Polymorphic adaptations in metazoans to establish and maintain photosymbioses

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ABSTRACT

Mutualistic symbioses are common throughout the animal kingdom. Rather unusual is a form of symbiosis, photosymbiosis, where animals are symbiotic with photoautotrophic organisms. Photosymbiosis is found among sponges, cnidarians, flatworms, molluscs, ascidians and even some amphibians. Generally the animal host harbours a phototrophic partner, usually a cyanobacteria or a unicellular alga. An exception to this rule is found in some sea slugs, which only retain the chloroplasts of the algal food source and maintain them photosynthetically active in their own cytosol – a phenomenon called ‘functional kleptoplasty’. Research has focused largely on the biodiversity of photosymbiotic species across a range of taxa. However, many questions with regard to the evolution of the ability to establish and maintain a photosymbiosis are still unanswered. To date, attempts to understand genome adaptations which could potentially lead to the evolution of photosymbioses have only been performed in cnidarians. This knowledge gap for other systems is mainly due to a lack of genetic information, both for non-symbiotic and symbiotic species. Considering non-photosymbiotic species is, however, important to understand the factors that make symbiotic species so unique. Herein we provide an overview of the diversity of photosymbioses across the animal kingdom and discuss potential scenarios for the evolution of this association in different lineages. We stress that the evolution of photosymbiosis is probably based on genome adaptations, which (i) lead to recognition of the symbiont to establish the symbiosis, and (ii) are needed to maintain the symbiosis. We hope to stimulate research involving sequencing the genomes of various key taxa to increase the genomic resources needed to understand the most fundamental question: how have animals evolved the ability to establish and maintain a photosymbiosis?

Key words: evolutionary genomics, biodiversity, photosynthesis, photosymbiosis, kleptoplasty.

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Evolution of photosymbiosis

I. INTRODUCTION

In 1878, Heinrich Anton de Bary defined symbiosis as a long-term relationship between organisms from different species (de Bary, 1878). It is found among all domains of life and classified as either mutualistic (both partners benefit), commensalistic (just one partner benefits, but without harming the other), or parasitic (one partner is negatively affected by the other) (Decelle, Colin & Foster, 2015). A particular form of symbiosis is endosymbiosis, in which one symbiotic partner lives within the other (Sagan, 1967; Kutscher & Niklas, 2005). A special form of mutualistic symbiosis is photosymbiosis (Cowen, 1988). This term is used when a heterotrophic organism acquires the benefits of photosynthesis by establishing an extra- or intracellular mutualistic symbiosis with a phototrophic organism (Buchner, 1921; Yonge, 1934; Cowen, 1988). Perhaps surprisingly, photosymbioses in animals are widespread across multiple phyla including sponges, cnidarians, acoelomorphs, platyhelminths, molluscs, ascidians, and even some vertebrates (Yonge, 1934; Venn, Loram & Douglas, 2008; Rumpho, Summer & Manhart, 2000). The vast majority of photosymbiotic animals inhabit marine environments, with the notable exception of few freshwater species (see online Supporting Information, Table S1) (e.g. Jensen & Pedersen, 1994; Huss, 1999; McCoy & Balzer, 2001). Generally, the phototrophic symbionts are either oxygenic photosynthetic bacteria, cyanobacteria, or unicellular algae (Trench, 1987; Venn et al., 2008; Kirk & Weis, 2016). A functionally unique system of acquiring the benefits of photosynthesis in animals is found among members of sacoglossan sea slugs. These marine gastropods are able to ‘steal’ and retain only the chloroplasts of their food algae: these are referred to as kleptoplasts (‘stolen plastids’) (Rumpho et al., 2011). In some species, the kleptoplasts remain photosynthetically active even during times of starvation (Wägele et al., 2011; Rumpho et al., 2011; Christa et al., 2015). This is referred to as functional kleptoplasy (Waugh & Clark, 1986), for which the term photosymbiosis is not entirely accurate, because the endosymbiosis only involves a non-reproducing organelle. However, the kleptoplasts may (perhaps transiently) benefit from their intracellular presence in the animal host due to enriched availability of carbon dioxide (Serôdio et al., 2014). In metazoans, functional kleptoplasy is taxonomically restricted to Sacoglossa, but it is also found in some protists, including Ciliates and Foraminifera (Pilet, de Vargas & Pawlowski, 2011; Pillet & Pawlowski, 2012; Not et al., 2016).

