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Metazoan parasites associated with marine mollusks inhabiting the China Seas: a review

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Parasites in mollusks are often neglected by humans, while some species were reported to be harmful to economic mollusks and caused production decrease. Metazoan parasites of mollusk studies from the China Seas started relatively later than other countries. To promote long-term studies on the distribution and diversity of metazoan parasites of mollusks from the China Seas, a comprehensive review has been carried out based on the available literature. The purpose of this study was to perform a critical review about the metazoan parasites associated with mollusks that are useful for the discovery of new metazoans. This publication summarizes information on metazoan parasites of Chinese mollusks from 1932 to 2024. The information is presented and contains 128 species of parasites, distributed among the higher taxa as follows: Turbellaria (2 species), Trematoda (34 species), Cestoda (1 species), Annelida (38 species), Arthropoda (48 species), Porifera (2 species), Cnidaria (1 species), and Mollusca (2 species). Many records of parasites not identified to the species level are also included. Collectively, this review provides a synopsis of the known metazoan parasites of mollusks from the China Seas, as well as presents the known relationship between metazoan parasites and the mollusks, which will broaden our knowledge on the metazoan parasites of mollusks. It is important as it highlights the lack of metazoan parasite studies done in the China Seas and the need for more parasite biodiversity work.

KEYWORDS

metazoan parasites, mollusks, distribution, diversity, the China Seas

1 Introduction

Mollusks [soft-bodied animals that have a hard shell (majority of the species)] have a tremendous role in the ecosystem and economy of various countries. Certain species of this group are edible and delicious and have a market value; therefore, they have attracted attention for cultivation. Members of this phylum inhabit the terrestrial world, fresh waters, and marine waters, with the highest number of species found in marine waters. Many species belonging to different classes of the phylum are edible, such as species of class Gastropoda (Haliotis corrugata, Turbo bruneus, and Rapana venosa), Bivalvia (Tegillarca granosa, Perna viridis, and Magallana gigas), and Cephalopoda (Amphioctopus fangsiao, Octopus minor, and Loligo vulgaris). It has been reported that 65 species of mollusks have been farmed globally until the year 2020 (Tacon, 2020). China has approximately 14,500 km of coastline and mollusks are being cultured all along the Chinese coast. It is one of the top mollusk exporter countries in the world. The increase in the number of cultured species also led to an increase in per-capita consumption.

Nevertheless, certain species of parasites are harmful to the breeding industry of mollusks around the world including China. The parasite is an important causative agent that can harm the industry and brings significant mass mortality. Parasitic infestation investigations are lacking especially from Chinese waters. Metazoan parasites of mollusks are members of the main phyla like Platyhelminthes, Annelida, and Arthropoda. Moreover, there have been few reports on Porifera, Cnidaria, Nemertea, Nematoda, and Mollusca (Russell, 1967; Rohde, 2005). To promote long-term studies on the distribution and diversity of metazoan parasites of mollusks from the China Seas, a comprehensive review has been carried out based on the available literature, which would be useful for understanding the present and forthcoming infestation and migration.

2 Methods

A scoping review was performed to characterize and summarize the available information on metazoan parasites of mollusk research from the China Seas. Web of Science, Scopus, and PubMed databases were searched using combinations of the terms "metazoa*", "parasit*", "mollusk or mollusc", "Platyhelminth*", "Turbellaria*", "Trematod*", "Cestod*", "Annelid*", "Polychaet*", "Arthropod*", "copepod*", "Malacostraca*", "pea crab", "Pinnotherid*", "prawn", "Palaemonoid*", "Pontoniinae", "sea spider", "Pycnogonid*", "sponge", "Porifera", "Cnidaria*", "Nemertea*", "Nematod*", and "Mollusca*" plus the name of the China Seas. For each search result obtained, the abstract was reviewed to determine relevance. In addition to the databases, gray literature from university theses and the conference presentations were searched.

3 Results

Platyhelminthes (Turbellaria, Trematoda, and Cestoda) (Figure 1A): Two species of turbellarians were recorded; *Stylochus* sp. was found inside oysters from Fujian in the East China Sea and

Guangdong in the South China Sea. *Stylochoplana maculata* (Quatrefage, 1845) was inside bivalves from Hong Kong in the South China Sea (Figure 1D). There are 23 known species of trematodes in the East China Sea and the South China Sea, and a few undefined species existed in the China Seas. Additionally, the hosts including bivalves and gastropods (see Table 1; Figure 1D) and *Tylocephalum* sp. belonging to the order Lecanicephalidea parasitize oysters in Taiwan, the East China Sea (Sun and Chen, 2007) (Figure 1D).

Annelida: Studies on the parasitic polychaetes of mollusks were recorded in the China Seas. More than 30 species of polychaetes belong to Polychaeta, and the hosts are marine bivalves and gastropods. There are 27 known species of polychaetes in the China Seas. A few undefined species are found in the Yellow Sea and the South China Sea (see Table 2; Figures 1B, D).

Arthropoda (Copepoda, Malacostraca, and Pycnogonida) (Figure 1C): Studies on the copepods of mollusks in the China Seas focus on cyclopoid copepods. There are 14 species of parasitic copepods from the China Seas and the hosts are bivalves and cephalopods (see Table 3; Figure 1D). There are 34 species of parasitic malacostracans from the China Seas, and the hosts are bivalves and gastropods (see Table 4; Figure 1D). Parasitic sea spiders of mollusks in the China Seas have not been recorded.

Porifera: *Suberites carnosus* (Johnston, 1842) (Suberitida: Suberitidae) was recorded at Xiagu Strait from Xiamen, the East China Sea attached to the outer shell of oysters. Another recorded species is *Mycale phyllophila* Hentschel, 1911, which was attached to the farmed oysters in the southern part of Hong Kong Island (Huang and Lin, 2012) (Figure 1D).

Cnidaria: In the China Seas, one species of parasitic cnidarian of mollusks has been recorded. *Paraiptasia radiata* (Stimpson, 1856) was found on *Nassarius* sp. at Wu Kai Sha, Hong Kong (Huang and Lin, 2012) (Figure 1D).

Nemertea: No records available.

Nematoda: No records available.

