Vampyroteuthis pseudoinfernalis sp. nov.: the second extant widespread deep sea squid species of Vampyromorpha (Cephalopoda: Coleoidea)

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Running title: The second species of Vampyromorpha

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Abstract

The vampire squid, *Vampyroteuthis infernalis* Chun, 1903, is currently the only extant species in the family Vampyroteuthidae Chun, 1903. However, specimens from the Gulf of Guinea, Africa, and California suggested the possibility of additional taxa. Here, we report the second species of *Vampyroteuthis*, collected from the South China Sea, China, which differs from *V. infernalis* by the tail shape, the lower beak, and the phylogenetic analysis of mitochondrial COI and nuclear large subunit ribosomal DNA (LSU) sequences: *V. infernalis* present by the lacking of the tail, photophores located approximately one-third of the points between the fins and end, and the lower beak with a broad, short wing; *V. pseudoinfernalis* Qiu, Liu & Huang, **sp. nov.** present by an acuate tail, a pair of photophores located at the midpoints between the fins and tail, and a lower beak with a broad, elongate wing.

Key words:

Nuclear gene, mitochondrial COI, phylogeny, morphology, South China Sea.

1 Introduction

Planktonic cephalopods are widely distributed in the world's oceans from the surface to abyssal depths, where they occupy epipelagic, mesopelagic and bathypelagic zones. One of these cephalopods, *Vampyroteuthis infernalis* Chun, 1903, is currently the only extant species in Vampyroteuthidae. The species was initially described by Chun (1903) under the order Octopoda (Chun, 1903; Pickford, 1946). Then, at least seven genera and ten species were reported by different authors (Robson, 1932). Pickford (1939) reclassified the eleven extant species as a single species, *V. infernalis*, and transferred it from the order Octopoda to the new order Vampyromorpha (Pickford, 1939, 1946).

The recognized distribution of *V. infernalis* includes temperate and tropical Pacific, Indian, and Atlantic oceans (Yokobori *et al.*, 2007; Jereb *et al.*, 2010; Hoving & Robison, 2012), where it typically occurs between 600 m and 900 m at oxygen concentrations of *ca*. 0.4 mL/L in the northeastern Pacific (Hoving & Robison, 2012). However, morphological differences had been reported among specimens from the Gulf of Guinea, Africa, and California (Young, 1972), and genetic differences or population structure analysis suggest that two or multiple extant species may exist in this family (Braid & Bolstad, 2019; Timm *et al.*, 2020).

The family Vampyroteuthidae and the genus *Vampyroteuthis* was not previously reported from the South China Sea, where presents 153 cephalopod species (Norman *et al.*, 2016). Here we describe a new species, namely *Vampyroteuthis pseudoinfernalis* Qiu, Liu & Huang, **sp. nov.**, with its small (SSU) and large (LSU) rDNA and mitochondrial

cytochrome c oxidase subunit I (COI) sequences.

2 Materials and methods

2.1 Sample collection, research ethics, and observations

The specimen was collected during an open cruise near Hainan Island, northwestern South China Sea (Stn 30: 17°59′28″N, 112°29′58″E), on 13 September 2016 (Fig. 1) from a depth between 800 m and 1000 m depth using a Hydro-Bios Multinet system (Type Max, mouth area 0.5 m^2, 300 µm mesh; HydroBios Inc., Kiel, Germany) hauled vertically at approximately 0.5 m/s. The temperature at this station ranged 5.75–8.86°C, and the salinity ranged 34.46–34.36 PSU. The net was equipped with internal and external flow meters and a depth transducer, all of which were monitored and logged in real time; sampling of the water column otherwise occurred in 1000–800 m, 800–600 m, 600–400 m, 400–300 m, 300–200 m, 200–100 m, 100–50 m, 50–25 m and 25–0 m.

Immediately after sorting, the specimen was photographed, and counts and measures were taken following Roper and Voss (1983). The specimen was then frozen at -20°C and kept in darkness for subsequent molecular and morphological analyses, deposited in the Marine Biodiversity Collection of South China Sea, South China Sea Institution of Oceanology, Chinese Academy of Sciences.

2.2 DNA extraction, PCR, and gene sequencing

A tissue sample was resuspended in 0.5 mL of DNA lysis buffer (0.1 MEDTA pH 8.0, 1% SDS, 200 µg/mL proteinase K) in a 1.5 mL tube and then incubated for 48 hours

at 55°C. DNA extraction and purification were performed according to the protocols of Qiu *et al.* (2011). After extraction, the sample DNA was eluted in 50 µL of Tris-HCl solution before 1 µL of DNA was subjected to PCR with pairs of primers (SSU, LSU, and COI) to amplify the SSU rDNA, LSU rDNA, and mitochondrial COI genes, respectively. Primer sequences are detailed in Table 1.

PCR amplification was carried out in 25 µL reaction volumes under thermocycling conditions, including a denaturing step of 94°C for 4 min; 35 cycles of 94°C for 30 sec, 56°C for 30 sec, and 72°C for 45 sec; and a final extension step of 72°C for 10 min. PCR products were resolved by agarose gel electrophoresis with a DL2000 DNA Ladder (TaKaRa Bio, Dalian, China) before bands of the expected sizes were excised to remove primer dimers. The DNA was purified and directly sequenced as described by Qiu *et al.* (2011).

2.3 Phylogenetic analyses

The sequences were trimmed with primers, and the two strands were merged. The assembled sequences were analyzed against the GenBank database using the Basic Local Search Tool (BLAST). Sequences showing significant similarity in BLAST to our sequences were downloaded. Phylogenetic analysis based on partial SSU (1899 bp), partial LSU (D1-D2, 408 bp), and mitochondrial COI (702 bp) regions was done to investigate the phylogenetic position of *Vampyroteuthis* specimens. The combined sequences were aligned with ClustalW. The alignment was run through ModelTest to select the most appropriate evolutionary model. The selected general time-reversible

model with a gamma distribution was subjected to maximum likelihood analysis using MEGA 5.0. Categories of substitution rates were set at 4, and other parameters were estimated based on the datasets. The sequences obtained in this study were deposited in GenBank under accession numbers MN044751, OP526744, OP531921, and OP549780.

3 Results

The result strongly supports the existence of two distinct *Vampyroteuthis* species which differ in tail shape, photophore position, lower beak morphology, and evolutionary distance between the respective LSU rDNA and mitochondrial COI sequences. We propose that one of these taxa, the South China Sea specimen, represents a new species, namely *V. pseudoinfernalis* Qiu, Liu & Huang, **sp. nov.**

3.1 Taxonomy

***Vampyroteuthis pseudoinfernalis* Qiu, Liu & Huang, sp. nov.**

Diagnosis. The new species is different from its sibling species *V. infernalis* by with an acuate tail. It is characterised by the following combination of morphological characters: a pair of photophores located at the midpoints between the fins and tail, and a lower beak with a broad, elongate wing.

Description. Mature female specimen (Fig. 2) small, extensively gelatinous, with black and reddish-brown chromatophores interspersed over body surfaces. Total length 9.5 cm, mantle length 5.2 cm and width 5.0 cm. Mantle conical and rounded, with an

acuate tail (Fig. 2). Head fused with mantle; brachial and nuchal constrictions poorly demarcated. Eyes brown (0.7 cm diameter), recessed into head tissues, and covered by a crystalline membrane. Arms with comparable length to mantle, subequal, with tapering ends. Web depth *ca*. 2.5 cm, *ca.* 50% arm length. Suckers small, in single series, on distal half of arms only, unstalked, without cuticular lining. Two rows of cirri extend along each arm for length. Threadlike arm ends naked at medial of it and web margin. A pair of long and paddle-shaped fins (width *ca*. 5 cm, length *ca.* 0.9 cm), lacking a cartilaginous base, protruded from posterior mantle. A pair of large photophores (*ca.* 0.3 cm diameter) lies between fins and tail. Distances from fins to photophores and from photophores to tail were 1.0 cm, 1.0 cm, respectively. All distance data are presented in Table 2.

