

Interoceanic occurrence of species of *Aristocleidus* Mueller, 1936 (Monogenoidea: Dactylogyridae) parasitizing the gills of gerreid fishes in the Neotropics

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Abstract During investigations of fish parasites in the Neotropics (including the state of Veracruz and the Yucatán Peninsula in the Gulf of Mexico, the Chautengo Lagoon on the Pacific coast of the state of Guerrero in Mexico, and Lake Gatun in the Panama Canal), three monogenoidean (Dactylogyridae) species were found parasitizing the gills of gerreids (Gerreidae): *Aristocleidus hastatus* Mueller, 1936, was recovered from *Eugerres plumieri* (Cuvier) and *Diapterus auratus* Ranzani in Veracruz, from *D. auratus* and *Diapterus rhombeus* (Cuvier) in Yucatán, from *Eugerres brasilianus* (Cuvier) in Panama (all new hosts and geographical records), and from *D. peruvianus* (Cuvier) and *Gerres cinereus* (Walbaum) in Guerrero; *Aristocleidus*

lamothei Kritsky and Mendoza-Franco, 2008, was recovered from *E. plumieri* in Veracruz and from *D. rhombeus* in Yucatan (new hosts and geographical records), and *Aristocleidus* sp. was recovered from *G. cinereus* in Guerrero. Results from this study suggest that species of *Aristocleidus* exhibit wide host specificity within gerreid fishes and that geminate species within this parasite genus may have originated with the formation of the Isthmus of Panama (3.1 to 3.5 ma). Evidence is also presented suggesting the potential role of the Panama Canal as a passageway allowing the interoceanic dispersal of *Aristocleidus* species across the isthmus.

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Introduction

Aristocleidus (Mueller 1936) (Monogenoidea: Dactylogyridae) is currently represented by two species: *Aristocleidus hastatus* (type species) from the striped bass, *Roccus lineatus* Bloch, 1792 (type host) (= *Morone saxatilis* [Walbaum, 1792]) (Moronidae), in the Peace River, Florida (Atlantic), and from *Diapterus peruvianus* Cuvier, 1830 (Gerreidae), in the Tres Palos Lagoon, Mexico (Pacific), and *Aristocleidus lamothei* Kritsky and Mendoza Franco, 2008, from *D. peruvianus* also in the Tres Palos Lagoon (Mueller 1936; Violante-González et al. 2007; Kritsky and Mendoza-Franco 2008). During a study of monogenoids infecting the gills of gerreid fishes, specimens of *A. hastatus*, *A. lamothei*, and *Aristocleidus* sp. were recovered from six species of Gerreidae (*Diapterus auratus* Ranzani, 1842; *D. peruvianus*; *Diapterus rhombeus* [Cuvier, 1829]; *Eugerres brasilianus* [Cuvier, 1830]; *Eugerres plumieri* [Cuvier, 1830]; and *Gerres cinereus* [Walbaum, 1792]) in the Atlantic and Pacific Oceans, as well as in the Panama

Canal. Here, we provided illustrations of the sclerotised structures of *A. hastatus* and *Aristocleidus* sp., data on biometrical variability of individual species from different hosts, and information about the prevalence and intensity of infections at each site. In addition, the occurrence of species of *Aristocleidus* on the Atlantic and Pacific coasts of North America is discussed in relation to the formation of the Isthmus of Panama (3.1 to 3.5 ma) and the possible role of the Panama Canal as a passageway for interoceanic dispersal.

