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Gershwinia thailandensis Wutthituntisil, Xiao and Aungtonya: A NEW GENUS AND SPECIES OF BOX JELLYFISH (Cubozoa: Carybdeida: Carukiidae) FROM THAI WATERS

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ABSTRACT: Specimens of a species of box jellyfish were collected from the Andaman Sea and Gulf of Thailand. The specimens were characterized by having cuboid bell shape, no gastric phacellae; pedalial bends volcano-shaped, broad pedalial canal where it joints flattened tentacle; inner keel greatly rounded. The frown-shaped rhopaliar niche ostium and presence of rhopaliar horns suggest the most appropriate placement is as a member of the family Carukiidae (Irukandji family), but additionally it is distinct from the currently described genera. Molecular analyses contextualizing these specimens with exemplars of other genera in this family is consistent with evidence from morphological traits suggesting that the lineage is distinct. Here, we present measurements and descriptions of the morphological features, photographs, and phylogenetic relationships of this new genus and species, *Gershwinia thailandensis* Wutthituntisil, Xiao and Aungtonya.

Key words: morphological study, molecular analysis, Andaman Sea, Gulf of Thailand

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INTRODUCTION

Box jellyfishes are widely distributed across the Indo-Pacific and Atlantic oceans (Bentlage and Lewis 2012) and consist of two taxonomical groups - order Chirodropida Haeckel, 1880 and order Carybdeida Gegenbaur, 1857 - which can be identified by the presence of gastric saccules and by the pedalium shape (Gershwin 2005a; 2005b; 2006a; 2006b; Daly *et al*. 2007). Members in the order Chirodropida possess gastric saccules with a branched or unbranched pedalium, while the order Carybdeida, except *Tripedalia*, is identified with only 2–4 unbranched pedalia without any gastric saccules (Gershwin *et al.* 2013; Toshino *et al.* 2015). Some box jellyfishes are well-known to produce a severe, painful, or deadly venom to humans. Envenomation by some species in the order Chirodropida can cause cardiac arrest within minutes (Lumley *et al*. 1988). On the other hand, members in Carybdeida seem to be less venomous, though several species are reported to cause an Irukandji syndrome, which comes with lower back and abdominal pain, vomiting, hypertension, and sweating. Many patients felt an impending doom and panic about death (Williamson *et al*. 1996).

Knowledge about box jellyfish in Thai waters remains very limited because there are only a few taxonomic studies available and the existence of many questionable species (Aungtonya and

Chanachon 2012; Aongsara *et al*. 2012; Sucharitakul *et al*. 2016; Aungtonya *et al*. 2018; Department of Marine and Coastal Resources 2020). The lack of understanding in many aspects of venomous jellyfishes causes inaccurate reports and records on these harmful organisms and negative impacts on tourism, fisheries, and residents (De Donno *et al*. 2014). One of the most important fundamental knowledge for a better understanding about unknown species is taxonomy. Taxonomical study and improved nomenclature will allow for more studies to investigate their distribution, dispersal patterns and population fluctuations.

In the past decade, several unknown box jellyfishes have been collected from the Andaman Sea and the Gulf of Thailand during venomous jellyfish surveys. At least 11 species of box jellyfish have been recorded, four of which belong to described species including *Chiropsoides buitendijki* (van der Horst, 1907), *Tripedalia binata* Moore, 1988, *Tripedalia cystophora* Conant, 1897, and the recently described species *Chironex indrasaksajiae* Sucharitakul, 2017. However, the other seven putative species cannot be identified to any described taxonomical species unit with current knowledge (Department of Marine and Coastal Resources 2020; Sucharitakul *et al*. 2017).

From all box jellyfishes collected from this survey, one morphologically distinct group was identified from both Andaman Sea and Gulf of Thailand. The specimens in this group are morphologically characterized by having rhopaliar niche ostium with rhopaliar horns while lacking stomach gastric phacellae, which are the key characters to the family Carukiidae, order Carybdeida. The most recent study reports a total of four genera belonging to Carukiidae, namely *Carukia, Gerongia, Malo*, and *Morbakka* (Bentlage and Lewis 2012). Given the morphological and genetic distinction from other described genera in this family, we propose a new genus, *Gershwinia*, and describe its type species *Gershwinia thailandensis*, including morphological observations and genetic characterization of the new species. Phylogenetic analyses including the proposed genus and species confirm its close relationship to, and distinctness from, other exemplars from the family Carukiidae available in public databases.

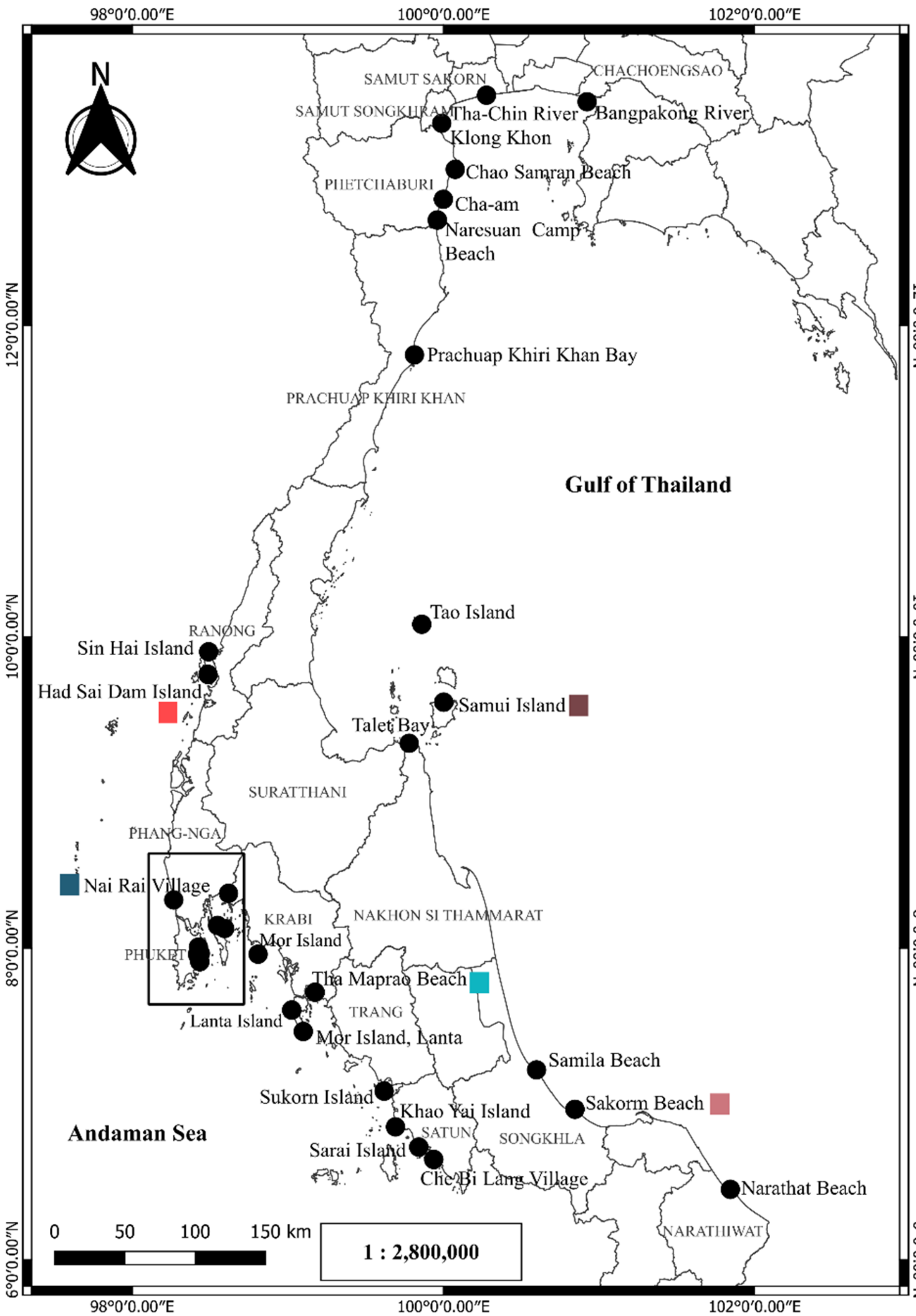
MATERIALS AND METHODS

Specimen collection and treatment

Samples from this study were collected during the surveys of venomous jellyfish in the Andaman Sea during 2009–2016 and in the Gulf of Thailand during 2010–2018. The surveys were conducted in the morning during the northeast monsoon (November–April) and during the southwest monsoon (May–October). The Andaman Sea covers the coastal areas in the provinces of Ranong, Phang-nga, Phuket, Krabi, Trang, and Satun while the Gulf of Thailand coastal provinces include Chachoengsao, Samut Sakhon, Samut Songkhram, Phetchaburi, Prachuap Khiri Khan, Surat Thani, Nakhon Sri Thammarat, Songkhla, and Narathiwat (Fig.1).

