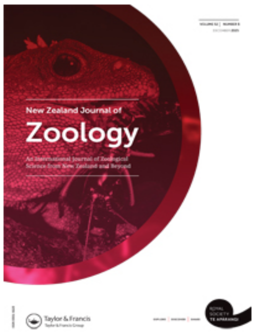

New Zealand Journal of Zoology

ISSN: 0301-4223 (Print) 1175-8821 (Online) Journal homepage: www.tandfonline.com/journals/tnzz20

Diversity of the ‘eerie’ glass squid genus *Taonius* Steenstrup, 1861 (Cephalopoda: Oegopsida) in the Pacific Ocean

Aaron Evans, Nancy Voss, Heather Braid, Tsunemi Kubodera & Kathrin Bolstad

To cite this article: Aaron Evans, Nancy Voss, Heather Braid, Tsunemi Kubodera & Kathrin Bolstad (2025) Diversity of the ‘eerie’ glass squid genus *Taonius* Steenstrup, 1861 (Cephalopoda: Oegopsida) in the Pacific Ocean, New Zealand Journal of Zoology, 52:5, 461-496, DOI: 10.1080/03014223.2024.2416207

To link to this article: https://doi.org/10.1080/03014223.2024.2416207

NEW ZEALAND JOURNAL OF ZOOLOGY
2025, VOL. 52, NO. 5, 461–496
https://doi.org/10.1080/03014223.2024.2416207

Taylor & Francis
Taylor & Francis Group

RESEARCH ARTICLE

OPEN ACCESS Check for updates

Diversity of the ‘eerie’ glass squid genus *Taonius* Steenstrup, 1861 (Cephalopoda: Oegopsida) in the Pacific Ocean

Aaron Evans[a], Nancy Voss[b], Heather Braid[a], Tsunemi Kubodera[c] and Kathrin Bolstad[a]

[a]AUT Lab for Cephalopod Ecology and Systematics (ALCES), Auckland University of Technology, Auckland, New Zealand; [b]Rosentstiel School of Marine, Atmospheric, and Earth Science, University of Miami, Key Biscayne, FL, USA; [c]National Museum of Nature and Science, Collection Center, Tsukuba, Japan

ABSTRACT
‘Glass’ squids (family Cranchiidae Prosch, 1849) are diverse and widely distributed, but many cranchiid genera are in need of global taxonomic revision. Although two species of *Taonius* are generally recognised from the Pacific Ocean (*T. belone* and *T. borealis*), a recent review of material from this basin has revealed the presence of at least six species, including at least four new to science, described here as *T. expolitus*, *T. notalia*, *T. robisoni*, and *T. tanuki*. Morphological species identities are supported by several characters, including arm sucker count, and arm and manus sucker dentition. Proposed species delimitations are further supported by differences in mitochondrial DNA (cytochrome *c* oxidase subunit I). Although a full systematic review of the Cranchiidae is still needed tripling the known diversity of *Taonius* in the Pacific Ocean and clarifying identities of its locally occurring species represent an important step forward.

ARTICLE HISTORY
Received 16 June 2024
Accepted 9 October 2024
First published online
3 December 2024

HANDLING EDITOR
Cor Vink

KEYWORDS
Taxonomy; systematics; integrative taxonomy; cephalopod; morphology; new species

Introduction

Representatives of the ‘eerie’ glass squid genus *Taonius* Steenstrup, 1861, have been known from the Atlantic and Pacific Oceans for more than 150 years. However, the systematics of this group remain notoriously unstable. Accurate understanding of these species’ biodiversity and zoogeography are important, both for characterising regional faunal assemblages, and because they can be key components of deep-sea trophic webs. For example, many cetaceans have been shown to feed on cranchiids, and the genus *Taonius* can constitute up to 35% of an individual’s diet (MacLeod et al. 2003); large individuals are also important prey for lancetfish (Chen et al. 2022). Yet distinguishing these species remains challenging (even when specimens are in good condition), and many ecological surveys identify *Taonius* only to the generic level.

Before the establishment of the Cranchiidae Prosch, 1849, species of this family were attributed to *Loligo* Lamarck, 1798, along with species that would later be moved to

CONTACT Kathrin Bolstad kathrin.bolstad@aut.ac.nz

several other genera and families. The earliest described species that would later be placed into *Taonius* was the type species, *Loligo pavo* Lesueur, 1821, from the western North Atlantic. Although the *L. pavo* description noted several useful characters, Lesueur did not mention the fusion between the head and mantle, an unusual feature for any squid species known at that time. His description focused on the elongated mantle and fins, as well as the large eyes protruding from a small head, a feature that was also emphasised by future authors. Unfortunately, Lesueur was not able to comment on the tentacular clubs and the ends of the arms, as these had been removed by the fishermen who provided the original specimen, a mature female. He described the tissues as being a mottled rusty brown colour, and illustrated a large egg mass protruding from the siphon (Lesueur 1821).

Several later authors recognised that *Loligo* was not the correct placement for *T. pavo* and attempted to resolve this. It was moved into *Loligopsis* d'Orbigny, 1845, (d'Orbigny, 1845), and later *Leachia* Lesueur, 1821, by Steenstrup (1861), who believed this to be the oldest available generic name for any squid with fusions at the head and mantle. Over the next few decades, new genera and species were erected as various authors attempted to provide some stability in the family Cranchiidae. Unfortunately, this profusion of names had the opposite effect, since many were proposed for specimens that ultimately proved to represent different growth stages of previously described taxa. Some of these nominal species were attributed to *Taonius*, and have since been synonymised with older names or moved to other cranchiid genera (see synonymies below).

Chun (1906) described the next new species that is still attributed to *Taonius*, although he placed it into a new genus, *Toxeuma* Chun, 1906. *Toxeuma belone* Chun, 1906, was described, from the Indian Ocean, as a slender squid with moderately stalked eyes that were elongated. Chun felt this differentiated it from *Taonius* because all known *Taonius*, at that time, had large, sessile eyes (Chun 1910). Chun's description of *T. belone* also lacked detail regarding the armature, a feature used in subsequent descriptions to distinguish it from other species found in the same region. Lane (1957) erected another new genus, *Belonella* Lane, 1957, for *T. belone* and this name replaced *Toxeuma* in the literature, as *Toxeuma* was an invalid junior homonym for an insect genus. Two further Pacific species were soon added to *Belonella*: *B. borealis* Nesis, 1972; and *B. pacifica* Nesis, 1972; the former is still considered a valid species, while the latter was synonymised with *Taonius belone* by Nesis in 1987. Voss (1980) considered *Belonella* a junior synonym of *Taonius* but upheld both *T. belone* and *T. borealis*, which are the two *Taonius* species now generally recognised from the Pacific basin. *Taonius borealis* was (and is still considered to be) distributed throughout the northern Pacific, throughout the waters of Japan, the Bering Sea, and the upper west coast of North America. *Taonius belone* is thought to occur throughout the central eastern Pacific as well as Indonesia and in the Indian Ocean (Young 2014b); however, the geographic distribution of this species is less well understood than that of *T. borealis*.

Lu and Clarke (1974) were the next to contribute to *Taonius* taxonomy (albeit inadvertently); they described what they believed to be a new species of *Galiteuthis, G. triluminosa*. The specimen was quite long and slender, and possessed unusual eye morphology: slightly stalked eyes, with three luminous organs on the ventral surface, and an unusual eye shape caused in part by their oblique upward orientation (Lu and Clarke 1974). Shortly thereafter, Young (1975) reported that *Taonius* species develop telescopic eyes as a transitional stage between paralarval and adult morphology, which enabled subsequent authors' recognition of '*G. triluminosa*' as a junior synonym of the known *T. belone* (= *T. belone*, *fide* Imber, 1978; Nesis, 1987; but see Remarks for *T.* cf. *belone*).

Taxonomic debate has continued through to the most recent studies. Voss's (1980) revision of the Cranchiidae placed *Belonella* into synonymy with *Taonius*, while Nesis' (1987) summary of the family retained *Belonella* as a valid genus. Nesis supported this choice by suggesting that autotomy of the tentacles was a distinguishing characteristic of *Taonius*, and due to this, he did not discuss the tentacle club armature. Although *Taonius* is largely believed to be the correct generic designation, *Belonella* has been maintained in some ecological reports (Arkhipkin 1996; Poltev 2007). It appears that a combination of molecular and morphological analyses is required to resolve the status of these genera and species.

Methods

Taxonomic conventions

Herein, many junior genus and species names are discussed, due to considerable historic systematic instability. When discussed, the senior name follows the junior name in parentheses, with an equal sign and the attributing author, e.g. *Loligopsis pavo* (=*Taonius pavo fide* Steenstrup, 1861). The synonymy for individual taxa is limited to previous taxonomic descriptions providing adequate morphological detail. In some instances, where previous literature lacked sufficient written detail, species identity could be confirmed based on the illustrations.

Fifty-one specimens were examined, mostly representing coastal areas, but also some more central regions of the Pacific Ocean (Figure 1). Specimens from the Southern Ocean and Antarctic waters were relatively scarce and no material from the eastern South Pacific was available. Some material could not be confidently identified due to either material condition, age, or size and is therefore excluded from systematic treatment.

Prior to examination, most specimens had been fixed in ~5–10% formalin and stored in 70–80% ethanol or ~40% isopropyl. Morphological measures and counts follow Roper and Voss (1983) with some modifications. Measurements and counts for symmetrical features (those appearing on both sides of the midline, e.g. arms, eyes) were taken from the more complete side of the specimen. Ranges of indices are provided in text as X–*Y*–Z, where X is the lowest observed value, *Y* is the mean, and Z is the highest observed value. If both sides of the specimen were equally damaged, a 'minimal estimation' value was taken and noted; however, these values were not included in the mean value calculation. Mean values were not calculated for sucker counts (on either arms or tentacle clubs) as the presence of suckers, particularly on the distal portion of the arms, varied due to damage.

Arm and tentacle club suckers were imaged using a traditional microscope or a scanning electron microscope (SEM) if available, after being critical-point dried and then sputter-coated in gold–palladium. Due to restrictions on destructive sampling, beaks and gladii could not be removed from most specimens housed in overseas collections.

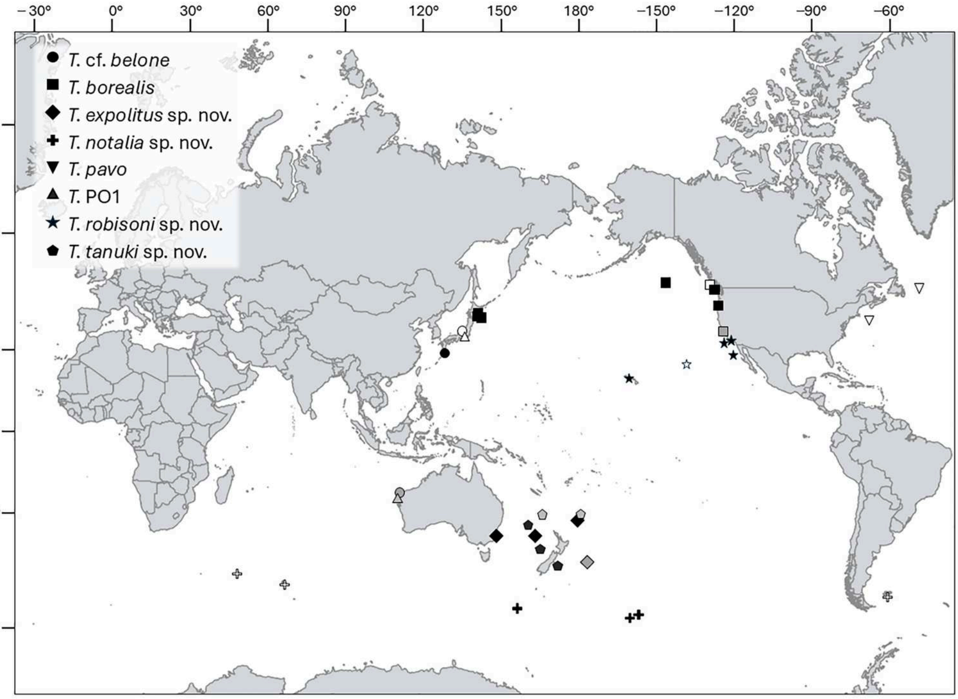

Figure 1. Distribution of examined *Taonius* material. Symbols corresponding to species are defined in the legend; solid black shapes represent specimens that were morphologically identified, hollow shapes indicate genetic vouchers, solid grey shapes identify vouchers where both morphological and molecular data were compared.

This was a limitation of this research, as the beak in particular is a vital component of identification in trophic and ecological research.

When sufficient material was present, paralarval and juvenile developmental stages were identified based on morphological differences, with divisions made when several physical features changed markedly, or developed where absent in the previous stage (as for *Teuthowenia pellucida* [Chun, 1910]; see Evans and Bolstad 2014). In most species the sub-adult (or juvenile) form was characterised by attaining all diagnostic morphological features other than those relating to sexual maturity (as per Young and Harman 1988); in ‘adult’ specimens, primary and secondary sexual characteristics were fully developed.

DNA barcoding

Tissue samples were fixed in 80–100% EtOH and maintained at room temperature until analysis. Samples were extracted using EconoSpin (Epoch Life Science) spin columns with QIAGEN reagents following the protocols for the DNeasy Blood & Tissue Kit (QIAGEN). PCR amplification for the DNA barcode region was carried out in 12.5 µl reaction volumes with: 6.25 µl 10% trehalose, 2 µl ddH$_2$O, 1.25 µl 10X buffer, 0.625 µl MgCl$_2$ (50 mM), 0.1 µl primer LCO1490 (Folmer et al. 1994) (10 µm), 0.1 µl primer HCO2198 (Folmer et al. 1994) (10 µm), 0.0625 µl 10 mM dNTPs, 0.06 µl Platinum Taq polymerase (5 U/µl), and 2 µl of DNA. A two-step amplification was run using the following reaction profile: hot start of 94°C for 1 min; 5 cycles of 94°C for 40 s, 45°C for 40 s, 72°C for 1 min; 35 cycles of 94°C for 40 s, 51°C for 40 s, 72°C for 1 min; extension at 72°C for 5 min, hold 4°C indefinitely. PCR products were run on a 1% agarose gel stained with GelRed and only products showing a single clear band were sent for sequencing.

