

# Resolving the taxonomic status of *Asperoteuthis lui* Salcedo-Vargas, 1999 (Cephalopoda, Chiroteuthidae) using integrative taxonomy

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Received: 11 April 2016 / Revised: 2 July 2016 / Accepted: 14 July 2016 / Published online: 7 November 2016  
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**Abstract** The biology and systematics of the squid genus *Asperoteuthis* Nesis, 1980, are poorly known. Although there have been four named and five described species in this genus, it now appears that there are only three valid species: *A. acanthoderma* (Lu, 1977), *A. mangoldae* Young, Vecchione & Roper, 2007a, and *A. lui* Salcedo-Vargas, 1999. Using a combination of mitochondrial DNA sequences (cytochrome *c* oxidase subunit I [COI], 16S rRNA, and 12S rRNA) and morphology, *A. nesis* Arkhipkin & Laptikhovskiy, 2008, and Clarke's (1980) '?*Mastigoteuthis* A' both appear to be junior synonyms of *A. lui*. The most distinctive feature of this species is the aboral tentacle club photophore distribution, which is chiral, with more photophores dorsally (~11–16) than ventrally (~9–12). Genetically, there is low intraspecific variation within *A. lui* and higher interspecific variation between this species and other chiroteuthids. Previously only known from the type description, *A. lui* now appears to have a circumpolar distribution in the Southern Ocean and is the most commonly encountered *Asperoteuthis* species in the diet of marine predators.

**Keywords** DNA barcode · Mollusca · Chiroteuthidae · Revision · Taxonomic description

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Communicated by M. Vecchione

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## Introduction

*Asperoteuthis* Nesis, 1980, is an enigmatic genus of poorly known meso-bathypelagic squids in the family Chiroteuthidae Gray, 1849. This genus is characterized by the presence of a tail structure, the absence of arm photophores, and unique tentacle clubs, each of which lacks suckers on the proximal half and is surrounded by a wide protective membrane (Young and Roper 2015). The exact use of asperoteuthid tentacles remains unknown and there is currently no data available on the feeding ecology of *Asperoteuthis*.

The type species *Asperoteuthis* was originally described as '*Chiroteuthis*' *acanthoderma* Lu, 1977. Nesis (1980) established a new genus for this species after examining additional specimens of *A. acanthoderma*. However, he incorrectly synonymized *A. acanthoderma* with '*Chiroteuthis*' *famelica* Berry, 1909 (now *Echinoteuthis famelica*, see Joubin 1933; Braid et al. 2014), which was poorly known at the time, because of similarities with Berry's description (e.g., skin tubercles and lanceolate fin), despite previous publications that supported the validity of this species (e.g., Roper and Young 1975; Young 1978). Young (1991) supported the validity of *E. famelica* and its place in the family Mastigoteuthidae, and suggested that the type species for the genus *Asperoteuthis* should be '*Chiroteuthis*' *acanthoderma*. Young et al. (2007a) officially fixed '*C.*' *acanthoderma* as the type species for *Asperoteuthis*.

There are currently four named species in this genus. *Asperoteuthis acanthoderma* was described from two immature individuals collected in the Celebes Sea in the Western Pacific Ocean (Lu 1977). This species has also been reported from the Northwestern Pacific Ocean near Okinawa (Tsuchiya and Okutani 1993), the Eastern Pacific near Hawaii (Young and Roper 2010), the North Atlantic Ocean in the Gulf of Mexico (Judkins et al. 2009), Straits of Florida (Judkins

et al. 2009), the Caribbean (Judkins et al. 2009), and the Indian Ocean off western Australia (Judkins et al. 2009). *Asperoteuthis lui* Salcedo-Vargas, 1999, was described from a single specimen from Cook Strait in New Zealand waters. *Asperoteuthis mangoldae* Young, Vecchione & Roper, 2007a, was described from specimens captured in Hawaiian waters. Most recently, *Asperoteuthis nesisi* Arkhipkin & Laptikhovskiy, 2008, was described from a single specimen that was captured around the Falkland Islands in the Southern Ocean. A fifth species was reported by Clarke (1980) as “*Mastigoteuthis A*”, but is now believed to belong in *Asperoteuthis* rather than in the family Mastigoteuthidae Verrill, 1881 (Arkhipkin and Laptikhovskiy 2008).

The purpose of this paper is to review the systematics of *A. lui*, which was originally described from a single, partial specimen that was from the stomach contents of a ling (*Genypterus blacodes*), and was damaged due to digestion (Salcedo-Vargas 1999). A redescription was possible because of additional, recently collected, material. The status of the species described in the genus *Asperoteuthis* is assessed using a combination of mitochondrial genes (cytochrome *c* oxidase subunit I [COI], 16S rRNA, and 12S rRNA) and morphology.

## Methods

### Genetic analysis

DNA was extracted from eight specimens. Frozen tissue was available for four specimens (one whole individual, three tentacles only), which were identified by tentacle-club morphology as *A. lui* (Table 1). Tissue fixed in 80 % ethanol was available for the other four specimens (one whole individual without tentacles, three that were beaks and buccal mass only), which were identified as “*Mastigoteuthis A*” based on beak morphology (by Darren Stevens) (Table 1). Additional sequences were obtained from GenBank for the type specimen of *A. nesisi* and the outgroup species *A. mangoldae*, which was chosen based on the results from Braid et al. (2016). Their study showed some support for a close relationship between *A. lui* and *A. mangoldae*. This outgroup was included to show the relationship between *A. lui*, *A. nesisi*, and “*Mastigoteuthis A*”. *Asperoteuthis acanthoderma* was not included in this phylogeny because it does not form a monophyletic clade with these species (Braid et al. 2016), but comparative sequences are available for this species in the Barcode of Life Data System (BOLD; CHSQX002-16, CHSQX001-16) and GenBank (KX783171, KX783229, KX783197, KX783172, KX783230, KX783198, and KT326921).

DNA was extracted using EconoSpin columns with QIAGEN reagents following protocols for the DNeasy Blood & Tissue Kit (QIAGEN). Three mitochondrial gene regions (COI, 16S rRNA, and 12S rRNA) were amplified and

sequenced following protocols and using primers in Braid et al. (2014). Bidirectional sequencing reactions were performed by Macrogen (Korea) using the same primers used for the polymerase chain reaction (PCR). Sequences were assembled into contigs and edited using Sequencher v.4.9 (Gene Codes) and then uploaded to the BOLD (Ratnasingham and Hebert 2007) public project titled ‘Resolving the taxonomic status of *Asperoteuthis lui*’ (project code: ALUI) and subsequently submitted to GenBank (Table 1). Sequences were checked for potential contamination using the Basic Local Alignment Search Tool (BLAST) through GenBank.

Sequences were aligned separately for each gene using the Multiple Alignment using Fast Fourier Transform (MAFFT) online server (Kato and Standley 2013), then concatenated in SequenceMatrix 1.8 (Vaidya et al. 2011). The concatenated alignment was analyzed in PartitionFinder 1.1.1 (Lanfear et al. 2012) to determine optimal partitioning and models using all substitution models included under the Bayesian Information Criterion (BIC). Each gene, as well as all codon positions for COI, were searched separately for a maximum of five partitions. The model TrN was chosen for both 16S rRNA and 12S rRNA. Different models were chosen for each codon position of COI as TrNef, F81, and HKY, respectively. A maximum-likelihood combined phylogeny with 1000 bootstrap replicates was created in GARLI 2.0.1 (Zwickl 2006). A consensus tree was created in Geneious 7.1.7 (Biomatters, Auckland, New Zealand) and branches were collapsed when bootstrap support values were less than 50. The final phylogeny was visualized in FigTree 1.4.0 (Rambaut 2012). The Barcode Index Number (BIN) system was also used to test the species boundaries of *A. lui*, *A. nesisi*, and “*Mastigoteuthis A*” (Ratnasingham and Hebert 2013). Intra- and interspecific distances for each gene region (COI, 16S rRNA, and 12S rRNA) were calculated using MEGA 6.06 (Tamura et al. 2013) using the Tamura–Nei (Tamura and Nei 1993) model with gamma correction.

### Morphological analysis

Original type descriptions for all asperoteuthid species were reviewed. The type specimen for *A. lui* from the National Museum of New Zealand Te Papa Tongarewa (NMNZ) was examined, and photographs of the type specimen for *A. nesisi* from the British Museum of Natural History (BMNH) were observed. All specimens that were used for DNA sequencing were examined. A specimen of *A. mangoldae* was examined from the Field Museum of Natural History (FMNH). The entire national collections of asperoteuthid specimens were loaned and examined from the NMNZ and the National Institute of Water and Atmospheric Research Ltd. (NIWA) in Wellington. Additional non-morphological abbreviations used are: MNHN—Muséum National d’Histoire Naturelle; RV—research vessel; Stn—station; USNM—U.S. National Museum of Natural History, USA.

