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ORIGINAL PAPER

Diversity of the squid genus *Leachia* (Oegopsida: Cranchiidae) in the Pacific Ocean

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Abstract

Leachia is a cosmopolitan tropical/temperate genus of 'glass' squids (Cranchiidae) whose taxonomy has been plagued with instability typical of the family. Eight species are currently believed to exist worldwide, including some not yet described. This review assesses the Pacific taxa, describes a novel species, *L. separata*, and provides updated diagnoses for the other Pacific species. Type material and original descriptions are compared, and brief remarks provided on the Atlantic taxa. The most useful characters for identifying *Leachia* species appear to be the number of ocular photophores and the configuration of the ventral cartilaginous strips and associated tubercles on the mantle, with arm and sucker-ring dentition also proving useful in some taxa. Further work on the genus is needed, ideally including molecular tools.

Keywords Biodiversity · Taxonomy · Squid · Systematics · Cephalopod

Introduction

Cranchiids ('glass' squids) are abundant and diverse oegopsids, with representatives found in all oceans except apparently the Arctic. Many species undergo ontogenic descent (Young 1978; Evans 2018), occupying different ecological niches across their growth and development, and being preyed on by fishes, seabirds, and whales (Evans 2013). The appearance of most taxa also changes considerably across the lifespan (as shown in Evans and Bolstad 2014 for the genus *Teuthowenia*), and specimens are often not identified beyond genus or even family. Systematic instability, fragile morphological characters, and specimen rarity all further complicate identification and taxonomic resolution, and several undescribed species are still believed to exist (Voss 1980). Due to the scale of the family (60 + described species [Evans 2018]), its geographic extent, and the factors outlined above, recent advances in our understanding have focused on subsets of the group and/or specific regions, such as a recent review of the Pacific cranchiid taxa (Evans 2018).

Within the Cranchiidae, untangling members of the genus *Leachia* has provided some of the greatest taxonomic challenges. Steps toward resolving this group have been taken by a succession of authors working both globally and on local scales. The genus *Leachia* was first erected by Lesueur (1821) for a specimen collected from 37°S, 33°E (southeast of South Africa, although Lesueur stated that it "inhabits the Pacific Ocean"). He based the description of his new species, *L. cyclura*, on an illustration by Mr. Nicolas-Martin Petit (later published in Grant 1833), but did not examine the specimen himself. Lesueur placed *Leachia* into a new family, Loligoidea, which he proposed to separate "the *Loligos*" (= squids) from cuttlefish (*Sepia*); the species he included in Loligoidea would later be recognized as members of the oegopsid families Ommastrephidae, Onychoteuthidae, Cranchiidae, and the myopsid family Loliginidae. He characterised the genus *Leachia* as having an elongated cylindrical body, transparent tissue, and third arms that were longer and more robust than the other arm pairs.

Some authors rejected the generic status of *Leachia* (e.g. d'Blainville 1823) due to its description being based on imperfect illustrations, but Grant (1833) believed it to represent the same taxon as *Loligopsis* Lamarck 1812 (another genus described solely from illustrations, which had also received little support from other authors). Grant resurrected

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Loligopsis and placed *L. cyclura* within it, alongside his new species *L. guttata* (=*L. cyclura*, *fide* Pfeffer 1912), with the type specimen of the genus being *L. peronii* (=*nomen dubium*, *fide* Berry 1932). In the *L. guttata* description, Grant mentioned lines of rough cartilaginous tubercles on the ventral surface, extending halfway down the mantle from the funnel (Grant 1833)—now recognized as one of the distinguishing features of *Leachia* species—but did not mention the presence of the cartilaginous line on which the tubercles are found.

A better understanding of the ecology, biology, and diversity of the genus was gained throughout the twentieth century, with authors noting the presence of luminous organs on the eyes (Joubin 1905), describing the secondary sexual characteristics of both males and females of taxa within the genus (Joubin 1931), and documenting maturation and spawning habits (Young 1975). Several new species (and genera) were described in the northern Pacific Ocean during this time including *Drechselia danae* Joubin 1931 (=*L. danae*, *fide* Voss 1980), *Zygaenopsis pacificus* Issel, 1908 (=*L. pacifica*, *fide* Young 1972) and *Leachia dislocata* Young 1972; however, few reports on the cranchiid fauna of the Southern Hemisphere were available until the late 1970s. In a much-criticised attempt to revise the New Zealand teuthofauna, Imber (1978) reported two locally occurring species of *Leachia*: *L. cyclura* and *L. eschscholtzii* (previously *Perothis eschscholtzii* Rathke 1833) and synonymized several geographically distant species to fit within those two taxa. These synonymies, which 'lumped' geographically separate and morphologically distinct species, were soundly refuted by Voss (1980).

As part of a larger work on identifying paralarval cephalopods, Voss et al. (1992) examined paralarval members of all nominal *Leachia* species. They concluded that six of the nominal 14 species appeared valid, but also acknowledged that the number might be revised upward to 11. They examined morphometric features of five (*L. atlantica*, *L. danae*, *L. dislocata*, *L. lemur*, and *L. pacifica*; *L. cyclura* was considered valid but was not described/compared) focussing on eye development, tubercle patterns and maturation size. Most of these species appeared to inhabit discrete, but adjacent geographic ranges, although some overlap was also noted. These observations represented a considerable advance in resolving *Leachia*, but the authors lacked access to specimens from several key geographic areas, such as the southern Pacific. They alluded to further forthcoming research on this genus, but this does not appear to have been published to date.

In Evans' recent review of the Pacific cranchiid fauna (2018), five *Leachia* species were identified (Table 1). These include two that are new to science, one of which is described below (the other, while possessing a unique suite of morphological characters, remains insufficiently known to permit formal description). For comparison, the three established Pacific species, plus *L. cyclura*, are re-diagnosed below with a summary of key characters (with further remarks in Discussion).

Methods

Material was examined from the following institutions

Australian Museum (AMS), Australia.
California Academy of Science (CAS), United States.
Museum für Naturkunde (ZMB Germany.
Muséum National d'Histoire Naturelle (MNHN), France.
National Institute of Weather and Atmospheric Research, Ltd (NIWA), New Zealand.

Table 1 Characters used to distinguish Pacific *Leachia* species

Species	Ventral tubercles	Strip length	Eye photophores	Arm sucker dentition	Manus sucker dentition
L. danae	8 complex, with occasional simple in between	9–*11*–15% ML	20	3 angular (curved in larger individuals)	15–22 teeth
L. dislocata	~7 complex (3 simple in between), offset tubercle at anterior margin	13–*16*–21% ML	15	6–12 angular	15–28 teeth
L. pacifica	~15 (6 complex with 1 or 2 two simple in between)	15–20%	~5	~10 rounded	12 peg-like teeth
L. separata sp. nov*	10 complex and 9–11 individual tubercles posteriorly, not connected to strip	15–*16*–20% (up to 45% with extra tubercles)	8	7–10 pointed	24 teeth
L. sp. NZ*	6 complex tubercles, simple tubercle at fusion	18–20% ML	10 or 11	6–12 pointed	~24 teeth

*New in this research

National Museum of New Zealand Te Papa Tongarewa (NMNZ), New Zealand.

