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# Cladobranchia (Gastropoda, Nudibranchia) as a Promising Model to Understand the Molecular Evolution of Photosymbiosis in Animals

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Symbiosis with photoautotrophic organisms has evolved in various species and even whole animal lineages, which allowed them to directly benefit from photosynthesis. This so-called *photosymbiosis* is best studied in cnidarians, which primarily establish symbioses with dinoflagellates from the family Symbiodiniaceae. In most other animals the mechanisms of establishing photosymbiosis, the physiological basis, and the evolution of a photosymbiotic life history remain poorly understood. Sea slugs belonging to the Cladobranchia (Gastropoda, Nudibranchia) are no exception, and are a rather neglected animal lineage in the research field of photosymbiosis. Yet, studying these sea slugs holds great potential to establish a unique photosymbiosis model, as they are the only known taxon that has evolved two different strategies to acquire their symbiont: either from cnidarian prey (thus becoming a secondary host) or directly out of the water column. The mechanisms for photobiont uptake and maintenance are unknown for these sea slugs, but might be similar to those of cnidarians. However, in terms of the evolution of photosymbiosis, Cladobranchia seem to share many commonalities with more closely related sea slugs belonging to the Sacoglossa, which only maintain the chloroplasts of the algae they feed on. Hence, Cladobranchia have the potential to shed light on the evolution of photosymbiosis in taxonomically divergent animals that also harbor photobionts of different evolutionary lineages.

**Keywords: Nudibranchia, photosynthetic symbiosis, sea slugs, Symbiodiniaceae, symbiont recognition**

## INTRODUCTION

Symbiotic relationships shape genomic and morphological plasticity, which is a driving force of evolution within prokaryotes and eukaryotes (Margulis, 1981; Burki et al., 2020). Most common are symbioses between heterotrophic organisms, but some protists (Decelle, 2013; Decelle et al., 2015; Foster and Zehr, 2019) and a few animal lineages (Melo Clavijo et al., 2018) engage in symbioses with photoautotrophic organisms (photobionts) – the so-called *photosymbiosis* (Cowen, 1988; Stanley, 2006). Among animals, stony corals (Scleractinia) are probably the best-known example of a successful photosymbiosis. Corals primarily form a mutualistic symbiosis with dinoflagellates of the family Symbiodiniaceae (Fensome, 1993), that are referred to zooxanthellae when *in hospite*. Yet, more recently the mutualism of the photosymbiosis has been questioned and some authors refer to a host-controlled parasitism of the photobiont (Wooldridge, 2010; Blackstone and Golladay, 2018). Independent on the exact nature of the symbiosis, the photosymbiosis of corals and Symbiodiniaceae is based on an interdependent nutrient exchange cycle between the host and the photobiont (Stanley and Helmle, 2010; Tornabene et al., 2017). It has been shown that the coral host obtains nutritional support by the photobiont in the form of sugars, amino acids and some other essential nutrients, sometimes even superseding its nutritional requirements, allowing the coral host to thrive in oligotrophic waters (Muscatine and Porter, 1977; Falkowski et al., 1984; Lin et al., 2015) and enhances their ability to form skeletons and build up the coral reef structure (Stanley and Lipps, 2011; Tambutté et al., 2011; Roth, 2014). In return, the coral host provides carbon dioxide and ammonium, which are key limiting compounds for the photobiont (e.g., Yellowlees et al., 2008). The coordination of this nutrient exchange cycle is complex. Its disruption, for instance caused by heat stress, can lead to the breakdown of the symbiosis and can result in the expulsion of the photobionts. This process is known as bleaching and often eventually results in the coral's death leading in extreme cases to mass bleaching events, as seen in recent years, that are endangering entire reef communities across the globe (Suggett and Smith, 2020).