**Table 1** Specimen information for sequences used in this study. Under ‘Original morphological ID, the feature used for the identification is indicated in brackets. Identifications based on beak morphology were conducted by Darren Stevens from the National Institute of Water and

Atmospheric Research Ltd. (NIWA). ‘Specimen ID’ is the registration number. The ‘BOLD (Barcode of Life Data Systems) ID’ is the unique identifier given to each specimen

Original morphological ID	Genetic ID	Specimen ID	BOLD ID	GenBank ID			Reference
				COI	16S rRNA	12S rRNA	
‘?Mastigoteuthis A’ (beak)	<i>A. lui</i>	NIWA 95040	ALUI008-16	KX675425	KX675433	KX675441	Present study
‘?Mastigoteuthis A’ (beak)	<i>A. lui</i>	NIWA 95039	ALUI007-16	KX675426	KX675434	KX675442	Present study
‘?Mastigoteuthis A’ (beak)	<i>A. lui</i>	NIWA 93270	ALUI006-16	KX675427	KX675435	KX675443	Present study
‘?Mastigoteuthis A’ (beak)	<i>A. lui</i>	NIWA 95041	ALUI005-16	KX675428	KX675436	KX675444	Present study
<i>A. lui</i> (tentacle club)	<i>A. lui</i>	NIWA 96166	ALUI004-16	KX675429	KX675437	KX675445	Present study
<i>A. lui</i> (tentacle club)	<i>A. lui</i>	NIWA 96168	ALUI003-16	KX675430	KX675438	KX675446	Present study
<i>A. lui</i> (tentacle club)	<i>A. lui</i>	NIWA 93268	ALUI002-16	KX675431	KX675439	KX675447	Present study
<i>A. lui</i> (tentacle club)	<i>A. lui</i>	NIWA 97258	ALUI001-16	KX675432	KX675440	KX675448	Present study
<i>A. nesisi</i> (type description)	<i>A. lui</i>	BMNH 20070615	GBCPH775-09	EU421718	EU421719	EU421720	Arkhipkin and Laptikhovskiy (2008)
<i>A. mangoldae</i>	<i>A. mangoldae</i>	FMNH 278099	CHSQX003-16	KX783173	KX783231	KX783199	Braid et al. (2016)

Distribution maps of *Asperoteuthis* species (Fig. 1) and *A. lui* specimens, found in New Zealand waters (Fig. 2), were created with ArcGIS 10.2 (Environmental Systems Research Institute [ESRI], Redlands, CA). The distribution for *A. acanthoderma* is based on specimen records from the Smithsonian National Museum of Natural History (USNM 1111098, USNM 1179399, USNM 1179402, USNM 1179422, USNM 1179632, and USNM 1179696) and MNHN (MNHN-IM-2002-2266), and localities from Lu (1977), Nesis (1980), Tsuchiya and Okutani (1993), Judkins et al. (2009), Young and Roper (2010), and Braid et al. (2016). The distribution for *A. mangoldae* is based on Young et al. (2011). The locality for ‘?Mastigoteuthis A’ (Clarke 1980) and the type localities for *A. nesisi* (BMNH 20070615) and *A. lui* (NMNZ M.143859) are indicated.

Collection data for some specimens were not available (ex-gut-content material). Collection dates are listed as dd/mm/yyyy. Specimens are listed by order of decreasing latitude, and secondarily by lower rostral length (LRL). Specimens were sexed when a viscera was present, while badly damaged specimens or beak-only specimens where sex could not be determined were designated ‘sex indet.’. Measurements were taken from the most complete side of the specimen and ranges are given in the format of lowest value (X), mean (Y), and largest value (Z) in the format of X–Y–Z; when the range was less than 5 % ML, only the mean is provided. Measurements of damaged features are indicated by an asterisk (\*). Morphological examinations focused on both internal (beak, palps, and radula) and external anatomy following Braid and Bolstad (2015).

The species description was made in accordance with the guidelines provided by Roper and Voss (1983), with some modification (see Braid and Bolstad 2015). Beaks were described following Clarke (1986) and drawn using a camera

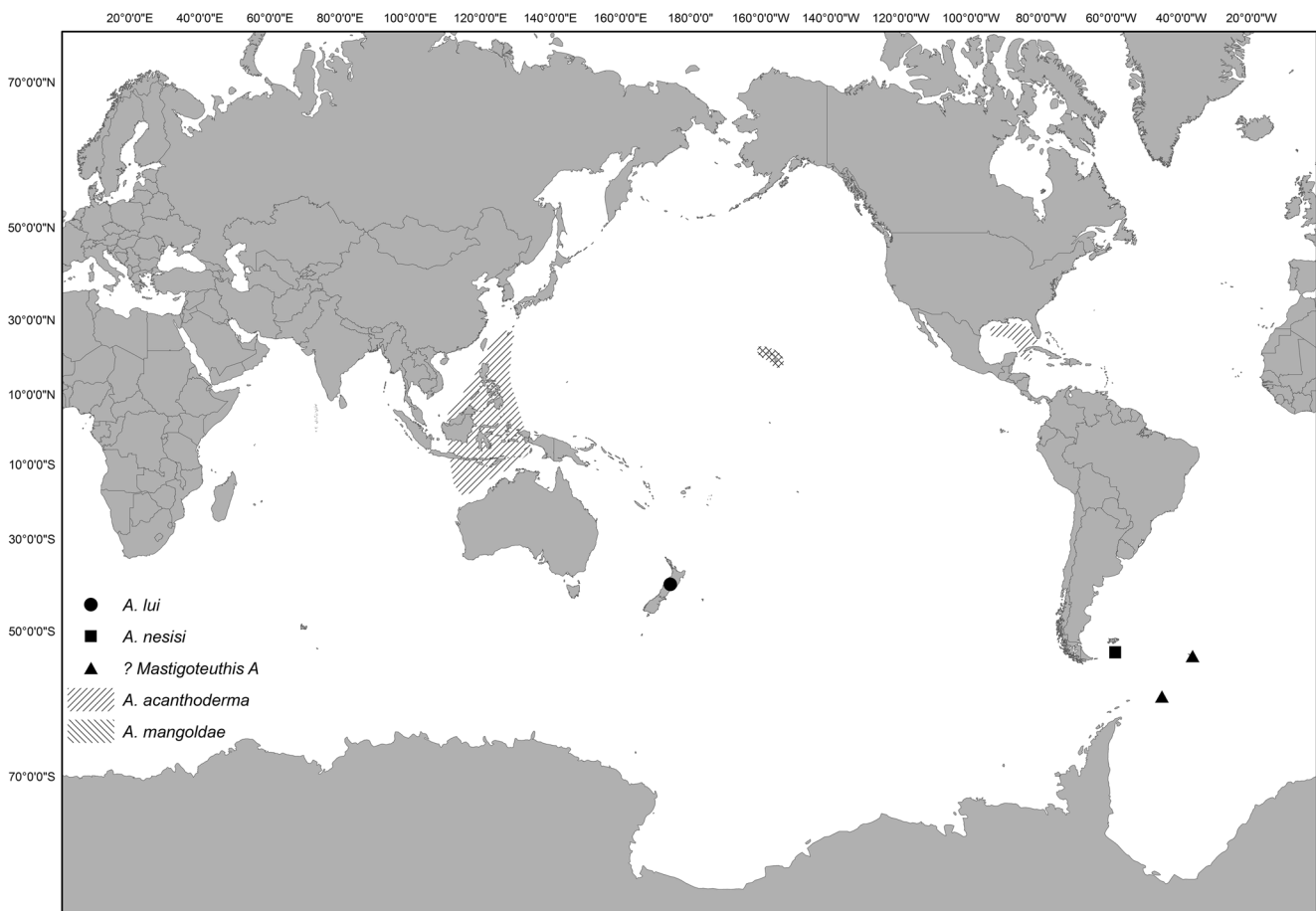
lucida. For scanning electron microscopy (SEM), specimens were critical-point dried at the University of Auckland, then platinum plated and imaged at the Auckland University of Technology. Sucker descriptions were based on Salcedo-Vargas (1995), with some modifications (see Braid and Bolstad 2015). Palatine teeth on the lateral buccal palps are described following Bolstad (2010). Radular tooth descriptions followed Bolstad (2010), with some modifications (see Braid and Bolstad 2015).

Specimen measurements used in the text and tables include the following: ML—dorsal mantle length (measured to the end of the fin); MW—mantle width; FL—fin length; FW—fin width; HL—head length (measured from anterior tip of nuchal cartilage to separation of Arms I); HW—head width; ED—eye diameter; AL—arm length (arms measured from most-proximal sucker to arm tip); TnL—tentacle length; CL—tentacle club length; LRL—lower rostral length; URL—upper rostral length.

