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New species and suborder records reveal unusually high thaliacean (Chordata, Tunicata) diversity in the South China Sea

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1 **New species and suborder records reveal unusually high**
2 **thaliacean (Chordata, Tunicata) diversity in the South**
3 **China Sea**

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16

17 Running head: New records of Thaliacea from the South China Sea

18 **Abstract**

19 In the context of global biodiversity decline, the monitoring and assessment of
20 marine biodiversity have gained increasing importance. Thaliaceans, a representative
21 group of filter-feeding gelatinous zooplankton, play crucial roles in the carbon cycle
22 and pelagic food webs, yet their diversity remains poorly documented due to challenges
23 in sampling and identification. This knowledge gap is particularly evident in the South
24 China Sea, a highly dynamic subtropical marginal sea. To achieve a comprehensive
25 assessment of thaliacean diversity in the South China Sea, we conducted two cruises in
26 the western South China Sea during the summers of 2020 and 2022. A total of 28 species
27 were recorded, representing the highest species richness ever reported from a single
28 study in the South China Sea. Among these, five species are newly recorded, all
29 belonging to the family Doliolidae (order Doliolida): *Dolioletta mirabilis* Korotneff,
30 1891, *Dolioletta tritonis* Herdman, 1888, *Doliolina (Doliolina) krohni* Herdman,
31 1888, *Doliolina (Doliolina) sigmoides* Garstang, 1933, and *Doliolina (Doliolinetta)*
32 *indica* Neumann, 1906. In addition, taxa of the suborder Doliopsidina are reported in
33 the South China Sea for the first time. This study expands current knowledge of
34 thaliacean diversity and distribution in the South China Sea, highlighting the need to
35 reassess their diversity and distribution using integrated methodologies.

36

37 **Key words:** Thaliacean, Doliolids, Salps, Gelatinous zooplankton, Taxonomy, Marine
 38 biodiversity
 39

40 **Introduction**

41 Knowledge of biodiversity provides a critical foundation for understanding
 42 ecosystem structures and functions (Duffy and Stachowicz 2006, Da Silva et al. 2025).
 43 The sharp global biodiversity decline driven by climate change and human disturbances
 44 creates an urgent need for comprehensive biodiversity monitoring (Ratnarajah et al.
 45 2023, Keck et al. 2025). However, this poses a particular challenge for gelatinous
 46 zooplankton due to their fragile and easily damaged bodies, which impedes a
 47 comprehensive understanding of their diversity and ecological functions (Greer and
 48 Chiaverano 2026, Stukel et al. 2018, Biard et al. 2016).

49
 50 Thaliaceans are an important group of filter-feeding gelatinous zooplankton
 51 containing three orders: Pyrosomatidae, Salpidae, and Doliolidae, with 78 known valid
 52 species (WoRMS 2026). Their remarkable reproductive capacity and short generation
 53 times facilitate the frequent formation of dense swarms. In recent years, the crucial role
 54 of thaliaceans in the marine biological carbon pump and ecosystem has garnered
 55 significant scientific interest. They efficiently transfer carbon to the deep sea through
 56 the production of substantial quantities of fast-sinking fecal pellets and carcasses
 57 (Stenvers et al. 2021, Décima et al. 2023, Orlov and Pakhomov 2024). Their dense
 58 aggregations can rapidly consume primary productivity, thereby accelerating the
 59 transfer of energy to higher trophic levels (Batta-Lona et al. 2024). Moreover,
 60 thaliaceans can have cascading effects on pelagic food web structure by competing for
 61 phytoplankton and preying on other zooplankton eggs and larvae (Köster and
 62 Paffenhöfer 2022, Pietzsch et al. 2023).

63
 64 Despite this growing recognition of their ecological importance, studies on the
 65 diversity of thaliaceans remain scarce. This is particularly true for species within the
 66 Doliolida order. For instance, although 25 species have been documented (WoRMS
 67 2026), only a few, such as *Doliolum denticulatum*, *Doliolum nationalis*, and *Dolioletta*
 68 *gegenbauri*, have received widespread attention. This gap is largely attributed to the
 69 fact that these gelatinous organisms are highly susceptible to damage during both
 70 capture and subsequent preservation processes, posing significant challenges to
 71 accurate species identification.

72
 73 The South China Sea (SCS), the largest subtropical marginal sea, is influenced by
 74 a complex interplay of dynamic forces, including currents (e.g., the Kuroshio and China
 75 Coastal Currents) and other physical processes such as fronts, upwelling, and eddies
 76 (Chu and Wang 2003, Su 2004). Combined with the seasonal monsoon effects, the SCS
 77 harbors diverse and unique ecological niches, resulting in a high diversity of plankton

78 (Guo et al. 2025, Liu et al. 2025, Tao et al. 2025). These characteristics establish the
 79 SCS as a key region for understanding plankton diversity in marginal seas. However,
 80 research on thaliaceans in the SCS remains scarce, detailed distribution and associated
 81 environmental information are available for only a few species (e.g., *D. denticulatum*
 82 and *D. gegenbauri* within Doliolida; *Thalia democratica* and *Iasis cylindrica* within
 83 Salpida), while the majority of other recorded species, particularly within Doliolida
 84 (e.g., *Doliolina obscura*), lack such detailed data. Furthermore, the few existing studies
 85 were conducted over a decade ago (Table 1). Given the ongoing environmental and
 86 plankton community shifts under global climate change (Cai et al. 2025, Wu et al. 2025),
 87 it remains unknown whether the thaliacean fauna of the SCS has undergone significant
 88 alterations in composition or biogeography. This gap hinders a comprehensive
 89 assessment of their distribution and ecological role, as well as the identification of local
 90 extinctions, non-native species, and biogeographic shifts.
 91

92 Table 1. Summary of primary historical studies on thaliaceans in the South China Sea

Sample Time	Region	Net length (cm)	Mouth diameter (cm)	Mesh size (μm)	Total thaliacean species number	Reference
Sep. 1983; Apr., Aug., and Dec. 1984	The central SCS (12–20° N, 111–118° E)	270	80	500	23	(Lin and Lin 2006)
Mar., May, Jul., Oct., and Dec. 1997	The coastal waters southwest of Taiwan (approximately 22°10' N, 120°10' E)		56	330	17	(Tew and Lo 2005)
Dec. 1997; May 1998; Jun.–Jul. 1999	The eastern waters of the Taiwan Strait (23°30'–25°30' N, 118°30'–121°00' E)	270	80	505	11	(Zhang et al. 2003b)
Feb., Sep., Nov., and Dec. 1998; Apr.–May 1999	The Beibu Gulf (16.5–21.5° N, 106–110° E)	280	80	505	9	(Wang et al. 2010)
Nov. and Dec. 2001	Nanwan Bay, Taiwan (21°52'12"–21°57'7" N, 120°43'12"–120°51'0" E)	180	45	200 and 333	16	(Zhang et al. 2003a)
Feb. and Aug. 2004	The waters around Taiwan (21–26° N, 118–123° E)		160	330	18	(Liao et al. 2013)

Jul.–Aug. 2006; Dec. 2006 – Jan. 2007	The northern SCS (17–22° N, 109–114° E)	80	505	14	(Li et al. 2011)
May–Jun 2009; Nov 2010; Aug– Sep 2012	The central SCS (6– 18° N, 108–119° E)	280	80	505	13 (Lai et al. 2024)
Aug. and Nov. 2014; Mar. and May 2015	The waters adjacent to the First and Second Nuclear Power Plants in Taiwan (25.2– 25.34° N, 121.58– 121.72° E)	180	45	333	4 (Franco et al. 2016)
Jul. 2015	The waters surrounding Taiwan	180	45	333	13 (Franco et al. 2017)
Mar., Jul.–Aug., and Nov. 2014; Jan. 2015	The sea area around the Zhongsha and Xisha Islands in the SCS (12°30′–17°32′ N, 110°00′–110°11′ E)	280	80	505	18 (Li et al. 2016)

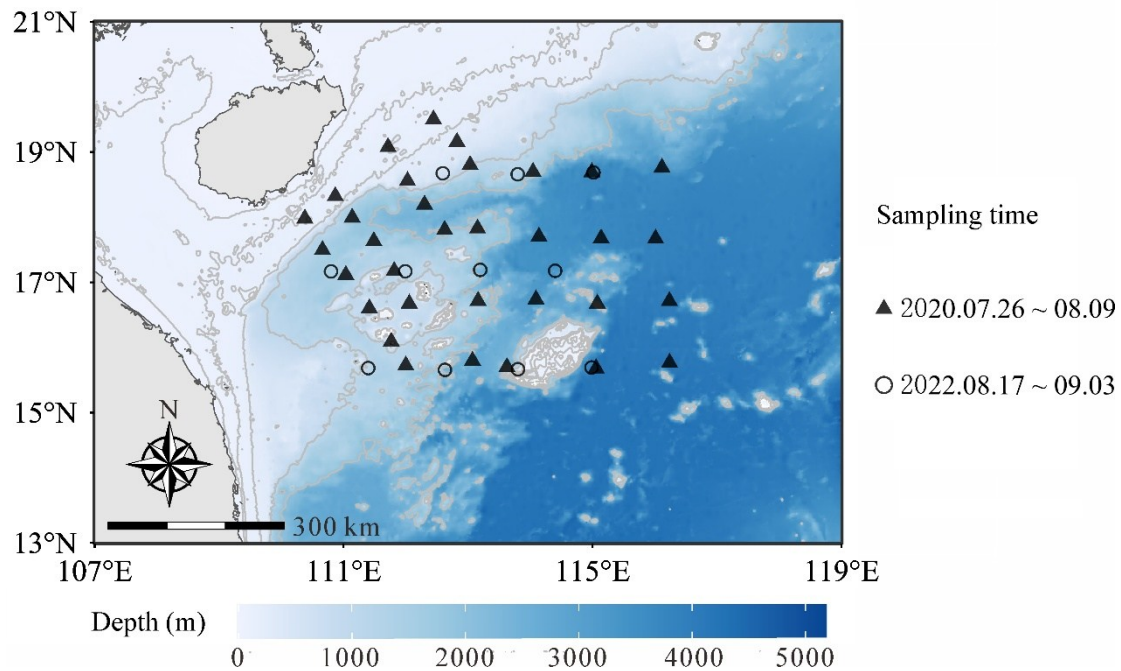
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94 To address this knowledge gap, the present study aimed to systematically assess
95 the thaliacean community in the SCS via two summer cruises in 2020 and 2022. This
96 study provides fundamental information on thaliacean diversity changes in the SCS
97 under climate change, offering a scientific basis for future ecological monitoring and
98 conservation strategies.

