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Ontogenetic comparison of larvae and juveniles of *Diaphus garmani* and *Benthosema pterotum* (Myctophidae, Pisces) collected from Korea

Hye-Lyang Lee[1], Jin-Koo Kim[1*], Hyo-Jae Yu[1,2] and Jung-Nyun Kim[2]

Abstract

During June 2017, we collected two postflexion larvae (6.01 and 7.56 mm in standard length [SL]) and two juveniles (7.72 and 9.62 mm SL) belonging to Myctophidae in the waters of Jejudo Island. Those four individuals were identified as *Diaphus garmani*, which had not been reported in Korea. They were distinguished from *Benthosema pterotum* by melanophores in the abdominal cavity (absent in *D. garmani* vs. present in *B. pterotum*) and the development of photophores (developed in *D. garmani* vs. rudimentary in *B. pterotum*) when shorter than 10.0 mm SL. Analysis of 16S rRNA sequences showed that the sequences of four individuals matched those of adult *D. garmani* (Kimura 2-parameter distance: 0.6–0.8%). This is the first record of larvae and juveniles of *D. garmani* in Korean waters, and we propose a new Korean name, *Gar-ma-ni-sat-bi-neul-chi*.

Keywords: *Diaphus garmani*, *Benthosema pterotum*, Larvae, Juvenile, Myctophidae, New record, 16S rRNA, Korea

Background

The family Myctophidae in the order Myctophiformes contains 251 species in 33 genera worldwide (Fricke et al. 2019), of which four species in three genera (*Benthosema pterotum*, *Myctophum asperum*, *Myctophum affine*, and *Notoscopelus japonicus*) occur in Korean waters (MABIK 2019; Park et al. 2019). The lanternfishes (Myctophidae) are mesopelagic fish that undertake diel vertical migration as a unique environmental adaptation (Ozawa 1986; Mini and James 1990; Moser and Ahlstrom 1996; Watanabe et al. 1999). They have a compressed body shape, large mouth, rows of small teeth, a swim bladder, bioluminescent photophores, and adipose fins (Nafpaktitis 1978, 1982, Nafpaktitis et al. 1995; Paxton et al. 1984; Martin et al. 2018).

The genus *Diaphus* in the family Myctophidae comprises 77 recognized species worldwide (Nelson et al. 2016; Froese and Pauly 2019) and has not been reported in Korea. The species in the genus *Diaphus* are classified into the *Diaphus* A and B groups depending on the presence and absence, respectively, of photophores on the suborbital organ (So), mouth morphology of early larvae, position of the anus, expression of melanophores and photophores, and timing of metamorphosis(Javadzadeh et al. 2012). Of which, *Diaphus garmani* is a small fish (~ 60 mm total length) belonging to the *Diaphus* B group and thus lacks photophores on the So (Nafpaktitis 1978; Nelson et al. 2016). Some studies of *Diaphus* have examined its early life history (Bineesh et al. 2010) and the first recorded species (Sassa et al. 2003). In Korea, studies of mesopelagic fish have examined the early life history of *Maurolicus muelleri* (Kim and Yoo 1999; Kim et al. 2007) and a new record for *Sigmops gracilis* (Lee and Kim 2013).

As the Myctophidae larvae collected in this study had similar morphological features to those of *Benthosema*

* Correspondence: taengko@hanmail.net
[1]Department of Marine Biology, Pukyong National University, Busan 48513, Korea
Full list of author information is available at the end of the article

pterotum, we confirmed the correctness of species identification by using 16S rRNA sequences. Afterward, in-depth morphological data related to ontogenetic features of these two species were compared with each other, which are barely distinguishable at the larval stage.

Methods

Sampling

Four larval specimens (PKUI 618-621) of *Diaphus garmani* were collected from the southern Jejudo Island in June 2017 by a research vessel from the National Institute of Fisheries Science using a bongo net (mouth diameter 80 cm; mesh size 500 μm). The collected specimens were immediately fixed in 5% formalin for 1 h on the vessel and then washed before being placed in a 1L polyethylene container, where they were fixed in 99% alcohol. Four *Benthosema pterotum* larvae (PKUI 614-617) were also collected from the western Jejudo Island to the East Sea between July and December 2018 (Fig. 1). After the study, the specimens were deposited at Ichthyoplankton Laboratory of Pukyong National University (PKUI).

Morphological analysis

The larvae were identified according to their morphological characteristics and photophore features observed, following the methods described by Richards (2006), Okiyama (2014), Nakabo (2013), and Martin et al.