Mollusca: A kind of snail, *Brachystomia omaensis* (Nomura, 1938), which was semi-parasitic on *Turbo* sp. and abalone shells, was recorded in Beidaihe, Hebei, and Qingdao, Shandong, as well as in the East China Sea (Qi et al., 1989). In addition, *Crepidula onyx* Sowerby, 1824 was attached to the outer shell of *Perna viridis* (Linnaeus) from Hong Kong in the South China Sea (Huang and Lin, 2012) (Figure 1D).

4 Discussion

4.1 Platyhelminthes: Turbellaria, Trematoda, and Cestoda

4.1.1 Turbellaria

Turbellaria is considered as an invalid class because it is a paraphyletic group. (i.e., having descendants, namely, the parasitic classes, which are not classified within it) (Ehlers, 1985). Several species of turbellarians have been reported to be associated with commercially important marine mollusks (Russell, 1967). Wu et al. (1997) reported that some species of suborders Acotylea



(Rhabditophora: Polycladida) and Dalytyphloplanida (Rhabditophora: Rhabdocoela) are turbellarians that parasitize mollusks. Some species of Stylochus Ehrenberg, 1831 and Pseudostylochus Yeri and Kaburaki, 1918 (belonging to Acotylea) parasitize oysters and other invertebrates (Russell, 1967). Species of Graffilla Ihering, 1880 and Paravortex Wahl, 1906 (belonging to Dalytyphloplanida) were found in mollusks. Depending on species, they were located in the mantle and gills, in the stomach and digestive gland, or in the heart and the kidney (Rohde, 2005). In addition, turbellarians belonging to the order Fecampiida (belonging to Rhabditophora) were found in mollusks; Urastoma cyprinae (Graff, 1882) causes pathological reactions in the hosts, leading to disorganization of the gill filaments (Robledo et al., 1994) and Octopoxenus antarcticus Gordeev, Biserova, Zhukova and Ekimova, 2022 was found in the intestine and liver of the octopuses (Gordeev et al., 2022). The two species (Stylochus sp. and Stylochoplana maculata) of turbellarians discovered in our country belong to Acotylea from the East China Sea and the South China Sea, and their hosts are bivalves (Figure 1D). There should be more opportunities to discover parasitic turbellarians in other sea areas of our country.

4.1.2 Trematoda

Trematoda use mollusks as first and second intermediate hosts (Lauckner, 1983). There are two subclasses, the Aspidogastrea and Digenea, the species of which parasitize marine bivalves, gastropods, and cephalopods (Russell, 1967; Rohde, 2005; Magalhães, 2018; Hochberg, 1990; Paladini et al., 2017; Madsen and Stauffer, 2024). As an important intermediate host in the life cycle of trematodes, the problem of diseases caused by the parasitic trematode larvae in economic mollusks is becoming increasingly prominent. Many kinds of trematodes often infect the liver, heart, and gonads of mollusks, and destroy the tissues and organs and their functions, resulting in poor growth, low condition factor, and low nutritional value. They even damage the reproductive capacity of mollusks and lead to death in severe cases (Yang and Shi, 2000). In China, there are more than 30 species of trematodes recorded and they are all affiliated to Digenea

TABLE 1 Taxon of trematode parasitizing mollusks in the China Seas.

Trematode	Hosts Geographic locations		References	
Cercaria armata	Gastropoda: Cerithium coralium ¹ ; Clypeomorus pellucida ¹ ; Pirenella alata ¹	S: Hong Kong	Tang, 1989; 1990b	
Cercaria cloacicola	Gastropoda: Terebralia sulcata ¹	S: Hong Kong	Tang, 1989; 1990a; 1990b	
Cercaria elegans	Bivalvia: <i>Ruditapes philippinarum</i> ¹	E: Fujian: (Xiamen, Zhangzhou); S: Hong Kong	S: Chen, 1994; Tang, 1992; Yang and Shi, 2000	
Cercaria gedoelsti	Gastropoda: Cerithidea rhizophorarum ¹	S: Hong Kong	Tang, 1989; 1990a; 1990b	
Cercaria hezuiensis	Gastropoda: Echinolittorina pascua ¹	S: Hong Kong	Tang, 1995	
Cercaria himasthloides	Gastropoda: Cerithidea rhizophorarum ¹	S: Hong Kong	Tang, 1989; 1990b	
Cercaria hongkongensis	Gastropoda: Pirenella alata ¹ ; Pirenella cingulata ¹	S: Hong Kong	Tang, 1989; 1990a; 1990b	
Cercaria longicauda	Gastropoda: Cerithidea rhizophorarum ¹ ; Pirenella alata ¹ ; Terebralia sulcata ¹	S: Hong Kong	Tang, 1989; 1990a; 1990b	
Cercaria magnicaudata	Gastropoda: Batillaria multiformis ¹ ; Batillaria sp. ¹ ; Pirenella alata ¹ ; Pirenella cingulata ¹ ; Terebralia sulcata ¹	S: Hong Kong	Tang, 1989; 1990b	
Cercaria meretrix	Bivalvia: <i>Meretrix meretrix</i> ¹	E: Taiwan	Shin et al., 1996	
Cercaria mesostephanus	Gastropoda: Pirenella alata ¹	S: Hong Kong	Tang, 1989; 1990b	
Cercaria minus	Gastropoda: Echinolittorina millegrana ¹ ; Echinolittorina pascua ¹ ; Echinolittorina radiata ¹ ; Nodilittorina pyramidalis ¹ ; Planaxis sulcatus ¹	S: Hong Kong	Tang, 1989; 1990b; 1995	
Cercaria mortoni	Gastropoda: Echinolittorina millegrana ¹ ; S: Hong Kong Nodilittorina pyramidalis ¹ S: Hong Kong		Tang, 1989; 1990a; 1990b	
Cercaria pernaviridis	Bivalvia: Perna viridis ¹ S: Hong Kong		Liu, 2008; Tang, 1992	
Cercaria spelotremoides	Gastropoda: Batillaria multiformis ¹ ; Cerithidea rhizophorarum ¹ ; Clypeomorus batillariaeformis ¹ ; Clypeomorus bifasciata ¹ ; Pirenella alata ¹ ; Pirenella cingulata ¹	S: Hong Kong	Tang, 1989; 1990b	
Cercaria tangi	Gastropoda: Echinolittorina pascua ¹ ; S: Hong Kong Echinolittorina radiata ¹ S: Hong Kong		Tang, 1995	
Heterophyes heterophyes	Gastropoda: Pirenella alata ¹	S: Hong Kong	Tang, 1989; 1990b	
Monorchis xiamenensis	Bivalvia: Sinonovacula constricta ²	E: Zhangzhou	Shi, 2000	
Podocotyle tetrastyla	Gastropoda: Lunella coronata ¹	S: Hong Kong	Tang, 1989; 1990b	
Proctoeces orientalis	peces orientalis Bivalvia: Arcuatula senhousia ^{1,2} ; Cyclina sinensis ² ; Dosinia japonica ² ; Modiolus modulaides ² ; Paratapes undulatus ² ; Placamen lamellatum ² ; Protapes gallus ² ; Pteria penguin ² ; Ruditapes philippinarum ² ; Tegillarca granosa ²		Cao, 1989; 1990; Tang, 1989; 1990b; Yang and Shi, 2000	
Proctotrematoides pisodontophidis	Bivalvia: Sinonovacula constricta ²	E: Zhejiang: Ningbo; Fujian: Zhangzhou	Wang et al., 1983; Shi, 2000	
Prosorhynchus facilis	Bivalvia: Arcuatula senhousia ¹	E: Fujian: Xiamen	Liu, 1993; 1994	
Vesicocoelium solenophagum	Bivalvia: Sinonovacula constricta ¹	E: Fujian: (Xiamen, Zhangzhou)	Shi and Wang, 2001; Tang and Xu, 1979; Tang et al., 1975; Yang and Shi, 2000	
Bucephalidae gen. et sp.	Bivalvia: <i>Brachidontes variabilis</i> ¹	S: Hong Kong	Tang, 1992	
Bucephalidae gen. et sp.	Bivalvia: <i>Meretrix meretrix</i> ¹	B: Shandong: Laizhou	Ren and Song, 2002	
Bucephalidae gen. et sp.	Bivalvia: <i>Meretrix meretrix</i> ¹	B: Shandong: Laizhou	Lv et al., 2003, 2004	
Bucephalidae gen. et sp.	Bivalvia: Dosinia japonica [?] ; Meretrix meretrix [?] ; Modiolus modulaides [?] ; Ruditapes philippinarum [?] ; Tegillarca granosa [?]	E: Fujian: (Xiamen, Zhangzhou)	Yang and Shi, 2000	