99

100 **Materias and methods**

101 Thaliacean samples were collected during two cruises aboard the research vessel
102 *Shiyan 3* in the western SCS (15°N–20°N, 110°E–117°E) from July 26 to August 9,
103 2020, and from August 17 to September 3, 2022 (Fig. 1). Vertical trawling for
104 zooplankton was performed at a depth of 200 m, or from the bottom to the surface when
105 the water depth was less than 200 m, using a plankton net with an 80 cm mouth diameter
106 and a mesh size of 330 μm , equipped with a flowmeter (Digital Flow Meter 438115,
107 HYDRO-BIOS, Germany). The net towing speed was maintained at 0.8 m s^{-1} . The
108 samples were preserved with 5% formaldehyde solution. Thaliacean specimens were
109 sorted, and then identified and quantified under a stereo microscope (Leica M165C,
110 Leica Microsystems, Germany), following established references (Godeaux 1998a,
111 1998b, 2003; Adam and Ishak 2018; Ishak *et al.* 2018). Thaliacean abundance was
112 expressed as the number of individuals per cubic meter (ind m^{-3}). The occurrence rate
113 (%) of each species was defined as the proportion of samples where the species
114 occurred to the total number of samples.



115

116 **Figure 1.** Sampling stations in the western South China Sea during the 2020 and 2022
 117 cruises

118 We obtained global records of thaliacean species from several key biodiversity
 119 databases, including the Global Biodiversity Information Facility
 120 (<https://www.gbif.org/>), Ocean Biodiversity Information System (<https://obis.org/>),
 121 Jellyfish Database Initiative (<https://doi.org/10.1575/1912/7191>), SeaLifeBase
 122 (<https://www.sealifebase.ca/>), and World Register of Marine Species
 123 (<https://www.marinespecies.org/>)

124 Results

125 Environmental background

126 Remote sensing maps and in situ measurements indicated complex hydrological
 127 dynamics in the SCS during the sampling periods, resulting in diverse environmental
 128 conditions (Supplementary Material). During the summer 2020 sampling period,
 129 environmental conditions were influenced by a low-salinity plume from the Mekong
 130 River in the southwest and a warm eddy extending across the region. Sea surface
 131 temperature ranged from 29.97 to 31.65 °C, with cooler waters in the west associated
 132 with the Qiongdong Upwelling and warmer waters in the east within the eddy center.
 133 Sea surface salinity varied between 33.72 and 34.23, showing lower values in the south
 134 consistent with the river plume. Sea surface chlorophyll *a* concentrations (0.03–0.40
 135 $\mu\text{g L}^{-1}$) were higher in the western upwelling area and lower in the eastern
 136 eddy-influenced region. In 2022, sea surface temperature ranged from 29.07 to 30.33 °C,
 137 sea surface salinity was lower in the south (33.19–33.52), and sea surface chlorophyll
 138 *a* concentrations (0.07–0.10 $\mu\text{g L}^{-1}$) decreased from west to east, with the southern

139 stations located at the edge of a warm eddy.

140

141 **Thaliacean species**

142 A total of 4090 thaliacean individuals were identified. Specimens of the order
 143 Pyrosomatida were not identified to species level, with occurrence rates of 12.12% in
 144 2020 and 27.27% in 2022 (Table 2). Within the order Salpida, all individuals except
 145 those with damaged morphology were identified to the species level. The 16 identified
 146 species belong to eight genera in the family Salpidae (Table 2). In 2020, *Thalia*
 147 *orientalis* exhibited the highest occurrence rate of 100%, followed by *Brooksia*
 148 *rostrata* (42.42%) and *T. democratica* (39.39%). In 2022, *T. orientalis* again showed
 149 the highest occurrence rate (100%), followed by *T. democratica* (81.82%) and *B.*
 150 *rostrata* (63.64%).

151

152 For the order Doliolida, individuals belonging to the suborder Doliopsidina were
 153 not identified to species, with occurrence rates of 48.48% in 2020 and 54.55% in 2022
 154 (Table 2). In the suborder Doliolidina, specimens in the phorozoid and gonozoid
 155 stages were identified to species, whereas those in other stages or with damaged
 156 morphology were identified only to genus. A total of 12 species were identified,
 157 representing four genera (Table 2). In 2020, *D. denticulatum* had the highest occurrence
 158 rate (100%), followed by *Doliolina (Doliolina) krohni* (72.73%) and *D.*
 159 *obscura* (63.64%). In 2022, *D. denticulatum* again recorded the highest occurrence rate
 160 (100%), followed by *D. gegenbauri* (90.91%), *Dolioloides rarum* (81.82%), and *D.*
 161 *obscura* (81.82%).

162

163 Table 2. Occurrence rate and mean abundance of thaliaceans identified in this study.

Order	Genus	Species	2020		2022	
			Occurren- -ce rate (%)	Average abundance (ind m ⁻³)	Occurren- -ce rate (%)	Average abundance (ind m ⁻³)
Doliolida	Dolioletta	<i>D. gegenbauri</i>	36.36	0.03 ± 0.08	90.91	0.16 ± 0.20
Doliolida	Dolioletta	<i>D. mirabilis</i>	3.03	0.01 ± 0.05	0	0 ± 0
Doliolida	Dolioletta	<i>D. tritonis</i>	3.03	0.01 ± 0.05	0	0 ± 0
Doliolida	Dolioletta	<i>Dolioletta</i> spp.	78.79	0.15 ± 0.14	90.91	0.12 ± 0.09
Doliolida	Doliolina	<i>D. indica</i>	57.58	0.04 ± 0.05	36.36	0.03 ± 0.06
Doliolida	Doliolina	<i>D. krohni</i>	72.73	0.09 ± 0.09	63.64	0.12 ± 0.19
Doliolida	Doliolina	<i>D. muelleri</i>	0	0 ± 0	9.09	0 ± 0.01
Doliolida	Doliolina	<i>D. obscura</i>	63.64	0.05 ± 0.07	81.82	0.1 ± 0.14
Doliolida	Doliolina	<i>D. separata</i>	9.09	0 ± 0.01	45.45	0.05 ± 0.07
Doliolida	Doliolina	<i>D. sigmoides</i>	6.06	0.01 ± 0.03	27.27	0.02 ± 0.06
Doliolida	Doliolina	<i>Doliolina</i> spp.	100	0.35 ± 0.19	100	0.57 ± 0.55

Doliolida	Dolioloides	<i>D. rarum</i>	12.12	0.01 ± 0.01	81.82	0.25 ± 0.28
Doliolida	Dolioloides	<i>Dolioloides</i> spp.	54.55	0.06 ± 0.09	90.91	0.15 ± 0.21
Doliolida	Doliolum	<i>D. denticulatum</i>	100	0.32 ± 0.39	100	0.22 ± 0.19
Doliolida	Doliolum	<i>D. nationalis</i>	15.15	0.05 ± 0.19	27.27	0.01 ± 0.02
Doliolida	Doliolum	<i>Doliolum</i> spp.	81.82	0.09 ± 0.10	90.91	0.1 ± 0.08
Doliolida	Undefined	Doliopsidina spp.	48.48	0.08 ± 0.15	54.55	0.11 ± 0.15
Salpida	Brooksia	<i>B. rostrata</i>	42.42	0.04 ± 0.07	63.64	0.2 ± 0.27
Salpida	Cyclosalpa	<i>C. bakeri</i>	3.03	0 ± 0.02	0	0 ± 0
Salpida	Cyclosalpa	<i>C. floridana</i>	6.06	0 ± 0.01	9.09	0.01 ± 0.02
Salpida	Cyclosalpa	<i>C. pinnata</i>	3.03	0 ± 0.02	9.09	0 ± 0.01
Salpida	Cyclosalpa	<i>C. polae</i>	9.09	0.01 ± 0.06	0	0 ± 0
Salpida	Cyclosalpa	<i>C. virgula</i>	3.03	0 ± 0.010	0	0 ± 0
Salpida	Iasis	<i>I. cylindrica</i>	12.12	0.02 ± 0.08	18.18	0.05 ± 0.13
Salpida	Pegea	<i>P. confoederata</i>	0	0 ± 0	9.09	0.01 ± 0.04
Salpida	Ritteriella	<i>R. amboinensis</i>	6.06	0 ± 0.01	0	0 ± 0
Salpida	Salpa	<i>S. fusiformis</i>	6.06	0.01 ± 0.07	0	0 ± 0
Salpida	Thalia	<i>T. cicar</i>	6.06	0 ± 0.01	18.18	0.01 ± 0.02
Salpida	Thalia	<i>T. democratica</i>	39.39	0.03 ± 0.05	81.82	0.22 ± 0.35
Salpida	Thalia	<i>T. orientalis</i>	96.97	0.83 ± 0.72	100	2.68 ± 2.49
Salpida	Thalia	<i>T. rhomboides</i>	36.36	0.06 ± 0.18	36.36	0.16 ± 0.38
Salpida	Thalia	<i>T. sibogae</i>	6.06	0 ± 0.01	27.27	0.02 ± 0.04
Salpida	Thalia	<i>Thalia</i> spp.	57.58	0.06 ± 0.10	100	0.21 ± 0.24
Salpida	Traustedia	<i>T. multitentaculata</i>	12.12	0.04 ± 0.14	9.09	0 ± 0.01
Pyrosomatida	Undefined	Pyrosomatida spp.	12.12	0.01 ± 0.02	27.27	0.17 ± 0.38
Undefined	Undefined	Undefined	57.58	0.07 ± 0.10	63.64	0.06 ± 0.07

