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From Microscale Interactions to Macroscale Patterns in Copepod-Crinoid Symbiosis

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Simple Summary: Crinoids, echinoderms, engage in diverse symbiotic relationships with copepod crustaceans, but understanding these interactions remains limited. Our analysis reveals 166 instances with 35 copepod species across 6 families associated with 33 Comatulida species. These associations span five of the 12 World Ocean ecoregions, with the highest diversity in the Central and Western Indo-Pacific regions. Atlantic copepod-crinoid associations are less documented. Most copepods form ectosymbiotic relationships, with some instances of endosymbiosis. Genera *Collocheres* and *Pseudanthessius* are prominent, and Comasteridae exhibits diverse copepod associations. While some copepod families specialize in crinoids, others show species-specific preferences. Only 5% of potential crinoid host diversity is currently known, highlighting the need for further research.

Abstract: Crinoids (Echinodermata) exhibit unique characteristics that facilitate a wide range of symbiotic relationships with diverse organisms. Nonetheless, the comprehension of their interactions with microscopic copepod crustaceans is still in a nascent and fragmented state. Our analysis identifies 166 instances involving 35 copepod species representing in 6 families in association with 33 species of the Comatulida. The majority of these associations have been singularly reported, with their distribution covering five out of the 12 World Ocean ecoregions. A notable concentration of diversity is observed in the Central and Western Indo-Pacific regions, while documentation of Atlantic copepod-crinoid associations is markedly limited. Copepods are predominantly found in ectosymbiotic relationships, with a lesser incidence of endosymbiotic interactions. Among these, the genus *Collocheres* and *Pseudanthessius* emerge as particularly prominent, and the Comasteridae family is distinguished by its diverse copepod associations. While certain copepod families exhibit a specialization towards crinoids, others demonstrate specificity at the species level. The current scope of knowledge encompasses merely 5% of the potential crinoid host diversity, underscoring the critical need for more extensive research in this area.

Keywords: copepod associations; symbiotic relationships; crinoids; comatulida; marine biodiversity; marine ecology; marine invertebrates; host-symbiont interactions; marine parasitology

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1. Introduction

The echinoderm class Crinoidea represents a diverse and enduring clade with a fossil record stretching back nearly half a billion years (Hess et al., 1999; Wright et al., 2017). Its modern-day diversity is predominantly found within the order Comatulida, which is documented to comprise a wealth of 671 distinct species (Pawson, 2007; Messing et al. 2023). These crinoids, characterized by their limited locomotive capabilities, rudimentary self-cleaning mechanisms, and the absence of saponin secretions, have provided a structural foundation for a diverse of vertebrate and invertebrate

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organisms (Burnell, ApSimon, 1983; Britayev, Mekhova, 2011). While direct predation on crinoids remains uncommon, their anatomical design—comprising mobile arms, pinnules, and cirri—and their unique filter-feeding method, wherein alimentary particles travel conspicuously along ambulacral grooves, serve as a habitat conducive to a plethora of symbionts (Fabricius, Dale, 1993; Deheyn, 2006; Britayev, Mekhova, 2011). The symbiotic taxa often found in association with crinoids range across gastropods, polychaetas, myzostomes, decapod and copepod crustaceans, ophiuroids, and fish (Clark, 1931; Fishelson, 1974; Humes, 2000; Mekhova, Britayev 2012).

Historical examinations within marine biology underscore a sustained interest in the relationships between crinoids and their symbiotic partners. The investigations have been conducted in various coastal ecosystems around the world, with notable studies including those conducted in the Bay of Bengal (Rao, Sowbhagyavathi, 1972), the Red Sea (Fishelson, 1974), the Marshall Islands (Zmarzly, 1984), the Maldives Archipelago (Tchesunov et al., 1989), Hong Kong (Morton and Mladenov, 1992), the Great Barrier Reef (Fabricius and Dale, 1993), Taiwan (Huang et al., 2005), New Guinea (Deheyn et al., 2006), South Africa (Hempson and Griffiths, 2008), Vietnam (Britayev and Mekhova, 2011; Britayev et al., 2016), and North Sulawesi (Virgili et al., 2020). Comprehensive investigations pertaining to this subject have consistently emphasized the prevalence of specialized fauna engaged in symbiotic associations with crinoids. However, it is imperative to exercise prudence in the interpretation of these findings, given the inherent discrepancies in the accuracy of species identification. Furthermore, a conspicuous gap in data persists regarding the diverse insufficiently studied microscopic symbionts (such as myzostomid polychaetes and copepod crustaceans) inhabiting crinoids (Humes, 1987; Summers et al. 2014). These relatively obscure organisms, despite their diminutive size, potentially exert a notable influence on the broader ecosystem dynamics intertwined with their host crinoids.

Microscopic copepods, a type of crustacean, play a significant, though still insufficiently explored, role in a wide range of ecological interactions within marine ecosystems (Humes, 1994; Ho, 2001; Bron et al., 2011; Bernot et al., 2021). Their establishment of symbiotic relationships with various echinoderm species across diverse marine environments underscores their remarkable ecological adaptability and highlights the intricate network of biotic interactions in aquatic ecosystems. Copepods from various families have been observed residing in association with echinoderm hosts representing Crinoidea (feather stars), Asteroidea (sea stars), Echinoidea (sea urchins), Holothuroidea (sea cucumbers), and Ophiuroidea (brittle stars) (Humes, 1986; Ivanenko et al., 2001; Boxshall and Halsey, 2004; Kim et al., 2007, Mahatma et al., 2008; Venmathi Maran et al. 2017; Yeom et al., 2018). This diverse range of symbiotic relationships underscores the pivotal role of copepods in marine ecosystems and provides valuable insights into the evolutionary intricacies governing these associations (Boxshall and Halsey, 2004; Bernot et al., 2021). The investigation of these interactions not only reveals the ecological significance of copepods but also contributes to a deeper understanding of the evolutionary mechanisms that underlie symbiosis within marine ecosystems.

This study is a component of a broader project aimed at elucidating patterns and assessing the depth of understanding pertaining to copepod symbionts found in various invertebrates, with a particular focus on echinoderms, sponges, and corals (Ivanenko et al. 2018; Korzhavina et al. 2019, 2021, 2023). Through an exhaustive analysis and synthesis, we aspire to offer a holistic view of these relationships, focusing on their ecological, evolutionary, and taxonomical dimensions, thereby enhancing our comprehensive understanding of marine symbiotic systems and the pivotal roles copepods play within them.

2. Materials and Methods

We have developed a comprehensive Microsoft Access database to meticulously analyze the symbiotic interactions between copepods and crinoids. This database comprises four intricately connected tables: 'Hosts,' 'Symbionts,' 'Sites,' and 'Publications,' which collectively merge into a comprehensive 'Literature Records' table (Table 1, Table A1, Table S1). Adhering to the standards set by the World Register of Marine Species (WoRMS 2022), this database provides a thorough record of the taxonomic classifications of hosts and symbionts. It also encompasses a broad spectrum of data, including detailed information on symbiotic relationships, geographical locations, sampling depths, and timestamps, as further elucidated in Table A2. Spatial data management involved extracting specific coordinates for each sampling location from the original literature and subsequently georeferencing them. All these data have been meticulously incorporated into the dataset entries, adhering to the Darwin Core standards (Wieczorek et al., 2012). To ensure consistency and accuracy in taxonomic nomenclature, we employed the 'Taxon Match' tool from WoRMS, a crucial step, especially given the evolving nomenclature for crinoid hosts. The classification of oceanic ecoregions adheres to the methodology advocated by Spalding et al. (2007). We do not endorse the recently proposed taxonomic status changes for the order Poecilostomatoida, as we believe they warrant further investigation (Mikhailov and Ivanenko, 2019, 2021). Visualization of these geographic data points was achieved using digital mapping platforms, including Google Maps and RStudio Version 1.2. To visualize and generate plots, we employed RStudio version 1.2.5001, harnessing the capabilities of various packages such as tidyverse [121], dplyr [122], ggplot2 [123], ggExtra [124], ggpubr [125], gridExtra [126], magrittr [127], maps [128], stringr [129], and RColorBrewer [130]. Additionally, all graphical representations were crafted using Adobe Photoshop CC.