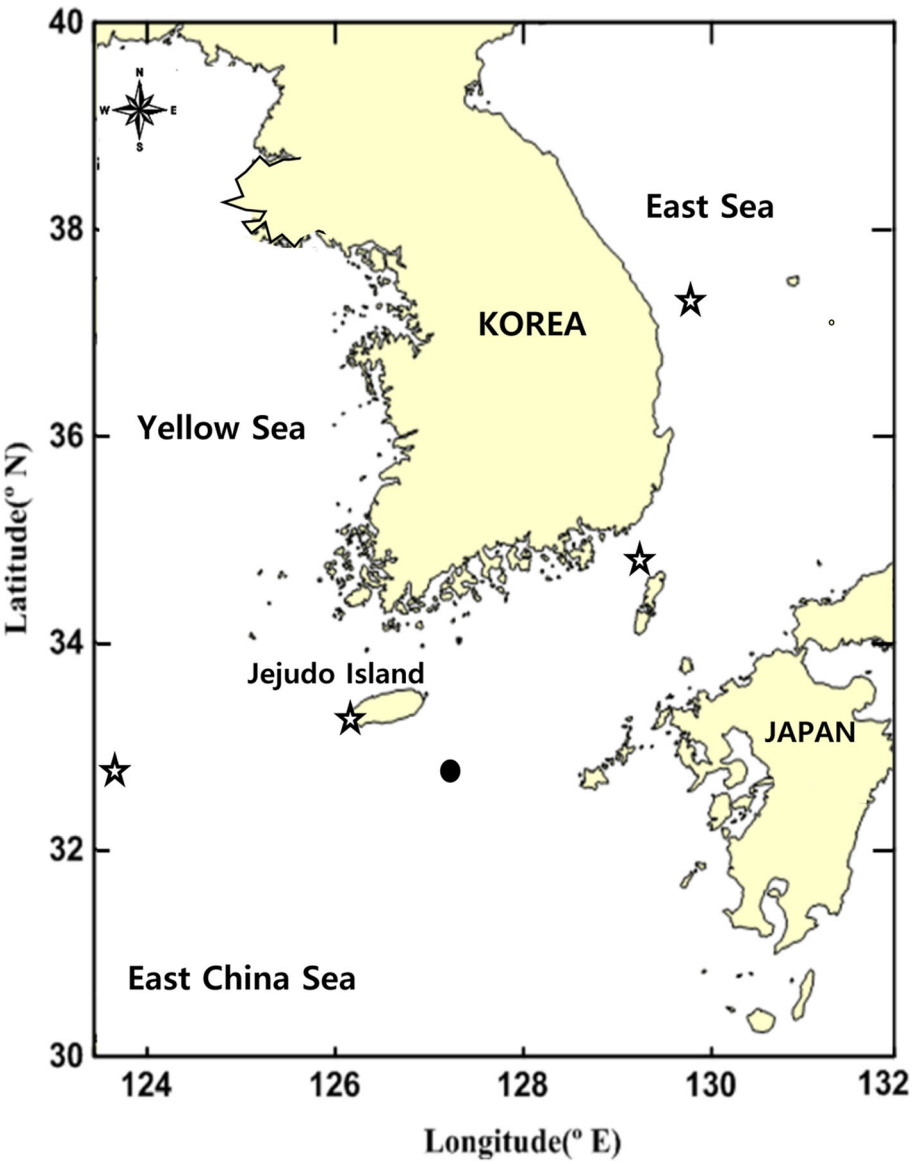

Fig. 1 Map showing the sampling sites of *Diaphus garmani* larvae ($n = 4$, PKUI 618-621) and *Benthosema pterotum* larvae ($n = 4$, PKUI 614-617) (black circle (●): *Diaphus garmani*; star (☆): *Benthosema pterotum*)

(2018). Morphometric characters included total length (TL), standard length (SL), body depth (BD), head depth (HD), head length (HL), preanus length (PaL), eye diameter (ED), pre-dorsal fin length (PDFL) and pre-anal fin length (PAFL), which were observed under a stereomicroscope (SZH-16, Olympus, Japan) and then measured to the nearest 0.01 mm using an Image-Pro plus (ver. 2.0, Media Cybernetics) (Fig. 2). Meristic characters included the dorsal fin rays (D), anal fin rays (A), pectoral fin rays (P1), and pelvic fin rays (P2), which were stained with alizarin red S for counting under a stereomicroscope (SZH-16, Olympus, Japan). Each stage of larval development was sketched using a camera lucida attached to the stereomicroscope.

Molecular analysis

Total DNA was extracted from eyeballs removed from the right side of the larvae using 150 μL Chelex 100 resin (Bio-Rad Laboratories, USA). The mitochondrial 16S rRNA region was amplified using the primers 5′-CGC CTG TTT ATC AAA AAC AT-3′ and 3′-CCG GTC TGA ACT CAG ATC ACG T-5′ (Ivanova et al. 2007). The polymerase chain reaction (PCR) conditions were as follows: initial denaturation at 95 °C for 11 min; 35 cycles of denaturation at 94 °C for 1 min, annealing 52 °C for 1 min, extension at 72 °C for 1 min; and a final extension at 72 °C for 5 min. The same conditions were used for PCR analysis of *B. pterotum*, except that the annealing temperature was 54 °C. The sequences were aligned using ClustalW in the program BioEdit (ver. 7.0.5.3; Hall 1999), and genetic distances were calculated using the Kimura 2-parameter model (Kimura 1980) using Mega X (ver. 10.0.5). The genetic relationships were analyzed by constructing a neighbor-joining tree using Mega X (ver. 10.0.5) with 1000 bootstrap replications. The 16S rRNA sequences of *D. garmani* (KR231737) and *B. pterotum* (JX133756) were also obtained from the National Centre for Biology Information database to compare eight specimens of Myctophidae larvae between the two species. The 16S rRNA sequence of *B. pterotum* and *D. garmani* used in this study was assigned the following registration number from NCBI(MT242581-242587).

Results

Molecular identification

A 479 bp of 16S rRNA sequence was obtained from each of the four Myctophidae larvae for comparison with the sequence from adults of the candidate species *D. garmani* (KR231737). The genetic distances ranged from 0.6 to 0.8%, indicating close consistency. We also compared the 16S rRNA gene sequences of the four *B. pterotum* larvae with that of the adult *B. pterotum* (JX133756) and found complete consistency, with a genetic distance of 0%. The *D. garmani* larvae, juveniles, and adult were clearly separated from the four *Diaphus* spp. and *B. pterotum* in the neighbor joining tree (Fig. 3).