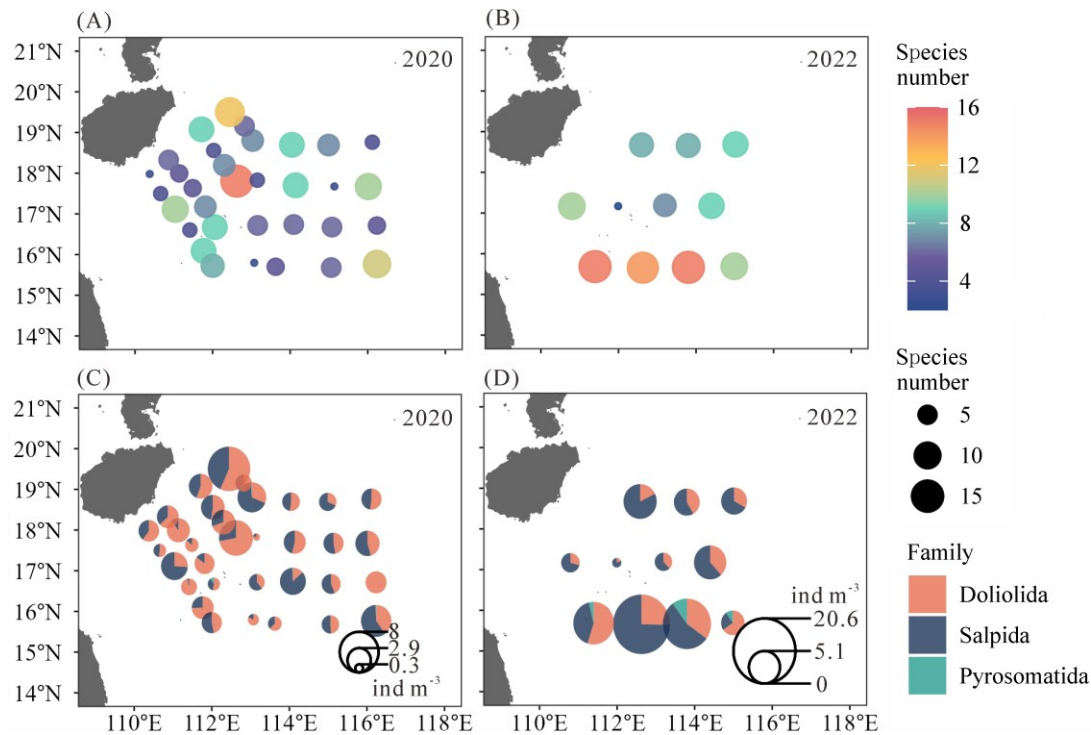
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165 In 2020, species richness ranged from 3 to 16, showing considerable regional
 166 variation. The highest value was recorded at station S10. Stations in the northwest and
 167 southwest exhibited relatively high species numbers (>8), while richness in the
 168 southeastern area was generally below 7 (Fig. 2A). In 2022, species richness varied
 169 between 2 and 15. Stations along the edge of the warm eddy showed higher species
 170 numbers (≥ 14), while other regions exhibited less variation, with values around 8 (Fig.
 171 2B).

172

173 Total thaliacean abundance in 2020 was generally higher at southwestern stations,
 174 peaking at 9.63 ind m⁻³, whereas southern stations had lower abundances, mostly below
 175 3 ind m⁻³ (Fig. 2C). In 2022, high total thaliacean abundance was observed along the
 176 edge of the warm eddy, reaching a maximum of 17.22 ind m⁻³, while stations on the
 177 central transect showed lower abundances, with a minimum of 0.45 ind m⁻³ (Fig. 2D).

178



179

180 **Figure 2.** Spatial distribution of thaliacean species richness in 2020 and 2022 and total
 181 thaliacean abundance in 2020 and 2022 during the sampling period. A. Species richness
 182 in 2020; B. Species richness in 2022; C. Total abundance in 2020; D. Total abundance
 183 in 2022.

184

185 **Morphology and distribution of newly recorded species**

186 Compared to historical records in the SCS (Table 1), this study reports the highest
 187 species richness of Thaliacea documented in the region to date. A total of five newly
 188 recorded species were identified, all belonging to the family Doliolidae within the order
 189 Doliolida: *Dolioletta mirabilis* and *Dolioletta tritonis* in the genus *Dolioletta*, and *D.*
 190 *krohni*, *Doliolina (Doliolina) sigmoides*, and *Doliolina (Doliolinetta) indica* in the
 191 genus *Doliolina*. In addition, taxa of the suborder Doliopsidina are reported in the SCS
 192 for the first time.

193

194 **Taxonomic**

195 **Phylum: Chordata Haeckel, 1874**

196 **Subphylum: Tunicata Lamarck, 1816**

197 **Class: Thaliacea Van der Hoeven, 1850**

198 **Order: Doliolida Delage and Hérouard, 1898**

199 **Suborder: Doliolidina Godeaux, 1996**

200 **Family: Doliolidae Bronn, 1862**

201 **Genus: Dolioletta Garstang, 1933**

202 ***Dolioletta mirabilis* Korotneff, 1891**

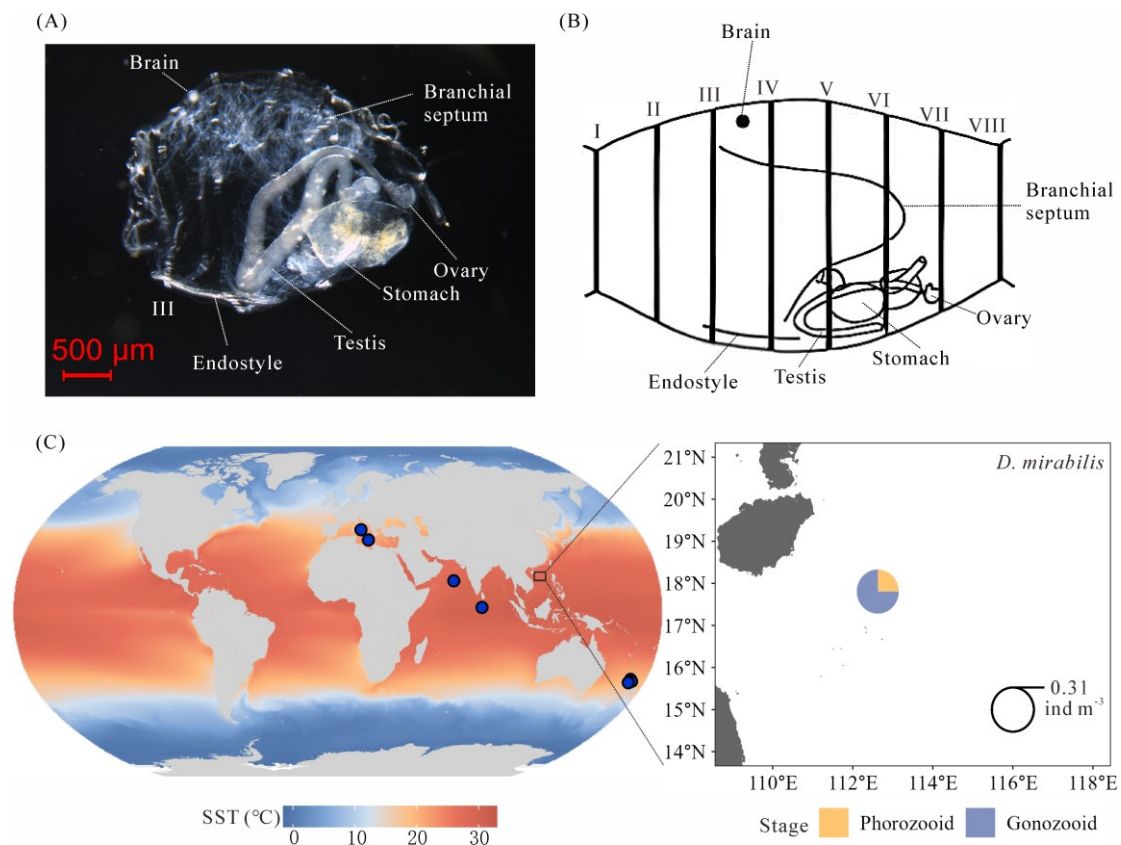
203 Materials examined: CHINA • 6 gonozooids; South China Sea; 112.625°E,

204 17.806°N; 28 Jul. 2020; Y.J. Lai leg.; SDRI 202001, 202003, 202009, 202012, 202019,
 205 202020 • 2 phorozoids; same data as for preceding; SDRI 202007, 202013

206 Description: Length 1.1–3.3 mm. Short endostyle extending from MII 4/5 to MIV
 207 1/2. Branchial septum starting from MIII, ventrally close to MIV, and ending close to
 208 MVI. Brain located between MIII and MIV. Tubular testis coiled on the left side of the
 209 stomach; ovary located anterior to MVII. MVI thin or ventrally open (Godeaux 2003).
 210 Intestine dextrally coiled (Fig. 3A, B).

211 Remarks: This species is primarily distinguished from the commonly occurring *D.*
 212 *gegenbauri* by the position and morphology of the tubular testis, which extends straight
 213 in *D. gegenbauri* but is coiled near the stomach in *D. mirabilis*.

214 Distribution: In this study, this species was only found in S10 (17.806°N,
 215 112.625°E,) during the summer of 2020, with abundance of 0.31 ind m⁻³ (Fig. 3C).
 216 According to the historical literature and biodiversity databases, this species was found
 217 in the Mediterranean, Indian Ocean, New Zealand (Godeaux 2003), Naples, tropical
 218 Atlantic Ocean, and the south of the Arabian Sea (Purushothaman et al., 2018).



