

***Philinopsis gigliolii* (Gastropoda: Heterobranchia: Aglajidae) from the Sea of Japan: validity, synonymy, and biogeography**

E.M. Chaban¹, I.A. Ekimova^{2*}, A.V. Chernyshev³

¹ Marine Research Laboratory, Zoological Institute, Russian Academy of Sciences, Universitetskaya emb. 1, St. Petersburg 199034 Russia.

² Invertebrate Zoology Department, Lomonosov Moscow State University, Leninskie gori 1-12, Moscow 119234 Russia.

³ A.V. Zhirmunsky National Scientific Center of Marine Biology, Far Eastern Branch, Russian Academy of Sciences, Palchevskogo str. 17, Vladivostok 690041 Russia.

* Corresponding author

Elena Chaban echaban@zin.ru ORCID 0000-0002-3433-5736

Irina Ekimova irenekimova@gmail.com ORCID 0000-0002-1846-0780

Alexey Chernyshev nemertea1969@gmail.com ORCID 0000-0002-2203-3001

ABSTRACT: *Philinopsis gigliolii* (Tapparone Canefri, 1874) was described under the name *Aglaja gigliolii* based on preserved material from the Pacific coast of Japan, collected during an expedition of the Italian warship *Magenta* in 1864–1868. Currently, this species is considered a subjective synonym of *P. speciosa* Pease, 1860, described from Hawaii, despite their morphological differences. To clarify the species status of *P. gigliolii* we have conducted a molecular phylogenetic analysis of the genus *Philinopsis* using COI, 16S, and histone H3 molecular markers, which included a specimen of *P. gigliolii* from Peter the Great Bay, the Sea of Japan. Our results confirm that *P. gigliolii* represents a distinct valid species, which shows both morphological and molecular differences with *P. speciosa*. The latter species is recovered paraphyletic and clearly needs further taxonomical revision. At the same time, the molecular analysis indicates that Australian species *P. taronga* (Allan, 1933) is conspecific to *P. gigliolii* (only two molecular substitutions were identified in 16S), and these species show many similarities in both external and internal morphology. We consider *P. taronga* a junior subjective synonym of *P. gigliolii*. Formally *Chelidonura aureopunctata* Rudman, 1968, described from New Zealand, is considered a junior subjective synonym of *P. gigliolii* as well. *Philinopsis gigliolii* has an antitropical distribution, its range includes subtropical and temperate areas of the Pacific Ocean in both hemispheres (the Sea of Japan, the Yellow Sea, the Pacific coast of Japan; South-East Australia and the northern coast of New Zealand). Three hypotheses may explain this distribution pattern. (1) The antitropical distribution results from the historical disjunction across tropical latitudes following the abiotic or biotic factors. (2) *Philinopsis gigliolii* may be widely distributed in temperate and tropical waters of the Pacific Ocean but be overlooked in the central part of its geographic range due to external similarities to other species of the genus. (3) The last hypothesis suggests the anthropogenic transportation of *P. gigliolii*. Further sampling activity and comparative genetic analyses may contribute to a better understanding of this very interesting biogeographic pattern.

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KEY WORDS: Mollusca, Cephalaspidea, North-West Pacific, morphology, taxonomy, integrative analysis.

***Philinopsis gigliolii* (Gastropoda: Heterobranchia: Aglajidae) из Японского моря: валидность, синонимия и биогеография**

Е.М. Чабан¹, И.А. Екимова^{2*}, А.В. Чернышев³

¹ Лаборатория морских исследований, Зоологический институт Российской академии наук, Университетская наб. 1, Санкт Петербург, 199034 Россия.

² Кафедра зоологии беспозвоночных, Московский государственный университет им. М.В. Ломоносова, Ленинские горы 1-12, Москва, 119234 Россия.

³ Национальный научный центр морской биологии им. А.В. Жирмунского Дальневосточного отделения Российской академии наук, ул. Пальчевского 17, Владивосток, 690041 Россия.

* Автор для корреспонденции: irenekimova@gmail.com

РЕЗЮМЕ: *Philinopsis gigliolii* (Tapparone Canefri, 1874) был описан как *Aglaja gigliolii* по фиксированному материалу, собранному у тихоокеанского побережья Японии во время экспедиции на итальянском военном корабле «Маджента» в 1864–1868 гг. В настоящее время этот вид считается младшим субъективным синонимом *P. speciosa* Pease, 1860, описанного с Гавайских островов, несмотря на их морфологические различия. Для уточнения таксономического статуса *P. gigliolii* мы провели молекулярно-филогенетический анализ рода *Philinopsis*, включая экземпляр *P. gigliolii* из залива Петра Великого Японского моря, с использованием трех молекулярных маркеров, представляющих частичные фрагменты цитохром с оксидазы субъединицы I (COI), 16S rRNA и гистона H3 (H3). Наши результаты подтверждают, что *P. gigliolii* представляет собой валидный вид, который имеет молекулярные и морфологические отличия от *P. speciosa*. Последний вид признан парафилетическим и явно нуждается в дальнейшей таксономической ревизии. В то же время молекулярный анализ показывает, что австралийский вид *P. taronga* (Allan, 1933) конспецифичен *P. gigliolii* (в 16S выявлены всего 2 молекулярные замены), и эти виды обнаруживают большое сходство как во внешней, так и во внутренней морфологии. Мы считаем *P. taronga* младшим субъективным синонимом *P. gigliolii*. Формально, *Chelidonura aureopunctata* Rudman, 1968, описанную из побережья Новой Зеландии, также следует считать младшим субъективным синонимом *P. gigliolii*. *Philinopsis gigliolii* имеет антитропическое распространение: его ареал включает субтропические и умеренные районы Тихого океана в обоих полушариях (Японское и Желтое моря, тихоокеанское побережье Японии; юго-восточная Австралия и северное побережье Новой Зеландии). Три гипотезы могут объяснить такую картину распределения: 1) антитропическое распределение является результатом исторического разделения ареала через тропические широты как следствие действия абиотических или биотических факторов; 2) *Philinopsis gigliolii* может быть широко распространен в тропических и умеренных водах Тихого океана, но не отмечен в центральной части ареала из-за внешнего сходства с другими видами рода; 3) последняя гипотеза предполагает антропогенный перенос *P. gigliolii*. Дополнительный сбор образцов и дальнейший генетический анализ могут способствовать лучшему пониманию этой очень интересной биогеографической модели.

