Journal of Species Research 9(2):131-146, 2020

Four new records of family Diphyidae (Hydrozoa: Siphonophorae) in Korean waters

Nayeon Park and Wonchoel Lee*

Department of Life Science, College of Natural Sciences, Hanyang University, Seoul 04763, Republic of Korea

**Correspondent: wlee@hanyang.ac.kr*

Siphonophores are unique, gelatinous zooplankton, which many individuals gather and live like one "Superorganism". The role of individuals in the colony differs greatly depending on their morphological difference, making them more unique. In this study, we report four species belonging to Diphyidae Quoy and Gaimard, 1827 sampled from the South Sea and off Jeju Island, Korea. Two *Chelophyes* Totton, 1932 (*C. appendiculata* (Eschscholtz, 1829); *C. contorta* (Lens and van Riemsdijk, 1908)) and two *Eudoxoides* Huxley, 1859 (*E. mitra* (Huxley, 1859); *E. spiralis* (Bigelow, 1911)) species are described with multi-focus stacked digital images. Our findings update the confirmed order Siphonophorae Eschscholtz, 1829 in Korea to be three suborders, five families, eight genera, and 13 species. In addition, we summarize the synonyms and global distributions of these four newly recorded species in Korean waters.

Keywords: Calycophorae, Cnidaria, eudoxid, nectophore, northwestern Pacific, polygastric

DOI:10.12651/JSR.2020.9.2.131

Introduction

Siphonophores are gelatinous zooplankton belonging to the phylum Cnidaria Hatschek, 1888 class Hydrozoa Owen, 1843. They are exclusively marine and mostly holoplanktonic organisms (Totton, 1965). Currently there are 187 described species in Siphonophorae, although it is expected that there will be more species (Munro *et al.*, 2018). Siphonophores are complex, polymorphic hydrozoans and have a unique colony stage in their life cycle (Pugh, 1974). Although siphonophores appear as one giant single creature, actually it is a colony composed of many individuals. For this unique colony, Mackie (1963) named it "Superorganism". Individual in the colony has significant morphological difference depending on the function (movement, feeding, defense, and reproduction).

Siphonophorae has been traditionally divided into three suborders (Totton, 1965; Pugh, 1999; Mapstone, 2014): Cystonectae Haeckel, 1887 (characterized by the presence of a pneumatophore and absence of nectophores), Physonectae Haeckel, 1888 (characterized by the presence of both a pneumatophore and nectophores), and Calycophorae Leuckart, 1854 (characterized by the absence of a pneumatophore and presence of nectophores).

Diphyidae, well known for bullet-shape, is the most diverse and representative group among seven families belonging to Calycophorae (Mapstone, 2009). Over 60% of known siphonophores are small, bullet-shaped colonies (Grossmann *et al.*, 2014). Diphyidae has two distinct phases, polygastric (creating eudoxid through asexual reproduction), and eudoxid (creating polygastric through sexual reproduction), as an adult (Dunn and Wagner, 2006). Diphyidae is typically composed of two dissimilar nectophores with mouth-plate and longitudinal ridges. Their somatocyst only exists in the anterior nectophore, not reaching the anterior end (Mapstone, 2009). Diphyidae is clearly distinguished from other families based on these unique characters. However, most species belonging to the Diphyidae share these characters within the family, so they were initially grouped into a single genus *Diphyes* Cuvier, 1817. Later on, they were divided 45 species in eight genera, based on detailed features such as the depth of hydroecium, the length of somatocyst, and the ostial teeth. In the past, *Diphyes* was the most diverse genus, however, currently *Lensia* Totton, 1932 is the most diverse one within Siphonophorae with 26 valid species (Grossmann *et al.*, 2014). In contrast, the smallest genus is *Dimophyes* Moser, 1925 with only one reported species. *Chelophyes* and *Eudoxoides*, addressed in this study, are the second smallest genera, including two species for each genus. Both of these genera were originally classified as *Diphyes*, and were reestablished in 1932 by Totton.

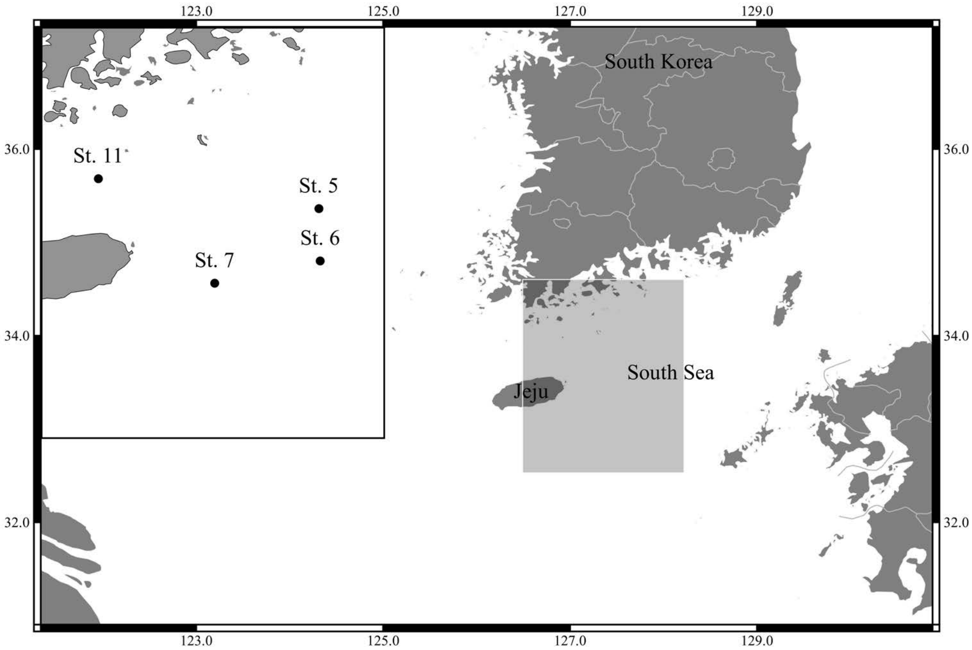

Fig. 1. The map of Korean waters and sampling stations marked with spot. The upper left box magnifies the stations on the map (gray area).

Only two genera (*Diphyes* Cuvier, 1817; *Muggiaea* Busch, 1851) and four species of Diphyidae have been recorded in Korea (NIBR, 2019). *Diphyes* and *Muggiaea* have round and deep hydroecium. The mouth-plate is undivided in *Diphyes* and divided in *Muggiaea*. On the other hand, *Chelophyes* and *Eudoxoides* have a medium depth hydroecium and divided mouth-plate, so they are clearly distinguished from other genera. However, the distinction between *Chelophyes* and *Eudoxoides* has been controversial, they are only discriminated from each other by fine discrepancies in the shape of the ventral notch, the ridges reaching the apex, and the shape of hydroecium cavity.

This study reports four unrecorded species belonging to Diphyidae found in the South Sea and off Jeju Island, Korea. Both genera, *Chelophyes* and *Eudoxoides*, are also reported for the first time in Korea.