219

220 **Figure 3.** Gonozoid of *Dolioletta mirabilis* and its distribution. A. Light
 221 micrograph of the specimen; B. Schematic diagram adapted from Godeaux (1998); C.
 222 Distribution of *D. mirabilis* in the South China Sea based on the present study and in
 223 the global ocean compiled from historical literature and biodiversity databases,
 224 including the Global Biodiversity Information Facility (GBIF), Ocean Biodiversity
 225 Information System (OBIS), Jellyfish Database Initiative (JeDI), SeaLifeBase, and

226 WoRMS. Dots on the global map represent approximate occurrence locations.

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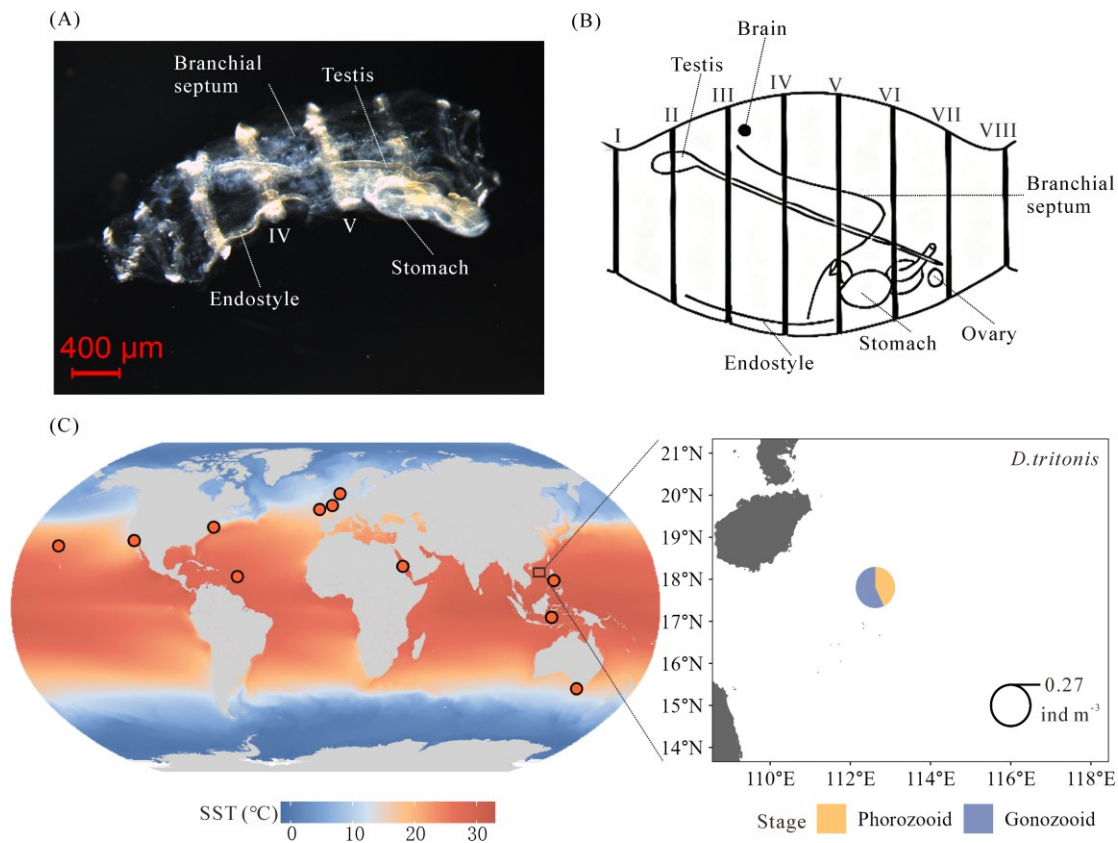
228 ***Dolioletta tritonis* Herdman, 1888**

229 Materials examined: CHINA • 10 gonozooids; South China Sea; 112.625°E,
230 17.806°N; 28 Jul. 2020; Y.J. Lai leg.; SDRI 202001, 202003, 202005, 202006, 202008,
231 202009, 202010, 202012, 202019, 202020 • 5 phorozoids; same data as for preceding;
232 SDRI 202004, 202007, 202013, 202014, 202015

233 Description: Length 1.1–3.9 mm. Endostyle extending from MII 1/2 to MIV 1/2.
234 Branchial septum starting from MII to MVI and ending at MIV 1/2. Brain located
235 between MIII and MIV. Testis tubular, running obliquely and starting from MII.
236 Intestine dextrally coiled.

237 Remarks: The position of branchial septum differs from that reported in previous
238 studies. In the present study, the branchial septum extends from MII to MVI (Fig. 4A),
239 in contrast to earlier descriptions in which it extended from MIII dorsally to MIV 1/2
240 ventrally (Fig. 4B; Godeaux 1998a, 2003; Purushothaman *et al.* 2018). This species
241 closely resembles *D. gegenbauri*, except that the branchial septum is ventrally attached
242 between MIV and MV.

243 Distribution: In this study, this species was only found in S10
244 (17.806°N, 112.625°E) during the summer of 2020, with abundance of 0.27 ind m⁻³ (Fig.
245 4C). According to the historical literature and biodiversity databases, this species was
246 found in the Bass Strait, Indian Ocean, Pacific Ocean, North Atlantic (Purushothaman
247 *et al.* 2018), the Gulf of 'Aqaba (Godeaux 2003), the English Channel, North Sea
248 (Harant and Vernières 1938), Red Sea (Godeaux 1987), and the North Pacific (Tokioka
249 1960).



250

251 **Figure 4.** Gonozooid of *Doliolitta tritonis* and its distribution. A. Light
 252 micrograph of the specimen; B. Schematic diagram adapted from Godeaux (1998); C.
 253 Distribution of *D. tritonis* in the South China Sea based on the present study and in the
 254 global ocean compiled from historical literature and biodiversity databases, including
 255 the GBIF, OBIS, JeDI, SeaLifeBase, and WoRMS. Dots on the global map represent
 256 approximate occurrence locations.

257

258 **Genus: Doliolina Borgert, 1894**

259 **Subgenus: Doliolina (Doliolina) Garstang, 1933**

260 ***Doliolina (Doliolina) krohni* Herdman, 1888**

261 Materials examined: CHINA • 3 gonozooids; South China Sea; 114.044°E,
 262 18.697°N; 26 Jul. 2020; Y.J. Lai leg.; SDRI 202136, 202137, 202138 • 1 phorozoid;
 263 same data as for preceding; SDRI 202134 • 2 gonozooids; South China Sea; 111.714°E,
 264 19.078°N; 27 Jul. 2020; Y.J. Lai leg.; SDRI 202174, 202175 • 2 phorozoids; same data
 265 as for preceding; SDRI 202173, 202176 • 2 gonozooids; South China Sea; 112.028°E,
 266 18.558°N; 27 Jul. 2020; Y.J. Lai leg.; SDRI 202177, 202182 • 2 gonozooids; South
 267 China Sea; 112.444°E, 19.503°N; 27 Jul. 2020; Y.J. Lai leg.; SDRI 202163, 202167 • 1
 268 phorozoid; same data as for preceding; SDRI 202169 • 1 gonozooid; South China Sea;
 269 112.300°E, 18.194°N; 28 Jul. 2020; Y.J. Lai leg.; SDRI 202191 • 13 gonozooids; South
 270 China Sea; 112.625°E, 17.806°N; 28 Jul. 2020; Y.J. Lai leg.; SDRI 202001, 202003,
 271 202005, 202006, 202008, 202009, 202010, 202012, 202017, 202018, 202019, 202020,

272 202024 • 9 phorozoids; same data as for preceding; SDRI 202004, 202007, 202011,
 273 202013, 202014, 202015, 202021, 202022, 202023 • 5 gonozoids; South China Sea;
 274 114.139°E, 17.703°N; 28 Jul. 2020; Y.J. Lai leg.; SDRI 202030, 202031, 202032,
 275 202033, 202034 • 1 phorozoid; same data as for preceding; SDRI 202026 • 2
 276 gonozoids; South China Sea; 115.078°E, 16.675°N; 29 Jul. 2020; Y.J. Lai leg.; SDRI
 277 202052, 202053 • 1 gonozoid; South China Sea; 116.014°E, 17.672°N; 29 Jul. 2020;
 278 Y.J. Lai leg.; SDRI 202036 • 1 phorozoid; same data as for preceding; SDRI 202039
 279 • 3 gonozoids; South China Sea; 116.236°E, 16.714°N; 29 Jul. 2020; Y.J. Lai leg.;
 280 SDRI 202042, 202043, 202044 • 1 phorozoid; same data as for preceding; SDRI
 281 202048 • 6 gonozoids; South China Sea; 112.056°E, 16.675°N; 30 Jul. 2020; Y.J. Lai
 282 leg.; SDRI 202058, 202061, 202062, 202066, 202067, 202073 • 1 phorozoid; same
 283 data as for preceding; SDRI 202068 • 1 gonozoid; South China Sea; 113.161°E,
 284 16.717°N; 30 Jul. 2020; Y.J. Lai leg.; SDRI 202057 • 1 phorozoid; same data as for
 285 preceding; SDRI 202056 • 4 gonozoids; South China Sea; 110.867°E, 18.325°N; 4
 286 Aug. 2020; Y.J. Lai leg.; SDRI 202094, 202095, 202096, 202097 • 1 phorozoid; South
 287 China Sea; 111.139°E, 17.994°N; 4 Aug. 2020; Y.J. Lai leg.; SDRI 202090 • 2
 288 gonozoids; South China Sea; 111.486°E, 17.633°N; 5 Aug. 2020; Y.J. Lai leg.; SDRI
 289 202088, 202089 • 2 gonozoids; South China Sea; 111.814°E, 17.175°N; 5 Aug. 2020;
 290 Y.J. Lai leg.; SDRI 202076, 202077 • 2 phorozoids; same data as for preceding; SDRI
 291 202074, 202086 • 1 gonozoid; South China Sea; 115.058°E, 15.681°N; 6 Aug. 2020;
 292 Y.J. Lai leg.; SDRI 202142 • 2 phorozoids; South China Sea; 116.239°E, 15.767°N; 6
 293 Aug. 2020; Y.J. Lai leg.; SDRI 202153, 202159 • 1 gonozoid; South China Sea;
 294 113.625°E, 15.700°N; 7 Aug. 2020; Y.J. Lai leg.; SDRI 202139 • 1 gonozoid; South
 295 China Sea; 111.414°E, 16.603°N; 8 Aug. 2020; Y.J. Lai leg.; SDRI 202108 • 5
 296 gonozoids; South China Sea; 111.767°E, 16.092°N; 8 Aug. 2020; Y.J. Lai leg.; SDRI
 297 202117, 202119, 202121, 202122, 202124 • 1 phorozoid; same data as for preceding;
 298 SDRI 202115 • 4 gonozoids; South China Sea; 112.000°E, 15.725°N; 8 Aug. 2020;
 299 Y.J. Lai leg.; SDRI 202125, 202126, 202129, 202131 • 1 gonozoid; South China Sea;
 300 110.661°E, 17.498°N; 9 Aug. 2020; Y.J. Lai leg.; SDRI 202101 • 2 gonozoids; South
 301 China Sea; 111.036°E, 17.114°N; 9 Aug. 2020; Y.J. Lai leg.; SDRI 202104, 202105 • 2
 302 phorozoids; South China Sea; 113.798°E, 18.659°N; 22 Aug. 2022; Y. Liu leg.; SDRI
 303 202206, 202207 • 1 gonozoid; South China Sea; 110.798°E, 17.168°N; 27 Aug. 2022;
 304 Y. Liu leg.; SDRI 202217 • 3 gonozoids; South China Sea; 114.400°E, 17.177°N; 28
 305 Aug. 2022; Y. Liu leg.; SDRI 202220, 202222, 202223 • 1 phorozoid; same data as
 306 for preceding; SDRI 202221 • 2 gonozoids; South China Sea; 114.985°E, 15.692°N;
 307 29 Aug. 2022; Y. Liu leg.; SDRI 202229, 202230 • 4 phorozoids; same data as for
 308 preceding; SDRI 202224, 202225, 202227, 202228 • 2 gonozoids; South China Sea;
 309 112.629°E, 15.656°N; 30 Aug. 2022; Y. Liu leg.; SDRI 202269, 202270 • 16
 310 gonozoids; South China Sea; 113.802°E, 15.666°N; 30 Aug. 2022; Y. Liu leg.; SDRI
 311 202237, 202240, 202244, 202247, 202248, 202251, 202254, 202255, 202256, 202258,
 312 202259, 202260, 202261, 202262, 202263, 202264 • 7 phorozoids; same data as for
 313 preceding; SDRI 202238, 202241, 202242, 202245, 202249, 202250, 202252 • 1

