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ORIGINAL PAPER

Phylogeny and Life Cycles of the Archiacanthocephala with a Note on the Validity of *Mediorhynchus gallinarum*

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Abstract

Purpose The molecular profile of specimens of *Mediorhynchus gallinarum* (Bhalero, 1937) collected from chickens, *Gallus gallus* L. in Indonesia was analysed. The aim of this study was to assess the phylogenetic position of species of *Mediorhynchus* within the order Giganthorhynchida.

Methods We used one mitochondrial gene (cytochrome oxidase 1) and one nuclear gene (18S ribosomal RNA) to infer phylogenetic relationships of class Archiacanthocephala.

Results The COI and 18S rDNA genes sequences showed that *M. gallinarum* had low genetic variation and that this species is sister to *Mediorhynchus africanus* Amin, Evans, Heckmann, El-Naggar, 2013. The phylogenetic relationships of the Class Archiacanthocephala showed that it is not resolved but, however, were mostly congruent using both genes. A review of host-parasite life cycles and geographic distributions of Archiacanthocephala indicates that mainly small mammals and birds are definitive hosts, while termites, cockroaches, and millipedes are intermediate hosts.

Conclusions While the intermediate hosts have wide geographic distributions, the narrow distribution of the definitive hosts limit the access of archiacanthocephalans to a wider range of prospective hosts. Additional analyses, to increase taxonomic and character sampling will improve the development of a robust phylogeny and provide more stable classification. The results presented here contribute to better understanding of the ecological and evolutionary relationships that allow the host-parasite co-existence within the class Archiacanthocephala.

Keywords Acanthocephala · *Mediorhynchus gallinarum* · Galliformes · Phylogeny

Introduction

Definitive hosts of Archiacanthocephala have been described as strictly terrestrial [1] and include hedgehogs, marsupials, rodents, carnivores and several orders of birds [1–8]. Archiacanthocephalans use invertebrates such as millipedes, termites and cockroaches [9–13] as intermediate hosts. Even when there are several species descriptions and ecological aspects of their natural history, the understanding of archiacanthocephalan evolution has not benefited from extensive usage of molecular data in phylogenetic analyses as is the case of the classes Palaeacanthocephala Meyer, 1931 and Eoacanthocephala Van Cleave, 1936 [14–18]. As such, relationships among members of Archiacanthocephala remain mostly unclear [1, 19–21].

The class Archiacanthocephala is composed of four orders and four families [22] including the family Gigantorhynchidae Hamman, 1982. The genus *Mediorhynchus* is one of the most diverse genera within that family. It

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encompasses 57 species [22] that have been mainly found in Africa and Asia. Species of *Mediorhynchus* use cockroaches as intermediate hosts and birds belonging to distinct orders, such as Accipitriformes, Bucerotiformes, Charadriiformes, Falconiformes, Galliformes and Passeriformes, as definitive hosts [19, 23–26]. Phylogenetic analyses indicate that *Mediorhynchus* is monophyletic [19], but studies centered on Gigantorhynchida or Archiacanthocephala are still scarce [19, 20, 27].

Specimens of *Mediorhynchus gallinarum* (Bhalerao, 1937) are parasites of the chicken *Gallus gallus* L. in diverse Asian areas, including Borneo (Indonesia), Palawan (Philippines) and India [27]. Specimens of *M. gallinarum* typically attach to the intestinal lining causing histological and metabolic changes [27]. Morphologically, *M. gallinarum* is characterized by a cylindrical, non-segmented trunk with few sensory pits. The proboscis has no apical pores and the posterior end of the female is pointed with a terminal gonopore. The proboscis armature is composed of 18–22 longitudinal rows of 5–6 hooks each on its anterior part and 30–34 longitudinal rows of 2–6 spine-like hooks each on its posterior area [19, 27]. Eggs measure 47–57 × 24–32 µm. Previous studies indicated that *M. gallinarum* is sister to *M. africanus* Amin, Evan, Heckmann and El-Naggar, 2013 and that both allopatric species present low divergence. However, this relationship was inferred based on only one individual of *M. gallinarum* [19].

The aim of this study is to further assess the phylogenetic position of *Mediorhynchus gallinarum* within the clade of Giganthorhynchida; our taxonomic sampling also allowed us to test relationships within Archiacanthocephala. To put our findings into perspective, we also discuss ecological relationships and global distribution of intermediate and definitive hosts of the class Archiacanthocephala.

