate intestinal environment to harbor the maturing worm. The trematode, if not expelled by peristalsis or other factors in the definitive host, will begin to produce eggs, which then are fertilized by sperm, also produced by the same worm, allowing viable eggs to be passed over time into the rectum of the bird. The life cycle is completed when bird feces containing the fertilized and developing trematode eggs are deposited in the marsh. These then are available to the snail for ingestion.

Anatomical features of these flukes include a so-called ascot (AS), (an ascot is a scarf usually worn around the neck—this worm has a feature resembling an ascot, hence the name *Ascocotyle*), (Figure 7). Other anatomical traits include the size and shape of the oral (OS) and ventral (VS) suckers; the number, shape, and position of spines (SP) around the oral sucker and on the body surface; and the size, position and distribution of certain internal organs (vitelleria (VI), ceca (CE), testes (TE), ovary (OV), excretory bladder (EB), pharynx (PH) and esophagus (ES)). The foregoing anatomical characteristics are typically used by taxonomists to distinguish different species, subgenera, or genera of these microscopic worms from each other. In addition, the location of the estuary, the specific hosts employed, the site of infection, the size and shape of the cyst used to maintain a presence in the intermediate host, and many other factors may be used to compare and contrast the many varieties of these parasites from each other, i.e., to delineate the different species within these groups.

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[*] Mark H. Armitage, M.S., Division of Natural Science and Mathematics, The Master's College, 587 Ventu Park Road, #304, Thousand Oaks, CA 91320

[+] Richard D. Lumsden, Ph.D., deceased

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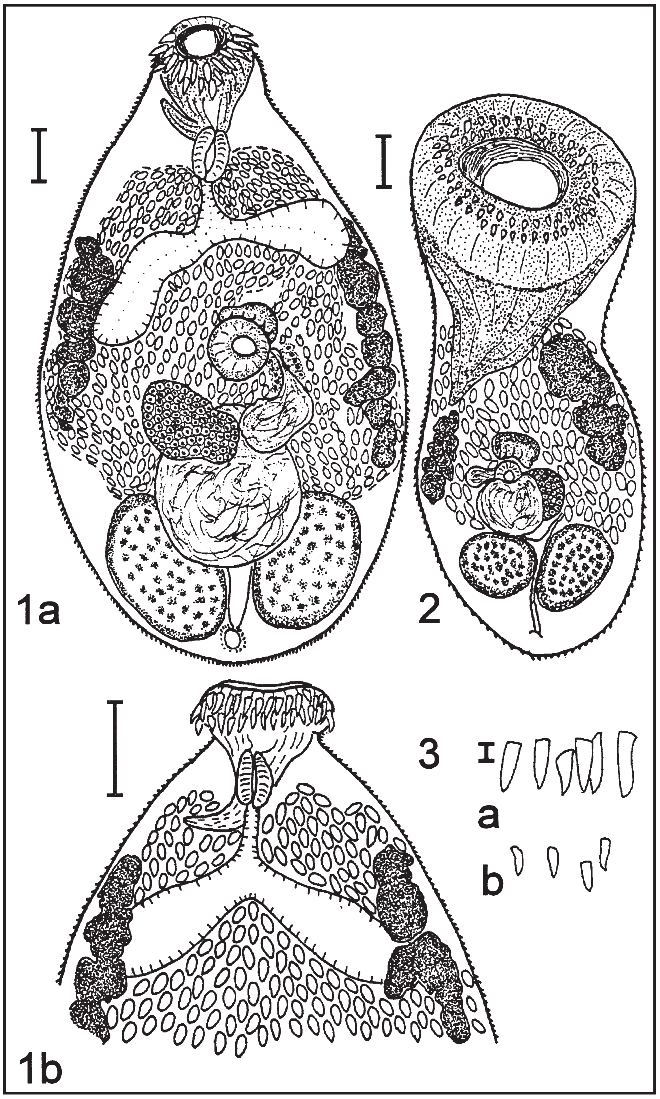

Figure 1. *Ascocotyle howei*, **n. sp. a. Ventral view of whole mount (scale is 75 µm). b. Forebody of a somewhat contracted specimen, with flattened oral sucker (scale is 110 micrometers).**

Figure 2. *A. megalocephala*, **dorsal view of whole mount (scale is 16 µm). (Drawn from Paratype #40158, U.S. Natl. Parasite Coll.).**

Figure 3. Spines of the circumoral coronet (dorsal and lateral views, scale is 12 µm). a. *A. howei* **b.** *A. megalocephala*.

