Marine fish parasites of Vietnam: a comprehensive review and updated list of species, hosts, and zoogeographical distribution

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Abstract – With a long coastline stretching from tropical to subtropical climate zones, and an immense exclusive economic zone with over 4000 islands, the Vietnamese marine waters support a rich and biodiverse parasite fauna. Although the first parasitological record was in 1898, systematic studies of the parasite fauna have increased during the last 50 years. This comprehensive review covers the current state of knowledge of marine fish parasites in Vietnam and lists 498 species found in 225 fish species, and their geographical distribution. In addition, 251 marine parasite species have newly been added to the already known fauna of 247 species since 2006 (more than two-fold increase). The most speciose group was the Digenea, which accounted for 43% of the total parasite species biodiversity, followed by Monogenea (23.5%), Crustacea (11.6%), Nematoda, and Acanthocephala (8.0% each). The shallow and muddy Gulf of Tonkin showed a rich parasite fauna, accounting for 66.3% of the whole marine parasite fauna of Vietnam, with Digenea accounting for 51% of the regional total parasite richness, followed by Monogenea (27%), Acanthocephala (8.8%), and Nematoda (5.8%). Only a few species belonged to Hirudinea, Myxozoa, and Cestoda, suggesting that these taxa may be understudied. Despite significant progress in studies of marine fish parasites in Vietnam since 2006, only about 12% and 13% of the total fish species have been examined for parasites in the whole country and the Gulf of Tonkin, respectively.

Key words: Marine fish parasites, Species richness, Diversity, Vietnam, Host, Distribution.

Résumé – Parasites des poissons marins du Vietnam : synthèse complète et mise à jour des listes d’espèces, des hôtes et de la distribution zoogéographique. Avec un long littoral s’étendant des zones climatiques tropicales à subtropicales et une immense zone économique exclusive incluant plus de 4 000 îles, les eaux marines vietnamiennes abritent une faune parasitaire abondante et riche en biodiversité. Le premier signalement parasitologique remonte à 1898 et les études systématiques de la faune parasitaire se sont multipliées au cours des 50 dernières années. Cette synthèse complète couvre l’état actuel des connaissances sur les parasites des poissons marins au Vietnam et répertorie 498 espèces trouvées dans 225 espèces de poissons et leur répartition géographique. De plus, 251 espèces de parasites marins ont été nouvellement ajoutées à la faune déjà connue de 247 espèces depuis 2006 (soit une augmentation de plus du double). Le groupe le plus riche en espèces était les Digenea, qui représentaient 43% de la biodiversité totale des espèces de parasites, suivis des Monogenea (23,5 %), des Crustacea (11,6 %), des Nematoda et des Acanthocephala (8,0 % chacun). Le golfe peu profond et boueux du Tonkin a montré une riche faune parasitaire, représentant 66,3 % de l’ensemble de la faune parasitaire marine du Vietnam, avec les Digenea représentant 51 % de la richesse parasitaire totale régionale, suivi des Monogenea (27 %), Acanthocephala (8,8 %) et Nematoda (5,8 %). Seules quelques espèces appartaient aux Hirudinea, Myxozoa et Cestoda, ce qui suggère que ces taxons pourraient être sous-étudiés. Malgré des progrès significatifs dans les études sur les parasites des poissons marins au Vietnam depuis 2006, seulement 12 % et 13 % des espèces de poissons ont été examinées, respectivement pour la faune des poissons marins du Vietnam et du golfe du Tonkin.
**Introduction**

Vietnam has a long coastline of more than 3260 km and an immense exclusive economic zone (one million km²), comprising the coastlines of more than 4000 islands and thousands of square kilometers of coral reefs [122, 131]. The Vietnamese Sea stretches from tropical to subtropical climate zones (from the Namazu Islands, 9°40’N, 104°22’E, in the Gulf of Thailand to Daochoa Island, 20°50’N, 107°20’E, in the Gulf of Tonkin), opening to the Pacific Ocean and being known for its biodiverse marine ecosystems supporting a rich fauna and flora, including fish parasites. Although Billet [26] recorded the first parasite, *Distomum hypselobagri* (Trematoda), systematic studies of the parasite fauna did not begin until the 1960s (e.g., [69, 71, 82, 97–99], etc.), and the first review was published only 16 years ago [19]. Recently, studies using both molecular [11–13, 16, 20, 24, 25, 36] and morphological methods [12, 13, 20, 24, 92] have been conducted in order to elucidate the systematics of marine parasites in Vietnam.

According to Palm and Bray [103], marine fish parasites are important in ecosystems. In open Hawaiian waters (Pacific Ocean), the authors discovered an average of 2.2 parasite species per marine fish species. In contrast, Klimpel et al. [66] discovered 1.5 metazoan parasite species per deep-sea fish species. According to Palm [102], each fish species in the world harbors up to 3–4 metazoan parasite species on average. In this sense, Arthur and Te [19] reported that the estimated number of parasite species per marine fish species in Vietnamese waters was as high as 3.0. There are currently 1876 species of marine fish reported in Vietnam’s marine waters [45]. Despite this, only 247 parasite species infecting 82 marine fish species were documented by 2006, accounting for about 4.4% of the total fish community [19]. Such data demonstrate that the number of parasites known to science is insufficient to provide credible estimates of the local parasite community.

Because of the importance of marine parasites in fisheries, aquaculture, and human health, more research has been conducted recently, focusing on commercially important fish (e.g., [88, 90, 132, 135]). Furthermore, because parasites can be used as a tool for monitoring climate change and environmental health [86, 102, 129], studies regarding these organisms are essential. However, no systematic update pertaining to parasites in marine fish from Vietnam has been published since 2006, and since that date, much has changed in the knowledge of such organisms. However, Poulin [123] asserts that, due to the absence of an adequate method for determining parasite diversity, species richness remains the most straightforward and thus most relevant indicator of diversity. Therefore, the present study is aimed at: (1) shedding more light on the marine parasite richness in Vietnam by listing, correcting, and arranging the latest information, including the host and geographical distribution of parasites of marine fish; and (2) providing a current state of knowledge on parasite research in the Vietnamese marine waters, with particular emphasis on the Gulf of Tonkin (GOT).

**Methods**

**Study sites and data collection**

Vietnam is a Southeast Asian country divided into three distinct geographical and climatic regions: North, Central, and South Vietnam. The aquaculture industry is vital to the Vietnamese economy, especially brackish and marine fish farming along the country’s coastline, particularly in the north [67].

A total of 137 references published between 1901 and 2022 were retrieved to gather knowledge on marine fish parasites and their occurrence in cultured and wild marine fish in Vietnam, focusing on the latest studies. This list was also based on information from the checklists of parasites of fishes in Vietnam [19], and it was expanded to provide a parasite-host list organized on a taxonomic basis, including information about each parasite species, sites of infection, the known geographical distribution in Vietnam, and references. More recently, reviews of individual species of parasites, including morphology, host-parasite distribution, zoogeography, and occasionally molecular analysis have become available; for instance, Amin et al. [2, 8, 14, 15] on *Rhadinorhynchus trachuri* Harada, 1935, *Neoechinorhynchus johnii* Yamaguti, 1939, *Sclerocotylus neourinbramis* Amin, Heckmann, Ha, 2018, respectively and *Serrasentis sagittifer* (Linton, 1889) Linton, 1932. The animal science databases (https://www.cabi.org/animalscience/disease-health/), MEDLINE, Scopus, Web of Science, and Google Scholar were searched using the keywords: parasite, fish, marine, and Vietnam.

In addition, we included our most recent results from the Gulf of Tonkin, which included 40 *Acanthopagrus latus*, 1 *Acanthocybium solandri*, 7 *Neotrygon kuhlii*, 47 *Protonibea diacanthus*, 37 *Trachinotus blochii*, 7 *Telatrygon zugei*, and 2 *Thynnus* sp. (from 2014 to 2015). The fish were collected in the local fish markets in Ha Long (20°94’96” N, 107°08’23” E) and Cat Ba (20°72’75” N, 107°04’67” E) between 2014 and 2015, kept on ice and transferred to the Fisheries College’s laboratory in Bac Ninh (close to Ha Noi). The parasite examination was performed using a Nikon SMZ-1 stereomicroscope and the standard procedures described by Palm [101] and Palm and Bray [103]. For taxonomic identification, permanent mounts were prepared following standard methods for Digenea, Monogenea, Nematoda, Cestoda, Acanthocephala, and Crustacea (Isopoda, Copepoda) according to Chisholm and Whittington [39], Dang et al. [41], and Hendrix [51]. The identification of crustaceans was based on Kabata and Margolis [59], Shultz [127], and Dojiri and Ho [42]. The digenean identification followed Bray et al. [32], Gibson et al. [47], Jones et al. [57], and Bray and Justine [30]. The identification of cestodes was based on Khalil [63] and Palm [101]. Identification of nematodes was based on Anderson et al. [17] and Gibbons [46]. The protozoan identification followed Bruno et al. [33], and Lom and Dyková [78].
Table 1. The abbreviated names of the municipalities, provinces, and sea or ocean parts where samples were collected.

| Full names                  | Abbreviation | Full names                  | Abbreviation |
|-----------------------------|--------------|-----------------------------|--------------|
| Bac Lieu province           | BL           | Nam Dinh province           | ND           |
| Binh Thuan province         | BT           | Ngo An province             | NA           |
| Gulf of Tonkin              | GOT          | Quang Binh province         | QB           |
| Gulf of Thailand            | GOTH         | Quang Ninh province         | QN           |
| Hai Phong city              | HP           | South China Sea             | SCS          |
| Ha Long Bay, Quang Ninh     | HL-QN        | Thanh Hoa province          | TH           |
| Thua Thien Hue province     | Hue          | Ba ria-Vung tau province    | VT           |
| Khanh Hoa province          | KH           |                            |              |
| Kien Giang province         | KG           | The Gulf of Tonkin (GOT)    |              |

Identification of acanthocephalans was based on Amin [1] and Arai et al. [18]. Other groups of invertebrates retrieved from the literature were identified using methods developed by different authors.

Furthermore, numerous scientific names for recorded hosts from the literature have been amended and corrected following the FishBase database (https://www.fishbase.in/search.php; 2021). The scientific names of existing parasites were carefully checked and corrected using various reliable sources, such as the World Register of Marine Species database (http://www.marinespecies.org/index.php), Ocean Biodiversity Information System (https://obis.org/), and Integrated Taxonomic Information System (https://www.itis.gov/).

Vietnam’s 3260 km of coastline is home to 25 coastal provinces and three cities by the sea. The following abbreviations are used to denote administrative and oceanic divisions where the parasites have been reported (Table 1).

Data analysis

The retrieved literature data, such as the reference, study period, study location, site of infection, fish host, taxa, and parasite species studied, were entered into an excel spreadsheet. This analysis only included parasites identified at the species level. In the list, the parasite taxon levels, i.e., subfamilies, genera, and species, were organized alphabetically. For the entire country of Vietnam and the Gulf of Tonkin, parasite species were classified into eight main taxa: Myxozoa (My), Ciliophora (Ci), Monogenea (Mo), Digenea (D), Cestoda (C), Nematoda (N), Acanthocephala (A), and Crustacea (Cr).

In order to have an insight into parasite richness, the total number of parasite species for Vietnam and the GOT was used to calculate the parasite species ratio per fish host. It is determined by dividing the total number of parasite species parasitizing fishes by the number of infected hosts. Microsoft Excel software was used to perform calculations and descriptive analysis of the collected data.

Results and discussion

Parasites in marine fish of Vietnam

Table 2 contains information about the parasite and host taxa, the site of infection, geographical localities, and literature sources.

Parasite richness

A total of 498 parasite species have been recorded from 225 marine fish in Vietnam belonging to the following taxa: Myxozoa and Ciliophora (8 each), Monogenea (117), Digenea (214), Cestoda (17), Nematoda (37), Acanthocephala (37), Hirudinea (2), and Crustacea (58), demonstrating the high diversity of the marine fish parasites inhabiting Vietnamese waters. The current average number of parasite species per fish species was 2.2, which was lower than the previously estimated species richness in Vietnamese (3.0) and German coastal waters (3.1) [19, 104]. This lower species richness appears to be due to a higher proportion of the fish community being investigated compared to 16 years ago (225 species vs. 82 fish species reported in 2006) so that a better prediction of the species richness can be made. It could also be explained by a decline in host species richness and population density, the major universal determinants of variations in parasite species richness [123]. However, the new figure of 2.2 is comparable to that of New Caledonia (1.9), the Indo-West Pacific (1.7), and Hawaii’s open Pacific waters (2.2) ([58, 103, 126], respectively). These regions’ similar latitudinal patterns could account for their parasite richness [28].

Our findings showed that only 225 of the total 1876 species of marine fish recorded in Vietnam [21] had been investigated for parasite species, accounting for only 12% of the entire fish community; this indicates that the parasite fauna of marine fishes in Vietnam is still poorly known.
Table 2. List of marine fish parasites in Vietnamese waters.

| Parasite                          | Taxa  | Hosts                  | Site of infection | Locality/ies | References |
|-----------------------------------|-------|------------------------|-------------------|--------------|------------|
| Phylum: Myzozoa Cavalier-Smith & Chao, 2004 |       |                        |                   |              |            |
| Class: Conoidasida Levine, 1988    |       |                        |                   |              |            |
| Order: Eucoccidiorida Léger, 1911 |       |                        |                   |              |            |
| Family: Eimeriidae Minchin, 1903   | My    | Lates calcarifer       | Sw                | KH           | [122]      |
| Phylum: Cnidaria Hatschek, 1888    |       |                        |                   |              |            |
| Class: Myxozoa Grassé, 1970        |       |                        |                   |              |            |
| Subclass: Myxosporea Bütschli, 1881|       |                        |                   |              |            |
| Order: Bivavulida Shulman, 1959    |       |                        |                   |              |            |
| Family: Ceratomyxidea Dolfin, 1899 |       |                        |                   |              |            |
| Ceratomyxa bsinthaumansensis Chinh, Ha, Doanh, Violettta My | My | Epinephelus fasciatus | Gb              | KH           | [38]       |
| Ceratomyxa sp.                     | My    | Epinephelus blekeri, E. coioides, E. malabaricus, E. taulvina, Lates calcarifer | Gb              | KH, HP, ND   | [122, 133, 135] |
| Family: Meglitschiidae Kovaleva, 1988 |       |                        |                   |              |            |
| Meglitschia insolita (Meglitsch, 1960) | My | Epinephelus coioides  | Gb                | KH           | [135]      |
| Phylum: Myxobolidae Thélohan, 1892 |       |                        |                   |              |            |
| Henneguya cerebralis Pronin, 1972 | My    | Lates calcarifer       | Gi                | KH           | [122]      |
| Henneguya lata Nguyen, Chinh, Ngo, Van Tuc, Itoh, Yoshinaga, Shirakashi & Doanh, 2021 in [Chinh NN et al. (2021)] | My | Acanthopagus latus   | Gi              | QN          | [37]       |
| Henneguya sp.                      | My    | Acanthopagus latus     | Gi, Sw            | QN           | Present study |
| Myxobolus sp.                     | My    | Epinephelus blekeri, E. coioides, E. taulvina | K              | KH           | [135]      |
| Phylum: Ciliophora Dolfin, 1901    |       |                        |                   |              |            |
| Class: Oligohymenophorea, Stein 1859 |       |                        |                   |              |            |
| Subclass: Peritrichia Stein, 1859 |       |                        |                   |              |            |
| Order: Mobilida Kahl, 1933        |       |                        |                   |              |            |
| Family: Trichodindia Claus, 1951  | Ci    | Epinephelus blekeri, E. coioides, E. malabaricus, E. taulvina | Gi              | KH           | [140]      |
| Trichodina japonica Imai, Miyazaki & Nomura, 1991 | Ci | Lates calcarifer   | Gi, Sk            | KH           | [122]      |
| Trichodina rostrate Kulemina, 1968 | Ci | Epinephelus bruneus, E. taulvina, E. sexfasciatus, E. coioides, Lutjanus erythropterus, Ruchycentron canadam, Sciaenops ocellatus | Gi, Sk | HP, QN, NA, KH, VT | [34, 121, 133, 140] |
| Trichodina sp.                    | Ci    |                        |                   |              |            |
| Order: Sessilida Stein 1933       |       |                        |                   |              |            |
| Family: Apistylididae Kahl, 1935  |       |                        |                   |              |            |
| Apiosoma sp.                      | Ci    | Epinephelus blekeri, E. coioides, E. malabaricus, E. taulvina | Sk              | KH           | [135]      |
| Family: Scyphidinidae Kahl, 1935  |       |                        |                   |              |            |
| Ambiphrya sp.                     | Ci    | Epinephelus blekeri, E. coioides, E. malabaricus, Lates calcarifer | Sk              | KH           | [140]      |
| Class: Phyllopharyngea de Puytorac, Batisse, Bohatier, Corliss, Deroux, Didier, Dragesco, Fryd-Versavel, Grain, Grollere, Horasse, Mode, Laval, Roque, Savoie & Tuffrau, 1974 |       |                        |                   |              |            |
| Order: Chlamydodontida Deroux, 1976 |       |                        |                   |              |            |
| Family: Chilodinellidae Deroux, 1970 |       |                        |                   |              |            |
| Chilodonella sp.                  | Ci    | Epinephelus blekeri, E. coioides | Sk              | KH           | [135]      |

