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## PHYLOGENETIC RELATIONSHIPS AMONG THE SPECIES OF *PYELOSOMUM* LOOSS, 1899 (DIGENEA: PRONOCEPHALIDAE)

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**ABSTRACT:** Comparative morphological study of 10 nominal species of pronocephalids forming a clade diagnosed by plump rounded bodies, sinuous ceca, and short esophagi supports the recognition of 7 species, with *Pyelosomum longicaecum* a junior synonym of *P. renicapite*, and *P. solum* and *Myosaccus chelonei* species incertae sedis. Phylogenetic analysis of the 7 recognized species, based on 18 morphological transformation series, produced a single tree with a consistency index of 86%. That tree suggests that *Pyelosomum* is paraphyletic unless *Astrorchis*, *Epibathra*, and *Myosaccus* are included in it. Accordingly, all are considered junior synonyms of *Pyelosomum*. *Epibathra stenobursata* is designated *Pyelosomum stenobursata* comb. n.

A group of species of Pronocephalidae Looss, 1902 form a clade diagnosed by plump rounded bodies, sinuous ceca, and short esophagi (Pérez Ponce de León and Brooks, 1995). Ruiz (1946) treated species having these traits as members of *Pyelosomum* Looss, 1899 in a revision of the Pronocephalidae. Other taxonomic treatments, e.g., Yamaguti (1958, 1971), however, have placed the species in as many as 4 genera: *Pyelosomum* Looss, 1899, including *Pyelosomum cochlear* Looss, 1899, *Pyelosomum longicaecum* Luhman, 1935, *Pyelosomum posterorochis* Oguro, 1936, and *Pyelosomum parvum* Prudhoe, 1944; *Epibathra* Looss, 1902, including *Epibathra crassa* (Looss, 1901) Looss, 1902; *Astrorchis* Poche, 1925, including *Astrorchis renicapite* (Leidy, 1856) Poche, 1925; and *Myosaccus* Gilbert, 1938, including *Myosaccus amblyrhynchus* Gilbert, 1938. Subsequent to Yamaguti's (1971) study, Chattopadhyaya (1972) described *Myosaccus chelonei* and *Pyelosomum solum* in *Chelonia mydas* from India, and Fischthal and Acholonu (1976) described *Epibathra stenobursata* in *Eretmochelys imbricata imbricata* from Puerto Rico, bringing to 10 the number of nominal species in this clade.

This study was undertaken to establish the validity of those 10 nominal species and to discern their phylogenetic relationships. In doing so, we have evaluated the classifications proposed by Ruiz and by Yamaguti.

### MATERIALS AND METHODS

#### Specimens examined

We examined all available published accounts and the following specimens: CHIBUNAM (Coleccion Helminologica del Instituto de Biología de la Universidad Nacional Autónoma de México, México City, México): *Pyelosomum cochlear*: 233-10 (6), 212-11 (1); *P. posterorochis*: 213-4 (1); *P. renicapite* (= *Astrorchis r.*): 250-12 (8). UNSMHWML (University of Nebraska State Museum, Division of Parasitology, Harold W. Manter Laboratory, Lincoln Nebraska, U.S.A.): *P. renicapite* (= *Astrorchis r.*): 1700 (1); *P. amblyrhynchi* (= *Myosaccus a.*): 1702 (2). USNMHC (United States National Museum Helminthological Collection, Beltsville, Maryland, U.S.A.): *P. cochlear*: 9665 (1); *P. posterorochis*: 73331 (2); *P. longicaecum*: 8910 (1); *P. renicapite* (= *Astrorchis r.*): 74860 (1); *P. stenobursata* (= *Epibathra s.*): 73313 (1).

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#### Taxa recognized

We recognize 7 valid species in this analysis. During our study, we failed to find any characters that separated *P. longicaecum* and *P. renicapite*; therefore, we consider *P. longicaecum* to be a junior synonym of *P. renicapite*. Illustrations of *M. chelonei* and *P. solum* presented by Chattopadhyaya (1972) suggest that the specimens were flattened excessively, with resultant displacement of internal organs. In addition, some aspects of the descriptions are difficult to interpret. For example, the trait that diagnoses *Myosaccus* as a distinct genus is a cirrus sac with a constriction in the middle, but *M. chelonei* is described as lacking that constriction. Attempts to obtain specimens for examination have failed. We therefore consider *P. solum* and *M. chelonei* species incertae sedis.

