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REVIEW PAPER

Pseudocollinia HISTOPHAGOUS CILIATES INFECT KRILL IN THE PACIFIC AND ATLANTIC OCEANS AND POSSIBLY WORLDWIDE

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ABSTRACT. The genus *Pseudocollinia* (Apostomatida, Pseudocolliniidae) currently includes four species (*P. beringensis*, *P. oregonensis*, *P. brintoni*, and *P. similis*) that infect adults of seven numerically dominant krill species (Order Euphausiacea) in the northeastern Pacific (Bering Sea-to-Gulf of California). In this review, we found four reports in other parts of the world of misidentified or unidentified protists infecting krill. Based on their morphology, cell size and infection of the hemocoel's host, we infer they are histophagous *Pseudocollinia* ciliates. We thus conclude that previous reports of protists (identified as microsporidians) infecting *Thysanoessa inermis* in the northwestern Atlantic Ocean (Bay of Fundy) and unidentified endoparasite ciliates infecting the *Euphausia superba* in the Southern Ocean (Admiralty Bay, King George Island), *Euphausia pacifica* in Sanriku, Japan and *Euphausia similis* var. *armata* in Tasmania, Australia are actually *Pseudocollinia* parasitoid ciliates that await to be morphologically and genetically described. This review provides strong evidence that apostome *Pseudocollinia* ciliates are widespread distributed in the Pacific and Atlantic Oceans, infecting at least nine krill species from Arctic–to–Antarctic zoogeographic regions, having perhaps worldwide distribution as several of their krill hosts. Future studies should focus on discovering parasitoid ciliates in other krill species, as well as in other phytoplankton and zooplankton taxonomic groups.

Keywords: *Collinia, Pseudocollinia,* Parasitoid, Apostome cilliates, Euphausiacea, distribution, zoogeography.

Ciliados histiófagos *Pseudocollinia* que infectan krill en los océanos Pacífico y Atlántico y posiblemente en el resto del mundo

RESUMEN. El género *Pseudocollinia* (Apostomatida, Pseudocolliniidae) actualmente incluye cuatro especies (*P. beringensis, P. oregonensis, P. brintoni* y *P. similis*) que han sido descubiertas infectando especímenes adultos de siete especies de krill (Orden Euphausiacea) numéricamente dominantes en el Pacífico nororiental (del Mar de Bering al Golfo de California). En esta revisión encontramos cuatro publicaciones que indican que estos ciliados se encuentran en otras partes del mundo pero que estos protistas han sido identificados erróneamente o no fueron identificados taxonómicamente. En la presente revisión se infiere que estos protistas son ciliados del género *Pseudocollinia* debido a que infectan krill, su morfología y tamaño celular, así como su localización de infección en el hemocele del huésped. Por lo tanto, concluimos que los reportes previos de protistas (identificados como microsporidios) descubiertos infectando a *Thysanoessa inermis* en el Océano Atlántico noroccidental (Bahía de Fundy) y los ciliados endoparásitos no identificados que infectan al krill Antárctico *Euphausia superba* en el Océano Austral (Bahía Almiralty, Isla King George), *Euphausia pacifica* en Sanriku, Japón y *Euphausia similis* var. *armata* en Tasmania, Australia también son ciliados parasitoides del género *Pseudocollinia*, pero que esperan ser descritos morfológicamente y genéticamente en el futuro. Esta revisión proporciona evidencia de que los ciliados *Pseudocollinia* están ampliamente distribuidos en los océanos Pacífico y Atlántico, infectando al menos nueve de las especies de hospederos de krill de regiones zoogeográficas Árticas a Antárticas teniendo una distribución probablemente mundial; como ocurre en varias especies de krill. Estudios futuros deben centrarse en descubrir los ciliados de parasitoides en otras especies de krill y en otros grupos taxonómicos de fitoplancton y zooplancton.

Palabras clave: *Collinia, Pseudocollinia*, parasitoide, ciliados apostómicos, distribución, zoogeografía.

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INTRODUCTION

A parasitoid is an organism that for most of its life is associated with a single host organism in a relationship that is in essence parasitic, but unlike a true parasite it ultimately sterilizes or kills, and sometimes consumes, the host (Parmentier & Michel, 2013; Gómez-Gutiérrez *et al*., 2015a,b). Two types of parasitoids are known to infect krill (Order Euphausiacea) worldwide (Gómez-Gutiérrez *et al*., 2017). Firstly, two species of dinoflagellates (*Chytriodinium roseum* and *C. affine*) that kill eggs of *Meganyctiphanes norvegica* (M Sars, 1857) in the Mediterranean Sea (Dogiel, 1906; Cachon & Cachon, 1968; Daugbjerg *et al*., 2000; Gómez *et al*., 2009) and eggs of *Euphausia pacifica* Hansen, 1911 off the Oregon coasts (USA) (Gómez-Gutiérrez *et al*., 2009). Secondly, apostome ciliates of the genus *Pseudocollinia*, discovered 80 years later (Capriulo & Small, 1986; Capriulo *et al*., 1991; Gómez-Gutiérrez *et al*., 2003, 2006, 2015a, b; Lynn *et al*., 2014). Apostome histophagous ciliates can cause massive die-offs of krill because they have short life cycles, relatively high transmission rates, and capacity to transform host biomass into reproduc-