(Continued)

TABLE 1 Continued

Trematode	Hosts	Geographic locations	References
Monorchiidae gen. et sp.	Bivalvia: Sinonovacula constricta ²	E: Fujian: (Xiamen, Zhangzhou)	Yang and Shi, 2000
Notocotylidae gen. et sp.	Bivalvia: <i>Meretrix meretrix</i> [?] ; <i>Modiolus modulaides</i> [?] ; E: Fujian: (Xiamen, Zhangzhou) <i>Ruditapes philippinarum</i> [?]		Yang and Shi, 2000
Plagiorchiidae gen. et sp.	Bivalvia: Modiolus modulaides?	E: Fujian: (Xiamen, Zhangzhou)	Yang and Shi, 2000
Digenea gen. et sp.	Bivalvia: <i>Meretrix meretrix</i> ¹	B: Shandong: Laizhou	Ren et al., 2005
Digenea gen. et sp.	Bivalvia: Ruditapes philippinarum ¹	Y: Liaoning: Dandong	Meng et al., 2019
Acanthoparyphium sp.	Bivalvia: Mactra quadrangularis ² ; Solen strictus ²	B: Shandong: Shouguang	Zhan et al., 1993
Bacciger sp.	Bivalvia: Meretrix meretrix ¹ Y: Jiangsu: Qidong		Shen and Yu, 1994

B, the Bohai Sea; Y, the Yellow Sea; E, the East China Sea; S, the South China Sea; 1, 2, and ? represent the first intermediate host, the second intermediate host, and the unknown intermediate host, respectively.

(belonging to Rhabditophora); the hosts are marine bivalves and gastropods from the China Seas, mostly in the East China Sea and the South China Sea. Mollusks often appear as the first intermediate host and occasionally as the second intermediate host (see Table 1; Figure 1D). At present, it is statistically found that all the mollusks acting as the second intermediate hosts are bivalves. It remains to be further studied in the future whether it is a coincidence.

4.1.3 Cestoda

As a group, mollusks are not common hosts for cestode parasites but have been reported to serve as intermediate hosts for cestodes in

TABLE 2 Taxon of polychaete parasitizing mollusks in the China Seas.

Polychaete	Hosts	Geographic locations	References
Arabella iricolor	Bivalvia: Pinctada fucata	S: Hainan: Lingshui County	Yang et al., 2012
Boccardiella hamata	Bivalvia: Pteria sp.	S: Guangdong: Shenzhen	Zhou et al., 2010
Capitella capitata	Bivalvia: Pinctada fucata	S: Hainan: Lingshui County	Yang et al., 2012
Composetia costae	Bivalvia: Pinctada fucata	_	Liang et al., 2007
Dipolydora pilikia	Bivalvia: Pinctada fucata	S: Hainan: Lingshui County	Yang et al., 2012
Hydroides fusicola	Bivalvia: Mizuhopecten yessoensis	Y: Liaoning: Dalian	Zhang et al., 2007
Leonnates indicus	Bivalvia: Pinctada fucata	_	Liang et al., 2007
Lysidice collaris	Bivalvia: Pinctada fucata	_	Liang et al., 2007
Lysidice ninetta	Bivalvia: Pinctada fucata	S: Hainan: Lingshui County	Yang et al., 2012
Marphysa sanguinea	Bivalvia: Pinctada fucata	_	Liang et al., 2007
Nereis falcaria	Bivalvia: Pinctada fucata	_	Liang et al., 2007
Nereis huanghaiensis	Bivalvia: Mizuhopecten yessoensis	Y: Liaoning: Dalian	Zhang et al., 2007
Nereis zonata	Bivalvia: Mizuhopecten yessoensis	Y: Liaoning: Dalian	Zhang et al., 2007
Perinereis cultrifera	Bivalvia: Pinctada fucata	_	Liang et al., 2007
Polydora aura	Bivalvia: Anadara broughtonii	Y: Shandong: Yantai	Tang, 2015
Polydora brevipalpa	Bivalvia: Mizuhopecten yessoensis; Gastropoda: Haliotis discus hannai	Y: Liaoning: Dalian; Shandong: Qingdao	Sato-Okoshi et al., 2013; Tang, 2015
Polydora ciliata	Bivalvia: <i>Mizuhopecten yessoensis</i> ; Pectinidae gen. et sp.; <i>Pinctada fucata</i> ; <i>Pteria penguin</i> ; Gastropoda: <i>Haliotis diversicolor</i>	B: Hebei: Qinhuangdao; Y: Liaoning: Dalian; S: Guangdong: (Shanwei, Shenzhen, Zhanjiang, Leizhou); Hainan: Lingshui County; Guangxi (Beihai, Fangchenggang)	Cui, 1995; Gao, 2011; Liang et al., 2007; Liu, 2003; Shi et al., 2004; Wang et al., 2004; Zhang et al., 2007
Polydora haswelli	Bivalvia: Ostrea sp.	S: Guangdong: (Shenzhen, Zhanjiang)	Tang, 2015
Polydora hoplura	Bivalvia: Ostrea sp.	E: Zhejiang: Wenzhou	Tang, 2015