National Museum of Victoria (MV), Australia.

Santa Barbara Museum of Natural History (SBMNH), United States.

Smithsonian National Museum of Natural History (NMNH), United States.

Tokyo National Museum (NSMT), Japan.

Prior to examination, most museum specimens had been fixed in ~ 4% formalin and stored in either 70–80% ethanol or 50% isopropanol. Morphological examinations and illustrations were made using a dissecting microscope (Leica WILD M3B); an attached camera lucida was used to illustrate small specimens and characters. Morphological measures and counts follow Roper and Voss (1983). 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, was variable due to damage.

Due to the unique morphology of the family Cranchiidae, with the head and mantle fused at three places, and coelomic compartments within the mantle, some specialised terms have been used to refer to specific features. 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. The cartilaginous connections at these ventral fusion points, which are thought to provide some structure for the otherwise gelatinous mantle, are generally linear and referred to as strips. These strips bear pointed tubercles, which may be simple (a single point) or complex (a cluster of points on a single tubercle). Cranchiid squid sucker dentition can be helpful in distinguishing between taxa; Fig. 1 provides examples of dentition morphology in *Leachia*.

Abbreviations used in text for morphological measurements and indices include 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). Collection gear abbreviations include MWT—Mid-Water Trawl; BT—Bottom Trawl.

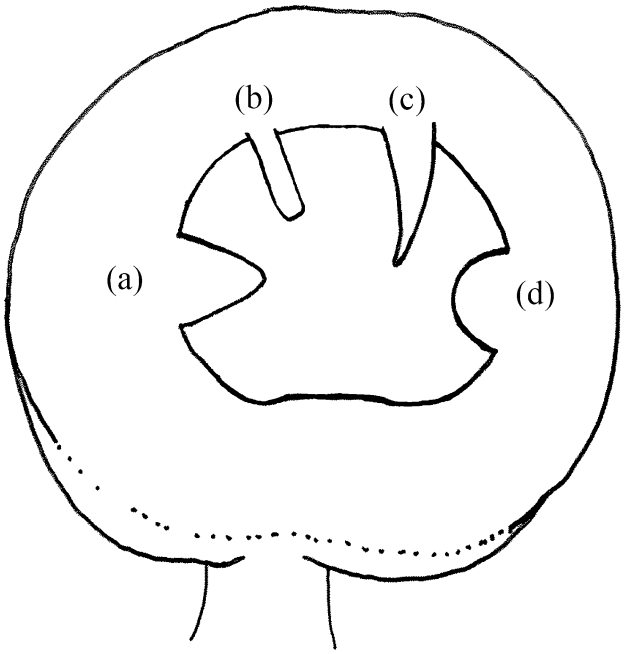

Fig. 1 Stylized sucker dentition morphology of *Leachia*: **a** angular, **b** peg-like, **c** pointed, **d** rounded

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

Inked images were scanned and then digitally compiled using Adobe Photoshop.

The synonymies for individual taxa are limited to previous taxonomic descriptions and/or illustrations providing sufficient morphological detail to attribute the taxon definitively to species. When discussed in text, synonymised taxa are referred to by the original (junior) name and author, followed by the current species designation and attributing author in parentheses, e.g. "*Zygaenopsis pacificus* Issel 1908 (= *Leachia pacifica*, *fide* Young 1972)".

Systematics

Leachia Lesueur 1821

Leachia Lesueur 1821: 12–13, Pl. VI; Steenstrup 1861: 34–37; Hoyle 1885: 326–329; Chun 1910: 271–276, Pl. LII 4–7; Pfeffer 1912: 650–656, Pl. 47 fig. 2–13; Voss 1960:

429–433; Young 1972: 80–83; Voss et al. 1992: 189–192, fig. 218a–j, fig. 219a–e; Reid 2016: 83–85.

Dyctydiopsis Rochebrune 1884: 16–17.

Pyrgopsis Rochebrune 1884: 23–24, Pl. II, fig. 1–6; Pfeffer 1912: 656–664, Pl. 47 fig. 14–17; Berry 1920: 298–299, Pl. 16, fig. 5; Robson 1924: 5–6.

Zygaenopsis Rochebrune 1884: 20; Pfeffer 1900: 193; Chun 1906: 84; Issel 1908: 223–228, Pl. 10, fig. 33–44.

Perothis Rathke 1833: 1–28; Rochebrune 1884: 25.

Euzygaena Chun 1910: 276–277.

Drechselia Joubin 1931: 197–208, fig. 33–46; De Silva-Dávila et al. 2010: 89–93, fig. 2–3.

Diagnosis

Small- to medium-sized cranchiids (ML to 150 mm in examined material), body slender, with subterminal fins, together ovoid, circular, or rhombic in outline. Ventral mantle surface with a single longitudinal series of cartilaginous tubercles extending posteriorly from each ventral funnel fusion point. Eyes each with four or more circular photophores. Third arm pair more robust and over twice the length of other pairs; tentacles slender with proportionally small club.

Remarks

The most useful morphological characters for distinguishing Pacific *Leachia* taxa include the relative length of the ventral cartilaginous strips and the number of associated tubercles, the number of eye photophores, and the sucker dentition on the arms and tentacles (Table 1).

Leachia cyclura Lesueur 1821

Type material

Specimen not extant [fide Voss (1962, p. 1)]. Type Locality: 37°00'S, 33°00'E (off the coast of South Africa).

Diagnosis

Ventral cartilaginous strips ~ 50% ventral mantle length, with 11–13 cartilaginous tubercles in a single series. Eye with 5–8 photophores.

Geographic distribution

The distribution of this taxon is not well understood. The original description cites *L. cyclura* as being from the 'Pacific Ocean' (Lesueur 1821), but the collection coordinates (37°S 33°E) for the holotype are located in the Indian Ocean off eastern Africa.