(Continued on next page)
### Table 2. (Continued)

| Parasite                                                                 | Taxa     | Hosts                                                                 | Site of infection         | Locality/ies | References |
|--------------------------------------------------------------------------|----------|-----------------------------------------------------------------------|---------------------------|--------------|------------|
| **Order: Dysteriida Deroux, 1970**                                        |          |                                                                       |                           |              |            |
| **Family: Hartmannulidae Poche, 1913**                                    |          |                                                                       |                           |              |            |
| *Brookynella hostilis* Lom & Nigrelli, 1970                              | Ci       | Epinephelus bleekeri, E. bruneus, E. sexfasciatus, E. tauvina*        | Gi, Sk                    | QN, KH       | [34, 140]  |
| **Class: Prostomatea Schewiakoff, 1896**                                  |          |                                                                       |                           |              |            |
| **Order: Prorodontida Corliss, 1974**                                     |          |                                                                       |                           |              |            |
| *Cryptocaryon irritans* Brown, 1951                                       | Ci       | Epinephelus bleekeri, E. coioides, E. malabaricus, Lates calcarifer, Sciaenops ocellatus | Gi, Sk                    | KH, HP, ND, QN | [133, 140] |
| **Phylum: Platyhelminthes Minot, 1876**                                   |          |                                                                       |                           |              |            |
| **Class: Monogenea Van Beneden, 1858**                                    |          |                                                                       |                           |              |            |
| **Subclass: Monopisthocotylea Odhner, 1912**                              |          |                                                                       |                           |              |            |
| **Order: Capsalidea Baird, 1853**                                         |          |                                                                       |                           |              |            |
| *Allobenedenia epinepheli* (Bychowsky & Nagibina, 1967) Yang, Kritsky & Sun, 2004 | Mo      | Epinephelus coioides                                                  | Gi                        | KH           | [140]      |
| *Allobenedenia yamagutii* (Egorova, 1994) Yang, Kritsky & Sun, 2004       | Mo       | Hypododus nigritus (Holbrook, 1855)                                   | Gi, Sk                    | KH, QN       | [88, 140]  |
| *Benedenia epinepheli* (Yamaguti, 1937) Meserve, 1938                    | Mo       | Epinephelus bleekeri, E. bruneus, E. coioides, E. malabaricus, E. sexfasciatus, E. tauvina*, Latjanus argentimaculatus | Sk, Fi                    | KH, QN       | [34, 135]  |
| *Benedenia sp.*                                                          | Mo       | Épínephelus brunus, E. coioides, E. sexfasciatus, E. tauvina*, Latjanus erythropterus, Rachycentron canadun | Sk                        | HP, ND, QN, KH | [34, 133, 140] |
| *Capsala affinis* (Mamaev, 1968) Chisholm & Whittington, 2007            | Mo       | Auxis thazard, Euthynnus affinis                                      | Gi                        | SCS          | [80]       |
| *Capsala notosinense* (Mamaev, 1968) Chisholm & Whittington, 2007         | Mo       | Euthynnus affinis                                                     | Gi                        | SCS          | [80]       |
| *Capsala paucispinosa* (Mamaev, 1968) Chisholm & Whittington, 2007        | Mo       | Euthynnus affinis, Thunnus thynnus                                    | Gi, Sk                    | SCS          | [80]       |
| *Capsula sp.*                                                            | Mo       | Thunnus thynnus                                                       | Gi                        | SCS          | [80]       |
| *Encotyllabe spari* Yamaguti, 1934                                        | Mo       | Gymnocranus griseus, Plectorhinchus sp.                               | Gi                        | GOT          | [81]       |
| *Megalocotylus latianus* Lebedev, 1970                                    | Mo       | Latjanus latianus                                                     | Gi                        | GOT          | [73]       |
| *Neobenedenia melleni* (MacCallum, 1927) Yamaguti, 1963                   | Mo       | Epinephelus bleekeri, E. coioides, E. malabaricus, Lates calcarifer, Latjanus argentimaculatus | Sk, Fi                    | KH           | [53, 140]  |
| *Neobenedenia sp.*                                                        | Mo       | Rachycentron canadun                                                  | Sk                        | KH           | [53]       |
| *Sessilorhis linopharynx* Mamaev, 1970                                    | Mo       | Platex orbicularis                                                    | Gi                        | GOT          | [81]       |
| *Sprostoniella multitetes* Bychowsky & Nagibina, 1967                     | Mo       | Platex orbicularis                                                    | Gi                        | GOT          | [81]       |
| *Trilobodiscus lutianus* Bychowsky & Nagibina, 1967                       | Mo       | Latjanus argentimaculatus                                             | –                         | GOT          | [43]       |
| *Trochopus antenniae* Egorova & Korotaeva, 1990                           | Mo       | Antignia rubescens                                                   | Gi                        | SCS          | [44]       |
| **Order: Dactylogyridea Bychowsky, 1937**                                 |          |                                                                       |                           |              |            |
| **Family: Ancyrocephalidae Bychowsky, 1937**                              |          |                                                                       |                           |              |            |
| *Ancyrocephalus macrogaster* Yamaguti, 1953                               | Mo       | Gerres filamentosus                                                  | Gi                        | GOT          | [81]       |
| *Ancyrocephalus paraspinicirrus* Mamaev, 1970                            | Mo       | Drepane punctata                                                     | Gi                        | GOT          | [81]       |
| Parasite | Taxa | Hosts | Site of infection | Locality/ies | References |
|----------|------|-------|-------------------|--------------|------------|
| Ancyrocephalus unicirrus | Mo | Pomadasys argenteus | Gi | GOT | [81] |
| Halictrema bilobatum (Yamaguti, 1953) | Mo | Drepane longimana, D. punctata | Gi | GOT | [81] |
| Bychowsky & Nagibina, 1970 | | | | | |
| Halictrema cromileptis Young, 1968 | Mo | Epinephelus bleekeri, E. coioides | Gi | KH | [41, 135] |
| Halictrema epinepheli Yamaguti, 1968 | Mo | Epinephelus bleekeri, E. coioides | Gi | KH | [41, 135] |
| Halictrema geminiotomada Bychowsky & Nagibina, 1971 | Mo | Leinognathus nuchalis | Gi | QN | [88] |
| Halictrema spinicirrus (Yamaguti, 1953) | Mo | Decapterus marnadsi, Drepane punctata | Gi | QN, GOT | [81, 88] |
| Present study | | | | | |
| Ligophorus hamulosus Pan & Zhang in Pan 1999 | Mo | Moolgarda engeli, M. seheli | Gi | QN | [88] |
| Metahaliotrema kulkarnii Venkatarasaiyah, 1981 | Mo | Scathophagus argus | Gi | GOT | [68] |
| Metahaliotrema mizellei Venkatarasaiyah, 1981 | Mo | Scathophagus argus | Gi | QN, GOTH | [68, 88] |
| Metahaliotrema scatophagi Yamaguti, 1953 | Mo | Scathophagus argus | Gi | QN | [68] |
| Metahaliotrema similile Krisky, Nguyen, Ha & Heckman, 2016 | Mo | Scathophagus argus | Gi | QN | [68] |
| Metahaliotrema yamaquatii Mizelle & Price, 1964 | Mo | Scathophagus argus | Gi | QN, GOTH | [68] |
| Metahaliotrema ypsilocleithrum Krisky, Nguyen, Ha & Heckman, 2016 | Mo | Scathophagus argus | Gi | QN, GOTH | [68] |
| Murraytrema pricei Bychowsky & Nagibina, 1977 | Mo | Nibea albiblora | Gi | QN | [88] |
| Paradiplectanotrema trachuri (Kovaleva, 1970) | Mo | Argyrosomus japonicus, Johnius carouuna | St | QN | [88] |
| Gerasov, Gayevskaya & Kovaleva, 1987 | | | | | |
| Platycephalotrema platycephali (Yin & Sproston, 1948) Kritsky & Nitta, 2019 | Mo | Platycephalus indicus | Gi | QN | [88] |
| Proteoactinotylus scapulasserus (Mamaev, 1970) Gusev, 1973 | Mo | Gerres filamentosus | Gi | GOTH | [81] |
| Family: Diplectanidae Monticelli, 1903 | | | | | |
| Calydiscoides flexuosus (Yamaguti, 1953) Young, 1969 | Mo | Nemipterus Japonicus | Gi | QN | [88] |
| Acleotrema nenu (Yamaguti, 1968) Dominques & Boeger, 2007 | Mo | Lates calcarifer | Gi, Sk | KH | [122] |
| Diplectanum sp. | Mo | Plectorhinchus cinctus | Gi | GOT | [81] |
| Laticola latesi (Tripathi, 1959) Yang, Kritsky, Sun, Zhang, Shi & Agrawal, 2006 | Mo | Lates calcarifer | Gi, Sk | KH | [122] |
| Laticola paralatesi (Nagibina, 1976) Yang, Kritsky, Sun, Zhang, Shi & Agrawal, 2006 | Mo | Lates calcarifer | Gi, Sk | KH | [122] |
| Murraytrema pricei Bychowsky & Nagibina, 1977 | Mo | Nibea albiblora | Gi | QN | [88] |
| Paradiplectanum blairense (Gupta & Khanna, 1974) Domingues & Boeger, 2008 | Mo | Sillago japonica, S. sihama | Gi | QN | [88] |
| Pseudorhabdosynochus coioidesis Bu, Leong, Wong, Woo & Foo, 1999 | Mo | Epinephelus bleekeri, E. coioides, E. malabaricus, E. tauvina | Gi | KH | [135] |
| Pseudorhabdosynochus cupatus (Young, 1969) Kritsky & Beverley-Burton, 1986 | Mo | Epinephelus sexfasciatus | Gi | QN | [34] |

(Continued on next page)
| Parasite                                         | Taxa | Hosts                                      | Site of infection | Locality/ies | References |
|--------------------------------------------------|------|--------------------------------------------|-------------------|--------------|------------|
| *Pseudorhabdosynochus epinepheli* (Yamaguti, 1938) | Mo   | *Epinephelus bleekeri, E. bruneus, E. coioides, E. sexfasciatus, E. tauvina* | Gi                | QN, KH      | [34, 135]  |
| *Pseudorhabdosynochus grouperi* (Bu, Leong, Wong, Woo & Foo, 1999) | Mo   | *Epinephelus bleekeri, E. coioides, E. malabaricus, E. tauvina, Lates calcarifer* | Gi                | KH          | [140]      |
| *Pseudorhabdosynochus lantaensis* (Beverley-Burton & Suriano, 1981) | Mo   | *Epinephelus bleekeri, E. coioides, E. malabaricus* | Gi                | KH          | [135]      |
| *Pseudorhabdosynochus serrani* (Yamaguti, 1953) | Mo   | *Epinephelus bleekeri, E. coioides, E. malabaricus* | Gi                | KH          | [135]      |
| *Pseudorhabdosynochus summanoides* | Mo   | *Epinephelus coioides, E. bleekeri* | Gi                | KH          | [135]      |
| *Pseudorhabdosynochus summanae* (Young, 1969) | Mo   | *Epinephelus coioides, E. bleekeri* | Gi                | QN, HP, ND   | [133]      |

**Order: Gyrodactylidea Price, 1943**

| Family: Tetraonchoididae Bychowsky, 1951 |
|------------------------------------------|
| *Paratetraonchoides inermis* Bychowsky, Gussev & Nagibina, 1965 | Mo | *Ichthyscopus lebeck* | Gi | GOT | [35] |
| *Pavlovskioites ichthyoscopei* Bychowsky, Gussev & Nagibina, 1965 | Mo | *Ichthyscopus lebeck* | Gi | GOT | [35] |
| *Pavlovskioites litoralis* Bychowsky, Gussev & Nagibina, 1965 | Mo | *Trachinocephalus myops* | Gi | GOT | [35] |

**Subclass: Polyopisthocotylea Odhner, 1912**

**Order: Mazocraeidea Bychowsky, 1957**

| Family: Allodiscocotylidae Tripathi, 1959 |
|------------------------------------------|
| *Allodiscocotyla chorinemi* Yamaguti, 1953 | Mo | *Caranx sp., Decapterus sp., Scomberoides lysan* | Gi | GOT, SCS | [73, 76, 118] |
| *Allodiscocotyla diacanthi* Unnithan, 1962 | Mo | *Acanthopagrus pacificus, Decapterus sp.* | Gi | QN, GOT, SCS | [73, 76, 93, 118] |
| *Camopia rachycentri* Lebedev, 1970 | Mo | *Rachycentron canadum* | Gi | GOT | [74] |
| *Metacamopia chorinemi* (Yamaguti, 1953) | Mo | *Scomberoides lysan, Selar crumenophthalmus* | Gi | GOT, SCS | [73, 76, 118] |

**Family: Bychowskicotylidae Lebedev, 1969**

| Mo | *Acanthopagrus pacificus* | Gi | QN | [93] |

(Continued on next page)
| Parasite                      | Taxa                        | Hosts                                      | Site of infection | Locality/ies | References |
|------------------------------|-----------------------------|--------------------------------------------|-------------------|--------------|------------|
| *Yamaguticotyla jucunda*     | Mo                          | Pomadasyidae gen. sp.                     | Gi                | GOT          | [74]       |
| *Osphobothrus bychowskyi*    | Mo                          | *Saurida tumbil*                          | Gi                | GOT, SCS     | [83, 114]  |
| *Gastrocotyle indica*        | Mo                          | *Anchoviella sp.*, *Thryssa mystax*       | Gi                | GOT          | [74]       |
| *Gastrocotyle kurra*         | Mo                          | *Decapterus sp.*                          | Gi                | GOT          | [74]       |
| *Gastrocotyle trachuri*      | Mo                          | *Decapterus sp.*, *Salar crumenophthalmus*, *Trachurus trachurus* | Gi | GOT, SCS | [73, 76, 118] |
| *Pseudaxine bivaginalis*     | Mo                          | *Carangoides malabaricus*, *Caranx sp.*, *Decapterus sp.* | Gi | GOT, SCS | [73, 76, 118] |
| *Pseudaxine bychowskyi*      | Mo                          | *Alectis indicus*, *Decapterus sp.*       | Gi                | GOT, SCS     | [72]       |
| *Pseudaxine caballeroi*      | Mo                          | *Alectis indicus*, *Alectis indicus*, *Decapterus sp.* | Gi | QN, GOT, SCS | [73, 76, 88, 118] |
| *Pseudaxine vietnamensis*    | Mo                          | *Caranx sp.*, *Decapterus sp.*, *Salar crumenophthalmus*, *Salaroides leptolepis*, *Seriola dumerili* | Gi | QN, GOT, SCS | [73, 76, 88, 118] |
| *Sibitrema poonui*           | Mo                          | *Auxis thazard*, *Euthynnus affinis*, *T. thynnus* | Gi | SCS | [74, 80] |
| *Gotoctyla laticauda*        | Mo                          | *Scomberomorus commerson*, *S. guttatus*. | Gi                | GOT, SCS     | [72, 73]   |
| *Gotoctyla acanthura*        | Mo                          | *Scomberomorus commerson*, *S. guttatus*. | Gi                | GOT          | [73]       |
| *Heteraxine parva*           | Mo                          | *Gymnocranius griseus*                    | Gi                | GOT          | [73]       |
| *Bicotide perpolita*         | Mo                          | *Pampus argenteus*, *Parastromateus niger* | Gi | GOT, SCS | [69, 81] |
| *Heteraxine heterocerca*     | Mo                          | *Caranx sp.*, *Salar crumenophthalmus*    | Gi, Phc           | GOT          | [69, 81]   |
| *Kannaphallus viridis*       | Mo                          | *Alectis indicus*, *Carangoides malabaricus*, *Otolithes ruber* | Gi | SCS, QB | [73, 76, 118] |
| *Karvolicola ruber*          | Mo                          | *Nibea albiflora*                         | Gi                | QB           | [94]       |
| *Karvolicola tayet*          | Mo                          | *Gymnocranius griseus*                    | Gi                | GOT          | [81]       |