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КЛЮЧЕВЫЕ СЛОВА: Mollusca, Cephalaspidea, северо-западная Пацифика, морфология, таксономия, интегративный анализ.

Introduction

Heterobranch sea slugs of the family Aglajidae typically represent colorful and active predators (Rudman, 1972a; Yonow, 1992; Malaquias, 2014; Zamora-Silva, Malaquias, 2016). Commonly the radula and gizzard plates are absent, the shell is internal, fragile, and reduced, and rarely used in species identification (Rudman, 1972b; Gosliner, 2011, 2015; Cooke *et al.*, 2014). As an exception, the recently described genus *Philinissima* Chaban, Ekimova, Lubin, Nikitenko et Schepetov, 2023 (Chaban *et al.*, 2023) has a well-developed external shell. Traditional taxonomical studies of the family Aglajidae were primarily based on the features of coloration, external morphology, and the morphology of digestive and reproductive systems (Rudman, 1972b, 1974, 1978; Gosliner, 2011, 2015). At the same time, molecular phylogenetic data has a crucial importance for the development of the alpha-taxonomy of the group (Camacho-García *et al.*, 2014). For instance, molecular phylogenetic analysis of the genus *Melanochlamys* Cheeseman, 1881 identified new cryptic species (Cooke *et al.*, 2014). Currently, the family Aglajidae comprises 17 genera (Zamora-Silva, Malaquias, 2018; Chaban *et al.*, 2022, 2023) and most of them are still pending a modern integrative revision. Among the most problematic taxa, the genus *Philinopsis* Pease, 1860 includes 15 species (Zamora-Silva, Malaquias, 2018), most of which are distributed in tropical and subtropical waters. One species, *Philinopsis gigliolii* (Tapparone Canefri, 1874) has its northern range border in the temperate waters of the Sea of Japan (Peter the Great Bay) and represents a single species of the genus *Philinopsis* recorded for Russian seas (Chaban, Martynov, 1998, 2006, 2013; Chaban, Chernyshev, 2017). At the same time, the species identity of *P. gigliolii* has been questioned recently. It was considered a subjective synonym of *P. speciosa* Pease, 1860 due to similarities in molecular data (Zamora-Silva, Malaquias, 2018), although these two species demonstrate several differences in copulatory organs (Rudman, 1972b). This conflict of molecular and morphological data needs further clarification.

The main goal of the present work is to revise the taxonomical status of *P. gigliolii* based on an integrative analysis of specimens from Peter the Great Bay (the Sea of Japan, Russia).

Material and methods

COLLECTION DATA. Material of *Philinopsis gigliolii* used in this study was collected in Peter the Great Bay, western part of the Sea of Japan: 1) Vostok Bay in the vicinity of the Vostok Marine biological station, National Scientific Centre of Marine Biology, one sample was fixed in 96° EtOH and stored at −18 °C to prevent DNA degradation, and two specimens were fixed in 70° EtOH; 2) in Posyet Bay, samples were fixed in 70° EtOH. The examined specimens are stored at the Zoological Institute, St. Petersburg, Russia (ZIN) and at the Museum of the National Scientific Center of Marine Biology, Vladivostok, Russia (MIMB).

MORPHOLOGICAL METHODS. The external morphology of the studied material was photographed with the help of a digital camera Olympus Pen3. Shells and penial morphology were photographed using a digital DCM-130 camera with the Scope Photo 3.0 software.

MOLECULAR METHODS. For molecular phylogenetic analysis, three molecular markers representing partial fragments of *cytochrome c oxidase subunit I* (COI), 16S rRNA, and *histone H3* (H3) were amplified and sequenced for a single specimen available for the analysis. Total genomic DNA was extracted from tissue sample following the invertebrate protocol of the Canadian Center for DNA Barcoding (Ivanova *et al.*, 2006). Polymerase chain reactions were performed with an “HS Taq” kit (Eurogen Lab, Russia), following the manufacturer’s protocol. Reaction conditions and primers were described in details in previous studies (Chaban *et al.*, 2019b, 2022) and are also available in Table S1.

For sequencing, 1 µL of successful amplicons were purified by EtOH + Ammonium acetate precipitation (Osterburg *et al.*, 1975) and used as a template for the sequencing reactions with a NovaDye Terminator sequencing kit by GeneQuest. Sequencing reactions were analyzed using an ABI 3500 Genetic Analyser (Applied Biosystems). All novel sequences were submitted to NCBI GenBank (Table 1).

DATA PROCESSING AND PHYLOGENETIC RECONSTRUCTION. All raw reads for each gene were assembled and checked for ambiguities and low-quality data in Geneious R10 (Kearse *et al.*, 2012). Edited sequences were verified for contamination using the BLAST-n algorithm run over the GenBank nr/nt database (Altschul *et al.*, 1990). For the phylogenetic reconstruction, sequences of the genus *Philinopsis* available in the public database (GenBank) were added to the dataset (Table 1). Two species of the genus *Tubulophilinopsis* Zamora-Silva et Malaquias, 2017, *Ossiania quadrata* (S.V. Wood, 1839), and *Diaphana globosa* (Lovén, 1846) were chosen as the closest and distant outgroups accordingly (Zamora-Silva, Malaquias, 2018). Original data and publicly available sequences were aligned with the MUSCLE

Table 1. Specimens used for phylogenetic analysis.
Таблица 1. Экземпляры, использованные для филогенетического анализа.