Materials and Methods

Sampling

Specimens of *Mediorhynchus gallinarum* were collected from 46 Isa brown chickens (*Gallus gallus*) from 2 different poultry farms located in the Kaliurang Sleman district, Daerah Istimewa Yogyakarta, Indonesia (107° 15′ 03″ E–7° 34′ 51″ S; 107° 29′ 30″ E–7° 47′ 30″ S). These poultry farms are situated in an open rural environment, where the chickens were maintained in extensive well-managed settings (More details, to read [27]. In 1 farm 26 chickens were examined, while in the other farm 20 were surveyed. Collected specimens were refrigerated for 2 days and then fixed in 70% ethanol.

Molecular Analysis

Genetic comparisons and phylogenetic analyses were based on DNA sequences of the mitochondrial cytochrome oxidase I (COI) gene and the nuclear 18S rDNA gene. Six Indonesian specimens of *Mediorhynchus gallinarum* were analyzed. Four samples were digested overnight at 55 °C and genomic DNA was isolated using a commercial extraction kit (Wizard® Genomic DNA Purification Kit, Promega, Madison, Wisconsin). A fragment of 620 bp of the COI gene was amplified using the primers detailed by Folmer *et al.* [28] following the protocol of Amin *et al.* [27]. Amplicons were sequenced using an external sequencing service (Macrogen Inc., Seoul, South Korea). Two other samples were used to acquire 18S rDNA sequences. Genomic DNA from individual worms was extracted using Qiagen DNeasy tissue kit (Qiagen Inc., Valencia, California, USA) according to manufacturer's instructions. PCR reactions were performed in 30 µL volumes containing 2 × red PCR premix (Ampliqon, Odense, Denmark), 20 pmol of each primer and 3 µL of extracted DNA. A 809 bp fragment of the partial 18S rRNA gene was amplified using the primers MGF (5′-GATCGGGGA GGTAGTGACG-3′) and MGR (5′-ACCCACCGAATC AAGAAAGAG-3′). PCR conditions for 18S rDNA gene amplification included of an initial denaturing step of 95 °C for 5 min and 35 cycles followed by denaturing step at 94 °C for 30 s, annealing step of 59 °C for 30 s, and 30 s of extension at 72 °C, and 72 °C for 5 min as a final extension. PCR products were analysed on 1.5% agarose gel and visualized with UV transluminator. Next, the PCR products were sequenced in both directions using the same PCR primers with ABI 3130 sequencer. All DNA sequences were edited using Codon-Code (Codon Code Aligner, Dedham, Massachusetts) and deposited in GenBank (OK094072–OK094075; MW282174–MW282175).

The four new COI sequences were integrated to a matrix with all sequences of members of Archiacanthocephala available in GenBank. Downloaded sequences include one of *Mediorhynchus gallinarum*, *M. africanus* and *Mediorhynchus* sp. together with one sequence of *Oligacanthorhynchus tortuosa* (Leidy, 1850), one of *Nephridiacanthus major* (Bremser, 1811 in Westrumb, 1821), two of *Prosthenorchis* Travassos, 1915 (*P. elegans* (Diesing, 1851) and *Prosthenorchis* sp.), three of *Oncicola* Travassos, 1916 (*Oncicola luehei* (Travassos, 1917) and *Oncicola* sp.), and five of *Macracanthorhynchus* Travassos, 1917 (*M. ingens* (von Linstow, 1879) and *M. hirudinaceus* (Pallas, 1781)) (Oligacanthorhynchidae). In addition, four sequences of *Moniliformis* Travassos, 1915 (*M. kalahariensis* Meyer, 1931; *M. moniliformis* (Bremser, 1811), *Moniliformis* sp.) (Moniliformidae) and one sequence of *Mayarhynchus* *karlae* Pinacho-Pinacho, Hernández-Orts, Sereno-Uribe, Pérez-Ponce de León, García-Varela, 2017 class Eoacanthocephala and one of *Heterosentis holospinus* Amin, Heckmann and Ha, 2011 and *Profilicollis altmani* (Perry, 1942) (Palaeacanthocephala), were also downloaded and used as outgroup (Table 1). As such, the analyzed matrix has a total of 26 sequences.

Sample size for the 18S rDNA gene was slightly smaller than for COI, including the 2 new sequences of *M. gallinarum* and 15 sequences of members of Archiacanthocephala available in GenBank including one sequence of *M. gallinarum*, *M. africanus*, *M. grandis* and *Mediorhynchus* sp. together with one sequence of *Intraproboscis sanghae* Amin, Heckmann, Sist and Basso, 2021. One of *O. tortuosa, N. major*, *M. ingens, M. hirudinaceus* and *Oncicola* sp, and five sequences of *Moniliformis* (two of *M. moniliformis,* and one of *M. kalahariensis, M. cryptosaudi* and *M. saudi*). Finally, one sequence of *Neoechinorhynchus agilis* (Rudolphi, 1819) (Eoacanthocephala) and one of *Echinorhynchus truttae* Schrank, 1788 (Palaeacanthocephala) were used as outgroup (Table 1). As such, the analyzed matrix has a total of 19 sequences.