Remarks

The type description of *L. cyclura* was based on an illustration and lacked sufficient detail to confidently attribute recent specimens to this taxon. The diagnosis above is compiled from reports by d'Orbigny (1845), Joubin (1905), Pfeffer (1912), and Nesis (1987). Some variation is apparent in these descriptions, as d'Orbigny failed to include the presence of ocular photophores, Joubin and Pfeffer reported *L. cyclura* having 5–6 ocular photophores, while Nesis described the species as having 8. As the type specimen is no longer extant, it is appropriate to use the earliest available information for comparison and therefore, as most material examined had more than 5–6 photophores, no specimens have been attributed to *L. cyclura*. Examination of *Leachia* material collected from the type locality would be useful in confirming diagnostic characters for *L. cyclura*, although multiple *Leachia* species may occur sympatrically (e.g. *L. danae* and *L. dislocata*).

Leachia danae Joubin 1931

Type material (not examined)

Drechselia danae **ZMUC Syntypes (2)** [fide Kristensen and Knudsen (1983:221)]. Type Locality: 6°40'N, 80°47'W (Pacific Ocean).

Diagnosis

Ventral cartilaginous strips ~ 10% ML (Fig. 2i). Eye with 20 photophores (Fig. 2a–c): 12 sub-orbital, 7 dorsal to lens, one on posterior of eye. Sucker rings on Arms III with three angular teeth (and 2–4 smaller cusps), central tooth enlarged.

Geographic distribution

Tropical Eastern Pacific, Baja California to Costa Rica.

Remarks

Leachia danae and *L. dislocata* can co-occur in the eastern Pacific, and younger individuals can be difficult to differentiate. The fins of *L. danae* are usually noticeably larger (FL 30–38–42% ML) than in *L. dislocata* (FL 20–27–35% ML). Perhaps most reliably, most specimens can easily be distinguished by the Arm III suckers: *L. danae* develop three distinct teeth from ~ 40 mm ML, while *L. dislocata* usually has 6–12 angular teeth (although several mature males examined

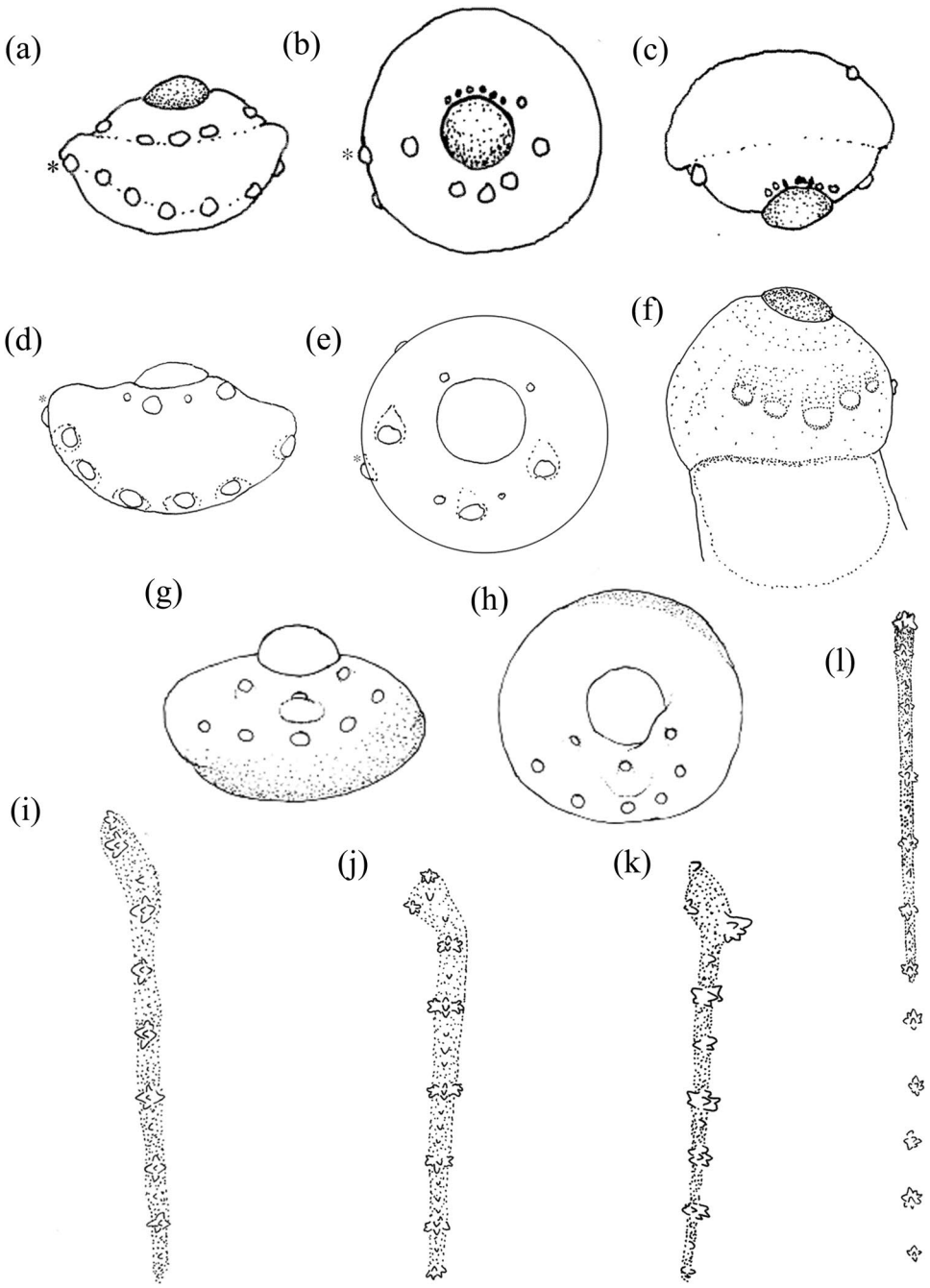

Fig. 2 *Leachia* distinguishing characters **a–c** *Leachia danae* eye **a** ventral **b** lateral **c** doral view; **d,e** *Leachia dislocata* eye **d** ventral **e** lateral view; **f** *Leachia pacifica* eye ventral view; **g,h** *Leachia separata* sp. nov eye **g** ventral **h** lateral view; **i–l** ventral cartilaginous strips **i** *L. danae*, **j** *L. dislocata*, **k** *L. pacifica*, **l** *L. separata* sp. nov

in this study had laterally compressed suckers on Arm III with small apertures and 3 or 4 small sharp teeth). The great variation in sucker counts (26–180 in mature individuals) appears to represent sexual dimorphism, as SBMNH 464440, a mature male, had the lowest sucker count of any specimen examined despite being the second largest specimen examined.

Leachia dislocata **Young 1972**

Type material

Leachia (*Pyrgopsis*) *pacifica* **SBMNH Holotype 34999** [fide Scott et al. (1990:20)]. Type locality: 32°35'N, 118°06'W, eastern North Pacific Ocean.

