Comments on the Gonotyl of *Proctocaecum macroclemidis* (Tkach and Snyder, 2003) n. comb. (Digenea: Acanthostomidae: Acanthostominae), with a Key to the Genera of Acanthostominae and New Phylogenetic Tree for *Proctocaecum* Baugh, 1957

Daniel R. Brooks
*University of Toronto*, dnlbrooks@gmail.com

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**COMMENTS ON THE GONOTYL OF PROCTOCAECUM MACROCLEMIDIS (TKACH AND SNYDER, 2003) N. COMB. (DIGENEA: ACANTHOSTOMIDAE: ACANTHOSTOMINAE), WITH A KEY TO THE GENERA OF ACANTHOSTOMINAE AND NEW PHYLOGENETIC TREE FOR PROCTOCAECUM BAUGH, 1957**

Daniel R. Brooks  
Department of Zoology, University of Toronto, Toronto, ON M5S 3G5 Canada. e-mail: dbrooks@zoo.utoronto.ca

**ABSTRACT:** The species recently described as Acanthostomum macroclemidis possesses the gonotyl in the form of a solid muscular pad uniquely diagnostic for species of Proctocaecum and is accordingly transferred to that genus. An artificial key to the 5 acanthostomine genera, as well as an updated phylogenetic hypothesis for the 10 known species of Proctocaecum, based on 11 characters and including 2 species described since the last phylogenetic analysis, are presented. The single most parsimonious phylogenetic tree with a consistency index of 87.5% suggests that Proctocaecum originated in Africa and spread to North America and South America before the breakup of Pangaea. As a result, the 2 North American and 1 South American species are closely related to different African members of the genus. African and Indo-Pacific species inhabit crocodylids; hence, the occurrence of North American species in alligatorids and chelonians and a South American species in alligatorids are the result of host switches.

Tkach and Snyder (2003) described Acanthostomum macroclemidis in the alligator snapping turtle Macrochelys temminckii (referred to by Tkach and Snyder, 2003 as Macrolemys temminckii) from Mississippi. Their description stated only that a gonotyl was present in members of the species, without providing any detailed illustrations of the gonotyl or associated terminal genitalia. They also noted that, based on the study by Brooks (1981) and Brooks and Holman (1993), the species seemed to belong in Proctocaecum. Nonetheless, they placed it in Acanthostomum, stating that because the gonotyl was homoplasious in the phylogenetic analysis of Brooks (1981) and Brooks and Holman (1993), they did not have confidence in the generic status of Proctocaecum.

Brooks and Overstreet (1977) first documented diversity in gonotyl structures when they described the morphology of 3 species of acanthostomes inhabiting Alligator mississippiensis. Brooks (1981) and Brooks and Holman (1993) found that this diversity provided useful indicators of phylogenetic relationships among the species of the Acanthostominae, in conjunction with analysis of numerous other characters. Phylogenetic analysis supported the interpretation that the plesiomorphic condition is the presence of a suckerlike gonotyl, exhibited by distantly and closely related outgroup taxa, and by some acanthostomes, i.e., Timoniella praeterita (Looss, 1901) Maillard, 1974, Timoniella imbutiforme (Molin, 1859) Brooks 1981, and Gymnatrema gymnarchi (Dollfus, 1950) Morozov, 1955. Members of Proctocaecum possess a gonotyl modified into a large muscular pad (Fig. 1; see also Brooks and Overstreet, 1977), a trait that is unique among acanthostomes. Thus, simple presence or absence of a gonotyl is insufficient grounds for distinguishing among acanthostomes. In addition, phylogenetic analysis suggests that the gonotyl has been lost twice, once in the common ancestor of Timoniella incognita Brooks, 1981, Timoniella ostrowskiae Brooks and Holman, 1993, Timoniella unami (Pelaez and Cruz, 1953) Brooks, 1981, Timoniella loossii (Perez Viguera, 1957) Brooks, 1981, and Timoniella albista Blair, Brooks, Purdie, and Melville, 1988, and once in the common ancestor of Caimanicola Teixeira de Freitas and Lent, 1938 + Acanthostomum Looss, 1899. It is therefore incorrect to state that the presence and absence of a gonotyl is homoplasious among the acanthostomes. Only the absence (secondary loss) of the gonotyl is homoplasious, and that occurs only twice, and in distantly related acanthostomes.

**MATERIALS AND METHODS**

I examined the holotype and 3 paratypes of A. macroclemidis deposited in the U.S. National Parasite Collection (USNPC 92147-8). This examination confirmed that all possess gonotyls in the form of the large and prominent muscular pad uniquely diagnostic for members of Proctocaecum (Fig. 1). I, therefore, transfer the species to Proctocaecum as Proctocaecum macrolemidis (Tkach and Snyder, 2003) n. comb. Tkach and Snyder’s (2003) failure to recognize the proper generic placement of Proctocaecum macroclemidis affected their discussion of potential closest relatives of P. macroclemidis, which they compared primarily with members of Caimanicola, all of which occur in the New World, most of them in Alligatoridae of Central and South America. In addition to P. macroclemidis, 1 additional member of Proctocaecum has been described since the study by Brooks and Holman (1993), i.e., Proctocaecum dorsale in Caiman jacare from Brazil (Catto and Amato, 1993). The 10 known species of Proctocaecum occur in tropical and subtropical habitats. Four species are known from the Indo-Pacific, 3 from Africa, 2 from North America, and 1 from South America. Six species inhabit members of the Crocodylidae, 2 inhabit members of the Alligatoridae, and 1 inhabits a chelonian.

