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ORIGINAL PAPER

Two new pygmy squids, *Idiosepius kijimuna* n. sp. and *Kodama jujutsu* n. gen., n. sp. (Cephalopoda: Idiosepiidae) from the Ryukyu Islands, Japan

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Abstract
Two new pygmy squid from the Ryukyu archipelago, Japan, are described: *Kodama jujutsu*, n. gen., n. sp. and *Idiosepius kijimuna*, n. sp. They differ from all other nominal species in a combination of traits, including the number of tentacular club suckers, shape of the funnel-mantle locking-cartilage, modification of the male hectocotylus and the structure of the gladius and nuchal-locking cartilage, in addition to mitochondrial DNA markers (12S, 16S and COI). They are both known from Okinawa Island and there is some overlap in their distributions. In a molecular phylogeny that includes all nominal Idiosepiidae, *Kodama jujutsu*, n. gen., n. sp. is sister taxon to a clade containing *Xipholeptos* Reid & Strugnell, 2018 and *Idiosepius* Steenstrup, 1881. *Xipholeptos* and *Idiosepius* are sister taxa. *Idiosepius* spp. now includes seven nominal species. In addition, aspects of the behaviour of the new species are described.

Keywords Pygmy squid · *Kodama* · *Idiosepius* · *Idiosepius kijimuna* · *Kodama jujutsu* · Ryukyu archipelago

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Introduction

In a recent study of *Idiosepius* Steenstrup, 1881 an undescribed species was recognised from Okinawa, Japan based on morphological and molecular traits (Reid and Strugnell 2018). It was represented by two males and a single female specimen held in the Australian Museum collections. The focus in Reid and Strugnell (2018) was on the Australian representatives of the family and because only two preserved specimens were available for examination at the time, the species was not formally described and was recognised as *'Okinawa'* n. sp. (Reid and Strugnell 2018: 472). Since then, more specimens have been collected enabling the species to be fully described here. It has been found at a number of locations in the Ryukyu Island archipelago, ranging from off Hamamoto, Okinawa Island in the north, and south to Sakiyama Bay, Iriomote Island.

Subsequently, a second idiosepiid was found in the region that did not appear to conform to other known idiosepiids. It shares some morphological traits with the southern Australian endemic *Xipholeptos notoides* (Berry, 1921). Both of the Japanese taxa were included in a molecular analysis with representatives of all known Idiosepiidae. The taxa within this family have historically proved difficult to identify based only on morphology (von Byern and Klepal 2010) but the application of molecular tools is facilitating a much better understanding of species boundaries and uncovering some hitherto interesting systematic depth within the family (von Byern et al. 2012; Reid and Strugnell 2018).

Both taxa are described below with some behavioural observations based on wild and laboratory-reared animals. Live animal videos of both species are included in the Supplementary information. These observations are compared with what is currently known about other members of the family.

Material and methods

Morphology

Terminology, measurements, indices, and abbreviations for anatomical structures follow Reid and Strugnell 2018 (based on Roper and Voss 1983) and are listed in Table 1. All measurements are in millimetres (mm). Measurements and counts for individual mature specimens of the new species are presented in Tables 3, 4, 6 and 7; the range of values for each character is expressed in the descriptions and in Tables 2 and 5 as: minimum–*mean*–maximum (SD). The values for each sex are given separately. In the case of discrete probability distributions, such as sucker-counts, standard deviations are not provided in cases where counts are few in number because these cannot be calculated using the same formula as can be applied to normally distributed data.

For scanning electron microscopy, arms, clubs and radulae were removed, mounted, then air dried and examined in a Zeiss Evo LS15 SEM using a Robinson Backscatter detector. Soft structures were mounted directly on carbon tape and air dried; some radulae and gladii were mounted on glass coverslips prior to SEM. Photomicrography using a compound microscope was also used to illustrate some structures.

Other abbreviations

AMS, Australian Museum, Sydney; NSMT, National Museum of Nature and Science, Tokyo, Japan; WAM, Western Australian Museum, Perth.

Table 1 Description of measurements and counts

Arm Length—AL: length of each designated (i.e. 1, 2 etc.) arm measured from first basal (proximal-most) sucker to distal tip of arm (Arm 1, dorsal; 2, dorso-lateral; 3, ventro-lateral; 4, ventral) [ALI]
Arm Length left hectocotylus—AL4l: length of left hectocotylised arm in males [AL4lI]
Arm Length right hectocotylus—AL4r: length of right hectocotylised arm in males [AL4rI]
Sucker Count ASC: total number of suckers on each designated arm (e.g. ASC2)
Arm Sucker Count hectocotylus—ASC4r: number of suckers on proximal end of hectocotylised right ventral arm
Arm Sucker Count hectocotylus—ASC4l: number of suckers on proximal end of hectocotylised left ventral arm
Arm Sucker diameter—AS: diameter of largest normal sucker on each designated (i.e. 1, 2 etc.) arm [ASIn]
Club Length—ClL: length of tentacular club measured from proximal-most basal suckers (carpus) to distal tip of club [ClLI]
Club Row Count—ClRC: number of suckers in transverse rows on tentacular club
Club Sucker diameter—ClS: diameter of largest sucker on tentacular club [ClSI]
Egg Diameter—EgD: diameter of largest egg present in the ovary or oviduct [EgDI]
Eye Diameter—ED: diameter of eye [EDI]
Fin Insertion anterior—FIa: anterior origin of fin measured from mantle margin to anterior-most junction of fin and mantle [FIIa]
Fin Length—FL: maximum length of single fin [FLI]
Fin Width—FW: greatest width of single fin [FWI]
Free Funnel length—FFu: the length of the funnel from the anterior funnel opening to the point of its dorsal attachment to the head [FFuI]
Funnel Length—FuL: the length of the funnel from the anterior funnel opening to the posterior margin measured along the ventral midline [FuLI]
Gill Lamellae Count—GLC: number of lamellae on one side of each demibranch (excluding the terminal lamella)
Gill Length—GilL: length of the gill measured from terminal lamella to origin of gill [GilLI]
Head Length—HL: dorsal length of head measured from point of fusion of dorsal arms to anterior tip of nuchal cartilage [HLI]
Head Width—HW: greatest width of head at level of eyes [HWI]
Mantle Length—ML: dorsal mantle length. Measured from anterior-most point of mantle to posterior apex of mantle
Mantle Width—MW: greatest width of mantle [MWI]
Ventral Mantle Length—VML: length of ventral mantle measured along ventral midline [VMLI]

Definitions largely follow Roper and Voss (1983). Indices (shown in square brackets) are calculated by expressing each measure as a percentage of mantle length

Table 2 *Idiosepius kijimuna* n. sp. ranges of arm length indices (ALI), arm sucker diameter indices (ASIn) and arm sucker counts (ASC) of ten mature males and ten mature females

	Males				Females			
	Min.	Mean	Max.	SD	Min.	Mean	Max.	SD
ALI1	21.6	*24.5*	29.2	2.3	16.4	*21.6*	28.2	3.7
ALI2	24.6	*29.0*	35.1	3.5	20.0	*24.8*	29.5	3.5
ALI3	24.6	*28.9*	37.5	4.2	20.0	*25.1*	28.6	2.8
ALI4R	37.0	*48.2*	61.4	7.2	22.0	*26.7*	31.8	3.0
ALI4L	35.8	*44.0*	58.3	6.3				
ASIn1	1.5	*2.7*	3.5	0.7	2.1	*2.4*	3.1	0.4
ASIn2	1.6	*2.6*	3.6	0.6	2.0	*2.4*	3.6	0.4
ASIn3	1.6	*2.5*	3.3	0.6	2.0	*2.6*	3.6	0.6
ASIn4	1.6	*2.5*	3.6	0.7	1.7	*2.3*	2.6	0.3
ASC1	13	*17*	20	2	20	*25*	30	3
ASC2	18	*20*	24	2	24	*27*	31	2
ASC3	16	*19*	24	2	22	*26*	32	3
ASC4r	2	*3*	4	1	22	*26*	30	2
ASC4l	3	*5*	6	1				

min. minimum, *max.* maximum, *R* right, *L* left

Taxon sampling and DNA isolation

Specimens were collected at night by wading, snorkelling, or on SCUBA from shore at Hamamoto (26° 40′ 17.90″ N, 127° 53′ 17.05″ E), Sunabe (26° 19′ 41.09″ N, 127° 44′ 35.98″ E), Maeda (26° 26′ 43.54″ N, 127° 46′ 20.01″ E), Onna Point (26° 40′ 17.90.4″ N, 127° 50′ 28.78″ E), Miyagi (26° 22′ N, 127° 59′ E), and Kaichyu-doro (26° 19′ N, 127° 55′ E) near Okinawa Island and Sakiyama Bay (24° 19′ N, 123° 40′ E) and Shirahama (24° 22′ N, 123° 44′ E) near Iriomote Island. Adults of both species were collected using dipnets or 200 ml transparent plastic containers. After collection they were transferred to 20 L buckets of fresh seawater and aerated with a battery powered bubbler and immediately transported to the Okinawa Institute of Science and Technology where they were gradually acclimated over one hour to 20 °C and other aquarium parameters and conditions used by Jolly et al. (2022). Adults were kept in a 70 L tank where they were observed until sacrificed. They were first transferred to a 500 ml container of filtered seawater and anaesthetised in a magnesium chloride solution (Abbo et al. 2021). Magnesium chloride was gradually added to a final concentration of 7% over 30 min. After no response to pinching stimuli and total cessation of breathing was observed, a small fin clip biopsy was performed for DNA extraction. The animal was then transferred to 4% methanol free paraformaldehyde in seawater and fixed for 72 h at 4 °C with gentle rocking. Specimens were then transferred to 70% ethanol for long-term preservation. Some specimens were fixed and preserved in 95% ethanol.

Freshly collected specimens were used for molecular study and analyses. Previously sequenced individuals were used to increase sample size with specimen data obtained from GenBank. Taxon names applied were those assigned by Reid and Strugnell (2018) and include: *Xipholeptos notoides* (Berry, 1921); *I. hallami* Reid and Strugnell 2018; *I. minimus* d'Orbigny in Férrusac and d'Orbigny 1835; *I. paradoxus* (Ortmann, 1888); *I. picteti* (Joubin, 1894); *I. pygmaeus* Steenstrup, 1881, and *I. thailandicus* Chotiyaputta et al, 1991. As used in that analysis, *Semirossia patagonica* (Smith, 1881) was selected as the outgroup taxon because among available mtDNA genomes, the *Idiosepius* sequence shows greatest similarity to that of *Semirossia* (Hall et al. 2014) and in addition, a sister taxon relationship between Idiosepiidae and Sepiolida is supported in the literature (Strugnell et al. 2017). Tissue from 16 new individuals that included both suspected new species was sampled (See Appendix Table 9). DNA was extracted using commercial kits (NucleoSpin; Machery-Nagel, Germany or DNeasy Blood & Tissue Kit; Qiagen, Hilden, Germany) according to the manufacturer's protocols.

PCR amplification and nucleotide sequencing

Partial sequences of three mitochondrial genes; 12S rRNA, 16S rRNA and cytochrome c oxidase subunit I (COI) were amplified in this study. Primers and annealing temperatures are detailed in Allcock et al. (2008). PCR was performed in a 20 µL volume, containing 2.0 µL Ex Taq buffer, 1.6 µL of dNTP, 0.1 µL of TaKaRa Ex Taq DNA Polymerase (TaKaRa), 1.0 µL of each primer, 12.3 µL of distilled H_2O and 2.0 µL template DNA. PCR products were sequenced by a commercial sequencing service (Fasmac, Japan) in both directions.

Table 3 *Idiosepius kijimuna* n. sp.: measurements (mm), counts and indices of 10 mature male specimens

Specimen	Paratype AMS C.575592	Paratype NSMT-Mo 85879	Paratype NSMT-Mo 85880	Paratype NSMT-Mo 85878	Paratype NSMT-Mo 85879	NSMT-Mo 85926	NSMT-Mo 85924	Paratype NSMT-Mo 85877	NSMT-Mo 85923	Holotype NSMT-Mo 85928
ML	5.4	5.6	5.7	6.0	6.2	6.2	6.5	6.6	7.4	8.1
MWI	61.1	60.7	70.2	63.3	69.4	59.7	46.2	57.6	56.8	48.1
VMLI	83.3	80.4	84.2	80.0	80.6	80.6	83.1	75.8	83.8	79.0
FWI	29.6	26.8	28.1	25.0	25.8	22.6	24.6	22.7	20.3	19.8
FIIa	74.1	78.6	71.9	75.0	64.5	74.2	80.0	75.8	77.0	71.6
FLI	38.9	39.3	42.1	33.3	35.5	37.1	38.5	33.3	31.1	37.0
FuLI	24.1	26.8	29.8	28.3	24.2	29.0	21.5	22.7	32.4	27.2
FFuI	16.7	14.3	14.0	16.7	16.1	16.1	21.5	13.6	17.6	12.3
HLI	41.7	41.1	43.9	50.0	36.3	48.4	46.2	51.5	47.3	39.5
HWI	57.4	57.1	66.7	56.7	59.7	45.2	42.3	50.0	45.9	39.5
EDI	14.8	8.9	8.8	8.3	8.1	11.3	8.5	13.6	10.8	8.6
AL1I	24.1	22.3	26.3	29.2	24.2	25.8	26.2	22.7	23.0	21.6
AL2I	27.8	28.6	35.1	33.3	32.3	27.4	24.6	28.0	28.4	24.7
AL3I	27.8	26.8	35.1	37.5	29.0	27.4	24.6	28.8	27.0	24.7
AL4rI	55.6	50.0	61.4	50.0	48.4	43.5	41.5	51.5	43.2	37.0
AL4lI	46.3	37.5	43.9	58.3	44.4	40.3	47.7	41.7	43.9	35.8
ASIn1	2.78	3.04	3.51	3.33	3.23	2.42	1.85	3.03	2.03	1.54
ASIn2	2.78	3.57	2.98	3.33	3.23	1.94	1.85	3.03	2.03	1.60
ASIn3	2.78	2.68	2.63	3.33	3.23	1.94	1.85	3.03	2.03	1.60
ASIn4	2.22	3.57	2.63	3.33	3.23	1.94	1.85	3.03	2.03	1.60
ASC1	15	17	13	16	16	18	20	18	18	17
ASC2	18	18	20	20	18	23	22	20	24	21
ASC3	16	18	18	20	17	20	24	21	20	20
ASC4r	3	2	3	2	2	3	4	3	4	3
ASC4l	3	3	5	4	5	4	6	6	6	4
ClLI	42.6	30.4	31.6	36.7	30.6	27.4	32.3	31.8	37.8	27.2
ClRC	2	2	2	2	2	2	2	2	2	2
CSC	32	36	34	32	32	38	40	32	39	33
ClSI	2.78	1.79	2.11	2.00	1.94	1.61	1.85	1.82	1.69	1.48
GilLI	25.9	17.9	24.6	25.0	24.2	27.4	26.2	22.7	28.4	24.7
GilLC	15	17	17	18	18	15	18	14	15	18
SpLI	32.4	31.4	30.7	28.7	30.6	–	–	33.3	–	–
SpWI	2.2	2.1	2.1	2.0	2.4	–	–	1.89	–	–

Molecular sequence analyses

DNA sequences were compiled in *Geneious* v 9.0.5 and sequences were aligned using MAFFT v7.222 (Katoh and Kuma 2002). *PartitionFinder* v1.1.1 (Lanfear et al. 2012) was used to select best-fit partitioning schemes and evolutionary models for the genes contained within the alignment. Maximum likelihood phylogenies were estimated for all datasets using *PhyML* (Guindon and Gascuel 2003), *IQ-TREE* (Nguyen et al. 2015) implemented within the W-IQ-TREE web interface (Trifinopoulos et al. 2016) and also *RAxML* (Stamatakis 2014) implemented within the *RAxML* BlackBox web server (Stamatakis et al. 2008).