Sequences were aligned in Clustal as implemented in MEGA 7 [29] using default parameter values. Observed genetic *p*-distances (*p*) between haplotype and sample pairs were calculated in MEGA 7. IQ-TREE [30] was used to select the model of nucleotide substitution for each matrix (TPM3 + G4). Two methods of phylogenetic inference were implemented, Maximum Likelihood (ML) and Bayesian inference (BI) for each matrix. The ML analysis was conducted with IQ-TREE using the online implementation W-IQ-TREE (http:/iqtree.cibiv.univie.ac.at; [31]), with perturbation strength set to 0.5 and stopping rule set to 100. Clade support was calculated with 1000 ultrafast bootstrap pseudo-replications (BS). The BI analysis was conducted with MrBayes 3.1 [32]. Two independent runs with 4 heated and 1 cold Markov chains each were run for 20 million generations, with trees sampled every 1000 generations. Model parameters were estimated in MrBayes. Convergence to stable log-likelihood values was checked by plotting log-likelihood values against generation time. The first 25% of the trees sampled were discarded as burn-in; remaining trees were used to compute a 50% majority rule consensus tree and to obtain posterior probability (PP) values for each clade.

Results

Both phylogenetic trees gathered via ML and BI for COI were mostly congruent. Archiacanthocephala was found to be monophyletic and with high support (PP = 1; BS = 93; Fig. 1A). Within the archiacanthocephalan clade, two of three orders were found monophyletic. One of these is Gigantorhynchida, whose members form a moderately supported clade (PP = 0.71; BS = 72); the other is Moniliformida that appears well supported (PP = 0.99; BS = 85). Meanwhile, the family Oligacanthorhynchidae was not proven monophyletic. Oligacanthorhynchid genera fall into two main lineages. One corresponds to a clade (PP = 0.85; BS = 80) formed by all oligacanthorhynchid genera except *Oligacanthorhynchus* (Fig. 1A); the other lineage is formed solely by *Oligacanthorhynchus.* Both oligacanthorhynchid main lineages form together with Moniliformidae a trichotomy at the base of a large clade (PP = 0.89; BS = 66), which is sister to Gigantorhynchidae. As such, one of the three possible resolutions of the mentioned trichotomy implies recovering a monophyletic Oligacanthorhynchidae. All species for which more than one sequence was analysed appear monophyletic and with good support. Similarly, all recovered genera are monophyletic. The exception being *Macracanthorhynchus* that is paraphyletic relative to *Nephridiacanthus*. *Macracanthorhynchus ingens* is sister (PP = 1; BS = 99) to *Nephridiacanthus major* and not to *M. hirudinaceus*.

Within Gigantorhynchidae sequences of *M. gallinarum* showed two distinct haplotypes (haplotype I: OK094073 - OK094075 - OK094072; haplotype II: OK094074) with extremely low genetic difference (0.2%) and that form a strongly supported monophyletic group (PP = 1; BS = 100), which is sister to *M. africanus* in a moderately supported clade (PP = 0.78; BS = 80). Haplotypes of both species differ by 25%. The clade formed by *M. gallinarum* and *M. africanus* is sister to *Mediorhynchus* sp. in a moderately supported clade (PP = 0.71; BS = 72); sequences of *Mediorhynchus* sp. differ on the average by 28% (Fig. 1). On the average, sequences of Gigantorhynchidae differ by 30% and 29% relative to the families Moniliformidae and Oligacanthorhynchidae, respectively. Other observed values of genetic differences are shown in Table 2.

The resulting ML and BI trees for 18S rDNA are less resolved than the COI trees (Fig. 1B). Archiacanthocephala was demonstrated to be monophyletic (PP = 0.83; BS = 89) and with a large polytomy at its base that involves seven lineages. One of these is the weakly supported clade of Oligacanthorhynchidae (PP = 0.6; BS = 51), which is the single family found monophyletic. Within this family *Oligacanthorhynchus tortuosa* is sister to a clade (PP = 0.95; BS = 79) formed by *Nephridiacanthus major*, *Macracanthorhynchus hirudinaceus*, *M. ingens* and *Oncicola* sp. Then, the family Gigantorhynchidae was not found monophyletic but forming two lineages involved in the basal polytomy. One corresponds to a clade formed by all species of *Mediorhynchus* (PP = 0.97; BS = 47) and the other is formed solely by *Intraproboscis sanghae* (Fig. 1B) formed by *Mediorhynchus* sp. and *M. grandis* that are sister to each other (PP = 1; BS = 92), while *M. africanus* is sister (PP = 0.56; BS = 44) to *M. gallinarum* (Fig. 1B). Finally,