The box jellyfish were collected from shrimp trammel nets (1.5 m in width, 400 m in length, mesh size ranged from 40 to 50 mm and 140 to 160 mm for inner and outer panels, respectively). Additional specimens were occasionally received from fishermen or collected from shrimp trammel nets from the Gulf of Thailand. Five hundred eighty-one specimens were preserved in 3% formalin seawater, then laid flat and measured using digital calipers following Gershwin (2005c) and Toshino *et al*. (2015).

For the bell shape measurement, bell height (BH) was measured from the base of the bell to the apex by excluding the perradial lappets, diagonal exumbrella width (DEW) was measured across from the base of outer pedalial keel to another diagonally opposite pedalium and diagonal subumbrella width (DSW) was measured across diagonal base of inner keel of pedalia. Interrhopaliar width (IRW) was measured as the length between two rhopalia, rhopalium height (RH), inner keel length (IKL), inner keel width (IKW), outer keel length (OKL), outer keel width (OKW), pedalial canal width (PCW), pedalial width (PW), tentacle base width (TBW), and velarial width (VW) (Fig.2). Those specimens were also photographed for morphological characters using a Canon 80D camera with EF 50 mm lens. Smaller features like rhopalia, rhopalial niche ostium and sex determination were observed and photographed through a stereo microscope. Bell heights of all samples were grouped by sampling locations and their means and standard deviations were calculated.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N
SAMUT SAKORN
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Tha-Chin River
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Klong Khon
Chao Samran Beach
PHETCHABURI
Cha-am
Naresuan Camp Beach
12°0′0.00″N
Prachuap Khiri Khan Bay
PRACHUAP KHIRI KHAN
Gulf of Thailand
Tao Island
RANONG
Sin Hai Island
10°0′0.00″N
Had Sai Dam Island
Samui Island
Talet Bay
SURATTHANI
PHANG-NGA
Nai Rai Village
KRABI
NAKHON SI THAMMARAT
Mor Island
PHUKET
8°0′0.00″N
Tha Maprao Beach
TRANG
Lanta Island
Mor Island, Lanta
Samila Beach
Sukorn Island
Sakorm Beach
Khao Yai Island
Andaman Sea
SATUN
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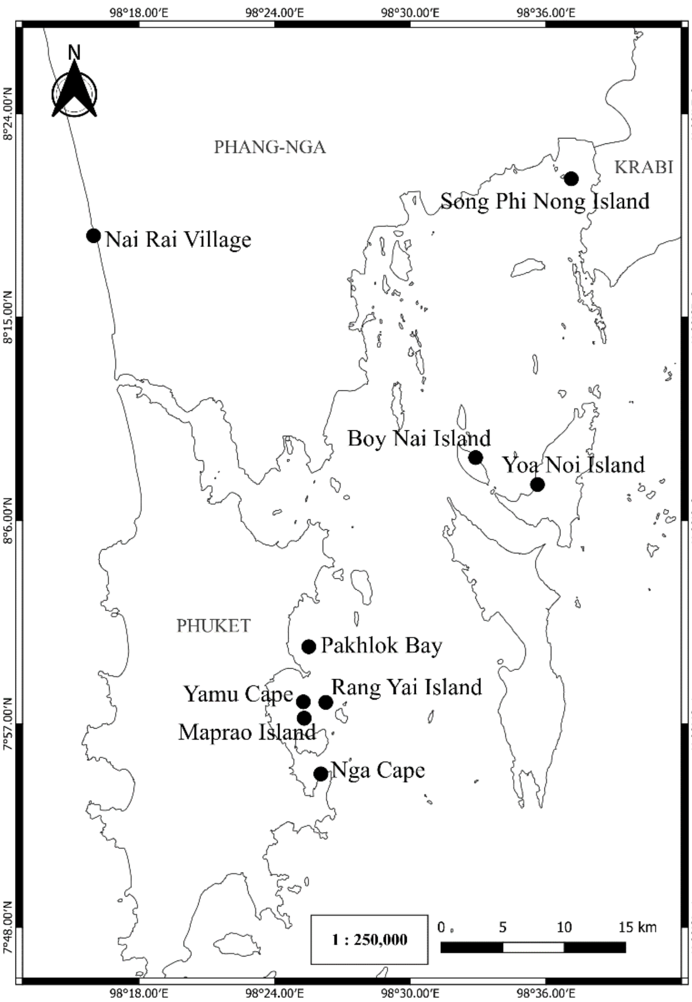

Figure 1. Localities in the Andaman Sea and the Gulf of Thailand where samples were collected. Localities in the rectangle in the upper map were enlarged in the lower map. [Color code corresponds to those of DNA sequences in Figure 5 (the phylogenetic trees)]

DNA extraction, PCR amplification and sequencing

A small piece (0.5 cm x 0.5 cm) of tentacle or rhopalia or mesoglea tissue was cut from the selected samples (see * in Appendix 1) and preserved in 99% ethanol at a ratio of 10- ethanol: 1 tissue (v:v). The preserved tissues were stored at 4°C for DNA analysis.

The genomic DNA was extracted using the commercial animal tissue extraction kit (OMEGA bio-tek, Inc., USA) or a CTAB/chloroform method described by Dawson *et al.* (1998). The nuclear 18S and mitochondrial 16S gene fragments were amplified using the primer pairs L18S: 5′-CGGAAGGGCACCACCAGGAG-3′, 18Sb: 5′-GATCCTTCTGCAGGTTCACCTAC-3′ and BRDGP-1: 5′-TCGACTGTTTACCAAAAACATAGC-3′, BRDGP-2: 5′-ACGGAATGAACTCAAATCATGTAAG-3′, respectively (Bayha, 2005; Bayha *et al*., 2010). PCR reactions were performed on the thermal cycler following the optimized protocol (Liu *et al.* 2016). The amplicons were directly sequenced bi-directionally on the ABI3130XL genetic analyzer (Applied Biosystems, Inc., USA). In cases that direct sequencing was not successful, amplicons were cloned using the TA cloning kits (Takara Biomedical Technology Co., Ltd., China) and then sequenced.

