The distribution of the introduced tapeworm *Bothriocephalus acheilognathi* in Australian freshwater fishes

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Abstract

Native and exotic fishes were collected from 29 sites across coastal and inland New South Wales, Queensland and Victoria, using a range of techniques, to infer the distribution of *Bothriocephalus acheilognathi* (Cestoda: Pseudophyllidea) and the host species in which it occurs. The distribution of *B. acheilognathi* was determined by that of its principal host, carp, *Cyprinus carpio*; it did not occur at sites where carp were not present. The parasite was recorded from all native fish species where the sample size exceeded 30 and which were collected sympatrically with carp: *Hypseleotris klunzingeri*, *Hypseleotris* sp. 4, *Hypseleotris* sp. 5, *Phylipnodon grandiceps* and *Retropinna semoni*. *Bothriocephalus acheilognathi* was also recorded from the exotic fishes *Gambusia holbrooki* and *Carassius auratus*. *Hypseleotris* sp. 4, *Hypseleotris* sp. 5, *P. grandiceps*, *R. semoni* and *C. auratus* are new host records. The parasite was not recorded from any sites in coastal drainages. The only carp population examined from a coastal drainage (Albert River, south-east Queensland) was also free of infection; those fish had a parasite fauna distinct from that of carp in inland drainages and may represent a separate introduction event. *Bothriocephalus acheilognathi* has apparently spread along with its carp hosts and is so far restricted to the Murray-Darling Basin. The low host specificity of this parasite is cause for concern given the threatened or endangered nature of some Australian native freshwater fish species. A revised list of definitive hosts of *B. acheilognathi* is presented.

Introduction

Like its original host, the carp *Cyprinus carpio*, *Bothriocephalus acheilognathi* Yamaguti, 1934 is native to the Amur River Basin of China. It has been distributed around the world along with several of its cyprinid host species, particularly *C. carpio* and *Ctenopharyngodon idella*, as these species have been translocated for use in providing fishing stocks, aquaculture and weed control (Andrews *et al*., 1981; Chubb, 1981; Heckmann *et al*., 1993; Font & Tate, 1994; Salgado-Maldonado *et al*., 1986; Scholz & Di Cave, 1992). In the process, host-switching events have occurred and the list of fish species which it infects has grown to include more than 50 species from six orders.

Bothriocephalus acheilognathi is present in Australia and has acquired native fish hosts (Dove *et al*., 1997). The aim of the present study was to provide evidence for the geographical distribution of this parasite in the eastern states of Australia and to reveal any native fish species which are being used as hosts. A secondary aim was the compilation of a list of definitive host species of *B. acheilognathi* around the world to provide a reference source for studies of this important fish pathogen and to allow conclusions to be drawn on the biology of the species based on its host-specificity patterns.

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https://doi.org/10.1017/S0022149X00700782 Published online by Cambridge University Press

Materials and methods

Fishes were collected from the sites identified in table 1 during January and February 1997. Sites were chosen to incorporate the following major drainage types: northern coastal, southern coastal, inland montane and inland lowland. Both lentic and lotic sites, with a wide range of physical and biological characteristics, were chosen. A list of sites, their abbreviations and drainage types is given in table 1. Collections were made by seine netting, dip netting, line fishing and backpack electrofishing. Fish were killed by pithing the brain or by overdose of benzocaine anaesthetic. Fish were identified using McDowall (1996) or Allen (1989), measured, sexed (if possible) and then dissected in saline. Identification of *Hypseleotris* spp. was problematic; discrimination of the undescribed species referred to as Midgely's carp gudgeon and Lake's carp gudgeon (*Hypseleotris* sp. 4 and *Hypseleotris* sp. 5 respectively) in Larson & Hoese (1996) and Allen (1989) was confirmed using Unmack (1997a,b). Records from unidentifiable gudgeons were excluded from the analysis (except table 3). Tapeworms were fixed by pipetting into boiling saline and then storing in 10% formalin. Specimens for whole mounts were stained in Mayer's haematoxylin, dehydrated through a graded alcohol series, cleared in methyl salicylate and mounted in Canada balsam. Permanent taxonomic preparations were made for representative specimens from each host and locality and lodged at the Queensland Museum.