(Continued)

TABLE 2 Continued

Polychaete	Hosts	Geographic locations	References
Polydora lingshuiensis	Bivalvia: Ostrea sp.; Pinctada fucata	S: Guangdong: (Shenzhen, Yangjiang, Zhanjiang); Hainan: Lingshui County	Tang, 2015; Ye et al., 2015
Polydora onagawaensis	Bivalvia: Chlamys farreri; Crassostrea giga; Mizuhopecten yessoensis; Gastropoda: Haliotis discus hannai; Tegula rustica	Y: Shandong: (Rongcheng, Qingdao)	Sato-Okoshi et al., 2013
Polydora triglanda	Bivalvia: Crassostrea gigas; Mytilopsis sallei	E: Taiwan: Taipei	Radashevsky and Hsieh, 2000
Polydora vicina	Bivalvia: Pinctada fucata	S: Hainan: Lingshui County	Yang et al., 2012
Polydora websteri	Bivalvia: Crassostrea gigas; Ostrea sp.	E: Zhejiang: Ningbo; Shanghai; S: Guangdong: Yangjiang	Sato-Okoshi et al., 2013; Tang, 2015
Syllis gracilis	Bivalvia: Pinctada fucata	_	Liang et al., 2007
Trypanosyllis taeniaeformis	Bivalvia: Pinctada fucata	S: Hainan: Lingshui County	Yang et al., 2012
Typosyllis maculata	Bivalvia: Pinctada fucata	S: Hainan: Lingshui County	Yang et al., 2012
Branchiomma sp.	Bivalvia: Pinctada fucata	S: Hainan: Lingshui County	Yang et al., 2012
Cirratulu sp.	Bivalvia: Pinctada fucata	S: Hainan: Lingshui County	Yang et al., 2012
Hydroides sp.	Bivalvia: Pteria penguin	S: Guangdong: Leizhou	Wang et al., 2006
Loimia sp.	Bivalvia: Pinctada fucata	S: Hainan: Lingshui County	Yang et al., 2012
Namalycastis sp.	Bivalvia: Pinctada fucata	S: Hainan: Lingshui County	Yang et al., 2012
Polydora sp.	Bivalvia: Pinctada fucata	S: Hainan: Lingshui County	Yang et al., 2012
Polydora sp.	Bivalvia: Pinctada fucata	S: Hainan: Lingshui County	Yang et al., 2012
Polydora sp.	Bivalvia: Pinctada fucata	S: Hainan: Lingshui County	Yang et al., 2012
Polydora sp.	Bivalvia: <i>Ostrea</i> sp.	Y: Jinagsu: Nantong; S: Guangdong: (Shenzhen, Yangjiang, Zhanjiang)	Tang, 2015
Polydora sp.	Bivalvia: Pteria penguin	S: Guangdong: Leizhou	Wang et al., 2006
Serpula sp.	Bivalvia: Pteria penguin	S: Guangdong: Leizhou	Wang et al., 2006

B, the Bohai Sea; Y, the Yellow Sea; E, the East China Sea; S, the South China Sea.

exceptional cases (Russell, 1967). A few species of cestodes have been reported from marine mollusks. Six orders of cestodes (Tetraphyllidea, Trypanorhyncha, Lecanicephalidea, Cyclophyllidea, Diphyllidea, and Tetrabothriidea), belonging to the subclass Eucestoda of the subphylum Rhabditophora, have been found in mollusks including cephalopods, pelecypods, and gastropods (Rohde, 2005). The life cycle of tetraphyllidean cestodes involves the mollusk as their hosts (Cake, 1978). Heavy infections of trypanorhynch larvae in the guts of pelecypod mollusks prevent the passage of food (Rohde, 2005). Heavy infections of larval lecanicephalideans may result in physiological stress and affect the growth and reproduction of pelecypod mollusks (Cake, 1978). Rohde (2005) recorded several marine animals serving as intermediate hosts for marine cestodes. As we can see from Figure 3.22 of that article, it clearly shows that cephalopods, pelecypods, and gastropods serve as intermediate hosts of cyclophyllideans, lecanicephalideans, tetraphyllideans, diphyllideans, trypanorhynchans, and tetrabothriideans (Rohde, 2005). Only one species (Tylocephalum sp.) parasitize oysters in Taiwan, the East China Sea (Figure 1D). There is an urgent need to discover more species.

4.2 Annelida

Several species of polychaetous annelids are known to live in association with marine mollusks. Polychaeta, a class of Annelida, parasitizes mollusks (Russell, 1967). Polychaetes exhibit great biodiversity in marine ecosystems, and many of them are involved in symbiotic relations (Martin and Britayev, 1998; Rouse and Pleijel, 2001). The molluscan hosts include bivalves, gastropods, limpets, chitons, squids, and octopuses (Jimi et al., 2019). Polychaetes parasitic on cultured shellfish such as pearls, oysters, scallops, and abalones affect the survival rate, yield, and quality of mollusks (Martin and Britayev, 1998; Nel et al., 1996; Caceres-Martinez et al., 1998; Fitzhugh and Rouse, 1999). Lankester (1868) has suggested that the polychaete can secrete a strong acid, which accounts for the tunnels that they burrow in the shell. In addition, the parasitic marine leech Pontobdella moorei Oka, 1910 along the northwest Mexican Pacific coast was described, and this ectoparasite was collected from the skin of the Octopus bimaculatus (Verrill) (López-Peraza et al., 2017). The annelids discovered in China all belong to the polychaetes. They are found

