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337 A new genus and a new species of onchidiid slugs from eastern Indonesia (Gastropoda: Euthyneura: Onchidiidae) Tricia C. Goulding 1,2, Munawar Khalil 3, Shau Hwai Tan 4,5, Benoît Dayrat 1* Abstract. The taxonomy of the Onchidiidae is currently being revised based on extensive sampling, molecular data, and examination of all type specimens available.

A new genus, *Alionchis* Goulding & Dayrat, new genus is described here for a new species, *Alionchis jailoloensis* Goulding & Dayrat, new species, which is highly distinct from all other onchidiids. *Alionchis jailoloensis* on mud mangrove and be identified in field its eye and hyponotum a white A genus is because *Alionchis jailoloensis* does not belong to any existing onchidiid genus.

The present study is based on an integrative approach to taxonomy, using nomenclatural history, comparative anatomy, molecular data, as well as natural field *Alionchis jailoloensis* is endemic to Halmahera, eastern Indonesia. *Onchidium meriakrii* Stantschinsky, 1907, with a type locality in Queensland, Australia, is transferred to *Alionchis* but is regarded as a nomen dubium. Key words.

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(print) 1Pennsylvania State University, Department of Biology, Mueller Laboratory 514, University Park, PA 16802, USA; Email: bad 25@psu.edu (*corresponding author)

2Current address: Bernice Pauahi Bishop Museum, 1525 Bernice St, Honolulu, HI 96817

3Department of Marine Science, Universitas Malikussaleh, Reuleut Main Campus,

Kecamatan Muara Batu, North Aceh, Aceh, 24355, Indonesia 4Marine Science Laboratory, School of Biological Sciences, Universiti Sains Malaysia, 11800 Minden Penang, Malaysia 5Centre for Marine and Coastal Studies, Universiti Sains Malaysia, 11800 Minden Penang, Malaysia INTRODUCTION Onchidiid slugs are found worldwide, but species and generic diversity is highest in the tropical Indo-West Pacific where they colonised a variety of microhabitats, especially in mangroves.

Onchidiids are unusual compared to many gastropods, because they breathe air through a lung but live in the intertidal. So, even though they are marine organisms, they die if they are submerged in water for just a few hours. Recent molecular studies have shown that onchidiids are pulmonates, closely related to land snails and slugs (Dayrat et al., 2011; White et al., 2011).

Onchidiid slugs are not the only marine pulmonates but they are the only pulmonate slugs to have greatly diversified in tropical, intertidal habitats, especially in mangroves. The systematics and biogeography of mangrove gastropods have only been studied for a few genera in Southeast Asia (e.g., Reid et al., 2010). So, even though onchidiids are some of the most abundant animals in mangroves of Southeast Asia, their diversity remains poorly known.

Most species are known only from the type material, with little to no information on their preferred habitat or their live colour and shape. Only a few studies have been published on onchidiid systematics since the 1930s, and mostly focusing on the genus *Onchidella*, which is not found in the tropical Indo-West (Dayrat, Our team is in the process of revising the entire Onchidiidae family, based on enormous effort spent collecting fresh material.

Onchidiid slugs were sampled at 300 stations worldwide, 260 in Indo-West especially Southeast Asia, which provides us with material for comparative anatomy and molecular systematics, as well as invaluable natural observations. many onchidiids are morphologically cryptic (even species from different genera can sometimes be very hard to distinguish collected at multiple sites across Southeast Asia could reveal their actual diversity.

The taxonomy of the family is now being revised through a series of revisions, each focusing on a distinct genus (Dayrat et al., 2016, 2017; Dayrat & Goulding, 2017; Goulding et al., in press-a, in press-b). By thoroughly examining the available types and the original descriptions of all existing onchidiid species, and comparing them to our own anatomical and molecular data, we have been able to determine the application of all onchidiid species- and genus-group names.

Here, *Alionchis* Goulding & Dayrat, new genus, is described for a new species (*Alionchis jailoloensis* Goulding & Dayrat, new species), which is anatomically distinct from all other onchidiids and cannot be placed in any existing genus. *Alionchis* slugs live in mangroves, where they are found directly on the surface of soft mud. Taxonomy & Systematics 338 *Alionchis jailoloensis* is known only from Halmahera, in eastern Indonesia, and no *Alionchis* slug was found at any of our 260 stations across the Indo-West Pacific, from South Africa to Australia, including in places near Halmahera, such as Ambon, Seram, the Kei Islands, or northern Sulawesi.

Only one existing species name, *Onchidium meriakrii* Stantschinsky, 1907 (with a type locality in Queensland, Australia) was found to belong to *Alionchis*, and it is regarded as a *nomen dubium*. In the general discussion, the geographic distribution of *Alionchis*, which seems to not be widely in Indo-West is to other onchidiid genera present in the region, such as *Peronia* Fleming, 1822 and *Platevindex* Baker, 1938. MATERIALS & METHODS Collecting.