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tive and transmission cells that kill the crustacean host (Gómez-Gutiérrez *et al*., 2003, 2006, 2012, 2015a,b; Chantangsi *et al*., 2013; Lynn *et al*., 2014). The genus *Pseudocollinia* currently includes four extant species: *P. beringensis* (Capriulo & Small, 1986), *P. oregonensis* (Gómez-Gutiérrez *et al*., 2006), *P. brintoni* Gómez-Gutiérrez *et al*., 2012, and *P. similis* Lynn *et al*., 2014. Here, we review cases of parasitoid ciliates of the genus *Pseudocollinia* that infect euphausiids (krill) showing observational evidence that those parasitoid (histophagous) apostome ciliates match the broad zoogeographical distribution patterns of their pelagic krill hosts. From a literature review of 162 published articles of krill parasites worldwide there are four other reports of unidentified endoparasitic apostome ciliates (Gómez-Gutiérrez *et al*., 2017) that we have subsequently interpreted here as ciliate species of the genus *Pseudocollinia*. They had been identified as other parasites or krill pathologies or simply unassigned to any taxonomic status: infection of adults of *Thysanoessa inermis* (Krøyer, 1846) in the Bay of Fundy, Canada (originally identified as microsporidians) (Kulka & Corey, 1984), unidentified endoparasitic ciliates infecting the Antarctic krill *Euphausia superba* Dana, 1850 in Admiralty Bay in King George Island (Stankovic & Rakusa-Suszczewski, 1996), *Euphausia pacifica* Hansen, 1911 in Sanriku coast, Japan (Shimazu, 2006) and *Euphausia similis* var. *armata* G.O. Sars, 1883 in the east coast of Tasmania, Australia (Gómez-Gutiérrez *et al*., 2017). The precise taxonomic classification of these endoparasites is still unknown and must be investigated in the future. Kawaguchi & Toda (1997) reported ciliates reproducing in the guts of *E. superba*, but later those gastro-intestinal parasites were correctly identified as gregarines (Apicomplexa) infecting larval-to-adult phases (Kawaguchi *et al*., 1999; Takahashi *et al*., 2003, 2011).

With this conceptual reinterpretation of previous records *Pseudocollinia* parasitoid ciliates infect at least nine numerically dominant krill species worldwide: the Arctic [*T. inermis*, *Thysanoessa raschi* (M. Sars, 1864) and *Thysanoessa longipes* Brandt, 1851], Arctic-temperate (*Thysanoessa gregaria* G.O. Sars, 1883), temperate (*Euphausia pacifica* and *Thysanoessa spinifera* Holmes, 1900), subtropical (*Nyctiphanes simplex* Hansen, 1911), sub Antartic (*E. similis* var. *armata*) , and Antarctic (*E. superba*). Thus, *Pseudocollinia* ciliates infect krill species that reproduce with sac-spawning (*N. simplex*) and mostly broadcast reproductive strategies. Infected krill include neritic (*T. spinifera* or *N. simplex*) and oceanic (*Thysanoessa longipes*) species, with host species ranging in total lenght from 8-19 mm (*N. simplex*) to 60 mm (*E. superba*).

Distribution of formally described *Pseudocollinia* species seems to be restricted to the Northeast Pacific, but observations of unidentified or misidentified protists from published literature suggest that those ciliates have considerably larger zoogeographic distribution patterns. The goal of this literature review is to conceptually present an integrative perspective about currently known *Pseudocollinia* parasitoid ciliate–krill host species distribution patterns in the Pacific Ocean, Northwest Atlantic Ocean, and the Southern Ocean.

Historical records of unidentified endoparasitic ciliates of krill

In a recent review of epibionts, micropredators, parasites and parasitoids that interact with krill worldwide, an unidentified protozoan infecting *Euphausia similis* var. *armata* was reported in the east coast of Tasmania, Australia (Gómez-Gutiérrez *et al*., 2017). Here, additional and more detailed information is provided on this infection report (Fig. 1 A–D, Table 1). In a zooplankton sample collected in 13 June 1981, near the South West Cape of Tasmania eleven *E. similis* var. *armata* krill specimens were collected; eight of them (16.7–21.7 mm total length; three males and five females) were infected with an unidentified endoparasitic ciliates of the genus *Pseudocollinia* (Table 1). All infected krill specimens were in late infection stage, when intensity is high and apostome ciliates in trophont and tomont stages invade all parts of the body, but quantification of intensity was not attempted (Fig. 1A–D). We failed to do scanning electron microscopy (SEM) and transmission electron microscopy (TEM) because infected krill was then preserved in formalin for 28 years.

The worldwide zoogeographic distributions of all krill species (Brinton, 1962, 1975; Brinton *et al*., 2000) that have been observed to be infected with *Pseudocollinia* are shown in Fig. 2A–C. Most of the research on krill infected with *Pseudocollinia* has been conducted exclusively in the region from the Bering Sea to the Baja California Peninsula (including the Gulf of California) (Fig. 3) (Lynn *et al*., 2014). The zoogeographic distribution of several krill species (Brinton, 1962, 1975; Brinton *et al*., 2000) infected with *Pseudocollinia* ciliates overlap suggesting potential krill interspecific infections. A single *Pseudocollinia* species could infect multiple krill host species, as it occurs in the Bering Sea (Capriulo & Small, 1986; Capriulo *et al*., 1991; Lynn *et al*., 2014) and along the west coast of USA (Gómez-Gutiérrez *et al*., 2003, 2006) (Fig. 2A–C, Fig. 3). There is a significant gap in knowledge about parasitoid infections of krill species in the Indian Ocean, the South Atlantic and for tropical latitudes worldwide. This is a result of the lack of parasitological studies of krill in broad regions of the ocean, rather than a natural biogeographic distribution of *Pseudocollinia*.