Aside from Scleractinia, photosymbiosis in metazoans is not well understood (Melo Clavijo et al., 2018). Considering its potential benefit for the heterotrophic host, it remains unclear why the symbiosis with a photobiont has evolved only in a few metazoan lineages. It is likely that photosymbiotic animals share components of a common genetic tool kit, which are essential for the initiation and maintenance of a photosymbiosis. This set of genes probably includes a large fraction related to the innate immune system (Gross et al., 2009; Davy et al., 2012; Mansfield and Gilmore, 2019), which is also highly relevant for other animal-microbe symbioses (e.g., McFall-Ngai et al., 2012; Schmittmann et al., 2021). Genomic data could help to understand these molecular mechanisms, but are still scarce for most photosymbiotic animal lineages (Melo Clavijo et al., 2018). Fortunately, genome-sequencing initiatives such as the recently launched Aquatic Symbiosis Genomics Project by the Welcome Sanger Institute and the Gordon and Betty Moore Foundation are addressing this lack of genomic data. Among others, this initative focuses on key photosymbiotic species in different lineages, which will provide a wealth of data and hence enable us to boost our understanding of photosymbioses. However, the acquisition of genomes of non-photosymbiotic congeners will be eminent to identify relevant genomic adaptations promoting photosymbiosis. Analyzing and comparing photosymbiotic and non-photosymbiotic animals within and between different lineages will have the potential to unravel their common genomic adaptations for photobiont recognition and maintenance. Such comparisons also hold the key to clarify at which point in the evolutionary history the animal host acquired distinct adaptations needed for photosymbiosis and if these adaptations evolved convergently or homologously.

We propose that a specific group of sea slugs, the Cladobranchia that belong to the Nudibranchia, should be studied in more detail. This lineage could considerably contribute to our understanding of photosymbiotic processes and the evolution of photosymbiosis in distantly related animals.

## "Butterflies of the Sea"

Nudibranchia are a morphologically diverse and colorful group of non-shelled sea slugs, belonging to the Heterobranchia (Burmeister, 1837) and consisting of the suborder Doridina and the suborder Cladobranchia. Over 4,000 nudibranch species have been described and, due to their colorful appearance, they fascinate scientists and non-scientists alike and are often called "butterflies of the sea" (Anderson, 1995). Current research on Nudibranchia focuses on assessing their biodiversity (e.g., Eisenbarth et al., 2018; Fritts-Penniman et al., 2020; Korshunova et al., 2021), their developmental biology and life cycle (Page, 1993; Kristof and Klussmann-Kolb, 2010; Ahmadian et al., 2016; Togawa et al., 2019), and phylogenetic relationships within the different groups (e.g., Carmona et al., 2013; Goodheart et al., 2015a,b; Karmeinski et al., 2021 Korshunova et al., 2021). Furthermore, because most Nudibranchia lost their protective shell, alternative defense strategies, such as mimicry of food sources (Gosliner and Behrens, 1990), calcareous needles (Cattaneo-Vietti et al., 1995), the synthesis of toxic metabolites (Bogdanov et al., 2017), and storing and using cnidocysts "stolen" from their cnidarian food source (Obermann et al., 2012; Goodheart et al., 2018) are investigated. Especially the potential pharmaceutical relevance of their secondary metabolites (reviewed by Cimino and Gavagnin, 2006; Putz et al., 2010; Fisch et al., 2017) makes them an interesting group for researchers. Photosymbiosis is only found in the Cladobranchia that comprise approximately 1,000 species and that can be identified by the lack of gills and their large dorsal appendices, the cerata, that also function as respiratory organ. However, photosymbiosis in Cladobranchia is not well understood.

