

ATROPHECAECUM LOBACETABULARE, N. SP.
(DIGENEA: CRYPTOOGONIMIDAE: ACANTHOSTOMINAE)
WITH DISCUSSION OF THE GENERIC STATUS OF
PARACANTHOSTOMUM FISCHTHAL AND KUNTZ, 1965,
AND *ATEUCHOCEPHALA* COIL AND KUNTZ, 1960

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Abstract.—A new species of *Atrophecaecum* is described from various sea snakes collected in northern Australia and Malaysia. The new species most closely resembles *A. burminis*, *A. simhai*, and *Paracanthostomum cerberi* in having one atrophied cecum, preovarian vitellaria, vitelline follicles not extending anteriorly to the posterior margin of the seminal vesicle, eggs attaining lengths greater than 30 μm , and a short prepharynx. It is unique among acanthostomes in possessing a flap of tissue on the posterior margin of the acetabulum, giving that organ a bipartite appearance. The new species further resembles *A. burminis* and *A. simhai* by possessing oral spines, and resembles *P. cerberi* in having a subterminal mouth. Inclusion of *Paracanthostomum cerberi* and *Ateuchocephala marina* in *Atrophecaecum* provides the most parsimonious hypothesis of phylogenetic relationships among the taxa involved, and produces a more efficient and stable classification.

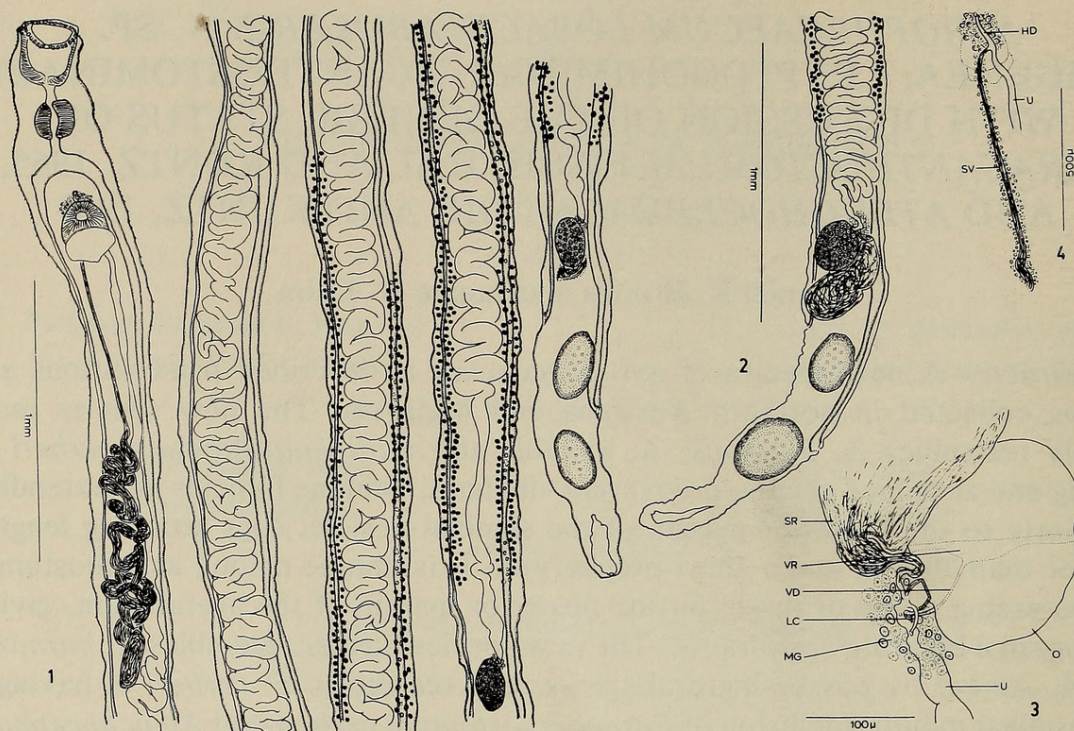
Brooks (1980) recently revised the digenean subfamily Acanthostominae Poche based on a phylogenetic analysis. In that monograph a new species of *Atrophecaecum* Bhalerao was discussed in terms of its effect on the classification of acanthostomes and two other cryptogonimid genera, *Paracanthostomum* Fischthal and Kuntz, and *Ateuchocephala* Coil and Kuntz. Specifically, the possibility was raised that *Ateuchocephala* and *Paracanthostomum* could not be recognized as natural (monophyletic) taxa unless *Atrophecaecum* was somehow subdivided. This report describes the new species of *Atrophecaecum* and, based on phylogenetic analysis, shows that the most useful classification for the taxa involved is one including *Ateuchocephala* and *Paracanthostomum* in the genus *Atrophecaecum*.