Diagnosis

Ventral cartilaginous strip about 15% ML, with simple and complex tubercles, complex tubercles antero-posteriorly compressed shape; second anterior tubercle displaced toward midline (Fig. 2j). Eye with 15 circular photophores (Fig. 2d,e), 6–12 angular teeth on distal third of sucker ring.

Geographic distribution

Tropical Pacific, reported from California to Mexico, and Hawaiian Islands.

Remarks

This species most closely resembles *L. pacifica* (which also has a dislocated tubercle near the funnel fusions); however, these species can be distinguished by the number of ocular photophores (*L. dislocata* with 15 and *L. pacifica* with 5 or 6). The geographic range of *L. dislocata* overlaps with that of *L. danae*, but these two can also be distinguished by the number of eye photophores (20 in *L. danae*) or by examining arm sucker dentition (*L. danae* with three angular teeth on sucker ring margin, the central one noticeably enlarged). Unfortunately, small paralarval specimens (below 20 mm ML) could not be examined in this study, so further research is needed in order to complete the ontogenic series.

Leachia pacifica Issel 1908

Type material

Zygaenopsis pacifica Type repository unresolved. Type locality: between Tahiti Island and Pago Pago Island (14°32'S, 167°43'W).

Diagnosis

Ventral cartilaginous strip 15–20% ML, usually with one anterior dislocated tubercle (Fig. 2k). Eyes with five ventral photophores (Fig. 2f).

Geographic distribution

Western to central Pacific (most known material from Hawaiian and Japanese waters).

Remarks

Two uncatalogued paralarval specimens from Hawaiian waters were examined, courtesy of Dr. Richard Young. These specimens seem to concur with a description of *P. pacificus* by Sasaki (1929); however, few other historical descriptions of this species provide enough detail to distinguish it confidently from other immature *Leachia*. The eye photophore pattern does appear unique among similarly sized specimens of all other *Leachia* taxa examined in this study. The most morphologically similar species is *L. dislocata*, which has a sympatric distribution and also has an offset tubercle at the anterior end of the ventral cartilaginous strip. These two species can be distinguished based on eye photophore pattern (*L. dislocata* with 15; 5 or 6 in *L. pacifica*). *Leachia dislocata* also often has two tubercle-like protrusions at the anterior end of the gladius, which are absent in *L. pacifica*.

Leachia separata, sp. nov. (Figs. 2, 3, 4 and 5)

Leachia eschscholtzii (not Rathke 1833): Chun 1910: 271–276, Pl. LII fig. 4–7; Pfeffer 1912: 654–656, Pl. XLVII fig. 11–13.

Leachia pacificus (not Issel 1908): Allan 1945: 338–339, Pl. XXVII fig. 5–11; Reid 2016: 84–85.

Leachia cyclura (not Pfeffer 1912): Imber 1978: 449–451, fig. 1C, D.

Leachia (*P.*) *rynchophorus* (not Rochebrune 1884); *Leachia* (*L*). sp. A Nesis: Nesis 1987: 270–271, figs. 69J, R.

Leachia sp. nov.: Braid and Bolstad 2019: 415, fig. 2, table 2–3.

Diagnosis

Ventral cartilaginous strip 12–20% ML, with additional tubercles extending past strip to 45% ML (Fig. 2l). Eye with 16 photophores (Fig. 2g, h). Arm suckers with 7–10 pointed teeth on distal margin.

Type material

Leachia separata **NMNZ Holotype M.067263**, **NMNZ Paratypes M.334423**, **M.334424**, **M.334425**, **M.334426**, Type locality: New Zealand (39.15°S, 178.83°E).

Material examined (32 specimens)

NMNZ M.067263 (holotype), ML 112 mm, ♀, 39.15°S, 178.83°E, New Zealand, 30 m over 1700 m, RV *James Cook*, Stn. J13/19/79, 01/10/1979, MWT; **NMNZ M.074202**, ML 16 mm, 32.40°S, 179.00°E, New Zealand, 274 m, RNZFA *Tui*, Stn.1962095, 25/07/1962; **NMNZ M.091514**, ML 74 mm, sex indet., 32.17°S, 167.91°E, New Zealand, 60 m over 750–1125 m, RV *James Cook*, MWT, Stn.J16/23/85, 24/10/1985; **NMV F163519**, ML 49 mm, sex indet., 32.82°S, 154.17°E–35.81°S, 155.14°E, New South Wales, 20–425 m, CSIRO RV *Soela*, 30/09/1981; **NMV F163601**,