Taxa	Voucher	Collection site	GenBank accession numbers		
			16S	COI	H3
<i>Tubulophilinopsis gardineri</i> (Eliot, 1903)	ZMBN95944	Australia	MF036412	MF036564	MF036667
<i>T. pilsbryi</i> (Eliot, 1900)	ZMBN95948	Australia	MF036416	MF036569	MF036670
<i>Philinopsis cyanea</i> (Martens, 1879)	CAS097543	Ecuador	JN825131	JN825189	JN825059
<i>P. giglioli</i> (Tapparone Canefri, 1874)	ZIN 63720/8	Russia, Sea of Japan	PP379058	PP379198	PP389021
<i>P. depicta</i> (Renier, 1807)	ZMBN94031	Italy	MF036397	–	–
<i>P. depicta</i>	E17	Spain	AM421831	AM421892	–
<i>P. pusa</i> (Ev. Marcus et Er. Marcus, 1966)	ZMBN95958	Bahamas	–	MF036552	MF036654
<i>P. pusa</i>	LACM173220	Bahamas	JN825144	JN825199	JN825072
<i>P. pusa</i>	LACM173221	Bahamas	JN825145	JN825200	JN825073
<i>P. pusa</i>	CAS175669	Bahamas	JN825143	JN825197	JN825071
<i>P. pusa</i>	CAS175770	Bahamas	–	JN825198	JN825070
<i>P. speciosa</i> Pease, 1860	ZMBN95967	Hawaii	MF036400	MF036555	MF036657
<i>P. speciosa</i>	ZMBN95997	Okinawa	MF036404	MF036558	MF036661
<i>P. speciosa</i>	ZMBN95995	Okinawa	MF036403	MF036557	MF036660
<i>P. speciosa</i>	ZMBN95951	Australia	MF036401	–	MF036658
<i>P. speciosa</i>	CAS175648	Papua New Guinea	JN825146	JN825201	JN825074
<i>P. taronga</i> (J.K. Allan, 1933)	KO2	Australia, Victoria	MF036405	–	–
<i>P. taronga</i>	KO6	Australia, Victoria	MF036406	–	MF036662
<i>Ossiania quadrata</i> (S.V. Wood, 1839)	ZMBN88012	Norway	JX022793	KJ022793	KJ022952
<i>Diaphana globosa</i> (Lovén, 1846)	ZMBN88018/ isolate_CN27	Norway	KJ022791	KF992162	KJ022930

(Edgar, 2004) algorithm in MEGA 7 (Kumar *et al.*, 2016). Additionally, all protein-coding sequences were translated into amino acids to verify reading frames and check for stop codons. Saturation was checked by plotting for all specimens including outgroup the total number of pairwise differences (transitions and transversions) against uncorrected *p*-distances. Phylogenetic reconstructions were conducted for the concatenated multi-gene partitioned datasets. The best-fit nucleotide evolution models were selected in MEGA 7 (Kumar *et al.*, 2016): GTR+G+I for the COI and 16S partitions, and K80+G for the H3 partition. Multi-gene analyses were done by applying evolutionary models separately to partitions representing single markers. The Bayesian phylogenetic analyses and estimation of posterior probabilities were performed in MrBayes 3.2 (Ronquist, Huelsenbeck, 2003). Markov chains were sampled at intervals of 500 generations. The analysis was initiated with a random starting tree and ran for 3×10^6 generations. Convergence was checked

in TRACER 1.7.1 (Rambaut *et al.*, 2018) with a 10% burn-in. Maximum likelihood phylogeny inference was performed in the HPC-PHREADS-AVX option of RaxML HPC-PHREADS 8.2.12 (Stamatakis, 2014) with auto-bootstrapping option. Bootstrap values were placed on the best tree found with SumTrees 3.3.1 from DendroPy Phylogenetic Computing Library 3.12.0 (Sukumaran, Holder, 2010). Final phylogenetic tree images were rendered in FigTree 1.4.0 and further modified in Adobe Illustrator CS 2015.

SPECIES DELIMITATION. To confirm the status of recovered clades as putative candidate species we tested the molecular species delimitation analysis ASAP (Assemble Species by Automatic Partitioning, Puillandre *et al.*, 2021). ASAP was run for the COI alignment using the online version of the program (<https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html>, accessed on 17 February 2024) with the Kimura 2-parameter model and other settings remained default.