Table 1. List of references reporting records of copepods, divided by world ocean regions and countries (for more details see **Tables A1, S1**).

Region	Country	Reference
Central Indo-Pacific	Australia	Humes, 1987
	Indonesia	Humes, 1987; Humes, 1990; Kim, 2007
	Marshall Islands	Humes, 1972
	New Caledonia	Humes, 1977; Humes, 1987
	Philippines	Humes, 1987
Temperate Northern Atlantic	France	Changeux, Delamare Deboutteville, 1956
	Ireland	Grainger, 1950
	Italy	Giesbrecht, 1900; Stock, 1959
	United Kingdom	Grainger, 1950
Temperate Northern Pacific	Japan	Ho, 1982; Ohtsuka, Kitazawa, Boxshall, 2010; Ohtsuka, Shimomura, Kitazawa, 2012
	Korea	Shin, Kim, 2004
Tropical Atlantic	Belize	Humes, 2000
	Brazil	Johnsson, 2002
	Jamaica	Kim, 2010
Western Indo-Pacific	India	Reddiah, 1968
	Israel	Stock, 1966; Stock, 1967; Stock, 1983
	Madagascar	Humes, 1990; Humes, Ho, 1970; Humes, Stock, 1973; Stock, 1967

3. Results and discussion

3.1. The history of research

Over the past century, the study of copepod symbionts associated with crinoids has culminated in the publication of 24 scientific articles, documenting a total of 166 symbiotic interactions between copepods and crinoids, as indicated in Figure 1. The research trajectory concerning crinoids can be divided into four significant stages, as identified by Wright et al. (2017). Notably, this trajectory demonstrates a notably greater taxonomic effort directed towards crinoids compared to copepod symbionts. This discrepancy can be attributed to the inherent challenges associated with collecting microscopic symbionts residing within galls, digestive systems, or on the surfaces of crinoids.

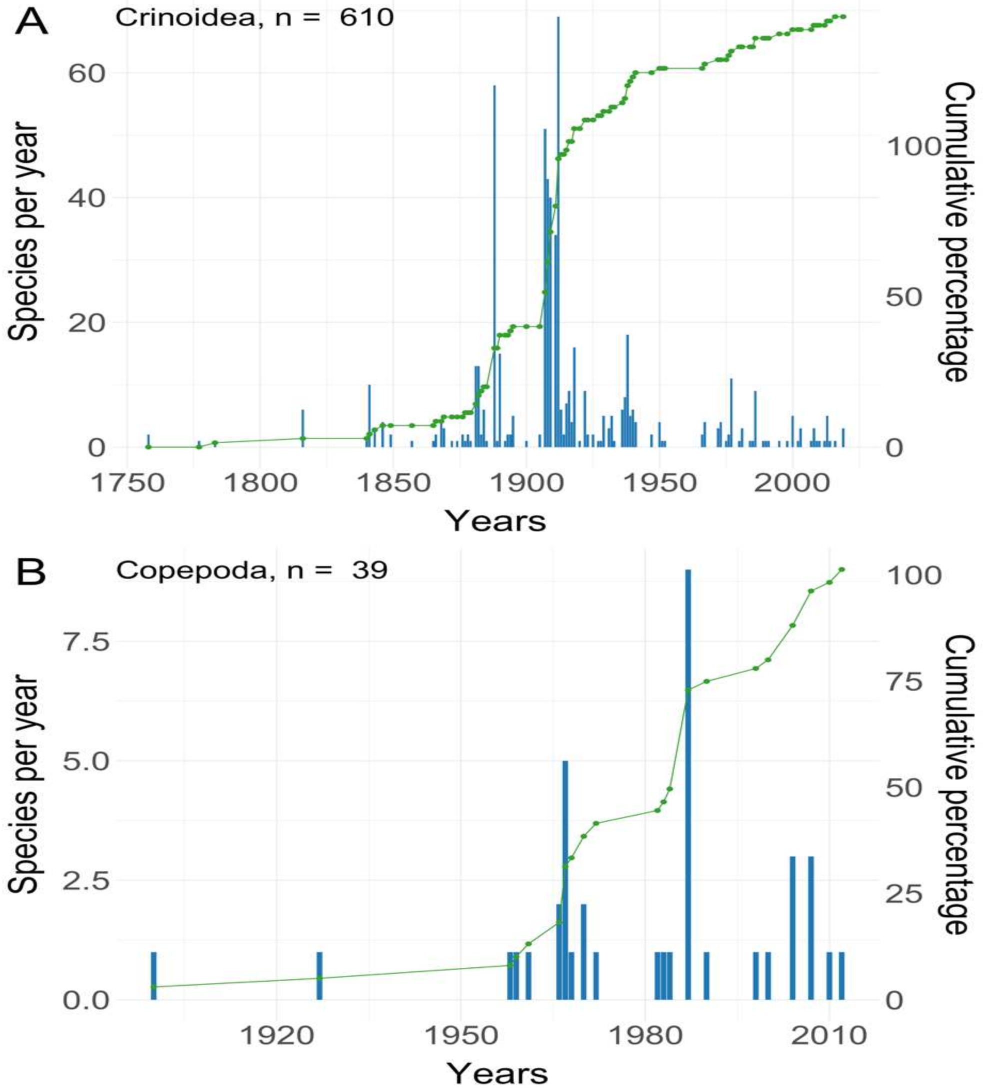

Figure 1. Numbers of new species and cumulative percentage (green line) of known species of (A) crinoids and associated with them (B) symbiotic copepods described published over time. Based on the WoRMS database (WoRMS 2022).

With the advent of methods for sampling shallow-water material using SCUBA diving, it became possible to gather copepods that are only weakly associated with shallow-water crinoids. However, over the past decade, there has been a noticeable decline in research activity. Few works have focused on morphological descriptions, with some providing brief comments on zoogeographical aspects and relationships between copepods and their hosts. This trend underscores the existence of numerous unexplored facets in the symbiotic relationship between copepods and crinoids, particularly concerning the nature of symbiosis and its implications for both partners.

3.2. Sampling methods and challenges

In the study of copepod-crinoid symbiosis, the prevailing methodology for copepod identification involves the use of a 5% ethanol solution to wash the crinoid hosts. This approach, although intricate and capable of recovering a significant diversity of microsymbionts, presents challenges when conducting quantitative assessments. The application of this methodology, which shapes our comprehension of copepod-host relationships, is applicable to the majority (155) of observations related to copepods on crinoids. Dissection has been relatively infrequent, limited to 11 instances (Table A1, Table S1).

The choice of methodology is inherently linked to the type of symbiotic interaction identified: specimens identified via washing are consistently categorized as ectosymbiotic, with descriptions typically lacking specific localization details on the host. Conversely, copepods identified through dissection are invariably classified as endosymbiotic, with precise intrahost localization described, such as within the intestinal tract (Giesbrecht in 1900 and 1950; Changeux and Delamare Deboutteville in 1956; Stock in 1959 and 1966), within galls (Ohtsuka, Kitazawa, Boxshall, 2010), or the coelom (Changeux, Delamare Deboutteville, 1956). The significant methodological influence on the types of copepods detected, as elucidated by Humes in 2000, suggests that the spectrum of endosymbiotic copepods associated with crinoids remains incompletely explored. Consequently, further research is imperative to ascertain the precise localization of the majority of ectosymbionts.

The research into copepod-crinoid symbiosis faces significant challenges, particularly the complexity of collecting loosely associated fauna from deep-sea specimens. This complexity is compounded by the current state of knowledge about microscopic copepods residing in or on crinoids, which is primarily characterized by a lack of an integrative approach, especially in the application of molecular methodologies. Additionally, much of the existing data is limited to faunistic or exploratory methodologies, which, while inevitable in the initial stages of researching any taxonomic group, constrain the breadth and depth of understanding. The absence of a comprehensive and multidisciplinary research approach thus represents a significant impediment to advancing the understanding of these intricate symbiotic associations.