## Results

### Genetic analysis

Bidirectional sequences were successfully recovered from all eight individuals for COI, 16S rRNA, and 12S rRNA. COI sequences were all 658 bp and did not contain stop codons or indels. The 16S rRNA sequences were 517 bp and the 12S rRNA sequences were 403 bp. All COI sequences for *A. nesisi*, *A. lui*, and ‘?Mastigoteuthis A’ were assigned to the same BIN (BOLD: AAJ9359) and these sequences also formed a single clade on the combined maximum-likelihood



**Fig. 1** Distribution of *Asperoteuthis* species

phylogeny that was distinct from *A. mangoldae* (Fig. 3). Within the sequences used in this study for *A. nesis*, *A. lui*, and “*Mastigoteuthis A?*”: COI showed an average divergence of 0.5 %, with a minimum of 0 %, and a maximum of 1.4 %; 16S rRNA showed no variation; and 12S rRNA showed an average divergence of 0.1 %, with a minimum of 0 %, and a maximum of 0.3 %. For the divergence between this clade and *A. mangoldae*: COI had an average interspecific divergence of 19.4 %, with a minimum of 19.0 %, and a maximum of 20.9 %; 16S rRNA showed a divergence of 5.4 %; and 12SrRNA showed an average divergence of 7.3 %, with a maximum of 7.6 %, and a minimum of 7.2 %.

## Systematics

### Genus *Asperoteuthis* Nesis, 1980

*Asperoteuthis* Nesis, 1980: 613. Type species *Chiroteuthis acanthoderma* Lu, 1977, by subsequent designation of Young et al. (2007a:357).

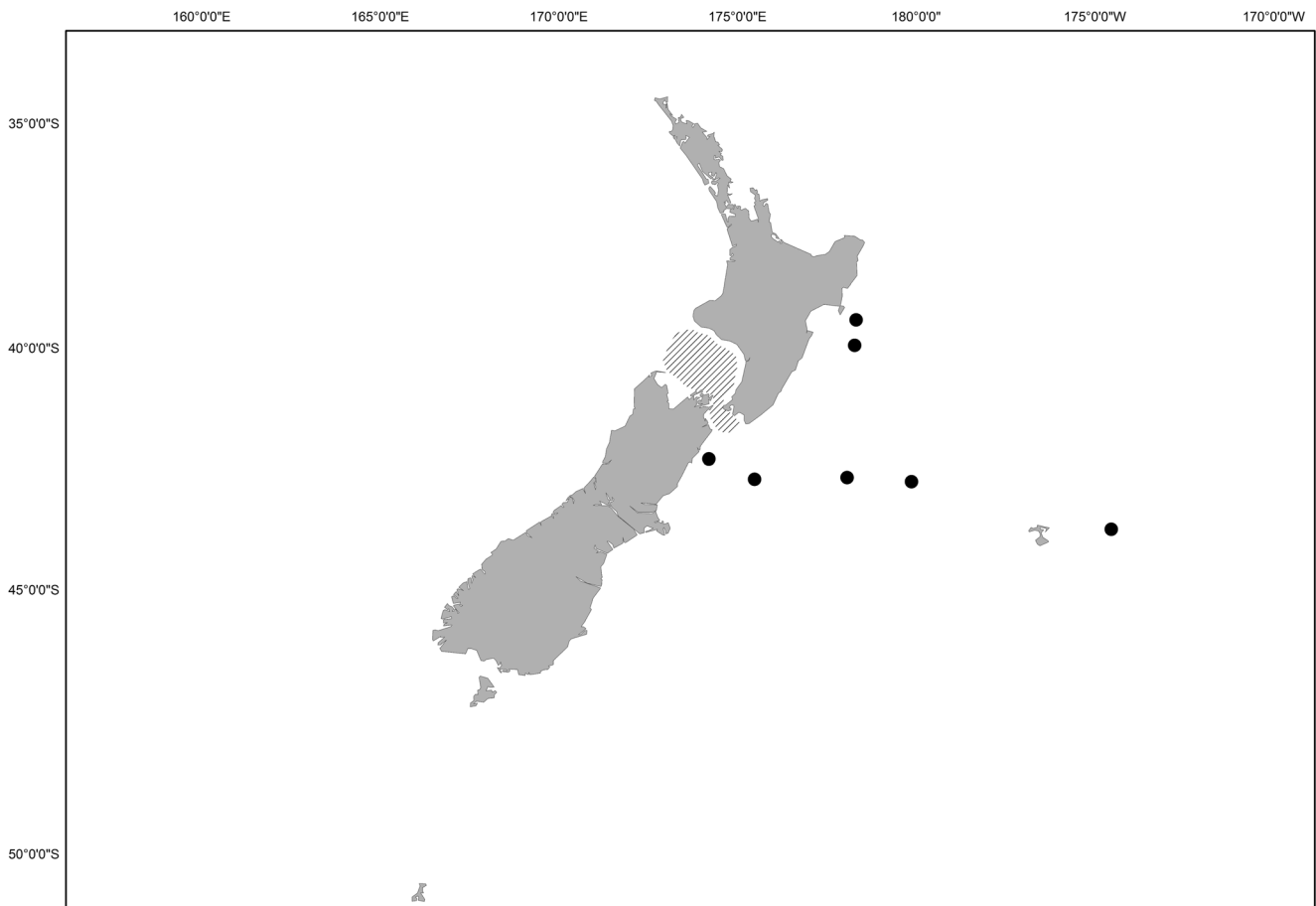
**Diagnosis:** Mantle length at maturity 100 mm to >780 mm. Fins circular to oval in outline when considered together; fin length ~40–65 % ML; tail structure

present. Funnel-locking cartilage inverted Y-shaped groove, comma shaped, or ear shaped, with weak tragus, antitragus variably present; funnel pocket absent; buccal formula DDVV. Mantle-locking cartilage inverted Y-shaped, crescent, or approximately oval. Arm suckers arranged in two distinct series, with sharp or blunt teeth; arm length approximately subequal (~50–115 % ML). Tentacular suckers present only on distal portion of club; trabeculate protective membrane present, expanded on proximal half of club; terminal-club photophore present, aboral club with small embedded photophores near lateral edges, photophores present on tentacular stalk. Photophore present on ventral surface of eye. Integumental photophores absent from mantle, fins, head, and arms.

**Remarks:** This diagnosis is based on descriptions of *A. acanthoderma* (Lu 1977), *A. nesis* (Arkhipkin and Laptikhovskiy 2008), *A. mangoldae* (Young et al. 2007a), and *A. lui* (Salcedo-Vargas 1999). Additional information was taken from Young et al. (2011) and the present findings.

***Asperoteuthis lui* Salcedo-Vargas, 1999** (Tables 2 and 3, Figs. 3, 4, 5, 6, 7, 8 and 9)





**Fig. 2** Distribution of *Asperoteuthis lui* specimens examined in this study. The shading indicates Cook Strait, where two specimens were caught without specific locality data

‘*Mastigoteuthis A*’ Clarke, 1980: 191–194, figs. 155, 156; Clarke (1986): 160, 161, fig. 83.

*Asperoteuthis lui* Salcedo-Vargas, 1999: 48, 49, fig. 1.

*Asperoteuthis nesisi* Arkhipkin & Laptikhovskiy, 2008: 203–205, figs. 1, 2.

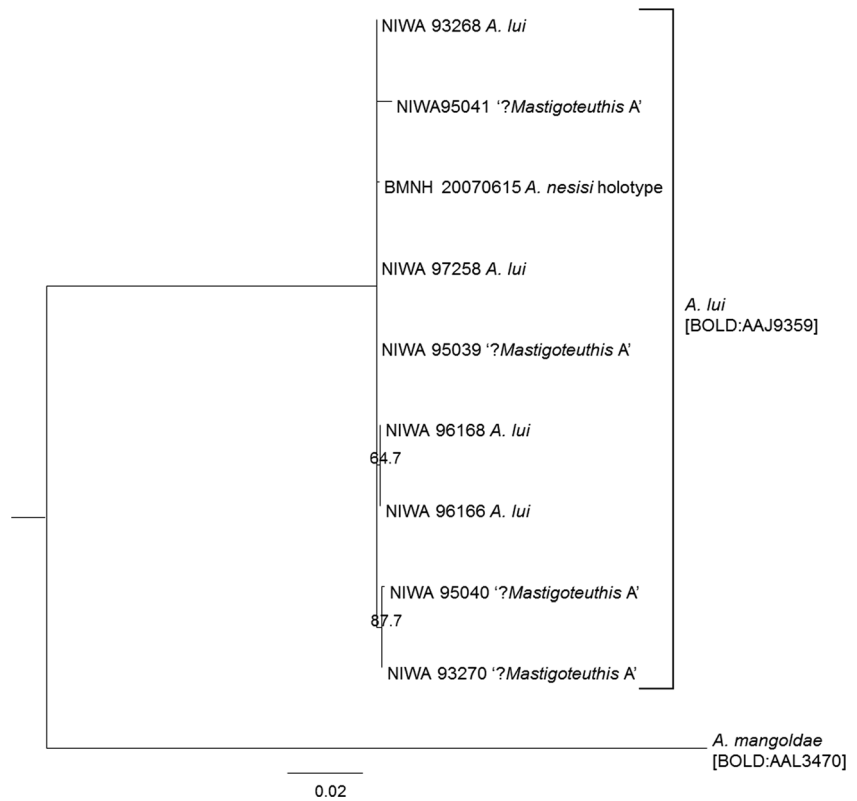
**Type material examined:** NMNZ M.143859, *A. lui* holotype, sex indet., head only, LRL 6.62 mm, no locality data, Cook Strait, *Genypterus blacodes* stomach content. Photographs of BMNH 20070615, *A. nesisi* holotype, ♀, ML 363 mm, 53°44’S, 58°46’W, 913 m, RV *Dorada*, pelagic trawl fishing near-bottom, 20/07/05, Stn 2132, cruise ZDLH1-07-2005, ‘*Asperoteuthis nesisi*’.