#### Analyses performed

Phylogenetic analyses were performed using the methods of phylogenetic systematics (Hennig, 1966; Wiley, 1981; Wiley et al., 1991). All results were confirmed using the PAUP (phylogenetic analysis using parsimony) computer program version 3.1.1 (Swofford, 1993), run on a MAC IIX computer. The following options were examined: Characters: All unordered, or only multistate characters unordered, or only characters 4 and 6 unordered; outgroups: plesiomorphic conditions determined by the generic level phylogenetic tree for the Pronocephalidae (see Pérez and Brooks, 1995); optimization: Acctran, Deltran; tree-building algorithm: Heuristic Search/Branch Swapping, Branch and Bound, Exhaustive Search.

#### Character argumentation

We identified the following characters and their states for use in phylogenetic analysis (characters are listed in order of their appearance in Table I). The character argumentation for each character:

1) Ceca. The plesiomorphic condition is straight ceca (0). *Pyelosomum cochlear*, *P. posterorochis*, *P. crassum*, and *P. amblyrhynchi* possess ceca that extend in a sinuous manner posteriorly from the cecal bifurcation (1); *P. parvum* and *P. renicapite* possess serpentine ceca (2).

2) Mehlis gland. The plesiomorphic condition is postovarian Mehlis glands (0); the Mehlis glands in *P. parvum* and *P. renicapite* are lateral to the ovary (1).

3) Anterior ends of the ceca. The plesiomorphic condition is for the ceca to extend posteriorly or posterolaterally from the cecal bifurcation (0); the ceca in *P. parvum* and *P. renicapite* loop anteriorly before passing posteriorly (1).

4) Egg size. The plesiomorphic condition is eggs 42–60  $\mu\text{m}$  long (0); *P. renicapite* and *P. parvum* have eggs 32–40  $\mu\text{m}$  long (1). *Pyelosomum stenobursata* was described as having eggs 32–39  $\mu\text{m}$  long, but the single specimen upon which the description is based is very young and the eggs are not fully developed. Consequently, we assign the plesiomorphic condition to this species.

5) Cecal tips. The plesiomorphic condition is cecal tips pointing directly posteriorly (0); in *P. renicapite* and *P. posterorochis*, the cecal tips point medially (1), and in *P. parvum*, the cecal tips point laterally (2).

6) Anterior extent of vitellaria. The plesiomorphic condition is vi-

telline follicles extending anteriorly at least to the middle of the body, and usually somewhat farther anteriorly (0); in *P. stenobursata* and *P. parvum* the vitelline follicles do not extend anteriorly to the middle of the body (1).

7) Egg filaments. The plesiomorphic condition for this character is 2 filaments (1 at either end of the egg) (0); *P. cochlear*, *P. posterorchis*, *P. crassum*, *P. stenobursata*, and *P. amblyrhynchi* have more than 2 filaments (1), and *P. renicapite* lacks egg filaments (2).

8) Orientation of testes relative to ceca. The plesiomorphic condition is extracecal testes (0); *P. renicapite*, *P. posterorchis*, *P. crassum*, *P. stenobursata*, and *P. amblyrhynchi* all exhibit testes that lie ventral to the ceca (1).

9) Structure of vitellaria. The plesiomorphic condition is follicular vitellaria (0); *P. renicapite* has acinous vitellaria (1).

10) Position of cirrus sac. The plesiomorphic condition is intercecal cirrus sacs (0); *P. renicapite* has an extracecal cirrus sac (1).

11) Anterior extent of uterine coils. The plesiomorphic condition is uterine coils not extending anterior to the posterior end of the cirrus sac (0); *P. cochlear* has uterine loops extending anterior to the posterior end of the cirrus sac (1).