During the first identification of a histophagous apostome ciliate infecting krill, *Collinia beringensis*

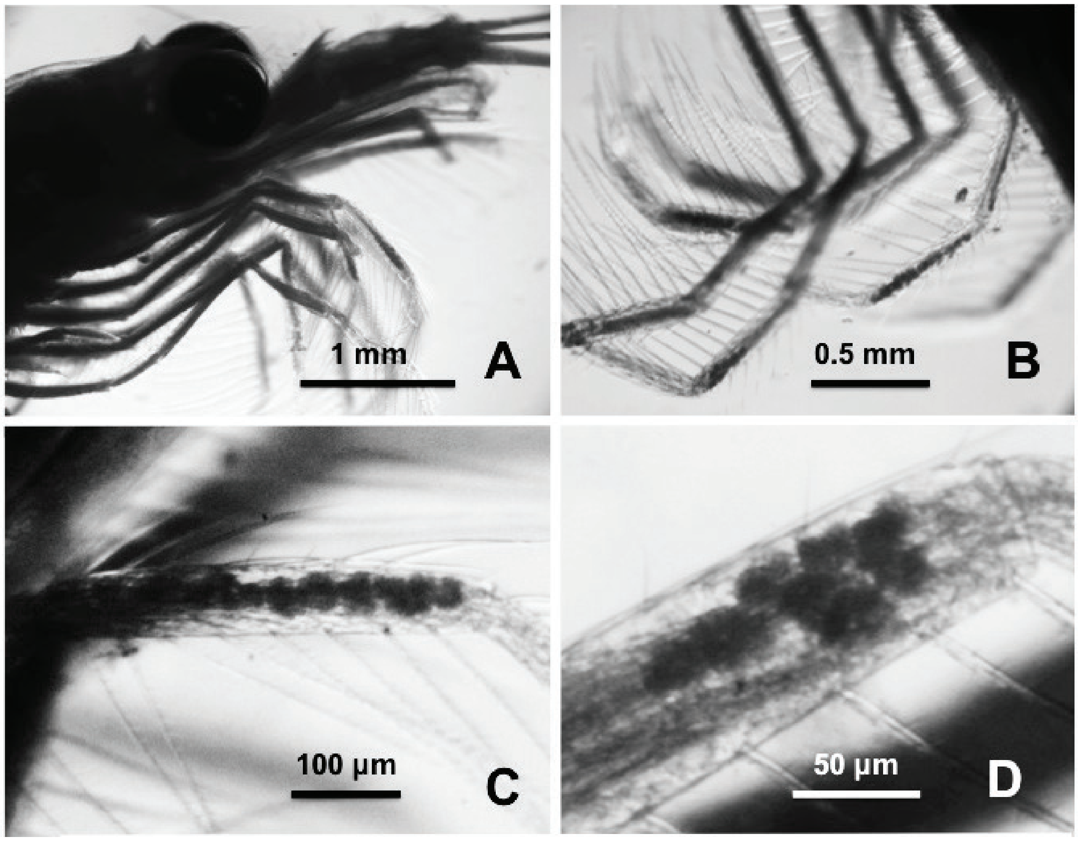

Figure 1. *Pseudocollinia* sp. parasitoid ciliates infecting the sub Antartic krill *Euphausia similis* var. *armata* GO Sars, 1883. Specimens collected during 13 June 1981 off the east coast of Tasmania, Australia.

(Collinidae) was reported for *Thysanoessa inermis* (Capriulo & Small, 1986). This species, along with the other histophagous ciliate species, *Collinia oregonensis* and the new species *Pseudocollinia brintoni* that infect krill, was later transferred to a new genus *Pseudocollinia* in the family Collinidae (Gómez-Gutiérrez *et al*., 2012). In 2013, on the basis of morphology and genetic information, *Pseudocollinia* was transferred to the newly established family Pseudocollinidae, which included the new genus

Table 1. Endoparasitic *Pseudocollinia* sp. ciliates infecting *Euphausia similis* var. *armata* collected during 13 June 1981 at Soft SW Cape in southeastern Tasmania, Australia (station CR Shot 2). * = Presence of *Pseudocollinia* ciliates, intensity of ciliate cells inside the krill body was not estimated. Molt stage according to Buchholz (1982)

Krill adult sex	Total length (mm)	Molt stage	*Pseudocollinia* sp. ciliates
male	11.7		
male	19.2		
female	16.7	B–C	
female	17.8		
female	19.5	B–C	
male	17.7		*
male	19.2	B–C	*
male	20.8		*
female	17.0	B–C	*
female	17.7	D	*
female	18.0	B–C	*
female	18.2	B–C	*
female	21.7	B–C	*