## Cladobranchia Evolved Different Strategies of Photobiont Acquisition

Like most photosymbiotic animals, Cladobranchia acquire their photobionts anew in each generation (i.e., horizontally, instead of vertically from their parents), which is the most common mechanism of photobiont acquisition in animals (reviewed in Melo Clavijo et al., 2018). However, only Cladobranchia evolved two different modes of horizontal photobiont acquisition – out of the water column or from photosymbiotic cnidarians (**Figure 1**). Within the Cladobranchia, members of the Dendronotoidea (Allmann, 1845), such as *Melibe engeli* Risbec, 1937 (**Figure 1**), experienced morphological modifications that resulted in a fan-like mouth opening (Gosliner, 1987), allowing them to effectively ingest the photobionts out of the water column

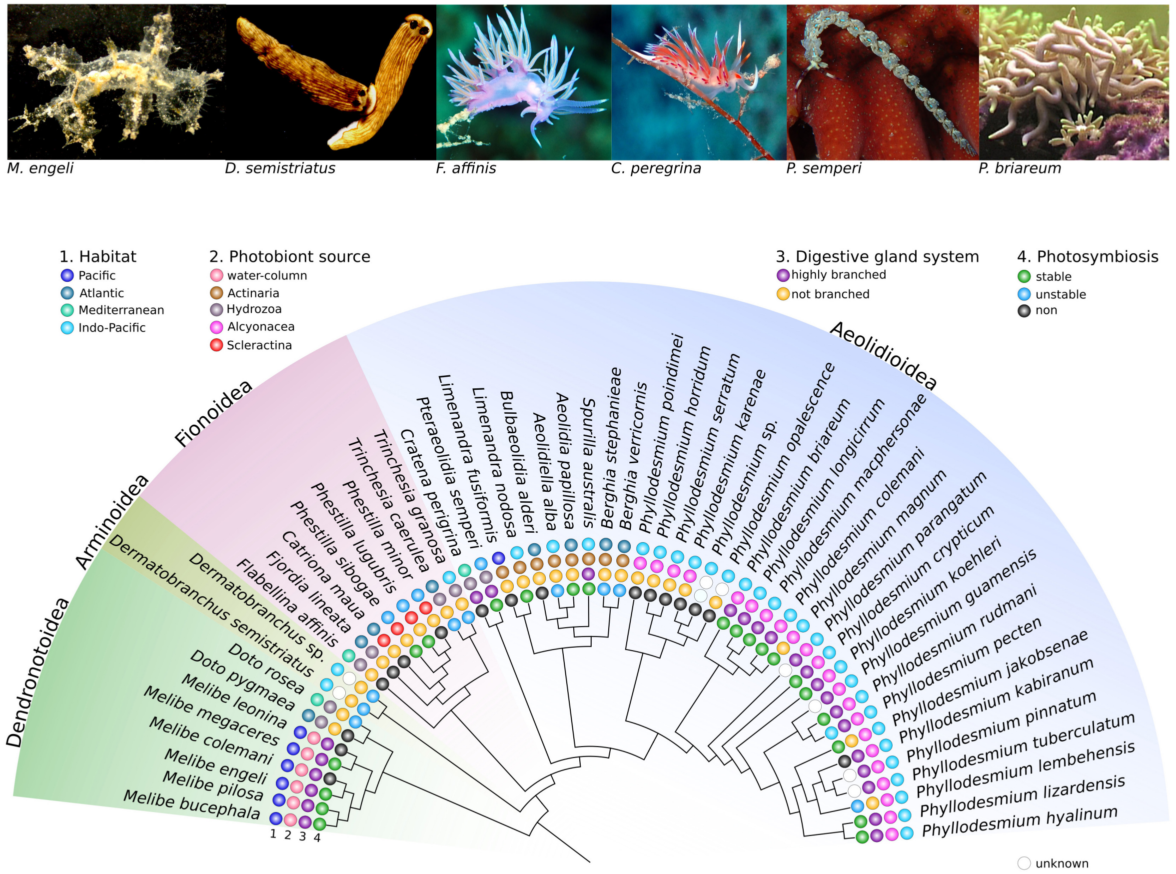

**FIGURE 1 |** Cladogram of selected Cladobranchia species showing different levels of photosymbiosis. Members of Cladobranchia are widespread distributed (1. Habitat) and acquire their photobiont horizontally either from the water column or by feeding on photosymbiotic cnidarians (2. Photobiont source). Different degree of ramification of the digestive gland system is present in Cladobranchia (3. Digestive gland system) that might be correlated to the stability of the photosymbiosis (4. Photosymbiosis). The cladogramm and the respective information are based on published data (Wägele and Willan, 2000; Johnson and Gosliner, 2012; Moore and Gosliner, 2014; Goodheart et al., 2018; Karmeinski et al., 2021). The images were taken by Heike Waegele (*Melibe engeli, Dermatobranchus semistriatus)*, Daniela Kupschus (*Flabellina affinis*, *Cratena peregrina*, *Pteraeolidia ianthina*), and Sabrina Bleidissel (*Phyllodesmium briareum*).