Copepod	Hosts	Geographic locations	References
Anthessius mytilicolus	Bivalvia: Perna viridis	E: Taiwan: Chiayi; S: Hong Kong	Humes and Lee, 1985; Lin and Ho, 1999
Anthessius pinnae	Bivalvia: Pinna bicolor	S: Hong Kong	Humes and Boxshall, 1988
Conchyliurus quintus	Bivalvia: Mactra chinensis; Mactra quadrangularis; Meretrix petechialis; Neotrapezium liratum; Ruditapes philippinarum	B: Shandong: Laizhou; Y: Shandong: (Haiyang, Qingdao); Jiangsu: (Lianyungang, Nantong)	Du and Sun, 2022; Du et al., 2024
Herrmannella soleni	Bivalvia: Mactra chinensis; Saxidomus purpurata	Y: Shandong: (Rongcheng, Haiyang)	Du and Sun, 2022
Lichomolgus similis	Bivalvia: Meretrix petechialis	B: Shandong: Laizhou; Y: Liaoning: Donggang; Jiangsu: (Lianyungang, Yancheng, Nantong)	Du and Sun, 2022; Du et al., 2024
Modiolicola bifida	Bivalvia: Leukoma jedoensis; Mactra chinensis; Mactra quadrangularis; Mytilus galloprovincialis; Ruditapes philippinarum	B: Shandong: Laizhou; Y: Shandong: (Haiyang, Qingdao); Jiangsu: Lianyungang	Du and Sun, 2022; Du et al., 2024
Myicola formosanus	Bivalvia: Cyclina sinensis	E: Taiwan: Chiayi	Lin and Ho, 1999
Mytilicola orientalis	Bivalvia: Crassostrea gigas; Mytilus galloprovincialis	Y: Shandong: (Rongcheng, Rushan, Qingdao)	Du and Sun, 2022; Du et al., 2024
Octopicola huanghaiensis	Cephalopoda: Amphioctopus fangsiao; Octopus minor	Y: Shandong: Qingdao	Du et al., 2018
Ostrincola koe	Bivalvia: Mactra quadrangularis; Meretrix lusoria; Meretrix petechialis	B: Shandong: Laizhou; Y: Jiangsu: (Lianyungang, Nantong); E: Jiangsu: (Nantong, Qidong); Taiwan: Changhua	Ho et al., 2012; Ho and Zheng, 1994; Du and Sun, 2022; Du et al., 2024
Ostrincola similis	Bivalvia: Crassostrea gigas; Perna viridis	E: Taiwan: Chiayi	Lin and Ho, 1999
Panjakus platygyrae	Bivalvia: Atrina vexillum	S: Hong Kong	Humes and Boxshall, 1988
Pseudomyicola spinosus	Bivalvia: Mytilus galloprovincialis; Ruditapes philippinarum	Y: Liaoning: Dalian; Shandong: Qingdao	Du and Sun, 2022; Du et al., 2024
Trochicola japonica	Bivalvia: Ruditapes philippinarum	B: Liaoning: Xingcheng; Y: Shandong: Qingdao; Jiangsu: (Lianyungang, Nantong)	Du and Sun, 2022; Du et al., 2024

TABLE 3 Taxon of copepod parasitizing mollusks in the China Seas.

B, the Bohai Sea; Y, the Yellow Sea; E, the East China Sea; S, the South China Sea.

in the China Seas; however, most of them are located in the South China Sea and the hosts are mainly bivalves, along with a small number of gastropods (see Table 2; Figures 1B, D).

4.3 Arthropoda: Copepoda, Malacostraca, and Pycnogonida

4.3.1 Copepoda

Among copepod crustaceans, numerous species have been reported as "parasites" or as "commensals" of mollusks including several from commercially important marine species (Russell, 1967). Copepods are typically small and inconspicuous aquatic crustaceans but they are extremely abundant. Two orders (Cyclopoida and Monstrilloida) of Copepoda were reported in mollusks (Rohde, 2005; Gejima et al., 1999; Suárez-Morales et al., 2010). Copepods parasitize most mollusk groups, ranging from aplacophorans and polyplacophorans to the cephalopods. Knowledge about the effects of copepod parasites on mollusks is still limited. Some species are reported to be harmful to economic mollusks. For example, the red copepod *Mytilicola intestinalis* Steuer, 1902 may be the cause of heavy mortalities for the mussel *Mytilus edulis* Linnaeus in Europe (Blateau et al., 1992); the scallop copepod *Pectenophilus ornatus* Nagasawa, Bresciani and Lutzen, 1988 can attain a prevalence of 100% and cause significant loss of condition in the Japanese scallop *Mizuhopecten yessoensis* (Jay) (Nagasawa and Nagata, 1992; Suzuki and Matsutani, 2009); *Mytilicola orientalis* Mori, 1935 and *Ostrincola koe* Tanaka, 1961 have been reported to harm mollusks (Ho and Zheng, 1994; Streftaris and Zenetos, 2006). The potential impact of the other copepod parasites on mollusks remains to be studied. Our findings in the China Seas all belong to Cyclopoida. Among them, in the East China Sea and the South China Sea, unknown species are urgently in need of discovery. *Octopicola huanghaiensis* Du, Dong and Sun, 2018 was found from cephalopods, and the remaining species were part of bivalves (see Table 3; Figure 1D).

4.3.2 Malacostraca

Castro (2015) stated that parasitic crabs including two families, namely, Aphanodactylidae and Pinnotheridae, have 322 species in 57 genera. All known members of the Aphanodactylidae for which

TABLE 4 Taxon of malacostracan parasitizing mollusks in the China Seas.