Results

Phylogenetic analysis

The best fit model was one where all three genes were contained within a single partition. The evolutionary model with the lowest BIC values was the Hasegawa-Kishino-Yano Model (HKY) + I + G (Hasegawa et al. 1985). The total evidence tree obtained from the sequence data is shown in Fig. 1.

A number of well-supported clades were retrieved from the analysis, with clear structuring within some of the larger clades. Two clades that include the newly sequenced

Table 4 *Idiosepius kijimuna* n. sp.: measurements (mm), counts and indices of 10 mature female specimens

Specimen	NSMT-Mo 85925	NSMT-Mo 85921	NSMT-Mo 85884	Paratype NSMT-Mo 85876	NSMT-Mo 85929	NSMT-Mo 85931	AMS C.477896	NSMT-Mo 85922	NSMT-Mo 85930	NSMT-Mo 85927
ML	9.8	10.0	10.0	10.3	11.0	11.0	11.2	11.4	11.5	11.8
MWI	63.3	52.0	61.0	58.3	57.3	56.4	62.5	54.4	56.5	56.8
VMLI	78.6	85.0	85.0	81.6	72.7	80.0	80.4	78.9	82.6	82.2
FWI	18.4	17.0	18.0	22.3	13.6	18.2	23.2	15.8	20.0	15.3
FIIa	78.6	78.0	70.0	73.8	69.1	66.4	67.9	71.9	69.6	72.0
FLI	34.7	35.0	38.0	31.1	27.3	33.6	35.7	32.5	36.5	29.7
FuLI	25.5	30.0	25.0	28.2	25.5	22.7	20.5	20.2	21.7	27.1
FFuI	13.3	13.0	14.0	14.6	13.6	12.7	13.4	12.3	13.9	15.3
HLI	35.7	32.0	30.0	35.0	28.2	38.2	28.6	35.1	32.2	29.7
HWI	40.8	41.0	47.0	45.6	36.4	40.0	40.2	39.5	39.1	38.1
EDI	8.2	7.0	8.0	11.7	6.4	8.2	8.9	7.9	8.7	8.5
AL1I	23.0	20.0	25.0	28.2	16.4	22.7	24.1	21.9	17.4	17.8
AL2I	25.5	20.0	29.5	29.1	22.7	26.4	28.6	21.9	21.7	22.0
AL3I	27.0	27.0	27.0	25.2	21.8	27.3	28.6	24.6	20.0	22.9
AL4I	23.5	27.0	25.0	27.2	26.4	31.8	31.3	26.3	26.1	22.0
ASIn1	2.24	2.50	3.00	2.14	2.27	2.27	3.13	2.19	2.17	2.12
ASIn2	2.04	2.50	2.60	2.62	2.27	2.27	3.57	2.19	2.17	2.12
ASIn3	2.04	2.50	3.60	2.91	2.27	2.27	3.57	2.19	2.17	2.12
ASIn4	2.55	2.50	2.40	2.62	2.27	1.82	2.41	2.19	2.61	1.69
ASC1	24	22	27	24	20	26	30	24	26	27
ASC2	30	26	26	27	26	31	24	26	25	28
ASC3	24	26	22	27	24	32	24	28	28	28
ASC4	27	28	28	26	22	30	24	24	26	28
ClLI	35.7	33.0	35.0	32.0	32.7	36.4	33.9	39.5	34.8	35.6
ClRC	2	2	2	2	2	2	2	2	2	2
CSC	50	48	42	45	48	51	44	48	47	49
ClSI	2.0	2.0	2.4	1.9	1.8	1.8	2.2	1.8	2.2	1.7
GilLI	30.6	25.0	30.0	22.3	27.3	20.0	18.8	26.3	27.8	29.7
GilLC	20	20	22	24	24	20	25	24	22	20
EgDI	8.2	10.0	10.0	12.6	9.1	9.1	7.1	8.8	8.7	9.3

taxa from the Ryukyu archipelago, are clearly distinct and well-supported. *Xipholeptos notoides* (IQ-tree bootstrap [IQ-BS] = 100%; RAxML bootstrap [R-BS], R-BS = 100%, PhyML bootstrap P-BS = 100%) was sister-taxon to a clade containing all *Idiosepius* (IQ-tree bootstrap [IQ-BS] = 98%; RAxML bootstrap [R-BS], R-BS = 77%, PhyML bootstrap P-BS = 93%). As reported in Reid and Strugnell (2018), the branch length separating *X. notoides* from *Idiosepius* is long relative to the branch lengths within *Idiosepius* indicating considerable molecular divergence.

Also on a long branch is a clade that includes one of the newly discovered Okinawan idiosepiids (IQ-tree bootstrap [IQ-BS] = 100%; RAxML bootstrap [R-BS], R-BS = 100%, PhyML bootstrap P-BS = 100%). This taxon is sister to the southern Australian endemic *X. notoides* and *Idiosepius* spp. Together with some significant morphological traits, deep evolutionary divergence is suggested based on analysis of the molecular data. For these reasons we place the members of this clade in its own genus, *Kodama* n. gen. as described below.

The second Japanese taxon forms a well-supported clade within *Idiosepius* (IQ-tree bootstrap [IQ-BS] = 100%; RAxML bootstrap [R-BS], R-BS = 91%, PhyML bootstrap P-BS = 99%). Members of this clade are recognised and described below as a new species, *Idiosepius kijimuna* n. sp. It includes the taxa referred to as '*Okinawa*' n. sp. in Reid and Strugnell (2018) and is sister to *Idiosepius minimus*. This clade shows some considerable internal structure, particularly among three termini that have a high support value on a relatively long branch (IQ-tree bootstrap [IQ-BS] = 92%; RAxML bootstrap [R-BS], R-BS = 82%, PhyML bootstrap P-BS = 84%).

Table 5 *Kodama jujutsu* n. sp. ranges of arm length indices (ALI), arm sucker diameter indices (ASIn) and arm sucker counts (ASC) of five mature males and two mature females

	Males				Females			
	Min.	Mean	Max.	SD	Min.	Mean	Max.	SD
ALI1	26.7	*29.4*	32.1	2.4	23.3	*27.7*	32.2	6.3
ALI2	26.7	*37.9*	47.2	7.6	25.2	*32.7*	40.2	10.6
ALI3	31.6	*34.3*	39.1	3.2	24.0	*29.3*	34.5	7.4
ALI4R	15.8	*23.4*	31.3	6.9	24.8	*26.8*	28.7	2.8
AL4L	16.7	*22.7*	28.1	4.3				
ASIn1	1.7	*2.3*	2.8	0.5	1.9	*2.1*	2.3	0.3
ASIn2	2.3	*2.6*	2.8	0.2	2.3	*2.3*	2.3	0
ASIn3	2.1	*2.5*	2.8	0.3	2.3	*2.6*	2.9	0.4
ASIn4	1.7	*2.3*	2.8	0.5	2.3	*2.6*	2.9	0.4
ASC1	14	*15*	16	1	15	*17*	20	3
ASC2	18	*21*	25	3	23	*23*	24	1
ASC3	18	*19*	22	2	19	*19*	19	0
ASC4r	8	*9*	10	1	19	*19*	19	0
ASC4l	8	*9*	10	1				

min. minimum, *max.* maximum, *R* right, *L* left

Systematic descriptions

Idiosepius kijimuna n. sp.

(Figs. 1, 2, 3, 4, 5, 6, Tables 2, 3, 4, 8, Appendix Table 9).

Common name: Ryukyu Pygmy Squid; Japanese name, Ryukyu-himeika.

Material examined

Type material

Holotype: Japan, Okinawa I., Motobu Hamamoto [Peninsula], 26° 40′ N, 127° 53′ E, coll. J. Jolly: 1♂, 8.1 mm ML, 22 Feb. 2019 (NSMT-Mo 85928).

Paratypes: Japan, Okinawa I., Motobu Hamamoto [Peninsula], 26° 40′ N, 127° 53′ E, coll. N. Sato: 1♀, 8.6 mm ML, 26 Jan. 2007 (NSMT-Mo 85875); 1♀, 10.0 mm ML, 19 Apr. 2007 (NSMT-Mo 85876); 1♂, 6.6 mm ML, 1♀, 7.2 mm ML, 3 May 2007 (NSMT-Mo 85877); 3♂, 3.8–6.5 mm ML, 4 May 2007 (NSMT-Mo 85878); 4♂, 4.0–6.2 mm ML, 1♀, 5.6 mm ML, 15 May 2007 (NSMT-Mo 85879); 5♂, 4.0–5.7 mm ML, 1♀, 7.3 mm ML, 18 May 2007 (NSMT-Mo 85880); 1♀, 7.4 mm ML, 29 Aug. 2007 (NSMT-Mo 85881); 1♂, 5.2 mm ML, 29 Oct. 2007 (NSMT-Mo 85882).

Other material examined

Japan: 4♀, 4.0–5.2 mm ML, Iriomote I., Sakiyama Bay, 24° 19′ N, 123° 40′ E, coll. N. Sato, 26 Aug. 2014 (AMS C.596044); 7♂, 6♀, Iriomote I., Shirahama, 24° 22′ N, 123° 44′ E, coll. N. Sato, 27 Aug. 2014 (AMS C.596045). Okinawa I.: Kaichyu-doro, 26° 19′ N, 127° 55′ E, coll. N. Sato: 1♂, 4.3 mm ML, 25 Jun. 2007 (AMS C.596040); 1♀, 9.4 mm ML, 3 Jul. 2007 (AMS C.596041). Miyagi I., 26° 22′ N, 127° 59′ E, coll. N. Sato: 1♂, 6.1 mm ML, 1♀, 10.0 mm ML, 23 Jan. 2008 (NSMT-Mo 85884); 1♂, 6.5 mm ML, 21 Feb. 2008 (AMS C.596042), 1♂, 5.2 mm ML, 3 Jun. 2008 (AMS C.596043). Motobu Hamamoto [Peninsula], 26° 40′ N, 127° 53′ E, coll. N. Sato, 9 Dec. 2007 (NSMT-Mo 85883); 2♂, 7.3 mm ML, 5.3 mm ML, data as for previous specimen, 22 Mar. 2007 (AMS C.596039). Okinawa, Hamamoto, 26° 40′ N, 127° 53′ E, coll. J. Jolly, 22 Feb. 2019: 1♂, 6.2 mm ML (NSMT-Mo 85926); 1♂, 7.4 mm ML, 1♀, 6.9 mm ML (NSMT-Mo 85923); 1♂, 6.5 mm ML, 1♀, 6.2 mm ML (NSMT-Mo 85924); 1♀, 10.0 mm ML (NSMT-Mo 85921); 1♀, 11.4 mm ML (NSMT-Mo 85922); 1♀, 9.8 mm ML (NSMT-Mo 85925); 1♀, 11.8 mm ML (NSMT-Mo 85927); 1♀, 7.8 mm ML (NSMT-Mo 85929); 1♀, 11.5 mm ML (NSMT-Mo 85930); 1♀, 11.0 mm ML (NSMT-Mo 85931); 1♀, 6.8 mm ML (AMS C.596046); 1♀, 6.8 mm ML (AMS C.596047); 1♀, 7.0 mm ML (AMS C.596048); 1♀, 9.3 mm ML (AMS C.596049); 1♀, 6.0 mm ML (AMS C.596050); 1♀, 6.5 mm ML (AMS C.596051); 1♀, 8.5 mm ML (AMS C.596052); 1♀, 7.0 mm ML (AMS C.596053); 1♀, 7.8 mm ML (AMS C.596054); 3 juv., 1.9–2.0 mm ML (AMS C.596055). Motobu Pen. Bise, 26° 42′ 31″ N, 127° 52′ 42″ E, 26 May 2013, coll. H. Fukumori, K. Hidaka & Y. Takano: 1♀, 11.2 mm ML (AMS C.477896); 1♂, 5.4 mm ML (AMS C.575592); 1♂, 4.7 mm ML (AMS C.575591).

Diagnosis

Tentacular club with two suckers in each transverse row; total number of club suckers 32–40♂, 42–50♀. Male

Table 6 *Kodama jujutsu* n. sp.: measurements (mm), counts and indices of mature male specimens

Specimen	Paratype NSMT-Mo 85933	Paratype NSMT-Mo 85938	Paratype NSMT-Mo 85940	Holotype NSMT-Mo 85932	Paratype NSMT-Mo 85939
ML	5.3	5.7	6.0	6.0	6.4
MWI	64.2	64.9	65.0	65.0	71.9
VMLI	75.5	87.7	80.0	81.7	89.1
FWI	28.3	28.1	31.7	33.3	25.0
FIIa	62.3	66.7	65.0	66.7	78.1
FLI	28.3	35.1	30.0	30.0	23.4
FuLI	45.3	43.9	41.7	46.7	45.3
FFuI	41.5	43.9	40.0	38.3	29.7
HLI	50.9	52.6	50.0	46.7	53.1
HWI	58.5	59.6	60.0	58.3	62.5
EDI	11.3	15.8	15.0	13.3	14.1
AL1I	32.1	31.6	26.7	28.3	28.1
AL2I	47.2	40.4	26.7	40.0	35.2
AL3I	35.8	31.6	33.3	31.7	39.1
AL4rI	28.3	15.8	16.7	25.0	31.3
AL4lI	22.6	21.1	16.7	25.0	28.1
ASIn1	2.83	2.28	2.08	1.67	2.73
ASIn2	2.83	2.63	2.50	2.50	2.50
ASIn3	2.83	2.63	2.08	2.67	2.34
ASIn4	2.83	2.63	2.08	1.67	2.34
ASC1	15	14	16	16	16
ASC2	18	20	24	25	19
ASC3	18	18	18	18	22
ASC4r	8	10	8	9	8
ASC4l	8	10	8	9	8
ClLI	41.5	70.2	75.0	83.3	35.2
ClRC	2	2	2	2	2
CSC	24	28	24	26	26
ClSI	3.4	2.6	2.1	2.5	2.7
GilLI	28.3	31.6	33.3	50	31.3
GilLC	15	15	16	15	16
SpLI	22.6	–	20.0	18.3	–
SpWI	2.26	–	2.33	1.67	–

hectocotylised arms 4 longer than remaining arms; right ventral arm longer than left ventral arm (Fig. 2a, b; Table 2). Female arms 1 shorter than remaining arms, rest similar in length. Hectocotylus: male left ventral arm with 3–6 suckers basally and large flap at tip of arm; right ventral arm with 2–4 suckers basally. GiLC males 14–18; females 20–25.