Gladius. Gladius broad, chitinous, and transparent, covering dorsal mantle beneath skin and a thick layer of loose connective tissue (Fig. 3). Gladius thin and flat in anterior, gradually thickening and arching strongly in posterior. Gladius consists of middle (ostracum), inner (hypostracum) and outer (periostracum) shell layers. Proostracum comprises five longi-tudinal elements: a middle plate (rachis), two lateral plates, and two wings (Fig. 3A).

Beaks. Upper beak rostrum long, curved, tip pointed. Jaw angle obtuse, lateral wall extends forward to wing, where becomes large and with a distinct false angle. Hood long, *ca.* 0.8 times of crest length. Posterior margins of hood/wing convex. Wing extends to base of anterior margin of lateral wall. Crest straight and unthickened (Fig. 3B). Lower beak rostral tip pointed, with a small hook. Wings very broad, elongate, and spread parallelly, with a very high wing fold and highest opposite jaw angle, forming a smooth

cutting edge. Crest short, wide, unthickened. Jaw angle obtuse. Shoulder tooth present (Fig. 3B). Beak measurements presented in Table 3.

Holotype. Hainan Island, northwestern South China Sea (Stn 30: 17°59′28″N, 112°29′58″E), 13 September 2016, coll. Dajun Qiu (SCSMBC030991). The specimen is barcoded in GenBank as follows: SSU 1-1899 (MN044751), D1-D2 LSU 1-408 rDNA (OP526744), and COI 1-702 (OP531921) sequences.

Etymology. The specific name is derived from the Latin word "*pseudo*" and the previous species *V. infernalis*.

Distribution. The species is known only in the South China Sea now. However, the molecular data shows it has a wider distribution, in the Gulf of Mexico, Atlantic Ocean, Cape Verde, northern Atlantic Ocean, off Tohoku (North Pacific Ocean), and western Pacific Ocean (D1–D2 LSU rDNA: MG263928, MG263931, MG263941, MG263942, MG263948, MG263949, MG263954, MG263969, MG263987, MG263992; COI: AB266515, AB385880, GU145060, MF432197, OR378923, OR379049, MG591300, MG591304, MG591313, MG591328, MG591329, MG591335, MG591338, MG591339, MG591358, MG591379, MG591380, MG591385, MG591386, MG591404, MG591438, MG591440, MG490128, NC009689; data from GenBank).

3.2 Phylogenetic position of *Vampyroteuthis* based on nuclear rRNA and mitochondrial COI genes

Nuclear-encoded partial SSU (MN044751) and LSU (OP526744) ribosomal RNA

genes and mitochondrial COI (OP531921) were obtained. The phylogenetic tree of SSU, LSU, and COI contain 40, 29, and 80 sequences, respectively, from GenBank, besides our sequences. The LSU tree topologies inferred from the dataset using neighbor joining (NJ) and maximum likelihood (ML) revealed well-supported long distances and clear separation of *V. pseudoinfernalis* Qiu, Liu & Huang, **sp. nov.** from *V. infernalis* and other genera (Fig. 4). Because our LSU rRNA gene sequence is almost identical to 10 sequences (MG263928, MG263931, MG263941, MG263942, MG263948, MG263949, MG263954, MG263969, MG263987, MG263992) from the Gulf of Mexico and Atlantic Ocean, they may be conspecific. The LSU phylogeny clusters *V. pseudoinfernalis* Qiu, Liu & Huang, **sp. nov.** in a distinct lineage separated from 14 other sequences of *V. infernalis* from the Gulf of Mexico (MG263894, MG263895, MG263896, MG263897, MG263926, MG263930, MG263940, MG263951, MG263953, MG263959, MG263985, MG263986) and two unknown localities (AH012197 and AY557548) (Fig. 4).

In the mitochondrial COI tree (Fig. 5), the South China Sea sequence is identical to the 21 sequences reported for *V. infernalis* from the Gulf of Mexico, the northeast and northwest Atlantic Ocean, and the North Pacific Ocean (off Tohoku) and forms a strongly supported distinct lineage that is well separated from 20 sequences referred to *V. infernalis* from the Gulf of Mexico, near New Zealand (South Pacific Ocean), the Indian Ocean, and the northwest Atlantic Ocean. Thus, the mitochondrial COI tree divided them into two groups. For COI, a total of 8 diagnostic positions were identified between the two groups (Table 4, Fig. S1). The sequences of AY557459 (SSU rDNA, Fig. 6), AY557548 (LSU rDNA, Fig. 4), and AF000071 (COI, Fig. 5) were sourced from the

same specimen referred to as *V. infernalis* by Carlini *et al.* (2001) and Lindgren *et al.* (2004). The sequence of MK186003 (COI, Fig. 5) clustered with the sequence AF000071 in a group that was sourced from New Zealand specimens and referred to as *V. infernalis*. In the SSU tree (Fig. 6), the 1899-bp SSU rDNA sequence from the South China Sea of *V. pseudoinfernalis* Qiu, Liu & Huang, **sp. nov.** (MN044751) differed by only 5 bp (0.3%) from that of *V. infernalis* (AY557459, AY145387). Therefore, the SSU rDNA sequence of *V. pseudoinfernalis* Qiu, Liu & Huang, **sp. nov.** could be difficultly separated from the *V. infernalis* sequence (AY557459) based on the sequence. As a result, the molecular phylogenies revealed that *V. pseudoinfernalis* Qiu, Liu & Huang, **sp. nov.** formed strongly supported lineages (Figs 4–6).

4 Discussion

4.1. *Vampyroteuthis infernalis sensu lato*

Molecular phylogeny indicates that *Vampyroteuthis infernalis sensu lato* is strongly bootstrap supported to be divided into two separated species, *V. pseudoinfernalis* Qiu, Liu & Huang, **sp. nov.** and *V. infernalis sensu stricto* (Figs 4–6, Table 4). In morphology, these two species can also be distinguished by their tail shape, lower beak, and photophore position.

The species *V. infernalis* was originally described by Chun (1903), however, he did not record the position of photophore (Fig. 7A). Similar situations are also present in its four synonyms, *Cirroteuthis macrope*, *Melanoteuthis beebei*, *Watasella nigra* and

Danateuthis schmidti (Figs 7B, G–I; Chun, 1903; Berry, 1911; Sasaki, 1920; Joubin, 1929; Robson, 1929; Pickford, 1949). Another five synonyms have the original description of the photophore position, such as *Retroteuthis pacifica* (Figs 7C), *Hansenoteuthis lucens* (Figs 7E–F), *Melanoteuthis lucens* (Fig. 7H), *Melanoteuthis schmidti* (Figs 7J–K), and *Melanoteuthis anderseni* (Figs 7I–M) (Joubin, 1912, 1929, 1931; Pickford, 1949). *Retroteuthis pacifica* showed the distortion of tail shape which did not present the true photophores positions (Fig. 7C-D; Joubin, 1929). Based on these descriptions/monographs, the ratio of the distance 'from fins to photophores' to the distance 'from photophores to tail' is far less than 1 (*Retroteuthis pacifica*) or approximately 0.5 (juvenile individuals of *Hansenoteuthis lucens* and *Melanoteuthis schmidti*, and mature individuals of *Melanoteuthis anderseni*). In this study, the corresponding ratio is 1 (Tables 2, 5, Fig. 7). Additionally, all monographs of *V. infernalis* and its synonyms not recorded the tail.

The new species is different from the *V. infernalis* populations of the southeastern and northeastern Pacific and central and eastern Atlantic (Clarke, 1986; Lu & Ickeringill, 2002; Schwarz *et al.*, 2020) by having a broad and elongated wing of lower beak. Its ratio of lower beak crest length (CL) to hood length (HL) is similar to that of previous studies, except specimen 8 (Table 3). The ratio of lower beak wing length (WL) to rostral length (RL) is significantly differed from specimen 2, 3 and 4, but was similar to specimen 7 and 8 (Table 3).