3.3. Diversity and taxonomy of symbiotic copepods

Literature analysis revealed 166 instances involving 35 copepod species representing 6 families in association with 33 species of the Comatulida. The data analysis has unveiled intricate symbiotic associations among three distinct orders of copepods — Cyclopoida, Poecilostomatoida, and Siphonostomatoida — and the Comatulida order of crinoids. Consequently, this taxonomic rearrangement necessitates additional scrutiny and detailed research to substantiate its validity. This symbiotic interaction constitutes more than 5% of the known diversity within the Comatulida order.

The study indicates that the Poecilostomatoida and Siphonostomatoida orders display parallel trends in their frequency of occurrence and the spectrum of crinoid taxa they are associated with, as elaborated in Table 2. Significantly, the Poecilostomatoida order is characterized by a broad spectrum of families and genera involved with crinoids, suggesting more elaborate symbiotic connections with this marine class. The predominance of Poecilostomatoida, evidenced by 82 instances in the study, points towards an in-depth exploration of their symbiotic links in comparison to other copepod orders. In contrast, the Siphonostomatoida order, with a considerable 19 species linked to crinoids, demonstrates a heightened level of specialization within this group.

Table 2. The families of Copepoda in relation to Octocorallia

Taxa	**# of known copepod species**	**# copepod species**	**# of copepod records found on crinoids**	**# crinoid families**	**# crinoid genera**	**# crinoid species**	**Mean of records per copepod species + SE**	**Mean of host species per copepod species + SE**	**% copepod species with a single crinoid host**
Cyclopoida									
Enterognathidae	7	4	11	5	6	7	2.75 + 0.85	1.75 + 0.48	50
Poecilostomatoida									

Kelleriidae	19	1	1	1	1	1	1 + NA	1 + NA	100
Pseudanthessiidae	61	7	77	6	13	14	13.57 + 5.03	3 + 0.93	28,57
Rhynchomolgidae	270	3	3	1	2	2	1 + 0	1 + 0	100
Synapticolidae	50	1	1	1	1	1	1 + NA	1 + NA	100
Siphonostomatoida									
Asterocheridae	271	19	73	5	12	17	3.84 + 1.17	2 + NA	63,16
Total	678	35	166	19	35	42			

* WoRMS database [33].

In the Cyclopoida order, encompassing 95 families, only the representatives from the Enterognathidae family have been identified in crinoids, comprising seven known copepod species. Of these, four species are associated with seven different further star species (Table 2). The average frequency of scientific mentions per copepod species stands at 2.75 (SE 0.85), reflecting variation in observations across different species. Half of the species in this family exhibit specialization for a single host, indicative of a selective adaptation towards specialization.

The Poecilostomatoida order is predominantly represented by the Pseudanthessiidae, with a high specialization, each of the three identified copepod species is exclusively linked to a singular further star species, demonstrating strict host specificity among these copepods. The Pseudanthessiidae family is noted for a considerable average of scientific mentions per species (13.57), with a standard error (SE) of 5.03, suggesting an extensive host range. The mean number of hosts per copepod species is three (SE 0.93), with approximately 28.57% of copepod species associated with a single further star species, indicative of a moderate degree of specialization in comparison to other families.

The Siphonostomatoida order has only one family associated with further stars (Table). The Asterocheridae family, uniquely identified within Siphonostomatoida, displays an average research mention frequency of 3.8 per species (SD ± 1.17), emphasizing the variability in species encounters. A substantial proportion of copepods (63.16%) within this order are associated solely with a single further star species, suggesting a trend towards species-specific symbiosis.

Despite the rich species diversity within the Asterocheridae, Rhynchomolgidae, and Pseudanthessiidae families, only a small fraction of these species is found in association with crinoids – 7% of 271 species, 2.5% of 270, and 5% of 61, respectively. This observation implies a selective nature of the relationships between copepods and crinoids, with Asterocheridae and Rhynchomolgidae exhibiting a high level of host specialization, whereas Pseudanthessiidae demonstrates a broader variation in associations.

3.4. Specialization in Copepod-Crinoid Symbiosis

The examination of morphological adaptations in copepods, particularly those engaged in endosymbiotic relationships with crinoids, reveals significant deviations from typical crustacean morphology, as depicted in Figure 2. This phenomenon is notably apparent in the Cyclopoid family Enterognathidae, which predominantly associates with crinoids and is represented by genera such as *Enterognathus* and *Parenterognathus*. Descriptions of different endosymbiotic or gall inducing show that endosymbiosis leads to considerable morphological changes in the copepods. In the case of Enterognathidae, these alterations include a swollen, vermiform body structure, reduced segmentation and sclerotization, obscured prosome and urosome demarcations, and a potential diminution or complete absence of antennae and maxillipeds. Such changes are markedly more pronounced in Enterognathidae compared to other crinoid-dwelling copepods and exhibit a less extreme form than those observed in the obligate symbionts of octocorals from the Lamippidae family (Korzhavina et al. 2021).

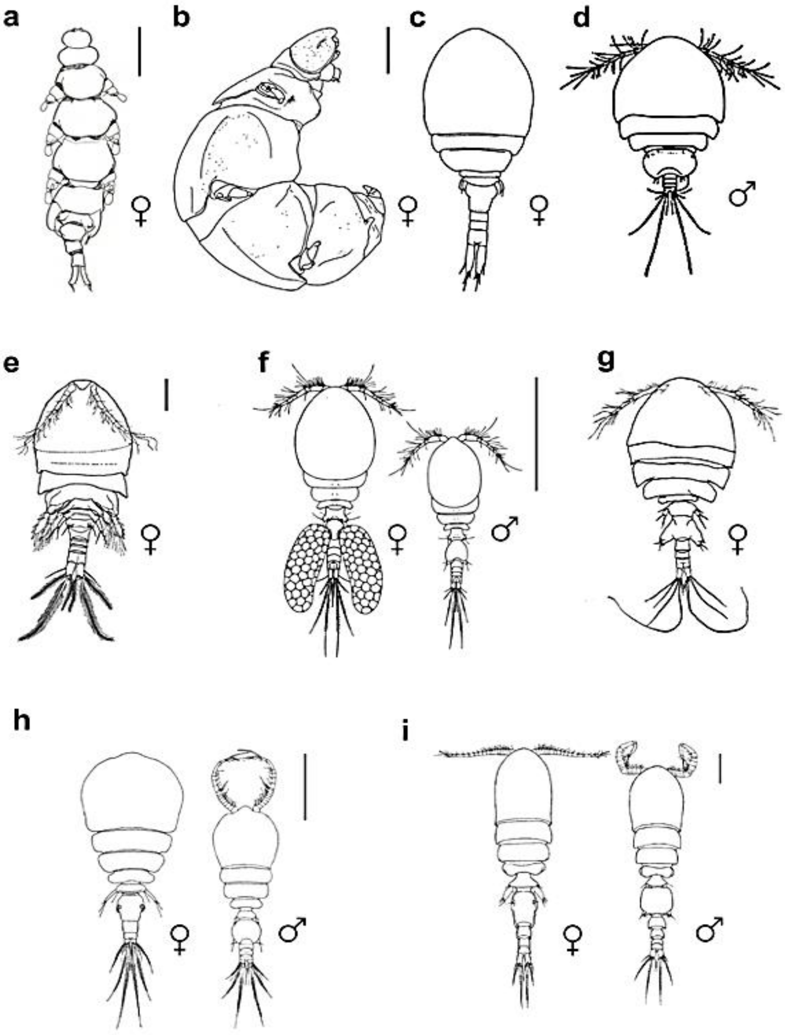

Figure 2. Habitus of copepod crustaceans living on crinoids: a – *Enterognathus inabai*, dorsal view, scale bar 1 mm; b – *Parenterognathus troglodytes*, dorsal view, scale bar 0.5 mm; c – *Critomolgus fishelsoni*, dorsal view, scale bar 0.5 mm; d – *Dordicola patulus*, dorsal view; e – *Kelleria gradata*, dorsal view, 0.2 mm; f – *Pseudanthessius comanthi*, dorsal view, 0.5 mm; g – *Scambicornus pillaii*, dorsal view, 0.1 mm; h – *Asterocheres crinoidicola*, dorsal view, 0.3 mm; i – *Collocheres brevipes*, dorsal view, 0.1 mm; (a-b – Cyclopoida, c-g – Poecilostomatoida, h-i – Siphonostomatoida). After Ohtsuka, Shimomura, Kitazawa, 2012 (a), Ohtsuka, Kitazawa, Boxshall, 2010 (b), Stock, 1967 (c, e), Humes, 1958 (d), Humes, 1972 (f), Stock, 1983 (g), Humes, 2000 (h), Shin, Kim, 2004 (i).