Results

Bothriocephalus acheilognathi was recovered from the introduced fishes *Cyprinus carpio*, *Carassius auratus* and *Gambusia holbrooki* and from the native fishes *Hypseleotris klunzingeri*, *Hypseleotris* sp. 4, *Hypseleotris* sp. 5, *Phylipnodon grandiceps* and *Retropinna semoni*. Table 1 shows the species of fish recovered at each site. Infected carp were all immature specimens of a size suggesting they were in the 0+ age group, whereas all other hosts were infected in the adult size range. Table 2 shows the infection details for infected species at each 'infected' site. Site 19, Gum Bend Lake near Condobolin, New South Wales, had the highest prevalence of infection in each host species. Sites 4, 6, 11 and 14 had infections recorded from hosts other than carp without records from carp; carp were nonetheless present at these sites and the failure to record the parasite from them is most likely an error resulting from small sampling size. The overall infection prevalences for all fish species examined, pooled across all sites, and the highest mean abundance and intensity shows that *Cyprinus carpio* was the principal host (table 3). Pooled data as presented in table 3 remove to some degree the problem of small sample sizes at any given site; it can be seen from these data that *B. acheilognathi* was recorded from all native hosts which live sympatrically with carp and with a sample size exceeding 30. Unidentified *Hypseleotris* spp. are included in table 2 to show that this group had a high prevalence of infection. This group was difficult to identify most often because they were small and had not developed the adult characteristics necessary for the identification of *Hypseleotris* species; the group probably includes representatives of *H. klunzingeri*, *Hypseleotris* sp. 4 and *Hypseleotris* sp. 5. The high prevalence of infection in this group is consistent with high prevalences of infection in young fishes found in other studies. *Bothriocephalus acheilognathi* was not recovered from any sites where carp were not present, nor any coastal sites including the only coastal carp population examined (Albert River, Queensland). Table 4 lists the published host records of *B. acheilognathi*. Five of the fish hosts in this study represent new host records for *B. acheilognathi*: the native species *Hypseleotris* sp. 4, *Hypseleotris* sp. 5, *P. grandiceps*, *R. semoni* and the exotic ornamental goldfish *Carassius auratus*. *Retropinna semoni* represents a new order of hosts, the Osmeriformes.

Discussion

Bothriocephalus acheilognathi must be considered one of the most successful of all freshwater fish parasites. Its principal host, *Cyprinus carpio*, is arguably the world's most widespread freshwater fish (Merrick & Schmida, 1984), as a result of its distribution for aquaculture, sport and weed control. The parasite has become established in nearly all environments to which its hosts have been introduced and, as such, now has a distribution incorporating all continents except Antarctica. Its low host specificity has facilitated host-switching and resulted in a host range including fish species from six orders and 11 families (see table 4). The importance of *B. acheilognathi* and its spread in non-native habitats makes the documentation of its native and non-native distribution and hosts desirable, so that future host colonizations and their effects may be better understood and managed.

Evidence from the present study suggests that *B. acheilognathi* has a distribution in Australia which is congruent with that of Boolarra strain carp and that it has apparently not spread beyond that range using other hosts. This pattern may reflect the failure of the parasite to mature properly in native hosts (gravid worms in native hosts are rare, A.D.M. Dove, personal observation), or the effective barrier to parasite spread represented by the Great Dividing Range, or some combination of both or other factors. More intensive sampling of coastal sites would be desirable before rigorous conclusions could be drawn on the distribution of the parasite in those drainages and the role of topography in defining the colonization patterns of the parasite. The northern and western tributaries of the Murray-Darling were not investigated in the present sampling regime. Although not found in the present study, juvenile percichthyids, terapontids, ambassids, atherinids, melanotaeniids and plotosids occur more frequently at those sites. As a result, the pattern of host range and parasite zoogeography may be most informative at these sites, where carp and other exotic fishes are less dominant (New South Wales Rivers Survey, 1998). There seems sufficient evidence to suggest that the parasite would most likely be present, and infecting native hosts, in far western and northern Darling drainages.

