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Luciferase of the Japanese syllid polychaete *Odontosyllis umdecimdonta*

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ABSTRACT

Odontosyllis undecimdonta is a marine syllid polychaete that produces bright internal and exuded bioluminescence. Despite over fifty years of biochemical investigation into *Odontosyllis* bioluminescence, the light-emitting small molecule substrate and catalyzing luciferase protein have remained a mystery. Here we describe the discovery of a bioluminescent protein fraction from *O. undecimdonta,* the identification of the luciferase using peptide and RNA sequencing, and the *in vitro* reconstruction of the bioluminescence reaction using highly purified *O. undecimdonta* luciferin and recombinant luciferase. Lastly, we found no identifiably homologous proteins in publicly available datasets. This suggests that the syllid polychaetes contain an evolutionarily unique luciferase among all characterized luminous taxa.

1. Introduction

Odontosyllis is a widely distributed genus of marine syllid polychaete worms that are noted for their striking bioluminescent courtship displays [1–5]. The bioluminescence (BL) of *Odontosyllis* is a luciferin-luciferase system [6], but the structure of the luciferin and the luciferase protein remain unknown despite several biochemical studies following the first in 1931 by Harvey [6–11]. More broadly, to date the enzyme sequences and luciferin structures remain a mystery for all polychaete species in the thirteen families containing luminous species [12].

Previous studies of the *Odontosyllis* bioluminescence system generated conflicting results regarding whether the system is a soluble oxygen-dependent luciferin-luciferase reaction [7,8], or is a photoprotein system in which the light-emitting small molecule substrate is covalently bound to the enzyme [10]. The above studies used a different *Odontosyllis* species, and the different colors of aqueous extracts identified from those species make it unclear whether there are multiple bioluminescent chemistries within *Odontosyllis*. However, both species have the same behavior of secreting luminescence during mating [1,4], so both species presumably share a homologous bioluminescent system.

Odontosyllis undecimdonta is a species found in Toyama Bay, Japan which engages in bioluminescent surface courtship displays around the first new moon in October [13]. Recently a protein-coding sequence from *O. undecimdonta* was patented that produces a recombinant protein with luminescence activity similar to that of crude worm extract mixed with crude luciferin isolate (WO2017155036A1). Here, we describe the identification, cloning, and characterization of the *O. undecimdonta* luciferase. In addition, our results suggest that the *O. undecimdonta* luminescence system is a luciferase-luciferin type without requisite cofactors, despite reports of magnesium ions as a necessary cofactor [14].

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2. Materials and methods

2.1. Specimen collection

Professor S. Inoue provided lyophilized *O. undecimdonta* worms collected in 1993 to develop the protein purification strategy [15]. The final specimens used in this study for protein purification, MS transcript identification, and nucleic acid purification were collected on October 06, 2016 in Toyama Prefecture Japan, Namerikawa City, at the coordinates 36° 46′ 40.3032" N 137° 20′ 42.378" E. At dusk, *Odontosyllis* worms were attracted to a handheld light at the surface and collected with a hand dip net. Worms were individually preserved in Invitrogen RNAlater or lyophilized for later analysis.

2.2. Molecular biology methods

2.2.1. DNA and RNA isolation

Methods for DNA and RNA isolation, as well as construction of the RNA-seq and genomic DNA libraries are as described in the Supplementary Information. Briefly, the *O. undecimdonta* transcriptome was assembled using 32, 457, 166 Illumina 2 × 150 read pairs and 343,752 Oxford Nanopore long reads using the Trinity assembler [16]. DNA from a single *O. undecimdonta* specimen was used to prepare both a 10X Genomics chromium library [17] and a PCR-free library. All sequencing reads are available to download from the European Nucleotide Archive under project PRJEB26709. Individual luciferase transcripts are available at NCBI accession numvers MH350412 and MH350413.