To date, we are not aware of any biochemical studies which can clarify how closely "related" these different species are, although such may be useful in the future. In addition, as will be discussed in the appendix, the "reproductive isolation" test, which often is applied to similar organisms to determine if they are validly distinct species, may be inapplicable. This could be the case since these organisms are true hermaphrodites, bearing both testes which produce sperm and an ovary which produces eggs within the same individual.

Self-fertilization seems to be the typical reproductive path employed by ascocotylids, although some authors are convinced otherwise with respect to platyhelminths in general (Nollen 1983). Nothing in the ascocotylid literature indicates that cross-fertilization has ever been observed by any worker, so they are, by their very nature, "reproductively isolated." This would preclude their assignment into species designations purely on that basis. Recent observations by the junior author, however, may cast doubt on the long-held belief that ascocotylids are strictly self-fertilizing. For example, worms collected by Price in 1932, and deposited into the U.S. National Parasite Collection as type specimens (#40158, *Ascocotyle megalocephala* Price) now are shown to be joined at the acetabulum, suggesting that genetic exchange (by means of eggs or sperm) may be taking place (Figure 8).

Looss erected the genus *Ascocotyle* with *A. coleostomum* (Looss, 1899) as the genotype. Excluding synonyms, there are at present more than 30 named species comprising the Ascocotyle complex as defined per Travassos (1930), Stunkard and Uzmann (1955), Sogandares-Bernal and Bridgman (1960), and Sogandares-Bernal and Lumsden (1963).

According to the taxonomic scheme proposed by Sogandares-Bernal and Lumsden (1963), *Ascocotyle* Looss, 1899 is divisible into three subgenera: *Ascocotyle* Travassos, 1930; *Leighia* Sogandares-Bernal and Lumsden, 1963; and *Phagicola* Faust, 1920. The primary basis at present for this subgeneric organization is cercarial type. Because of the paucity of life history information at the time, most of the assignments to these subgenera were made on the basis of adult and metacercarial morphology (Sogandares-Bernal and Lumsden, 1963).

Specimens of some ascocotylid trematodes collected by Dr. Dale Little from Colombian opossums ca. 1975, and generously provided for the senior author's study, appear to represent a new species, which is designated *A. (L.) howei* and is described herein.

The following species description is based on 11 specimens fixed in 10% formalin, stained with Mallory's triple stain and whole mounted, and five specimens embedded in paraffin and sectioned. Measurements are in micrometers (µm). Drawings were made with the aid of a camera lucida.

Description

Ascocotyle (Leighia) howei, n. sp. (Figures 1a–1b). Body distinctively flagon-shaped, 740 to 817 long, 490 to 521 in maximum width (at midbody); completely spinose. Short neck terminates in an oral sucker , 108 to 179 in di-