(Continued on next page)
| Parasite Taxa | Hosts | Site of infection | Locality/ies | References |
|--------------|-------|------------------|--------------|------------|
| Monaxine formionis Unnithan, 1957 | Mo | Parastromateus niger | Gi | GOT | [81] |
| **Family: Heteromicrocotylidae Unnithan, 1961** | | | | |
| Heterapta chorinemi (Tripathi, 1956) Unnithan, 1961 | Mo | Acanthopagrus pacificus | Gi | QN | [93] |
| Heteromicrocotyla carangis Yamaguti, 1953 | Mo | Carangoides malabaricus, Seriola sp., Seriolina nigrofasciata, Carangidae gen. sp. | Gi | GOT, SCS | [69, 73, 76, 118] |
| Heteromicrocotyla polyorchis Unnithan, 1961 | Mo | Carangidae gen. sp. | Gi | GOT, SCS | [73, 118] |
| Heteromicrocotyla vaginispina Unnithan, 1961 | Mo | Carangidae gen. sp., Carangoides malabaricus, Decapterus sp., Seriolaides leptolepis | Gi | GOT, SCS | [73, 118] |
| Family: Hexostomatidae Price, 1936 | | | | |
| Hexostoma thynni (Delaroche, 1811) Rafinesque, 1815 | Mo | Auxis thazard | Gi | SCS | [80] |
| Neohexostoma euthynni (Meserve, 1938) Price, 1961 | Mo | Auxis thazard, Euthynnus affinis | Gi | SCS | [80] |
| **Family: Mazocraeidae Price, 1936** | | | | |
| Neomazocraes dorosomatis (Yamaguti, 1938) Price, 1943 | Mo | Clupanodon thrissa | Gi | QN | [88] |
| Parmazocraes thrissocles Tripathi, 1959 | Mo | Thrissocles sp. | Gi | GOT | |
| **Family: Microcotylidae Taschenberg, 1879** | | | | |
| Caballeraxine chaimanica (Lebedev, Parukhin & Roitman, 1970) Lebedev, 1972 | Mo | Carangoides malabaricus | Gi | GOT, SCS | [118] |
| Diplostamenides sciaenae (Goto, 1894) Mamaev, 1986 | Mo | Seriola sp. | Gi | GOT, SCS | [73, 118] |
| Incisaxine dubia Mamaev, 1970 | Mo | Gerres sp. | Gi | GOT | [81] |
| Intracotyle orientalis Mamaev, 1970 | Mo | Pomadasys argenteus | Gi | GOT | [81] |
| Lutianicola haifoniensis Lebedev, 1972 | Mo | Lutjanus russelii, L. sebae | Gi | GOT | [73] |
| Microcotyle sp. | Mo | Carangoides malabaricus | Gi | GOT | [73] |
| Polylabroides cf. guangdongensis Zhang & Yang, 2000 | Mo | Acanthopagrus latus | Gi | QN | Present study |
| Polylabroides tienyenensis Nguyen, Nguyen, Ha, Ngoc, Ngoc, Le, Tatonova & Greiman, 2020 | Mo | Acanthopagrus pacificus | Gi | QN | [93] |
| | Mo | Acanthopagrus pacificus | Gi | QN | [93] |
| | Mo | Acanthopagrus pacificus | Gi | QN | [93] |
| **Family: Plectanocotylidae Monticelli, 1903** | | | | |
| Triglicola tonkinensis Mamaev & Parukhin, 1972 | Mo | Lepidotrigla sp. | Gi | GOT | [84, 119] |
| **Family: Protomicrocotylidae Johnston & Tiegs, 1922** | | | | |
| Bilaterocotyloides carangis Ramalingam, 1961 | Mo | Carangidae gen. sp., Megalaspis cordyla | Gi | GOT, SCS | [73, 118] |
| Bilaterocotyloides madrasensis Radha, 1966 | Mo | Megalaspis cordyla | Gi | GOT | [73, 118] |
| Vallisiopsis contorta Subhapradha, 1951 | Mo | Lactarius lactarius | Gi | GOT, SCS | [74] |
| **Family: Thoracocotylidae Price, 1936** | | | | |
| Pricea muliae Chauhan, 1945 | Mo | Scomberomorus commerson, S. guttatus | Gi | GOT | [73] |

(Continued on next page)
| Parasite                      | Taxa               | Hosts                                      | Site of infection | Locality/ies | References      |
|------------------------------|--------------------|--------------------------------------------|-------------------|--------------|-----------------|
| *Pseudothoracocotyla ovalis* (Tripathi, 1956) | Mo                 | *Scomberomorus commerson*, *S. guttatus* | Gi                | GOT, SCS     | [73, 119]       |
| *Monogenea gen. sp.* | Mo                 | *Abalistes stellaris*                      | Gi                | SCS          | [119]           |
| **Class: Trematoda Rudolphi, 1808** |                    |                                            |                   |              |                 |
| **Subclass: Digenea Carus, 1863** |                    |                                            |                   |              |                 |
| **Order: Diplostomida Olson, Cribb, Tkach, Bray & Littlewood, 2003** |                    |                                            |                   |              |                 |
| **Superfamily: Schistosomatoida Stiles & Hassall, 1898** |                    |                                            |                   |              |                 |
| **Family: Aporocotylidae Odhnner, 1912** |                    |                                            |                   |              |                 |
| *Cardicola congruentus* Lebedev & Mamaev, 1968 | D                  | *Euthynnus affinis*                        | Bvg               | GOT          | [75]            |
| *Cardicola grandis* Lebedev and Mamaev, 1968 | D                  | *Makaira sp.*                              | Iw                | GOT          | [75]            |
| *Cardallagium* cf. *anthicum* (Bullard & Overstreet, 2006) Yong, Cutmore, Jones, Gauthier & Cribb, 2017 | D                  | *Rachycentron canadum*                     | He                | KH           | [141]           |
| **Order: Plagiorchiida La Rue, 1957** |                    |                                            |                   |              |                 |
| **Suborder: Aporocotylida Olson, Cribb, Tkach, Bray & Littlewood, 2003** |                    |                                            |                   |              |                 |
| **Superfamily: Aporocotylidea Skrjabin, 1942** |                    |                                            |                   |              |                 |
| **Family: Aporocotylidae Skrjabin, 1942** |                    |                                            |                   |              |                 |
| *Homalometron* sp. | D                  | *Gerres filamentosus*                      | In                | GOT          | [81]            |
| *Schistorchis skrjabini* Parukhin, 1963 | D                  | *Abalistes stellaris, Triacanthus biaculeatus* | In                | GOT          | [106, 119]      |
| *Sphincteristomum acollum* Oshmarin et al., 1961 | D                  | *Abalistes stellaris*                      | In                | GOT          | [99, 119]       |
| **Suborder: Bivesiculata Olson, Cribb, Tkach, Bray & Littlewood, 2003** |                    |                                            |                   |              |                 |
| **Superfamily: Bivesiculoida Yamaguti, 1934** |                    |                                            |                   |              |                 |
| **Family: Bivesiculidae Yamaguti, 1934** |                    |                                            |                   |              |                 |
| *Bivesicula claviiformis* Yamaguti, 1934 | D                  | *Amphirrion clarkii, A. perideraion; A. polymnus* | S                  | KH           | [27]            |
| *Bivesicula* sp., Metaceraria | D                  | *Amphirrion clarkii, A. perideraion*       | In                | KH           | [142]           |
| *Pancivitelloides vietnamensis* Atopkin, Besprozvannykh, Ngo, Van Ha, Van Tang, Ermolenko & Beloded, 2016 | D                  | *Liza subviridis*                          | In                | GOT          | [20]            |
| **Suborder: Bucephalata La Rue, 1926** |                    |                                            |                   |              |                 |
| **Superfamily: Bucephaloidea Poche, 1907** |                    |                                            |                   |              |                 |
| **Family: Bucephalidae Poche, 1907** |                    |                                            |                   |              |                 |
| *Alicornis baylisi* Nagaty, 1937 | D                  | *Carangoides malabaricus*                  | In                | SCS          | [113]           |
| *Alicornis carangis* MacCallum, 1917 | D                  | *Caranx sp.*                               | In                | GOT, SCS     | [71, 73]        |
| *Bucephalus fragilis* Velasquez, 1959 | D                  | *Megalaspis cordyla, Scomberoides lysan*   | In                | SCS          | [113]           |
| *Bucephalus gorgon* (Linton, 1905) Eckmann, 1932 | D                  | *Seriolina nigrofasciata*                  | S                  | GOT          | [95]            |
| *Bucephalus introversus* Manter, 1940 | D                  | *Seriolina nigrofasciata*                  | In                | SCS          | [118]           |
| *Bucephalus varicus* Manter, 1940 | D                  | *Atropus atropos, Atale mate, Rachycentron canadum, Selar crumenophthalmus* | S, In             | SCS, GOT     | [113, 117, 118] |
| *Bucephalus paraheterotentaculatus* Velasquez, 1959 | D                  | *Seriola dumerili, Seriolina nigrofasciata* | In                | SCS          | [113, 118]      |
| *Bucephalus polymorphus* von Baer, 1827 | D                  | *Lates calcarifer*                         | In                | KH           | [140]           |
| *Bucephalus sp.* | D                  | *Gerres filamentosus*                      | S                  | SCS, GOT     | [81]            |
| *Prosorhynchus epinepheli* Yamaguti, 1939 | D                  | *Epinephelus coioidei, E. bleekeri, E. bruneus, E. malabaricus, E. sexfasciatus, E. tawinya, Latjanus argenticulatus* | In                | KH, QN       | [34, 90, 140]   |

(Continued on next page)
Table 2. (Continued)

| Parasite                          | Taxa                      | Hosts                                      | Site of infection | Locality/ies | References |
|-----------------------------------|---------------------------|--------------------------------------------|-------------------|--------------|------------|
| *Prosorhynchus pacificus* Manter, 1940 | D                         | *Epinephelus bleekeri*, *E. coioides*, *E. malarbaricus* | In                | KH           | [135]      |
| *Prosorhynchus luzonicus* Velasquez, 1959 | D                         | *Epinephelus coioides*                     | S, In, Py         | HP, ND, QN, TH | [132]      |
| *Prosorhynchus tonkinensis* Truong, Palm, Bui, Thy Ngo & Bray, 2016 | D                         | *Epinephelus coioides*                     | S, Py             | ND           | [132]      |
| *Prosorhynchus maternus* Bray & Justine, 2006  | D                         | *Epinephelus coioides*                     | S                 | HP           | [132]      |
| *Prosorhynchus sp. A*²            | D                         | *Epinephelus coioides*                     | S                 | HP           | [132]      |
| *Prosorhynchus sp. B*³            | D                         | *Acanthopagrus latus, Auxis thazard*       | In                | NA, QB, QN SCS | [80, 90]; Present study |
| *Rhipidocotyle laruei* Velasquez, 1959  | D                         | *Psettodes erumei*                         | S, In             | SCS, GOT     | [114, 119] |
| *Rhipidocotyle pentagonum* (Ozaki, 1924 Eckmann, 1932) | D                         | *Auxis thazard, Euthynnus affinis, Thunnus thynnus* | S, In             | SCS          | [95]       |
| *Rhipidocotyle sp.*               | D                         | *Drepane punctata, Ephippus orbis, Gerres filamentosus, Gymnocranius griseus, Leignathus equulus, Parastromateus niger, Leignathidae gen. sp., Sciaenidae gen. sp.* | Gi, Go, In, K, Ve | GOT, SCS   | [81, 95, 133] |
| *Prosorhynchinae* gen. sp.        | D                         | *Epinephelus coioides*                     | In                | QN           | [133]      |
| **Superfamily: Gorgoderoida Looss, 1901** |                           |                                            |                   |              |            |
| **Family: Callostomidae Odhner, 1910** |                           |                                            |                   |              |            |
| *Cholepotes* sp.                  | D                         | *Parapeneus multifasciatus*                | In                | KH           | [27]       |
| **Superfamily: Gymnohorhoroidea Odhner, 1905** |                           |                                            |                   |              |            |
| **Family: Fellodistomidae Nicoll, 1909** |                           |                                            |                   |              |            |
| *Complexobursa* vietnamensis Oshmarin & Mamaev, 1963 | D                         | *Terapon theraps*                          | In                | GOT          | [98]       |
| *Lintonium vixen* (Linton, 1900) Stunkard & Nigrelli, 1930 | D                         | *Abalistes stellaris, Aluterus monoceros, Monacanthus chinesis, Scomberoides lyyan, Scomberomorus commerson* | In, L             | GOT, SCS    | [73, 95, 113] |
| *Proctoeces* sp.                  | D                         | *Acanthopagrus latus*                      | In                | QN           | Present study |
| *Pseudosterigophorus* sp.         | D                         | *Ephippus orbis*                           | In                | GOT          | [81]       |
| *Tergestia laticollis* (Rudolphi, 1819) Stossich, 1899 | D                         | *Alepes melanoptera, Decapterus sp., Megalaspis cordyla, Selar crumenophthalmus, Selaroides leptolepis* | In                | SCS          | [118]      |
| **Family: Tandanicolidae Johnston, 1927** |                           |                                            |                   |              |            |
| *Buckleytemma indicum* Gupta, 1956 | D                         | *Arius sp.*                                | In                | GOT          | [98]       |
| *Monodhelmis torpeditinis* Dollfus, 1937 | D                         | *Arius arius*                              | In                | HP           | [90]       |
| **Suborder: Haplorora Pérez-Ponce de León & Hernández-Mena, 2019** |                           |                                            |                   |              |            |
| **Superfamily: Haplororidea Nicoll, 1914** |                           |                                            |                   |              |            |
| *Parahaploroporus elegans* Atopkin, Besprozvannykh, Ha, Nguyen & Nguyen, 2019 | D                         | *Osteomugil cunnesius*                     | In                | KH           | [23]       |
| *Parasaccocoelium mugil* Zhukov, 1971 | D                         | *Liza haematocheila*                       | In                | QN, HP       | [23]       |
| *Pseudohaploroporus vietnamensis* Atopkin, Besprozvannykh, Ha, Tang, Nguyen, Nguyen & Chalenko, 2018 | D                         | *Moolgarda seheli, Osteomugil engeli*      | In                | GOT          | [22]       |
| Parasite                                | Taxa | Hosts                        | Site of infection | Locality/ies | References |
|----------------------------------------|------|------------------------------|-------------------|--------------|------------|
| *Pseudohaplporus planilizum* Atopkin,  | D    | *Planiliza subviridi*        | In                | GOT          | [22]       |
| Besprozvannikh, Ha, Nguyen, Nguyen &   |      |                              |                   |              |            |
| Chalenko, 2018                         |      |                              |                   |              |            |
| *Pseudohaplporus pusitestis* Atopkin,  | D    | *Moolgarda seheli*           | HP                |             | [23]       |
| Besprozvannikh, Ha, Nguyen & Nguyen,   |      |                              |                   |              |            |
| 2019                                   |      |                              |                   |              |            |
| *Pseudohaplporus* sp.                  | D    | *Moolgarda seheli*           | In                | GOT          | [22]       |
| Skrjabinolecithum spasskii Belous, 1954| D    | *Liza haematocheila, Mugil*  |                   | HP           | [90]       |
|                                        |      | *cephalus*                   |                   |              |            |
| **Suborder:** Haplosplanchnata Olson,   |      |                              |                   |              |            |
| Cribb, Tkach, Bray & Littlewood, 2003  |      |                              |                   |              |            |
| **Superfamily:** Haplosplanchnoidea     |      |                              |                   |              |            |
| Poche, 1925                            |      |                              |                   |              |            |
| **Family:** Haplosplanchnidae Poche,   |      |                              |                   |              |            |
| 1926                                   |      |                              |                   |              |            |
| **Locality:** QQ, 1992                  |      |                              |                   |              |            |
| **Suborder:** Hemirura Skrjabin &       |      |                              |                   |              |            |
| Guschanskaja, 1954                     |      |                              |                   |              |            |
| **Superfamily:** Hemiouroidea Looss,   |      |                              |                   |              |            |
| 1899                                   |      |                              |                   |              |            |
| **Family:** Accacoeliidae Odhner, 1911  |      |                              |                   |              |            |
| *Tetrochetus hansoni* (Parukhin, 1964) | D    | *Aluterus monoceros*         | In                | GOT          | [107]      |
| Hafeezullah, 1982                      |      |                              |                   |              |            |
| *Tetrochetus* sp.                      | D    | *Nemipterus hexodon*         | S                 | KH           | [27]       |
| **Family:** Bathycotylidae             |      |                              |                   |              |            |
| Bathycotyle sp.                        | D    | *Pampus argenteus*           | Gic               | GOT          | [73]       |
| **Family:** Derogeniidae Nicoll, 1910   |      |                              |                   |              |            |
| *Derogenus varicus* (Müller, 1784)     | D    | *Rachycentron canadum,      | S, In             | GOT          | [117, 119] |
| Looss, 1901                            |      | *Triacanthus biaculeatus*    |                   |              |            |
| *Gonocercella pacifica* (Manter, 1940) | D    | *Drepane punctata*           | In                | GOT          | [81]       |
| *Gonocercella* sp.                     | D    | *Atropus atropos,           | In                |              |            |
|                                        |      | *Psettodes erumei, Scomberoides* |       |              |            |
|                                        |      | *lysan*                     |                   |              |            |
| **Family:** Dictycarcididae Skrjabin & |      |                              |                   |              |            |
| Guschanskaja, 1955                     |      |                              |                   |              |            |
| **Locality:** QQ, 1992                  |      |                              |                   |              |            |
| **Family:** Didymozoidae Monticelli,   |      |                              |                   |              |            |
| 1888                                   |      |                              |                   |              |            |
| **Locality:** QQ, 1992                  |      |                              |                   |              |            |
| **Family:** Elopogonorchis pneumatis   | D    | *Arius sp.*                  | Sb                | SCS          | [96]       |
| Rao, 1961                              |      |                              |                   |              |            |
| **Locality:** QQ, 1992                  |      |                              |                   |              |            |
| **Family:** Didymidiclinus epinepheli  | D    | *Scombrids gen. sp.*         | Bc, In            | SCS          | [80]       |
| (Abdul-Salam, 1963)                    |      | *Epinephelus coioides*       |                   |              |            |
| Sreeath & Farah, 1990                   |      |                              |                   |              | [135]      |
| Pozdnyakov, 1994                       |      |                              |                   |              |            |
| Lobatozoum multiscalatum Ishii, 1935    | D    | *Auxis thazard*              | Iw, S, Ve         | SCS          | [80]       |
| **Locality:** QQ, 1992                  |      |                              |                   |              |            |
| Metanematobothriophorus bivistilatum    | D    | *Auxis thazard, Euthynnus*   | Bc, Bvg, L, K     | SCS          | [80]       |
| Mamaev, 1968                           |      | *affinis*                    |                   |              |            |
| Monilicaecium ventricosum Yamaguti, 1942| D    | *Abalistes stellaris,        | Bvg, L            | GOT          | [119]      |
| Mamaev, 1970                           |      | *Psettodes erumei*           |                   |              |            |
| Multitubovarium amphibolum Mamaev, 1970| D    | *Platax orbicularis*         | Gi, Ht            | GOT          | [81]       |
| Nematothorium sp.                       | D    | *Euthynnus affinis, Thunnus* | L, Phc            | SCS          | [80]       |
| Neometadidymozoon polymorphis          | D    | *Thunnus thynnus*            |                   |              | [98]       |
| (Oschmarin & Mamaev, 1963) Yamaguti, 1971| D    | *Priacanthus tayenus*        | Be, Gi, Mu        | GOT          |            |
| Neometanematobothrioides rachycencri   | D    | *Rachycentron canadum*       | Bc, Gi            | GOT, SCS     | [116, 118] |
| (Parukhin, 1969) Yamaguti, 1971         |      |                              |                   |              |            |
| Oesophagocystis dissimilis (Yamaguti,  | D    | *Auxis thazard, Euthynnus*   | O, S, In          | SCS          | [80]       |
| 1938) Yamaguti, 1970                    |      | *affinis, Thunnus*           |                   |              |            |
| Torticaecum fenestratum (Linton, 1907)  | D    | *Psettodes erumei, Triacanthus* |       |              | [119]      |
| Yamaguti, 1942                          |      | *bivaculeatus*               |                   |              |            |