(Bleidissel, 2010; Burghardt and Wägele, 2014). To the best of our knowledge, adults of the genus *Melibe* are the only sea slugs to obtain their photobionts this way. The vast majority of Cladobranchia, however, acquire the photobionts by feeding on cnidarian prey and "stealing" the cnidarians' photobionts (Rudman, 1981; Kempf, 1984; Wägele, 2004). This is a unique photobiont acquisition strategy in animals that evolved in Cladobranchia probably multiple times in the superfamilies Arminoidea, Iredale and O'Donoghue (1923), Fionoidea Gray (1827), and Aeolidioidea Gray (1827) (**Figure 1**).

## Not All Cladobranchia Can Maintain Photobionts

Subsequent to the uptake, Cladobranchia selectively phagocytize the photobionts into epithelial cells of their digestive gland system (DGS). The DGS branches throughout the entire body and, particularly, into the cerata (**Figures 2A,B**). Once the algae are phagocytized in the epithelial cells, they remain in their coccoid state and are surrounded by the phagosomal membrane (**Figures 2C,D**; Wägele and Johnsen, 2001; Wakefield and Kempf, 2001). In most cladobranchs, like *Flabellina affinis* (Gmelin, 1791) or *Cratena peregrina* (Gmelin, 1791) (**Figure 1**), the algae are then rapidly digested, while some species, like *Berghia stephanieae* (Valdés, 2005) (**Figure 2A**) are capable to maintain the algae photosynthetically active for a few days (Monteiro et al., 2019). Regarding the organismic interaction that we describe in this review we refer to the general symbiotic terminology. Within that terminology, the existing subcategories of photosymbiosis are defined based on the beneficial aspects and the time-span of interaction, following the definitions by Kempf (1991). Based on this, maintaining the photobiont for a short term is here referred to an unstable photosymbiosis, because the algae reside intracellularly, but the slugs, like *B. stephanieae*, tend to digest the algae within a couple of days, or expel them from the cells and secrete them in a viable state in the feces. Species that have evolved an unstable photosymbiosis do not appear to benefit from the photosynthesis performed by the acquired photobionts. They are neither able to maintain their symbionts nor their biomass when solely relying on the photobiont as