Morphological features

***Diaphus garmani* Gilbert, 1906 (Fig. 4) (new Korean name: Gal-ma-ni-sat-bi-neul-chi)**

Diaphus garmani Gilbert, 1906: 258 (type locality: Cuba, western Atlantic) Masuda et al. 1984: 74; Hulley 1986: 291; Nakabo 2013: 473; Okiyama 2014: 336

Materials examined: PKUI 618, one specimen, 6.01 mm in standard length (SL), 32° 99.61′ N, 127° 05.18′ E, southern Jejudo Island, 24 June 2017, Bongo net; PKUI 619, one specimen, 7.50 mm SL, 32° 99.61′ N, 127° 05.18′ E, southern Jejudo Island, 24 June 2017, Bongo

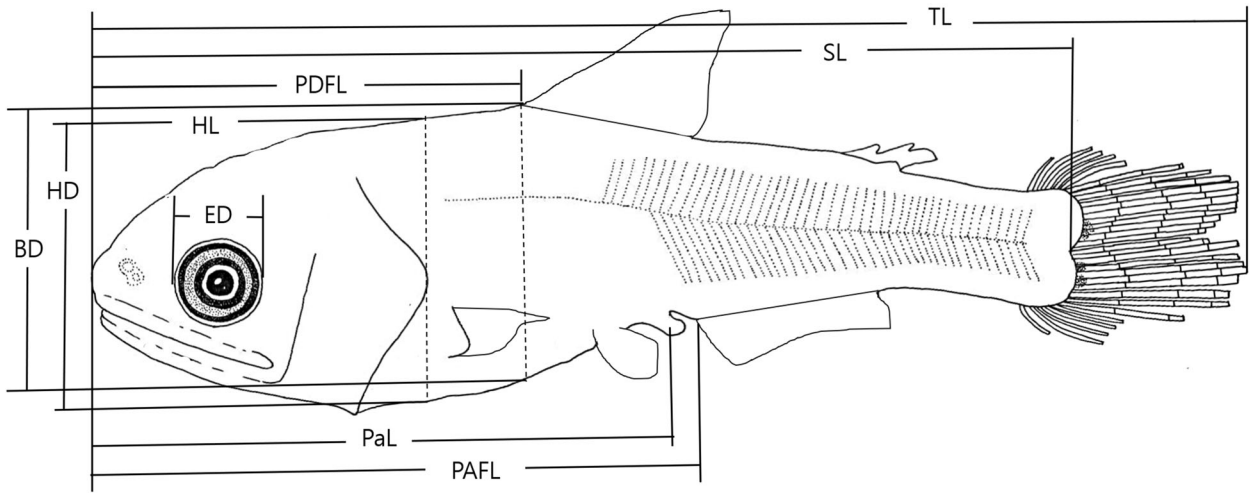

Fig. 2 Diagram showing measurements. TL, total length; SL, standard length; BD, body depth; HD, head depth; HL, head length; PaL, preanus length; ED, eye diameter; PDFL, pre-dorsal fin length; PAFL, pre-anal fin lengthTL, total length; SL, standard length; BD, body depth; HD, head depth; HL, head length; PaL, preanus length; ED, eye diameter; PDFL, pre-dorsal fin length; PAFL, pre-anal fin length