The mechanisms involved in the recognition and incorporation of a symbiont by the animal host are now under intensive investigation. The symbionts are either taken up from the environment (horizontal transmission) or they are passed from parent to offspring (vertical transmission) during reproduction (Muller-Parker, D’elia & Cook, 2015). Inside the animal host, the symbionts may enter a ‘vegetative cyst’ phase where the cell cycle is arrested and the symbionts are potentially under host control. For example, the dinoflagellate Symbiodinium is only found in non-motile forms inside hosts (Koike et al., 2004; Stambler, 2011) in which they are surrounded by a membrane, called a symbysome in corals (Stambler, 2011) or perialgal vacuole in Hydra (McNeil, 1981). These symbiont compartments are important to guarantee the regulation of molecular exchanges and of the symbiotic environment (Blackall, Wilson & Oppen, 2015). Whether kleptoplasts reside in such a membrane is still under debate (Rumpho, Summer & Manhart, 2000; Muniaín, Marin & Penchasazadeh, 2001; Hirose, 2005; Martin, Walther & Tomashko, 2013, 2015). The host shelters the symbiont or the kleptoplasts against predators and environmental fluctuations, and supplies sufficient inorganic compounds, such as CO₂, for photosynthesis (Pearse & Muscatine, 1971; Stat, Carter & Hoegh-Guldberg, 2006; Yellowlees, Rees & Leggat, 2008), although CO₂ limitation in the host can occur (Radecker et al., 2017). In turn, the host receives photosynthates, mainly in the form of fixed carbon, which can meet at least 50% of their overall nutritional requirements (Fitt, Fisher & Trench, 1986; Klump & Griffiths, 1994; Stat et al., 2006; Hernawan, 2008; Stanley & Lipps, 2011). In comparison, kleptoplasts are probably only able to supply their host slugs with between 1% (Rauch et al., 2017) and 60% (Raven et al., 2001) of their nutritional requirements. The discrepancy between the latter two values presumably arises from methodological differences, emphasising the need for further studies to unravel the true extent of nutritional support provided by kleptoplasts.

Extensive studies have been carried out on the biodiversity and physiology of symbionts and their hosts. However, the evolution of photosymbiosis is comparatively less well understood. Recent advances in next-generation-sequencing techniques now allow us to analyse these symbionts and hosts from an evolutionary genomics perspective. While many recent studies have focused on the transcriptomic and genomic properties of the symbiont, only a few have begun to examine the host. Comparative analyses involving multiple photosymbiotic and non-photosymbiotic animal lineages are important to answer the most fundamental question: what genomic adaptations have enabled the evolution of photosymbiosis in animals?
II. BIODIVERSITY OF PHOTOSYMBIOSIS IN ANIMALS

(1) Photosymbioses in Porifera

The photosymbiotic relationship of marine sponges is regarded as a driving force for the establishment of reefs over a wide geological timescale (Lipps & Stanley, 2016a). Sponges are probably the most diverse group in terms of number of photosymbiotic species and the variety of symbionts (Fig. 1). For example, in some temperate and tropical regions more than 60% of sponge species were found to harbour photosymbionts from multiple different lineages (Steindler, Beer & I’lan, 2002; Lemloh et al., 2009). Photosymbiosis is found in four Porifera classes: Demospongiae, Hexactinellida, Homoscleromorpha, and Calcarea (Diaz & Ward, 1999; Diaz et al., 2007; Fromont et al., 2016). While most species generally establish photosymbiosis with cyanobacteria (Fig. 1; Usher, 2008; Adams, Duggan & Jackson, 2012; Thacker & Freeman, 2012), demospongan sponges might also harbour green non-sulfur bacteria of the genus Chloroflexi (Rodríguez et al., 2011; Webster & Taylor, 2012), members of the Clionaidae are symbiotic with the dinoflagellate Symsagittifera roscoffensis (Kovacevic, 2012) or dinoflagellates (Muller-Parker, 1990; Carey et al., 2011). This uncertainty arises because of issues with culturing and the lack of proper morphological identification of the algae. The convolutids and other members are photosymbiotic with as yet undescribed algae (Ax, 1970). Shannon & Achatz, 2007). This uncertainty arises because of issues with culturing and the lack of proper morphological identification of the algae. The convolutids Symagnostifera roscoffensis and Convolutriloba longissima harbour the chlorophyte Tetraselmis convolutae (Bartolomaeus, 1997; Seródio et al., 2011), while Amphicolasopsis sp., A. langerhansi, Waminoa litus, and W. brickneri can harbour the dinoflagellates Symbiodinium and/or Amphidinium kelyhii (Taylor, 1971; Lopes & Silveira, 1994; Barneah et al., 2007; Hikosaka-Katayama et al., 2012). Convoluta convoluta harbours the diatom Licomorpha sp. (Fig. 1; Ax & Apelt, 1963; Apelt, 1969).

Photosymbiosis is also found in freshwater platyhelminths belonging to the Rhabdocoela, but this is probably the least-understood system. Here, particular members of the Provorticidae, Dalyeliidae, and Typhloplanidae are symbiotic. Members of the genus Pogaina of the Provorticidae, e.g. Pogaina kinnei, feed on diatoms and presumably retain them as symbionts (Ax, 1970). Dalyelidia viridis (Dalyelidiidae), Tylophlana viridata and Phaeocora typhlops (both Typhloplanidae) live symbiotically with the chlorophyte Chlorella sp. (Eaton & Young, 1975; Douglas, 1987). Various other members are photosymbiotic with as yet undescribed algae (Ax, 1970; Armonies, 1989; McCoy & Balzer, 2001).