The order Comatulida encompasses a diverse array of crinoid hosts for copepods, including eight families, 21 genera, and 33 species, as detailed in Table 3 and Supplement Table 2. The Comasteridae family emerges as a prominent symbiotic partner for copepods. Despite the Comatulidae family comprising 102 species, only 16% serve as hosts for copepods. Notably, this family is linked to half of all recorded copepod findings (81 out of 163) and half of the copepod species (20 out of 40) symbiotic with crinoids, as outlined in Tables 3 and Figure 3. The unique ambulacral architecture of the Comasteridae may provide specialized ecological niches conducive to symbiosis. Conversely, the Antedonidae family, despite its diversity (151 species), exhibits a minimal number of confirmed symbiotic relationships with copepods. These observations underscore the complexity and selectivity inherent in the symbiotic associations between copepods and crinoids, hinting at the potential influence of ecological and evolutionary factors that warrant further investigation. An alternative hypothesis might consider the uneven distribution of research efforts across different feather star species.

Table 3. Crinoidea families in relation to copepods

Host taxa	# of known crinoid genera	# host crinoid genera (%)	# of known species	# host crinoid species (%)	# records	# of copepod species found on crinoids	# of host species with 1 copepod species	2	3	4
Comatulida										
Antedonidae	50	1 (2%)	151	2 (1.32%)	5	1	2			
Charitometridae	8	1 (12.5%)	33	1 (3.03%)	2	1	1			
Colobometridae	18	3 (16.67%)	47	3 (6.38%)	11	6	1		2	
Comatulidae	23	8 (34.78%)	102	16 (15.69%)	81	20	7	5	3	1
Himerometridae	5	2 (40%)	39	3 (7.69%)	18	6		2		1
Mariametridae	7	4 (57.14%)	22	5 (22.73%)	24	4	1	3	1	
Tropiometridae	1	1 (100%)	4	2 (50%)	21	1	2			
Zygometridae	2	1 (50%)	10	1 (10%)	1	1	1			
Total	114	21	408	33	163	40	15	10	6	2

* WoRMS database [33]

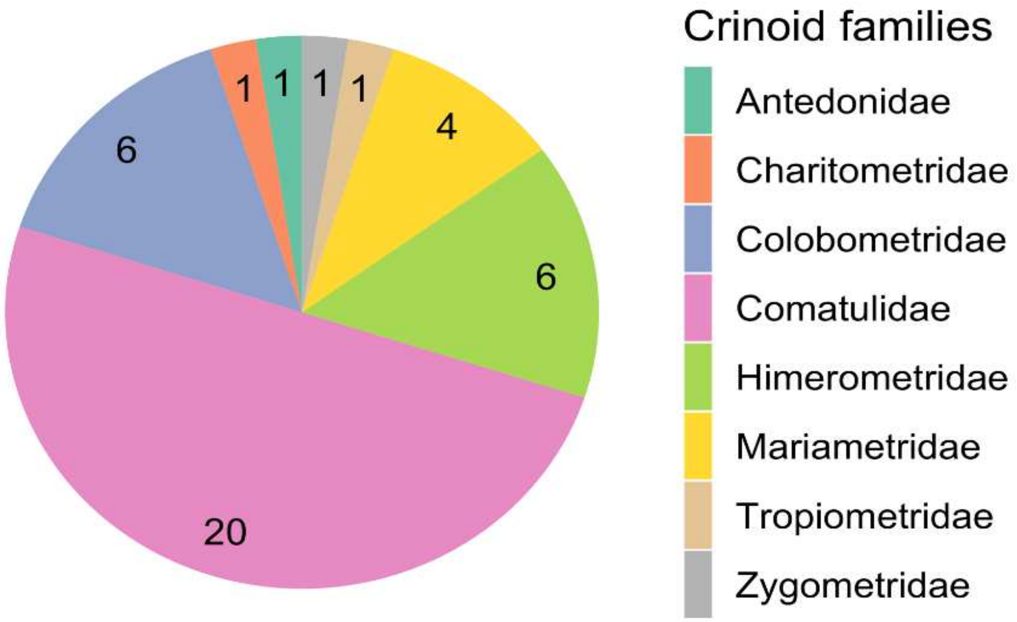

Figure 3. Distribution of copepod associations across different crinoid families.

The degree of host specialization exhibited by various copepod species in their interactions with crinoids displays a spectrum ranging from highly specialized to more generalized associations, indicative of diverse evolutionary trajectories. Notably, species-specific symbionts constitute 61% (comprising 20 species), as opposed to 39% (encompassing 13 species) associated with a variety of hosts. This pattern highlights the significance of specialized host-symbiont relationships in the evolutionary ecology of copepods (Figure 4).

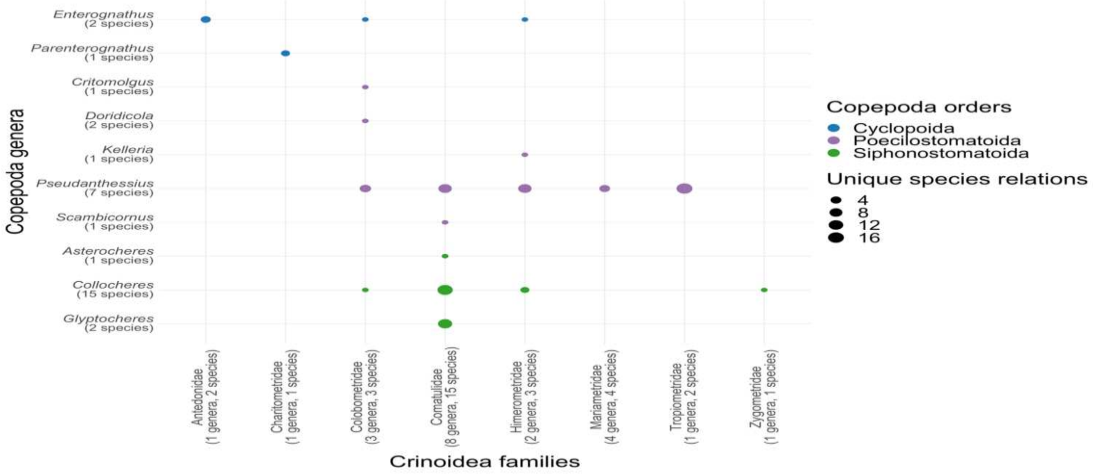

Figure 4. Number of records per association of symbiotic copepod genera with crinoid families. Size of figure means number of records.

The range of host interactions among copepod species exhibits considerable heterogeneity. For example, *Pseudanthessius major* and *P. minor* are distinguished by their extensive host interactions, involving multiple host species (eight and four, respectively) and genera (seven and four, respectively). Similarly, *Collocheres uncinatus* associates with three distinct host families: Colobometridae, Comatulidae, and Himerometridae, presenting a broad spectrum of ecological associations.

A reduction in the number of host species typically leads to the evolution of specific adaptive traits. This is exemplified by *P. angularis*, *P. comanthi*, and *P. madrasensis*, characterized by the development of prominent egg sacs in females, a feature commonly observed in symbiotic copepod species. This trait distinguishes them from species such as *P. major* and *P. minor*. Additionally, *Enterognathus comatulae* and *E. lateripes* display significant morphological adaptations, including a vermiform body structure with inflated, rounded body segments, and fringed swimming appendages.