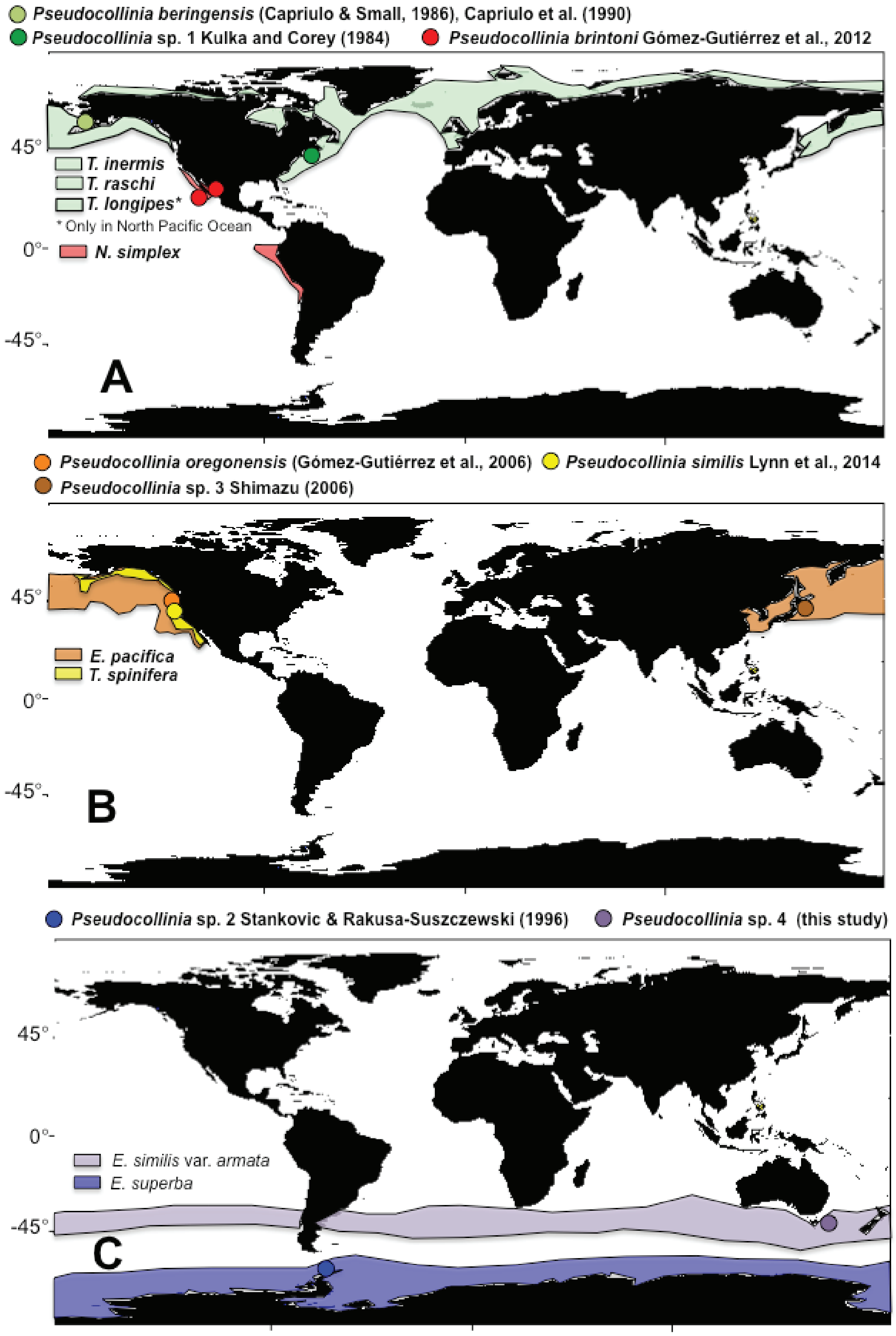

Figure 2. Distribution of *Pseudocollinia* parasitoid ciliates infecting nine krill species: (A) *Pseudocollinia beringensis* (Capriulo & Small, 1986) infecting Artic *Thysanoessa inermis*, *Thysanoessa raschi*, and *Thysanoessa longipes* in the Bering Sea (Capriulo & Small, 1986; Capriulo *et al*., 1990; Lynn *et al*., 2014), *Pseudocollinia* sp. in the northwest Atlantic (Kulka & Corey, 1984); *Pseudocollinia brintoni* infecting sub Tropical krill *Nyctiphanes simplex* in the west coast of the Baja California Peninsula and the Gulf of California (Gómez-Gutiérrez *et al*., 2012, 2015a, b); (B) *Pseudocollinia oregonensis* infecting temperate krill *Euphausia pacifica* in the west coast of USA (Gómez-Gutiérrez *et al*., 2006). *Pseudocollinia* sp. east coast of Japan (Shimazu, 2006), and *Pseudocollinia similis* infecting *Thysanoessa spinifera* and likely *Thysanoessa gregaria* in the west coast of USA (Lynn *et al*., 2014); C) In the Southern Ocean, the Antarctic krill *Euphausia superba* is infected with an unidentified *Pseudocollinia* sp. (Stankovic & Rakusa-Suszczewski 1996); and an unidentified *Pseudocollinia* sp. infects the sub Antartic *Euphausia similis* var. *armata* (Gómez-Gutiérrez *et al*., 2017, this study).