12) Relative development of the prostatic complex. The plesiomorphic condition is a relatively small prostatic complex with thinly muscled walls (0); *P. crassum* and *P. stenobursata* have well-developed prostatic complexes with thin walls (1); and *P. amblyrhynchi* has a well-developed prostatic complex with extremely thickly muscled walls (2).

13) Position of vitellaria. The plesiomorphic condition is vitelline follicles or acini lying ventral to the ceca as well as lateral to them (0); *P. crassum*, *P. stenobursata*, and *P. amblyrhynchi* have extracecal vitellaria only (1).

14) Relative degree of glandulation of metraterm. The plesiomorphic condition is a metraterm surrounded by relatively few gland cells (0); *P. crassum* has abundant gland cells lying along the metraterm (1).

15) Lateral extent of uterine loops. The plesiomorphic condition for *Pyelosomum* is uterine loops that are partly extracecal (0); *P. crassum*, and *P. amblyrhynchi* have intercecal uterine loops (1). For pronocceph-

TABLE I. Data matrix for *Pyelosomum*.\*

PA	2 1 1 1 2 1 0 0 0 0 0 0 0 0 0 0 0 1 1
RE	2 1 1 1 1 0 2 1 1 1 0 0 0 0 0 1 0 1 1
CO	1 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 0 0 1 1
PO	1 0 0 0 1 0 1 1 0 0 0 1 0 0 0 0 0 0 1 1
CR	1 0 0 0 0 0 1 1 0 0 0 1 1 1 1 0 1 0 1 1
ST	1 0 0 0 0 1 1 1 0 0 0 1 1 1 1 0 0 1 1 1 1
AM	1 0 0 0 0 0 1 1 0 0 0 2 1 0 1 1 1 0 1 1

\* PA = *P. parvum*; RE = *P. renicapite*; CO = *P. cochlear*; PO = *P. posterorchis*; CR = *P. crassum*; ST = *P. stenobursata*; AM = *P. amblyrhynchi*. 0 = Plesiomorphic; 1, 2 = apomorphic conditions.

alids as a whole, intercecal uterine loops are plesiomorphic, so this represents an evolutionary reversal.

16) Shape of cirrus sac. The plesiomorphic condition is elongate cirrus sacs (0); *P. crassum* and *P. amblyrhynchi* have cirrus sacs that are spherical or club-shaped posteriorly (1).

17) Testes shape. The plesiomorphic condition is spherical or sub-spherical testes (0); *P. renicapite*, *P. crassum*, *P. stenobursata*, and *P. amblyrhynchi* have lobate testes (1).

18) Posterior extent of vitellaria. The plesiomorphic condition is vitelline follicles (or acini) not extending posterior to the anterior margin of the testes (0); *P. stenobursata* exhibits vitelline follicles extending posteriorly to the anterior margin of the testes (1).

19) Esophagus length. The plesiomorphic condition is a relatively long esophagus (0); a short esophagus (1) is a synapomorphy for *Pyelosomum* (see also Pérez Ponce de León and Brooks, 1995).

20) Body shape. The plesiomorphic condition is relatively elongate bodies (0); relatively plump bodies (1) is a synapomorphy for *Pyelosomum* (see also Pérez Ponce de León and Brooks, 1995).