Description

Counts and indices for individual specimens are given in Tables 3 (males) and 4 (females). Ten mature male and ten mature females were measured.

Mature males smaller than females: ML males 5.4–*6.4*–8.1 mm (SD 0.8), females 9.8–*10.8*–11.8 mm (SD 0.7). Mantle blunt-cylindrical (Fig. 2a–c); MWI males 46.2–*59.3*–70.2 mm (SD 7.8), females 52.0–*57.8*–63.3 mm (SD 3.5). Dorsal mantle not joined to head, ventral mantle margin straight to slightly concave. Ventral skin tags present, one on each side of head posterior to eyes (Fig. 2d). Fins small, rounded, length approximately one-third mantle length, FLI males 31.1–*36.6*–42.1 mm (SD 3.3), females 27.3–*33.4*–38.0 mm (SD 3.3); positioned dorso-laterally on posterior end of mantle, FIIa males 64.5–*74.3*–80.0 mm (SD 4.3), females 66.4–*71.7*–78.6 mm (SD 4.1); fin width ~ 20% ML, FWI males 19.8–*24.5*–29.6 mm (SD 3.2), females 13.6–*18.2*–23.2 mm (SD 3.0); anterior and posterior margins with well-developed lobes, lateral lobes crescentic.

Table 7 *Kodama jujutsu* n. sp.: measurements (mm), counts and indices of mature female specimens

Specimen	Paratype NSMT-Mo 85936	Paratype NSMT-Mo 85936
ML	8.7	12.9
MWI	72.4	69.8
VMLI	70.1	69.8
FWI	27.6	36.4
FIIa	64.4	54.3
FLI	51.7	48.1
FuLI	40.2	35.7
FFuI	20.7	17.8
HLI	40.2	37.2
HWI	54.0	48.1
EDI	14.9	12.4
AL1I	32.2	23.3
AL2I	40.2	25.2
AL3I	34.5	24.0
AL4I	28.7	24.8
ASIn1	2.3	1.9
ASIn2	2.3	2.3
ASIn3	2.9	2.3
ASIn4	2.9	2.3
ASC1	15	20
ASC2	24	23
ASC3	19	19
ASC4	19	19
ClLI	41.4	33.3
ClRC	2	2
CSC	35	34
ClSI	2.3	2.3
GilLI	34.5	29.5
GilLC	16	18
EgDI	6.9	11.6

Funnel conical, base broad, tapered anteriorly (Fig. 2e); FuLI males 21.5–*26.6*–32.4 mm (SD 3.4), females 20.2–*24.6*–30.0 mm (SD 3.3); free for about 1/3 of its length, FFuI males 12.3–*15.9*–21.5 mm (SD 3.4), females 20.2–*24.6*–30.0 mm (SD 3.3). Funnel-locking cartilage (Fig. 2f), deep, oval, with defined outer rim. Mantle-locking cartilage (Fig. 2g) compliments funnel member, an ear-shaped lug, broadest posteriorly, tapering towards mantle margin. Funnel valve small, flaplike, rounded anteriorly, dorsal element broad, inverted V-shape with pointed anterior tip; ventral elements ovoid (Fig. 3a). Nuchal locking cartilage oval, not well-defined, indistinct (Fig. 3b).

Head broader than long in both sexes, HLI males 36.3–*44.6*–51.5 mm (SD 4.9), females 28.2–*32.5*–38.2 mm (SD 3.4); HWI males 39.5–*52.0*–66.7 mm (SD 8.7), females 36.4–*40.8*–47.0 mm (SD 3.2). Eyes large, EDI males 8.1–*10.2*–14.8 mm (SD 2.4), females 6.4–*8.3*–11.7 mm (SD 1.4); ventral eyelids free. Eye covered by corneal membrane. Distinct, large olfactory pit on latero-posterior surface of head, posterior and ventral to eyes, close to mantle opening.

Arms, broad basally, tapered distally, hectocotylised arms much longer than unmodified arms in males 4.3.2.1 or 4.2.3.1 (Tables 2 and 3), arm formula variable in females, with arm 4 usually longest and arms 1 shorter than lateral arms (Tables 2 and 4). Arm length index of longest arm in males (ALI4 right) 37.0–*48.2*–61.4 mm (SD 7.2), females (ALI4) 22.0–*26.7*–31.8 mm (SD 3.0). All arms similar in shape, U-shaped in section (Fig. 3c). Sucker pedicels broad, short, suckers joined closely to arms and club. Chitinous inner ring of arm suckers without teeth, smooth or slightly crenulated on inner margin (Fig. 3d). Infundibulum with 2–3 rows of shallow cup-like broad-based pegs, innermost row of pegs larger, slightly more elongate, cylindrical surrounding inner ring, more elongate on one side of the sucker than the other; processes contain low papillae, outer-most sucker rim processes rectangular, flat, radially arranged (Fig. 3d, e). Male and female arm suckers similar in size (Table 2). Sucker counts range from 13–24 on male normal arms, 20–32 in females. All arms connected by relatively shallow webs, protective membranes absent.

Both ventral arms of males hectocotylised: (Fig. 3f–h). Right ventral arm with 2.0–*3.0*–4.0 suckers proximally remainder of arm without suckers; aboral side of arm with broad, thin, ventro-lateral flanges attached laterally on each side of arm; flange broadest proximally, tapering to distal tip of arm (Fig. 3f). Right ventral arm slightly longer than left ventral arm (Table 2). Left ventral arm with 3.0–*5.0*–6.0 suckers proximally (generally a greater number of suckers on left than on right ventral arm), remainder of arm without suckers; distal tip of arm flattened forming a blunt tongue-like flange and proximal to this a slightly shorter blunt flap; in preserved specimens, distal flap often recurved to cover distal tip of arm (Fig. 3g, h).

Tentacles similar to arms in appearance, semicircular in section; oral surface convex. Club relatively long; ClLI males 27.2–*32.8*–42.6 mm (SD 4.8), females 32.0–*34.9*–39.5 mm (SD 2.2), cylindrical, tapers to blunt end distally. Sucker-bearing face of club only slightly convex. Suckers ~ 0.1–0.2 mm diameter in centre of club, arranged in two rows in both sexes. Total number of club suckers in males 32.0–*35.0*–40.0 (SD 3); females 42.0–*47.2*–51.0. Swimming keel on aboral side of carpus broad, extends posteriorly beyond carpus. Keel forms groove on oral side. Club sucker dentition (Fig. 4a): inner ring without teeth; infundibulum with 3 rows of pegs; shallow, cup-like distally bearing numerous papillae. At periphery, pegs narrower and with fewer papillae. Outer-most sucker rim processes flattened, rectangular.

Table 8 Idiosepiidae nominal species distinguishing features

Species	GiLC	No. rows club suckers*	Total no. club suckers	No. sucker rows left ventral arm 4 ♂	No. sucker rows right ventral arm 4 ♂	Relative lengths of ventral arms compared with other arms (males)	Female relative arm lengths	Hectocotylus left ventral arm IV (with flap)	Hectocotylus right ventral arm 4	Other
Idiosepius hallami Reid abd Strugmell, 2018 Status: valid Misidentifications: *I. paradoxus*	14–18 ♂, 18–20 ♀	2 ♂, 2 ♀	27–37 ♂, 37–46 ♀ Sucker rim pegs with papillae	7–10	6–9	Arms 4 slightly longer than remaining arms; arms 1 shortest, arms 2 and 3 similar in length	All similar in length, with arms 1 only slightly shorter than rest	Longer than right with large, flap-like lobe attached obliquely ventro-laterally towards distal tip	Shorter, broader than remaining arms Strong keels on aboral side	Tentacles possibly used for spermatophore transfer† Radula rachidian teeth homodont or bidentate in repeating series Spermatophore cement body bipartite
I. kijimuna n. sp. Status: valid Misidentifications: *I. paradoxus*	14–18 ♂, 20–25 ♀	2	32–40 ♂, 42–50 ♀	3–6	2–4	Arms 1–3 similar in length. Arms 4 longer than rest	Arms 1 shorter than rest. Rest similar in length	Shorter than right. Distal tip of arm with blunt tongue-like flange and proximal to this a slightly, shorter blunt flap	Keels on aboral side	Mate head-to-head Hectocotylus used for transferring spermatophores
I. minimus d'Orbigny in Férrusac and d'Orbigny 1835 Status: valid Syn. *I. biserialis* Voss, 1962; *I. macrocheir* Voss, 1962	?	2–4	39 ♂, 32–44 ♀	4	4	4.3.2.1 Arms 4.5 × length of remaining arms	4.3.2.1	Left arm shorter than right, with two small flaps separated by a deep cleft	Slightly wider than left Keels on aboral side	Oral side of ventral arms in males with dark pigment spots

Table 8 (continued)

Species	GiLC	No. rows club suckers*	Total no. club suckers	No. sucker rows left ventral arm 4 ♂	No. sucker rows right ventral arm 4 ♂	Relative lengths of ventral arms compared with other arms (males)	Female relative arm lengths	Hectocotylus left ventral arm IV (with flap)	Hectocotylus right ventral arm 4	Other
I. paradoxus (Ortmann, 1888) Status: valid Misidentifications: 'Okinawa' n. sp.	29	4	~48.0 ♂; 54–62 ♀	3–7 suckers basally;	3–7 on right ventral arm	Similar in length to other arms	All similar in length, arms 1 and 4 slightly shorter than remaining arms	Same length as right, semi-circular membrane on dorsal side, tip enlarged as a cap-like cover	Same length as left; slightly thicker. Keels on aboral side Transverse ridges and grooves orally	Tentacles as thick as arms Hectocotylus used for transferring spermatophores
I. picteti (Joubin, 1894) Status: questionable	34	2–4		2	2	Much shorter than other arms. Remaining arms similar in length		Slender and bilobed at tip. Lobe tiny	Shorter and thicker than left. Strong keels on aboral side transverse ridges and grooves on oral side	
I. pygmaeus Steenstrup, 1881 Status: valid Misidentifications: *O. pygmaeus*	28–30 ♂, 39–45 ♀	2**–4 **Hylleberg and Nateewathana (1991)	45–62 ♂, 51–63 ♀	1–4 (usually 1–3)	1–3	Much shorter than other arms. Remaining arms similar in length	Arm 1 shortest	Longer than right; thinner than right, slender; with transverse ridges and grooves on oral side; bilobed at tip. Lobe tiny	Shorter than left; stout, thick, blunt. Keels on aboral side; fleshy transverse ridges on oral side	Live animals sometimes reverse countershade: pale dorsally, dark ventrally Males grasp females during mating Hectocotylus used for transferring spermatophores

Table 8 (continued)

Species	GiLC	No. rows club suckers*	Total no. club suckers	No. sucker rows left ventral arm 4 ♂	No. sucker rows right ventral arm 4 ♂	Relative lengths of ventral arms compared with other arms (males)	Female relative arm lengths	Hectocotylus left ventral arm IV (with flap)	Hectocotylus right ventral arm 4	Other
I. thailandicus Chitiyaputta et al. (1991) Status: valid Misidentifications: *I. biserialis* (SE Asia)	15–17	2	28–39 ♂, 32–45 ♀	2–7	2–5	Arms 4 1.5 × as long as arms 1–3	Arms 1 shortest	Slightly shorter than right Tiny flap at tip of arm	Slightly longer than left. Broad with keels on aboral side	Tentacles used for transferring spermatophores Females light brown, males dark brown
Kodama jujutsu n. gen., n. sp.	15–16 ♂, 16–18 ♀	2 ♂, 2 ♀	24–28 ♂ 34–35 ♀ Sucker rim pegs with papillae	8–10	8–10	All similar in length, arms 4 slightly shorter than remaining arms	All similar	Similar to right Large, flap-like lobe attached obliquely ventro-laterally towards distal tip	Similar to left. No keels on aboral side	Body squat, rounded Males approach females from below when mating Hectocotylus used for transferring spermatophores Radula rachidian teeth homodont; first lateral teeth short, hooked
Xipholeptos notoides (Berry, 1921)	30♂, 28–30 ♀	2–3 ♂, 2–3 ♀	45–62 ♂ 51–78 ♀	7–11	7–11	All similar length	All similar length	Longer than right, bifurcates at tip	No keels on aboral side	Body narrow, elongate Radula rachidian teeth homodont Spermatophore cement body with bipartite structure

Data has been compiled from the examination of preserved specimens and published literature. Included taxa follow the taxonomic conclusions reached in this paper and Reid and Strugnell (2018). Some information was derived from taxa now deemed to be in synonymy with valid species. Misidentifications refer to those in previous publications, GenBank and likely among museum collections. Not all *Idiosepius* species have yet been examined for all characters in the light of the taxonomy proposed in this paper and this should be a focus for future study

*These traits have been used historically to distinguish *Idiosepius*, but their usefulness is questionable (von Byern and Klepal 2010)

†To be confirmed. Traits for *I. picteti* were scored following examination of the purported holotype. (Table modified from Reid and Strugnell (2018), Table 5 to include new species.) See also generic diagnoses. Distinguishing generic characters are not tabulated here

Gills with 14–*16*–18 (SD 1.6) lamellae per demibranch in males, females with 20–*22*–25 (SD 2.0) lamellae per demibranch; GiLI 17.9–*24.7*–28.4 mm (SD 2.9) males, 18.8–*25.8*–30.6 mm (SD 4.2) females.