(Continued on next page)
| Parasite                      | Taxa             | Hosts                                                                 | Site of infection | Locality/ies | References |
|-------------------------------|------------------|----------------------------------------------------------------------|------------------|--------------|------------|
| Didymozoidae gen. sp.         | D                | Atule mate, Auxis thazard, Carangoides malabaricus, Echeneis naucrates, Epinephelus coioide, Euthynus affinis, Leiognathus equulus, Psetteodes crumei, Rachycentron canadum, Selar crumenophthalmus, Seriolina nigrofasciata, Thunnus thynnus, Leiognathidae gen. sp. | Be, Ve, Gi, In, K, L | GOT, SCS | [80, 81, 113, 115, 117, 133] |

**Family: Hemiuridae Looss, 1899**

| Allostomachicola secundus (Srivastava, 1939) | D | Chirocentrus dorab | S | GOT | [81] |
| Aphanurus mugilis Tang 1981 | D | Moolgarda engeli | I | HP | [21] |
| Aphanurus stossichii (Monticelli, 1891) | D | Drepane punctata, Ehippus orbis, Pampus argenteus, Thunnus thynnus | S, In | GOT, SCS | [73, 80, 81] |
| Aphanurus sp. | D | Magil sp. | In | GOT | SCS | [80] |
| Dinurus euhynmi Yamaguti, 1934 | D | Auxis thazard, Euthynus affinis, Thunnus sp. | In | GOT | SCS | [113, 118] |
| Dinurus longuisinos Looss, 1907 | D | Carangoides malabaricus | S | GOT | SCS | [19, 111, 113, 118] |
| Dinurus selari Parukhin, 1966 | D | Atropus atropos, Atule mate, Carangoides malabaricus, Decapterus sp., Rachycentron canadum, Selar crumenophthalmus, Selaroides lepotelesis, Carangidae gen. sp. | S, In | GOT, SCS | [34, 73, 112, 113, 118, 121] |
| Dinurus sp. | D | Mene maculata | S | GOT | SCS | [81] |
| Ectenurus selari (Parukhin, 1966) | D | Atule mate, Caranx sp., Epinephelus bruneus, E. coioide, E. sexfasciatus, E. tauvina*, Megalaspi cordyli, Rachycentron canadum, Selar crumenophthalmus, Selaroides lepotelesis, Carangidae gen. sp. | S, In | GOT, SCS | [71, 73] |
| Ectenurus theraponae Oshmarin, 1965 | D | Terapon theraps | S | GOT | SCS | [95] |
| Ectenurus trachuri (Yamaguti, 1934) | D | Caranx sp., Selar crumenophthalmus, | S | GOT, SCS | [19, 111, 113, 118] |
| Ectenurus sp. | D | Pampus argenteus | S | GOT | SCS | [118] |
| Ectenurus sp. | D | Scler crumenophthalmus | S | GOT | SCS | [95] |
| Erilepturus formosae Reid, Coil & Kuntz, 1966 | D | Decapterus sp., Dussumieria elopoides | S | GOT | SCS | [73, 91] |
| Erilepturus hamati (Yamaguti, 1934) | D | Eleutheronema tetradactylum, Epinephelus bleekeri, E. coioide, E. malabaricus, Platyccephalus indicus, Nibeal albilora, Lates calcarifer | S | GOT | SCS | [90, 138] |
| Erilepturus neopaciificus (Velasquez, 1962) | D | Acanthopagrus latus, Sciaenidae gen. sp. | S | GOT, HL | [95]; Present study |
| Elytrophalloides sp. | D | Thryssa mystax | S | ND | [90] |
| Hemurias arelesci Yamaguti, 1938 | D | Scomberoides lysan | S | QN, ND | [88, 90] |
| Lecithichthirium alectis Yamaguti, 1970 | D | Nibeal albilora | S | QN, ND | [88, 90] |
| Lecithichthirium imovacuum (Looss, 1907) | D | Auxis thazard, Euthynus affinis, Ilsha sp., Thunnus thynnus, Thunnus sp. | S | GOT | SCS | [113] |
| Lecithichthirium magnuportor Manter, 1940 | D | Atropus atropos | S | SCS | [113] |
| Lecithichthirium microstomum Chandler, 1935 | D | Atropus atropos | S | SCS | [113] |

(Continued on next page)
| Parasite Class | Taxa | Hosts | Site of infection | Locality/i.e.s | References |
|----------------|------|-------|-------------------|----------------|------------|
| Lecithochirium monticellii (Linton, 1898) | D | Amphiprion clarkia, Atropus atropos, Echeneis naucrates, Salar crumenophthalmus | S | KH, SCS | [27, 113, 115] |
| Skrjabin & Guschanska, 1955 | | | | | |
| Lecithochirium sp. | D | Mene maculata, Seriolina nigrofasciata | S | GOT, SCS | [81, 113] |
| Lecithochirium apolecti Velasquez, 1962 | D | Epiphippus orbis, Gerres filamentosus, Parastromateus niger, Rastrelliger kanagurta, Leiognathidae gen. sp. | S, In | GOT | [73, 81] |
| Lecithochirium excisiforme Cohn, 1902 | D | Alepes melanoptera, Caranx sp., Selaroides leptolepis | S | GOT, SCS | [118] |
| Lecithochirium excisum (Rudolphi, 1819) | D | Alepes melanoptera, Caranx sp., Decapterus maruadsi, Decapterus sp., Eleutheronema tetradactylum, Sardinella sp., Salar crumenophthalmus, Scomberoides kyphos | S | GOT, SCS | [73, 81, 88, 118] |
| L. K., 1901 | | | | | |
| Lecithochirium harpodontis Srivastava, 1942 | D | Atropus atropos, Decapterus sp., Dussumieria elopsoides, Ilisha sp., Salar crumenophthalmus | S | GOT, SCS | [81, 113, 118] |
| Lecithochirium megalaspis Yamaguti, 1953 | D | Megalaspis cordyla | S, In | SCS | [113] |
| Lecithochirium pampi Lebedev, 1968 | D | Pampus argenteus | In | GOT, SCS | [70, 73] |
| Lecithochirium seriolae Manter, 1954 | D | Carangoides melanopterus, Salar crumenophthalmus | S, In | SCS | [113, 118] |
| Lecithochirium sp. | D | Mene maculata | S | GOT | [81] |
| Merlucciotrema praeclarum (Manter, 1934) | | | | | |
| Parahemiurus clupeae Yamaguti, 1971 | D | Herklotsichthys quadridentatus | S | KH | [64] |
| Parahemiurus merus (Linton, 1910) Manter, 1940 | D | Atropus atropos, Decapterus sp., Sardinella sp., Scomberoides kyphos | S, In | GOT, SCS | [81, 118] |
| Parahemiurus sp. | D | Alepes kleinii | S | GON, SCS | [80, 113, 118] |
| Plerurus digitatus (Looss, 1899) Looss, 1907 | D | Auxis thazard, Euthynnus affinis, Thunnus sp., Carangidae gen. sp. | S, In | GON, SCS | [80, 113, 118] |
| Stomachicola muraenesocis Yamaguti, 1934 | D | Congrinos talabonoides | S | GON (QB) | [88, 90] |
| Tubulovesicula angusticauda (Nicoll, 1915) | D | Euphelinus merus, Rachycentron canadum, Trachinoccephalus sp. | S, In | GON, SCS | [64, 95, 118] |
| Yamaguti, 1934 | | | | | |
| Tubulovesicula lindbergi (Rayman, 1930) | D | Echeneis naucrates, Pseiotodes erumei, Carangidae gen. sp. | S | GON, SCS | [115, 118, 119] |
| Yamaguti, 1934 | | | | | |
| Tubulovesicula marsupialis Oshmarin, 1965 | D | Saurotida tumbl | In | GON, SCS | [95] |
| Tubulovesicula sp. | D | Euthynne affinis, Thunnus thynnus, Thunnus thynnus, Thunnus thynnus | S, In | GON, SCS | [80] |
| Hemirimadiidae gen. sp. | | | | | |
| Family: Hirudinellidae Dollfus, 1932 | | | | | |
| Hirudinella ventricosa (Pallas, 1774) Baird, 1853 | D | Euthynnus affinis, Seriolina nigrofasciata, Thunnus thynnus | S | SCS | [80, 113] |
| Family: Lecithasteridae Odhner, 1905 | | | | | |
| Aponurus carangis Yamaguti, 1952 | D | Decapterus sp., Rachycentron canadum, Salar crumenophthalmus | S, In | GON, SCS | [73, 113, 118] |
| Aponurus lapponicus Looss, 1907 | D | Amphiprion polyzona, Atropus atropos, Doplania punctata, Dussumieria elopsoides, Ilisha sp., Leiognathidae gen. sp. | S, In | GON, SCS | [80, 113, 118, 142] |
| Aponurus pyriformis (Linton, 1910) | D | Amphiprion clarckii, Parastromateus niger, Platax orbicularis | In, S | GON, SCS | [81, 142] |
| Overstreet, 1973 | D | Epiphippus orbis, Parastromateus niger | | | |
| Apontus sp. | D | Epiphippus orbis, Parastromateus niger | S | GON, SCS | [133] |

(Continued on next page)
### Table 2. (Continued)

| Parasite                          | Taxa                     | Hosts                                                                 | Site of infection | Locality/ies | References |
|-----------------------------------|--------------------------|----------------------------------------------------------------------|-------------------|--------------|------------|
| *Hysterolecitha nahaensis* Yamaguti, 1942 | D                        | Amphiprion clarkei, A. frenatus, A. perideraion, A. polymopus, Dascyllus trimaculatus | S                 | SCS          | [64, 142]  |
| *Lecithaster mugilis* Yamaguti, 1970     | D                        | Moolgarda engeli, M. seheli, Liza subviridis                        | In                | GOT          | [25]       |
| *Lecithaster stellatus* Looss, 1907     | D                        | Seriolina nigrofasciata                                             | S                 | SCS          | [113]      |
| *Trifoliovarium triacanthi* (Parukhin, 1964) | D                        | Triacanthus biculeatus                                             | In                | GOT          | [108]      |
| **Family: Sclerodistomidae Odhner, 1927** |                           |                                                                      |                   |              |            |
| *Prosogonotrema bilabiatum* Vigueras, 1940 | D                        | Abalistes stellaris, Ephippus orbis, Platax orbicularis             | S                 | GOT          | [81, 107, 119] |
| *Prosogonotrema symmetricum* Oshmarin, 1965 | D                        | Latjanus sp., Pristipomoides typus                                   | S                 | GOT          | [95, 118]  |
| *Prosorchis chainanensis* Lebedev, 1970  | D                        | Ephippus orbis, Pampus argenteus, Parastramaeus niger                | S                 | GOT          | [73, 81]   |
| *Hemiuroidea gen. sp.*              | D                        | Alectis indicus, Gnathanodon species, Megalaspis cordyla, Rachycentron canadum, Seriolina nigrofasciata, Terapon theraps, Carangidae gen. sp. | In                |              |            |
| **Suborder: Lepocreadiata Olson, Cribb, Tkach, Bray & Littlewood, 2003** |                           |                                                                      |                   |              |            |
| **Superfamily: Lepocreadioidea Odhner, 1905** |                           |                                                                      |                   |              |            |
| **Family: Aephnidiogenidae Yamaguti, 1934** |                           |                                                                      |                   |              |            |
| *Aephiphanides barbarus* Nicoll, 1915   | D                        | Pomadasys argenteus                                                 | In                | GOT          | [81]       |
| **Family: Gyliauchenidae Fukui, 1929**  |                           |                                                                      |                   |              |            |
| *Gyliauchen tarachodes* Nicoll, 1970    | D                        | Siganus fuscescens                                                 | In                | HP           | [90]       |
| **Family: Lepocreadiidae Odhner, 1905** |                           |                                                                      |                   |              |            |
| *Diploproctacium drepanei* Mamaev, 1970 | D                        | Drepane punctata                                                    | In                | GOT          | [81, 90]   |
| *Diploproctoidea haustrum* (MacCallum, 1919) | D                        | Alaterus monoceros                                                | In                | QB           | [90]       |
| *Diploproctoidea longipygum* (Oshmarin, Mamaev & Parukhin, 1961) | D                        | Abalistes stellaris                                                | In                | GTh, GOT     | [99]       |
| *Oshmarin, Mamaev & Parukhin, 1961*   | D                        | Platax orbicularis                                                  | In                | GTh, GOT     | [99]       |
| *Diploproctoidea macracetabulum* Oshmarin, Mamaev & Parukhin, 1961 | D                        | Abalistes stellaris, Triacanthus biculeatus                        | In                | GTh, GOT     | [99]       |
| *Diploproctoidea plataxi* Mamaev, 1970 | D                        | Platax orbicularis                                                  | In                | GTh          | [81]       |
| *Diploproctoidea rutellum* (Mamaev, 1970) | D                        | Ephippus orbis, Platax orbicularis                                  | In                | GTh          | [81]       |
| Bray, Cribb & Barker, 1996             | D                        | Echeneis naucrates, Psettodes erumei                                | In, S             | GTh, GOT, SCS | [112, 119] |
| *Hypocreadium cavitum* Bray & Cribb, 1966 | D                        | Abalistes stellaris                                                 | In                | GTh          | [95]       |
| **Hypocreadium scaphosomum** (Manter, 1990) | D                        | Abalistes stellaris, Alaterus monoceros, Triacanthus biculeatus     | In                | GTh, GOT     | [119]      |
| **Bravo Hollis & Manter, 1957**       | D                        |                                                                      |                   |              |            |
| *Hypocreadium sp.*                   | D                        | Abalistes stellaris                                                 |                   | GTh          | [119]      |
| *Lepidapedon megalaspi* Parukhin, 1966 | D                        | Caranxoides malabaricus, Decapterus sp., Megalaspis cordyla, Rachycentron canadum | In                | GTh, SCS     | [112, 113] |
| *Lepocreadium sp.*                   | D                        | Ephippus orbis, Triacanthus biculeatus                              | In                | GTh          | [81, 119]  |
| *Multitestis magnacetabulum* Mamaev, 1970 | D                        | Ephippus orbis, Platax orbicularis                                  | In                | GTh          | [81]       |
| **Neoallolepidapedon fistulariae** (Oshmarin, 1965) | D                        | Fistularia petimba                                                 | S                 | GTh          | [96]       |
| *Opechona formiae* Oshmarin, 1965      | D                        | Pampus argenteus, Parastramaeus niger, Leiognathiidae gen. sp.      | S, In             | GTh          | [73, 95]   |