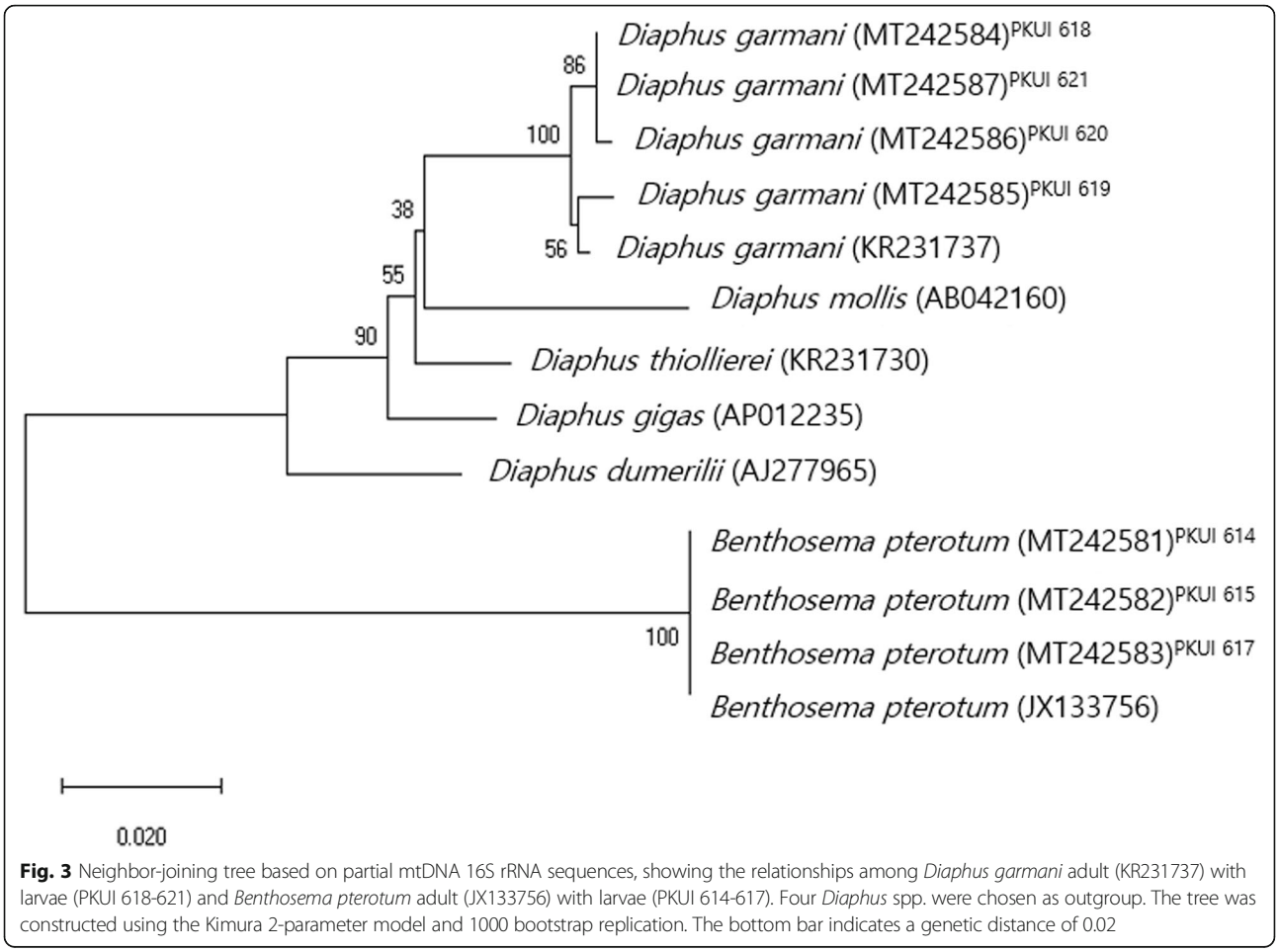

Fig. 3 Neighbor-joining tree based on partial mtDNA 16S rRNA sequences, showing the relationships among *Diaphus garmani* adult (KR231737) with larvae (PKUI 618-621) and *Benthosema pterotum* adult (JX133756) with larvae (PKUI 614-617). Four *Diaphus* spp. were chosen as outgroup. The tree was constructed using the Kimura 2-parameter model and 1000 bootstrap replication. The bottom bar indicates a genetic distance of 0.02

net; PKUI 620, one specimen, 7.72 mm SL, 32° 99.61′ N, 127° 05.18′ E, southern Jejudo Island, 24 June 2017, Bongo net; PKUI 621, one specimen, 9.62 mm SL, 32° 99.61′ N, 127° 05.18′ E, southern Jejudo Island, 24 June 2017, Bongo net.

The 6.01 mm standard length (SL) post-flexion larva of *D. garmani* (Fig. 4a) has large eyes with a pair of small nostrils situated in front. The mouth is large and slopes, with the rear end of the upper jaw reaching the posterior rim of the eye. There is a row of small sharp teeth in the jaws. The anus is positioned slightly behind the middle of the body. The end of the operculum tapers to a triangular shape. The myomeres show a clear M shape. Br_2 photophores are found on the middle part of the lower jaw, and only a trace of PO_5 photophore remain in front of the pelvic fin. The larva has an adipose fin, 13 dorsal fin rays, 14 anal fin rays, nine pectoral fin rays, and seven pelvic fin rays (Table 1). A few melanophores are present on the opercular organ, a series of three melanophores on the ventral side, one star-shaped melanophore on the anus, and one large dot-shaped melanophore at the posterior end of the anal fin base.

The 7.56 mm SL post-flexion larva of *D. garmani* (Fig. 4b) has a heavier head. Br_2 photophores are observed on the middle part of the lower jaw, a line of PO_{1235} photophores is arranged along the ventral side of the abdominal cavity, and a raised PO_4 photophore is situated between PO_3 and PO_5. A PVO_{12} photophore is observed between the base of the opercular organ and the pectoral fin, a VO_1 photophore on the base of the pelvic fin, and VO_{45} photophores on the anus. There are 14 dorsal fin rays, 15 anal fin rays, 10 pectoral fin rays, and 8 pelvic fin rays (Table 1). The occurrence of melanophores is similar to that of the 6.01 mm SL larva, but with the addition of two star-shaped melanophores in front of the pectoral fin and one and two on the upper and lower lobes, respectively, of the caudal fins.

The 7.72 mm SL juvenile of *D. garmani* (Fig. 4c) has a sharper snout than that at the previous stage, with the anus shifted forward toward the head. Br_{123} photophores are arranged in a line in the lower jaw. OP_2 is recognized in the opercular organ under the eye. PLO is situated posterior to the operculum between the lateral line and pectoral fin. PO_{1235} photophores are aligned in the

