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Systematic Status of Copepods Infecting the Rosy Goatfish (*Parupeneus rubescens*)

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ABSTRACT

Fish represent one of the most important sources of protein. All fish species are vulnerable to great hazards due to infection with various parasitic taxa and other disease agents. The rosy goatfish (*Parupeneus rubescens*) is one of the most widely distributed and edible species. Little information about the copepod parasites infecting this fish remains. This review included all related published scientific articles in the electronic databases NCBI, ScienceDirect, Saudi digital library and GenBank database. Relevant studies were reviewed through the generic features and molecular analysis of copepods. Parasitologists use many scientific tools to classify copepods and the morphological and morphometric levels are a basic key to identifying copepods. The presence of many copepod species makes it difficult to confirm their taxonomic status. Therefore, scientists focused on the molecular tools to identify each copepod species based on nuclear ribosomal genes as markers to discriminate copepodid species. Scientists can confirm the parasite species' systematic status by combining fundamental and innovative identification tools.

Key words: Classification, Copepods, Fish, Parasites, Phylogeny.

Fish are a good source of quality protein. Still, various diseases, including parasitic infections, threaten fish cultivation, which is a valuable source of food and employment in developing countries (Yooyen *et al.*, 2006; Abdel-Gaber *et al.*, 2023a,b). Goatfishes are tropical marine perciform fish of the family Mullidae, including more than 60 species (Uiblein, 2007). The rosy goatfish, *Parupeneus rubescens* is considered one of the most important goatfish species used as seafood at fish markets in Saudi Arabia. Despite its economic and ecological importance, the ichthyoparasitological problems related to *Parupeneus rubescens* are generally scarce in this region, particularly those of parasitic copepods that may affect them. Several research projects have focused on parasites of goatfishes of the genus *Mullus*, *e.g.*, argentine goatfish, *Mullus argentinae* (Luque *et al.*, 2002) and red mullet, *Mullus surmuletus* (Hassani *et al.*, 2015). Our parasitological studies have focused on our community's most important and edible fish species, the rosy goatfish of the genus *Parupeneus* (Abdel-Gaber *et al.*, 2020a,b,c). In addition, Paperna (1972) reported five monogenean species infecting goatfishes in the Gulf of Eilat. Justine (2010) also documented some parasites of New Caledonian coral reef fishes, including *Parupeneus multifasciatus*.

In the present critical review of the copepods, the proper classification, the criteria of generic and unique diagnosis and the cosmopolitan distribution of copepods among fish are examined because of their relevant characteristics and taxonomic revisions.

This review included all related published scientific articles from January 1840 to December 2022. This article was conducted by searching the electronic databases NCBI, ScienceDirect, Saudi digital library and GenBank database, to check scientific articles related to the research topic of this review. Studies published in the English language were only included and otherwise excluded. Relevant studies were reviewed through numerous steps. In the first step, target published articles were identified by using general related terms related to the morphological features, such as "Crustacea" and "Copepoda". The second step involved screening the resulting articles by using highly specific keywords of the generic features for stages in the life cycle of sea lice. The last step of the review focused on selected studies involving the use of molecular analysis for accurate taxonomic identification by using highly specific keywords, including "PCR", "Genetic markers", "Variable regions", "ribosomal rRNA gene" and "Phylogenetic analysis".

In this review, the different parasitic taxa were used to identify copepods. However, in most cases, their assignment to one or another genus cannot be considered more than provisional. Crustaceans are largely aquatic and more than 36,000 species have been described, including copepods, branchiurans and isopods (Boxshall and Halsey, 2004; Boualleg *et al.*, 2010). Copepods are small crustaceans