The infection-free status of the carp population in the Albert River (Beenleigh Crayfish Farm), coastal Queensland may be the result of a separate carp introduction event (initially infection-free) or intolerance of summer water temperature by the parasite. The other parasites

Table 1. Sites and host species examined for *Bothriocephalus acheilognathi*.

Site no.	Site name	Lat./Long.	Characteristics	Species recovered
1	Concrete Crossing, Pierce's Creek, ACT	35°17′S 149°08′E	Inland montane creek	*Galaxias olidus*
2	Warri Bridge, Shoalhaven R., NSW	34°49′S 150°13′E	Coastal lowland river	***Carassius auratus, Gambusia holbrooki, Oncorhynchus mykiss***, *Galaxias maculatus, G. olidus*
3	Araluen Creek, NSW	35°46′S 149°54′E	Coastal montane creek	*G. maculatus, Gobiomorphus coxii, Retropinna semoni*
4	Black Mountain Peninsula, Lake Burley-Griffin, ACT	35°17′S 149°09′E	Inland artificial lake	***C. auratus, Cyprinus carpio, G. holbrooki***, *Hypseleotris klunzingeri*
5	Ginninderra Ck, Macgregor, ACT	35°16′S 149°09′E	Inland, disturbed suburban creek	***Misgurnus anguillicaudatus***
6	Ginninderra Ck, Ginninderra Falls, NSW	35°16′S 149°08′E	Inland, pools below waterfall	***C. carpio, G. holbrooki***
7	Ovens River, Victoria	36°25′S 146°32′E	Inland, lowland, wetland surrounding river	***C. auratus, C. carpio, G. holbrooki***, *H. klunzingeri, Hypseleotris* sp. 5, *Nannoperca australia*
8	The Broken Creek, Victoria	36°07′S 145°23′E	Inland lowland, creek	***C. carpio***
9	The Gulf, Murray River, Barmah Forest, NSW	35°55′S 145°23′E	Inland lowland, billabongs adjacent to river	***C. carpio, G. holbrooki, Perca fluviatilis***, *H. klunzingeri, Hypseleotris* sp. 4, *Hypseleotris* sp. 5, *Macquaria ambigua, Phylipnodon grandiceps, R. semoni*
10	Bangarang Rd Billabong, Murray River, Victoria	36°08′S 144°47′E	Inland lowland, periodically-flushed billabong	***C. auratus, C. carpio, G. holbrooki, P. fluviatilis***, *H. klunzingeri, Hypseleotris* sp. 4, *Hypseleotris* sp. 5, *P. grandiceps, R. semoni*
11	Barmah Lake, NSW	35°52′S 145°20′E	Inland lowland, shallow lake	***C. auratus, C. carpio***, *R. semoni*
12	Barmah Forest Creek, NSW	35°52′S 145°20′E	Inland lowland, creek feeding Barmah Lake	***C. auratus, G. holbrooki***, *Craterocephalus stercusmuscarum, H. klunzingeri, Hypseleotris* sp. 4, *Hypseleotris* sp. 5
13	Skeleton Creek, Victoria	35°55′S 145°36′E	Inland lowland, creek	***C. carpio, G. holbrooki***, *Hypseleotris* sp. 4, *Hypseleotris* sp. 5, *P. grandiceps*