Materials and Methods

Sample collections

Zooplankton samples were collected in April and August 2018 during an oceanographic vessel, R/V Dongbaek, in the South Sea and off Jeju Island of South Korea (Fig. 1). We towed a plankton net (mesh size: 200 μm, Ø: 60 cm) vertically from the bottom to surface. The net mouth was equipped with a flowmeter (Hydro-Bios, Germany) to determine the volume of filtered water at each tow. Temperature and salinity of surface layer of seawater were recorded using a CTD (CastAway-CTD, Sontek, USA) at each station (Table 1). Zooplankton samples were immediately split into two aliquots using a Folsom plankton splitter. One aliquot was fixed in 5 or 10% neutralized formalin solution for morphological observation and stored at room temperature. The other aliquot was fixed in 99.9% ethanol and stored in 4°C for further molecular study. Siphonophores were sorted out from zooplankton samples using a Live Insect Forceps (26029-10, F.S.T, Germany) under a stereomicroscope (Olympus SZX7, Japan) and stored in 20 mL glass vials filled with 5% neutralized formalin at room temperature. All materials of four newly recorded species were deposited in the invertebrate collection of the National Institute of Biological Resources (NIBR), Korea.

Morphological analysis

Siphonophore individuals were observed on a petri dish (Ø: 5 cm) filled with 5% neutralized formalin solution under a stereomicroscope (Olympus SZX7, Japan). All specimens were identified using descriptions and illustrations from literature including Totton (1954; 1965), Kirkpatrick and Pugh (1984), and Mapstone (2009). We used the terminology proposed by Mapstone (2009) to describe the specimens. Digital photographs of specimens were taken using a digital camera (Olympus PEN Lite E-PL3, Japan) connected to the stereomicroscope (Olympus SZX7, Japan), and side lights on dark field. Photographs were

Table 1. CTD (Conductivity, Temperature, and Depth) data and sample fixation methods of each station.

Station	Latitude	Longitude	Date	Depth (m)	Temperature (°C)	Salinity (PSS)
5	33°41′17.9376″N	127°53′22.6860″E	2018. 04. 27	107	17.87	34.47
			2018. 09. 14	108	26.77	33.88
6	33°25′27.6924″N	127°53′45.6252″E	2018. 04. 27	111	18.02	34.49
			2018. 09. 14	117	26.99	33.71
7	33°18′43.6968″N	127°21′52.8552″E	2018. 04. 26	133	18.35	34.32
			2018. 09. 13	127	26.71	33.58
11	33°50′21.2388″N	126°46′43.7880″E	2018. 04. 26	95	15.86	34.43
			2018. 09. 12	88	23.20	33.48

taken at various focus distances and multi-focus stacking was performed using Helicon Focus 7 (version: 7.5.1, Helicon Soft, Ukraine). The objects of the photographs were cropped and moved to a black background with a scale bar by using Adobe Photoshop CS6 (Version: 13.0 ×64, Adobe, USA). Size measurements of the right lateral and dorsal views (up to 15 individuals) were performed using Axiovision Rel. 4.8 (Version: AxioVs40 V 4.8.1.0, Carl Zeiss, Germany). The measurement points were determined by reference to Nishiyama *et al.* (2016).

Systematics

Class Hydrozoa Owen, 1843
Subclass Hydroidolina Collins, 2000
Order Siphonophorae Eschscholtz, 1829
Suborder Calycophorae Leuckart, 1854
Family Diphyidae Quoy and Gaimard, 1827
Subfamily Diphyinae Quoy and Gaimard, 1827
Genus *Chelophyes* Totton, 1932

Diagnosis

Bullet-shaped anterior nectophore with pointed apex. Five serrated ridges. Five ridges that only partly reaching the apex. A short hydroecium compared to *Eudoxoides*. Claw-shaped hydroecium. Small serrated hydroecium and mouth-plate. Pentagonal cross section. Anterior nectophore and posterior nectophore, both existing. Divided mouth-plate with two trapezoidal serrated wings equal. A club-shaped somatocyst with long peduncle. Somatocyst that does not reach nectosac apex. Canal that follows the shape of a nectosac. No baso-dorsal or lateral ostial teeth at the level of the ostial. The end of the mouth-plate with the point. Hydroecium cavity with made of slanted arches from the lateral view. U-shaped shallow notch from the ventral view.

1. *Chelophyes appendiculata* (Eschscholtz, 1829) (Fig. 2)

Synonymy

Diphyes appendiculata Eschscholtz, 1829: 138–139, pl. 12, fig. 7; Huxley, 1859: 34, pl. 1, figs. 2a–c; Bigelow, 1911: 248–249, pl. 7, figs. 5–6, pl. 8, figs. 7–8, pl. 9, fig. 6, pl. 10, fig. 6, pl. 11, fig. 1.
Diphyes gracilis Gegenbaur, 1853: 309–315, pl. 16, figs. 5–7.
Chelophyes appendiculata Totton, 1932: 354; 1954: 127, pl. 4, figs. 1, 3; 1965: 185–187; pl. 32, fig. 4, pl. 33, fig. 6; Stepanjants, 1967: 191, figs. 131–132a; Kirkpatrick and Pugh, 1984: 108, fig. 48; Daniel, 1985: 263, figs. 72a–e; Mackie *et al.*, 1987: fig. 36; Pagès and Gili, 1992: 95, fig. 40; Gamulin and Krsinić, 2000: 103, figs. 59a–c; Mapstone, 2009: 201, fig. 55.

Material examined

Five anterior nectophores (NIBRIV0000862385, one vial), St. 6 (33°25′27.6924″N, 127°53′45.6252″E), South Sea, Korea, 14 September 2018, collected by Jaehyeon Kim and Jisu Yeom.

Descriptions

Polygastric phase (Fig. 2)

Mean length and width, 10.50 mm and 3.52 mm, respectively (Table 2). Long bullet-shaped anterior nectophore with pointed apex (Fig. 2A–D). Sharp tip of nectosac facing to apex (Fig. $2E_1$; Subscripts indicate arrow number). Canal passing along surface of nectosac (Fig. $2E_2$). Five serrated ridges. Pentagonal cross section. Right lateral, right, and left lower ridges reaching anterior nectophore apex (Fig. $2E_3$). Claw-shaped short hydroecium (Fig. 2F). Small serrated margin and tip of hydroecium (Fig. $2F_{1,2}$). Horizontal-patterned surface of nectosac (Fig.