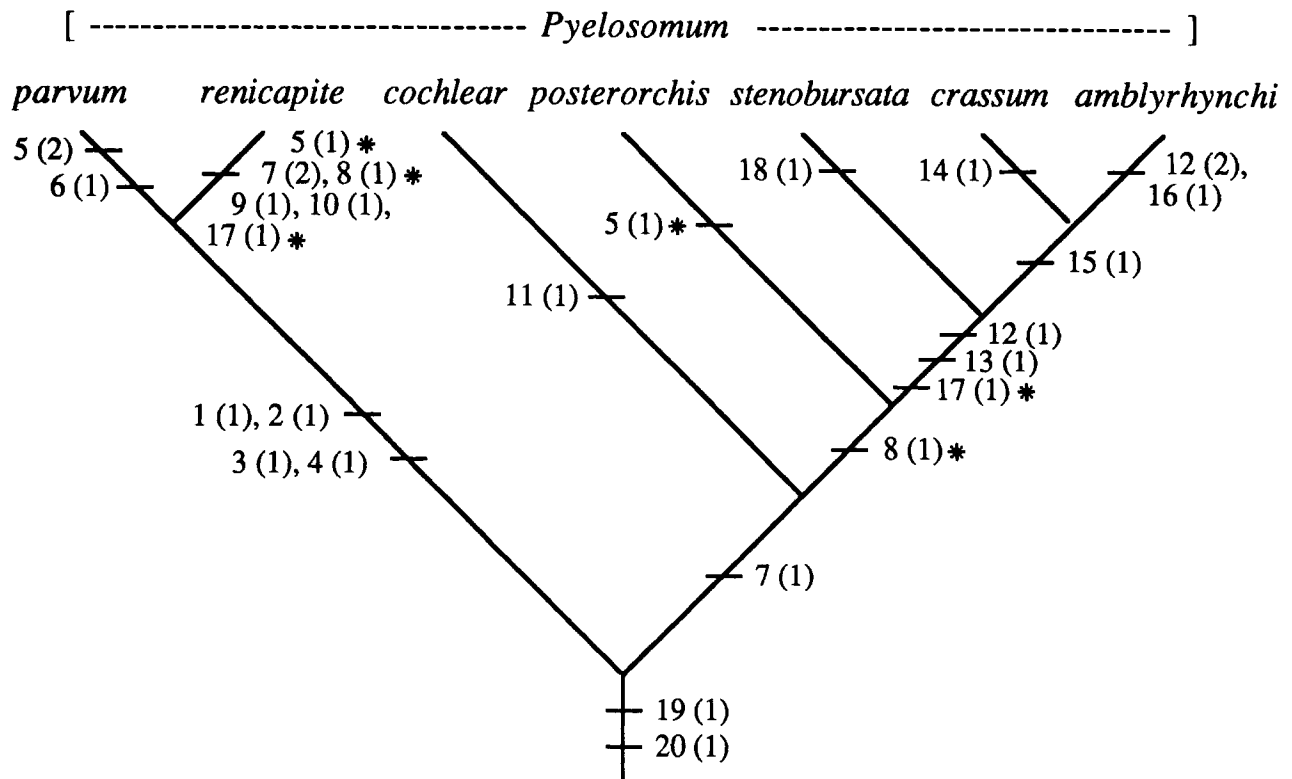


FIGURE 1. Phylogenetic tree for 6 species of *Pyelosomum*. Numbers accompanying slash marks on the tree indicate putative synapomorphies (character number followed by character state in parentheses) supporting the phylogenetic relationships. For identities of characters, refer to text. \*, Homoplasious character state.

## RESULTS

Phylogenetic analyses of the 7 species we consider valid, using all combinations of the above options, produced a single most parsimonious phylogenetic tree (Fig. 1) with a consistency index of 86%. The tree suggests that *Pyelosomum* is paraphyletic unless *Astororchis*, *Epibathra*, and *Myosaccus* are included in it. This supports the synonymies proposed by Ruiz (1946). Accordingly, *E. stenobursata* Fischthal and Acholonu, 1976 becomes *P. stenobursata* (Fischthal and Acholonu, 1976) comb. n.

## DISCUSSION

As with the pronocephalids as a whole, *Pyelosomum* is a group that primitively and predominantly comprises parasites of marine turtles, and which occurs worldwide. The highly derived position of *P. amblyrhynchi* in the phylogenetic tree of *Pyelosomum* argues strongly that this species inhabits the Galapagos iguana as the result of a host switch. From the biogeographic perspective, we note that at present, *P. parvum* and *P. amblyrhynchi* are known only from the Pacific Ocean, *P. crassum* and *P. stenobursata* are known only from the Atlantic Ocean, whereas *P. cochlear*, *P. renicapite*, and *P. posterorchis* are known from both.

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