Cadherin switch marks germ layer formation in the diploblastic sea anemone *Nematostella vectensis*

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Abstract

Morphogenesis is a shape-building process during development of multicellular organisms. During this process the establishment and modulation of cell-cell contacts play an important role. Cadherins, the major cell adhesion molecules, form adherens junctions connecting epithelial cells. Numerous studies in Bilateria have shown that cadherins are associated with the regulation of cell differentiation, cell shape changes, cell migration and tissue morphogenesis. To date, the role of Cadherins in non-bilaterians is unknown. Here, we study the expression and the function of two paralogous classical cadherins, cadherin1 and cadherin3, in the diploblastic animal, the sea anemone *Nematostella vectensis*. We show that a cadherin switch is accompanying the formation of germ layers. Using specific antibodies, we show that both cadherins are localized to adherens junctions at apical and basal positions in ectoderm and endoderm. During gastrulation, partial EMT of endodermal cells is marked by a step-wise down-regulation of cadherin3 and up-regulation of cadherin1. Knockdown experiments show that both cadherins are required for maintenance of tissue integrity and tissue morphogenesis. Thus, both sea anemones and bilaterians use independently duplicated cadherins combinatorially for tissue morphogenesis and germ layer differentiation.

Introduction

Morphogenesis is a process of tissue and organ formation during organism development (Gilbert, 2013), driven by coordinated cell shape changes, cell migration, cell proliferation and cell death and cell adhesion. The key morphogenetic events during early development are gastrulation and germ layer formation, folding of the neural tube and body axis elongation. Cadherins are transmembrane cell adhesion molecules, which play an important role in these processes. They do not only provide the mechanical connection between cells, but also control cell-cell recognition, cell sorting, tissue boundary formation, signal transduction, formation of cell and tissue polarity, cell migration, cell proliferation and cell death (Gumbiner, 2005; Halbleib and Nelson, 2006). In adult tissues, cadherins preserve stable and ordered tissue integrity (Angst et al., 2001; Halbleib and Nelson, 2006).

Classical cadherins are conserved molecules present in all animals whose genomes have been analyzed (Alberts, 2007). They are major components of the adherens junctions between cells, which are conserved structures of epithelial cells in most animals (Meng and Takeichi, 2009). In adherens junctions, cadherins form homophilic (more rarely heterophilic), calcium dependent interactions with other cadherin molecules from neighboring cells. The cytoplasmic domain of cadherins is highly conserved among metazoans, distinguishing classical cadherins from other cadherin subfamilies (Hulpiau and van Roy, 2011; Oda and Takeichi, 2011). It contains β-catenin and p120 binding sites, which connect catenins with the actin cytoskeleton in a dynamic manner (Meng and Takeichi, 2009). In comparison with other cadherin subfamilies, classical cadherins are unique by showing the most noticeable variation in their extracellular region among different species (Hulpiau and van Roy, 2011). Indeed, the extracellular domain consists of a variable number of cadherin repeats of about 110 amino-acids each, and - depending on the species - the presence of laminin G and EGF-like domains.

During development, the regulation of specific cadherin expression correlates with the formation of new tissues. For instance, the folding of the neural tube in vertebrates occurs in parallel with down-regulation of epithelial cadherin (E-cadherin) and up-regulation of neuronal cadherin (N-cadherin) (Nandadasa et al., 2009). Such cadherin switches are characteristic of several different morphogenetic processes, for example, during gastrulation and neural crest development (Basilicata et al., 2016; Dady et al., 2012; Detrick et al., 1990; Giger and David, 2017; Hatta and Takeichi, 1986; Pla et al., 2001; Rogers et al., 2013; Scarpa et al., 2015; Schäfer et al., 2014; Shoval et al., 2007). During mesoderm formation of *Drosophila*, *Dme*_E-cadherin becomes replaced by *Dme*_N-cadherin (Oda et al., 1998), similar to the switch from E- to N-cadherin during mesoderm formation in chicken (Hatta and Takeichi, 1986). It has also been shown that N-cadherin expression triggers active endodermal cell migration, which leads to the cell segregation and germ layer formation (Ninomiya et al., 2012). Moreover, a cadherin switch allows efficient Wnt, BMP and FGF signaling, required for proper mesoderm differentiation in both fruitfly and mouse (Basilicata et al., 2016; Giger and David, 2017; Ninomiya et al., 2012; Schäfer et al., 2014). For example, N-cadherin can interact with the FGF receptor and modulate the signaling pathway (Francavilla et al., 2009; Williams et al., 1994). Therefore, accurate control of the expression of cadherin is important for proper cell movements during gastrulation, like epiboly, or convergence and extension of the tissue during axis elongation (Babb and Marrs, 2004; Basilicata et al., 2016; Shimizu et al., 2005; Winklbauer, 2012).

While the role of cadherins has been studied in model bilaterian species, very little is known in diploblastic organisms, such as cnidarians. Most of our knowledge on cell adhesion molecules in cnidarians is restricted to genome analyses (Hulpiau and van Roy, 2009; Hulpiau and van Roy, 2011; Tucker and Adams, 2014) or biochemical studies (Clarke et al., 2016). The sea anemone *Nematostella vectensis* has become one of the prime model organisms for embryonic development during the last two decades (Genikhovich and Technau, 2009a; Layden et al., 2016; Technau and Steele, 2011). A bioinformatic analysis of the available genome sequence of *Nematostella vectensis* (Putnam et al., 2007) revealed 16 different cadherins from all main groups of the cadherin superfamily (classical, flamingo, FAT, dachsous, FAT-like, protocadherins and cadherin-related proteins) (Hulpiau and van Roy, 2011). It has been shown that adherens junctions in *Nematostella* ultrastucturally resemble those in bilaterians (Fritzenwanker et al., 2007). However, the molecular composition of these junctions has not yet been described, and a recent report questioned the presence of adherens junctions in the inner layer of *Nematostella* (Salinas-Saavedra et al., 2018).

Germ layers are formed in *Nematostella* by invagination of the endoderm at the animal pole (Kraus and Technau, 2006; Magie et al., 2007). However, whether classical cadherins play a role in germ layer formation of a non-bilaterian is not known. Here, we show that classical cadherins of *Nematostella*, Cadherin1 (Cdh1) and Cadherin3 (Cdh3), form the adherens junctions of the epithelium of both germ layers. Germ layer differentiation in *Nematostella* is marked by a cadherin switch, where Cdh3 is down-regulated in the inner, endodermal layer, while Cdh1 is up-regulated and remains the only cadherin expressed in the endoderm. Unexpectedly, we found that in addition to apical adherens junctions both Cdh1 and Cdh3 are also involved in cell junctions between cells on the basal-lateral side. Knockdown experiments of *cdh1* and *cdh3* indicate important roles of cadherins in cell adhesion and tissue morphogenesis of this diploblastic metazoan.

Results

Structure of classical cadherins of *Nematostella vectensis*

Three genes encoding classical cadherins have been predicted in the genome of *Nematostella vectensis – cadherin1, cadherin2, cadherin3 (cdh1, cdh2, cdh3)* (Hulpiau and van Roy, 2011). However our analysis of the *cadherin2* gene model showed that it is a fusion of two separate gene models for which we have no evidence of its complete transcription. *cdh2* is not detectable by *in situ* hybridization. Furthermore, the hallmarks of the cadherin intracellular domain are absent. Therefore, *cdh2* may be either a pseudogene or the result of an incorrect assembly. Hence, this gene model is not further investigated here.

Hulpiau and van Roy predicted 25-32 EC repeats for *Nematostella* cadherins (Hulpiau and van Roy, 2011). However, in a recent publication, two cadherins with 14 and 30 EC repeats, respectively, were reported (Clarke et al., 2016). We cloned both cadherin1 and cadherin2 in overlapping fragments of 2-3kb length, resulting in full-length cDNA clones of >13 kb, predicting a protein size of about 480 kDa for both cadherins. The protein model suggest a structure similar to classical cadherins, composed of a typical intracellular domain with binding sites for ß-catenin and p-120, and a large extracellular domain consisting of three EGF-like and two interspaced Laminin G domains, followed by 31 (cdh1) or 32 (cdh3) extracellular (EC) repeats. This is similar to the original model of Hulpiau and van Roy (Fig. 1) and we therefore follow their gene terminology. By comparison, fruit fly cadherin has 17 EC repeats, and chick cadherin has 13 EC repeats, mouse cadherin has only 5 EC repeats (Hulpiau and van Roy, 2011).

We also interrogated the genomes and transcriptomes of several other cnidarians and found that all investigated cnidarian cadherins have 30-32 EC domains and the EGF/Laminin domains in the extracellular part. Notably, corals and hydrozoans have only a single classical cadherin while the sea anemones underwent a lineage-specific gene duplication (Fig. 1; Fig. S1). Mammals have lost the extracellular EGF and LamG domains and have retained only a few EC domains (Hulpiau and van Roy, 2011). Interestingly, platypus has several paralogs of the short version with no EGF/LamG domains, typical for mammals, but also one classical cadherin with EGF/LamG domains and many EC domains, like other non-mammals. This suggests that an ancestral "long" cadherin gene duplicated in the ancestor of placental mammals and platypus and one of the duplicates underwent a drastic loss of EC and EGF/LamG domains. Platypus has kept both versions, while other mammals have retained only duplicates of the short classical cadherin version.

Expression of classical cadherins is highly dynamic during early development of *Nematostella*

To characterize the pattern of classical cadherin expression during normal development, *in situ* hybridization has been performed on developmental stages from early cleavage through adult polyp. *cdh3* is maternally expressed at significant levels, which are detectable at the earliest cleavage stages. *cdh3* is then strongly expressed in all cells starting from the egg until gastrula stage (Fig. 2A-D,M). During early gastrulation *cdh3* expression is decreased in the presumptive endoderm (Fig. 2B,C), and completely down-regulated in the endoderm by the planula stage (Fig. 2B-E).

By comparison, *cdh1* expression could not be detected by *in situ* hybridization until early gastrula stage (Fig. 2G-I), although RNAseq data suggest that it also maternally expressed at lower levels (Casper et al., 2018). During gastrulation *cdh1* expression first appears and intensifies in the pre-endodermal plate (Fig. 2H,I). At late gastrula stage *cdh1* starts being expressed in the aboral ectoderm and then expands orally during planula development (Fig. 2J,K). Interestingly, at the late planula stage, the strongest *cdh1* expression is detected in the endoderm and in the subpopulation of ectodermal cells, which give rise to a sensory apical organ (Fig. 2K).

In primary polyp, *cdh3* expression remains strongly expressed in the tentacles and in the pharynx and weakly in the body-wall ectoderm (Fig. 2F). Interestingly, *cdh3* in juveniles and adults is detectable only in the ectoderm of the pharynx and tentacles, ciliated tract, septal filaments and developing eggs, with hardly any expression in the body-wall ectoderm (Fig. S2A,B). Almost complementary to that, *cdh1* is expressed both in the ectoderm and endoderm, but it is completely excluded from the ectoderm of the pharynx and tentacles (Fig. 2L). In juveniles, *cdh1* is expressed in the endoderm and body-wall ectoderm, but not in the ectoderm of most of the pharynx. Interestingly, the part of the pharynx carrying siphonoglyph and the ciliary tract below the pharynx specifically expresses low levels of *cdh1* (Fig. S2C-H*)*. In adults, *cdh1* is expressed in the body-wall endoderm and in small oogonia (Fig. 2N; Fig. S2I).

Cdh3 is the main component of adherens junctions during cleavage and gastrulation

We wished to visualize the subcellular localization of Cdh3 protein during development. We generated specific polyclonal and monoclonal antibodies against two recombinant fragments of Cdh1 and three peptides of Cdh3, respectively (Fig. S3). All antibodies against the different fragments and peptides consistently showed the same pattern for Cdh1 and Cdh3, respectively (Fig. S4; Materials and Methods) (Madeira et al., 2019). Immunocytochemistry experiments were carried out at all stages of development. Cdh3 protein is already accumulated at the apical cell junctions at the first cell divisions, suggesting a role in establishing early cell polarity. It is also detectable in less confined areas at the lateral contacts between cells (Fig. 3A-C). Interestingly, cells maintain their polarity during cell divisions. In contrast to the Par system proteins (Ragkousi et al., 2017; Salinas-Saavedra et al., 2018) Cdh3 stays localized at the apical cell junctions at different cell cycle stages (Fig. 4). It is possible that the polarized Cdh3 at the junctions may guide the Par system proteins during their transient loss of polarity during cell division. Later, during blastoderm formation, apical cell junctions become more pronounced (Fig. 3D-F). Strikingly, we found that Cdh3 also localizes on the basal-lateral side of the cells (Fig. 3D-L), in addition to the apical localization. Ultrastructural analysis by transmission electron microscopy revealed that the cell-cell junctions at the basal side resemble the adherens junctions at the apical side (Fig. 3M,N). However, during blastula stage, asynchronously dividing cells lose transiently the basal-lateral localization of Cdh3 (Fig. 3E, a yellow star), similar to the early cleavage stage, when cells are synchronously dividing (Fig. 3B,C; Fig. 4). Thus, *Nematostella* has a unique epithelium, where cells form cell-cell contacts on both apical and basal sides. These Cdh3-positive junctions develop before any contact to an endodermal layer or presence of the mesoglea, the extracellular matrix of Cnidaria. This is remarkable, and has to our knowledge not been described in any other animal. Interestingly, as the pre-endodermal plate (PEP) starts to invaginate and the cells adopt a partial EMT phenotype, Cdh3 disappears from the basal junctions of the invaginating cells (Fig. 3G,H,I). Meanwhile, ectodermal cells of the blastoderm retain both apical and basal cell contacts. As the pre-endodermal cells lose basal junctions, its epithelium becomes less rigid and columnar. Pre-endodermal cells form filopodia and become more motile on the basal side (Fig. 3O). This event is possibly one of the crucial steps of the incomplete EMT, which pre-endodermal cells undergo during gastrulation (Kraus and Technau, 2006; Salinas-Saavedra et al., 2018). Notably, apical cell junctions expressing Cdh3 are preserved in the pre-endodermal cells during the course of gastrulation (Fig. 3J-L).

After the invagination process is completed, Cdh3 fully disappears from the cell junctions of the endoderm, concordant with the decrease of mRNA expression in the whole endoderm. Cdh3 remains expressed exclusively in the ectoderm, forming apical and basal cell junctions (Fig. 5A-E). Notably, while the boundary between ectoderm and endoderm is very difficult to discern by morphological criteria, Cdh3 localization at the cell junctions in the pharynx precisely marks the boundary between the last ectodermal and the first endodermal cell (Fig. 5B,E). At the polyp stage Cdh3 remains exclusively expressed in the ectoderm, with especially strong expression in the pharynx and the tentacles (Fig. 5F,G).

Cdh1 protein expression marks a cadherin switch during endoderm formation

After completion of gastrulation, Cdh1 protein forms pronounced cellular junctions. At early planula larva Cdh1 localizes to the apical and basal junctions of the endoderm (Fig. 6A-D). Hence, the formation of the endoderm is marked by a cadherin switch from Cdh3 to Cdh1.

It should be noted, though, the transcriptome data suggest some maternal deposition of *cdh1* in the embryo, even though *in situ* hybridization does not detect *cdh1* till the late gastrula stage. Indeed, the anti-Cdh1 antibody detects a fuzzy signal beneath the apical cell membrane in all cells at the early gastrula stage, which might be maternal Cdh1 protein that has not yet localized to the cell junctions.

In addition to endodermal expression, Cdh1 is strongly expressed in the apical organ ectoderm and then expands into a wider domain in the aboral ectoderm, where Cdh1 and Cdh3 are co-expressed (Fig. 6). At the ectodermal surface, expression of the Cdh1 decreases along a gradient towards the oral pole (Fig. 6L). Interestingly, the ectodermal cell population that gives rise to the apical tuft is also different from the rest of the ectoderm in terms of cadherin expression. These cells lose Cdh3 basal junctions, while keeping the apical junctions (Fig. 5C). This specific arrangement may be connected with the special function of these cells (Fig. S5). Indeed, the loss of Cdh3 expression in the ectodermal apical tuft cells goes hand in hand with an up-regulation of Cdh1 in these cells (Fig. 2K; Fig. 6A,C).

We have demonstrated that Cdh3 is the major component of adhesion complexes during cleavage and gastrulation and is present in all cells until late gastrula stage. Cdh3 forms apical and basal cell junctions in the blastodermal epithelium, which during invagination of the pre-endodermal plate disappear from basal cell junctions of the future endoderm. Further endoderm differentiation leads to the complete Cdh3 to Cdh1 replacement. Therefore, there is a distinct boundary between ectoderm and endoderm which is defined by Cdh1 / Cdh3 localization.

Cdh3 in apical ectodermal junctions co-localize with β-catenin

A recent biochemical study showed that the intracellular domain of the classical cadherins can form a ternary complex with α-catenin and β-catenin (Clarke et al., 2016). To explore further the molecular composition of the cadherin cell junctions, we co-stained the embryos with the antibody against Cdh3 and with the previously described for *Nematostella* antibody against β-catenin (Leclère et al., 2016; Salinas-Saavedra et al., 2018). At blastula stage Cdh3 is co-localized with ß-catenin at the apical junctions whereas basal junctions do not show such pronounced co-localization (Fig. 7A-C; G-I). Interestingly, at planula stage β-catenin was detected only in the body wall ectoderm but neither in the ectodermal pharynx nor the endoderm (Fig. 7D-F; Fig. S6). These results could mean that not all the cell contacts of *Nematostella* epithelium contain β-catenin, in line with other recent findings (Salinas-Saavedra et al., 2018). This is surprising, as no ultrastructural differences in the junctions of endoderm and ectoderm could be detected (Fig. S7).

Function of classical cadherins in early development

To examine the function of cadherins we performed knockdown experiments using morpholinos and shRNA. First, we injected independently two non-overlapping translation blocking *cdh3* morpholinos (MO). However, we could still detect Cdh3 in apical and basal cell junctions in the whole mount MO injected embryos (Fig. 8). Indeed, on the ultrastructural level, the adherens cell junctions looked similar in morphants and in control embryos (Fig. 8C,G; 7D,H). These results can be explained by the significant maternal deposition mRNA and protein. However, development of Cdh3 morphants was arrested after gastrula stage, presumably due to the block of translation of zygotically expressed *cdh3*. As a result, when Cdh3 protein becomes limited, post-gastrula embryos are unable to develop further (Fig. 8A,B).