14	Steven's Weir, Edward River, NSW	35°52′S 144°58′E	Inland lowland, riverine wetlands	***C. auratus, C. carpio, G. holbrooki***, *H. klunzingeri, Nematolosa erebi, P. grandiceps*
15	Riverside, Edward River, Deniliquin, NSW	35°52′S 145°00′E	Inland lowland river, main channel	***C. auratus, C. carpio, P. fluviatilis***, *H. klunzingeri, R. semoni*
16	NFC/Murrumbidgee Junction, Narranderra, NSW	34°44′S 146°34′E	Drainage Creek from Inland Fisheries Research Station	***C. auratus, C. carpio, G. holbrooki***, *H. klunzingeri, Hypseleotris* sp. 4, *Hypseleotris* sp. 5, *M. ambigua**
17	NFC pondage creek, Narranderra, NSW	34°44′S 146°34′E	Drainage Creek from Inland Fisheries Research Station	***C. auratus, C. carpio, G. holbrooki***, *H. klunzingeri, M. ambigua,** *R. semoni*
18	Wallaroi Ck, Condobolin, NSW	33°11′S 147°03′E	Inland lowland, creek	***G. holbrooki***, *Hypseleotris* sp. 4, *Hypseleotris* sp. 5, *P. grandiceps, Tandanus tandanus*
19	Gum Bend Lake, Condobolin, NSW	33°04′S 147°11′E	Inland lowland, 10 year old artificial lane	***C. auratus, C. carpio, G. holbrooki, P. fluviatilis***, *H. klunzingeri, Hypseleotris* sp. 4, *Hypseleotris* sp. 5, *P. grandiceps, R. semoni*
20	Gwydir River, near Armidale, NSW	30°30′S 151°36′E	Inland montane river	***G. holbrooki***
21	Boorolong Creek, near Armidale, NSW	30°30′S 151°59′E	Inland montane creek	*G. olidus*
22	Wollomombi River, near Armidale, NSW	30°37′S 151°40′E	Inland montane river	***G. holbrooki, O. mykiss***
23	Condamine headwaters, NSW	28°19′S 152°18′E	Inland montane creek	***G. holbrooki***, *Craterocephalus stercusmuscarum fulvus, Hypseleotris* sp. 4, *R. semoni, T. tandanus*
24	Marylands River, NSW	28°35′S 152°35′E	Coastal montane river	***G. holbrooki***, *Hypseleotris compressa, Hypseleotris galii, H. klunzingeri, Mogurnda adspersa*
25	Boonoo Boonoo River, NSW	29°02′S 152°02′E	Coastal montane creek	*G. olidus*
26	Leslie Dam, Warwick, Queensland	28°12′S 152°00′E	Inland impoundment	***G. holbrooki***, *Ambassis agassizi, Bidyanus bidyanus,*** *C. stercusmuscarum, H. klunzingeri*
27	Condamine River, Warwick, Queensland	28°13′S 152°02′E	Inland river	*C. stercusmuscarum, H. klunzingeri, Melanotaenia fluviatilis, N. erebi, R. semoni*
28	Below Leslie Dam, Warwick Queensland	28°12′S 152°00′E	Inland impoundment	***G. holbrooki***, *A. agassizi, C. stercusmuscarum, H. klunzingeri, Hypseleotris* sp. 4, *M. adspersa, Leiopotherapon unicolor, T. tandanus*
29	Beenleigh Crayfish Farm, Beenleigh, Queensland	27°43′S 153°13′E	Coastal crayfish farm ponds	***C. carpio, G. holbrooki***, *H. galii, H. klunzingeri, L. unicolor*