**Additional local material examined** (10 specimens): NIWA 95041, ♀, beak only, LRL 7.34 mm, 39.40°S, 178.32°E, 998 m, RV *Tangaroa*, 26/03/2010, Stn TAN1003/64; NIWA 93270, sex indet., beak only, LRL 6.70 mm, 39.95°S, 178.28°E, 1285 m, RV *Tangaroa*, 26/03/2010, Stn TAN1003/65; NIWA 95040, sex indet., ML 345 mm, LRL 7.70 mm, 42.35°S, 174.20°E, 1226 m, RV *Tangaroa*, 01/04/2010, Stn TAN1003/119; NIWA 96168, sex indet., tentacle only, CL

138 mm, 42.74°S, 178.07°E, 42.75°S, 178.05°E, 868–822 m, RV *Tangaroa*, 16/11/2011, TAN1116/115; NIWA 96166, sex indet., tentacle only, CL 144 mm, 42.74°S, 178.07°E, 42.75°S, 178.05°E, 868–822 m, RV *Tangaroa*, 16/11/2011, TAN1116/115; NIWA 97258, sex indet., tentacle only, CL 170 mm, 42.77°S, 175.48°E, 886–889 m, RV *Tangaroa*, 20/01/2014, TAN1401/102; NIWA 95039, sex indet., beak only, LRL 5.16 mm, 42.82°S, 179.87°E, 42.83°S, 179.83°E, 960–962 m, RV *Tangaroa*, 16/06/2010, Stn TAN1008/04; NIWA 93268, ♀, fins missing, CL 79 mm, LRL 5.43 mm, 43.79°S, 174.54°W, 810–811 m, RV *Tangaroa*, 11/01/2014, Stn TAN1401/56; unaccessioned, ♀, ML 315 mm, LRL 6.51 mm, no locality data, New Zealand; NMNZ M.302215, sex indet., head only, LRL 3.26 mm, no locality data, Cook Strait, *Genypterus blacodes* stomach content.

**Comparative material examined:** *Asperoteuthis mangoldae*, FMNH 278099, ♂, ML 144\* mm, 21.33°N, 158.33°W, 21.58°N, 158.58°W, 975–1040 m RV *New Horizon*, 04/07/1996, Stn 962-sta#76, mother tucker trawl. *Asperoteuthis acanthoderma*, unaccessioned, sex indet., ML 1030\* mm, Indian Ocean, no locality data.

**Fig. 3** Combined maximum-likelihood phylogeny based on COI, 16S rRNA, and 12S rRNA for specimens identified as *Asperoteuthis nesisii*, *A. lui*, and ‘?*Mastigoteuthis A*’, with *A. mangoldae* as an outgroup, with 1000 bootstrap replicates



**Distribution:** Circumpolar distribution in the Southern Ocean; New Zealand in Cook Strait and the Chatham Rise; South Atlantic around the Falkland Islands.

**Diagnosis:** Fins circular in outline when considered together, length ~64 % ML, width 52–60–68 % ML; circular skin depressions present. Single elongate photophore on ventral surface of eye. Funnel-locking cartilage ear shaped, weak tragus, strong antitragus; mantle-locking cartilage approximately oval. Largest suckers of all located mid Arms II and III (~75 % arm width); arm suckers with 7–11 blunt, rectangular or sharp, conical teeth. Tentacles with ~120–160 suckers with 5–7 sharp, conical teeth; aboral tentacle-club surface midline with five smaller proximal and two larger distal photophores; small embedded photophores near lateral edges bilaterally asymmetrical with more photophores dorsally (~11–16) than ventrally (~9–12); trabeculae present on protective membrane, trabeculae on distal portion of expanded proximal membrane fused to form a solid muscular area.

**Description:** Mantle cone shaped anteriorly, with mantle cavity terminating approximately one third of FL from anterior of fins (thereafter gladius and surrounding musculature continue as narrow cylinder), widest (~28 % ML) at anterior margin; dorsal anterior mantle margin triangular with point produced over nuchal-locking cartilage. Fins circular in outline when considered together, length ~64 % ML, width 52–60–68 %

ML; anterior lobes absent; tail structure missing due to damage from all specimens examined. Integumental photophores absent from mantle, fins, head, and arms; skin tubercles not observed (skin always damaged); circular skin depressions present on dorsal and ventral surface of fins, and all external surfaces of mantle, head, and funnel (absent from collar).

Head narrowly conical, length 24–32–39 % ML, widest posteriorly (width at midline ~11 % ML). Olfactory papilla cylindrical. Eye diameter ~8 % ML. Single elongate photophore on ventral surface of eye (Fig. 4d–f). Funnel widely conical with recurved end, width ~13 % ML, length ~13 % ML; aperture posterior to eyeball; funnel pocket absent. Funnel-locking cartilage ear shaped (Fig. 4a), ~5 % ML; anterior groove concave due to strong antitragus; weak tragus along inner/medial margin; nearly straight along outer/lateral margin. Mantle-locking cartilage approximately oval (Fig. 4b), ~4 % ML; posteriorly undercut.

Arm formula  $IV \geq III \geq II > I$ ; arm length 83–99–108 % ML (Table 2); arms of approximately subequal thickness, with Arms IV thickest and Arms I thinnest; oral faces of arms bordered by membranes, trabeculae absent; aboral keels present on Arms I–III; expanded lateral membrane present on Arms IV. Each arm with ~122–206 suckers in two series; largest suckers of all located on Arms II (~75 % arm width) at about row 18–21 (~30–40 % arm length) and Arms III (~75 % arm width) at about row 18–23 (~30–40 % arm length).

**Table 2** Measurements for *Asperoteuthis lui* and mean indices for *A. lui*, *A. acanthoderma*, and *A. mangoldae*. Specimen indices are abbreviated as follows: MWI—mantle width index as % of ML; FLI—fin length index (measured from anterior edge of fin to end of tail); FWI—fin width index; HLJ—head length index; HWI—head width index; EDI—eye diameter index; ALI—arm length index; TnLI—tentacle length index; CLI—tentacle club length index as % of TnL; LRL—lower rostral length; URL—upper rostral length. Measurements for Whale 524 specimens from Clarke (1980) and BMNH 20070615 measurements from Arkhipkin and Laptikhovsky (2008). All specimens measured on the right side except for NIWA 93268, and Arm IV on NMNZ M.143859

Reference	Clarke (1980)	Clarke (1980)	Arkhipkin and Laptikhovsky (2008)	Salcedo-Vargas (1999)	Present study	Present study	Present study	Mean Indices
Specimen ID	Whale 524, specimen 1	Whale 524, specimen 2	BMNH 20070615	NMNZ M.143859	Unaccessioned	NIWA 95040	NIWA 93268	<i>A. lui</i> <i>A. acanthoderma</i> <sup>a</sup> <i>A. mangoldae</i> <sup>b</sup>
Type status	None	None	Holotype	Holotype	None	None	None	
Sex	M	M	F	Sex indet.	F	Sex indet.	F	
ML	175	185	363	–	315	345	–	
MW	N/A	N/A	100	–	90	70	55	MWI 25 16
FL	115	118	220	–	218	210	–	FLI 64 51
FW	92	96	246	–	215	205	–	FWI 60 37
HL	62	56.5	88	–	103	135	72	HLJ 32 27
HW	20	18.3	36	40	38	35	26	HWI 11 10
ED	–	–	27	30	30	35*	–	EDI 8 12
Arm I	150	150	312	255	258	310	153	ALI 84 109
Arm II	166	195	335	304	310	375	195	ALI2 102 123
Arm III	215	210	303	327	297	392	197	ALI3 108 128
Arm IV	175	177	377	354	362	390*	224	ALI4 102 139
TnL	–	–	–	2065	–	–	986	TnLI ~570 605
CL	–	–	–	138	–	–	79	CLI ~40 24

\* indicates a damaged feature

– indicates a missing feature

<sup>a</sup>Based on Lu (1977), Nesis (1980), and Tsuchiya and Okutani (1993)

<sup>b</sup>Based on Young et al. (2007a, b)

**Table 3** Comparison of characters for *Asperoteuthis* species

Character	<i>A. acanthoderma</i> <sup>a</sup>	<i>A. mangoldae</i> <sup>b</sup>	<i>A. lui</i>
Fin shape	Oval	Circular	Circular
Photophores			
Eye	Oval	Large oval patch	Elongate
Medial club	Large, at club tip	Small, at club tip	Series along midline, enlarged photophore at club tip
Aboral lateral club margins	12–13 on each side	8 distal, 5 proximal on each side	More on dorsal (9–12) than ventral (11–16)
Funnel-locking cartilage	Inverted Y	Comma-shaped	Ear-shaped
Tragus	Present	Present	Present, weak
Antitragus	Present	Absent	Present
Mantle-locking cartilage	Inverted Y	Crescent	Approximately oval
Arm suckers			
Dentition	3–4 rounded to truncated teeth	9–10 separate, truncated teeth	7–11 blunt, rectangular or sharp, conical teeth
Location of largest sucker	Arms II and III	Arms III	Arms II and III
Tentacles			
Sucker dentition	3–4 triangular teeth	Truncated teeth, 8 large distally, 17 small proximally	5–7 sharp, conical teeth
Number of suckers	~50	~50	~120–160
Skin morphology			
Circular depressions	Absent	Absent	Present
Tubercles	Present	Absent	Not observed in this study*

