1. Introduction

Sponges lack muscles, a gut and a nervous system, and consequently have emerged as a model to study complex character evolution in Metazoa. But sequencing has revealed substantial genetic complexity despite an apparently simple body plan (Srivastava et al., 2010; Riesgo et al., 2014). The presence of so-called ‘neural’ genes and evident sensory behaviour in sponges intuitively suggests that the latter emerges from the former. The proposal that ctenophores are basal to all other metazoans (Dunn et al., 2008; Ryan et al., 2013; Moroz et al., 2014), has led to discussion about whether these genes are characters of a ‘pre-nervous’ system or the remnants of a lost nervous system (Richards et al., 2008; Nickel, 2010; Ryan and Chiodin, 2015). However it is not yet possible to distinguish between these two hypotheses; our paper examines the data from the perspective that nervous system loss has not occurred. Additionally, there is no evidence for the presence of an extant poriferan neuron and thus we do not search for one. Instead, we ask if the available data are sufficient to test whether the last common ancestor of sponges and eumetazoans possessed the genetic modules underlying the nervous system’s sensory and coordinating phenotype. By inference this suggests that these genetic modules led to a specialized sensory cell type in the last common ancestor. Alternatively, if these modules arose after the divergence of sponges the co-opted genes may have held non-sensory functions in the last common ancestor. Thus it is problematic to refer to these genes as ‘neural’, especially given the fact that gene function may diverge in an extant animal. Instead, we use the term ‘sensory-neural markers’ (SNM) to indicate genes involved in the sensory and neural systems of neuralians.

Sponges, a quintessential non-model organism, have so far resisted the development of direct tests of gene function. The vast majority of data on SNMs has arisen from gene expression studies which have localized these genes to specific structures and cell types in sponges. With few exceptions there is very little access to higher-level genetic data, such as gene network interactions (e.g. Arendt et al., 2016) and more nuanced approaches to homology are currently not possible.
Instead, the presence/absence data of in situ hybridization is often interpreted as a kind of genetic signal, in which the collection of genes expressed in a structure is inferred to suggest heritage to another cell type. In this way, the genetic signal approximates a molecular fingerprint. However these are two distinct concepts with subtle differences. A neural hypothesis defines a molecular fingerprint as the unique set of both the transcription factors and the effectors they govern that give rise to a specific cell type. While effectors are indicative of a cell’s phenotype, regulatory genes may be either used in neural or non-neural functions.

In this framework investigating the possibility of a neural heritage within sponges faces several distinct difficulties. First, the majority of genes expressed in a neuron are not neural-specific (Bucher and Anderson, 2015). Second, it is not readily apparent what to compare this genetic signal to. The genetic repertoire of neurons is vastly diverse – no gene is universally and uniquely expressed in all neurons (Bucher and Anderson, 2015) – though non-exclusive “pan-neuronal” genes have been studied (Stefanakis et al., 2015; Arendt et al., 2016). Indeed, the definition of a neuron as drawn at the genetic, morphological, or functional level is not wholly agreed upon (Bucher and Anderson, 2015). Thus, the question arises as to what degree SNMs allow us to trace neural heritage and infer a sensory function of a sponge sensory structure.

Current research aims to infer homology of a sponge structure to the nervous system by attempting to determine whether SNMs are expressed in that structure and hold a sensory function. The idea that the sensory and nervous systems are intimately related stems from Mackie (1970) who theorized that a cell type specialized for signaling may have emerged through separation of functions in an ancestral neuro-sensory precursor cell. A step-wise evolution of the complete sensory cell system was envisioned, starting with a single sensory cell acquiring an effector property, and then separation of sensor and effector with the addition of a nerve cell (Mackie, 1970). The genes underlying the sponge sensory system may be distinct from those of the nervous system.