All specimens examined were collected by hand at low tide by Munawar Khalil and party, which provided fresh material for comparative anatomy, DNA sequencing, and natural history observations. Live animals order to document their natural appearance (slugs contract when touched and can take a long time to relax again). Specimens individually in field that photographs can be linked to each preserved individual.

A piece of tissue was cut from specimens for DNA extraction, the rest of the specimen being relaxed in magnesium chloride and preserved in 70% ethanol for comparative anatomy. Specimens. DNA extraction numbers used in the phylogenetic analyses are indicated in the list of material examined as well as in the figure captions (numbers are between brackets).

Sizes (length/width) are indicated in millimeters for each specimen. Eleven specimens are included here for the new species being described. Many additional specimens were examined in the context of our worldwide revision of the family, including all available types and hundreds of onchidiids representing all the known genera and nearly all species.

Museum abbreviations are: Senckenberg Naturmuseum Frankfurt, Germany (SMF), for some type material mentioned in the discussion, and Universitas Malikussaleh, North Aceh, Sumatra, Indonesia (UMIZ), where all freshly-collected specimens of *Alionchis* were deposited as vouchers. Anatomical preparations. All anatomical observations were made under a dissecting microscope. Radulae were prepared for scanning electron

microscopy (SEM).

The radulae were cleaned in 10% NaOH for several days, rinsed in distilled water for a week, sputter-coated with gold-palladium, and examined by SEM. The structure of the copulatory organs drying, so copulatory organs are illustrated with drawings. DNA extraction and PCR amplification. DNA was extracted using a phenol-chloroform extraction protocol with cetyltrimethyl-ammonium bromide (CTAB).

The mitochondrial cytochrome oxidase I region (COI) and 16S region amplified the primers LCO1490 GGT CAA CAA ATC ATA AAG ATA TTG G and HCO2198 TAA ACT TCA GGG TGA CCA AAR AAY CA (Folmer et al., 1994), 16Sar-L CGC CTG TTT ATC AAA AAC AT (Palumbi, 1996), and 16S 972R CCG GTC TGA ACT CAG ATC ATG T (Dayrat et al., 2011). The ITS2 was with following GTG and (5'-3') TTC CAC ACT TG (Wade & Mordan, 2000).

The PCRss for COI and 16S were μl containing μl water, μl 10X Buffer, μl 25 MgCl₂, μl each μM primer, 2 μl of dNTP Mixture, 0.2 μl (1 unit) of TaKaRa Taq No. 1 of BSA Serum reactions for ITS2 used the reagents in the same amounts as and except water reduced 14.8 amount template reduced 0.5 The and 16S was: minutes 94°C; cycles 40 seconds 94°C, minute 46°C, 1 at and minutes 72°C.

thermoprofile for extension 10 at The products cleaned with ExoSAP-IT (Affymetrix, Santa Clara, CA, USA) prior to sequencing. Untrimmed sequence fragments represent approximately 680 bp for COI, 530 bp for 16S, and 790 bp for ITS2. Phylogenetic analyses. Chromatograms were consulted to resolve rare ambiguous base calls. DNA sequences were aligned using Clustal W in MEGA 7 (Kumar et al., 2016).

Ten COI sequences, ten 16S sequences and eight ITS sequences for *Alionchis jailoloensis* were used for the alignments. Eleven other onchidiid species were selected as outgroups from previous studies from our lab (Dayrat et al., 2011, 2016, 2017; Dayrat & Goulding, 2017) to represent existing genera in the Onchidiidae: *Onchidella celtica* (Cuvier in Audouin and Milne-Edwards, 1832), *Onchidella floridana* (Dall, 1885), *Onchidium typhae* Buchannan, 1800, *Onchidium stuxbergi* (Westerlund, 1883), *Onchidina australis* (Semper, 1880), *Platevindex luteum* (Semper, 1880), *Peronina tenera* (Stoliczka, 1869), *Peronia* sp. (Okinawa), *Peronia* sp.

(Hawaii), *Melayonchis annae* Dayrat, 2017, and *Melayonchis siongkiati* Dayrat & Goulding, 2017. DNA sequences were all deposited in Genbank and vouchers deposited in museum collections (Table 1). The ends of each alignment were trimmed and sequences were concatenated. The concatenated mitochondrial alignment included 1,052 nucleotide positions: 614 (COI) and 438 (16S). The ITS2 alignment included 815

positions, including gaps.

Pairwise genetic distances between COI sequences were calculated in 7. to analyses, best-fitting evolutionary model was selected for each locus separately using the Model Selection option from Topali v2.5 (Milne et al., 2004). A GTR + G model was independently selected for COI and 16S, and a HKY + G model was selected for ITS2.