The mild knockdown effect on the presence of Cdh3 in the junctions also suggests that there is relatively little turnover in established junctions. Therefore, to assess the function of Cdh3 in establishing new cell junctions we used an aggregate assay. *Nematostella* gastrulae can be dissociated into single cells and small clusters and can be re-aggregated by centrifugation into the cell aggregates (Kirillova et al., 2018). We followed the establishment of cell contacts and the formation of the epithelium in the developing cell aggregates (Fig. 9). Dissociated cells do not show any signs of polarization: Cdh3 is not localized to any side (Fig. 9C). Only 30 min after re-aggregation, Cdh3 becomes localized to the apical side of the outer cells of the aggregate and the first signs of epithelialization become apparent (Fig. 9E,F,M). 12 hours after re-aggregation the outer epithelial layer is completely formed and Cdh3 is localized at the apical and basal cell junctions (Fig. 9H,I). 24 hours after re-aggregation two epithelial layers – ectoderm and endoderm are formed (Kirillova et al., 2018). Both cell layers possess basal and apical cadherin cell junctions (Fig. 9K,L,S). Cdh1 starts being expressed in both ectoderm and endoderm at 24 hours of aggregate development (Fig. 9N,Q,T,W). Similar to the normal embryo, ectoderm expresses both Cdh1 and Cdh3, while endoderm expresses exclusively Cdh1 (Fig. 9U,X).

To address the question how Cdh3 down-regulation influences the establishment of new cell contacts in the aggregate, we dissociated an equal amount of *cdh3* MO injected gastrulae and standard MO injected gastrulae as a control. The first difference we observed was that the size of the aggregates from *cdh3* morphant cells was significantly smaller than control aggregates ($p<0.0001$) (Fig. 10M-O). Moreover, aggregates from *cdh3* morpholino injected embryos start falling apart into cells immediately after re-aggregation (Fig. 10; Movies 1,2). Cdh3 knockdown in the aggregate at the protein level was shown by immunostaining (Fig. 10I;J). Ultrastructural imaging with TEM confirmed that cells in Cdh3 MO aggregates do not form well-defined subapical adherens junctions, while in the control aggregate cell contacts are well developed (Fig. 10K,L). Interestingly, cells in the Cdh3 MO aggregates make lamella-like protrusions extending to the neighboring cell on the apical surface (Fig. 10K). These results show that *cdh3* knockdown impairs the *de novo* formation of the cell contacts, although it does not affect the earlier established contacts built from the maternal protein.

To further explore the role of Cdh1 protein, we down-regulated *cdh1* using an independent approach, shRNA-mediated knockdown (He et al., 2018). As in MO knockdown, shRNA knockdown leads to the significant decrease of the Cdh1 protein as assayed by immunohistochemistry (Fig. S8; Fig. 11). Although early development including gastrulation appears largely unaffected, in the subsequent planula stage, mesenteries do not form upon *cdh1* knockdown. In all MO and shRNA injected embryos mesenteries were absent or impaired, while there are eight mesenteries developed in all control embryos at this stage (Fig. 11; Fig. 12D,H).

Besides the predominant expression in the endoderm, *cdh1* is also expressed in the apical tuft region of the ectoderm (Fig. 2K). Interestingly, *cdh1* knockdown abolishes expression of FGFa1, which is responsible for apical organ development (Rentzsch et al., 2008). In most *cdh1* MO injected embryos the apical organ does not form and there is lack of *FGFa1* expression (Fig. 12). These results suggest that Cdh1 is crucial for morphogenesis and differentiation of the endoderm as well as the development of the apical organ.

Discussion

Evolution and structure of cadherins

Although proteins with cadherin domains are present in choanoflagellates, cadherins with intracellular catenin binding domains are an important class of cell adhesion molecules that arose only in metazoans (Nichols et al., 2012). They are mediating not only cell adhesion between epithelial cells, but are strongly involved in the differentiation of specific cell types. Recently, cadherins have been shown to also convey mechanotransduction, i.e. the activation of gene expression to the nucleus upon mechanical stress, which in Drosophila and *Nematostella* is mediated by β-catenin (Lyer et al., 2019; Pukhlyakova et al., 2018; Röper et al., 2018). However, most studies on the role of cadherins have been carried out in bilaterian model organisms like mouse or *Drosophila*. Here, we show the localization and function of both classical cadherins in a representative of the Cnidaria, the sea anemone *Nematostella vectensis*. The phylogenetic analysis suggests that sea anemone have duplicated an ancestral classical cadherin, while corals and hydrozoans have retained a single copy. The two investigated *cadherin* genes code for large proteins with 31-32 EC domains each, largely confirming previous predictions from the genome (Hulpiau and van Roy, 2011) and gene models based on our transcriptome assembly (Fredman et al., 2013). This significantly extends the structure of the recently published gene model for Cdh3 (termed Cad1 in (Clarke et al., 2016). Thus, cnidarians as well as other non-bilaterians have substantially larger classical cadherins than most bilaterians and their extracellular domain structure is reminiscent of the FAT-like proteins (Hulpiau and van Roy, 2009; Hulpiau and van Roy, 2011). It will be interesting to determine which extracellular domains are engaged in homophilic or heterophilic interactions.

Cadherins are localized to apical and basal junction in both germ layers

Interestingly, both cadherins localize to apical junctions as well as to basal cell-cell junctions in the epithelial cells of both ectoderm and endoderm (Fig. 13A). Electron and confocal microscopy analyses show actin filaments attaching to the junction, suggesting that these are adherens junctions (Fig. 3G,N; Fig. 8D,H). This is in contrast to a recent study, which claimed that the endodermal epithelium does not contain adherens junctions, since neither Par complex components nor β-catenin could be detected (Salinas-Saavedra et al., 2018). Yet, in line with this study (Salinas-Saavedra et al., 2018), we could detect β-catenin in the apical adherens junctions and weakly in the basal junction of the ectoderm, but not in the pharyngeal ectoderm and the endoderm (Fig. 7; Fig. S6). This could indicate that the basal junctions in the ectoderm and all endodermal junctions are qualitatively different. However, apical adherens junctions in the ectoderm and endoderm have a very similar structure on the ultrastuctural level (Fig. S7). As we observe co-localized actin fibers at these junctions, we assume that either another protein replaces β-catenin or β-catenin is simply not detected at these junctions. Indeed, we note that the antibody also fails to stain nuclear β-catenin after early cleavage stages. Therefore, as a cautionary note, we cannot fully rule out that the failure to stain β-catenin in the pharynx and the endoderm is due to technical reasons.

While to our knowledge the basal-lateral junctions involving specific cadherins has not been described in other animals yet, more fuzzy basal-lateral localization of cadherins has been observed in other systems. For instance, the midgut epithelium of *Drosophila* shows a basal-lateral localization of a cadherin (Chen et al., 2018), albeit much less defined as described here for *Nematostella*.

Basal junctions might be an innovation of Cnidaria and can play a crucial role in morphogenesis of the epithelium. The formation of the basal junctions can be connected to the special properties and functions of the cnidarian epithelium. For example, in Hydra epithelia are composed of the multifunctional epithelia-muscular cells. These cells form basal myonemes, connected between the neighboring cells by the desmosomal-like junctions (Seybold et al., 2016). These basal connections can be associated with the contractile actin bundles and can be used for the increased synchronized contractile activity within large epithelia sheets. Basal cellular contractions have also a major contribution in the process of the bud formation in Hydra (Holz et al., 2017). Such basal contacts are absent from bilaterian embryos, which are mainly connected by apical junction belts.

Cadherin and formation of epithelia

The establishment of the adherens junctions is crucial for normal development of the embryo. Knockdown of *cdh3* in normal embryos does not lead to a dissociation of the embryonic tissue, suggesting that maternally expressed cadherin protein, localized in cell junctions might have a slow turnover and be sufficient for the early stages of development. This is consistent with knockdown of E-Cadherin in mouse embryos (Capaldo and Macara, 2007). However, proper formation of epithelial layers is disrupted in embryonic aggregates upon knockdown of *cdh3*. Notably, while knockdown of the endodermal *cdh1* does not disrupt gastrulation itself, the endoderm does not develop endodermal structures, such as mesenteries. Thus, proper development of the inner germ layer is dependent on the expression of Cdh1.

The role of cadherins in germ layer formation

The role of cadherins in the formation of germ layers in a diploblast animal is of particular interest, as we might learn about the evolution and potential homology of germ layers. We find that the formation of the inner layer is accompanied by a step-wise cadherin switch. At the blastula stage, Cdh3 forms apical and basal adherens junctions. The onset of gastrulation is characterized by a change of shape of the endodermal cells, which adopt a partial EMT phenotype: They apically constrict, lose the Cdh3-positive basal junctions, the nucleus migrates basally, the cells develop filopodia and become rather motile (Fig. 13B). We propose that the changes in the adhesion properties of the endodermal cells are crucial for the morphogenetic behavior and further differentiation. In a second step, after completion of invagination, Cdh3 also disappears from the apical junctions in the endoderm and is replaced by Cdh1 both at apical and basal junctions of the endoderm. Thus, we observe a cadherin switch in *Nematostella* that is analogous to the cadherin switch in vertebrates and insects. As *cdh1* and *cdh3*, like E- and N-cadherins in mammals and insects are lineage-specific duplications (Fig. 1), we conclude that the cadherin switch evolved convergently in these animals.

However, while Cdh3 is not expressed in the endoderm after the gastrula stage, Cdh1 shows partially overlapping expression with Cdh3 in the ectoderm. Cdh1 seems to form a decreasing gradient from aboral to oral, but the significance of this gradient is unclear at this point. Notably, the oral region and tentacles are completely devoid of Cdh1 expression. Interestingly, *cdh1* knock down does not disrupt oral patterning. For example, the expression of the blastopore marker *brachyury* was normal. However the expression of the aboral patterning gene *FGFa1* was abolished. Since the aboral part is an area of strong Cdh1 expression, we assume, that normal Cdh1 expression is necessary for FGF signaling and apical organ development. Our results show that *Nematostella* cadherins are important for germ layer morphogenesis and the maintenance of tissue integrity . However, so far we have no evidence that cadherins play role in initial germ layer differentiation, as shown similarly for the knock-down of α-catenin, another component of the adhesion junction complex (Clarke et al., 2019). We conclude that like in bilaterians (Basilicata et al., 2016; Giger and David, 2017; Huang et al., 2016; Nakagawa and Takeichi, 1998; Pla et al., 2001; Schäfer et al., 2014; Shoval et al., 2007), different combinations and concentrations of Cdh1 and Cdh3 convey different tissue properties and identities in different regions of the developing embryo. Thus, the combinatorial and differential use of cadherins is a recurring feature of metazoans (Fig. 1; Fig. S1; Fig. 13C), although the paralogous molecules have evolved independently.

Interestingly, our phylogenetic analysis of the classical cadherins showed that hydrozoans and stony corals have only cadherin protein, which groups basally with two classical cadherins of sea anemones, suggesting that *cdh1* and *cdh3* arose by a lineage-specific gene duplication within the sea anemones (Fig.1). The expression and function of the single cadherin in other cnidarians is unknown. However, they do have a *dachsous* gene, which also encodes a cytoplasmic cadherin domain and has a similar structure as classical cadherins, except that they lack the EGF/LamininG domains found in most invertebrate cadherins. It remains to be shown whether Dachsous and classical cadherin could interact during early germ layer formation in other cnidarians.

Homology of germ layers

Our study has established that cadherins play an important role in the formation and differentiation of the germ layers in a diploblastic animal. This revives the question to which germ layers in Bilateria these two cell layers are homologous. Traditionally, they have been homologized with endoderm and ectoderm, with the mesoderm missing. The identification of a number of mesodermal transcription factors in cnidarians and their expression in the endoderm led to the notion of an inner "mesendoderm" (Fritzenwanker et al., 2004; Kumburegama et al., 2011; Martindale, 2004; Salinas-Saavedra et al., 2018; Scholz and Technau, 2003). However, a recent analysis of many endodermal and mesodermal marker genes has suggested that segregation has already taken place in the *Nematostella* polyp. In fact, the inner layer rather corresponds to mesoderm, while all endodermal functions reside in the ectodermally derived extensions of the pharynx, the septal filaments (Hashimshony, 2017; Steinmetz et al., 2017). In the light of those new findings, it is interesting to note that Cdh1 is specific to the inner cell layer, which would correspond to the mesoderm of bilaterians. Notably, this cell layer also expresses the zinc finger transcription factor *snailA* (Fritzenwanker et al., 2004; Martindale, 2004). Snail proteins regulate the downregulation of *E-cadherin* in vertebrates and insects in the ingressing mesoderm (Nieto, 2002). In line with this, *snail* genes appear to play a role in regulating invagination and partial EMT in *Nematostella* (Salinas-Saavedra et al., 2018). It will be of interest to investigate how the cadherins are regulated by Snail in *Nematostella*.

Conclusion:

This first analysis of the expression and function of classical cadherins in a diploblast shows that these molecules play a conserved role in cell adhesion, tissue morphogenesis and germ layer specification during embryogenesis. The invaginating cells show partial EMT, accompanied by a cadherin switch. The evolutionarily recurring mechanism of a cadherin switch suggests that the evolution of germ layer formation and tissue morphogenesis was facilitated by the differential expression of cadherins.

Material and Methods:

Animals and embryo culturing

Animals were kept in artificial seawater at 18°C the dark. Spawning was induced by temperature shift to 24°C and light exposure over 10 hours (Fritzenwanker and Technau, 2002). In vitro fertilized embryos were collected and kept at 21°C as described (Fritzenwanker and Technau, 2002; Genikhovich and Technau, 2009c).

Identification of Cdh1 and Cdh3 protein sequences

To retrieve the coding sequences of *cdh1* and *cdh3* genes the 1-3Kb overlapping coding fragments of *cdh1* and *cdh3* were amplified from cDNA of mixed embryonic stages, cloned using pJet1.2/blunt vector system (ThermoFisher Scientific) and sequenced. The full-length sequences of Cadherin1 and Cadherin3 have been deposited at Genbank (accession numbers MK253651 and MK253652).

Assembled *cdh1* and *cdh3* protein coding sequences were derived *in silico* using Expasy translation tool (Artimo et al., 2012). Cadherin protein domain annotation was performed using SMART protein domain annotation resource (Letunic and Bork, 2018).

Morpholino injection

cdh1 and *cdh3* knockdowns were performed by independent zygote injections of two non-overlapping translation blocking morpholinos (Gene Tools, LLC):

cdh1MO1 - 5’ CCGGCCAGCACTCATTTTGTGGCTA 3’;
cdh1MO2 - 5’ ACCCGTGAGTTTAAAAACCCATAGC 3’;
cdh3MO1 5’ ACGAGTTGCGGTGAACGAAAATAAC 3’;

cdh3MO2 5’ TAGCAGAACCGTCCAGTCCCATATC 3’ at concentration of 500 µM.
Standard morpholino injection at 500 µM was used as a control.
SdtMO – 5’ CCTCTTACCTCAGTTACAATTTATA’

Non-overlapping morpholinos for *cdh1* and *cdh3* knockdown had similar phenotypes. Injection equipment used: FemtoJet (Eppendorf), CellTram Vario (Eppendorf), micromanipulator (Narishige), needles were pulled from the glass capillaries type GB 100TF-10 (Science Products GmbH) with a micropipette puller (Sutter Instrument CO., Model P-97). We used holding capillaries from Eppendorf for the injection (Renfer et al., 2010).

Short hairpin RNA (shRNA) knockdown

cdh1 shRNA design and synthesis were performed as described (He et al., 2018). The following primers were used for *cdh1* shRNA synthesis:
cdh1 shRNA F:
TAATACGACTCACTATAGAAGCGCGCTCAGGTAAATGTTTCAAGAGA
cdh1 shRNA R:
AAGAAGCACGTTCGGGTAAATGTTCTCTTGAAACATTTACCTGAGCGC
Purified shRNA was injected into zygotes at concentration of 500 ng/µl. As a negative control shRNA against mOrange was injected at 500 ng/µl. Uninjected embryos from the same batch were used as a control for injection. After the injection embryos were raised at 21°C.

Generation of Cdh1 and Cdh3 antibodies

To generate antibodies against Cdh1 we expressed the protein domains cdh1:domain1 (extracellular) and cdh1:domain3 (intracellular) in *E.coli*. The fragment sequences were the following:

Cdh1 domain1 (extracellular):
NAPKDGSLLIIVNAYDGNFTGGVIGKPYYQDDDFDGDENTYELNSQSPGSYFRVNEG
NGDITAAPMIPMGEYNLKIRVTEKKDSPSTVTSSVRVLVRRIDKEAVDNGVAVEFTD
MRKVGYFVGDYYKGFEDVLASTLGVPTGDIKIFSVQKAHDNGLAVVVFFTVAAKDS
YMPHWDVVSKLVDAKKPLESLGLKVSRLGMD

Cdh1 domain3 (intracellular):

RRPEPVVVYADSTDTGHVHDNVRLYHDDGGGEEDNLGYDITKLMKYTYIETTIAPPS
VAPSKASEDKISTSSDQPLLQGRPPDAVFGLTGKEPGPKMPKYMEGDDVGDFITTRV
KITDREVFLAVDELHIYRYEGDDTDVD

The column-based affinity purified recombinant protein fragments were used for immunization. Specifically, the extracellular fragment was used for immunization of two rats (polyclonal Cdh1 antibodies 1 and 2) and the intracellular fragment was used for immunization of a rabbit (polyclonal Cdh1 antibody 3). All Cdh1 antibodies resulted in the same staining pattern (see Fig. S4). Cdh1 antibody2 was used for most experiments in this paper.

For visualization of Cdh3, monoclonal antibodies were produced in mice. The following peptides were used for immunization: SSSDRNRPPV (for Cdh3 antibody1); DEKDPPQFSQ (for Cdh3 antibody2). Both epitopes are located in the extracellular part of Cdh3 in the third and seventh cadherin repeats, respectively. Both antibody clones - Cdh3 antibody1 and Cdh3 antibody2 resulted in the same staining patterns (see Fig. S4). Cdh3 antibody2 was used for antibody staining in this paper.

