Molecular phylogeny and evolution of bioluminescence in Odontosyllis (Annelida, Syllidae)

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\textbf{ABSTRACT}

Marine worms of the genus \textit{Odontosyllis} (Syllidae, Annelida) are well known for spectacular bioluminescent courtship rituals. During the reproductive period, the benthic marine worms leave the ocean floor and swim to the surface to spawn, using bioluminescent light for mate attraction. The behavioural aspects of the courtship ritual have been extensively investigated but little is known about the origin and evolution of light production in \textit{Odontosyllis} that may be a key factor shaping the natural history of the group. To investigate the speciation patterns and evolutionary history of \textit{Odontosyllis}, we inferred phylogenies following a gene concatenation approach using both maximum likelihood and Bayesian inference with a multilocus molecular dataset including nuclear (\textit{18S} rRNA) and mitochondrial markers (\textit{16S} rRNA and cytochrome \textit{c} oxidase subunit I) from 51 \textit{Odontosyllis} specimens. We also used the resulting phylogenetic tree to perform an ancestral state reconstruction analysis to trace the origin of bioluminescence within the group. Our results reveal that the genus \textit{Odontosyllis} as currently delineated is a paraphyletic group that needs to be taxonomically revised to reflect evolutionary relationships. Nevertheless, our analyses recover two supported clades with bioluminescent species and suggest that the most recent common ancestor of luminous syllids was not bioluminescent, providing evidence that bioluminescence has evolved independently twice in the group. We discuss possible scenarios for the origin and evolution of light production and the potential role of bioluminescence courtship as a driver of speciation. Our results shed light on the evolutionary history of luminous syllids and suggest that bioluminescence might represent a key factor shaping the evolution of these organisms.

\textbf{Keywords:} ancestral reconstruction, bioluminescence, Eusyllinae, evolution, luminous syllids, \textit{Odontosyllis}, phylogeny, Syllidae.

\textbf{Introduction}

Bioluminescence, the ability of living organisms to produce visible light, has evolved independently in several annelid lineages (Haddock \textit{et al.} 2010; Verdes and Gruber 2017), including remarkable species like the deep-sea \textit{Swima bombiviridis} Osborn, Haddock, Pleijel, Madin & Rouse, 2009 that releases defensive luminescent ‘bombs’ (Osborn \textit{et al.} 2009) or the pelagic tomopterids that emit yellow light for communication, an extremely rare colour among marine luminous taxa (Widder 2010). Bioluminescent annelids occupy a variety of habitats from terrestrial to marine ecosystems and display a wide range of bioluminescent colours associated with different functions, such as defence or intraspecific communication (Verdes and Gruber 2017). In luminous syllids of the genus \textit{Odontosyllis} Claparède, 1863 (Fig. 1a–h), bioluminescent light is used for mate attraction, acting as a swarming cue during reproduction (see video in Verdes and Gruber 2017). During the summer months, a few days after a full moon and shortly after sunset, the benthic marine worms leave the ocean floor and swim to the surface to reproduce. In most cases, females appear first and swim in circles while releasing gametes in a cloud of bright green luminous mucus that attracts the males that dart towards the females to spawn (Galloway and Welch 1911; Markert \textit{et al.} 1961; Verdes and Gruber 2017). This courtship...
ritual and the precise timing have been thoroughly described from a behavioural point of view (Huntsman 1948; Markert et al. 1961; Tsuji and Hill 1983; Fischer and Fischer 1995; Gaston and Hall 2000), but knowledge about the origin and evolution of light production in the group is rather limited. Nevertheless, luminous syllids have recently received increased attention, with a handful of species being the focus of studies describing the properties of the bioluminescent system (Brugler et al. 2018; Mitani et al. 2018; Schultz et al. 2018; Kotlobay et al. 2019; Mitani et al. 2019), rendering these as an excellent model to investigate the evolution of luminous lineages. Moreover, lineages with this type of bioluminescent courtship display have been shown to be more speciose and have significantly higher rates of diversification than the non-luminous sister groups (Ellis and Oakley 2016), suggesting that the luminous ritual of Odontosyllis may represent a key innovation shaping the evolution and natural history of this group of marine annelids.