Specimens upon which the description of the new species is based were collected from sea-snakes quick-frozen shortly after capture and kept frozen until returned to the laboratory, where they were thawed and examined. Most were partially thawed, eviscerated, and the viscera refrozen and shipped to the University of Alberta. Collected helminths were fixed with cold AFA, stained with Harris' hematoxylin and mounted in Permount (Fisher). Measurements are in micra unless otherwise stated, with mean values ($\bar{x}$) and number of observations (n) for some traits; figures were drawn with the aid of a drawing tube.

Atrophecaecum lobacetabulare, new species

Figs. 1–4

Description (based on 34 specimens).—Body elongate, 4.32–12.30 mm long (n = 27) by 0.24–0.75 mm wide (n = 27); widest point variable in hindbody; ratio



Figs. 1-4. *Atrophecaecum lobacetabulare*: 1, Ventral view of holotype; 2, Close-up of posterior end of paratype, showing position of seminal receptacle, which is not apparent in holotype; 3, Close-up of ootype region; 4, Dorsal view of acetabular region of holotype, showing terminal genitalia. Abbreviations: HD = hermaphroditic duct; LC = Laurer's canal; MG = Mehlis' gland; O = ovary; SR = seminal receptacle; SV = seminal vesicle; U = uterus; VR = vitelline reservoir; VD = vitelline duct.

of body width to length 1:9.1-33.8 ($\bar{x}$ = 1:18.1, n = 27). Tegument spinose; extent of spination not determined due to fixation methods. Eyespot pigment lacking. Oral sucker cup-shaped, terminal with subterminal mouth, 154-297 (n = 24) long by 143-231 (n = 24) wide, surrounded by single uninterrupted row of 24-26 spines; spines 22-38 (n = 20) long by 12-29 (n = 20) wide. Acetabulum 105-231 long (n = 23) by 95-209 wide (n = 23), with posterior lobe giving bipartite appearance; lobe not apparent in many specimens. Forebody 6.4-14.1% of total body length. Ratio of oral sucker width to acetabular width 1:0.64-1.07 ($\bar{x}$ = 1:0.84, n = 20). Prepharynx 60-242 long (n = 21), thin-walled. Pharynx barrel-shaped, 108-148 long (n = 22) by 99-214 wide (n = 22). Ratio of oral sucker width to pharyngeal width 1:0.50-0.89 ($\bar{x}$ = 1:0.71, n = 16). Ratio of acetabular width to pharyngeal width 1:0.59-1.15 ($\bar{x}$ = 1:0.87, n = 16). Esophagus usually extremely short, not measured. Cecal bifurcation less than 5% of total body length pre-acetabular; ceca lined with epithelium, opening separately and laterally near posterior end of body; one cecum atrophied.