To better reassess the relationships of P. macroclemidis, I added the relevant character information for it and for P. dorsale to produce a new phylogenetic analysis of the genus. The analysis is based on 11 characters comprising 14 derived states, polarized using other acanthostomes as outgroups (see Brooks and Holman, 1993) (TBL = total body length). Table I includes the data matrix.

1. Gonotyl in the form of a solid muscular pad. As noted above, this trait is uniquely diagnostic for members of Proctocaecum (Fig. 1; see also Brooks and Overstreet, 1977), and is the primary synapomorphy for the genus.
2. Uterine loops occupying >45% TBL (0); uterine loops occupying <45% TBL (1).
3. Anal pores opening laterally, at the same level (0); anal pores opening laterally, at different levels (1); anal pores opening at posterior end (2); anal pores opening dorsolaterally (3).
4. Vitelline follicles extending anterior to posterior margin of seminal vesicle (0); vitelline follicles not extending anterior to posterior margin of seminal vesicle (1).
5. Ceca not atrophied (0); 1 cecum atrophied (1).
6. Oral spines < 100 μm long (0); oral spines > 100 μm long (1).
7. Ratio of Body length: width < 7.5: 1 (0); 7.5-15: 1 (1); > 20: 1 (2).

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TABLE I. Data matrix for 10 species of Proctocaecum and 11 comparative morphological characters. For identities of characters and states, see text.

<table>
<thead>
<tr>
<th>Species</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
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<td>P. coronarium</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>P. vicinum</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>P. gonotyl</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>P. macroclemidis</td>
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<td>0</td>
<td>1</td>
<td>0</td>
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<tr>
<td>P. productum</td>
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<td>1</td>
</tr>
<tr>
<td>P. elongatum</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>P. crocodili</td>
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<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>P. atae</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>P. nicolli</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>P. dorsale</td>
<td>1</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
</tbody>
</table>

RESULTS

Phylogenetic systematic analysis of the 11 characters, all run unordered, produced 1 most parsimonious tree, with a consistency index of 87.5% (16 steps for 14 apomorphy traits: Fig. 2). That tree retains the relative phylogenetic relationships among the 8 species analyzed in previous studies (Brooks, 1980; Brooks and Holman, 1993) but adds P. dorsale in a trichotomy with Proctocaecum productum and a clade of Proctocaecum crocodili + Proctocaecum elongatum + Proctocaecum atae + Proctocaecum nicolli and P. macroclemidis in a trichotomy with the common ancestor of Proctocaecum gonotyl + Proctocaecum vicinum + Proctocaecum coronarium and the common ancestor of the clade containing P. dorsale + P. productum + P. crocodili + P. elongatum + P. atae + P. nicolli. Proctocaecum spp. form a morphologically conservative group, and the basal placement of P. macroclemidis within that clade explains its general (sympleiomorphic) similarity with the members of Caimanicola, with which Tkach and Snyder (2003) compared P. macroclemidis.
DISCUSSION

Figures 3 and 4 summarize host groups and geographical distributions, respectively, for the various members of Proctocaecum optimized on the phylogenetic tree. The evolution of host relationships among members of the group is most parsimoniously explained by inferring that the common ancestor of the group originated in crocodylids and that host switching to alligatorids occurred twice (P. dorsale and P. coronarium) and to chelonians once (P. macroclemidis) (Fig. 3). The biogeographic origins of the group are most parsimoniously explained by inferring that the group originated in Africa, then dispersed North America (2 times), South America (1 time), and the Indo-Pacific (1 time) before the breakup of Pangaea (Fig. 4). Recent phylogenetic analyses of another morphologically conservative group, the frog lung flukes, Haematoloechus, have also found evidence of a Pangaean origin, with North and South American species not being each other’s closest relatives (Snyder and Tkach, 2001; León-Régagnon and Brooks, 2003).

Brooks (1981) and Brooks and Holman (1993) recognized 5 genera within this group, which can be readily distinguished by the following key, which is artificial by virtue of the fact that it groups Gymnatrema Morozov, 1955 and Proctocaecum, whereas phylogenetic analysis places Proctocaecum as the sister group of Caimaniola + Acanthostomum (Brooks, 1981; Brooks and Holman, 1993):

Artificial key to genera of Acanthostominae

1a. Seminal receptacle thick-walled, preovarian.

.............................................................................. Timoniella Rebecq, 1960
1b. Seminal receptacle thin-walled, postovarian ............. 2
2a. Gonotyl present ........................................ 3
2b. Gonotyl absent ........................................... 4
3a. Gonotyl suckerlike ............................... Gymnatrema Morozov, 1955
3b. Gonotyl a solid muscular pad ........................ Proctocaecum Baugh, 1957
4a. Tegumental spines greatly enlarged in forebody ........ Caimanicola Teixeira de Freitas and Lent, 1938
4b. Tegumental spines not greatly enlarged in forebody .... Acanthostomum Looss, 1899

This study underscores the importance of a phylogenetic perspective in speeding up the global census of life and in making the results of basic taxonomy more broadly useful to the scientific community (Brooks, 2003).

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LITERATURE CITED