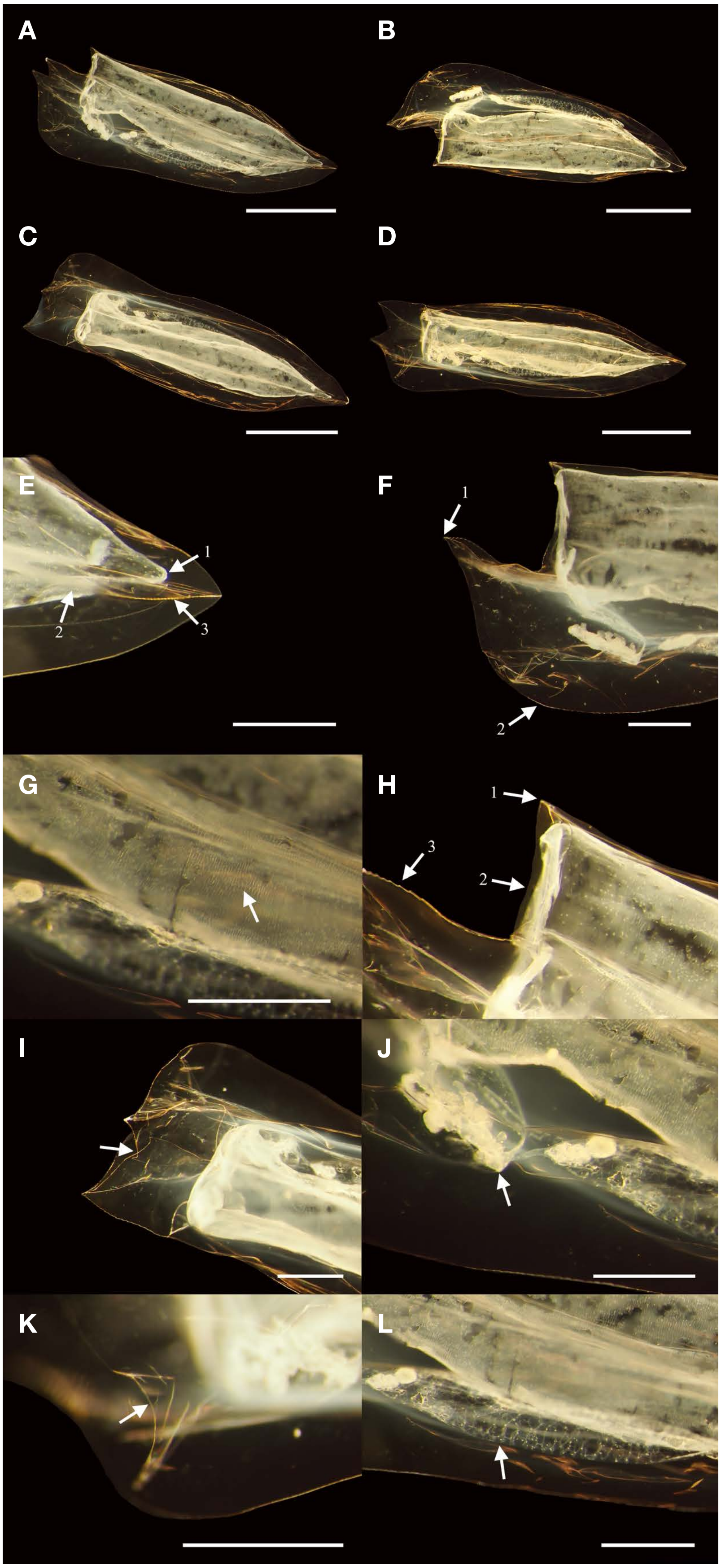

Fig. 2. *Chelophyes appendiculata* anterior nectophore. (A) Right lateral view, (B) Left lateral view, (C) Dorsal view, (D) Ventral view, (E) Apex; 1: Tip of Apex; 2: Canal; 3: Ridge, (F) Hydroecium; 1: Tip of hydroecium; 2: Serrated right ventral ridge, (G) Surface of nectosac; Horizontal-pattern of nectosac, (H) Ostial teeth; 1: No baso-dorsal ostial teeth; 2: No baso-lateral ostial teeth, 3: Serrated wing, (I) Dorsal view of mouth-plate; Divided mouth-plate, (J) Right lateral view of stem; Stem attachment point, (K) Ventral view of hydroecium; U-notch, (L) Right lateral view of somatocyst; somatocyst with oil droplets. Scale bars: A–D (3 mm); E–L (1 mm).

2G). No baso-dorsal or lateral ostial teeth at level of ostial (Fig. $2H_{1,2}$). Serrated ridge of wing (Fig. $2H_3$). Mouth-plate divided with two trapezoidal wings; equal on both sides, or larger on right one (Fig. 2I). Sharp pointed end of mouth-plate. Hydroecium cavity with slanted arches (Fig. 2J). Gastrozooid originating at end of hydroecium cavity arch. Stem originating at apex of hydroecium cavity. Stem attachment point with broad rootlike-shape. U-shaped shallow notch in ventral view (Fig. 2K). Oval-shaped somatocyst with small circular materials (Fig. 2L). Round oil droplets at end of somatocyst. Somatocyst reaching 3/4 nectosac length (Fig. 2A–D).

Remarks

Chelophyes appendiculata has a claw-shaped hydroecium, no conspicuous ostial teeth, and the long cylindrical somatocyst as the original description (Eschscholtz, 1829). Most of the morphological characters are confirmed from our materials, although there are minor discrepancies compared to the original description; in the original description the somatocyst narrows more sharply towards the end and no oil droplets, while in present specimens it has oval shaped somatocyst with oil droplets. We regard these differences as variation within the range of individual because the shape of the overall somatocyst was the similar, and the oil droplets are easy to damage.

Gegenbaur (1853) described *C. appendiculata* as *Diphyes gracilis*; the illustrations are almost perfectly consistent with the present materials, although there is no report on the serrated ridges being clearly visible in the present specimen (Fig. $2F_{1,2}$). Totton (1932) established the genus *Chelophyes* characterizing with no baso-dorsal and lateral teeth from anterior and posterior nectophores; the apical wall is oblique and runs into the dorsal wall without the marked angle. Based on those synapomorphic characters, Totton (1932) reallocated *D. appendiculata* into the genus *Chelophyes*.

2. *Chelophyes contorta* (Lens and van Riemsdijk, 1908) (Fig. 3)

Synonymy

Diphyes contorta Lens and van Riemsdijk, 1908: 39–41, pl. 6, figs. 48–50; Bigelow, 1911: 254–255, pl. 7, figs. 7–8, pl. 8, fig. 3, pl. 11, fig. 2.

Chelophyes contorta Totton, 1932: 357–358, fig. 27; 1954: 130, fig. 65; 1965: 187–188, figs. 125–126, pl. 32, figs. 7–8.

Material Examined

Ten anterior nectophores (NIBRIV0000862386, one vial), St. 6 (33°25′27.6924″N, 127°53′45.6252″E), South Sea, Korea, 14 September 2018, collected by Jaehyeon Kim and Jisu Yeom.

Descriptions

Polygastric phase (Fig. 3)

Mean length and width, 4.94 mm and 1.87 mm, respectively (Table 2). Bullet-shaped anterior nectophore with pointed apex (Figs. 3A–D). Bluntly pointed anterior nectophore compared with *Chelophyes appendiculata*. Sharp tip of nectosac facing to anterior nectophore apex (Fig. $3E_1$). Small circular material covering tip of nectosac. Canal passing along surface of nectosac. Five serrated ridges (Fig. $3E_2$). Pentagonal cross section. Right ventral ridge not reaching anterior nectophore apex (Fig. 3A). Horizontal-patterned surface of nectosac (Fig. 3F). Claw-shaped hydroecium (Fig. 3G). Short hydroecium compared with *C. appendiculata*. Serrated tip of hydroecium (Fig. $3G_1$). No baso-dorsal or lateral teeth at level of ostial (Fig. $3G_{2,3}$). Smooth ostial regions. Narrow hydroecium cavity with slanted arches. Gradual apex of hydroecium cavity compared with *C. appendiculata*. Stem originating at apex of hydroecium cavity (Fig. $3H_1$). Gastrozooid originating at end of hydroecium cavity arch. Stem attachment point with broad rootlike-shape. Club-shaped somatocyst with long peduncle (Fig. $3H_2$). Right bending head of club. Opaque white somatocyst. Oil droplets at various positions of somatocyst. Somatocyst reaching 1/2–2/3 nectosac length (Fig. 3A–D). Mouth-plate divided with two trapezoidal wings; equal on both sides, or larger on right one (Fig. 3I). Small serrated mouth-plate. Sharp pointed end of mouth-plate (Fig. $3J_1$). U-shaped shallow notch in ventral view (Fig. $3J_2$).