Testes spherical to subspherical, smooth, tandem, not contiguous; anterior testis 209-345 long by 132-208 wide, posterior testis 220-396 long by 132-352 wide; post-testicular space 3-11% of total body length ($\bar{x}$ = 7%, n = 26). Seminal vesicle consisting of posterior saccate part and anterior sinus part, sinuous, median, intercecal, extending 4.6-11.7 times acetabular length postacetabular ($\bar{x}$ = 9.1, n = 18). Prostatic duct surrounded by few prostatic cells free in parenchyma. Preacetabular pit without spines, with transverse aperture 80-83 wide, surround-

ed by gland cells; gonotyl lacking. Genital pore immediately preacetabular, opening immediately posterior to preacetabular pit. Postacetabular pit lacking.

Ovary approximately one ovarian diameter pretesticular, not contiguous with anterior testis, spherical to subspherical, 120–264 long by 99–242 wide. Seminal receptacle posterodorsal to ovary, 132–506 long by 77–198 wide. Ootype region as in Fig. 3. Uterus wound in ascending loops intercecal between ovary and acetabulum; loops occupying 63–75% of total body length ($\bar{x}$ = 70%, n = 23); joining hermaphroditic duct posterior to acetabulum. Vitellaria follicular; follicles in 2 longitudinal rows dorsal and lateral to ceca, extending from immediately preovarian to 8–50% of total body length postacetabular ($\bar{x}$ = 27%, n = 24), terminating at uneven levels. Left vitellarium follicles extending anteriorly to 8–46% of total body length postacetabular, right vitellarium follicles extending anteriorly to 9–50% of total body length postacetabular. Follicles not reaching anteriorly to posterior margin of seminal vesicle, 14–33 long by 12–29 wide. Eggs 25–35 ($\bar{x}$ = 28, n = 34) long by 13–20 ($\bar{x}$ = 16.5, n = 34) wide. Excretory vesicle Y-shaped; bifurcation posterodorsal to acetabulum; pore terminal with muscular sphincter surrounded by gland cells.

Hosts.—*Disteira major* (Shaw), *Hydrophis caeruleus* (Shaw), *H. spiralis* (Shaw), *Enhydrina schistosa* (Daudin) (type), *Lapemis hardwicki* Gray (Ophidia: Hydrophiidae: Hydrophiinae: Hydrophiini).

Site of infection.—Small intestine.

Localities.—Penang, Malaysia (type) (*E. schistosa*, *H. spiralis*, *L. hardwicki*); Western Gulf of Carpentaria, Australia (*D. major*, *H. caeruleus*).

Holotype.—USNM Helm. Coll. No. 77161. *Paratypes*.—USNM Helm. Coll. No. 77162, 77163, 77164.

Etymology.—The species is named for its lobate acetabulum, a feature unique among acanthostomes.

Atrophecaecum lobacetabulare most closely resembles the species *A. burminis* (Bhalerao, 1926) Khalil, 1963, and *A. simhai* Khalil, 1963, and *Paracanthostomum cerberi* Fischthal and Kuntz, 1965, by having one atrophied cecum, preovarian vitellaria, vitelline follicles not extending anteriorly to the posterior margin of the seminal vesicle, eggs attaining lengths greater than 30 μ m, and a very short prepharynx. The new species is unique among known acanthostomes by virtue of its possessing a lobate acetabulum. It resembles *A. burminis* and *A. simhai* by having oral spines, although they are relatively much smaller than those of most other acanthostomes. It resembles *P. cerberi* by possessing a subterminal mouth with terminal oral sucker. Thus, *A. lobacetabulare* occupies a systematic position intermediate between the taxa listed above.

Discussion

Brooks (1980) alluded to possible taxonomic problems arising from the discovery of *A. lobacetabulare*. The nature of the problem, and of its solution, may be seen best by examining the relative positions of *A. lobacetabulare*, *P. cerberi*, and *Ateuchocephala marina* in a cladogram depicting the phylogenetic relationships of *Atrophecaecum* spp. (Fig. 5). Synapomorphies (shared special traits) linking the new species and the other two taxa above to *Atrophecaecum* are listed on the cladogram (simplified from that of Brooks 1980).