Materials and methods

Fishes were captured using gill and throw nets, as well as by hook-and-line, between December 2004 and June 2007. Three estuaries and one river were sampled in the Gulf of Mexico: Ría Lagartos (21°35'8.88"N; 87°00'19.68"W) and Ría Celestún (20°49'15.4"N; 90°23'31"W) in the Yucatán Peninsula and Las Barrancas (18°59'46"N; 95°57'54"W) and Ría Maquinas (18°36'41"N; 95°06'27"W) in the state of Veracruz. Other sampling locations included Lake Gatun near Barro Colorado Island (9°10'2.68"N; 79°50'13.90"W) in Panama and the Chautengo Lagoon (16°38'36.48"N; 99°02'48.14"W) on the Pacific coast of the state of Guerrero, Mexico. Fishes were kept on ice until their gills were removed in the laboratory and fixed in 4–5% formalin to examine ectoparasites. Parasites were isolated and stained with Gomori's trichrome and mounted in Canada balsam. Some specimens were also mounted unstained in Gray and Wess's medium to obtain measurements and line drawings of the haptor structures and the copulatory complex. All other measurements were obtained from unflattened specimens stained with Gomori's trichrome. Drawings were made with the aid of a drawing tube using an Olympus microscope with Nomarski interference contrast. Measurements, in micrometers (µm), represent straight-line distances between extreme points and are expressed as the mean followed by the range and number (*n*) of structures measured in parentheses; body length includes that of the haptor. Prevalence of infection in a sample was calculated as the percentage of hosts infected with a species of *Aristocleidus* and intensity as the mean number of monogenoids per infected fish (Bush et al. 1997). Voucher specimens were deposited in the National Helminthological Collection of Mexico (CNHE), Institute of Biology, National Autonomous University of Mexico, Mexico; the helminthological collection of the Institute of Parasitology, České Budějovice, Czech Republic (IPCAS); and the United States National Parasite Collection, Beltsville, Maryland (USNPC). Scientific names of the hosts are consistent with FishBase (Froese and Pauly 2008) and host body lengths are expressed as total length (TL).

Results

Aristocleidus hastatus Mueller 1936 (Fig. 1, parts 1–5)

Host: *E. plumieri* (Perciformes, Gerreidae).

Site of infection: Gills.

Locality and collection date: Ría Maquinas (18°36'41"N; 95°06'27"W), 3–4 km from the town of Montepio in Veracruz, Mexico, March 2006.

Prevalence and intensity of infection: two fish (mean TL 16 cm; range 14–18) infected of two examined (100%); intensity of infection, two worms.

Measurements (based on two specimens): Pharynx, 42 wide. Haptor, 125 (*n*=2). Ventral anchor, 46 (45–47; *n*=4) long. Dorsal anchor, 44 (42–47; *n*=4) long. Ventral bar, 20–23 long. Dorsal bar, 36–37 long. Hooks, 13 (11–13; *n*=6) long. Copulatory complex, 23–29 long.

Measurements of *A. hastatus* specimens from other gerreid host species are provided in Table 1, along with the prevalence and intensity of infections at each location.

Specimens deposited: 19 vouchers in CNHE (6582, 6584, 6588–6591), 19 in IPCAS (M-484), and 16 in USNPC (101543–46).

Aristocleidus lamothei Kritsky and Mendoza-Franco 2008

Host: *E. plumieri* (Perciformes, Gerreidae).

Site of infection: Gills.

Locality and collection date: Ría Maquinas in Veracruz, Mexico, March 2006.

Other host and locality: *D. rhombeus* from Ría Celestún in Yucatán, Mexico.

Prevalence and intensity of infection: two fish (mean TL 14 cm; range 8–6) infected of two examined (100%); intensity of infection, three worms.

Measurements (based on three specimens from *E. plumieri* and one from *D. rhombeus* [brackets]): Pharynx, 16–34 [16] wide. Haptor, 67–100 [50] wide. Ventral anchor, 42 (39–43; *n*=6) [26–28] long, with elongate and curved shaft and point. Dorsal anchor, 41 (38–42; *n*=6) [22] long. Ventral bar, 26 (24–29; *n*=3) [19] long. Dorsal bar, 30 (30–31; *n*=3) [21] long. Hooks, 12 (*n*=5) long. Copulatory complex, 35–36 long. Accessory piece, 28 long.

Specimens deposited: three vouchers from *E. plumieri* and one from *D. rhombeus* in CNHE (6583 and 6593, respectively).

Aristocleidus sp. (Fig. 1, parts 6–12)

Host: *Gerres cinereus* (Perciformes, Gerreidae).