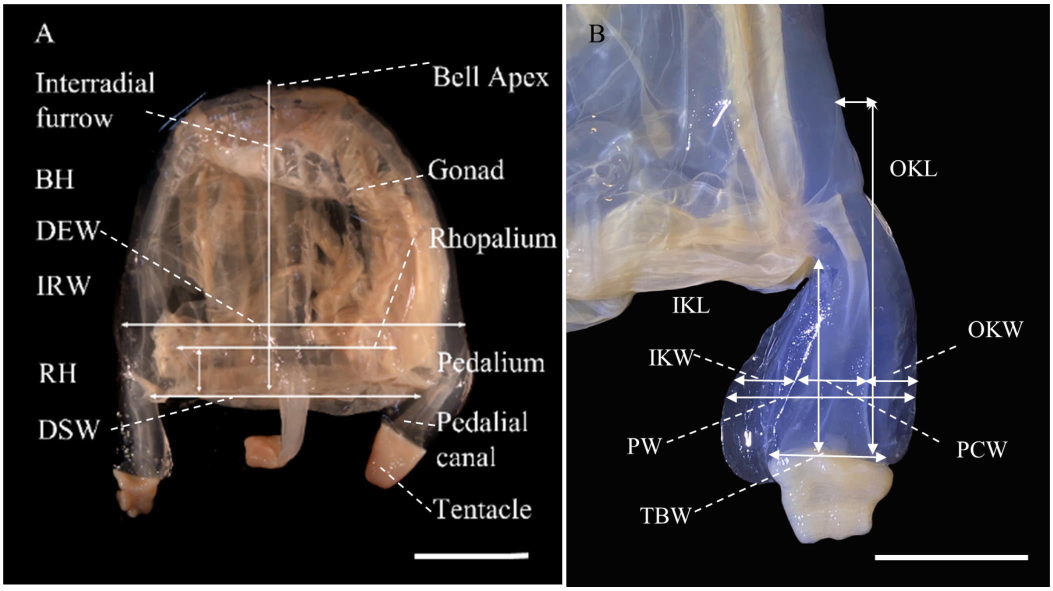

Figure 2. Morphological characters and measurements of *Gershwinia thailandensis* Wutthituntisil, Xiao and Aungtonya gen. et sp. nov. A. Lateral view, tentacles missing. B. Pedalium, tentacle missing. A. PMBC 21325, holotype, B. PMBC 30174. Scale bar: 3 cm (A), 1 cm (B). Abbreviations: BH = bell height; DEW = diagonal exumbrella width; DSW = diagonal subumbrella width; IRW = interrhopaliar width; RH = rhopalium height; IKL = inner keel length; IKW = inner keel width; OKL = outer keel length; OKW = outer keel width; PCW = pedalial canal width; PW = pedalial width; TBW = tentacle base width.

Sequence analysis

The resulting sequences were cleaned for vector sequences, primers, and ambiguous nucleotides then subsequently aligned with the reference sequences downloaded from GenBank using Clustal W algorithm (Thompson *et al*. 1994). The genetic distances (number of base substitutions per site) within and among species groups were estimated using the Tamura-Nei model with a gamma distribution (Tamura and Nei 1993). The phylogenetic relationships among newly described specimens and references was analyzed using maximum likelihood (ML), neighbor joining (NJ) and Bayesian Inference (BI) methods. ML and NJ analyses were conducted in MEGA6 (Tamura *et al*. 2013) with General Time Reversible (GTR) model. Robustness of resulting phylogenetic trees was assessed by bootstrapping method for 1000 replicates. BI analysis was performed using MrBayes 3.1 (Huelsenbeck and Ronquist 2001) with GTR substitution model, gamma-distributed rate variation, 2 million generations, Markov chains (Nchains) = 4, sampled frequency = 100. A consensus tree of the last 1000 resulting trees is presented here. For comparison, six partial 16S sequences (GQ849097-8, GQ849119-22, JN184782) derived from the various taxa in the family Carukiidae and four sequences from *Tamoya* spp. (GQ849122, GQ849095, KR093033, HQ824528) were retrieved from the NCBI database. Sequences of *Alatina* spp. (GQ507004, GQ506983, GA506990, GA506984, GA506998 and GA506999) were used as the outgroup. Four partial 18S sequences (GQ849083-4, AF358105, AF358107) from Carukiidae and two sequences from Tamoyidae (GQ849085-6) were downloaded for 18S analysis, while the sequence GQ849082 from *Alatina* was used as the outgroup.

RESULTS

SYSTEMATICS

Family Carukiidae Bentlage, Cartwright, Yanagihara, Lewis, Richards, and Collins, 2010

Genus *Gershwinia* Wutthituntisil, Xiao and Aungtonya gen. nov.

Type species. *Gershwinia thailandensis* Wutthituntisil, Xiao and Aungtonya n. sp., designated herein. Gender: neuter.

Diagnosis. Carukiidae with a ratio of bell height and diagonal exumbrella width as 1:1, pedalial canal bend volcano-shaped; broad pedalial canal at the joint of flatten tentacle; inner keel rounded; no gastric phacellae.

Etymology: The name is dedicated to Dr. Lisa-Ann Gershwin, in honor of her many contributions to medusozoan taxonomy. A search of the World Register of Marine Species has her down as the taxonomic author of 43 accepted species within Medusozoa. She recognized this new genus when she was lecturing in the WESTPAC Training Workshop on the Identification of Box Jellyfish in the Eastern Indian Ocean and the Gulf of Thailand, held at Phuket Marine Biological Center, Phuket, Thailand, on June 13–17, 2016.

Gershwinia thailandensis Wutthituntisil, Xiao and Aungtonya n. sp.

Figs. 2A–B, 3A–F, 4A–F, Table 1–2, Appendix 2

Morbakka fenneri – Aungtonya and Chanachon 2012: 18, fig. 11; 44.

Morbakka sp. C - Marine and Coastal Resources Research and Development Institute. 2015: 31–37.

Holotype: PMBC 21325, 1, Lanta Island, Krabi Province. 24/09/13 (Fig. 4A).

Paratype: PMBC 21326, 1, Mor Island, Lanta Island, Krabi; PMBC 30174, 1, Nga Cape, Phuket Province; PMBC 30175, 1, Sarai Island, Satun Province; PMBC 30176, 1, Mor Island, Lanta Island, Krabi Province; PMBC 30177, 1, Lanta Island, Krabi Province (Fig. 4B–F).

Material examined. A total of 581 specimens measured had a minimum bell height of 23.36 mm and a maximum bell height of 127.62 mm (Table 1). Only 154 specimens were deposited at the Reference Collection of Phuket Marine Biological Center (Appendix 1).

Description. Adult cubomedusa with scattered nematocyst warts on the exumbrella, pedalia, and velarium. Bell height (BH), measured from bell apex to turnover velarium range 23.36–127.62 mm from the Andaman Sea and range 50.58–104.21 mm from the Gulf of Thailand (Table 2). Diagonal exumbrella width (DEW), a length from one edge side to another side range 29.68–128.31 mm measured from specimens sample from the Gulf of Thailand. Thick mesoglea on the apex of the bell and four interradial pillar, with median furrow around 3 of 4 of the BH (Fig. 2A). Two vertical adradial shallow and narrow to each other in lower half of the bell, flank both side of rhopalium, become wider in the upper half, then disappear just below the apex.

Four pedalia, interradial on each corner of the bell (Figs. 3A, 4). Well-developed inner keel, greatly rounded (Fig. 3A–B). Obvious scattered nematocyst warts on outer keel but inconspicuous on inner keel (Fig. 3A–B). Large angle bending of pedalial canal, slightly pointed upward at the angle. Enlarged pedalial canal at the meeting point between canal and tentacle. Flattened tentacle with enlarged base (Fig. 3B).

Four rhopalia, perradial, with a frown-shaped rhopaliar niche ostium and two rhopaliar horns. The rhopaliar horns broad, long, swollen at the middle and pointed at the tip, similar to rabbit-ear shape (Fig. 3C–D). Nematocyst warts on rhopaliar stem absent. Two median lensed eyes, no lateral eyes were observed in all preserved specimens (the color of lateral eyes may be degraded by formalin) (Fig. 3D).

Velarium broad, about 20 mm of velarial width. Velarial canal 4 per octant, branched vertically, without nematocyst warts. Perradial lappets narrows, isosceles triangular shape with two rows of four nematocyst warts, cascading in size, larger on the outer edge to inner side (Fig. 3E). Frenulum narrows, attach to velarium at a proximal half of velarial width.