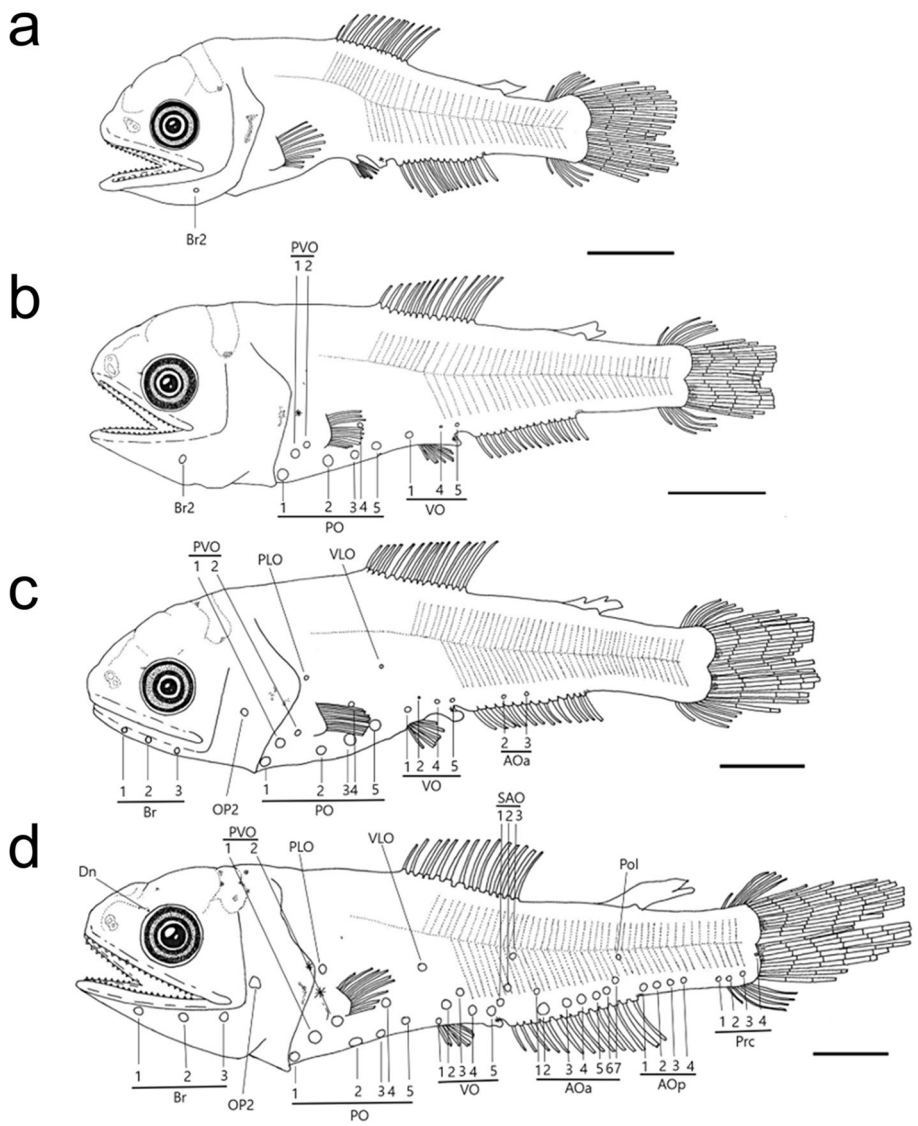

Fig. 4 Morphological development of *Diaphus garmani* (**a** post-flexion stage, PKUI 618, 6.01 mm SL; **b** post-flexion stage, PKUI 619, 7.56 mm SL; **c** juvenile stage, PKUI 620, 7.72 mm SL; **d** juvenile stage, PKUI 621, 9.62 mm SL). AOa, anterior anal organs; AOp, posterior anal organs; Br, branchiostegal organs; Dn, dorsonasal organ; OP, opercular organs; PLO, suprapectoral organ; PO, pectoral organs; Pol, postero-lateral organ; Prc, precaudal organs; PVO, subpectoral luminous glands; SAO, supraanal organs; VLO, supraventral organ; VO, ventral organs. Scale bars indicate 1.0 mm

Table 1 Number of dorsal (D), anal (A), pectoral (P1), and pelvic (P2) fin rays of *Diaphus garmani*

Voucher number	D	A	P1	P2	Stage
PKUI 618	13	14	9	7	Post-flexion
PKUI 619	14	15	10	8	Post-flexion
PKUI 620	14	15	13	8	Juvenile
PKUI 621	14	14	-	8	Juvenile

abdominal cavity. The PO_4 photophore is raised between PO_3 and PO_5. The PVO_{12} photophore is situated obliquely between the base of the opercular organ and the pectoral fin. VLO is raised slightly from the middle between the base of the pelvic fin and the lateral line. VO_{145} photophores are arranged in a line behind the pelvic fin. The VO_2 photophore is raised between VO_1 and VO_4. AOa_{23} photophores are lined on the anal fin. There are 14 dorsal fin rays, 15 anal fin rays, 13 pectoral fin rays, and 8 pelvic fin rays (Table 1). Several melanophores are present on the opercular organ. Two star-shaped melanophores are aligned on the abdominal cavity. One star-

shaped melanophore is present on the anus. A dot-shaped melanophore is present at the end of the anal fin base. There are one and two melanophores dotted on the upper and lower lobes, respectively, of the caudal fin.

The 9.62 mm SL juvenile of *D. garmani* (Fig. 4d) has a similar morphology to that of the previous developmental stage. A D_n photophore is present in front of the eye. Br_{123} photophores are lined in the lower jaw. A OP_2 is located under the eye. PO_{1235} photophores are arranged in a line in the abdominal cavity. PO_4 is raised between PO_3 and PO_5. The PVO_{12} photophore is situated obliquely between the base of the opercular organ and the pectoral fin. PLO is situated between the base of the pectoral fin and the lateral line. VLO is raised slightly from the middle between the base of the pelvic fin and the lateral line. The VO_{145} photophores are arranged in a line behind the pelvic fin. The VO_{23} photophores are situated obliquely between VO_1 and VO_4. The SAO_{123} photophores are gradually raised behind VO_5. AOa_1 is slightly raised from the anal fin base and follows the line of AOa_{23456} photophores arranged along the anal fin base. AOa_7 is raised more. Pol is near the lateral line at the end of the anal fin base. The AOp_{1234} photophores are arranged in a line along the caudal peduncle base behind the anal fin base. A line of Prc_{123} photophores is near the caudal peduncle, and Prc_4 is observed under the lateral line of the caudal peduncle. There are 14 dorsal fin rays, 14 anal fin rays, and 8 pelvic fin rays (Table 1). Of the melanophores, one is observed above the left side of the eye, a few are recognized on the top of the head and the opercular organ with two star-shaped melanophores nearby. One melanophore is dotted on the anus, and one on the upper lobe and two dotted on the lower lobe of the caudal fin.