Table 1 Species of acanthocephalans, their hosts, locations and GenBank accession number of the sequences used in the phylogenetic analysis

Species	Host	Location	Genbank access COI	Genbanck access 18S	References
Oligacanthorhynchidae					
Oligacanthorhynchus tortuosa (Leydi, 1850) Schmidt, 1972	*Didelphis virginiana*	Florida, USA	KT881245		[11]
Oligacanthorhynchus tortuosa	–	–	–	AF064817	[54]
Nephridiacanthus major (Bremser, 1811 in Westrumb, 1821)	*Hemiechinus auritus*	Razavi Khorasan, Iran	MN612080	MN612079	[20]
Macracanthorhynchus ingens (von Linstow, 1879)	*Chicobolus spinigerus*	Florida, USA	KT881247		[11]
Macracanthorhynchus ingens	*Procyon lotor*	–	AF416997		[14]
Macracanthorhynchus ingens	*Procyon lotor*	–		AF001844	[55]
Macracanthorhynchus hirudinaceus (Pallas, 1781)	*Sus scrofa*	Bakony, Hungary	FR856886		[56]
Macracanthorhynchus hirudinaceus	*Sus scrofa*	Bakony, Hungary	NC019808		[56]
Macracanthorhynchus hirudinaceus	*Sus scrofa leucomystax*	Japan	LC350021	LC350000	[43]
Oncicola luehei (Travassos, 1917) Schmidt, 1972	*Didelphis virginiana*	Veracruz, Mexico	NC016754		[44]
Oncicola luehei	*Didelphis virginiana*	Veracruz, Mexico	JN710452		[44]
Oncicola sp.	*Nasua narica*	–	AF417000		[14]
Oncicola sp.	*Nassua narica*	–	–	AF064818	[54]
Prosthenorchis elegans (Diesing, 1851)	*Saguinus leucopus*	Colombia	KT818504		[45]
Prosthenorchis sp.	*Blattella germanica*	Moscow, Russian	KP997253		[46]
Moniliformidae					
Moniliformis moniliformis (Bremser, 1811)	*Rattus rattus*	–	AF416998		[14]
Moniliformis moniliformis (Bremser, 1811)	*Rattus rattus*	Spain	–	HQ536017	Foronda Rodríguez *et al.* (unpublished)
Moniliformis moniliformis (Bremser, 1811)	Laboratory rat	England	–	ZI9562	[57]
Moniliformis kahalariensis Meyer, 1931	*Atelerix frontalis*	South Africa	MH401040	MH401042	[18]
Moniliformis cryptosaudi Amin, Heckmann, Sharifdini and Yaseen Albayati, 2019	*Hemiechinus auritus*	Baquba, Iraq	MH401041	MH401043	[18]
Moniliformis Saudi Amin, 1916	*Parachinus aethiopicus*	Unaizah, Saudi Arabia	KU206783	KU206782	[4]
Gigantorhynchidae					
Mediorhynchus sp.	*Quiscalus mexicanus*	–	AF416996		[14]
Mediorhynchus sp.	*Casidis mexicanus*	–		AF064816	[54]

Table 1 (continued)

Species	Host	Location	Genbank access COI	Genbanck access 18S	References
Mediorhynchus africanus Amin, Evans, Heckmann and El-Naggar, 2013	*Numida meliagris*	Africa	KC261351	KC261353	[19]
Mediorhynchus grandis Van Cleve, 1916	*Sturnella magna*	–		AF001843	[55]
Mediorhynchus gallinarum (Bhalerao, 1937)	*Gallus gallus*	Indonesia	KC261352	KC261354	[27]
Mediorhynchus gallinarum	*Gallus gallus*	Indonesia	OK094073	–	This study
Mediorhynchus gallinarum	*Gallus gallus*	Indonesia	OK094075	–	This study
Mediorhynchus gallinarum	*Gallus gallus*	Indonesia	OK094072	–	This study
Mediorhynchus gallinarum	*Gallus gallus*	Indonesia	OK094074	–	This study
Mediorhynchus gallinarum	*Gallus gallus*	Indonesia	–	MW282174	This study
Mediorhynchus gallinarum	*Gallus gallus*	Indonesia	–	MW282175	This study
Intraproboscis sanghae	*Phataginus tetradactyla*	Central Africa Republic	–	MN996986	[21]
Neoechinorhynchidae					
Mayarhynchus karlae Pinacho-Pinacho, Hernández-Orts, Sereno-Uribe, Pérez-Ponce de León, García-Varela, 2017	*Thorichthys ellioti*	Southeastern, Mexico	KY077085		[58]
Arhytmacanthidae					
Heterosentis holospinus Amin, Heckmann and Ha, 2011	*Leiognathus equulus*	Gulf of Tonkin, Vietnam	MN715352		[39]
Polymorphidae					
Profilicollis altmani (Perry, 1942)	*Leucophaeus modestus*	Curiñanco beach, Valdivia, Chile	KX702245		[34]
Neoechinorhynchus agilis (Rudolphi, 1819)	*Chelon labrosus*	Arousa river, Spain		MN148895	[59]
Echinorhynchus truttae Schrank, 1788	*Thymallus thymallus*	–		AY830156	[14]