The sequencing reaction was performed by Macrogen (Korea) using the same primers used for PCR. Bidirectional sequences were assembled into contigs and edited in CodonCode v 9.0.1 (Richterich 2004). These sequences were combined with publicly available sequences for *Taonius* and the outgroup *Cranchia scabra* Leach, 1817 (Table 1). The outgroup species was chosen because it belongs to the Cranchiidae, but is in a separate subfamily (Cranchiinae) from *Taonius* (Taoniinae). Sequences were submitted to NCBI (National Center for Biotechnology Information) and checked for contamination through the Basic Local Alignment Search Tool (BLAST) through NCBI. Sequences were uploaded to the Barcode of Life Data System (BOLD) (Ratnasingham and Hebert 2007) in a public project titled 'Taonius Sequences' (project code: TAONI). All BOLD sequences used in the present study were compiled into a public dataset titled 'Taonius Taxonomy' (dataset code: DS-TAONI24).

Sequence analysis

Sequences were aligned using the Multiple Alignment using Fast Fourier Transformation (MAFFT) online server (Katoh and Standley 2013). This dataset was analysed in jModelTest (under Bayesian Information Criterion) to determine the appropriate model. Nodes with low support (below 75%) were collapsed. The maximum-likelihood phylogeny was generated in MEGA 7.0.26 (Kumar et al. 2016) using Hasegawa-Kishino-Yano (HKY) + I + G. Intra- and interspecific distances were calculated in MEGA 7.0.26 (Kumar et al. 2016) using uncorrected p-distances. The distances in COI among taxa were used to calculate the 'barcode gap', which is the separation between the largest intraspecific distance and the smallest interspecific distance (Meier et al. 2008). Species delimitation was determined using two methods. The Barcode Index Number (BIN) system uses an algorithm to form clusters of barcode sequences that have a high congruence with species (Ratnasingham and Hebert 2013). This system is integrated in BOLD and automatically generates BINs for sequences that are added to the database, and that meet the quality criteria (Ratnasingham and Hebert 2013). The species delimitations were also assessed using the maximum-likelihood solution based on the Bayesian Poisson tree processes (bPTP) model (Zhang et al. 2013).

Instruments used

Illustrations were made by hand or using a camera lucida attachment and Leica WILD M3B microscope when the specimen was too small. Inked images were scanned and then digitally compiled using Adobe Photoshop. Global distribution maps were made using ArcGIS Online (ESRI) to plot geographic coordinates.

Table 1. Specimen data for *Taonius* (and outgroup *Cranchia scabra*) sequences used in the present study.

Taxon ID	BIN	BOLD Process ID	Specimen ID	GenBank ID	Locality	Reference
T. cf. *belone*	BOLD: ADH3661	NZCRA004-17	NSMT 016	PQ388246	Pacific Ocean	Present study
T. cf. *belone*	BOLD: ADH3661	NZCRA049-17	NSMT 030	PQ388243	Pacific Ocean	Present study
T. cf. *belone*	BOLD: ADH3661	NZCRA074-17	NSMT 254	PQ388253	Pacific Ocean	Present study
T. cf. *belone*	BOLD: ADH3661	TAONI002-24	WAMS 116598	PQ388245	Indian Ocean	Present study
T. cf. *belone*	BOLD: ADH3661	TAONI003-24	WAMS 116586	PQ388242	Indian Ocean	Present study
T. borealis	BOLD: ACD9245	GBCPH1829-14	N/A	KF309244	Mid-Atlantic Ridge	Bolstad et al. (2015)
T. borealis	BOLD: ACD9245	RBCMI492-14	RBCM: 011-00132-002	PQ388248	NE Pacific Ocean (BC)	BOLD project 'RBCM Invertebrates' (project code: RBCMI)
T. expolitus	BOLD: ADH3662	KERCE125-17	AIM 124798 A	MK185995	New Zealand (Kermadec Islands)	Braid and Bolstad (2019)
T. expolitus	BOLD: ADH3662	KERCE127-17	AIM 124798 C	MK185994	New Zealand (Kermadec Islands)	Braid and Bolstad (2019)
T. expolitus	BOLD: ADH3662	KERCE126-17	AIM 124798 B	MK185997	New Zealand (Kermadec Islands)	Braid and Bolstad (2019)
T. expolitus	BOLD: ADH3662	KERCE128-17	AIM 124798 D	MK185998	New Zealand (Kermadec Islands)	Braid and Bolstad (2019)
T. expolitus	BOLD: ADH3662	KERCE129-17	AIM 124798 E	MK185996	New Zealand (Kermadec Islands)	Braid and Bolstad (2019)
T. expolitus	BOLD: ADH3662	NZCRA018-17	NIWA 92488	PQ388255	New Zealand	Present study
T. notalia	BOLD: AFX4200	TAONI005-24	Cherel-628	PQ388252	Falklands	Present study
T. notalia	BOLD: AFX4200	TAONI006-24	MNHN-CG651-0001	PQ388254	Indian Ocean	Present study
T. notalia	BOLD: AFX4200	TAONI007-24	MNHN-CG654-0002	PQ388250	Indian Ocean	Present study
T. pavo	BOLD: AAM9951	GBCPH1057-10	N/A	EU735381	N Atlantic Ocean	Lindgren (2010)
T. pavo	BOLD: AAM9951	GBMNC29582-20	USNM 1531375	MT223328	N Atlantic Ocean	Taite et al. (2020)
T. pavo	BOLD: AAM9951	GBMNC29581-20	USNM 1531117	MT223406	N Atlantic Ocean	Taite et al. (2020)
T. sp. PO1	BOLD: ADH3660	NZCRA035-17	NSMT 245	PQ388251	Pacific Ocean	Present study
T. sp. PO1	BOLD: ADH3660	TAONI004-24	WAMS 116670	PQ388249	Indian Ocean	Present study
T. robisoni	BOLD: AAK0251	TAONI001-24	Young Y38	PQ388247	N Pacific Ocean (Hawaii)	Present study
T. robisoni	BOLD: AAK0251	NZCRA050-17	FMNH 278101	PQ388244	N Pacific Ocean (Hawaii)	Present study
T. tanuki	BOLD: ADH3663	KERCE062-17	AIM 124799	MK185999	New Zealand (Kermadec Islands)	Braid and Bolstad (2019)
Cranchia scabra	BOLD: AAJ6514	KERCE002-17	AIM 124785	MK185908	New Zealand (Kermadec Islands)	Braid and Bolstad (2019)

Due to the unique morphology of the Cranchiidae, with the head and mantle fused in three places, some specialised terms are used to refer to specific parts of the cranchiid anatomy. The dorsal fusion between the head and the mantle is referred to as the nuchal fusion, while the two ventral fusion points (which are almost always identical to each other morphologically, symmetrical across the midline) are referred to as the funnel–mantle fusions. Cartilaginous connections are usually present at these ventral fusion points, which are thought to provide some structure for the otherwise gelatinous mantle. The shape of these cartilaginous areas in cranchiids are genus specific and can sometimes help distinguish between species as well. In *Taonius*, these cartilaginous 'windows' are often rounded (whereas in other genera they could be angular or linear [e.g. Figure 14]).

Commonly used morphological abbreviations

ML—Mantle length (dorsal); MW—Mantle width; FL—Fin length; FW—Fin width; HL—Head length; HW—Head width; FB—Funnel base width; FA—Funnel aperture width; ED—Eye diameter; TnL—Tentacle length (including stalk and club); CL—Tentacle club length; LRL—Lower rostral length (of beak).

Non-morphological abbreviations

MWT—Mid-water trawl; BT—Bottom Trawl

Specimens were examined from natural history collections around the Pacific Ocean, and further abroad for certain type specimens. The following institutions were visited:

- Australian Museum (AMS), Sydney, Australia
- Auckland War Memorial Museum Tāmaki Paenga Hira (AIM)
- Field Museum of Natural History (FMNH), Chicago, United States
- Muséum National d'Histoire Naturelle (MNHN), Paris, France
- Museum of New Zealand Te Papa Tongarewa (NMNZ), Wellington, New Zealand
- National Museum of Victoria (MV), Melbourne, Australia
- National Institute of Water and Atmospheric Research, Ltd (NIWA), Wellington, New Zealand
- Smithsonian National Museum of Natural History (NMNH), Washington, D.C., United States (previously known as United States National Museum [USNM])
- National Museum of Nature and Science (NSMT), Tokyo, Japan
- Rosenstiel School of Marine, Atmospheric, and Earth Science (RSMAS), Miami, United States
- Santa Barbara Museum of Natural History (SBMNH), Santa Barbara, United States

Results

Genetic results

COI sequences for 24 *Taonius* individuals representing eight species were included in our analysis, including 11 sequences that were available from previous studies, and 13 that were generated in the present study (Table 1). COI sequences were 658 bp long, except for one specimen of *T. notalia* sp. nov. (MNHN-CG651-0001) that was only 600 bp because of non-specific binding that occurred at the start of the sequence, which was truncated before analysis. All sequences used in the analysis were free from indels and stop codons.

All species where multiple individuals were sequenced (*T.* cf. *belone*, *T.* sp. PO1, *T. robisoni* sp. nov., *T. borealis*, *T. pavo*, *T. notalia* sp. nov, and *T. expolitus* sp. nov.) formed distinct species clusters on the phylogeny (Figure 2). The one species represented by a single specimen (*T. tanuki* sp. nov.) was well separated from all other species (4.4% divergent from its nearest neighbour, *T.* cf. *belone*). The smallest interspecific distance was found between *T.* cf. *belone* and *T.* sp. PO1 (2.4%), which showed a strongly supported sister relationship. The largest interspecific distance was found between *T. borealis* and *T. notalia* sp. nov. (13.6%), with the next-largest interspecific distance found between *T. notalia* and *T. expolitus* (12.7%).

Very low intraspecific variation was found (with a maximum of 0.6% found within *T.* cf. *belone*) (Table 2). However, it should be noted that our sample size for each species was quite low, with most species represented by three individuals or fewer. The largest sample size for a single species was *T. expolitus* sp. nov., which was represented by six individuals (this species had a maximum intraspecific divergence of 0.3%). BINs were assigned to all barcode clusters generated in this study using a spectral clustering

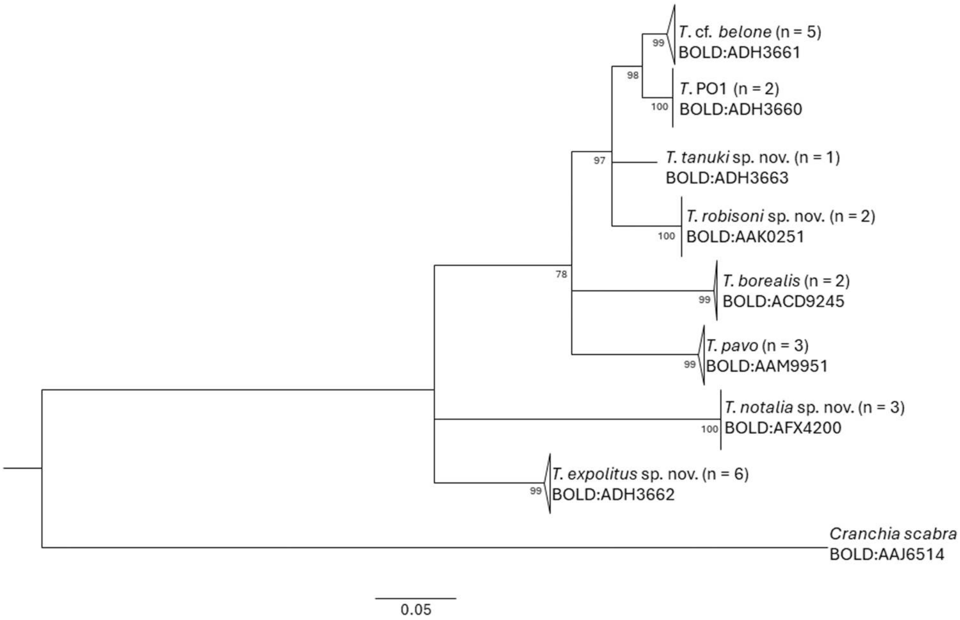

Figure 2. Maximum-likelihood phylogeny of all *Taonius* specimens sequenced for this study and from previously published sequences for cytochrome *c* oxidase subunit 1 (COI)generated in MEGA 7.0.26 (Kumar et al. 2016) using Hasegawa-Kishino-Yano (HKY) + I + G. Bootstrap support values are indicated at nodes and based on 1000 bootstrap replicates. Nodes with bootstrap support below 75% have been collapsed. The scale bar indicates in the number of substitutions per site.

method implemented in BOLD v4 (Ratnasingham and Hebert 2013). All eight species were recognised as distinct in the bPTP analysis (Appendix A).

Systematics

Taonius Steenstrup, 1861 (Table 3)
Taonius Steenstrup, 1861: 37–38; Voss 1980: 390–392, fig. 8.
Toxeuma Chun, 1906: 86; Pfeffer 1912: 699–700.
Belonella Lane, 1957: 287; Nesis 1987: 274, fig. 71 F–J.

Diagnosis

Mantle usually long and narrow, tapering gradually to point; conus of gladius long (~50% ML). Fins slender (often 10–20% ML), lanceolate, attaching to conus at its widest point. Tubercles absent at all head–mantle fusion points. Eyes large in adults, with two ventral photophores: one large, crescent shaped, on ventral surface of eye; one smaller, crescent shaped or linear, ventral or posteroventral to lens. Arms robust, of variable relative length but none markedly longest; arm-sucker teeth blunt, rounded, or adentate. Tentacles shorter than ML; clubs with suckers in four longitudinal series; those in two medial series largest, with 2–8 enlarged hook-like teeth in most species.

Taonius belone (Chun, 1906) (Tables 1–3, Figure 3)

Toxeuma cf. *belone* (Chun, 1906): 86; Chun 1910: 296–297, Pl. LVI fig. 10, Pl. LVIII fig. 1–5; Pfeffer 1912: 700–702.
Taonius pavo (not Lesueur, 1821) Sasaki 1920: 201.
Belonella pacifica pacifica Nesis, 1972: 80–82, fig. 1.
Galiteuthis triluminosa Lu and Clarke, 1974: 991–994, fig. 3–4.
?*Taonius belone* (Chun, 1906) [see Remarks]: Imber 1978: 458–459, 1H, 3, 4, 5C.
Belonella belone (Chun, 1906): Nesis 1987: 264, fig. 71 F–J.
Taonius belone (Chun, 1906): Evans 2018: 163–165, fig. 10.2.

Diagnosis

Mantle slender (mean MW ~20% ML); arm suckers with 20–30 blunt teeth evenly distributed around entire margin (*fide* Voss 1963). Tentacle club mid-manus suckers in medial two series with two enlarged primary cusps; secondary cusps absent.

