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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

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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 most 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 *Macrochelys 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 loossi* (Perez Viguera, 1957) Brooks, 1981, and *Timoniella absita* 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 malaclemidis* (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 μ m long (0); oral spines > 100 μ m long (1).
7. Ratio of Body length: width < 7.5: 1 (0); 7.5–15: 1 (1); > 20: 1 (2).

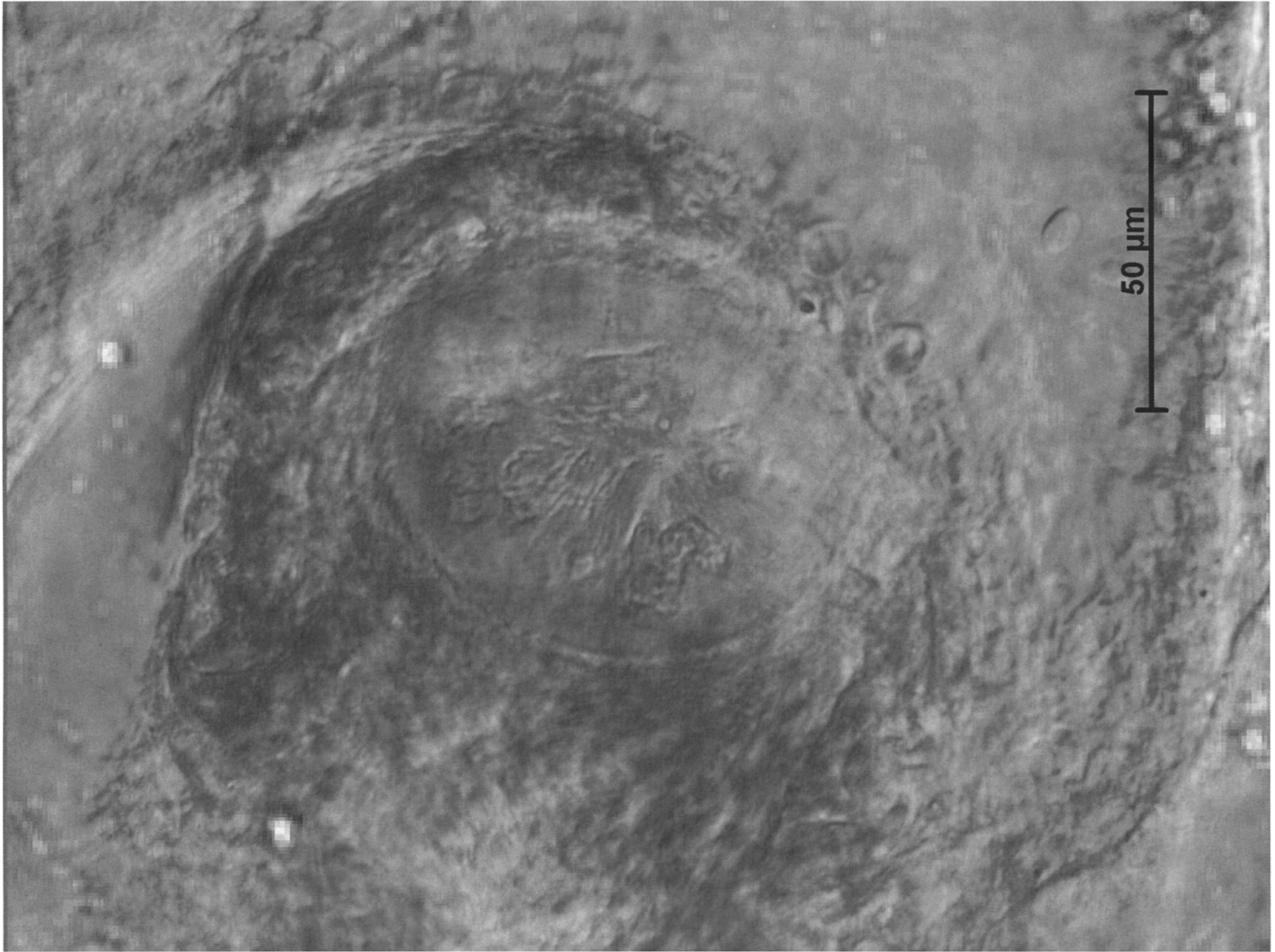


FIGURE 1. Digital image of the solid muscular padlike gonotyl of *Proctocaecum macroclemidis*. Scale bar = 50 μm.