Animal sensory cells are generally associated with nerves. The sensory cell functions as a ‘receptor’ and transmits information to an ‘effector’ via the neuron. However, without nerves, what does a sponge sensory cell do? Examples in which a sensory cell directly activates separate effector cells include kidney epithelia, in which primary cilia detect changes in flow and provide feedback to other cells, which change their secretion/absorption of solutes (reviewed in Berbari et al. (2009)). Cnidarian nematocytes show a graded receptor and effector interaction. Some cells can be triggered to fire the nematocyst capsule by activation directly via a sensory neuron, or as independent effectors via cilia on the nematocyte itself that receive a mechanical or chemical trigger (Holstein, 2012). At least one example of a sensor-effector cell in sponges is seen in the ciliated pigmented cells of the *Amphimedon queenslandica* larval photoreceptive organ, which acts to both detect light and steer the larva in response (Leys and Degnan, 2001).

In light of these considerations, context is paramount when interpreting a genetic signal. Alone, a genetic signal presents a limited hypothesis. It does not consider the sponge’s unique biology, which has been shaped over evolutionary time by highly specific selective forces. Yet morphological, functional and genetic pieces of the puzzle are often missing in the study of the sponge sensory system. Here we aim to provide some context by providing a broad, objective view of gene expression in both sensory and non-sensory features, and providing an analysis of how this genetic data may be informative about the above hypotheses.

### 2. Sensory cells in sponges

Several types of evidence are used to identify sensory regions and cells in sponges, including phototaxis or geotaxis of larvae, contractions of the osculum or ostia of whole sponges, and more recently, expression...
of marker genes. Original workers saw the osculum retract in response to mechanical or chemical stimuli (Parker, 1910; McNair, 1923; Prosser et al., 1962; reviewed in Leys, 2015). Pore cells are also responsive (Elliott and Leys, 2007), as are cells or sphincters around canals that vent into the atrial cavity, although these are often hidden within the osculum and so difficult to see (Reiswig, 1971). All these cells may share a developmental origin as ‘sieve cells’, ‘pore cells’ and contractile sphincters, because at least in one freshwater sponge, a small (20 µm diameter) ostium was found to develop into the osculum (Weissenfels, 1980). In general sponges contract (see examples in Nickel (2010)) and it is usually considered that canal epithelia are responsible (Nickel et al., 2011) but the best-known examples of sponge sensation come from studies of larval behaviour.

Phototaxis in parenchymella larvae results from rapid bending or straightening of long cilia in cells at the posterior pole of the larva (Leys and Degnan, 2001; Leys et al., 2002; Maldonado et al., 2003; Collin et al., 2010). These cells are elongate, with a basal nucleus, and they lie just adjacent to cells containing many inclusions with pigment granules, as well as cells with large globular inclusions at the posterior pole (Weissenfels, 1980). In general sponges contract (see examples in Nickel (2010)) and it is usually considered that canal epithelia are responsible (Nickel et al., 2011) but the best-known examples of sponge sensation come from studies of larval behaviour.

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in other animals, and (b) the function of the feature in which the gene is expressed. The vast majority of genes have been solely or most thoroughly characterized in Bilateria. Thus, underlying this premise is the assumption that function is conserved in clades that arose after the divergence of Porifera. Inversely the second approach extends conclusions from feature to gene. This is a top-down method which suggests that sensory function, a highly emergent character, can be used to extend inferences down to the genetic level. These two approaches provide different views. The first focuses a bilaterian 'lens', coined by Dunn et al. (2015), on gene function, while the second provides a more immediate poriferan-centred approach.

There are caveats to both approaches. Without additional context it is precarious to use either method of inference alone, a fact that becomes especially evident when their conclusions contradict each other. For instance when a gene has been characterized as non-sensory or non-neural in other animals it is rarely suggested to be sensory in sponges, even if it is expressed in a sponge sensory feature (Larroux et al., 2006; Gauthier and Degnan, 2008). Similarly when SNM expression occurs in a non-sensory feature that gene is generally not proposed to be sensory (Okamoto et al., 2012; Fortunato et al., 2014b; Nakayama et al., 2015). Yet until the function of that gene is directly tested both hypotheses remain viable. Furthermore, the presence of a greater number of SNMs expressed within the same structure is interpreted as stronger evidence for a sensory function, especially given the fact that the in situ hybridization technique involves whole sample exposure. But in situ hybridization studies also face the challenge of being limited by the number of genes that can be examined. Sampling bias and a smaller sample size can distort the catalogue of gene expression observed for a feature. Thus a comprehensive view of both SNM and putatively non-sensory genes is required.