Figure 5 clearly shows that *A. lobacetabulare*, *P. cerberi*, and *Ateuchocephala*

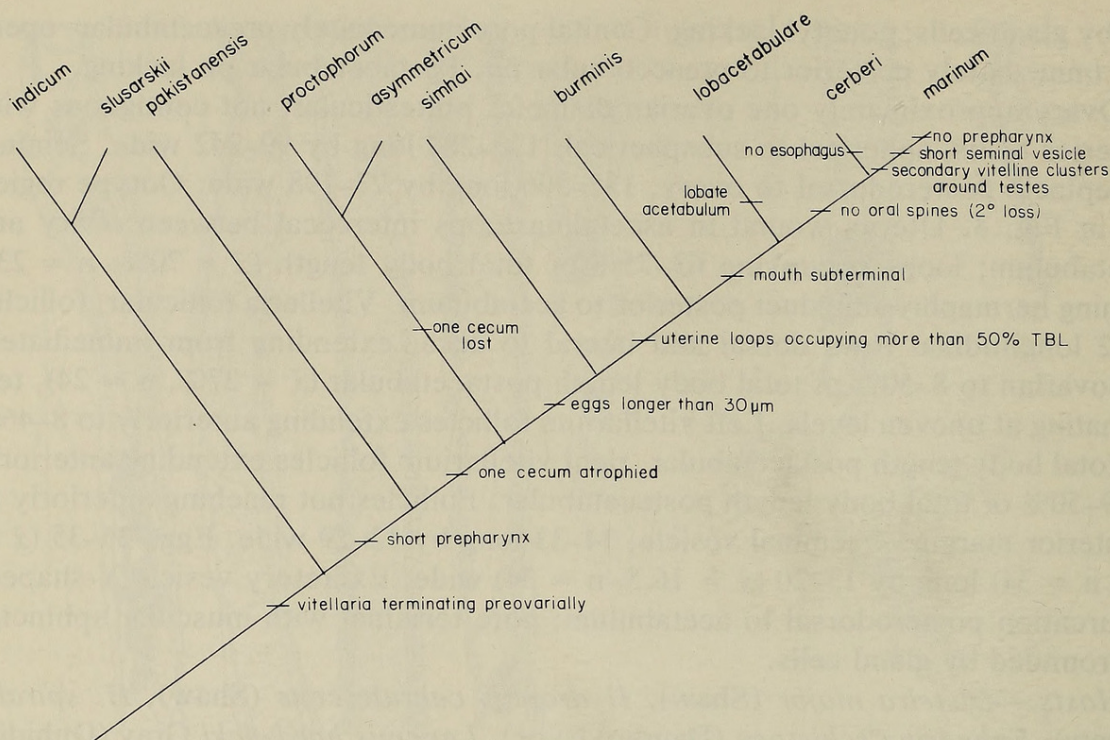


Fig. 5. Cladogram, partly modified from that of Brooks (1980), depicting phylogenetic relationships of *Atrophecaecum* spp. plus *Paracanthostomum cerberi* and *Ateuchocephala marina*. Modifications comprise deletion of some characters from the cladogram for the sake of clarity in viewing, and addition of *A. lobacetabulare* and *P. cerberi* and *A. marina*.

marina form a monophyletic group most closely related to *Atrophecaecum burminis* and *A. simhai*, hence our choice of comparisons above. This arrangement would require that *Paracanthostomum* and *Ateuchocephala* be considered junior synonyms of *Atrophecaecum* if *A. lobacetabulare* and all other members of the genus are to be retained in a single genus. Despite the perceived morphological distinctness of oral structures possessed by *P. cerberi* and *Ateuchocephala marina*, they represent only secondary loss of traits (oral spines) already reduced in size in their closest relative and a tilting of the mouth orientation. *Paracanthostomum* and *Ateuchocephala* are therefore characterized in part by the absence of traits. Conversely, *Atrophecaecum* would not exist as a natural taxon if *P. cerberi* and *Ateuchocephala marina* are excluded from it.