- 8. Maximum TBL < 7 mm (0); 7–16 mm (1).
- 9. Forebody > 10% TBL (0); forebody < 10% TBL (1).
- 10. Average ratio of oral sucker width: pharynx width 1: 0.4 (0); < 1: 0.40; and > 1: 0.25 (1)
- 11. Vitelline follicles not extending anterior to acetabulum (0); vitelline follicles extending anterior to acetabulum (1).

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 apomorphous 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 (symplesiomorphic) similarity with the members of *Caimanicola*, with which Tkach and Snyder (2003) compared *P. macroclemidis*.

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

<i>P. coronarium</i>	1	1	1	1	1	1	0	0	0	0	0	0
<i>P. vicinum</i>	1	1	1	0	0	0	0	0	0	0	0	0
<i>P. gonotyl</i>	1	1	0	0	0	0	0	0	0	0	0	0
<i>P. macroclemidis</i>	1	0	0	1	0	0	0	0	0	0	0	0
<i>P. productum</i>	1	0	0	0	0	0	1	0	0	0	0	0
<i>P. elongatum</i>	1	0	2	0	0	0	2	1	0	0	0	0
<i>P. crocodili</i>	1	0	2	0	0	0	1	1	1	0	0	0
<i>P. atae</i>	1	0	2	0	0	0	1	1	0	1	0	0
<i>P. nicolli</i>	1	0	2	0	0	1	1	1	0	1	1	1
<i>P. dorsale</i>	1	0	3	0	0	0	1	0	0	0	0	0

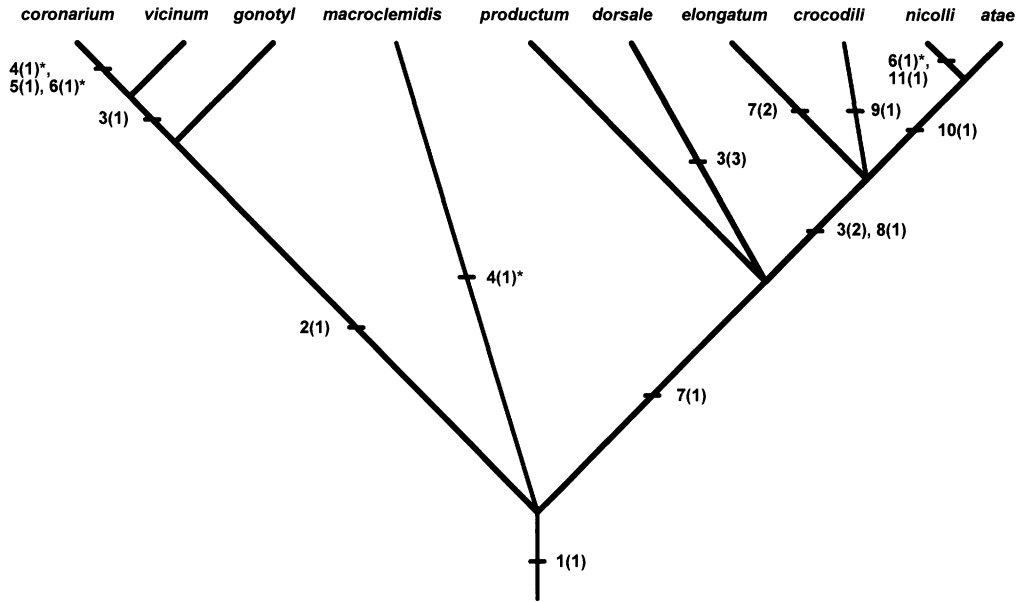


FIGURE 2. Phylogenetic tree for 10 species of *Proctocaecum*. Slash marks on branches denote apomorphic traits, identified as character number (character state). For identities of characters and their states, see text.