Buccal membrane with six lappets and fringed inner margin; suckers absent. Radula with seven transverse rows of homodont teeth (Fig. 4b). Rachidian teeth, and second lateral teeth broad basally, tapering distally, second laterals asymmetrical with cusp of displaced toward midline of radula ribbon (Fig. 4b, c), second lateral teeth triangular, pointed, symmetrical in shape; marginal teeth narrow, scythe-like (Fig. 4b).

Upper beak (Fig. 4d) with short, triangular rostrum, and, as for lower beak, flanked by row of smaller teeth. Lower beak (Fig. 4e) with large median rostrum, flanked on either side with a row of similar-sized small teeth. Distinct dark pigmentation restricted to rostrum of upper and lower beaks.

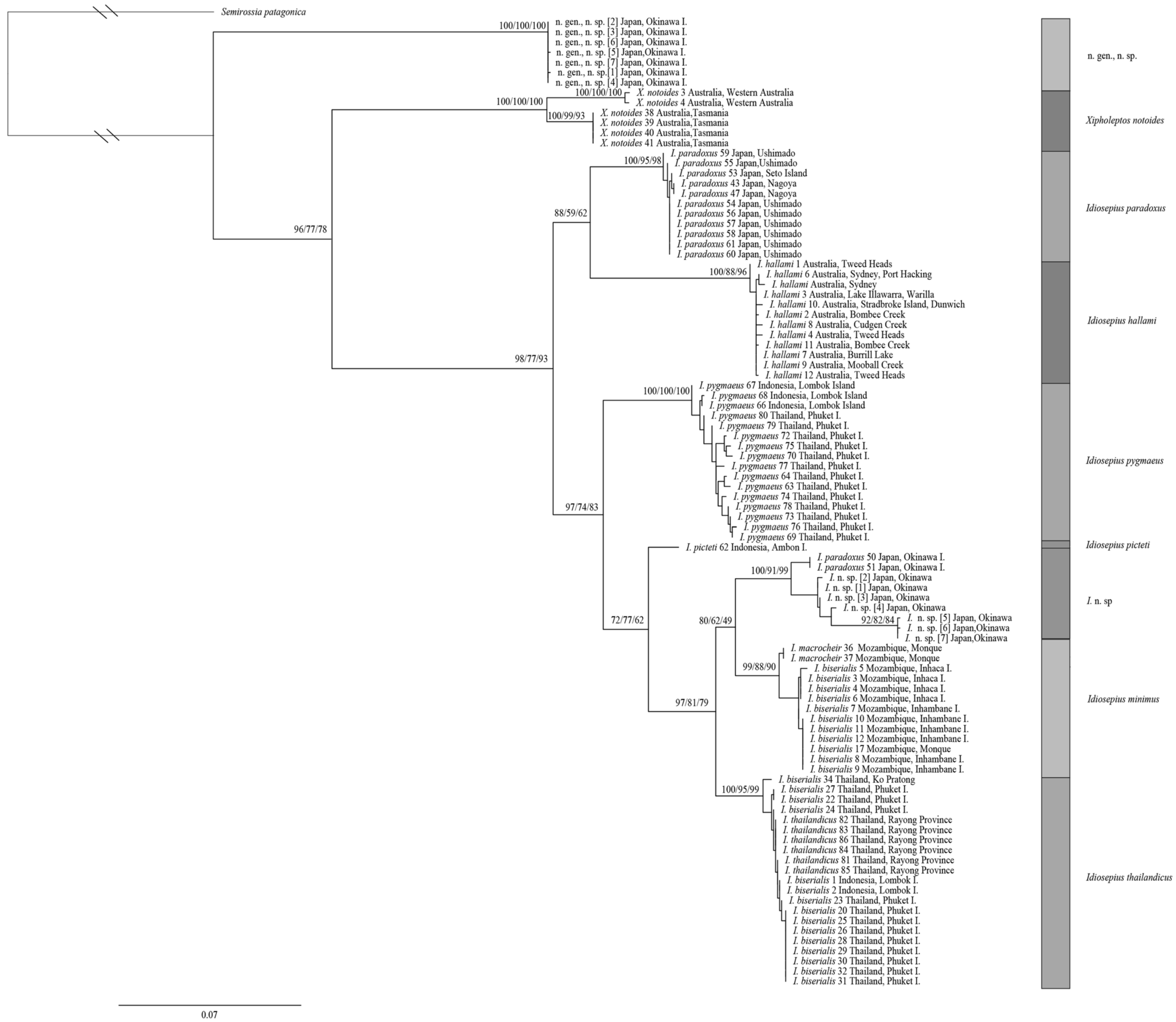

Fig. 1 Maximum Likelihood phylogenetic tree generated using PhYML (GTR + I + G) from the analysis of partial fragments of 12S rRNA, 16S rRNA and CO1. *Semirossia patagonica* was used the outgroup. Bootstrap values (1000 replicates) were generated from maximum likelihood analysis using IQ-tree/RAMxML/PhyML. Taxon names to the left of the shaded bar refer to the species names used in GenBank records and associated publications, in addition to the new taxa identified in this analysis. Taxon names to the right of the bar are those we believe should be assigned to the studied taxa. Numbers to the right of the taxon names refer to sample numbers corresponding to individual specimens sequenced that are listed in the Appendix Table 9; numbers in square brackets were sequenced for this study, those without brackets correspond to specimens included in Reid and Strugnell (2018)

Male reproductive tract similar in structure to congeners (not illustrated). Spermatophores approximately 1/3 mantle length; SpLI 28.7–*31.2*–33.3 mm (SD 2.9), SpWI 1.9–*2.1*–2.4 mm (SD 0.2). Sperm reservoir simple, without coiled sperm cord. Cement body unipartite; aboral end cup-shaped, cylindrical, oral end tapering toward ejaculatory apparatus (Fig. 4f). Oral end of ejaculatory apparatus with 3–4 simple coils.

Female reproductive tract: Ovary large, occupies approximately half of mantle cavity. Eggs of various sizes suggesting protracted multiple spawning. Ovary opens via single thick-walled oviduct at anterior end on left side of animal. Nidamental glands paired, broad, leaf-shaped, located ventral to ovary toward, and overlying anterior half. Accessory nidamental glands absent. Eggs ovoid, 0.8–1.3 mm diameter; EgDI 7.1–*9.3*–12.6 mm (SD 1.4).

Gladius reduced to a thin, ovoid, chitinous structure embedded in ventral side of dorsal mantle below adhesive pad; does not extend full length of mantle. Rachis absent.

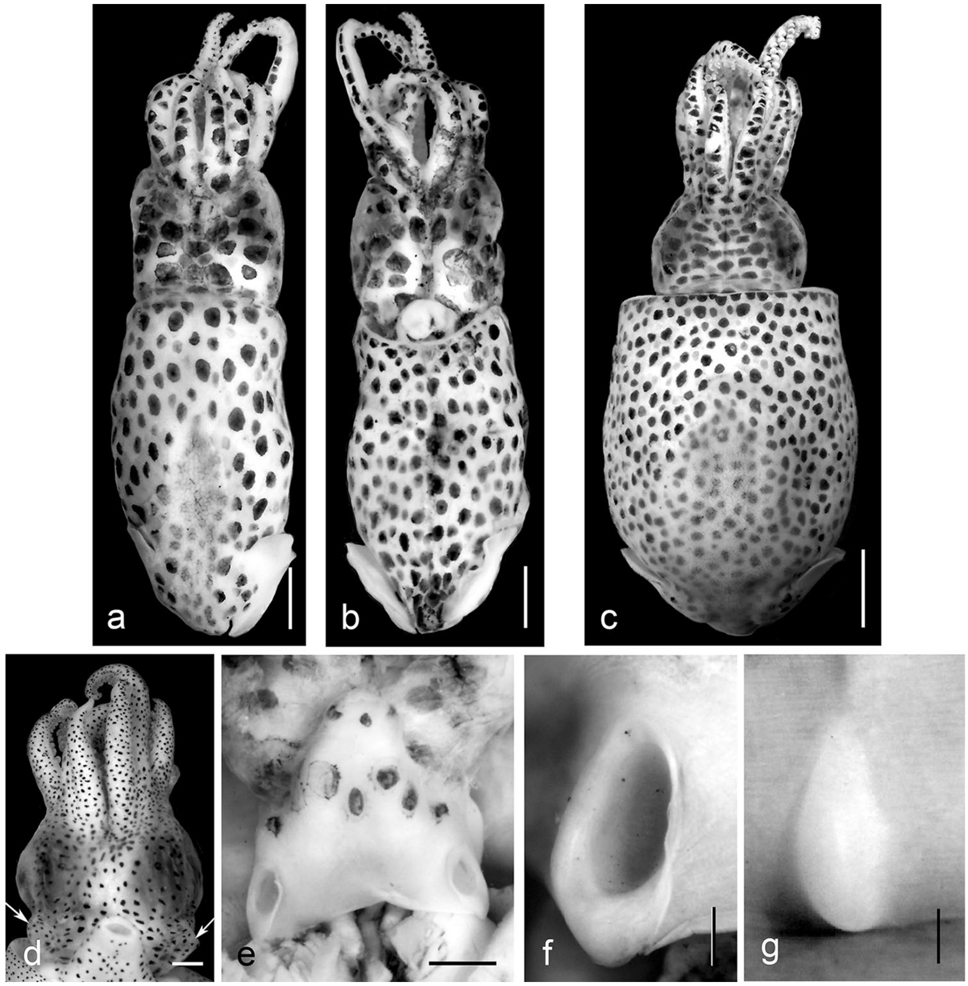

Fig. 2 *Idiosepius kijimuna* n. sp. **a** dorsal view, male, 5.4 mm ML, AMS C.575592. **b** ventral view, same specimen. **c** dorsal view, female, 11.2 mm ML, AMS C.477896. **d** ventral view of head showing ventro-lateral skin tags (arrows), male, 5.4 mm ML, AMS C.575592. **e** funnel, paratype female, 8.6 mm ML, NSMT Mo-85875. **f** funnel-locking cartilage, paratype male, 7.2 mm ML, NSMT-Mo 85881. **g** mantle-locking cartilage, male as in **f**. Scale bars: **a**, **b** = 1 mm; **c** = 2 mm; **d** = 0.5 mm; **e** = 1 mm; **f**, **g** = 200 µm

Preserved animals cream with purple chromatophores evenly peppered dorsally and ventrally on mantle and arms, largest on head (Fig. 2a–c). Large chromatophores on arms appear as block-like bands. Chromatophores on fins confined to junction with mantle, do not extend to outer fin margins. Ventral side of funnel with chromatophores. Chromatophores often in a row at distal tip. Chromatophores in tissue overlying internal viscera. Live animals (Fig. 5) mid-brown to greenish brown with relaxed chromatophores giving a predominantly uniform colouration (Fig. 5a).

Type locality

Japan, Okinawa I., Motobu Hamamoto [Peninsula], 26° 40′ N, 127° 53′ E.

Distribution

Japan: Ryukyu Islands: Iriomote I., Sakiyama Bay, 24° 19′ N, 123° 40′ E to Okinawa, Motobu Pen. Bise, 26° 42′ 31″ N, 127° 52′ 42″ E (Fig. 6).

Habitat and biology

Idiosepius kijimuna have primarily been collected from shallow (less than 2 m) seagrass beds in Okinawa in winter from November to March. During this time, they have also been observed, albeit rarely, in coral habitats. Their whereabouts during the warmer months are largely unknown.

Etymology

The species name is used for creatures in Okinawan mythology. The Kijimunā are said to be elfin creatures that make their home in the banyan trees that grow over the Ryukyu Archipelago. Their diet consists entirely of seafood and they are excellent fishers. They avoid octopuses at all costs. The name is used as a noun in apposition.

Remarks

Characters that distinguish *I. kijimuna* from *Kodama jujutsu*, n. sp. n. gen. and *X. notoides* are provided in the Diagnosis and Remarks under *K. jujutsu* n. sp. n. gen. below. The

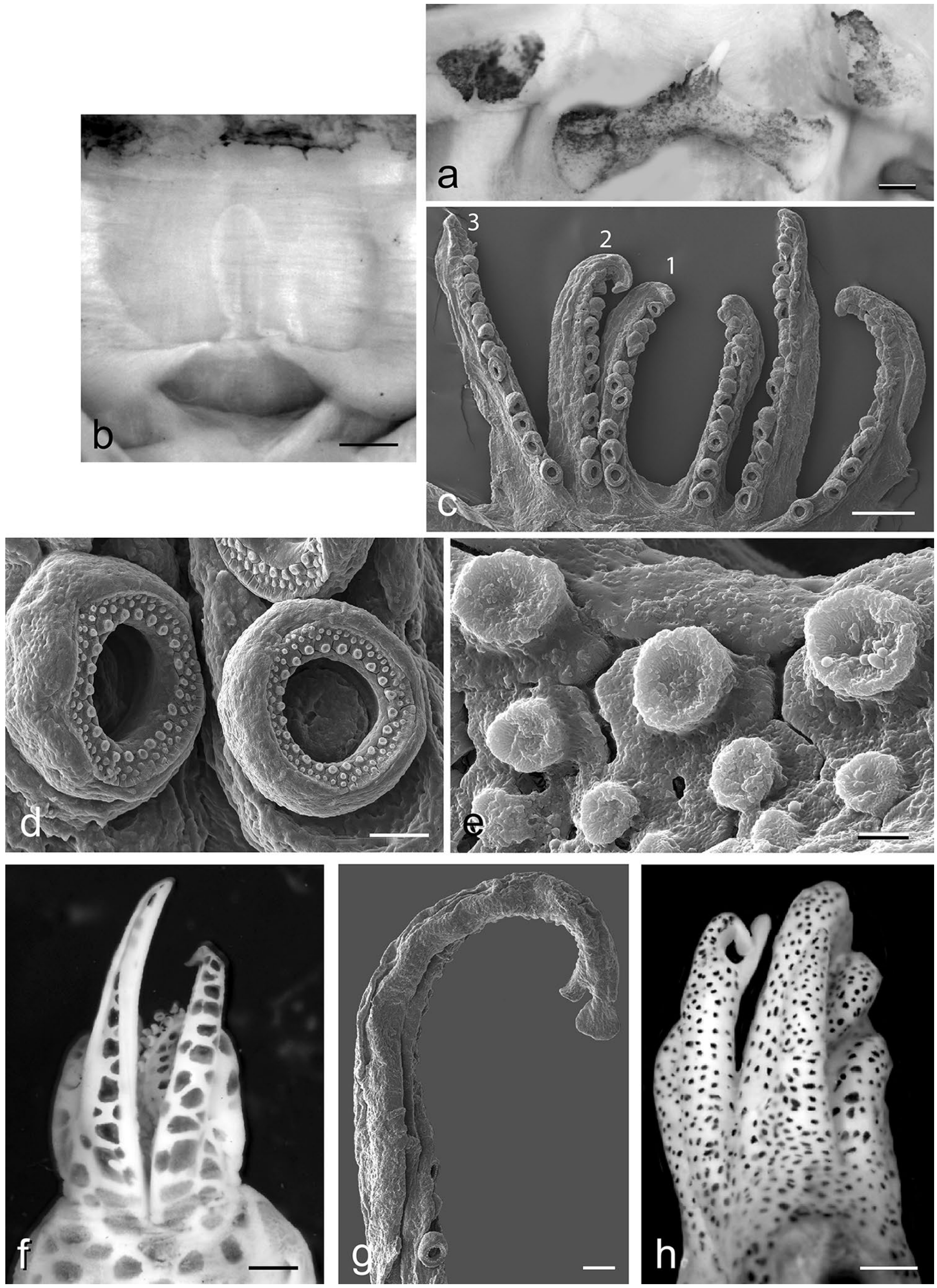

Fig. 3 *Idiosepius kijimuna* n. sp. **a** funnel organ stained with methylene blue, paratype male, 7.2 mm ML, NSMT-Mo 85881. **b** nuchal cartilage, specimen as in a. **c** SEM ventral view of portion of arm crown (arms 1–3, numbered), paratype male, 6.0 mm ML, NSMT-Mo 85878. **d** SEM enlargement of arm 2 (left) and arm 3 (right) suckers, specimen as in c. **e** enlargement of individual sucker rim, arm 3 left, specimen as in c. **f** ventral arms, male 5.4 mm ML (AMS C.575592). **g** SEM hectocotylised left arm 4, paratype male 6.0 mm ML, NSMT-Mo 85878. **h** far left, hectocotylised left ventral arm (tip recurved during fixation), male AMS C.575592, 5.4 mm ML. Scale bars: **a**, **b**, = 200 µm; **c** = 300 µm, **d** = 30 µm, **e** = 3 µm, **f** = 0.5 mm. **g**, **h** = 200 µm

combination of characters that separate *I. kijimuna* from other nominal *Idiosepius* are provided in Table 8.