Bold type denotes an exotic fish species.
* These fish almost certainly escaped from the NFC hatchery.
** These fish probably the result of a stocking from hatchery raised fry.

Table 2. The infection prevalence of *Bothriocephalus acheilognathi* in fish hosts at various sites in Australia.

Site no.	Host	% Prevalence (no. examined)
4	*Hypseleotris klunzingeri*	12 (8)
4	***Carassius auratus***	**7 (55)**
6	***Gambusia holbrooki***	**40 (5)**
7	***Gambusia holbrooki***	**17 (6)**
9	***Cyprinus carpio***	**13 (15)**
10	***Cyprinus carpio***	**60 (5)**
10	*Hypseleotris* sp. 4	4 (27)
10	*Hypseleotris* sp. 5	6 (31)
10	*Phylipnodon grandiceps*	15 (26)
11	*Retropinna semoni*	3 (29)
13	***Cyprinus carpio***	**3 (35)**
14	*Hypseleotris klunzingeri*	8 (12)
15	***Cyprinus carpio***	**100 (1)**
15	***Carassius auratus***	**100 (1)**
16	***Gambusia holbrooki***	**31 (16)**
16	***Cyprinus carpio***	**33 (9)**
17	***Cyprinus carpio***	**40 (5)**
17	***Gambusia holbrooki***	**10 (20)**
19	***Cyprinus carpio***	**88 (24)**
19	*Hypseleotris klunzingeri*	50 (66)
19	*Hypseleotris* sp. 4	60 (5)
19	*Phylipnodon grandiceps*	75 (4)
19	***Gambusia holbrooki***	**48 (21)**

Exotic host species are shown in bold.

present in that population support the former hypothesis; fish from that site support a number of dactylogyrid monogeneans and gill-parasitic copepods which were not recovered from inland carp populations (A.D.M. Dove, unpublished data).

Bothriocephalus acheilognathi has been shown to be pathogenic (Scott & Grizzle, 1979; Hoole & Nisan, 1994), and has been responsible for mass mortalities in cultured fishes elsewhere (Korting, 1975). It may play a significant role in the interaction between native and exotic fishes in Australia. To determine the extent to which it affects native and exotic fishes in Australia, more information must be gathered on which other native fishes can act as hosts for the parasite and the impact of the parasite on their populations. Of particular interest in such investigations would be the effect of the parasite on host species which form significant fisheries or are in decline, species such as: golden perch (*Macquaria ambigua*); silver perch (*Bidyanus bidyanus*); Murray cod and trout cod (*Machullochella peeli* and *M. macquariensis*); catfish (*Tandanus tandanus*); and many of the declining smaller eleotrids, ambassids, atherinids and melanotaeniids.

The list of definitive host species for *Bothriocephalus acheilognathi* includes species from 12 families of fish across six orders (table 4). The list is dominated by species of cyprinids, which is, perhaps, not surprising given that its original hosts are also cyprinids and that cyprinids dominate the fish fauna of the populous regions of the northern hemisphere where carp introductions have been the most extensive. More informative are the host records

Table 3. Infection prevalence, mean intensity and mean abundance of *Bothriocephalus acheilognathi* in various fish hosts in Australia.

Species	No. examined	% *B. acheilognathi*	Mean intensity	Mean abundance
Ambassis agassizi	45	0	–	–
Bidyanus bidyanus	16	0	–	–
Carassius auratus	**38**	**7.9**	**1**	**0.08**
Craterocephalus stercusmuscarum	30	0	–	–
Craterocephalus fulvus	2	0	–	–
Cyprinus carpio	**124**	**25.8**	**5.4**	**1.23**
Galaxias maculatus	13	0	–	–
Galaxias olidus	69	0	–	–
Gambusia holbrooki	**331**	**6.7**	**2.1**	**0.14**
Gobiomorphus coxii	7	0	–	–
Hypseleotris sp. ?	18	27.8	4.3	0.76
Hypseleotris sp. 4	118	3.4	3.2	0.11
Hypseleotris sp. 5	79	2.5	1	0.03
Hypseleotris compressa	2	0	–	–
Hypseleotris galii	31	0	–	–
Hypseleotris klunzingeri	243	15.2	2.8	0.35
Leiopotherapon unicolor	2	0	–	–
Macquaria ambigua	23	0	–	–
Melanotaenia fluviatilis	3	0	–	–
Misgurnus anguillicaudatus	**13**	**0**	–	–
Mogurnda adspersa	6	0	–	–
Nannoperca australis	4	0	–	–
Nematolosa erebi	4	0	–	–
Oncorhynchus mykiss	**4**	**0**	–	–
Perca fluviatilis	**11**	**0**	–	–
Phylipnodon grandiceps	66	9.1	3.4	0.36
Retropinna semoni	62	1.6	1	0.02
Tandanus tandanus	20	0	–	–

Exotic host species are shown in bold.

https://doi.org/10.1017/S0022149X00700782 Published online by Cambridge University Press

Table 4. Known definitive hosts of *Bothriocephalus acheilognathi*.