Maximum Likelihood analyses were performed using PhyML (Guindon & Gascuel, 2003) as implemented in Topali v2.5 for the mitochondrial and ITS2 data separately. 339 Mitochondrial and nuclear sequences were not concatenated precisely to demonstrate that these two data sets support exactly the same phylogenetic relationships (i.e., only one species of *Alionchis*). Node support was evaluated using bootstrapping with 100 replicates. Bayesian analyses were performed using MrBayes v3.1.2

(Ronquist & Huelsenbeck, 2003) as implemented in Topali v2.5, with five simultaneous runs of 1.5×10^6 generations each, sample frequency of 100, and burn in of 25% (and posterior probabilities were also calculated). Topali did not detect any issue with respect to convergence.

Other (unpublished) analyses were performed using different combinations of outgroups, which all yielded identical results. PHYLOGENETIC RESULTS Molecular phylogenetic analyses (Figs. 1, 2). DNA sequences are used here to test for the potential presence of cryptic species within *Alionchis*, and whether *Alionchis* is a distinct clade or nested within an existing genus. Phylogenetic analyses of mitochondrial sequences (COI and 16S) and nuclear sequences (ITS2) both yielded one molecular unit (species).

Its monophyly is strongly supported here with a bootstrap value of 100 and posterior probability of 1.0 in both the mitochondrial and nuclear phylogenetic analyses. Also, *Alionchis* is not included within any of the existing onchidiid genera. Pairwise genetic divergences. Pairwise genetic distances also support the existence of a single *Alionchis* species because all pairwise COI distances between *Alionchis* sequences are below 0.5%.

This maximum genetic distance (0.5 %) is between the COI sequence of individual 6084 (station 219) and that of individual 5137 (station 218), and both of these stations are on the west side of the island. Pairwise genetic distances were lower than 0.5% between individuals from the western side of the island (stations 218 and 219) and the central bay (station 208), indicating there is no geographic population structure between sampling localities with the mitochondrial data. Fig. 1.

Phylogenetic tree showing relationships between individuals of *Alionchis jailoloensis*

based on COI and 16S sequences. Numbers above branches are the bootstrap values (Maximum Likelihood analysis) and below are the posterior probabilities (Bayesian analysis); only numbers and are All sequences as Information individually-identified specimens can be found in the list of material examined. 340 Fig. 2.

Phylogenetic tree showing relationships between individuals of *Alionchis jailoloensis* based on ITS2 sequences. Numbers above branches are the bootstrap values (Maximum Likelihood analysis) and below are the posterior probabilities (Bayesian analysis); only significant numbers (>80% and >0.9) are indicated. All other sequences serve as outgroups. Information on individually-identified specimens can be found in the list of material examined.

Table 1. Genbank accession numbers for COI and 16S DNA sequences. All *Alionchis* sequences and all ITS2 sequences are new. Mitochondrial sequences of outgroups (*Melayonchis*, *Onchidella*, *Onchidina*, *Onchidium* and *Peronia*) were obtained from other publications (Dayrat et al., 2011, 2016, 2017; Dayrat & Goulding, 2017; Goulding et al., in press-b) and studies in progress.

Species	Individual (DNA)	Locality	Genbank COI	Genbank 16S	Genbank ITS2	<i>Alionchis</i>
<i>jailoloensis</i>	5137	Halmahera, Indonesia	MG953528	MG953538	MG953548	5023
<i>jailoloensis</i>		Halmahera, Indonesia	MG953529	MG953539	MG953549	5039
<i>jailoloensis</i>		Halmahera, Indonesia	MG953530	MG953540	MG953550	5040
<i>jailoloensis</i>		Halmahera, Indonesia	MG953531	MG953541	MG953551	5093
<i>jailoloensis</i>		Halmahera, Indonesia	MG953532	MG953542	MG953552	5135
<i>jailoloensis</i>		Halmahera, Indonesia	MG953533	MG953543	MG953553	5136
<i>jailoloensis</i>		Halmahera, Indonesia	MG953534	MG953544	MG953554	5028
<i>jailoloensis</i>		Halmahera, Indonesia	MG953536	MG953546	6084	
<i>Platevindex luteum</i>	1001	Singapore	MG958714			
<i>Peronina tenera</i>	960	Malaysia	MG958740	MG958796		
<i>Onchidina australis</i>	1523	New South Wales, Australia	KX179548	KX179561	MG958719	
<i>Onchidium typhae</i>	965	Peninsular Malaysia	KX179509	KX179525	MG958720	
<i>Onchidium stuxbergi</i>	5605	Vietnam	KX179520	KX179537	MG958721	
<i>Melayonchis annae</i>	1010	Singapore	KX240015	KX240039		
<i>Melayonchis siongkiati</i>	1002	Singapore	KX240020	KX240044		
<i>Peronia</i> sp.		Okinawa, Japan	HQ660043	HQ659911		
<i>Peronia</i> sp.						