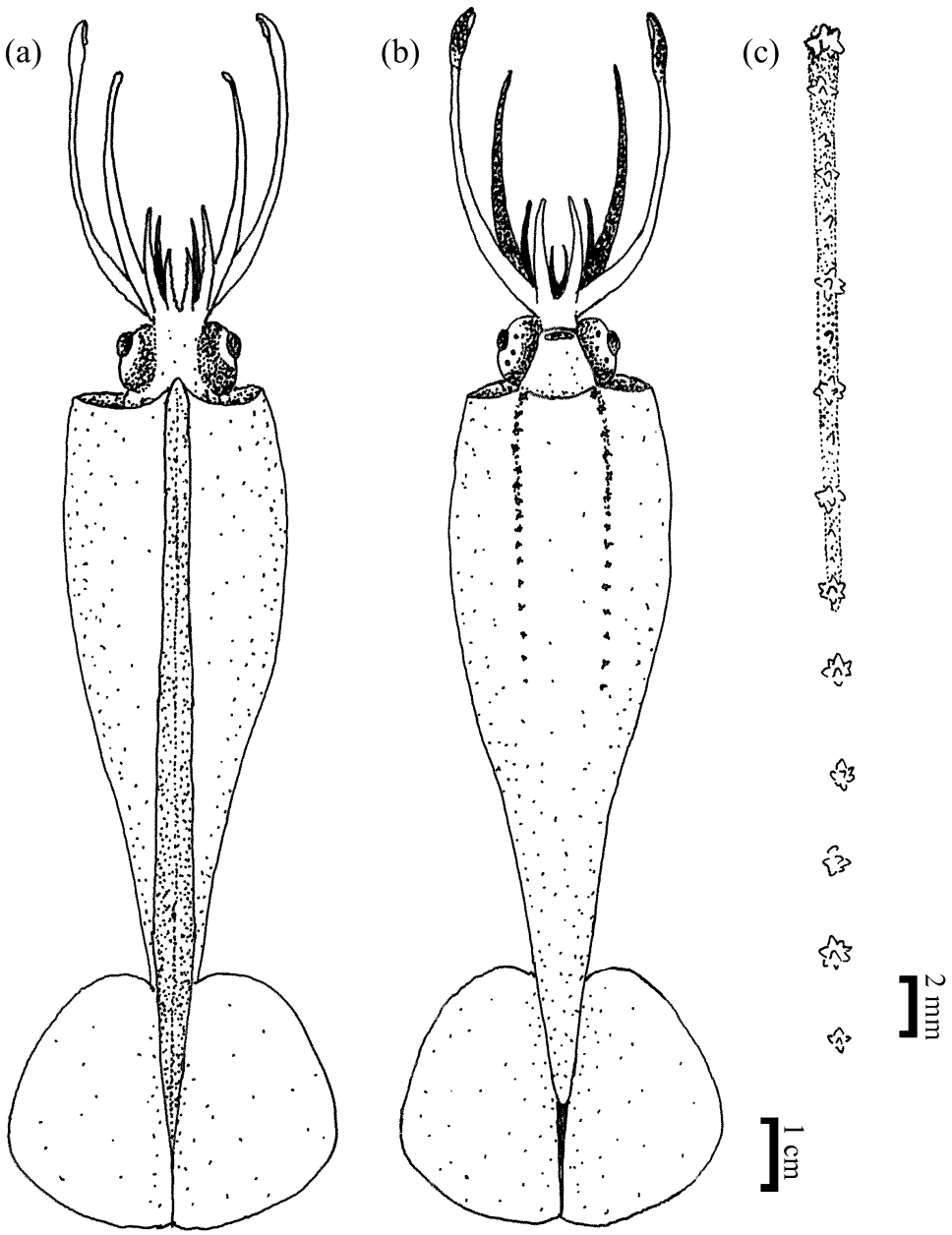

Fig. 3 Adult *L. separata* **a** dorsal view, **b** ventral view, **c** left cartilaginous strip (NMNZ M.067263, ML 112 mm)

ML 94 mm, sex indet., 33.14°S 154.87°E, New South Wales, East of Newcastle, 20 m, CSIRO RV *Soela*, 12/10/1981; **NMV F163558**, ML 97 mm, sex indet., 33.80°S, 154.87°E, New South Wales, 20 m, CSIRO RV *Soela*, 10/10/1981; **NMV F163533**, ML 55 mm, sex indet., 34.46°S, 154.49°E, New South Wales, 20 m, CSIRO RV *Soela*, 30/09/1981; **NMV F163563**, ML 81 mm, sex indet., 34.67°S, 155.01°E, New South Wales, 210 m, CSIRO RV *Soela*, 08/10/1981; **NMNZ M.091689** (2 specimens), ML 42, 41 mm, sex indet., 34.95°S, 173.95°E, New Zealand, North Island off Cavalli Islands, 04/09/1977; **NMV F163526**, ML 35 mm, sex indet., 34.95°S, 151.13°E–35.00°S, 151.12°E, New South Wales, off Nowra, MWT, 0–250 m, CSIRO RV *Franklin*, 14/07/1986; **NMV F163576**, ML 42 mm. sex indet., 35.63°S, 154.24°E, New South Wales, 40 m, CSIRO RV *Soela*, 05/10/1981; **NMV F163577**, ML 81 mm, sex indet., 35.64°S 154.35°E, New South Wales, 20 m, CSIRO RV *Soela*, 05/10/1981; **NMNZ M.070963**, ML 102 mm, sex indet., 39.15°S, 178.85°E, New Zealand, 60 m over 1700 m, RV *James Cook*, MWT, Stn. J13/27/79, 02/10/1979; **NMNZ M.091573** (2 specimens), ML 108, 107 mm, sex indet., 39.23°S 179.67°E, New Zealand, North Island, East of Mahia Peninsula, 30 m over 3595–3604 m, RV *James Cook*, MWT, Stn. J12/19/87, 15/09/1987; **NMNZ M.091560**, ML 72, 61 mm, sex indet., 39.23°S, 179.83°E, New Zealand, 30 m over 3600 m, RV *James Cook*, MWT,