Remarks

Chelophyes contorta is characterized by the absolute contortion of the somatocyst, and the related facets (Lens and van Riemsdijk, 1908). In addition, the club-shaped somatocyst curved to the right is unique character within the family. The key characters are confirmed from our present materials, except for few minor characters; the incomplete median ridge beginning at the base of facet near the velum is visible in the original description, while it is not present in our materials; the peduncle of somatocyst is short (Lens and van Riemsdijk, 1908, fig. 48 in pl. 6), but present materials have long somatocyst similar to those in the fig. 49 in pl. 6 (Lens and van Riemsdijk, 1908). As in the case of *C. appendiculata*, Totton (1932) reallocated *C. contorta* from *Diphyes* to *Chelophyes* based on the characteristic of no baso-dorsal and lateral teeth at the level of ostial.

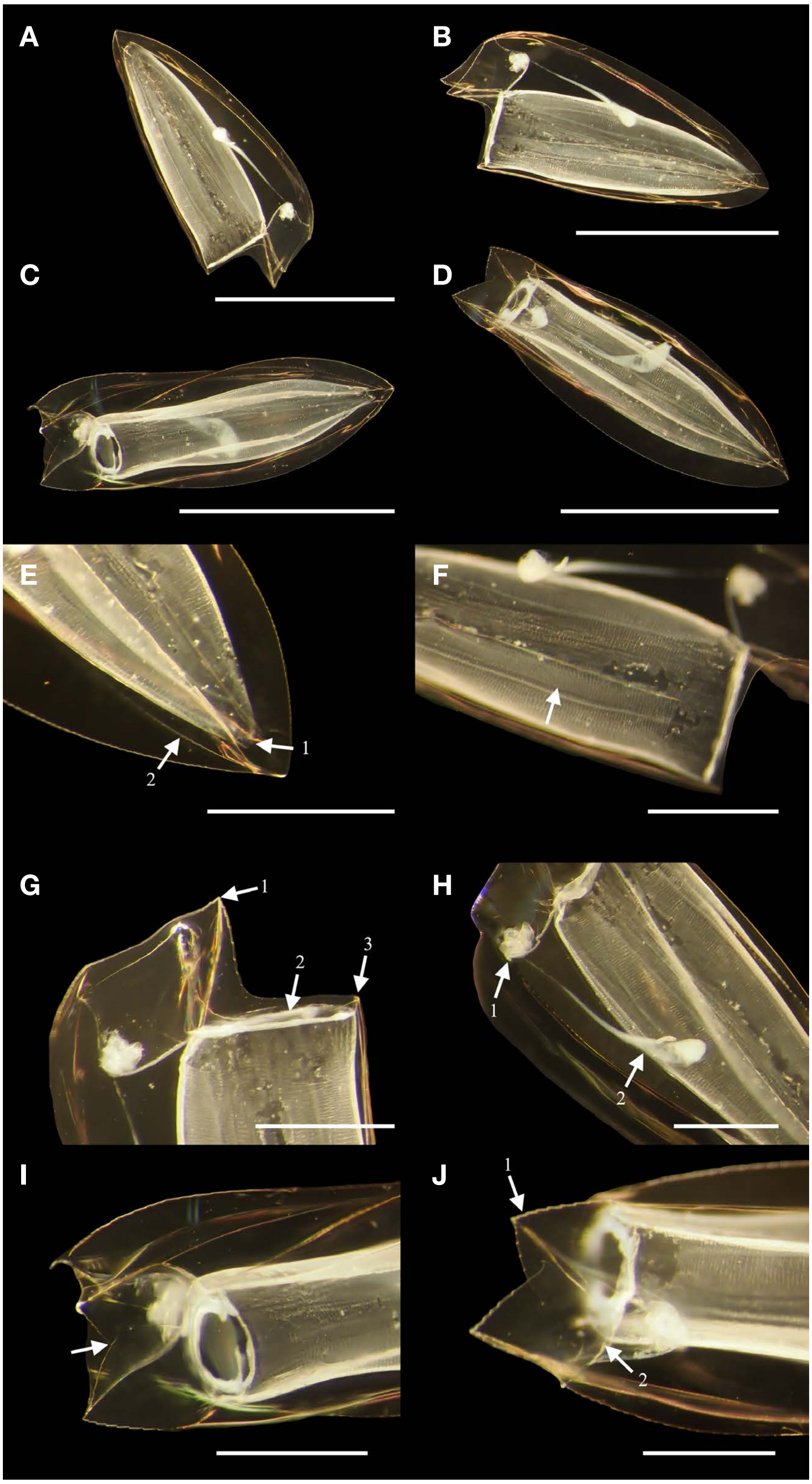

Fig. 3. *Chelophyes contorta* anterior nectophore. (A) Right lateral view, (B) Left lateral view, (C) Dorsal view, (D) Ventral view, (E) Apex; 1: Tip of Apex; 2: Serrated ridge, (F) Surface of nectosac; Horizontal-pattern of nectosac, (G) Hydroecium and ostial teeth; 1: Tip of hydroecium; 2: No baso-lateral ostial teeth; 3: No baso-dorsal ostial teeth, (H) Right lateral view of somatocyst and stem; 1: Stem attachment point; 2: Somatocyst, (I) Dorsal view of mouth-plate; Divided mouth-plate, (J) Ventral view of hydroecium; 1: Serrated wing; 2: U-notch. Scale bars: A–D (3 mm); E–J (1 mm).

Table 2. Size measurement of unrecorded four Diphyidae species.

Specimen	N	Average (Min–Max) (mm)												
		TL	ANH	ANW	NH	OW	SH	SW	HH	HW	LMH	LMW	RMH	RMW
Chelophyes appendiculata	5	10.50 (9.76–11.15)	9.11 (8.59–9.57)	3.52 (3.14–3.87)	8.51 (7.67–9.15)	1.89 (1.46–2.11)	5.53 (4.94–5.94)	0.35 (0.15–0.68)	1.48 (1.23–1.75)	2.37 (1.71–2.91)	1.19 (0.92–1.55)	0.95 (0.74–1.17)	1.32 (1.14–1.48)	1.18 (0.98–1.44)
Chelophyes contota	10	4.94 (3.10–5.45)	4.13 (2.58–4.58)	1.87 (0.99–2.21)	3.86 (2.37–4.39)	1.03 (0.46–1.28)	2.00 (1.25–2.43)	0.33 (0.13–0.47)	0.80 (0.55–0.91)	1.12 (0.68–1.31)	0.72 (0.40–0.84)	0.47 (0.25–0.57)	0.75 (0.47–0.91)	0.54 (0.30–0.67)
Eudoxoides mitra	15	9.42 (8.21–10.41)	7.84 (6.92–8.70)	2.64 (2.32–3.10)	7.07 (6.32–7.71)	1.55 (1.14–1.91)	2.32 (1.86–2.99)	0.47 (0.17–0.88)	1.69 (1.35–1.94)	1.50 (1.24–1.71)	1.57 (1.14–1.84)	0.63 (0.41–0.83)	1.48 (1.23–1.70)	0.79 (0.42–1.05)
Eudoxoides spiralis	15	4.48 (3.88–5.41)	3.38 (2.98–3.97)	1.36 (1.07–1.77)	3.07 (2.69–3.61)	0.77 (0.43–1.13)	1.33 (0.88–1.58)	0.29 (0.15–0.49)	1.09 (0.78–1.54)	0.89 (0.67–1.02)	1.02 (0.88–1.21)	0.26 (0.18–0.35)	1.10 (0.98–1.28)	0.46 (0.35–0.61)
		TL	TW	BH	BW	GH	GW							
Eudoxoides spiralis (Eudoxid)	1	4.08	0.93	1.97	0.93	2.76	0.98							

N: Numbers, TL: Total length, ANH: Anterior nectophore height, ANW: Anterior nectophore width, NH: Nectosac height, OW: Ostium width, SH: Somatocyst height, SW: Somatocyst width, HH: Hydroecium height, HW: Hydroecium width, LMH: Left mouth-plate height, LMW: Left mouth-plate width, RMH: Right mouth-plate height, RMW: Right mouth-plate width, TW: Total width, BH: Bract height, BW: Bract width, GH: Gonophore height, GW: Gonophore width.