2.3. Protein extraction from biomaterial

Five ml of phosphate buffer (5 mM sodium phosphate buffer, pH 7.4) was added to 150 mg of lyophilized worms. Then this mixture was dropped in to the liquid nitrogen, using a 1 ml pipette, to create small drops of frozen material. These small ice drops were ground in a mortar. Frozen powder was added to 10 ml of phosphate buffer (5 mM sodium phosphate buffer, pH 7.4) and incubated 40 min on an ice bath with stirring. After incubation this solution was centrifuged at 40000 g (4 °C) for 40 min. The supernatant, containing luciferase, was then collected and used for further purification by anion exchange chromatography.

2.4. Protein purification

2.4.1. Anion exchange chromatography of water extract

An extract of *O. undecimdonta* was applied to a DEAE Sepharose (GE Healthcare, Uppsala, Sweden) HiTrap Fast Flow column (1.6 × 2.5 cm), equilibrated and washed with 5 mM sodium phosphate buffer, pH 7.4 at rate of 5 ml/min. The elution was done by linear NaCl gradient from 0 to 0.4 M (80 ml) and 5 ml fractions were collected. To minimize bioluminescent reactions, the solvent, fractions and column were maintained at 4 °C. Automatic fraction collection and solvent application was controlled with an Akta Prime chromatography system (GE Healthcare, Uppsala, Sweden). After elution, fractions containing luciferase and luciferin were detected by pairwise mixing all possible fraction combinations. The reaction was monitored with a custom-made luminometer Oberon-K (Krasnoyarsk, Russia).

2.4.2. Ultrafiltration and concentration

To discard additional proteins from the luciferase-containing fractions the ultrafiltration procedure was used. First, the active fraction was filtered on a 50 kDa Amicon® Ultra centrifugal filter unit (Merck Millipore, Germany). BL activity was measured for the concentrated retentate and the permeate. We found that only the permeate was bioluminescent. The bioluminescent permeate was then concentrated on 30 kDa Amicon® Ultra centrifugal filter unit (Merck Millipore, Germany). The resulting retentate possessed BL activity while the permeate did not. Thus this concentrated luciferase sample was used for size exclusion chromatography.

2.4.3. Size exclusion chromatography

The bioluminescent retentate from ultrafiltration was applied to a Superdex 200 column (Phenomenex, USA) on a Shimadzu chromatography system (Shimadzu, Japan). The loaded column was washed with 5 mM sodium phosphate buffer, 150 mM NaCl, pH 7.4 at rate of 0.4 ml/min. During separation 0.5 ml fractions were collected. The solvent, fractions, and column were maintained at 4 °C. BL-active fractions were used in the subsequent gel electrophoresis experiments.

2.5. Denaturing polyacrylamide gel electrophoresis and amino acid sequence analysis

SDS-PAGE of the BL-active fractions was performed using a 10–25% gradient gel according to [18]. Gel staining was done according to the silver staining protocol from [19], or using a standard Coomassie G250 staining protocol. Protein bands were excised from the gel and subjected to in-gel trypsinolysis [20]. LC-MS was performed on the Ultimate 3000 Nano LC System (Thermo Fisher Scientific), connected to a Q Exactive HF mass spectrometer (Thermo Fisher Scientific). For data analysis, Mascot software (Matrix Science) with the *O. undecimdonta* transcriptome as a reference was used.

2.5.1. Molecular cloning

Four Odontosyllis luciferase candidate genes were codon-optimized for expression in mammalian cells, domesticated for compatibility with MoClo assembly [21] and ordered from a commercial supplier (Twist Biosciences, USA) as linear dsDNA fragments. Molecular cloning is described in detail in the Supplementary Materials.

2.5.2. Mammalian cell culture

HEK293NT cells were grown under standard conditions and transfected with FuGene 6 reagent (Promega, Fitchburg, WI, USA) in accordance to the manufacturer's protocol. For more details see Supplementary materials.

2.6. In vitro bioluminescence assay

The reaction was monitored with a custom-made luminometer Oberon-K (Krasnoyarsk, Russia) at room temperature. For each measurement 100 μl of reaction mix (10 mM sodium phosphate buffer, 150 mM NaCl, pH 7.4, 2 μl of luciferase fraction, 2 μl of highly purified luciferin [22] were used. In experiments with mammalian cells lysates, the same amount of cells was used for each clone in each bioluminescence analysis to make results comparable.