Hawaii, USA HQ660038 HQ659906 MG958722 *Onchidella* Tobago HQ660035 HQ659903 *Onchidella celtica* 5013 France MG958715 MG958717 341 SYSTEMATICS *Onchidiidae* 1815 *Alionchis* Goulding & Dayrat, new genus Type species: *Alionchis jailoloensis*, designated here Etymology. The genus *Alionchis* is a combination of Ali, a collector and assistant to Alfred Russel Wallace during his travels across the Malay Archipelago, and *Onchis*, one of the names used to refer to onchidiid slugs.

Ali began working for Wallace in Borneo, first serving as cook, and later collecting and preparing specimens (Van Wyhe & Drawhorn, 2015). Ali's collections of birds and natural history observations greatly contributed to Wallace's knowledge of the fauna in the region. This genus is named to honor Ali's contribution to studies of biodiversity in the Malay Archipelago.

Ali actually got married on the island of Ternate, near Halmahera, and settled there, which, given the geographic distribution of *Alionchis*, the genus especially *Diagnosis*. Body slightly flattened. Notum soft (gelatinous). No dorsal gills. Dorsal eyes present on notum. Retractable, central papilla (with four dorsal eyes) present. Foot wide, approximately two thirds of total width. Eye tentacles thick and long.

Eyes at tip of ocular tentacles. Pneumostome median, at posterior margin of hyponotum. Female opening adjacent to anus. Male opening below right ocular tentacle. Intestinal loops of type II, type III, and intermediate between types II and III. No rectal gland. No penial hooks. No accessory penial gland. Diagnostic features.

Externally, *Alionchis* can be reliably distinguished from other onchidiid genera by the unusually thick eye tentacles and the pneumostome at the very posterior end of the hyponotum. The squishy, gelatinous texture of the notum is also distinctive (in live animals). Remarks. A new generic name is needed for the new species described here because it does not belong to any of the known genera and no existing generic name could apply to it (for a recent review of the application of all onchidiid genus-group names, see Dayrat et al., 2017). The position of the pneumostome in *Alionchis* is unique.

It is at the posterior end of the hyponotum, close to the hyponotum edge (but still on the hyponotum surface), which cannot be confused with any other onchidiid genus. In Peronina Plate, 1893, the pneumostome also is at the posterior end of the hyponotum, but it is not on the hyponotum surface (Goulding et al., in press-b). Instead, it is right at the margin between the ventral hyponotum and the dorsal notum.

In other onchidiids, the pneumostome is on the hyponotum, approximately equally distant between the foot and the hyponotum edge. The eye tentacles of *Alionchis* are also unique. They are much thicker than in all other onchidiid genera. Only one species of *Alionchis* is described here, but the position of the pneumostome and the unique eye tentacles will likely be shared by other species in this genus because these traits usually do not vary within a genus. For instance, all three species of *Onchidium* share long and thin eye tentacles (Dayrat et al.,

2016) and all three species of *Peronina* (Goulding et al., in press-b) share the same pneumostome position. *Alionchis jailoloensis* Goulding & Dayrat, new species (Figs. 3–7) Type locality. Jailolo, S, E, station 218, *Sonneratia* and *Rhizophora* mangrove near a creek. Type material. Holotype, 43/22 mm [5137], designated here (UMIZ 00117). Additional material examined.

Indonesia, Halmahera,], 48/24 [5040], 45/27 [5023], 63/35 [#1], and 29/19 [5093] mm), station 208, mangrove by the beach, soft mud with *Rhizophora*, *Avicennia* and *Nypa* palms (UMIZ 00118); Halmahera, 01°03.76'N, 2 (64/28 [5135] and 33/19 [5136] mm), station 218, *Sonneratia* and *Rhizophora* mangrove near a creek (UMIZ 00119); Gamkonora, 127°31.63'E, 3 specimens (61/31 [5028], 69/34 [6083] and 23/27 [6084] mm), station 219, mostly *Rhizophora* mangrove with a mix of open sandy and muddy areas (UMIZ 00120). Distribution.

Halmahera, eastern Indonesia. Etymology. *jailoloensis* comes from the type locality, the small port of Jailolo, on Halmahera's western coast. Jailolo also happens to be one of the former names of the entire Island of Halmahera. Table Intra-specific (based COI in genera to divergences *Alionchis* and *Onchidina* both being monotypic).