The presence of relatively long male ventral arms is not unique to *I. kijimuna.* This trait is shared by its sister taxon *I. minimus* and also *I. thailandicus.* These three taxa together form a well supported clade within the broader *Idiosepius* clade (IQ-tree bootstrap [IQ-BS] = 97%; RAxML bootstrap [R-BS], R-BS = 81%, PhyML bootstrap P-BS = 79%) that appears to be sister to *I. picteti* (Fig. 1).

Kodama n. gen.

Type species

Here designated. *Kodama jujutsu*, n. sp.

Diagnosis

Mantle-locking cartilage a straight ridge, funnel-locking cartilage a corresponding straight, narrow furrow. Eight to 10 pairs of suckers, extend along length of both ventral

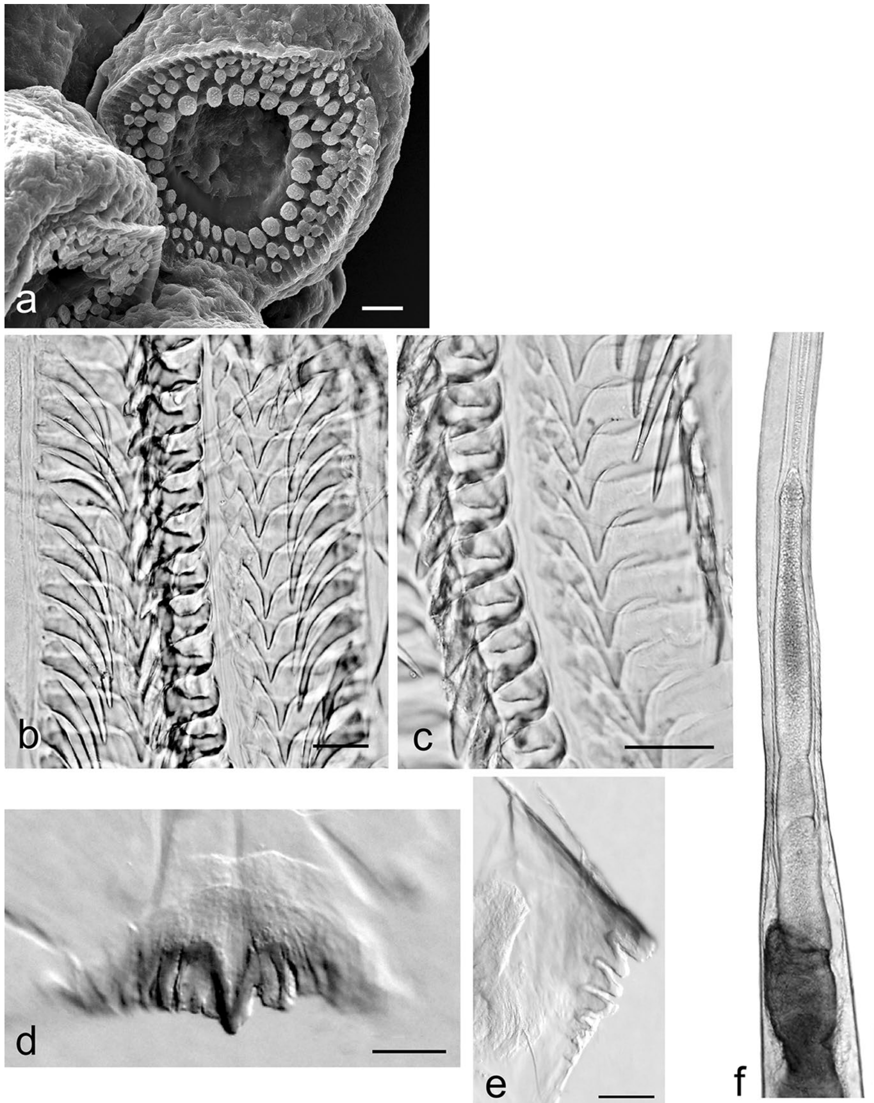

Fig. 4 *Idiosepius kijimuna* n. sp. **a** SEM, tentacular club sucker, male paratype, 6.0 mm ML, NSMT-Mo 85858. **b** radula, female, 10.2 mm ML, AMS C.477896. **c** enlargement of portion of radula. **d** upper beak, specimen as in **b**. **e** lower beak, lateral view, specimen as in **d**. **f** enlargement of oral end of spermatophore, male, 6.5 mm ML, NSMT-Mo 85924. Scale bars: **a** = 10 μm; **b**, **c** = 1 mm; **d**, **e** = 2 mm; **f** = 1 mm

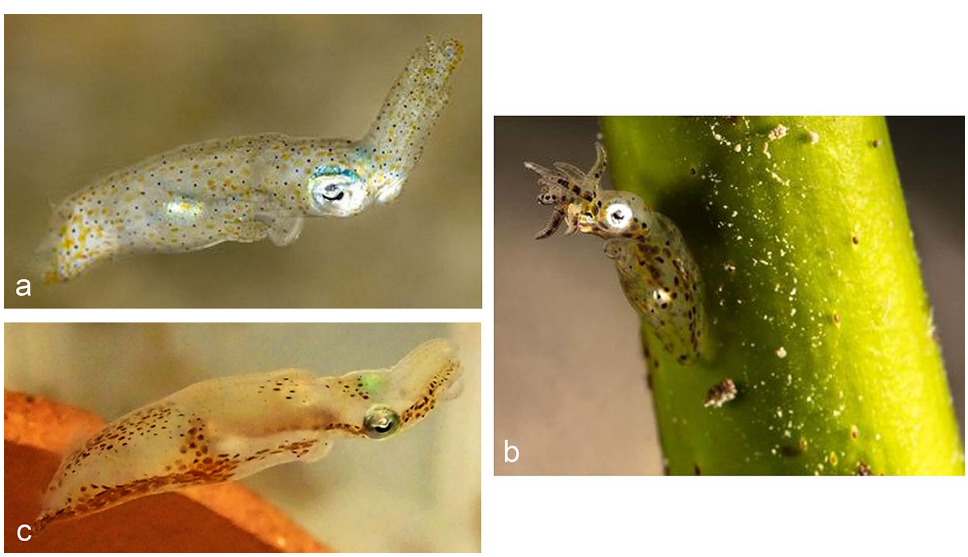

Fig. 5 Live *Idiosepius kijimuna* n. sp. **a**, **c** swimming; **b** attached to vegetation using dorsal adhesive pad. Photos **a**, **c** © Jeff Jolly; **b** © Brandon Hannan

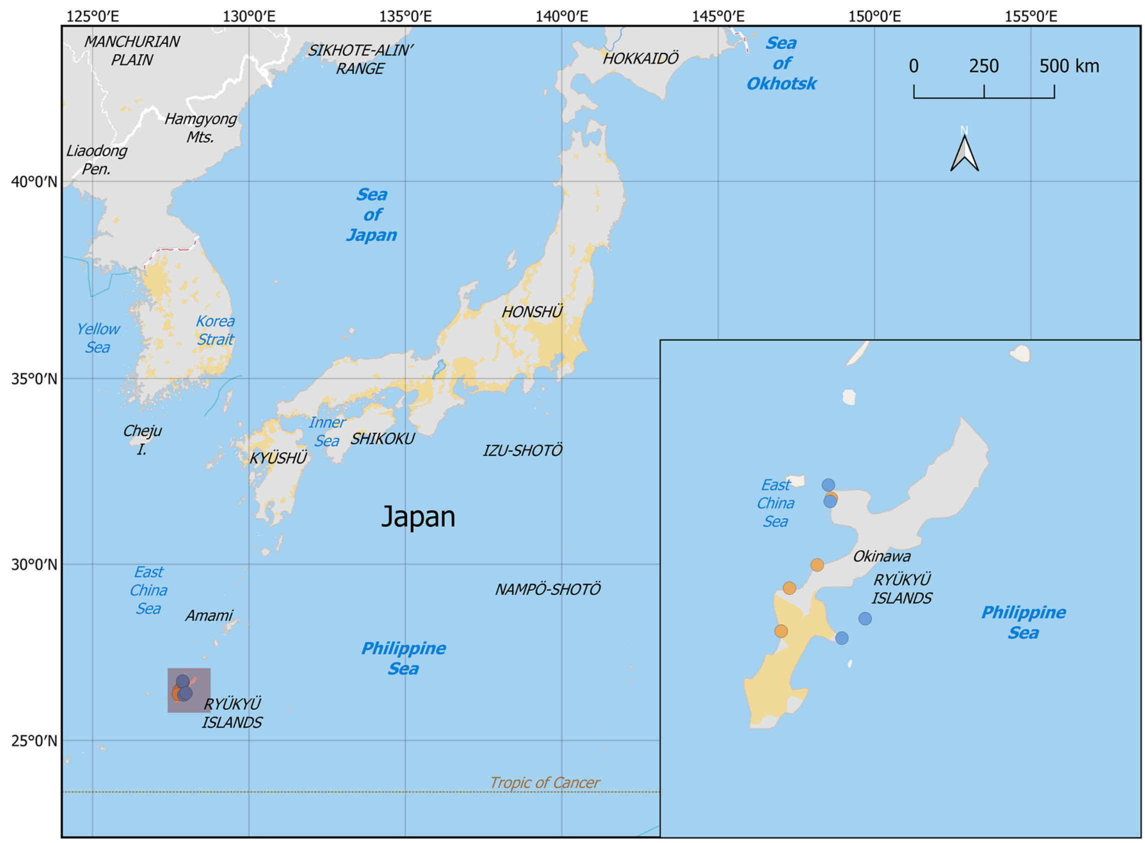

Fig. 6 Distribution of idiosepiids examined in this study: *Idiosepius kijimuna* n. sp. blue circles, *Kodama jujutsu* n. gen., n. sp. orange circles. Shaded area on main map corresponds to Ryuku Isds inset in bottom right of figure

arms in males; aboral side of right ventral arm not modified, smooth; only left ventral arm modified as the hectocotylus. Tentacular club with two rows of suckers in transverse rows. Gills with 15–18 lamellae per demibranch. Rachidian teeth of radula homodont; first lateral teeth short, much smaller than other teeth and cusps low. Gladius extends full length of mantle, paddle-shaped, narrow, pointed anteriorly, broadens midway along its length; remainder of gladius, clear non-sclerotised. Nuchal-locking cartilage distinct, well-defined. Prominent skin tags, one on each side, posterior to eyes; anterior to eyes on ventral side of head with pair of prominent, small rounded, protruding papillae.

Etymology

The generic name *Kodama* refers to a tree spirit in Japanese folklore. It has a reputation of being rounded in shape. The presence of Kodama is a sign of a healthy forest. We have chosen this name to suggest its extension to representing a healthy reef.

Remarks

Some traits of *Kodama* n. gen. are shared with *Xipholeptos.* Both of these monotypic taxa have a straight mantle-locking cartilage, and the funnel-locking cartilage is a corresponding straight furrow. Both have a medial rachis in the gladius and the arms of males are all similar in length. The aboral side of the right ventral arm is without a keel, and posterior to the eyes is a pronounced skin tag. These traits separate *Kodama* n. gen. and *Xipholeptos* from *Idiosepius.* However, the distinct, folded bipartite structure seen in the aboral end of the spermatophore cement body reported for *X. notoides* in Reid and Strugnell (2018) is not present in *Kodama* n. gen. In addition, the club has two transverse rows of suckers in *Kodama*, n. gen. and four rows in *Xipholeptos.* The body of *Xipholeptos* is cylindrical and elongate, while that of *Kodama* is squat and rounded.

Kodama jujutsu, n. sp.

(Figs. 1, 6, 7, 8, 9, 10, 11, 12, Tables 5, 6, 7, 8, Appendix Table 9).

Common name: Hannan's Pygmy Squid; Japanese name Tsuno-himeika.

Material examined

Type material

Holotype: Japan, Okinawa I, Hamamoto: 1♂, 6.0 mm ML, 26° 40′ 17.90″ N, 127° 53′ 17.05″ E, 24 Feb 2019, coll. C. Sugimoto and J. Jolly (NSMT-Mo 85932).