(2) Photosymbioses in Cnidaria

Together with sponges, corals are the main contributors in establishing reefs (Stanley & Lipps, 2011; Lipps & Stanley, 2016b) and the diversity of species that harbour photosymbionts is comparable between these two taxa. Yet, cnidarians are either photosymbiotic with chlorophytes (Kovacevic, 2012) or dinoflagellates (Muller-Parker et al., 2015); in rare cases even with both (Fig. 1; Verde & McCloskey, 1996). Their photosymbiosis with Symbiodinium is thought to underlie the ability of corals to form massive reefs: more than 95% of the energy required is provided by the symbiont’s photosynthetic activity (Muscatine, Pool & Trench, 1975; Stat et al., 2006; Hariri, Yamamoto & Hoehl-Guldberg, 2010; Stanley & Lipps, 2011). This energetic boost provides the needed energy for light-enhanced calcification (Goreau, 1959; Muscatine et al., 1975; Roth, 2014). In particular tropical and temperate members of Anthozoa, Hexacorallia and Octocorallia harbour photosymbionts, while the sister group to Hexacorallia, the Ceriantharia, are photosymbiont-free (Rodriguez et al., 2014; Stampar, Morandini & Da Silveira, 2014). Sister to Anthozoa is the clade Medusozoa which includes Hydrozoa, Scyphozoa, Staurozoa and Cubozoa. While the latter two taxa are not reported to be symbiotic, some members of the Scyphozoa, the upside-down jellyfish of the genus Cassiopea, harbour Symbiodinium (Thornhill et al., 2006; Lampert, 2016). In Hydrozoa, the situation is more complex: the H. viridissima group (also referred to as green Hydra), the H. vulgaris group and the H. oligactis group are symbiotic with chlorophyte algae of the genus Chlorella or Chlorococcum (Matthias, Frederike & Thomas, 2003; Bosch, 2012; Kawaida et al., 2013), but only in H. viridissima is the symbiosis stable (Kawaida et al., 2013; Ishikawa et al., 2015). The H. braueri group, however, is completely symbiont-free (Kovacevic, 2012).

(3) Photosymbioses in basal bilaterians

Acoelomorphs are particularly abundant in marine and brackish water habitats but are rather poorly investigated with regard to photosymbiosis (McCoy & Balzer, 2001). All photosymbiotic members belong to the Convolutidae of the ‘Acoelomorpha’ (Paps, Baguñà & Riutort, 2009). The ‘Acoelomorpha’ were previously assigned to Platychelminthes but recent phylogenetic studies indicate a paraphyletic nature, and place the Acoela as the sister group to all bilaterians (Hejnol et al., 2009; Mwinyi et al., 2010; Philippe et al., 2011). The nature of the symbionts of Acoela is poorly understood. In some taxonomic reports the symbiont is simply described as zoochlorella or zooxanthellla (Fig. 1; Ax, 1970; Shannon & Achatz, 2007). This uncertainty arises because of issues with culturing and the lack of proper morphological identification of the algae. The convolutid Symagnostifera roscoffensis and Convolutriloba longissima harbour the chlorophyte Tetraselmis convolutae (Bartolomaeus, 1997; Seródio et al., 2011), while Amphicolasopsis sp., A. langerhansi, Waminoa litus, and W. brickneri can harbour the dinoflagellates Symbiodinium and/or Amphidinium kelyhii (Taylor, 1971; Lopes & Silveira, 1994; Barneah et al., 2007; Hikosaka-Katayama et al., 2012). Convoluta convoluta harbours the diatom Licomorpha sp. (Fig. 1; Ax & Apelt, 1963; Apelt, 1969).

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(4) Photosymbioses in molluscs

In Mollusca, photosymbiosis is taxonomically restricted to some bivalves and gastropods. Tropical marine bivalves from the family Cardiidae host the dinoflagellate Symbiodinium (Ohno, Katoh & Yamasu, 1995; Maruyama et al., 1998; Hernawan, 2008). This bivalve family encompasses large
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Fig. 1. Sankey diagram of animal taxa that are photosymbiotic and their respective symbiotic partner. Most animal lineages establish a symbiosis with dinoflagellates or with chlorophytes, but may also with cyanobacteria or even, in rare cases, diatoms. Diatoms are, however, reported to be parasitic in arctic sponges. Some members of Porifera might also be symbiotic with green-sulfur bacteria or red algae, but as this is only known from a few taxa, they are not included in the figure. Some members of the sacoglossan sea slugs only incorporate chloroplasts, which are then referred to as kleptoplasts.

species that can reach up to 1 m in diameter, like Tridacna, and are occasionally referred to as giant clams (Vermeij, 2013). Their exceptionally large sizes are thought to result from the establishment of symbioses (Griffiths & Klumpp, 1996) often with several clades of Symbiodinium (Bailleul, Belela-Baillie & Maruyama, 2000; DeBoer et al., 2012; Ikeda et al., 2017). The major characteristic of cardiids is an enlarged and colourful mantle, in which Symbiodinium is hosted in extracellular spaces (Hernawan, 2008). This is different from other photosymbiotic systems, in which the symbiont resides intracellularly (Wakefield & Kempf, 2001). Besides Tridacincae (Hirose, 2005), photosymbiosis in the Cardiidae is also found in members of the Fraginaceae (Farmer, Fitt & Trench, 2001), but is lacking in the Laevicardiidae and Trachycardiidae (Maruyama et al., 1998). The only known photosymbiotic freshwater bivalve belongs to the genus Anodonta and hosts the chlorophyte Chlorella (Goetsch & Scheuring, 1926; Pardy, 1980). In contrast to the photosymbiotic Cardiidae, the symbionts in Anodonta reside in the gills and mantle (Pardy, 1980).