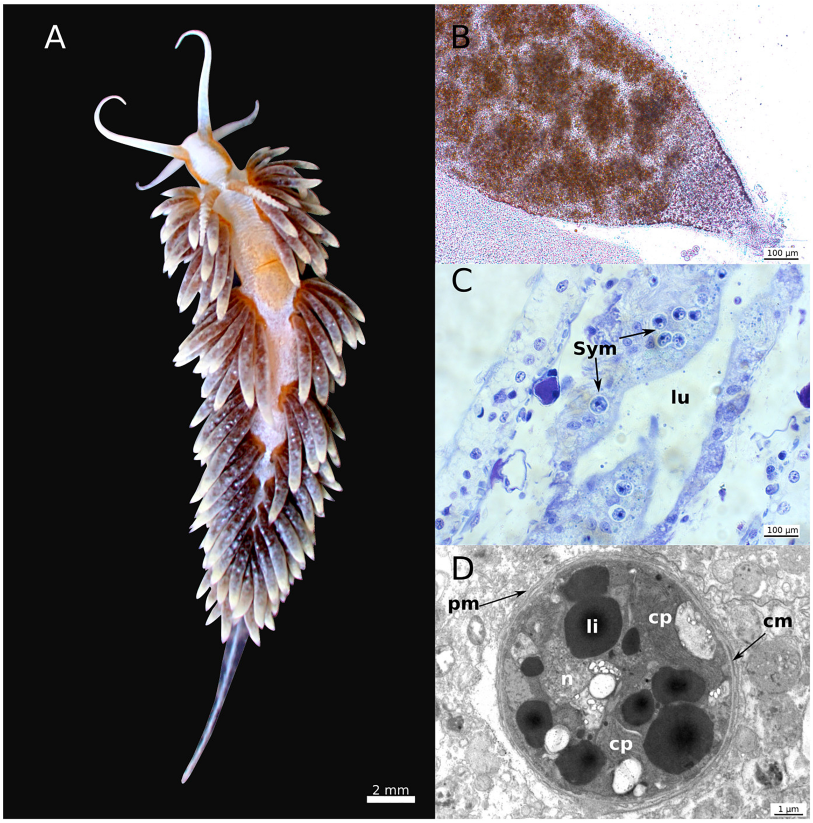

**FIGURE 2 |** Morphology and microscopic details of *Berghia stephanieae*. Morphology of *B. stephanieae* **(A)**. Detail of a cerata of *B. stephanieae* bearing the photobionts **(B)**, histological cross-section through a cerata showing the host cells of the cerata bearing the photobiont **(C)**, and detail of the coccoid (non-motile) stage of intracellular Symbiodiniaceae **(D)**. cm: Symbiodiniaceae cell membrane, cp: chloroplast, li: lipid droplets, lu: lumen of the host digestive gland, n: nucleus, pm: host phagosomal membrane, Sym: Symbiodiniaceae. The images were taken by Gregor Christa **(A,B)**, Jenny Melo **(C)** and Elise Laetz **(D)**.

source of nutrition (Kempf, 1991; McFarland and Muller-Parker, 1993; Bleidissel, 2010; Monteiro et al., 2019). Yet, some taxa have evolved the ability to establish a stable photosymbiosis, maintaining the photobionts for months. For a couple of these photosymbiotic species, like *Melibe engeli* and *Phyllodesmium briareum* (Bergh, 1896), it has been shown that the photobiont can fully support the host, enhancing growth and the ability of long-term reproduction without a reduction in the quantity and quality of egg-masses under regular light conditions (Kempf, 1984; Burghardt and Wägele, 2004, 2006, 2014; Burghardt et al., 2005, 2008a,b; Burghardt and Gosliner, 2006). These observations support the idea that at least these Cladobranchia species and Symbiodiniaceae are involved in a mutualistic symbiosis, which is unique in gastropods. More closely related Sacoglossa sea slugs, that are in a sort of photosymbiosis with chloroplasts of their algal prey, are not able to grow, or even maintain their biomass, if they are exclusively dependent on their ingested chloroplasts for more than a couple of weeks (Pelletreau et al., 2012; Christa et al., 2014). Further, they are not able to maintain the quantity and quality of egg-masses during periods of food depletion (Cartaxana et al., 2019). Hence, Cladobranchia provide a unique opportunity to understand which genomic adaptations are needed to evolve a mutualistic photosymbiosis in sea slugs. Comparative analyses of photosymbiotic and non-photosymbiotic Cladobranchia with Sacoglossa and Cnidaria might uncover if these genomic adaptations are based on convergent evolution or if, for instance, epigenetic modifications are involved in activating specific genes in photosymbiotic slugs.