In conclusion, *V. pseudoinfernalis* Qiu, Liu & Huang, **sp. nov.** is characterized by having an acuate tail, photophores located at the midpoints between the fins and tail, and

a broad and elongated wing of lower beak (Tables 2, 5), while *V. infernalis sensu stricto* has no recorded tail, photophores located about one-third of the fins and end, and the lower beak with a broad and short wing.

According to the molecular phylogenies, *V. pseudoinfernalis* Qiu, Liu & Huang, **sp. nov.** branched at a basal position to *V. infernalis sensu stricto*; these two species indisputably share common ancestry (Figs 4–5). Timm *et al.* (2020) reported that evidence of two populations of *Vampyroteuthis* was found in the Gulf of Mexico and northwestern Atlantic Ocean based on population structure analysis.

4.2 Phylogenetic position of Vampyromorpha

The phylogenetic analyses support the point that Vampyromorpha occupies an intermediate phylogenetic position between Decabrachia and Octobrachia (Fig. 6). Among the surveyed taxa, Vampyromorpha appears to be more closely related to *Psychroteuthis* sp. (AY557513, differing in 345 bp (15.92%)) than to *Stauroteuthis syrtensis* (differing in 851 bp (32.78%)). The result is similar to the views of Lindgren *et al.* (2004), Pickford (1939, 1940), Young (1977), Healy (1990), Young & Vecchione (1996) and Young *et al.* (1998), that Vampyromorpha was more closely related to Decabrachia (or Teuthida) than Octobrachia (particularly cirrate octopuses) based on either molecular or morphological data. On the contrast, Yokobori *et al.* (2007) suggested than Vampyromorpha was more closely related to Octobrachia based on mitochondrial gene sequence information.

However, our results and historical data have yet to unequivocally demonstrate the

monophyly of Decabrachia and Vampyromorpha or Octobrachia and Vampyromorpha. Further analyses are needed to determine the phylogenetic relationships between these taxa.

Authorship contribution

Dajun Qiu: Conceptualization, Investigation, Methodology, Data curation, Formal analysis, Writing – original draft, Writing – review & editing, Project administration, Funding acquisition. Bilin Liu: Methodology, Formal analysis, Writing – original draft, Writing – review & editing. Liangmin Huang: Supervision, Project administration, Funding acquisition. Yupei Guo: Formal analysis. W.A.S.W Lakmini: Formal analysis. Yehui Tan: Analysis tools. Gang Li: Investigation. Zhixin Ke: Investigation. Kaizhi Li: Analysis tools.

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Figure legends:

Figure 1. Map of study site. The *Vampyroteuthis* was collected from Station 30.

Figure 2. Fresh-collected *Vampyroteuthis pseudoinfernalis* Qiu, Liu & Huang, sp. nov.: A) dorsal, B) lateral views. Scale bar = 1 cm.

Figure 3. Gladius (A), upper and lower beak (B) of *Vampyroteuthis pseudoinfernalis* Qiu, Liu & Huang, sp. nov. Scale bar = 1 cm.

Figure 4. Cephalopod phylogeny inferred from LSU rDNA. Nodal support based on bootstrap values of ML/NJ with 1000 resamplings each; only values > 60 are shown (if a phylogenetic method yielded support < 60, it is denoted by ‘‘-’’). *Thaumeledone gunteri* was used as an outgroup to root the tree.

Figure 5. Cephalopod phylogeny inferred from mitochondrial COI. Nodal support based on bootstrap values of ML/NJ with 1000 resamplings each; only values > 60 are shown (if a phylogenetic method yielded support < 60, it is denoted by ‘‘-’’). *Chaetoderma nitidulum* was used as an outgroup to root the tree.

Figure 6. Cephalopod phylogeny inferred from SSU rDNA. Nodal support based on bootstrap values of ML/NJ with 1000 resamplings each; only values > 60 are shown (if a phylogenetic method yielded support < 60, it is denoted by ‘‘-’’). *Chaetoderma nitidulum* was used as an outgroup to root the tree.

Figure 7. Drawings of *Vampyroteuthis infernalis*, *Melanoteuthis* spp., *Watasella nigra*, *Danateuthis schmidti*, *Retroteuthis pacifica*, and *Hansenoteuthis lucens* from the literature. (a) Lateral view of *Vampyroteuthis infernalis* from Chun (1903). (b) Dorsal view of *Watasella nigra* from Sasaki (1920). (c-d) Dorsal and lateral view of *Retroteuthis pacifica* from Jubin (1929, Fig.13, 15). (e) Dorsal view of *Hansenoteuthis lucens* from Jubin (1929, Fig.17). (f) Dorsal view of *Hansenoteuthis lucens* from Pickford (1949, Fig. 9). (g) Dorsal view of *Danateuthis schmidti* from Jubin (1929, Fig.7). (h) Dorsal view of *Melanoteuthis lucens* from Jubin (1912, Fig. 2). (i) Outline drawing of *Melanoteuthis beebei* (ventral view, partly restored) from Roboson (1929). (j) Dorsal view of *Melanoteuthis schmidti* from Jubin (1929, plate III, Fig.3). (k) Dorsal view of *Melanoteuthis schmidti* from Pickford (1949, plate III, Fig.2, 4). (l-m) Dorsal and lateral view of *Melanoteuthis anderseni* from Pickford (1949, plate II, Fig. 4; plate I, Fig. 1).

Table 1. Primers used in this study.

Primer name	Application	Sequences (5′–3′)	References
18SF	SSU for *Vampyroteuthis*	AAGGGTTGTGTTYATTAGNTACARAAC	This study
18ScomR	SSU for *Vampyroteuthis*	CACCTACGGAAACCTTGTTACGAC	This study
28Sa	LSU for *Vampyroteuthis*	GACCCGTCTTGAAACACGGA	Lindgren *et al*., 2004
28Sb	LSU for *Vampyroteuthis*	TCGGAAGGAACCAGCTAC	Lindgren *et al*., 2004
LCO1490	COI for *Vampyroteuthis*	GGTCAACAAATCATAAAGATATTGG	Lindgren *et al*., 2004
HCO2198	COI for *Vampyroteuthis*	TAAACTTCAGGGTGACCAAAAAATCA	Lindgren *et al*., 2004

Table 2. Distances from the fins to the photophores and from the photophores to the tail or end of *Vampyroteuthis*.

Specimen number	Species	From fins to photophores (cm)	From photophores to tail or end (cm)	Reference
1	*Vampyroteuthis pseudoinfernalis*	1.0	1.0	This study
2	*V. infernalis*	0.6	1.15	Pickford, 1949: plate II, fig. 4.
3	*V. infernalis*	0.2	0.4	Pickford, 1949: plate III, fig. 8.
4	*V. infernalis*	0.3	0.7	Pickford, 1949: plate III, fig. 9.
5	*V. infernalis*	0.15	0.3	Pickford, 1949: plate III, fig. 7.

Table 3. Lengths of the upper and lower beak characters of *Vampyroteuthis* in this study and literature data. HL—hood length; RL—rostral length; CL—crest length; LWL—lower wing length; WL—wing length.