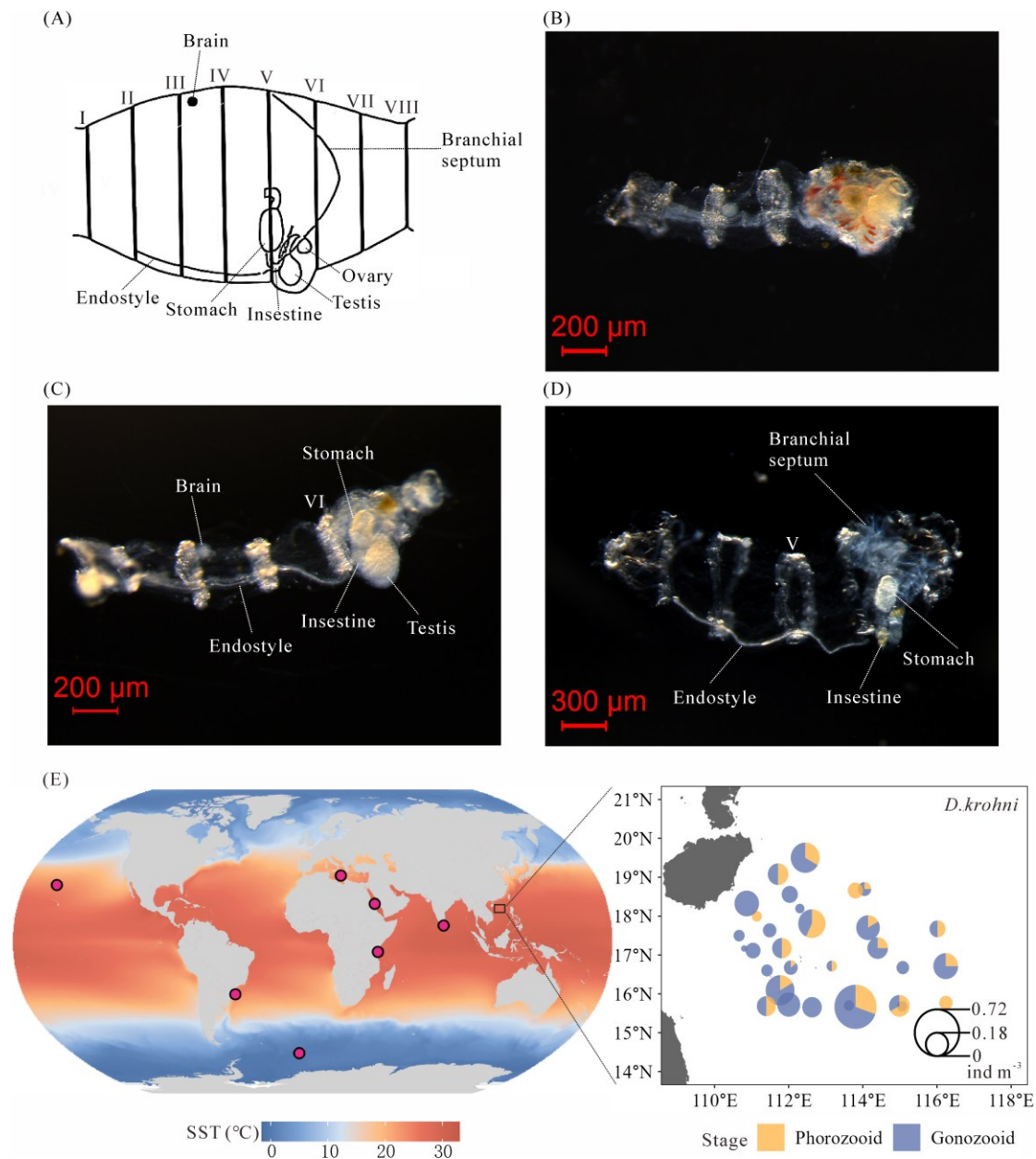
314 gonozoid; South China Sea; 111.396°E, 15.684°N; 31 Aug. 2022; Y. Liu leg.; SDRI
315 202279 • 1 phorozoid; same data as for preceding; SDRI 202282

316 Description: Length 0.5–2.4 mm. Long endostyle extending from MII to MV (Fig.
317 5A, C, D). Branchial septum arched, between MV and MVI. Brain between MIII and
318 MIV. Testis pear-shaped, swollen, protruding ventrally below intestine. Ovary anterior
319 to MVI. In some specimens, bright red streaks or patches were observed near the
320 stomach, a feature not previously described (Fig. 5B).

321 Remarks: Most specimens appeared flattened and contracted, likely due to fixation
322 in formaldehyde solution. This species closely resembles *Doliolina (Doliolina)*
323 *müelleri*, but can be clearly distinguished by its markedly longer endostyle. Although
324 *D. müelleri* has been reported multiple times in the SCS, *D. krohni* has not been
325 recorded previously. In the present study, however, the pattern was reversed: *D. krohni*
326 occurred frequently, while *D. müelleri* was rarely observed.

327 Distribution: In this study, this species was widely distributed, exhibiting high
328 occurrence rates in both 2020 (72.73%) and 2022 (63.64%; Table 2). In the
329 southwestern area, where phorozoid was the dominant stage, and abundances were
330 low. In contrast, higher abundances were observed in the northwestern and southeastern
331 areas, coinciding with the dominance of gonozoid (Fig. 5D). According to the
332 historical literature and biodiversity databases, this species was found in European
333 waters, Mediterranean, Indian Ocean, Arabian Sea (Purushothaman et al. 2018), South
334 Atlantic, Brazilian waters (Da Silva Rodrigues et al. 2024), Red Sea (Godeaux 1987),
335 and the North Pacific (Tokioka 1960).

336



337

338 **Figure 5.** *Doliolina (Doliolina) krohni* and its distribution. A. Schematic diagram of
 339 the gonozooid adapted from Godeaux (1998); B. Light micrograph of a gonozooid
 340 specimen showing red streaks; C. Light micrograph of a phorozooid specimen; D.
 341 Light micrograph of a gonozooid specimen; E. Distribution of *D. krohni* in the South China
 342 Sea based on the present study and in the global ocean compiled from historical
 343 literature and biodiversity databases, including the GBIF, OBIS, JeDI, SeaLifeBase,
 344 and WoRMS. Dots on the global map represent approximate occurrence locations.

345

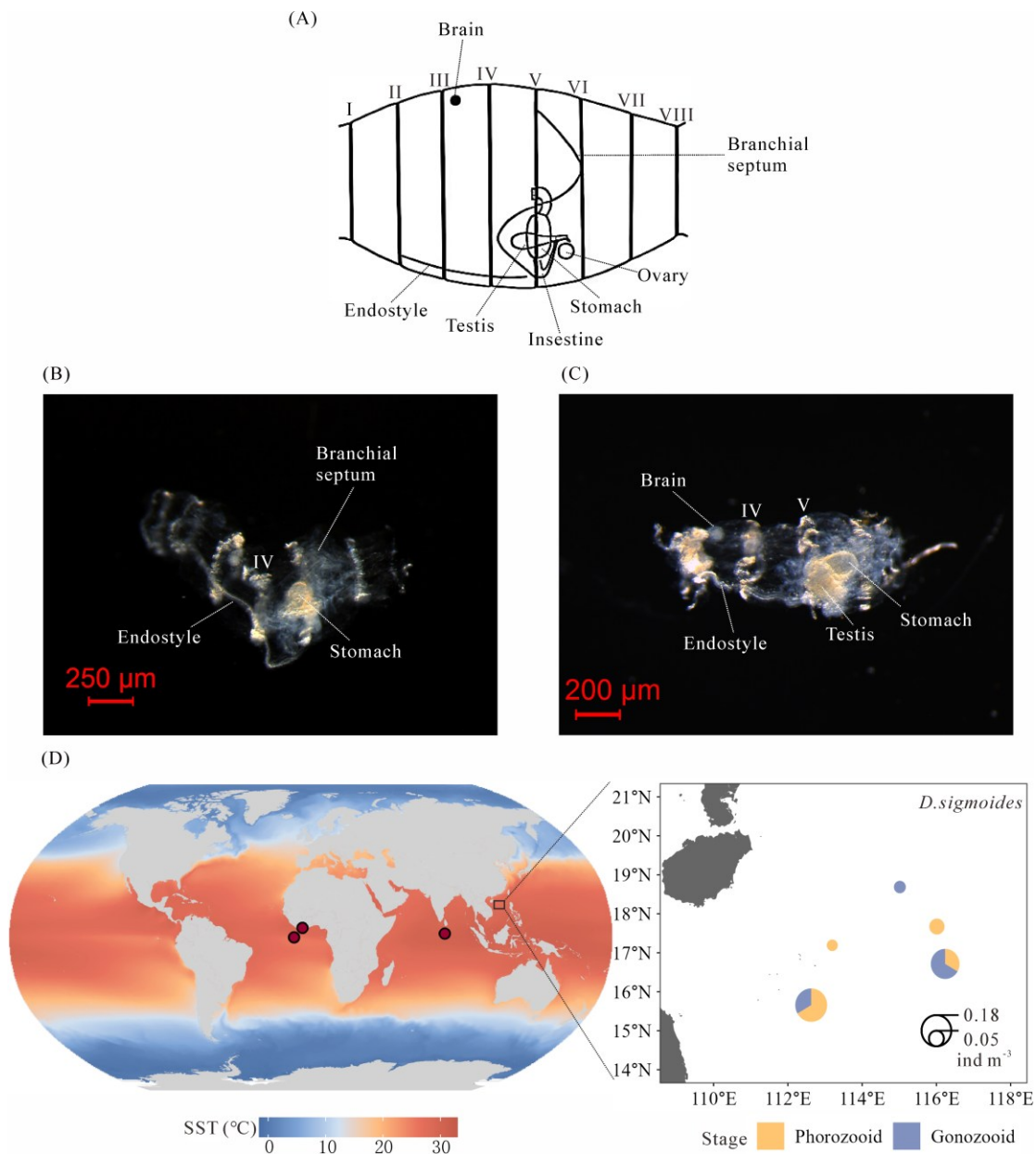
346 ***Doliolina (Doliolina) sigmoides* Garstang, 1933**