Paratypes: Japan: Okinawa I.: Miyagi I., 1♀, 6.8 mm ML, 26° 22′ N, 127° 59′ E, 23 Jan 2008, coll. N. Sato (NSMT-Mo 85935). Maeda Pt, 1♂, 3.5 mm ML, 26° 26′ 43.54″ N, 127° 46′ 20.01″ E, 26 Jun 2018, coll. J. Jolly and K. Asada (NSMT-Mo 85934). Onna Pt, 1♂, 5.3 mm ML, 26° 40′ 17.90.4″ N, 127° 50′ 28.78″ E, 24 Feb 2019, coll. K. Asada and C. Derup (NSMT-Mo 85933). Sunabe Sea Wall, 26° 19′ 41.09″ N, 127° 44′ 35.98″ E: 1♀, 8.7 mm ML (NSMT-Mo 85936); 1♀, 12.9 mm ML (NSMT-Mo 85937); 1♂, 5.7 mm ML, (NSMT-Mo 85938); 1♂, 6.4 mm ML (NSMT-Mo 85939); ♂, 6.0 mm ML (NSMT-Mo 85940), 24 Feb 2019, coll. B. R. Hannan.

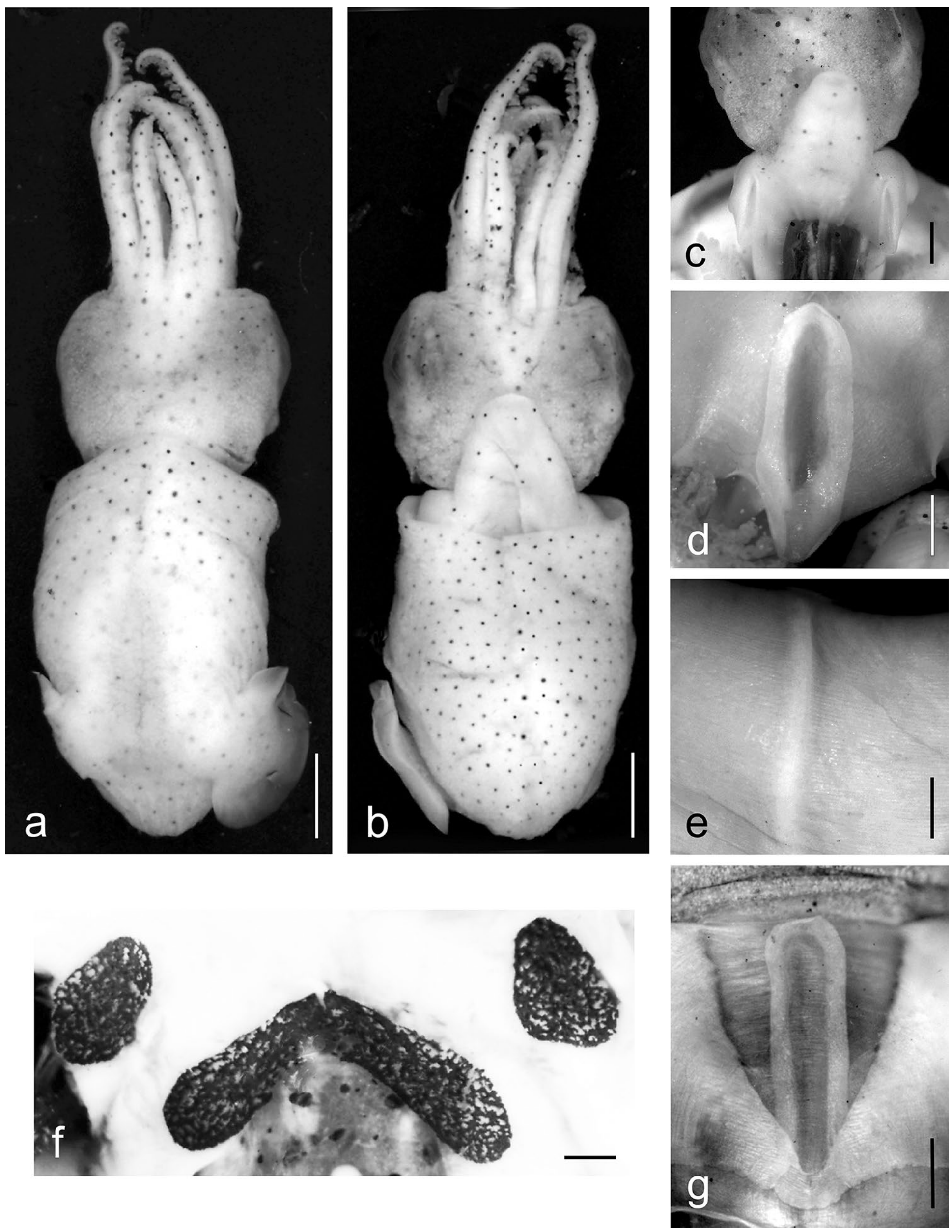

Fig. 7 *Kodama jujutsu* n. gen., n. sp. **a** dorsal view, male paratype, 5.3 mm ML, NSMT-Mo 85933. **b** ventral view, specimen as in a. **c** funnel, ventral view, specimen as in **b**. **d** funnel-locking cartilage, paratype female, 12.9 mm ML, NSMT-Mo 85937. **e** mantle-locking cartilage, specimen as in **d**. **f**, funnel organ stained with methylene blue, male paratype, 5.3 mm ML, NSMT-Mo 85933. **g** nuchal-locking cartilage, female paratype 8.7 mm ML. Scale bars: **a**, **b** = 1 mm, **c** = 1 mm, **d**, **e** = 0.5 mm, **f** = 200 µm, **g** = 0.5 mm

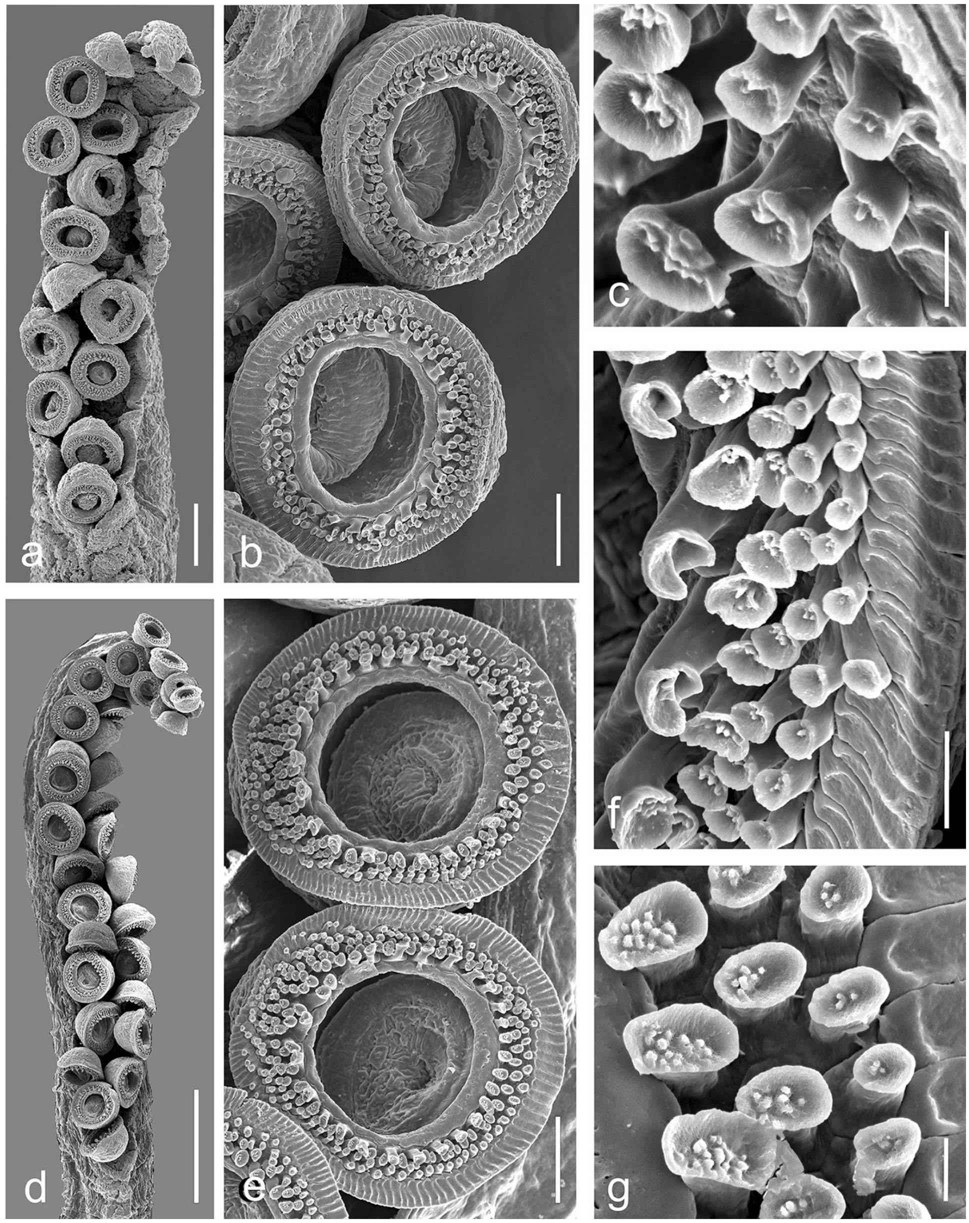

Fig. 8 *Kodama jujutsu* n. gen., n. sp. SEMs female paratype, 12.9 mm ML, NSMT-Mo 85937: **a** arm 1, **b** arm 1 suckers. **c** arm 1 enlargement of sucker rim. **d** tentacular club. **e** tentacular club suckers. **f**, **g** enlargement of club sucker rim. Scale bars: **a** = 200 µm, **b**, **e**, **f** = 50 µm, **c**, **g** = 5 µm, **d** 250 µm

Other material examined

Sunabe: 2 juv., 26° 19′ 41.09″ N, 127° 44′ 35.98″ E, 29 Mar 2019, coll. B. R. Hannan (NSMT-Mo 85941).

Diagnosis

As for genus.

Description

Counts and indices for individual specimens are given in Tables 6 (males) and 7 (females). Only mature specimens (five males and two females) were measured.

Males smaller than females: ML males 5.3–*5.9*–6.4 mm (SD 0.4), females 8.7–*10.8*–12.9 mm (SD 3.0). Mantle, short, rounded, blunt posteriorly (Fig. 7a, b) may be narrowed, nipple-like in live animals (Fig. 11a, c–e, h); MWI males 64.2–*66.2*–71.9 mm (SD 3.2), females 69.8–*71.1*–72.4 mm (SD 1.9). Ventral mantle margin straight to slightly concave (Fig. 7b). Fins rounded, maximum length approximately half mantle length, FLI males 29.7–*38.7*–43.9 mm (SD 5.4), females 48.1–*49.9*–51.7 mm (SD 2.6); positioned dorso-laterally on posterior third of mantle, FIIa males 62.3–*67.7*–78.1 mm (SD 6.1), females 54.3–*59.3*–64.4 mm (SD 7.1); fin width ~ 30% ML, FWI males 25.0–*29.3*–33.3 mm (SD 3.3), females 27.6–*32.0*–36.4 mm (SD 6.3); posterior margins curved;

Fig. 9 *Kodama jujutsu* n. gen, n. sp. hectocotylised left ventral arm (middle of field) male paratype 5.3 mm ML, NSMT-Mo 85933. Scale bar 5 mm

anterior margins with well-developed lobes, lateral lobes crescentic.

Funnel conical, base broad, tapered anteriorly (Fig. 7c); FuLI males 29.7–*38.7*–43.9 mm (SD 5.4), females 48.1–*49.9*–51.7 mm (SD 2.6); free for about 1/5 of its length, FFuI males 13.2–*17.3*–21.1 mm (SD 2.9), females 17.8–*19.3*–20.7 mm (SD 2.0). Funnel-locking cartilage (Fig. 7d), strait. Mantle-locking cartilage (Fig. 7e) compliments funnel member. Funnel valve small, flaplike, rounded anteriorly. Funnel organ, dorsal element broad, inverted V-shape with pointed anterior tip; ventral elements ovoid (Fig. 7f). Nuchal locking-cartilage (Fig. 7g) pronounced, deep, cylindrical, with raised margin of uniform width and median longitudinal furrow corresponding to rachis of gladius.

Head 40–50% ML, HLI males 46.7–*50.7*–53.1 mm (SD 2.6), females 37.2–*38.7*–40.2 mm (SD 2.1); slightly broader than ML in both sexes, HWI males 58.3.0–*59.8*–62.5 mm (SD 1.7), females 48.1–*51.0*–54.0 mm (SD 4.2). Eyes large, EDI males 11.3–*13.9*–15.8 mm (SD 1.7), females 12.4–*13.7*–14.9 mm (SD 1.8); ventral eyelids free. Eye covered by corneal membrane. Distinct, large olfactory pit on latero-posterior surface of head, posterior and ventral to eyes, close to mantle opening. Posterior-ventral to each eye is a prominent skin tag positioned ventrolaterally on the head. Lobes particularly prominent in live animals (Fig. 11b, c, e, g). Slightly anterior to eyes on ventral side of head are a pair of more prominent, small, rounded whitish projections.

Arms, broad basally, tapered distally, all similar length (particularly in females); arm formula usually 2.3.1.4 or 3.1.2.4 in males (Table 5), arm formula variable in females (Table 7). Arm length index of longest arm in males (ALI2) 26.7–*37.9*–47.2 mm (SD 7.6), females (ALI2) 25.2–*32.7*–40.2 mm (SD 10.6). All arms similar in shape, U-shaped in section. Sucker pedicels narrow. Chitinous inner ring of arm suckers without teeth, smooth or slightly crenulated on inner margin (Fig. 8a, b). Infundibulum with 4–5 rows of polygonal processes, innermost row of pegs elongate, cylindrical, with pegs decreasing in size toward outer margin of sucker, more elongate on one side of the sucker than the other (Fig. 8b); processes expanded, shallow dish-like distally contain tufts of low lobe-like papillae (Fig. 8c), outer-most sucker rim processes rectangular, tile-like, radially arranged, smooth, without papillae (Fig. 8b). Male and female arm suckers similar in size (Table 5). Sucker counts range from 18–25 on male normal arms, 15–24 in females. All arms connected by relatively shallow webs, protective membranes absent.

Male left ventral arm hectocotylised. Hectocotylus with 8.0–*8.6*–10.0 (SD 0.9) suckers proximally, remainder of arm without suckers; distal end of arm with large tongue-like flap attached dorso-laterally to arm a short distance proximal to distal arm tip (Fig. 9). Right ventral arm unmodified, with 8.0–*8.6*–10.0 (SD 0.9) suckers proximally (generally a greater number of suckers on left than on right ventral arm) remainder of arm without suckers. Left and right ventral arms similar in length (Table 5).