The involvement of additional cofactors in the *O. undecimdonta* bioluminescence reaction was tested using an *in vitro* assay with only purified luciferase and highly purified luciferin. Since previous studies suggest the involvement of Mg^{2+} in the *Odontosyllis* bioluminescence reaction (optimum conc is 30 mM; [14]), we also testing the *in vitro* bioluminescence assay with 30 mM–60 mM Mg^{2+} with cell lysate.

2.7. Protein structure and homology analysis

We used HMMER and the BLAST suite to predict structural domains and interspecies homology of transcripts that produced

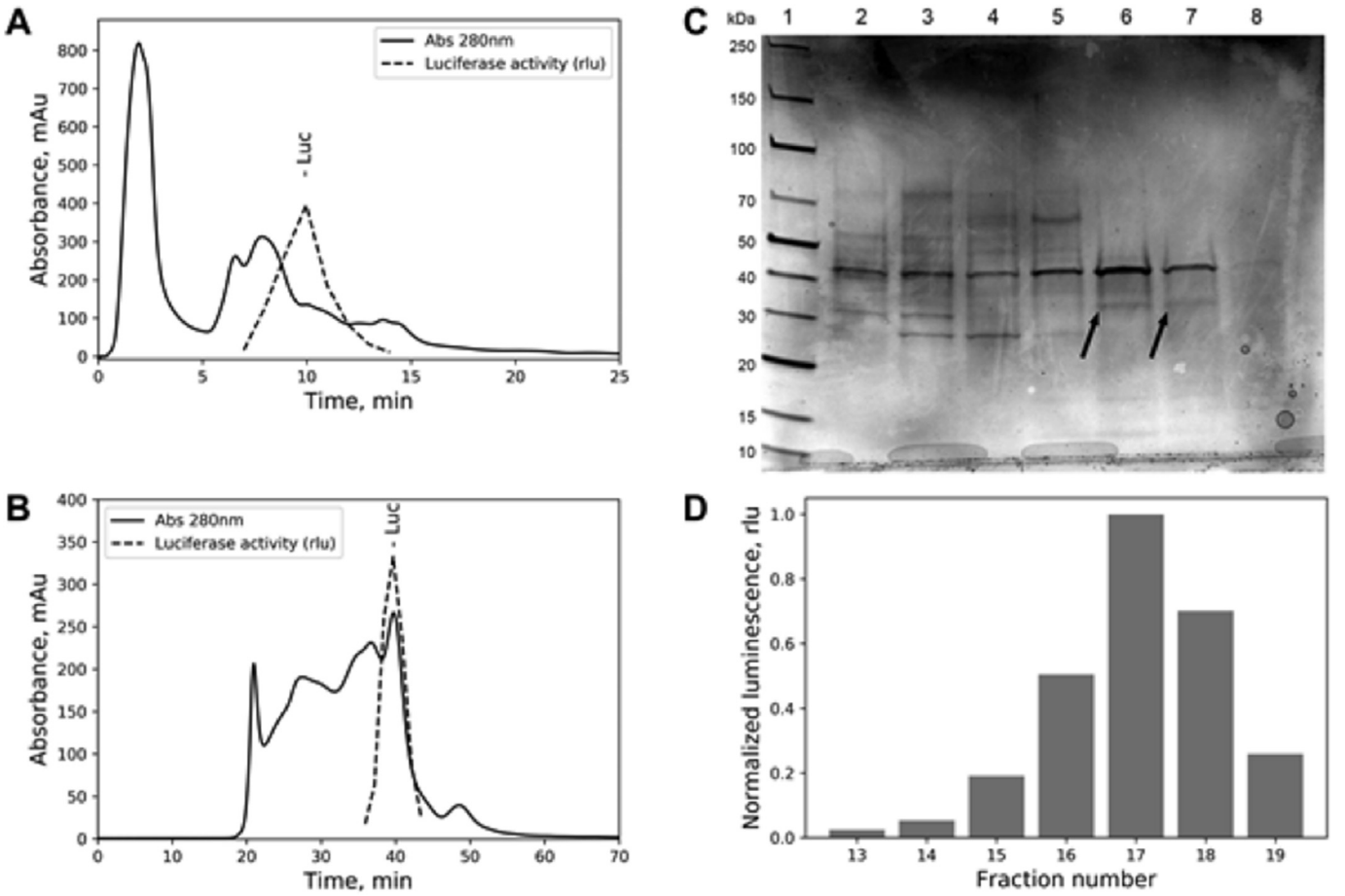

Fig. 1. Purification and isolation of *O. undecimdonta* luciferase. **A** - Chromatographic profile of water extract from lyophilized *O. undecimdonta* worms anion-exchange chromatography on DEAE Sepharose HiTrap Fast Flow column. Solid line – 280 nm absorption signal. Activity profile of *Odontosyllis* luciferase shown as dashed line. **B** – Size exclusion chromatographic profile of anion-exchange chromatography concentrated luciferase fractions on Superdex 200 column. Solid line – 280 nm absorption signal. Activity profile of *O. undecimdonta* luciferase shown as dashed line. **C** - SDS-PAGE analysis of size exclusion chromatography fractions. Lanes: 1 - PageRuler protein ladder (Thermo Scientific), lanes from 2 to 8 - size exclusion chromatography fractions 13–19 respectively. Arrows shows protein bands excised from gel and analyzed by LC-MS. **D** – Normalized luminescence activity of size exclusion chromatography fractions, used for SDS-PAGE analysis.