Type material

(not examined) *Toxeuma belone* **Type repository unresolved** [species not traced by Glaubrecht and Salcedo-Vargas (2000)]. Type locality: 10.13°S, 97.23°E (Indian Ocean) [*fide* Chun (1910: 380)].

Material examined (3 specimens)

NSMT-Mo.75441, ML 270 mm, sex indet., 29.68°N, 130.66°E, off Okinawa, 1000 m, Tansei-Maru, 23/10/2004; **WAMS_116598** [BOLD Process ID TAONI002-24], ML ~240 mm, sex indet., 22.02°S, 113.64°E, 792 m, RV *Investigator*, scampi trawl, 8/12/

Table 2. Intra- and interspecific variation within *Taonius* (in percentages) for cytochrome *c* oxidase subunit I (COI). These values represent uncorrected p-distances calculated using MEGA 7.0.26 (Kumar et al. 2016).

	Intraspecific variation (%)				
Species	Min	Mean	Max	Nearest species	Min distance to nearest species (%)
T. borealis	–	0.2	–	*T.* sp. PO1	7.5
T. cf. *belone*	0	0.3	0.6	*T.* sp. PO1	2.4
T. expolitus sp. nov.	0	0.1	0.3	*T. tanuki* sp. nov.	10.3
T. notalia sp. nov.	0	0	0	*T. tanuki* sp. nov.	9.8
T. pavo	0	0.2	0.3	*T.* cf. *belone*	7.7
T. sp. PO1	–	0	–	*T.* cf. *belone*	2.4
T. robisoni sp. nov.	–	0	–	*T. tanuki* sp. nov.	4.4
T. tanuki sp. nov.	–	–	–	*T.* cf. *belone*	4.4

Table 3. Comparison of morphological characters across all known *Taonius* species.

Species	Mantle	Mean fin length	Relative arm lengths	Maximum arm sucker count	Arm sucker tooth number and shape	Manus sucker tooth arrangement
T. cf. *belone*	Slender (MW 15–20% ML)	20%–40% ML	III>II>IV>I	30–52	20+, rounded	2 primary
T. borealis	Stout (MW 15–40% ML)	~35% ML	III>II>IV>I	90	16–22, rounded	2 primary, 3–6 secondary
T. expolitus sp. nov.	Slender (MW 12–19% ML)	~28% ML	III>II≈IV>I	54	adentate	5–11 teeth (no primary)
T. notalia sp. nov.	Slender (MW 11–17% ML)	~35% ML	III≈II>IV>I	36–48	5–7, blunt	1 primary, 4–6 secondary
T. robisoni sp. nov.	Slender (MW 10–25% ML)	~50% ML	III≥II≥IV>I	28–48	3 or 4, blunt	2 primary, 2–4 secondary
T. tanuki sp. nov.	Slender (MW 13–28% ML)	~35% ML	III>II>IV>I	50	12–18, blunt	2 primary, 0–2 secondary
T. pavo	Slender (MW ~13% ML) (d'Orbigny 1845)	~28% ML (d'Orbigny 1845)	NA	NA	4 or 5, blunt	2 primary, no secondary

2022. **WAMS_116586** [BOLD Process ID TAONI003-24], ML ~430 mm, sex indet., 22.22°S 113.63°E, RV *Investigator*, scampi trawl, 5/12/2022.

Non-localised material examined (2 specimens)

NSMT-Mo.67349, ML 121, 116 mm, sex indet., 480 m, 04/08/1986.

Description

(ML 113–270 mm; Figure 3)—Mantle elongate, slender (MW 15–*20*–27% ML); fins lanceolate (FL ~40% ML in specimens ML ~120 mm, ~20% at ML ~250 mm), FW ~14% ML. HL ~9% ML, eyes proportionally small, ED ~9% ML, HW ~18% ML. Eyes with two crescentric photophores: outer photophore traverses ventral half of eye circumference;

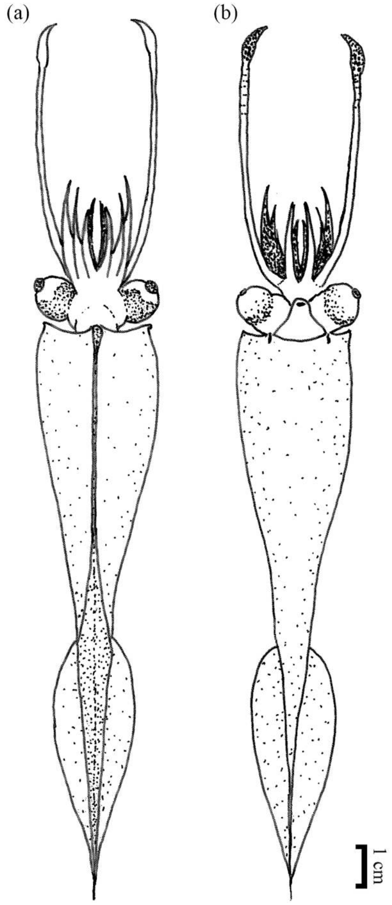

Figure 3. *Taonius* cf. *belone,* (a) dorsal view and (b) ventral view (NMST Mo.75114; ML 113 mm).

inner photophore linear or slightly curved, spanning ~50% ED just ventral to lens. Funnel narrows to small aperture, FA 33–*37*–44% FB; ventral fusion cartilaginous windows appear slightly wider than in other species.

Arm formula III>II≈IV>I: Arm I 10–*13*–16% ML, Arm II 15–*17*–26% ML, Arm III 17–*20*–26% ML, Arm IV 13–*17*–23% ML, with aboral keel; minimal webbing between arms. Arms with 30–52 small subequal suckers, largest arm sucker with at least 22 blunt teeth. Tentacles 20–*35*–45% ML, stalks with ~14 suckers. Clubs ~9% ML (16–*25*–32% TnL) with up to 90 suckers. Largest manus suckers with two enlarged primary cusps and no small secondary cusps.

Known distribution. Generally thought to be an Indo-Pacific species (as reported by Nesis 1987). Material examined herein was from Japan and the northeastern Indian Ocean (Figure 1).

Remarks. Unfortunately, only five specimens of *T.* cf. *belone* were available for examination, none of which appeared to be mature. Morphologically, *T.* cf. *belone* appears most similar to *T. tanuki* sp. nov. These species can be differentiated by their eye photophores, arm-sucker dentition, and manus dentition. *Taonius* cf. *belone* has noticeably more teeth on the arm suckers (>22 teeth, compared to 12–18 teeth in *T. tanuki*), and only two large primary cusps (no secondary) on the largest manus suckers, whereas *T. tanuki* has additional smaller cusps along the lateral sucker margins (see Figure 21). Genetically, *T. belone* shows a sister relationship to *T.* sp. 'PO1' and these species form a clade with *T. tanuki* and *T. robisoni*. All four species were assigned separate BINs.

Lu and Clarke (1974) diagnosed their novel *Galiteuthis triluminosa* (=*T. belone*, *fide* Nesis 1987) by the presence of three distinct photophores on the ventral surface of stalked, tubular eyes. Tubular eyes are now understood to occur during an intermediate ontogenetic stage of the genus *Taonius*, but as all known species of both *Galiteuthis* and *Taonius* only have two eye photophores, the presence of three would be unusual for either genus. Although Nesis (1987) placed *G. triluminosa* into synonymy with *T.* cf. *belone*, the status of this species is not clear. The type locality of *G. triluminosa* is in the northern Atlantic Ocean, while *T.* cf. *belone* presently appears restricted to Indo-Pacific waters (Young 2014b), which makes this synonymy unlikely. Because the taoniins are so poorly known, *G. triluminosa* could represent a junior synonym of a different species of *Taonius*, or a valid species in this subfamily.

***Taonius borealis* (Nesis, 1972) (Tables 1–3, Figures 4–7)**

Belonella pacifica borealis Nesis, 1972: 82–86, fig. 2; Arkhipkin 1996: 123–132, fig. 1, 2, 4.
Taonius borealis (Nesis, 1972): Voss et al. 1992: 198–200; Evans 2018: 165–169, figs 10.3–10.6.

Diagnosis

Mantle stout (MW up to 40% ML). Arm suckers with 16–22 rounded teeth distributed around entire ring margin. Tentacle club manus suckers with two enlarged primary cusps and a total of three to six smaller cusps around sucker margin.

Type material

(not examined) *Belonella pacifica borealis* **ZIN Holotype** [*fide* Nesis (1987:274)]. Type locality: 44.12°N, 150.44°E (North Pacific Ocean).

Material examined (15 specimens)

RBCM 979-11242-1, ML 185 mm, sex indet., 50.00°N, 145.00°W, Ocean Stn. Papa, 23/08/1979; **RBCM 979-11252-4**, ML 154 mm, sex indet., 50.00°N, 145.00°W, Ocean Stn. Papa, 31/08/1979; **RBCM 979-11230-2**, ML 145 mm, sex indet., 50.00°N, 145.00°W, Ocean Stn. Papa, 04/08/1979; **RBCM 979-11252-4**, ML 58 mm, sex indet., 50.00°N, 145.00°W, Ocean Stn. Papa, 31/08/1979; **RBCM 010-00251-008**, ML 118 mm, sex indet., 48.71°N, 126.52°W–48.71°N 126.49°W, Pacific Ocean, Father Charles Canyon, offshore of Vancouver Island, 561–563 m, 30/08/2001; **RBCM 010-00264-001**, ML 245 mm, sex indet., 48.52°N, 126.47°W–48.52°N, 126.45°W, Pacific Ocean, offshore to SW of Ulcuelet, Vancouver Island, 1268–1270 m, 04/09/2001; **RBCM 010-00247-015**, ML 133 mm, sex indet., 48.37°N, 126.46°W–48.38°N, 126.47°W, Pacific Ocean, Loudoun Canyon, 1416–1433 m, 13/04/2011; **SBMNH 464441**, ML 144 mm, sex

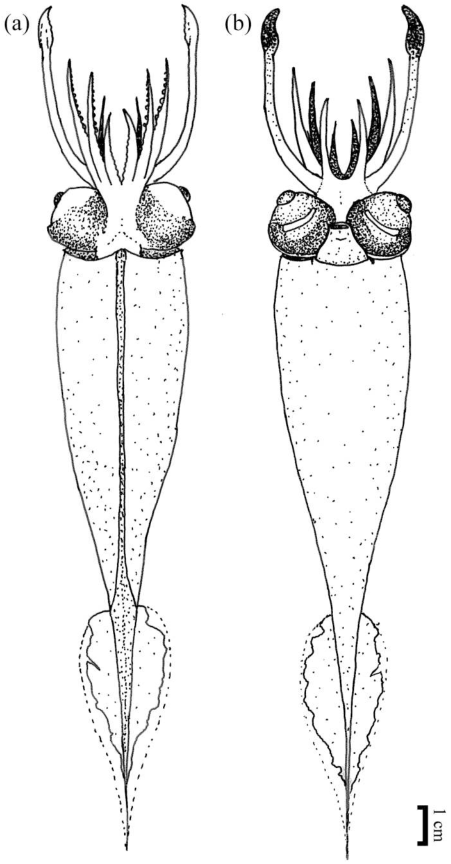

Figure 4. *Taonius borealis*, adult (a) dorsal, and (b) ventral views (RBCM 988-00212-003, ML 141 mm).

indet., 44.00°N, 125.00°W, USA, Oregon, OSU MT 2340; **NSMT-Mo. 71705**, ML 450 mm, sex indet, 42.30°N, 144.02°E, off Kushiro, Japan, NW Pacific Ocean, 867 m, *Wakataka-Maru*, 23/07/1999; **NSMT-Mo.85452**, ML 250 mm, sex indet., 41.57°N,

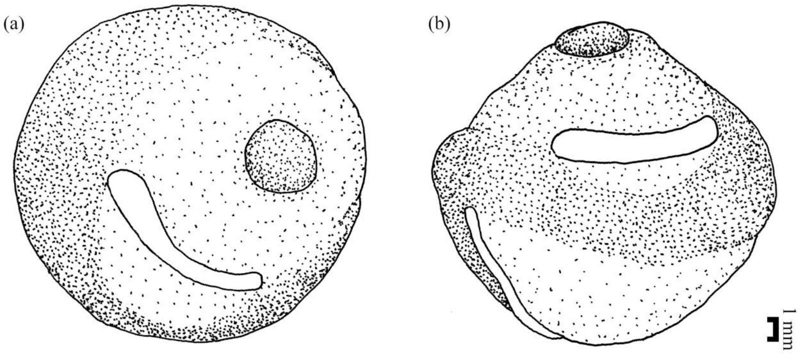

Figure 5. *Taonius borealis*, right eye schematic (a) lateral view, (b) ventral view (RBCM 988-00212-003; ML 141 mm).

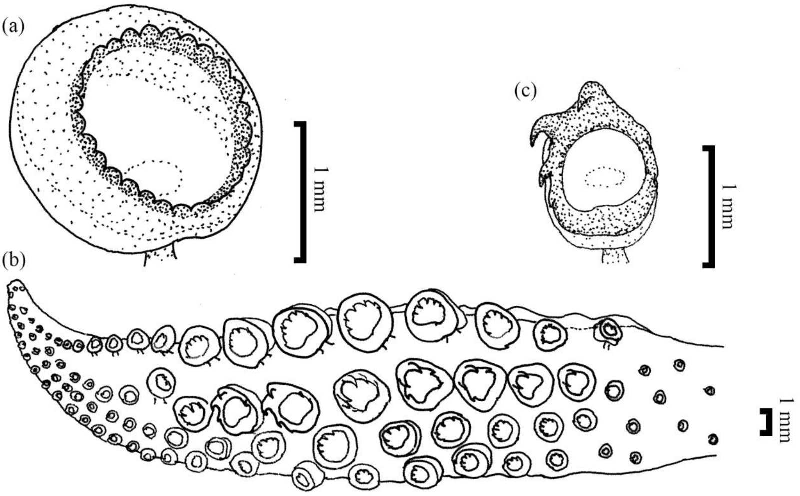

Figure 6. *Taonius borealis*, armature (a) Mid-Arm III sucker, (b) right tentacle club with (c) largest manus sucker (RBCM 988-00212-003; ML 141 mm).