Manubrium about one-third long of bell height. Four well-developed broadly quadrate lips (Fig. 3F). Inner stomach wall with parallel corrugations, gastric phacellae absent. The gamete of females

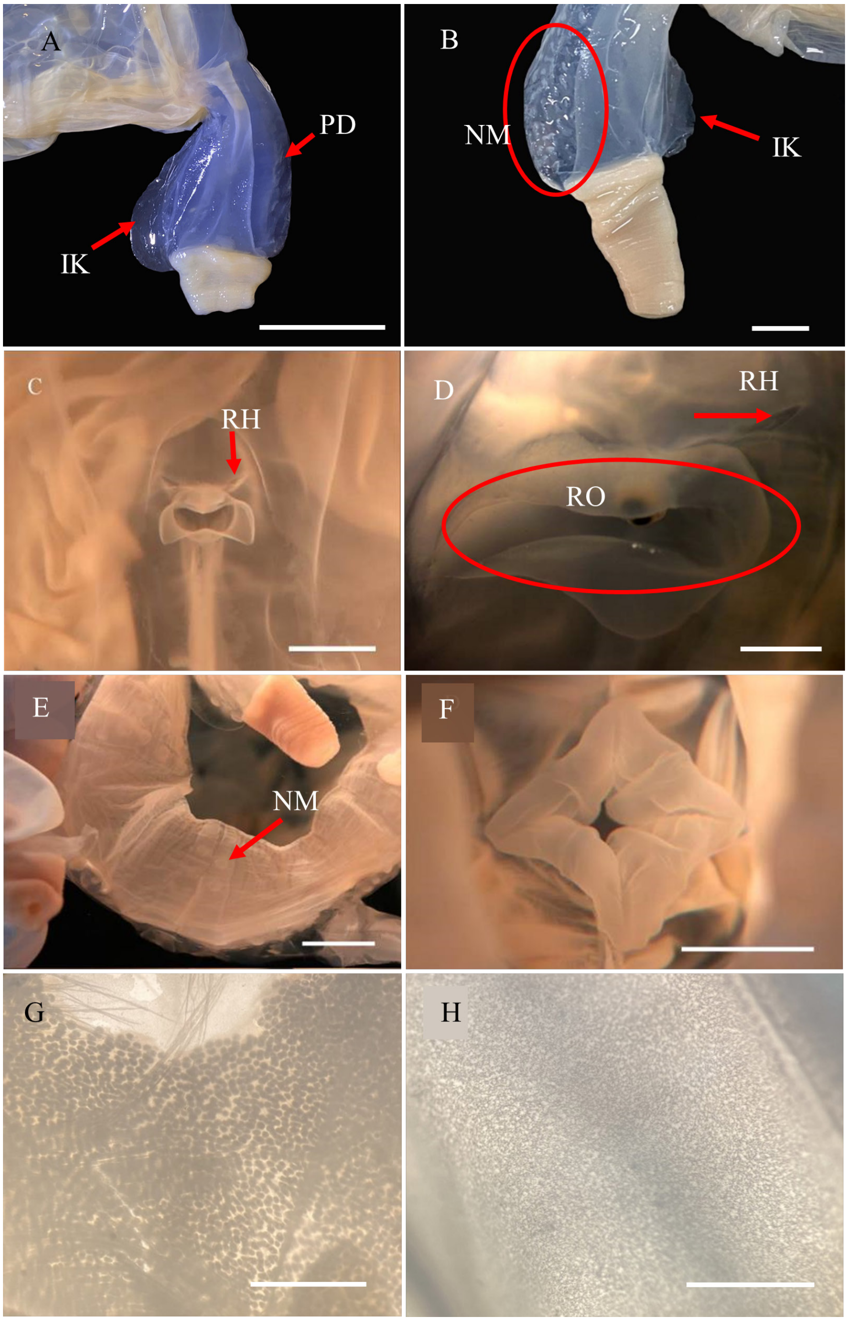

Figure 3. Morphological characters of *Gershwinia thailandensis* Wutthituntisil, Xiao and Aungtonya gen. et sp. nov.; A. Pedalium, tentacle missing. B. Nematocyst warts, tentacle missing. C. Rhopalium with rhopaliar horns (arrow). D. Two median lensed eyes. E. Velarial lappet (arrow). F. Mouth oral lips. G. Gametes of female. H. Gametes of male. A. PMBC 30174 (paratype), B. PMBC 21279, C–F. PMBC 21325 (holotype), G. PMBC 21332, H. PMBC 21270. Scale bar: 1 cm (A), 5 mm (B, D), 10 mm (C, E–H). Abbreviation: PD: Pedalia, NM: Nematocyst, IK: Inner keel, RH: Rhopaliar horn and RO: Rhopaliar niche ostium.

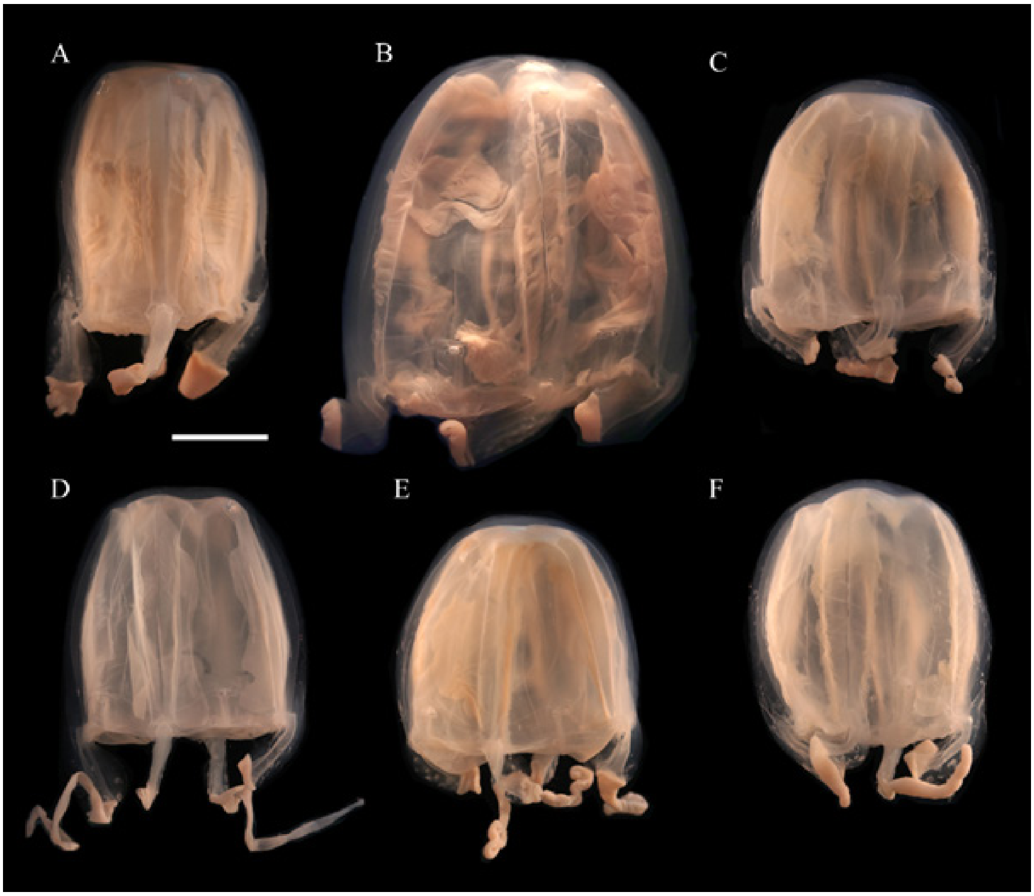

Figure 4. The type specimens of *Gershwinia thailandensis* Wutthituntisil, Xiao and Aungtonya gen. et sp. nov.; Holotype: A. PMBC 21325. Paratype: B. PMBC 30177, C. PMBC 30175, D. PMBC 30176, E. PMBC 30174, F. PMBC 21326. Scale bar indicates 3 cm. Tentacle missing in all type specimens.

Table 1. Bell height of *Gershwinia thailandensis* Wutthituntisil, Xiao and Aungtonya gen. et sp. nov. from the Andaman Sea and the Gulf of Thailand; BH = Bell height.