Site of infection: Gills.

Locality and collection date: Chautengo Lagoon in the state of Guerrero, Mexico, December 2004.

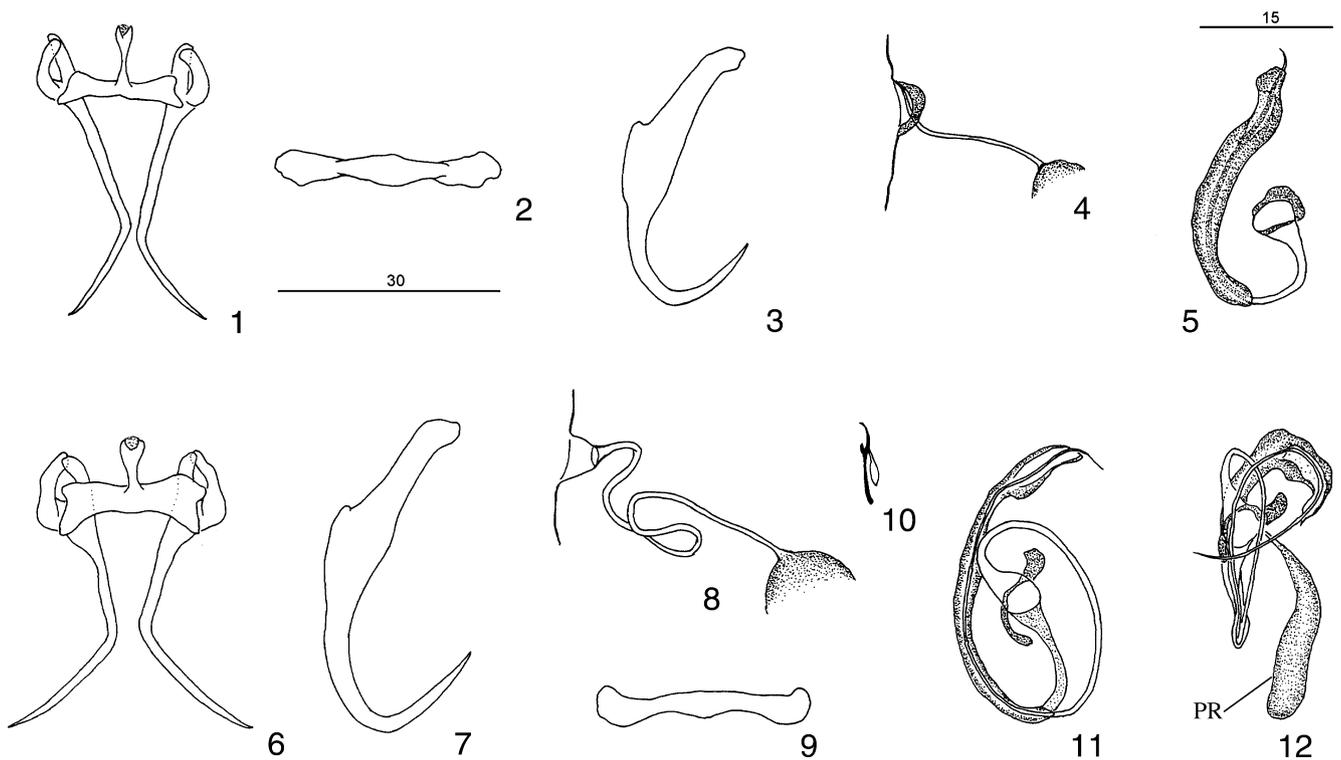


Fig. 1 *Aristocleidus* spp. from *Gerres cinereus* in the Chautengo Lagoon, Guerrero, Mexico. 1–5 *Aristocleidus hastatus*. 1 Ventral anchor/bar complex. 2 Dorsal bar. 3 Dorsal anchor. 4 Vagina (dextral). 5 Copulatory complex (ventral). 6–12 *Aristocleidus* sp. 6 Ventral

anchor/bar complex. 7 Dorsal anchor. 8 Vagina (dextral). 9 Dorsal bar. 10 Hook. 11, 12 Copulatory complexes (ventral). PR prostatic reservoir. All images were drawn to a scale of 30 μ m, except for 5 (15 μ m)

Prevalence and intensity of infection: Only three specimens of this species were found with *A. hastatus* on *G. cinereus*.