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living in diverse marine and freshwater environments (Costello, 2006; Suárez-Morales *et al*., 2008; Gargan *et al*., 2016). Humes (1994) counted 11,500 described species of copepods and mentioned that many species are yet to be described. Huys (2014) counted the number of described copepod species as 12,500. Although some copepods constitute the most important plankton organisms in aquatic ecosystems, about half of the described species are known to be parasites (or associates). The Siphonostomatoida and Cyclopoida, among the nine orders in the subclass Copepoda, contain parasitic copepods, with most members of the former and many of the latter being parasites of fish. The gills of fish are the preferred attachment site for several parasitic copepods (Lester and Hayward, 2006). About 25% of fish-parasitic copepods belong to Cyclopoida. Kabata (1981) reviewed the effects of copepod infections on their fish hosts and divided them into two categories: The first local effects are those limited to the immediate vicinity of the copepod's attachment site and are mainly due to the mechanical influences of its attachment and feeding activities. The second general effect manifests itself at sites remote from the permanent habitat of the adult parasite.

Family Taeniacanthidae

This is a unique family in the copepod order Cyclopoida, containing members that are either parasitic on marine fish or associated with sea urchins (Dojiri and Humes, 1982). Taeniacanthids exhibit high host specificity at both the generic and specific levels (Boxshall and Halsey, 2004). This family, along with Bomolochidae, Tuccidae and Tegobomolochidae, are members of the bomolochiform complex (Dojiri and Cressey, 1987) and characterized by the presence of an indistinctly four-segmented antenna; bearing two pectinate processes, claw-like spines and setae; a mandible with two sub-equal spinulated blades; a maxilla bearing spinulated elements; a concave ventral surface of the cephalothorax; and a lamelliform leg 1. There are 25 genera containing more than 91 species in the Taeniacanthidae (Ho and Lin, 2006; Walter and Boxshall, 2019) and these genera are *Tucca, Haemaphilus, Anchistrotos, Irodes, Phagus, Haematophilus, Taeniacanthodes, Parataeniacanthus, Pseudotaeniacanthus, Echinirus, Echinosocius, Metataeniacanthus*, *Scolecicara, Taeniastrotos, Clavisodalis, Taeniacathus, Cirracanthus*, *Nudisodalis*, *Biacanthus*, *Caudacanthus*, *Umazuracola*, *Saging*, *Triacanthus, Cepolacanthus* and *Suncheonacanthus*.