Details **can be found in the** paper corresponding to each genus (Dayrat et al., 2016, 2017; Dayrat & Goulding, 2017). Genus Intra-specific Inter-specific *Alionchis* 0.5% N/A *Onchidina* 1.2% N/A *Onchidium* 0.0–5.1% 15.0–28.3% *Melayonchis* 0.0–5.2% 14.1–21.4% 342 Fig. 3. Habitats for *Alionchis jailoloensis*, Indonesia, Halmahera.

A, Mangrove by the beach, soft mud with *Rhizophora*, *Avicennia* and *Nypa* (station 208); B, Close up of the mud and roots (station 208); C, *Sonneratia* and *Rhizophora* mangrove near a creek (station 218); D, Close up of the mud and roots (station 218). Habitat (Fig. 3). *Alionchis jailoloensis* lives on open patches of mud in mangrove forests, where trees are not too close together.

It typically is found on dark mud saturated with water, near *Nypa*, *Avicennia*, *Sonneratia* or *Rhizophora*. Animals usually are together in small clusters, rather than scattered randomly in the mangrove. Colour and morphology of live animals (Fig. 4). Natural colour of live animals usually observed without having to wash off any mud. Dorsal notum colour usually dark brown, but occasionally orangish-brown or red.

Hyponotum (ventral) brown grey-brown small of and margin. Foot brown or grey-brown. Animal oval, slightly flattened, often contracts when disturbed. Dorsal notum granular. Papillae with so-called 'dorsal eyes' present, including a slightly raised central papilla. eight fifteen papillae with three or four eyes per papilla. Eye papillae

distributed near midline of notum.

Animals occasionally dig into mud when approached and may completely disappear. Dorsal gills absent. Hyponotum width about one third of animal width, but hyponotum may be hidden anteriorly by foot. Anus posterior, median, close to edge of pedal sole. Female opening very close to anus.

Peripodial groove runs longitudinally at junction between foot and hyponotum on right side (left in ventral view), from buccal area to posterior end, and ending with female opening. Pneumostome median, at posterior end of ventral hyponotum. Eyes at tip of paired ocular tentacles. A pair of oral lobes above mouth, each with an elongated (transversal) bump, likely with sensitive receptors. Male opening inferior to right ocular tentacle.

Visceral cavity and pallial complex. Visceral cavity not pigmented. Heart enclosed in pericardium, on right side of visceral cavity, slightly posterior to middle. Large, anterior, ventricle becomes large aorta that branches into smaller vessels delivering blood to visceral organs. Posterior auricle significantly smaller than ventricle. Pericardium communicates through small hole with right part of renal- pulmonary complex.

Kidney intricately attached to pulmonary cavity and more or less symmetrical. Digestive system Each radular row contains a rachidian tooth and two half rows of lateral teeth. Examples of radular formulae are presented in Table 3. Half 343 Fig. 4. Live specimens, *Alionchis jailoloensis*, Indonesia, Halmahera.

A, Dorsal view, 63 mm long [#1], station 208 (UMIZ 00118); B, Dorsal view, 48 mm long [5040], station 208 (UMIZ 00118); C, Dorsal view, holotype, 43 mm long [5137], station 218 (UMIZ 00117); D, Dorsal view, 64 mm long [5135], station 218 (UMIZ 00119); E, Dorsal view (the arrow points to the pneumostome), same as A; F, Dorsal view, 51 mm long [5039], station 208 (UMIZ 00118); G, Dorsal view, 61 mm long [5028], station 219 (UMIZ 00120); H, Lateral view, 69 mm long [6083], station 219 (UMIZ 00120); I, Ventral view, 33 mm long [5136], station 218 (UMIZ 00119); J, Ventral view, 45 mm long [5023], station 208 (UMIZ 00118). 344 Fig. 5.

External morphology, digestive system, and nervous system, *Alionchis jailoloensis*. A, Ventral, anterior view, scale bar = 5 mm [5023] (UMIZ 00118); B, Ventral, posterior view, scale bar = 3 mm [5028] (UMIZ 00120); C, Digestive system (type III), dorsal view, scale bar = 4 mm [6084] (UMIZ 00118); D, Stomach, dorsal view, scale bar = 3 mm, same as C; E, Digestive system (type II), dorsal view, scale bar = 3 mm, same as B; F, Digestive system (intermediate between type II and type III), dorsal view, scale bar = 4 mm, same

as A; G, Nervous system, dorsal view, scale bar = 1 mm [5093] (UMIZ 00118).

Abbreviations: a, anus; ddg, dorsal lobe of digestive gland; e, esophagus; f, foot; fo, female opening; hn, hyponotum; i, intestine; lcg, left cerebral ganglion; lplg, left pleural ganglion; mo, male opening; oddg, opening of the dorsal lobe of the digestive gland; ol, oral lobe; opdg, opening of the posterior lobe of the digestive gland; ot, oral tentacle; pdg, posterior lobe of the digestive gland; pn, pneumostome; ppg, peripodial groove; r, rectum; rcg, right cerebral ganglion; rplg, right pleural ganglion; st, stomach; st1, stomach chamber 1; st2, stomach chamber 2; st3, stomach chamber 3; st4, stomach chamber 4; tb, transversal bump; vg, visceral ganglion. Table 3. Radular formulae in *Alionchis jailoloensis*.