The species-specific *Parenterognathus troglodytes* exhibits a more pronounced degree of body modification compared to its *Enterognathus counterparts*. Distinct adaptations are also evident in *P. planus* and *P. rostellatus*, including broader and rounder thoracic segments in the former, and an abundance of long setae on the antennae and urosome in the latter. *Kelleria gradata*, another species-specific symbiont, demonstrates elongated setae, particularly on the swimming legs, and thoracic segment expansion, a feature also observed in *Critomolgus fishelsoni* and *Doridicola patulus*.

However, conducting a comprehensive comparative analysis presents considerable challenges, primarily due to the variability in research depth, taxonomic precision, and accuracy in species identification. Moreover, our understanding of host specificity is significantly constrained by the fragmentary nature of the available data and the absence of a systematic approach to this issue. This limitation is not exclusive to these copepods but also extends to the majority of copepods associated with invertebrates, underscoring a significant gap in our comprehensive understanding of symbiotic relationships in marine ecosystems, as noted by Ivanenko et al. (2018).

3.5. Distribution of Crinoid-Associated Copepods

Copepods engaged in symbiosis with crinoids are distributed across a wide range of ecosystems, extending from tropical to temperate latitudes in both Western and Eastern hemispheres, as depicted in Figure 5. Predominantly, the distribution of observational data is concentrated in the temperate zones of both hemispheres, with a comparatively reduced dataset originating from tropical regions. These symbiotic interactions are documented in five out of the twelve delineated marine ecoregions, according to Spalding et al. (2007), with regions such as the Central and Western Indo-Pacific epitomizing the richness in biodiversity, detailed in Table 4. Conversely, the temperate Northern

Pacific and Atlantic regions are characterized by a notably lower diversity of these symbiotic associations.

Table 4. The distribution of symbiotic copepods and their hosts in the ecoregions *

Region	# of localities	# of records	# of symbiont orders	# of symbiont families	# of symbiont genera	# of symbiont species	# of host families	# of host genera	# of host species
Central Indo-Pacific	21	74	2	2	3	17	4	9	14
Temperate Northern Atlantic	4	5	1	1	1	1	1	1	2
Temperate Northern Pacific	5	11	2	2	3	6	4	4	5
Tropical Atlantic	1	2	1	1	1	1	1	2	2
Western Indo-Pacific	23	71	3	6	7	13	5	11	12

* WoRMS database

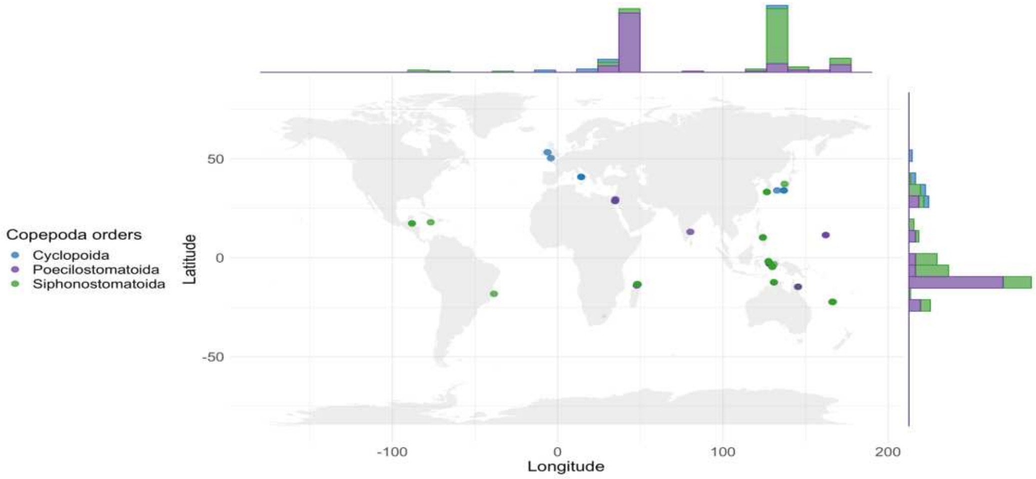

Figure 5. Distribution of the copepods associated with crinoids in the World Ocean. The marginal histogram illustrates the latitudinal and longitudinal distribution of the reports of copepods.

The paucity of data in certain geographical areas can be attributed to either the absence of copepod populations or to the lack of extensive research in these locales. The distribution pattern of existing data may reflect the habitat preferences inherent to copepod species, as well as highlight areas of specific interest within the research community. This pattern underscores the critical need for enhanced research efforts in under-explored regions to attain a holistic understanding of the global distribution patterns of these marine symbionts.

Several taxa within the copepod community, namely *Collocheres prionotus*, *C. uncinatus*, *Pseudanthessius madrasensis*, and *P. major*, alongside crinoids such as *Capillaster multiradiatus* and *Stephanometra indica*, demonstrate a pan-Indo-Pacific distribution. Biodiversity hotspots for these organisms are identified in regions including Madagascar, Australia, and the Indo-West Pacific archipelagos, with notable biodiversity concentrations in Madagascar's northern area, the Moluccas of Indonesia, and New Caledonia. The heightened diversity observed in regions like Indonesia and Madagascar is likely a result of intensive sampling efforts, suggesting that further research could reveal additional, cryptic species. The Atlantic region, with rare findings like the parasitic *Enterognathus comatulae*, remains largely uncharted in this context.

The genus *Scambicornus* is observed in a limited number of localities, in contrast to the more widespread geographical presence of *Collocheres* and *Enterognathus*. Species such as *Collocheres comanthiphilus*, *Pseudanthessius major*, and *Glyptocheres extrusus* are of particular interest due to their extensive transmarine distribution. Additionally, the cosmopolitan presence of the scarcely documented *Enterognathus* genus, spanning from the northeast Atlantic to Japanese waters, presents a compelling case for further investigation. The morphological adaptations observed in these copepods, especially in terms of specialized oral structures and appendages, are indicative of their advanced symbiotic relationships. Yet, these taxa do not exhibit any distinct morphological characteristics that would differentiate them from their congeneric counterparts.

3.6. Bathymetric Distribution

The analysis of depth-related data offers an enhanced understanding of the habitat preferences in symbiotic relationships between copepods and their hosts. The concentration of research efforts within a depth range of 47 meters, contrasted with sporadic findings in deep-sea environments, points to two possible interpretations: a depth-specific specialization in these symbiotic relationships or a research bias towards sampling in more accessible, shallower waters. The discovery of the copepod species *Parenterognathus troglodytes* in deep-sea habitats underscores the remarkable adaptability of certain copepod taxa to diverse environmental conditions.

A significant correlation is observed between the bathymetric distribution of copepods and the preferred habitats of stalked crinoids, predominantly within the 0–200-meter depth range (Figure 5). This correlation may indicate a potential co-evolutionary relationship between these organisms, shaped by their long-term interactions in shared ecological niches. The depth range preference suggests that environmental factors associated with shallower marine zones play a crucial role in facilitating and maintaining these symbiotic relationships. The presence of copepods in deeper waters, albeit less frequently documented, opens avenues for further exploration into the adaptive capabilities and ecological breadth of these symbiotic copepods.