(Continued on next page)
| Parasite                          | Taxa                      | Hosts                                                | Site of infection | Locality/ies | References |
|----------------------------------|---------------------------|------------------------------------------------------|-------------------|--------------|------------|
| *Trigonotrema alatum* Goto & Ozaki, 1929 | D                         | *Brachiostegus japonicus, Drepane longimana, D. punctata, Ephippus orbis* | In, S             | GOT          | [95]       |
| Lepocreadiidae gen. sp.          | D                         | *Plectonichus cinctus*                               | In                | GOT          | [81]       |

**Superorder: Monorchidia Olson, Cribb, Tkach, Bray & Littlewood, 2003**

**Family: Monorchiidae Olson, 1911**

| Parasite                          | Taxa                      | Hosts                                                | Site of infection | Locality/ies | References |
|----------------------------------|---------------------------|------------------------------------------------------|-------------------|--------------|------------|
| *Alloinfundiburictus cacuminatus* (Nicoll, 1915) | D                         | *Pomadasys argenteus*                                | In, S             | GOT          | [95]       |

**Superfamily: Monorchioida Odhner, 1911**

| Parasite                          | Taxa                      | Hosts                                                | Site of infection | Locality/ies | References |
|----------------------------------|---------------------------|------------------------------------------------------|-------------------|--------------|------------|
| *Alloinfundiburictus cryptostoma* (Oshmarin, 1966) | D                         | *Pomadasys argenteus*                                | In, S             | GOT          | [81]       |

| Parasite                          | Taxa                      | Hosts                                                | Site of infection | Locality/ies | References |
|----------------------------------|---------------------------|------------------------------------------------------|-------------------|--------------|------------|
| *Ancylocelaimus tropicium* (Manter, 1940) Wee, Cutmore, Pérez-del-Olmo & Cribb, 2020 | D                         | *Carangoides malabaricus, Megalaspis cordyla*        | In                | GOT          | [81]       |
| *Hurleytrematoides chaetodoni* (Manter, 1942) Yamaguti, 1954 | D                         | *Chaetodon sp.*                                       | In                | GOT          | [81]       |

**Suborder: Monorchidia Olson, Cribb, Tkach, Bray & Littlewood, 2003**

**Superfamily: Opisthorchioida Loos, 1899**

**Family: Cryptoconidiidae Ward, 1917**

| Parasite                          | Taxa                      | Hosts                                                | Site of infection | Locality/ies | References |
|----------------------------------|---------------------------|------------------------------------------------------|-------------------|--------------|------------|
| *Beluesca plectonichus* (Mamaev, 1970) | D                         | *Plectonichus cinctus*                                | In, S             | GOT          | [81]       |

**Superfamily: Opisthorchioida La Rue, 1957**

| Parasite                          | Taxa                      | Hosts                                                | Site of infection | Locality/ies | References |
|----------------------------------|---------------------------|------------------------------------------------------|-------------------|--------------|------------|
| *Pseudometadena celebesensis* Yamaguti, 1952 | D                         | *Lates calcarifer*                                    | In                | KH           | [140]      |
| *Siphoderina echinostomus* (Oshmarin, Mamaev & Parukhin, 1961) Miller & Cribb, 2008 | D                         | *Pristonichus cinctus*                                 | In                | GOT          | [99]       |
Table 2. (Continued)

| Parasite | Taxa | Hosts | Site of infection | Locality/ies | References |
|----------|------|-------|------------------|--------------|------------|
| *Siphoderina morosovi* (Parukhin, 1965) | D | *Rachycentron canadum* | In | GOT, SCS | [110, 118] |
| Miller & Cribb, 2008 | | *Siphoderina sp.* | D | *Lutjanus argentimaculatus* | In | QB | [90] |
| **Family: Heterophyidae Leiper, 1909** | | | | | |
| *Centrocestus* sp. | D | *Epinephelus coioides* | Mu, Fi | GOT | [133] |
| *Heterophyopsis continua* (Onji & Nishio, 1916) | D | *Epinephelus bleekeri, E. coioides* | Mu, Fi | KH | [130, 135, 137] |
| *Procerovum varium* Onji & Nishio, 1916 | D | *Epinephelus bleekeri, E. coioides* | Mu, Fi | KH | [135] |
| *Heterophyidae gen. sp.* | D | *Epinephelus coioides, Protonibea dicanthus, Sardinella sp.* | In | GOT, SCS | [81, 133]; Present study |
| **Suborder: Pronocephalata Skrjabin, 1955** | | | | | |
| **Superfamily: Paramphistomoidea Fischoeder, 1901** | | | | | |
| *Cleptodiscus* sp. | D | *Triacanthus biauleatus* | In | GOT | [119] |
| **Suborder: Transversotremata Olson, Cribb, Tkach, Bray & Littlewood, 2003** | | | | | |
| **Superfamily: Transversotrematoidea Witenberg, 1944** | | | | | |
| *Transversotrema patialense* (Soparkar, 1924) | D | *Epinephelus bleekeri, E. coioides* | Us | KH, ND | [133, 140] |
| Cruz & Sathanathan, 1960 | | | | | |
| **Suborder: Xiphidiata Olson, Cribb, Tkach, Bray & Littlewood, 2003** | | | | | |
| **Superfamily: Brachycladioidea Odhner, 1905** | | | | | |
| *Acanthocolpus liodorus* Lühe, 1906 | D | *Chirocentrus dorab, Ilisha sp., Sardinella sp.* | Ve | GOT | [82] |
| *Pleorchis haianensis* Shen, 1983 | D | *Johnius caroana, Nibea albiflora, Pennahia argentata* | In | QN, QB | [90] |
| *Pleorchis sciænae* Yamaguti, 1938 | D | *Acanthopagrus berda, Nibea albiflora, Sciaenidae gen. sp.* | In | QN, HP | [90, 95] |
| *Stephanostomum bicornutum* (Stossich, 1883) | D | *Johnius caroana* | In | | |
| Fuhmann, 1928 | | | | | |
| *Stephanostomum ditrenais* (Yamaguti, 1939) | D | *Scomberoides lysan, Seriola dumerili, Seriolina nigrofasciata* | In | SCS, QN, ND | [49, 113] |
| Manter, 1947 | | | | | |
| *Stephanostomum fistulæ* (Yamaguti, 1940) | D | *Fistularia petimba, Harpadon nehereus* | In | GOT, HP | [90, 95] |
| Manter & Van Cleave, 1951 | | | | | |
| *Stephanostomum hispidum* (Yamaguti, 1934) | D | *Seriolina nigrofasciata* | In | SCS | [113] |
| Manter, 1940 | | | | | |
| *Stephanostomum imparispine* (Linton, 1905) | D | *Abalistes stellaris, Aluterus monoceros, Echeneis naucrates, Psettodes erumei, Rachycentron canadum, Seriolina nigrofasciata, Triacanthus biauleatus* | Bc, Gi, In | GOT, GOTH, SCS | [113, 114, 119] |
| Manter, 1940 | | | | | |
| *Stephanostomum orientale* (Srivastava, 1939) | D | *Seriola dumerili, Seriolina nigrofasciata* | In | SCS | [113] |
| Madhavi, 1976 | | | | | |
| *Stephanostomum tenue* (Linton, 1898) | D | *Chirocentrus dorab* | S | GOT | [84] |
| Linton, 1934 | | | | | |
| *Stephanostomum sp.* | D | *Ephippus orbis, Epinephelus coioides, Sciaenidae gen. sp.* | In | GOT | [81, 114, 133] |
| *Tormosolus carangi* Parukhin, 1976 | D | *Carangoides malabaricus* | In, S | SCS | [118] |

(Continued on next page)
| Parasite                        | Taxa                | Hosts                                | Site of infection | Locality/ies | References          |
|--------------------------------|---------------------|--------------------------------------|------------------|--------------|---------------------|
| **Tormopsolus filiformis**     | D                   | Carangoides malabaricus, Rachycentron canadum | In               | GOT, SCS     | [113, 119]          |
| Sogandares-Bernal & Hutton, 1958 |                    |                                      |                  |              |                     |
| **Tormopsolus orientalis**     | D                   | Carangoides malabaricus              | S                | GOT, SCS     | [71, 73, 113]       |
| Yamaguti, 1934                 |                     |                                      |                  |              |                     |
| **Superfamily: Opecoelioidea** |                     |                                      |                  |              |                     |
| Ozaki, 1925                    |                     |                                      |                  |              |                     |
| **Family: Opecoelidae**        |                     |                                      |                  |              |                     |
| Ozaki, 1925                    |                     |                                      |                  |              |                     |
| **Allopodocotyle epinepheli**  | D                   | Drepane punctata                     | In               | GOT          | [81]                |
| Yamaguti, 1942                 |                     |                                      |                  |              |                     |
| **Allopodocotyle sp.**         | D                   | Epinephelus coioides                 | In               | QN, HP       | [133]               |
| Pritchard, 1966                |                     |                                      |                  |              |                     |
| **Cainocreadium labracis**     | D                   | Scorpaenopsis cacopis, Synodus variegatus | S                | KH          | [27]                |
| (Dujardin, 1845)              |                     |                                      |                  |              |                     |
| **Coitoacecum gymnophallum**   | D                   | Acanthopagrus berda, A. latus        | In               | QN, HP       | [90], Present study |
| Nicoll, 1909                   |                     |                                      |                  |              |                     |
| **Helmicemina fasciata**       | D                   | Epinephelus bleekeri, E. coioides, E. malabaricus, E. quoyanus, E. sexfasciatus | In               | GOT, KH     | [34, 90, 139]       |
| Rudolphi, 1819                 |                     |                                      |                  |              |                     |
| **Odher, 1902**                |                     |                                      |                  |              |                     |
| **Helicometra pisodonophi**    | D                   | Pisodonophis cancrivorus             | In               | QN, HP       | [48]                |
| Nguyen Van Ha, 2012            |                     |                                      |                  |              |                     |
| **Helicometrina ninia**        | D                   | Epinephelus sexfasciatus             | In               | QB          |                     |
| Linton, 1910                   |                     |                                      |                  |              |                     |
| **Helicometra sp.**            | D                   | Acanthopagrus latus, Epinephelus coioides | In               | QN          | [133]; Present study |
| **Superfamily: Gorgoderoidea** |                     |                                      |                  |              |                     |
| Looss, 1901                    |                     |                                      |                  |              |                     |
| **Family: Gorgoderidae**       |                     |                                      |                  |              |                     |
| Looss, 1899                    |                     |                                      |                  |              |                     |
| **Phyllodistomum carangis**    | D                   | Scomberoides lysan                   | In               | QN, HP, SCS | [90, 113]           |
| MacCallum, 1913                |                     |                                      |                  |              |                     |
| **Cutmore & Cribb, 2018**      |                     |                                      |                  |              |                     |
| **Phyllodistomum lancea**      | D                   | Acanthopagrus amblycephalus          | In               | QB          | [90]                |
| Mamayev, 1915                  |                     |                                      |                  |              |                     |
| **Phyllodistomum parukhini**   | D                   | Tetrapturus spp., Tetrapturus brachysoma | In               | GOR, SC      | [73, 90]            |
| Yamaguti, 1934                 |                     |                                      |                  |              |                     |
| **Pseudopecoeloides carangis** | D                   | Aleiostoma lamellosiphonophorum      | In               | QN          | [90]                |
| Yamaguti, 1938                 |                     |                                      |                  |              |                     |
| **Phyllodistomum strictum**    | D                   | Parastromateus niger                 | In               | GOT          | [95]                |
| Oshmarin, 1965                 |                     |                                      |                  |              |                     |
| **(Continued on next page)**   |                     |                                      |                  |              |                     |
Table 2. (Continued)