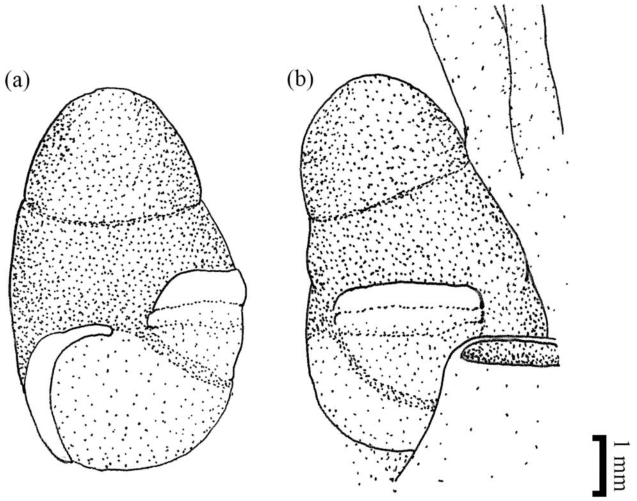

Figure 7. *Taonius borealis*, juvenile tubular right eye (a) lateral view and (b) ventral view (RBCM 987-00076-001; ML 57 mm).

143.48°E, off Enmo-misaki, Hokkaido, 850 m, *Tansei-maru*, 28/05/2010; **NSMT-Mo.76413**, ML 160 mm, sex indet., 41.03°N, 144.84°E, off Sanriku, Japan, Western North Pacific, 650 m, *Marusada-maru*, 06/07/1996.

Non-localised material examined (4 specimens)

RBCM 988-00212-003, ML 141 mm, sex indet., Pacific Ocean, off Clayquot Canyon, 29/02/1998; **RBCM 987-00076-001**, ML 46, 57, 54 mm, sex indet., 0–500 m, Stn. 1, 03/03/1969.

Description

Adult (ML 118–450; Figures 4–7)—Mantle stout, MW 17–*27*–38% ML; skin reticulate in adults. Fin length 31–*39*–43% ML, FW 9–*12*–16% ML (55–80% MW). HL 10–*13*–17% ML; eyes large, often extending beyond remainder of head tissue (ED 9–*12*–16% ML, ED 80–*96*–133% HL, HW 75–*94*–140% MW). Eyes sessile from ~60 mm ML, with two crescentric photophores (Figure 5). Funnel narrows to small aperture, FA 32–*36*–42% FB, cartilaginous fusion windows rounded.

Arms robust basally, slender distally; low protective membrane present along arm length; formula III>II>IV>I (although relative lengths vary only slightly): Arm I 9–*21*–28% ML, Arm II 17–*26*–35% ML, Arm III 17–*28*–39% ML, Arm IV 15–*22*–29% ML. Longest arms with 40–*52*–90 suckers, subequal in diameter along proximal ¾ of arm then rapidly decreasing in size distally; largest arm suckers with 16–22 rounded teeth (Figure 6a), dentition decreasing on distal arm suckers. No sexual arm modifications observed on material examined (to ML 450 mm). Tentacles 33–*56*–74% ML, with ~20 suckers on tentacular stalk. Tentacle clubs (Figure 6) 6–*12*–17% ML (12–25% TnL); wide trabeculate membrane present along dorsal and ventral margins; total of 80–100 suckers: three or four pairs on carpal locking apparatus, 24–36 manus suckers, largest mid-manus suckers with two enlarged primary cusps and 1–3 secondary cusps on each side (Figure 6c); 50–60 dactylus suckers, largest with ~8 long pointed teeth on distal margin and several smaller teeth on opposite margin.

Known distribution. Northern Pacific Ocean (north of 40°N) from Japanese waters to Bering Sea and northern Vancouver Island (Figure 1). Present material collected from 250–1425 meters; previously recorded from 400–700 meters (Watanabe et al. 2006) and reported not to perform diel vertical migrations.

Remarks. *Taonius borealis* is often proportionally stouter than other species, with a maximum observed MW of 40% ML, while the maximum observed MW in other species is ~20–25% ML. Specimens of *T. borealis* are genetically distinct from other species in the genus, with a minimum nearest-neighbour distance of 7.5% (with *T.* sp. PO1) and forming a distinct BIN (BOLD:ACD9245; Figure 2). The genetic relationship of this species to others in this genus is not clear (Figure 2). This species is most likely to be confused with the sympatric *Galiteuthis phyllura* Berry, 1911; however, *Galiteuthis* taxa have large hooks on their tentacle clubs which begin to develop by 40 mm ML (Evans 2018). It is possible that *T. borealis* may also be confused with *T. robisoni* sp. nov., as there appears to be some geographic overlap between the two species in southern Californian waters. These species can usually be distinguished using mantle width, or by arm and tentacle sucker dentition (Table 3). *Taonius borealis* has 16–22 rounded teeth on the arm sucker margins and up to six small secondary cusps laterally along the manus sucker aperture (Figure 5c), whereas *T. robisoni* has around four teeth on the distal margin of the arm suckers and four secondary cusps on the manus suckers (Figures 13, 16).

When describing *Taonius borealis*, Nesis (1972) stated that on his smallest specimens (40 mm ML), the eyes were sessile and ocular photophores had already developed. The smallest specimens examined in this study were of similar size (ML 46–57 mm) and had telescopic eyes in transitional states of development (Figure 7). As these specimens are slightly larger than those examined by Nesis (1972), this could indicate that the development of mature features can occur over a fairly wide ontogenetic range in this species.

***Taonius expolitus* sp. nov.** (Tables 1–3, Figures 8–10)

Taonius pavo (not Lesueur, 1821): Imber 1978: 453–455, figs 3, 4.
Taonius sp. 1: Marshall et al. 2023: 237.
Taonius sp. KER1: Braid & Bolstad 2019: 402–425.

Diagnosis

Mantle slender (mean MW 17% ML); largest arm suckers adentate; tentacular suckers with 5–8 long pointed teeth, without greatly enlarged primary cusps. Modified portions of male Arms I–III potentially lacking suckers at distal tips.

Type material

[Holotype] **NIWA 95946**, ML 285 mm, ♂. Type locality: North-west of Aotearoa New Zealand (35.9°S, 165.7°E), depth 1071 m; [Paratype] **AIM MA124798** (5 specimens) [BOLD Process ID KERCE-125-17 to -129-17] ML damaged, 31.4°S, 178.6°W–31.4°S, 178.6°W, Rangitāhua/Kermadec Islands, 1000–110 m, *RV Tangaroa*, TAN1612/120, 03/11/2016.

Additional material examined (5 specimens)

AMS C.9070 (4 specimens): ML 223–282 mm, ♂/♀, NSW, Australia, off Batemans Bay, 35.70°S 150.70°E, 940–975 m, FRV *Kapala*, Stn.K87-25-08, 17/12/1987, **NIWA 92488** [BOLD Process ID NZCRA018-17], 43.79°S 174.53°W, depth 811 m, TAN1401/56.

Description

Adult (ML 223–285 mm; Figure 8)—Mantle slender, conical (MW 12–*17*–19% ML). Fins narrow, lanceolate, FL 23–*28*–33% ML, FW <9% ML (fins damaged in all known specimens). HL 10–*12*–14% ML; eyes damaged on all known specimens, estimated ED 6–*9*–13% ML; HW 10–*12*–13% ML. Funnel narrows markedly anteriorly, FA 18–*42*–73% FB; cartilaginous window at funnel–mantle fusion expands posteriorly, curving slightly towards ventral midline.

Arm formula III>II≈IV>I: Arm I 13–*16*–22% ML, Arm II 15–*19*–25% ML, Arm III 18–*22*–28% ML, Arm IV 17–*19*–22% ML. Arms with up to 54 suckers, increasing greatly in size mid-arm; suckers lack dentition basally and mid-arm; distal arm suckers with 5–12 blunt/rounded teeth. Male Arms I–III modified at maturity (Figure 9) with four series of large round suckers starting mid-arm, possibly lacking suckers entirely on distal portion with triangular dermal pads with linear ridges (Figure 9a), 15–20% arm length. Tentacles 40–*43*–45% ML, stalks with five or six pairs of adentate suckers. Clubs 9–*11*–12% ML (22–26% TL) with 84–125 suckers. Largest manus suckers (Figure 10) with 5–11 long, pointed, slightly curved teeth, none forming strong primary cusps although medial two may be slightly enlarged.

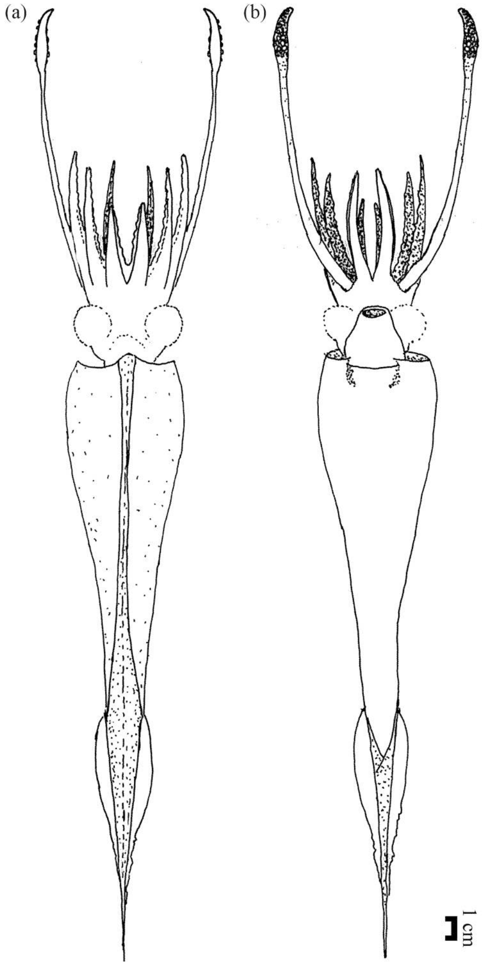

Figure 8. *Taonius expolitus* sp. nov., (a) dorsal and (b) ventral view (composite illustration based on mantle and head of NIWA 95946; ML 285 mm; tentacles of AIM 124798; CL 27 mm).

Known distribution. Eastern Australian waters to northern Aotearoa New Zealand (Rangitāhua/Kermadec Islands; 30°S–35°S; Figure 1). Present material collected from 110–1071 meters depth.

Remarks. *Taonius expolitus* sp. nov. is the only *Taonius* lacking the unique enlarged primary cusps on the manus suckers, a feature that can be readily used to separate its congeners from all other known cranchiid taxa. This species is additionally distinguished by the notable separation between the basal-most arm sucker (or pair of suckers) and the other sucker pairs. However, some morphological traits do align *T. expolitus* with other members of *Taonius*. The mantle width, mean fin width, relative arm lengths, and maximum arm sucker count for *T. expolitus* all fall within the range of other *Taonius* species (Table 3).

The placement of this species in the genus *Taonius* requires further investigation. Morphologically and genetically, this species is quite distinct (with the largest distance to the nearest neighbour in this genus; 10.3% divergent from *T. tanuki* sp. nov.). Our

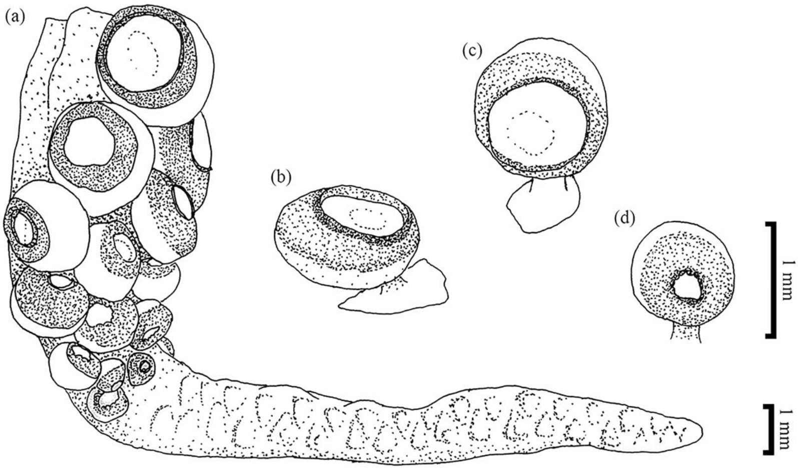

Figure 9. *Taonius expolitus* sp. nov., male arm suckers (a) hectocotylus? and (b–d) arm suckers: (b, c) medial suckers and (d) distal suckers (NIWA 95946; ML 285 mm).

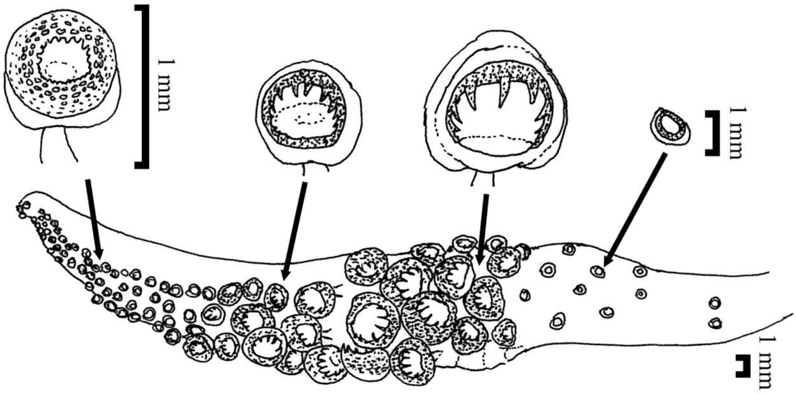

Figure 10. *Taonius expolitus* sp. nov., left tentacle club and club armature (AIM 124798; CL 27 mm).

phylogeny did not resolve a placement for *Taonius expolitus* in this family (Figure 2). However, these results are based only on the COI gene, and additional genes are needed to help resolve the placement of this species within the genus, family, and subfamily.

The generic diagnosis above (slightly amended from other recent diagnoses, e.g. Young 2014a) includes the atypical manus sucker morphology of *T. expolitus*. Specimens of *T. expolitus* that are missing their tentacular clubs could be confused with *Galiteuthis*, as the two genera appear superficially quite similar, and some species of *Galiteuthis* also lack arm-sucker dentition. However, all known *Taonius* species (including *T. expolitus*) lack pointed tubercles at the ventral funnel–mantle fusion, which are present in all known *Galiteuthis*. This species is morphologically and genetically distinct from all other cranchiids, but the generic placement could change with additional information in the future.

Etymology. This species is named for the smooth (adentate) margins on both the basal and the mid-arm suckers (from the Latin '*expolitus*' meaning 'smooth'), a feature unique among the presently known *Taonius* species. Although other species of *Taonius* may lack dentition on the basal most sucker pairs, in all other species, dentition is visible towards the mid-arm suckers.