Antibody and Phalloidin staining

For Cdh1 antibody staining embryos were fixed for 1h at 4°C with Lavdovsky's fixative (3,7% formaldehyde (FA)/50% ethanol/4% acetic acid). For Cdh3 and β-catenin antibody and phalloidin staining embryos were fixed for 1h with 3,7% FA in PBS at 4°C. Primary polyps were relaxed prior the fixation in 0,1 M $MgCl_2$ in *Nematostella* medium for 10 min. After fixation, embryos were incubated on ice in ice cold acetone (chilled at -20°C) for 7 min followed by 5 washes with PBSTx 0,2% (PBS with 0,2% of TritonX-100).

Then embryos were incubated in blocking solution (20% sheep serum, 1% Bovine Serum Albumin (BSA) in PBSTx (0,2%) for 2h at room temperature (RT). Primary mouse anti-Cdh3 antibody (1:1000), rabbit β-catenin antibody (Sigma C2206, 1:500) (Leclère et al., 2016; Salinas-Saavedra et al., 2018) and/or rat/rabbit anti-Cdh1 antibodies (1:500) were diluted in blocking solution and incubated with the embryos overnight at 4°C, followed by washing in PBSTx 0,2% at RT (10x 10 minutes each). at RT. After incubation in blocking solution for 2 h at RT, embryos were placed in a secondary antibody solution: goat anti-mouse Alexa Fluor 568 antibodies (1:1000), goat anti-rat Alexa Fluor 488 antibodies (1:1000) and DAPI overnight at 4 °C. When fixed with FA, phalloidin Alexa Fluor 488 (1:30) (Thermo Fisher Scientific) was added to the secondary antibody solution, since phalloidin staining is not compatible with the Lavdovsky's fixation. Embryos were washed in PBSTx 0,2% at RT (10x 10 minutes each), infiltrated with Vectashield antifade mounting medium (Vector laboratories) at 4°C overnight. For β-catenin staining of the embryo sections, fixed embryos were embedded in 10% gelatine in PBS. Gelatine blocks were post-fixed in 3,7% FA in PBS overnight at 4°C and sectioned on a vibratome Leica VT 1200S. 50 µm embryo sections were stained with β-catenin antibody, phalloidin and DAPI as described for the whole-mount embryos. Imaging was performed with Leica TCS SP5 DM-6000 confocal microscope.

In situ hybridization

In situ hybridizations of embryos were conducted as previously described (Genikhovich and Technau, 2009b; Kraus et al., 2016). The following regions of the CDS of cadherins were used to produce the *in situ* hybridization probes: for *cdh1* (7054-9126bp); for *cdh3* (2728-5091bp). Adult animals and juveniles were relaxed for 20 min in 0,1M $MgCl_2$ solution in *Nematostella* medium followed by fixation and *in situ* hybridization as described (Steinmetz et al., 2017). After *in situ* hybridization embryos, adult and juvenile pieces were embedded in 10% gelatine in PBS. Gelatine blocks were post-fixed in 3,7% FA in PBS overnight at 4°C and sectioned on a vibratome Leica VT 1200S. Embryos and adult and juvenile 50 µm sections were embedded in 80% glycerol and imaged with the Nikon Eclipse 80i compound microscope equipped with DIC optics and Zeiss AxioCam camera.

Time-lapse microscopy

Time-lapse imaging was carried out with the use of a Nikon Eclipse 80i compound microscope. Pictures were taken Zeiss AxioCam camera. Time-lapse movies were made with the use of FIJI software (Schindelin et al., 2012).

Transmission electron microscopy (TEM)

TEM was performed as previously described (Fritzenwanker et al., 2007).

Phylogenetic analysis

The protein complements of *Mus musculus* (GRCm38) (Schneider et al., 2017) and *Drosophila melanogaster* (FB2018_03) (Thurmond et al., 2019) were downloaded from Ensembl (Zerbino et al., 2018), *Strongylocentrotus purpuratus*, *Capitella teleta*, *Lottia gigantica* and *Tribolium castaneum* from Ensembl metazoan (Kersey et al., 2018), *Hydra vulgaris* and *Ornithorhynchus anatinus* from RefSeq at NCBI (O'Leary et al., 2016), *Acropora millepora* (PRJNA74409) (Moya et al., 2012), *Anemonia viridis* (PRJNA260824) (Rachamim et al., 2015), *Exaptasia pallida* (PRJNA386175) (Baumgarten et al., 2015), *Stylophora pistilata* (PRJNA281535) (Voolstra et al., 2017) from the Sequence Read Archive at NCBI (Leinonen et al., 2011), *Acropora digitifera* from marine genomics at OIST (Shinzato et al., 2011). Sequences were selected which had a significant domain hit (domE $< 1 \times 10^{-5}$) to the Cadherin cytoplasmic Pfam family (PF01049) according to HMMER 3.2.1 (Finn et al., 2011). When multiple isoforms were present, the longest one was used. The genes were filtered against truncated and misassembled gene models manually. Sequences were aligned using MAFFT v7.307 in E-INS-i mode and a maximum of 1000 iterations of refinement (Katoh and Standley, 2013). The WAG+F+R6 model was determined as optimal by the Bayesian Information Criterion using ModelFinder (Kalyaanamoorthy et al., 2017). This was used to infer a maximum likelihood tree using IQTREE (Nguyen et al., 2015). Support values were determined with 1000 standard bootstrap replicates. Domain architectures were determined using standalone interproscan (Mitchell et al., 2019). Sequence, alignment files and Subtree files can be obtained upon request.

Analysis of the size of the cell aggregates

50 Cdh3 morpholino (MO) embryos and 50 Std MO control embryos were dissociated into cells at the gastrula stage. Cell aggregates were generated by slow centrifugation as described (Kirillova et al., 2018) and photographed immediately after centrifugation. The size of the aggregates was analyzed with FIJI software. (FIJI/Image/Adjust/Threshold tool and FIJI/Analyze/Analyze particles). The threshold was set to 50. The experiment was repeated three times.

Image processing

Images were processed and adjusted for brightness and contrast using FIJI software (Schindelin et al., 2012). Focus stacking of ISH images was done using Helicon Focus software (Helicon Soft Ltd, Kharkov, Ukraine). Images were cropped and assembled into the figures as well as schemes were made using Adobe Illustrator CS6 software (Adobe, San Jose, USA).

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Author contributions

E.P, U.T. conceived the study; E.P. and U.T. designed the experiments; E.P. performed the experiments; E.P. and A.K. performed the aggregate experiments; Y.K. and A.K. performed transmission electron microscopy imaging; B.Z. and E.P. performed statistical analysis of the aggregate sizes and phylogenetic analysis; ,E.P. and U.T. wrote the paper.

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Figures

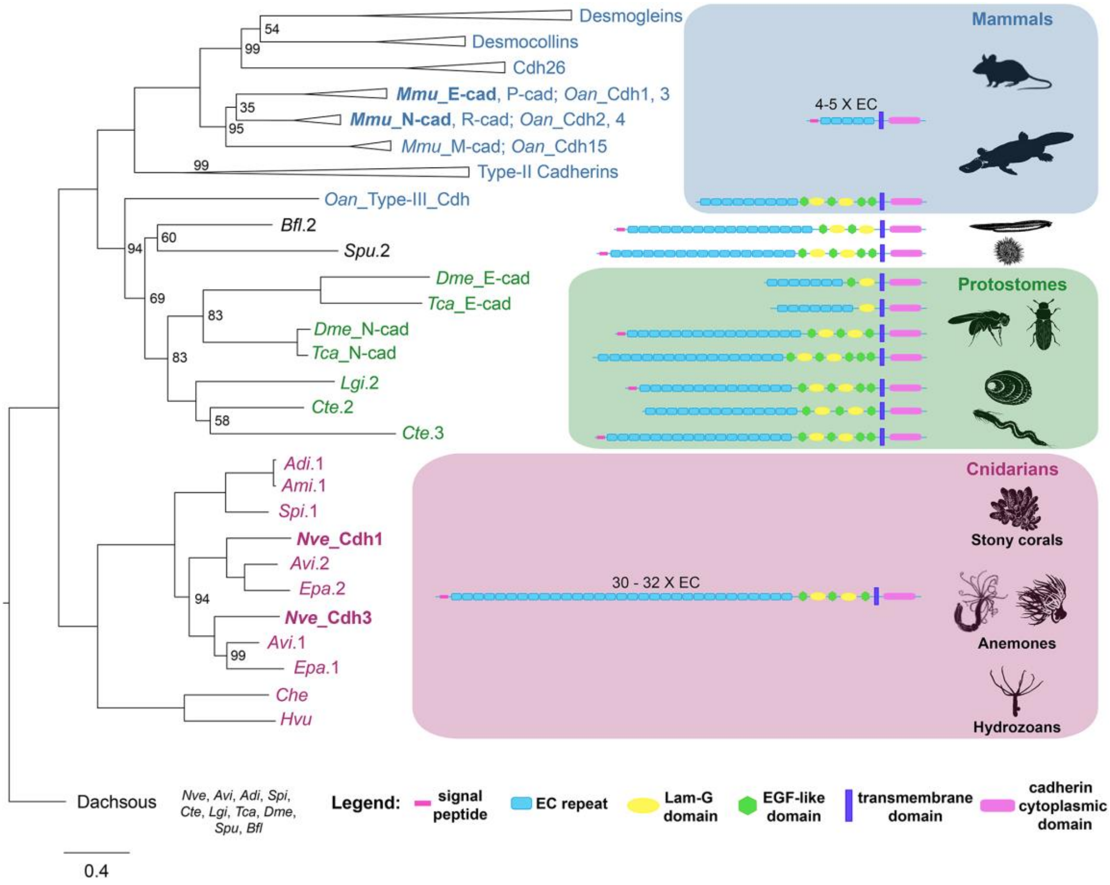


Fig. 1. Maximum likelihood phylogenetic tree of classical and other cadherins. Sequences of all proteins containing a cytoplasmic cadherin domain were extracted from the genomes and transcriptomes of *Mus musculus* (*Mmu*), *Ornithorhynchus anatinus* (*Oan*), *Branchiostoma floridae* (*Bfl*), *Drosophila melanogaster* (*Dme*), *Tribolium castaneum* (*Tca*), *Capitella teleta* (*Cte*), *Lottia gigantea* (*Lgi*), *Nematostella vectensis* (*Nve*), *Anemone viridis* (*Avi*), *Exaiptasia pallida (Epa)*, *Acropora millepora* (*Ami*), *Acropora digitifera* (*Adi*), *Stylophora pistillata* (*Spi*) *Clytia hemisphaerica* (*Che*), *Hydra vulgaris* (*Hvu*). Proteins with no annotation in their respective databases were assigned an arbitrary number. All gene names are based on the respective databases' annotations, except for Oan Type-III Cdh, Nve Cdh1 and Nve Cdh3, which were annotated based on the findings from Hulpiau and van Roy (2011). Dachsous cadherin proteins, which also contain a cytoplasmic

cadherin domain, were used as an outgroup. The number at the nodes indicates the bootstrap support; nodes with no label have 100 % support. Domain organization is shown on the right. Some proteins lack a signal peptide. It is either an indication of a truncated protein (e.g. *Che*, *Avi*) or can be a result of assembly mistakes in a gene model.

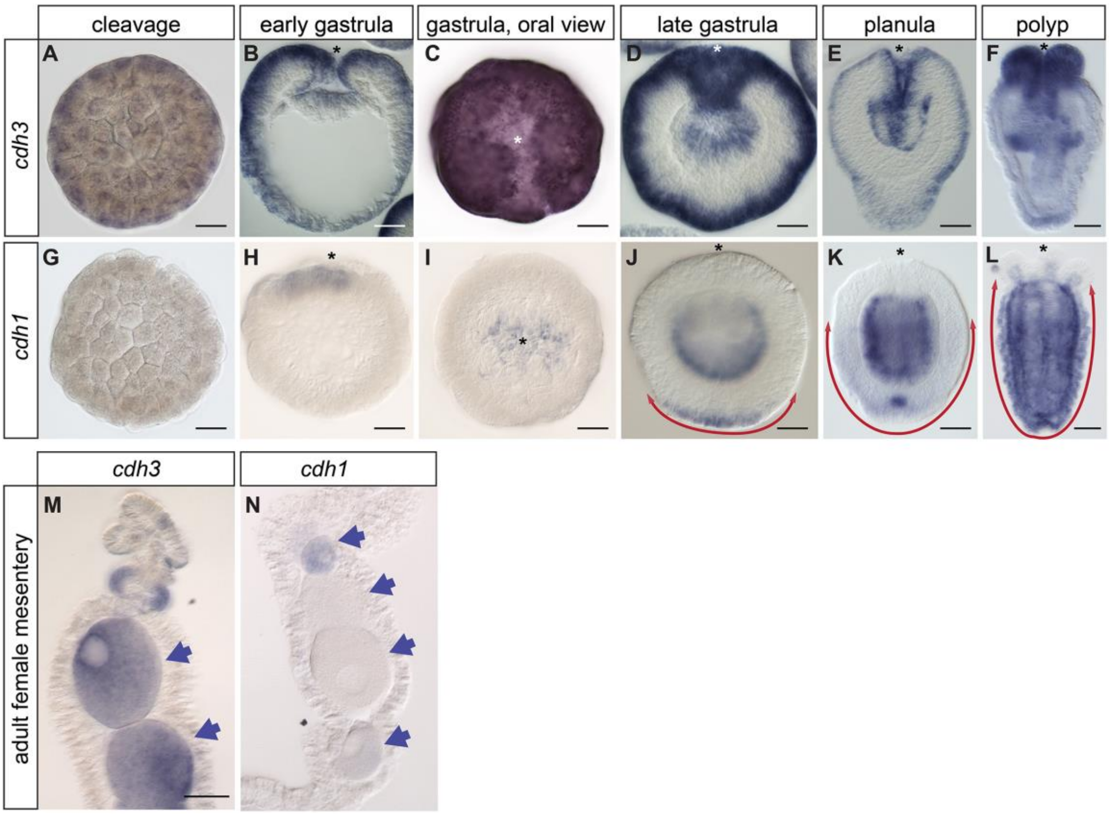


Fig. 2. *cadherin3* and *cadherin1* expression is highly dynamic during early development and polyp growth. (A, G) Cleavage. (B, H) Early gastrula, lateral section. C, I: Early gastrula, oral view. D, J: Late gastrula, lateral section. (E, K) Planula, lateral section. (F, L) Primary polyp. (M, N) Adult mesentery section. Double-headed arrows show an expansion of *cdh1* expression on the aboral pole. Arrows show the eggs. Asterisk indicates an oral pole. Scale bar (A-L) 50 µm; (M,N) 100 µm.

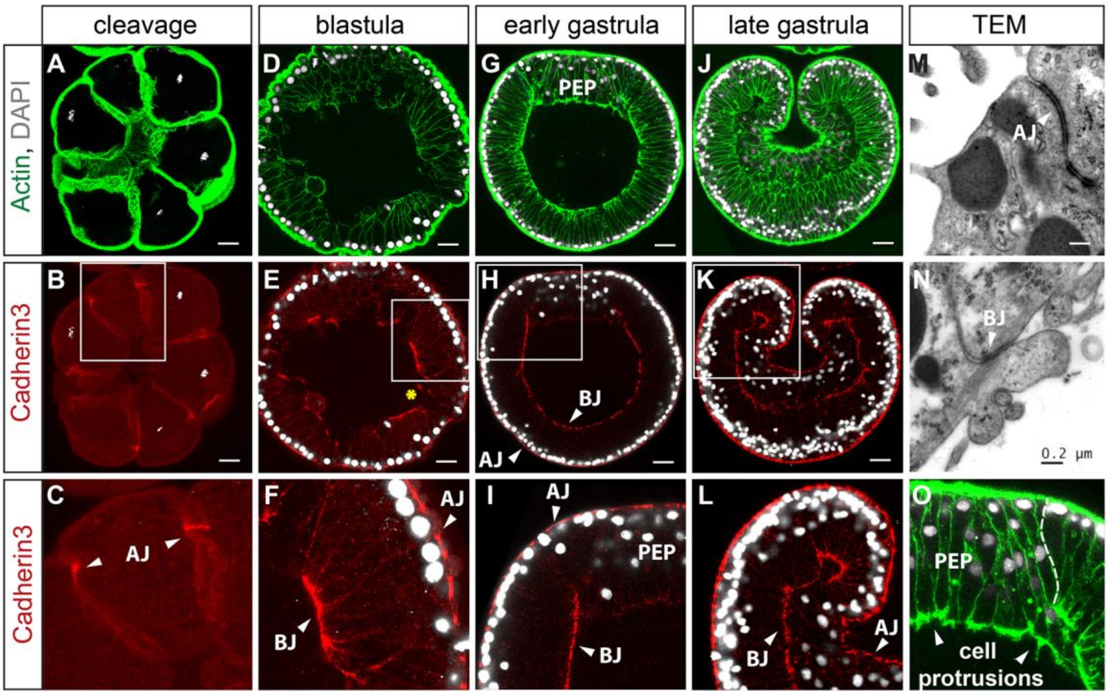


Fig. 3. Cdh3 is a major component of adhesion complexes during cleavage and gastrulation. (A-F) Besides apical junctions (AJ), strong basal epithelial contacts (BJ) form in the blastula during epithelialization. (G-I) As the pre-endodermal plate (PEP) starts to invaginate, Cdh3 disappears from the basal junctions and decreases in the apical junctions in the pre-endodermal plate. Ectodermal cells preserve both apical and basal cell contacts. (J-L) Late gastrula. Apical junctions are present in the ectoderm and in the endoderm. (M-N) Transmission electron microscopy (TEM) of the *Nematostella* epithelium. (O) Cell protrusions on the basal side of the PEP. Apical cell-cell junctions (AJ); basal cell-cell junctions (BJ). Yellow star (*) is located next to the dividing blastula cell. Scale bar 20 µm; Scale bar M-N: 0,2 µm.