(**–**) Location not indicated

the family Moniliformidae was not found monophyletic; four moniliformid lineages fall to the polytomy at the base of the Archiacanthocephala clade; one of these is *Moniliformis saudi*, another is *M. moniliformis*, the third is *M. kalahariensis*, and the last lineage is *M. cryptosaudi* (Fig. 1B).

Discussion

Our molecular analysis showed that *Mediorhynchus gallinarum,* a parasite of *G. gallus* from Indonesia, exhibits extremely low-level of genetic variation. Analysed haplotypes differ on average by 0.1%. We note however, that our analysed sample is small and that all specimens were collected at a single locality (a farm in this case), therefore the low level of genetic variance is not unexpected. Additional analyses should further assess the level and pattern of the genetic variation of *M. gallinarum.* The low divergence value found for *M. gallinarun* is in line with those reported for other acanthocephalans. For example, low genetic diversity has been found within species of the genera *Andracantha* Schmidt, 1975; *Corynosoma* Lühe, 1904; *Profillicollis* Meyer, 1931 and *Heterosentis* Van Cleave, 1931 [17, 18, 33–35]. The drivers behind those low levels of divergence

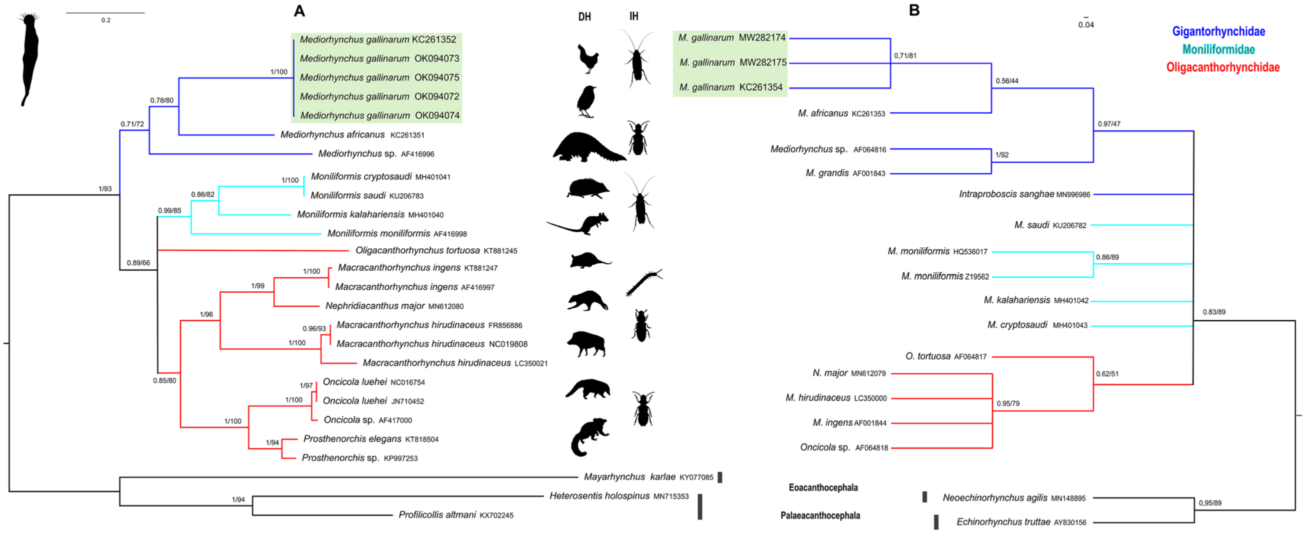

Fig. 1 Genealogical relationships of haplotypes based on partial COI (**A**) and 18S (**B**) gene sequences of specimens of the class Archiacanthocephala recovered in a Bayesian inference analysis. Numbers next to nodes refer to support values. Bayesian posterior probability values are shown left of the diagonal. Bootstrap support values found in the Maximum Likelihood analysis (COI: L*n* = − 6930.5649; 18S: L*n* = − 1553.391) are found left of the diagonal. GenBank accession numbers are included in the terminal labels. Animal silhouettes next to the tree indicate host of each family (*DH* definitive host, *IH* intermediate host) (colour figure online)