Taonius notalia **sp. nov.** (Tables 1–3, Figures 11, 12)

Belonella sp.: Nesis 1987: 274.

Diagnosis

Mantle slender (mean MW 15% ML), mid-arm suckers with 5–7 blunt teeth, basal arm suckers adentate. Largest manus suckers on tentacle clubs with single enlarged primary cusp and approximately six smaller secondary cusps (usually three on each side).

Type material

[Holotype] **MV F53273**, ML 245 mm, 56.01°S, 155.00°E, S. E. of Tasmania, 1700 m, 29/11/1968.

Additional material examined (5 specimens)

MV F163703, ML 307 mm, sex indet., 54.61°S, 158.74°E–54.87°S, 158.68°E, Tasmania, Macquarie Island, 802 m, 02/01/1995; **MV F163704**, ML 263 mm, sex indet., 54.72°S, 158.70°E, Tasmania, Macquarie Island, 815–875 m, 08/01/1995; **MV F163706**, ML 310 mm, sex indet., 54.72°S, 158.70°E–54.55°S 158.77°E, Tasmania, Macquarie Island, 700–915 m, FV *Austral Leader*, 29/01/1995; **ZMO, uncatalogued**: ML 265 mm, sex indet., 56.50°S, 158.70°W, 2000 m, SS *Norvegia*.

Non-localised material examined

RSMAS #782-20, ML 225, sex indet., 'sub-Antarctic', MWT, 3039 m, 20/10/63.

Description

Adult (ML 225–310 mm; Figures 11, 12)—Mantle slender, MW 11–*15*–17% ML; gladius barely visible through dorsal tissue; rachis expanded, sagittate, anterior tip pointed. Fins narrow, lanceolate, FL 32–*36*–43% ML, FW ~13% ML. HL 8–*12*–17% ML; HW 10–20% ML; ED ~10% ML; inner eye photophore positioned slightly anteriorly. Funnel narrows to small distal aperture, FA 28% FB; ventral fusion window 'angular'.

Arm formula III≈II>IV>I (although lengths vary only slightly): Arm I 15–*20*–29% ML, Arm II 18–*24*–30% ML, Arm III 19–*24*–33% ML, Arm IV 16–*21*–27% ML. Short web present between arms; protective membranes flank both sucker series along entire arm length; aboral keel absent from all arms. Arms with 40–50 suckers that decrease in size from basal-most pair to mid-arm, then increase slightly around pair 10; largest arm suckers with five to seven blunt teeth. Tentacles 32–*44*–61% ML, stalk with ~18 suckers. Clubs (Figure 12) ~9% ML (16–*23*–29% TnL) with 80–100 suckers. Largest manus suckers with one enlarged primary cusp and two or three secondary cusps on each side (Figure 12a).

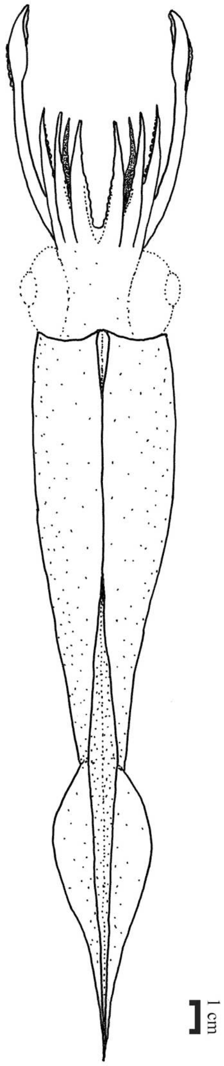

Figure 11. *Taonius notalia* sp. nov., dorsal view (RSMAS #782-20, ML 225 mm).

Known distribution. Southern Pacific Ocean, south-east of New Zealand, possibly sub-Antarctic (Figure 1). Material examined in this study was collected between 700 and 3032 meters depth.

Remarks. Although both *T. notalia* and *T. borealis* are known from high latitudes and have similarly shaped tentacular clubs, their mantle shapes differ considerably. *Taonius borealis* is the stoutest member of this genus (maximum MW 40% ML), while *T. notalia* has the more typical slender mantle (maximum MW 17% ML). This species is genetically distinct from all others in the genus, but its relationship to other species is not resolved (Figure 2). The nearest neighbour to *T. notalia* is *T. tanuki* sp. nov., with a minimum distance of 9.8% (Table 1).

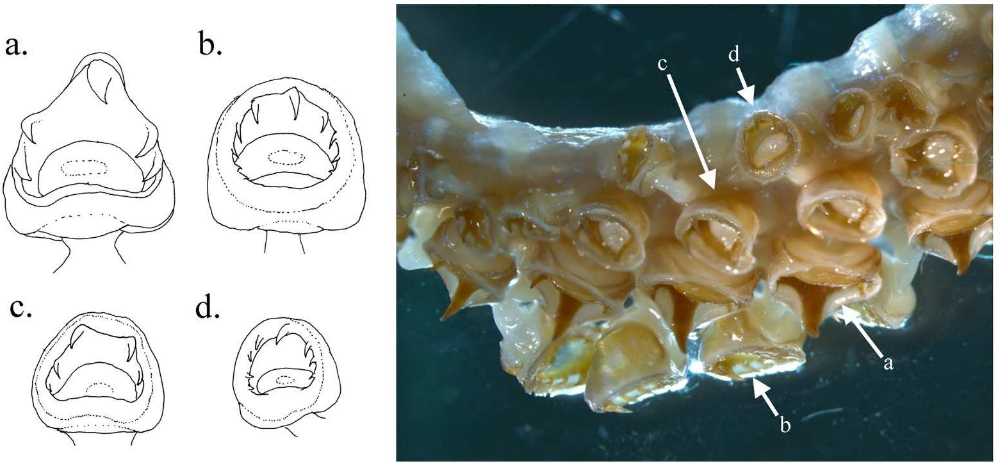

Figure 12. *Taonius notalia* sp. nov., tentacle armature (RSMAS #782-20; ML 225 mm): (left) schematic diagram of tentacular club suckers from (a,c) inner manus series and (b,d) outer manus series; (right) photograph of right tentacular club.

As limited material of *T. notalia* was available for study, the full geographic distribution of this species is not currently fully understood; however, it appears to overlap with *G. glacialis* (which can be differentiated by its small, spherical mantle tubercles and elongated hooks on the tentacle club). It is highly likely this was the species Nesis (1987) reported as *Belonella* sp. (and N. Voss in unpublished data as '*Taonius* sp. B'; see, e.g. Cherel 2020) from the notalian-Antarctic, since this taxon was characterised by a singular large tooth on the manus suckers and 1–5 smaller teeth along the lateral ring margins, and large protective membranes on the arms.

Etymology. The species name derives from the Notalian-Antarctic (the region of ocean between tropical waters and the Southern Ocean). This area includes southern Aotearoa New Zealand and Macquarie Island, where the type specimens were collected.

***Taonius robisoni* sp. nov. (Tables 1–3, Figures 13–16).**

Taonius sp.: Young 1972: 98.

Diagnosis

Mantle slender (mean MW 18% ML); gladius visible along entire dorsal mantle length; conus of gladius broadest posterior to fin insertion. Arm suckers with three or four large, blunt teeth; largest manus suckers with two enlarged cusps and about two smaller secondary cusps on each lateral margin.

Type material

[Holotype] **SBMNH 464424**, ML 143 mm, sex indet., 32.93°N, 120.42°W, USA, California, 3657 m, 16/02/1966.

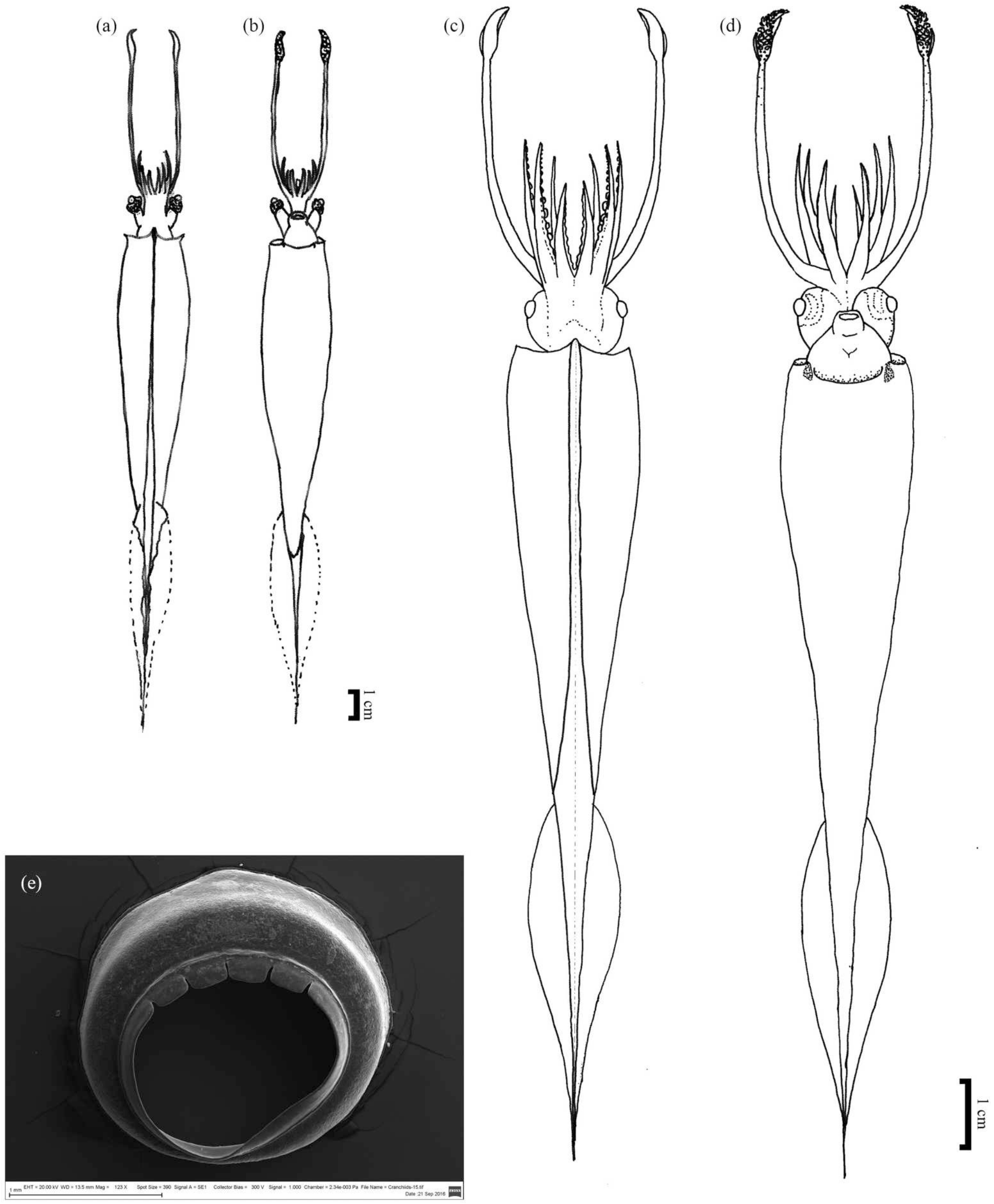

Figure 13. *Taonius robisoni* sp. nov., (a,b) juvenile (SBMNH 460944; ML 165 mm), (c – e) adult (SBMNH 464982; ML 210 mm) (a,c) dorsal and (b,d) ventral, (e) largest Arm III sucker.

Additional material examined (4 specimens)

SBMNH 464422, ML 69 mm, sex indet., 33.38°N, 118.76°W, USA, California, Santa Catalina Island, 1280 m, 16/04/1964; **SBMNH 464421**, ML 96, sex indet., 29.97°N, 119.20° W, Mexico, Baja California, Isla Guadalupe, 07/08/1964; **FMNH 278101** [BOLD Process ID NZCRA050-17] 21.33°N 158.33°W; **SBMNH 460944**, ML 165, sex indet., 21.38°N, 158.30°W, USA, Hawaii, Oahu, FIDO XVI tow 85, 22/03/1980.

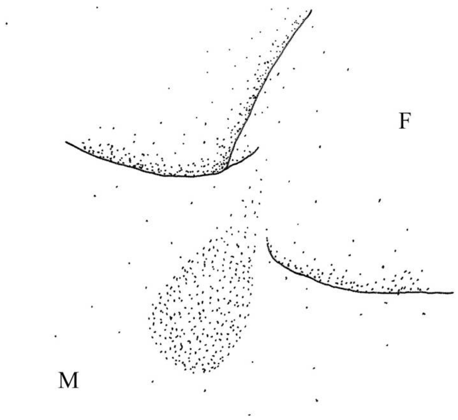

Figure 14. *Taonius robisoni* sp. nov., right funnel-mantle fusion window, schematic of connection between mantle (M) and funnel (F) shown (SBMNH 464982, ML 210 mm).

Non-localised material examined (1 specimen)

SBMNH 464982, ML 210 mm, 02/10/1992.

Description

Adult (ML 69–210 mm; Figures 13–16)—Mantle conical, slender, MW 10–*18*–25% ML; gladius visible along entire dorsal mantle length, widening slightly at anterior margin; conus long, over 50% ML. Fins narrow, lanceolate, FL ~50% ML, FW 10% ML. HL 8–*9*–10% ML, HW 9–*14*–18% ML, eye diameter 4–*7*–10% ML with two crescentric photophores. Funnel tapers gradually from base to aperture; funnel length 6–*7*–9% ML, FA 30–*34*–40% FB; cartilaginous fusion windows rounded (Figure 14).

Arm formula III≥II≥IV>I (but nearly sub-equal): Arm I ~11% ML, Arm II 9–*14*–17% ML, Arm III 10–*15*–17% ML, Arm IV 10–*13*–16% ML. Sucker counts vary slightly, with

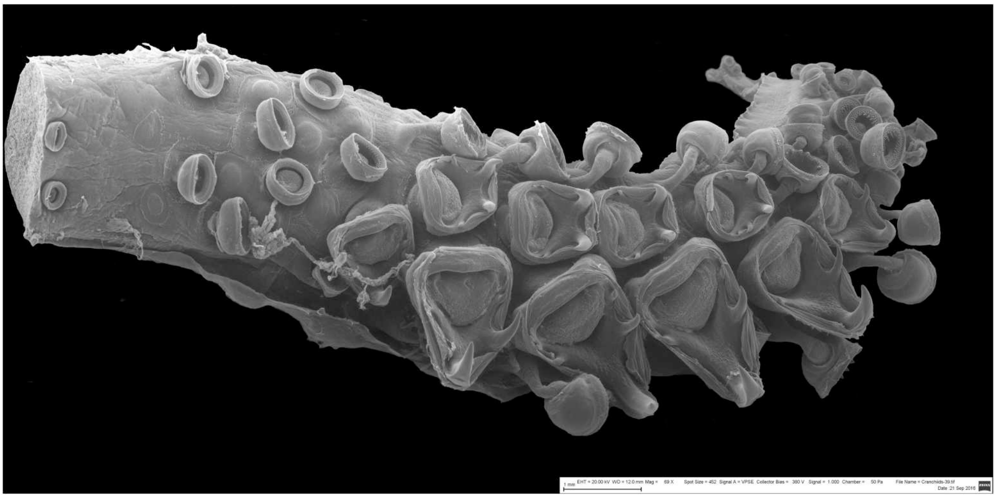

Figure 15. *Taonius robisoni* sp. nov., right tentacle club (SBMNH 464982; ML 210 mm).