Benthosema pterotum (Alcock, 1890) (Fig. 5) (Korean name: Git-bi-neul-chi)

Scopelus pterotus Alcock, 1890: 217 (type locality: Madras coast, India)

Benthosema pterotum: Masuda et al. 1984: 65; Hulley 1986: 285; Nakabo 2013: 451; Okiyama 2014: 364.

Materials examined: PKUI 614, one specimen, 9.81 mm SL, 34° 83.28′ N, 129° 10.75′ E, eastern Korea Strait, 9 Dec 2018, Bongo net; PKUI 615, one specimen, 5.75 mm in standard length (SL), 32° 68.40′ N, 123° 88.52′ E, western Jejudo Island, 16 Sep 2018, Bongo net; PKUI 616, one specimen, 7.27 mm SL, 33° 09.68′ N, 126° 38.57′ E, East Sea, 9 Dec 2018, Bongo net; PKUI 617, one specimen, 8.07 mm SL, 37° 18.53′ N, 129° 67.90′ E, East Sea, 20 July 2018, Bongo net.

The 5.75 mm SL post-flexion larva of *B. pterotum* (Fig. 5a) has a small body depth and large head depth, with the head depth decreasing from the nape. At this stage of development, the larva has large eyes and a sharp snout. The anus is positioned slightly behind the middle of the body. A Br_2 photophore is found in the lower jaw under the eye and Bu under the rear of the eye. The adipose fin is present. There are 10 dorsal fin rays, 14 anal fin rays, 11 pectoral fin rays, and 7 pelvic fin rays (Table 2). Observed melanophores include one on the end of the lower jaw snout, a line of melanophores in the lower jaw, one on the central upper part of the gut, many melanophore dots around the anus, and a line of very short, indistinct melanophores on the anal fin.

The 7.27 mm SL juvenile of *B. pterotum* (Fig. 5b) has a Dn photophore in front of the eye, Br_2 on the lower jaw under the eye, and Bu under the rear of the eye. There are 12 dorsal fin rays, 18 anal fin rays, 11 pectoral fin rays, and 8 pelvic fin rays (Table 2). Observed melanophores include one on the end of the lower jaw, one around the nostrils, a line of four melanophores at the base of the opercular organ, in addition to irregularly distributed small dots of melanophores, and a few on the anus. During this stage of development, existing melanophores disappear from the central anus and central muscle of the anal fin.

The 8.07 mm SL juvenile of *B. pterotum* (Fig. 5c) has a Dn photophore in front of the eye, Br_2 on the lower jaw under the eye, and Bu under the rear of the eye. There are 12 dorsal fin rays, 18 anal fin rays, 11 pectoral fin rays, and 8 pelvic fin rays (Table 2). Observed melanophores include one at the tip of the lower jaw snout, one under the nostrils, a line of dark dots on the base of the opercular organ, and a large melanophore dot on the anus.

The 9.81 mm SL juvenile of *B. pterotum* (Fig. 5d) has a Dn photophore in front of the eye, Br_2 on the lower jaw under the eye, Cp on the opercular organ, a series of PO_{1234} photophores followed by a raised PO_5 in the isthmus, PVO_1 in front of the base of the pectoral fin behind the operculum organ, VO_1 under the pelvic fin followed by a raised VO_2, AOa_{12} on the anal fin, and Prc_2 below the lateral line of the anal fin. There are 10 (?) dorsal fin rays, 18 anal fin rays, 11 pectoral fin rays, and 8 pelvic fin rays (Table 2). Observed melanophores include a series of dots under the operculum organ, one dot on the anus, one melanophore each on the upper and lower lobes of the base of the caudal fin.

Discussion

We performed a molecular identification of Myctophidae larvae and juveniles collected in the waters around Jeju Island and the East Sea in June 2017 and found that four of the larvae had 99.2–99.4% identity to the sequence of a *D. garmani* adult and the other four larvae 100% identity to the sequence of a *B. pterotum* adult. *Diaphus garmani* has not been recorded in Korea, and its morphological features and measurements according to developmental stage obtained in this study were