3.1. Gene expression studies: A survey

An encompassing review of gene expression data may give a broader, objective platform from which to base inferences. We have performed a meta-analysis of all currently available in situ hybridization data (Figs. 2, 3; Supplementary Fig. 1). SNMs were defined as those possessing a conserved role in sensory or neural systems across Bilateria. These include developmental regulatory as well as effecter genes, those genes responsible for sensory functions themselves. Features in which gene expression has been predominantly reported are included for the three sponges (Amphimedon queenslandica, Sycon ciliatum, Ephydatia fluviatilis/muelleri) in which sensory structures or cell types have been hypothesized or investigated (Supplementary

![Fig. 2, 3]. A. queenslandica and S. ciliatum have gained prominence in gene expression studies due to the availability of a genome, while E. fluviatilis and E. muelleri have benefited from their ability to be grown and maintained on the lab bench. For our meta-analysis, we used gene expressions that were clearly corroborated by images shown in published work. In some instances we were unable to confirm that gene expression occurred in a particular cell type because images showed regional expression. However, these patterns were still included (Supplementary Fig. 3).

Non-model organisms offer little from which to infer gene function. However, there is a rich database of functional gene data as characterized in other animals, and the dominant approach has been to use this data to test functional hypotheses in non-model organisms. Indeed, as demonstrated in cnidarian and ectenophore neuredevelopment, the genes of non-bilaterian metazoa do display functional conservation (Marlow et al., 2009; Simmons et al., 2012). Being aware of the fact that in situ hybridization data can be open to interpretation and methodological difficulties, analysis of gene expression data nevertheless reveals distinct insights into sponge biology.

SNMs are indeed expressed in sponge sensory structures, supporting the hypothesis that they play a sensory role in sponges. By corollary this also suggests homology to the sensory structures of other animals, though the story is complex. One example is the expression of SNMs in the A. queenslandica photoreceptive organ (Fig. 2). The presence of a 440 nm peak on the action spectrum prompted Leys et al. (2002) to first hypothesize that a flavin or carotenoid may be the photopigment underlying the photoreceptive organ. No peak was seen at 500 nm, the characteristic absorption peak of opsin (Leys et al., 2002), and searches of the A. queenslandica and O. carmela genomes have not yet found this protein (Plachetzkii et al., 2007; Feuda et al., 2012). Instead, Rivera et al. (2012) found that the photoreceptive organ of the Amphimedon larva expresses a cryptochrome, rather than an opsin. Opsin expression unites morphologically distinct photoreceptors across non-poriferan animals (Arendt, 2008), but opsins have yet to be found in sponge genomes. Thus, while colloquially called an ‘eye’ the photoreceptive organ in the sponge larva is most likely a convergent structure. However, patterning of the underlying sensory domain may yet be homologous to other sensory regions, as evidenced by the expression of NK5/6/7B, Lhx3/4 and Lhx1/5 (Fig. 2).

The osculum expresses comparatively fewer SNMs than the photoreceptive organ (Fig. 2), but as oscular expression data is available for only two species of sponges (Sycon ciliatum and Halisarca dujardini) low sample size may play a factor (Fortunato et al., 2012, 2014a; Leininger et al., 2014; Borisenko et al., 2016). SNMs in H. dujardini have not yet been explored but in S. ciliatum H6-like-homeobox (Hmx
and muscle segment homeobox (Msx) show osmolar expression patterns (Fortunato et al., 2014a). Hmx is involved in CNS development in bilaterians, but little non-bilaterian data is currently available (Wang and Lufkin, 2005). Among its many roles, Msx is involved in muscle development in both bilaterians (Lord et al., 1995; Houzelstein et al., 1999) and non-bilaterians (Galle et al., 2005), in addition to neural functions (Wang et al., 1996; Miljkovic-Licina et al., 2004; Ramos and Robert, 2005). The difficulty of drawing conclusions from genes with multiple functions is not limited to Msx. Osmolar expression patterns may yet occur in other sponges, such as Ephydatia, but difficulties in viewing the osmolar obscures this.