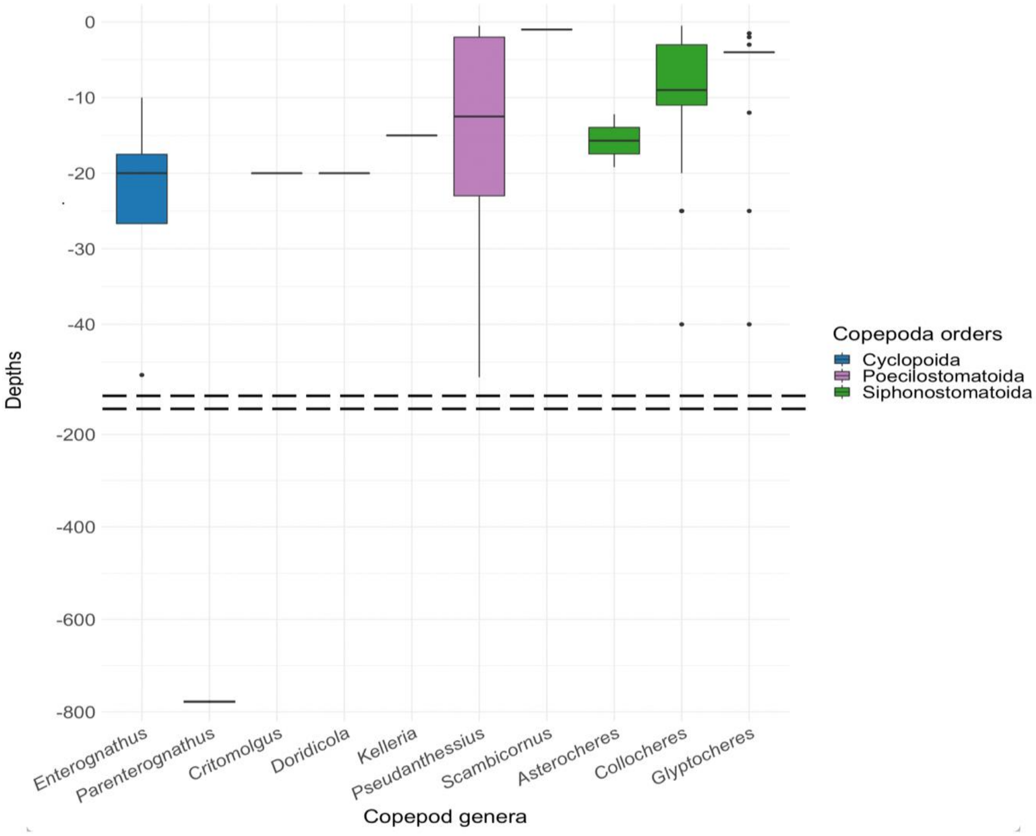

Figure 5. Distribution of symbiotic copepods associated with crinoids by depth. This box plot illustrates the data distribution. The horizontal line within each box represents the median of the dataset. The box defines the interquartile range, covering the 25th to 75th percentiles. Whiskers

extending from each box show the minimum and maximum data values. Data points appearing outside of these whiskers are identified as outliers.

Differences in the bathymetric distribution of symbiotic copepods across various orders are observed. For instance, the Cyclopoida order is represented by a single genus favouring relatively shallow waters, predominantly around -20 meters. In contrast, the Poecilostomatoida order exhibits a more extensive range of habitat depths, ranging from shallow waters (-10 meters) to deeper locations (-40 meters and below), indicating a significant diversity in their living conditions. The copepods of the order Siphonostomatoida also shows adaptation to various depths, but with a narrower depth range than Poecilostomatoida, focusing around -10 meters. It is noteworthy that certain copepod genera, such as *Collocheres*, *Enterognathus*, and *Scambicornus*, inhabit a very narrow depth range. Exceptions in the data, particularly within the Poecilostomatoida order, may signal the presence of rare species that prefer significantly deeper waters compared to their counterparts. Overall, the data reflect a broad spectrum of adaptations among different copepod orders to living conditions at various depths, demonstrating their ecological flexibility and the diversity of ecological niches in the marine environment.

4. Conclusions

This investigation leads to a series of conclusions, tempered by the recognition of substantial gaps in the existing body of research. These gaps manifest as disparities in the depth and scope of studies, variations in taxonomic precision, and inconsistencies in the identification of specific copepod taxa. It is imperative to emphasize the need for the enhancement and standardization of research methodologies, specifically tailored to the study of microsymbiotic relationships within marine invertebrates. Such methodological advancements are crucial for addressing and bridging the conspicuous knowledge gaps in this field.

The exploration of copepod-crinoid symbiosis, representing a substantial yet largely uncharted domain within scientific inquiry, faces notable challenges. These challenges include a prevailing research bias towards macro-symbionts, the inherent complexities in the collection and analysis of microsymbiont data, and the nascent stage of marine invertebrate symbiosis research. To advance our understanding of these complex ecological interactions, concerted efforts aimed at overcoming these obstacles are imperative.

Current knowledge in the field of copepod-crinoid symbiosis represents only a fraction—approximately 5%—of the hypothesized diversity of crinoid hosts. Preliminary calculations, based on the observed diversity of copepods associated with crinoids and relying solely on morphological studies, suggest that a minimum of 600 copepod species remain to be described. The potential application of molecular methodologies, which have successfully identified previously unrecognized species diversity in other taxa at the morphological level, is expected to significantly and exponentially increase these preliminary estimates (Ivanenko et al., 2018; Martínez et al., 2020). This underscores the urgent need for more comprehensive and in-depth research efforts focused on microscopic crustaceans (Bron et al., 2011; Zeppilli et al., 2015). Future research initiatives in this area are encouraged to broaden their scope of investigation and to employ robust and innovative methodologies. Such approaches are essential for fully unraveling the complexities and nuances of symbiotic relationships within marine ecosystems. The advancement of this field critically hinges on the integration of interdisciplinary methods and a dedicated commitment to enhancing our understanding of these intricate ecological interactions. This collective effort will not only illuminate the intricate symbiotic dynamics but also make a substantial contribution to the broader understanding of marine biodiversity and ecosystem functioning.

Supplementary Materials: The following supporting information can be downloaded at: www.mdpi.com/xxx/s1, **Table S1**: Crinoids as hosts of copepod crustaceans.

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Appendix A

Table A1. Copepod crustaceans recorded as associated with octocorals (see also **Table S1**. Octocorals as hosts of copepod crustaceans).

Copepod	Host species: valid name (and as in original record)	Host abbreviation *	Symbiosis nature abbreviation **	Site abbreviation **	Depth (m)	Reference
Cyclopoida						
Enterognathidae						
Enterognathus comatulae Giesbrecht, 1900	*Antedon bifida* (Pennant, 1777)	A	en	GB, IE		Grainger, 1950
Enterognathus comatulae Giesbrecht, 1901	*Antedon mediterranea* (Lamarck, 1816)	A	en	FR, IT		Changeux, Delamare Deboutteville, 1956; Giesbrecht, 1900; Stock, 1959
Enterognathus inabai Ohtsuka, Shimomura, Kitazawa, 2012	*Lamprometra* sp.	M	en	JP	46.7-46.9	Ohtsuka, Shimomura, Kitazawa, 2012
Entherognathus lateripes Stock, 1966	*Decametra chadwicki* (Clark, 1911)	Col	en	IL	20	Stock, 1966
Entherognathus lateripes Stock, 1966	*Oligometra serripinna* (Carpenter, 1811)	Col	en	IL	20	Stock, 1966
Entherognathus lateripes Stock, 1966	*Heterometra savignii* (Müller, 1841) (= *Heterometra savignyi* (Müller, 1841))	H	en	IL	10	Stock, 1966
Parenterognathus troglodytes Ohtsuka, Kitazawa, Boxshall, 2010	*Glyptometra crassa* (Clark, 1912)	Ch	en	JP	775, 780.8-787.1	Ohtsuka, Kitazawa, Boxshall, 2010
Poecilostomatoida						
Kelleriidae						
Kelleria gradata Stock, 1967	*Heterometra savignii* (Müller, 1841) (= *Heterometra savignyi* (Müller, 1841))	H	ec	IL	15	Stock, 1967
Pseudanthessiidae	*Dichrometra flagellata* (Müller, 1841)					