Radular formula Animal length (mm) Voucher DNA extraction number 73 × (110-1-110) 61 UMIZ 00120 5028 66 × (105-1-105) 45 UMIZ 00118 5023 58 × (85-1-85) 33 UMIZ 00019 5136 57 × (85-1-85) 29 UMIZ 00118 5093 345 with rachidian axis. Rachidian teeth tricuspid: median cusp always present; two lateral cusps, on lateral sides of base of the rachidian tooth, present but small (Fig. 6A).

Lateral aspect of base of rachidian teeth straight (neither concave nor convex). Length of rachidian teeth about 20 to 30 μm. Lateral teeth with and hook. of lateral teeth from 35 to 90 μm, gradually increasing towards outer lateral teeth, excluding few innermost and outermost lateral (significantly Lateral bear pointed spine on lateral expansion of base (Fig. 6F).

Spine rarely observed because most often hidden below hook of next, outer lateral tooth; spine only observed when teeth not too close or when placed in unusual position; spine absent on outermost lateral teeth. Esophagus narrow and straight, entering stomach anteriorly. Stomach on left side of visceral mass. Only a portion of stomach seen in dorsal view because partly covered by lobes of digestive gland. Dorsal lobe on right side of visceral mass. Fig. 6.

Radula, *Alionchis jailoloensis*, Halmahera. Rachidian innermost teeth, bar 20 [5023] 00118); Lateral with teeth, bar 20 [5093] 00118); Left teeth, bar 50 same as D, lateral scale = μm, as E, lateral scale = μm, same B; Underside lateral scale = μm, as Abbreviations: first, lateral 1rlt, right, tooth; second, lateral tooth; 2rlt, second, right, lateral tooth; bls, basal lateral spine; hlt, hook of lateral tooth; lc, lateral cusp of rachidian tooth; mc, median cusp of rachidian tooth; rt, rachidian tooth.

346 Left, lateral lobe ventral. Posterior lobe covers posterior aspect of stomach. Stomach is U-shaped sac divided into four chambers (Fig. 5D). First chamber, distal to esophagus,

delimited by thin layer of tissue, receives ducts from dorsal and left lateral lobes of digestive gland. Second chamber delimited by thick, muscular layer of tissue, receives duct from posterior lobe of digestive gland.

In third stomach chamber, thick ridges extend towards middle of chamber. Fourth chamber externally similar to third chamber, but characterised by thin internal ridges. Intestine long and narrow, with loops of type II (Fig. 5E), type III (Fig. 5C), or intermediate between types II and III (Fig. 5F). No rectal gland. Nervous (Fig. Circum-esophageal nerve ring post-pharyngeal and pre-esophageal. Cerebral commissure between paired cerebral ganglia short but length varies among individuals.

Paired pleural and pedal ganglia all distinct. Visceral commissure short but present and visceral ganglion approximately median. Cerebro-pleural and pleuro-pedal connectives very short and pleural and cerebral ganglia touch each other. Nerves from cerebral ganglia innervate buccal area and ocular tentacles, and penial complex on right side. Nerves from pedal ganglia innervate foot.

Nerves from pleural ganglia innervate lateral and dorsal regions of mantle. Nerves from visceral ganglia innervate visceral organs. Reproductive system (Fig. 7A). Sexual maturity correlated with body length. Individuals reach reproductive maturity at large (> mm). Mature have female organs and fully-developed, anterior, male, copulatory parts.

Immature individuals (< 30 mm long) may have small, inconspicuous, or simply no female organs. Hermaphroditic gland a single mass. Hermaphroditic duct starts with multiple proximal branches at hermaphroditic gland subsequently merging into single, distal, short duct. Hermaphroditic duct conveys eggs and autosperm from hermaphroditic gland to fertilisation chamber, which connects to large receptaculum seminis.

Receptaculum seminis narrow and elongated. Female gland mass contains various glands (mucus and albumen) of which exact connections remain uncertain. Distally, spermoviduct branches into deferent duct (which conveys autosperm to anterior region, running through body wall) and oviduct. Oviduct conveys eggs up to female opening and exosperm from female opening up to fertilisation chamber.

Distal region of oviduct (from female opening to duct of spermatheca) short and wide. Spherical spermatheca connects to proximal portion of oviduct through wide, short duct. Male anterior organs composed of penial complex (penis, vestibule, deferent duct, and retractor muscle). No accessory penial gland.