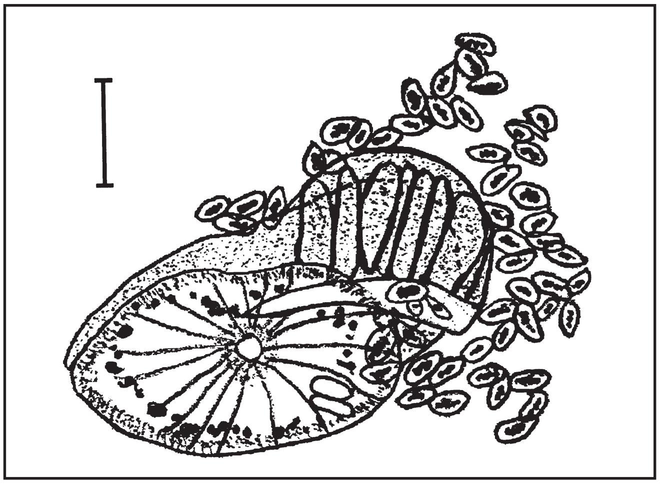

Figure 4. **Gonotyl,** *A. howei*, **(scale is 25 micrometers).**

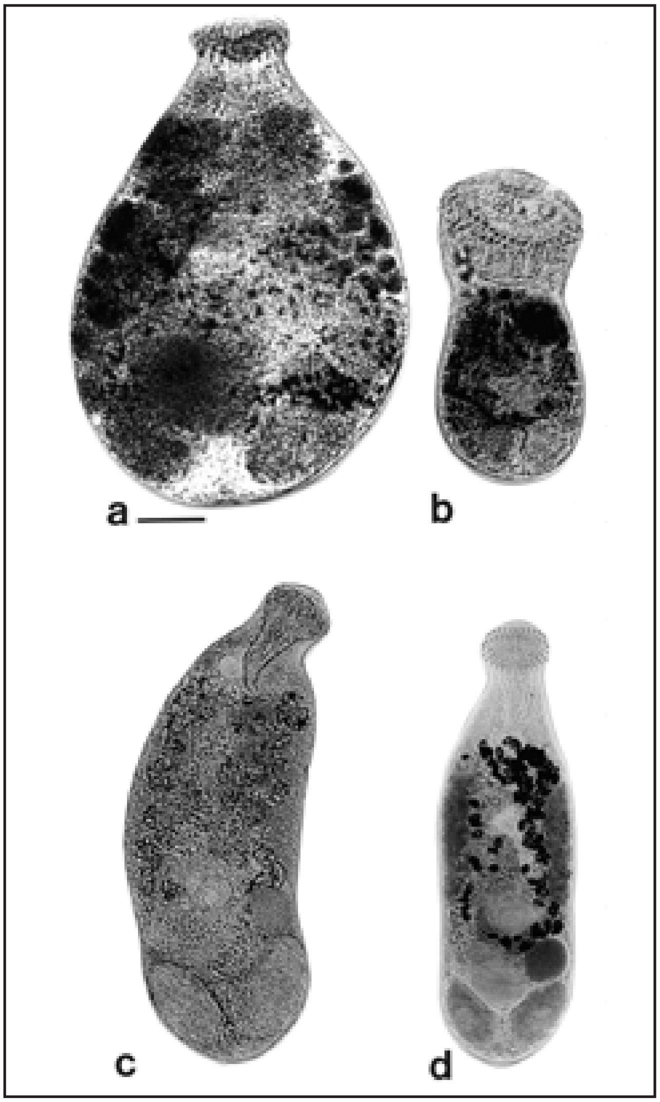

Figure 5. a. *A. howei* **(scale is 95 µm) b.** *A. megalocephala*. **(USNPC # 40158). c.** *A. sexidigita* **(Alan Hancock Foundation # AHF691). d.** *A. gemina* **(AHF # F-1-9-21-81).**

ameter, tapering into a caudally directed, conical muscular appendage. Pre-oral lip reduced or absent. Oral sucker with two complete rows of scalpel-shaped spines, 25 to 39 long by 5 to 9 wide at base, 24 - 28 per row. Pre-pharynx present. Pharynx ovoid to nearly cylindrical in shape, 58 to 87 long by 35 to 42 wide. Short esophagus bifurcates into two cecal pouches which do not generally extend past the acetabulum. Acetabulum equatorial, subspherical in shape, 78 to 83 in diameter, enclosed with gonotyl in a genital sac. Genital pore medial, immediately preacetabular. Gonotyl a single pad, immediately anterior to the acetabulum, sinestromedial bearing at least six digitiform pockets or lobes; followed by a more or less sigmoid-shaped seminal vesicle with sperm duct surrounded by prostatic gland cells. Testes broadly ovoid with mostly regular margins, in posterior region of hindbody, 185 to 220 long by 116 to 154 wide. Ovary dextral to body midline, pretesticular, ovoid, 108 to 135 long by 65 to 96 wide. Mehlis gland and Laurer's canal present. Seminal receptacle subspherical, 193 to 251 in diameter, postovarian, mediodextral. Gravid uterine coils extending from anterior margin of testes to pharynx, terminating at genital sac; uterus does not penetrate gonotyl. Eggs operculate, embryonated, 17 to 19 long by 7 wide.