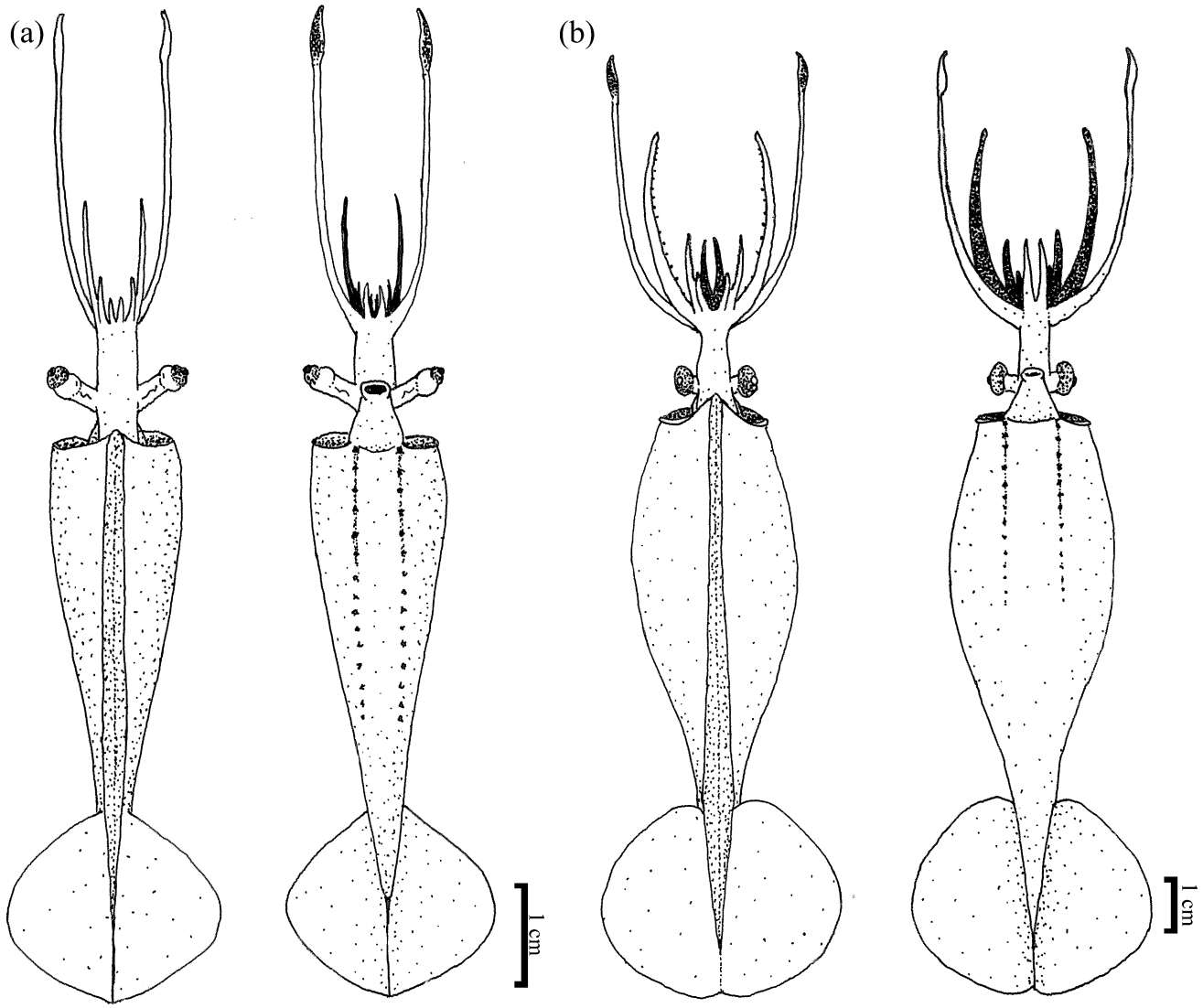

Fig. 4 *Leachia separata* ontogenic growth: dorsal and ventral views of **a** juvenile (NMNZ M.091554, ML 53 mm), **b** sub-adult (NMNZ M.091657, ML 117 mm)

Stn. J12/16/87,14/09/1987; **NMNZ M. 091,543**, ML 83 mm, sex indet., 39.25°S, 187.59°E, New Zealand, 30 m, RV *James Cook*, 13/09/1987, midwater trawl, Stn. J12/09/87; **NMNZ M.091568** (3 specimens), ML 113, 93, 74 mm, sex indet., 39.26°S, 179.84°E, New Zealand, 30 m over 3600 m, RV *James Cook*, MWT, Stn.J12/18/87, 14/09/1987; **NIWA 90,004**, ML 102 mm, sex indet., 40.76°S 165.31°E, 4215 m, Station: TAN1311/33, 13/10/2013; **NMV F163518**, ML 31 mm, sex indet., 41.14°S, 148.75°E–41.14°S, 148.75°E, 1000 m, 18/07/1991; **NMV F52269**, ML 24 mm, sex indet., 42.67°S, 148.30°E, South Eastern Tasmania, 10–12 m over 104 m, RV *Soela*, 20/06/1984; **NMV F52113**, ML 90 mm, sex indet., 42.71°S, 148.42°E, Eastern Tasmania, RV *Soela*, Stn.84/20, 18/08/84; **NMNZ M.091657**, ML 117 mm, ♀, 46.56°S, 164.06°E, New Zealand, 75–495 m over 4793 m, RV *Kaiyo Maru*, Bongo Nets, Stn. KM/111A/85, 29/07/1985.

Non-localized material examined (four specimens)

NMV F163592, ML 27 mm, sex indet., RV *Sprightly*, SP8/82/34, 29/08/1982; **NZB 110,359**, ML 64 mm, Borneo, 1875; **NMNZ M.074350**, ML 78 mm, sex indet., New Zealand, RV *W. J. Scott*, 08/05/1976; **NMNZ M.074228**, ML 74 mm, New Zealand, South Island, Cloudy Bay, 27–37 m, RV *W. J. Scott*, 20/09/1971.

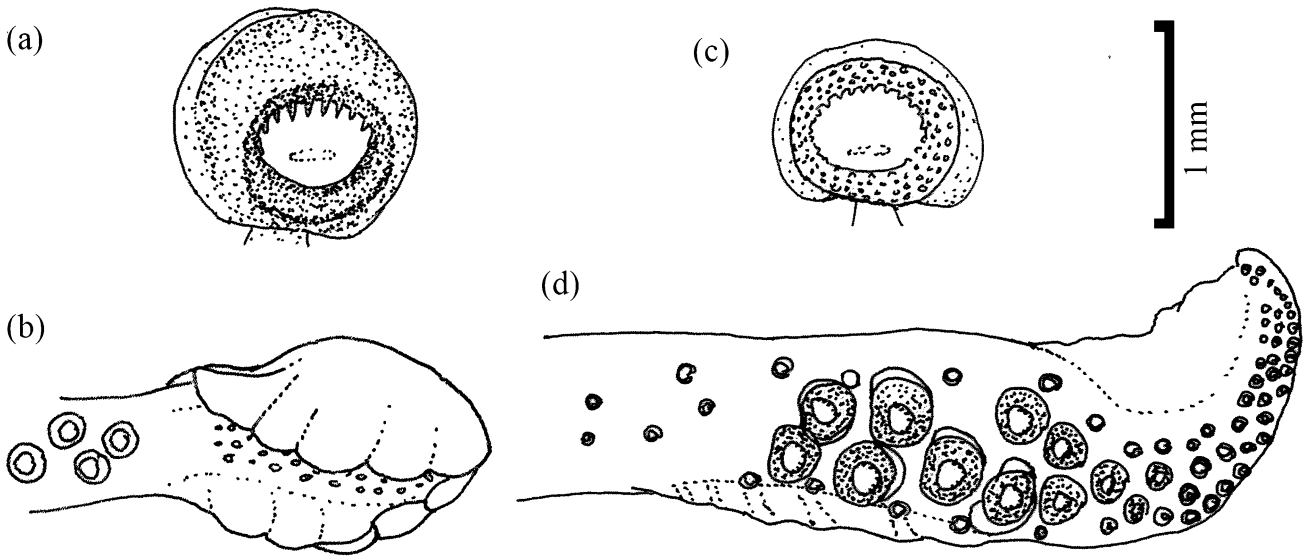

Fig. 5 Armature for *L. separata*: **a** mid-Arm III sucker, **b** female brachial end-organ, **c** largest manus sucker on **d** left tentacular club (NMNZ M.067263, ML 112 mm)

Description (ML 35–117 mm; Fig. 3)

Mantle width 10–*21*–35% ML; ventral cartilaginous strip 12–*16*–20% ML with 5–10 complex tubercles (each tubercle with 5–7 points), several single-pointed tubercles interspersed between each; tubercle series extends posteriorly past cartilaginous strip (a further 7–12 complex tubercles; Fig. 2l), up to ~ 45% ML (starting from anterior mantle fusion). Fins together rhombic in outline, FL 20–*29*–42% ML, FW 17–*38*–55% ML (FW 110–*132*–157% FL), attaining greatest width at posterior third. Head with extended brachial pillar at smaller sizes; ventral surface of head appears as a flat rectangular surface; HL 8–*13*–20% ML, HW 10–*15*–25% ML; HL proportionally shorter as ML increases while HW varies with ontogeny. Eyes small, set on stalks (decreasing in length with ontogeny; Fig. 4) through at least ML 100 mm; ED ~ 5% ML stalked-eye specimens, ~ 8% ML once eyes are sessile (Fig. 3; but see Remarks); eight sub-equal, round photophores on ventral surface: five elliptical photophores on ventral surface, three circular photophores closer to lens; olfactory papilla appears as rounded or cup-shaped protrusion on ventral surface of eye or on eye stalk. Funnel base ~ 30% MW with aperture size varying greatly with preservation of specimen. Dorsal pad of funnel organ appears as inverted 'V' with large angular flaps at lateral arms and single small papilla at anterior midpoint; ventral pads appear as elongated ovals, pointed slightly at anterior end.