In gastropods photosymbiosis is found in various genera. The ceanogastropod Strombus gigas hosts Symbiodinium (Banaszak, Ramos & Goulet, 2013). The snails acquire the symbiont during the larval stage (Garcia-Ramos & Banaszak, 2007) and the symbiosis only appears to be mutualistic at this stage. In adults it takes a parasitic form: the snails provide nutrition to their symbiont because the presence of a shell reduces the possibility of photosynthesis (Banaszak et al., 2013). This is the only known member of the Caenogastropoda reported to be photosymbiotic (Garcia-Ramos & Banaszak, 2007).

Among heterobranch sea slugs (Gastropoda) two very different systems of photosynthetic symbiosis have been described. (i) Some members of the Nudibranchia acquire symbionts by feeding on photosymbiotic cnidarians and subsequently embed the symbiotic algae (Symbiodinium) in their own cytosol (Burghardt et al., 2005; Burghardt, Stemmer & Wägele, 2008). Several different taxa are able to carry Symbiodinium: Melibe engeli (Dendronotida) harbours a dinoflagellate acquired from an unknown source (Burghardt et al., 2008); members of the Aeolidiida, e.g., Berghia stephanoeae and Sparilla neapolitana, ingest Symbiodinium after feeding on Anthozoa (Carroll & Kempf, 1990; Schlesinger et al., 2009; Dionísio et al., 2013); and the fricellinididean Phylloidesmium briaeum obtains its symbionts from feeding on the soft coral Briareum violaceum (Burghardt et al., 2008). (ii) Members of the Sacoglossa remove the cell contents of their macroalgal food and specifically sequester the chloroplasts, which are then
called kleptoplasts (Fig. 1), in cells of their digestive system (Händeler et al., 2009). However, the basal-branching shelled Ossyoacea, e.g. Cylindrobulla schatti or Oxynoe antillarum, and most Limapontioidea (e.g. Placida dendritica), are not able to ingest the kleptoplasts in a functional state and instead digest them rather quickly (Christa et al., 2015). By contrast, some members of the Costasiellidae, such as Costasussia ocellifera or C. karoshiinae and most Plakobranchaceae, e.g. Elysia timida or Plakobranchus ocellatus, are able to retain photosynthetic activity in the kleptoplasts, even during starvation (Christa et al., 2014, 2015; de Vries, Christa & Gould, 2014; Wagele & Martin, 2014).

(5) Photosymbioses in chordates

A few chordates are known to be able to establish photosymbiosis. Knowledge about the diversity and physiology of this phenomenon is, however, scarce. A lifelong and obligate relationship in chordates is found only in the tropical colonial ascidians from the family Didemnidae. These ascidians are mainly associated extracellularly with cyanobacteria from the genus Prochloron (Hirose et al., 2018). These symbiotic associations are generally considered to be primary producers of open ocean planktonic communities (Decelle et al., 2015). Photosymbiotic foraminiferans play a major ecological role contributing to the global carbon cycle and to 25% of carbonate calcium deposits (Langer, Silk & Lipps, 1997; Erez, 2003; Lipps & Stanley, 2016). Foraminifera acquire their symbionts either vertically or horizontally (Fay, Weber & Lipps, 2009). They associate with a variety of symbionts including dinoflagellates, diatoms, rhodophytes, chlorophytes and cyanophytes (Hansen & Buchardt, 1977; Hansen & Dalberg, 1979; Smith, 1991; Lee, 2006; Lipps & Stanley, 2016), a range that covers all known symbionts from animal lineages. Of the 150 foraminiferan families, 10% are hosts of algal symbionts (Lee & Anderson, 1991). Benthic foraminiferans either establish symbioses with Symbiodinium (Schmidt, Kucera & Uthicke, 2014) or, as in Sacoglossa, retain only the chloroplasts from their algal prey (Bernhard & Bowser, 1999; Pillet et al., 2011; Pillet & Pawlowski, 2012). Planktonic foraminiferans, however, mainly associate with the dinoflagellate Pelagodinium, a sister taxon of Symbiodinium (Decelle et al., 2015). The symbiotic relationship between photosynthetic partners and Foraminifera is sensitive to environmental stressors that can cause a massive release of symbionts known as bleaching (Hallock, Forward & Hansen, 1986; Hallock et al., 2003, 2006). In this sense, Foraminifera have been used as indicators of water quality and temperature of the reef ecosystem (Reymond, Uthicke & Pandolfi, 2012).

III. EVOLUTION OF PHOTOSYMBIOSES IN ANIMALS

Although there are many records showing the biodiversity of photosymbioses in animals, we lack information on the evolution of these symbioses across most lineages. Figure 2 provides a brief overview of the phylogenetic relationships among non-photosymbiotic or photosymbiotic taxa. Given the tremendous diversity of photosymbiotic species, this figure contains only hypothetical origins or losses of photosymbiosis in the respective clades.

Sponges are probably the sister taxon to all other metazoans (Philippe et al., 2009; Jékely, Paps & Nielsen, 2015; Pisani et al., 2015; Whelan, Kocot & Halanych, 2015). Surprisingly, no studies of the great diversity of photosymbiosis in sponges have been carried out. On the basis of current evolutionary hypotheses (Worheide et al., 2012; Simion et al., 2017) and the fact that photosymbiotic species exist in all sponge classes, it is possible that the ability to incorporate symbionts either evolved in the last common ancestor (LCA) of all sponges with subsequent multiple losses in different lineages or that several independent acquisitions occurred (Fig. 2).