But the correlation between SNMs and sensory structures is not exclusive; non-sensory cells also express SNMs (Fig. 2). Choanocytes, pinacocytes, archaeocytes, and skeletogenic elements do not appear to have a sensory function, yet all express SNMs. But if we are to maintain the view that SNM gene function is conserved in sponges, new hypotheses emerge: putatively non-sensory cell types may hold cryptic sensory functions. In Ephydatia muelleri Pax6 is regulated Six1/2 (Rivera et al., 2013) and both are expressed in the pinacocytes lining the canals. Canal growth is a dynamic process, likely in response to flow. One possibility may be that these cells provide sensory feedback contributing to canal maintenance (Rivera et al., 2013).

The presence of SNM expression in functionally uncharacterized cell types has also prompted novel hypotheses. The A. queenslandica larva possesses globular/mucous cells and flask cells and the larva of S. ciliatum possesses cross cells (Dubosq and Tuzet, 1938, 1941; Leys and Degnan, 2001; Richards and Degnan, 2012). Both larvae are phototactic (Leys and Degnan, 2001; Elliott et al., 2004), and the A. queenslandica larva has also been shown to settle in response to various cues (Jackson et al., 2002). In the face of these behaviors the expression of SNMs in these specialized cell types has led to suggestions that they are sensory (Richards et al., 2008; Fortunato et al., 2014b; Nakanishi et al., 2015; Ueda et al., 2016). However, such hypotheses remain a priori until direct functional tests on these cell types are performed.

The hypotheses that globular cells and flask cells are sensory are based on different classes of evidence. The expression of an atonal-like gene (Richards et al., 2008), several post-synaptic density genes (Sakarya et al., 2007), and NOS (Ueda et al., 2016) in globular cells suggest a sensory function, although the morphology of globular cells is not similar to that of other animal sensory cells. They lack a cilium, and though the apex of globular cells extends beyond the surface of the larva the cell also possesses large inclusions indicative of mucous. Thus follows the first functional interpretation of this cell, which is that it serves to secrete mucous externally (Leys and Degnan, 2001). In contrast, flask cells do possess a recessed cilium suggestive of a possible sensory functionality (Leys and Degnan, 2001) yet they do not appear to express any of the SNMs censused to date (Fig. 2). However, given the diversity and proximity of cell types in the sponge epithelium we cannot rule out the possibility that some of these expression patterns may have been associated with the wrong cell type. Thus in these two examples the traditional measure of morphology and the untested evidence of molecular data are in dispute. It is relevant to note that although globular cells, flask cells, and the photoreceptive organ are all hypothesized to be sensory, no SNM expression is shared amongst them (Fig. 2).

If functional hypotheses are to be built upon gene expression, the entire repertoire of expressed genes must be considered. Globular cells express the innate immunity genes TIR1, pellino, and NF-κb, while cross cells also express the germline genes vasa and nanos (Fig. 3). The sensory potential of these cells is most often emphasized, yet these expression patterns suggest a multi-modal functionality or even the possibility that a sensory function is secondary. For example, perhaps expression of both synaptic and innate immunity genes in globular cells and the apposition of ciliated flask cells hints at the ancestry of the immunological synapse (Angus and Griffiths, 2013; Le Borgne and Shaw, 2013). It is much easier to infer gene function if expression occurs in a cell type that is recognizable comparable to that of other animals. But sponge cells allow few parallels and the relation of these specialized, but functionally uncharacterized, cell types remains elusive.