Arms tapering rapidly to tip, arm formula III ≫ II≈IV > I: Arm I 4–*7*–15% ML, Arm II 7–*13*–20% ML, Arm III 20–*30*–45% ML, Arm IV 5–*11*–18% ML. Low protective membrane bordering suckers along entire length, webbing absent. Up to 50 suckers on arms in most specimens (two immature male specimens with 70 suckers on third arms), suckers spherical, with those at arm bases slightly largest, on slender peduncles; sucker rings with 7–10 pointed teeth (Fig. 5a); proximal margin of sucker ring with wide lip. Sex-specific arm-tip modifications: Arms III in females with fleshy membrane surrounding small suckers on distal tip of arm, lacking pigmentation (Fig. 5b), starting around 110 mm ML; Arm IVR in males with sucker series displaced to outer edge of arm on distal 25% and membranous keel along ventral margin of arm, starting around 90 mm ML.

Tentacles slender, TnL 42–*55*–74% ML; club slightly expanded (Fig. 5d); CL 4–*7*–10% ML. Tentacular stalk with 10 small suckers; carpal-locking apparatus with five suckers and pads alternating; 10–12 mid-manus suckers enlarged (~ 3 × larger than adjacent manus suckers), dactylus with ~ 50 suckers (Fig. 5d). Manus sucker rings with ~ 24 min peg-like teeth around entire margin, distal 12–16 teeth easiest to distinguish (Fig. 5c); sucker ring wide with rough texture; protective membrane on dorsal surface of club, large keel on ventral surface.

Known distribution

New Zealand to Southern Australia; however, *L. separata* may have appeared in earlier accounts under other names and may ultimately prove to have a southern circumglobal distribution.

Molecular information

Fresh material of *L. separata* sp. nov. was fortuitously encountered in a concurrent study; tissue samples were taken, extracted, and DNA barcoded (cytochrome *c* oxidase subunit I [COI]; Hebert et al. 2003) for 11 individuals, reported as '*Leachia* sp. nov.' (Braid and Bolstad 2019). The edited COI sequences (BIN BOLD:ADH5276) are available on the Barcode of Life Data Systems (BOLD) under the project name 'Cephalopod Fauna of the Kermadec Islands (project code KERCE).

Remarks

L. separata specimens have previously been attributed to several other names, but careful examination shows that published descriptions of these taxa do not match the present material. For instance, *Leachia cyclura* was originally described from an illustration of the dorsal surface of the type specimen; however, several sources (Joubin 1905; Pfeffer 1912) mentioned the presence of six eye photophores (whereas *L. separata* sp. nov. has eight). Both *L. rhynchophorus* and *L. schneehagenii* were described from small, damaged specimens, making detailed comparisons challenging; however, Pfeffer (1912) did describe the cartilaginous strip of *L. schneehagenii* as being < 25% of the mantle length and no additional cartilaginous tubercles were noted posterior to this strip. The type specimen of *Pyrgopsis rynchophorus* also has a short (~ 10% ML, although mantle was damaged) ventral cartilaginous strip, with no additional ventral tubercles occurring posterior to it, and examination of the eye revealed only four photophores present (although the eyes were both extremely damaged). Type material for *Perothis dussumeiri* Rochebrune 1884 (= *Leachia* sp.? *fide* Voss 1980) was described from a location close to that of *L. cyclura*, and has a ventral strip of tubercles that extend approximately 40% of the mantle length. Despite the specimen's poor condition, close examination reveals all tubercles faintly connected by the cartilaginous strip and that the strip is not linear; each strip of tubercles curves away from the ventral mid-line, forming a shallow "Z" shape. Based on existing descriptions and type material, these species all differ morphologically from *L. separata*.

The final possible existing name for this species was *L. eschscholtzii*, which was described by Rathke (1833) as having 8–12 [ventral mantle] tubercles connected by a "cartilaginous thread", ~ 50% ML, and eight eye photophores—based on the holotype collected near Madagascar (no longer extant). Chun (1910) described a specimen he reported as a 'syntype' (ZMB 110359) of *L. eschscholtzii*, although it was collected 40 years later and off Borneo. This paralarval specimen differs from Rathke's description in having a cartilaginous strip ~ 40% ML with additional tubercles posterior to the strip itself. It is in fact quite similar to *L. separata* and could represent the same species, but given the differences from Rathke's description, is not *L. eschscholtzii*. Rathke (1833) both described and illustrated how the tubercles on the cartilaginous strip were connected and there is no mention of unconnected tubercles further along the ventral mantle. As Rathke provided detailed information about the outer mantle and chromatophores of the specimen, these are clearly not absent due to specimen degradation. Nesis (1987) later synonymized Rathke's missing type with *L. cyclura*. Comparison of historical descriptions and extant type material therefore distinguishes the taxon more commonly encountered in Aotearoa New Zealand from all known *Leachia* names from the Pacific and Indian Oceans. Its characters also do not align with either of the named Atlantic species, *L. atlantica* or *L. lemur*, which have cartilaginous strips 15–25% ML and lack individual tubercles posterior to the strip itself; the limited genetic information available for the genus (see "Discussion") also supports its status as distinct from these.

Leachia separata appears to retain some character states typically associated with juvenile life stages through to larger sizes than other Pacific *Leachia* species; among the material examined, only one specimen, a female (ML 112 mm), possessed sessile eyes (a character state normally attained by ML 40 mm in most Pacific congeners), and in several other larger specimens the eye stalks were still resorbing. Male arm modifications appeared to be developing on several mid-size specimens (ML 91, 94 mm), producing the unusual combination of stalked eyes and near-mature arm characters. Males may also mature at smaller sizes than females, as the arm-tip modifications were only just beginning to develop on the largest examined female specimen (ML 112 mm).

Leachia separata occurs sympatrically with a second apparently novel species (*L.* 'sp. NZ' sensu Evans 2018). While the latter remains insufficiently known to permit formal description (two juvenile specimens), preliminary characters include 10 or 11 eye photophores (eight in *L. separata*), and about six complex ventral tubercles that do not extend beyond the cartilaginous strip.

Etymology

Leachia separata is named for the separate cartilaginous tubercles, found posterior to the cartilaginous strip, on the ventral mantle (from the Latin 'separata' meaning 'separated'). This feature appears to be unique among known *Leachia* taxa.