In cnidarians, several analyses on single taxa have been performed to clarify the evolution of photosymbiosis (Kawaiida et al., 2013; Schwentner & Bosch, 2015; Ishikawa et al., 2016). Phylogenetic analyses in Hydra (Kawaiida et al., 2013; Schwentner & Bosch, 2015) suggest the evolution of
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Fig. 2. Legend on next page.
non-stable symbiosis in the LCA of the *Hydra* group, while stable symbiosis originated in the LCA of the *H. viridissima* group (Fig. 2). Under this scenario, non-stable symbiosis has been secondarily lost in the LCA of the *H. baueri* group (Fig. 2). Thus, symbiosis in *Hydra* was established first followed later by mechanisms allowing a long and stable symbiosis (e.g. oxidative stress tolerance) (Ishikawa et al., 2016). Among cnidarians four distinct taxa evolved photosymbiosis, i.e. Hexacorallia, Octocorallia, Scyphozoa, and Hydrozoa (Fig. 2; Kayal et al., 2013; Stampar et al., 2014; Zapata et al., 2015). Yet, whether this reflects independent acquisitions of symbiotic taxa or multiple losses is unclear (Fig. 2).

Phylogenetic analyses in Acoela are mainly focused on their taxonomic position within bilaterians (Paps et al., 2009) or on the evolution of selected morphological characters (Jondelius et al., 2011). Based on published, unresolved phylogenies, photosymbiosis evolved in the LCA of the Convolutidae clade of the Acoela (Fig. 2; Jondelius et al., 2011).

The phylogeny of Platyhelminthes is also under intense investigation. The photosymbiotic *Dalyellia viridis* and *Typhloplana viridata* are distantly related to photosymbiotic members of the Provoirticidae, such as *Pogaina kinnei* (Fig. 2; Jondelius & Thollesson, 1993; Littlewood et al., 1999; Zamparo et al., 2001; Van Steenkiste et al., 2013). Thus, photosymbioses may have evolved at least twice independently in the platyhelmithes (Fig. 2), or was lost in the Dugesidae, such as *Schmidtia mediterranea* (Fig. 2).

Recent phylogenetic analyses in molluscs (Giribet & Wheeler, 2002) suggest that photosymbioses evolved at least twice in bivalves, once in *Anodonta* sp. (Pardy, 1980) and once in the Cardiidae. For the latter, two scenarios for the evolution of photosymbioses are feasible, based on their phylogenetic position (Maruyama et al., 1998): either photosymbiosis evolved in the LCA of Cardiidae and was subsequently lost in the sister taxa Laevicardiinae (e.g. *Fulvia*) and Trachycardiinae (e.g. *Vasicardium*) (Fig. 2) or two independent acquisitions occurred, once in the LCA of Fraginiae (e.g. *Coreium*) (Kirkendale, 2009) and once in the LCA of Trochidinae (e.g. *Fragum*) (Fig. 2; Maruyama et al., 1998).

In Nudibranchs, photosymbioses evolved at least twice, once in the LCA of *Melibe* and once in Aeolidida (Fig. 2). In Aeolidida several gains or losses of photosymbioses are conceivable, as most genera include photosymbiotic and non-photosymbiotic members (Fig. 2). No analyses have yet been conducted with regard to the most likely evolutionary scenarios and the phylogenetic reconstructions in this group are still ongoing. In sacoglossans, functional kleptoplasty was acquired at least twice, once in the LCA of Costasiellidae and once in the LCA of the Plakobranchacea (Fig. 2; Christa et al., 2015).

There is little information on the evolution of photosymbioses in chordates. In Ascidia, more than 30 species from four genera of the Didemnidae are photosymbiotic, but their congeners are mostly non-symbiotic (Fig. 2). This suggests multiple origins of this symbiosis (at least once in each genus) in the ascidians (Fig. 2; Yokobori et al., 2006), but further work is needed. In amphibians, the photosymbiotic salamanders of the genus *Ambystoma* and *Hynobius* and frogs of the genus *Lithobates* are only distantly related. Thus, again photosymbiosis is likely to have evolved several times independently (Fig. 2).

**IV. EVOLUTIONARY GENOMICS OF PHOTOSYMBIOSES**

In addition to the uncertainties in scenarios of how photosymbioses evolved, the underlying molecular mechanisms needed to establish and maintain photosymbioses also remain largely unknown.

(1) **Onset and maintenance of photosymbioses**

In corals, detailed work unravelling the genomic adaptations that enable photosymbiosis has increased our understanding of the onset and maintenance of this symbiosis significantly (Baumgarten et al., 2015; Neubauer et al., 2016, 2017; van der Burg et al., 2016). Discrimination by the coral host among symbionts, pathogens, and food particles is key to symbiosis establishment and depends most likely on features of the host innate immune system (Davy, Allemand & Weis, 2012). It involves the recognition of specific microbial-associated molecular patterns (MAMPs) of the symbiont or pathogen by pattern-recognition receptors (PRRs) (Davy et al., 2012). In symbiotic cnidarians a set of PRRs has been identified.