3.2. Challenges of tracing homology within Porifera

Both the pre-nervous system and nervous system loss hypotheses predict that a sensorineural-like cell was present at the stem of Porifera, implying that a homologous representative could be present in extant sponges. Thus, cell type comparisons between sponge species are invaluable. However, sponges offer several challenges. Porifera lineages are characterized by long branches allowing ample time for divergence (Philippe et al., 2009). This evolutionary distance is embodied by the presence of unique, class-specific cell types including the globular, flask, and cross cells. All three are hypothesized to possess neural links (Richards et al., 2008; Fortunato et al., 2014b, 2015; Nakanishi et al., 2015) but none can be compared to the other. Attempts at cross-species comparisons have been made but the criteria used is broad by necessity. For instance, morphological similarities have been drawn between various larval cells and globular cells: they are bottle or oval-shaped larval cells with or without cilia possessing numerous small vesicles (Renard et al., 2009). Even differentiating between cell types within the same species can be challenging. For example, there was early confusion in the identification of globular vs. flask cells (Sakarya et al., 2007; Richards et al., 2008; Renard et al., 2009). Furthermore, undescribed cell types may exist. Globular cells are often treated as a single cell type (Richards et al., 2008; Gauthier et al., 2010) but Sakarya et al. (2007) noted gene expression in some cells and not others. In fact a closer look at the ultrastructure shows that there are a number of different cell types in the larval epithelium that have not been described (Fig. 1), so perhaps selective gene expression is not to be unexpected. Thus, a deeper understanding of basic sponge cytology is required if new hypotheses on cell function are to be made.

In situ hybridization studies follow the candidate gene approach, and what we learn is strongly dependent on what is tested. Most genes selected for study, including many SNMs, are transcription factors. Perhaps unsurprisingly they are expressed extensively during development. As more in situ hybridization studies have been published an increasing number of gene expressions have been replicated across species. However of the SNMs studied so far only a handful have been investigated in more than one species (Fig. 2). Interestingly, of all genes examined so far, only one gene - Gata - is expressed in the same structure or cell type in different species (Fig. 2). This may be due to the limited number of structures available for study in each species. The most well-studied life stage in Amphiomedon queenslandicus is the larva while the juvenile sponge is the most common subject of study in Ephydatia. In contrast, studies featuring Sycon ciliatum examine both the juvenile and larval stages as the adult is small and tends to contain all the developmental stages. Work is done on whole small sponges, or portions of these sponges, containing embryos and larvae. Finally, sponge genes themselves offer additional challenges. A common scenario is for sponge genes to be most closely related to other sponge genes, clustering amongst themselves rather than within better characterized bilaterian clades (Tompkins-MacDonald et al., 2009; Fortunato et al., 2014b).

3.3. Higher-level approaches

Several SNM studies have introduced higher-level multi-dimensional data beyond that of expression patterns. Most often protein function, as deduced from domain structure, is not tested despite the fact that protein interactions in sponges may very well not match that of bilaterians. Richards et al. (2008) demonstrated through hetero-
logous expression that an atonal-related bHLH from Amphimedon queenslandica has proneural properties in Xenopus laevis and Drosophila. Similarly the A. queenslandica cryptochromes, which lie in a clade sister to both photolyase and cryptochromes, were tested for bona fide photoreceptive abilities through in vitro assays (Rivera et al., 2012). Other studies have examined potential gene interactions. Rivera et al. (2013) found that PaxB may regulate Scl1/2 in E. muelleri, and indeed these two genes localize to the same cell type. In contrast, Conaco et al. (2012) found that many post-synaptic density genes are not co-expressed and thus may not assemble into a unified scaffold. Globular cells however, do express five post-synaptic density genes (Sakarya et al., 2007) and Conaco et al. (2012) note that small modules of interactions may persist. Evidence for gene interactions may also derive from the temporal and spatial information in situ hybridizations provide. Richards et al. (2008) hypothesized that the order of expression of notch, delta, and bHLH in globular cells and putative globular cell precursors suggests the presence of a genetic circuit.

Ultimately, the underlying goal is to link SNMs to organismal behaviour and sensation. Ludeman et al. (2014) found that fluorescent molecules that function as calcium channel blockers label both primary cilia in the osculum and inhibit the inflation-contraction behaviour, leading to the hypothesis that TRP channels may localize to the cilia and function in detection of water flow. Ueda et al. (2016) demonstrated that nitric oxide triggers larval metamorphosis in A. queenslandica, suggesting a link between nitric oxide synthase in the globular cells and detection of nitric oxide. Studies characterizing SNMs at a higher-level represent invaluable progress, but still face challenges until direct tests of gene function are available. Those that investigate protein function or gene network interactions struggle to link to higher-level organismal behaviours and studies that do examine organismal behaviour must draw links to genes by association.