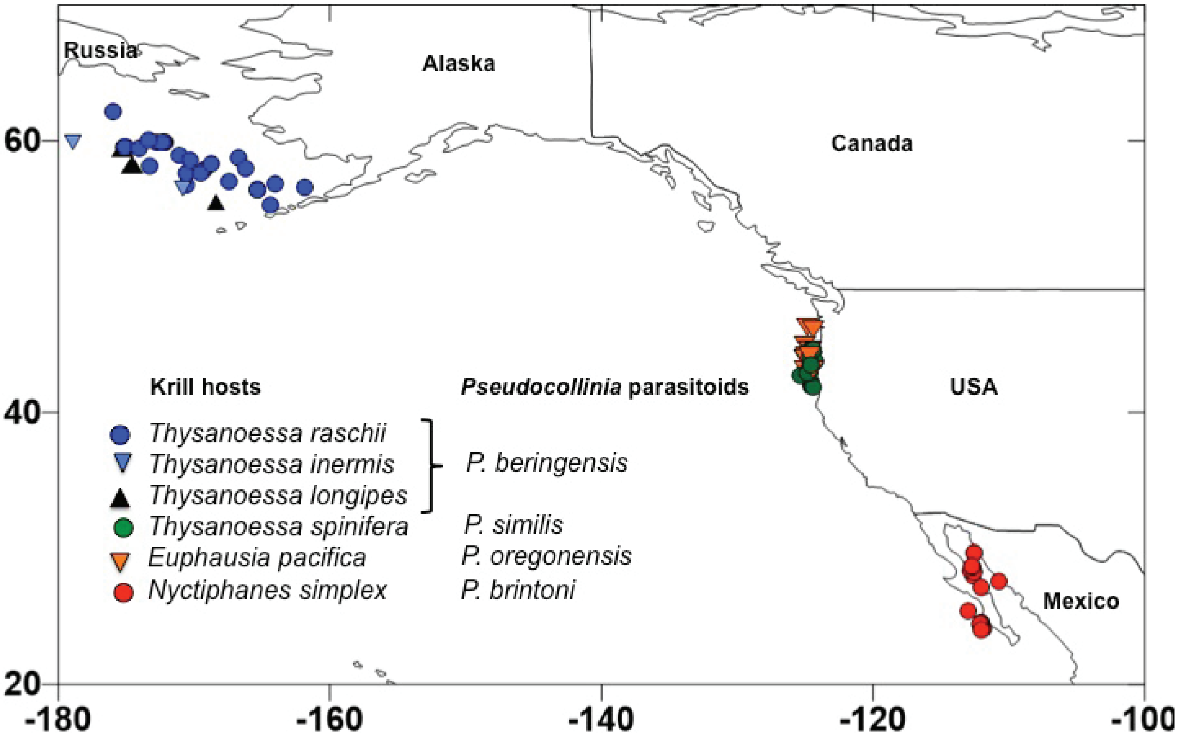

Figure 3. Distribution of krill species infected with *Pseudocollinia* ciliates collected in the region from Bering Sea-to-Baja California Peninsula (including the Gulf of California) where most of the parasitological research has been done.

and species *Fusiforma themisticola*, that infects the hyperiid amphipod *Themisto libellula* (Lichtenstein in Mandt, 1822) in the Beaufort Sea (Chantangsi *et al*., 2013). Two years earlier than the formal description of *Pseudocollinia beringensis* (Capriulo & Small, 1986), Kulka and Corey (1984) were the first to discover the then completely unknown protozoans endoparasites currently known as *Pseudocollinia* ciliates. However, they misidentified them as microsporidians, infecting *T. inermis* of specimens of both sexes and anomalous ova (Fig. 4A, B). Carefully inspecting the photographs in Kulka and Corey (1984) and with current knowledge on such apostome ciliates and all types of epibionts, micropredators, parasites and parasitoids that interact with krill worldwide (Gómez-Gutiérrez *et al*., 2017), they are here interpreted as *Pseudocollinia* endoparasitic ciliates (tentatively identified as *P. beringensis* for the *T. inermis* host and Arctic zoogeographic region) (Fig. 4A, B). Their figure 2a of Kulka and Corey (1984) shows a histological section of a krill infected with trophont cells with characteristic oval shape of 40-µm diameter; ciliates are observed surrounding the cell that has a large macro-nucleus. Their figure 4 clearly shows a tomont cell dividing by palintomy (not an anomalous ova) (Fig. 4B). All these morphological characteristics are similar to histological observations of *Pseudocollinia brintoni* infecting the subtropical krill *N. simplex* showing abundant trophonts (feeding stage) (Fig. 4C) and tomonts (reproductive stage) dividing by palintomy to produce two smaller tomite cells (infective transmission stage) (Fig. 4D). The comparison of this histological evidence strongly confirms the identity and type of parasite reported in Bay Fundy, Canada (Fig. 4A–D).

Stankovic and Rakusa-Suszczewski (1996) published photographs in their figures 1-4, reported as "unidentified endoparasitic ciliates...that may have a negative (lethal) consequence for the host", unambiguously show ciliates of the genus *Pseudocollinia* (although of an unknown species), infecting *Euphausia superba.* Those ciliates also closely resemble the morphology and sizes of *Pseudocollinia* sp. ciliates photographed in the present study (Fig. 4C, D) and the distinctive infection pattern reproducing in the hemocoel and filling other body cavities like periopods and pleopods (Fig. 1A-D) infecting *E. similis* var. *armata* collected near Tasmania and other previous studies (Gómez-Gutiérrez *et al*., 2003, 2006, 2012; Lynn *et al*., 2014). Shimazu (2006) reported (in Japanese) unidentified ciliates in the hemocoel of *Euphausia pacifica* collected in waters off Sanriku, Japan (unfortunately without photographs to corroborate morphology and cell size). However, these ciliates are likely to be *Pseudocollinia oregonensis,* that also infect *E. pacifica* in the California Current System (Gómez-Gutiérrez *et al*., 2003, 2006) and it is the only known type of endo-