Provinces	No. of specimens	BH (mm)		
		Mean	S.D.	Range (min-max)
Ranong	4	53.19	7.82	48.61–58.69
Phang-nga	189	51.46	11.81	24.49–89.88
Phuket	67	46.18	12.22	23.36–71.88
Krabi	97	63.92	17.57	30.76–127.62
Trang	9	54.91	11.40	39.64–73.97

Provinces	No. of specimens	BH (mm)		
		Mean	S.D.	Range (min-max)
Satun	210	75.29	20.39	31.09–123.58
Chachoengsao	1	79.8		
Samut Sakhon	2	77.69	18.31	64.75–90.64
Samut Songkhram	4	64.38	8.65	49.49–70.79
Phetchaburi	5	75.77	14.78	50.58–91.71
Prachuap Khiri Khan	2	79.06	2.93	76.13-81.98
Surat Thani	4	72.92	13.86	57.01–100.87
Nakhon Sri Thammarat	1	119.77		
Songkhla	20	63.73	16.53	40.93–102.08
Narathiwat	18	81.68	11.86	56.72–104.21

Table 2. Measurement (mm) of the type specimens of *Gershwinia thailandensis* Wutthituntisil, Xiao and Aungtonya, Holotype: PMBC 21325; Paratypes: PMBC 21326, 30174–30177. Abbreviations: BH = bell height; IRW = interrhopaliar width; DEW = diagonal exumbrella width; DSW = diagonal subumbrella width; RH = rhopalium height; IKL = inner keel length; IKW = inner keel width; PCW = pedalial canal width; OKL = outer keel length; OKW = outer keel width; PW = pedalial width; TBW = tentacle base width; VW = velarial width.

Specimens	BH	IRW	DEW	DSW	RH	IKL	IKW
PMBC 21325	75.41	42.11	78.62	68.57	10.83	17.43	7.17
PMBC 21326	69.81	39.33	70.20	57.14	13.02	17.15	6.96
PMBC 30174	64.37	41.53	69.04	63.33	7.66	16.30	6.69
PMBC 30175	72.00	42.80	78.17	67.20	12.10	18.49	7.55
PMBC 30176	74.21	39.32	75.92	61.67	10.11	22.32	7.74
PMBC 30177	106.99	52.37	114.69	96.21	15.82	27.43	7.54
Specimens	**PCW**	**OKL**	**OKW**	**PW**	**TBW**	**VW**	**SEX**
PMBC 21325	5.02	29.43	4.21	15.38	12.32	19.51	Female
PMBC 21326	4.18	30.81	6.48	16.47	8.70	14.41	Female
PMBC 30174	5.68	28.80	4.67	15.94	9.84	14.50	Male
PMBC 30175	3.99	33.59	3.97	16.78	8.87	14.19	Female
PMBC 30176	6.04	29.78	5.61	18.62	11.04	16.66	Female
PMBC 30177	8.43	43.32	6.23	21.25	16.06	25.33	Female

with a milky white to light yellowish and the gamete of males with pale white in color. The specimens from the Gulf of Thailand with bell height (BH) from 35.02 mm and up, were observed to have mature gonads.

Remarks. Rows of cascade size nematocyst warts on the perradial lappets present in most of samples, however, there are some samples that lack nematocyst warts, possibly due to degradation during preservation or as a variation in the population.

This genus differs from *Morbakka* in having a cuboid bell shape, smooth surface on rounded apex without warts; pedalial canal spread out on both sides at tentacle base with rounded inner keel, volcano-shaped in bend; nematocyst warts on velarium canals absent, except on frenulum, while that of *Morbakka* according to Gershwin (2008) having bell shape taller than wide, flat apex with nematocyst warts; well developed 'spike' in bend of pedalial canal (thorn-like), inner pedalial canal broaden at tentacle base with straight inner keel; nematocyst warts scattered on velarium canals and frenulum (Figs. 7–9).

Most specimens in the present study exhibit volcano-shaped pedalial canal bends, except for a few specimens (*i.e*., PMBC 21325, some specimens of PMBC 21332 and PMBC 21335) having two volcano-shaped arranged parallel on pedalia canal bend. This likely represents intraspecific variation based on the molecular analysis (Figs. 5–6), which indicates that the samples represent a single species.

Molecular phylogenetics

The genetic distances between groups were much higher than those within each taxon group for both genes (Table 3 and 4). And the distances estimated from 16S were larger than 18S indicating higher mutation rates of 16S gene, as one would expect. The 16S and 18S sequences generated from the representative specimens of PMBC 21328, 21329, 21336, 30178, 30179, 30180, 30196, 30197

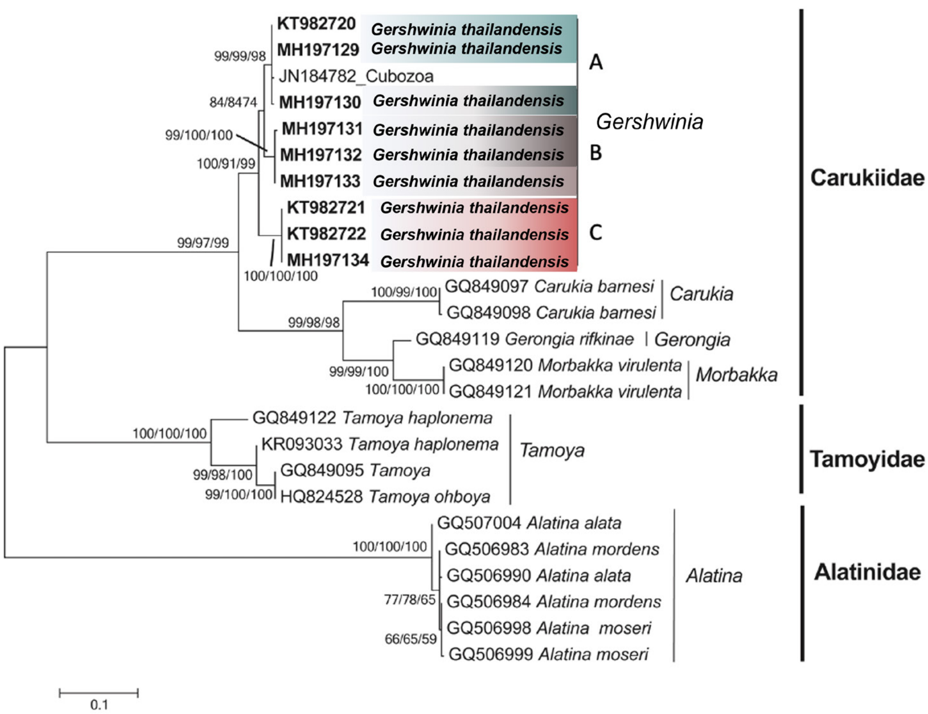

Figure 5. Phylogenetic tree showing the phylogenetic affinity of *Gershwinia thailandensis* with other box jellyfish based on the partial 16S gene sequences. Numbers on each node are bootstrapping support for NJ/ML analyses and the credibility of BI analysis. Sequences of *Alatina* spp. (GQ507004, GQ507983, GQ506990, GQ506984, GQ506998, GA506999) were treated as the outgroup. Bold fonts indicate the samples from this study. Color code corresponds to the localities where the samples were collected, as in Fig. 1. Identifiers A, B, and C indicate each sub-clade in the *G. thailandensis* population.

and 30198 were aligned with reference sequences retrieved from Genbank. All ML, NJ and BI analyses resulted in identical tree topologies for both 16s and 18s trees (Figs. 5–6). The nine 16S sequences from this study were grouped together in a clade with a sequence JN184782, from an unknown cubozoan specimen in Malaysia (Maghsoudlou and Siti-Azizah 2011), suggesting that *Gershwinia thailandensis* is also present in Malaysian waters. The sequences from three genera *Morbakka*, *Gerongia* and *Carukia* in the family Carukiidae, each represented by a single species, were clustered

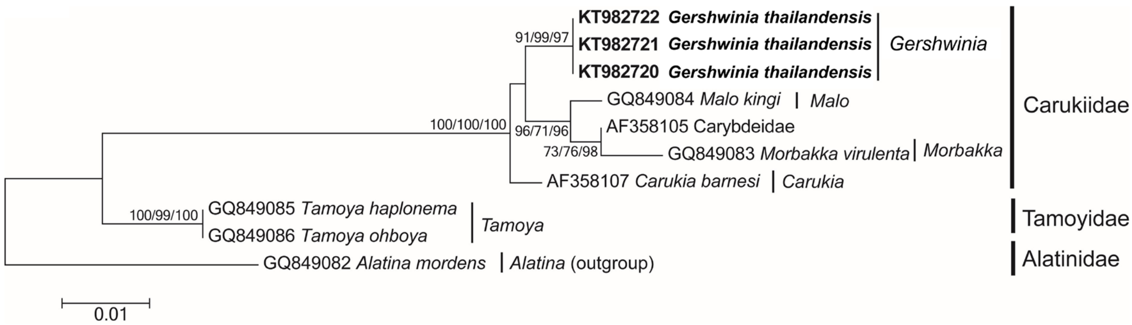

Figure 6. Phylogenetic tree showing the phylogenetic affinity of *Gershwinia thailandensis* with other box jellyfish based on the partial 18S gene sequences. Numbers on each node are bootstrapping support for NJ/ML analyses and the credibility of BI analysis. The sequence of *Alatina mordens* (GQ849082) was treated as the outgroup. Bold fonts indicate the samples from this study.

