Phylogenetic Analysis of *Opisthadena* (Digenea: Hemiuridae)

Virginia León-Règagnon  
*Universidad Nacional Autónoma de México*

Gerardo Pérez-Ponce de León  
*Universidad Nacional Autónoma de México*, ppdleon@servidor.unam.mx

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

Follow this and additional works at: https://digitalcommons.unl.edu/parasitologyfacpubs

Part of the Parasitology Commons

León-Règagnon, Virginia; Pérez-Ponce de León, Gerardo; and Brooks, Daniel R., "Phylogenetic Analysis of *Opisthadena* (Digenea: Hemiuridae)" (1996). *Faculty Publications from the Harold W. Manter Laboratory of Parasitology*. 285.  
https://digitalcommons.unl.edu/parasitologyfacpubs/285

This Article is brought to you for free and open access by the Parasitology, Harold W. Manter Laboratory of at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Faculty Publications from the Harold W. Manter Laboratory of Parasitology by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.
PHYLLOGENETIC ANALYSIS OF OPISTHADENA (DIGENA: HEMIURIDAE)

Virginia León-Régagnon, Gerardo Pérez-Ponce de León, and Daniel R. Brooks*  
Laboratorio de Helminthología, Instituto de Biología, U.N.A.M.,  

ABSTRACT: Systematic study of the closely related hemiurid genera Mitrostoma, Neopisthadena and Opisthadena revealed that Opisthadena cortesi is a junior synonym of Opisthadena dimidia and Opisthadena fujianensis and Opisthadena marina are species inquirendae. Phylogenetic analysis of the 7 recognized species, based on 21 transformation series derived from comparative morphologic characters, produced a single tree with a consistency index of 0.735. The five species of the genus Opisthadena constitute a monophyletic clade and Neopisthadena habei is their sister group. Mitrostoma nototheniae is the sister group of the other 6 members of the clade. Geographic distribution suggests an ancient circum-Pacific distribution of the group. The association between phykosphis and this group of hemiurids appeared with the ancestor of Neopisthadena and Opisthadena.

The Hemiuridae (sensu Brooks et al., 1985) is 1 of the most diverse, and characteristic, groups of digenans inhabiting marine fishes. Gibson and Bray (1979) grouped together the genera Opisthadena Linton, 1910, Genolinea Manter, 1925, Neotheletrum Gibson and Bray, 1979, and Mitrostoma Manter, 1954 in the subfamily Opisthadeninae. Neopisthadena Machida, 1980 was described as a group closely related to Opisthadena. Mitrostoma and Opisthadena are both monotypic; Mitrostoma nototheniae Manter, 1925 was described by Manter (1954) from Notothenia macrocephala (Günther) off New Zealand and Neopisthadena habei Machida, 1980 was described from Kyphosus cinerascens (Forskål) off Japan (Machida, 1980). Opisthadena comprises 8 nominal species. The type species, Opisthadena dimidia Linton, 1910, was first described from Kyphosus sectatrix (Linn.) and Kyphosus incisor (Cuvier and Valenciennes) off Florida (Linton, 1910). Opisthadena dimidia was subsequently recorded in Kyphosus spp. off Florida (Manter, 1947; Overstreet, 1969), the Pacific coast of Panama and the Caribbean Sea (Sogandares-Bernal, 1959), South Australia (Manter, 1966), Japan (Machida, 1980), the Caribbean Sea (Sierra, 1984), and the Pacific coast of México (León-Régagnon et al., 1997). The other species of Opisthadena have restricted geographic distributions. Opisthadena kawaii Al-Yamani and Nahhas, 1981 was first described from the Arabian Gulf in Valamugil seheli (Forskål) (Al-Yamani and Nahhas, 1981). Opisthadena cortesi Bravo-Hollis, 1965 was described from Kyphosus elegans (Peters) off the Gulf of California (Bravo-Hollis, 1965). Yamaguti (1970) described Opisthadena kyphosi Yamaguti, 1970 from Kyphosus cinerascens off Hawaii. Opisthadena bodogensis Johnson and Copsey, 1953 and Opisthadena cheni Martin, 1978 were described off the coast of California from Cebidichthys violaceus (Girard) (Johnson and Copsey, 1953) and Girella nigricans (Ayers) (Martin, 1978). Finally, Tang et al. (1983) described Opisthadena fujianensis Tang, Shi, Cao, Guan and Pan, 1983 and Opisthadena marina Tang, Shi, Cao, Guan and Pan, 1983 from Fujian, China, in Mugil engeli (Bleeker) and Ambassis gymnocephalus (Lacépède), respectively.