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 Pangaeian origin, with North and South American species not being each other's closest relatives (Snyder and Tkach, 2001; León-Règagnon 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

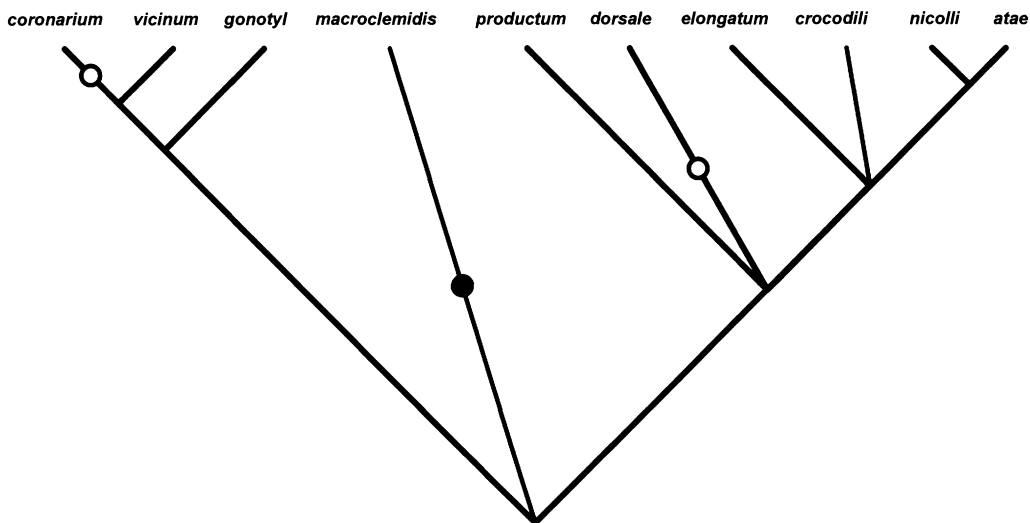


FIGURE 3. Host distributions for species of *Proctocaecum* optimized phylogenetically onto the phylogenetic tree from Figure 2. Open circle = host switch from crocodylids to alligatorids; solid circle = host switch from crocodylids to chelonians.

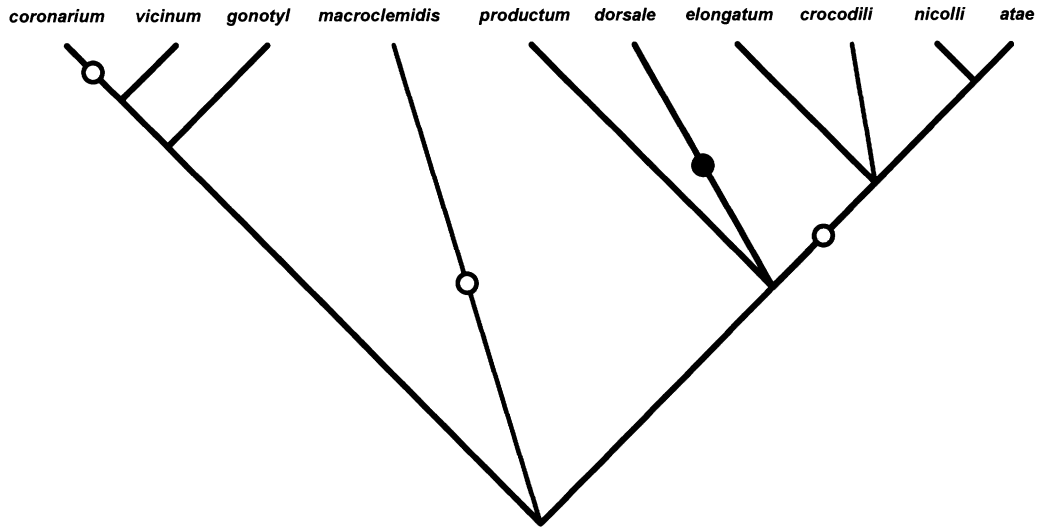


FIGURE 4. Geographic distributions for species of *Proctocaecum* optimized phylogenetically onto the phylogenetic tree from Figure 2. Open circles = dispersal from Africa to North America; solid circle = dispersal from Africa to South America; dotted circle = dispersal from Africa to the Indo-Pacific. Note that North American and South American members of the genus are more closely related to different African species than to each other.

- 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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