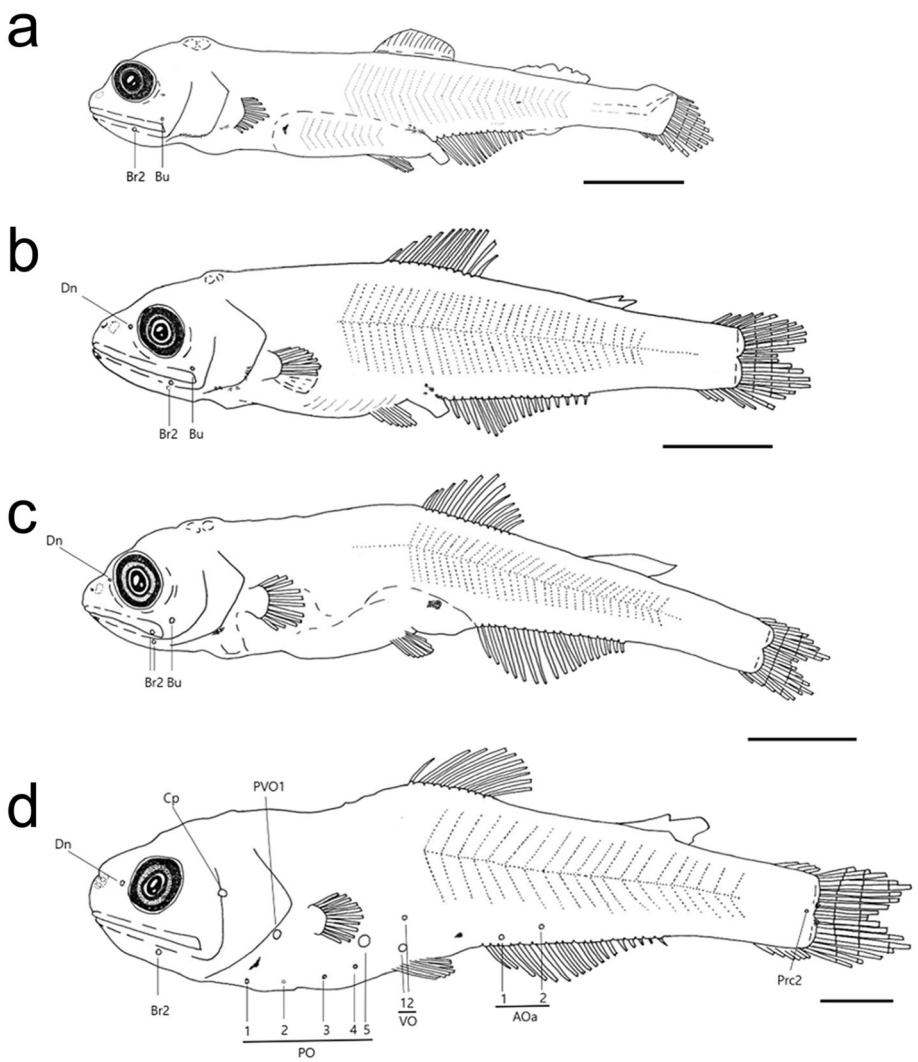

Fig. 5 Morphological development of *Benthosema pterotum* (**a** post-flexion stage, PKUI 615, 5.75 mm SL; **b** juvenile stage, PKUI 616, 7.27 mm SL; **c** juvenile stage, PKUI 617, 8.07 mm SL; **d** juvenile stage, PKUI 614, 9.81 mm SL). AOa, anterior anal organs; Br, branchiostegal organs; Bu, buccal organ; CP, cheek photophore; Dn, dorsonasal organ; PO, pectoral organs; Prc, precaudal organs; PVO, subpectoral luminous glands; VO, ventral organs. Scale bars indicate 1.0 mm

found to be generally consistent with previous reports (Gilbert 1906; Kawaguchi and Shimizu 1978; Sassa et al. 2003; Richards 2006; Bineesh et al. 2010; Okiyama 2014). Okiyama (2014) suggested that the completion of metamorphosis and photophore development occurs later in *B. pterotum* (12–13 mm SL) than in *D. garmani* (11 mm SL), which is consistent with our results. In this study, a juvenile *D. garmani* (PKUI 621, 9.62 mm BL) developed AOa_{1-7}. This result is consistent with that in the original descriptive paper (Gilbert 1906), but differs from the results of Nakabo (2013) and Bineesh et al. (2010) which described only AOa_{1-6}. In addition, *D. garmani* juveniles in this study had a Prc_4 photophore under the lateral line inside of the caudal fin, which is consistent with Bineesh et al. (2010) but clearly different than that present under the lateral line outside of the caudal fin from Nakabo (2013). It is thought that the discrepant results for the AOa photophores are due to individual variations, but further study will be needed with regard to the Prc4 photophore location. The species *D. garmani* and *B. pterotum* share the characteristics of

Table 2 Number of dorsal (D), anal (A), pectoral (P1), and pelvic (P2) fin rays of *Benthosema pterotum*

Voucher number	D	A	P1	P2	Stage
PKUI 615	10	14	11	7	Post-flexion
PKUI 616	12	18	11	8	Juvenile
PKUI 617	12	18	11	8	Juvenile
PKUI 614	10 (?)	18	11	8	Juvenile

body shape, eye size, and photophore arrangement, but the two species can be differentiated by the photophore development process and relative growth of individuals of similar size. In terms of photophore development, *B. pterotum* first develops Dn in front of the eye, whereas *D. garmani* first develops OP_2 at the base of the opercular organ. *B. pterotum* has Bu under the right eye and Cp on the isthmus, which are not present in *D. garmani*. The two species can also be differentiated by the position of the PO photophores; *D. garmani* has PO_4 at the highest raised position, whereas *B. pterotum* has PO_5 as the highest PO photophore. The arrangement of VO photophores can also clearly differentiate the two species: VO_3 is located at the top in *D. garmani* versus VO_2 in *B. pterotum*. AOa_1 is positioned higher than the other AOa photophores in *D. garmani*, whereas the AOa photophores are arranged horizontally in *B. pterotum*.