Order	Family	Species	Reference
Cypriniformes	Cyprinidae	*Acheilognathus rhombea*	Schmidt, 1986
	Cyprinidae	*Gnathopogon elongatus*	Schmidt, 1986
	Cyprinidae	*Cyprinus carpio*	Schmidt, 1986
	Cyprinidae	*Ctenopharyngodon idella*	Schmidt, 1986
	Cyprinidae	*Opsariichthys uncirostris*	Schmidt, 1986
	Cyprinidae	*Cyprinella lutrensis*	Heckmann *et al.*, 1993
	Cyprinidae	*Gila robusta*	Heckmann *et al.*, 1993
	Cyprinidae	*Gila cypha*	Brouder & Hoffnagle, 1997
	Cyprinidae	*Notemigonus chrysoleucas*	Heckmann *et al.*, 1993
	Cyprinidae	*Rhinichthys osculus*	Heckmann *et al.*, 1993
	Cyprinidae	*Lepidomeda mollispinis*	Heckmann *et al.*, 1993
	Cyprinidae	*Plagopterus argentissimus*	Heckmann *et al.*, 1993
	Cyprinidae	*Ptychocheilus lucius*	Heckmann *et al.*, 1993
	Cyprinidae	*Tinca tinca*	Scholz & Di Cave, 1992
	Cyprinidae	*Notropis lutrensis*	Marcogliese & Esch, 1989
	Cyprinidae	*Pimephales promelas*	Brouder & Hoffnagle, 1997
	Cyprinidae	*Hypophthalmichthys molitrix*	Salih *et al.*, 1988
	Cyprinidae	*Carassius carassius*	Alarcon-Gonzales, 1988
	Cyprinidae	*Leuciscus cephalus*	Nedeva, 1988
	Cyprinidae	*Leuciscus idus*	Grabda-Kazubska & Pilecka-Rapacz, 1987
	Cyprinidae	*Chondrostoma nasus*	Nedeva, 1988
	Cyprinidae	*Alburnus alburnus*	Nedeva, 1988
	Cyprinidae	*Rutilus rutilus*	Salgado-Maldonado *et al.*, 1993
	Cyprinidae	*Barbus barbus*	Grabda-Kazubska & Pilecka-Rapacz, 1987
	Cyprinidae	*Barbus bynni*	Pool, 1987
	Cyprinidae	*Barbus altianilis*	Pool, 1987
	Cyprinidae	*Barbus sharpyi*	Khalifa, 1986
	Cyprinidae	*Barbus capito*	Grigoryan & Pogosyan, 1983
	Cyprinidae	*Barbus callensis*	Meddour, 1988
	Cyprinidae	*Barbus kimberleyensis*	Brandt *et al.*, 1981
	Cyprinidae	*Barbus mattozzi*	Brandt *et al.*, 1981
	Cyprinidae	*Barbus trimaculatus*	Brandt *et al.*, 1981
	Cyprinidae	*Aspius aspius*	Grabda-Kazubska & Pilecka-Rapacz, 1987
	Cyprinidae	*Alburnoides bipunctatus*	Dzhalilov & Daniyarov, 1979
	Cyprinidae	*Varicorhinus heratensis*	Dzhalilov & Daniyarov, 1979
	Cyprinidae	*Puntius binotatus*	Leong, 1986
	Cyprinidae	*Rhinichthys osculus*	Brouder & Hoffnagle, 1997
	Cyprinidae	*Plagopterus argentissimus*	Heckmann *et al.* 1986
	Cyprinidae	*Algansea lacustris*	Mendoza-Garfias *et al.*, 1996
	Cyprinidae	*Gobio gobio*	Scholz, 1989; cited in Scholz & Di Cave, 1992
	Cyprinidae	*Mylocheilus caurinus*	Scholz, 1997
	Cyprinidae	*Ptychocheilus oregonensis*	Scholz, 1997
	Cyprinidae	*Melaniris balsanus*	Scholz, 1997
	Balitoridae	*Nemacheilus angorae*	Mikailov & Ibragimov, 1981
Cyprinodontiformes	Poeciliidae	*Gambusia holbrooki*	Heckmann *et al.*, 1993
	Poeciliidae	*Gambusia yucatana*	Scholz *et al.*, 1996
	Poeciliidae	*Xiphophorus helleri*	Font & Tate, 1994
	Goodeidae	*Alloophorus robustus*	Peresbarbosa-Rojas *et al.*, 1994
	Goodeidae	*Neoophorus diazi*	Peresbarbosa-Rojas *et al.*, 1994
	Goodeidae	*Goodea atripinnis*	Peresbarbosa-Rojas *et al.*, 1994
	Fundulidae	*Fundulus zebrinus*	Brouder & Hoffnagle, 1997
Perciformes	Centrarchidae	*Lepomis gibbosus*	Nedeva, 1988
	Centrarchidae	*Micropterus salmoides*	Salgado-Maldonado *et al.*, 1993
	Gobiidae	*Awous guamensis*	Font & Tate, 1994
	Eleotridae	*Eleotris sandwicensis*	Font & Tate, 1994
	Eleotridae	*Hypseleotris klunzingeri*	Dove *et al.*, 1997
	Eleotridae	*Hypseleotris* sp. 4	present study
	Eleotridae	*Hypseleotris* sp. 5	present study
	Eleotridae	*Phylipnodon grandiceps*	present study
Atheriniformes	Atherinidae	*Chirostoma estor*	Osorio-Sarabia *et al.*, 1986
	Atherinidae	*Chirostoma attenuatum*	Perez-Ponce de Leon *et al.*, 1994
Osmeriformes	Retropinnidae	*Retropinna semoni*	present study
Siluriformes	Clariidae	*Clarias gariepinus*	Anosike *et al.*, 1992
	Plotosidae	*Siluris glanis*	Salgado-Maldonado *et al.*, 1986
Acipenseriformes	Acipenseridae	*Pseudoscapirhynchus kaumanni*	Salgado-Maldonado *et al.*, 1986
Urodela (Amphibia)	Amblystomatidae	*Amblystoma* sp.	Garcia-Prieto & Osorio-Sarabia, 1992