| Parasite                      | Taxa      | Hosts                          | Site of infection | Locality/ies | References |
|-------------------------------|-----------|--------------------------------|-------------------|--------------|------------|
| *Phyllodistomum* sp.          | D         | *Nibea albi-flora*             | Ub                | QN, HP       | [88, 90]   |
| *Xystretrum abalisti* Parukhin, 1963 | D         | *Triacanthus biauculeatus*     | Ub                | GOT          | [19]       |
| **Superfamily: Microphalloidea Ward, 1901** |           |                                |                   |              |            |
| Family: Faustulidae Poche, 1926 |           |                                 |                   |              |            |
| *Paradiscogaster drepanei* Mamaev, 1970 | D         | *Drepane longimana, D. punctata* | In                | GOT          | [81]       |
| **Family: Microphallidae Ward, 1901** |           |                                 |                   |              |            |
| *Microphallus* sp.            | D         | *Parapeneus multifasciatus*     | In                | KH           | [27]       |
| **Family: Zoogonidae Odhner, 1902** |           |                                 |                   |              |            |
| *Plectognathotrema ovatum* Parukhin, 1964 | D         | *Aluterus monoceros*           | In                | GOT, SCS     | [107, 119] |
| **Digenea gen. sp.**          |           |                                 |                   |              |            |
| **Class: Cestoda Rudolphi, 1808** |           |                                 |                   |              |            |
| **Subclass: Eucestoda Southwell, 1930** |           |                                 |                   |              |            |
| **Order: Bothriocephalidea Kuchta, Scholz, Brabec & Bray, 2008** |           |                                 |                   |              |            |
| Family: Bothriocephalidae Blanchard, 1849 |           |                                 |                   |              |            |
| *Bothriocephalus manubriiformis* (Linton, 1889) | C         | *Makaira sp.*                  | In                | GOT          | [73]       |
| **Ariola, 1900**              |           |                                |                   |              |            |
| **Order: Diphyllobothriidea Kuchta, Scholz, Brabec & Bray, 2008** |           |                                 |                   |              |            |
| Family: Diphyllobothriidae Lühe, 1910 |           |                                 |                   |              |            |
| *Diphyllobothrium* sp.        |           | *Alepes melanoptera, Atule mate* | In, Mu            | SCS          | [113]      |
| **Order: Lecanicephalidea Hyman, 1951** |           |                                 |                   |              |            |
| Family: Cephalobothriidae Pintner, 1928 |           |                                 |                   |              |            |
| *Tylodelphalum* sp.           |           | *Epinephelus bleekeri, E. coioides, E. malabaricus, Lates calcarifer* | In                | KH           | [140]      |
| **Order: Onchoproteocephalidea Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014** |           |                                 |                   |              |            |
| Family: Proteocephalidae La Rue, 1911 |           |                                 |                   |              |            |
| *Proteocephalus* sp.          |           | *Lates calcarifer*             | In                | KH           | [122]      |
| **Order: Tetraphyllidea Carus, 1863** |           |                                 |                   |              |            |
| Family: Tetraphyllidea *incertae sedis* |           |                                 |                   |              |            |
| *Scolex* sp.                  |           | *Auxis thazard, Thunnus sp.*   | Bc, L             | SCS          | [80]       |
| **Tetraphyllidea gen. sp. plerocercoid** |           |                                 |                   |              | [19, 73, 81, 119, 133]; Present study |
| Parasite | Taxa | Hosts | Site of infection | Locality/ies | References |
|----------|------|-------|------------------|--------------|------------|
| **Order: Trypanorhyncha Diesing, 1863** | | | | | |
| **Suborder: Trypanobatoida Olson, Caira, Jensen, Overstreet, Palm & Beveridge, 2010** | | | | | |
| **Superfamily: Tentacularioidea Poche, 1926** | | | | | |
| **Family: Tentaculariidae Poche, 1926** | Nybelinia sp. | C | Alectis indicus, Carangoides malabaricus, Caranx sp., Cepola schlegelli, Decapterus muroadi, Decapterus sp., Leiognathus sp., Megalaspis cordyla, Mene maculata, Parastromateus niger, Platix orbicularis, Pomadasys argenteus, Rastrelliger kanagura, Scomberoides lysan, Scomberomorus commerson, S. guatamai, Scorpaenoides sp., Selar crumenophthalmus, Selaroides leptolepis, Selaroides sp., Seriola dumerili, Seriola sp., Seriola nigrofasciata, Triacanthus biaucleatus, Carangidae gen. sp., Leiognathidae gen. sp., Scombrids gen. sp. | Bc, Go, In, K, L, S | GOT, SCS [73, 81, 119, 143] |
| | | | | | |
| | Tentacularia coryphaenae Bosc, 1802 | C | Acanthocybium solandri | SW | HP | Present study |
| **Superfamily: Eutetrarhynchoidea Guiart, 1927** | | | | | |
| **Family: Eutetrarhynchidae Guiart, 1927** | Dollfusiella sp. A⁴ | C | Telatrygon zugei | Sv | HP | Present study |
| | Dollfusiella sp. B | C | Neotrygon kuhlii | Sv | HP | Present study |
| | Oncomegas wageneri (Linton, 1890) Dollfus, 1929 | C | Acanthocepola limbata, Cepola schlegelli, Cepola sp. | Bc | GOT | [81] |
| | Prochristianella sp. | C | Telatrygon zugei | Sv | HP | Present study |
| | Eutetrarhynchidae gen. sp. | C | Chirocentrus dorab, Ilisha sp. | Bc | GOT | [81] |
| **Family: Rhinoptericolidae Carvajal & Campbell, 1975** | Shirleyhynchus cf. butleri Beveridge & Campbell, 1988 | C | Neotrygon kuhlii, Telatrygon zugei | Sv | HP | Present study |
| **Suborder: Trypanoselachoida Olson, Caira, Jensen, Overstreet, Palm & Beveridge, 2010** | | | | | |
| **Superfamily: Lacistorhynchoidea Guiart, 1927** | | | | | |
| **Family: Pterobothriidae Pintner, 1931** | Pterobothrium platycephalum (Shipley & Hornell, 1906) Dollfus, 1930 | C | Mene maculata, Parastromateus niger, Platix orbicularis | Bc | GOT | [81] |
| **Family: Lacistorhynchidae Guiart, 1937** | Grillotia sp. | C | Drepane punctata, Platix orbicularis | Bc | GOT | [81] |
| **Superfamily: Otobothrioidae Dollfus, 1942** | | | | | |
| **Family: Lacistorhynchidae Guiart 1937** | Callitetrarhynchus gracilis (Radophli, 1819) Pintner, 1931 | C | Ausis thazard, Epinephelus coioideus, E. malabaricus, Euthynnus affinis, Thunnus thynnus, Thunnus sp. | S | SCS, KH | [80, 140] |
| **Family: Otobothriidae Dollfus, 1942** | Otobothrium sp. | C | Abalistes stellaris, Aluterus monoceros, Ausis thazard, CepolaBc, Sw, In schlegelli, Cepola sp., Drepane punctata, Ephippus orbis, Gymnocraniu griseus, Leiognathus equula, Leiognathus sp., Parastromateus niger, Platix orbicularis, Pomadasys argenteus, Leiognathidae gen. sp. | Bc, Sw, In | GOT | [80, 81, 119] |

(Continued on next page)
| Parasite | Taxa | Hosts | Site of infection | Locality/ies | References |
|----------|------|-------|------------------|--------------|------------|
| Family: Pseudotobothriidae Palm, 1995 | | | | | |
| Parotobothrium balli (Southwell, 1929) | C | Epinephelus bleekeri, E. coioides, E. malabaricus | S | KH | [135] |
| Trypanorhyncha gen. sp. | C | Abalistes stellaris, Acanthocepoloida limbata, Alectis melanoptera, Aturus monoceros, Atule mate, Carangoides malabaricus, Caranx sp., Cepola schlegeli, Decapterus sp., Echeneis naucrates, Ephippus orbis, Gymnocranius griseus, Mene maculata, Parastromateus niger, Pomadasys argenteus, Psettodes erumei, Rachycentron canadum, Selaroides leptolepis, Carangidae gen. sp. | Bc, Gi, In, Mu | GOT, GOTH, SCS | [19, 81, 109, 113, 115, 117, 119] |
| Cestoda gen. sp. | C | Abalistes stellaris, Alectis indicus, Alectes melanoptera, Atropus atropos, A. oreolatus, Atule mate, Carangoides chrysophrys, C. malabaricus, Caranx sp., Decapterus sp., Echeneis naucrates, Epinephelus coioides, Gnathanodon speciosus, Megalaspis cordyla, Psettodes erumei, Rachycentron canadum, Selar crumenophthalmus, Selaroides leptolepis, Seriola dumerili, Seriolina nigrofasciata, Carangidae gen. sp. | GOTH | | [19, 109, 133] |

Phylum: Nematoda Rudolphi, 1808
Class: Chromadorea Inglis, 1983
Order: Rhabditida Chitwood, 1933
Suborder: Spirurina Railliet & Henry, 1915
Infraorder: Ascaridomorpha De Ley & Blaxter, 2002
Superfamily: Ascaridoidea Baird, 1853
Family: Anisakidae Railliet & Henry, 1912
Anisakis sp. Larvae | N | Abalistes stellaris, Acanthocepoloida limbata, Alectis indicus, Alectes melanoptera, Atropus atropos, A. oreolatus, Atule mate, Aaxis thazard, Carangoides chrysophrys, Carangoides malabaricus, Caranx sp., Cepola schlegeli, Cepola sp., Chirocentrus dorab, Decapterus muroadi, Decapterus sp., Drepane longimana, D. punctata, Dussanieria elopsoides, Echeneis naucrates, Ephippus orbis, Epinephelus bleekeri, E. coioides, E. malabaricus, Euthynnus affinis, Gerres filamentosus, Gerres sp., Gymnocranius griseus, Ilisha sp., Leiognathus equulus, Leiognathus sp., Latj anus russelsii, L. sebae, Makaira sp., Megalaspis cordyla, Mene maculata, Pampus argenteus, Parastromateus niger, Platax orbicularis, Pomadasys argenteus, Psettodes erumei, Rachycentron canadum, Rastrelliger kanagura, Sardinella sp., Scombridae gen. sp., Xiphias sp., Carangidae gen. sp., Chaetodontidae gen. sp., Scombridae gen. sp., Leiognathidae gen. sp. | Bc, Sw, In | GOT, SCS, GOTH | [19, 73, 80, 113, 118, 119, 140] |

(Continued on next page)
| Parasite          | Taxa                     | Hosts                                                                 | Site of Infection | Locality/ies | References |
|-------------------|--------------------------|-----------------------------------------------------------------------|-------------------|--------------|------------|
| Contracaecum sp.  | N                        | Abalistes stellaris, Alectis indicus, Alepes melanoptera, Atropus atropos, Atule mate, Aucis thazard, Carangoides malabaricus, Caranx sp., Decapterus sp., Echeneis naucrates, Euthynnus affinis, Lutjanus russelii, L. sebae, Makaira sp., Megalaspis cordyla, Mene maculata, Pampus argenteus, Parastromateus niger, Platix orbicularis, Psettodes erumei, Rachycentron canadum, Rastrelliger kanagurta, Sardinella sp., Scomberoides lysan, Scomberomorus commerson, S. guttatus, Scomberomorus sp., Selar crumenophthalmus, Selar sp., Selaroides leptolepis, Selaroides sp., Seriola dumerili, Seriola sp., Seriolina nigrofasciata, Thunnus thynnus, Xiphius sp., Carangidae gen. sp., Scombridae gen. sp. | Bc, Sw, In, K | GOT, SCS | [19, 73, 113, 118, 119, 140] |
| **Family: Ascarididae Baird, 1853** | | | | | |
| Porrocaecum sp.   | N                        | Abalistes stellaris, Alectis indicus, Alepes melanoptera, Atropus atropos, Atule mate, Carangoides chrysophrys, C. malabaricus, Caranx sp., Chirocentrus dorab, Decapterus muroadsi, Decapterus sp., Dussumieria elopsoides, Echeneis naucrates, Gnathanodon speciosus, Ilisha sp., Lutjanus lutjanus, L. russelii, L. sebae, Megalaspis cordyla, Pampus argenteus, Psettodes erumei, Rastrelliger kanagurta, Sardinella sp., Scomberoides lysan, Scomberomorus commerson, S. guttatus, Scomberomorus sp., Selar crumenophthalmus, Selar sp., Selaroides leptolepis, Selaroides sp., Seriola dumerili, Seriola sp., Seriolina nigrofasciata, Triacanthus bicusculus, Carangidae gen. sp., Scombridae gen. sp. | Bc, In | GOT, SCS | [73, 81, 109, 113, 119] |
| **Family: Raphidascarididae Hartwich, 1954** | | | | | |
| Hysterothylacium aduncum (Rudolphi, 1802) | N | Epinephelus bleekeri, E. coioides, E. malabaricus | Sw | KH | [135] |
| Hysterothylacium chorinemi (Parukhin, 1966) | N | Atule mate, Scomberoides lysan | In | SCS | [113] |
| Bruce & Cannon, 1989 | | | | | |
| Hysterothylacium incurvum (Rudolphi, 1819) | N | Xiphius sp. | In | SCS | [73] |
| Deardorff & Overstreet, 1980 | | | | | |
| Hysterothylacium saba (Yamaguti, 1941) | N | Scombridae gen. sp. | In | GOT | [73] |
| Deardorff & Overstreet, 1980 | | | | | |
| Hysterothylacium sp. | N | Amphiprion clarkii, A. frenatus, A. polynnus | L | KH | [142] |
| Deardorff & Overstreet, 1980 | | | | | |
| Iheringascaris inquies (Linton, 1901) | N | Rachycentron canadum | In | GOT, SCS | [118] |
| Deardorff & Overstreet, 1980 | | | | | |
| Raphidascaris sp. (Larva) | N | Echeneis naucrates, Epinephelus bleekeri, E. coioides, E. malabaricus | SCS | | [115, 135] |
| **Superfamily: Seuratoidea Hall, 1916** | | | | | |
| **Family: Cucullanidae Cobbold, 1864** | | | | | |
| Cucullanus decapteri Parukhin, 1966 | N | Decapterus sp. | In | SCS | [113] |
| Cucullanus heterochrous Rudolphi, 1802 | N | Psettodes erumei | In | SCS | [114] |
| Parasite                          | Taxa       | Hosts                                      | Site of infection | Locality/ies | References          |
|----------------------------------|------------|--------------------------------------------|-------------------|--------------|---------------------|
| *Cucullanus* sp.                 | N          | *Drepane punctata, Gymnocranius griseus*   | In                | GOT          | [81]                |
| **Infraorder: Gnathostomatoforma De Ley & Blaxter, 2002** |            |                                            |                   |              |                     |
| **Superfamily: Gnathostomatoidea Railliet, 1895** |            |                                            |                   |              |                     |
| *Echinocephalus spinosissimus* (von Linstow in Shipley et Hornell, 1905) | N          | *Abalistes stellaris, Echeneis naucrates* | Io                | SCS, GOT     | [118, 119]          |
| *Echinocephalus* sp.             | N          | *Acanthopagrus latus, Echeneis naucrates, Ilisha sp., Triacanthus biauculeatus,* | In                | GOT, SCS     | [81, 115, 119]      |
| **Infraorder: Spirurina incertae sedis** |            |                                            |                   |              |                     |
| **Superfamily: Dracunculoida Stiles, 1907** |            |                                            |                   |              |                     |
| *Buckleyella* buckleyi Rasheed, 1963 | N          | *Scomberoides lysan*                      | Py                | SCS          | [111, 118]          |
| *Philometra* balistii (Rasheed, 1963) | N          | *Abalistes stellaris*                     | Oe                | GOTH, GOT    | [116, 119]          |
| Vidal-Martínez, Aguirre- Macedo & Moravec, 1995 |            |                                            |                   |              |                     |
| *Philometra spinosa* Vo, 2010 | N          | *Epinephelus coioide*                     | Fi                | KH           | [135]               |
| *Philometra* sp.                | N          | *Abalistes stellaris, Carangoides malabaricus, Caranx sp., Decepterus sp., Epinephelus bleekeri, E. coioide, E. malabaricus, Megalaspis cordyla, Parastromateus niger, Psettodes erumei, Sardinella sp., Triacanthus biauculeatus,* | Op, Fi            | GOT, SCS, QN, KH | [19, 71, 73, 117–119] |
| *Philometroides* atropi (Parukhin, 1966) Moravec & Ergens, 1970 | N          | *Epinephelus coioide*                     | Fi                | ND           | [133]               |
| *Philometroides* sp.            | N          | *Epinephelus coioide*                     | eyes              | HP           | [133]               |
| *Philometroides* atropi (Parukhin, 1966) Moravec & Ergens, 1970 | N          | *Abalistes stellaris*                     | Fi                | KH           | [140]               |
| *Philometroides* sp.            | N          | *Atropus atropos*                        | Bc                | GOTH, SCS    | [112, 113]          |
| *Philometroides* sp.            | N          | *Euthynnus affinis, Rachiocentron canadum* | Bc                | GOTH         | [117]               |
| **Infraorder: Spiruromorpha De Ley & Blaxter, 2002** |            |                                            |                   |              |                     |
| **Superfamily: Camallanoidea Travassos, 1920** |            |                                            |                   |              |                     |
| *Camallanus* sp.                | N          | *Echeneis naucrates, Psettodes erumei*     | In                | GOT, SCS     | [114, 115]          |
| *Procamallanus* (Spirocamallanus) guttatusi (Andrade-Salas, Pineda-López & García-Magaña, 1994) | N          | *Epinephelus bleekeri, E. coioide, E. malabaricus* | In                | KH           | [140]               |
| *Procamallanus* istiblenni (Noble, 1966) Moravec & Sey, 1988 | N          | *Amphipror clarkii, A. frenatus, A. perideraion, A. polynmus* | In                | KH           | [142]               |
| **Superfamily: Habronematoida Ivaschkin, 1961** |            |                                            |                   |              |                     |
| **Family: Cystidicolidae Skrabin, 1946** |            |                                            |                   |              |                     |
| *Ascarophis* sp.                | N          | *Echeneis naucrates, Epinephelus malabaricus, Gymnocranius griseus* | In                | GOT, SCS     | [81, 114, 115, 140] |
| *Ctenascarophis* gastricus Mamaev, 1968 | N          | *Auxis thazard, Euthynnus affinis,*       | In                | SCS          | [80]                |
| *Prospininctes* mollis (Mamaev, 1968) Petter, 1979 | N          | *Auxis thazard, Euthynnus affinis,*       | In                | SCS          | [80]                |
| *Spininctes* echenei Parukhin, 1967 | N          | *Echeneis naucrates*                      | In                | SCS          | [115]               |
| *Spininctes* sp.                | N          | *Auxis thazard*                           | In                | SCS          | [80]                |
| (Continued on next page)
Table 2. (Continued)