In the adult stage, the two species can be clearly identified by the number of Prc photophores: four in *D. garmani* and two in *B. pterotum* (Nakabo 2013). We also found four Prc photophores in *D. garmani* and one in *B. pterotum*. Comparing the body ratios of the two species at each developmental stage, the ratios of head depth, head length, preanus length, eye diameter, and pre-anal fin length to SL differentiated the two species (Fig. 6a–e), except the ratio of pre-dorsal fin length to SL (Fig. 6a–f). Okiyama (2014) suggested that in *D. garmani*, the ratios of pre-anal fin length, head length, and body depth to SL

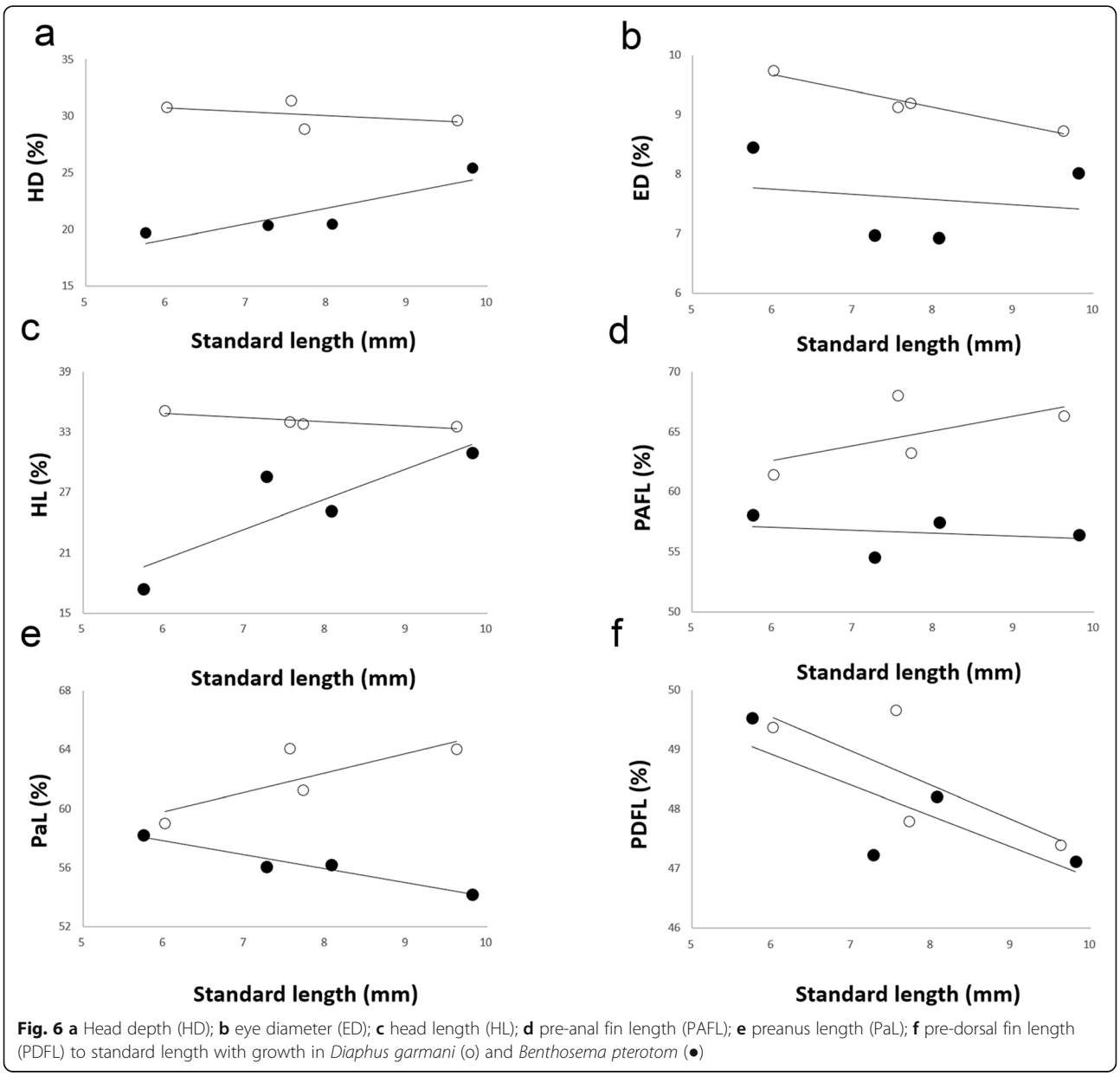

Fig. 6 **a** Head depth (HD); **b** eye diameter (ED); **c** head length (HL); **d** pre-anal fin length (PAFL); **e** preanus length (PaL); **f** pre-dorsal fin length (PDFL) to standard length with growth in *Diaphus garmani* (o) and *Benthosema pterotom* (●)

increase linearly until the larvae grow to 7 mm SL, after which the ratios gradually decrease until they reach the juvenile stage. In contrast to that previous study, we showed that the pre-anal fin length increased with SL in *D. garmani*, but with no change in head length. This result may be related to the trivial difference in genetic distance (0.6–0.8%) in terms of the 16S rRNA sequence between Japanese *D. garmani* adults and the *D. garmani* larvae collected in Korean waters, which requires further study.

Conclusions

Based on mitochondrial DNA 16S rRNA sequences, two larvae and two juveniles were identified as *Diaphus garmani*, which is the first record in Korean waters. Among myctophid species previously recorded in Korea, *Benthosema pterotum* seems to be very similar to *D. garmani* in external morphology. The two species were distinguished by melanophores in the abdominal cavity (absent in *D. garmani* vs. present in *B. pterotum*) and the development of photophores (developed in *D. garmani* vs. rudimentary in *B. pterotum*) when shorter than 10.0 mm standard length. We propose a new Korean name *Gar-ma-ni-sat-bi-neul-chi*, a combination of the specific name *garmani* and the Korean name of the family Myctophidae *Sat-bi-neul-chi*.

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Authors' contributions
HLL and JKK conducted the research, analyzed the materials, and prepared the draft manuscript. JKK, HJY, and JNK designed and directed the study and finalized the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials
All datasets analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Author details
[1]Department of Marine Biology, Pukyong National University, Busan 48513, Korea. [2]Fisheries Resources Research Center, National Institute of Fisheries Science, Tongyeong 53064, Korea.

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