Measurements (based on three specimens): Pharynx, 20–23 wide. Haptor, 66 wide. Ventral anchor, 36 (34–37; $n=5$) long, with the shaft bent on its midportion. Dorsal anchor, 42 (41–43; $n=4$) long. Ventral bar, 21 ($n=2$) long. Dorsal bar, 28 (28–29; $n=3$) long. Hooks, 11 (11–12; $n=8$) long. Male copulatory organ (MCO), a coiled tube with one complete and one half ring, 23 (23–24; $n=3$) diameter of the first ring. Accessory piece, 30 long, apparently articulated to the base of the MCO. Vagina, a looping tube opening dextrally.

Specimens deposited: three vouchers in CNHE (6592).

Discussion

While specimens of *A. hastatus* exhibited morphological similarities across their respective hosts and locations, there were size differences in the length of the anchors between specimens recovered from *Diapterus* spp. and those recovered from *Gerres* and *Eugerres* spp. (see Table 1 and measurements of specimens from *E. plumieri*). In the Atlantic, as well as in the Pacific, these differences may

reflect the different environmental influences placed on the parasites by their respective hosts (*Diapterus* vs *Gerres* and/or *Eugerres*) and/or the geographical distribution of these hosts. For instance, in the Atlantic, species of *Diapterus* occur throughout the western region, whereas species of *Eugerres* are restricted to the transitional zone between Belize and Panama, including Cuba (Deckert and Greenfield 1987). Similarly, specimens of *A. lamothei* exhibited metrical variation between *Diapterus* and *Eugerres* host species. Notably, the lengths of the ventral and dorsal anchors of *A. lamothei* specimens from *D. rhombeus* in the Atlantic (present study) and *D. peruvianus* in the Pacific (original description in Kritsky and Mendoza-Franco 2008) were smaller than those from *E. plumieri* in the Atlantic (present study): 26–28, 26–33 vs 39–43 and 22, 30–33 vs 38–42, respectively.

Aristocleidus hastatus was the most common species of the genus and occurred simultaneously with *A. lamothei* and *Aristocleidus* sp. on individual gerreid hosts. The scarcity of specimens from the latter two species found in mixed infections supports this observation and suggests that a large sample size of host specimens may be necessary to recover these species of *Aristocleidus*. The identification of *Aristocleidus* sp. was restricted to three specimens found on *G. cinereus* from the Chautengo Lagoon in Guerrero,

Table 1 Measurements (in micrometers; mean with range and number of measurements [*n*] in parentheses) of *Aristocleidus hastatus* Mueller, 1936 (Monogenoidea, Dactylogyridae) from the gills of gerreid (Gerreidae) fishes in the Neotropics