Genus *Taeniscanthus*

Taeniacanthus Sumpf (1871) is the largest genus of the family Taeniacanthidae consisting of 62 species of poecilostome copepods parasitic on both cartilaginous and bony fish (Walter and Boxshall, 2019; Abdel-Gaber *et al*., 2020a). These species are *Taeniacanthus balistae* Claus (1864), *Taeniacanthus ostracionis* Richiardi (1870), *Taeniacanthus carchariae* Sumpf (1871), *Taeniacanthus tetradonis* Bassett-Smith (1898), *Taeniacanthus zeugopteri* Scott (1902), *Taeniacanthus onosi* Scott (1902), *Taeniacanthus albidus* Wilson (1911), *Taeniacanthus flagellans* Wilson (1913), *Taeniacanthus coelus* Wilson (1922), *Taeniacanthus occidentalis* Wilson (1924), *Taeniacanthus wilsoni* Scott (1929), *Taeniacanthus laqueus* Leigh-Sharpe (1935), *Taeniacanthus longichela* Yamaguti and Yamasu (1959), *Taeniacanthus acanthocepolae* Yamaguti (1939), *Taeniacanthus neopercis* Yamaguti (1939), *Taeniacanthus sebastisci* Yamaguti (1939), *Taeniacanthus monacanthi* Yamaguti (1939), *Taeniacanthus platycephali* Yamaguti (1939), *Taeniacanthus sebastichthydis* Yamaguti (1939), *Taeniacanthus pseudorhombi* Yamaguti (1939), *Taeniacanthus lagocephali* Pearse (1952), *Taeniacanthus upenei* Yamaguti (1954), *Taeniacanthus rotundiceps* Shiino (1957), *Taeniacanthus pteroisi* Shen (1957), *Taeniacanthus yamagutii* Shiino (1957), *Taeniacanthus kitamakura* Yamaguti and Yamasu (1959), *Taeniacanthus sabafugu* Yamaguti and Yamasu (1959), *Taeniacanthus hapalogenyos* Yamaguti and Yamasu (1959), *Taeniacanthus fugu* Yamaguti and Yamasu (1959), *Taeniacanthus sauridae* Yamaguti and Yamasu (1959), *Taeniacanthus inimici* Yamaguti and Yamasu (1959), *Taeniacanthus pectinatus* Yamaguti and Yamasu (1959), *Taeniacanthus cynoglossi* Rangnekar and Murti (1960), *Taeniacanthus narcini* Pillai (1963), *Taeniacanthus longicaudus* Pillai (1963), *Taeniacanthus indicus* Pillai (1963), *Taeniacanthus longicervis* Pillai (1963), *Taeniacanthus miles* Pillai (1963), *Taeniacanthus dentatus* Sebastian (1964), *Taeniacanthus canthigasteri* Izawa (1967), *Taeniacanthus moa* Lewis (1967), *Taeniacanthus alutei* Avdeev (1977), *Taeniacanthus anguillaris* Devi, Uma and Shyamasundari (1980), *Taeniacanthus lucipetus* Holmes (1985), *Taeniacanthus petilus* Dojiri and Cressey (1987), *Taeniacanthus similis* Dojiri and Cressey (1987), *Taeniacanthus glomerosus* Dojiri and Cressey (1987), *Taeniacanthus pollicaris* Dojiri and Cressey (1987), *Taeniacanthus papulosus* Dojiri and Cressey (1987), *Taeniacanthus williamsi* Dojiri and Cressey (1987), *Taeniacanthus nudicauda* Dojiri and Cressey (1987), *Taeniacanthus digitatus* Dojiri and Cressey (1987), *Taeniacanthus comparatus* Dojiri and Cressey (1987), *Taeniacanthus spiniferus* Ho and Lin (2006), *Taeniacanthus kiemae* Tang (2011), *Taeniacanthus mcgroutheri* Tang, Uyeno and Nagasawa (2011), *Taeniacanthus thackerae* Tang *et al*. (2011), *Taeniacanthus larsonae* Tang *et al*. (2011), *Taeniacanthus brayae* Tang *et al*. (2011), *Taeniacanthus singularis* Kim and Moon (2013), *Taeniacanthus ryukyuensis* Tang *et al*. (2016) and *Taeniacanthus dojirii* Tang *et al*. (2016).

Family Caligidae

This family comprises more than 450 valid species, which are known as sea lice (Ho, 1963; Lucky, 1977; Ho *et al*., 2001; Krkôsek *et al*., 2005; Morales *et al*., 2008; Hayes *et al*., 2012), that belong to the genera *Caligus* Müller (1785) and

Lepeophtheirus von Nordmann (1832). They are predominantly external parasites of marine fish (Dojiri and Ho, 2013). Caligid copepods attach themselves to the mouth cavity, gills and operculum of their hosts (Boxshall and Montú, 1997). However, adult caligids can also be found in the water column and some species are known only from plankton surveys (Venmathi Maran and Ohtsuka, 2008). Each of these two main genera of the Caligoida, *Caligus and Lepeophtheirus*, appears to have a well-defined tendency to distribute at different latitudes.