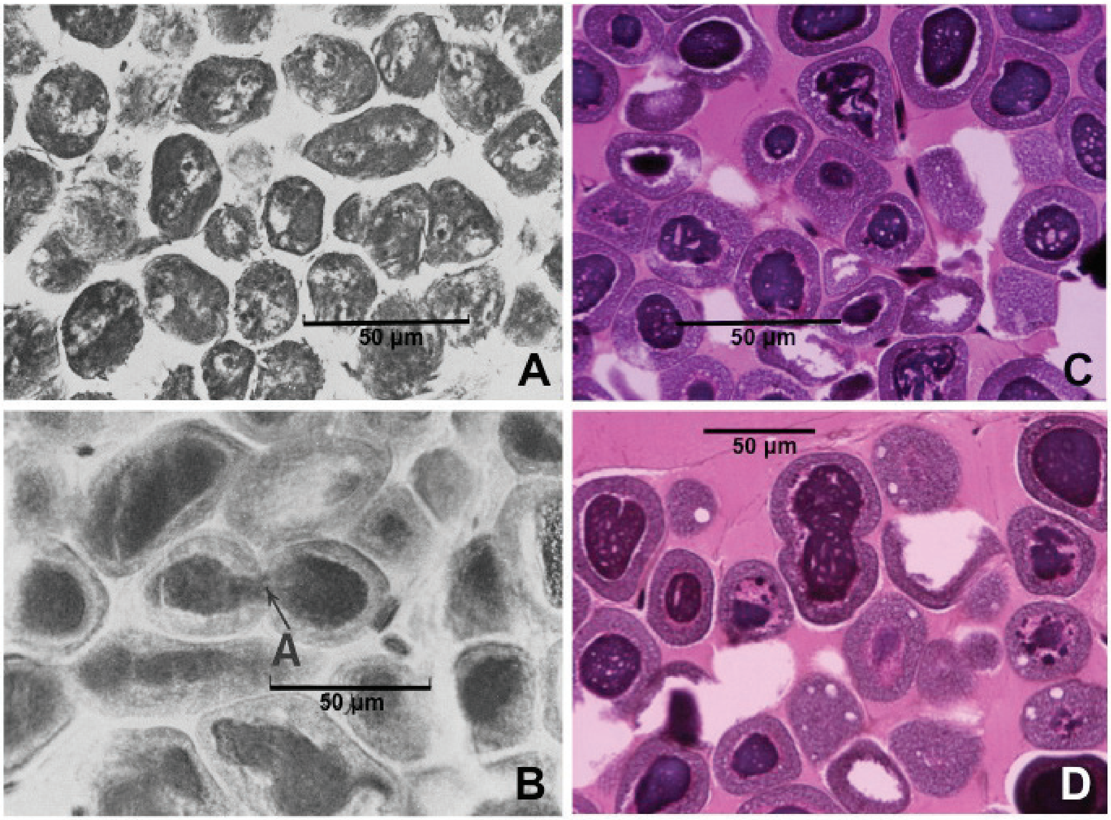

Figure 4. Comparison of longitudinal histological cuts of the krill's hemocoel with endoparasitoids infecting (A,B) *Thysanoessa inermis* collected at Bay Fundy, Canada (Kulka & Corey, 1984) and (C,D) *Nyctiphanes simplex* collected in the Gulf of California, Mexico (Gómez-Gutiérrez pers. observ.). (A) endoparasites originally described as "a massive infection of a microsporidian" (Fig. 3b from Kulka & Corey, 1984); (B) cells originally described as "an abnormal ovum in cell division" (Fig. 4 from Kulka & Corey, 1984). These endoparasites are here interpreted as *Pseudocollinia beringensis* apostome ciliates; (C) *Pseudocollinia brintoni* trophont stage apostome ciliates infecting the krill hemocoel; and (D) *Pseudocollinia brintoni* tomont dividing by palintomy, the small separate ciliates are in tomite transmission ciliate stage. A and B reproduced and modified with permission of Crustaceana.

parasitic ciliate that infect hemocoels of krill worldwide (Gómez-Gutiérrez *et al*., 2017). If the species identity is confirmed, this would be the first report of *Pseudocollinia* ciliates infecting krill in the west Pacific Ocean.

An unusually deep observation of *Euphausia superba* feeding in bathypelagic habitat (550-3500 m depth) where orange swollen cephalothorax individuals were originally interpreted by scientists as gravid females in Marguerite Bay, western Antarctic Peninsula (3000 m depth) (Clarke & Tyler, 2008). However, when females of *E. superba* become gravid, their gonads are gray not orange. This observation lead us to speculate that those *E. superba* individuals were likely individuals in advanced infection phase with *Pseudocollinia* sp. ciliates (typically causing swollen cephalothorax) as result of a mass mortality event. All specimens in the ROV photographs (including photographs of their supplemental material) looked orange individuals with swollen cephalothorax and they observed large numbers of "exuviae" (cast exoskeletons) that we interpreted as dead animals after the histophagous ciliates consume the infected euphausiids (carcasses). Those images resemble mass epizootic event observed with ROPOS ROV in Astoria Canyon, Oregon, USA, with dead specimens sinking (Gómez-Gutiérrez *et al*., 2003). This may also explain the massive krill "dead body rain" observed in *E. superba* in the Antarctic Sea (Sokolova, 1994). Future parasitological and ethological studies of *E. superba* will test our, so far, hypothetical interpretation.