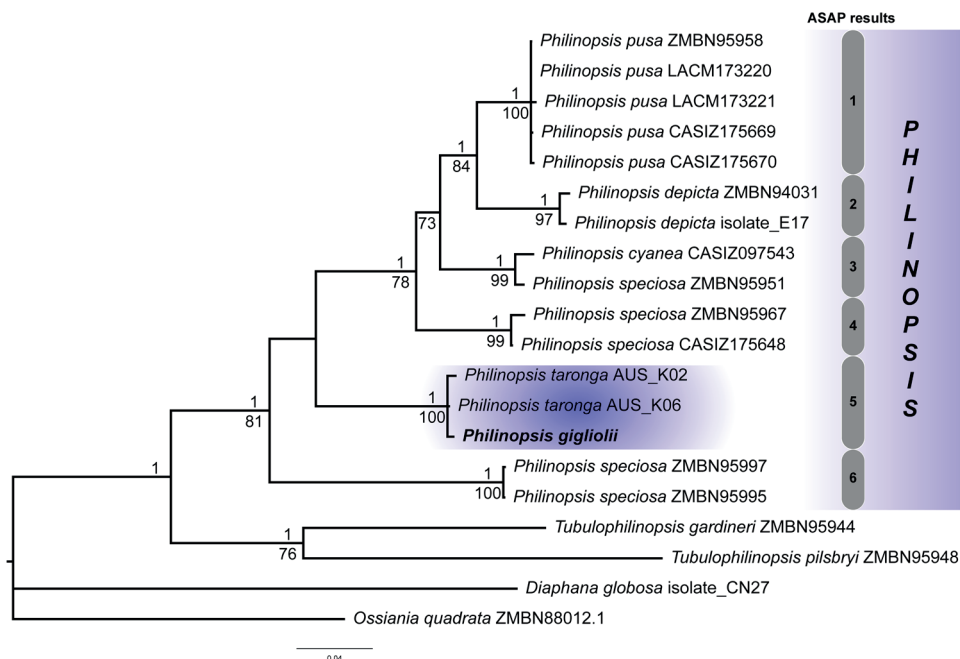


Fig. 1. Molecular phylogenetic hypothesis of the genus *Philinopsis*, Bayesian Inference, concatenated dataset of three markers (COI + 16S + H3). Numbers above branches indicate posterior probabilities from Bayesian Inference (only values higher 0.9 are shown), and numbers below branches – bootstrap support from Maximum Likelihood (only values higher 60 are shown). The results of ASAP analysis are given on the right.

Рис. 1. Молекулярно-филогенетическая гипотеза отношений рода *Philinopsis*, построенная по данным комбинированного датасета трех маркеров (COI + 16S + H3) с применением Байесовского анализа. Цифры над ветвями обозначают апостериорные вероятности (PP) Байесовского анализа (показаны только значения PP > 0,9), цифры под ветвями — бутстреп-поддержки (BS) метода Максимального правдоподобия (показаны только значения BS > 60).

Results

MOLECULAR PHYLOGENY. The molecular phylogenetic analysis based on three molecular markers (COI, 16S, H3) revealed similar topologies of the phylogenetic trees reconstructed with a help of the Maximum likelihood analysis (ML) and the Bayesian inference (BI) (Fig. 1). The genus *Philinopsis* was recovered as monophyletic with a high support in both ML and BI (posterior probabilities from BI (PP) = 1; bootstrap support from ML (BS) = 81). Within it, *Philinopsis gigliolii* formed a single species-level clade with Australian species *P. taronga* (Allan, 1933) (PP = 1; BS = 100). Type species of the genus, *P. speciosa*, formed three distinct clades: (1) ZMBN95967 from Hawaii (type locality) and CASIZ175648 from Papua New Guinea (PP = 1; BS = 99), (2) ZMBN95997 and ZMBN95995 from Okinawa (PP = 1; BS = 100) and (3) ZMBN95951 from Australia and *P. cyanea* CASIZ097543 from Ecuador (PP = 1; BS = 99). Two other studied species, *P. pusa* (Ev. Marcus et Er. Marcus, 1966) and

P. depicta (Renier, 1807) formed two distinct clades (PP = 1; BS = 97–100) with sister relationships (PP = 1; ML = 84). Overall, our molecular phylogenetic analysis supported the separate species status of *P. gigliolii* as a distinct species from *P. speciosa*. At the same time it provided evidence that *P. taronga* and *P. gigliolii* represent a single species. This result was supported by the ASAP analysis. It suggested six candidate species, which fully corresponded the six reciprocal monophyletic clades recovered in the molecular phylogenetic analysis based on the concatenated dataset (Fig. 1).

Systematics

Order Cephalaspidea
 Family Aglajidae Pilsbry, 1895 (1847)
Philinopsis Pease, 1860
Philinopsis gigliolii
 (Tapparone Canefri, 1874)
 Figs 1–3.