\*Skin tubercles were reported for *A. nesisi* in the type description (Arkhipkin and Laptikhovskiy 2008), but no tubercles were observed on specimens examined herein; however, the skin was badly damaged on all specimens examined

<sup>a</sup>Based on the type description by Lu (1977)

<sup>b</sup>Based on the type description by Young et al. (2007a, 2011)

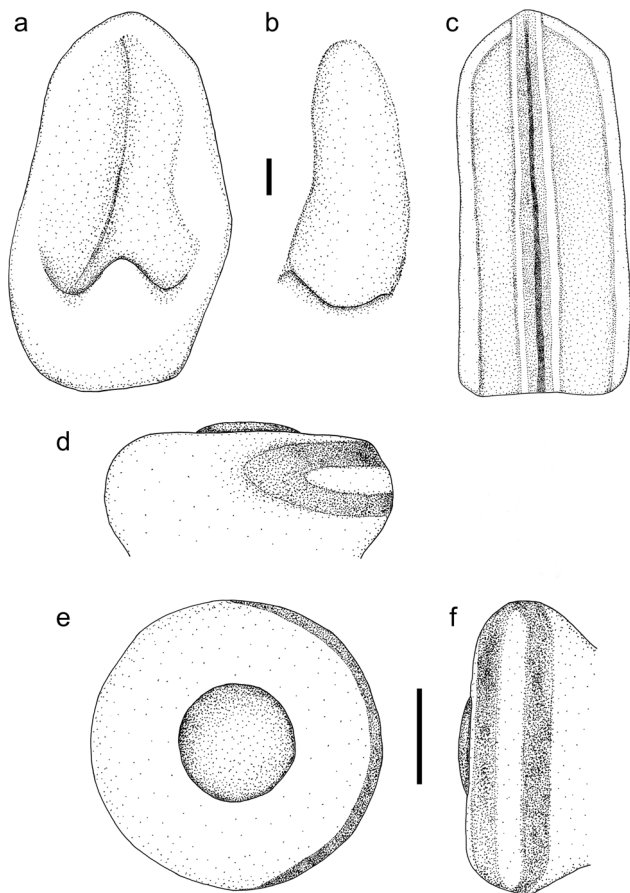
Arm-sucker infundibular rings (Fig. 5) proximally adentate, distally with ~7–11 blunt, rectangular or sharp, conical teeth. Polygonal processes on oral surface of sucker papillated ring often damaged, in ~2–4 concentric rings; distally, central and intermediate rings with ovate, porous pegs; proximally, central and intermediate rings nearly flat or slightly raised proximally, peripheral ring with flat rectangular or ovate processes.

Tentacle length ~570 % ML, club length ~6 % TnL (~40 % ML), sucker-covered surface ~75 % club length; proximal protective membrane ~25 % of club length, widest portion of club surface ~30 % maximum membrane width; stalk width at base of club ~70 % club surface width, mid-stalk width ~40 % club surface width. Distal club with ~120–160 suckers in four series (Fig. 6). Proximal rounded expanded portion of protective membrane trabeculate, distally fused to form a solid muscular area; distal non-expanded protective membrane trabeculate; medial aboral club with proximal series of ~6–8 smaller photophores, medium-sized photophore distally, large club-tip photophore; lateral aboral club with more ventral photophores (~11–16) than dorsal (~9–12); tentacle-stalk photophores alternating between larger (~75–100 % stalk width) and smaller (~25 % stalk width) along length of stalk, most distal ~5 % stalk length with only smaller

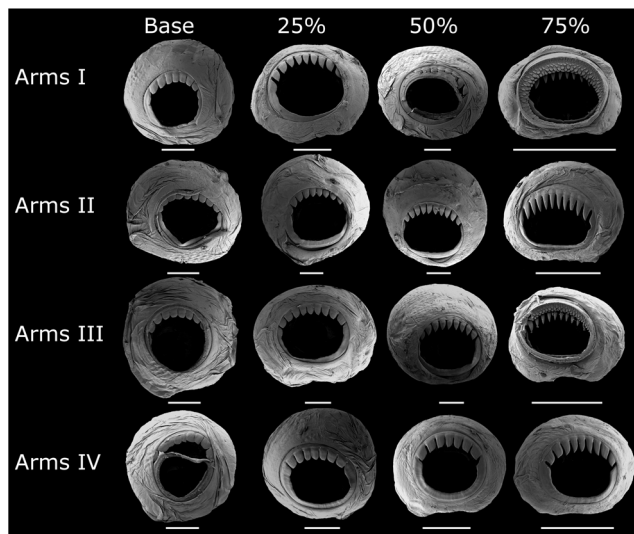
photophores, which decrease in size distally. Sucker infundibular rings (Fig. 7d–m) proximally adentate, distally with ~5–7 sharp, conical teeth; proximal polygonal processes in papillated ring flat, often irregularly shaped varying from ovate to spindle shaped, in ~4–6 concentric rings; distal polygonal processes approximately circular to rectangular, slightly elevated proximally, in ~3 rings.

Lower beak, lateral profile (Fig. 8a, d, g, j, m): lower rostral length ~43 % wing length, rostral edge with strong curve, rostral tip without hook, rostral tip behind leading edge of wing by 20–28–35 % baseline; wing angle slightly obtuse (nearly right angle), jaw angle obscured by prominent wing fold, shoulder groove present; height 79–87–92 % baseline; hood close to crest, hood length ~64 % crest length, crest length 54–57–63 % of baseline, visible portion of crest nearly straight; broad lateral-wall fold extending to posterior edge of lateral wall; no or slight notch in lateral wall. Lateral oblique view (Fig. 8b, e, h, k, n) with wing narrowest level with jaw angle, 48–58–68 % of greatest width. Ventral view with broad notch in hood, free corners well separated. Wings remain entirely clear at LRL 3.26 mm, anterior edge of wing below shoulder clear at LRL 5.43 mm, anterior and posterior edge of wing remains clear through at least LRL 7.70 mm.





**Fig. 4** *Asperoteuthis lui*. **a–c** NIWA 93268, ♀, LRL 5.43 mm; **d–f** NMNZ M.143859, sex indet., LRL 6.62 mm. **a** Right funnel-locking cartilage; **b** right mantle-locking cartilage; **c** nuchal-locking cartilage; **d** left eye photophore, anterior view; **e** left eye photophore, lateral view; **f** left eye photophore, ventral view. Scale bars: **a**, **b** = 1 mm; **c** = 5 mm; **d–f** = 10 mm



**Fig. 5** *Asperoteuthis lui* arm suckers, NIWA 93268, ♀, LRL 5.43 mm. Scale bars = 500 µm

Upper beak, lateral profile (Fig. 8c, f, i, l, o): upper rostral length  $\sim 32\%$  hood length; hood length  $\sim 67\%$  beak length; hood height  $\sim 39\%$  beak width. Lateral-wall fold absent; shoulder produced into point or smooth curve, shoulder step 6–43–92 % URL; jaw edge slightly curved; jaw angle nearly right angle.

Radula (Fig. 7a) with tricuspid rachidian, base width  $\sim 60\%$  height, proximal margin of base rectangular, with broad, sharp triangular mesocone and small, sharp lateral cusps, slightly laterally directed, their height  $\sim 45\%$  mesocone height. First lateral tooth strongly bicuspid; inner cusp broad, triangular, slightly curved towards rachidian, its height  $\sim 100\%$  that of overall rachidian; outer cusp sharply pointed, medially directed, its height  $\sim 60\%$  that of inner cusp. Second lateral tooth simple, curved slightly towards rachidian,  $\sim 125\%$  rachidian height. Marginal tooth simple, straight,  $\sim 145\%$  height of rachidian. Marginal plate absent (Fig. 7b). Palatine palp (Fig. 7c) with  $\sim 70$  narrow, flat teeth, each  $\sim 15\text{--}45\%$  rachidian height, evenly distributed over palp.