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*Fig. 2.* Metazoan lineages in which photosymbioses occurs. Several animal lineages from different habitats (column 1: marine, cyan circles; freshwater, blue circles; terrestrial, green circles) have a symbiotic relationship with a phototrophic partner. For almost all metazoan lineages, evolutionary scenarios of how photosymbioses evolved are not available. For Sacoglossa, two studies investigated the most likely evolution of functional kleptoplasty (blue circles in the tree). Based on studies on photosymbiotic and non-photosymbiotic taxa (column 2: green and white circles, respectively), different hypothesis of evolving (red circles in the tree) or losing (white circles in the tree) photosymbioses are feasible. Unfortunately, for the vast majority of taxa neither genome (column 3) nor transcriptome (column 4) data exist (black circles, present; white circles, absent). Tree assembled from published studies (Maruyama et al., 1998; Zamparo et al., 2001; Yokobori et al., 2006; Kirkendale, 2009; Jondelius et al., 2011; Pyron & Wiens, 2011; Wörheide et al., 2012; Carmona et al., 2013; Kawaïda et al., 2013; Kayal et al., 2013; Van Steenkiste et al., 2013; Rodríguez et al., 2014; Christa et al., 2015; Schwemmer & Bosch, 2015; Zapata et al., 2015). Photograph credits: Heike Wägelle (*Didemnum, Costasiella, Phyllodesmium, Tridacna, Briareum, Halicona*), João Serôdio (*Symosugilifera* and Jenny Melo (*Ambystoma*).
that is absent in non-symbiotic species: a repertoire of thrombospondin-type-1 repeat protein (TSR) (Neubauer et al., 2017) and a set of expanded scavenger receptors (SRs), including a unique c-type lectin domain (LOX1), several scavenger receptor cystein-rich (SRCR) receptors, and a specific set of Class B scavenger receptors (CD36) (Neubauer et al., 2016). Experimental studies on SRs and TSRS support their role in symbiont recognition (Rodriguez-Lanetty, Phillips & Weis, 2006; Lehnert et al., 2014; Neubauer et al., 2016, 2017). Additionally, cnidian ficolin-like (CniFL) proteins are found in symbiotic and non-symbiotic cnidarians, but their role in symbiont recognition is still debated (Baumgarten et al., 2015; van der Burg et al., 2016). Recently, a study in a functional kleptoplast bearing sea slug showed that similar factors as in corals might be involved in plastid recognition (Chan et al., 2018).

(2) Maintenance of the symbiont includes phagosome arrest and ROS tolerance

Stable and long-lasting photosymbiosis is thought to be dependent on cellular response mechanisms coping with elevated levels of reactive oxygen species (ROS) (Kawano et al., 2004; Johnson, 2011; Ishikawa et al., 2016). In Hydra vulgaris and H. viridissima, the host first establishes the photosymbiosis and later develops tolerance to oxidative stress. Gene expression studies showed that H. vulgaris is less tolerant to ROS in an aposymbiotic state than in symbioses (Ishikawa et al., 2016). Under stress conditions, such as excessive light or high temperature, corals suffer from ROS stress generated by their symbionts (although the host itself is also stressed by high temperature). The symbiosis is then disrupted and the symbionts are expelled by various cellular mechanisms (Weis, 2008). In Sacoglossa, ROS tolerance was recently hypothesized to play a role in enduring long periods of starvation (de Vries et al., 2015). Although not studied in detail, it seems that coping with elevated ROS levels, potentially produced by the symbiont, is a common mechanism in different animal lineages to maintain the symbiosis. Besides ROS tolerance, stopping or delaying digestion allows stable integration and maintenance of the symbioses (Rodriguez-Lanetty et al., 2006; Dunn, Schnitzler & Weis, 2007; Voolstra et al., 2009). The mechanism behind such digestion control is unknown. For corals, the ‘arrested phagosome’ hypothesis attempts to provide one explanation (Hill & Hill, 2012), although experimental verification and analyses of genomic regulation that would enable this are still missing. This is of particular interest as selective forces could act on genomic adaptations to allow the evolution of photosymbiosis. For instance, nutritional support provided by the symbiont might lead to (i) better survival in oligotrophic waters, (ii) reduced predation through an associated increase in body size, or (iii) the ability to endure periods of starvation (especially in gastropods). Such ecological benefits could also explain why photosymbiosis apparently evolved multiple times independently within various taxa. However, nutritional support may not be the only factor. Often non-photosymbiotic species are sympatric within the same habitat and in the case of gastropods, non-photosymbiotic species often have the same survival during periods of starvation as photosymbiotic species. It remains important to identify potential evolutionary forces leading to genome adaptations to identify the relevant genome adaptions.

(3) Most lineages lack genomic information

Unfortunately, analyses focusing on genomic adaptations that allow the establishment and maintenance of photosymbiosis in most symbiotic species other than corals are absent. This is partly due to the lack of available genome sequences, especially of photosymbiotic species.

In sponges, analyses of genomic and transcriptomic data have focused on carbon and nitrogen metabolism, vitamin biosynthesis, and proteins that act as symbiont factors (Hentschel et al., 2012). However, data for candidate sponge species to understand the evolutionary genomics involved in photosymbioses are still lacking (Pita, Fraune & Hentschel, 2016).