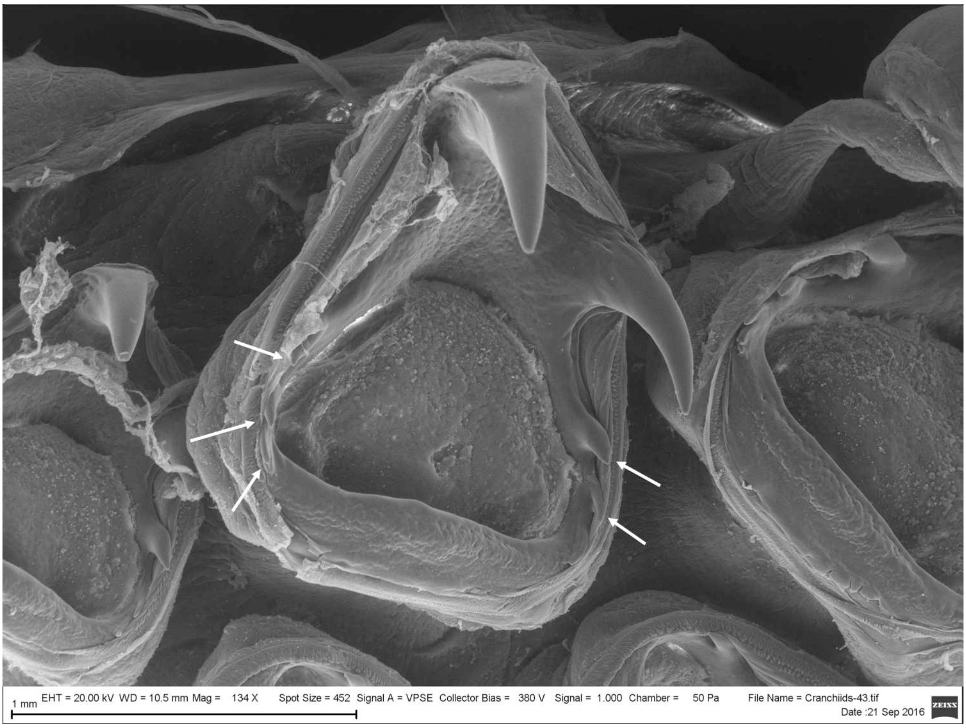

Figure 16. *Taonius robisoni* sp. nov., mid-manus medial sucker (SBMNH 464982; 210 mm); arrows indicate secondary cusps.

28–48 suckers on longest arm. Sucker size increases slightly mid-arm, then decreases distally; basal-most arm suckers lack dentition, largest mid-arm suckers and remaining distal suckers with three or four low, blunt teeth (Figure 13e). Tentacles ~35% ML; clubs (Figure 15) ~5% ML (15–22% TnL) with ~60 suckers. Largest manus suckers with two enlarged primary cusps and two small secondary cusps (Figure 16) on each side; smaller manus suckers with two primary cusps and three or four smaller secondary cusps on each side.

Known distribution. North-eastern sub-tropical Pacific Ocean (Figure 1), from California to Mexico (29°N–33°N) and the Hawaiian Islands; elsewhere reported as '*Taonius* sp.' from southern Californian waters (Young 1972).

Remarks. *Taonius robisoni* sp. nov. is most easily distinguished by the number of arm-sucker teeth. This species has, at most, four blunt teeth on the largest arm suckers, while all other species with arm-sucker teeth have at least five. This species has frequently been identified in museum collections as *T. pavo,* which is presently known only from the Atlantic Ocean. Although their distribution is not known to overlap, these two species do share some morphological similarities. The holotype of *T. pavo* also has arm suckers with four or five blunt teeth on the distal ring margin. Unfortunately, the holotype of *T. pavo* lacks tentacles, so it was not possible to compare them to the clubs of *T. robisoni*, but previous descriptions of *T. pavo* report only two large, curved teeth on the manus suckers (Voss 1980) and do not mention any smaller secondary cusps along the ring margin, such as are present on the manus suckers of *T. robisoni*. This is consistent with other non-type specimens of *T. pavo* (from the Atlantic) that were examined (Evans 2018).

Taonius robisoni is genetically distinct from all other *Taonius* species (BOLD: AAK0251; Figure 2). Although this species is most morphologically similar to *T. pavo*, it formed a clade with *T. tanuki* sp. nov., *T.* cf. *belone,* and *T.* sp. PO1. The nearest neighbour for *Taonius robisoni* is *T. tanuki* (minimum interspecific distance of 4.4%). The genetic relationship between *T. pavo* and *T. robisoni* is not resolved in the current analysis.

Etymology. This species is named in honour of Dr Bruce Robison, from the Monterey Bay Aquarium Research Institute (MBARI), Monterey, CA, USA. Mid-water ecology research voyages, often led by Dr Robison, have captured extensive footage of *Taonius* and numerous otherwise rarely observed cephalopods off the coast of California, providing considerable insight into these animals' distribution and ecology.

***Taonius tanuki* sp. nov.** (Tables 1–3, Figures 17–21)

Taonius sp. 2: Marshall et al. 2023: 237.

Taonius sp. KER2: Braid & Bolstad 2019: 402–425. *Diagnosis*: Mantle slender (mean MW 19% ML). Inner eye photophore resembles the typographical curly bracket symbol ({). Arm suckers with 12–18 blunt teeth; largest tentacle club suckers with two primary cusps and one small secondary cusp on each side.

Type material

[Holotype] **AM C.607890** (previously **NMNZ M.172910)**, ML 453 mm, ♂, 28.83°S, 167.57°E, Norfolk Ridge, S of Norfolk Island, 1000–1050 m, Stn.2003030, ethanol 80%; [Paratype] **NMNZ M.172913**, ML 395 mm, ♂, 29.53°S, 167.63°E, Norfolk Ridge, 200–1200 m; [Paratypes] **NMNZ M.172908** (7 specimens), ML 283, 276, 272, 270, 261, 260, 237 mm, ♂/♀, 32.43°S, 161.76°E, Lord Howe Rise SE of Lord Howe Island, 1200–1300 m, Stn.2003074.

Additional material examined (4 specimens)

AIM 124799 [BOLD Process ID KERCE062-17], 30.3°S 178.2°W, Kermadec Islands, 1000 m, MWT, TAN1612/69, 28/10/2016; **NMNZ M.09146**, ML 250 mm, sex indet., 40.07°S, 167.90°E, New Zealand, 900 m, BT, Stn.J19/12/84; **NMNZ M.091403**, ML 208 mm, sex indet., 40.08°S, 168.11°E, New Zealand, 900 m, BT, Stn.J19/06/84; **NMNZ M.091392**, ML 235 mm, sex indet., 44.69°S, 173.53°E, New Zealand, 700 m, MWT, Stn.J15/52/83.

Description

(ML 235–453 mm; Figures 17–21)—Mantle slender, conical (MW 13–*19*–28% ML). Fins narrow, lanceolate; FL 33–*37*–41% ML; FW <15% ML (fins damaged in majority of

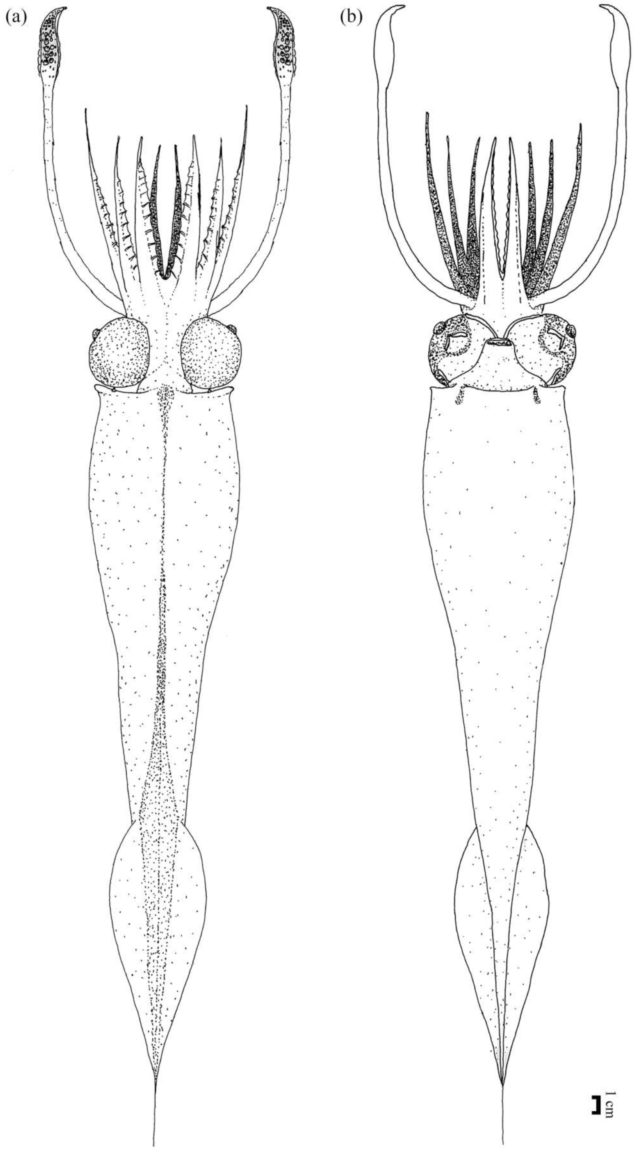

Figure 17. *Taonius tanuki* sp. nov., schematic (a) dorsal view, (b) ventral view (NMNZ M.172913; ML 395 mm).

examined specimens). HL 8–*13*–22% ML; HW 8–*13*–20% ML; eyes large, ED *9*% ML, with two near-crescent shaped photophores, outer photophore terminates just anterior to arm crown, inner photophore ~40% ED, resembles curly bracket ({) (Figure 18). Funnel narrows slightly, FA 26–*49*–73% FB, cartilaginous window at funnel fusion oval, curved towards ventral mid-line (Figure 19).

Arms robust basally, slender distally; formula III>II>IV>I (although lengths vary only slightly): Arm I 11–*18*–26% ML, Arm II 15–*21*–30% ML, Arm III 18–*24*–30% ML, Arm IV 17–*21*–25% ML. Arms with up to 50 suckers increasing slightly in size toward mid-

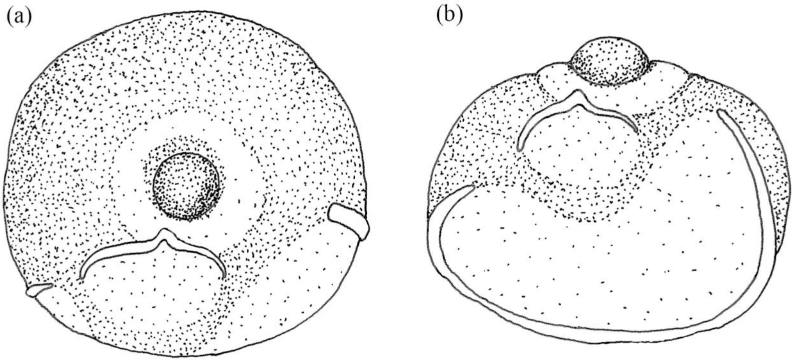

Figure 18. *Taonius tanuki* sp. nov., right eye schematic (a) lateral view, (b) ventral view (AM C.607890; ML 453).

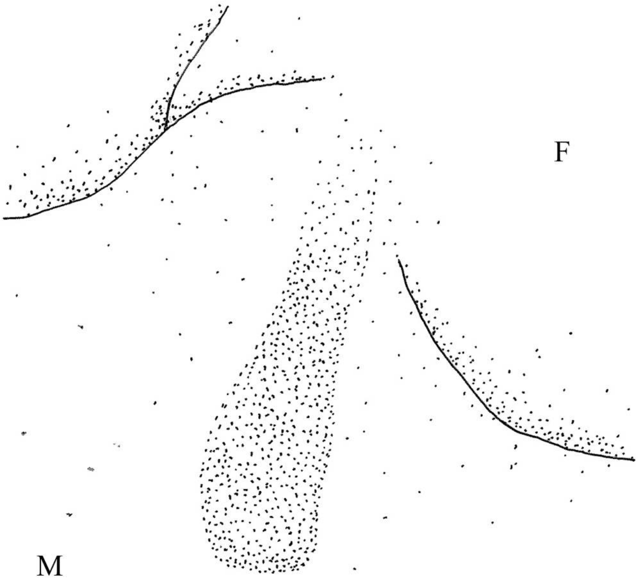

Figure 19. *Taonius tanuki* sp. nov., right funnel-mantle fusion window, schematic of connection between mantle (M) and funnel (F) shown (NMNZ M.172938; ML 221 mm).

arm; largest arm sucker with 12–18 teeth, decreasing along arm length to four or five in distal suckers. Oral surfaces of arms narrow, causing biserial suckers to appear uniserial on proximal half of arm. Distal 25–30% of male Arms I–III modified, with about six longitudinal series of small oblong suckers (Figure 20). Tentacles 42–*57*–67% ML, stalks with 11–24 pairs of adentate suckers (Figure 21a). Clubs 7–*9*–11% ML (13–24% TnL) with 68–108 suckers. Largest manus suckers (Figure 21d) with two enlarged primary cusps and 0–1 small secondary cusps on each side.

Known distribution. Southern Pacific species presently known from Norfolk Island to southern Aotearoa New Zealand (28°S–45°S) (Figure 1), 200–1200 meters.