Genus *Eudoxoides* Huxley, 1859

Diagnosis

Bullet-shaped anterior nectophore with pointed apex. Small serrated 5 longitudinal ridges. Pentagonal cross section. Complete dorsal ridge. Claw-shaped hydroecium. Divided mouth-plate. Somatocyst not reaching apex of nectosac. Lancet-shaped and serrated wings. Small serrated hydroecium and mouth-plate. Posterior nectophore which is present or absent.

3. *Eudoxoides mitra* (Huxley, 1859) (Fig. 4)

Synonymy

Diphyes mitra Huxley, 1859: 36–37, pl. 1, fig. 4.
Diphyes gracilis Bedot, 1896: 370–372, pl. 12, figs. 4, 8.
Eudoxoides mitra Totton, 1932: 358–360, figs. 28–29; 1936: 234; 1965: 188–189, pl.33, figs. 4–5; Leloup, 1934: 28; Moore, 1949: 17, figs. 30–36; Sears, 1950: 3.

Material Examined

Six anterior nectophores (NIBRIV0000862387, one vial), St. 5 (33°41′17.9376″N, 127°53′22.6860″E), South Sea, Korea, 27 April 2018, collected by Eunha Choi and Nayeon Park; nine anterior nectophores (NIBRIV 0000862388), St. 6 (33°25′27.6924″N, 127°53′45. 6252″E), South Sea, Korea, 14 September 2018, collected by Jaehyeon Kim and Jisu Yeom.

Descriptions

Polygastric phase (Fig. 4)

Mean length and width, 9.42 mm and 2.64 mm, respectively (Table 2). Bullet-shaped with pointed apex (Fig. 4A–D). Not spirally twisted. Small circular material covering tip of nectosac facing to apex (Fig. 4E$_1$). Canal passing along surface of nectosac (Fig. 4E$_2$). Small serrated five longitudinal ridges reaching apex (Fig. 4E$_3$). Hydroecium with pointed tip (Fig. 4F$_1$). Long hydroecium part below ostial level compared with part above. Gastrozooid originating at end of hydroecium cavity arch (Fig. 4F$_2$). No lateral ostial teeth (Fig. 4G$_1$). Ostial teeth originating from junction of baso-dorsal ridge and ostial (Fig. 4G$_2$). Acute outer angles of mouth-plate wing. Concave distal edges of wing. Small serrated mouth-plate (Fig. 4F, H). Mouth-plate divided with two lanceolate wings; equal in both sides, or larger in left one (Fig. 4H). Oval-shaped somatocyst with short peduncle (Fig. 4I$_1$). Round oil droplets at end of somatocyst (Fig. 4I$_2$). Somatocyst with small circular materials. Somatocyst reaching 1/2–1/3 nectosac length (Fig. 4A–C). Stem attachment point with broad rootlike-shape (Fig. 4I$_3$). Horizontal-patterned surface of nectosac (Fig. 4J).

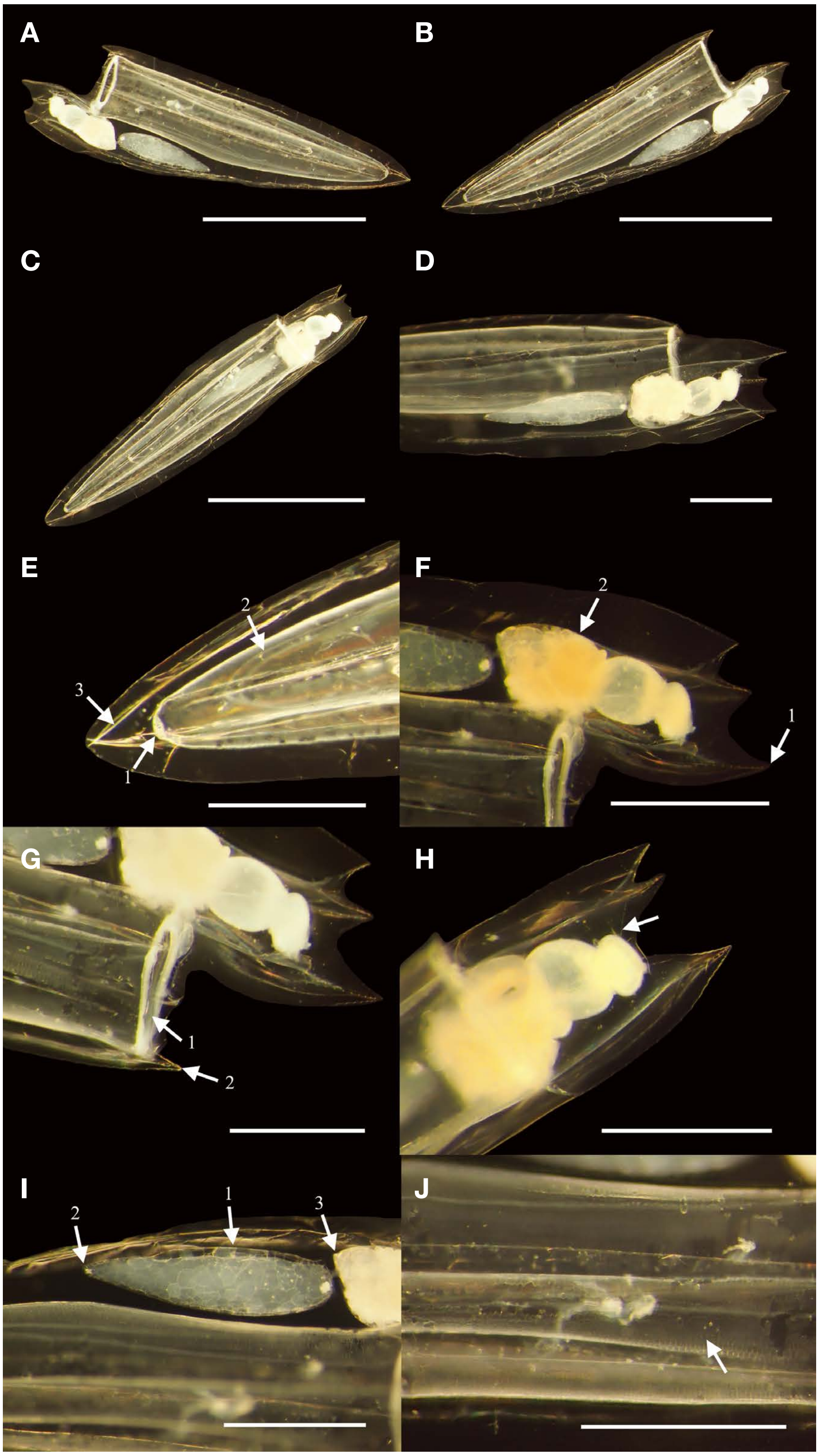

Fig. 4. *Eudoxoides mitra* anterior nectophore. (A) Right lateral view, (B) Left lateral view, (C) Dorsal view, (D) Ventral view, (E) Apex; 1: Tip of Apex; 2: Canal; 3: Ridge, (F) Hydroecium; 1: Tip of hydroecium; 2: Gastrozooid, (G) Ostial teeth; 1: No baso-lateral ostial teeth, 2: Baso-dorsal ostial teeth, (H) Dorsal view of mouth-plate; Divided mouth-plate, (I) Somatocyst; 1: Somatocyst; 2: Oil droplets; 3: Stem attachment point, (J) Surface of nectosac; Horizontal-pattern of nectosac. Scale bars: A–C (3 mm); D–J (1 mm).