	Atlantic (Veracruz State and Yucatán Peninsula, Gulf of Mexico)			Panama Canal		Pacific (Guerrero State, Mexico)	
	<i>D. auratus</i> TL 8 (6–10) <i>P</i> =100, <i>I</i> =6 <i>n</i> =2 Ría Lagartos	<i>D. rhombeus</i> TL 9 <i>I</i> =33 <i>n</i> =1 Ría Celestún	<i>D. rhombeus</i> TL 7 <i>I</i> =34 <i>n</i> =1 Ría Lagartos	<i>D. auratus</i> TL 13 (12–14) <i>P</i> =50, <i>I</i> =4 <i>n</i> =2 Las Barrancas	<i>E. brasiliensis</i> TL 20 (18–21) <i>P</i> =100, <i>I</i> =15 <i>n</i> =10 Barro Colorado Island	<i>Diapterus peruvianus</i> TL 14 (9–22) <i>P</i> =100, <i>I</i> =16 <i>n</i> =33 Chautengo Lagoon	<i>Gerres cinereus</i> TL 14 (10–26) <i>P</i> =87.5, <i>I</i> =7 <i>n</i> =24 Chautengo Lagoon
Body length	165–173	206 (98–210; <i>n</i> =3)	180 (162–198; <i>n</i> =8)	–	364 (268–470; <i>n</i> =18)	328 (268–370; <i>n</i> =11)	281 (205–335; <i>n</i> =10)
Greatest width	73–81	53 (47–67; <i>n</i> =3)	47 (43–50; <i>n</i> =6)	–	62 (50–77; <i>n</i> =17)	60 (50–70; <i>n</i> =12)	49 (43–54; <i>n</i> =7)
Pharynx width	25 (19–33; <i>n</i> =4)	21 (21–24; <i>n</i> =3)	21 (18–24)	37 (33–40; <i>n</i> =3)	27 (24–33; <i>n</i> =14)	26 (22–31; <i>n</i> =9)	20 (15–23; <i>n</i> =6)
Haptor width	64 (60–67; <i>n</i> =4)	55 (50–60; <i>n</i> =3)	58 (55–65; <i>n</i> =5)	106 (97–125; <i>n</i> =4)	67 (62–82; <i>n</i> =11)	56 (53–60; <i>n</i> =5)	52 (50–53; <i>n</i> =3)
Ventral anchor length	37 (35–39; <i>n</i> =7)	37 (35–38; <i>n</i> =5)	38 (35–39; <i>n</i> =8)	44 (42–46; <i>n</i> =8)	42 (40–45; <i>n</i> =26)	37 (35–38; <i>n</i> =17)	45 (42–48; <i>n</i> =8)
Dorsal anchor length	31 (<i>n</i> =2)	32	34 (34–35; <i>n</i> =3)	41 (39–42; <i>n</i> =8)	42 (40–43; <i>n</i> =17)	36 (33–38; <i>n</i> =15)	40 (38–43; <i>n</i> =7)
Ventral bar length	18 (<i>n</i> =2)	16	18 (16–20; <i>n</i> =3)	18 (17–18; <i>n</i> =4)	22 (20–23; <i>n</i> =7)	18 (16–19; <i>n</i> =8)	19
Dorsal bar length	24–25	23 (22–23; <i>n</i> =3)	26 (25–28; <i>n</i> =3)	31 (30–32; <i>n</i> =4)	34 (30–36; <i>n</i> =10)	30 (28–31; <i>n</i> =9)	29 (27–33; <i>n</i> =5)
Hooks	11–12	11	12 (12–13; <i>n</i> =3)	11 (10–12; <i>n</i> =21)	11 (11–12; <i>n</i> =23)	11 (10–12; <i>n</i> =13)	11–12
C. complex length	–	–	–	27 (26–29; <i>n</i> =4)	26 (22–29; <i>n</i> =9)	26 (22–29; <i>n</i> =10)	24 (22–25; <i>n</i> =3)
Germaarium length	–	30 (26–30; <i>n</i> =3)	30 (28–33; <i>n</i> =3)	–	36 (30–40; <i>n</i> =4)	–	33
Germaarium width	–	9–16	12 (8–13; <i>n</i> =5)	–	11 (9–14; <i>n</i> =4)	–	9

C. copulatory, TL total length (cm) of the host with range in parentheses, *P* (%) infection prevalence [% infected], *I* mean number of parasites per infected host, *N* number of examined host

Mexico. *Aristocleidus* sp. resembles *A. hastatus* in the general morphology of the reproductive organs and haptor structures (see Fig. 1, parts 1–12), but differs from *A. hastatus* by having the shaft of the ventral anchors bent on their midportion (bent on the distal third portion in *A. hastatus*, see Fig. 1, parts 1 and 6), a looping vaginal tube (short tube in *A. hastatus*, see Fig. 1, parts 4 and 8), an MCO comprising a coiled tube with one complete and one half ring (almost a complete ring in *A. hastatus*, see Fig. 1, parts 5, 11, and 12), and an accessory piece articulated to the base of the MCO (Fig. 1, parts 11 and 12) [not articulated in *A. hastatus* (see Figs. 5 and 3 in Kritsky and Mendoza-Franco, 2008)]. An emendation of *Aristocleidus* may be possible based on the morphology of the accessory piece, given a more extensive revision of specimens to formally describe this characteristic.