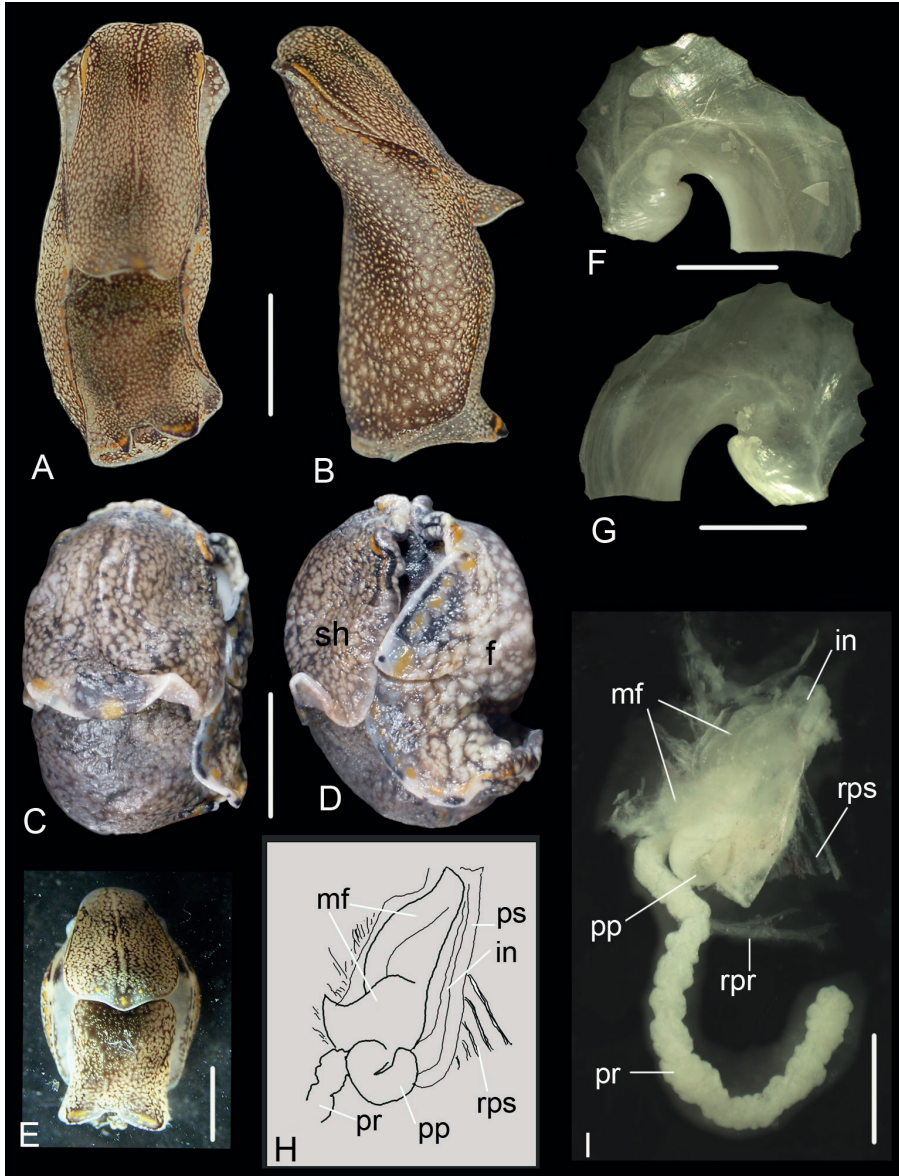


Fig. 2. *Philinopsis gigliolii*. A–D, E — specimens from the Vostok Bay, the Sea of Japan (A, B — photographs of a live specimen; C, D — photographs of a fixed specimen; E — subadult living specimen). F–G — shell (F — dorsal view, G — ventral view). H–I — a copulatory complex (H — drawing, the prostate is shown incompletely).

Abbreviations: sh — cephalic shield; f — foot; in — incurrent seminal duct; mf — muscle fold; ps — penial sac; pp — penial papilla; pr — prostate; rpr — retractor of prostate; rps — retractor of penial sac. Scale bars: A, B — 10 mm; C, D — 5 mm; E — 2 mm; F, G, I — 1 mm.

Рис. 2. *Philinopsis gigliolii*. A–D, E — экземпляры из залива Восток Японского моря (A, B — фотографии живой особи; C, D — фотографии фиксированного экземпляра; E — неполовозрелый живой экземпляр). F–G — раковина (F — дорсально, G — вентрально). H–I — копулятивный аппарат (H — рисунок, простата показана не полностью).

Обозначения: sh — головной щит; f — нога; in — внутренняя семенная борозда; mf — мышечная складка; ps — мешок пениса; pp — пениальная папилла; pr — простата; rpr — ретрактор простаты; rps — ретрактор мешка пениса. Масштаб: A, B — 10 мм; C, D — 5 мм; E — 2 мм; F, G, I — 1 мм.

Aglaja gigliolii Tapparone Canefri, 1874: 110–111, pl. I, fig. 48.

Aglaja gigliolii: Pilsbry, 1895-1896: 50, pl. 1, fig. 6; Golikov, Scarlato, 1967: 82, fig. 71.

Doridium gigliolii: Abe, 1964: 19, pl. 1, fig. 4; Habe, 1964: 140, pl. 43, fig. 24.

Philinopsis gigliolii: Rudman, 1972b: 390; Lin Guangyu *et al.*, 1986: 27; Chaban, Martynov, 1998: 147–150, fig. 1A–C; 2006: 253, pl. 125, figs G–H; Chernyshev, 2007: 148–149, photo 164; Chaban, Chernyshev, 2017: 45–46, pl. 2, figs A, B.

Doridium depictum var. *minor*: Tchang Si, 1934: 49, figs 25–31, pl. 2, figs 1–3, pl. 3, figs 7–8, pl. 10, 11 — syn. Chaban, Martynov, 1998.

Philinopsis minor: Rudman, 1972b: 396.

Aglaja taronga J.K. Allan, 1933: 444, pl. LVI figs 1–3 — **syn.n.**

Philinopsis taronga: Rudman, 1972b: 381, 391, figs 2–4, 6, 10, 11, 13B, 14C–D — **syn.n.**

Chelidonura aureopunctata Rudman, 1968: 211, figs 1A–C, 2A–C — **syn.n.**

TYPES. Not traced.

TYPE LOCATION. “Regione Giapponese” (Tapparone Canefri, 1874: 156) (most probably, Yokohama, see Chaban, Martynov, 2006).

MATERIAL EXAMINED. Sea of Japan. ZIN 23633/1, Posyet Bay, Vityaz Bay, July 1962, at 5 m depth, clay silt, collected by L.V. Mikulich, 1 specimen, dissected. ZIN 63720/8, Vostok Bay, Tikhaya Zavod’ Bay, ~3 m depth, 24.06.2005, collected by A.V. Chernyshev, 1 specimen. Vostok Bay, Tikhaya Zavod’ Bay, ~2–3 m depth, 19.07.2008, collected by A.V. Chernyshev, 2 specimens, MIMB, uncatalogued.

DIAGNOSIS. Body brown or blackish, covered with white spots; headshield, parapodia, and posterior shield bordered by a broken yellow line. Shell thin, its convex plate consisting of central relatively strong half-circled area and thinner periphery. Male copulatory system consists of large penial sac and long thin prostate. Penial sac with large flat muscular flap and short thick convoluted penial papilla.

DESCRIPTION. Preserved specimens up to 11.5 mm in length, short and thick; cephalic shield without tentacles; its posterior edge with rounded tips. Foot wide, long, anterior edge with small lateral outgrowths; its posterior edge reaches posterior mantle lobes. Posterior mantle lobes small, equal in size. Body covered with small white spots. Edges of foot, posterior mantle lobes and posterior edge of cephalic shield with small orange spots.