## Mechanisms for Photobiont Recognition and Maintenance Are Unknown in Cladobranchia

The selective incorporation of photobionts in Cladobranchia is a complex process. It remains unknown how the slugs are able to distinguish between photobionts and plankton and further digest all plankton (e.g., in *Melibe*) or tissues of the cnidarian prey while maintaining the photobionts intact. The mechanisms of photobiont recognition by the epithelial cells of the DGS have not yet been addressed, while in cnidarians the photobiont recognition is based on a set of animal host pattern recognition receptors (PRRs). Specific microbe associated molecular patterns (MAMPs) of the photobiont (Neubauer et al., 2016, 2017; Mansfield and Gilmore, 2019) bind to the PRRs, which triggers downstream signaling cascades to maintain the photobiont (Davy et al., 2012). The PRRs of Cladobranchia might be similar to those of their cnidarian host, as they incorporate the same photobiont and hence need to recognize the same MAMPs. However, Cladobranchia could also just use different PRRs to recognize other MAMPs to identify the equivalent photobiont. The incorporation process might even be more similar to the selective uptake of chloroplasts by more closely related members of sea slugs belonging to the Sacoglossa (Chan et al., 2018; Melo Clavijo et al., 2020). Using phylogenetic and domain specific analyses of the respective receptors will help to understand if the relationship of the respective PRRs is matching the taxonomy of the host. In combination with subsequent functional analyses, for instance by gene expression and manipulation, a list of candidate genes can be generated that could be involved in photobiont recognition. Therefore, Cladobranchia are the only animals that could permit a direct comparison of photobiont recognition mechanisms, in particular PRRs, between a primary (Cnidaria) and secondary (Cladobranchia) host of the same photobiont. At the same time, Cladobranchia allow comparisons with mechanisms of chloroplast recognition in the more closely related Sacoglossa. These analyses may provide insights into the relevance of PRRs in photosymbiosis across taxonomically divergent animal taxa. Furthermore, they may elucidate how conserved the signaling pathways for initiating photosymbiosis are – independent from the taxonomic lineage of the photobiont.

## Evolution of Stable Photosymbiosis in Cladobranchia

The evolution of a stable photosymbiosis in Cladobranchia is still not well understood. It appears that photosymbiosis evolved several times independently in different Cladobranchia superfamilies (**Figure 1**). For instance, it might have evolved independently in the Dendronotoidea and a monophyletic group including Arminoidea, Fionoidea, and Aeolidioidea. This would explain the evolution of the two different acquisition modes. Alternatively, photosymbiosis could also have evolved in each of the superfamilies independently. It is furthermore unknown whether unstable and stable photosymbiosis evolved separately, or if stable photosymbiosis evolved from unstable photosymbiosis.

Commonly, photosymbiotic Cladobranchia have a highly branched digestive gland system and specialized digestive structures, such as large circular chambers, fine tubules and cisternae that are located at the tips and harbor the photobionts (Burghardt and Wägele, 2014). These structures are considered to enlarge colonizable space and optimize light attenuation, increasing photobiont density and photosynthesis, respectively (Rudman, 1991; Burghardt et al., 2008a,b; Moore and Gosliner, 2011). Yet, despite of having a highly branched digestive gland system, species of *Phestilla* or *Limenandra* (**Figure 1**), and species like *Melibe leonina* (Gould, 1852) or *Phyllodesmium kabiranum* Baba, 1991, are non-photosymbiotic (**Figure 1**). Aside of this exception the genus *Phyllodesmium* shows a correlation between photosymbiosis and a highly branched digestive gland system (Rudman, 1991; Burghardt et al., 2008a,b; Moore and Gosliner, 2011). A highly branched DGS might not be a prerequisite to evolve a stable photosymbiosis, but it appears to be advantageous to harbor larger numbers of photobionts and to optimize photosynthesis.