Results from this study indicate that *A. hastatus* occurs on several host species spanning a broad geographical range: *D. auratus*, *D. rhombeus*, *E. plumieri*, and *G. cinereus* from the Gulf of Mexico; *E. brasiliensis* from the Panama Canal (all new hosts and geographical records); and *D. peruvianus* from the Pacific coast of Mexico. In addition, *A. lamothei*, which was recently described from *D. peruvianus* on the Pacific coast of Mexico (Kritsky and Mendoza-Franco 2008), was recovered from *E. plumieri* and *D. rhombeus* (new hosts and geographical records) in the Gulf of Mexico.

Two hypotheses may explain the current zoogeographical distribution of these monogenean species: (1) *A. hastatus* and *A. lamothei* may be exceptionally old species that were present on either side of the Isthmus of Panama before its formation (3.1 to 3.5 ma), and specimens recovered from either side may represent distinct species that cannot be differentiated morphologically (see Kritsky and Mendoza-Franco 2008), and (2) *A. hastatus* and *A. lamothei* may be geminate species having originated from a common ancestor with an ampho-American distribution before the formation of the Isthmus of Panama, and the occurrence of both species in the Atlantic and Pacific basins may be explained by the dispersal of their hosts through the Panama Canal.

Other possible examples from the Monogenea representing potential geminate species in the Neotropics have been documented with *Rhabdosynochus hargisi* Kritsky, Boeger and Robaldo, 2001, and *Rhabdosynochus alterinstitus* Mendoza-Franco, Violante-González and Vidal-Martínez, 2008 (Diplectanidae), from the gills of the centropomids, *Centropomus undecimalis* (Bloch, 1792) in the Atlantic Ocean and *Centropomus nigrescens* Günther, 1864 in the Pacific Ocean, respectively (Mendoza-Franco et al. 2008).

Several lines of evidence support the second hypothesis mentioned above. For instance, although the family Gerreidae is primarily marine, various species are known to enter rivers [Deckert and Greenfield 1987; see also *G. cinereus*

from the Río Maquinas (present study)]. The ability of gerreids to tolerate freshwater is exemplified in this study by specimens of *E. brasiliensis* collected from Lake Gatun in the Panama Canal. The fact that these fish were parasitized by *A. hastatus* also supports the possibility that this parasite species was carried into the Pacific through the Panama Canal by its host, *E. brasiliensis*, native to the Caribbean Sea (see Deckert and Greenfield 1987). Consistent with this hypothesis, it is also possible that *E. brasiliensis* has been in direct contact with other gerreid species such as *D. peruvianus* (originally dispersed in the Pacific) and *G. cinereus* (occurring naturally in the Atlantic), which have previously been reported in the Gatun Lake and the Pacific entrance of the Panama Canal (i.e., Miraflores Lake) (see McCosker and Dawson 1975; Panama Canal Authority 2004). Although these gerreid species from the Pacific coast of Panama have not yet been reported as hosts of *Aristocleidus* species, the occurrence of *A. hastatus* and *A. lamothei* on these same host species from the Pacific coast of the state of Guerrero, in Mexico, supports this hypothesis. Since its construction in 1914, the Panama Canal has been viewed as a potential pathway for the interoceanic dispersal of marine fishes, and previous studies have documented the migration of several species from the Pacific to the Atlantic, and vice versa (see Rubinoff and Rubinoff 1968; McCosker and Dawson 1975; Cohen 2006).

Undoubtedly, the formation of the Isthmus of Panama is tightly linked to the evolutionary history of *Aristocleidus* species. However, determining the evolutionary time of diversification of this parasite genus in the neotropics and the potential role of the Panama Canal in explaining the broad zoogeographical distribution of individual species will further require the use of molecular tools.

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