The genomes of the anthozoans Acropora digitifera, Aiptasia pallida and Nematostella vectensis, several transcriptomes of other anthozoan species, the genome of the hydrozoan Hydra vulgaris (Chapman et al., 2010) and the transcriptome of H. viridissima (Ishikawa et al., 2016) have been published (see online Supporting Information, Table S1). The Hydra genome is highly complex and exhibits dramatic changes in genome size. The smallest genome is estimated for H. viridissima (380 Mbp) based on microphotometry of Feulgen-stained nuclei of epithelial and interstitial cells (Zacharias et al., 2004; Chapman et al., 2010; Bosch, 2012). According to Bosch (2012) this small genome size could be related to the small cell size of H. viridissima and contributions of the symbiont to the host’s metabolism. Likewise, the highly reduced genome of streptosiberian insects is hypothesized to be a result of their parasitic lifestyle (Niehuis et al., 2012). Because stable symbioses only evolved in the H. viridissima group, comparative analyses of genomes of the other three Hydra groups could shed light on adaptations needed to maintain photosymbiosis.

Unfortunately, no genomic or transcriptomic data are accessible for any photosymbiotic member of the Acoela or Platyhelminthes (Fig 2). Only the genome of the free-living freshwater planarian Schmidtea mediterranea has been sequenced to date, a non-photosymbiotic species frequently used in regeneration, tissue homeostasis, and stem-cell research (Robb et al., 2015).

Few studies using genomic resources have been performed among molluscs. Among bivalves only the genome of the pacific oyster Crassostrea gigas has been sequenced (Zhang et al., 2012). For the photosymbiotic Tridacna maxima, Mies et al. (2017b) showed that four specific genes are expressed during the onset of the symbiosis: a clam-specific actin, a symbiont-specific Ribulose-1,5-bisphosphate-carboxylase/-oxygenase (RuBisCO) gene, a symbiosis-specific H+ -ATPase gene and an aldo-keto oxidoreductase gene. The H+ -ATPase gene is considered
a symbiosis indicator, since it is expressed in symbiotic cells of *Symbiodinium* and not in free-living or aposymbiotic cells (Bertucci et al., 2009). By contrast, *Symbiodinium* expresses aldo-keto oxidoreductase only in the presence of light, both in free-living and in symbiotic forms (Mies et al., 2017b). This protein is necessary for glycerol synthesis (Jez et al., 1997), which might be continuously translocated to *Tridacna* (Mies et al., 2017b). Yet, no genomic sequences of these bivalve hosts are available to facilitate the search for further genetic factors that might underpin the establishment or maintenance of symbiosis.

In sea slugs, only the draft genome of *Aplysia californica* is currently available (https://www.broadinstitute.org/ alysia/alysisa-genome-project, last updated in 2013). For the kleptoplastic sacoglossan *Elysia chlorotica* a non-assembled short-read draft genome exists (Bhattacharya et al., 2013). Transcriptomic data sets have been generated for 13 nudibranch species (Goodheart et al., 2015) and five sacoglossans (Schwartz, Curtis & Pierce, 2010; Wägele et al., 2010; Han et al., 2013; de Vries et al., 2015): in Nudibranchia only one out of the 13 sequenced species is symbiotic, in Sacoglossa four. In Sacoglossa one study compared the transcriptomic response of two species that differed in longevity of plastid retention (de Vries et al., 2015). Yet, we still do not understand what sets functional kleptoplasty species apart from non-kleptoplastic sister taxa.

Among Ascidia the genome of the carpet sea squirt, *Didemnum vexillum* (Didemnidae), has been sequenced (Velanda-Huerto et al., 2016). This non-symbiotic species (Lin et al., 2016) is currently considered a highly successful invasive taxon (Bullard et al., 2007; Lengyel, Collie & Valentine, 2009; Locke & Carman, 2009; Stefaniak et al., 2012). In addition, the genomes of seven non-photosymbiotic species, i.e. *Ciona intestinalis* (Dehal et al., 2002), *Ciona savignyi* (Small et al., 2007), *Botryllus schlosseri* (Voskoboynik et al., 2013), *Oikopleura dioica* (Seo et al., 2001), and three species of *Molgula* (Stolfi et al., 2014), have been sequenced (see online Supporting Information, Table S1). No genetic and transcriptomic data regarding the unique association between didemnidaen ascidians and *Prochloron* are available.

No studies have reported genomic information from amphibian–algae symbioses. The closest species to photosymbiotic salamanders with a sequenced genome and available transcriptome is the non-symbiotic Mexican axolotl *Ambystoma mexicanum*, well known for its ability to regenerate amputated limbs and for its neotenic form with external gills and caudal fin (Wu et al., 2013; Keinath et al., 2015). Recently, thorough comparative transcriptomic analysis of the expression of cells of photosymbiotic *Ambystoma maculatum* bearing *Ophilia* algae, algae-free cells, and eggs with extracellular algae have been performed (Burns et al., 2017). Interestingly, algae in host cells show stress responses and a shift in energy acquisition compared to algae inside the egg capsule. Under low light conditions and low oxygen levels, intracellular algae obtain phosphates and glutamine from their host, but rely on fermentation instead of photosynthesis (Burns et al., 2017). Salamander cells with intracellular algae show inhibition of immune responses to tolerate the symbiont (Burns et al., 2017). To what degree this process might also occur in other photosymbiotic clades is not known.