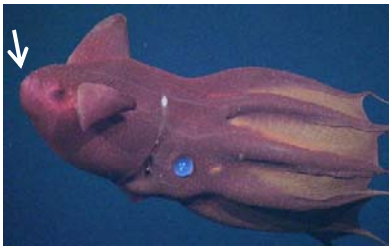
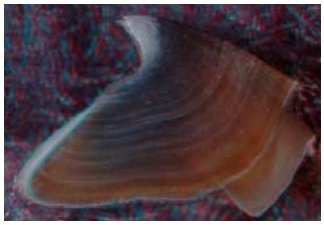
Specimen number	Species	Beak position	HL (mm)	RL (mm)	CL (mm)	LWL (mm)	WL (mm)	
1	*Vampyroteuthis pseudoinfernalis*	Upper beak	8.718	2.249	11.590	8.005	2.924	This study
		Lower beak	5.436	2.077	6.559	6.905	4.630	
2	*V. infernalis*	Upper beak	/	/	/	/	/	http://tolweb.org/Vampyroteuthis_infernalis/20084
		Lower beak	3.41	1.00	3.78	3.91	2.81	
3	*V. infernalis*	Upper beak	/	/	/	/	/	
		Lower beak	7.57	2.20	9.12	9.62	7.75	http://tolweb.org/notes/?note_id=5249
4	*V. infernalis*	Upper beak	/	/	/	/	/	
		Lower beak	16.59	5.30	20.16	19.87	14.26	
5	*V. infernalis*	Upper beak	13.23	3.67	16.13	13.49	4.31	Schwarz *et al*., 2020
		Lower beak	/	/	/	/	/	
6	*V. infernalis*	Upper beak						Clarke, 1986
		Lower beak	10.786	/	13.000	12.91	/	
7	*V. infernalis*	Upper beak	7.10	2.61	9.45	5.84	1.58	Pickford, 1949
		Lower beak	5.00	2.04	6.09	/	4.12	
8	*V. infernalis*	Upper beak	5.04	/	7.02	4.80	/	
		Lower beak	3.66	0.91	5.21	4.84	1.95	

Table 4. Molecular diagnostic characters obtained from cytochrome c oxidase subunit I (COI)

Position	*Vampyroteuthis infernalis*	*V. pseudoinfernalis* **sp. nov.**	*Gonatus madokai*	*Graneledone verrucosa*
72	G	A	A	A
180	G	A	G	A
372	G	A	C	T
474	A	T	A	A
517	C	T	T	T
528	A	T	A	A
618	A	T	G	T
639	C	T	T	T

The alignment is provided in Supporting FASTA File S1 to name each nucleotide position unambiguously.

Table 5. Morphological characteristics and distributions of *Vampyroteuthis* species

	Vampyroteuthis infernalis s.s.	*Vampyroteuthis pseudoinfernalis* sp. nov.
Tail	No tail  © 2007 MBARI	Acuate tail
Photophores	A pair of photophores located around the one third points between the fins and end. © 2007 MBARI	A pair of photophores located at the midpoints between the fins and tail.
Lower beak wing	Broad and short  http://tolweb.org/notes/?note_id=5249 	Broad and elongate
Distributions	The Gulf of Mexico, northwest Atlantic Ocean, near New Zealand (South Pacific Ocean), North Pacific Ocean, and Indian Ocean.	South China Sea, off Tohoku, Smith Caldera (North Pacific Ocean), the Gulf of Mexico, northeast and northwest Atlantic Ocean, Cape Verde, Atlantic Ocean.
References	Lu & Ickeringill, 2002; Young, 2019; http://tolweb.org/notes/?note_id=5249.	This study

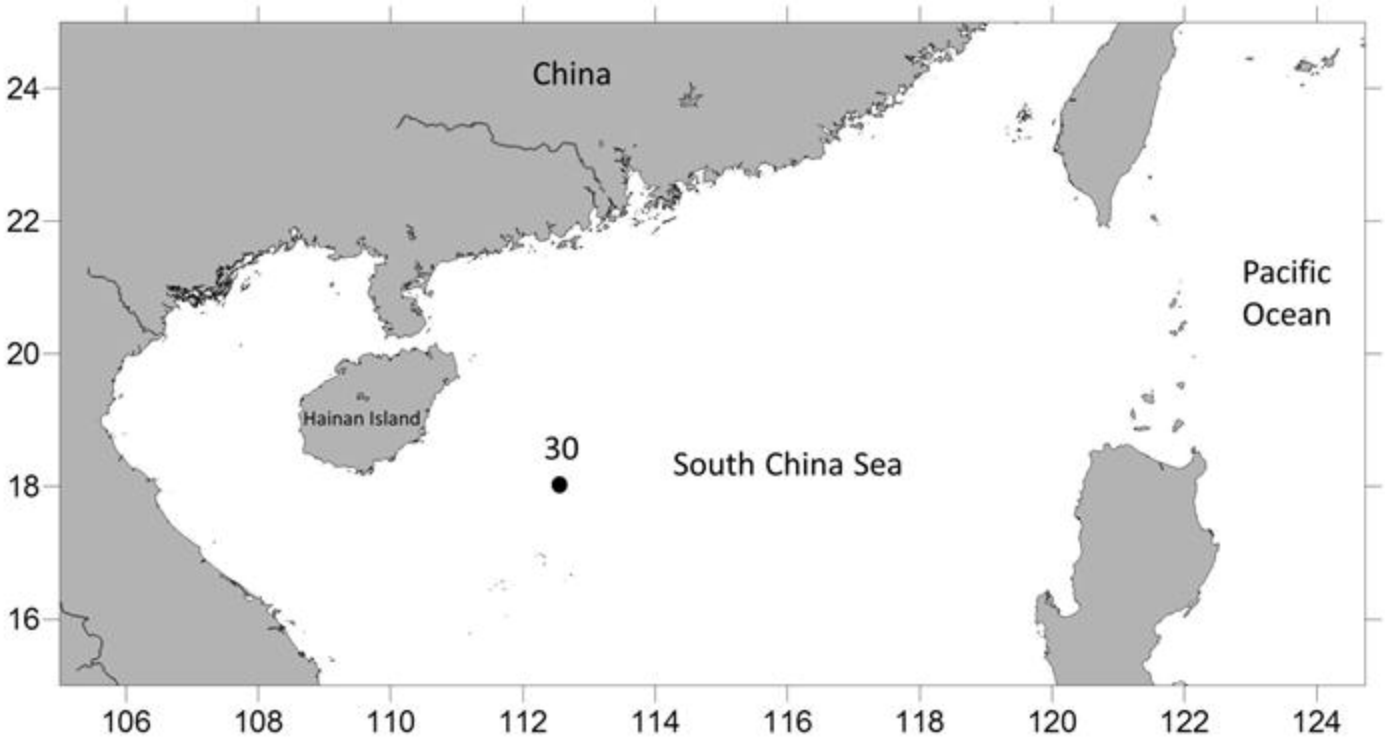

China
Pacific
Ocean
Hainan Island
30
South China Sea
24
22
20
18
16
106
108
110
112
114
116
118
120
122
124