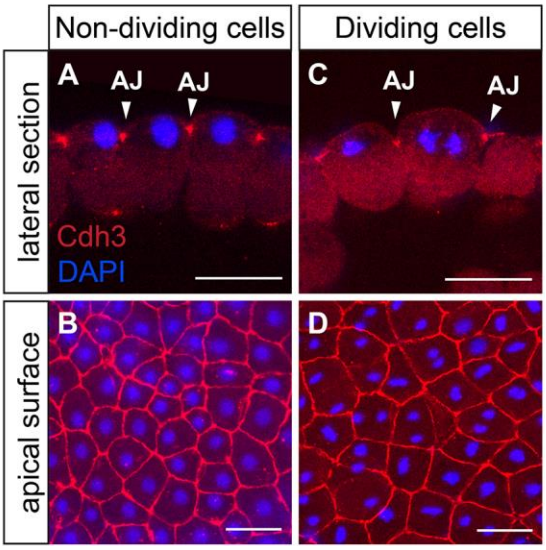


Fig. 4. Cdh3 apical junctions localization and cell polarity are preserved during the cell division. (A, B) Non-dividing blastula cells. (C, D) Dividing blastula cells at different mitotic phases. Scale bar 25 µm.

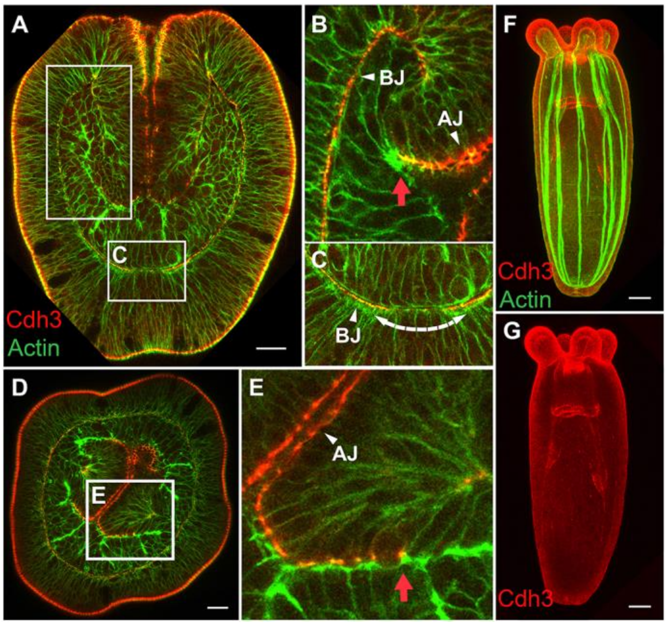


Fig. 5. Cdh3 marks the boundary between ectoderm and endoderm.

(A-C) Lateral section of planula. (D, E) Cross-section of planula. Ectodermal-endodermal boundary in the pharynx is distinctly labeled by Cdh3 localization in the cell junctions. (F, G) Primary polyp. Cdh3 is expressed exclusively in the ectoderm, forming apical and basal adherens junctions. Red arrow indicates the boundary between the last ectodermal and the first endodermal cell. Scale bar 20 µm.

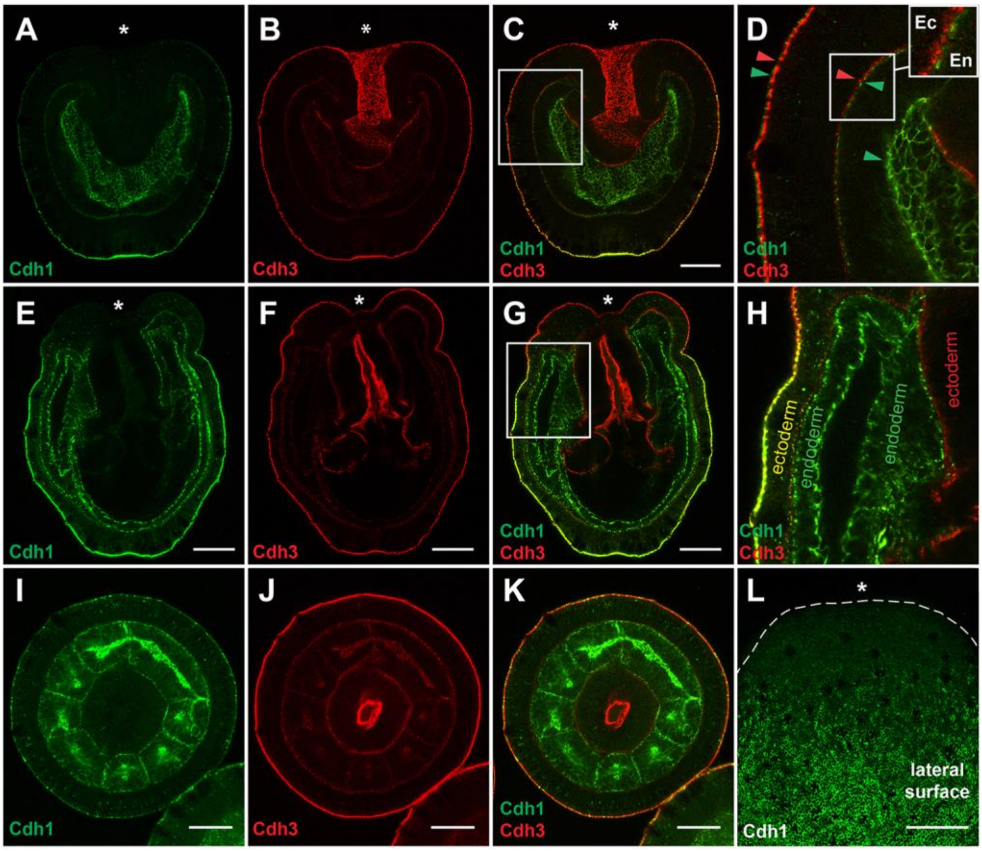


Fig. 6. Cdh1 and Cdh3 protein localization during germ layer differentiation. (A-D) Planula lateral section. D is an enlargement of an area shown in C. (E-H) Lateral lection of the primary polyp. H is an enlargement of an area shown in G. (I-K) Planula cross-section. (L) Surface of the planula, oral part of the ectoderm is free of Cdh1. Cdh1 is localized in the apical and basal junctions of the endoderm, as well as in the apical junctions and basal junctions of the aboral ectoderm, especially in the area of the apical organ. Cdh1 is gradually disappearing from the ectoderm towards the oral pole and completely excluded from the ectoderm of the tentacles and the pharynx Cdh3 is localized to the apical and basal junctions of the body wall ectoderm, ectoderm of the pharynx and is completely excluded from the endoderm. Asterisk marks an oral pole. Scale bar 50 µm.

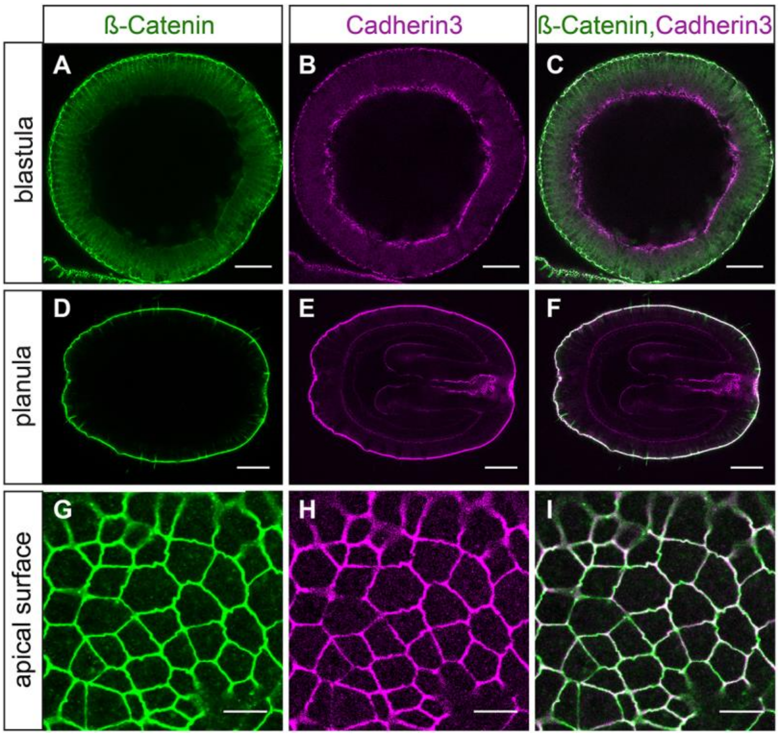


Fig. 7. Cdh3 and beta-catenin are co-localized at the apical cell junctions of the ectoderm. (A-C) blastula stage. (D-F) planula stage. (G-I) Apical surface of the ectoderm. Note that only weak beta-catenin staining can be detected at the basal ectodermal junction and none in the endoderm. Scale bar (A-F) 50 µm; (G-I) 10 µm.

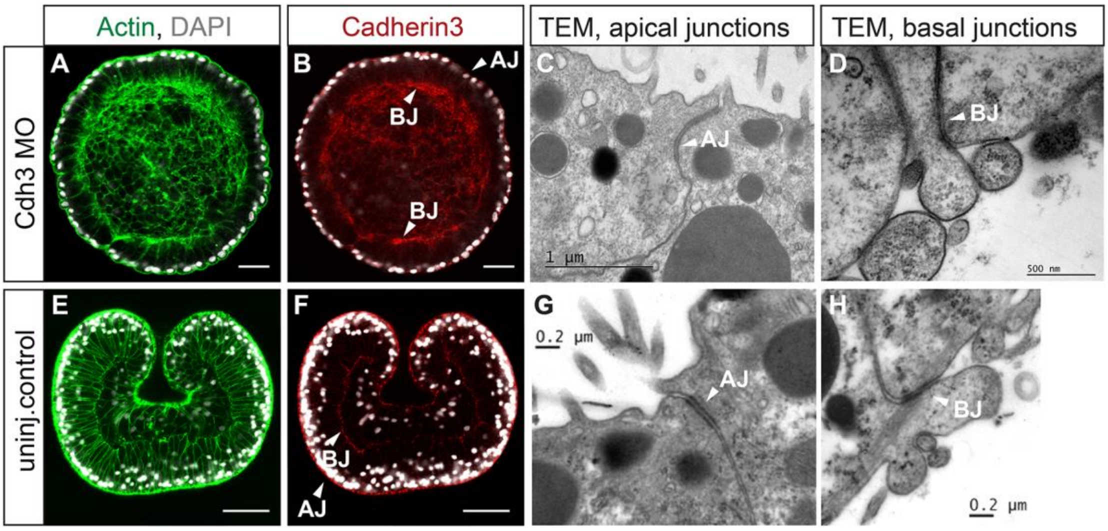


Fig. 8. Cdh3 knockdown blocks gastrulation movements. (A-D) Cdh3 morpholino (MO) injected embryos, 28 hours post-fertilization (hpf). (E-H) Control embryos, 28 hpf. Apical (AJ) and basal (BJ) cell junctions of Cdh3 morphants look very similar to the cell junctions of the control gastrulae. Scale bar (A,B,E,F) 40 µm.

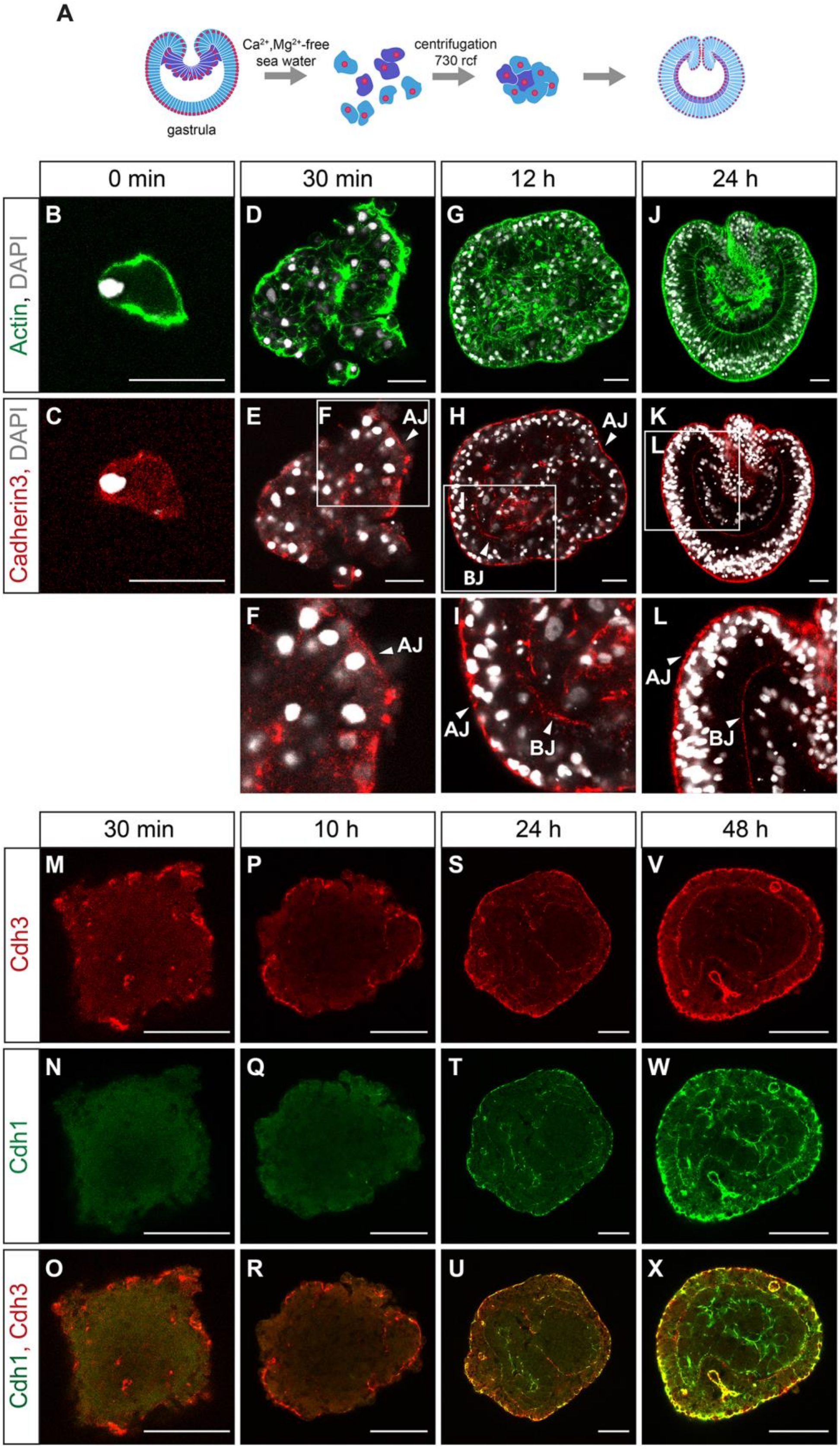

A
Ca²⁺,Mg²⁺-free sea water
centrifugation 730 rcf
gastrula
0 min
30 min
12 h
24 h
Actin, DAPI
Cadherin3, DAPI
B
C
D
E
F
G
H
I
J
K
L
AJ
BJ
30 min
10 h
24 h
48 h
Cdh3
Cdh1
Cdh1, Cdh3
M
N
O
P
Q
R
S
T
U
V
W
X

Fig. 9. Reestablishment of the polarity and de novo germ layer formation in the cell aggregate. (A) Scheme of the experiment. (B,C) Dissociated cells do not show polarized Cdh3 localization. (D-F) Epithelialization of the cell aggregate starts ~30 min after re-aggregation in small groups of cells. (G-I) 12h after dissociation the ectoderm of the aggregate is fully epithelialized. (J-L) 24h. Aggregate forms two germ layers. (M-X) Cdh1 protein appears at the junctions at 24h of aggregate development. At 48h after re-aggregation Cdh1 is broadly expressed in both germ layers. Apical junctions (AJ); Basal junctions (BJ). Scale bar (B-K) 20 µm; (M-X) 50 µm.

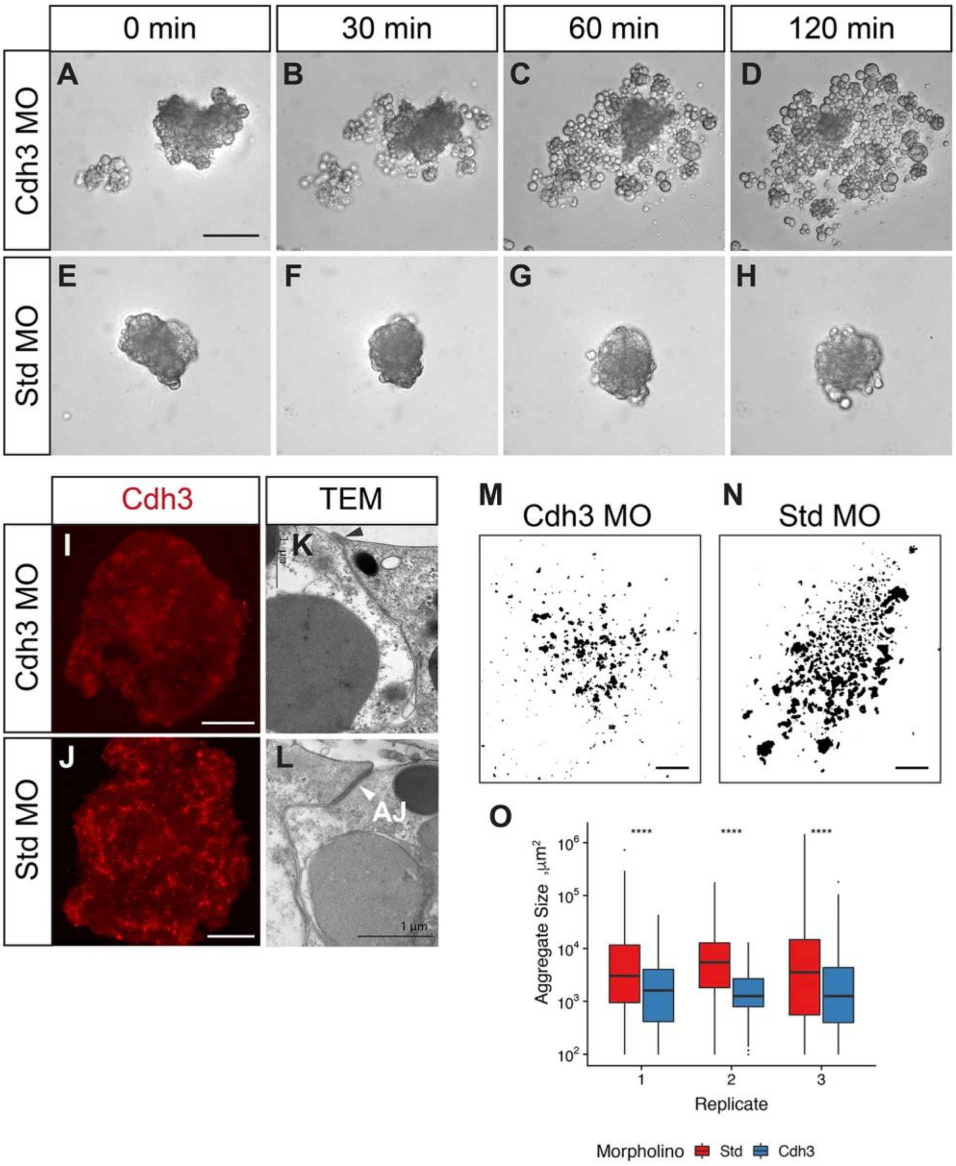


Fig. 10. Cdh3 MO aggregates fail to form adherens junctions *de novo*. (A-D) Cdh3 morpholino (MO) aggregates do not form new cell contacts, fail to develop and fall apart into cells. (E-H) Standard (Std) MO control aggregates stay compact. (I,J) Down-regulation of Cdh3 protein in the Cdh3 MO aggregates. Confocal microscopy, Cdh3 antibody staining. (K,L) TEM of the apical adherens junctions. Apical cell junctions (AJ) of the Cdh3 MO aggregates are much less pronounced than AJ in the control aggregates. (M,N,O) Cdh3 MO aggregates are significantly smaller than Std MO aggregates. Distribution means within each replicate were tested for significance using a two-sided unpaired Wilcoxon rank-sum test (****: $p < 0.0001$). Scale bar (A-J) 50 µm; (K, L) 1 µm. (M,N) 1 mm.