The inference of species boundaries and robust phylogenetic hypotheses are fundamental for any evolutionary study but these features are currently lacking for the genus Odontosyllis. The genus belongs to the family Syllidae Grube, 1850, one of the most diverse families in the phylum Annelida with almost 1000 species described to date (Pamungkas et al. 2019). Odontosyllis species are characterised by a combination of morphological characters including the presence of a well-developed occipital flap covering the posterior part of the prostomium (Fig. 1a, b, g) and a short pharynx with a few teeth directed backwards (San Martin and Hutchings 2006; Verdes et al. 2011; Fukuda et al. 2013). This unique pharyngeal armature, referred to as denticled arc, is considered the main diagnostic feature of the genus (San Martin and Hutchings 2006). Though identifying Odontosyllis species based on this distinctive structure may seem straightforward, many of the 56 species that currently comprise the genus (http://www.marinespecies.org at VLIZ,
accessed 5 May 2022) correspond to single reports whose descriptions lack crucial information regarding the pharyngeal armature, hindering any revisionary effort to clarify the taxonomy and systematics of the group (Verdes et al. 2011; Fukuda et al. 2013). Additionally, identification to the species level is rather difficult since many species have been described using different combinations of characters representing a continuum of variation of certain morphological features, sometimes resulting in descriptions based on slight morphological variations (Fukuda et al. 2013).

In this study, we used phylogenetic analyses and ancestral state reconstruction methods to clarify the evolutionary history and relationships among Odontosyllis species, and investigate the origin and evolution of bioluminescence. We inferred phylogenies using DNA sequence data from nuclear marker 18S rRNA and mitochondrial markers 16S rRNA and cytochrome c oxidase subunit I (COI) from 51 Odontosyllis specimens, representing 26 species. We followed a gene concatenation approach using both maximum likelihood (ML) and Bayesian inference (BI) analyses. We discuss the taxonomic implications of our results and explore possible scenarios for the origin and evolution of light production, and the role of bioluminescence courtship as a possible driver of speciation within luminous syllids.

Material and methods

Sample collection and identification

Samples were collected from a variety of substrates in intertidal and subtidal zones by hand, snorkeling or SCUBA diving during biological surveys undertaken between 2012 and 2016. Information regarding collection dates, locality and substrates is listed in Supplementary Table S1. Specimens were sorted in the field using light microscopy and fixed in 96% ethanol or RNA for morphological and molecular analyses. Prior to fixation, selected specimens were anaesthetised with 7% magnesium chloride buffered in seawater and photographed under a microscope. Further examinations and identifications were completed using a Nikon Optiphot light microscope with a differential interference contrast system (Nomarsky) at the Universidad Autónoma de Madrid (UAM).

DNA extraction, amplification and sequencing

Genomic DNA was extracted using the DNeasy Blood & Tissue Kit (Qiagen), following manufacturer’s protocols. Fragments of the nuclear gene 18S rRNA (2157 bp), and the mitochondrial 16S rRNA (546 bp) and COI (659 bp) were amplified by polymerase chain reaction (PCR). Three overlapping pairs of primers were used to amplify 18S rRNA: 18S1F-18S4R, 18S3F-18SBi and 18Sa2.0-18S9R (Giribet et al. 1996). Primers 16SaRl and 16SBrH (Palumbi 1996) were used to amplify 16S rRNA, and the modified primers with inosine jgLCO1490 and jgHCO2198 (Geller et al. 2013) were employed to amplify COI in all specimens. The PCR reactions consisted of 1 µL of DNA template in 25-µL reaction volumes containing 18 µL of H2O; 5 µL of buffer, 0.25 µL of each of 10-µM primers, 0.5 µL of 10 mM of dNTPs, and 0.13 µL of 1.25 U L⁻¹ GoTaq DNA Polymerase (Promega). The temperature profile for the 18S rRNA nuclear markers was as follows: initial denaturing step at 95°C for 120 s; 35 cycles with denaturing at 95°C for 30 s; annealing at 47°C for 30 s; and extension at 72°C for 180 s; and a final extension at 72°C for 300 s. For 16S rRNA: initial denaturing step at 95°C for 5 min; 35 cycles with denaturing at 95°C for 30 s; annealing at 45°C for 30 s; and extension at 72°C for 60 s; a final extension at 72°C for 10 min. For COI: initial denaturing step at 95°C for 15 min; 40 cycles with denaturing at 94°C for 30 s; annealing at 45°C for 70 s; and extension at 72°C for 90 s; a final extension at 72°C for 10 min. 1.5 µL of the PCR product was used for sequencing using the forward primer of the primers described above at the Servicio de Secuenciación Sanger, Unidad de Genómica (Universidad Complutense de Madrid) and at Genewiz Inc. (South Plainfield, NJ, USA). Sequences were edited in Geneious (ver. 8.1.9, see https://www.geneious.com/; Kearse et al. 2012), to remove primers from all markers and merge the three overlapping fragments of the 18S rRNA into a consensus sequence. Multiple sequence alignments for the three different genes were built in the online server of MAFFT (ver. 7, see https://mafft.cbrc.jp/alignment/software/; Katoh and Standley 2013) under default parameters.