Table 2 Observed values of genetic differences (*p*-distances) between haplotypes of the distinct samples of *Mediorhynchus* and other species of the family Oligacanthorhynchidae

	Mediorhynchus	*Macracanthorhynchus ingens*	*Nephridiacanthus major*	*Macracanthorhynchus hirudinaceus*	*Oncicola luehei*
M. ingens	0.320				
N. major	0.301	0.192			
M. hirudinaceus	0.312	0.254	0.257		
O. luehei	0.278	0.290	0.261	0.277	
P. elegans	0.288	0.263	0.253	0.288	0.184

are so far unclear. Further studies would clarify the effect of this pattern, if any, of the particularities of their natural history, including strict parasite-environmental links and specific host-parasite relationships [17, 34, 35].

Mediorhynchus gallinarum is highly divergent from the analysed congenerics *M. africanus* (25%) and *Mediorhynchus* sp. (28%). This result strongly supports the distinction at the species level of *M. africanus* from *gallinarum*, which was questioned by various authors since 1932 [19]. Later, molecular studies on *Mediorhynchus* by Amin *et al.* [19, 27] showed that specimens from chicken from Indonesia (*M. gallinarum*) are distinct from those recovered from African birds (*M. africanus*). In this study, we corroborate those results showing that both species are genetically highly divergent.

Both analyses show that phylogenetic relationships into the Class Archiacanthocephala are not fully resolved. For example, the resulting COI tree showed that the family Oligacanthorhynchidae is not monophyletic (Fig. 1A). Genera of this family fall in two main lineages; one formed by the genera *Macracanthorhynchus, Nephridiacanthus, Oncicola*, and *Prosthenorchis*, and the other by *Oligacanthorhynchus*, the type genus. In contrast, the resulting 18S rDNA tree showed that the family Oligocanthorhynchidae is monophyletic (Fig. 1B). This result needs to be further explored as the lack of monophyly may be due to the short sequence fragment analysed not having enough information to resolve some relationships. We also note that our sampling of oligocanthorhynchid is incomplete as samples of six genera were not included; as such, the monophyly of the family should be further tested with broader taxonomic sampling. Having said that, we note that the systematics of Acanthocephala is still unstable; most groups have been proposed on the basis of morphological trenchant characters and have not been tested with an explicit phylogenetic approach [15, 33, 36]. Even for the classification of the class Palaeacanthocephala, which has been the focus of diverse studies based on morphological and molecular data, several authors suggested that it still needs adjustments due to the lack of monophyly in some families [14, 16–18]. These conclusions agree with our findings regarding Oligacanthorhynchidae. Due to the lack of molecular data available for several members of Archiacanthocephala, our finding should be regarded as preliminary. Future studies, including a wider taxonomic and character sampling should generate a robust phylogeny that would be the basis for a more stable classification of the Archiacanthocephala.

Host-Parasite Relationships and Distribution (Fig. 2)

A high degree of host specificity has been reported for *Mediorhynchus* [25, 37]. Adult specimens of *M. gallinarum* are commonly found in chickens of the family Phasianidae from diverse Asian locations [27]. In contrast, adults of *M. africanus* are mostly found in birds of the families Numididae and Phasianidae from Africa [19]. However, most of the other species of *Mediorhynchus* use as definitive hosts passeriform birds from diverse continents [23–25]. Species of termites and cockroaches have been reported as intermediate hosts [23]. Aspects such as the vagility and capacity of migration of definitive hosts have been indicated as having a direct effect on the genetic variation of acanthocephalans [34, 35, 38]. In addition, narrow host-parasite relationships could be related to low presence of intermediate or paratenic hosts, that accumulate the infective stage and also, probably, limits the accessibility to a wide range of predators [25, 37].