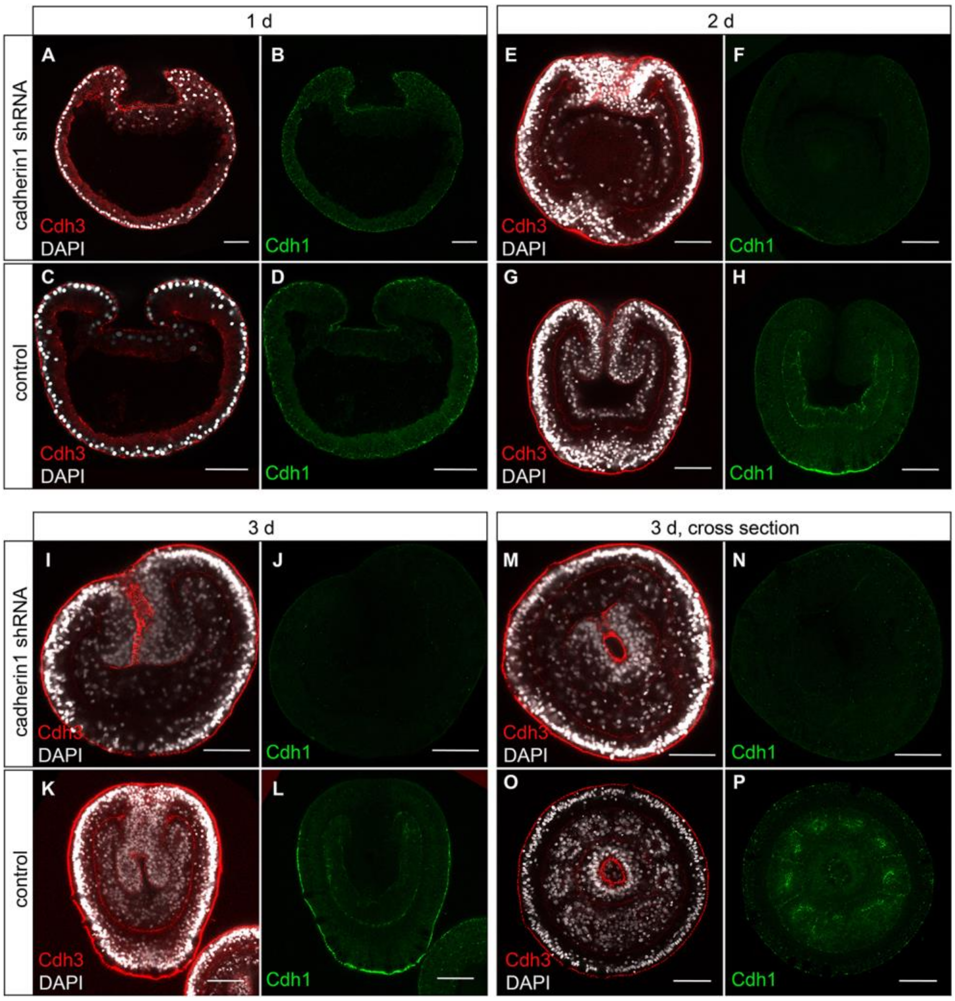


Fig. 11. Mesenteries do not develop upon Cdh1 knock-down by shRNA injection. Cdh1 protein expression is strongly down regulated. (A-D) 1 dpf, gastrula stage, lateral section. (E-H) 2 dpf planula, lateral section. (I-L) 3 dpf planula, lateral section. (M-P) 3 dpf planula, cross section.

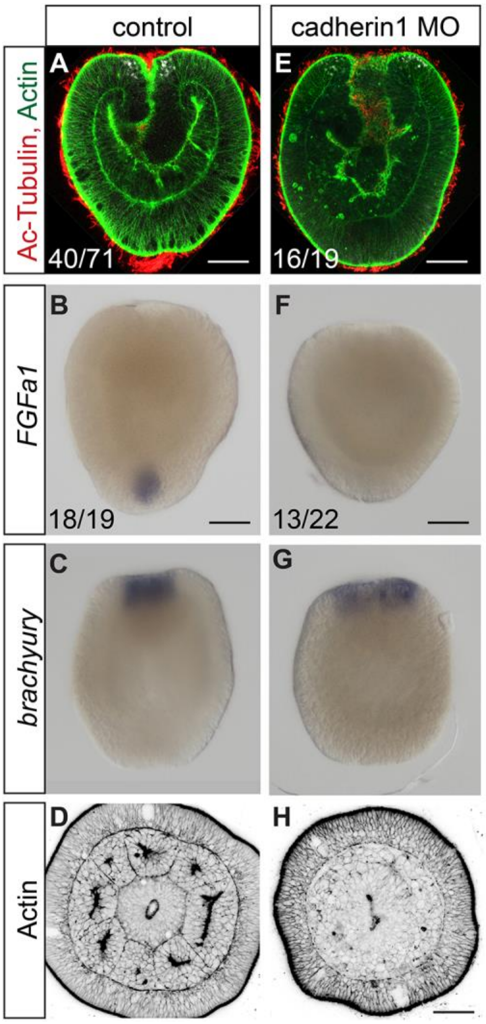


Fig. 12. Cdh1 knock-down impairs apical organ development. (A-D) Control embryo. (E-H) Cdh1 MO knockdown. Apical organ fail to develop (acetylated tubulin antibody staining). *FGFa1* is not expressed. Mesenteries do not form (phalloidin staining). *Brachyury* expression is normal. Scale bar 50 µm.

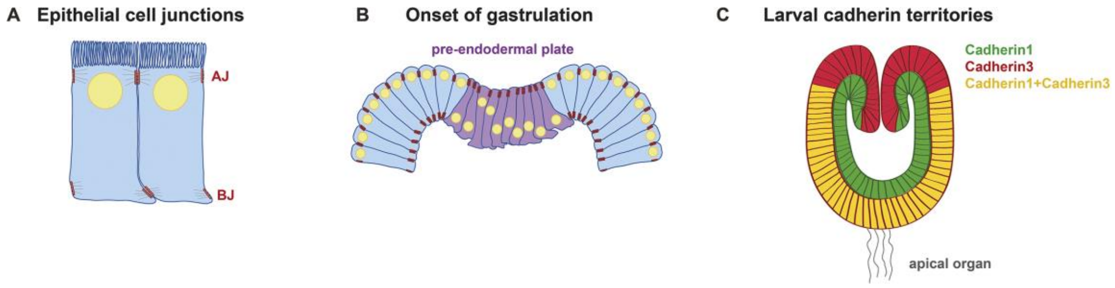


Fig. 13. Cadherin localization during early development of *Nematostella*.

(A) Schematic depiction of the apical and basal adherens junctions in both epithelial cell layers. (B) The onset of gastrulation is characterized by a downregulation of Cdh3 in the basal junctions, accompanied by apical constriction, migration of nuclei to basal positions, formation of filopodia. (C) Overlapping and specific expression domains of Cdh1 and Cdh3 in a planula larva.

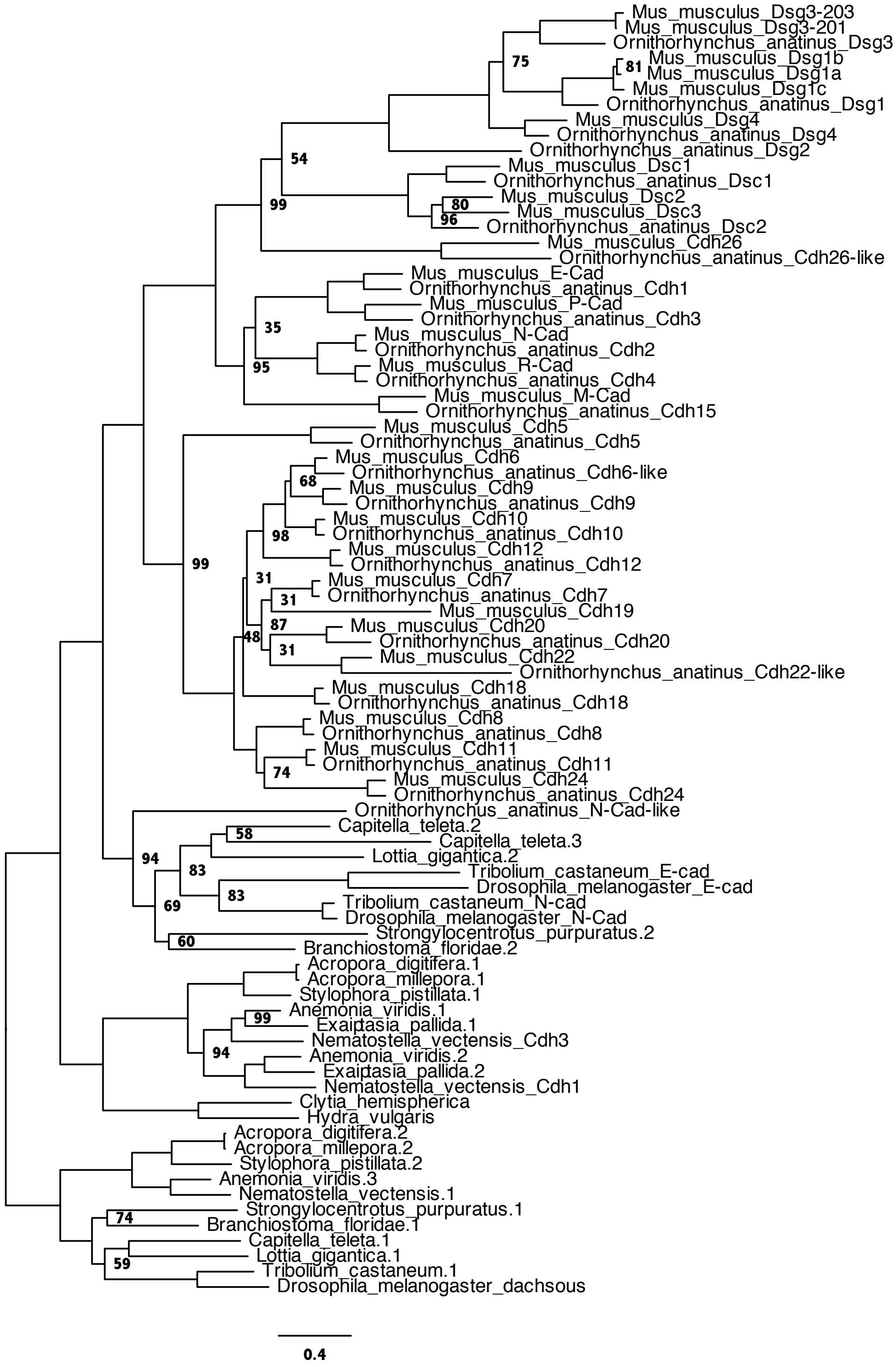


Fig. S1. Phylogenetic analysis of classical cadherins. Extended version of the tree in Fig.1. Dachsous cadherin proteins were used as an outgroup. The phylogenetic tree was constructed with the maximum likelihood method in IQ-tree. The number at the nodes indicates the bootstrap support from the maximum likelihood method.

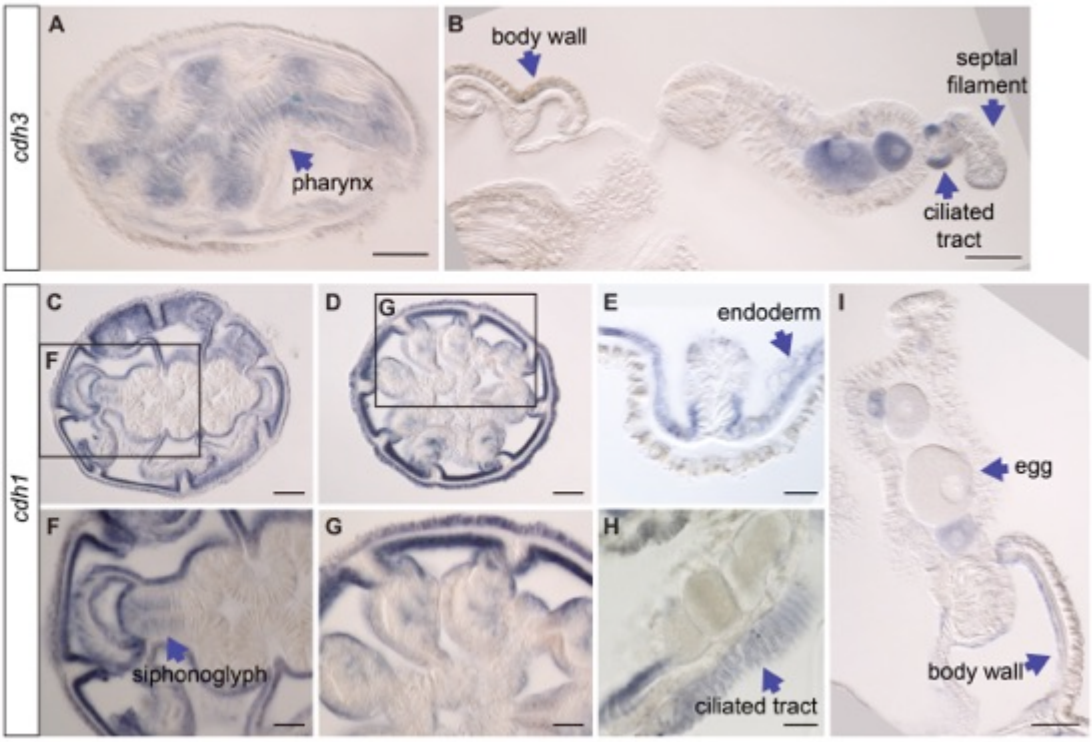
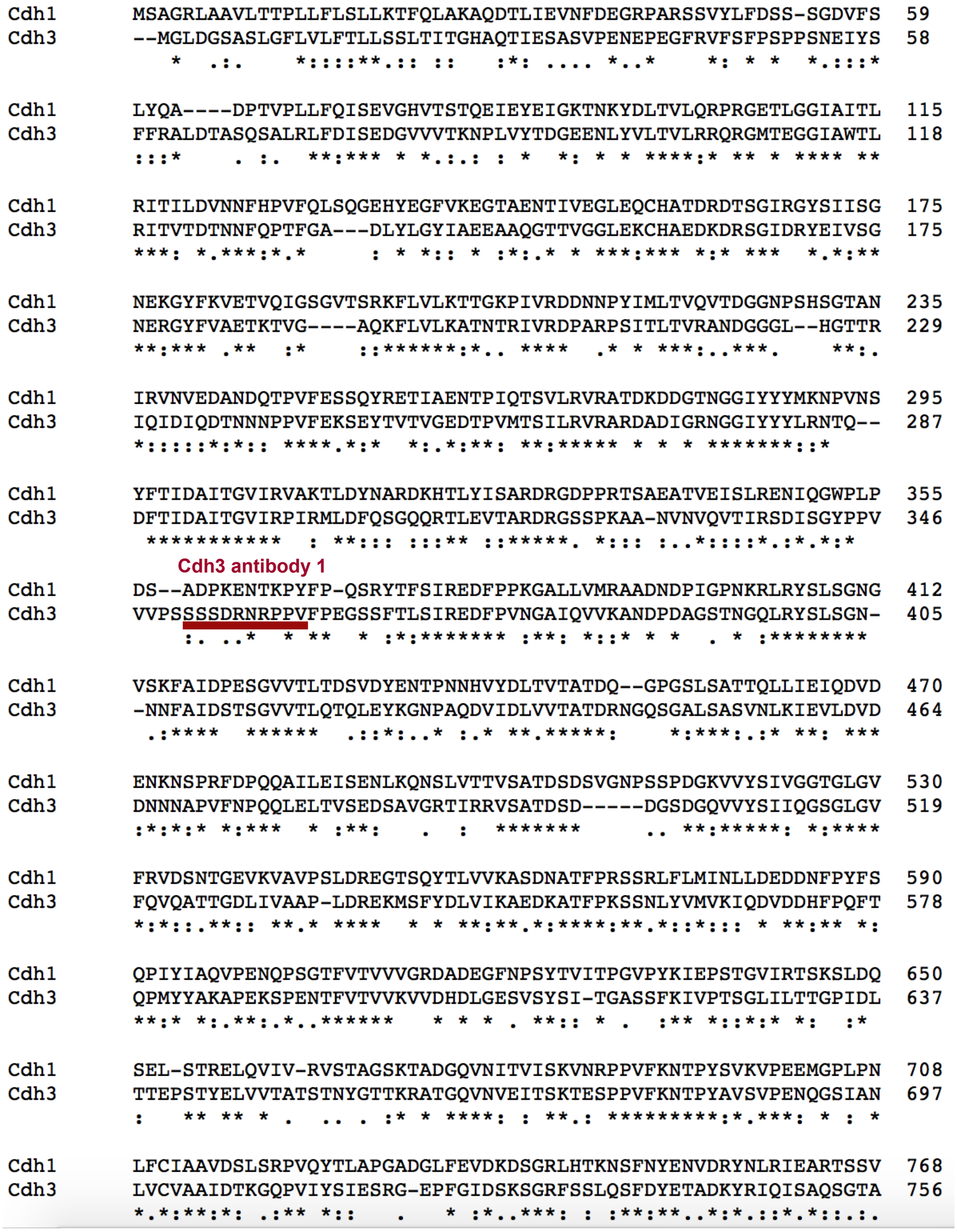