Figure 1

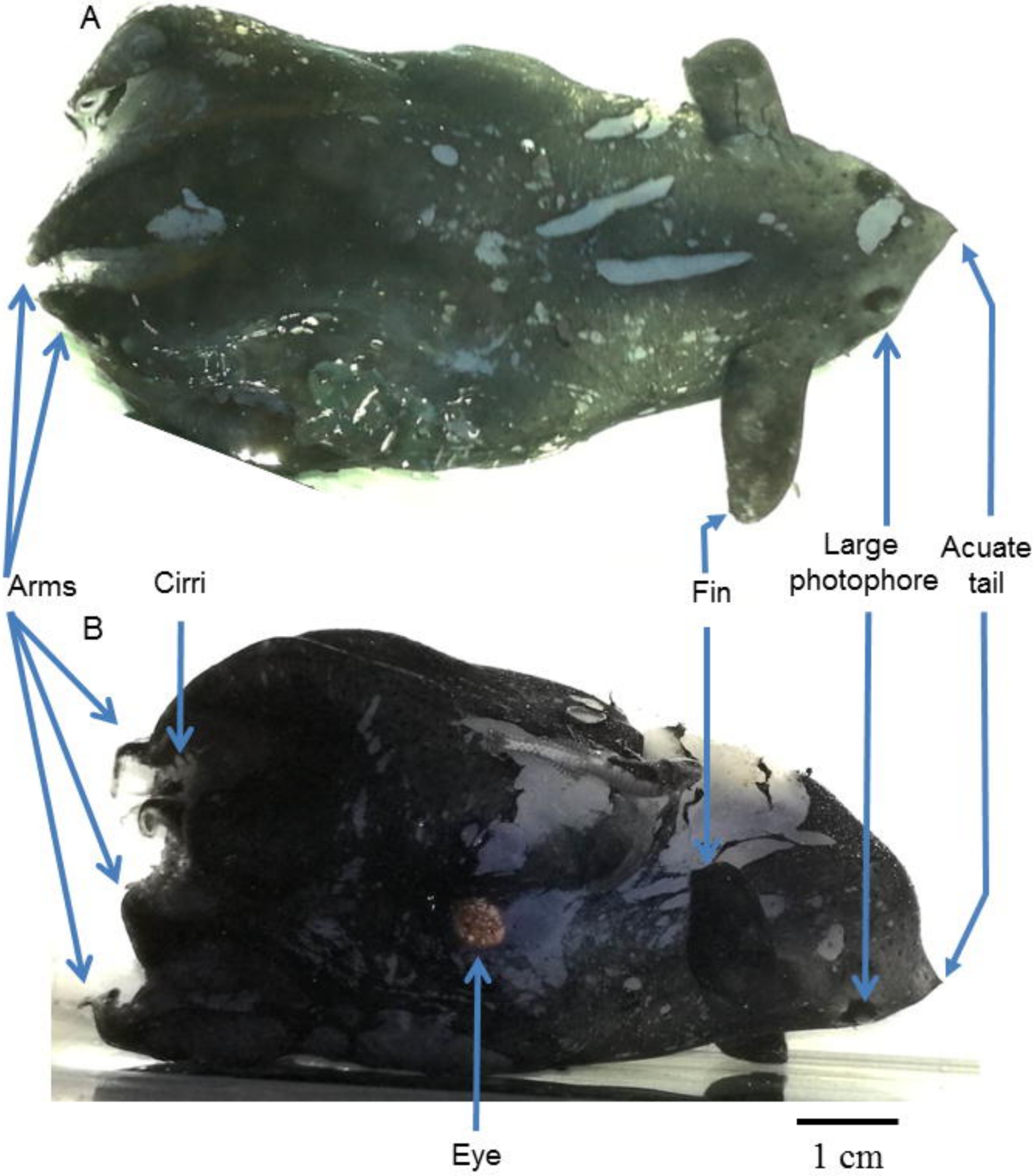
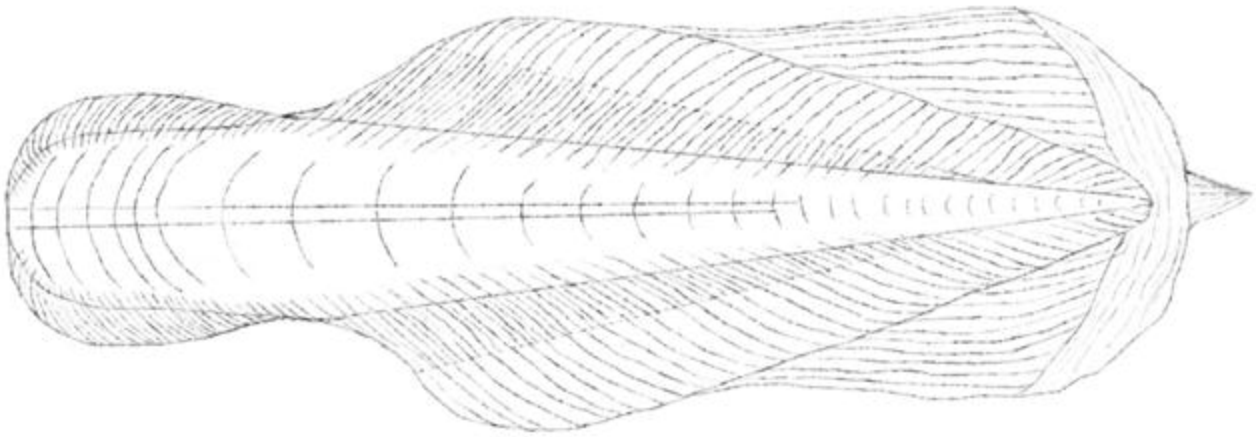