3.4. Emerging molecular approaches and future directions

Despite challenges, bottom-up molecular approaches may provide a path forward. RNAseq offers unbiased access to the entire genetic complement of a sensory feature, providing greater genetic context from which to base homology inferences. In particular single cell RNAseq may allow targeted access of sponge sensory cells, which are often sparsely distributed within tissues. Importantly, these sequencing techniques allow access to uncharacterized proteins. Testing uncharacterized orthologs shared among non-bilaterian metazoan sensory structures may be key to understanding sensory function origins. In this vein, interactome studies may be invaluable. Given that many genes fundamental to the neurons are not neural-specific understanding the emergence of the molecular interactions underlying the neural phenotype will be insightful. Interactions conserved in basal metazoans, but since lost in Bilateria, may provide the molecular context within which neurons evolved. RNAi has so far been tested in Ephydatia muelleri and Tethya wilhelma (Rivera et al., 2011, 2013) and further development of this technique in other sponge species will prove promising. CRISPR is not yet accessible due to lack of access to early embryos and difficulties in delivering the molecules into cells, but techniques are continually being refined. Finally, while molecular techniques are powerful this data cannot be interpreted without an understanding of an organism’s basic biology. Morphological, functional, and physiological characterizations provide a foundation for discovery. Molecular data often supersedes morphological data, but larvae clearly have many undescribed cell types (Fig. 1). Studies that closely describe ultrastructure and cell interactions coupled with gene expression will lead to a better understanding of function (Richards et al., 2008; Nakayama et al., 2015; Kahn and Leys, 2016).

The genetic resources available for sponges have advanced in step with the increasing efficiency and affordability of molecular technology. As of the writing of this article, four genomes (Amphimedon queenslandica (Srivistava et al., 2010), Syccon ciliatum (Fortunato et al., 2014a; Leininger et al., 2014), Tethya wilhelma (Francis et al., 2017), and Oscarella carmela (Nichols et al., 2012)) are available. Other genomes are in progress. In addition, assembled transcriptomes have been published or made available for at least 24 species of sponges (Table S2). These include the transcriptomes of closely related species, which may offer insight into how divergence affects genetic interpretations (e.g. Sycon ciliatum vs Sycon coactum (Leininger et al., 2014; Riesgo et al., 2014), Haliclonia tubifera vs Haliclonia amboinensis (Guzman and Conaco, 2016) and Ephydatia flaviatilis vs Ephydatia muelleri (Allie et al., 2015; Pena et al., 2016)).

4. Think like a sponge

As noted by Dunn et al. (2015) most organismal knowledge has been gathered in Bilateria, but non-bilaterian biology extends beyond this perimeter. Functional data from other animals affords a limited window of insight into sponge genes. Another source of information, the function of the sponge feature gene expression occurs in, presents alternate hypotheses. Might SNMs contribute to non-sensory functions in sponges? As noted previously, SNM expression occurs in non-sensory cells. Musashi, which is involved in neural stem cell maintenance in Bilateria (Richter et al., 1990; Nakamura et al., 1994), is expressed in the archaeocytes of Ephydatia flaviatilis (Okamoto et al., 2012) (Fig. 2). Archaeocytes act as stem cells in sponges presenting the possibility that musashi may be involved in the broader function of general stem cell maintenance (Okamoto et al., 2012). Another striking example is that SoxB acts a marker for spicule transporting cells in E. flaviatilis (Nakayama et al., 2015) (Fig. 2). So far no stem cell function has been uncovered for these spicule transporters and SoxB is not expressed in archaeocytes (Nakayama et al., 2015), leaving the function of SoxB uncertain. Of course, sponges are not the only non-bilaterian that displays this phenomenon. Pang and Martindale (2008), for example, found it surprising that brain-specific homebox is expressed in the tentacle apparatus rather than sensory apical organ of the Mnemiopsis leidyi larva.