Vitellaria generally preacetabular but often extending to pharynx, with 6 to 8 relatively large (50 to 116 by 38 to 85) ovate follicles twisted into a serpentine array on each side of body between ovary and cecal bifurcation. Excretory bladder intertesticular, globlet or tulip-shaped, with smooth margins. Excretory pore terminal with subjacent sphincter.

Taxonomic Summary

Type host: Opossum, *Didelphis marsupialis* L.
Type locality: vicinity of Cali, Colombia, S.A..
Site of infection: intestine.
Etymology: Named in honor of Dr. George F. Howe, in recognition of his contributions to the concept of sibling speciation.
Specimens deposited: Holotype and paratypes: Biosystematic Parasitology Laboratory, U.S.D.A., Bethesda, MD (Holotype USNPC No. 87600, Paratypes 87601).

Remarks

Adult morphology places *A. howei* in the subgenus *Leighia*, where it most closely resembles *A. megalocephala* (Figure 2, USNPC# 40158), in that it bears a large oral sucker, a reduced to absent pre-oral lip, ceca which do not descend past the acetabulum and vitellaria which generally are restricted between the testes and the

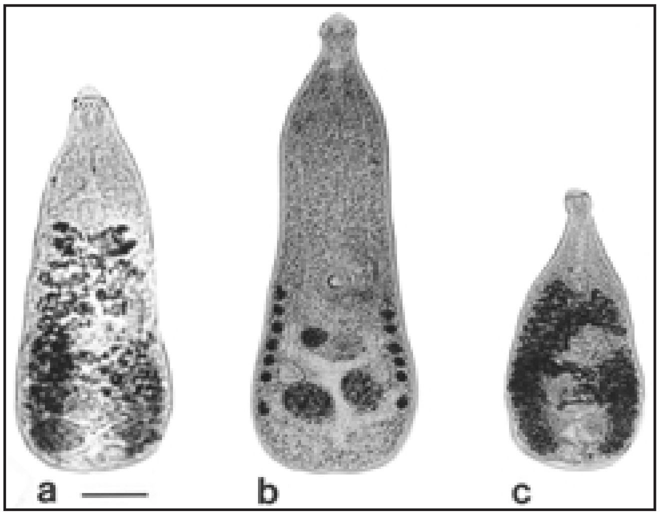

Figure 6. a. A. *(L.) mcintoshi* **(scale is 11 microns) (USNPC # 42211) b.** A. *(L.) chandleri* **(USNPC # 59894) c.** A. *(L.) hadra* **(USNPC # 84045).**