This study was undertaken to propose a hypothesis of the phylogenetic relationships of the species of Opisthadena, Neopisthadena, and Mitrostoma, and to examine the biogeographic and coevolutionary history of the group.

MATERIALS AND METHODS

Specimens examined


Analyses performed

Phylogenetic analyses were performed using the methods of phylogenetic systematics (Hennig, 1966; Wiley, 1981; Wiley et al., 1991). Results were confirmed quantitatively using the PAUP (Phylogenetic Analysis Using Parsimony) computer program version 3.1.1. (Swofford, 1993), run on a Macintosh LCII computer. The following options were examined: (1) characters: all unordered, or only character 18 unordered. (2) Outgroups: plesiomorphic conditions determined by the state observed in the genera Genolinea and Neotheletrum, which are recognized to be the most related genera of bunocotylids (Gibson and Bray, 1979) as a primary outgroup and the Hemihirius (Hemihirius, Parahemihirius, and Anahemihirius). The hemihirius were recognized to be the sister group of bunocotylids by Brooks et al. (1985) and within them, the hemihirius were considered to be the most related group of the bunocotylids (Gibson and Bray, 1979). (3) optimization: Acetran, Deltran. (4) Tree-building algorithms: exhaustive search.
Table I. Data matrix for *Opisthadena*, *Neopisthadena*, and *Mitrostoma*. Characters are numbered as in the text; for descriptions of characters and polarity arguments, see text. 0 = plesiomorphic condition; 1, 2 = apomorphic conditions; ? = condition unknown.

<table>
<thead>
<tr>
<th>Taxa*</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
<th>14</th>
<th>15</th>
<th>16</th>
<th>17</th>
<th>18</th>
<th>19</th>
<th>20</th>
<th>21</th>
</tr>
</thead>
<tbody>
<tr>
<td>HE</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>GE</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>NE</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>MN</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>NH</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>DI</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>CH</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>?</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>KU</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>?</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>?</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>KY</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>BO</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

* HE = Hemiurini (outgroup); GE = Genolinea (outgroup); NE = Neoteleuran (outgroup); MN = Mitrostoma notototheniae; NH = Neopisthadena habeli; DI = *Opisthadena dimidia*; CH = *O. cheni*; KU = *O. kawaiti*; KY = *O. kyphos*; BO = *O. boegegensis*.

**RESULTS**

**Taxa recognized**

Of the 10 nominal species in this group, we recognize 7 as valid in this study; 5 species of *Opisthadena* and the monotypic *Neopisthadena habeli*, and *Mitrostoma notototheniae*. Overstreet (1969) synonymized *O. cortesi* with *O. dimidia*. We examined the type specimens of *O. cortesi* and agree with Overstreet's evaluation. Machida (1980) proposed that *O. kyphos* was synonymous with *O. dimidia*. He argued that the number of oral papillae was not a useful character for distinguishing species because in Japanese specimens of *O. dimidia* the number of oral papillae varied from 5 pairs, as originally described by Manter (1947), to 3 pairs. We have noticed the same variation in number of papillae in the specimens of *O. dimidia* that we examined, but we also found that at least 3 pairs of oral papillae are always present. *Opisthadena kyphos*, by contrast, bears no oral papillae, and for that reason we consider it a valid species. Finally, *O. fujianensis* and *O. marina* were described based on a single specimen each, and the characters used to separate them from other species, such as body length, the presence of annulations in the tegument, and the shape of the genital cone, vary greatly with fixation techniques. The shape of vitelline masses in *O. fujianensis* indicates that this specimen might belong in the Lecithasterinae (sensu Brooks et al., 1985), and the male genital ducts of *O. marina* differ greatly from those of other members of *Opisthadena*. We therefore consider those taxa species inquirendae in this analysis.

**Character argumentation**

We used the following characters and their states in the phylogenetic analysis (characters are listed in order of their appearance in Table I): 0 = plesiomorphic; 1, 2 = apomorphic; ? = unknown. The polarity argumentation for each character is:

1. Seminal vesicle. Three states: 0 = saccate; 1 = tubular; 2 = seminal sac. In the species of the genus *Opisthadena* there is a sac containing a very coiled tubular seminal vesicle.
2. Egg size. Two states: 0 = larger than 25 μm; 1 = 13–18 μm.
3. Pharynx size. Two states: 0 = pharynx smaller than the oral sucker; 1 = pharynx and oral sucker the same size.
4. Testes location. Two states: 0 = in the second third of the body; 1 = in the posterior third of the body.
5. Excretory ducts. Two states: 0 = nonbranched anteriorly to the acetabulum; 1 = branched anteriorly.
6. Oral papillae. Two states: 0 = absent; 1 = present. As noted above, the number of oral papillae is variable within a species.
7. Testes position. Three states: 0 = symmetrical; 1 = oblique; 2 = tandem. In most of the genera of the Hemiurini (outgroup) testes are symmetrical, so we considered this state as plesiomorphic.
8. Distance between posterior testis and ovary. Two states: 0 = posterior testis lies more than its own length from the ovary; 1 = posterior testis lies less than its own length from the ovary.
9. Location of the vitellaria and ovary. Two states: 0 = in the third quarter of the body; 1 = in the fourth quarter of the body.
10. Muscular sphincter around acetabulum. Two states: 0 = absent; 1 = present.
11. Seminal vesicle wall. Two states: 0 = thin; 1 = thick.
12. End of pars prostatica. Three states: 0 = at the level of the acetabulum; 1 = posterior to the acetabulum; 2 = anterior to the acetabulum.
13. Acetabular papillae. Two states: 0 = absent; 1 = present. This is a unique state for *O. cheni*.
14. Extension of excretory ducts. Two states: 0 = running forward of the acetabulum; 1 = forward of the acetabulum and back posteriorly to testes level.
15. Postacetabular transverse fold. Two states: 0 = absent; 1 = present. In the description of the Arabian species, there is no mention made of the presence or absence of the fold. Because we could not examine type specimens, we coded this character as "unknown" (?).
16. Ejaculatory duct. Two states: 0 = absent; 1 = present.
17. Seminal receptacle. Two states: 0 = absent; 1 = present.
18. Preacetabular pit. Two states: 0 = absent; 1 = present.
19. Excretory vesicle bifurcation. Two states: 0 = near the posterior margin of the acetabulum; 1 = at the level of testes.
The condition of this character is not described in detail for *O. kuwaiti* and *O. cheni*, we coded this character as "unknown" (?) for those two species.

20. Uterine seminal receptacle. Two states: 0 = present; 1 = absent.


**Phylogenetic analysis of Bunocotylinae**

Phylogenetic analyses of the 7 taxa we consider valid, using all combinations of above options, produced a single most parsimonious phylogenetic tree (Fig. 1), with a consistency index of 0.735 (34 transformations to account for 25 apomorphic states). This result predicts that *O. kuwaiti* possesses a postacetabular fold and that *O. kuwaiti* and *O. cheni* possess excretory vesicles that bifurcate at the level of the testes; verification of these predictions requires examination of specimens. Only 2 of the 34 evolutionary changes postulated by this tree represent an evolutionary loss (the loss of oral papillae in *O. kyphosi* and *O. kuwaiti*), indicating a minimal amount of secondary simplification in the evolution of these parasites. The loss of the ecisoma and cuticular plications present in the Hemiurini are not considered herein because those are the result of a previous simplification event in some basal point of the ancestral states of bunocotilds. The tree supports the monophyly of *Mitrostoma + Neopisthadena + Opisthadena*; the presence of a postacetabular transverse fold is the synapomorphy diagnosing the clade. The tree further suggests that the monotypic *Mitrostoma* is the sister group of the remaining species and *Neopisthadena habei* is the sister species of the genus *Opisthadena*, which is monophyletic.

**DISCUSSION**

The level of homoplasy encountered in this study is comparable to those found in other phylogenetic systematic studies of digeneans (Brooks and McLennan, 1993a, 1993b; Pérez-Ponce de León and Brooks, 1995a, 1995b), although substantially less than postulated by intuitive or evolutionary taxonomic studies (e.g., Pearson, 1992). The low amount of simplification in this genera of bunocotilds provides additional support
for previous observations by Brooks and McLennan (1993a, 1993b) and Pérez-Ponce de León and Brooks (1995a, 1995b) that parasitic platyhelminths seem to have experienced little secondary simplification during their evolutionary history.

Manter (Van Cleave and Manter, 1948; Manter, 1949, 1965) considered the reef fish genus *Kyphosus* to be an interesting system for biogeographic and coevolutionary studies using helminth parasites. *Kyphosus* spp. and their helminth fauna laid the cornerstone for Manter’s thoughts about what he called “parascript” (see Brooks and McLennan, 1993a). Manter (1965) proposed an Indo-Pacific origin of *Kyphosus*, with secondary dispersion to the Americas via Japan and Hawaii and to the Caribbean Sea via the eastern Pacific Ocean. Several *Opisthadena* species inhabit kyphosid and related girellid hosts, so this study provides an opportunity to examine Manter’s ideas in the light of current methods of phylogenetic and biogeographic analysis.