	(= *Dichrometra afra* Clark, 1912)					
Pseudanthessius angularis Humes, Ho, 1970	*Stephanometra indica* (Smith, 1876) (= *Stephanometra spicata* (Carpenter, 1881))	M	ec	MG	1	Humes, Ho, 1970
Pseudanthessius angularis Humes, Ho, 1970	*Anneissia bennetti* (Müller, 1841) (= *Comanthus bennetti* (Müller, 1841))	M	ec	MG	2, 6	Humes, Ho, 1970
Pseudanthessius comanthi Humes, 1972	*Comanthus wahlbergii* (Müller, 1843)	Com	ec	MH	4, 8	Humes, 1972
Pseudanthessius comanthi Humes, 1972	*Oxycomanthus bennetti* (Müller, 1841) (= *Comanthus bennetti* (Müller, 1841))	Com	ec	ID	25	Humes, 1987
Pseudanthessius comanthi Humes, 1972	*Heterometra savignii* (Müller, 1841) (= *Heterometra savignyi* (Müller, 1841))	Com	ec	AU, ID, PH	2, 3, 4, 10, 12, 40	Humes, 1987
Pseudanthessius madrasensis Reddiah, 1968	Comatulida		ec	IN		Reddiah, 1968
Pseudanthessius madrasensis Reddiah, 1968	*Tropiometra afra* (Hartlaub, 1890)	T	ec	NC	1.5, 2, 3	Humes, 1977
Pseudanthessius madrasensis Reddiah, 1968	*Tropiometra carinata* (Lamarck, 1816)	T	ec	MG	0.5, 1, 1.5, 2, 3, 15	Humes, Ho, 1970
Pseudanthessius major Stock, 1967	*Cenometra emendatrix* (Bell, 1892)	Col	ec	MG	10, 20	Stock, 1967
Pseudanthessius major Stock, 1967	*Heterometra africana* (Clark, 1911)	H	ec	MG	17, 18, 25, 29, 34	Stock, 1967
Pseudanthessius major Stock, 1967	*Heterometra savignii* (Müller, 1841) (= *Heterometra savignyi* (Müller, 1841))	H	ec	IL	10, 15	Stock, 1967
Pseudanthessius major Stock, 1967	*Himerometra robustipinna* (Carpenter, 1881) (= *Himerometra magnipinna* Clark, 1908)	H	ec	NC	1	Humes, 1977

Pseudanthessius major Stock, 1967	*Dichrometra flagellata* (Müller, 1841) (= *Dichrometra afra* Clark, 1912)	M	ec	MG	1, 2, 6	Stock, 1967
Pseudanthessius major Stock, 1967	*Lamprometra palmata* (Müller, 1841) (= *Lamprometra klunzingeri* (Hartlaub, 1890))	M	ec	MG	1, 13	Stock, 1967
Pseudanthessius major Stock, 1967	*Liparometra sp.*	M	ec	MG	15, 23, 27, 35	Stock, 1967
Pseudanthessius major Stock, 1967	*Stephanometra indica* (Smith, 1876) (= *Stephanometra spicata* (Carpenter, 1881))	M	ec	MG, NC	2, 3, 13, 17	Stock, 1967; Humes, 1977
Pseudanthessius minor Stock, 1967	*Heterometra africana* (Clark, 1911)	H	ec	MG	18	Stock, 1967
Pseudanthessius minor Stock, 1967	*Dichrometra flagellata* (Müller, 1841) (= *Dichrometra afra* Clark, 1912)	M	ec	MG	2	Stock, 1967
Pseudanthessius minor Stock, 1967	*Lamprometra palmata* (Müller, 1841) (= *Lamprometra klunzingeri* (Hartlaub, 1890))	M	ec	IL, MG	0.5, 13	Stock, 1967
Pseudanthessius minor Stock, 1967	*Liparometra sp.*	M	ec	MG	15, 23, 27, 35	Stock, 1967
Pseudanthessius planus Kim, 2007	*Himerometra robustipinna* (Carpenter, 1881) (= *Himerometra magnipinna* Clark, 1908)	H	ec	ID	2	Kim, 2007
Pseudanthessius rostellatus Humes, Ho, 1970	*Phanogenia distincta* (Carpenter, 1888) (= *Comaster distinctus* (Carpenter, 1888))	Com	ec	MG	47	Humes, Ho, 1970
Rhynchomolgidae						
Critomolgus fishelsoni (Stock, 1967)	*Oligometra serripinna* (Carpenter, 1811)	Col	ec	IL	20	Stock, 1967
Doridicola patulus (Humes, 1959)	*Cenometra emendatrix* (Bell, 1892)	Col	ec	MG	20	Humes, Stock, 1973
Doridicola venustus (Humes, 1958)	*Cenometra emendatrix* (Bell, 1892)	Col	ec	MG	20	Humes, Stock, 1973
Synapticolidae						

Scambicornus pillaii Stock, 1983	*Capillaster multiradiatus* (Linnaeus, 1758) (= *Capillaster multiradiata* (Linnaeus, 1758))	Com	ec	IL	1	Stock, 1983
Siphonostomatoida						
Asterocheridae						
Asterocheres crinoidicola Humes, 2000	Comatulida		ec	JM		Kim, 2010
Asterocheres crinoidicola Humes, 2000	*Davidaster rubiginosus* (Pourtalès, 1869)	Com	ec	BZ	12.2	Humes, 2000
Asterocheres crinoidicola Humes, 2000	*Nemaster grandis* Clark, 1909	Com	ec	BZ	32.2	Humes, 2000
Asterocheres spinopaulus Johnsson, 1998	Comatulida		ec	BR		Johnsson, 2002
Collocheres amicus Kim, 2007	*Comanthus briareus* (Bell, 1882) (= *Comantheria rotula* Clark, 1912)	Com	ec	ID	17	Kim, 2007
Collocheres brevipes Shin, Kim, 2004	*Anneissia solaster* (Clark, 1907) (= *Comanthus solaster* Clark, 1907)	Com	ec	KP	25	Shin, Kim, 2004
Collocheres comanthiphilus Humes, 1987	*Comanthus parvicirrus* (Müller, 1841)	Com	ec	NC	1.5, 5	Humes, 1987
Collocheres comanthiphilus Humes, 1987	*Comanthus sp.*	Com	ec	NC	1, 3	Humes, 1987
Collocheres comanthiphilus Humes, 1987	*Comanthus wahlbergii* (Müller, 1843)	Com	ec	ID, NC	0.5, 2, 25	Humes, 1987
Collocheres comanthiphilus Humes, 1987	*Oxycomanthus bennetti* (Müller, 1841) (= *Comanthus bennetti* (Müller, 1841))	Com	ec	AU, ID, PH	2, 3, 4, 12, 40	Humes, 1987
Collocheres humesi Kim, 2007	*Comanthus briareus* (Bell, 1882) (= *Comantheria rotula* Clark, 1912)	Com	ec	ID	17	Kim, 2007
Collocheres inaequalis Ho, 1982	*Anneissia japonica* (Müller, 1841)	Com	ec	JP		Ho, 1982

	(= *Comanthus japonica* (Müller, 1841), *Comanthus japonicus* (Müller, 1841))					
Collocheres inflatiseta Humes, 1987	*Phanogenia multibrachiata* (Carpenter, 1888) (= *Comaster multibrachiatus* (Carpenter, 1888))	Com	ec	ID	10	Humes, 1987
Collocheres marginatus Humes, 1987	*Comaster multifidus* (Müller, 1841) (= *Comanthina variabilis* (Bell, 1882))	Com	ec	AU	9	Humes, 1987
Collocheres parvus Humes, 1987	*Davidaster rubiginosus* (Pourtalès, 1869)	Com	ec	ID	10	Humes, 1987
Collocheres prionotus Humes, 1990	*Nemaster grandis* Clark, 1909	Com	ec	ID, MG	0.5, 1	Humes, 1990
Collocheres serrulatus Humes, 1987	Comatulida	Com	ec	ID	10	Humes, 1987
Collocheres solidus Shin, Kim, 2004	*Comanthus briareus* (Bell, 1882) (= *Comantheria rotula* Clark, 1912)	Com	ec	KP	25	Shin, Kim, 2004
Collocheres solidus Shin, Kim, 2004	*Anneissia solaster* (Clark, 1907) (= *Comanthus solaster* Clark, 1907)	Com	ec	KP	25	Shin, Kim, 2004
Collocheres tamladus Shin, Kim, 2004	*Comanthus parvicirrus* (Müller, 1841)	Z	ec	KP		Shin, Kim, 2004
Collocheres thysanotus Humes, 1987	*Comanthus sp.*	Com	ec	AU	9	Humes, 1987
Collocheres thysanotus Humes, 1987	*Comanthus wahlbergii* (Müller, 1843)	Com	ec	AU	9	Humes, 1987
Collocheres titillator Humes, 1987	*Oxycomanthus bennetti* (Müller, 1841) (= *Comanthus bennetti* (Müller, 1841))	Com	ec	ID	10	Humes, 1987
Collocheres uncinatus Stock, 1966	*Comanthus briareus* (Bell, 1882) (= *Comantheria rotula* Clark, 1912)	Col	ec	IL	20	Stock, 1966
Collocheres uncinatus Stock, 1966	*Anneissia japonica* (Müller, 1841)	Com	ec	ID, MG	0.5, 1, 3	Humes, 1990