Genus *Caligus*

Caligus is the largest genus of parasitic copepods, containing more than 250 species (Ho and Lin, 2004; Abdel-Gaber *et al.*, 2020b). So far, 43 species of this genus have been reported from the fishes of the Far East, but only eight of them are known from Taiwan. These eight species are *Caligus coryphaenae* Steenstrup and Lüitken (1861), *Caligus polycanthi* Gnanamuthu (1950), *Caligus orientalis* Gusev (1951), *Caligus oviceps* Shiino (1952), *Caligus punctatus* Shiino (1955), *Caligus multispinosus* Shen (1957), *Caligus epidemicus* Hewitt (1971), *Caligus chanos* Lin (1989) and *Caligus acanthopagri* Lin *et al*. (1994). In addition, ten species were recorded from Turkish marine habitats. These ten species are *Caligus minimus* Otto (1821), *Caligus pelamydis* Krøyer (1863), *Caligus brevicaudatus* Scott (1901), *Caligus bonito* Wilson (1905), *Caligus ligusticus* Brian (1906); *Caligus apodus* Brian (1924), *Caligus solea* Demirkale *et al*. (2014), *Caligus temnodontis* Brian (1924), *Caligus pageti* Russell (1925) and *Caligus lagocephali* Pillai (1961). These caligid species influence host survival or cause unsightly changes in the flesh (Oğuz and Öktener, 2007; Özak *et al.*, 2010; Bakir *et al.*, 2014; Demirkale *et al.*, 2015).

The morphological feature of *Caligus* species, distinguishing them from the closely related *Lepeophtheirus* species, is the presence of a pair of lunules on the anterior margin of the adult parasites (Kabata, 1979). The main differences between the *Caligus* species are the relative sizes of the body parts, the armature and structure of the fourth leg, particularly the shape and size of the genital complex and the length and segmentation of the abdomen (Öktener and Trilles, 2009; Agusti-Ridaura *et al.*, 2018; Abdel-Gaber *et al.*, 2020b). The sea louse *Caligus elongatus* has been found on many hosts. Its host list includes more than 80 different fish species (Parker, 1969; Margolis *et al.*, 1975; Boxshall and Halsey, 2004; Suárez-Morales *et al.*, 2008; Özak *et al.*, 2012). *Caligus elongatus* is reported as common on sea-farmed salmonids along the Atlantic coast of Canada (Hogans and Trudeau, 1989a,b), in Ireland (Wallace, 1998), in Scotland (Bron *et al.*, 1993; Grant and Treasurer, 1993) and in Norway (Margolis and Berland, 1984). Salmonid hosts include *Oncorhynchus mykiss*, *Salvelinus fontinalis, Salmo salar* and *Salmo trutta* (brown trout) (Kabata, 1979; Sanches *et al.*, 2012; Noor El-Deen *et al.*, 2013).

Genus *Lepeophtheirus*

Caligids are the most widely distributed group of siphonostomatoid copepods in the world (Ho *et al.*, 2000; Boxshall and Halsey, 2004; Abdel-Gaber *et al.*, 2020c). *Lepeophtheirus* von Nordmann (1832) is the second most diverse genus of the family Caligidae; the most speciose is *Caligus*, which contains more than 250 species. Currently, it is known to contain 124 valid species and 2 recognized subspecies (Ho *et al.*, 2001; Boxshall and Walter, 2016) and of these, the life cycle of five species has been revealed, namely, *Lepeophtheirus dissimulatus* Wilson (1905), *Lepeophtheirus hospitalis* Fraser (1920), *Lepeophtheirus pectoralis* Müller (1776), *Lepeophtheirus salmonis* Krøyer (1837) and *Lepeophtheirus elegans* Gusev (1951). Members of this genus are known as parasites of many teleosts and elasmobranchs (Kabata, 1979; Cressey and Cressey, 1980; Ho and Lin, 2004) and one species, *Lepeophtheirus salmonis* Krøyer (1837) is deemed as the most serious parasite of farmed fish (Johnson *et al.*, 2004; Costello, 2006). Morphologically, this genus is characterized by the lack of lunules, a three-segmented exopod of the fourth leg and the presence of a post-antennary process (Ho and Lin, 2004).