In living specimens body elongated, almost rectangular, up to 37 mm in length (Fig. 2A, B). Cephalic shield ca. ½ of body length, with almost straight anterior edge and parallel lateral edges, rounded tip of posterior edge. This pointed crest raised while animal moving (Fig. 2B) and clearly seen in subadult specimen (Fig. 2E). Parapodia well developed, but not reaching midline of body. Body brown, covered with white spots. Cephalic shield with white median line and anterior-lateral orange lines. Edges of foot,

posterior mantle lobes and posterior edge of cephalic shield with small orange spots.

Shell internal, thin, calcified, white, covered with yellowish periostracum (Fig. 2F, G). Its convex plate consisting of central relatively strong half-circled area and thinner periphery.

Radula, jaws and gizzard plates absent. Buccal bulb large, capable of partial eversion.

Male copulatory system (Fig. 2H, I) consists of large penial sac and long thin prostate. Prostate opening distally into penial sac. Penial sac with large flat muscular flap and short thick convoluted penial papilla. Ciliated incurrent sperm groove running from sac opening down to opening of prostate. Flap attached to penial sac along the incurrent sperm groove. Penial sac attached to body wall with several parallel muscle beams and prostate with a single muscle beam.

GEOGRAPHIC RANGE (Fig. 3). The North-West Pacific: Pacific coast of Kyushu Is. and Honshu Is., where this species is “rather common among eel grass below the tide mark in bays” (Habe, 1964: 140); the Sea of Japan (Toyama Bay, Japan (Abe, 1964)), including Posyet Bay (Chaban, Martynov, 1998), Vostok Bay, Peter the Great Bay (Chaban *et al.*, 2003; Rudman, 2003; Chaban, Chernyshev, 2017). The Yellow Sea: Qingdao Bay (Tchang Si, 1934, as *Doridium depictum* var. *minor*) and Yantai Bay (Chaban, Martynov, 1998). South-East Australia and the North of New Zealand (Rudman, 1972b as *Philinopsis taronga*).

BIOLOGY. In the Sea of Japan this species was collected at a depth of 2–5 m, and sporadically found at 8–10 m in semi-closed bays of the Peter the Great Bay on sand and silty soil, where it eats *Cylichnatis angusta* (Gould, 1859) (Chaban, Martynov, 1998; Chaban, Chernyshev, 2017, this study). On the Pacific coast of Japan, it was collected on silty soil between *Zostera nana* (Rudman, 1972b). In the Yellow Sea, this species inhabits silty-sand soil at a depth of 8 m in Qingdao Bay (Tchang Si, 1934), and on stone littoral below an oyster belt (Chaban, Martynov, 1998). In Australia and north New Zealand *P. gigliolii* was collected at a depth of 2–3 m burrowing in mud (Allan, 1933; Rudman, 1998).

REMARKS. A detailed description of the morphology of *Philinopsis gigliolii* was presented by Rudman (1972b, as *P. gigliolii* and *P. taronga*), Tchang Si (1934, as *Doridium depictum* var. *minor*), and Chaban & Martynov (1998).

Discussion

TAXONOMY OF *PHILINOPSIS GIGLIOLII*. *Philinopsis gigliolii* was described under the name *Aglaja gigliolii* based on preserved material, collected during an expedition of the Italian warship *Magenta* in 1865–1868 off Japan,