Fig. S2. *cdh1* and *cdh3* expression in adults and juveniles. (A-B) *cdh3* is expressed in the ectoderm of the pharynx, septal filaments and ciliated tract and in the oocytes. (C-I) *cdh1* is expressed in the endoderm, ciliated tract, ciliated lobe of the pharynx – siphonoglyph and small oocytes. Scale bar A-D, I: 100 µm. Scale bar E-H: 50 µm.



```
Cdh1            MSAGRLAAVLTTPLLFLSLLKTFQLAKAQDTLIEVNFDEGRPARSSVYLFDSS-SGDVFS   59
Cdh3            --MGLDGSASLGFLVLFTLLSSLTITGHAQTIESASVPENEPEGFRVFSFPSPPSNEIYS   58
                   *  .:.    *::::**.:: ::   :*: .... *..*    *: * *  *.:::*

Cdh1            LYQA----DPTVPLLFQISEVGHVTSTQEIEYEIGKTNKYDLTVLQRPRGETLGGIAITL   115
Cdh3            FFRALDTASQSALRLFDISEDGVVVTKNPLVYTDGEENLYVLTVLRRQRGMTEGGIAWTL   118
                :::*    . :.  **:*** * *.:.: : *  *: * * ****:* ** * **** **

Cdh1            RITILDVNNFHPVFQLSQGEHYEGFVKEGTAENTIVEGLEQCHATDRDTSGIRGYSIISG   175
Cdh3            RITVTDTNNFQPTFGA---DLYLGYIAEEAAQGTTVGGLEKCHAEDKDRSGIDRYEIVSG   175
                ***: *.***:*.*     : * *:: * :*:.* * ***:*** *:* ***  *.*:**

Cdh1            NEKGYFKVETVQIGSGVTSRKFLVLKTTGKPIVRDDNNPYIMLTVQVTDGGNPSHSGTAN   235
Cdh3            NERGYFVAETKTVG----AQKFLVLKATNTRIVRDPARPSITLTVRANDGGGL--HGTTR   229
                **:*** .**  :*    ::******:*.. ****  .* * ***:..***.    **:.

Cdh1            IRVNVEDANDQTPVFESSQYRETIAENTPIQTSVLRVRATDKDDGTNGGIYYYMKNPVNS   295
Cdh3            IQIDIQDTNNNPPVFEKSEYTVTVGEDTPVMTSILRVRARDADIGRNGGIYYYLRNTQ--   287
                *:::::*:*:: ****.*:*  *:.*:**: **:***** * * * *******::*

Cdh1            YFTIDAITGVIRVAKTLDYNARDKHTLYISARDRGDPPRTSAEATVEISLRENIQGWPLP   355
Cdh3            DFTIDAITGVIRPIRMLDFQSGQQRTLEVTARDRGSSPKAA-NVNVQVTIRSDISGYPPV   346
                 ***********  : **::: :::** ::*****. *::: :..*::::*.:*.*:*
                    Cdh3 antibody 1
Cdh1            DS--ADPKENTKPYFP-QSRYTFSIREDFPPKGALLVMRAADNDPIGPNKRLRYSLSGNG   412
Cdh3            VVPSSSSDRNRPPVFPEGSSFTLSIREDFPVNGAIQVVKANDPDAGSTNGQLRYSLSGN-   405
                    :. ..*   * **  * :*:******* :**: *::* * *  . * :********

Cdh1            VSKFAIDPESGVVTLTDSVDYENTPNNHVYDLTVTATDQ--GPGSLSATTQLLIEIQDVD   470
Cdh3            -NNFAIDSTSGVVTLQTQLEYKGNPAQDVIDLVVTATDRNGQSGALSASVNLKIEVLDVD   464
                 .:****  ******  .::*:..* :.* **.*****:    *:***:.:* **: ***

Cdh1            ENKNSPRFDPQQAILEISENLKQNSLVTTVSATDSDSVGNPSSPDGKVVYSIVGGTGLGV   530
Cdh3            DNNNAPVFNPQQLELTVSEDSAVGRTIRRVSATDSD-----DGSDGQVVYSIIQGSGLGV   519
                :*:*:* *:***  * :**:   .  :  *******     .. **:*****: *:****

Cdh1            FRVDSNTGEVKVAVPSLDREGTSQYTLVVKASDNATFPRSSRLFLMINLLDEDDNFPYFS   590
Cdh3            FQVQATTGDLIVAAP-LDREKMSFYDLVIKAEDKATFPKSSNLYVMVKIQDVDDHFPQFT   578
                *:*::.**:: **.* ****  * * **:**.*:****:**.*::*::: * **:** *:

Cdh1            QPIYIAQVPENQPSGTFVTVVVGRDADEGFNPSYTVITPGVPYKIEPSTGVIRTSKSLDQ   650
Cdh3            QPMYYAKAPEKSPENTFVTVVKVVDHDLGESVSYSI-TGASSFKIVPTSGLILTTGPIDL   637
                **:* *:.**:.*..******   * * * . **:: * .  :** *::*:* *:  :*

Cdh1            SEL-STRELQVIV-RVSTAGSKTADGQVNITVISKVNRPPVFKNTPYSVKVPEEMGPLPN   708
Cdh3            TTEPSTYELVVTATSTNYGTTKRATGQVNVEITSKTESPPVFKNTPYAVSVPENQGSIAN   697
                :   ** ** * .  .. . :* * ****: : **.: *********:*.***: * : *

Cdh1            LFCIAAVDSLSRPVQYTLAPGADGLFEVDKDSGRLHTKNSFNYENVDRYNLRIEARTSSV   768
Cdh3            LVCVAAIDTKGQPVIYSIESRG-EPFGIDSKSGRFSSLQSFDYETADKYRIQISAQSGTA   756
                *.*:**:*: .:** *::   .   * :*..***: : :**:**..*:*.::*.*::.:.
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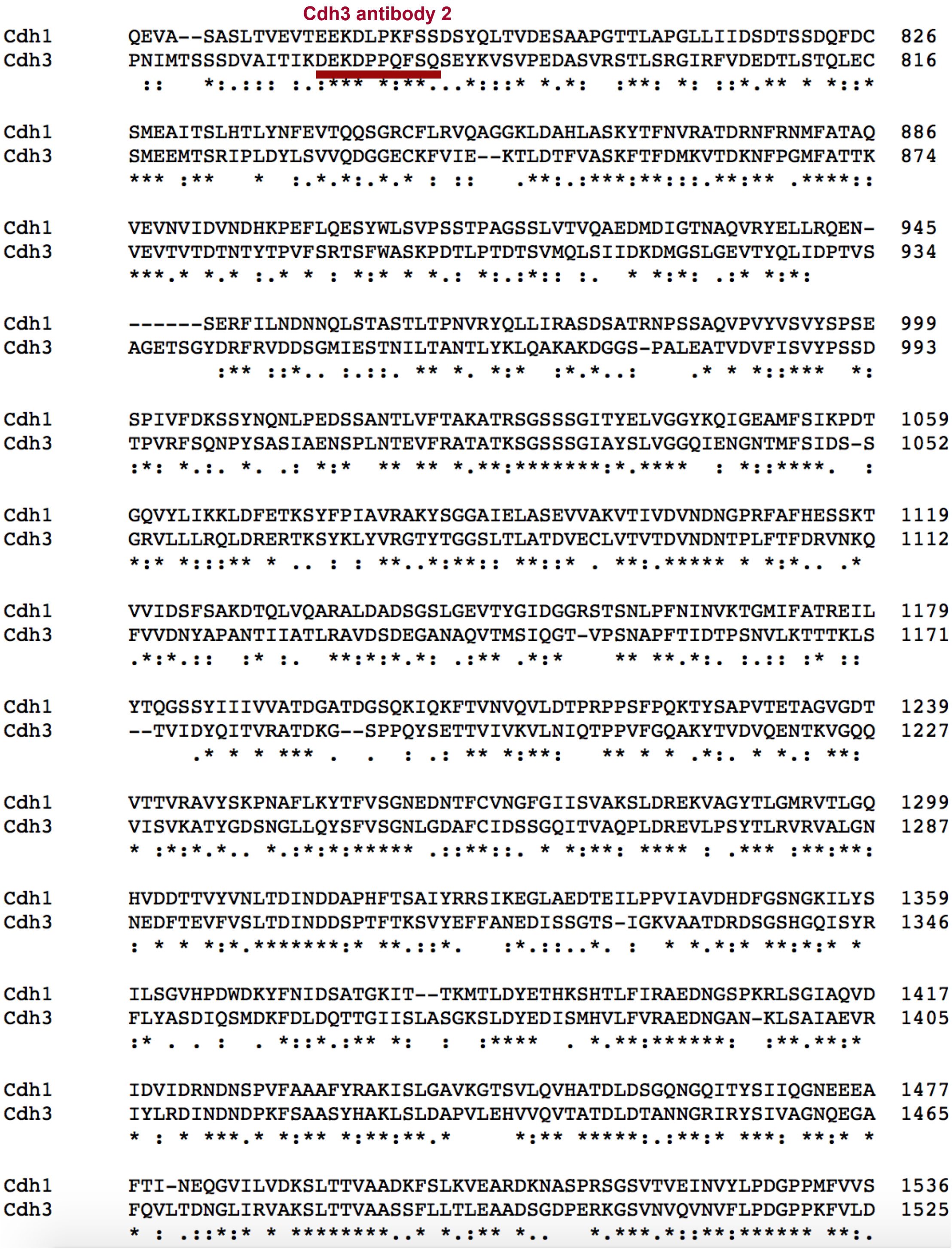

```
Cdh1            QEVA--SASLTVEVTEEKDLPKFSSDSYQLTVDESAAPGTTLAPGLLIIDSDTSSDQFDC  826
Cdh3            PNIMTSSSDVAITIKDEKDPPQFSQSEYKVSVPEDASVRSTLSRGIRFVDEDTLSTQLEC  816
                 ::   *:.::: :.:*** *:**...*:::* *.*:  :**: *: ::*.** * *::*

Cdh1            SMEAITSLHTLYNFEVTQQSGRCFLRVQAGGKLDAHLASKYTFNVRATDRNFRNMFATAQ  886
Cdh3            SMEEMTSRIPLDYLSVVQDGGECKFVIE--KTLDTFVASKFTFDMKVTDKNFPGMFATTK  874
                *** :**   *  :.*.*:.*.* : ::   .**:.:***:**:::.**:** .****::

Cdh1            VEVNVIDVNDHKPEFLQESYWLSVPSSTPAGSSLVTVQAEDMDIGTNAQVRYELLRQEN-  945
Cdh3            VEVTVTDTNTYTPVFSRTSFWASKPDTLPTDTSVMQLSIIDKDMGSLGEVTYQLIDPTVS  934
                ***.* *.* :.* * : *:* * *.: *:.:*:: :.  * *:*: .:* *:*:

Cdh1            ------SERFILNDNNQLSTASTLTPNVRYQLLIRASDSATRNPSSAQVPVYVSVYSPSE  999
Cdh3            AGETSGYDRFRVDDSGMIESTNILTANTLYKLQAKAKDGGS-PALEATVDVFISVYPSSD  993
                       :** ::*.. :.::. ** *. *:*  :*.*..:    .* * *::***  *:

Cdh1            SPIVFDKSSYNQNLPEDSSANTLVFTAKATRSGSSSGITYELVGGYKQIGEAMFSIKPDT  1059
Cdh3            TPVRFSQNPYSASIAENSPLNTEVFRATATKSGSSSGIAYSLVGGQIENGNTMFSIDS-S  1052
                :*: *.:. *. .: *:*  ** ** *.**:*******:*.****  : *::****.  :

Cdh1            GQVYLIKKLDFETKSYFPIAVRAKYSGGAIELASEVVAKVTIVDVNDNGPRFAFHESSKT  1119
Cdh3            GRVLLLRQLDRERTKSYKLYVRGTYTGGSLTLATDVECLVTVTDVNDNTPLFTFDRVNKQ  1112
                *:* *:::** * .. : : **..*:**:: **::* . **:.***** * *:*.. .*

Cdh1            VVIDSFSAKDTQLVQARALDADSGSLGEVTYGIDGGRSTSNLPFNINVKTGMIFATREIL  1179
Cdh3            FVVDNYAPANTIIATLRAVDSDEGANAQVTMSIQGT-VPSNAPFTIDTPSNVLKTTTKLS  1171
                .*:*.::  :* :.  **:*:*.*: .:** .*:*    ** **.*:. :.:: :* ::

Cdh1            YTQGSSYIIIVVATDGATDGSQKIQKFTVNVQVLDTPRPPSFPQKTYSAPVTETAGVGDT  1239
Cdh3            --TVIDYQITVRATDKG--SPPQYSETTVIVKVLNIQTPPVFGQAKYTVDVQENTKVGQQ  1227
                     .* * * *** .  .  : .: ** *:**:   ** * * .*:. * *.: **:

Cdh1            VTTVRAVYSKPNAFLKYTFVSGNEDNTFCVNGFGIISVAKSLDREKVAGYTLGMRVTLGQ  1299
Cdh3            VISVKATYGDSNGLLQYSFVSGNLGDAFCIDSSGQITVAQPLDREVLPSYTLRVRVALGN  1287
                * :*:*.*.. *.:*:*:***** .::**::. * *:**: **** : .*** :**:**:

Cdh1            HVDDTTVYVNLTDINDDAPHFTSAIYRRSIKEGLAEDTEILPPVIAVDHDFGSNGKILYS  1359
Cdh3            NEDFTEVFVSLTDINDDSPTFTKSVYEFFANEDISSGTS-IGKVAATDRDSGSHGQISYR  1346
                : * * *:*.*******:* **.::*.   :*.::..*. :  * *.*:* **:*:* *

Cdh1            ILSGVHPDWDKYFNIDSATGKIT--TKMTLDYETHKSHTLFIRAEDNGSPKRLSGIAQVD  1417
Cdh3            FLYASDIQSMDKFDLDQTTGIISLASGKSLDYEDISMHVLFVRAEDNGAN-KLSAIAEVR  1405
                :* . . :  . *::*.:** *:  :  :****  . *.**:******:  :**.**:*

Cdh1            IDVIDRNDNSPVFAAAFYRAKISLGAVKGTSVLQVHATDLDSGQNGQITYSIIQGNEEEA  1477
Cdh3            IYLRDINDNDPKFSAASYHAKLSLDAPVLEHVVQVTATDLDTANNGRIRYSIVAGNQEGA  1465
                * : * ***.* *:** *:**:**.*     *:** *****:.:**:* ***: **:* *

Cdh1            FTI-NEQGVILVDKSLTTVAADKFSLKVEARDKNASPRSGSVTVEINVYLPDGPPMFVVS  1536
Cdh3            FQVLTDNGLIRVAKSLTTVAASSFLLTLEAADSGDPERKGSVNVQVNVFLPDGPPKFVLD  1525
                * : .::*:* * ********..* *.:** *..   *.***.*::**:****** **:.
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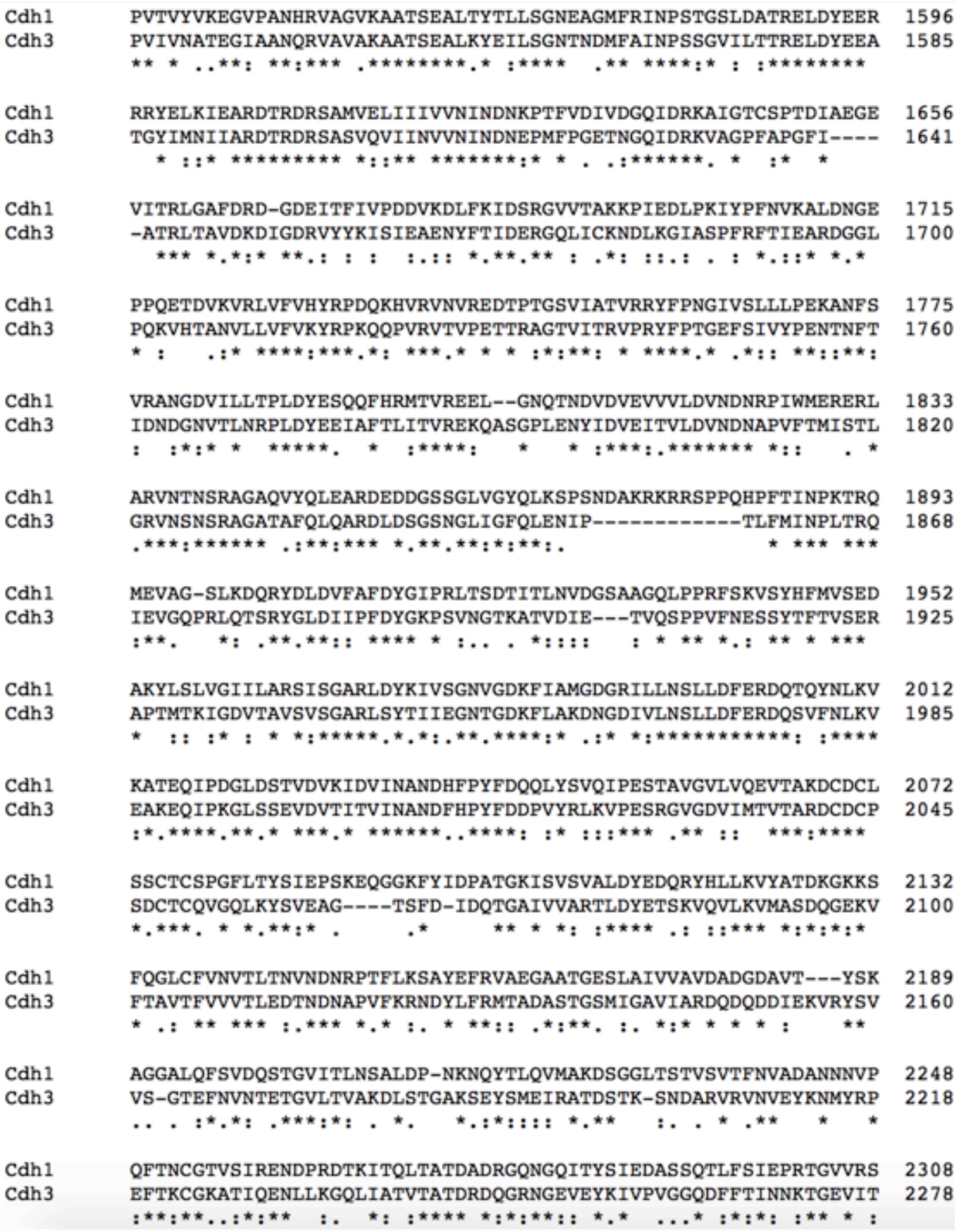