https://doi.org/10.1017/S0022149X00700782 Published online by Cambridge University Press

outside the Cyprinidae. These are spread across the subdivision Euteleostei, incorporating members of three superorders: the Ostariophysi (Siluriformes and Cypriniformes); Protacanthopterygii (Osmeriformes); and Acanthopterygii (Perciformes from the Series Percomorpha, and Cyprinodontiformes and Atheriniformes from the Series Atherinomorpha) (Nelson, 1994). This pattern amounts to an extremely low level of host-specificity and confirms that the parasite does not rely on phylogenetic (i.e. physiological) cues for completion of the life-cycle. Instead, *B. acheilognathi* seems capable of infecting a majority of fish species which will eat the copepod hosts during the first year or so of life. The success of the parasite will also depend on its specificity within the intermediate stage, but data on copepod hosts are limited. We can infer from the degree of success shown by *B. acheilognathi* to date, that it is likely to show a similar absence of host-specificity at the copepod stage, perhaps being restricted only to the Cyclopoida.

Acknowledgements

We are extremely grateful to Mark Lintermans and Mark Jeckabsons of Environment ACT; Andrew Pinner, Craig Schiller, Ian Wooden, and Gavin Kenny at Narranderra Inland Fisheries Research Station; Shirl, Bert, Cheezel and Ross McGann; and Hugh and Marj Dove for their help with the field work. AD was supported by an Australian Postgraduate Award during the study.

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(Accepted 9 November 1999)