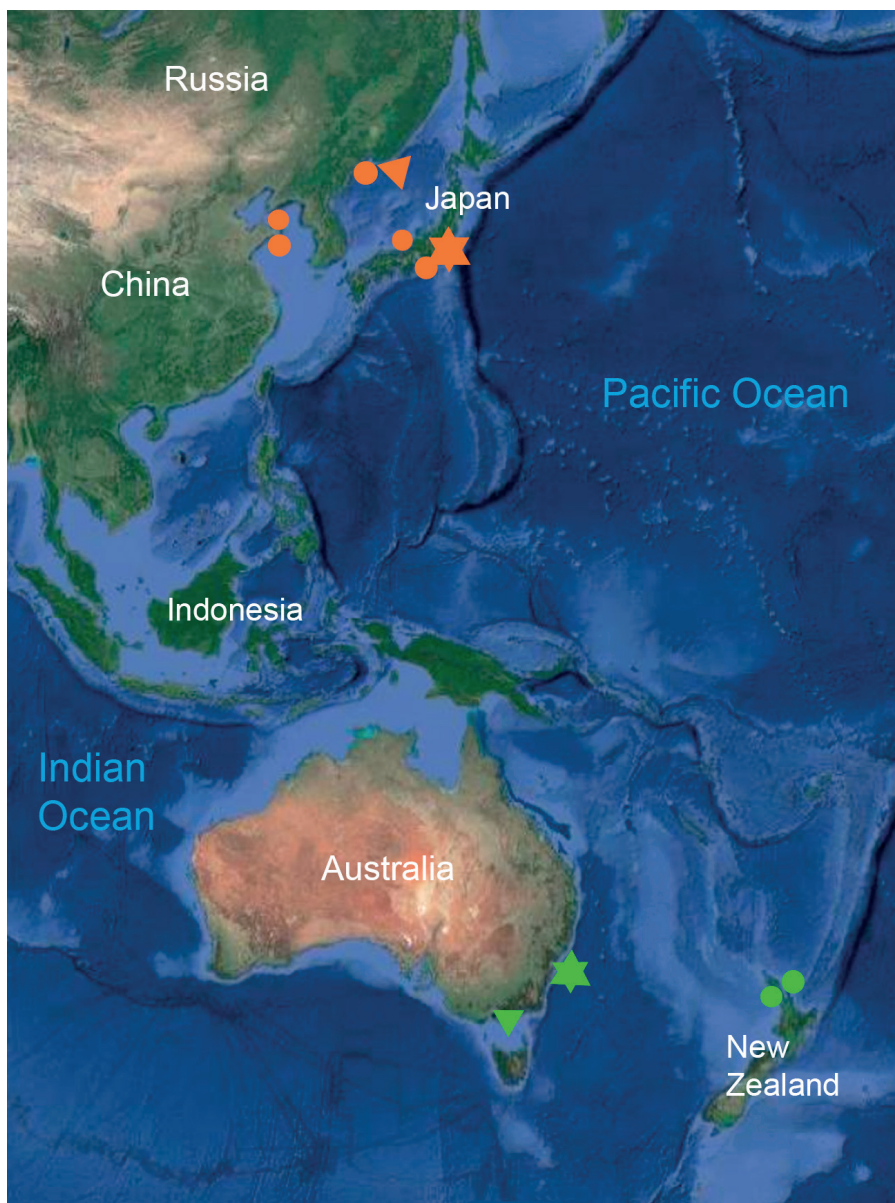


Fig. 3. Map of distribution of *Philinopsis gigliolii*. The North-West Pacific, where the species was known as *P. gigliolii* (the Sea of Japan, the Yellow Sea, Pacific coast of Japan), localities are marked in orange. The South-West Pacific, where the species was known as *P. taronga* (South-East Australia, the North of New Zealand), localities are marked in green. The type localities *P. gigliolii* and *P. taronga* are designated with a polygon. The localities of sequenced specimens are designated with a triangle. Data are seen in the text.

Рис. 3. Карта распространения *Philinopsis gigliolii*. В Северо-Западной Пацифике вид был известен как *P. gigliolii* (Японское море, Желтое море, Тихоокеанское побережье Японии), места находок отмечены оранжевым цветом. В Юго-Западной Пацифике вид был известен как *P. taronga* (Юго-Восточная Австралия, север Новой Зеландии), места находок отмечены зеленым цветом. Типовые местонахождения *P. gigliolii* и *P. taronga* обозначены многоугольниками. Места сборов секвенированных экземпляров обозначены треугольниками. Данные сборов указаны в тексте.

presumably near Yokohama (Chaban, Martynov, 2006). The original description is short, noting that the length of the body is 32 mm, the cephalic and mantle shields with short, paired appendages, and the coloration is “*un bianco sudicio e giallognolo... reticolato di fosco e di cenerino o turchiniccio*” [a dirty white and yellowish... reticulated of dark and ash or blue] (Tapparone Canefri, 1874: 111). It was also indicated that the internal morphology of this species is similar to that of *Acera carnosa* (Cuvier, 1810) (= *Philinopsis depicta*). This description fully corresponds to the morphology of specimens from Peter the Great Bay (Chaban, Martynov, 1998). The living coloration was described for specimens from Japan: “*Yellow dots speckle the surface, and the headshield, parapodia, and posterior shield are bordered by a broken yellow line*” (Rudman, 1972b: 390). Studied specimens from Vostok Bay have similar coloration (Chaban *et al.*, 2003; Rudman, 2003; Fig. 2A, B, E), and the yellowish pigmentation remains in fixed material for some time (Fig. 2C, D). The morphology of copulatory organs in *P. gigliolii* from Osaka Bay, Japan (Rudman, 1972b), and the northwestern Sea of Japan (this study) is similar.

COMPARATIVE MORPHOLOGY OF *PHILINOPSIS GIGLIOLII* AND *PHILINOPSIS TARONGA*. *Philinopsis taronga* was described as a member of the genus *Aglaja* Renier, 1807, based on a single specimen (holotype, deposited in the Australian Museum, Sydney). It was collected on the eastern Australian coast (Athol Bay, Sydney Harbour) from a depth of 3 m (Allan, 1933). The holotype of *P. taronga* is a large specimen, 65 mm in length. The color of the animal in life was rich velvety dark brown, with sometimes a bluish bloom over it. Edges of the cephalic shield have a distinct yellow-orange line, the posterior point of the cephalic shield with a small orange spot on the apex. A broad band of orange was on each side of the tail lobes. Over the whole-body surface patches of small creamy-white splashes were scattered (Allan, 1933). Rudman noted that the coloration may vary overall, but this patchy pattern is characteristic of *P. taronga* (see Rudman, 1998). The same pattern is found in *P. gigliolii* (Chaban *et al.*, 2003; this study). These two species show considerable similarities in internal morphology as well. Rudman concluded the lack of differences between these two species, he noted: “... this species [*P. taronga*]

has a great similarity to *P. gigliolii*”, and “More extensive collecting may show that *P. gigliolii*, from the northern limit of the western Pacific, and *P. taronga*, from the southern extreme, may be variations of one species” (Rudman, 1972b: 391). Our molecular phylogenetic analysis supported these two species are conspecific (Fig. 1) and thus we designate *P. taronga* as a subjective synonym of *P. gigliolii*.

Chelidonura aureopunctata described from New Zealand was designated as a synonym of *P. taronga* due to similarities in both external and internal morphology (Rudman, 1972b). Thus, we also consider this species as a subjective synonym of *P. gigliolii*.