Table 3. Genetic distances estimated using the Tamura-Nei model with a gamma distribution based on 16S gene sequences within (bold fonts) and between taxa groups (n.d. is not determined since only one sequence of *Gerongia* was involved).

	Gershwinia	*Carukia*	*Gerongia*	*Morbakka*	*Tamoya*	*Alatina*
Gershwinia	**0.03**					
Carukia	0.23	**0.00**				
Gerongia	0.26	0.24	**n.d.**			
Morbakka	0.23	0.22	0.14	**0.01**		
Tamoya	0.36	0.41	0.51	0.46	**0.08**	
Alatina	0.46	0.53	0.51	0.51	0.47	**0.01**

Table 4. Genetic distances estimated using the Tamura-Nei model with a gamma distribution based on 18S gene sequences within (bold fonts) and between taxa groups (n.d. is not determined since only one sequence in this group was involved).

	Gershwinia	*Malo*	*Carybdeidae*	*Morbakka*	*Carukia*	*Tamoya*	*Alatina*
Gershwinia	**0.00**						
Malo	0.02	**n.d.**					
Carybdeidae	0.02	0.01	**n.d.**				
Morbakka	0.04	0.02	0.01	**n.d.**			
Carukia	0.01	0.02	0.01	0.02	**n.d.**		
Tamoya	0.15	0.17	0.17	0.22	0.16	**0.00**	
Alatina	0.58	0.38	0.38	0.60	0.46	0.11	**n.d.**

together, forming a sister group to this novel genus *Gershwinia*. The clade of Carukiidae, comprised of *Gershwinia, Morbakka, Gerongia* and *Carukia*, is sister to Tamoyidae. Three sub-clades within *Gershwinia*, with short distance from each other, had high bootstrapping support based on both ML and NJ analyses, indicating a possible genetic structure within this genus.

All 18S sequences from these nine *G. thailandensis* samples were 100% identical, hence the only three sequences deposited in Genbank were applied in the phylogenetic analysis. In a similar pattern as the 16S tree, the clade of *Gershwinia* in phylogenetic tree generated from 18S sequences was nested with *Malo, Morbakka* and *Carukia*, forming a monophyletic group of Carukiidae, as a sister clade of Tamoyidae (Fig. 6). In the 18S analysis, *Carukia* is sister to the other representatives of Carukiidae.

DISCUSSION

Gershwinia thailandensis Wutthituntisil, Xiao and Aungtonya is characterized by having a ratio of bell height and diagonal exumbrella width as 1:1, pedalial canal bends volcano-shaped; broad pedalial canal at the joint with flatten tentacle; rounded inner keels at the joint with tentacle; no gastric phacellae. The differences among genera in the Carukiidae, *i.e*., *Carukia*, *Gerongia*, *Malo*, *Morbakka* and *Gershwinia* are shown in Table 3. The monophyletic status of this new genus and species is also strongly supported by the molecular phylogenetic trees from partial 16S and 18S mitochondrial genes (Figs. 5–6).

At the beginning of the jellyfish survey in 2010, the *G. thailandensis* samples in this study were identified as *Morbakka* spp. according to their morphological characters (rhopaliar horn, rhopaliar niche ostium and ribbon-like single tentacle). The pedalial canal bend, which is a main diagnostic feature of this new genus, was described initially as a variation of *Morbakka* spp. However, with the result from phylogenetic analyses and closer examination of the morphological traits, we found that *G. thailandensis* is clearly distinct from *Morbakka* spp., forming its own clade, apart from the genera *Carukia*, *Gerongia*, and *Morbakka* (Fig. 5) and possessing sufficient morphological differences. These findings suggest that *Gershwinia* is the earliest diverging genus within the family Carukiidae, as it was the first to diverge from a Carukiidae ancestor. However, the incomplete taxon sampling of members in the family Carukiidae still leaves some uncertainties about the relationship among members in this family. The phylogenetic relationship also shows that there is within-group genetic differentiation of *G. thailandensis* from three locations (northern, southern Andaman Sea, and Gulf of Thailand).

The structure of 16S sequences of *G. thailandensis* partitions individuals into three sub-groups corresponding to their geographic distribution: clade A from southern Andaman and Malaysia (PMBC 21336, PMBC 30179, PMBC 30180, and JN184782 (KT982720, MH197129, JN184782 and MH197130)), clade B from Gulf of Thailand (PMBC 30196 (MCRRC C14), PMBC 30197 (MCRRC C15), and PMBC 30198 (MCRRC L1) (MH197131, MH197132 and MH197133)), and clade C from northern Andaman (PMBC 21328, PMBC 21329, and PMBC 30178 (KT982721, KT 982722 and MH 197134)). Despite the northern and southern Andaman Sea having no observed physical barrier, clade A (southern Andaman) is sister to clade B (Gulf of Thailand). The common ancestor of clade A and B was then paired with clade C from northern Andaman (specifically from Hat Sai Dam Island, Ranong).

One possible explanation of this tree topology of *G. thailandensis* populations could be geographic barriers related to seasonal monsoons. During the northeast monsoon, a water mass flows down from the north of the Andaman Sea to the south, while another water mass enters the Andaman Sea from Malacca Strait from the south. These two water masses are reported to intersect with one another around Phuket Island before changing direction and leaving the coast around the area of Phuket, Phang-nga and Krabi (Chan *et al.* 2022; Pongparadon *et al*. 2015; Rizal *et al*. 2012). The north-to-south ocean current potentially mediates *G. thailandensis* dispersal from a parental population in the northern Andaman Sea, while the south-to-north current brought a population from another population source in the south. Consequently, the combined water mass that leaves the Phuket coast acts as a physical barrier to these two populations and prevents their offspring from mixing in the coastal area of Thailand. However, a deeper genetic analysis is needed to answer the question how much genetic material is exchanged between the sub-populations. With the current information, we hypothesize that the population of clade 3 came from a northern Andaman source while clades 1 and 2 were derived from southern Andaman.

A similar pattern of geographical genetic differentiation is also present in the study of a box jellyfish, *C. buitendijki* (Aungtonya *et al*. 2018), community structure in barnacle, *Tetraclita* spp. (Chan *et al*. 2022), giant clams, *Tridacna maxima* (Kittiwattanawong 1997) and macroalgae, *Halimeda* spp. (Pongparadon *et al*. 2015). With the shared geographic structure observed in these species across the tree of life, there is a high possibility that the population genetic structure here is strongly associated with environmental influences especially the characteristics of the ocean current between northern and southern Andaman Sea as explained above. Further studies on the population genetics of box jellyfish, their life history, and other high dispersal marine invertebrates will provide more solid evidence and assess and refine this hypothesis.

Table 3. Comparison of the genera within the family Carukiidae (adapted from Gershwin, 2008 and present study).