Zoogeography of *Pseudocollinia* and krill hosts

Pseudocollinia ciliates can successfully complete their life cycles by preferentially infecting the most abundant krill. These krill species typically form massive aggregations and in some cases, have broad zoogeographic range that suggests their *Pseudocollinia* also are widely distributed. Lynn *et al*. (2014) speculated that krill abundance and behavior imposes co-evolutionary interaction between krill and parasitoid ciliates. However, using *cox1* and SSU rDNA sequences of the krill host and the histophagous ciliates, to test three distinct models, Lynn *et al*. (2014) statistically rejected the co-diversification hypothesis at the geographical scale of species found in the northeastern Pacific (Bering Sea-to-Gulf of California) (Fig. 3). Co-diversification processes may however exist if comparisons of parasitoids and krill cover a larger area such as comparing species from the Northern and Southern Hemispheres or different oceans (not done yet). Euphausiids seem to be the definitive host where ciliate reproduction occurs, apparently without the need of other host species; thus zoogeographic distribution of their krill host must influence *Psedocollinia* distribution patterns. *Pseudocollinia* ciliates infecting krill species from Arctic-to-Antarctic suggests *Pseudocollinia* ciliates may potentially infect any krill species where there are overlapping zoogeographic distributions (interspecific zoonosis) and intraspecific epizootic infections (Gómez-Gutiérrez *et al*., 2003). Similar large-scale distribution patterns have been observed in tiny ectoparasitic isopods (family Dajidae) infecting two krill species of the genus *Stylocheiron* (Gómez-Gutiérrez & Shields, 1998; Gómez-Gutiérrez & Castellanos-Osorio, 2010). This worldwide distribution pattern suggests that, for krill, parasites have broad distribution ranges like their krill species hosts, but this emerging pattern has been so far overlooked. Here we propose that *E. pacifica* is infected with *P. oregonensis* in the west coast of USA (Gómez-Gutiérrez *et al*., 2006) and at Sanriku coast, Japan (Shimazu, 2006) indicating transoceanic distribution ranges. The presence of *T. inermis* infected with *Pseudocollinia* ciliates in the northeastern Pacific (Bering Sea) (Capiulo & Small, 1986; Capriulo *et al*., 1990; Lynn *et al*., 2014) and northwestern Atlantic (Kulka & Corey, 1984) indicates that populations of this parasite may be connected in the Arctic Ocean. We assume it is the same *P. beringensis* species distributed in the Arctic Ocean. Reports of endoparasitic ciliates in the southern hemisphere in *E. superba* (Stankovic & Rakusa-Suszczewski, 1996) and *E. similis* var. *armata* (Gómez-Gutiérrez *et al*., 2017) greatly extend distribution range of previous confirmed reports restricted in the northern hemisphere but future taxonomic and genetic investigations should discover the species identity.

D'Amato *et al.* (2008) proposed a possible krill dispersal speciation mechanisms using genetic information to tie speciation with tectonic plates theory concluding that founder dispersal rather than vicariance speciation processes may have played a major role in the generation of the current disjunctive geographical distribution among the four *Nyctiphanes* species. We propose the hypothesis that *Pseudocollinia* may also have such disjunctive geographical distribution as the krill hosts (Fig. 5). The 16S consensus tree of the relaxed molecular clock analysis show that *E. pacifica* and *E. superba* are phylogenetic closely related, and diverged earlier than the *Thysanoessa* and *Nyctiphanes* species (Fig. 5) (D'Amato *et al*., 2008). Several of these krill species are now known to interact with *Pseudocollinia* ciliates, which are phylogenetically related with ancestral krill populations originating from the same "hydroplates" and "hydrotectonic system" (Van der Spoel *et al*., 1990). This phylogenetic tree may also indicate long-term association of krill species with apostome histophagous ciliates.

Future discovery of euphausiid parasitoids in other regions of the world could show species parasitoid ciliate–krill co-diversification evidenced by integrative taxonomy. So far, statistically rejected for krill–parasitoid species assemblages inhabiting the northeastern Pacific (Lynn *et al*., 2014). D'Amato *et al*. (2008), speculate that the presence of *N. simplex* in the northern Pacific is possibly a result of recent dispersal from the south. If future studies indicate that *N. simplex* populations in the southern hemisphere are not infected with *Pseudocollinia* ciliates, it would suggest that *P. brintoni* evolved in the relatively recent past among northern krill species. Because *Pseudocollinia* ciliates seem to complete their life cycle parasitizing only krill (Gómez-Gutiérrez *et al*., 2003, 2006, 2012, 2015a) we propose the hypothesis that these parasites have quite similar zoogeographic patterns as their krill host species (Fig. 2A–C, Fig. 3). Clamp *et al*. (2008) mentioned there is currently a debate about the biogeography of free-living protists, with two competing hypotheses seeking to explain observed patterns of distribution. On one hand, the Ubiquitous Dispersal Hypothesis (UDH) asserts that species of free-living protists should be everywhere because of their small size and almost infinite population numbers (Finlay, 2002). On the other hand, the Moderate Endemism Hypothesis (MEH) argues that as many as 30% of free-living protist species could be endemic owing to their large size, very specialized niche requirements (Foissner, 2006), and parasitic-like life cycles. The UDH and MEH both admit that symbiotic protists probably will have patterns of distribution related to those of their hosts (Clamp *et al.,* 2008). However, current evidence of *Pseudocollinia*-krill species in the Northeast Pacific suggest MEH occur at such geographical scale (Lynn *et al*., 2014), but corroboration of these hypotheses must be seek in the future over larger geographical scales.