347 Materials examined: CHINA • 2 gonozooids; South China Sea; 116.236°E,
 348 16.714°N; 29 Jul. 2020; Y.J. Lai leg.; SDRI 202045, 202047 • 2 phorozooids; same data
 349 as for preceding; SDRI 202049 • 1 phorozooid; South China Sea; 116.014°E, 17.672°N;

350 29 Jul. 2020; Y.J. Lai leg.; SDRI 202040 • 1 gonozooid; South China Sea; 115.016°E,
 351 18.686°N; 22 Aug. 2022; Y. Liu leg.; SDRI 202203 • 1 phorozoid; South China Sea;
 352 113.196°E, 17.191°N; 28 Aug. 2022; Y. Liu leg.; SDRI 202219 • 1 gonozooid; South
 353 China Sea; 112.629°E, 15.656°N; 30 Aug. 2022; Y. Liu leg.; SDRI 202267 • 2
 354 phorozoids; same data as for preceding; SDRI 202266, 202268

355 Description: Length 1.0–1.9 mm. Endostyle slender, extending from MII to MV.
 356 Branchial septum S-shaped, extending from MV to MVI, ending at MIV. Brain located
 357 between MIII and MIV. Testis short, horizontal, swollen anterior to MV. Ovary
 358 positioned immediately posterior to testis (Fig. 6A–C).

359 Distribution: This species was recorded in the western part of the study area, with
 360 occurrence rates of 6.06% in 2020 and 27.27% in 2022 (Table 2, Fig. 6D). Global
 361 records are scarce (Fig. 6D), with reported occurrences primarily limited to the Guinea
 362 Basin and the Indian Ocean (Purushothaman et al. 2018).



364 **Figure 6.** *Doliolina (Doliolina) sigmoides* and its distribution. A. Schematic diagram
 365 of the gonozooid adapted from Godeaux (1998); B. Light micrograph of a phorozoid
 366 specimen; C. Light micrograph of a gonozooid specimen; D. Distribution of *D.*
 367 *sigmoides* in the South China Sea based on the present study and in the global ocean
 368 compiled from historical literature and biodiversity databases, including the GBIF,
 369 OBIS, JeDI, SeaLifeBase, and WoRMS. Dots on the global map represent approximate
 370 occurrence locations.

371

372 **Subgenus: Doliolina (Doliolinetta) Godeaux, 1998**

373 ***Doliolina (Doliolinetta) indica* Neumann, 1906**

374 Materials examined: CHINA • 1 gonozooid; South China Sea; 112.625°E,
 375 17.806°N; 28 Jul. 2020; Y.J. Lai leg.; SDRI 202016 • 2 gonozooids; South China Sea;
 376 114.139°E, 17.703°N; 28 Jul. 2020; Y.J. Lai leg.; SDRI 202028, 202029 • 2 gonozooids;
 377 South China Sea; 116.014°E, 17.672°N; 29 Jul. 2020; Y.J. Lai leg.; SDRI 202037,
 378 202038 • 2 gonozooids; South China Sea; 116.236°E, 16.714°N; 29 Jul. 2020; Y.J. Lai
 379 leg.; SDRI 202041, 202046 • 1 phorozoid; South China Sea; 115.078°E, 16.675°N; 29
 380 Jul. 2020; Y.J. Lai leg.; SDRI 202051 • 1 gonozooid; South China Sea; 114.092°E,
 381 16.739°N; 30 Jul. 2020; Y.J. Lai leg.; SDRI 202054 • 1 phorozoid; same data as for
 382 preceding; SDRI 202055 • 1 phorozoid; South China Sea; 112.056°E, 16.675°N; 30
 383 Jul. 2020; Y.J. Lai leg.; SDRI 202059 • 2 gonozooids; South China Sea; 111.814°E,
 384 17.175°N; 5 Aug. 2020; Y.J. Lai leg.; SDRI 202075, 202081 • 2 phorozoids; same data
 385 as for preceding; SDRI 202079, 202080 • 1 gonozooid; same data as for preceding;
 386 SDRI 202078 • 2 gonozooids; South China Sea; 111.036°E, 17.114°N; 9 Aug. 2020;
 387 Y.J. Lai leg.; SDRI 202102, 202103 • 2 gonozooids; South China Sea; 111.414°E,
 388 16.603°N; 8 Aug. 2020; Y.J. Lai leg.; SDRI 202106, 202107 • 1 gonozooid; South
 389 China Sea; 111.767°E, 16.092°N; 8 Aug. 2020; Y.J. Lai leg.; SDRI 202116 • 3
 390 phorozoids; same data as for preceding; SDRI 202118, 202120, 202123 • 1 gonozooid;
 391 South China Sea; 112.000°E, 15.725°N; 8 Aug. 2020; Y.J. Lai leg.; SDRI 202128 • 1
 392 gonozooid; South China Sea; 114.044°E, 18.697°N; 26 Jul. 2020; Y.J. Lai leg.; SDRI
 393 202135 • 1 phorozoid; South China Sea; 113.625°E, 15.700°N; 7 Aug. 2020; Y.J. Lai
 394 leg.; SDRI 202140 • 1 gonozooid; same data as for preceding; SDRI 202141 • 2
 395 gonozooids; South China Sea; 115.058°E, 15.681°N; 6 Aug. 2020; Y.J. Lai leg.; SDRI
 396 202149, 202150 • 3 gonozooids; South China Sea; 116.239°E, 15.767°N; 6 Aug. 2020;
 397 Y.J. Lai leg.; SDRI 202155, 202157, 202158 • 2 gonozooids; South China Sea;
 398 112.822°E, 19.156°N; 27 Jul. 2020; Y.J. Lai leg.; SDRI 202160, 202161 • 1 gonozooid;
 399 South China Sea; 112.444°E, 19.503°N; 27 Jul. 2020; Y.J. Lai leg.; SDRI 202166 • 2
 400 gonozooids; South China Sea; 112.300°E, 18.194°N; 28 Jul. 2020; Y.J. Lai leg.; SDRI
 401 202187, 202189 • 1 gonozooid; South China Sea; 110.798°E, 17.168°N; 27 Aug. 2022;
 402 Y. Liu leg.; SDRI 202218 • 1 gonozooid; South China Sea; 114.985°E, 15.692°N; 29
 403 Aug. 2022; Y. Liu leg.; SDRI 202226 • 5 gonozooids; South China Sea; 113.802°E,
 404 15.666°N; 30 Aug. 2022; Y. Liu leg.; SDRI 202246, 202253, 202257 • 1 phorozoid;