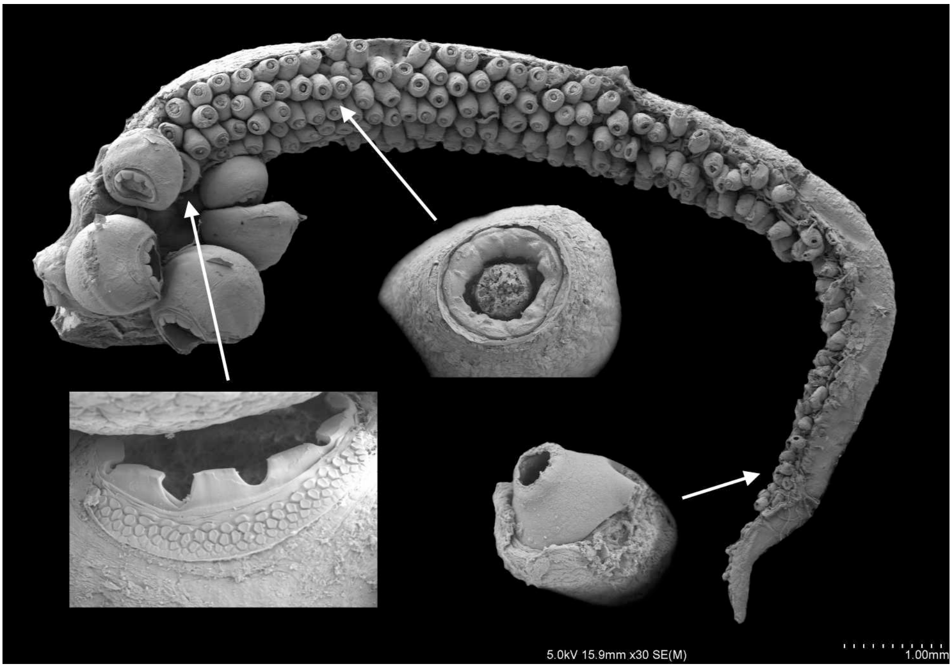

Figure 20. *Taonius tanuki* sp. nov., Arm III male modification (NMNZ 172913; ML 395 mm).

Remarks. *Taonius tanuki* can be distinguished from all other *Taonius* species by the arm and tentacle sucker morphology (Table 3). This species is morphologically similar to the North Atlantic *T. pavo*, and much of the Pacific *Taonius* material has previously been attributed to *T.* '*pavo*'. The holotype of *T. pavo* (described by Lesueur [1821] as elongated with large eyes and short arms) was examined to facilitate accurate comparisons, and while *T. pavo* and the South Pacific *Taonius* specimens share some morphological characteristics common to the genus (such as an elongated mantle and proportionally shorter arms), the holotype of *Taonius pavo* also has four blocky teeth on the basal arm suckers (unfortunately, the distal arm tips and tentacles had been removed). This differs from both known southern Pacific taxa, which have at least 12 teeth (*T. tanuki* sp. nov.) or lack teeth (*T. expolitus* sp. nov.).

Taonius tanuki is genetically distinct from other species in the genus (BOLD: ADH3663), including *T. pavo* (BOLD:AAM9951; Figure 2). The relationship between this species and others in the genus is currently unresolved, but it does form a clade with *T. robisoni* sp. nov. *T.* sp. PO1, and *T.* cf. *belone*. The nearest neighbour of *T. tanuki* is *T.* cf. *belone* and these species have a minimum interspecific distance of 4.4% (Table 2). Only a single individual of *T. tanuki* was available for sequence analysis, so the intraspecific variation in this species is not known.

Taonius tanuki appears to occur in the southern Pacific Ocean around Aotearoa New Zealand and the Tasman Sea (Figure 1). No evidence was found in the present study for the occurrence of *T. pavo sensu stricto* in the Pacific Ocean; at present, it appears restricted to the Atlantic Ocean. *Taonius tanuki* occurs sympatrically with *T. expolitus* sp. nov. around the Rangitāhua/Kermadec region north of Aotearoa New Zealand, but

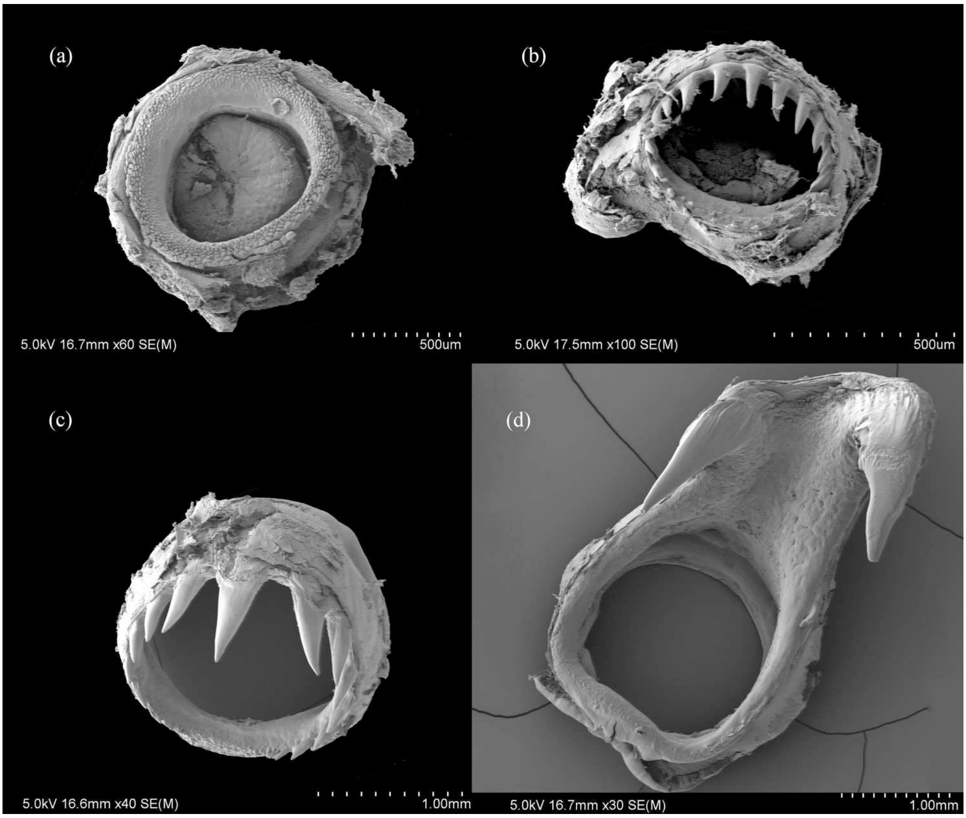

Figure 21. *Taonius tanuki* sp. nov., tentacle suckers: (a) tentacle stalk, (b) small manus sucker, (c) dactylus sucker, (d) largest manus sucker (NMNZ 172913; ML 395 mm).

can be readily differentiated since *T. expolitus* has adentate arm suckers, whereas *T. tanuki* has 12–18 blunt teeth. The nearest neighbour for *T. tanuki* is *T. expolitus*, but these species were assigned separate BINs (BOLD:ADH3662 for *T. expolitus*) and have a minimum interspecific distance of 10.3% (Table 1).

Etymology. The tanuki is a mammal endemic to Japan, and a common trickster figure in Japanese myth and folklore, notorious for being a mischievous shape-shifter. This seems apt, given both the historical systematic instability of this genus and a series of perplexing complications that arose while designating the type series. This name additionally pays homage to the extensive Japanese contributions to cephalopod research, as was made evident at the 2015 Cephalopod International Advisory Council proceedings in Hakodate.

Discussion

This work triples the known diversity of *Taonius* in the Pacific Ocean and provides useful characters for distinguishing among species. Four of the six Pacific species are new to science: *T. expolitus*, *T. notalia*, *T. robisoni*, and *T. tanuki*. A seventh potential species is currently only known from genetics (*T.* sp. PO1; BOLD:

ADH3660), and will require further investigation as additional specimens become available. Yet more taxa may be recognised as further morphological and genetic material becomes available for study; little material is yet available for the western equatorial, northern central, and southeastern parts of the Pacific Ocean basin in particular.

Several morphological features appear most helpful for identifying and delimiting *Taonius* species, but as is typical for cranchiids, many of these are vulnerable to damage during collection. For material in good condition, sucker armature (both arm and tentacle) is particularly valuable, although the number of teeth on the arm suckers decreases distally, so care must be taken to compare suckers from similar locations on the arms. The shape and proportions of the mantle and fins are less useful, being very similar in many species, although *T. robisoni* can be distinguished by its relatively long fins (Figure 13, Table 3), while the mantle of *T. borealis* is stouter than that of other species (Figure 4, Table 3). Only slight variation has been observed in the arm lengths. Eye photophore patterns can also be helpful, but are often difficult to compare due to the delicacy of—and therefore frequent damage to—the eyes. Beaks have been used extensively in other families for species identification from predator stomachs (e.g. Cherel and Weimerskirch 1999; Cherel et al. 2004; Xavier and Cherel 2009), but their variability in cranchiids remains less well known, partly because specimens of many species are relatively rare in collections and the potential for damage during beak removal is too great. Pending additional fresh material, a more thorough investigation of the beak and gladius morphology may reveal additional characters, which would be of particular value for dietary work on these squids' predators.

While the present work focuses on Pacific taxa, some Atlantic specimens including the holotype of *T. pavo* were examined. *Taonius pavo* has at times functioned as a cosmopolitan 'catch-all' name for specimens that fit a broad set of characteristics—long, slender, conical mantle with lanceolate fins approximately half the mantle length—many of which were eventually re-identified as a range of other taxa (including some from other genera, e.g. *Galiteuthis phyllura*). Lesueur's (1821) original description of *Loligo pavo*, from 'Sandy Bay' somewhere along the North American east coast, reported an elongated and pointed mantle, rusty-brown colouration, and extremely large eyes that were slightly anteriorly directed. The description did not provide details regarding sucker armature; the tentacles and distal arm tips of the specimen were missing. The holotype has deteriorated significantly in the meantime, but some of the larger remaining arm sucker rings have four or five blunt teeth on their distal margin, most similar to the three or four present in *T. robisoni*. On more complete *Taonius* specimens recently examined from the western North Atlantic (e.g. NMNH 1080249, ML 227 mm) and reported by Young (2014a), the large central manus suckers possess two large, curved teeth, and have no smaller secondary cusps along the lateral margins. While it is possible that additional *Taonius* species will be recognised in the Atlantic, at present we attribute specimens with these morphological characters to *T. pavo* and use this as a basis for comparison with (and differentiation from all known) Pacific taxa. Sequences obtained from specimens identified as *T. pavo* (M. Vecchione pers. comm.), collected from the western North Atlantic, are also genetically distinct from the six Pacific species treated in this study (Appendix A, Figure 2). However, a full redescription of *T. pavo* and a review of material collected throughout the Atlantic region should be undertaken.

The six known Pacific *Taonius* species are all morphologically and genetically distinct from our current understanding of *T. pavo* (*s.s.*). *Taonius* cf. *belone* is most morphologically similar, possessing similar manus sucker morphology. However, *T.* cf. *belone* differs in the arm-sucker dentition, with 20–30 small blunt teeth around the entire sucker ring margin (whereas *T. pavo* has fewer teeth and only on the distal margin). Interestingly, our COI analyses show that *T.* cf. *belone* is also the nearest genetic neighbour of *T. pavo* (7.7% divergent; Table 2), although the nearest neighbour of *T.* cf. *belone* itself is the unresolved *T.* sp. PO1 (a potentially new species currently known from the Indian Ocean and Japan). We note that Nesis (1972) described '*Belonella pacifica pacifica*' from Japanese waters, and later (1987) synonymised it with *T.* cf. *belone*. Pending additional morphological investigations, it may prove that '*B. pacifica pacifica*' represents the taxon herein sequenced as *T.* sp. PO1, which does appear to co-occur with *T.* cf. *belone* in both the northeastern Indian Ocean and the western North Pacific. *Taonius borealis* is also found in northern Japanese waters but differs morphologically from *T.* cf. *belone* (and *T. pavo*), both in sucker armature and in being noticeably stouter (Figure 4, Table 3), and genetically from *T.* cf. *belone* and *T.* sp. PO1 (and *T. pavo*).

Two of the remaining three Pacific species, *T. tanuki* and *T. expolitus* (currently known from waters surrounding Aotearoa New Zealand and Australia) have similarly been previously reported as '*T. pavo*'. These can now also be morphologically and genetically distinguished from each other, all north Pacific species, and Atlantic *T. pavo. Taonius tanuki* possesses a unique combination of arm and manus sucker dentition: the largest manus suckers have two large distal primary cusps and one or two smaller secondary cusps along each lateral margin, and the largest arm suckers have approximately 18 teeth, with an adentate proximal section (Table 2). In addition, the inner eye photophore of *T. tanuki* resembles a pinched crescent (or a curly bracket), also a unique character within the genus. *Taonius tanuki* can also be distinguished genetically from all other species in this genus, and shows a close relationship with *T. robisoni* (4.8% divergent).

Taonius expolitus can be distinguished from all known congeners by its unique arm-sucker morphology, the manus sucker tooth arrangement, and genetics. Although the existing material for this taxon is severely damaged, *T. expolitus* is the only known *Taonius* species to lack dentition on the larger mid-arm suckers (although several other *Taonius* species do lack dentition on the basal-most arm suckers). The manus suckers of this taxon also differ from other known *Taonius*, as they lack the enlarged primary cusps otherwise characteristic of this genus, instead having 5–11 subequal pointed teeth set around the distal margin (Figure 10). Both of these characters are unique within the genus *Taonius*, and this combination of characters also differs from any other known cranchiid. In our COI analyses, the relationship of *T. expolitus* to other *Taonius* species was not resolved (Figure 2). This species had the largest nearest neighbour divergence (10.3% divergence), but not the largest divergence found within this genus (13.6%, which was found between *T.* cf. *borealis* and *T. notalia*). Given these differences, it is possible that *T. expolitus* may later be moved into a new genus. However, this will require additional specimens and gene regions; for the moment, *Taonius* remains the most suitable available genus.

Taonius notalia is the first *Taonius* species known to occur in sub-Antarctic waters (Figure 1). Although this species has a similar mantle width, fin length, and arm formula to other *Taonius* species, it can be distinguished by arm-sucker morphology, and manus-sucker structure (Figure 12, Table 3). The manus suckers of this taxon are most similar to those of *T. borealis*; however, *T. notalia* has only a single primary cusp (as opposed to the two primary cusps present in *T. borealis*) and two or three smaller secondary cusps along each lateral margin (progressively decreasing in size proximally). In addition, *T. notalia* has a more slender mantle (mean MW 15% ML) compared to *T. borealis*, which is often stout (mean MW 27% ML). Although the available material for *T. notalia* was limited, the gladius of specimens is visible only as a narrow line through the dorsal outer integument, whereas most other *Taonius* species have a gladial vane visibly wider than two millimetres. Genetically, *T. notalia* specimens form a single clade, distinct from all other *Taonius* species (Figure 2). This species appears to be quite distinct from others in this genus, and has a nearest-neighbour relationship with *T. tanuki* (9.8% divergent; Table 1).