For parasites belonging to the family Moniliformidae, host-parasite relationships seem to be even stricter. Mammals have been identified as definitive hosts including the family Erinaceidae from Africa and Asia, the giant anteater, primates, and rodents mainly from South America, and occasionally birds [1, 2, 4, 39]. Intermediate hosts are mostly cockroaches [1, 4]. Morphologically cryptic species of *Moniliformis*, which are basically differentiated genetically [18], differ in their hosts; *Moniliformis saudi* Amin, Heckman, Mohammed and Evans, 2016 parasites the desert hedgehog *Paraechinus aethiopicus* (Ehrenberg, 1832) from Saudi Arabia [4], while, *M. cryptosaudi* Amin, Heckmann, Sharifdini, Albayati, 2019 parasitizes the long-eared hedgehog *Hemiechinus auritus* (Gmelin, 1770) in Iraq [18]. Cases of cryptic speciation have been commonly suggested for acanthocephalans in distinct classes [35, 38–40]. These authors concluded that their genetic variation, in part, could be explained likely by environmental influences together with host specificity [35, 38, 40].

The family Oligacanthorhynchidae is the most diverse of Archiacanthocephala [22]. Hosts reported for members of this family such as *Oligacanthorhynchus tortuosa*, include the Virginia opossum *Didelphis virginiana* Allen, 1900 and the millipede *Narceus amaricanus* (Palisot de Beauvois, 1817) as intermediate host [11]. Raccoons, *Procyon*

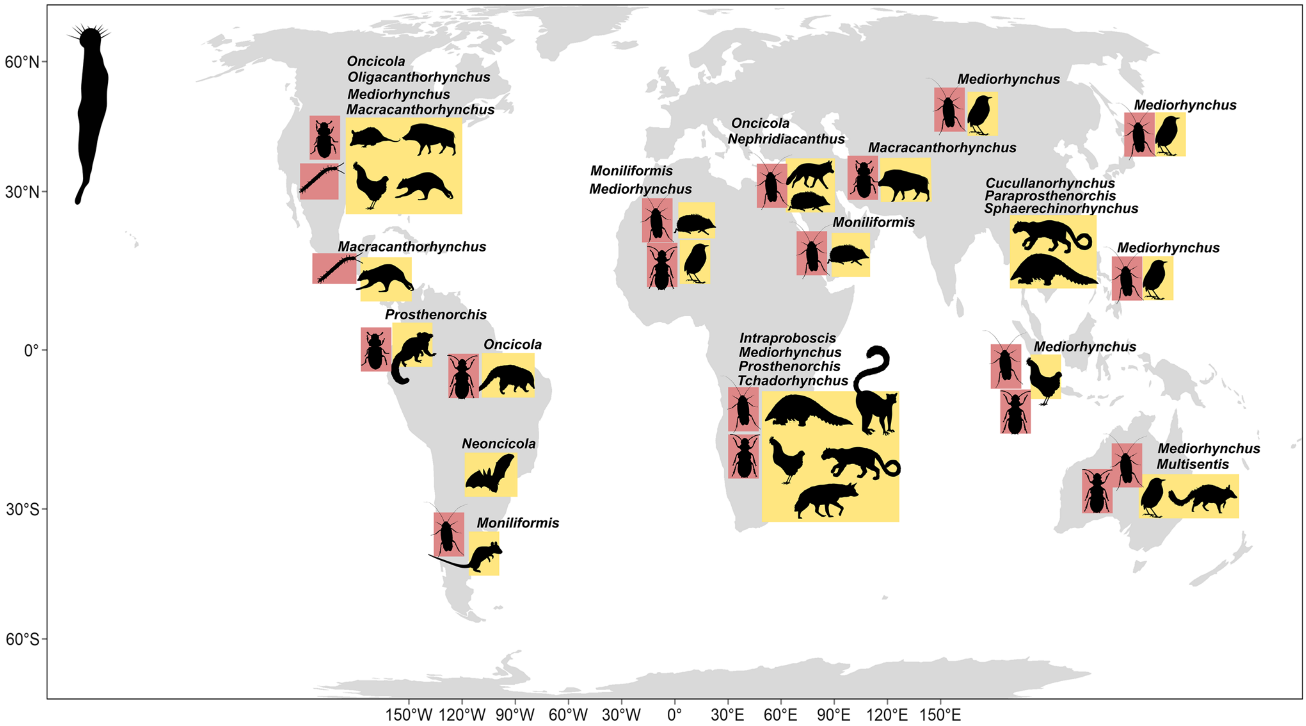

Fig. 2 Map indicating the global distribution of intermediate hosts (pink square) and definitive hosts (yellow square) of members of the class Archiacanthocephala. Genera of representative acanthocephalans for different places around continent are reported in bold (colour figure online)

lotor Linnaeus, 1758 from USA and *Bassariscus astutus* (Lichtenstein, 1830) from Nicaragua are the definitive hosts of *Macracanthrohynchus ingens*, while its intermediate host is the millipede *Chicobolus spinigerus* (Wood), 1864 from USA [7, 11]. *Macracanthrohynchus hirudinaceus* has been reported parasitizing the wild boar *Sus scrofa* from Iran, Japan and USA and beetles of the family Scarabaeidae family are the intermediate hosts [41–43]. For *Nephridiacanthus major,* the erineaceid long-eared hedgehog *Hemiechinus auritus* was reported as definitive host in Iran [20], while the intermediate hosts are beetles of the family Tenebrionidae and cockroaches [20].