	(= *Comanthus japonica* (Müller, 1841), *Comanthus japonicus* (Müller, 1841))					
Collocheres uncinatus Stock, 1966	*Phanogenia multibrachiata* (Carpenter, 1888) (= *Comaster multibrachiatus* (Carpenter, 1888))	H	ec	IL	1, 15	Stock, 1966
Glyptocheres comanthinae Humes, 1987	*Comaster multifidus* (Müller, 1841) (= *Comanthina variabilis* (Bell, 1882))	Com	ec	ID	4	Humes, 1987
Glyptocheres extrusus Humes, 1987	*Davidaster rubiginosus* (Pourtalès, 1869)	Com	ec	NC	1.5	Humes, 1987
Glyptocheres extrusus Humes, 1987	*Nemaster grandis* Clark, 1909	Com	ec	ID	25	Humes, 1987
Glyptocheres extrusus Humes, 1987	Comatulida	Com	ec	AU, ID, PH	2, 3, 4, 12, 40	Humes, 1987

* Host Abbreviations: A – Antedonidae, Ch – Charitometridae, Col – Colobometridae, Com – Comasteridae, H – Himerometridae, M – Mariametridae, T – Tropiometridae, Z – Zygometridae. ** Symbiosis nature abbreviation: ec – ectosymbiont, en – endosymbiont. *** Country abbreviation: AU – Australia, BR – Brazil, BZ – Belize, FR – France, GB – United Kingdom, ID – Indonesia, IE – Ireland, IL – Israel, IN – India, IT – Italy, JM – Jamaica, JP – Japan, KP – Korea, MG – Madagascar, MH – Marshall Islands, NC – New Caledonia, PH – Philippines.

Table A2. Description of the dataset with specific information relative to column names, description, units, and attribute type.

Attribute	**Column_name**	**Description**	**Units**	**Attribute_Type**
Record number	rID	Unique number corresponding to specific occurrence		Integer
Record ID	recordID	A structured code incorporating a concise article reference, region and country observation identifiers, shorthand for the location coordinates, and specific abbreviations for the symbiont and host families, complemented by a distinct number.		Text
Aphia ID of symbiont	aphiaID_Symbiont	Unique number for taxon from WoRMS database		Integer
Kingdom of symbiont	kingdom_Symbiont	Taxonomic rank below Domain		Text
Phylum of symbiont	phylum_Symbiont	Taxonomic rank below Kingdom		Text
Class of symbiont	class_Symbiont	Taxonomic rank below Phylum		Text
Order of symbiont	order_Symbiont	Taxonomic rank below Class		Text
Family of symbiont	family_Symbiont	Taxonomic rank below Order		Text
Genus of symbiont	genus_Symbiont	Taxonomic rank below Family and first element in the Latin binomial name		Text
Specific epithet of symbiont	specificEpithet_Symbiont	Second element in the Latin binomial name		Text
Scientific name authorship of symbiont	scientificNameAuthorship_Symbiont	Third element in the Latin binomial name		Text

Symbiont ID	symbiontID	Reviewed species name		Text
Taxon rank of symbiont	taxonRank_Symbiont	Taxonomic rank information (e.g., genus, species)		Text
Taxonomic status of symbiont	taxonomicStatus_Symbiont	Taxonomic status information (e.g., accepted, unaccepted)		Text
Link of symbiont	link_Symbiont	Link to taxon in WoRMS database		Text
Female Body Length	femaleLength	The length of the female specimen, measured from head to tail	μm	Text
Female Body Weight	femaleWeight	The total weight of the female specimen	μm	Text
Male Body Length	maleLength	The length of the male specimen, measured from head to tail	μm	Text
Male Body Weight	maleWeight	The total weight of the male specimen	μm	Text
Aphia ID of host	aphiaID_Host	Unique number for taxon from WoRMS database		Integer
Kingdom of host	kingdom_Host	Taxonomic rank below Domain		Text
Phylum of host	phylum_Host	Taxonomic rank below Kingdom		Text
Class of host	class_Host	Taxonomic rank below Phylum		Text
Order of host	order_Host	Taxonomic rank below Class		Text
Family of host	family_Host	Taxonomic rank below Order		Text
Genus of host	genus_Host	Taxonomic rank below Family and first element in the Latin binomial name		Text
Specific epithet of host	specificEpithet_Host	Second element in the Latin binomial name		Text
Scientific name authorship of host	scientificNameAuthorship_Host	Third element in the Latin binomial name		Text
Host ID	hostID	Reviewed species name		Text
Taxon rank of host	taxonRank_Host	Taxonomic rank information (e.g., genus, species)		Text
Taxonomic status of host	taxonomicStatus_Host	Taxonomic status information (e.g., accepted, unaccepted)		Text
Link of host	link_Host	Link to taxon in WoRMS database		Text
Site ID	siteID	Unique number for locality		Text
Region code	regionCode	Unique number for region		Text
Region	region	Division of the World Ocean (Spalding et al., 2007)		Text
Ocean	ocean	The name of the ocean in which the locality occurs.		Text
Water body	waterBody	The name of the water body in which the locality occurs.		Text
Island	island	The name of the island near which the locality occurs.		Text
Country	country	The name of the country in which the locality occurs.		Text
Country code	countryCode	The standard code (ISO 3166-1-alpha-2) for the country in which the locality occurs.		Text
Locality	locality	Particular area where the taxon was found		Text
Exact Location Description	verbatimLocalition	A comprehensive description of the location from the original article		Text
Geocoordinates	geocoordinates	A combined representation of both latitude and longitude	Degrees Minutes Seconds (DMS)	Text
Latitude	latitude	Coordinate that specifies the N–S position of a point on the Earth surface	Degrees Minutes Seconds (DMS)	Text

Longitude	longitude	Coordinate that specifies the E–W position of a point on the Earth surface	Degrees Minutes Seconds (DMS)	Text
Decimal geocoordinates	decimalGeocoordinates	A combined representation of both latitude and longitude	Decimal degrees, WGS84	Numeric
Decimal latitude	decimalLatitude	Coordinate that specifies the N–S position of a point on the Earth surface	Decimal degrees, WGS84	Numeric
Decimal longitude	decimalLongitude	Coordinate that specifies the E–W position of a point on the Earth surface	Decimal degrees, WGS84	Numeric
Coordinate uncertainty	coordinateUncertaintyInMeters	The horizontal distance from the given decimal latitude and longitude describing the smallest circle containing the whole of the Location.	m	Integer
Minimum depth	minimumDepthInMeters	Vertical distance under sea level	m	Integer
Maximum depth	maximumDepthInMeters	Vertical distance under sea level	m	Integer
Collecting method	collectingMethod	The method of taking sample		Text
Finding method	findingMethod	The method of finding copepods in sample		Text
Type of association	note	Describes the nature of the interaction.		Text
Host interaction site	locationAtHost	The general location or site on the host where the copepod interacts or resides.		Text
Event date	eventDate	Date of sampling.		Date
Year	year	The four-digit year in which the Occurence recorded. Format: yyyy.		Integer
Month	month	The ordinal month in which the Occurence recorded. Format: mm.		Integer
Article ID	articleID	Short reference		Text
Reference	reference	Full reference to article		Text

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