COMPARATIVE MORPHOLOGY OF *PHILINOPSIS GIGLIOLII* AND *PHILINOPSIS SPECIOSA*. *Philinopsis speciosa* was described from Hawaii based on specimens collected among seaweed on the coral reefs (Pease, 1860). The original description includes only the shell morphology, external features and coloration, but no illustration was provided. The shell is “*concealed in the truncated end, white, thin, fragile, pellucid, subtriangular, with a curved callous apex; surface with furrows of growth*” (Pease, 1860: 21). Although the morphology of fragile and thin shells is not very useful for species identification of *Philinopsis* species, in the case of *P. speciosa* the shell is subtriangular, and thus it differs from rounded shells of both *P. gigliolii* (this study) and *P. taronga* (Allan, 1933). The coloration of *P. speciosa*, initially described by Pease (1860), was further specified by Rudman (1972b), based on the material from the type locality. Rudman (1972b) identified two color morphs of this species. The dark-brown morph has a blue edge of parapodia with distinct yellow spots (Rudman, 2006: Upper photo). This morphotype is similar in coloration to *P. cyanea* (Martens, 1879), which is now considered a junior synonym of *P. speciosa* (Zamora-Silva, Malaquias, 2018). The light morph has numerous light-colored patches overlaying and partly masking yellow spots, but overall, this coloration pattern resembles that in *P. taronga* and *P. gigliolii* (Rudman, 2006: lower photo). Perhaps a similar color pattern has led to the initial identification of two *Philinopsis* specimens belonging to one species from Okinawa as *P. cyanea* (ZMBN95997) and *P. gigliolii* (ZMBN95995) (see Zamora-Silva, Malaquias, 2018). This was

a reason for further synonymizing of *P. gigliolii* and *P. speciosa*. Our results clearly show that *P. gigliolii* and *P. speciosa* represent more than two distinct species, which have considerably different copulatory system morphology. According to Rudman (1972b), in *P. gigliolii* the penial papilla is broad and short (as well as in our specimen, see Fig. 2H, I), but in *P. speciosa* it is long and narrow as in *P. troubridgensis* (Verco, 1909) (see Rudman, 1972b: 385, fig. 7A). In external morphology these two species differ in the position of yellow lines on anterior side of the cephalic shield: in *P. gigliolii* they are located laterally, and in *P. speciosa* they lay dorsally, in parallel to a midline (Rudman, 1972b, 2006). The molecular analysis also supports this result, as our specimens of *P. gigliolii* represent a distinct clade apart from *P. speciosa*, and the latter species is recovered paraphyletic and clearly needs further taxonomical revision.

DISTRIBUTION OF *PHILINOPSIS GIGLIOLII*. The current geographic range of *P. gigliolii* constitutes two distant regions (Fig. 3): 1) the North-West Pacific, from the Sea of Japan (Peter the Great Bay and Toyama Bay) to the Pacific coast of Japan and the Yellow Sea (Yantai and Qingdao Bay); and 2) South-East Australia and north of New Zealand. This range is similar to so-called antitropical distribution, where species inhabit subtropical waters in both hemispheres with a break in tropical equatorial parts (Hubbs, 1952). The phenomenon of antitropical distribution is well-known in the literature (see Ludt, 2021 for review). One of the main models to explain this phenomenon (glacial model) assumes that ancestors of antitropical species may have originated in the equatorial region during the cooler geological periods (e.g. cooling of the Oligocene, glacial cycles of the Pleistocene) and with consequent equatorial warming (e.g. mid-Miocene warming, Pleistocene interglacials) they became extinct in the tropical part of their range, which resulted in disjunction across tropical latitudes (Berg, 1933; Briggs, 1887a,b). Another explanation is the vicariance model, suggesting that suitable tropical habitats are predicted to reduce and be less continuous due to non-abiotic factors, resulting in prevention of species from residing in abiotically suitable tropical habitats today (Briggs, 1987a; Ludt, Myers, 2021). Regardless of the precise speciation mechanism, many

studies date the divergence between antitropical species back to the Pliocene or the Pleistocene (see Ludt, 2021 for review), but the intraspecific divergence dated back to the last 100,000 years was also shown (Tea *et al.*, 2019). The glacial nature of antitropical distribution may be also a case of *P. gigliolii*, although further sampling and population genetic studies are needed to confirm these hypotheses.

Taking into account the limited material available for our study, we may suggest two alternative hypotheses. Firstly, *P. gigliolii* may be widely distributed in temperate and tropical waters of the Pacific Ocean but be overlooked in the central part of its geographic range due to external similarities to other similar-looking species as *P. speciosa* and especially to *P. cyanea* Pease, 1860. The last species is widespread throughout the Indo-West Pacific, a species with similarities in colour to *P. gigliolii* (Rudman, 2006), but is considered as a junior synonym of *P. speciosa* (Zamora-Silva, Malaquias, 2018). Among heterobranchs sea slugs such a wide range is known for several aplysiids, e.g. *Bursatella leachii* de Brainville, 1817, this range is confirmed by molecular data (Bazzicalupo *et al.*, 2020). The second possibility is the anthropogenic transportation of *P. gigliolii*. There are several confirmed examples of anthropogenic transportation among heterobranch sea slug molluscs, including species that recently invaded Australia, e.g., *Bermudella pellucida* (Burn, 1967) (see Wells *et al.*, 2009); or highly invasive and globally distributed species, which is, however, absent in Australian waters at the moment (*Haloe japonica* Pilsbry, 1895) (Hanson *et al.*, 2013). At the same time, the anthropogenic hypothesis seems to be not highly likely as our specimens from the Sea of Japan and those from Australia show two substitutions in the mitochondrial 16S marker, suggesting some genetic divergence between these populations exists.

It should be also noted that possible antitropical distribution found for *P. gigliolii* is not exceptional among heterobranch sea slugs, but this issue has not received specific attention yet. There are only a few examples of interspecific (e.g. nudibranch genus *Felimare* Ev. Marcus et Er. Marcus, 1967, see Hoover *et al.*, 2017) and intraspecific [e.g. nudibranchs *Limacia ornata* (Baba, 1937), see Toms *et al.*, 2021; and *Anteaeolidiella cacaotica* (Stimpson, 1855),

see Carmona *et al.*, 2014] trans-equatorial disjunction available to date in heterobranch sea slugs' studies, but further sampling activity and comparative genetic analyses may contribute to the better understanding of this very interesting biogeographic pattern.

Supplementary data. The following materials are available online.

Table S1. Amplification and sequencing primers and PCR conditions.

Compliance with ethical standards

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

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