Figure 2

A



1 cm

B

1 cm

Figure 3

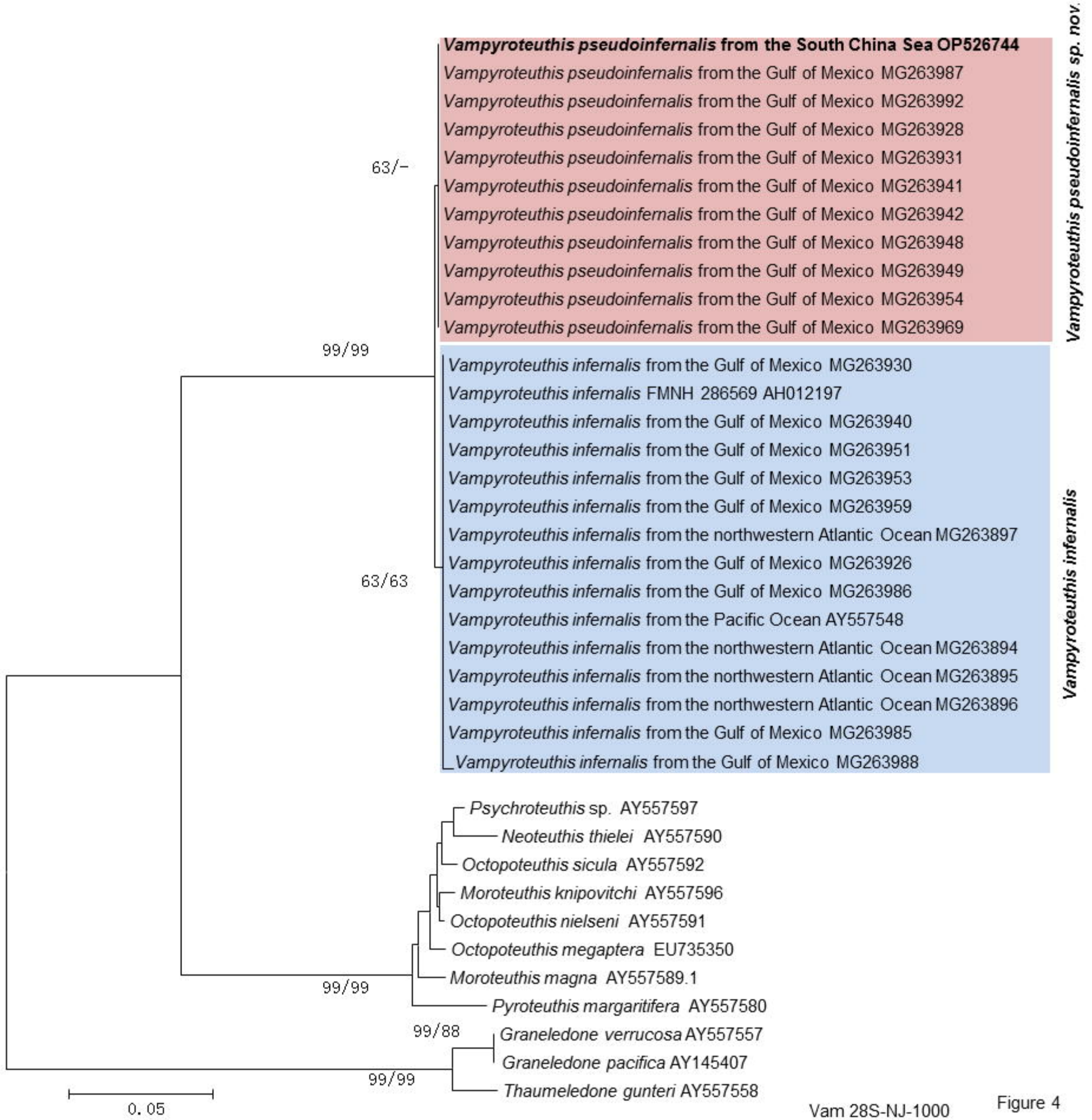
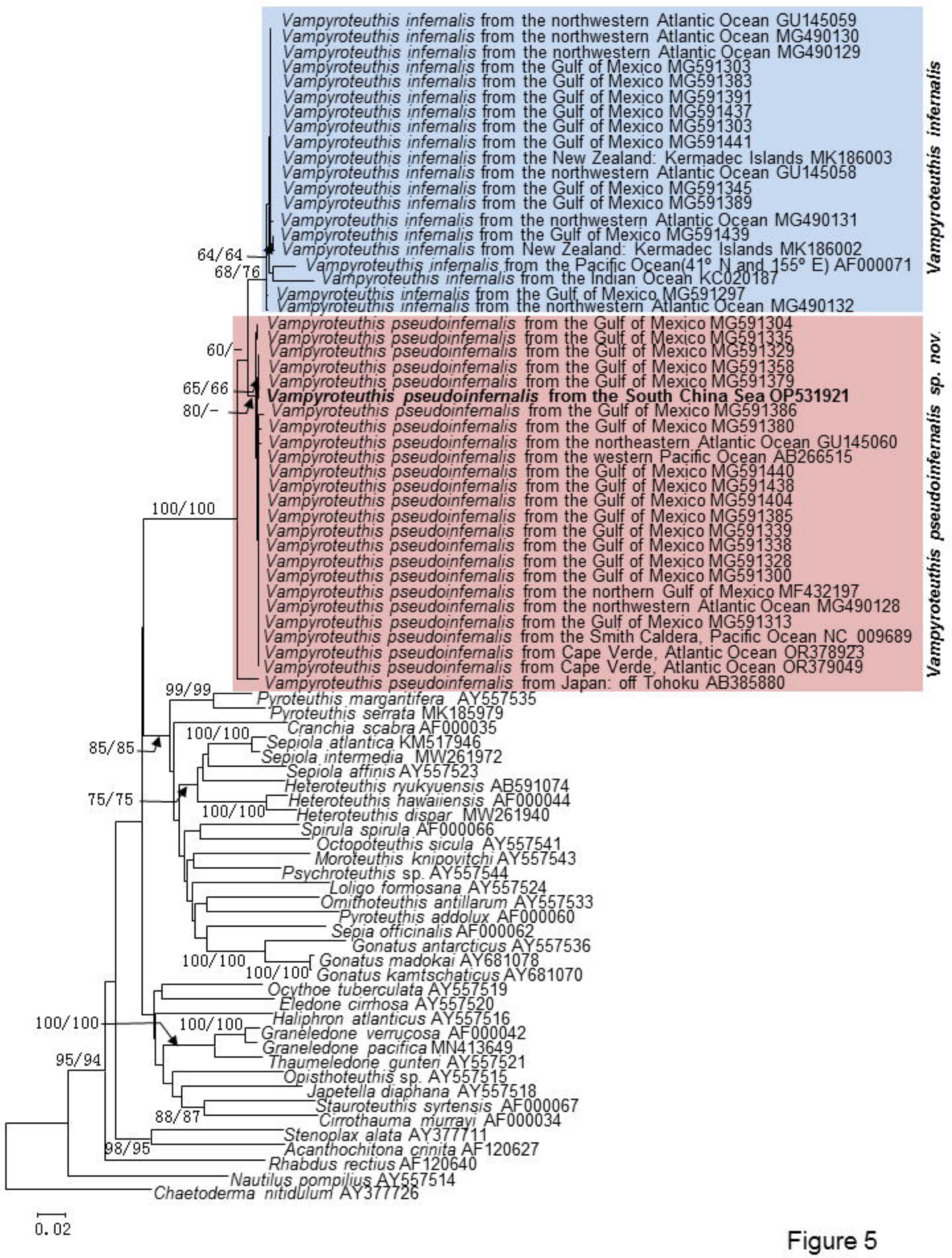

Vampyroteuthis pseudoinfernalis from the South China Sea OP526744
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG263987
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG263992
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG263928
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG263931
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG263941
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG263942
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG263948
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG263949
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG263954
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG263969
Vampyroteuthis pseudoinfernalis sp. nov.
63/-
99/99
Vampyroteuthis infernalis from the Gulf of Mexico MG263930
Vampyroteuthis infernalis FMNH 286569 AH012197
Vampyroteuthis infernalis from the Gulf of Mexico MG263940
Vampyroteuthis infernalis from the Gulf of Mexico MG263951
Vampyroteuthis infernalis from the Gulf of Mexico MG263953
Vampyroteuthis infernalis from the Gulf of Mexico MG263959
Vampyroteuthis infernalis from the northwestern Atlantic Ocean MG263897
Vampyroteuthis infernalis from the Gulf of Mexico MG263926
Vampyroteuthis infernalis from the Gulf of Mexico MG263986
Vampyroteuthis infernalis from the Pacific Ocean AY557548
Vampyroteuthis infernalis from the northwestern Atlantic Ocean MG263894
Vampyroteuthis infernalis from the northwestern Atlantic Ocean MG263895
Vampyroteuthis infernalis from the northwestern Atlantic Ocean MG263896
Vampyroteuthis infernalis from the Gulf of Mexico MG263985
Vampyroteuthis infernalis from the Gulf of Mexico MG263988
Vampyroteuthis infernalis
63/63
Psychroteuthis sp. AY557597
Neoteuthis thielei AY557590
Octopoteuthis sicula AY557592
Moroteuthis knipovitchi AY557596
Octopoteuthis nielseni AY557591
Octopoteuthis megaptera EU735350
Moroteuthis magna AY557589.1
99/99
Pyroteuthis margaritifera AY557580
99/88
Graneledone verrucosa AY557557
Graneledone pacifica AY145407
99/99
Thaumeledone gunteri AY557558
0.05
Vam 28S-NJ-1000