A sister hypothesis is that predominantly non-neural genes hold sensory functions in sponge sensory structures. For instance, Wnt has widespread developmental roles (McMahon and Moon, 1989) and is expressed in two polarized sponge structures: the larval photoreceptive organ of A. queenslandica and the osculum (Fig. 3). However, Wnt is also involved in neurodevelopment in Bilateria (Thomas and Capecchi, 1990). Thus Wnt may also hold sensory patterning roles in these sponge structures, though it may not be possible nor meaningful to delineate between these two possibilities.

Thus a conundrum is presented when gene function, as characterized in other animals, conflicts with the function of the structure it is expressed in. But should we expect gene function to be conserved in sponges if these functions were characterized in later diverging clades? Instead, alternate hypotheses directly drawn from poriferan characters may offer insight that is not constrained within a bilaterian framework.

5. Conclusion

The study of nervous system evolution seeks to understand at what node the genetic modules underlying sensorineural functions originated. Most published work suggests that SNMs are associated with sensory abilities in the last common ancestor to sponges and eumetazoans. But our analysis suggests that the correlation is weak. While sponge sensory structures do express some SNMs, many putatively non-sensory cell types do too (Fig. 2). When forming hypotheses about the function of uncharacterized cell types based on gene expression we must be exceedingly cautious. Indeed, conceiving hypotheses in general is a difficult task as insight is narrowed by a lack of broader genetic context. The fact that some SNMs are expressed alongside genes suggestive of alternate functions raises the question of whether other hypotheses exist beyond the small window of candidate genes selected
for study. Furthermore, drawing correlations between gene expression in sponges and gene function as characterized in other animals may be misleading when working with a non-bilaterian non-model organism. This top-down approach lends a bilaterian ‘lens’ (Dunn et al., 2015) when interpreting genetic data in sponges when equally viable hypotheses emerge from a more poriferan-centred approach. Currently, we lack sufficient data to conclude that the sponge sensory and eumetazoan nervous systems are homologous. Our analysis suggests that the null hypothesis, that SNMs may hold non-sensorial functions, is equally possible, if not more likely. But this is a nascent and exciting field, and further advances may yet transform the enticing insights genetic data has delivered so far.

Definitions list

Pinacyctes: Plate-like cells that form the sponge epithelium. Pinacyctes form the outer surface of the sponge as well as line the canals of the canal system.

Choanocytes: A specialized feeding cell. Choanocytes are arrayed in chambers connected to the sponge canal system. Choanocytes possess an apical crown of micrornicles encircling a beating flagellum, which drives water through the canals. Food particles entrained in the current are filtered out and subsequently phagocytized by the sponge.

Archaeocytes: Motile stem cells found within the middle layer of the sponge. Archaeocytes give rise to several sponge cell types, including choanocytes and pinacyctes.

Spicules: Spicules are structural elements which act as a lattice to support sponge tissues. They are made of silica or calcite.

Skeletogenic elements: All cell types involved in the creation and organization of spicules. These include sclerocytes, which directly secrete and shape spicules, as well as cells that are involved in transporting spicules throughout the sponge body.

Ostia: Incurrent openings on the outer surface of the sponge through which water enters.

Atrial cavity: A space to which all excurrent canals converge. Water is deposited into the atrium before exiting through the osculum.

Osculum: The single excurrent vent through which water exits the sponge.

Pore cells: Cells or groups of cells that form the pores through which water enters the sponge.

Sieve cells: A sieve-like contractile cell which may serve to regulate water flow through the canal system (Steinmetz et al., 2012).

Amphiblastula: A calcareous free-swimming larva possessing an anterior hemisphere of ciliated columnar cells and a posterior hemisphere of large cells.

Cross cells: Four cells of unknown function spaced equidistantly around the equator of the calcareous amphiblastula.

Parenychymella: An ovoid free-swimming larva found in Demospongiae.

Globular or mucous cells: large cells with electron-dense inclusions found embedded within the epithelium of the parenychymella larva Amphimedon queenslandica (Leys and Degnan, 2001).

Flask cells: Bottle-shaped cells embedded within the epithelium of the A. queenslandica parenychymella larvae. Flask cells have clear cytoplasmic vesicles and a single sunken epithelium extending from the apical surface (Leys and Degnan, 2001).

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ydbio.2017.06.012.

References