Berland and Margolis (1983) reviewed the early history of the salmon louse, *Lepeophtheirus salmonis* and concluded that the earliest nomenclature applied to this species was *Binoculus salmoneus* (Müller, 1785). However, the name *Binoculus salmoneus* is considered unavailable by the International Commission on Zoological Nomenclature and *Lepeophtheirus salmonis* remains the valid name for this species (Margolis and Berland, 1984). Other scientific synonyms for *Lepeophtheirus salmonis* as listed in Kabata (1979) include: *Caligus salmonis* Krøyer (1837); *Caligus vespa* Milne-Edwards (1840); *Caligus strömii* Baird (1847); *Lepeophtheirus strömii* Baird (1850); *Caligus pacificus* Gissler (1883), *Lepeophtheirus pacificus* Gissler (1883); *Lepeophtheirus vesper* Bassett-Smith (1899), *Caligus vesper* Bassett-Smith (1899) and *Lepeophtheirus uenoi* Yamaguti (1939).

Lepeophtheirus salmonis has a circumpolar distribution in the northern hemisphere (Kabata, 1979; Margolis, 1958). This species is essentially limited to salmonid hosts including *Oncorhynchus clarki* (= *Salmo clarki*) (coastal cutthroat trout), *Oncorhynchus gorbuscha* (pink salmon), *Oncorhynchus keta* (chum salmon), *Oncorhynchus kisutch* (coho salmon), *Oncorhynchus masou* (cherry or masu salmon), *Oncorhynchus mykiss* (= *Salmo gairdneri*) (rainbow or steelhead trout), *Oncorhynchus nerka* (sockeye salmon), *Oncorhynchus tschawytscha* (chinook salmon), *Salmo salar* (Atlantic salmon), *Salvelinus fontinalis* (brook trout) (Kabata, 1979; Hogans and Trudeau, 1989b; Tully, 1989; Nagasawa *et al.*, 1987). Kabata (1979) lists four records of non-salmonid hosts but notes that such occurrences should be considered unusual. Bruno and Stone (1990) report low numbers of preadult *Lepeophtheirus salmonis* on saithe (*Pollachinus virens*) collected near sea farms.

The infestation most likely arose from farmed salmonids as saithe collected away from the sea farms were not infected with *Lepeophtheirus salmonis*. Chalimus stages were not recorded; therefore, it is impossible to determine if *Lepeophtheirus salmonis* had matured to the preadult stage on saithe or if transferring of preadults from salmon hosts occurred. *Lepeophtheirus salmonis* occurs on sea-farmed salmonids along the Pacific coast of Canada, in Norway (Bruno and Stone, 1990), along the Atlantic coast of Canada (Hogans and Trudeau, 1989b) and in Ireland (Tully, 1989). Although *Lepeophtheirus salmonis* is a marine parasite it has been reported to occur on salmonids recently entering freshwater (Hutton, 1923; White, 1940; Hahnenkamp and Fyhn, 1985). In contrast to *Lepeophtheirus salmonis*, the other species of sea lice occur naturally on a wider range of host species, mainly non-salmonids.

Developmental stages and life cycle of sea lice species

All species of sea lice studied have a direct life cycle with five phases and ten developmental stages. These stages include two free-living planktonic nauplius stages, one free-swimming infectious copepodid stage, four attached chalimus stages, two free-moving preadult stages and one free-moving adult stage (Johannessen, 1974; Johnson and Albright, 1991; Ho and Lin, 2004). The precise identification of different larval copepod stages of these species is difficult, if not impossible, owing to the poor descriptions and characterization of such parasites (Price *et al*., 2010; Özak *et al*., 2012; Bayoumy *et al*., 2013). Most parasitic copepods parasitize more than one host (De Meeûs *et al*., 1990), showing little specificity. Regarding their distribution, it is worldwide as they, like their hosts, occur in all warm and temperate seas.