Figure 4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Vampyroteuthis infernalis from the northwestern Atlantic Ocean MG490130
Vampyroteuthis infernalis from the northwestern Atlantic Ocean MG490129
Vampyroteuthis infernalis from the Gulf of Mexico MG591303
Vampyroteuthis infernalis from the Gulf of Mexico MG591383
Vampyroteuthis infernalis from the Gulf of Mexico MG591391
Vampyroteuthis infernalis from the Gulf of Mexico MG591437
Vampyroteuthis infernalis from the Gulf of Mexico MG591303
Vampyroteuthis infernalis from the Gulf of Mexico MG591441
Vampyroteuthis infernalis from the New Zealand: Kermadec Islands MK186003
Vampyroteuthis infernalis from the northwestern Atlantic Ocean GU145058
Vampyroteuthis infernalis from the Gulf of Mexico MG591345
Vampyroteuthis infernalis from the Gulf of Mexico MG591389
Vampyroteuthis infernalis from the northwestern Atlantic Ocean MG490131
Vampyroteuthis infernalis from the Gulf of Mexico MG591439
Vampyroteuthis infernalis from New Zealand: Kermadec Islands MK186002
Vampyroteuthis infernalis from the Pacific Ocean(41° N and 155° E) AF000071
Vampyroteuthis infernalis from the Indian Ocean KC020187
Vampyroteuthis infernalis from the Gulf of Mexico MG591297
Vampyroteuthis infernalis from the northwestern Atlantic Ocean MG490132
Vampyroteuthis infernalis
64/64
68/76
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG591304
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG591335
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG591329
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG591358
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG591379
Vampyroteuthis pseudoinfernalis from the South China Sea OP531921
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG591386
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG591380
Vampyroteuthis pseudoinfernalis from the northeastern Atlantic Ocean GU145060
Vampyroteuthis pseudoinfernalis from the western Pacific Ocean AB266515
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG591440
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG591438
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG591404
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG591385
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG591339
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG591338
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG591328
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG591300
Vampyroteuthis pseudoinfernalis from the northern Gulf of Mexico MF432197
Vampyroteuthis pseudoinfernalis from the northwestern Atlantic Ocean MG490128
Vampyroteuthis pseudoinfernalis from the Gulf of Mexico MG591313
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Vampyroteuthis pseudoinfernalis from Cape Verde, Atlantic Ocean OR378923
Vampyroteuthis pseudoinfernalis from Cape Verde, Atlantic Ocean OR379049
Vampyroteuthis pseudoinfernalis from Japan: off Tohoku AB385880
Vampyroteuthis pseudoinfernalis sp. nov.
60/-
65/66
80/-
100/100
99/99
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Pyroteuthis serrata MK185979
Cranchia scabra AF000035
100/100
Sepiola atlantica KM517946
Sepiola intermedia MW261972
85/85
Sepiola affinis AY557523
Heteroteuthis ryukyuensis AB591074
Heteroteuthis hawaiiensis AF000044
75/75
100/100
Heteroteuthis dispar MW261940
Spirula spirula AF000066
Octopoteuthis sicula AY557541
Moroteuthis knipovitchi AY557543
Psychroteuthis sp. AY557544
Loligo formosana AY557524
Ornithoteuthis antillarum AY557533
Pyroteuthis addolux AF000060
Sepia officinalis AF000062
Gonatus antarcticus AY557536
100/100
Gonatus madokai AY681078
100/100
Gonatus kamtschaticus AY681070
Ocythoe tuberculata AY557519
Eledone cirrhosa AY557520
Haliphron atlanticus AY557516
100/100
100/100
Graneledone verrucosa AF000042
Graneledone pacifica MN413649
95/94
Thaumeledone gunteri AY557521
Opisthoteuthis sp. AY557515
Japetella diaphana AY557518
Stauroteuthis syrtensis AF000067
88/87
Cirrothauma murrayi AF000034
Stenoplax alata AY377711
98/95
Acanthochitona crinita AF120627
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Nautilus pompilius AY557514
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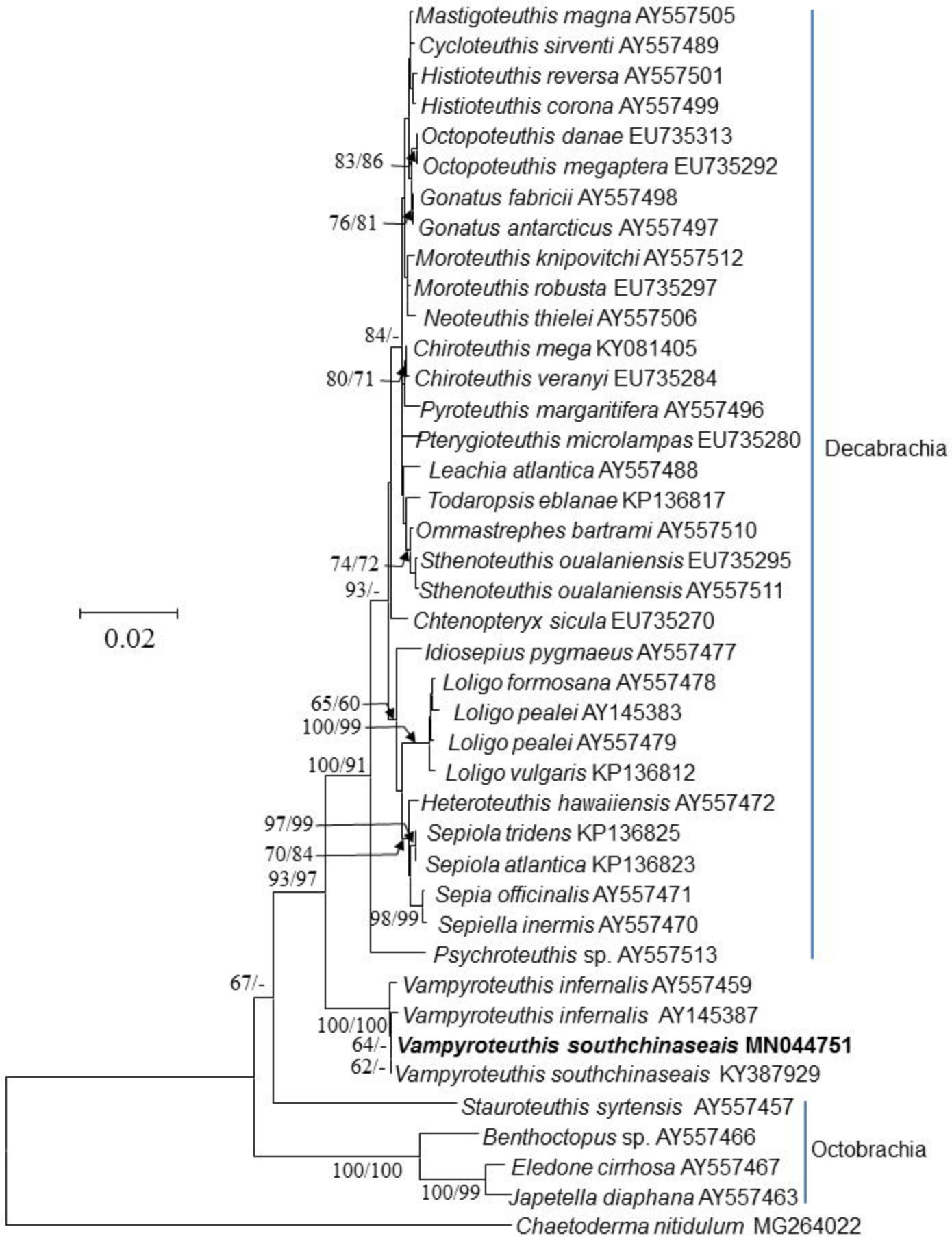
Figure 5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Cycloteuthis sirventi AY557489
Histioteuthis reversa AY557501
Histioteuthis corona AY557499
Octopoteuthis danae EU735313
83/86
Octopoteuthis megaptera EU735292
Gonatus fabricii AY557498
76/81
Gonatus antarcticus AY557497
Moroteuthis knipovitchi AY557512
Moroteuthis robusta EU735297
Neoteuthis thielei AY557506
84/-
Chiroteuthis mega KY081405
80/71
Chiroteuthis veranyi EU735284
Pyroteuthis margaritifera AY557496
Pterygioteuthis microlampas EU735280
Leachia atlantica AY557488
Todaropsis eblanae KP136817
Ommastrephes bartrami AY557510
74/72
Sthenoteuthis oualaniensis EU735295
93/-
Sthenoteuthis oualaniensis AY557511
Chtenopteryx sicula EU735270
Idiosepius pygmaeus AY557477
Loligo formosana AY557478
65/60
Loligo pealei AY145383
100/99
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100/91
Loligo vulgaris KP136812
Heteroteuthis hawaiiensis AY557472
97/99
Sepiola tridens KP136825
70/84
Sepiola atlantica KP136823
93/97
Sepia officinalis AY557471
98/99
Sepiella inermis AY557470
Psychroteuthis sp. AY557513
Decabrachia
67/-
Vampyroteuthis infernalis AY557459
Vampyroteuthis infernalis AY145387
100/100
64/-
Vampyroteuthis southchinaseais MN044751
62/-
Vampyroteuthis southchinaseais KY387929
Stauroteuthis syrtensis AY557457
Benthoctopus sp. AY557466
Octobrachia
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100/99
Japetella diaphana AY557463
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0.02