Remarks

Based on the original description (Huxley, 1859), *Eudoxoides mitra* has an interesting combination of characters including (1) anterior nectophore has obtusely pointed at its apex, (2) hydroecium attains hardly more than one fourth of the length, (3) the narrow neck of the somatocyst is obtusely conical with a slightly recurved apex, (4) the anterior wall of hydroecium is formed below by two triangular plates. The same characters are detected from our present materials although there are minor discrepancies including (1) nectophore is a bit blunter, (2) the somatocyst is slightly shorter, (3) the hydroecium is round and the serrate of ridge is larger. Present specimens also can be regarded as *Diphyes gracilis* originally reported by Bedot (1896), however Totton (1932) synonymized the species to *E. mitra*. Totton (1965) provides detailed illustrations of anterior nectophores, which are almost perfectly consistent with the present specimen, except that the somatocyst is relatively shorter in the earlier report.

4. *Eudoxoides spiralis* (Bigelow, 1911) (Fig. 5)

Synonymy

Diphyes spiralis Bigelow, 1911: 249–251, pl. 7, fig. 4, pl. 8, figs. 1–2, pl. 9, fig. 3, pl. 11, fig. 4.
Eudoxoides spiralis Totton, 1932: 360–363, fig. 30; 1936: 234; 1965: 189–191, pl. 32, figs. 5–6; Moore, 1949: 16, figs. 23–29; Sears, 1950: 3; Totton and Fraser, 1955: 55, figs. 2–3, 6; Kirkpatrick and Pugh, 1984: 110–111, fig. 49; Pugh, 1999: 154, pl. 60, fig. F.

Material Examined

Five anterior nectophores (NIBRIV0000862389, one vial), St. 6 (33°25′27.6924″N, 127°53′45.6252″E), South Sea, Korea, 14 September 2018, collected by Jaehyeon Kim and Jisu Yeom; six anterior nectophores (NIBRIV 0000862390, one vial) and one eudoxid (NIBRIV0000 862391, one vial), St. 5 (33°41′17.9376″N, 127°53′ 22.6860″E), South Sea, Korea, 14 September 2018, collected by Jaehyeon Kim and Jisu Yeom; three anterior nectophores (NIBRIV0000862382, one vial), St. 7 (33°18′43.6968″N, 127°21′52.8552″E), South Sea, Korea, 13 September 2018, collected by Jaehyeon Kim and Jisu Yeom; one anterior nectophores (NIBRIV0000862383, one vial), St. 11 (33°50′21.2388″N, 126°46′43.7880″E), South Sea, Korea, 26 April 2018, collected by Eunha Choi and Nayeon Park.

Descriptions

Polygastric phase (Fig. 5A–J)

Mean length and width, 4.48 mm and 1.36 mm, respectively (Table 2). Overall twisted bullet-shaped with pointed apex (Fig. 5A–D). Small circular material covering tip of nectosac facing to apex (Fig. $5E_1$). Nectosac with same twist-shaped as nectophore. Five twisted and serrated longitudinal ridges. Left ventral ridge combining to right before apex (Fig. $5E_2$). Serrated and pointed tip of hydroecium (Fig. $5F_1$). Hook-shape of hydroecium in lateral view (Fig. $5F_2$). Small serrated hydroecium (Fig. $5F_3$). No baso-dorsal or lateral ostial teeth at level of ostial (Fig. $5F_{4,5}$). Stem attachment point with broad rootlike-shape (Fig. $5G_1$). Oval-shaped somatocyst with short peduncle (Fig. $5G_2$). Somatocyst with small circular and column-shaped materials. Round oil droplets at end of somatocyst (Fig. $5G_3$). Somatocyst reaching 1/2–1/3 nectosac length (Fig. 5A–D). Oblique somatocyst to right of main axis (Fig. 5D). Slanted fish-scaly surface of nectosac (Fig. 5H). Deep V-shaped notch located in ventral wall (Fig. 5I). Right ventral ridges faced to notch. Curved basal end of left ventral ridge reaching the mid-ventral line before level of ostium. Dissimilar basal ends of two ventral ridges. Triangular space consisting of hydroecium converged to dorsal and opened to ventral. Small divided mouth-plate with two lanceolate wings (Fig. 5J). Larger right lanceolate wing than left one.

Eudoxid phase Eudoxid (Fig. 5K–L)

Conical shape with one longer downside (Fig. 5K). Sharp apex of ridges. Two serrated ridges. Long plump oval-shaped phyllocyst. Small circular materials in phyllocyst. Round oil droplets at end of phyllocyst. Tip of phyllocyst facing to bract apex (Fig. $5K_1$). Basal end of phyllocyst point with broad rootlike-shape (Fig. $5K_2$). About 2.76 mm in gonophore length and about 0.98 mm in gonophore width (Table 2). Junction of bract and gonophore (Fig. 5L). About 4.08 mm in eudoxid total length about 1.97 mm in bract length and about 0.93 mm in bract width (Table 2). Twisted column-shaped gonophore (Fig. 5L). Smooth attachment point (Fig. $5L_1$). Slanted fish-scaly surface same as anterior nectophore. Ovum attached inside of eudoxid (Fig. $5L_2$). Serrated ridges. Short and pointed hydroecium. No conspicuous baso-ostial teeth in ostium (Fig. $5L_3$).

Remarks

Based on the original description (Bigelow, 1911), the most remarkable feature of *Eudoxoides spiralis* is that the entire nectophore is spirally twisted in the same clockwise direction. This species has four ridges at the apex, the larger right wing, and neither baso-lateral nor baso-dorsal teeth as in our present specimens. There is a slight difference, with the original description showing plumper nectophore than the present one. Similar to the case of *E. mi-*