Penial sheath long, approximately half of body cavity length, and thin. Penis delimited by thin tissue touching penial sheath. Penis with proximal stalk and distal bulb-like tip. Both stalk and bulb are soft (not rigid). Penis stalk wide in diameter, between 0.7 mm (immature) and 2.0 mm. Distal region of penial stalk longitudinally folded with one fold. Internally, penis bears thin longitudinal ridges. Bulb-like tip of penis between 1.8 and 2.5

mm long and between 1 and 2 mm wide, often filled with fluid substance which supports flexible structure so that it appears inflated. No penial hooks. Vestibule delimited proximally by attachment of penial sheath to distal end of penis stalk. In mature specimens, retractor muscle cylindrical and thick (between 1 and 2 mm wide); 0.4 mm wide).

Retractor muscle inserts near heart on **right side of visceral cavity**. Retractor muscle marks separation between penial sheath and deferent duct. Deferent duct large and slightly convoluted, but shorter and less convoluted in immature specimens. Distinctive diagnostic features. Externally, the white band at the margin of the hyponotum is much brighter than in any other onchidiid species.

A white margin is occasionally present in a few *Platevindex* species, but *Alionchis jailoloensis* lives **directly on the surface of** soft mud, where *Platevindex* is not encountered, and *Platevindex* species can hardly be confused with any other onchidiids (because body strikingly and foot very narrow). Internally, the bulb-like tip of the penis and the large, cylindrical retractor muscle are unique. Remarks.

One existing onchidiid species name, *Onchidium meriakrii* Stantschinsky, 1907, must be transferred to *Alionchis*. The holotype (34/23 mm, SMF 15149), by monotypy, of *O. meriakrii* shares two diagnostic characters of *Alionchis*: a median pneumostome **at the posterior end of the** hyponotum, and large eye tentacles.

In addition, the intestinal loops of *O. meriakrii* are intermediate between type II and type (see 1934: fig. for comparison digestive types), as illustrated by Stantschinsky (1907: 360, Fig. and by examination the which is an unusual character known only in *Alionchis*, one *Onchidium* species, and two *Melayonchis* species (Dayrat et al., 2016, 2017).

The type locality of *A. meriakrii* is in and no DNA sequencing could be attempted). The name *A. meriakrii* is regarded here as a nomen dubium because the anatomy of the male copulatory apparatus, which is critical in distinguishing onchidiid species, is unknown. The penis of *A. meriakrii*, dissected by Stantschinsky, was not illustrated and is now missing from the holotype.

Stantschinsky's (1907: 374, our translation from German) description of an "anterior part that protrudes into the fore- cavity" is vague and could apply to the copulatory organs of many onchidiid species. However, Stantschinsky does not describe the actual shape of the penis, nor does he describe whether hooks were present or not. The diameter of the penial sheath and the cylindrical retractor muscle are similar in *A. jailoloensis* and *A.*

meriakrii, but these structures are frequently similar between related species. Also, Stantschinsky does not mention the live colour of *A. meriakrii* because he did not collect the animals himself. So, it is unknown whether the margin of the hyponotum of *A. meriakrii* is white, as in *A. jailoloensis*, or if any other external colour trait might distinguish it from *A. jailoloensis*. 347 The holotype of *O. meriakrii* is part of an *Alionchis* species.

However, it cannot be determined at this stage whether it is part of the same species as the Halmahera populations described here as *A. jailoloensis*. Our team has spent four weeks exploring mangroves of the eastern coast of Q from 29 s from 16° to 21° S. Unfortunately, we did not find any *Alionchis* there. If one single species of *Alionchis* was broadly distributed from Halmahera to Queensland, we could have found it at other localities in between, but we did not find any *Alionchis* in Ambon, Seram, the Kei Islands, or in Northern Territory (Australia).

Also, no *Alionchis* was found in the collections made during recent expeditions in Papua New Guinea (Madang and Kavieng) led by Philippe Bouchet for the Museum national d'histoire naturelle, Paris. Naturally, we may have missed *Alionchis* in Queensland and everywhere else between Queensland and Halmahera. Or, it could be that *A. meriakrii* is restricted to the more northern latitudes in Queensland (north of Cairns), close to the Torres Strait.

It is also possible (though less likely) that there are two allopatric species of *Alionchis*, one in eastern Indonesia and one in southern Queensland (south of Mackay), with no species in between. If *Alionchis* slugs are ever found in Queensland, it will be necessary to compare their DNA sequences to *A. jailoloensis*, because onchidiid species can be morphologically cryptic.