	***Carukia* Southcott, 1967**	***Gerongia* Gershwin and Alderslade, 2005**	***Malo* Gershwin, 2005**	***Morbakka* Gershwin, 2008**	***Gershwinia* Wutthituntisil, Xiao and Aungtonya gen. nov.**
Bell shape	small and pyramidal, with rounded apex	cuboid and robust, with rounded apex	taller than wide, with flat apex	taller than wide, flat apex with warts (Fig. 7A)	cuboid, smooth and rounded apex (Fig. 7B)
Exumbrellar warts	red warts	pale freckles	purple freckles	bright pink warts	no warts observed, any possible pigments degraded in formalin-preserved specimens
Rhopaliar horns	narrow, long, straight; thread-shaped	broad, short, curved; devil horn-shaped	broad, short, blunt or with pointed tips	broad or narrow, long, straight, pointy; rabbit-ear-shaped	*broad, long, swollen at middle and pointed at the tip; rabbit-ear-shaped
Number of eyes per rhopalium	6 (2 median, plus 4 lateral)	unknown, possibly 6	2 median lensed eyes only, lacking laterals	2 median lensed eyes only, lacking laterals	** 2 median lensed eyes
Pedalial canal	narrow canal, pedalial canal bend simple (lacking prominent thorn)	broadly rounded canal, bend of pedalial canal overhanging, upward pointing, thorn-like	narrow, knee-shaped pedalial canal bend, lacking prominent thorn	inner pedalial canal broaden at tentacle base with straight inner keel, well developed ‘spike’ in bend of pedalial canal, thorn-like (Fig. 8A)	pedalial canal broaden both side at tentacle base with rounded inner keel, volcano-shaped in bend (Fig. 8B)
Tentacle	round in cross section, with tailed bands	round in cross section, heavy, with enlarged base	round in cross section, fine	flat in cross section, heavy, with enlarged base	flat in cross section, with enlarged base

	Carukia **Southcott, 1967**	***Gerongia*** **Gershwin and Alderslade, 2005**	***Malo*** **Gershwin, 2005**	***Morbakka*** **Gershwin, 2008**	***Gershwinia*** **Wutthituntisil, Xiao and Aungtonya gen. nov.**
Mesenteries	flap-like halfway, cord-like to rhopalium	robust, flap-like halfway to rhopalium, without cord-like extension	flap-like one-third way to rhopalium; cord-like to rhopalium	robust, flap-like halfway to rhopalium, with fine cord-like extension to rhopalium	robust, flap-like halfway, poorly developed to rhopalium
Velarial canals (per octant)	2, simple or somewhat branched, lacking lateral diverticula and warts	7, with laminar branching, lacking lateral diverticula	1 root, with 3-4 unbranched fingers, lacking lateral diverticula, lacking warts	very complexly branched; too many to easily count, with lateral diverticula, scattered warts (Fig. 9A)	3-4, very complexly branched vertically with lateral diverticula, lacking warts (Fig. 9B)
Perradial lappets warts	lacking or single on one side	2 rows of 3–6 (typically 5)	2 rows of 1–4 (typically 2)	2 rows of large warts plus scattered warts	*** 2 rows of 4-6 warts, cascade in size from outer to inner

Remarks

* Rhopaliar horn originally described in the genus *Morbakka* was broad, long, straight, pointy; rabbit-ear-shaped. However, figure 2D (Gershwin 2008) and figure 4H, I (Bentlage and Lewis 2012) suggest that an angle between two rhopaliar horns of the genus *Morbakka* is narrow in *Morbakka fenneri*, and board in *Morbakka virulenta*, while broad rhopaliar horns are present in *Gerongia, Malo*, and *Gershwinia.*

** It is possible that lateral eye color was degraded during preservation process in formalin.

*** Rows of cascade size nematocyst warts on the perradial lappets are absent in some samples, which potentially caused by the preserving solution or the variation of the different populations.

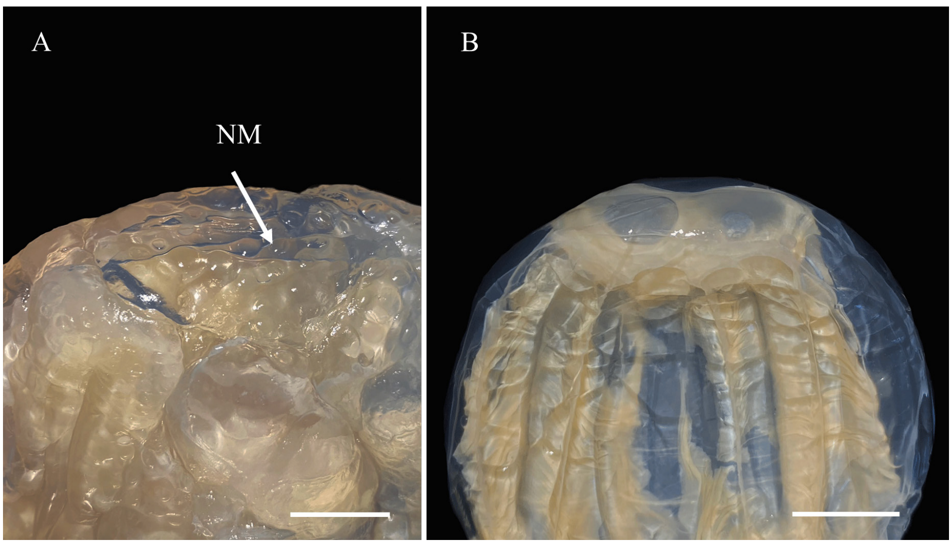

Figure 7. The character of exumbrella surface comparison between *Morbakka* cf. *virulenta* (left) and *Gershwinia thailandensis* (right): A. Nematocyst warts on apex of bell, B. Smooth surface without warts on top of bell. A: PMBC 15804, B: PMBC 21322. Scale bar: 1 cm (A–B). Abbreviation: NM: Nematocyst wart.

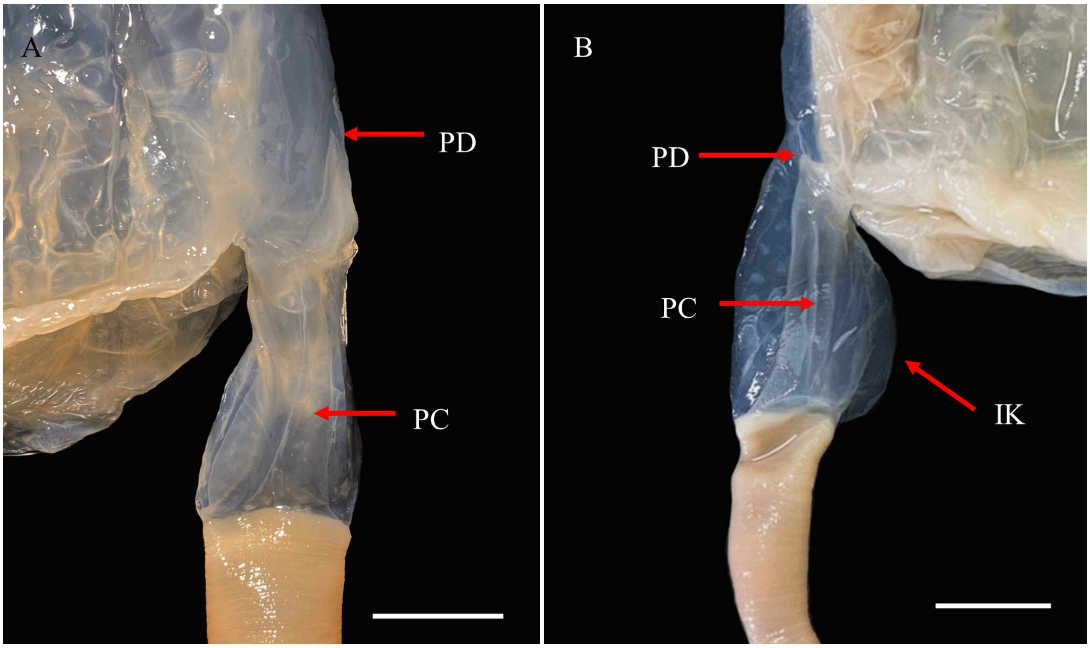

Figure 8. The characters of pedalia comparison between *Morbakka* cf. *virulenta* (left) and *Gershwinia thailandensis* (right): A. thorn-shape pedalia, B. knee with volcano-shaped pedalial bend and rounded inner keel. A: PMBC 15804, B: PMBC 21322. Scale bar 1 cm (A–B). Abbreviation: PC: Pedalial canal, PD: Pedalia and IK: inner keel.