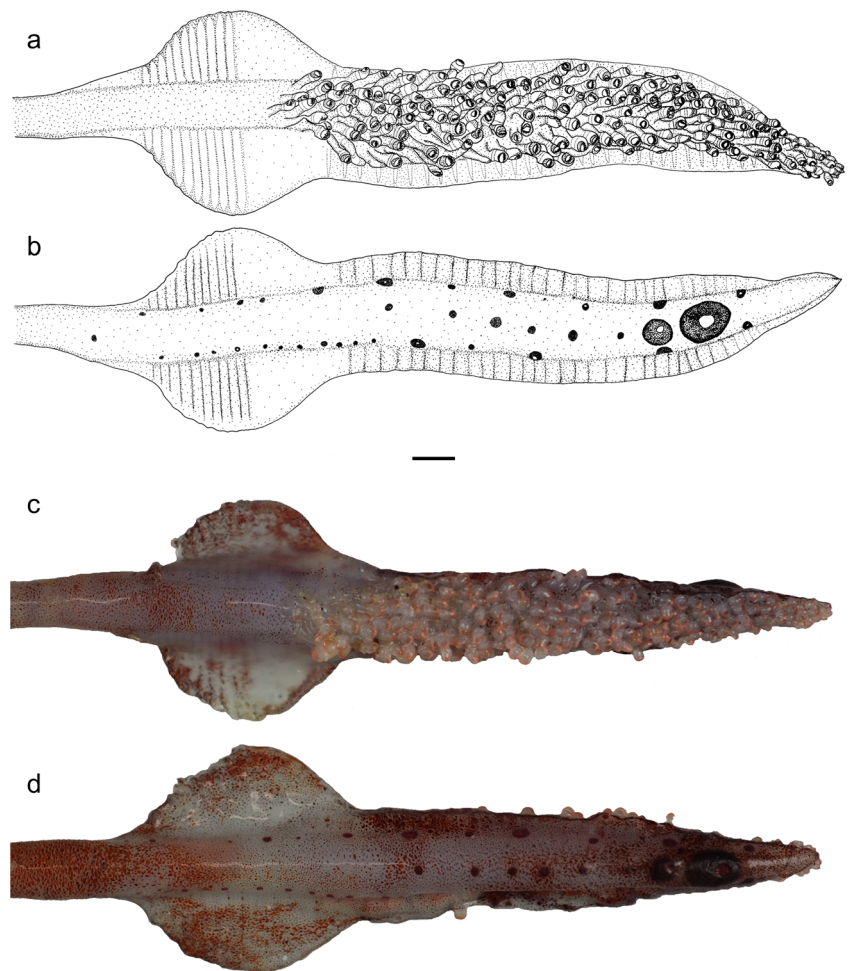
Epidermis damaged on all examined material. Translucent white when fresh, yellow when preserved; purple and red chromatophores dense and evenly distributed on all exterior surfaces, absent from internal mantle.

#### Taxonomic remarks

Additional, recently collected specimens made this review possible. The most complete specimen available for genetic analysis was in good condition, except that it lacked fins and eyes (NIWA 93268; Fig. 9). The tentacles (Fig. 6) and beaks (Fig. 8d–f) of this specimen are morphologically consistent with those of the holotype for *A. lui* (Fig. 8g–i). Some of the specimens examined herein consisted of only beaks (with buccal masses, which allowed for genetic analysis) or tentacles; these specimens were used to examine variation in beak morphology (Fig. 8) and tentacle-club photophore patterns, respectively. It appears that the tentacle-club photophores show some intraspecific variation, but a greater sample size will be needed to determine if this is related to sex, growth, or locality.

The original description of *A. lui* was based on a single, incomplete specimen that was taken from the stomach of a ling (*Genypterus blacodes*) (Salcedo-Vargas 1999). The specimen only consists of a head and arm crown, including two slightly damaged eyes and one tentacle (Salcedo-Vargas 1999). Unfortunately, the sucker rings from the tentacle club and arms were degraded due to digestion. The only images in the type description were of the eye photophore and the tentacle club and stalk (Salcedo-Vargas 1999). There are some inconsistencies with the type description for *A. lui* and the observations on that specimen made herein. The description of *A. lui* stated that the suckers on mid-Arms II and III were enlarged (Salcedo-Vargas 1999); however, they appear to be the largest suckers on the animal, rather than enlarged suckers.

**Fig. 6** *Asperoteuthis lui* tentacle club NIWA 93268, ♀, LRL 5.43 mm. **a, c** Oral; **b, d** aboral. **c, d** Photographs by Darren Stevens. Scale bars = 5 mm



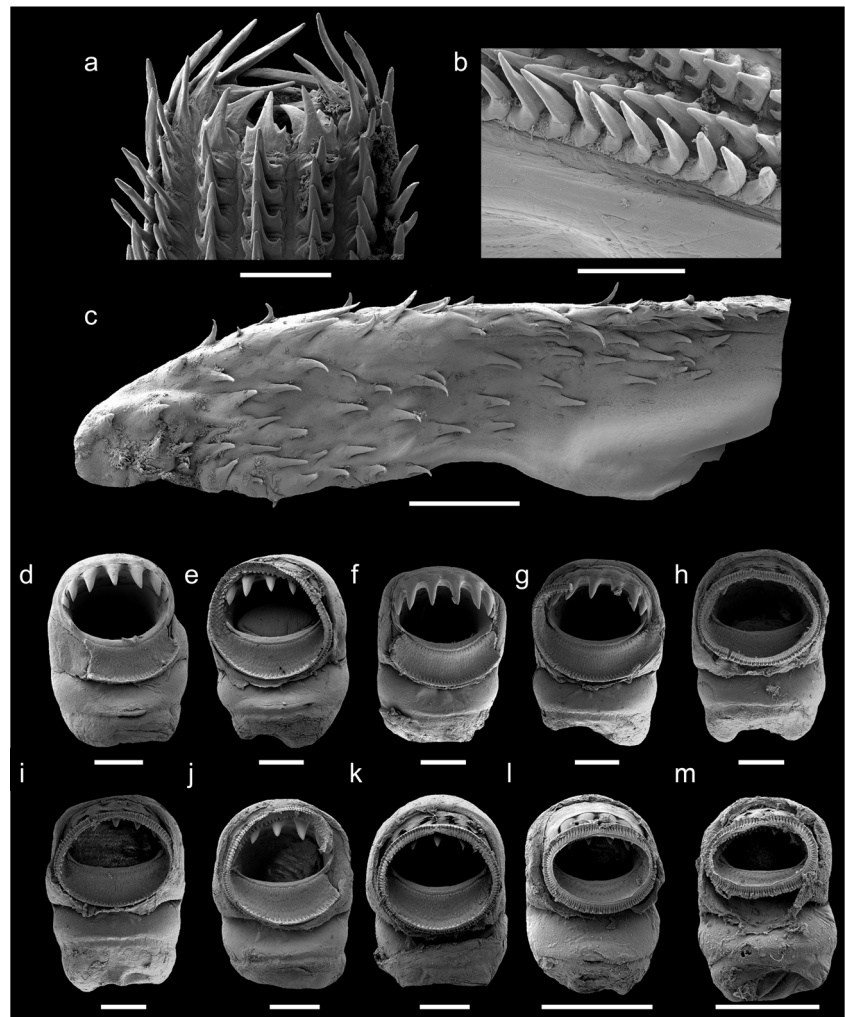
The eyeball photophore was described as a patch (Salcedo-Vargas 1999), but the examination herein found that it is elongate (Fig. 4d–f). Salcedo-Vargas (1999) stated that there was no tentacle-club-tip photophore; however, there is a photophore located near the tentacle-club tip (Fig. 6b, d), which is a characteristic of this genus. Two important features that were overlooked in this description were the small embedded photophores on the lateral edges of the aboral surface of the club (Fig. 6b, d) and the beak morphology (Fig. 8).

The characters that Arkhipkin and Laptikhovskiy (2008) used to distinguish *A. nesisi* from other species of *Asperoteuthis* were based on features that were missing from the *A. lui* holotype (mantle musculature, fin shape, mantle skin texture, funnel-locking cartilage morphology, and arm-sucker dentition) or not included in the original description of *A. lui* (arm sucker count and beak morphology). The specimens identified herein as *A. lui* have morphological characters that are consistent with those of *A. nesisi*, with some exceptions due to damage or size. The eye photophore was described as a single longitudinal photophore on the ventral surface of the eye (Arkhipkin and Laptikhovskiy 2008), which is consistent with the present findings (Fig. 4d–f). The arm suckers

described for *A. nesisi* had 12–14 sharp triangular teeth (Arkhipkin and Laptikhovskiy 2008), while the specimen examined herein had 7–11 blunt, rectangular or sharp, conical teeth (Fig. 5); this difference is likely related to size, because the specimen examined in the present study was smaller. Arkhipkin and Laptikhovskiy (2008) reported small cartilaginous tubercles on the skin of the head and mantle, which were not observed herein, likely due to the damaged skin on all specimens examined herein. Arkhipkin and Laptikhovskiy (2008) suggested that tentacles may be absent in maturing specimens; however, this seems unlikely because the holotype for *A. lui*, which has similar arm lengths and head width, has a tentacle attached (CL 138 mm) and larger tentacles have been found (NIWA 97258, CL 170 mm).