Figure 6

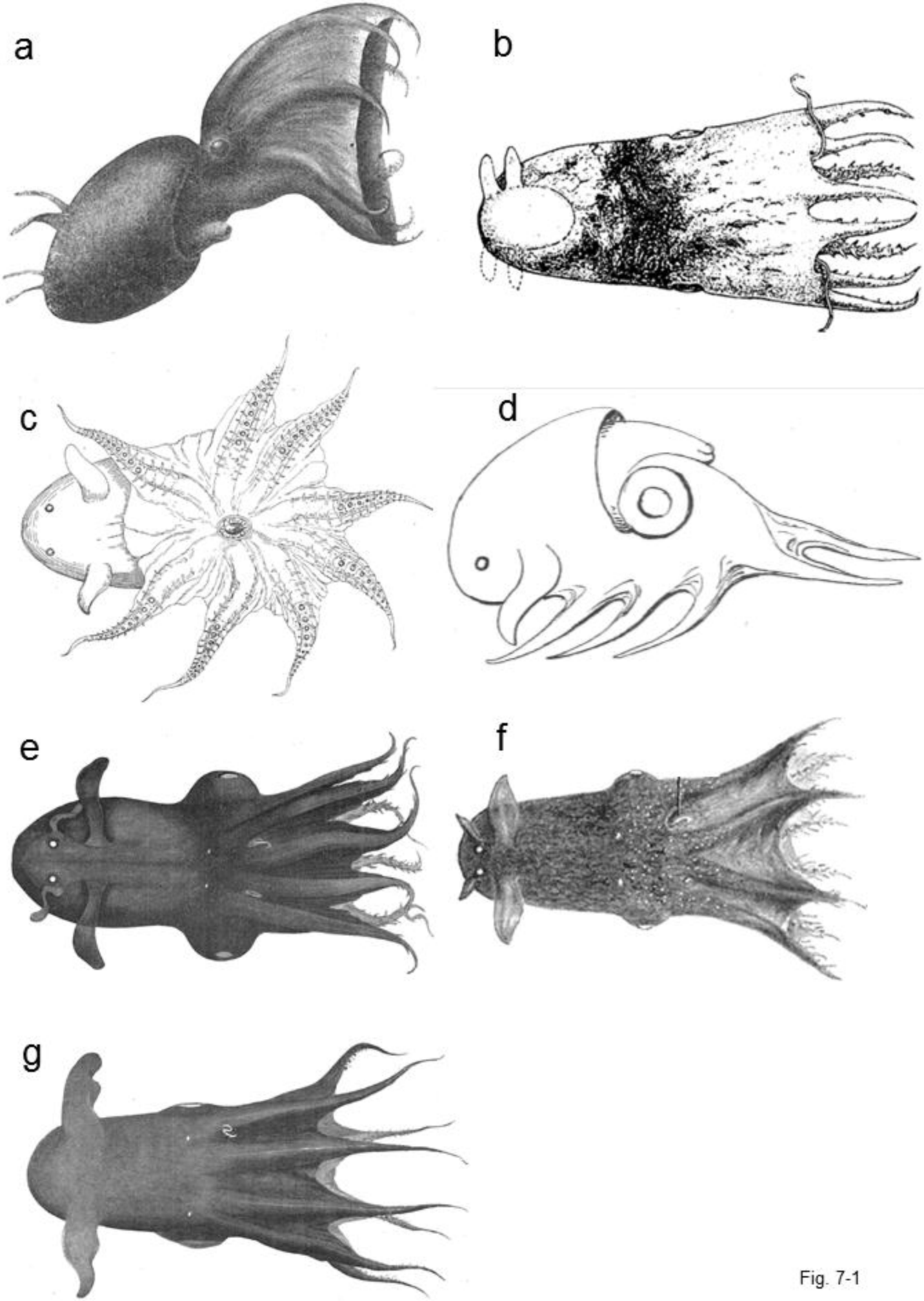

Fig. 7-1

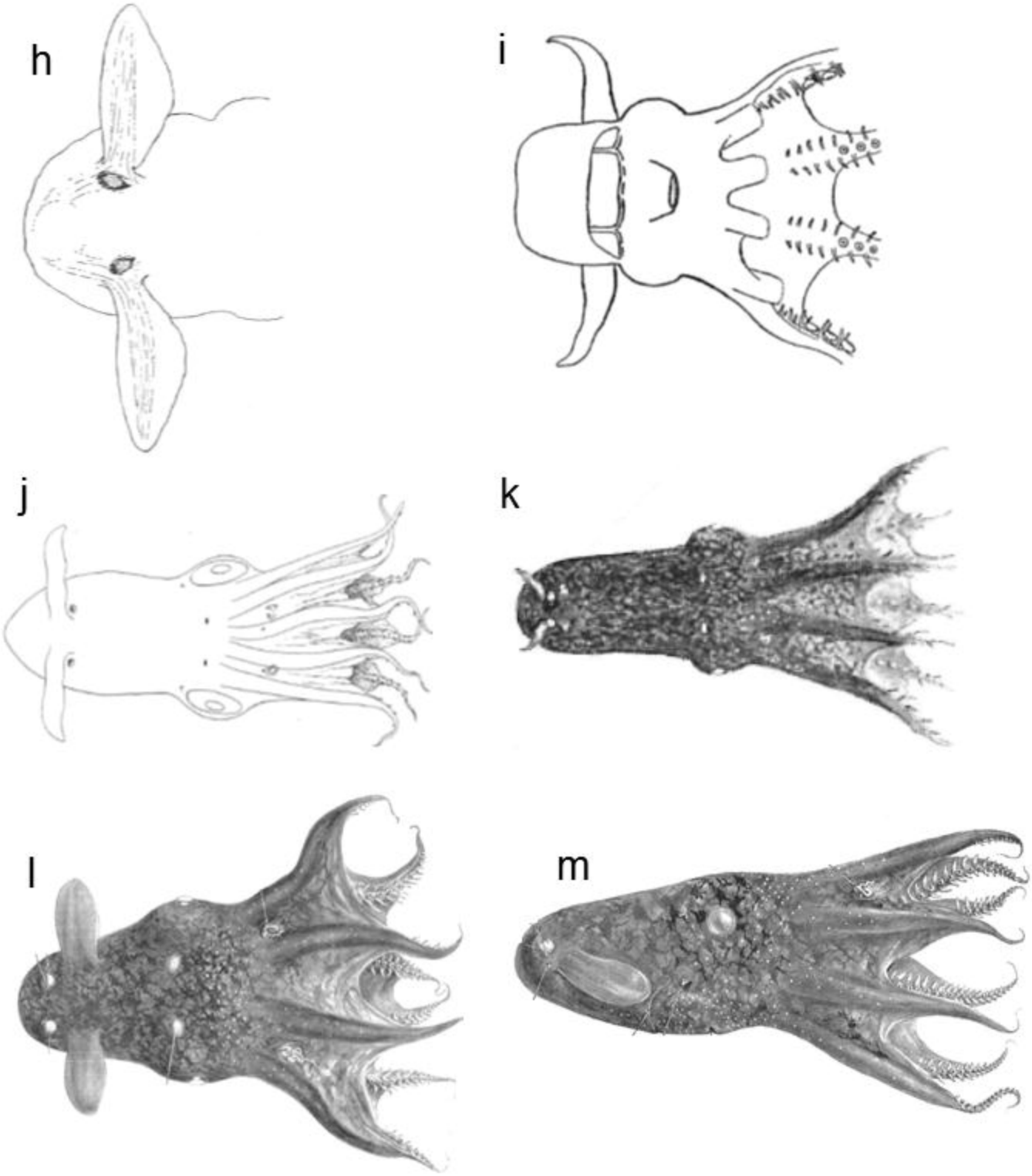

Fig. 7-2