Discussion

To clarify the Pacific *Leachia* fauna, physical specimens from throughout the region (and types from other regions) were examined, in conjunction with a global literature review of published *Leachia* records and accounts. The apparently restricted geographic ranges of most known *Leachia* species (Young et al. 2018) support the likelihood of the Pacific hosting a unique and characteristic species array, although detailed work is still needed on congeners from the Atlantic and Indian Oceans (including molecular data) to confirm this. A complete global review of the genus was not possible within the scope of Evans (2018), but is planned as a collaborative effort in the future, building upon groundwork laid by these observations.

Prior to this study, three *Leachia* species were known to inhabit the Pacific: *L. danae*, *L. dislocata*, and *L. pacifica*. Several additional names had been historically applied to subsets of Pacific *Leachia* material. The morphological characters of our new species were carefully compared with the three nominal taxa, and with accounts of the diagnostic features characterising the other three known species (*L. cyclura*, *L. ellipsoptera*, and *L. lemur*), as well as those associated with various historical names. All comparisons (see Table 1) led us to conclude that the New Zealand material represents at least one (likely two) undescribed *Leachia* species, to which none of the historical names can be applied. In the interest of improving the accuracy of Pacific biodiversity accounts, we therefore provide the present description of the novel species *Leachia separata*, which is well represented in NZ collections and has been sequenced (BIN BOLD:ADH5276). The two specimens we consider likely to represent a fifth Pacific species were collected farther north than the *L. separata* material, in an undersampled region of New Zealand's EEZ, where other more tropical oegopsid squid species are also known to occur (see Braid and Bolstad 2019). These small individuals do not yet provide enough evidence to justify a new name or full description, so we have acted conservatively. We hope that raising awareness of this possible additional taxon will enable fresh material, when encountered, to be recognised and preserved for further study.

One further name was investigated in the course of this study: *L. rynchophorus* Rochebrune 1884, described from the Cape of Good Hope. Despite a lack of detail in the original description, Nesis (1987, p. 270) reported this taxon as a "southern subtropical species found from Southern Africa to New Zealand," with long ventral cartilaginous strips (but no specified number of eye photophores). This bears some resemblance to our new species, but examination of the holotype of *L. rynchophorus* (MNHN 3.8.742, ML 20 mm, damaged) revealed clear differences from *L. separata:* short ventral cartilaginous strips (about 5–10% ML) and no additional posterior tubercles, which are already present at this size in *L. separata*. Only four circular photophores could be distinguished on the holotype's (albeit damaged) ventral eye surface. At present, we consider *L. rynchophorus* to be a nomen inquirendum, pending examination of additional material from the type locality, and perhaps further investigation of '*Leachia* sp. A' (sensu Young et al. 2018) from the western South Atlantic.

Leachia separata sp. nov. has certainly been encountered by other authors; in one of the clearer cases, it was reported from Australia as *Pyrgopsis pacificus* by Allan (1945), who both noted and clearly illustrated the separated posterior tubercles. *Pyrgopsis pacificus* (= *Leachia pacifica*, *fide* Nesis 1987) had also been described from Japanese waters by Sasaki (1929), with illustrations depicting an animal with comparatively short cartilaginous strips (and much rounder fins), establishing the currently accepted characters of *L. pacifica*—in the meantime also known from Hawaii—and clearly not the same taxon as that depicted by Allan (1945). However, as is often the case with cranchiids (particularly those whose appearance changes considerably throughout ontogeny), there are also records that have proven more difficult to unravel. Chun (1910) and Pfeffer (1912) both examined *Leachia* material (from Borneo and Argentina, respectively) with separated tubercles on the ventral mantle, which they attributed to *L. eschscholtzii* (= *L. cyclura*, *fide* Nesis 1987, characterised by eight ventral eye photophores and ventral tubercle strips 20–40% ML), but which, upon further re-examination, may prove referable to *L. separata*, which would extend the species' known distribution.

When identifying Pacific *Leachia* species, eye photophore patterns and the ventral cartilaginous strips and tubercles appear to be the most useful characters. In well-preserved material, eye photophores are the most reliable character, since each species possesses a unique pattern; however, cranchiid eyes are notoriously delicate and routinely damaged during collection, reducing the utility of this character in most cases. Ventral tubercles are more robust and thus of greater utility, because the ventral mantle surface is often intact in preserved specimens; however, the differences among species may be relatively minor and require a practiced eye to distinguish. *Leachia separata* is the only species with tubercles extending along the ventral mantle surface posteriorly beyond the cartilaginous strip (Fig. 2), making this the most helpful feature for identifying this species. The limited material available for *L.* 'sp. NZ' (sensu Evans 2018) has not yet permitted a wide survey of tubercle structure in this taxon; preliminarily, both regular and antero-posteriorly compressed complex tubercles appear to be present, in fewer numbers (6 or 7) than in *L. separata*. The specimens are relatively small (46 and 56 mm ML), so this character should be examined in larger material when possible, although little

intraspecific variation in tubercle morphology has been observed in other *Leachia* taxa examined to date.

Future *Leachia* work will benefit greatly from incorporating additional sequence data, ideally from all nominal *Leachia* taxa. Sequences are presently only available for *L. separata* and two Atlantic clades (each clade containing only one specimen identified to species, one each as *L. lemur* and *L. atlantica*, with the rest "*Leachia* sp."). COI sequences do show clear distinctions among these three clades (with 4.65–8.83% divergence between clades based on BOLD data). An additional unpublished GenBank sequence attributed to *L. pacifica* (KC020189) appears to be either a misidentification, a pseudogene, or a poor-quality sequence, since it most closely matches the sepiolid *Rossia palpebrosa* (and only at 84.62%). Sequences thus remain unknown for most *Leachia* species, including *L. cyclura*, *L. danae*, *L. dislocata*, *L. pacifica*, and the hypothesised southwestern Atlantic "*Leachia* sp. A" (sensu Young et al. 2018).

Conclusion

This research describes a novel *Leachia* species from Aotearoa New Zealand, and presents a concise, organised account of historical literature pertaining to the genus, forming a strong foundation for future systematic research on the genus. Three other Pacific species, *L. pacifica*, *L. danae* and *L. dislocata*, are treated briefly for comparison, and preliminary remarks made on a second potentially new *Leachia* species from the New Zealand region. Future research into *Leachia* will require detailed descriptions and comparisons with the morphological characteristics treated herein, and should be supported by molecular data whenever possible in order to avoid further systematic confusion.

Author contributions Both authors contributed to the study conception and design. Data collection and analysis were performed by AE. The manuscript was drafted by AE and edited by both authors. Both authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethics approval All material for this study was sources from existing natural history collections, precluding the need for further ethics approval.

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