Malacostracan	Hosts	Geographic locations	References
Amusiotheres obtusidentatus	Bivalvia: Amusium pleuronectes	E: Taiwan; S: Guangdong: (Shantou, Zhanjiang); Hong Kong; Hainan: (Danzhou, Sanya); Guangxi: Beihai	Chen, 2008; Dai et al., 1980; Huang and Lin, 2012; Jiang, 2006
Arcotheres boninensis	Bivalvia: <i>Crassostrea gigas</i> ; <i>Mytilus</i> sp.	E: Taiwan: Xinzhu; S: Guangdong: Zhanjiang; Hainan: Hainan Island (Xincun)	Chen, 2008; Dai et al., 1980; Huang, 2005; Huang and Lin, 2012; Jiang, 2006
Arcotheres cyclinus	Bivalvia: Barbatia virescens; Meretrix meretrix	Y: Shandong Peninsula; E: Taiwan: Taibei	Chen, 2008; Dai et al., 1986; Huang and Lin, 2012; Jiang, 2006; Shen and Dai, 1964
Arcotheres purpureus	-	S: Hainan: (Hainan Island (Xincun), Sanya); Guangxi: Qisha	Dai et al., 1980; Jiang, 2006
Arcotheres similis	Bivalvia: Mytilus unguiculatus	S: Guangdong: Shanwei; Hainan: (Hainan Island (Xincun), Sanya); Beibu Gulf	Dai et al., 1980; Huang and Lin, 2012; Jiang, 2006
Arcotheres sinensis	Bivalvia: Arcuatula japonica; Crassostrea angulata; Crassostrea gigas; Laternula gracilis; Mytilus edulis; Mytilus galloprovincialis; Venerupis aspera; Ostrea sp.	B: Liaoning: Huludao; Hebei: Qinhuangdao; Tianjin; Liaodong Peninsula; Y: Liaoning: (Zhuanghe, Dalian), Shandong: (Haiyang; Qingdao, Liaodong Peninsula); E: Taiwan: (Xinzhu, Zhanghua, Yunlin County, Chiayi, Tainan, Pingdong County); Fujian: Xiamen; S: Dapeng Bay	Chen, 2008; Huang, 2005; Huang and Lin, 2012; Jiang, 2006; Kuo et al., 2018; Shen and Dai, 1964; Sun and Chen, 2007; Sun et al., 2006; Wang et al., 2002; Zhang et al., 2019; Zhu et al., 1988
Durckheimia caeca	Bivalvia: Limopsidae gen. et sp.	S: Hong Kong	Huang and Lin, 2012
Magnotheres globosus	Bivalvia: <i>Pinna</i> sp.	S: Guangdong: Zhanjiang; Hainan: (Lingao County, Lingshui County, Hainan Island (Xincun), Sanya)	Dai et al., 1980; Huang and Lin, 2012; Jiang, 2006
Nepinnotheres affinis	-	Y: Shandong Peninsula	Shen and Dai, 1964; Sun and Chen, 2007
Nepinnotheres glaberrimus	Bivalvia: Venerupis aspera	E: Taiwan: Chiayi	Chen, 2008
Nepinnotheres taichungae	Bivalvia: Laternula gracilis	E: Taiwan: (Taizhong, Xinzhu)	Chen, 2008
Nepinnotheres tsingtaoensis	Bivalvia: Barnea dilatata; Hiatula acuta; Laternula gracilis; Mactra quadrangularis; Meropesta sinojaponica; Ostrea sp.; Venerupis aspera	B: Shandong: (Dongying, Liaodong Peninsula); Y: Shandong: (Longkou, Haiyang, Qingdao, Liaodong Peninsula, Shandong Peninsula); E: Taiwan: Bajhang River	Huang and Lin, 2012; Jiang, 2006; Shen and Dai, 1964; Soong, 1997
Orthotheres haliotidis	Gastropoda: Haliotis asinina	S: Taiwan: Dongsha Islands	Chen, 2008
Pinnaxodes major	-	Y: Shandong: Qingdao	Jiang, 2006
Pinnaxodes mutuensis	Bivalvia: Modiolus modiolus	Y: Liaoning: Dalian	Jiang and Liu, 2011
Pinnotheres dilatatus	Bivalvia: Venerupis aspera; Solen strictus; Venerupis aspera	E: Taiwan: Zhanghua; Y: Shandong: (Rushan, Shandong Peninsula)	Chen, 2008; Huang and Lin, 2012; Jiang, 2006; Shen and Dai, 1964
Pinnotheres excussus	Bivalvia: Gafrarium sp.; Marcia hiantina	E: Taiwan: Pingdong; S: Hong Kong; Hainan: Hainan Island (Xincun)	Chen, 2008; Dai et al., 1980; Huang and Lin, 2012; Jiang, 2006
Pinnotheres gordoni	Bivalvia: <i>Mytilus</i> <i>galloprovincialis</i> ; Bivalvia: Pinnidae gen. et sp.	B: Liaodong Peninsula; Y: Liaodong Peninsula, Shandong Peninsula; S: Hong Kong	Huang and Lin, 2012; Shen and Dai, 1964; Sun and Chen, 2007; Zhu et al., 1980
Pinnotheres haiyangensis	Bivalvia: Laternula gracilis	Y: Shandong: (Haiyang, Shandong Peninsula); E: Taiwan: Xinzhu; S: Hong Kong	Huang, 2005; Huang and Lin, 2012; Jiang, 2006; Shen and Dai, 1964
Pinnotheres luminatus	Bivalvia: Asaphis violascens	S: Hong Kong; Hainan: Lingao County	Dai et al., 1980; Huang and Lin, 2012; Jiang, 2006
Pinnotheres obscurus		S: Hong Kong	Huang and Lin, 2012
Pinnotheres parvulus	Bivalvia: Macridiscus aequilatera	E: Taiwan: Taizhong; S: Guangdong: ?; Hong Kong	Chen, 2008; Huang and Lin, 2012; Shen and Dai, 1964
Pinnotheres pholadis	Bivalvia: <i>Hiatula acuta</i>	B: ?; Y: Liaoning: Dalian, Shandong: (Rongcheng, Qingdao, Shandong Peninsula); E: Fujian: (Xiamen, Zhangzhou); S: Dapeng Bay	Huang and Lin, 2012; Jiang, 2006; Yang and Li, 1997; Yang et al., 1998

(Continued)