Phylogenetic analyses

To assess the monophyly of Odontosyllis, we analysed the three molecular markers (18S, 16S and COI) in a total of 94 specimens (51 Odontosyllis, 19 closely related Eusyllinae and 24 outgroups representing the main Syllidae subfamilies) following a gene concatenation approach using both maximum likelihood (ML) and Bayesian inference (BI). All mitochondrial and nuclear data sets were concatenated and the best-fitting model of sequence evolution was selected using the Akaike information criterion (AIC) in jModeltest (ver. 2, see https://github.com/ddarriba/jmodeltest2; Darriba 2012). The best model for the concatenated data set was a general time-reversible (GTR) with gamma-distributed rates across sites and a proportion of invariable sites (GTR + G + I). Partitions for each of the markers were used in all subsequent phylogenetic analyses: for ribosomal markers, non-codon-specific models were used; and for COI, we used codon-specific models. ML analyses were run in RAxML (ver. 1.31, see https://github.com/stamatak/standard-RAXML; Stamatakis 2006) using the GTR + G + I evolutionary model. Bootstrap support values were estimated using 1000 replicates and 10 starting trees (Stamatakis et al. 2008). BI analyses were run with MrBayes (ver. 3.2.1, see https://github.com/NBISweden/MrBayes/; Ronquist et al. 2012) in the CIPRES Science Gateway (ver. 3.1, see http://www.phylo.org/;
Miller et al. 2010). Analyses were run using the GTR + G + I evolutionary model, with four Markov chains that were started from a random tree, running simultaneously for 30 million generations, with trees sampled every 2000 generations, with trees sampled every 2000 generations (samplefreq = 2000); the initial 25% of trees were discarded as burn-in (burninfrac = 0.25) after assessing for convergence with Tracer (ver. 1.6, A. Rambaut and A. J. Drummond, see http://beast.bio.ed.ac.uk/Tracer).

Ancestral state character reconstruction

To investigate the evolution of bioluminescence within luminous syllids we performed ancestral state reconstructions (ASR) on the ML topology obtained in the phylogenetic analysis. The ability of each species to produce light was determined either from literature reports or personal observations by the authors and colleagues who collected the samples. Bioluminescence was coded as a binary character (0, absence; 1, presence) for the species for which information was available and ASR was performed in Mesquite (ver. 3.10, W. P. Maddison and D. R. Maddison, see http://www.mesquiteproject.org) using equally weighted, unordered states. ML optimisation was implemented under the Mk1 model to identify the state at each node that maximises the probability of the states observed in the terminal taxa (Pagel 1999). Species duplicates were excluded from the analyses.