| Parasite | Taxa | Hosts | Site of infection | Locality/ies | References |
|----------|------|-------|-------------------|--------------|------------|
| **Superfamily: Physalopteroidea Railliet, 1893** | | | | | |
| **Family: Physalopteridae Railliet, 1893** | | | | | |
| *Cestocephalus petterae* (Le-Van-Hoa, Pham-Ngoc-Khue & Nguyen-Thi-Lien, 1972) Moravec & Justine, 2018 | Polynemus plebeius | In | SCS | [52] |
| *Rasheedia deblocki* (Le-Van-Hoa, Pham-Ngoc-Khue & Nguyen-Thi-Lien, 1972) Moravec & Justine, 2018 | Eleutheronema tetradactylum | In | SCS | [52] |
| **Superfamily: Thelazioidea Skrjabin, 1915** | | | | | |
| **Family: Rhabdochonidae Skrjabin, 1946** | | | | | |
| *Heptochona dorabi* (Mamaev, 1968) Moravec, 1975 | | In | GOT | [81] |
| **Class: Enoplea Inglis, 1983** | | | | | |
| **Subclass: Dorylaimia Inglis, 1983** | | | | | |
| **Order: Trichinellida Hall, 1916** | | | | | |
| **Superfamily: Trichinelloidea Ward, 1907** | | | | | |
| **Family: Capillariidae Railliet, 1915** | | | | | |
| *Capillaria ariusi* (Parukhin, 1989) Arthur & Te, 2006 | Aries sp. | In | GOTH | [119] |
| Capillaria sp. | Acanthopagrus latus, Epinephelus coioides, Gerres filamentosus | In | GOT, SCS | [81] Present study |
| **Pseudocapillaria (Pseudocapillaria) echenei** (Parukhin, 1967) Moravec, 1982 | Echeneis naucrates | In | SCS | [115, 119] |
| Nematoda gen. sp. | Alectis indicus, Alepes melanoptera, Atropus atropos, A. oreolatus, Atule mate, Carangoides chrysophrys, C. malabaricus, Caranx sp., Chirocentrus dorab, Decapterus muroadi, Decapterus sp., Echeneis naucrates, Gnathanodon speciosus, Megalaspis cordyla, Psettodes erumei, Rachycentron canadum, Selar crumenophthalmus, Selar sp., Selaroides leptolepis, Seriola dumerili, Seriolina nigrofasciata, Carangidae gen. sp. | | | |
| **Phylum: Acanthocephala Kohlreuther, 1771** | | | | | |
| **Class: Eoacanthocephala Van Cleave, 1936** | | | | | |
| **Order: Neoechinorhynchidae Ward, 1917** | | | | | |
| **Family: Neoechinorhynchidae Ward, 1917** | | | | | |
| *Neoechinorhynchus ampullata* Amin, Ha & Ha, 2011 | Megalops cyprinoides | In | GOT | [4] |
| *Neoechinorhynchus* (Neoechinorhynchus) ascus Amin, Ha & Ha, 2011 | Moolgarda seheli | In | GOT | [4] |
| *Neoechinorhynchus* (Neoechinorhynchus) arnorpulposinus Amin & Sey, 1996 | Liza subviridis | In | KG | [14] |
| *Neoechinorhynchus* (Neoechinorhynchus) johnii Yamaguti, 1939 | Eleutheronema tetradactylus, Johnius carouna, Johnius sp. Otolithes ruber, Johnius carouna, Nibeal glabella | In | VT, BL, KH, QN, QB | [11] |
| *Neoechinorhynchus* (Neoechinorhynchus) longinculeatus Amin, Ha & Ha, 2011 | Strongylura strongylura | In | GOT | [4] |
| *Neoechinorhynchus* (Neoechinorhynchus) manubriatus Amin, Ha & Ha, 2011 | Johnius carouna, Nibeal glabella | In | GOT | [4] |

(Continued on next page)
| Parasite | Taxa | Hosts | Site of infection | Locality/ies | References |
|----------|------|-------|------------------|--------------|------------|
| Neoechinorhynchus (Neoechinorhynchus) pennahia | A | Pennahia argentata | In | GOT | [4] |
| Neoechinorhynchus (Neoechinorhynchus) plaquensis | A | Clupanodon thrissa | In | HP | [90] |

**Order: Gyracanthocephala Van Cleave, 1936**

**Family: Quadrigyridae Van Cleave, 1920**

- Neoechinorhynchus (Neoechinorhynchus) fusiformis Amin, Ha & Ha, 2011
  - Aria sp.
  - In HP [90]
- Neoechinorhynchus (Neoechinorhynchus) indicus Tripathi, 1959
  - Pomadasys argenteus,
  - In GOT [81]

**Class: Palaeacanthocephala Meyer, 1931**

**Order: Echinorhynchida Southwell & MacFie, 1925**

**Family: Arhythmacanthidae Yamaguti, 1935**

- Heterosentis holospinus Amin, Heckman & Ha, 2011
  - Acanthogyrus fusiformis
  - In SCS, BL [10]
- Heterosentis mongcai Amin, Heckmann & Ha, 2014
  - Acanthogyrus indicus Tripathi, 1959
  - Pomadasys argenteus,
  - In QN [5]
- Heterosentis paraholospinus Amin, Heckmann & Ha, 2018
  - Acanthogyrus paraholospinus
  - In QN [7]

**Family: Cavisomidae Meyer, 1932**

- Filisoma indicum Van Cleave, 1928
  - Scatophagus argus
  - In KG [7]
- Neorhadinorhynchus arctica Amin & Ha, 2011
  - Sigania fuscescens
  - In NA [3]
- Neorhadinorhynchus nudum (Harada, 1938) Yamaguti, 1939
  - Auxis thazard, Decapterus sp., Euthynnus affinis, Thunnus thynnus
  - In KH, SCS [9, 80, 119]

**Family: Echinorhynchidae Cobbold, 1879**

- Echinorhynchus sp.
  - Amphiprion clarkii
  - In KH [142]

**Family: Paracanthocephalidae Golvan, 1960**

- Acanthocephalus halongensis Amin & Ha, 2011
  - Decapterus kurroides
  - In NA [3]

**Family: Rhadinorhynchidae Lühe, 1912**

- Australorhynchus multipinosus Amin, Heckmann & Ha, 2018
  - Fistularia petimba
  - In KH [12]
- Cathayacanthus spiniruncatus Amin, Heckmann & Ha, 2014
  - Leiognathus equulus, Nuchequula flavaxilla
  - In HP, QN [50]
- Gorgorhynchus medius (Linton, 1908) Chandler, 1934
  - Selar crumenophthalmus
  - In BC, Io GOT [118]
- Gorgorhynchus tonkinensis Amin & Ha, 2011
  - Decapterus kurroides
  - In GN [3]
- Gorgorhynchus sp.
  - Abalistes stellaris
  - In GN [119]
- Micracanthorhynchina kawaiensis Amin & Sey, 1996
  - Strongyura strongylura
  - In GN [3]
- Rhadinorhynchus carangis Yamaguti, 1939
  - Carangoides malabaricus
  - In GOT, SCS [73, 118]
- Rhadinorhynchus circumsinus Amin, Rubtsova & Nguyen, 2019
  - Triacanthus bicaeleatus
  - In HP [13]
- Rhadinorhynchus ditrematii Yamaguti, 1939
  - Decapterus sp.
  - In GOT, GOTH, SCS [71, 73]
- Rhadinorhynchus doroventrospinosis Amin, Heckmann & Nguyen Van Ha, 2011
  - Decapterus maruadsi
  - In QN [6]

(Continued on next page)
| Parasite                                      | Taxa | Hosts                                      | Site of infection | Locality/ies | References |
|----------------------------------------------|------|--------------------------------------------|-------------------|--------------|------------|
| Rhadinorhynchus hiansi Soota & Bhattacharya, 1981 | A    | Sarda orientalis                           | –                 | KH           | [16]       |
| Rhadinorhynchus johnston Golvan, 1969         | A    | Cyprinodorus hexazona                      | –                 | QB           | [7]        |
| Rhadinorhynchus laterospinosus Amin, Heckmann & Nguyen Van Ha, 2011 | A    | Alectis ciliaris, Auxis rochei, A. thazard, Balistes sp., Harpodon neheures, Leiosgnathus equulus, Latijanus biatiaeniatus, Megalaspis cordyla, Nucchqua flavaxilla, Tylosurus sp. | In                | QN, HP, BT  | [6, 15]    |
| Rhadinorhynchus multispinosus Amin, Rubtsova & Ha, 2019 | A    | Decapteres maruadsi                        | In                | HP           | [13]       |
| Rhadinorhynchus pacificus Amin, Rubtsova & Ha, 2019 | A    | Auxis thazard                              | In                | HP           | [13]       |
| Rhadinorhynchus pristis (Rudolph, 1802)      | A    | Carangoides malabaricus                    | In                | GOT, SCS    | [73, 118]  |
| Rhadinorhynchus trachuri Harada, 1935        | A    | Auxis thazard, Megalaspis cordyla, Tylosurus sp | In                | KH, BT      | [2]        |
| Family: Transvenidae Pichelin & Cribb, 2001  | A    | Scataphagus argus                          | In                | GOT         | [50]       |
| Pararhadinorhynchus magnus Van Ha, Amin, Ngo & Heckmann, 2018 | A    | Siganus guttatus                           | In                | KH          | [12]       |
| Sclerocollum neorubrimaris Amin, Heckmann & Ha, 2018 | A    | Echeneis naucrates, Psettodes erumei       | GOT               |             | [109]      |
| Family: Isthosacanthidae Smales, 2012        | A    | Abalistes stellaris, Atropus atropos, Carangoides malabaricus, Echeneis naucrates, Euthynnus affinis, Gerres filamentosus, Gerres sp., Gymnoconrus griseus, Latijanus russelli, Pomadasys argenteus, Rachycytron cacadum, Sardinella sp., Scomberoides lysan, Trachurus declivis, Tricantus bianculeatus | Py, In, Bc        | GOT, Goth, SCS | [71, 73, 80, 81, 113, 118, 119] |
| Phyllum: Annelida Lamarck, 1809              | A    | Echeneis naucrates                         | GOT               |             | [109]      |
| Class: Clitellata Michaelsen, 1919           | H    | Lates calcarifer                           | Gi, Sk            | KH          | [122]      |
| Order: Rhyynchobellida Blanchard, 1894       | H    | Epinephelus bleeki, E. coioide, E. malabaricus, Lates calcarifer, Latijanus argentinmaculatus | Sk                |             | [139]      |
| Family: Piscicolidae Johnston, 1865          | H    |                                           |                   |             |            |
| Piscicola sp.                                |      |                                           |                   |             |            |
| Zeylanicobella arugamensis de Silva, 1963    | H    |                                           |                   |             |            |
| Phyllum: Arthropoda von Siebold, 1848        | Cr   | Epinephelus coioide, E. malabaricus        | Gi                | KH          | [139]      |
| Subphylum: Crustacea Brünnich, 1772          | Cr   |                                           |                   |             |            |
| Class: Hexanauplia Oakley, Wolfe, Lindgren & Zaharof, 2013 | Cr   |                                           |                   |             |            |
| Subclass: Copepoda Milne Edwards, 1840       | Cr   |                                           |                   |             |            |
| Order: Cyclopoida Burmeister, 1834           | Cr   |                                           |                   |             |            |
| Family: Ergasilidae Burmeister, 1835         | Cr   |                                           |                   |             |            |
| Ergasilus sp.                                |      |                                           |                   |             |            |
| Order: Siphonostomatoida Burmeister, 1835    | Cr   |                                           |                   |             |            |
| Family: Caligidae Burmeister, 1835           | Cr   |                                           |                   |             |            |
| Acanthocephala sp.                           |      |                                           |                   |             |            |

(Continued on next page)
| Parasite                          | Taxa | Hosts                                  | Site of infection | Locality/ies | References        |
|----------------------------------|------|----------------------------------------|-------------------|--------------|-------------------|
| Caligus arii Bassett-Smith, 1898 | Cr   | Arius sp                               | –                 | –            | [60]              |
| Caligus bonito Wilson, 1905      | Cr   | Euthynus affinis                       | –                 | –            | [61]              |
| Caligus confusus Pillai, 1961    | Cr   | Abalistes stellatus, Decapterus sp.    | Gi                | GOT          | [61]              |
| Caligus constrictus Heller, 1865 | Cr   | Decapterus sp.                          | Gi                | GOT          | [61]              |
| Caligus epidemics Hewitt, 1971   | Cr   | Epinephelus bleekeri, E. coioides, E. malabaricus, E. tawina, Lates calcarifer | Sk               | KH           | [122, 136]        |
| Caligus fortes Kabata, 1965      | Cr   | Abalistes stellatus                    | –                 | –            | [61]              |
| Caligus multispinosus Shen, 1957 | Cr   | Pampus argenteus                       | –                 | –            | [61]              |
| Caligus pelamys Krøyer, 1863     | Cr   | Sphyraena jello                        | –                 | –            | [61]              |
| Caligus robustus Bassett-Smith, 1898 | Cr    | Epinephelus bleekeri, Decapterus sp. | Gi                | GOT          | [61]              |
| Caligus stromatei Krøyer, 1863   | Cr   | Epinephelus bleekeri, E. coioides, E. malabaricus, E. tawina, Lates calcarifer | Gi               | KH           | [122, 136]        |
| Caligus sp.                      | Cr   | Acanthopagrus latus, Epinephelus bleekeri, E. coioides | Gi               | KH, QN       | [133, 140] Present study |
| Caligodes laciniatus (Krøyer, 1863) | Cr | Ablennes hians                        | –                 | –            | [61]              |
| Hermilius pyrventris Heller, 1865 | Cr | Unidentified Marine catfish           | –                 | –            | [61]              |
| Mappates platatus Rangnekar, 1958 | Cr | Platys tetra, Sarda sp.                | –                 | –            | [61]              |
| Lepeophtheirus arypicus Lin, Ho & Chen, 1996 | Cr | Siganus fuscescens                   | –                 | –            | [61]              |
| Lepeophtheirus longipalpus Bassett-Smith, 1898 | Cr | Arius acutirostris              | –                 | –            | [61]              |
| Lepeophtheirus sp.               | Cr   | Epinephelus tawina*                   | Sk               | GOT          | [34]              |
| Parapetalus hirsutus (Bassett-Smith, 1898) | Cr | Eleytheronema tetradactylum          | –                 | –            | [61]              |
| Parapetalus occidentalis Wilson, 1908 | Cr | Sphyraena jello                      | –                 | –            | [61]              |
| Synocaligus formicoides (Redkar, Rangnekar et Murti, 1949) | Cr | Dussumieria elopoides                | –                 | –            | [61]              |
| Synestius caliginus Steenstrup et Lutken, 1861 | Cr | Parastromateus niger                 | –                 | –            | [61]              |
| Parapetalus sp.                  | Cr   | Rachycentron canadum                 | Gi               | KH           | [53]              |
| **Family: Hatschekidae Kabata, 1979** |     |                                         |                   |              |                   |
| Hatschekia foliulata Redkar, Rangnekar & Murti, 1950 | Cr | Parastromateus niger, Nemipterus peronii | Gi               | GOT          | [61]              |
| Hatschekia hanguyenwani Kovaleva, Nguyen et Ngo, 2017 | Cr | Unidentified marine host            | –                 | –            | [61]              |
| Hatschekia rotundigenitalis Yamaguti, 1939 | Cr | Amphiprion polymnus                  | Gi               | KH           | [142]             |
| Hatschekia sp.                   | Cr   | Congroesox talabonoides              | –                 | –            | [61]              |
| Pseudocongricerola sp.           | Cr   |                                         |                   |              |                   |
| **Family: Kroyeriidae Kabata, 1979** |     |                                         |                   |              |                   |
| Kroyeria spatulata Pearse, 1948 | Cr   | Carcharhinus sorrah                   | –                 | –            | [61]              |
| **Family: Lernaeopodidae Milne Edwards, 1840** |     |                                         |                   |              |                   |
| Charopinopsis quaternia (Wilson C.B., 1935) | Cr | Scomberoides lysan                   | –                 | –            | [61]              |
| Parabrachiella trichuri (Yamaguti, 1939) | Cr | Lutjanus erythrolepturus         | Gi               | GOT          | [61]              |
| Neobrachiella sp.                | Cr   | Valamugil engeli                     | –                 | –            | [61]              |
| Naobranchia sp.                  | Cr   | Gerres filamentus                    | –                 | –            | [61]              |
| **Family: Lernanthropidae Kabata, 1979** |     |                                         |                   |              |                   |
| Chauvania chauvani Kazatchenko, Kovaleva, Nguyen and Ngo, 2017 | Cr | Alepes melanoptera                  | Gi               | GOT          | [61]              |