(4) Implications of the mode of symbiont transmission on the evolution of the host genome

In order to understand the genome adaptations that are needed to evolve photosymbiosis, the mode of symbiont transmission should also be considered. Acquiring symbionts horizontally always includes an aposymbiotic life stage present in all photosymbiotic animal lineages, which is usually the larval phase before metamorphosis into juveniles (e.g. Belda-Baillie et al., 1999; Weis et al., 2001; Harrison, 2011; Pelletreau et al., 2014; Mies et al., 2017a). Juveniles then successfully take up the symbiont from their environment, but there seems to be little co-evolution of species with horizontal transmission and their symbiont partners (van Oppen et al., 2001; Bright & Bulgheresi, 2010). The identification of symbionts in adult stages may mask potentially non-specific symbiont uptake during the juvenile stages. For example, in corals it has been shown that juveniles have a rather unspecific symbiont uptake and symbiont selection is based on intracellular sorting and adaptive bleaching (Buddemeier & Fautin, 1993) in adults (Little, van Oppen & Willis, 2004). This might also apply to Foraminifera (Fay et al., 2009). On what this sorting is based, i.e. if certain genome adaptations are needed or there is interspecific competition among symbionts or selection based on ecological factors, is unknown. Alternatively, the whole community of algal symbionts can be altered during re-colonization following a bleaching event [Jones et al., 2008]. Thus, analyses of symbionts only at a distinct adult stage will provide only restricted information about the potential diversity of the recognition mechanisms involved. Nevertheless, it seems reasonable to assume that acquiring a broad diversity of symbionts via horizontal transmission could represent a high level of diversity in symbiont-recognition mechanisms. In this scenario, species that are only able to incorporate symbionts from a distinct lineage may have a reduced set of recognition mechanisms.

Vertical transmission is found among sponges (Usher et al., 2001; Oren, Steindler & Ilan, 2005), corals (Baird, Guest & Willis, 2009; Padilla-Gamin˜no et al., 2012), acelomorphs (Barneah et al., 2007; Hikosaka-Katayama et al., 2012) and ascidians (Hirose, Oka & Akahori, 2004). For this mode of transmission the symbionts need to be translocated into the reproductive system, requiring a rather complicated mechanism in ascidia, for example (Hirose, 2000). In contrast to horizontal transmission, vertical transmission might well lead to genomic adaptations and co-evolution of symbionts and hosts is likely (Barneah et al., 2004). Further, because the symbionts are not necessarily acquired from the water column, genomic adaptations for symbiont recognition could be lost during evolution. As a result, the plasticity of the recognition system might become reduced. This could provide an explanation of higher specificity of endosymbiotic algae in corals with vertical transmission.
(Stat et al., 2008). Vertical transmission might also favour the successful colonization of environments in which the horizontally transmitted symbiont is not found (Oren et al., 2005). In species with both modes of transmission (Bright & Bulgheresi, 2010) genomic adaptation might even be more complex.

(5) Additional genomes of non-model organisms are needed

Analyses of already sequenced transcriptomes and genomes of various photosymbiotic and non-photosymbiotic taxa will certainly help to understand the genomic adaptations needed to establish and maintain photosymbiosis. Broad taxon sampling will uncover whether these mechanisms are evolutionarily ancient or whether they are the result of convergence. In this regard it will be of particular interest to investigate Foraminifera, because they share many features of photosymbiosis with animals. To obtain the necessary information more genome data sets are needed and are preferred over transcriptomic data sets. The absence of a transcript in a sequenced transcriptome does not translate into the absence of the gene or gene product and is thus only of limited use. Nevertheless, initial studies relying on a mixture of transcriptomic and genomic resources are a first step towards understanding the adaptations necessary to evolve photosymbiosis in animals. In the near future, techniques such as single-cell RNA sequencing (scRNA-seq) and long-read sequencing, will allow more accurate determination of the transcriptional state of an organism and the identification of stage- and tissue-specific expressed and alternatively spliced genes (Shapiro, Biezuner & Linnarsson, 2013; Kolodziejczyk et al., 2015; Garalde et al., 2018).

V. CONCLUSIONS

(1) The phenomenon of photosymbiosis in the animal kingdom is remarkably widespread. Many studies have increased our understanding of the biodiversity of the animal hosts and algal symbionts. However, in most lineages the evolution of photosymbiosis is still poorly known, especially with regard to selective forces leading to genome adaptations that enable the evolution of symbiont recognition and stable integration.

(2) Studies in corals should inspire future analyses: specific receptors of the host innate immune system have evolved in symbiotic corals that are most likely involved in the recognition of Symbiodinium. Similar analyses for other photosymbiotic animals are absent but will be fundamental to advancing our understanding of how photosymbioses evolved, whether there are common genomic adaptations in different lineages, and how the mode of transmission might influence the genome evolution.

(3) Such analyses will help to understand why some species harbour multiple symbionts of different lineages, while others are restricted to single species.

(4) Comparative analyses of photosymbiotic and non-photosymbiotic species are key to understanding what makes photosymbiotic species so special.

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article. Table S1. Genomes and transcriptomes of photosymbiotic animals and their close relatives.