Results

Phylogenetic analyses recover a paraphyletic Odontosyllis

Multiple sequence alignments used for phylogenetic reconstruction included partial sequences of nuclear marker 18S rRNA (2157 bp) from 84 specimens, and mitochondrial genes 16S rRNA from 68 specimens (546 bp) and COI from 70 specimens (659 bp). Both ML (Fig. 2, Supplementary Fig. S1) and BI (Supplementary Fig. S2) analyses of the three concatenated genes recovered a paraphyletic Odontosyllis, as species of the closely related genera Eusyllis Malmgren, 1867, Pionosyllis Malmgren, 1867 and Nudisyllis Knox & Cameron, 1970 are found nested within Odontosyllis (Fig. 2). Since the two topologies obtained from the ML and BI analyses are almost identical, we present the ML tree with both bootstrap (bs) and posterior probability (pp) support values mapped on each node (Fig. 2).

Our analyses recovered a paraphyletic Odontosyllis, with two main clades labelled Clade 1 and Clade 2 (Fig. 2). Clade 1 is strongly supported in both the ML and BI analyses (90/1) whereas Clade 2 is strongly supported in the BI (0.99 pp) but shows weaker support in the ML (71 bs) (Supplementary Fig. S1, S2). Clade 1 includes Odontosyllis fulgurans (Audouin & Milne Edwards, 1833), Odontosyllis undecimdonta Imajima & Hartman, 1964 and an unidentified Odontosyllis species. Clade 2 groups all remaining Odontosyllis and includes the type species Odontosyllis gibba Claparède, 1863. Within Clade 2, both analyses recovered a well-supported clade (0.98/1 bs/pp) that includes the type species O. gibba and other species characterised by unidentate chaetae with long blades (see insets in Fig. 2), including Odontosyllis freycinetensis Augener, 1913, Odontosyllis globulocirrata Hartmann-Schröder, 1981 and Odontosyllis maculata Uschakov in Annenkov (1938). This latter species might have been misidentified as O. maculata as this falls within O. gibba specimens, but unfortunately there is no voucher available to corroborate the identity. The only other species with this type of unidentate chaetae is O. detecta Augener, 1913, also nested within Clade 2 but the blades are much shorter than those in the lineage including O. gibba. Within Clade 2, a lineage comprising Odontosyllis australiensis Hartmann-Schröder, 1979, Odontosyllis cf. fulgurans and an unidentified species from Indonesia (Odontosyllis sp. 6) was also well supported (96/0.99 bs/pp) in both analyses, along with a clade containing most of the species known to use bioluminescence for courtship, including Odontosyllis phosphorea Moore, 1909, Odontosyllis guillermitoi Fukuda & Nogueira, 2006 and several undescribed Caribbean Odontosyllis (90/1 bs/pp) (Fig. 2, Supplementary Fig. S1, S2).

There were slight differences in the node support values of a handful of clades recovered in the ML and BI analysis. Specifically, Clade 2 was strongly supported in the BI analysis (0.99 pp), but support was weaker in the ML analysis (71 bs). Similarly, within Clade 2, the lineage containing O. detecta and numerous luminous courting syllids including O. phosphorea and O. guillermitoi, showed strong support in the BI tree (0.99 pp) but was weakly supported in the ML tree (76 bs) (Fig. 2, Supplementary Fig. S1, S2).

Bioluminescence evolved independently in two distinct syllid lineages

Results from the ASR analysis using the ML topology obtained in the phylogenetic analysis support the notion that bioluminescence was not the ancestral state for syllids, nor for the Eusyllinae lineage to which Odontosyllis and all other luminous syllids belong (Fig. 3, Supplementary Fig. S3). Specifically, the ML reconstruction suggests with high probability that bioluminescence evolved twice within Eusyllinae (indicated by asterisks in Fig. 3, Supplementary Fig. S3), once in the most recent common ancestor (MRCA) of a lineage including Clade 1, and Eusyllis blomstrandii Malmgren, 1867 and Pionosyllis enigmatica (Wesenberg-Lund, 1950) (0.981 likelihood), and once in the MRCA of Clade 2 (0.999 likelihood), with possible secondary losses in several lineages (Fig. 3, Supplementary Fig. S3). Therefore our results suggest that the MRCA of extant luminous syllids did not have the ability to produce light and provide evidence that bioluminescence is a trait that evolved independently in two distinct evolutionary lineages within the subfamily Eusyllinae.
Discussion