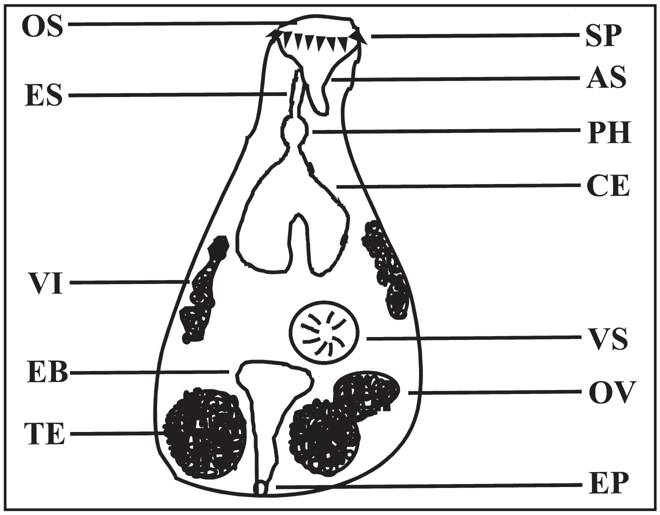

Figure 7. Taxonomic morphology of a typical *Ascocotyle* **parasite.**

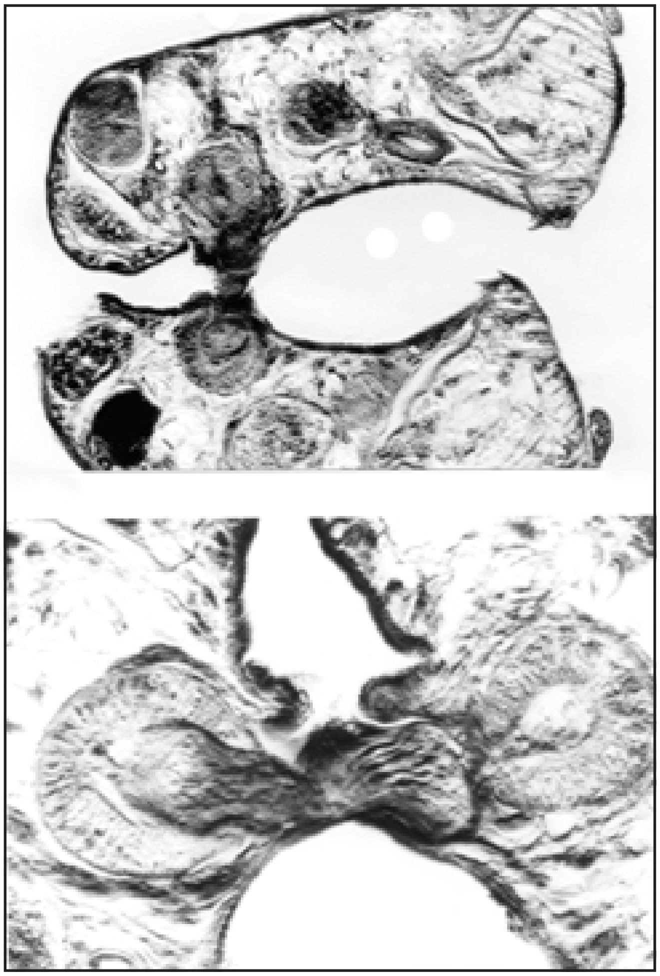

Figure 8. A. *megalocephala*, **serial section (Price 1932), worms joined at the acetabula.**

pharynx, although some of these features would place it in *Phagicola* or *Ascocotyle*. Alternately, the subgenus *Phagicola* is characterized by one single complete row of circumoral spines and a second incomplete or accessory row, in addition to an incompletely spinose body, among other traits which do not characterize A. *howei*.

The short ceca, and the vitelline distribution of A. *howei* fit well with the subgenus *Ascocotyle*, as represented by A. *sexigita* and A. *gemina*; yet the number of circumoral spines is generally fewer than expected for *Ascocotyle*. Additionally the vitellaria of A. *howei* extend anteriorly to the level of the pharynx but are disposed as large ovate follicles, versus the smaller and more numerous follicles, otherwise similarly distributed, in A. *sexidigita* and A. *gemina*.

In A. *megalocephala*, the most posterior extent of the vitellaria is the middle of the acetablum, versus A. *howei* where it is the ovary; in A. *sexidigita* and A. *gemina*, it is the posterior margin of the acetabulum. The margins of the excretory bladder in A. *howei* and A. *megalocephala* are evenly contoured (as they are also in A. *gemina* and A. *sexidigita*), versus the robustly lobate, or deeply scalloped configuration of the bladder evidenced by other members of the subgenus *Leighia*. Martin and Steele (1970) described the bladder of A. *sexidigita* as "scalloped," but our examination of the type specimens revealed a smooth margined structure with only a pair of *cul de sacs* extending laterally in the posttesticular region of the hindbody. In A. *howei*, the acetabulum is equatorial, versus subequatorial in A. *megalocephala* and its postequatorial position in other *Leighia* species. Much like the description of A. *nunezae* (Scholtz, Vargas-Vasquez, Vidal-Martinez, and Aguirre-Macedo, 1997), in which the authors lament, "The morphology of A. *(A.) nunezae*, which shares some features for all 3 subgenera of *Ascocotyle*, casts doubts upon the present classification of the subgenera within the genus *Ascocotyle*," the description of A. *(L.)*

howei, likewise muddies the taxonomic waters. We do point out, however, that contrary to the report by Scholtz et al. (1997), A. *megalocephala* does not exhibit "vitelline follicles confined to the post acetabular region," but rather vitelleria which can be found from the level of the testes to the pharynx, as also seen in A. *howei (*Figures 1a, 2 and 5a,b).