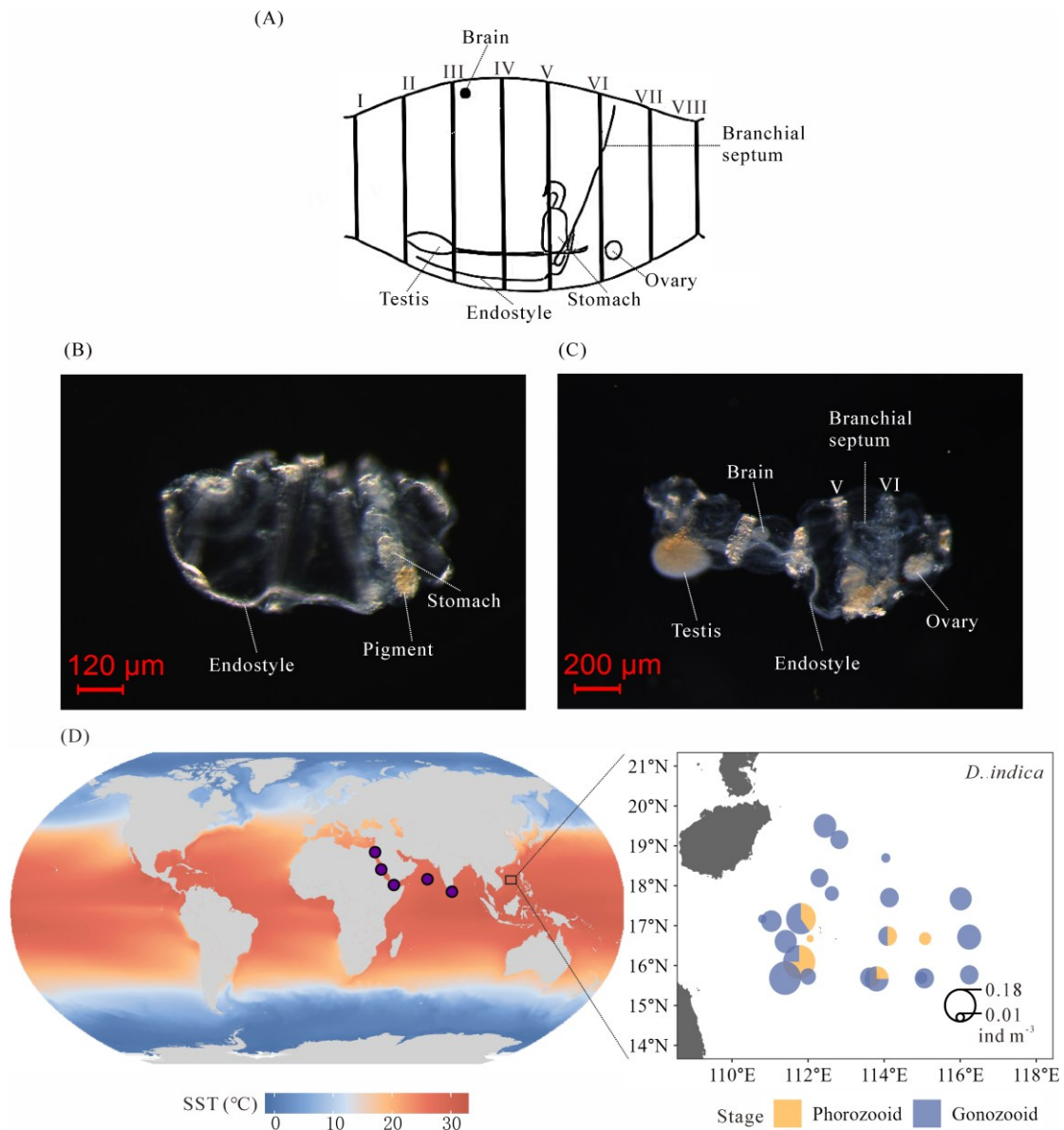
405 same data as for preceding; SDRI 202239 • 3 gonozooids; South China Sea; 111.396°E,
406 15.684°N; 31 Aug. 2022; Y. Liu leg.; SDRI 202278, 202280, 202281

407 Description: Length 0.4–2.1 mm. Endostyle slender, extending from MII to MV.
408 Branchial septum oblique between MV and MVI. Brain located between MIII and MIV.
409 Testis tubular, horizontal, swollen at MII. Stomach masked by a cloud of yellow
410 pigment. Ovary anterior to MVII (Fig. 7A–C).

411 Remarks: This species is readily distinguishable by the yellow pigment cloud
412 around the stomach both in the phorozoid and gonozoid stages, and by the swollen
413 testis at M II in the gonozoid stage (Fig. 7C).

414 Distribution: This species was widely distributed within the study area, exhibiting
415 a high occurrence rate of 57.58% in 2020 (Table 2, Fig. 7D). Globally, records are
416 scarce (Fig. 7D) with documented occurrences primarily limited to the Indian Ocean,
417 Gulf of Aden, Red Sea, Gulf of Aqaba, and Arabian Sea (Purushothaman et al. 2018).
418 Its occurrence in the SCS is consistent with its tropical–subtropical distribution and
419 may be facilitated by the SCS acting as a biogeographic transition zone within the Indo–
420 Pacific.

421



422

423 **Figure 7.** *Doliolina (Doliolinetta) indica* and its distribution. A. Schematic diagram of
 424 the gonozooid adapted from Bone (1998); B. Light micrograph of a phorozooid
 425 specimen; C. Light micrograph of a gonozooid specimen; D. Distribution of *D.*
 426 *indica* in the South China Sea based on the present study and in the global ocean
 427 compiled from historical literature and biodiversity databases, including the GBIF,
 428 OBIS, JeDI, SeaLifeBase, and WoRMS. Dots on the global map represent approximate
 429 occurrence locations.

430

431 **Suborder:** Doliopsidina Godeaux, 1996

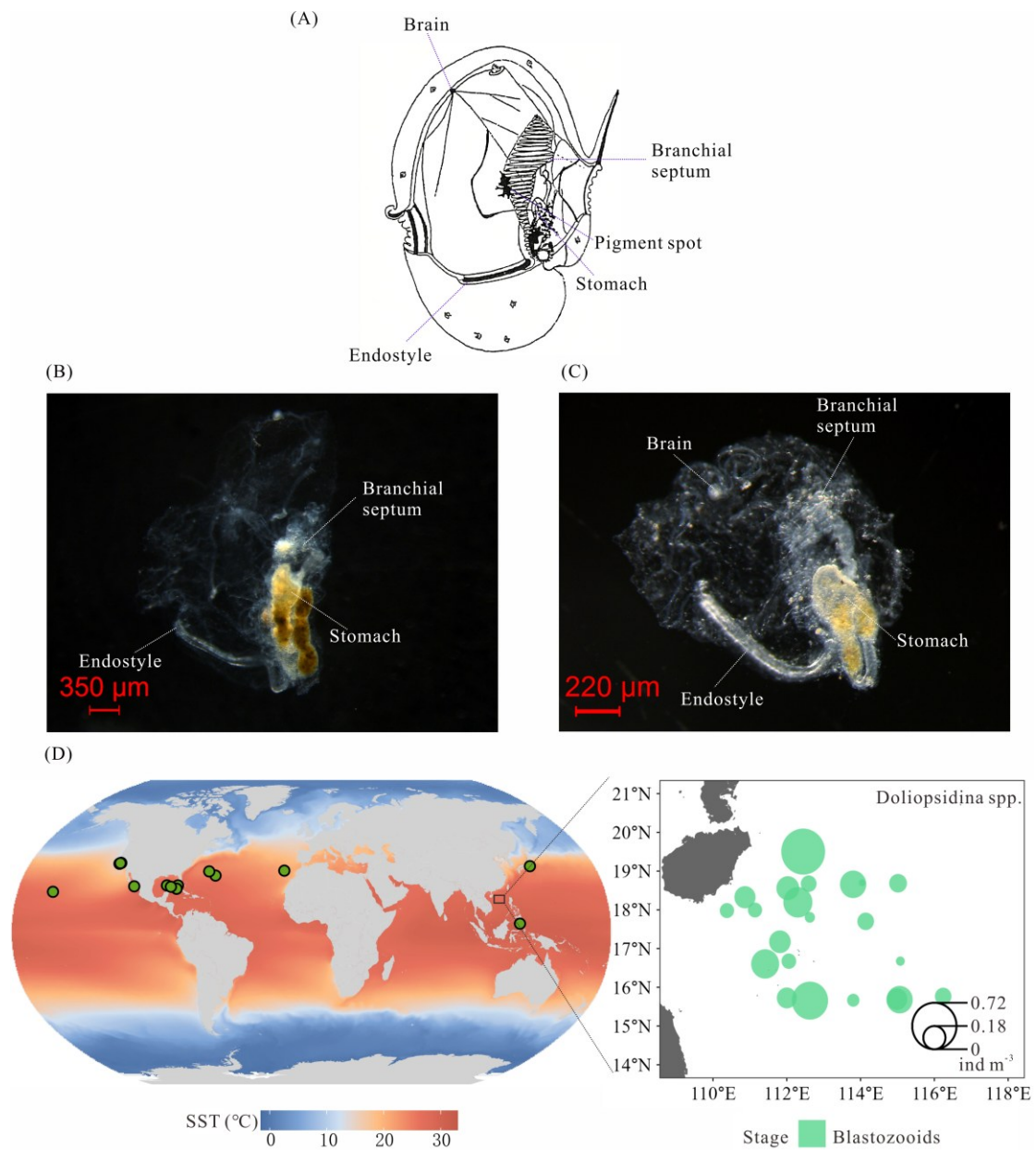
432 Materials examined: CHINA • 1 specimen (sex undefined); South China Sea;
 433 112.625°E, 17.806°N; 28 Jul. 2020; Y.J. Lai leg.; SDRI 202002 • 3 specimens (sex
 434 undefined); South China Sea; 114.139°E, 17.703°N; 28 Jul. 2020; Y.J. Lai leg.; SDRI
 435 202025, 202027, 202035 • 1 specimen (sex undefined); South China Sea; 115.078°E,