The phylogenetic analyses completed in this study show congruent results with both methodologies used (ML or BI) indicating that *Odontosyllis* is a paraphyletic group, with species of the closely related genera *Eusyllis*, *Pionosyllis* and *Nudisyllis* nested within (Fig. 2) this. The paraphyly of *Odontosyllis* had been suggested in the most recent molecular phylogeny of Syllidae (Aguado et al. 2012), however this only included 11 species of the genus *Odontosyllis* and no lineages were supported, except the one including the type species *O. gibba*. On the other side,
our phylogenetic reconstruction included 51 *Odontosyllis* specimens, representing 26 different species. We recovered two main clades of *Odontosyllis* (Clade 1 and Clade 2) supported in both the ML and BI analyses. In addition, within Clade 2, all analyses recovered a strongly supported lineage that includes *O. freycinetensis*, *O. cf. gibba*, *O. globulocirrata*, *O. maculata* and *O. gibba*. Since *O. gibba* is the type species of the genus, this lineage would represent the taxonomically valid *Odontosyllis* (Fig. 2, Supplementary Fig. S1, S2). Morphological examination showed that this lineage mainly comprised species with unidentate chaetae and long blades that are not found in other lineages (see insets in Fig. 2). Despite small discrepancies in the support values assigned to a handful of nodes by each analysis, our results clearly show that *Odontosyllis* as currently delineated is a paraphyletic group and needs to be taxonomically revised to reflect evolutionary relationships. However, we did not identify shared distinctive morphological features in most supported lineages and as a consequence, we do not consider taking any taxonomic action appropriate until additional material is available for molecular study and a more thorough morphological analysis can be completed.

It is well known that many species of *Odontosyllis* are bioluminescent (Fig. 1a, c, g, h) but there are also reports of luminous species in other closely related syllid genera including *Eusyllis* (Fig. 1f) and *Pionosyllis* (Zörner and Fischer 2007; Haddock *et al.* 2010; Verdes and Gruber 2017). Several *Odontosyllis* species, including *O. australiensis*, *O. enopla*, *O. phosphorea*, *O. polycera* and *O. undecimdonta* display a bioluminescence courtship ritual in which light is used for mate attraction and functions as a swarming cue during reproduction (Tsuji and Hill 1983; Gaston and Hall 2000; Verdes and Gruber 2017). For other *Odontosyllis* species such as *O. fulgurans* and *O. ctenostoma*, and *Eusyllis blomstrandii*, only a few reports document the capability of the worms to glow when disturbed and whether bioluminescence is used for courtship or only as a defence mechanism is not clear. A recent study showed that lineages with bioluminescent courtship displays are associated with higher species richness and faster rates of species accumulation than the non-luminous relatives, but this pattern was not observed for lineages that use bioluminescence as a defence mechanism (Ellis and Oakley 2016). For the reason that bioluminescence courtship is almost certainly a sexually selected trait, this study provides further evidence to support the theory that sexual selection promotes speciation at a macroevolutionary scale (Seddon *et al.* 2008; Ellis and Oakley 2016).

Our ancestral state reconstruction analyses tracing the evolution of bioluminescence in luminous syllids provides evidence suggesting that the capability to produce light evolved twice within the group, independently in the most recent common ancestors of two distinct evolutionary lineages (Fig. 3, Supplementary Fig. S3). Interestingly, most of the species known to use bioluminescence for courtship, including *O. australiensis*, *O. phosphorea* and *O. polycera* fall within Clade 2, the most speciose lineage. Clade 1 is a less diverse lineage and includes only a single species with bioluminescent courtship, the Japanese *O. undecimdonta*. There are different reasons that could explain why this particular lineage is less speciose despite also having a luminous courting species, including environmental factors such as temperature, historical ones such as more recent colonisation events (Stephens and Wiens 2003; Tittensor *et al.* 2010) or simply insufficient sampling coverage or undescribed diversity. Nevertheless, the Eusyllinae clade that includes all luminous syllids (i.e. *Odontosyllis*, *Eusyllis*, *Pionosyllis*) is clearly remarkably more speciose than the sister clade that includes
non-luminous *Synmerosyllis* species and *Eusyllis lamelligera* (Fig. 2). These results provide support for the hypothesis that the use of bioluminescence and particularly bioluminescent courtship, might be associated with an increase in speciation rates, potentially leading to higher species richness in luminous syllids (Ellis and Oakley 2016).