Three types of objections commonly raised concerning cladistic classification include: (1) they involve loss of information about "gaps" or degrees of difference between taxa (anagenetic information), (2) they produce confusing and unusable diagnoses and keys, and (3) any attempts to preserve cladistic information produce long unwieldy classifications. All of these objections have been treated empirically in papers published by various authors primarily in *Systematic Zoology* during the past ten years. This study provides an opportunity to demonstrate the efficacy of phylogenetic classification using a set of real taxa.

Loss of information.—Consider the three genera *Atrophecaecum*, *Paracanthostomum*, and *Ateuchocephala* in the classification presented by Yamaguti (1971). *Paracanthostomum* and *Atrophecaecum* (as a subgenus of *Acanthostomum*) belong in the Acanthostominae and *Ateuchocephala* comprises the sole

member of the Ateuchocephalinae. Such a classification does not represent any information concerning any members of *Atrophecaecum* which exhibit traits intermediate between the other taxa, nor does it recognize any of the similarities between *Ateuchocephala* and *Paracanthostomum*. Yamaguti's classification proposed a set of relationships opposite to the phylogenetic relationships supported by known data; *Ateuchocephala* was considered the sister-lineage of *Paracanthostomum* plus all other acanthostomes, and *Paracanthostomum* was considered the sister-lineage of all armed acanthostomes, including *Atrophecaecum*. Even if *Paracanthostomum* were considered a member of the Ateuchocephalinae, the classification would suggest that *Atrophecaecum* excluding *Paracanthostomum* and *Ateuchocephala* comprises a monophyletic group. Such a notion is not supported by any known data. In such cases, because *Atrophecaecum lobacetabulare* possesses traits intermediate between *Atrophecaecum* and *Paracanthostomum* plus *Ateuchocephala*, the "gap" between the taxa no longer exists, and existed originally only as an artifact of sampling error. Insofar as gaps represent either large numbers of character differences, which may be an artifact of data type or of sampling, or large-scale character differences, which may also be an artifact of data type, information concerning such occurrences should not be a basis for classification. Such occurrences are represented in every cladogram but do not alter the branching pattern or classification produced. A cladistic classification does not indicate directly such gaps, but the diagnoses for which the taxon names stand do.

Confusion in diagnoses and keys.—It has been suggested (Mayr 1969; Sneath and Sokal 1973) that cladistic classifications are not very stable. One aspect of that instability would be wholesale changes in diagnoses and keys every time a new taxon is included in the classification. It is true that the inclusion of the taxa in question within *Atrophecaecum* requires changes in some diagnoses and keys. However, we think the changes are few and minor, especially when compared with the number of unnecessary redundancies in diagnoses required if *Paracanthostomum* and *Ateuchocephalus* were maintained separately from the other acanthostomes.

Inclusion of *Paracanthostomum* and *Ateuchocephalus* in the Acanthostominae requires the following changes (in italics) in the subfamilial diagnosis presented by Brooks (1980):

Acanthostominae Poche, 1926

Diagnosis (emended from that of Brooks 1980).—Body elongate, eyespotted or not. Oral sucker terminal, *with terminal or subterminal mouth*, surrounded by uninterrupted single row of spines *or lacking spines*. Prepharynx and esophagus present and variable in length *or lacking*. Ceca extending to near posterior end of body. Acetabulum median, embedded in parenchyma or enclosed in body fold. Preacetabular pit present. Postacetabular pit present or lacking. Testes 2, intercecal, tandem or oblique, in hindbody. Seminal vesicle present. Cirrus sac lacking. Gonotyl present or lacking. Genital pore immediately preacetabular, not in preacetabular pit. Ovary spherical or subspherical, pretesticular in hindbody. Seminal receptacle and Laurer's canal present. Vitellaria follicular, in lateral fields in hindbody. Uterus postacetabular, usually not extending postovarially. Eggs em-

bryonated, not filamented. Excretory vesicle Y- or V-shaped, with post- or pre-acetabular bifurcation. Parasites of estuarine and freshwater fishes and reptilians. Pantropical. Type-genus: *Acanthostomum* Looss, 1899.