(Continued on next page)
| Parasite                       | Taxa                          | Hosts                                      | Site of infection | Locality/ies | References |
|-------------------------------|-------------------------------|--------------------------------------------|-------------------|--------------|------------|
| Lernanthropus alatus Pillai, 1964 | Cr                            | Alipes melanoptera, Caranx sp., Decapterus sp. | –                 | –            | [61]       |
| Lernanthropus carangis Pillai, 1964 | Cr                            | Upeneus sulphureus                        | –                 | –            | [61]       |
| Lernanthropus chirocentrosus Tripathi, 1959 | Cr                            | Chirocentrus dorab                        | –                 | –            | [61]       |
| Lernanthropus cornutus Kirtisinghe, 1937 | Cr                            | Ablennes hians                            | –                 | –            | [61]       |
| Lernanthropus franci Nunes-Ruivo, 1962 | Cr                            | Larimichthys croceus                      | –                 | –            | [61]       |
| Lernanthropus laitis Yamaguti, 1954 | Cr                            | Lates calcarifer                          | Gi                | KH           | [140]      |
| Lernanthropus laplaceus Wilson, 1912 | Cr                            | Eleutheronema tetradactylum, Arius maculatus | –                 | –            | [61]       |
| Lernanthropus opisthopteri Pillai, 1964 | Cr                            | Bisha elongata                            | –                 | –            | [61]       |
| Lernanthropus otolithi Pillai, 1963 | Cr                            | Johnius carouna                           | –                 | –            | [61]       |
| Lernanthropus polyenmi Richardi, 1881 | Cr                            | Unidentified host                        | –                 | –            | [61]       |
| Lernanthropus sanguineus Song, 1976. | Cr                            | Latjanus johnii                           | –                 | –            | [61]       |
| Lernanthropus trifoliatus Bassett-Smith, 1898 | Cr                            | Arius maculatus, Arius sp., Polydactylus sextarius | –                 | –            | [61]       |
| Lernanthropus villiersi Delamare-Deboutteville et Nunes-Ruivo, 1954 | Cr                            | Gerres filamentosus                       | –                 | –            | [61]       |
| Lernanthropus decapertii (Pillai, 1964) Pillai, 1967 | Cr                            | Decapterus maruadsi, Elisha filigera      | –                 | –            | [61]       |
| Lernanthropus gibbosus (Pillai, 1964) | Cr                            | Saurida tumbil                            | –                 | –            | [61]       |
| Lernanthropus sphyraenae (Yamaguti et Yamasu, 1959) | Cr                            | Mene maculata                             | –                 | –            | [61]       |
| Sagum sanguineus (Song, 1976) | Cr                            | Latjanus johnii                           | –                 | –            | [61]       |
| Sagum vietnamiensis Kazachenko, Kovaleva, Nguyen and Ngo, 2017 | Cr                            | –                                          | Gi                | GOT          | [61]       |

**Family: Pseudocycnidae Wilson C.B., 1922**

| Cybicola armatus (Bassett-Smith, 1898) Kensley et Grindley, 1973 | Cr | Sphyraena jello, Euthynnus alletteratus, Scomberomorus commerson | – | – | [61] |
| Pseudocycnus appendiculatus Heller, 1865 | Cr | Auxis thazard, Euthynnus affinis, E. alletteratus | – | – | [61] |

**Family: Trebiidae Wilson C.B., 1905**

| Trebius elongatus Capart, 1953 | Cr | Taeniura meyeni | – | – | [61] |

**Class: Malacostraca Latreille, 1802**

**Order: Isopoda Latreille, 1817**

| Alcirona sp. | Cr | Epinephelus coioides | Sk | QN, HP | [133] |
| Corallana sp. | Cr | Epinephelus taivuna* | Sk | GOT  | [34] |

**Family: Cymothoidae Leach, 1818**

| Ceratothoa verrucosa (Schioedte & Meinert, 1883) | Cr | Epinephelus coioides | Gi | KH | [135] |

**Family: Gnathiidae Leach, 1814**

| Gnathia sp. | Cr | Epinephelus bleeki, E. coioides | Gi | KH | [133, 140] |
| Gnathiidae gen. sp. | Cr | Epinephelus coioides | Gi | GOT | [133] |

1. This species has not been registered in WoRMS and not confirmed by international experts.
2. *Prosorhynchus* sp. A & *Prosorhynchus* sp. B have not been identified, but they are distinct based on some morphological characters.
3. This species has not been confirmed by international experts.
4. *Dollfusiella* sp. A and B were not identified to species level, but it was possible to distinguish them based on morphology.
5. Temporary name: This species has not been registered in WoRMS and not confirmed by international experts.
6. *Philometra* sp. 1 and 2 were not fully identified, but it was possible to distinguish them based on morphology.
Parasite composition and proportion in marine fish of Vietnam

The present results showed that the proportion of marine fish parasites observed in Vietnam is similar to that previously described in Hawaiian waters ([103]; Fig. 2b). As mentioned, the proximity of the latitudinal range between Vietnam and Hawaii might be the reason for such similarities in the proportion of the parasite taxa.

Digenea and Monogenea were the most common taxa, accounting for 43% and 23.5% of Vietnam’s total marine fish parasite fauna, respectively. The overall taxon proportions are similar to those found in Hawaii, except for Nematoda and Acanthocephala, which were higher in Vietnam than in Hawaii (7.4% and 7.4% in Vietnam vs. 3.1% and 1.4% in Hawaii, respectively). Many factors can influence the richness of these two parasite taxa, e.g., the zooplankton (e.g., Copepoda, Amphipoda), which may act as intermediate hosts for Nematoda and Acanthocephala and were reported to be more diverse and abundant in Vietnam than in Hawaii [56, 87]. Furthermore, since acanthocephalans use amphipods or ostracods more frequently as intermediate hosts, they are abundant in shallow waters in Ha Long Bay but not on the Hawaiian coast [56, 87]; these parasites are typically found in benthic and bentholgalic fish final hosts [54]. As a result, when compared to the 2006 list, 29 additional acanthocephalans have been added to the current local list [3–13, 50], 22 of which are new parasite species that have never been recorded anywhere other than Vietnam. Those 22 species are Acanthocephalus halongensis Amin & Ha, 2011; Acanthohyrax (Acanthosentis) fusiformis Amin, Chaudhary, Heckmann, Ha & Singh, 2019; Neoechinorhynchus amplulata Amin, Ha & Ha, 2011; Neoechinorhynchus ascus Amin, Ha & Ha, 2011; Neoechinorhynchus longinucleatus Amin, Ha & Ha, 2011; Neoechinorhynchus manubriatus Amin, Ha & Ha, 2011; Neoechinorhynchus pennatius Amin, Ha & Ha, 2011; Neoechinorhynchus plaquensis Amin, Ha & Ha, 2011; Heterosentis hokosinus Amin, Heckmann & Ha, 2011; Heterosentis mongol Amin, Heckmann & Ha, 2014; Heterosentis paraholosinus Amin, Heckmann & Ha, 2018; Australorhynchus multispinosus Amin, Heckmann & Ha, 2018; Cathayacanthus spinuruncatus Amin, Heckmann & Ha, 2014; Rhabdorhynchus circumspinosus Amin, Rubtsova & Nguyen, 2019; Rhabdorhynchus doroventrospinosus Amin, Heckmann & Ha, 2011; Rhabdorhynchus laterospinosus Amin, Heckmann & Ha, 2011; Rhabdorhynchus pacificus Amin, Rubtsova & Ha, 2019; Rhabdorhynchus multispinosus Amin, Rubtsova & Ha, 2019; Neorhabdinorhynchus atypicus Amin & Ha, 2011, Pararhabdinorhynchus magnus Ha et al., 2018; Gorgorhynchus tonkinensis Amin & Ha, 2011, and Sclerocollum neobrinaris Amin, Heckmann & Ha, 2018.

These findings suggest that prior to 2006, acanthocephalans were neglected in the parasitological studies regarding marine fish from Vietnam.

To date, it is known that the Cestoda, particularly the orders Trypanorhyncha and Tetraphyllidea, are found in a wide range of marine fish species worldwide [101, 103]. They are tapeworms from elasmodbranchs that have been considered excellent indicators of host ecology [105]. In Vietnam, cestodes accounted for only 3.4% of the total parasite fauna in marine fish (17 out of 498 species; Fig. 2a), a much lower proportion than in Hawaii (9.2% represented by 60 species; [103]; Fig. 2b); this could be because of a lack of definitive hosts (elasmodbranchs) due to shallow waters or, more likely, a lack of research interest in these parasites in Vietnam.

The hirudinean parasites were in very low proportion compared to other parasite taxa. These annelids have one of the largest body sizes among the groups of parasites in marine fish and are well known to be pathogenic in farmed finfish [40]. Moreover, hirudineans occur mainly in freshwater [134] which may explain their low proportion of occurrence in marine fish observed here (0.4%; Fig. 2a). This low proportion was also observed by Palm and Bray [103] in Hawaiian waters (0.5%; Fig. 2b).

In comparison to data from Hawaii [103], Crustacea were found in similar proportions in Vietnamese marine fish (11.6% vs. 10.3%; Fig. 2a), but Myxozoa proportions were higher (1.6% vs. 0.9%), and no Ciliophora were found in Hawaii, while there was 1.6% in Vietnam. However, myxozoans have recently been reported in a low proportion in Vietnamese marine waters (0.09% equal to 2 species) when compared to other groups. However, Mackenzie and Kalavati [79] reported 223 myxosporean parasites from North Pacific marine fish, identifying them as one of the most common parasite groups in marine fish [79]. Thus, the true diversity of myxozoans in Vietnam is expected to be much higher than the current findings. The lack of information and data for this group could be attributed to rudimentary sampling methods and a lack of well-trained personnel to investigate this parasite group. Similarly, the Ciliophora, a worldwide distributed parasite of aquatic teleosts, was only found in small numbers. Depending on their host species, this taxon can range from harmless ectocommensals to dangerous parasites in fish aquaculture [79]. Bui [34] and Phan [121] reported Ciliophora as parasites causing disease in Vietnam’s finfish mariculture. These parasites that infected marine fish in Vietnam were mostly likely reported as multi-species groups (e.g., Trichodina spp.), making identification difficult. This means that the actual number of ciliates in Vietnamese marine waters may be much higher than the eight species found so far.

Parasitic crustacean species accounted for 11.6% of total marine fish parasites reported in Vietnam thus far, slightly higher than the figure found in Hawaiian marine waters (10.3%; Fig. 2). This parasite group has been identified as the most diverse and widespread subphylum of arthropods in marine fish [29, 126]. They have also been identified as critical pathogenic agents of cultured marine fish in the Asian-Pacific region [77]. Given the critical role that disease control plays in ensuring the success of aquaculture, further research on parasites is both necessary and warranted.

Parasite composition and proportion in the Gulf of Tonkin

The current study presents 330 marine fish parasite species in the GOT. They are classified into eight taxa, Myxozoa (3), Ciliophora (3), Monogenea (89), Digenea (168), Cestoda (11), Nematoda (19), Acanthocephala (29), and Crustacea (8), demonstrating a high number and rich species composition in the GOT. The parasite richness in the GOT may be influenced
by several factors, including geographical latitude, the environment, and the availability of intermediate hosts [55, 85]. The GOT is in South-East Asia, a region with a diverse range of parasites and hosts [125, 126], including the first intermediate host, mollusks [91], which may be the primary factor affecting endoparasite diversity, such as the digeneans (168 species) we discovered here. However, the GOT’s shallow water depth and muddy sediment limit the distribution of open-water

Figure 1. A map of Vietnam with abbreviated names of municipalities, provinces, and sea or ocean areas where samples were collected.
elasmobranchs (e.g., sharks and rays), the expected final hosts of marine Cestoda, particularly Trypanorhyncha (Fig. 3). As a result, only seven Trypanorhyncha species have been identified in the GOT so far.

Most of the recorded marine parasite species in Vietnam (66.3%) have been found in the GOT, indicating that the GOT is a hotspot for interested collectors and institutions supporting research due to its high parasite biodiversity. However, apart from its natural biodiversity, most parasitological research may be concentrated in the GOT due to the urgency of fish disease research serving the high-density aquaculture area in the GOT or because conducting research here is more convenient than in other regions. The composition related to the parasite fauna in the GOT was generally similar to that of all Vietnamese marine environments (Figs. 2a and 3a). Digenea were proportionally the taxon in the GOT with the highest species richness (51%; Fig. 3a). This proportion in the GOT was higher than that observed for the whole of Vietnam (this study; Fig. 2a) and similar to that reported in Hawaii [103], Fig. 2b). A possible explanation for the previous results relates to the environmental features of the GOT, i.e., muddy and shallow waters with rocky and limestone substrates [89, 120] which support an abundant fauna of mollusks that act as intermediate hosts for digenetic trematodes. This is also consistent with the findings of Sujatha and Madhavi [128] and Bray et al. [31], which indicated that the Digenea were typically shallow-water parasites.

Other major parasite groups in the GOT reported in this study (Fig. 3a) include Monogenea (27%), Acanthocephala (8.8%), Nematoda (5.8%), Cestoda (3.3%), Crustacea (2.4%), Ciliophora (0.9%), and Myxozoa (0.9%). It is worth noting that, of the 330 species of marine fish parasites discovered in the GOT, up to 235 species (71%) are found only here and nowhere else in Vietnam (Fig. 3b). For example, the current effort revealed that up to 21/29 acanthocephalans are found only in the GOT (Fig. 3b), suggesting that they are GOT native species.

The parasite-host ratio of 2.7 was calculated based on a total of 330 parasite species that have been recorded in 122 marine fish species in the GOT. This ratio is higher than the average for Vietnamese marine water (2.2), Hawaii (2.2), New Caledonia (1.9), and the Indo-West Pacific (1.7) [58, 103, 126]. Since the GOT is thought to have around 928 marine fish species [144], only a tiny portion of the fish species has been

Figure 2. Proportion (%) of (a) the recorded fish parasite species in Vietnam (498 species, present study), and (b) fish parasites species in Hawaii (652 species [103]).

Figure 3. Marine fish parasites in the Gulf of Tonkin: (a) Proportion of the total recorded fish parasite species (%), and (b) Composition (species richness) of parasite species only found in the Gulf of Tonkin.
examen for parasites (13.1%), indicating that more attention needs to be paid to exploring the region’s high diversity of marine fish parasites.

Conclusions

This is a comprehensive review to understand the diversity and richness of Vietnam’s marine parasite fauna. In 225 fish species, 498 marine fish parasite species have been identified, compared to 247 parasites in 82 fish species in 2006. Digenea (43%) and Monogenea (23.5%) had the highest levels of species richness. According to the data currently available, most parasites in Vietnamese fish come from the GOT (330 species, equivalent to 66.3%).

In Vietnam, the estimated marine parasite richness decreased from 3.0 in 2006 to 2.2 in 2022. Only 12% of the marine fish species have been studied for parasites, so a large part of the fish community still needs to be studied to evaluate and predict better parasite richness and diversity in this tropical-subtropical country. This compilation of parasite records shows significant progress in studying marine fish parasites in Vietnam over the last 16 years. However, it is still in its infancy, leaving a sizable task for the future, as species classification is the first critical step in characterizing any ecosystem. It is a challenging but fascinating task to learn about evolutionary biology and the history of nature, while discovering the true diversity of these marine ecosystems. Understanding pathogenic threats is critical for Vietnam’s growing finfish mariculture industry. Recent research shows that parasites can be used to study climate change and the environment. Thus, studying marine fish parasites in Vietnam is urgently needed in the future, especially using molecular data to characterize and classify the fauna.

The findings of this study will help create a database for marine fish parasites in Vietnam. Additionally, it promotes aquaculture success in Vietnam, reduces the risk of fish disease transmission between countries, and reduces the risk of consuming parasite-infected fishery and aquaculture products in Vietnam and elsewhere.

Author contributions

Truong, T.V.: Conceptualization, writing-original draft, editing, investigation, resources, methodology, software, analysis, visualization; Ngo, H.T.T.: Conceptualization, writing-review, and editing, investigation, methodology, software, analysis, visualization; Bui, T.Q.: Analytical tools, investigation; Palm, H.W.: Conceptualization, investigation, and editing; Bray, R.A.: writing-review and editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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