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Cdh1            PVTVYVKEGVPANHRVAGVKAATSEALTYTLLSGNEAGMFRINPSTGSLDATRELDYEER  1596
Cdh3            PVIVNATEGIAANQRVAVAKAATSEALKYEILSGNTNDMFAINPSSGVILTTRELDYEEA  1585
                ** * ..**: **:*** .********.* :****  .** ****:* : :********

Cdh1            RRYELKIEARDTRDRSAMVELIIIVVNINDNKPTFVDIVDGQIDRKAIGTCSPTDIAEGE  1656
Cdh3            TGYIMNIIARDTRDRSASVQVIINVVNINDNEPMFPGETNGQIDRKVAGPFAPGFI----  1641
                  * ::* ********* *::** *******:* * . .:******. *  :*  *

Cdh1            VITRLGAFDRD-GDEITFIVPDDVKDLFKIDSRGVVTAKKPIEDLPKIYPFNVKALDNGE  1715
Cdh3            -ATRLTAVDKDIGDRVYYKISIEAENYFTIDERGQLICKNDLKGIASPFRFTIEARDGGL  1700
                  *** *.*:* **.: : :  :.:: *.**.** : .*: ::.: . : *.::* *.*

Cdh1            PPQETDVKVRLVFVHYRPDQKHVRVNVREDTPTGSVIATVRRYFPNGIVSLLLPEKANFS  1775
Cdh3            PQKVHTANVLLVFVKYRPKQQPVRVTVPETTRAGTVITRVPRYFPTGEFSIVYPENTNFT  1760
                * :   .:* ****:***.*: ***.* * * :*:**: * ****.* .*:: **::**:

Cdh1            VRANGDVILLTPLDYESQQFHRMTVREEL--GNQTNDVDVEVVVLDVNDNRPIWMERERL  1833
Cdh3            IDNDGNVTLNRPLDYEEIAFTLITVREKQASGPLENYIDVEITVLDVNDNAPVFTMISTL  1820
                :  :*:* *  *****.  *  :****:   *   * :***:.******* *::   . *

Cdh1            ARVNTNSRAGAQVYQLEARDEDDGSSGLVGYQLKSPSNDAKRKRRSPPQHPFTINPKTRQ  1893
Cdh3            GRVNSNSRAGATAFQLQARDLDSGSNGLIGFQLENIP------------TLFMINPLTRQ  1868
                .***:****** .:**:*** *.**.**:*:**:.                * *** ***

Cdh1            MEVAG-SLKDQRYDLDVFAFDYGIPRLTSDTITLNVDGSAAGQLPPRFSKVSYHFMVSED  1952
Cdh3            IEVGQPRLQTSRYGLDIIPFDYGKPSVNGTKATVDIE---TVQSPPVFNESSYTFTVSER  1925
                :**.   *: .**.**:: **** * :.. . *::::   : * ** *.: ** * ***

Cdh1            AKYLSLVGIILARSISGARLDYKIVSGNVGDKFIAMGDGRILLNSLLDFERDQTQYNLKV  2012
Cdh3            APTMTKIGDVTAVSVSGARLSYTIIEGNTGDKFLAKDNGDIVLNSLLDFERDQSVFNLKV  1985
                *  :: :* : * *:*****.*.*:.**.****:* .:* *:***********: :****

Cdh1            KATEQIPDGLDSTVDVKIDVINANDHFPYFDQQLYSVQIPESTAVGVLVQEVTAKDCDCL  2072
Cdh3            EAKEQIPKGLSSEVDVTITVINANDFHPYFDDPVYRLKVPESRGVGDVIMTVTARDCDCP  2045
                :*.****.**.* ***.* ******..****: :* :::*** .** ::  ***:****

Cdh1            SSCTCSPGFLTYSIEPSKEQGGKFYIDPATGKISVSVALDYEDQRYHLLKVYATDKGKKS  2132
Cdh3            SDCTCQVGQLKYSVEAG----TSFD-IDQTGAIVVARTLDYETSKVQVLKVMASDQGEKV  2100
                *.***. * *.**:* .     .*     ** * *: :**** .: ::*** *:*:*:*

Cdh1            FQGLCFVNVTLTNVNDNRPTFLKSAYEFRVAEGAATGESLAIVVAVDADGDAVT---YSK  2189
Cdh3            FTAVTFVVVTLEDTNDNAPVFKRNDYLFRMTADASTGSMIGAVIARDQDQDDIEKVRYSV  2160
                * .: ** *** :.*** *.* :. * **:: .*:**. :. *:* * * * :    **

Cdh1            AGGALQFSVDQSTGVITLNSALDP-NKNQYTLQVMAKDSGGLTSTVSVTFNVADANNNVP  2248
Cdh3            VS-GTEFNVNTETGVLTVAKDLSTGAKSEYSMEIRATDSTK-SNDARVRVNVEYKNMYRP  2218
                .. . :*.*: .***:*: . *.   *.:*:::: *.**   :. . * .**   *   *

Cdh1            QFTNCGTVSIRENDPRDTKITQLTATDADRGQNGQITYSIEDASSQTLFSIEPRTGVVRS  2308
Cdh3            EFTKCGKATIQENLLKGQLIATVTATDRDQGRNGEVEYKIVPVGGQDFFTINNKTGEVIT  2278
                :**:**..:*:**  :.  *: :**** *:*:**:: *.*  ...* :*:*: :** * :
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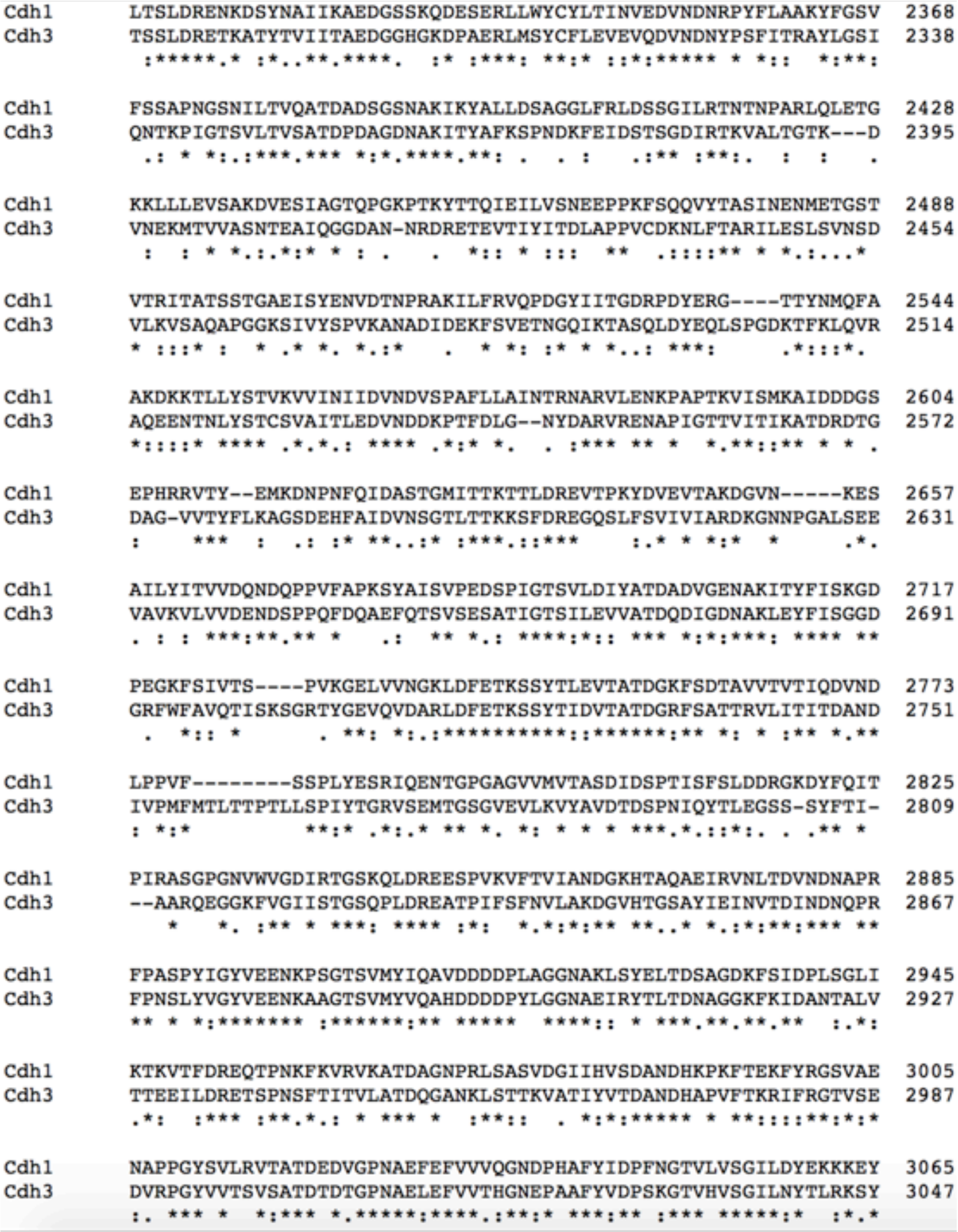

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Cdh1            LTSLDRENKDSYNAIIKAEDGSSKQDESERLLWYCYLTINVEDVNDNRPYFLAAKYFGSV  2368
Cdh3            TSSLDRETKATYTVIITAEDGGHGKDPAERLMSYCFLEVEVQDVNDNYPSFITRAYLGSI  2338
                 :*****.* :*..**.****.  :* :***: **:* ::*:***** * *::  *:**:

Cdh1            FSSAPNGSNILTVQATDADSGSNAKIKYALLDSAGGLFRLDSSGILRTNTNPARLQLETG  2428
Cdh3            QNTKPIGTSVLTVSATDPDAGDNAKITYAFKSPNDKFEIDSTSGDIRTKVALTGTK---D  2395
                 .: * *:.:***.*** *:*.****.**: .  . :   .:** :**:.  :  :   .

Cdh1            KKLLLEVSAKDVESIAGTQPGKPTKYTTQIEILVSNEEPPKFSQQVYTASINENMETGST  2488
Cdh3            VNEKMTVVASNTEAIQGGDAN-NRDRETEVTIYITDLAPPVCDKNLFTARILESLSVNSD  2454
                 :  : * *.:.*:* * : .   .  *:: * :::  **  .::::** * *.:...*

Cdh1            VTRITATSSTGAEISYENVDTNPRAKILFRVQPDGYIITGDRPDYERG----TTYNMQFA  2544
Cdh3            VLKVSAQAPGGKSIVYSPVKANADIDEKFSVETNGQIKTASQLDYEQLSPGDKTFKLQVR  2514
                * :::* :  * .* *. *.:*   .  * *: :* * *..: ***:     .*:::*.

Cdh1            AKDKKTLLYSTVKVVINIIDVNDVSPAFLLAINTRNARVLENKPAPTKVISMKAIDDDGS  2604
Cdh3            AQEENTNLYSTCSVAITLEDVNDDKPTFDLG--NYDARVRENAPIGTTVITIKATDRDTG  2572
                *::::* **** .*.*.: **** .*:* *.  . :*** ** *  *.**::** * * .

Cdh1            EPHRRVTY--EMKDNPNFQIDASTGMITTKTTLDREVTPKYDVEVTAKDGVN-----KES  2657
Cdh3            DAG-VVTYFLKAGSDEHFAIDVNSGTLTTKKSFDREGQSLFSVIVIARDKGNNPGALSEE  2631
                :    ***  :  .: :* **..:* :***.::***    :.* * *:*  *     .*.

Cdh1            AILYITVVDQNDQPPVFAPKSYAISVPEDSPIGTSVLDIYATDADVGENAKITYFISKGD  2717
Cdh3            VAVKVLVVDENDSPPQFDQAEFQTSVSESATIGTSILEVVATDQDIGDNAKLEYFISGGD  2691
                . : : ***:**.** *   .:  ** *.: ****:*:: *** *:*:***: **** **

Cdh1            PEGKFSIVTS----PVKGELVVNGKLDFETKSSYTLEVTATDGKFSDTAVVTVTIQDVND  2773
Cdh3            GRFWFAVQTISKSGRTYGEVQVDARLDFETKSSYTIDVTATDGRFSATTRVLITITDAND  2751
                 .  *:: *      . **: *:.:**********::******:** *: * :** *.**

Cdh1            LPPVF--------SSPLYESRIQENTGPGAGVVMVTASDIDSPTISFSLDDRGKDYFQIT  2825
Cdh3            IVPMFMTLTTPTLLSPIYTGRVSEMTGSGVEVLKVYAVDTDSPNIQYTLEGSS-SYFTI-  2809
                : *:*         **:* .*:.* ** *. *: * * * ***.*.::*:. . .** *

Cdh1            PIRASGPGNVWVGDIRTGSKQLDREESPVKVFTVIANDGKHTAQAEIRVNLTDVNDNAPR  2885
Cdh3            --AARQEGGKFVGIISTGSQPLDREATPIFSFNVLAKDGVHTGSAYIEINVTDINDNQPR  2867
                   *   *. :** * ***: **** :*:  *.*:*:** **..* *.:*:**:*** **

Cdh1            FPASPYIGYVEENKPSGTSVMYIQAVDDDDPLAGGNAKLSYELTDSAGDKFSIDPLSGLI  2945
Cdh3            FPNSLYVGYVEENKAAGTSVMYVQAHDDDDPYLGGNAEIRYTLTDNAGGKFKIDANTALV  2927
                ** * *:******* :******:** *****  ****:: * ***.**.**.**  :.*:

Cdh1            KTKVTFDREQTPNKFKVRVKATDAGNPRLSASVDGIIHVSDANDHKPKFTEKFYRGSVAE  3005
Cdh3            TTEEILDRETSPNSFTITVLATDQGANKLSTTKVATIYVTDANDHAPVFTKRIFRGTVSE  2987
                .*:  :*** :**.*.: * *** *  :**::  . *:*:***** * **::::**:*:*

Cdh1            NAPPGYSVLRVTATDEDVGPNAEFEFVVVQGNDPHAFYIDPFNGTVLVSGILDYEKKKEY  3065
Cdh3            DVRPGYVVTSVSATDTDTGPNAELEFVVTHGNEPAAFYVDPSKGTVHVSGILNYTLRKSY  3047
                :. *** *  *:*** *.*****:****.:**:* ***:** :*** *****:*  :*.*
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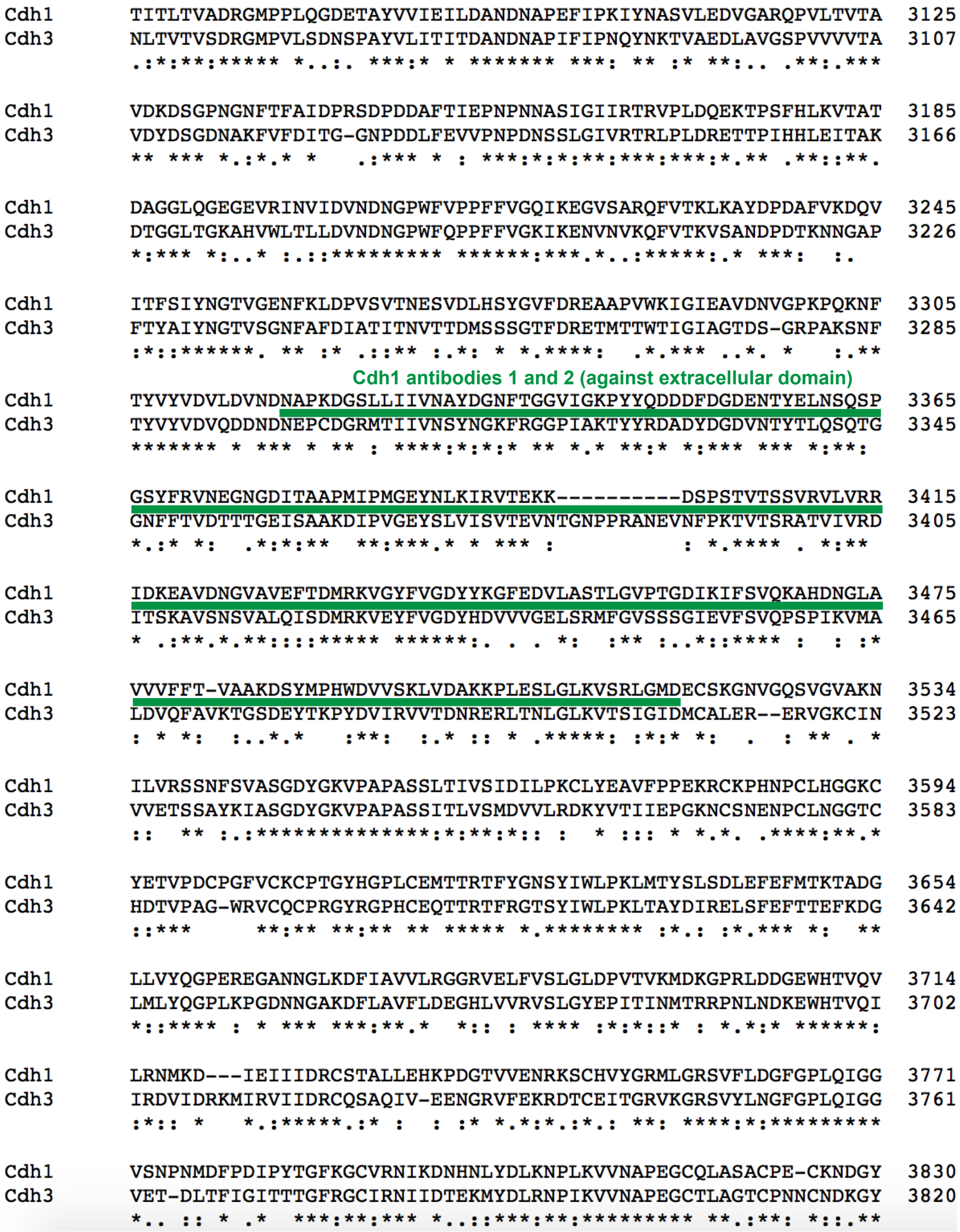

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Cdh1       TITLTVADRGMPPLQGDETAYVVIEILDANDNAPEFIPKIYNASVLEDVGARQPVLTVTA  3125
Cdh3       NLTVTVSDRGMPVLSDNSPAYVLITITDANDNAPIFIPNQYNKTVAEDLAVGSPVVVVTA  3107
           .:*:**:***** *..:. ***:* * ******* ***: ** :* **:.. .**:.***

Cdh1       VDKDSGPNGNFTFAIDPRSDPDDAFTIEPNPNNASIGIIRTRVPLDQEKTPSFHLKVTAT  3185
Cdh3       VDYDSGDNAKFVFDITG-GNPDDLFEVVPNPDNSSLGIVRTRLPLDRETTPIHHLEITAK  3166
           ** *** *.:*.* *   .:*** * : ***:*:*:**:***:***:*.** .**::**.