Inclusion of *Paracanthostomum* and *Ateuchocephala* in *Atrophecaecum* requires the following emendations to the generic diagnosis presented by Brooks (1980):

Atrophecaecum Bhalerao, 1940

Ateuchocephala Coil and Kuntz, 1960:145–150.

Paracanthstomum Fischthal and Kuntz, 1965:124–136.

Diagnosis.—Acanthostominae. Tegumental spines uniform in size. Oral sucker armed with single uninterrupted row of spines or lacking spines. Mouth terminal or subterminal. Prepharynx and esophagus variable in length or one lacking. Ceca opening separately and laterally; ceca not atrophied, one cecum atrophied or one cecum lacking. Gonotyl lacking. Seminal vesicle coiled. Vitelline follicles terminating preovarially; secondary cluster of follicles surrounding testes may be present. Seminal receptacle posterodorsal to ovary. Uterine loops preovarian. Excretory vesicle Y-shaped, with pre- or postacetabular bifurcation. Parasites of crocodilians and ophidians. India, Pakistan, Burma, Malaysia, Australia. Type-species: *Atrophecaecum burminis* (Bhalerao, 1926), Bhalerao, 1940.

The above additions to the diagnoses of Acanthostominae and of *Atrophecaecum* eliminate the need for separate diagnoses of *Paracanthostomum*, *Ateuchocephala* and the Ateuchocephalinae. Additionally, the phylogenetic relationships of the taxa involved are represented in the classification and the new classification differs little from the previous classification of the acanthostomes with the exception of the addition of three new species. Thus, the cladistic system is demonstrably more stable and less ambiguous than any other. The above additions do not require any changes in the generic key presented by Brooks (1980) but do require a new key to the species of *Atrophecaecum*, as follows:

- 1a. Prepharynx less than 3 times longer than pharynx, one cecum partially or completely atrophied, parasites of ophidians 3
- 1b. Prepharynx at least 3 times longer than pharynx, ceca not atrophied, parasites of crocodilians 2
- 2a. Oral spines 18–19 in number *slusarskii*
- 2b. Oral spines 22 in number *indicum*
- 3a. One cecum lacking 4
- 3b. Both ceca present 5
- 4a. Oral spines 20–22 in number, vitellaria confluent preovarially *proctophorum*
- 4b. Oral spines 24–28 in number, vitellaria not confluent preovarially *asymmetricum*
- 5a. Oral spines 23 in number, vitelline follicles extending anteriorly to posterior margin of seminal vesicle *pakistanense*
- 5b. Oral spines 24–29 in number or lacking, vitelline follicles not extending anteriorly to posterior margin of seminal vesicle, eggs reaching more than 30 μ m in length 6

- 6a. Cecal bifurcation more than 10% of total body length preacetabular, uterine loops occupying less than 50% of total body length *simhai*
- 6b. Cecal bifurcation less than 5% of total body length preacetabular, uterine loops occupying more than 50% of total body length 7
- 7a. Mouth terminal *burminis*
- 7b. Mouth subterminal 8
- 8a. Oral spines present, acetabulum bipartite *lobacetabulare*
- 8b. Oral spines lacking, acetabulum unipartite 9
- 9a. Esophagus present, prepharynx lacking, secondary vitelline cluster surrounding testes, seminal vesicle short *marinum*
- 9b. Esophagus lacking, prepharynx short, secondary vitelline cluster lacking, seminal vesicle elongate *cerberi*

Coil and Kuntz (1960) reported lateral ani for *Ateuchocephala marina*, but Yamaguti (1971) reported no ani after examining a paratype. We examined the specimens in question and found lateral ani and slight cecal atrophy. Yamaguti further reported a fairly long prepharynx in *Paracanthostomum cerberi*, but we found the prepharynx of the holotype and of specimens reported by Brooks and Palmieri (1981) to be as short as or shorter than the pharynx.