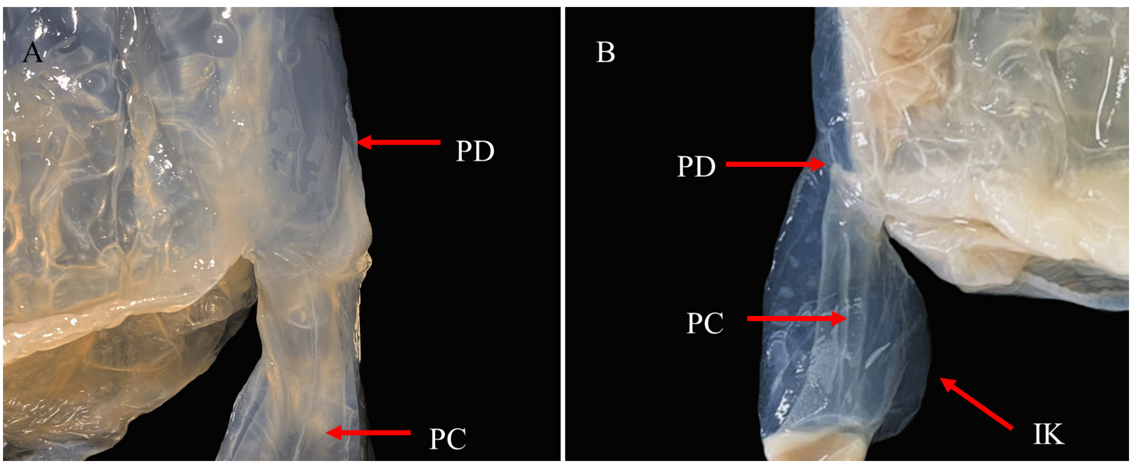

Figure 9. The character of velarium comparison between *Morbakka* cf. *virulenta* (left) and *Gershwinia thailandensis* (right): A. nematocyst warts scattered on velarial canals and frenulum, B. velarial canals without nematocyst except on frenulum. A: PMBC 15804, B: PMBC 21322. Scale bar 2 cm (A), 1 cm (B). Abbreviation: NM: Nematocyst warts, PL: Perradial lappets and VE: Velarial canals.

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Appendix 1. *Gershwinia thailandensis* Wutthituntisil, Xiao and Aungtonya gen. et sp. nov.: selected materials deposited in the PMBC Reference Collection.

PMBC No.	No. ind.	Type	Locality	Province	Lat	Long	Date	DNA Code
21325	1 (F)	Holotype	Lanta Island	Krabi	7.602829	99.024908	24/9/2013	
30174	1 (M)	Paratype	Nga Cape	Phuket	7.913198	98.434154	21/9/2010	
21326	1 (F)	Paratype	Mor Island, Lanta Island	Krabi	7.465185	99.099175	17/10/2013	
30175	1 (F)	Paratype	Mor Island, Lanta Island	Krabi	7.465185	99.099175	14/8/2013	
30176	1 (F)	Paratype	Lanta Island	Krabi	7.602829	99.024908	24/9/2013	
30177	1 (F)	Paratype	Sarai Island	Satun	6.722878	99.841518	18/6/2012	
21327	1 (F)		Sin Hai Island	Ranong	9.903394	98.490799	24/6/2014	
21328	1 (F)		Had Sai Dam Island	Ranong	9.757935	98.48712	21/4/2015	KT982721
30178	1 (F)		Had Sai Dam Island	Ranong	9.757935	98.48712	21/4/2015	KT982722
21329	1 (F)		Had Sai Dam Island	Ranong	9.757935	98.48712	21/7/2015	MH197134
21330	2 (F)		Yoa Noi Island	Phang-gna	8.126669	98.593769	20/6/2012	
21331	2 (F)		Song Phi Nong Island	Phang-gna	8.352118	98.618702	21/5/2012	
25278	17 (10F, 4M, 3W)		Boy Nai Island	Phang-gna	8.146495	98.548179	14/05/2012	
30180	1 (W)		Nai Rai Village	Phang-gna	8.310188	98.266656	28/11/2014	MH197130
26288	3 (1F, 2W)		Nga Cape	Phuket	7.913198	98.434154	21/9/2010	
25269	5 (3F, 2M)		Yamu Cape	Phuket	7.96636	98.4212	21/9/2010	
26293	4 (2F, 2W)		Pakhlok Bay	Phuket	8.007028	98.425222	21/9/2010	
21332	11 (9F, 2M)		Rang Yai Island	Phuket	7.965972	98.437722	22/9/2010	
26291	6 (5F, 1W)		Maprao Island	Phuket	7.954306	98.421833	21/09/2010	
21333	1 (M)		Maprao Island	Phuket	7.954306	98.421833	3/7/2015	
21334	3 (1F, 1M, 1W)		Mor Island	Krabi	7.961473	98.80855	14/08/2013	
21335	10 (7F, 3M)		Lanta Island	Krabi	7.60282	99.024908	24/9/2013	
21336	1 (M)		Tha Maprao Beach	Krabi	7.717108	99.175038	15/10/2015	KY982720
30179	1 (M)		Tha Maprao Beach	Krabi	7.717108	99.175038	15/10/2015	MH197129
21337	7 (4F, 2M, 1W)		Sukorn Island	Trang	7.082117	99.618702	3/11/2014	
21338	2 (F)		KhaoYai Island	Satun	6.852782	99.691813	23/7/2009	
21322	1 (F)		Che Bi Lang Village	Satun	6.643444	99.937528	30/11/2010	
26360	2 (F)		Che Bi Lang Village	Satun	6.643444	99.937528	19/12/2010	
21360	4 (1F, 1M, 2W)		Sarai Island	Satun	6.722878	99.841518	18/6/2012	
21276	1 (F)		Bangpakong River	Chachoengsao	13.43538448	100.9229045	2/4/2010	
21282	2 (1F, 1W)		Tha-Chin River	Samut Sakhon	13.47721696	100.276367	20/5/2016	

PMBC No.	No. ind.	Type	Locality	Province	Lat	Long	Date	DNA Code
21279	4 (3F, 1W)		Klong khon	Samut Songkhram	13.29749071	99.98865737	10/8/2016	
21274	1 (F)		Chao Samran Beach	Phetchaburi	13.00102194	100.0754502	10/5/2016	
21281	1 (F)		Naresuan Camp Beach	Phetchaburi	12.67577171	99.9609427	20/7/2017	
21275	1 (F)		Naresuan Camp Beach	Phetchaburi	12.67577171	99.9609427	10/8/2017	
21277	1 (M)		Naresuan Camp Beach	Phetchaburi	12.67577171	99.9609427	12/7/2018	
21278	1 (F)		Cha-am	Phetchaburi	12.80922008	99.99944169	22/2/2017	
21271	1 (M)		Prachuap Khiri Khan Bay	Prachuap Khiri Khan	11.809987	99.81368	20/9/2017	
30196	1 (M)		Samui Island	Surat Thani	9.579778	100.001472	22/1/2015	MH197131
30197	1 (M)		Samui Island	Surat Thani	9.579778	100.001472	22/1/2015	MH197132
21286	2 (1F, 1M)		Tao Island	Surat Thani	10.079873	99.860721	6/7/2012	
21272	1 (F)		Talet Bay	Nakhon Sri Thammarat	9.315936	99.779896	24/12/2019	
30198	1 (W)		Sakom Beach	Songkhla	6.96539	100.84484	29/12/2014	MH197133
30199	1 (W)		Sakom Beach	Songkhla	6.96539	100.84484	29/12/2014	
21287	20 (10F, 6M, 4W)		Samila beach	Songkhla	7.21851	100.59807	6/1/2012	
21270	20 (14F, 4M, 2W)		Narathat Beach	Narathiwat	6.451268	101.843892	9/1/2020	

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