Price (1932) differentiated A. *megalocephala* from other ascocotylids on the basis of body shape. For this species, in particular, the present authors concur that this is a valid characteristic. In its distinctly flagon-shaped body, A. *howei* readily is distinguished from A. *megalocephala*, with its characteristically beaker-shaped form, and from the other species comprising the subgenus where the shape of the body is essentially cylindrical. Realizing that body shape frequently is impacted by the fixation protocol, the senior author believes, on the basis of his experience with the microtechnical preparation of A*scocotyle* spp., that the comparison of body morphotypes is valid. He also is aware that body shape may vary somewhat for otherwise putatively conspecific forms developing in different hosts (see, e.g., Sogandares-Bernal and Lumsden, 1963, regarding variant morphotypes of A *(P.) angrense*).

A. *howei* further differs from A. *megalocephala* in the number of circumoral spines (2 x 24-28 v. 2 x 36, respectively), and the oral sucker: acetabulum ratio (ca 2: 1 v. 5: 1, respectively). In other species of the genus A*scocotyle*, the sucker ratio is ca. 1 - 1.5 : 1. The circumoral spination for A. *sexidigita* and A. *gemina* is 2 x 28 - 32. Additionally in A. *howei*, the testes are more widely separated. In our opinion, this does not appear to be a function altogether of an anatomical response to fixation. As is the case for other species of *Leighia*, the gonotyl in A. *howei* and A. *megalocephala* bears digitiform lobes, or pockets, although the exact number of these structures and the presence (or absence) of supportive rodlets noted for some of the other species of this subgenus could not be resolved definitively in the specimens available in the present study. Gonotyl microstructure has been used to distinguish between A. *gemina*, and A. *sexidigita* by Font, Heard and Overstreet (1984) and is probably a valid species criterion, but such features are best discerned in live worms.

The geographic range of A. *megalocephala* is Puerto Rico (Price, 1932) westward to south Florida (Stein, 1968) (cf. the northwestern coast of Colombia, S.A., for A. *howei*); the only known definitive hosts for A. *megalocephala* are herons i.e. *Butorides* (cf.opossums for A. *howei*).

As exemplified by A. *angrense*, there are species of ascocotylids which infect both birds and mammals with equal facility and have an extensive (intercontinental) geographic range (Sogandares-Bernal and Lumsden, 1963). However, the possibility of at least strain differences within the context of this nominally singular species exists. Indeed, Ostrowski de Nunez (1993) contends that North American populations of "A. *angrense*" are a distinct species, A. *diminuta* (Stunkard and Haviland, 1924), which Sogandares-Bernal and Lumsden (1963) had reduced to synonomy with the species described by Travassos (1916) from specimens parasitizing *Butorides striata* in Brazil. Another synonym of A. *angrense*, A. *nana* (Ransom, 1920), appears to be a valid species based on life history data obtained by Font, Overstreet and Heard (1984). The broad range of definitive hosts reported for the *angrense* group may be a reflection of the short maturation time (Sogandares-Bernal and Lumsden, 1964) and the relatively non-specific requirements for the excystment of ascocotylid metacercariae (Stein, 1968).

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Appendix

Sibling species are morphologically similar or possibly almost identical natural populations of sexually reproducing organisms. They are held to be reproductively isolated, because they have never been observed to mate, even though they may inhabit the same locality. This definition has caused no small stir in taxonomic biology because morphotypes (shape characteristics) are thought to be passed down through generations by parental genes; yet morphologically "related" and almost identical organisms (sibling species) exist without the sharing of genes. Dobzhansky (1955) has stated, "The definition of species as reproductively isolated populations has, however, no meaning where sexuality is lost or where self-fertilization is the usual or exclusive method or begetting progeny." We know that even though there is a distinct possibility that A*scocotyle* worms share genes (Figure 8), it is more likely that they exclusively self-fertilize. This would mean that the similarities we observe between such groups do not depend upon gene exchange, supporting our claim that they are sibling species.