Members of the genus *Taonius* appear to be widely distributed throughout the Pacific, and sympatric species are now recognised in several regions. In the south-western Pacific Ocean, *T. tanuki* and *T. expolitus* co-occur, and off the west coast of North America, *T. borealis* and *T. robisoni* co-occur (Figure 1). In addition, the potentially new species *T.* sp. ‘PO1’ appears to co-occur with *T.* cf. *belone* in both the northeastern Indian Ocean, and—along with *T. borealis*—in the north-western Pacific Ocean (Figure 1). While only a single species is presently known from sub-Antarctic waters, the Atlantic Ocean, and Hawaiian waters, material from these regions remains sparse (and entirely unknown from other regions such as the eastern South Pacific) and future research may well reveal additional taxa and/or wider distributions than those currently recognised. It seems highly likely that, given the diversity seen in the Pacific Ocean, undescribed species remain to be discovered in other major bodies of water, and future research should focus on a worldwide systematic revision of *Taonius*.

Conclusion

This research re-describes the two previously reported *Taonius* taxa from Pacific waters and describes four additional novel species. Pending additional material, future research into *Taonius* diversity should examine the hard internal structures (beak and gladius), to support ecological research, as these features may be isolated and identified as prey remains in the stomach contents of marine predators. Additionally, fresh tissue samples of *Taonius* specimens should be collected for molecular analysis, and additional gene regions investigated in order to fully understand the phylogenetic relationships among *Taonius* species, and within the Cranchiidae.

Acknowledgements

Many research programmes and institutions provided material in support of this research. For specimens collected within the Aotearoa New Zealand EEZ, we thank the Scientific Observer Programme and its observers, funded by Ministry for Primary Industries (Fisheries New Zealand); NIWA (particularly S. Mills, D. Stevens, D. MacPherson, K. Schnabel, D. Stotter and C. Chin) and Fisheries New Zealand for material collected by fisheries trawl surveys; and the Museum of New Zealand Te Papa Tongarewa (particularly B. Marshall and K. Walton). For specimens collected as part of the project ‘Biodiversity of the Kermadec Islands and offshore waters of the

Kermadec Ridge – a coastal, marine mammal and deep-sea survey (TAN1612)', we acknowledge and appreciate funding from the Marine Funding Advisory Research Group, NIWA (project COBR1705), Ministry for the Environment, Museum of New Zealand Te Papa Tongarewa, Auckland War Memorial Museum and The Pew Charitable Trust. We also thank the crew, support staff, and organisers of the following vessels and voyages: RV *Tangaroa*; RV *Dorada*; Marine National Facility RV *Investigator* (J. Keesing, T. Sime, J. Wakeford), Gascoyne Marine Park (Western Australia) in 2022; Monterey Bay Aquarium Research Institute's RV *Western Flyer* (S. Bush, H.-J. Hoving, K. Reisenbichler, B. Robison, R. Sherlock); Y. Cherel (CEBC, France), fishery observers from the Terres Australes et Antarctiques Françaises (Crozet and Kerguelen waters), and the fishery team from the MNHN (Paris); A. Choy (North Pacific Trophic Research Programme). We also thank the staff at the National Museum of Nature and Science (Tokyo), the Australian Museum (A. Reid), Museum Victoria (C. Rowley), National Museum of Science and Technology, Royal British Columbia Museum (H. Gartner), and Santa Barbara Museum of Natural History (D. Geiger). This research was supported by the International Seabed Authority's Sustainable Seabed Knowledge Initiative: One Thousand Reasons Campaign (co-financed by the European Maritime and Fisheries Fund of the European Union, Project 101071214 — SSKI-I — EMFAF-2021-ISA-SSKI-IBA) and by Auckland University of Technology.

Disclosure statement

No potential conflict of interest was reported by the author(s).

ORCID

Aaron Evans http://orcid.org/0000-0003-0808-2293
Heather Braid http://orcid.org/0000-0003-0428-5800
Tsunemi Kubodera http://orcid.org/0000-0003-0783-7148

References

Arkhipkin A. 1996. Statolith microstructure and age of early life stages of planktonic squids *Galiteuthis phyllura* and *Belonella borealis* (Oegopsida, Cranchiidae) from the northern North Pacific. Journal of Plankton Research. 18(1):123–132. doi: 10.1093/plankt/18.1.123.

Berry SS. 1911. Preliminary notices of some new Pacific Cephalopods. Proceedings of the United States National Museum. 40(1838):589–592. doi: 10.5479/si.00963801.1838.589.

Bolstad KSR, Perez JAA, Strugnell JM, Vidal EAG. 2015. Cranchiids of the South Atlantic Mid-Oceanic Ridge: results from the first southern MAR-ECO expedition. Journal of Natural History. 49(21-24):1351–1371. doi: 10.1080/00222933.2013.867375.

Braid HE, Bolstad KS. 2019. Cephalopod biodiversity of the Kermadec Islands: implications for conservation and some future taxonomic priorities. Invertebr Syst. 33(2):402–425.

Chen RS, Portner EJ, Choy CA. 2022. Gelatinous cephalopods as important prey for a deep-sea fish predator. Marine Biology. 169(12):155. doi: 10.1007/s00227-022-04116-w.

Cherel Y. 2020. A review of Southern Ocean squids using nets and beaks. Marine Biodiversity. 50 (6):98. doi: 10.1007/s12526-020-01113-4.

Cherel Y, Duhamel G, Gasco N. 2004. Cephalopod fauna of subantarctic islands: new information from predators. Marine Ecology Progress Series. 266:143–156. doi: 10.3354/meps266143.

Cherel Y, Weimerskirch H. 1999. Spawning cycle of onychoteuthid squids in the southern Indian Ocean:new information from seabird predators. Marine Ecology Progress Series. 188:93–104. doi: 10.3354/meps188093.

Chun C. 1906. System der Cranchien. Zoologischer Anzeiger. 31(2):82–86.

Chun C. 1910. Die Cephalopoden. I. Oegopsida. Wissenschaftliche Ergebnisse Der Deutschen Tiefsee-Expedition Valdivia. 18:1–401.

d'Orbigny A. 1845. Mollusques vivants et fossiles ou description de toutes les espèces de Coquilles et de Mollusques. Paris: Gide et Cie., éditeurs.

Evans AB. 2018. A systematic review of the squid family Cranchiidae (Cephalopoda: Oegopsida) in the Pacific Ocean [Doctoral Thesis]. Auckland (New Zealand): Auckland University of Technology.

Evans AB, Bolstad KSR. 2014. Ontogeny of the deep-sea cranchiid squid Teuthowenia pellucida (Cephalopoda: Cranchiidae) from New Zealand waters. Journal of Natural History. 49(21–24):1327–1349. doi: 10.1080/00222933.2013.840747.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molec Mar Biol Biotechnol. 3:294–299.

Glaubrecht M, Salcedo-Vargas MA. 2000. Annotated type catalogue of the Cephalopoda (Mollusca) in the Museum für Naturkunde, Humboldt University of Berlin. Zoosystematics and Evolution. 76(2):269–282. doi: 10.1002/mmnz.20000760209.

Imber MJ. 1978. The squid families Cranchiidae and Gonatidae (Cephalopoda: Teuthoidea) in the New Zealand region. New Zealand Journal of Zoology. 5(3):445–484. doi: 10.1080/03014223.1978.10428331.

Katoh K, Standley DM. 2013. MAFFT Multiple Sequence Alignment Software Version 7: improvements in performance and usability. Molecular Biology and Evolution. 30(4):772–780. doi: 10.1093/molbev/mst010.

Kumar S, Stecher G, Tamura K. 2016. MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for bigger datasets. Molecular Biology and Evolution. 33(7):1870–1874. doi: 10.1093/molbev/msw054.

Lane FW. 1957. Kingdom of the Octopus, the life-history of the Cephalopoda. London: Jarrolds Publishers Ltd.

Lesueur CA. 1821. Description of several new species of cuttlefish. Journal of the Academy of Natural Sciences of Philadelphia. 2(1):86–101.

Lindgren AR. 2010. Molecular inference of phylogenetic relationships among Decapodiformes (Mollusca: Cephalopoda) with special focus on the squid order Oegopsida. Molecular Phylogenetics and Evolution. 56(1):77–90. doi: 10.1016/j.ympev.2010.03.025.

Lu CC, Clarke MR. 1974. Two new species of cranchiid cephalopod from the North Atlantic, *Uranoteuthis bilucifer* n. gen., n. sp. Journal of the Marine Biological Association of the United Kingdom. 54(4):985–994. doi: 10.1017/S0025315400057702.

MacLeod CD, Santos MB, Pierce GJ. 2003. Review of data on diets of beaked whales: evidence of Niche separation and geographic segregation. Journal of the Marine Biological Association of the United Kingdom. 83(3):651–665. doi: 10.1017/S0025315403007616h.

Marshall BA, Bolstad KSR, Enderby A. 2023. Checklist of extant Mollusca known from the New Zealand EEZ. In: Kelly M, Mills S, Terezow M, Sim-Smith C, Nelson W, editors. The marine biota of Aotearoa New Zealand: updating our marine biodiversity inventory. Wellington: NIWA Biodivers Mem, Vol. 136. p. 221–237.

Meier R, Zhang G, Ali F. 2008. The use of mean instead of smallest interspecific distances exaggerates the size of the "barcoding gap" and leads to misidentification. Systematic Biology. 57 (5):809–813. doi: 10.1080/10635150802406343.

Nesis KN. 1972. A review of the squid genera *Taonius* and *Belonella* (Oegopsida, Cranchiidae). Zool Zhurnal. 51(3):341–350.

Nesis KN. 1987. Cephalopods of the world; Squids, cuttlefishes, octopuses, and allies. Neptune City (NJ): T.F.H. Publications.

Pfeffer G. 1912. Die cephalopoden der plankton-expedition. Zugleich eine monographische übersicht der oegopsiden cephalopoden. Ergebnisse der plankton-expedition der Humboldt-Stiftung. 2:1–815.

Poltev YN. 2007. Specific features of spatial distribution of Pacific cod *Gadus macrocephalus* in waters off the eastern coast of the northern Kuril Islands and the southern extremity of Kamchatka. Journal of Ichthyology. 47(9):726–738. doi: 10.1134/S0032945207090068.

Prosch V. 1849. Nogle nye Cephalopoder. K Dansk Vidensk Selsk. 5(1):53–72.

Ratnasingham S, Hebert PD. 2007. BOLD: The barcode of life data system (http://www.barcodinglife.org). Molecular Ecology Notes. 7(3):355–364.

Ratnasingham S, Hebert PD. 2013. A DNA-based registry for all animal species: The Barcode index number (BIN) system: the Barcode index number (BIN). PLoS ONE. 8(7):e66213. doi: 10.1371/journal.pone.0066213.

Richterich P. 2004. New products. Genetics in Medicine. 6:162–163. doi: 10.1097/00125817-200405000-00012.

Roper CFE, Voss GL. 1983. Guidelines for taxonomic descriptions of cephalopod species. Memoirs of the National Museum of Victoria. 44:48–63. doi: 10.24199/j.mmv.1983.44.03.

Sasaki M. 1920. Report on cephalopods collected during 1906 by the United States Bureau of Fisheries steamer Albatross in the northwestern Pacific. Proceedings of the United States National Museum. 57(2310):163–203. doi: 10.5479/si.00963801.57-2310.163.

Steenstrup J. 1861. Overblik over de i Kjobenhavns Museer opbevarede Blaeksprutter fra det aabne Hav (1860-61). Overs Kongel Dansk Vidensk Selsk Forhandlinger. 1861:69–86.

Taite M, Vecchione M, Fennell S, Allcock AL. 2020. Paralarval and juvenile cephalopods within warm-core eddies in the North Atlantic. Bulletin of Marine Science. 96(2):235–262. doi: 10.5343/bms.2019.0042.

Voss GL. 1963. Cephalopods of the Philippine Islands. Bulletin of the United States National Museum. 234:1–180. doi: 10.5479/si.03629236.234.1.

Voss NA. 1980. A generic revision of the Cranchiidae (Cephalopoda; Oegopsida). Bulletin of Marine Science. 30(2):365–412.

Voss NA, Stephen SJ, Dong Z. 1992. Family Cranchiidae Prosch, 1849. In: Sweeney MJ, Roper CFE, Mangold KM, Clarke MR, Boletzky SV, editors. Larval" and juvenile cephalopods: a manual for their identification. Washington (DC): Smithsonian Institution Press; p. 187–210.

Watanabe H, Kubodera T, Moku M, Kawaguchi K. 2006. Diel vertical migration of squid in the warm core ring and cold water masses in the transition region of the western North Pacific. Marine Ecology Progress Series. 315:187–197. doi: 10.3354/meps315187.

Xavier JC, Cherel Y. 2009. Cephalopod beak guide for the Southern Ocean. Cambridge: British Antarctic Survey.

Young RE. 1972. The systematics and areal distribution of pelagic cephalopods from the seas off Southern California. Smithsonian Contributions to Zoology. 97:1–159. doi: 10.5479/si.00810282.97.

Young RE. 1975. Transitory eye shapes and the vertical distribution of two midwater squids. Pac Sci. 29(3):243–255.

Young RE. 2014a. *Taonius pavo* (Lesueur, 1821). Version 06 December 2014 (under construction). http://tolweb.org/Taonius_pavo/19611.

Young RE. 2014b. *Taonius belone* (Chun, 1906). Version 21 January 2014 (under construction). http://tolweb.org/Taonius_belone/120159.

Young RE, Harman RF. 1988. "Larva", "paralarva" and "subadult" in cephalopod terminology. Malacologia. 29(1):201–207.

Zhang J, Kapli P, Pavlidis P, Stamatakis A. 2013. A general species delimitation method with applications to phylogenetic placements. Bioinformatics. 29:2869–2876. doi: 10.1093/bioinformatics/btt499.

Appendix A: Bayesian Poisson Tree Processes (bPTP) analysis of cytochrome *c* oxidase subunit I (COI) Taonius sequences analysed in the present study. Red lines connect members of the same species, and blue lines show connections between separate species.