The life cycle of these small aquatic crustacean parasites is described in De Meeûs *et al*. (1990). Generally, they have a direct cycle with a fairly long free-swimming phase (at least three days). Once attached to the host, the parasite becomes mucophagous. Mating occurs on the host's body surface and once fertilized, females colonize the gill cavity, where they lay eggs that develop and give birth to free-swimming larvae (Rodríguez-Santiago *et al*., 2015). The female louse carries her eggs in egg sacs extruding from her abdomen. The number of eggs per sea louse varies with the time of year, louse size, louse age and host species. Based on earlier studies, it is generally assumed that sea lice on farmed salmon carry an average of 500 ova, while those on wild salmon have 1000 ova (Costello, 2006). Generally, following egg hatch, two sequential stages of free-swimming nauplii give rise to a free-swimming copepodid. The copepodid seeks and attaches to the host. Once attached, the parasite develops by molting through four chalimus stages firmly attached to the host by a frontal filament and therefore considered non-motile. The fourth chalimus is followed by pre-adult and adult stages, which are termed motile. Adults mate while on the fish and the fertilized female produces egg strings.

Water temperature and salinity regulate the copepod development rate and nauplii and copepodid survival. Development is accelerated with increased water temperature and survival is enhanced with increased salinity. Dispersal of planktonic stages depends on tidal flows and when near a potential host, copepodids rely on chemical, optical and mechanical cues for host location (Heuch and Karlsen, 1997; Ingvarsdóttir *et al*., 2002). Planktonic stages do not feed and their longevity depends on the availability of stored energy. Adults and pre-adults may also be found as a movement of these stages among hosts is not uncommon (Pike and Wadsworth, 1999). Adult Caligus survives without food for 5-8 days at 19-26°C and may swim from fish to larval. As a result, this group of pathogens is widespread, particularly in marine and brackish waters of tropical regions, often resulting in serious health problems for fish, including heavy mortalities (Hallett and Roual, 1995).

Impact of parasitic copepods on mariculture

Fish parasites harm the commercial fishery industry (Mehl, 1970; Grabda, 1977; Palm and Overstreet, 2000). Several interacting factors can influence the fish's susceptibility to parasitic infection, including the host's stress and nutritional status, the effectiveness of the host's immune system and the genetically determined susceptibility of the host (Palm and Overstreet, 2000). A copepod infection can substantially affect hosts by impacting changes in appetite and the levels of hematological parameters (Vargas-Chacoff *et al*., 2016). Sea lice are responsible for most fish disease outbreaks (Berland and Margolis, 1983; Yuniar *et al*., 2007; Wagner *et al*., 2008). The gills are a favorite site for the attachment of several parasitic copepods. They damage the gills by feeding on the delicate tissue of the gill lamellae or on the blood circulating within the lamellae, leading to a loss of respiratory surface area (Lester and Hayward, 2006). There is extensive gill damage and severe hemorrhage, with inflammation and exsanguination associated with the attachment and feeding of the parasite (Lester and Hayward, 2006). Blood vessels in the gill filaments are blocked, leading to atrophy of gill tips (Dogiel *et al*., 1961). Sea lice produce secretory products, such as prostaglandin E2, which may protect the parasite from the host's immune response, creating a more favorable environment for the parasite (Fast *et al*., 2004). In addition, Fast *et al.* (2003) described proteases released by *L. salmonis* in response to the host mucus. The impact of sea lice is well known to cause serious cutaneous lesions, growth retardation and mortality in farmed teleosts (Boxshall and El-Rashidy, 2009; Dezfuli *et al*., 2011; Demirkale *et al*., 2015; Thorstad *et al*., 2015). Due to their feeding activities on host mucous, tissue and blood, it has been suggested that parasitic copepods may serve as vectors of viral and bacterial diseases in fish (Ho and Lin, 2004; Suárez-Morales *et al*., 2008). No doubt, parasites infecting fish indirectly affect human welfare by transmitting different pathogens such as parasites, viruses and bacteria (Bayoumy *et al*., 2013).