The phylogenetic tree depicts *Mitrostoma nototheniae* from New Zealand as the sister species of the rest of the clade (Fig. 2). The next branching point separates *Neopisthadena habeii*, found in Japan from the 5 species of *Opisthadena* found in the Arabian Sea, Pacific Ocean, and Caribbean Sea. The New Zealand, then Japan plus Arabian Sea, and American Pacific distributions suggest a circum-Pacific ancient distribution of the group. Within the *Opisthadena* clade, the Arabian species *O. kuwaitii* is the sister species of the rest. The next 2 species, *O. cheni* and *O. bodegensis*, occur along the California coast. *Opisthadena bodegensis* is the sister species of *O. kyphosi*, the
Hawaiian endemic, plus *O. dimidia*, which is widely distributed throughout the Pacific Ocean and is the only member of the genus currently known from the Caribbean Sea. This particular geographic pattern does not support Manter’s view of a progressive dispersion from the western to the eastern Pacific Ocean, suggesting rather that the Hawaiian endemic and its widespread sister species are derived from the eastern Pacific Ocean. The geographic distribution of *O. dimidia* is also interesting. Other hemiurids, such as *Deroeges varicus*, are extremely widespread in the marine environment, but those species tend to exhibit little host specificity. *Opisthadena dimidia*, by contrast, inhabits only members of the genus *Kyphosus*. The species is found in geographic areas lacking other members of the genus (the Caribbean Sea and Australia) and also symptomatically with its sister species, *O. kyphosi*, and with non-sister species inhabiting kyphosids and girellids (*O. habei* and *O. cheni*). Its occurrence in the Caribbean Sea supports Manter’s (1965) views of colonization of the Caribbean Sea from the eastern Pacific Ocean. Because *O. dimidia* is a highly derived, rather than a basal, member of its clade, it is not reasonable to suggest that it is a widespread ancestral generalist from which the other members of the group are derived. Its distribution pattern is more likely the result of secondary colonization of areas and hosts that are suitable for its survival (the occurrence of its sister species in the same species of host in Hawaii might indicate that *O. kyphosi* originated as a result of allopatric speciation). It is also possible that the widespread occurrence of *O. dimidia*, including its presence in the Caribbean Sea, is the result of anthropogenic phenomena, thus representing recent dispersal of the species. In either case, the species is a highly successful colonizer.

Four species of *Opisthadena* and *Neopisthadena* (*O. dimidia, O. kyphosi, N. habei*) are restricted to fishes of the Kyphosidae or the related Girellidae (*O. cheni*) and they, together with *O. kuwaiti* and *O. bodengensis*, which do not inhabit kyphosids or girellids, constitute a clade in the phylogenetic tree. The hosts for *Mitrostoma nototeniæ* and for *Genolina* and *Neothelstraßeum* are not kyphosids or girellids, suggesting that the association between kyphosids and girellids and this clade of digneans originated with the common ancestor of *Opisthadena* plus *Neopisthadena*. If so, the occurrence of *O. kuwaiti* and *O. bodengensis* in a host that is neither a kyphosid nor a girellid would best be interpreted as the result of speciation via host switching (a form of peripheral isolates allopatric speciation, see Brooks and McLennan, 1993a).

The host and geographic distribution patterns discussed above make it difficult to interpret the degree of evolutionary association between kyphosids and girellids and *Opisthadena*. A possible solution would be to treat *Opisthadena* as a single data source, then assemble additional phylogenetic trees for other parasite groups inhabiting the same hosts and combine them in a single analysis to see if the parasite groups supported any general geographic or host relationships (Brooks parsimony analysis in Wiley, 1988a, 1988b; Brooks, 1981, 1990; Brooks and McLennan, 1991, 1993a). In this case, phylogenetic studies of groups such as *Cadenatella* Dollfus, 1948, *Jeancadenatia*, Dollfus, 1948, *Euneterum* Linton, 1910, *Deontaciliis* Linton, 1910 (Digeana), and *Filisoma* Van Cleave, 1928 (Acanthocephala) could provide the additional parasite data necessary to ask if the geographic distribution and host patterns indicated by *Opisthadena* are unique to that group or are part of a general pattern of marine evolutionary diversification.

**ACKNOWLEDGMENTS**

Funding for this study was provided by PADEP-UNAM prox. 3333-1994 and 3344-1996 to V.L.R., PAPIIT-UNAM prox. IN201593 to GPPL and NSERC Operating Grant No. A7696 to D.R.B. Special thanks to Dr. Ralph Lichtenfels, curator, and Dr. Eric Hoberg, United States National Parasite Collection, Dr. Masaaki Machida, curator, National Science Museum Helmhin Collection, Tokyo, and Dr. Shunya Kamegai, curator, and Dr. Jun Araki, Meguro Parasitological Museum for the loan of specimens.

**LITERATURE CITED**