Arkhipkin and Laptikhovskiy (2008) proposed that, due to a similar appearance, *A. nesisi* was probably synonymous with Clarke's (1980) ‘?Mastigoteuthis A’, which is supported by the results of the present study. There are few differences between Clarke's (1980) description and the specimens examined herein. Clarke's (1980) description is consistent with *A. lui* based on the characteristic gelatinous tissue that overlies the posterior portion of the mantle, the acutely pointed dorsal

**Fig. 7** *Asperoteuthis lui*. **a–c** NIWA 93268, ♀, LRL 5.43 mm; **d–m** NIWA 97258, sex indet., tentacle only, CL 170 mm. **a** Radula; **b** radula margin; **c** palatine palp; **d** most-proximal tentacle sucker; **e** outer tentacle sucker close to base; **f** inner sucker 25 % from most-proximal sucker; **g** outer sucker 25 % from most-proximal sucker; **h** inner sucker 50 % from most-proximal sucker; **i** outer sucker 50 % from most-proximal sucker; **j** inner sucker 75 % from most-proximal sucker; **k** outer sucker 75 % from most-proximal sucker; **l** inner sucker tentacle-tip sucker; **m** outer sucker tentacle-tip sucker. Scale bars = 500  $\mu$ m



mantle, the long and narrow head, radula morphology, funnel- and mantle-locking-cartilage morphology, eye photophore shape, beak morphology, and general appearance. However, Clarke (1980) described a small muscular pad on each side of the posterior end of the mantle in both of the specimens he examined, which was not observed herein or reported by Arkhipkin and Laptikhovskiy (2008). It is possible that this was either an artefact due to damage caused by being eaten and partially digested, or possibly a character that is only associated with males (the specimens examined in this study were female or sex indet.). No swimming membranes were described on the arms, but these are easily damaged.

The taxonomic placement of ‘*Mastigoteuthis A*’ remained unclear for some time. Nesis (1987) suggested that his new species, ‘*Chiroteuthis*’ n. sp. Nesis, 1974, from the South Atlantic was synonymous with ‘*Mastigoteuthis A*’ and placed this species in a new unnamed genus, n. gen. B. However, there are several morphological differences that distinguish Nesis’s (1974) ‘*Chiroteuthis*’ n. sp. from *Asperoteuthis*: six series of suckers on the developing club; photophore present on the ink sac; Arms IV longer than other

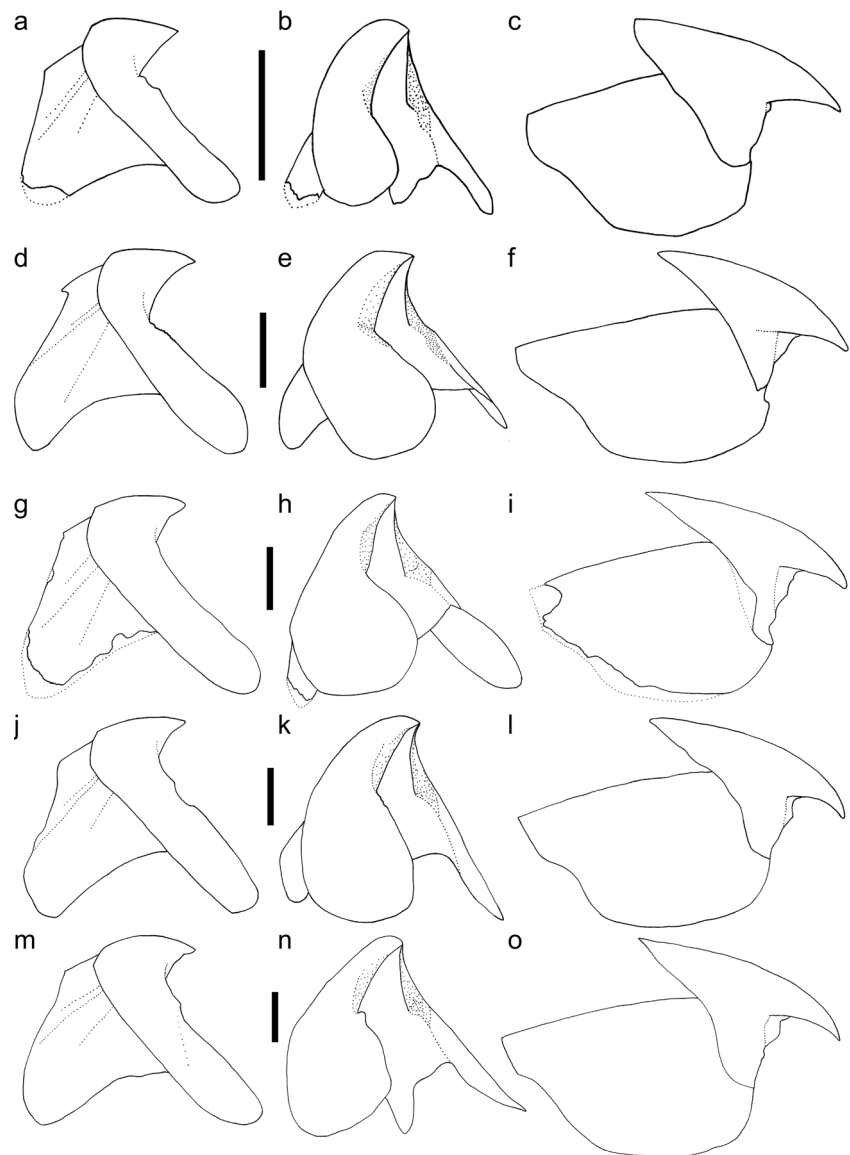
arms; and funnel-locking cartilage with rounded antitragus and without tragus (Nesis 1974). Because of these differences, the species reported by Nesis (1974) is now considered to belong in a new genus in the family Chiroteuthidae (Nesis and Nikitina 1999).

There are many similarities between tentacle suckers of *A. lui* and those of the chiroteuthid genus ‘New Genus C’ (Young and Roper 2000a). The tentacle suckers for both have approximately the same number of conical teeth and are surrounded by a wide papillated ring (Young and Roper 2000b). The only known specimen found to represent this new genus was a badly damaged brachial crown from Antarctic waters (Young and Roper 2000a), which is within the distribution for *A. lui*. It is possible that the ‘New Genus C’ is actually *A. lui*. Previously, this specimen could not be compared to *A. lui* because the present study is the first report to describe the tentacle suckers in *A. lui*.

A comparison of characters found in *A. lui*, *A. mangoldae*, and *A. acanthoderma* is summarized in Table 3 and mean indices are found in Table 2. *Asperoteuthis lui* is distinguished from both of these species by: (1) an elongate ventral eye



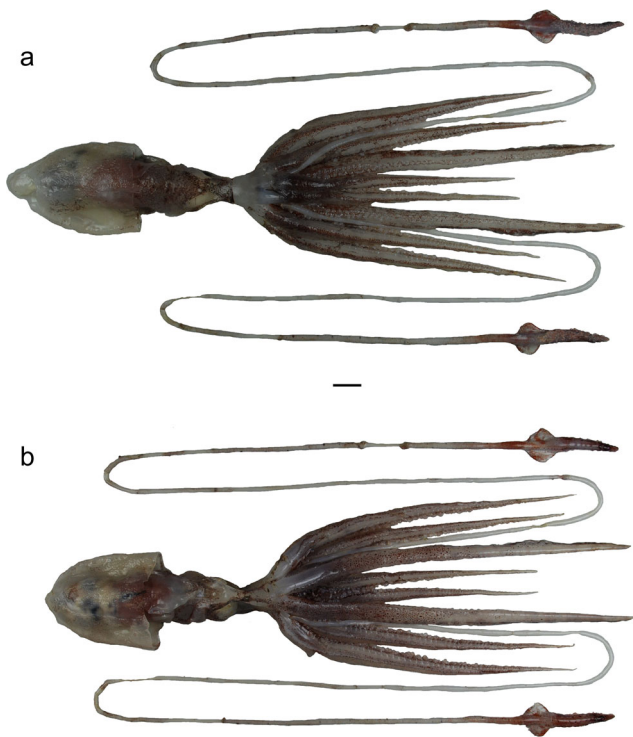
**Fig. 8** *Asperoteuthis lui* beaks. **a–c** NMNZ M.302215, sex indet., head only, LRL 3.26 mm; **d–f** NIWA 93268, ♀, LRL 5.43 mm; **g–i** NMNZ M.143859, sex indet., LRL 6.62 mm; **j–l** NIWA 95041, ♀, beak only, LRL 7.34 mm; **m–o** NIWA 95040, sex indet., beak only, LRL 7.70 mm. **a, d, g, j, m** Lower beaks in lateral profile view; **b, e, h, k, n** lower beaks in lateral oblique view; **c, f, i, l, o** upper beaks. Scale bars = 5 mm



photophore; (2) a medial row of photophores on the aboral tentacle club; (3) chiral photophores on the lateral margins of the aboral tentacle club with more ventral photophores than dorsal; (4) ear-shaped funnel-locking cartilage with a weak tragus; (5) approximately oval mantle-locking cartilage; (6) tentacle suckers with 5–7 sharp, conical teeth; (7) more than twice as many tentacle-club suckers (~120–160); (8) circular skin depressions; (9) a relatively wide mantle; (10) a relatively longer club; and (11) a lack of trabeculae in the distal portion of the proximal, expanded region of the tentacle-club protective membrane. *Asperoteuthis lui* and *A. mangoldae* both have approximately circular fins, while *A. acanthoderma* has an oval fin, but the fin of *A. lui* is relatively larger. *Asperoteuthis acanthoderma* is additionally distinguished from the other two species by a larger club-tip photophore, inverted Y-shaped funnel- and mantle-locking cartilages, less teeth on arm and tentacle suckers, and a larger size at maturity

(Lu 1977). *Asperoteuthis acanthoderma* and *A. mangoldae* both have an oval ventral-eye photophore and lack circular skin depressions. *Asperoteuthis acanthoderma* has the longest arms relative to mantle length, *A. mangoldae* has the shortest arms, and *A. lui* arms are intermediate in length.