Control

Different chemicals control sea lice but increasing resistance to antiparasitic drugs has been reported (Aaen *et al.*, 2015). Currently, the only effective method for controlling sea lice on farmed salmonids is the organophosphorus insecticide, dichlorvos, marked as 'Nuvan 500EC' or in its related trichlorphon form as 'Neguvon'. Brandal and Egidius (1977) reported the first use of trichlorphon to treat salmonids infected with sea lice. In their study, oral trichlorphan administration caused a significant amount of fish mortality and a decline in sea lice. Dichlorvos and trichlorphon have been used in pond fish culture since the 1960s as bath treatments for parasites (Brandal and Egidius, 1979). These treatments effectively remove both the preadult and adult stages of sea lice but not the chalimus larvae; therefore, successive treatments, usually at two- to four-week intervals, are required to control the infection (Schmahl *et al.*, 1989). Physical damage and high levels of stress imposed during treatment commonly result in fish developing secondary diseases (*e.g.* vibriosis, furunculosis). In addition, production levels of treated stocks are lower due to lowered growth and feed conversion rates. There needs to be published information on alternative treatment methods for sea lice. Palmer *et al.* (1987) report the results of preliminary studies on the efficacy of oral doses of Ivermectin for controlling sea lice on Atlantic salmon. Ivermectin is effective in reducing populations of sea lice; however, the drug has a narrow margin of safety. Currently, studies are underway to: (1) further investigate the toxicity of Ivermectin to salmonids; (2) determine the minimum dosage required to control sea lice and (3) determine tissue clearance times.

Molecular phylogenetic analysis of Copepods

Although molecular approaches have been applied exhaustively to copepods to ensure accurate taxonomic identification of species, more information is needed for cyclopoid copepods (Blanco-Bercial *et al.*, 2011). Molecular studies on Copepoda have focused on the species-to-superfamily level relationships of Calanoida (Bucklin and Frost, 2009; Marszalek *et al.*, 2009; Makino and Tanabe, 2009; Figueroa, 2011), Harpacticoida (genus *Tigriopus*), Cyclopoida and Poecilostomatoida (families Xarifiidae, Chondracanthidae and Umazuracolidae, Oithonidae and Cyclopidae) (Huys *et al.*, 2006,2009,2012; Castro-Longoria *et al.*, 2003; Al-Quraishy *et al.*, 2021). DNA sequence variation of the large-subunit (28S) rRNA gene has been extensively used to examine phylogenetic relationships among marine invertebrate species, including echinoderms (Borchiellini *et al.*, 2004), cnidarians (Ortman, 2008), nematodes (Bik *et al.*, 2010), mollusks (Holznagel *et al.*, 2010) and annelids (Struck *et al.*, 2011), among others. The broad application of this gene as a character for the taxonomic identification of species with subtle or ambiguous morphological characteristics makes it a useful marker for copepod species (Cepeda *et al.*, 2012).

No molecular-level phylogeny of copepods is currently available, but phylogenetic relationships based on morphological characteristics have been postulated in the past (Huys and Boxshall, 1991). Apomorphies used in morphological analyses are largely based on adaptations of the locomotory and feeding appendages and body shape to newly colonized environments and associations with invertebrates and fish (including ecto- and endoparasites). In the past, the form of the mouthparts has been a key evolutionary characteristic complex for the high-level classification of copepods (Thorell, 1859), but subsequent authors did not adopt this view (Sars, 1903). A comprehensive investigation of homologies in the body plan, segmentation and setation of copepod appendages was performed by Huys and Boxshall (1991), resulting in a cladistic phylogeny of the 10 orders of the subclass Copepoda. The morphological phylogenetic analyses of Copepoda have been extensively investigated and there are general agreements, such as the monophyletic status of Copepoda (Ho, 1990; Dahms, 2004). Furthermore, copepods can be divided into two infraclasses, Progymnoplea and Neocopepoda (Huys and Boxshall, 1991). Progymnoplea contains only one order Platycopioida and Neocopepoda can be further classified into two superorders, Gymnoplea and Podoplea (Huys and Boxshall, 1991; Ho, 1994). The latter was divided into two main clades, the so-called "MHPSM-clade" containing Mormonilloida, Harpacticoida, Poecilostomatoida, Siphonostomatoida, Monstrilloida and the "MCG-clade" including the Misophrioida, Cyclopoida and Gelyelloida. This phylogenetic concept has been revised by many authors (Martınez Arbizu, 2000; Huys *et al.*, 2002; Ho *et al.*, 2003; Schizas *et al.*, 2015).