Stantschinsky (1907) described three species of onchidiids from Queensland, only one of which (*Onchidium buetschlii* Stantschinsky, 1907) was found during our exploration of the mangroves of Queensland (Goulding et al., in press-a). It surprising we not the other described by Stantschinsky from Queensland (*O. meriakrii* Stantschinsky, 1907 and *O.*

fungiforme Stantschinsky, 1907) despite wide and intense sampling in Queensland, as

we have been able to locate most other existing onchidiid species by returning to type localities. Also, most early descriptions of onchidiid species were based on fairly common species (people were not traveling deep into mangrove forests to find them) and so it is strange that one of the few specimens sent to Stantschinsky from Queensland was an *Alionchis* (which, based on our experience, are extremely rare slugs) and that we not any though collected of onchidiid slugs there.

This leads us to wonder whether the localities of Stantschinsky's specimens may have possibly been mixed up. In the same paper, Stantschinsky (1907) described an onchidiid species from Mindanao, Philippines, which is just north of Halmahera, and maybe the holotype of *O. meriakrii* was from Mindanao and not Queensland.

Unfortunately, that is something that we will never know, even if Queensland mangroves were to be explored in much greater depth. At any rate, because of all the issues mentioned above, we consider that, for now, *A. jailoloensis* is endemic to Halmahera and that *A. meriakrii* is a name of doubtful application. Fig. 7. Reproductive system, *Alionchis jailoloensis*, Indonesia, Halmahera [5023] (UMIZ 00118).

A, Posterior, hermaphroditic parts, scale bar = 3 mm; B, Anterior, male copulatory parts, scale bar = 3 mm. Abbreviations: dd, deferent duct; fgm, female gland mass; hd, hermaphroditic duct; hg, hermaphroditic gland; ov, oviduct; pb, penis bulb-like tip; ps, penial sheath; rm, penial retractor muscle; rs, receptaculum seminis; sp, spermatheca; v, vestibule.

348 DISCUSSION Intra-specific variation in the intestinal loops, as shown here for *Alionchis jailoloensis*, is extremely unusual in onchidiids. In the other onchidiid species that we have studied, individuals of the same species always share the same type of intestinal loops. We found only one species for which this rule does not apply, but that species is widely distributed in the Indo-West and characterised high structure across its range. In contrast, *A. jailoloensis* is the only onchidiid species in which three distinct types of intestinal loops can be found within the same population.

Indeed, DNA sequences show that there is extremely low genetic divergence between individuals of *A. jailoloensis* in Halmahera, and that this variation in intestinal loops is clearly not related to the presence of any cryptic diversity. The geographic distribution of *Alionchis* is also unusual.

Other onchidiid genera found in the Coral Triangle, such as *Peronia* Fleming, 1822 and *Platevindex* Baker, 1938, are widely distributed but *Alionchis* was not found elsewhere in Indonesia (Ambon, Bali, Kei Islands, Lombok, Seram, Sulawesi, Sumatra, and Timor), the

Philippines (Bohol and Luzon), or Australia (Northern Territory, Queensland, and New South Wales). *Alionchis* may not be widely distributed but there is no reason to think that it is endemic to Halmahera.

If the type locality of *A. meriakrii* is correct, then *Alionchis* is present in Queensland too (likely in northern Queensland). Also, it may possibly be found in Mindanao (Philippines) or West Papua (eastern Indonesia), which are close to Halmahera and which we have not been able to explore so far.

That *Alionchis jailoloensis* is found at only one island in the Indo-West Pacific could be due to the fact that it is specialised to a very specific and rare microhabitat (even though the soft mud on which individuals we collected does not seem too distinct from the soft mud found elsewhere), or it may be part of the mangrove fauna of West Papua, which has not been explored properly.

Unfortunately, there are few onchidiids from eastern Indonesia in museum collections, and it cannot be determined if *Alionchis* was formerly present in Ambon or northern Sulawesi when mangroves were less impacted. It also is possible that *Alionchis* is a relict taxon which has only survived in the core of the Coral Triangle (and possibly the Torres Strait too, if the type locality information for *A. meriakrii* is correct).

The embryonic development of onchidiids has been studied in only a few onchidiid species in the genus *Onchidella*, with some species characterised as having planktonic development and others direct development (Fretter, 1943; Stringer, 1963). have broad geographic distributions, likely through planktonic dispersal. As the diversity and geographic distributions of onchidiid species becomes clearer through this series of taxonomic revisions, studies of embryonic development in onchidiids reveal planktonic influences the geographic distributions of onchidiid species. If *A.*

jailoloensis is endemic to Halmahera, limited dispersal may be factor its Additional of mangroves in eastern Indonesia and Papua New Guinea is also necessary to determine if *Alionchis jailoloensis* requires a habitat needs Only conserving mangroves which have not yet been degraded or destroyed by development will *Alionchis* and other rare mangrove species continue to persist. ACKNOWLEDGEMENTS Accessing mangrove sites would have been impossible without from fishermen villagers.

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