There are many commonalities in the aboral tentacle - club photophores in the genus *Asperoteuthis*. The tentacle-club structure of all three species shares a lack of suckers in the proximal region of the tentacle, but the structure of the tentacles of *A. acanthoderma* is much more similar to *A. mangoldae* in terms of trabeculae distribution, sucker count, club length index, and photophores. Photophores in the lateral margins of the tentacle club have been reported for *A. mangoldae* (Young et al. 2007a), *A. acanthoderma* (Lu 1977), and were found herein for *A. lui*. However, unlike the other species in this genus, *A. lui* photophores are chiral, which is a type of asymmetry in which a structure cannot be



**Fig. 9** *Asperoteuthis lui* NIWA 93268, ♀, LRL 5.43 mm. **a** Dorsal; **b** ventral. Photographs by Darren Stevens. Scale bar = 20 mm

superimposed on its mirror image. In *A. lui*, the left and right tentacle clubs have an asymmetric distribution of photophores and the clubs are mirror images of each other—more photophores are present along the ventral margin (11–16) than along the dorsal margin (9–12). Although chirality is common in squid tentacles, the small embedded aboral photophores are symmetrical in *A. acanthoderma* (Young and Roper 2010) and *A. mangoldae* (Young et al. 2007a). In addition, bilaterally asymmetric photophore patterns are found in other squid; for example, the photophore patterns of histioteuthids (Young and Vecchione 2003). *Asperoteuthis lui* has a series of medial club photophores with approximately five to eight smaller proximal photophores and two larger photophores distally, while *A. mangoldae* and *A. acanthoderma* only have a single medial club-tip photophore.

## Discussion

The taxonomic study of chiroteuthids is especially difficult because specimens are not frequently caught and are almost always damaged by capture. In addition, species in this family are especially delicate, and nearly all *Asperoteuthis* specimens lose their tail structure and tentacles during capture, which are important morphological features for their identification. Genetic analyses, such as DNA barcoding (Hebert et al. 2003), can be used for species identification of even badly damaged (St-Onge et al. 2008) and juvenile specimens

(Victor et al. 2009). The DNA barcode, along with 16S rRNA and 12S rRNA, has been helpful in species delimitation and the recognition of new species in the chiroteuthid families (Young et al. 2008; Braid et al. 2014, 2016). Herein, the DNA barcode, 16S rRNA, and 12S rRNA, in conjunction with a morphological analysis, have been used to determine that *A. 'nesisi'* and '*?Mastigoteuthis A*' are junior synonyms of *A. lui*.

*Asperoteuthis 'nesisi'* and *A. lui* were both described from single, damaged specimens that were unfortunately missing different morphological features: *A. lui* had a tentacle present, but the arm and tentacle suckers were damaged, and it lacked a mantle (Salcedo-Vargas 1999), while *A. 'nesisi'* was intact other than the missing tentacles, tail, and damaged fin (Arkhipkin and Laptikhovskiy 2008). Because the description for *A. lui* primarily focused on the tentacle-club morphology, the relationship between *A. 'nesisi'* and *A. lui* was not clear when *A. 'nesisi'* was described. The type description for *A. 'nesisi'* included GenBank accession numbers for three mitochondrial genes from the holotype (Arkhipkin and Laptikhovskiy 2008). There were no DNA sequences associated with the *A. lui* holotype because this specimen was formalin-fixed and described before DNA sequences were regularly included with species descriptions.

Sequences for COI, 16S rRNA, and 12S rRNA from the holotype of *A. 'nesisi'* were compared with specimens collected in New Zealand waters with tentacle-club morphology consistent with *A. lui* and beaks with morphology consistent with '*?Mastigoteuthis A*', and they all formed a single cluster on the maximum-likelihood phylogeny, with very little variation within that clade, and a large gap between that clade and *A. mangoldae* (Fig. 3). These three taxa were also assigned the same BIN (Fig. 3), and there is a high concordance between BINs and species (Ratnasingham and Hebert 2013). BINs have been successfully used to delimitate species in other species in the Chiroteuthidae (Braid et al. 2016) and in the closely related squid family Mastigoteuthidae (Braid et al. 2014).

The relationship between the three valid species in this genus remains unclear. Arkhipkin and Laptikhovskiy (2008) suggested that, based on morphology, *A. acanthoderma* and *A. 'nesisi'* have a closer relationship to each other than to *A. mangoldae*. Herein, it appears that there are more similarities in the tentacle-club morphology of *A. acanthoderma* and *A. mangoldae* than with *A. lui*. However, Braid et al. (2016) found that the genus *Asperoteuthis* was polyphyletic, and their Bayesian phylogeny showed some support for a sister relationship between *A. lui* and *A. mangoldae*. Their results suggested the possibility that there may be additional species of *Asperoteuthis* that have not been sequenced yet, or that this genus needs to be reassessed.

There are very few records of specimens identified as *Asperoteuthis* in the stomach contents of predators. However, they have been reported from the gut contents of



sperm whales (*Physeter macrocephalus*) (Gómez-Villota 2007), ling (*Genypterus blacodes*) (Salcedo-Vargas 1999), and blue sharks (*Prionace glauca*) (Kubodera et al. 2007). It was only recently recognized that Clarke's (1980) ‘?Mastigoteuthis A’ is an *Asperoteuthis* species (Arkhipkin and Laptikhovsky 2008; Young 2015); therefore, this species has been previously incorrectly attributed to the family Mastigoteuthidae in dietary analyses. Even recent ecological studies continue to apply the original incorrect mastigoteuthid classification (e.g., Alvito et al. 2015; Bloom 2012; Guerreiro et al. 2015). Beaks identified as ‘?Mastigoteuthis A’ have been reported from the stomach contents of southern bottlenose whales (*Hyperoodon planifrons*) (Clarke and Goodall 1994), sperm whales (*P. macrocephalus*) (Clarke 1980; Pascoe et al. 1990), grey-headed albatrosses (*Thalassarche chrysostoma*) (Cherel et al. 2002; Richoux et al. 2010; Alvito et al. 2015), wandering albatross (*Diomedea exulans*) (Guerreiro et al. 2015; Rodhouse et al. 1987; Xavier et al. 2011), white-chinned petrels (*Procellaria aequinoctialis*) (Bloom 2012), Antarctic fur seals (*Arctocephalus gazelle*) (Lea et al. 2002), Patagonian toothfish (*Dissostichus eleginoides*) (Cherel et al. 2004), and porbeagles (*Lamna nasus*) (Cherel and Duhamel 2004). Herein, ‘?Mastigoteuthis A’ has been recognized as a junior synonym of *A. lui*. Therefore, the previous importance of ‘?Mastigoteuthis A’ in the diet of marine predators must be transferred to *A. lui*. The role of *Asperoteuthis* in the feeding ecology of other species has been dramatically underestimated.

Using a combination of morphology and mitochondrial genes, the identity of *A. lui*, *A. nesisi*, and ‘?Mastigoteuthis A’ has been resolved. This demonstrates the importance of including genetic sequences with species descriptions whenever possible. The ecological importance of *Asperoteuthis* in the diet of marine mammals, birds, and fish has been underestimated because the identity of ‘?Mastigoteuthis A’ remained unknown until recently. It appears that the biodiversity of the genus *Asperoteuthis* has been overestimated, with a previous estimate of five species (Young and Roper 2015). Currently, only three valid species are recognized in this genus: *A. acanthoderma*, *A. mangoldae*, and *A. lui*. This study highlights the significance of critical taxonomic revisions as additional material for poorly known species becomes available. Accurate species identification is fundamental for all biological research, with ramifications for predator-prey relationships and conservation.

**Acknowledgments** I am grateful to the Royal Society of New Zealand's Hutton Fund, which supported the genetic analysis for this study. I would like to thank the Museum of New Zealand Te Papa Tongarewa, particularly Bruce Marshall, and the National Institute of Water and Atmospheric Research Ltd. (NIWA), especially Darren Stevens for help with specimen collection, beak identification, access to his beak collection, and photographs of *Asperoteuthis lui*. Many thanks go to the scientists and crew of the RV *Tangaroa* for always checking

carefully for cephalopods and especially Ian “Hearn” Smith for finding the most complete *A. lui* specimen available for genetic analysis. Thanks to Adrian Turner at the Auckland University for assistance with critical-point drying, and Patrick Conner at AUT for platinum plating and imaging assistance. Many thanks go to Jesse Kelly for insightful comments and encouragement, Kat Bolstad for her endless patience, and to Steve O’Shea for the most intact *A. lui* specimen available from New Zealand waters for morphological examination.

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