Sibling species, then, even though sexual organisms, are separated by a barrier which may be characterized as a sterile separation. Because of this so-called 'sterility barrier,' it is assumed that these close morphotypes diverged from a common ancestor in the recent past, and thus must, at the very least, be related on that basis (Dodson and Dodson, 1985). Creationists would be tempted to assert that the origin of sibling species occurred soon after the original Creation events, and such might be the case.

That sibling species exist in nature is hardly in question. As elucidated by Mayr in his description of sibling species(1963), "Many examples will be listed...from the enormous number of such cases in the taxonomic literature. There is hardly a taxonomic monograph or revision that does not give new instances of sibling species." It is a valid exercise, then, to pursue the distinctions of sibling species as we seek a greater understanding of the very origin of new species which appears to be a true function of biology. William Stansfield has noted (1977), "Populations that live in the same locality without interbreeding must be accorded species recognition regardless of the degree of morphological distinctions they exhibit." Yet there was one anonymous reviewer of this paper, after it was presented in a reduced form to a major parasitological journal, who stated, "to call the two species sibling species is absurd...In fact, not only is A. *megalocephala not* a sibling species, it is probably not even the most closely related species." Although it may be true that there exist other more closely related ascocotylids, the reviewer would have done well to study the very taxonomic literature of this diverse group of parasites because it yields several published examples of sibling speciation in journals from his own field.

Bowers, et al. (1990, 1996) demonstrated that sibling species of *Meiogymnophallus*, (a digenean trematode not unlike the one in this study), collected along the French Mediterranean and British coasts are morphologically almost identical, but that they employ different second intermediate hosts in their life cycle.

Russell-Pinto and Bowers (1998) further elucidated the differences between the sibling species of *Meiogymnophallus*, differences that are observable only under scanning and transmission electron microscopy. Further, Font et al. (1984) described a very closely related member of this ascocotylid group, *Ascocotyle gemina* (placed within the subgenus *Ascocotyle*, c.f. *Leighia* for the worm in the present study), and stated "We consider *Ascocotyle gemina* to be a sibling species to A. *sexidigita* . . . " even though the two parasites "displayed different specificity for cyprinodontid [host] fishes . . . ", and " . . . an explanation of the widely separated geographical distribution of these sibling species is problematical." It is quite clear then that sound justification exists for the consideration of A. *howei* and A. *megalocephala* as distinct, yet sibling species.

It may be that this area of sibling speciation is troubling for evolutionary systematists because it does not clearly support the theory of descent by means of gradual selection which leads slowly to reproductive isolation. It fits quite well, however, with the creationist position that the basic kinds (baramins) were created at the beginning and that they were plastic enough to yield sibling species in later development (Robinson and Cavanaugh, 1998).

That certain members of the *Ascocotyle* group share distinct phenotypes is not in question. What is problematical is, as in the pairs of A. *sexidigita*/A. *gemina and* A. *megalocephala*/A. *howei*, that such similar phenotypes could be shared when gene pools are not exchanged. These are, after all, hermaphroditic organisms which are widely geographically separated, and this would cause us to puzzle over their similarity on the basis of descent with gradual selection.

Anatomical features in the metacercarial and adult stages of these trematodes (such as the pattern of circumoral spination combined with the anatomical distribution of the ceca, uterus and vitellaria) are believed to be congruent with cercarial type. Within each subgenus, species groups have been differentiated by the arrangement and number of circumoral spines and microstructure of the gonotyl. Among the representatives of the *Ascocotyle* complex are forms which are almost identical in morphology, but exhibit other significant differences in their biology. Host specificity, particularly in the preadult stages, is important in the identification of what might be sibling species among the *Ascocotyle* complex (e.g., Font, Heard and Overstreet, 1984, concerning the validity of A. *gemina* Font, Heard and Overstreet 1984, and A. *sexidigita* Martin and Steele, 1970).