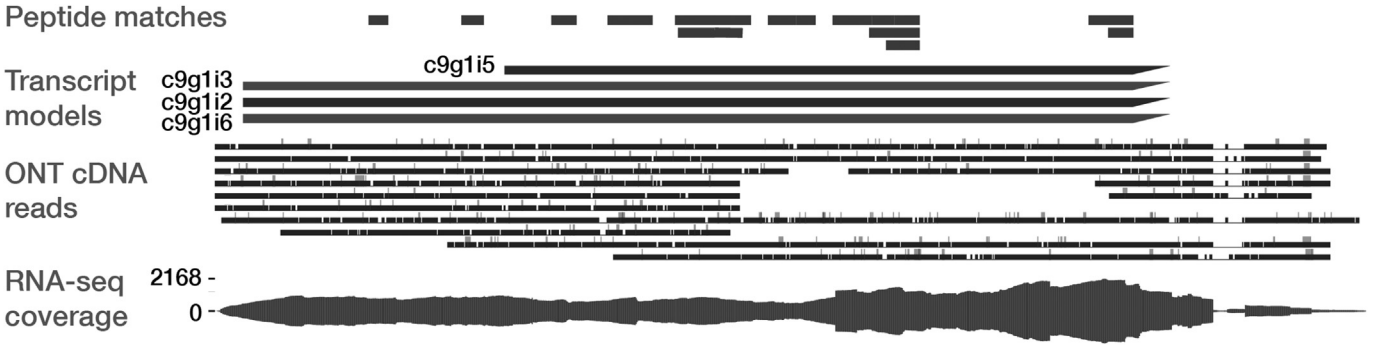

Fig. 2. Supporting evidence for transcript models aligned to the c9g1i2 transcript, including 5′ and 3′ UTR. The *Peptide Matches* track shows unique peptide hits to any of the four transcript models that match by DNA and amino acid sequence similarity. All transcript models except c9g1i5 share the same structure, whereas c9g1i5 lacks 93 N-terminal amino acids. The *ONT cDNA Reads* track shows individual Oxford Nanopore 2D cDNA reads that align to the c9g1i2 transcript. Three reads span the complete 5′ UTR, transcript, and 3′ UTR of the long isoforms (c9g1i2, c9g1i3, c9g1i6), and four additional reads support the 5′ UTR of the long isoforms. The *RNA-seq coverage* track supports the 5′ and 3′ UTR of the long isoforms, despite the predictable 3′ bias inherent to polyA-selecting library preparation techniques.

bioluminescence [23–25]. We also used Phobius and SignalP to detect signal peptides and transmembrane domains of the same transcripts [26,27]. Lastly, we used the I-TASSER server for structural prediction [28]. See the supplementary materials for a detailed descripton of the search for homologous sequences in other polychaetes.