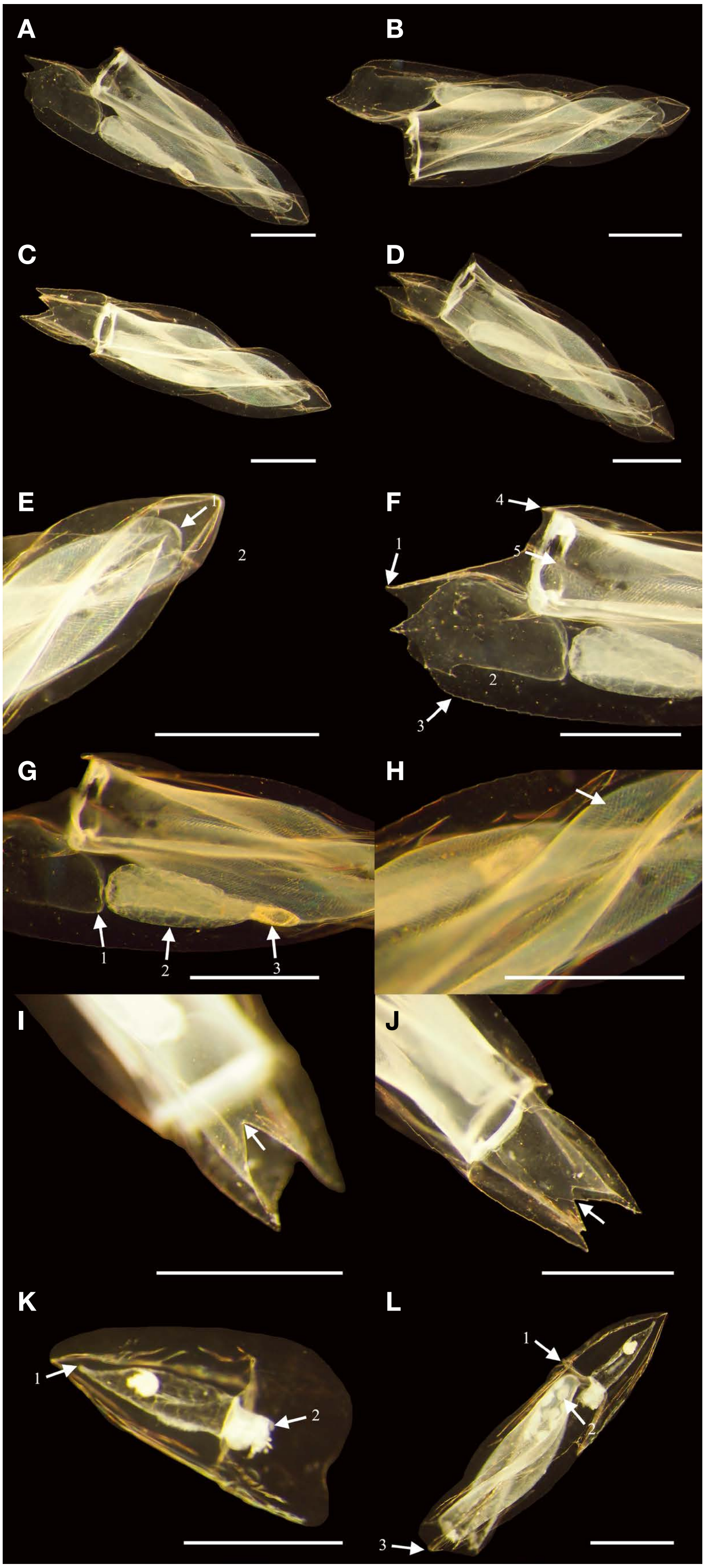

Fig. 5. *Eudoxoides spiralis* anterior nectophore and Eudoxid. (A) Right lateral view, (B) Left lateral view, (C) Dorsal view, (D) Ventral view, (E) Apex; 1: Tip of Apex; 2: Ridge, (F) Hydroecium; 1: Tip of hydroecium; 2: Hook of hydroecium; 3: Serrated right ventral ridge; 4: No baso-dorsal ostial teeth; 5: No baso-lateral ostial teeth, (G) Somatocyst; 1: Stem attatchment point; 2: Somatocyst; 3: Oil droplets, (H) Surface of nectosac; Slanted fish-scaly pattern of nectosac, (I) Ventral view of hydroecium; V-notch, (J) Dorsal view of mouth-plate; Divided mouth-plate, (K) Bract of Eudoxid; 1: Apex of phyllocyst; 2: Gastrozooid, (L) Gonophore of Eudoxid; 1: Attatchment point; 2: Ovum; 3: Ostium. Scale bars: 1 mm.

Table 3. Global distribution of four Diphyidae species described in this paper. Records after the original descriptions were integrated. St. 5–7, 11 can be found in the fig. 1.

Ocean	Regions	Newly recorded species				References
		Chelophyes appendiculata	*Chelophyes contorta*	*Eudoxoides mitra*	*Eudoxoides spiralis*	
North Pacific	Canada, Canadian Pacific water	●				Mapstone, 2009
	China, East China Sea			●	●	Gao *et al*., 2002; Tao *et al*., 2005; Xu *et al*., 2008
	China, South China Sea	●	●	●	●	Li et al, 2012; Lo *et al*., 2012; 2014; Tao *et al*., 2005; Zhang and Xu, 1980; Zhang *et al*., 2005
	Costa Rica		●	●		Gasca and Suárez, 1992
	Japan, Sagami Bay	●	●	●	●	Grossmann and Lindsay, 2013
	Korea, St. 5			●	●	This study
	Korea, St. 6	●	●	●	●	This study
	Korea, St. 7				●	This study
	Korea, St. 11				●	This study
	Philippines, Celebes Sea		●	●	●	Bigelow, 1928; Grossmann *et al*., 2015
	Philippines, Sulu Sea		●		●	Grossmann *et al*., 2015
	Taiwan	●	●	●	●	Hsieh *et al*., 2013; Lo *et al*., 2012; 2014; Zhang *et al*., 2005
	USA, California	●			●	Alvariño, 1991; Lluch-Cota *et al*., 2007; Longhurst, 1967
South Pacific	Australia, Coral Sea: Great Barrier Reef			●		Totton, 1932
	Chile	●	●	●	●	Palma and Silva, 2006
	Chile, Easter Island	●	●	●	●	Palma and Silva, 2006
	New Zealand, Exclusive Economic Zone (EEZ)	●		●	●	Cairns *et al*., 2009
	Papua New Guinea		●	●	●	Pagès *et al*., 1989
	Peru			●	●	Ayón *et al*., 2008
North Atlantic	Adriatic Sea	●			●	Gamulin and Krsinić, 2000; Hure *et al*., 2018
	British Isles, North and West of the British Isles				●	Fraser, 1967
	Caribbean Sea	●			●	Alvariño, 1974; Michel and Foyo, 1977
	Colombia		●	●	●	Palomino *et al*., 2019
	France, Villefranche-Sur-Mer	●			●	Leloup, 1935
	Italy, Tyrrhenian Sea				●	Zagami *et al*., 1996
	Mediterranean Sea	●	●	●	●	Andersen *et al*., 2001; Bouillon *et al*., 2004; Mapstone, 2001; Sardou and Andersen, 1993
	Mexico, Gulf of Mexico	●	●	●	●	Felder and Camp, 2009; Pugh and Gasca, 2009
	Porcupine Seabight	●				Kirkpatrick and Pugh, 1984
	Sargasso Sea	●				Purcell, 1981
	Spain, Canary Island			●	●	Owre and Foyo, 1972; Soldevilla and Hernández, 1991
	United Kingdom, Bermuda	●		●	●	Hela *et al*., 1953; Lo and Biggs, 1996; Moore, 1949
	USA, Florida Current			●		Moore and Corwin, 1956

Table 3. Continued.