For several decades, however, the phylogenetic relationships among the copepod orders have been controversial (Boxshall and Halsey, 2004). Owing to the extreme diversity of body forms, the phylogenetic relationships based on traditional morphological data have led to much controversy. For example, Huys and Boxshall (1991) analyzed 21 and 54 morphological characters across ten copepod orders. They agreed that Platycopioida and Calanoida were the most basal groups. However, the cladogram from Ho (1990) depicted Harpacticoida and Gelyelloida were closely related, but this group was a distinct cluster from the group of Siphonostomatoida, while that of Huys and Boxshall (1991) appeared to indicate that Harpacticoida had a close affinity to a sister-group of Siphonostomatoida but was discrete from Gelyelloida. Later, some modifications for the morphological phylogenetic models have been proposed (Ho, 1990). However, as Ho *et al.* (2003) pointed out, the inconsistent position of Harpacticoida which represents an important ecological group in aquatic environments, has still been problematic.

Furthermore, some molecular-based studies were not congruent with morphological evidence. Braga *et al.* (1999) focused on the phylogenetic relationships within the copepod family Euchaetidae and showed the three copepod orders

(Harpacticoida, Calanoida and Poecilostomatoida with a barnacle, Semibalanus balanoides as an outgroup) using the large subunit ribosomal RNA (28S rRNA) gene. The tree appeared to be markedly inconsistent with morphological phylogenies; Harpacticoida was closer to Calanoida than to Poecilostomatoida, which conflicted with the superorder Podoplea. Later, other molecular studies recovered and supported the monophyletic podoplean group using the 18S small subunit ribosomal RNA gene (18S rRNA), but they still left unresolved the phylogenetic position of Harpacticoida (Huys *et al*., 2006; Huys *et al*., 2007; Tung *et al*., 2014; Schizas *et al*., 2015; Dkhil *et al*., 2022).

A recent study using concatenated twelve mitochondrial genes showed that Harpacticoida (*Tigriopus californicus*) was more closely related to Siphonostomatoida (*Lepeophtheirus salmonis* and *Caligus rogercresseyi*) than Calanoida (*Calanus sinicus*) (Minxiao *et al*., 2011). This mitochondrial phylogenetic hypothesis was congruent with most of the morphological phylogenies (Ho *et al*., 2003), except for the phylogenetic position of Poecilostomatoida. Moreover, in the 18S rRNA gene trees of Poecilostomatoida, the Clausidiiform complex and the remaining poecilostomatoid taxa appeared to be paraphyletic (Huys *et al*., 2012; Tung *et al*., 2014). Harpacticoida also may be a paraphyletic taxon with Polyarthra (consisting of the families Canuellidae and Longipediidae) and Oligoarthra (all remaining harpacticoid families) (Dahms, 2004). From the 28S rRNA gene tree, two Polyarthra taxa (*Canuella perplexa* and *Longipedia gonzalezi*) were more closely related to other copepods than Oligoarthra (Schizas *et al*., 2015). All these molecular phylogenetic studies used relatively short sequences (<2.000 bp) or fast-evolving genes that were not acceptable for interordinal relationships (Khodami *et al*., 2017; Sun and Cheng, 2021).

CONCLUSION

The present study supplied valuable information on the taxonomy of copepod parasites infecting the rosy goatfish (*Parupeneus rubescens*). Further studies should be conducted to survey more ectoparasitic taxa infecting the solider bream fish species. The upcoming studies should include more genes to provide more knowledge about all the observable parasite species. Different measures should be determined to control the transmission of water-related parasitic diseases to various fish species.

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Data availability statement

All datasets generated during this study are included in this article.

Conflicts of interest

The authors declare no conflicts of interest.

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