3. Results

The isolation and purification of *O. undecimdonta* luciferase

required ion exchange chromatography, size exclusion chromatography, and ultrafiltration. (Fig. 1). The presence of luciferase in samples was controlled by an *in vitro* BL assay for all stages of purification. Several bands that corresponded to BL activity in the size exclusion chromatography fractions were identified by polyacrylamide gel electrophoresis (Fig. 1C). These bands were excised from gel and were identified by LC-MS.

The transcriptome assembled with Illumina paired-end reads and ONT 2D reads extracted with poretools "fwd" parameter yielded 256,027 transcripts and a median transcript length of 737 base pairs. Four transcripts were identified as potential luciferases (Fig. 2) based on coverage and quantity of MS matches. Three long transcripts c9g1i2 (990 bp), c9g1i3 (993 bp), c9g1i6 (990 bp) had c-terminal amino acid variation. Transcript c9g1i5 (711 bp) was homologous to the aforementioned three transcripts but lacked 118 n-terminal amino acids (Fig. 4). These four transcripts were verified by presence of two ONT whole-cDNA reads that spanned from the 5′ UTR to the 3′UTR. Non-spliced mapping of an Illumina paired-end polyA RNA-seq library also confirmed that the longest of the four transcripts were expressed. The BLOSUM-alignment for the protein products of these four transcripts were identical at 92% of sites.

All four candidate DNA sequences were synthesized as linear dsDNA fragments and cloned using MoClo technology. Then, mammalian cells were transfected by resulting constructs. Mammalian cell culture lysate from two of the above four candidates produced bioluminescence when assayed with purified luciferin (c9g1i2 and c9g1i6) (Fig. 3). The bioluminescence spectra of positive clones were similar to that of native *O. undecimdonta* worms (Fig. 3). However, cell culture lysate from expressed transcripts c9g1i3 and c9g1i5 were not luminous. None of the non-lysed cell cultures produced luminescence when purified luciferin was applied.