The definitive hosts of the genus *Oncicola* are small mammals. For example, adult *O. luehei* parasiteze the opossum *D. virginiana* and the coatis *Nasua narica* (Linnaeus, 1766) distributed in North, Central and South America [44]. For other species of *Oncicola*, other mammals like the feral cat *Felis catus* Linnaeus, 1758, the Indian mangoose *Herpestes auropunctatus* Hodgson, 1836, the foxes *Vulpes vulpes* Linnaeus, 1758 from Lebanon and the ocelot *Leopardus pardalis* Linnaeus, 1758 were reported as definitive hosts, and the Caribbean termite *Nasutitermes acajutlae* (Holmgren) as the intermediate host [8–10, 12, 48]. Additionally, lizards, African green monkeys and birds serve as paratenic hosts for species of *Oncicola* [8, 9].

Acanthocephalans of the genus *Prosthenorchis* have been reported parasitizing neotropical primates, mainly individuals of the family Callitrichidae, distributed in the Brazilian Atlantic forest and Colombia [5, 6, 45]. Also, adult specimens have been collected from lemurs in Madagascar and vertebrates belonging to the family Felidae in Africa [49, 50]. Likewise, individuals of this genus have been reported in primates of the neotropical origin housed at a zoo collection in Moscow, and the larvae were found in cockroaches *Blattela germanica,* captured around primate cages [46]. In general, species of Blattodea and Coleoptera contains the larval stages of *Prosthenorchis* [5, 46, 47]. Other members of this family such as adults of *Tchadorhynchus* sp. have been reported in *Hyaena hyaena* (Linnaeus, 1758) from Africa [49]. Individuals of *Cucullanorhynchus constrictruncatus* Amin, Van Ha and Heckmann, 2008, collected from the leopard *Panthera pardus* (Linnaeus), adults of *Paraprosthenorchis ornatus* Amin, Van Ha and Heckmann, 2008 from Chinese pangolin *Manis pentadactyla* Linnaeus, and adult species of *Sphaerechinorhynchus macropisthospinus* Amin, Wongsawad, Marayong, Saehoong, Suwattanacoupt, and Sey, 1998, collected in tiger, *Panthera tigris* (Linnaeus). These last three species were collected in hosts from Hanoi Zoological Park, Hanoi, Vietnam [51].

Individuals of the genus *Multisentis* sp. have been reported from termites as the intermediate host, and as the definitive hosts in the numbat *Myrmecobius fasciatus* from Australia [52]. Additionally, acanthocephalan adults of *Neoncicola* sp. were obtained from bats around Paraguay, South America [53].

Conclusion

This study suggests that the link between definitive hosts and the acanthocephalan parasites is mediated by the selection of their intermediate hosts as food items. Also, even if some intermediate hosts have distribution across distinct continents, i.e., cockroaches, being able to extend the parasite transmission in distant geographic localities, the definitive hosts, that disperse infective stages, have a more limited distribution, resulting in more or less geographically restricted dispersal for members of Archiacanthocephala. In summary, the results presented here contribute to further understanding of the ecological and evolutionary relationships that allow the host-parasite co-existence within the class Archiacanthocephala, which needs adjustments due to inapparent monophyly of some families. Also, due to the lack of molecular data available for several members of Archiacanthocephala, our finding should be regarded as preliminary. Future research needs increased collection efforts, integrating morphological and molecular data, as well as increased field-based observations of parasitic life cycle, to further our understanding of ecological and phylogenetic relationships of members of the class Archiacanthocephala.

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Author Contributions OMA and RAH collected samples and provided original descriptions and research of the species reported and reviewed the manuscript. SMR and GD analysed and interpreted data. SMR wrote the first draft of the manuscript. All authors reviewed and approved the text.

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Availability of Data and Material Sequences are available in GenBank.

Code Availability Not applicable.

Declarations

Conflict of interest There is no competing interest among the authors and compliance with all relevant ethical standards.

Ethical approval The authors declare that this study was conducted in compliance with all guidelines on the care and use of animals.

Consent to participate All authors approve the participation.

Consent for publication All authors approve the publication.

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