The cnidarian prey is considered important for the stability of the photosymbiosis in Cladobranchia (Wägele et al., 2010). For instance, members of the genus *Phyllodesmium*, in which most species have a stable photosymbiosis, feed exclusively on xeneid cnidarians belonging to the Alcyonacea. However, *Pteraeolidia semperi* (Bergh, 1970), also in a stable photosymbiosis, obtains the photobionts from Hydrozoa, so that the food source is not strictly connected to photosymbiosis (**Figure 1**). Instead, it seems to be based on obtaining specific secondary metabolites for defense purposes (Bogdanov et al., 2017) and the feeding preference is rather taxon-specific. Independent of the source of the photobiont, the efficiency of the photosymbiosis may be further influenced by the specific algal taxon. For instance, in other stable photosymbiotic systems, such as Cnidaria-Symbiodiniaceae and Bivalvia-Symbiodiniaceae associations, the animal hosts could benefit from more physiologically resilient photobionts during increased ambient temperature (Hume et al., 2016; Cziesielski et al., 2018; Mies, 2019; Cunning and Baker, 2020). When corals are in symbiosis with multiple symbiodiniacean genera, the active removal of less resilient strains results in an adaptive bleaching, which might increase the animal's fitness and improve the stability of the symbiosis considerably (Ziegler et al., 2014; Bayliss et al., 2019; Chen et al., 2019). So far, only a few studies have investigated the diversity and composition of Symbiodiniaceae in Cladobranchia (Loh et al., 2006; FitzPatrick et al., 2012; Ziegler et al., 2014; Wecker et al., 2015; Yorifuji et al., 2015). Nevertheless, these studies have not uncovered any correlation between specific Symbiodiniaceae taxa and the ability to establish a photosymbiosis with Nudibranchia. It rather seems that symbionts are taken up from the cnidarian prey indiscriminately. Future analyses of photobiont abundance in cladobranchs in comparison to their cnidarian prey will help to understand if the slugs are able to distinguish between Symbiodiniaceae taxa and selectively expel less beneficial photobionts. Comparative metabarcoding analyses, as available for some cnidarians and their Symbiodiniaceae composition (Fujise et al., 2021), is still lacking for sea slugs, but are needed to reveal the relevance for a stable photosymbiosis in Cladobranchia. It might be further worth to investigate, if the slugs play a role in genotype dispersion of symbiodiniaceans in marine habitats. The fact that symbionts are transferred from a sessile to a motile host could potentially enhance the dispersion of symbiodiniaceans and could change the composition of clades and strains in environmental populations (Parker, 1984). This could be beneficial for other sessile photosymbiotic animals and their symbiont uptake, facing environmental changes with different adapted symbionts (Umeki et al., 2020).

Regardless of the stability of the photosymbiosis, little is known on how nutrients are exchanged between the slugs and the algae. The phagosomal membrane surrounding photobionts in cnidarians is known as symbiosome (Hill and Hill, 2012). The symbiosome plays a crucial role in the successful establishment of the symbiosis. Transporters relevant for nutrient exchange, i.e., sugars from the algae to the animal and dissolved inorganic compounds from the animal to the algae, are situated in the symbiosomal membrane (Sproles et al., 2018). In cladobranchs it is unknown if and which transporters are present on the phagosomal membrane and how comparable it is to the symbiosome in terms of functionality. Future immuno-histochemical studies could give valuable insights into the localization of photosymbiosis-relevant receptors and their role in the nutritional exchange between the two partners, while metabolomics could provide important information on the interdependent nutrient exchange between both partners. Further, it remains to be shown whether in species with a stable photosymbiosis the symbiosis is beneficial for the host and whether the symbiosis is mutualistic or even some sort of parasitism as proposed for other photosymbiotic animals by some authors (Lesser et al., 2013; Blackstone and Golladay, 2018; Androuin et al., 2020).

## CLADOBRANCHIA CAN SHED LIGHT ON PHOTOSYMBIOSIS

Cladobranchia are a promising model to deepen the knowledge on fundamental processes that lead towards the evolution of photosymbiosis in animals as they resemble a connecting link between the well studied photosymbiosis in cnidarians and the less understood animal lineages such as sea slugs. Future research combining genomics, metabolomics, physiological, and immuno-histochemical studies, as well as phylogenetic analyzes of key receptors or proteins involved in photosymbiosis, will highlight if photosymbiosis evolved convergently or homologously in the different animal lineages.

## AUTHOR CONTRIBUTIONS

MR, JM, and GC designed the figures. All authors searched and analyzed the literature, wrote the draft, and reviewed and accepted the final version of the manuscript.

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