Both the light emitting molecule (luciferin) and the enzyme that catalyses the bioluminescence reaction (luciferase), have recently been characterised in luminous syllids of the genus *Odontosyllis* and these represent unique compounds that do not share sequence or structural similarity with any other known bioluminescent systems (Brugler et al. 2018; Mitani et al. 2018; Schultz et al. 2018; Kotlobay et al. 2019). The results presented here suggest that these compounds might have evolved independently in luminous syllids, but the evolutionary origins, as for most bioluminescent organisms, remain unclear. One of the most accepted evolutionary theories proposes that bioluminescence might have originated as a mechanism to reduce oxidative stress due to the strong antioxidative properties of luciferin and the high reactivity with reactive oxygen species (Rees et al. 1998; Devillers et al. 1999; Labas et al. 2001; Haddock et al. 2010). This might also apply to syllids, as oxygen levels in the ocean have seen strong fluctuations through evolutionary time (Baker et al. 2017; Dahl et al. 2019). Therefore, a ‘proto luciferin’ with antioxidative properties might have appeared in annelid lineages subjected to oxidative stress pressures, to cope with deleterious oxygen derivatives when ocean oxygen levels were high. This proto luciferin would have shifted from a detoxifying to a light-emitting function when exposure to oxidative stress was reduced, allowing syllids to harness luminescence for defence or mate attraction. Similar cases have previously been reported in other taxa, for example, luminous fungi produce luciferin from an antioxidant precursor called hispidin that is also found in non-luminous fungi (Oba et al. 2017), whereas the antioxidant properties of firefly luciferin suggest this might have evolved as a scavenger of toxic oxidants (Dubuisson et al. 2004). The *Odontosyllis* luciferin could also function as an antioxidant to protect gametes as this is found within the luminous mucus where gametes are released. The oxidative properties of the luciferin and increased viscosity of the mucus that limits gamete dilution provide a microenvironment that might facilitate successful fertilisation (Thomas 1994; Dehney and Latz 2009). Indeed, the luminous mucus appears to be ‘charged with oxygen’ and could protect gametes from chemical degradation or biological consumption from small grazers (Dehney and Latz 2009; Limatola et al. 2020). Although plausible, these hypotheses need to be further evaluated through evolutionary analysis with a time-calibrated and comprehensive phylogeny including a dense taxon sampling within Syllidae, and tests to identify trait-dependent shifts in diversification rates.

In conclusion, our results suggest that *Odontosyllis* is a paraphyletic group that needs to be taxonomically revised to accurately reflect evolutionary relationships when additional morphological and molecular data become available. Nevertheless, our analyses recover two well-supported clades of *Odontosyllis* that include bioluminescent species and provide evidence that the most recent common ancestor of luminous syllids did not have the ability to produce light, suggesting that bioluminescence evolved twice in the group. Coincidently, the Eusyllinae lineage that groups all bioluminescent species (i.e. *Pionosyllis, Eusyllinae* and *Odontosyllis*) including mostly species that use bioluminescence for mate attraction has higher species richness than the sister clade, providing support for the hypothesis that bioluminescent courtship behaviours might increase speciation rates (Ellis and Oakley 2016). Our results shed light on the evolutionary history of luminous syllids and suggest that bioluminescence might represent a key factor shaping the evolution.

**Supplementary material**

Supplementary material is available online.

**References**


Ellis EA, Oakley TH (2016) High rates of species accumulation in animals with bioluminescent courtship displays. Current Biology 26, 1–6. doi:10.1016/j.cub.2015.06.043


Data availability. The data presented in this study have been deposited in public databases. All relevant information and accession numbers can be found in the Supplementary material.

Conflicts of interest. The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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