Malacostracan	Hosts	Geographic locations	References
Pinnotheres pilulus	Bivalvia: Barnea manilensis; Barbatia virescens; Martesia sp.	S: Guangdong: Yangjiang, Hainan: Sanya; Guangxi: Fangchenggang	Dai et al., 1980; Huang and Lin, 2012; Jiang, 2006
Tridacnatheres whitei	-	S: Hainan: Sanya	Jiang, 2006
Xanthasia murigera	Bivalvia: <i>Tridacna</i> sp.	S: Xisha Islands	Dai et al., 1986; Huang and Lin, 2012; Jiang, 2006
Anchistus demani	Bivalvia: <i>Tridacna</i> sp.	S: Nansha Islands	Huang and Lin, 2012
Anchistus miersi	Bivalvia: Tridacna sp.; Hippopus hippopus; Pinna sp.; Pinctada sp.	S: Northern South China Sea; Nansha Islands	Bruce, 1979; Huang and Lin, 2012; Li, 1997
Conchodytes biunguiculatu	Bivalvia: <i>Pinna</i> sp.	E: Taiwan; S: Hainan; South China Sea; Xisha Islands	Huang and Lin, 2012; Li and Liu, 2002
Conchodytes meleagrinae	Bivalvia: Pinctada margaritifera	S: Zhaoshu Island	Huang and Lin, 2012; Li, 1997
Conchodytes monodactylus	Bivalvia: Pinna atropurpurea	S: Guangdong; Hong Kong; Hainan; South China Sea	Bruce, 1979; Huang and Lin, 2012
Conchodytes nipponensis	Bivalvia: <i>Pinna</i> sp.	E: East China Sea; S: Hainan; Northern South China Sea	Huang and Lin, 2012; Li and Liu, 2002
Conchodytes tridacnae	Bivalvia: <i>Tridacna</i> sp.	S: Northern South China Sea; Central South China Sea; Nansha Islands; Yongxing Island	Bruce, 1979; Huang and Lin, 2012; Li, 1997
Ensiger custos	Bivalvia: Pinna sp.; Tridacna sp.	S: Guangdong; Hong Kong; Hainan; Northern South China Sea	Bruce, 1979; Huang and Lin, 2012; Li, 1997; Li and Liu, 2002

TABLE 4 Continued

B, the Bohai Sea; Y, the Yellow Sea; E, the East China Sea; S, the South China Sea; - represents the unknown host; ? represents the unknown locality.

hosts have been recorded are associated with tube building polychaete worms (belonging to Terebellidae) (Ahyong and Ng, 2009). Species of Pinnotheridae are associated with various invertebrates including mollusks (Dai et al., 1980). Among the malacostracans, a number of decapods are known to live symbiotically with commercially important marine mollusks at least during one phase of their life cycles (Russell, 1967). Specifically, certain species of crabs of Pinnotheridae are known to live within the mantle cavities of oysters and other pelecypods (Russell, 1967). Pea crabs have been shown to cause damage to the gills of their bivalve hosts. Infected mussels have been shown to have lower tissue weights and slightly greater shell weights than equivalent uninfected mussels (Seed, 1969). They retard the growth of some commercial mollusks and cause millions of dollars in losses in aquaculture (Trottier and Jeffs, 2015). All the pea crabs found in China so far belong to Pinnotheridae. They were found in the China Seas. Most of their hosts are bivalves, and only an extremely small number are gastropods (see Table 4; Figure 1D).

The crabs belong to the family Pinnotheridae, especially the genus *Pinnotheres*. Meanwhile, the prawns are members of the family Palaemonidae. Most species of the family are commensal and are mainly associated with coelenterates, sponges, bivalve mollusks, echinoderms, and tunicates, and several species are cleaners of fishes (Li, 2004). The association between bivalves and pinnotherid crabs is relatively well known and has often been studied but little attention has been paid to the palaemonid commensals (Johnson and Liang, 1966). In terms of both the number of host species and the number of shrimp associates, the most important group of host organisms seems to be Scleractinia (Grave, 1999). Nevertheless, bivalve mollusks are also important as hosts for shrimps. Commensalism with bivalve mollusks is not restricted to

palaemonid shrimps, but also occurs in Alpheidae (Grave, 1999). We have not been able to show any damage to host tissues caused by prawns. The amount of food consumed by prawns is minimal. Thus, even in cases of multiple infections, it is likely to be insignificant compared to the total food supply available to bivalves. Therefore, prawns seem to be harmless commensals (Johnson and Liang, 1966). Eight species of palaemonid prawns have been reported in China. They are distributed in the East China Sea and the South China Sea and all their hosts are bivalves (see Table 4; Figure 1D). The parasitic prawns still need further investigation and research.

4.3.3 Pycnogonida

All pycnogonids parasitic on mollusks belong to the order Pantopoda, and the hosts are gastropods and bivalves (Arnaud and Bamber, 1988). Pycnogonids are most often found attached to the foot and mantle of the host by means of their chelifores, with their proboscides piercing and destroying the host tissue (Benson and Chivers, 1960). Juvenile ammotheid pycnogonid species of the genus Nymphonella Ohshima, 1927 have been reported to be living parasitically in several species of infaunal and epifaunal bivalve mollusks in Japanese waters. The young and adults of Achelia chelata (Hilton, 1939) were also found infesting the mussel Mytilus californianus Conrad, partly destroying the tissue (Benson and Chivers, 1960). Opisthobranchs are a diverse group of mollusks that include the bubble shells, the sea hares, and the nudibranchs, all of which have a documented parasitic association with pycnogonids. Young stages of Ammothea Leach, 1814 were recorded as ectoparasites on the nudibranch Armina variolosa (Bergh) (Ohshima, 1933). At present, there is no record of sea spiders in the China Seas and they are waiting to be discovered in the future.

4.4 Porifera

Porifera parasitic in mollusks belong to the class Demospongiae (Rohde, 2005; Huang and Lin, 2012). The parasitic sponges have been responsible for extensive damage to commercial shellfish and other molluscan hosts (Lauckner, 1983; Rosique et al., 1996). The most visibly destructive cases of bioeroding sponge infections can be observed in edible oyster cultures infected with Pione vastifica (Hancock, 1849). Reported infection rates can reach up to 50% in some commercial oysters such as Saccostrea glomerata (Gould) (Wesche et al., 1997). The common practice of translocating young oyster spat between commercial oyster beds has led to nearly cosmopolitan distributions for some species (e.g., P. vastifica) (Rohde, 2005). Parasitic sponges are a major pest of commercial molluscan fisheries (Rohde, 2005). Two species of parasitic sponges (Suberites carnosus and Mycale phyllophila) are discovered from the East China Sea and the South China Sea (Figure 1D). The Bohai Sea and the Yellow Sea have no records of parasitic sponges and there are more species waiting to be discovered.