Tentacles slender, stalks naked, semicircular in section; oral surface convex. Club arm-like in form, just slightly narrower, cylindrical, tapers to blunt end distally (Fig. 8d); ClLI males 35.2–*61.0*–83.3 mm (SD 21.4) females 33.3–*37.4*–41.4 mm (SD 5.7). Sucker-bearing face of club only slightly convex. Suckers ~ 0.1–0.3 mm diameter in centre of club; arranged in two oblique transverse rows in both sexes. Total number of club suckers in males 24.0–*25.6*–28.0; females 34.0–*34.5*–35.0. Club sucker dentition (Fig. 3e): inner ring without teeth; infundibulum with 3–4 rows of polygonal processes; pegs narrow, elongate shallow, cup-like distally bearing papillae in depression. At periphery, pegs narrower and more elongate, with fewer papillae (Fig. 8f, g). Some inner pegs longer on inner side and recurved to cover depression. Outer-most sucker rim processes flattened, rectangular (Fig. 3f).

Gills with 15.0–*15.4*–16.0 (SD 0.5) lamellae per demibranch in males; 16.0–*17.0*–18.0 (SD 1.4) lamellae per demibranch in females.

Buccal membrane with six lappets and fringed inner margin; suckers absent. Radula with seven transverse rows of teeth (Fig. 10a). Rachidian teeth, broad rectangular basally, do not vary in shape along length of radula ribbon; teeth homodont, without cusps. First lateral teeth much smaller than rest, triangular, pointed, displaced toward second laterals; second laterals broad-based, much larger in size than

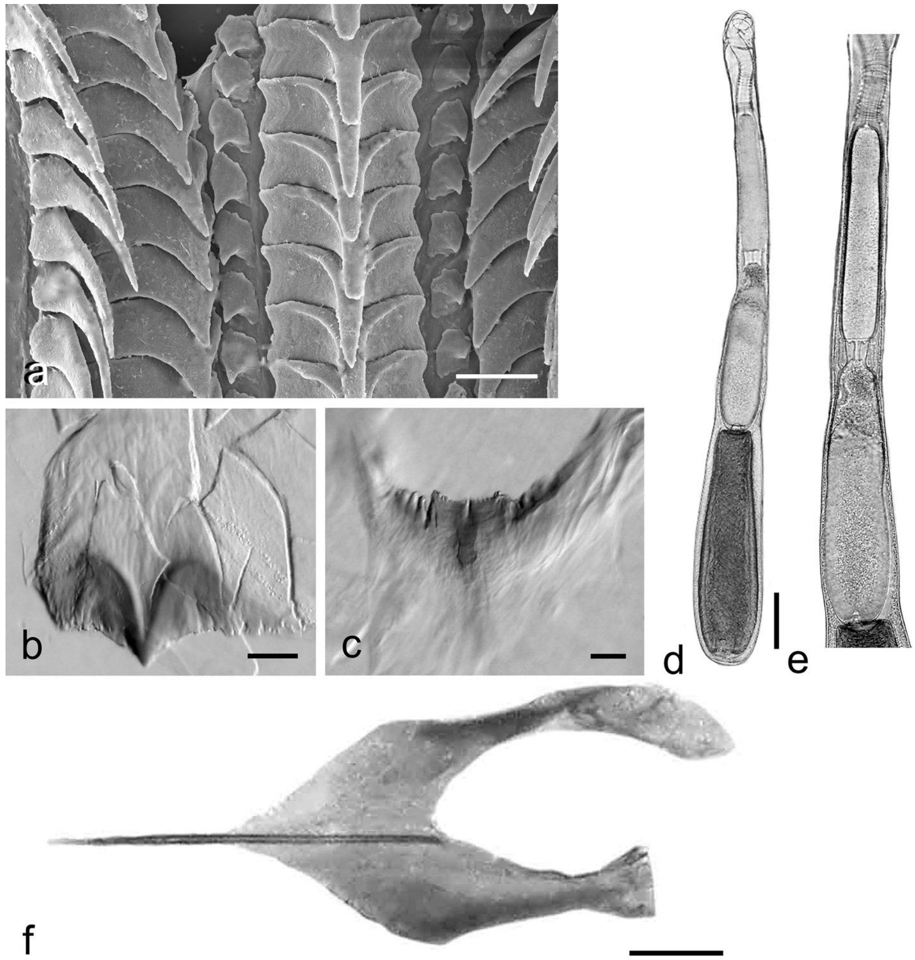

Fig. 10 *Kodama jujutsu* n. gen., n. sp. **a** radula, male, unregistered specimen collected 7 Dec 2019. **b** upper beak, male paratype, 6.0 mm ML, NSMT-Mo 85940. **c** lower beak, specimen as in **b**. **d** spermatophore, male paratype 5.3 mm ML, NSMT-Mo 85933. **e** enlargement of oral end of spermatophore, male paratype 5.7 mm ML, NSMT-Mo 85938. **f** gladius (part), unregistered specimen as in a. Scale bars: **a** = 20 µm; **b**, **c**, **f** = 1 mm; **d**, **e** = 0.1 mm. (Note: due to its delicate nature, the posterior end of the gladius beyond the rachis was damaged and lost during staining and mounting.)

first laterals and displaced toward midline. Marginal teeth narrow basally, scythe-like.

Upper beak (Fig. 10b) with short, triangular rostrum, hood curved; lateral margins with row of low teeth. Lower beak (Fig. 10c) with concave, finely toothed rostrum, flanked laterally by larger conical teeth. Distinct dark pigmentation restricted to rostrum and hood of upper and lower beaks.

Male reproductive tract (not illustrated) similar in structure to that of congeners. Spermatophores (Fig. 10d) approximately 1/5 mantle length; SpLI 18.3–*20.3*–22.6 mm (SD 2.2). Sperm reservoir simple, without coiled sperm cord. Cement body bipartite; aboral end elongate, cylindrical, narrows at oral end, connects to sperm reservoir via a narrow duct, connects via a narrow neck to long, narrower cylindrical portion leading to ejaculatory apparatus (Fig. 10e). Oral end of ejaculatory apparatus with 2–3 simple coils (Fig. 10d).

Female reproductive tract: Ovary large, occupies approximately half of mantle. Eggs of various sizes suggesting protracted multiple spawning. Ovary opens via single thick-walled oviduct at anterior end on left side of animal. Nidamental glands paired, broad, leaf-shaped located ventral to ovary toward, and overlying anterior half. Accessory nidamental glands absent. Eggs ovoid, 0.6–1.5 mm diameter; EgDI 6.9–*9.3*–11.6 mm (SD 3.3).

Gladius a thin, elongate, chitinous structure embedded in ventral side of dorsal mantle below adhesive pad; extending full length of mantle. Sclerotised rachis present (Fig. 10f).

Preserved animals cream with sparse dark purple chromatophores peppered evenly dorsally and ventrally on mantle, aboral side of arms and tentacles, and on ventral side of free portion of funnel. A row of dark chromatophores surrounds distal tip of funnel dorsally and ventrally. Single dark chromatophore on base of funnel on each side, anterior to tip of funnel-locking cartilage. Fins with evenly scattered chromatophores dorsally and ventrally, closest to junction with mantle. Outer rim of fins devoid of chromatophores. Chromatophores in a band dorsal to anus and in tissue overlaying viscera internally and in a patch on each side of anus. Between dark chromatophores are evenly scattered orange chromatophores.

Live animals with overall orange to yellow 'base' colouration. In some body patterns, chromatophores contract (appear large) at the same time on the head, in a transverse

Fig. 11 *Kodama jujutsu* n. gen., n. sp. **a**–**h**, live animals photographed in the wild. **i** laboratory reared hatchling, dorsal view. **j** ventral view same specimen. The large white testis toward the posterior end of the mantle is clearly visible in images **c**, **e** and **h**. Prominent skin tags posterior to the eyes can be seen in **c**, **e**, **g** and **h**, and the nipple-like posterior tip of the mantle apparent in some postures is shown in **a**, **c**, and **h**. Curling and recurving the arms appears to be a common posture. Photos: **a**, **c**, **d**–**h**, © Shawn Miller; **b** © Brandon Hannan; **i**, **j** © Jeff Jolly

band toward the anterior end of the mantle and around the posterior end of the mantle (Fig. 10a, d).

Type locality

Japan, Okinawa I, Hamamoto: 1♂, 6.0 mm ML, 26° 40′ 17.90″ N, 127° 53′ 17.05″ E.

Distribution

Japan, Okinawa Island from Miyagi I., 1♀, 6.8 mm ML, 26° 22′ N, 127° 59′ E to Sunabe 26° 19′ 41.09″ N, 127° 44′ 35.98″ E. Visual observations made by Brandon Hannan (personal communication) extend the northernmost extent of the range to 26° 30′ 43.02″ N, 127° 52′ 07.92″ E. Depth range 1–20 m.

Habitat and biology

Kodama jujutsu is found around coral reefs and has been seen hunting and foraging after sunset, often in open water near reef cuts. Underwater naturalist and photographer, Shawn Miller, has captured a typical, possibly defence posture (Fig. 10a, c–h) in which the animal spreads the arms and sometimes the tentacles out widely in a circle surrounding the mouth, with the distal tips of these appendages curved inwards. Sometimes the arms are extended dorsally above the head. This can be accompanied by the contraction of the mantle posterior to the fins forming a rounded nipple-like tip. They readily follow shrimp attracted to dive camera lights or torches at night. The species has also been found in shallow seagrass beds.

It first attracted Brandon Ryan Hannan's attention in 2019 when he noticed the unusual protrusions below the eyes and observed the species attaching itself to the underside of coral or any underwater substrate. At the popular Sunabe Seawall dive site in Okinawa he observed *K. jujutsu* attached to the undersides of various hydroids to which the hydroid nematocysts (stinging cells) do not deter *K. jujutsu*. A further interesting observation was made in 2019 of the pygmy squid attached to a hydroid that the swimming nudibranch, *Bornella anguilla* S. Johnson, 1984 was eating (Fig. 12a). When the nudibranch reached the end of the hydroid it did not touch the squid and the squid didn't move. Clearly the

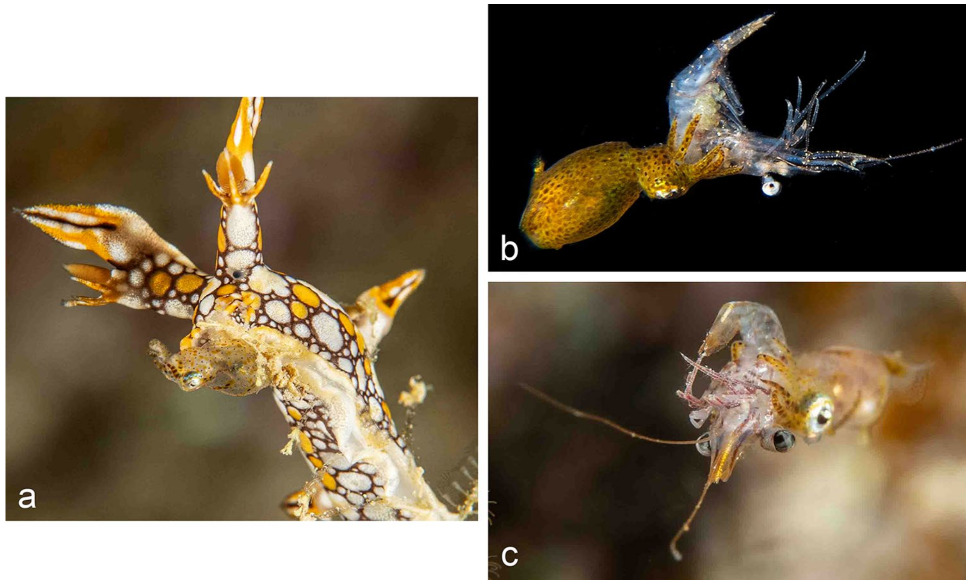

Fig. 12 *Kodama jujutsu* n. gen., n. sp. **a** stuck to a hydroid that is being consumed by the nudibranch *Bornella anguilla*. **b** side view and **c** antero-lateral foreshortened view, capturing ovigerous caridean shrimp. Photos: © Brandon Hannan

squid was not concerned about the nudibranch—testament to the fact that nudibranchs are generally highly specialised feeders. In this case, the hydroid, and not the pygmy squid is the target for *B. anguilla*. (The species is known to extend its buccal bulb and hydroid branches are drawn into the mouth to be stripped of its polyps.)

The species has been observed numerous times during diving around Okinawa at night and sometimes at dusk in water with temperatures ranging between 20 and 27 °C. When observed eating, the prey was always small shrimp with bodies smaller or similar in size to themselves (B. Hannan, personal observations, Fig. 12b, c).

Etymology

The specific name *jujutsu* is derived from the Japanese word jūjutsu that is a martial art of the same name, translating to 'gentle art'. The goal of the sport is to control your opponents by grappling them. This pygmy squid has been seeing grappling shrimp in a similar fashion. The name is used as a noun in apposition.

Remarks

Traits that separate *K. jujutsu* from *X. notoides* and *Idiosepius* are described in the generic diagnosis above. The character combination that separates *Kodama jujutsu* from individual *Idiosepius* spp. are tabulated in Table 8.

Some females have spermatophores embedded at the base of the ventral arm pair. The 3.5 mm ML male specimen from Maeda Point has well-developed spermatophores indicating this species matures at a very small size.

Behaviour in captivity

Idiosepius kijimuna and *K. jujutsu* habitually attach to substrate including aquarium plants and tank walls where they remain unless swimming to change positions, hunt, or mate. Both species were observed to attack the dorsal side of prey to immobilise it within seconds and both swam or attached to substrate while consuming prey (Online Resource 1, MOESM1; Fig. 5b). Adults of both species swam by pumping water through the funnel and moving the fins in a high frequency figure-eight motion. *Idiosepius kijimuna* swam in sudden and quick movements, sometimes swinging the mantle in a bobbing motion with the arms recurved or positioned above the head. The mantle is often inflated, and rounded and the posterior end is constricted, making a nipple-like projection (Online Resource 2, MOESM2 and Fig. 11). The arms of *Kodama jujutsu* were usually splayed outwards and above the head and the tip of the ventral mantle was produced into a nipple. Sometimes while swimming, the head and arms appeared fixed as the body moved in a vertical bobbing motion. In this way the outline of the animal is disrupted perhaps making it look more like a bit of floating debris. *Idiosepius kijimuna* exhibits a more streamlined and controlled swimming motion (Online Resources 3 MOESM3, 4 MOESM4; Fig. 5a, c). Prior to mating, *Idiosepius kijimuna* males approached females head on and mating occurred in the head-to-head position (Online Resource 5, MOESM5). The males appear to deposit the spermatophores on the oral side of the arm crown, perhaps in the buccal region. In contrast, *Kodama jujutsu* males approached the female from below (i.e., both facing the same direction) and extended the hectocotylus toward the female, appearing to deposit spermatophores on the ventral side of the head (Online Resource 6, MOESM6). Both sexes exhibited a row of two white papillae posterior-laterally on either side of the mantle and on the ventral side of the head when mating and approaching to mate. (While assuming the hectocotylus in both species was used to deposit spermatophores, it is difficult to determine from the video footage whether the hectocotylus or the tentacles are being used to place them.) One specimen captured in Okinawa at Mizugama (north wall) laid fertile eggs that successfully hatched one week after capture. As there were no males present, clearly the sperm had been stored by the female for at least one week.