Additional features useful for discrimination of sibling species include cercarial behavior and metacercarial cyst structure (Schroeder and Leigh, 1965, and Stein and Lumsden, 197l a, b, re: A. *leighi* Burton 1956, and A. *pachycystis* Schroeder and Leigh, 1965). For all their subtlety, these characteristics, we believe, are still profound indicators of species diversification. If shared cercarial behavior and cyst structure, along with the overt anatomical disparaties we have already discussed do not derive from genetic variation, then the case for sibling speciation as a function of the Creation events is made even more strongly.

Sibling species are identified by the extent to which variants overlap in "morphological space" (as defined and discussed by Remine, 1993) while diverging along other trajectories in the totality of their biology. The sibling species concept would tangibly address the ecological, physiological, and genetic principles underpinning the differentiation process, perhaps more than the traditional concept of geographic separation of morphologically variant populations. We also note that the sibling species of *Ascocotyle* complex in particular are commonly sympatric (e.g., A. *leighi* and A. *pachycystis*, A. *mcintoshi* Price, 1932 and A. *chandleri* Lumsden, 1963) although this is not the case for A. *howei* and A. *megalocephala*. Such a "test of sympatry" without interbreeding would support calling such pairs "sibling species."

A. *howei* and A. *megalocephala* are sibling species, we believe. They overlap in most of their anatomical features but they are distinguishable by body shape (Figures 1a and 2); relative size of the oral sucker; and number, size, and shape of the spines in the oral coronet (Figure 3). (Spine shape may be influenced, however, by the age of the metacercaria at the time of infection - Sogandares-Bernal and Lumsden, 1963 - and fixation - Font, Overstreet and Heard, 1984).

We believe that A. *howei* is a sibling species of A. *megalocephala*: we speculate that A. *howei* has arisen since the time of Creation and we believe that it is a part of the same baramin as A. *megalocephala*.

It is our hope that further study into the area of sibling speciation may provide answers to the question of speciation and baraminology in general.

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Book Review

T. Rex and the Crater of Doom by Walter Alvarez.
Princeton University Press, Princeton, NJ. 1997. 185 pages. $24.95.
Paperback edition from Random House $13.00
Reviewed by Eugene F. Chaffin

When the idea was first proposed that a giant impact caused the Cretaceous-Tertiary extinctions, two of the principal investigators were physicist Luis Alvarez and his geologist son. Walter Alvarez, the author of this book, was that son. The book tells the story in very interesting, chronological style. Neither of the pair appears to have been a creationist, but the story is interesting nonetheless. Walter was studying a continuous, apparently complete limestone outcrop in a valley in Italy. Paleontological work using foraminifera placed the boundary between two geological "eras" at a thin clay layer. Happily for the father-son team, Walter obtained a job at the University of California, Berkeley in near proximity to his father. The teamwork between the two was able to identify iridium in the clay boundary layer, and in cooperation with Frank Asaro, to rule out a supernova as the agency of the extinction (due to the absence of Pu-244). The book tells of the formulation of the asteroid or comet impact hypothesis, and how the doctrine of uniformitarianism proved to be a formidable barrier to its acceptance. Many references are given at the end of the book, documenting the various episodes in this drama, which lasted from the 1970's to the present. Readers wishing to read opposing viewpoints may wish to consult a Web page by Dewey McLean:
http://www.vt.edu:10021/artsci/geology/mclean/oldDinosaur_Volcano_Extinction/.

Recently, the Chicxulub (pronounced Cheek-shoe-lube) crater below the surface in the Yucatan Peninsula of Mexico has been identified as the likely impact site. Supporting evidence includes tsunami deposits in northeast Mexico, Texas, Haiti, and Belize. One wonders whether the submarine deposits which Alvarez mentions can attest to the Flood model. An article by Don DeYoung and Carl Froede appeared in the June, 1996 Quarterly, and attempted to answer some of the questions. Many of us have been following news articles and such for more than a decade, and it is interesting to read this book and fill in some of the details with which we might have been unfamiliar.