436 16.675°N; 29 Jul. 2020; Y.J. Lai leg.; SDRI 202050 • 1 phorozoid; South China Sea;
 437 112.056°E, 16.675°N; 30 Jul. 2020; Y.J. Lai leg.; SDRI 202060 • 7 specimens (sex
 438 undefined); same data as for preceding; SDRI 202063, 202064, 202065, 202069,
 439 202070, 202071, 202072 • 5 specimens (sex undefined); South China Sea; 111.814°E,
 440 17.175°N; 5 Aug. 2020; Y.J. Lai leg.; SDRI 202082, 202083, 202084, 202085, 202087
 441 • 2 specimens (sex undefined); South China Sea; 111.139°E, 17.994°N; 4 Aug. 2020;
 442 Y.J. Lai leg.; SDRI 202091, 202092 • 3 specimens (sex undefined); South China Sea;
 443 110.867°E, 18.325°N; 4 Aug. 2020; Y.J. Lai leg.; SDRI 202093, 202098, 202099 • 1
 444 specimen (sex undefined); South China Sea; 110.378°E, 17.981°N; 9 Aug. 2020; Y.J.
 445 Lai leg.; SDRI 202100 • 6 phorozoids; South China Sea; 111.414°E, 16.603°N; 8 Aug.
 446 2020; Y.J. Lai leg.; SDRI 202109, 202110, 202111, 202112, 202113, 202114 • 1
 447 phorozoid; South China Sea; 112.000°E, 15.725°N; 8 Aug. 2020; Y.J. Lai leg.; SDRI
 448 202127 • 2 specimens (sex undefined); same data as for preceding; SDRI 202130,
 449 202132 • 1 phorozoid; South China Sea; 114.044°E, 18.697°N; 26 Jul. 2020; Y.J. Lai
 450 leg.; SDRI 202133 • 7 specimens (sex undefined); South China Sea; 115.058°E,
 451 15.681°N; 6 Aug. 2020; Y.J. Lai leg.; SDRI 202143, 202144, 202145, 202146, 202147,
 452 202148, 202151 • 3 specimens (sex undefined); South China Sea; 116.239°E, 15.767°N;
 453 6 Aug. 2020; Y.J. Lai leg.; SDRI 202152, 202154, 202156 • 7 specimens (sex
 454 undefined); South China Sea; 112.444°E, 19.503°N; 27 Jul. 2020; Y.J. Lai leg.; SDRI
 455 202162, 202164, 202165, 202168, 202170, 202171, 202172 • 4 specimens (sex
 456 undefined); South China Sea; 112.028°E, 18.558°N; 27 Jul. 2020; Y.J. Lai leg.; SDRI
 457 202178, 202179, 202180, 202181 • 1 specimen (sex undefined); South China Sea;
 458 112.300°E, 18.194°N; 28 Jul. 2020; Y.J. Lai leg.; SDRI 202183 • 1 phorozoid; same
 459 data as for preceding; SDRI 202184 • 6 specimens (sex undefined); same data as for
 460 preceding; SDRI 202185, 202186, 190, 192, 193, 194, 195 • 1 phorozoid; same data
 461 as for preceding; SDRI 202188 • 4 specimens (sex undefined); South China Sea;
 462 115.016°E, 18.686°N; 22 Aug. 2022; Y. Liu leg.; SDRI 202201, 202202, 202204,
 463 202205 • 6 specimens (sex undefined); South China Sea; 113.798°E, 18.659°N; 22 Aug.
 464 2022; Y. Liu leg.; SDRI 202208, 202209, 202210, 202211, 202212, 202213 • 3
 465 specimens (sex undefined); South China Sea; 112.594°E, 18.674°N; 23 Aug. 2022; Y.
 466 Liu leg.; SDRI 202214, 202215, 202216 • 6 specimens (sex undefined); South China
 467 Sea; 114.985°E, 15.692°N; 29 Aug. 2022; Y. Liu leg.; SDRI 202231, 202232, 202233,
 468 202234, 202235, 202236 • 2 specimens (sex undefined); South China Sea; 113.802°E,
 469 15.666°N; 30 Aug. 2022; Y. Liu leg.; SDRI 202243, 202265 • 7 specimens (sex
 470 undefined); South China Sea; 112.629°E, 15.656°N; 30 Aug. 2022; Y. Liu leg.; SDRI
 471 202271, 202272, 202273, 202274, 202275, 202276, 202277

472 Description: Length 0.7–6.4 mm. The suborder Doliopsidina differs from the more
 473 commonly reported suborder Doliolidina in possessing only five muscle bands,
 474 whereas the latter has eight muscle bands (Godeaux 2003, Robison et al. 2005). The
 475 specimens examined in this study had a transparent, spherical body (Fig. 8B, C). The
 476 muscle bands were slender and transparent, and the digestive tract was U-shaped (Fig.
 477 8A–C).

478 Remarks: Owing to the extreme slenderness and transparency of the muscle bands,
 479 identification to the species level, or even to the family level, was unsuccessful in this
 480 study. Nevertheless, based on morphological observations, Doliopsidina in the SCS
 481 likely comprises more than one species.

482 Distribution: The suborder Doliopsidina comprises three families, four genera, and
 483 five described species, none of which have previously been reported from the SCS. All
 484 known members of Doliopsidina are warm-temperate species. Based on the global
 485 records (Fig. 8D), Doliopsidina species have been recorded from the coastal waters off
 486 Japan, the Pacific coast of the United States, the California Current system, the North
 487 Atlantic, the Caribbean Sea, the Mediterranean Sea, and the Gulf of Mexico.



488

489 **Figure 8.** Doliopsidina spp. and their distribution. A. Schematic diagram of the
 490 gonozoid adapted from Kowalevsky and Barrois (1883); B. Light micrograph of an

491 undefined specimen; C. Light micrograph of another undefined specimen; D.
492 Distribution of *Doliopsidina* spp. in the South China Sea based on the present study and
493 in the global ocean compiled from historical literature and biodiversity databases,
494 including the GBIF, OBIS, JeDI, SeaLifeBase, and WoRMS. Dots on the global map
495 represent approximate occurrence locations.

496

497 **Discussion**

498 **Unusual rich biodiversity of thaliaceans in the SCS**

499 This study provides the most comprehensive taxonomic assessment of thaliaceans
500 conducted to date in the SCS, documenting 28 species, which represents the highest
501 richness reported for this region (Table 1). Previous studies conducted in adjacent areas
502 reported lower richness, with only 18 and 23 species recorded (Lin and Lin 2006, Li et
503 al. 2016). Methodological differences may partly account for this discrepancy, as earlier
504 surveys employed 500 μm nets, whereas the finer mesh used in the present study (330
505 μm) is more effective at retaining small-sized thaliaceans, particularly doliolids.
506 Differences in net type and mesh size are well known to influence observed
507 zooplankton assemblages (Garcia et al. 2021).

508

509 However, methodological differences alone cannot explain the exceptionally high
510 richness observed, as studies conducted elsewhere in the SCS using comparable mesh
511 sizes have not reported similarly high thaliacean diversity (Table 1). Moreover, the
512 species richness documented here is also unusually high compared with that of other
513 regions where thaliacean diversity and ecology have been relatively well studied,
514 including the North Atlantic, the Pacific Ocean, and various coastal systems (Van Soest
515 1975, Martin et al. 2016, Ishak et al. 2020, 2022, Pitt et al. 2023, Da Silva Rodrigues et
516 al. 2024). The exceptionally high species richness observed in the SCS likely reflects
517 the combined influence of its biogeographic setting and local physical forcing. During
518 the sampling period, monsoon-driven circulation, mesoscale cyclonic and anticyclonic
519 eddies, and coastal upwelling generated pronounced hydrographic heterogeneity
520 (Supplementary Material), which likely enhanced habitat diversity and facilitated the
521 coexistence of species with different ecological affinities (Liu 2013, Diao et al. 2022).
522 This physical complexity may partly account for the higher thaliacean richness
523 observed relative to other regions of the SCS. Moreover, as a central component of the
524 Indo–Pacific biogeographic province, the SCS may function as a biological
525 convergence zone, allowing the co-occurrence of thaliacean species from the tropical
526 Indian Ocean, the western Pacific, and locally adapted taxa (Diao et al. 2022, Liu et al.
527 2024, Lai et al. 2025), which further contributes to the elevated species richness
528 compared with other regions globally.

529

530 However, the lack of time-series data, multi-gear sampling, and standardized

531 regional comparisons constrain our interpretation of this high diversity. It remains
532 unclear whether this pattern represents a localized and seasonal phenomenon or reflects
533 actual shifts in thaliacean species composition, possibly driven by global climate
534 change. These findings underscore the need for long-term, multi-method monitoring of
535 thaliaceans.

536

537 **New records reveal expanded doliolida biodiversity in the SCS**

538 This study documents five newly recorded species and one suborder of Doliolidae,
539 thereby expanding current knowledge of doliolid diversity and distribution in the SCS.
540 The discovery of *D. mirabilis* and *D. tritonis* fills a taxonomic gap for the genus
541 *Dolioletta* in the SCS, which was previously only represented by *D. gegenbauri*. Both
542 species have been rarely reported globally, likely due to their morphological similarity
543 to *D. gegenbauri*, particularly during the phorozoid stage (Godeaux 1998a), which
544 may have led to frequent misidentification.

545

546 Three other new species belong to the genus *Doliolina*. This genus has been rarely
547 documented in previous studies of the SCS but was frequently encountered in this study
548 (Table 2). *D. indica* has previously been reported mainly from the Indian Ocean,
549 Arabian Sea, and Red Sea (Fig. 7D). Its occurrence in the SCS is consistent with its
550 tropical-subtropical distribution and may be facilitated by the SCS acting as a
551 biogeographic transition zone within the Indo-Pacific. *D. krohni* is considered one of
552 the few doliolid species capable of thriving under both tropical and subpolar conditions
553 (Weikert and Godeaux 2008). Although suitable niches likely exist in the SCS, this
554 species is recorded here for the first time. *D. sigmoides* was rarely recorded in previous
555 studies. In this study, it occurred more frequently in offshore waters (Fig. 6D), which
556 may account for its rare records in conventional coastal surveys.

557

558 The suborder Doliopsidina, although first described in 1996, had not previously
559 been recorded in the SCS. Its detection in this study therefore filled a major
560 biogeographic gap. In this study, Doliopsidina exhibited relatively high occurrence
561 rates, reaching up to 54.55%. All known members of Doliopsidina are warm-temperate
562 species, and thus, the occurrence of Doliopsidina in the SCS is biogeographically
563 plausible. However, determining whether the observed specimens represent any known
564 species or a potentially undescribed taxon will require additional material and further
565 investigation.

566

567 Overall, these findings suggest that doliolids in the SCS are far more diverse and
568 ecologically differentiated than previously recognized, with important implications for
569 regional biodiversity assessments and for the reevaluation of the biogeographic patterns
570 of pelagic tunicates.

571 **Conclusion**

572 This study provides the most comprehensive assessment of thaliaceans in the SCS
573 to date, documenting 28 species that represent the highest species richness reported in
574 this region. These include five newly recorded species and one suborder. These findings
575 reveal an unusually complex species composition and ecological differentiation,
576 highlighting the previously underestimated diversity of thaliaceans in the SCS.

577

578 Despite increasing global trends of biodiversity loss under climate warming and
579 ocean acidification, we observed exceptionally high thaliacean diversity using plankton
580 net trawling. This suggests that marine biodiversity may still be substantially
581 underestimated and that our understanding of pelagic ecosystem diversity and function
582 requires further refinement.

583

584 However, as this study was conducted during a single season, we cannot determine
585 whether the observed high diversity is a localized, seasonal phenomenon or reflects
586 actual shifts in thaliacean species composition potentially linked to global climate
587 change. These uncertainties highlight the need for establishing long-term, cross-
588 regional monitoring networks that integrate multiple sampling approaches, including
589 eDNA and *in situ* imaging technologies, to achieve a more comprehensive
590 understanding of gelatinous zooplankton diversity and ecosystem function.

591

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599

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