Discussion

Kodama jujutsu is sister to a clade containing *X. notoides* and all *Idiosepiidae*. It shares a number of morphological traits with the southern Australian endemic species, *Xipholeptos notoides*. Most significantly, both species have a straight, narrow funnel-mantle locking cartilage and the gladius extends along the full length of the mantle and has a distinct medial rachis. The presence of a fully developed gladius with sclerotised rachis seems to be a primitive trait in this family that is lost in the genus *Idiosepius* in which the gladius is reduced to a chitinous shield. *Kodama jujutsu* and *X. notoides* clearly differ, however, in some other morphological traits, and are clearly separated on molecular grounds.

The spermatophore transfer method shown by *I. kijimuna* is similar to that of *I. thailandicus* (Nabhitabhata and Suwanamala 2008) and differs from *I. paradoxus* (Ortmann, 1888), where males transfer spermatophores while grasping females (Sato et al. 2013). The mating behaviour of *X. notoides* has not yet been described. Given that *K. jujutsu* and *X. notoides* do not have dimorphic hectocotyli, it may be that they exhibit similar mating behaviour that differs from that of *Idiosepius* spp., with males approaching the females from below. Observation of the deposition of spermatophores in all idiosepiids using high speed photography as used in Sato et al. (2013) would be valuable to compare strategies. In addition, it would be useful to re-confirm whether *I. thailandicus* Chotiyaputta et al. (1991) uses the tentacles for spermatophore transfer as reported by Nabhitabhata and Suwanamala (2008).

Very apparent from this study is evidence of the importance of live animal observations in defining taxa within this family. As these tiny cephalopods are easy to culture in captivity, and are found at depths readily accessible to divers, future behavioural studies and observations will undoubtedly yield many useful insights to aid our understanding of this particularly enigmatic group of tiny cephalopods.

Appendix

See Table 9.

Table 9 Specimens with locality, GenBank voucher information and accession numbers used in this study

Species	Sample #	Location	COI	16S rRNA	12S rRNA
S. patagonica			NC_016425	NC_016425	NC_016425
K. n. gen., n. sp.	NMST-Mo 85938[1]	Japan, Okinawa I., Sunabe Sea Wall	LC749837	LC746832	LC746818
K. n. gen., n. sp.	NMST-Mo 85940[2]	Japan, Okinawa I., Sunabe Sea Wall	LC749838	LC746833	LC746819
K. n. gen., n. sp.	NMST-Mo 85939[3]	Japan, Okinawa I., Sunabe Sea Wall	LC749839	LC746834	LC746820
K. n. gen., n. sp.	NMST-Mo 85933[4]	Japan, Okinawa I., Onna Pt	LC749840	LC746835	LC746821
K. n. gen., n. sp.	NMST-Mo 85932[5]	Japan, Okinawa I., Hamamoto	LC749841	LC746936	LC746822
K. n. gen., n. sp.	NMST-Mo 85936 [6]	Japan, Okinawa I., Sunabe Sea Wall	LC749842	LC746837	LC746823
K. n. gen., n. sp.	NMST-Mo 85937 [7]	Japan, Okinawa I., Sunabe Sea Wall	LC749843	LC746838	LC746824
X. notoides	WAM S.67769(3)	Australia Western Australia	MG097850	MG062709	MG062721
X. notoides	WAM S.67770(4)	Australia, Western Australia	MG097851	MG062710	MG062722
X. notoides	38	Australia, Tasmania, Snug	EU008975	EF684980	EF680148
X. notoides	39	Australia, Tasmania, Snug	EU008976	EF684981	EF680149
X. notoides	40	Australia, Tasmania, Snug	EU008977	EF684982	EF680150
X. notoides	41	Australia, Tasmania, Snug	EU008978	EF684984	EF680151
I. paradoxus	59	Japan, Ushimado	EU008995	EF685003	EF680169
I. paradoxus	55	Japan, Ushimado	EU008991	EF684999	EF680165

Table 9 (continued)

Species	Sample #	Location	COI	16S rRNA	12S rRNA
I. paradoxus	61	Japan, Ushimado	EU008997	EF684997	EF680171
I. paradoxus	60	Japan, Ushimado	EU008996	EF685004	EF680170
I. paradoxus	58	Japan, Ushimado	EU008994	EF685002	EF680168
I. paradoxus	57	Japan, Ushimado	EU008993	EF685001	EF680167
I. paradoxus	54	Japan, Ushimado	EU008990	EF684998	EF680164
I. paradoxus	56	Japan, Ushimado	EU008992	EF685000	EF680166
I. paradoxus	53	Japan, Ushimado	EU008989	EF684996	EF680163
I. paradoxus	43	Japan, Nagoya	EU009065	EF684986	EF680153
I. paradoxus	47	Japan, Nagoya	EU008984	EF684990	EF680157
I. hallami	AMS C.483477	Australia, S of Tweed Heads	MG097849	MG062708	MG062720
I. hallami	AMS C.477702	Australia, Bombee Creek	MG097842	MG062701	MG062713
I. hallami	AMS C.477949	Australia, Lake Illawarra, Warilla*	MG097844	MG062703	–
I. hallami	AMS C.483437	Australia, Tweed Heads	MG097847	MG062706	MG062718
I. hallami	4–2000	Australia, Sydney	AY293708	AY293658	AY293634
I. hallami	AMS C.477952	Sydney, Port Hacking, Maianbar	MG097841	MG062700	MG062712
I. hallami	AMS C.479165	Australia, Burrill Lake	MG097840	MG062699	MG062711
I. hallami	AMS C.269823	Australia, Cudgen Creek	MG097845	MG062704	MG062716
I. hallami	AMS C.483476	Australia, Pottsville, Mooball Ck	MG097848	MG062707	MG062719
I. hallami		Australia, Stradbroke I. Dunwich	KF647895	KF647895	KF647895
I. hallami	C.477703	Australia, Bombee Creek	MG097843	MG062702	MG062714
I. hallami	C.477930	Australia, Tweed Heads	MG097846	MG062705	MG062717
I. pygmaeus	67	Thailand, Lombok I., Ekas Bay	EU009003	EF685017	EF680177
I. pygmaeus	66	Thailand, Lombok I., Ekas Bay	EU009002	EF685016	EF680176
I. pygmaeus	68	Thailand, Lombok I., Ekas Bay	EU009004	EF685018	EF680178
I. pygmaeus	80	Thailand, Phuket I., Klong Mudong, PMBC Pier	EU009016	EF685026	EF680190
I. pygmaeus	79	Thailand, Phuket I., Klong Mudong	EU009015	EF685025	EF680189
I. pygmaeus	75	Thailand, Phuket I., Klong Mudong	EU009010	EF685022	EF680185
I. pygmaeus	72	Thailand, Phuket I., Klong Mudong	EU009007	EF685006	EF680182
I. pygmaeus	70	Thailand, Phuket I., Klong Mudong	EU009006	EF685020	EF680180
I. pygmaeus	77	Thailand, Phuket I., Klong Mudong	EU009013	EF685024	EF680187
I. pygmaeus	63	Thailand, Phuket I., Klong Mudong	EU008999	EF685012	EF680173
I. pygmaeus	64	Thailand, Phuket I., Klong Mudong	EU009000	EF685013	EF680174
I. pygmaeus	74	Thailand, Phuket I., Klong Mudong	EU009009	EF685008	EF680184
I. pygmaeus	78	Thailand, Phuket I., Klong Mudong	EU009014	EF685010	EF680188
I. pygmaeus	73	Thailand, Phuket I., Klong Mudong	EU009008	EF685007	EF680183
I. pygmaeus	69	Thailand, Phuket I., Klong Mudong	EU009005	EF685019	EF680179
I. pygmaeus	76	Thailand, Phuket I., Klong Mudong	EU009012	EF685023	EF680186
I. picteti	62	Indonesia, Ambon I			
I. paradoxus[a]	50	Japan, Okinawa I	EU008986	EF684993	EF680160
I. paradoxus[a]	51	Japan, Okinawa I	EU008987	EF684994	EF680161
I. n. sp.	AMS C.596046[1]	Japan, Okinawa I., Hamamoto	LC749830	LC746825	LC746811
I. n. sp.	NMST-Mo 85922[2]	Japan, Okinawa I., Hamamoto	LC746831	LC746826	LC746812
I. n. sp.	AMS C.596048[3]	Japan, Okinawa I., Hamamoto	LC746832	LC746827	LC746813
I. n. sp.	AMS C.596049[4]	Japan, Okinawa I., Hamamoto	LC746833	LC746828	LC746814
I. n. sp.	NMST-Mo 85875[5]	Japan, Okinawa I. Motobu Hamamoto	LC749834	LC746829	LC746815
I. n. sp.	NMST-Mo 85878[6]	Japan, Okinawa I. Motobu Hamamoto	LC749835	LC746830	LC746816
I. n. sp.	NMST-Mo 85876[7]	Japan, Okinawa I. Motobu Hamamoto	LC749836	LC746831	LC746817
I. macrocheir[b]	36	Mozambique, Monque	EU008973	EF684978	EF680146

Table 9 (continued)

Species	Sample #	Location	COI	16S rRNA	12S rRNA
I. macrocheir[b]	37	Mozambique, Monque	EU008974	EF684979	EF680147
I. biserialis[b]	7	Mozambique, Inhambane I	EU008947	EF684950	EF680117
I. biserialis[b]	6	Mozambique, Inhaca I	EU008946	EF684948	EF680116
I. biserialis[b]	3	Mozambique, Inhaca I	EU008943	EF684945	EF680113
I. biserialis[b]	4	Mozambique, Inhaca I	EU008944	EF684946	EF680114
I. biserialis[b]	5	Mozambique, Inhaca I	EU008945	EF684947	EF680115
I. biserialis[b]	12	Mozambique, Inhambane I	EU008952	EF684955	EF680122
I. biserialis[b]	17	Mozambique, Monque	EU008956	EF684959	EF680127
I. biserialis[b]	11	Mozambique, Inhambane I	EU008951	EF684954	EF680121
I. biserialis[b]	10	Mozambique, Inhambane I	EU008950	EF684953	EF680120
I. biserialis[b]	8	Mozambique, Inhambane I	EU008948	EF684951	EF680118
I. biserialis[b]	9	Mozambique, Inhambane I	EU008949	EF684952	EF680119
I. biserialis[c]	34	Thailand, Ko Pratong, Type: Hylleberg PMB7957	EU008971	EF684976	EF680144
I. biserialis[c]	22	Thailand, Phuket I., Klong Bangrong	EU008959	EF684964	EF680132
I. biserialis[c]	27	Thailand, Phuket I., Klong Bangrong	EU008964	EF684969	EF680137
I. biserialis[c]	24	Thailand, Phuket I., Klong Bangrong	EU008961	EF684966	EF680134
I. thailandicus[c]	82	Thailand, Rayong Province, Chantaburi Ban Phe	EU009018	EF685028	EF680192
I. thailandicus[c]	83	Thailand, Rayong Province, Chantaburi Ban Phe	EU009020	EF685029	EF680193
I. thailandicus[c]	84	Thailand, Rayong Province, Chantaburi Ban Phe	EU009020	EF685030	EF680194
I. thailandicus[c]	86	Thailand, Rayong Province, Chantaburi Ban Phe	EU009022	EF685032	EF680196
I. thailandicus[c]	81	Thailand, Rayong Province, Chantaburi Ban Phe	EU009017	EF685027	EF680191
I. thailandicus[c]	85	Thailand, Rayong Province, Chantaburi Ban Phe	EU009021	EF685031	EF680195
I. biserialis[c]	2	Indonesia, Lombok I., Ekas Bay	EU008942	EF684944	EF680112
I. biserialis[c]	1	Indonesia, Lombok I., Ekas Bay	EU008941	EF684943	EF680111
I. biserialis[c]	23	Thailand, Phuket I., Klong Bangrong	EU008960	EF684965	EF680133
I. biserialis[c]	20	Thailand, Phuket I., Klong Bangrong	EU008958	EF684962	EF680130
I. biserialis[c]	25	Thailand, Phuket I., Klong Bangrong	EU008962	EF684967	EF680135
I. biserialis[c]	26	Thailand, Phuket I., Klong Bangrong	EU008963	EF684968	EF680136
I. biserialis[c]	31	Thailand, Phuket I., Klong Bangrong	EU008968	EF684973	EF680141
I. biserialis[c]	30	Thailand, Phuket I., Klong Bangrong	EU008967	EF684972	EF680140
I. biserialis[c]	29	Thailand, Phuket I., Klong Bangrong	EU008966	EF684971	EF680139
I. biserialis[c]	28	Thailand, Phuket I., Klong Bangrong	EU008965	EF684970	EF680138
I. biserialis	32	Thailand, Phuket I., Klong Bangrong	EU008969	EF684974	EF680142

Species refer to the names used in GenBank records and associated publications. Names for clades recognised in Reid and Strugnell (2018) include: [a], '*Okinawa*' n. sp. (and described here as *I. kijimuna* n. sp.); [b], *Idiosepius minimus*; [c], *I. thailandicus.* Numbers listed under 'Sample #' refer to numbers used in Fig. 1; corresponding museum specimen registration voucher numbers are included where known

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Author contributions NS and JJ: led the sample collection, fixed animals, extracted DNA and sequenced specimens. JS: analysed the molecular data and generated the phylogenetic tree. JJ: managed the culture of live animals. AR: wrote the species descriptions and prepared Figs. 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12. All authors contributed to the writing and the final editing of the manuscript. All authors read and approved the final manuscript.

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Data/code availability Genetic sequence data are available from GenBank, https://www.ncbi.nim.nih.gov/genbank/.

Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethical approval Cephalopods are not covered under the Japanese legislation 'Act on Humane Treatment and Management of Animals' (Ogden et al. 2016). Procedures and rearing protocols followed the guidelines set by Directive 2010/63/EU for cephalopods (Fiorito et al. 2015) and animal welfare guidelines set by OIST Animal Care and Use Committee. The highest quality of care was taken to reduce the suffering of animals.

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