A number of species of *Ateuchocephala* have been described in addition to *A. marina*, but their validity and identities remain in question pending acquisition of material for study. Therefore, we make only the following new combinations: *Paracanthostomum cerberi* Fischthal and Kuntz, 1965 becomes *Atrophecaecum cerberi* (Fischthal and Kuntz, 1965), n. comb., and *Ateuchocephala marina* Coil and Kuntz, 1960 becomes *Atrophecaecum marinum* (Coil and Kuntz, 1960), n. comb.; *Ateuchocephalinae* Yamaguti, 1971 becomes a junior subjective synonym of *Acanthostominae* Poche, 1926.

Inclusion of all cladistic information in classifications produces long unwieldy classifications.—Do attempts to preserve all the information in a cladogram necessarily produce long unwieldy classifications? In order to examine this question, we formulated a complete classification of the acanthostomes according to the convention of phyletic sequencing (see Wiley 1979) in which every taxon is considered the sister-group of all taxa of equivalent position below it. That classification:

- Subfamily Acanthostominae
 - Genus *Timoniella*
 - Subgenus 1
 - species *praeterita*
 - species *imbutiformis*
 - Subgenus 2
 - species *incognita*
 - species *scyphocephala*
 - species *unami*
 - species *loossi*
 - Genus *Gymnatrema*
 - species *gymnarchi*
 - species *pambanense*
 - Genus *Proctocaecum*
 - Subgenus 1
 - Infrasubgenus 1

- species *coronarium*
- species *vicinum*
- Infrasubgenus 2
 - species *productum*
 - species *gonotyl*
- Subgenus 2
 - Infrasubgenus 1
 - species *nicolli*
 - Infrasubgenus 2
 - species *atae sedis mutabilis*
 - species *elongatum sedis mutabilis*
 - species *crocodili sedis mutabilis*
- Genus *Caimanicola*
 - species *caballeroi*
 - species *pavidus*
 - species *marajoara*
 - species *brauni*
- Genus *Acanthostomum*
 - Subgenus 1
 - species *absconditum*
 - species *knobus*
 - species *niloticum*
 - species *spiniceps*
 - Subgenus 2
 - Infrasubgenus 1
 - species *gnerii*
 - species *minimum*
 - species *astorquii*
 - Infrasubgenus 2
 - species *americanum*
 - species *megacetabulum*
- Genus *Atrophecaecum*
 - Subgenus 1
 - species *indicum*
 - species *slusarskii*
 - Subgenus 2
 - species *pakistanense*
 - Subgenus 3
 - species *proctophorum*
 - species *asymmetricum*
 - Subgenus 4
 - species *simhai*
 - species *burminis*
 - species *lobacetabulare*
 - species *cerberi*
 - species *marinum*

This classification is only 16 lines longer than a classification listing only genera and their included species, and only 6 lines longer than a classification using subgeneric designations. Thus, a fully-resolved cladistic classification need not be substantially longer than a less informative syncretistic scheme.

This report demonstrates the utility of a cladistic classification scheme as a general reference system for helminth systematics. Theoretical claims in support of the stability, consistency, predictivity, information content, and applicability of Hennigian systematics are upheld in this practical demonstration. We strongly

urge helminthologists to investigate the use of such an approach in classifying other taxa.

Acknowledgments

We express appreciation to Dr. John C. Holmes, University of Alberta, for providing the specimens of *Atrophecaecum lobacetabulare*. Funds for this study were provided through a grant to DRB from the Natural, Applied and Health Sciences Grant Committee of the University of British Columbia.

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