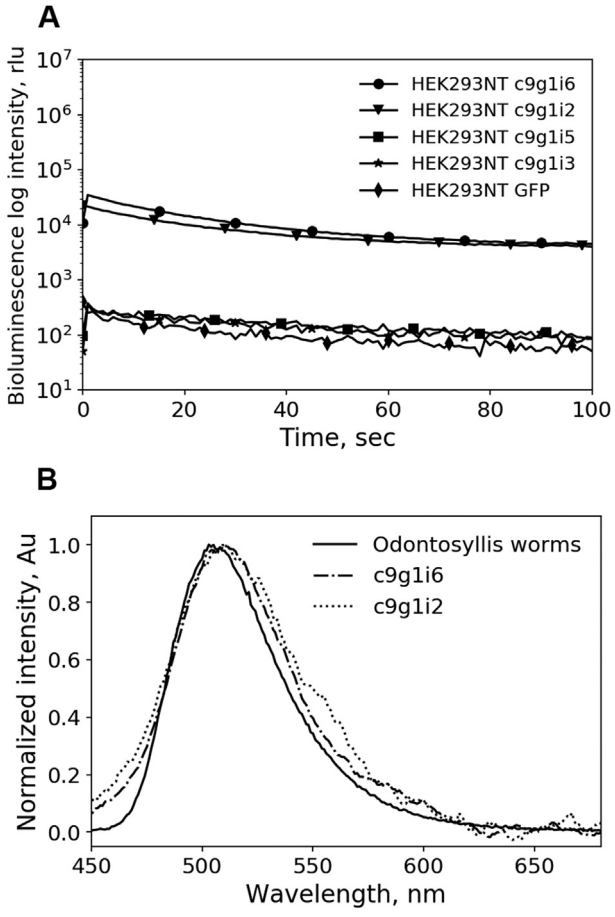

Fig. 3. *O. undecimdonta* luciferase properties. **A** - Kinetics of bioluminescence of transfected by *O. umdecimdonta* luciferase genes candidates HEK293NT cells lysates (log scale). For HEK293NT cells lysates, transfected by plasmids with c9g1i6, c9g1i2, c9g1i5, c9g1i3 - circle, triangle, square and asterisks markers were used respectively, and rhombus marker for GFP control. **B** - Normalized bioluminescence spectra of natural *O. undecimdonta* luciferase (solid line), c9g1i6 recombinant protein (dash-dotted line) and c9g1i2 recombinant protein (dotted line). The spectral maxima are near 510 nm.

The protein product of c9g1i2 is 329 amino acids long. The signal peptide prediction software Phobius had a posterior probability of 1 that the first 21 c-terminal peptides are a signal peptide. The SignalP service has a probability of 0.28 that the first 21 amino acids are signal peptides. The only HMMER and PHMMER results for this protein product were an insignificant match (E-value = 0.8) to a prokaryotic protein involved in mRNA production. I-TASSER protein structure and function prediction results found that nine of the top ten structural homologs to the protein product of c9g1i2 were adenosine deaminase/hydrolases. A tblastn search with the c9g1i2 protein product only found an insignificant match (E-value = 3.1) to a predicted gerbil transcription factor (sequence XM_021634012.1). A blastn search returned no significant matches. Blast searches against the assembled transcriptomes of publicly available polychaete RNA-seq read data also yielded no significant matches (see SI results).

The mixture of purified *O. undecimdonta* luciferase and luciferin in TBS (50 mM Tris-HCl, 150 mM NaCl, pH 8.0) was luminescent, even in the absence of Mg^{2+} ions. Increasing the Mg^{2+} concentration in the reaction buffer of recombinant luciferase cell lysate did not affect the yield of the bioluminescence reaction (data not shown).

4. Discussion

Given our lack of fresh specimens we opted to extract and purify the *Odontosyllis* luciferase directly from the lyophilized worms and successfully identified the luciferase gene using classic protein purification, luciferin purification, and recent whole-cDNA sequencing techniques. We then reconstructed native *Odontosyllis* bioluminescence *in vitro* using purified protein and highly purified luciferin [22] with no additional cofactors. Lastly, we verified the identity of the *Odontosyllis* luciferase gene by showing that recombinant protein and purified luciferin in cell-lysate is luminous, in which the luminescence spectra (max, near 510 nm) matches that of the *Odontosyllis in vivo* luminescence.

It is notable that using purified components in studying bioluminescence reactions is important to verify that off-target reactions are not the source of luminescence and to avoid erroneous interpretation of the results [14]. Given that the protein and luciferin purification products were luminous and that luminescence of recombinant luciferase cell lysates were not enhanced with Mg^{2+} the *O. undecimdonta* luciferase-luciferin reaction does not appear to require additional cofactors. It is also important to note that the recombinant protein is not secreted by eukaryotic cells and that the luminescence reaction only occurs when cells containing the recombinant luciferase are lysed. This suggests that the highly purified *O. undecimdonta* luciferin is not membrane-permeable, thus limiting the potential for applications of this luciferase in optogenetics or other cellular expression-based technology.

While the bioluminescence emitted during mating is well-characterized in *Odontosyllis* spp., the luciferase structure and the mechanism of the luciferin-luciferase reaction remains unclear. Despite this uncertainty, protein ortology searches using BLAST and HMMER show that syllid luciferase is unique both among sequenced polychaetes and other sequenced organisms in public