SUMMARY

The emerging perspective of the present review includes findings of *Pseudocollinia* in the northeastern and northwestern Pacific, southwestern Pacific, northeastern Atlantic, and southeastern Atlantic (Figs. 2A–C) infecting krill with broad and sometimes multi-ocean zoogeographic ranges (Brinton, 1962, 1975, Brinton *et al*., 2000). All these records suggest that the *Pseudocollinia*–krill association is more widespread in the Order Euphausiacea than previously recognized (Gómez-Gutiérrez *et al*., 2003, 2006, 2010, 2012, 2015a, b; 2017, Lynn *et al*.,

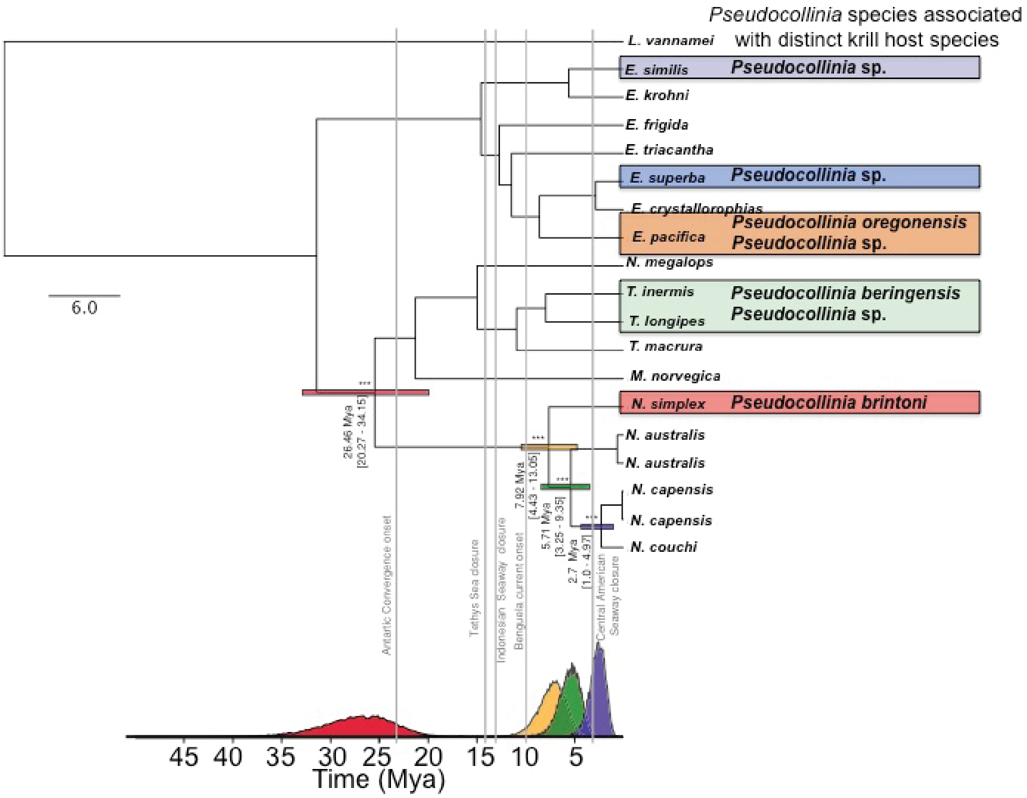

Figure 5. The 16S consensus tree of the relaxed molecular clock analysis modified from D'Amato *et al*. (2008) that matches records of krill–*Pseudocollinia* species. The ends of the tree correspond to the sampled species. Length of branch reflects the mean of the posterior probability density. The posterior probability density for the time of most recent common ancestor (TMRCA) for speciation of *N. couchi* and *N. capensis* is shown in dark blue. The TMRCA of the speciation event between *N. australis*, *N. capensis*, and *N. couchi* is presented in green. The TMRCA of the speciation of *N. simplex* from the other three *Nyctiphanes* species is shown in yellow. The TMRCA of the speciation event from the sampled *Nyctiphanes* and other euphausiids in shown in red. The TMRCA means and the 95% highest probability density intervals are shown by the horizontal bars in the internal nodes of the *Nyctiphanes* clade and are indicated in text in the figures. Krill–*Pseudocollinia* species colors correspond to Figure 2. Genetic data is not available for this phylogenetic model for *Thysanoessa spinifera*, *T. gregaria*, and *T. raschii* that are known to be hosts of *Pseudocollinia* species. Republished and modified with permission of Marine Biology, Springer.

2014) and that *Pseudocollinia* histophagous ciliates match the widespread zoogeographic patterns of their krill host species. The hypothesis of co-diversification of *Pseudocollinia* and euphausiids seems to be still a possibility if infected specimens from different Oceans, hemispheres, or transoceanic regions are analyzed as was done by Lynn *et al*. (2014) for the Northeast Pacific. Parasitoid apostome ciliates are currently known to infect other crustaceans such as copepods, amphipods and decapods (Bradbury, 1994); but it is likely apostome histophagous ciliates also infect other non-crustacean taxonomic groups in the planktonic realm.

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