4.5 Cnidaria

Cnidarians parasitic in mollusks are generally found in the class Hydrozoa (Rohde, 2005). Cnidarians living on gastropod shells containing living mollusks or hermit crabs are either simple epibionts or even mutualists. Polyps of three hydrozoan species, Kinetocodium danae Kramp, 1921, Perigonella sulfurea (Chun, 1889), and Pandea conica (Quoy and Gaimard, 1827), live on the shells of pteropods and feed on their epithelium and on their embryos (i.e., they are real parasites). Polyps of five hydrozoan species live in the mantle cavity of bivalve mollusks, attached to the tissues of the mantle cavity by stolonal sucker-like structures or by hydrorhizae penetrating into the host tissues. They utilize food collected by the ciliary movements of the bivalve gills and the labial palps, but their exact parasitic relationships are not known. Some have been observed feeding on the larvae of other parasites of their hosts. The species include Eugymnanthea inquilina Palombi, 1936, Eugymnanthea japonica (Yamada, 1950), Eutima commensalis Santhakumari, 1970, Eutima ostrearum (Mattox and Crowell, 1951), and Eutima sapinhoa Narchi and Hebling, 1975 (Rohde, 2005). Additionally, Paraiptasia radiata (belonging to Hexacorallia) was found on the outer shell of the Perna virdis in the South China Sea, and more species need to be found in the China Seas (Huang and Lin, 2012) (Figure 1D).

4.6 Nemertea

The parasitic nemerteans of mollusks are relatively few. The species of two orders Monostilifera and Heteronemertea have been recorded to date (Rohde, 2005). The Malacobdellidae belonging to Monostilifera contains a single genus, *Malacobdella* Blainville, 1872, with six valid species (Gibson, 1995; Ivanov et al., 2002). They predominantly inhabit the mantle cavity of bivalves of the subclass Heterodonta, Protobranchia, and Pteriomorphia (Rohde, 2005).

Tetrastemma fozensis Gibson and Junoy, 1991 (Monostilifera: Tetrastemmatidae) lives in the mantle cavity of the bivalve *Scrobicularia plana* (da Costa) (Gibson, 1995). There is no reliable evidence to indicate that *Malacobdella* spp. (Monostilifera: Malacobedellidae) are in any way injurious to their hosts (Russell, 1967). In addition, *Uchidana parasita Iwata*, 1967 (Heteronemertea: Valenciniidae) was collected from the cavity and the gap between the mantle and shell of the bivalve *Mactra chinensis* Philippi in Japan (Iwata, 1967). Currently, there is no documentation of nemerteans in the China Seas and they remain to be discovered in the future.

4.7 Nematoda

The species of the nematodes belong to the order Rhabditida (Russell, 1967). Only a few species of nematodes have been reported from commercially important marine mollusks, although they have been recorded in some unimportant marine mollusks either as larvae or as adults (Russell, 1967). Sulcascaris sulcata (Rudolphi, 1819), an anisakine parasite of marine turtles, however, has a relatively simple life cycle with marine bivalves (such as scallops and oysters) serving as intermediate hosts (Lauckner, 1983). The presence of S. sulcata at the larval stage in edible scallops has significant implications for the depreciation of the product and also has consequences for health and hygiene requirements in accordance with legislation (Marcer et al., 2020). Millemann (1951) described the larva of the species Echinocephalus pseudouncinatus Millemann, 1951, encysted in the foot of the pink abalones, Haliotis corrugata Wood (Millemann, 1951). Nemerteans have not been recorded in the China Seas and they are yet to be found.

4.8 Mollusca

Several species of mollusks belonging to the family Pyramidellidae have been reported as parasites of commercially important marine mollusks (Russell, 1967). All pyramidellids are ectoparasites as they are generally attached on the exterior, near the edges of the valves of pelecypods, and insert their long proboscis into the hosts' soft tissues to feed on blood or tissue fluids (Russell, 1967). As foraging animals, pyramidellids are constantly moving between the host and the habitat substrate rather than parasitizing the host for life (Robertson and Mau-Lastovicka, 1979). Odostomia Fleming, 1813 have been reported as a pest of oysters and mussels (Cole and Hancock, 1955). Additionally, species of the mollusks from the family Modiolidae and Calyptraeidae are also reported as epibionts of the mollusk hosts. For example, Leiosolenus patagonicus (d'Orbigny, 1846) and Crepidula sp. are parasites of Aulacomya atra (Molina) and Ostrea puelchana (d'Orbigny) from Argentina (Cremonte et al., 2005). Moreover, bivalves of the family Mytilidae, such as internal bioeroders, boring bivalves Lithophaga spp. are parasites of mollusks (Cortés and Jiménez, 2003). The abalone piddock clam, Penitella conradi Valenciennes, 1846, and mussels of Lithophaga spp. bore into substrates including the shells

of live abalone (Moore, 2023). In China, two species (*Brachystomia omaensis* and *Crepidula onyx*) of parasitic mollusks have been discovered from the China Seas and the hosts are all gastropods (Figure 1D). Research on parasitic mollusks of the mollusk hosts needs to be further carried out.

5 Conclusion

Collectively, Figure 1 indicates that arthropods, annelids, and platyhelminths take up a relatively large proportion. The largest phylum is Arthropoda, while other phyla have a relatively small proportion. This review provides a synopsis of the known metazoan parasites of mollusks from the China Seas and presents the known relationship between metazoan parasites and mollusks, which will broaden our knowledge on the metazoan parasites of mollusks. Compared with other countries, scientific research on the metazoan parasites of mollusks from the China Seas is relatively scarce. Higher species diversity may be uncovered if other mollusks are examined intensively in the future. The knowledge about the effects of metazoan parasites on mollusks is still limited. Most species are reported to be more or less harmful to economic mollusks, with the exception of prawns and nemerteans. The potential impact of other metazoan parasites on mollusks still needs to be studied. For instance, anisakine parasites that pose a threat to human health should be given more attention. It should be emphasized that the biology of zoosymbionts of marine mollusks, regardless of their economic or medical importance, has a great deal to contribute to our understanding of the nature of symbiotic relationships and deserves increased attention (Russell, 1967).

Author contributions

XD: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Writing – review & editing, Funding acquisition, Project administration, Resources, Software, Supervision, Validation, Writing – original draft. JS: Conceptualization, Data curation, Resources, Writing – review & editing, Investigation. HJ: Conceptualization, Resources, Writing – review & editing, Formal Analysis, Funding acquisition, Software,

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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