Ocean	Regions	Newly recorded species				References
		Chelophyes appendiculata	*Chelophyes contorta*	*Eudoxoides mitra*	*Eudoxoides spiralis*	
South Atlantic	Angola, Benguela Current	●	●	●	●	Pagès and Gili, 1992; Pagès *et al*., 1991
	Brazil			●	●	Gusmão *et al*., 2015; Lang da Silveira *et al*., 2011
Indian Ocean	Arab emirates		●			Sharaf and Al-Ghais, 1997
	Arabian Sea			●		Peter *et al*., 2018
	Australia, Western Australia				●	McCosker, 2016
	India, Bay of Bengal				●	Li *et al*., 2017
	Indonesia	●	●			Wang *et al*., 2018
	Jordan, Gulf of Aqaba		●	●		Mańko *et al*., 2017
	Madagascar			●		Patriti, 1970
	Pakistan	●	●			Morandini *et al*., 2015

tra, Totton (1932) reallocated *E. spiralis* from *Diphyes* to *Eudoxoides*. The eudoxid phase of *E. spiralis* is identified by Totton (1932) with the conical bract as in other eudoxid. It is easily identified as *E. spiralis* due to the twisted gonophore.

Discussions

We conducted a morphological study of four unrecorded species of Diphyidae found in the South Sea and off Jeju Island, Korea. Two species belong to *Chelophyes* and another two species to *Eudoxoides*.

Chelophyes appendiculata is the type species of *Chelophyes*, and the most abundant species in the family Diphyidae (Totton, 1965). Up to 20 mm in length, it is larger than the other species in the same family (Kirkpatrick and Pugh, 1984). Specimens observed in this study were about 10 mm in length, twice as large as *C. contorta* (Table 2). *Chelophyes appendiculata* has a big difference in the shape of somatocyst compared with *C. contorta*, so the distinction between them is clear. Interestingly, *E. mitra* has a similar shape of somatocyst and size of anterior nectophore compared with *C. appendiculata*, so they are difficult to distinguish especially in lateral view. According to the previous reports (*C. appendiculata*: Gegenbaur, 1853; *E. mitra*: Bedot, 1896), these two species were identified as a single species, *Diphyes gracilis*. For clear identification, we need to check the apex view, whether there are three ridges reaching the apex (*C. appendiculata*) or five ridges (*E. mitra*), as suggested in Totton (1965).

Chelophyes contorta is about 7 mm in length (Totton, 1965). The mean length of present specimens is 5 mm, and about half size of *C. appendiculata* (Table 2). *Chelophyes contorta* has a unique club-shaped somatocyst curved to the right. The number of ridges reaching the apex is four, which is the same as *E. spiralis*. However, the right-ventral ridge does not reach the apex in *C. contorta*, while the left-ventral ridge does not reach the apex in *E. spiralis* (Totton, 1965).

Eudoxoides mitra is the type species of *Eudoxoides*. It has been recorded up to 12 mm in length (Totton, 1965). Specimens observed in this study were about 10 mm in length. It is a large species like *C. appendiculata* (Table 2). *Eudoxoides mitra* has a straight body shape, and also has a posterior nectophore. Therefore, the distinction between *E. mitra* and *E. spiralis* is quite clear based on their body form.

Eudoxoides spiralis is 2–6 mm in length in the original description (Bigelow, 1911) and up to 11–12 mm in subsequent studies (Totton, 1965; Kirkpatrick and Pugh, 1984). The present specimens were about 5 mm in length, which fits well into the size range of the original report. *Eudoxoides spiralis* has a unique anterior nectophore which is completely twisted. In addition, *E. spiralis* has four ridges reaching the apex, while *E. mitra* has five ridges reaching the apex (Totton, 1965).

The genus *Eudoxoides* has a debatable history. Huxley (1859) established the genus, however it was Totton (1932) who defined and allocated *E. mitra* to *Eudoxoides*. This genus has a medium depth hydroecium and divided mouth-plate, and their anterior nectophore has a complete dorsal ridge. Since *Chelophyes* shares these characters with *Eudoxoides*, and their differences are not clear, it is necessary to check the generic identity of *Eudoxoides* in further molecular analysis.

Chelophyes appendiculata and *E. mitra* are the most abundant species in the family Diphyidae (Totton, 1965) and they occur mainly in warm waters (Kirkpatric and Pugh, 1984). *Chelophyes contorta* and *E. spiralis* are rarer compared to other species belonging to Diphyidae (Totton, 1965). However, in the tropical western Indian Ocean, *C. contorta* is more abundant than *C. appendiculata* (Totton, 1954). The type localities of these four species are the Mediterranean Sea (*C. appendiculata*, Eschscholtz, 1829), Malay Archipelago (*C. contorta*, Lens and van Riemsdijk, 1908), southeast of Mauritius (*E. mitra*, Huxley, 1859) and tropical eastern Pacific Ocean (*E. spiralis*, Bigelow, 1911). Since their original reports, their distributions have been limited to warm waters (Mapstone, 2009). However, high temperature does not necessarily cause their high abundance. In the case of the Gulf of Mexico, where siphonophores appear frequently, colonies decrease at conditions of over 28.1°C (Sanvicente-Añorve *et al.*, 2009) and extreme salinity ($>$36.5 or $<$34 PSU, Sanvicente-Añorve *et al.*, 2007). According to Pakhomov *et al.* (1994), *C. appendiculata* and *E. spiralis* appear in the subtropical convergence regions but are absent in the Antarctic Polar Fronts showing limited distribution in low temperature.

These four species have been reported in the northwestern Pacific Ocean (Table 3). During the surveyed period, temperature and salinity were about 15.3°C and 34.6 PSU in Sagami Bay, Japan (Grossmann and Lindsay, 2013). In the Taiwan Strait, temperature ranged 14.7–24.4°C in winter and 25.18–30.08°C in summer, while salinity ranged 32.3–34.7 PSU in winter and 32.1–34.3 PSU in summer (Hsieh *et al.*, 2013). In the present study, conditions ranged 15.86–26.99°C in temperature and 33.48–34.49 PSU in salinity (Table 1). Those values are within the ranges of temperature and salinity in previous reports.

These four species are distributed globally except for the Antarctic and Arctic Oceans (Table 3). They are epipelagic (Mapstone, 2009), eurythermic, and euryhaline showing cosmopolitan distribution (Hsieh *et al.*, 2013). However, morphological identification of siphonophores can be confusing due to their phenotypic plasticity. Their gelatinous bodies are easily damaged, and many records have been described based on dissociated specimens (Totton, 1965; Dunn *et al.*, 2005). In addition, siphonophores have intraspecific size variation. For example, *E. spiralis* has a difference up to six times in adult size (2–12 mm). This size difference is quite large although gelatinous zooplanktons normally have variability in size depending on the habitat (Bouillon and Boero, 2000). This suggests the presence of cryptic species, although there are many difficulties in determining the cryptic species due to the lack of data (Moura *et al.*, 2008; Pontin and Cruickshank, 2012). It would be useful if we can compare molecular markers of Siphonophorae in further study.

In conclusion, our findings update the confirmed Siphonophorae in Korea to be three suborders, five families, eight genera, and 13 species. These data suggest basic information on the biodiversity of siphonophores in Korean waters.

Acknowledgements

The study was supported by following research grants: Study of Undiscovered Invertebrate Species from Korea (IV) from the National Institute of Biological Resources (NIBR201902106), and Marine Biotechnology Program of the Korea Institute of Marine Science and Technology Promotion (KIMST) funded by the Ministry of Oceans and Fisheries (MOF) (No. 20170431). Authors express sincere thanks to professor Ho Young Soh (Faculty of Marine Technology, Chonnam National University) for permitting us to be participated in the cruise, and to captain, professor Daejin Kim and crew members of R/V Dongbaek (Training Ship Administrative Center, Chonnam National University) for their genuine helps during the sampling processes.

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Submitted: October 30, 2019
Revised: April 30, 2020
Accepted: April 30, 2020