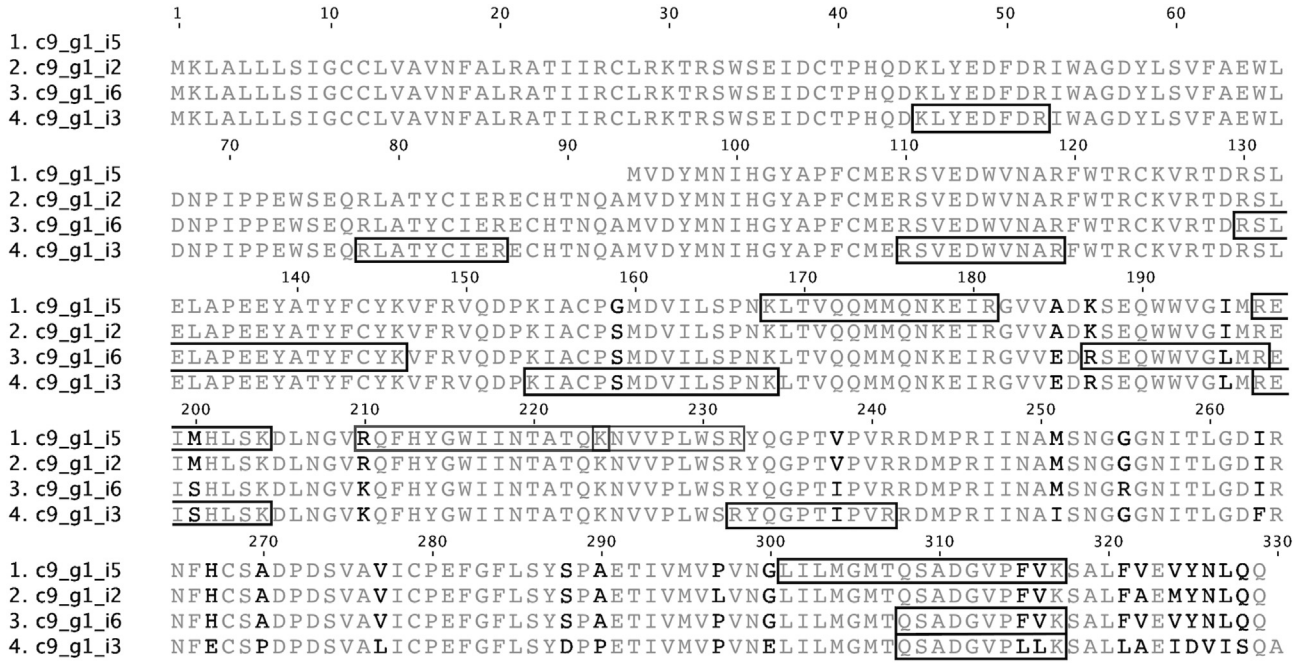

Fig. 4. The amino acid alignment of the four luciferase transcripts. Black boxes surrounding the alignment indicate regions to which there were exact MS peptide matches. The fours transcripts are on average 94% similar to one another. Transcript c9g1i5 lacks 93 N-terminal amino acids. All transcripts have a highly variable C-terminus.

databases. The lack of evidence for a conserved protein in the transcriptomes of other luminous polychaetes leaves open the theory that bioluminesc evoled more than three times in the annelids. In this conservative estimate, we only include the evolution of two unique bioluminescent systems for which either the structure of the luciferin, luciferase, or both have been determined (earthworms [29] and *Odontosyllis*) plus at least one event for other annelids with uncharacterized bioluminescent systems. Given that the structure of other polychaete luciferins is still unknown, this leaves the question of polychaete bioluminescence unanswered. Identification of the *O. umdecimdonta* luciferase sequence is the most important step to further characterization of this worm's bioluminescent system and the screening of other purified polychaete luciferins for cross-reactivity.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.bbrc.2018.05.135.

Transparency document

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Corrigendum

Corrigendum to "Luciferase of the Japanese syllid polychaete Odontosyllis undecimdonta" [Biochem. Biophys. Res. Commun. 2018 Jul 20;502(3):318–323]

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The authors regret that the polychaete worm was incorrectly referred to as *Odontosyllis umdecimdonta* in several parts of the text rather than the accepted nomenclature, *Odontosyllis undecimdonta.* The authors would like to apologise for any inconvenience caused.

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