Cdh1       DAGGLQGEGEVRINVIDVNDNGPWFVPPFFVGQIKEGVSARQFVTKLKAYDPDAFVKDQV  3245
Cdh3       DTGGLTGKAHVWLTLLDVNDNGPWFQPPFFVGKIKENVNVKQFVTKVSANDPDTKNNGAP  3226
           *:*** *:..* :.::********* ******:***.*..:*****:.* ***:  :.

Cdh1       ITFSIYNGTVGENFKLDPVSVTNESVDLHSYGVFDREAAPVWKIGIEAVDNVGPKPQKNF  3305
Cdh3       FTYAIYNGTVSGNFAFDIATITNVTTDMSSSGTFDRETMTTWTIGIAGTDS-GRPAKSNF  3285
           :*::******. ** :* .::** :.*: * *.****:  .*.*** ..*. *   :.**

                                 Cdh1 antibodies 1 and 2 (against extracellular domain)
Cdh1       TYVYVDVLDVNDNAPKDGSLLIIVNAYDGNFTGGVIGKPYYQDDDFDGDENTYELNSQSP  3365
Cdh3       TYVYVDVQDDNDNEPCDGRMTIIVNSYNGKFRGGPIAKTYYRDADYDGDVNTYTLQSQTG  3345
           ******* * *** * ** : ****:*:*:* ** *.* **:* *:*** *** *:**:

Cdh1       GSYFRVNEGNGDITAAPMIPMGEYNLKIRVTEKK----------DSPSTVTSSVRVLVRR  3415
Cdh3       GNFFTVDTTTGEISAAKDIPVGEYSLVISVTEVNTGNPPRANEVNFPKTVTSRATVIVRD  3405
           *.:* *:  .*:*:**  **:***.* * *** :          : *.**** . *:**

Cdh1       IDKEAVDNGVAVEFTDMRKVGYFVGDYYKGFEDVLASTLGVPTGDIKIFSVQKAHDNGLA  3475
Cdh3       ITSKAVSNSVALQISDMRKVEYFVGDYHDVVVGELSRMFGVSSSGIEVFSVQPSPIKVMA  3465
           * .:**.*.**::::***** ******:. . . *:  :** :..*::**** :  : :*

Cdh1       VVVFFT-VAAKDSYMPHWDVVSKLVDAKKPLESLGLKVSRLGMDECSKGNVGQSVGVAKN  3534
Cdh3       LDVQFAVKTGSDEYTKPYDVIRVVTDNRERLTNLGLKVTSIGIDMCALER--ERVGKCIN  3523
           : * *:  :..*.*   :**:  :.* :: * .*****: :*:* *:   .  : ** . *

Cdh1       ILVRSSNFSVASGDYGKVPAPASSLTIVSIDILPKCLYEAVFPPEKRCKPHNPCLHGGKC  3594
Cdh3       VVETSSAYKIASGDYGKVPAPASSITLVSMDVVLRDKYVTIIEPGKNCSNENPCLNGGTC  3583
           ::  ** :.:**************:*:**:*:: :  * ::: * *.*. .****:**.*

Cdh1       YETVPDCPGFVCKCPTGYHGPLCEMTTRTFYGNSYIWLPKLMTYSLSDLEFEFMTKTADG  3654
Cdh3       HDTVPAG-WRVCQCPRGYRGPHCEQTTRTFRGTSYIWLPKLTAYDIRELSFEFTTEFKDG  3642
           ::***     **:** **:** ** ***** *.******** :*.: :*.*** *:  **

Cdh1       LLVYQGPEREGANNGLKDFIAVVLRGGRVELFVSLGLDPVTVKMDKGPRLDDGEWHTVQV  3714
Cdh3       LMLYQGPLKPGDNNGAKDFLAVFLDEGHLVVRVSLGYEPITINMTRRPNLNDKEWHTVQI  3702
           *::**** : * *** ***:**.*  *:: : **** :*:*::* : *.*:* ******:

Cdh1       LRNMKD---IEIIIDRCSTALLEHKPDGTVVENRKSCHVYGRMLGRSVFLDGFGPLQIGG  3771
Cdh3       IRDVIDRKMIRVIIDRCQSAQIV-EENGRVFEKRDTCEITGRVKGRSVYLNGFGPLQIGG  3761
           :*:: *   *.:*****.:* :  : :* *.*:*.:*.: **: ****:*:*********

Cdh1       VSNPNMDFPDIPYTGFKGCVRNIKDNHNLYDLKNPLKVVNAPEGCQLASACPE-CKNDGY  3830
Cdh3       VET-DLTFIGITTTGFRGCIRNIIDTEKMYDLRNPIKVVNAPEGCTLAGTCPNNCNDKGY  3820
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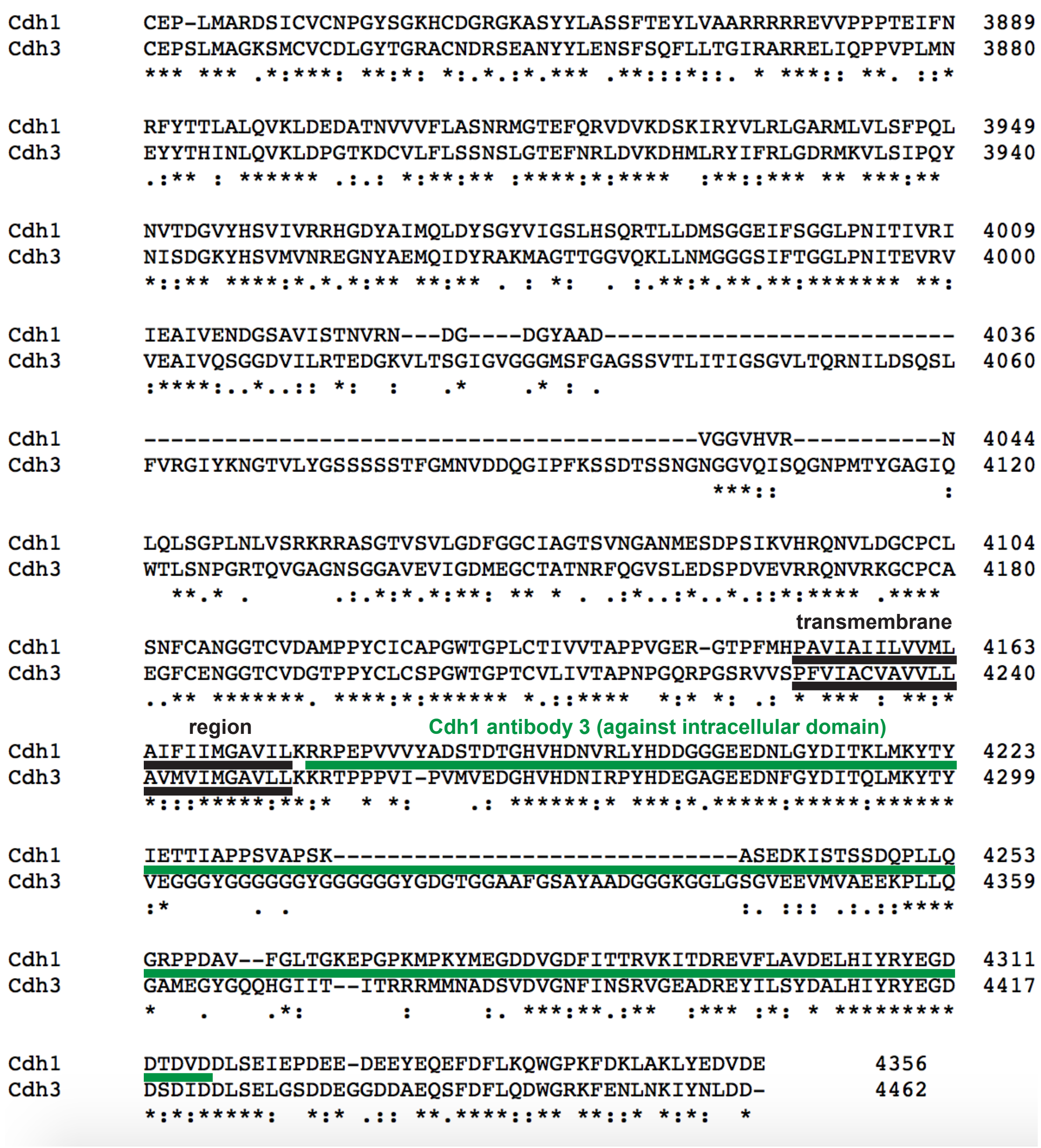

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Cdh1          CEP-LMARDSICVCNPGYSGKHCDGRGKASYYLASSFTEYLVAARRRRREVVPPPTEIFN  3889
Cdh3          CEPSLMAGKSMCVCDLGYTGRACNDRSEANYYLENSFSQFLLTGIRARRELIQPPVPLMN  3880
              *** *** .*:***: **:*: *:.*.:*.*** .**:::*::. * ***:: **. ::*

Cdh1          RFYTTLALQVKLDEDATNVVVFLASNRMGTEFQRVDVKDSKIRYVLRLGARMLVLSFPQL  3949
Cdh3          EYYTHINLQVKLDPGTKDCVLFLSSNSLGTEFNRLDVKDHMLRYIFRLGDRMKVLSIPQY  3940
              .:** : ****** .:.: *:**:** :****:*:****  :**::*** ** ***:**

Cdh1          NVTDGVYHSVIVRRHGDYAIMQLDYSGYVIGSLHSQRTLLDMSGGEIFSGGLPNITIVRI  4009
Cdh3          NISDGKYHSVMVNREGNYAEMQIDYRAKMAGTTGGVQKLLNMGGGSIFTGGLPNITEVRV  4000
              *::** ****:*.*.*:** **:** . : *:  . :.**:*.**.**:******* **:

Cdh1          IEAIVENDGSAVISTNVRN---DG----DGYAAD--------------------------  4036
Cdh3          VEAIVQSGGDVILRTEDGKVLTSGIGVGGGMSFGAGSSVTLITIGSGVLTQRNILDSQSL  4060
              :****:..*..:: *:  :   .*    .* : .

Cdh1          -----------------------------------------VGGVHVR-----------N  4044
Cdh3          FVRGIYKNGTVLYGSSSSSTFGMNVDDQGIPFKSSDTSSNGNGGVQISQGNPMTYGAGIQ  4120
                                                        ***::            :

Cdh1          LQLSGPLNLVSRKRRASGTVSVLGDFGGCIAGTSVNGANMESDPSIKVHRQNVLDGCPCL  4104
Cdh3          WTLSNPGRTQVGAGNSGGAVEVIGDMEGCTATNRFQGVSLEDSPDVEVRRQNVRKGCPCA  4180
                **.* .      .:.*:*.*:**: ** * . .:*..:*..*.::*:**** .****
                                                               transmembrane
Cdh1          SNFCANGGTCVDAMPPYCICAPGWTGPLCTIVVTAPPVGER-GTPFMHPAVIAIILVVML  4163
Cdh3          EGFCENGGTCVDGTPPYCLCSPGWTGPTCVLIVTAPNPGQRPGSRVVSPFVIACVAVVLL  4240
              ..** *******. ****:*:****** *.::****  *:* *: .: * *** : **:*
                 region          Cdh1 antibody 3 (against intracellular domain)
Cdh1          AIFIIMGAVILKRRPEPVVVYADSTDTGHVHDNVRLYHDDGGGEEDNLGYDITKLMKYTY  4223
Cdh3          AVMVIMGAVLLKKRTPPPVI-PVMVEDGHVHDNIRPYHDEGAGEEDNFGYDITQLMKYTY  4299
              *:::*****:**:*  * *:    .: ******:* ***:*.*****:*****:******

Cdh1          IETTIAPPSVAPSK------------------------------ASEDKISTSSDQPLLQ  4253
Cdh3          VEGGGYGGGGGGYGGGGGGYGDGTGGAAFGSAYAADGGGKGGLGSGVEEVMVAEEKPLLQ  4359
              :*      . .                                 :. ::: .:.::****

Cdh1          GRPPDAV--FGLTGKEPGPKMPKYMEGDDVGDFITTRVKITDREVFLAVDELHIYRYEGD  4311
Cdh3          GAMEGYGQQHGIIT--ITRRRMMNADSVDVGNFINSRVGEADREYILSYDALHIYRYEGD  4417
              *   .    .*:       :     :. ***:**.:**  :*** :*: * *********

Cdh1          DTDVDDLSEIEPDEE-DEEYEQEFDFLKQWGPKFDKLAKLYEDVDE        4356
Cdh3          DSDIDDLSELGSDDEGGDDAEQSFDFLQDWGRKFENLNKIYNLDD-        4462
              *:*:*****:  *:* .:: **.****::** **::* *:*:  *
```

Fig. S3. Protein alignment of the full-length sequences of the Cdh1 and Cdh3. Cdh1 and Cdh3 antibody epitopes and transmembrane protein regions are underlined and recognized with the colors. Transmembrane regions were identified with the SMART protein domain annotation resource. Alignment was performed with the Clustal Omega Multiple Sequence Alignment tool.

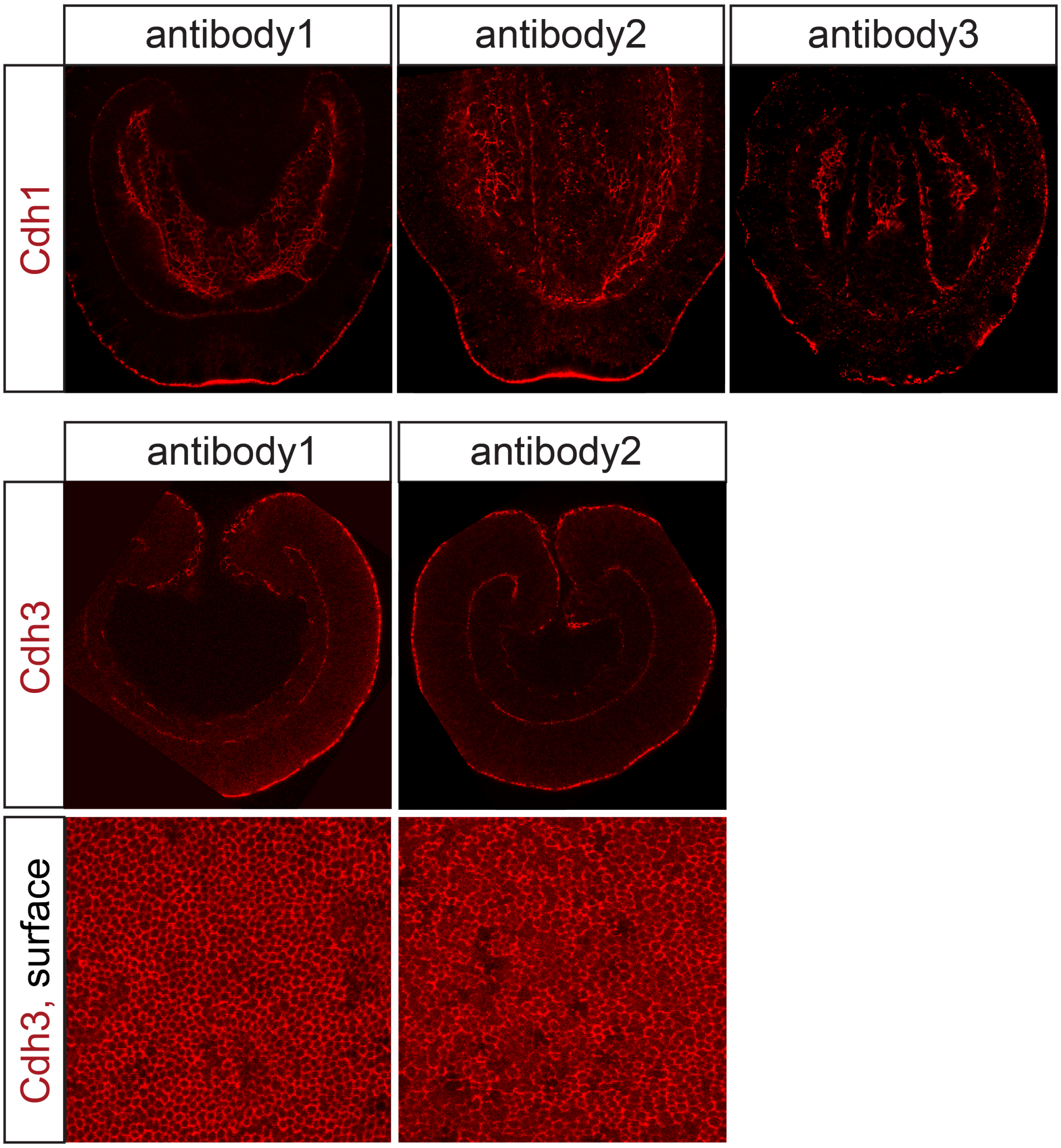


Fig. S4. Custom antibodies generated in different animals against different protein domains result in the same staining pattern. Cdh1 antibody1:domain1 (extracellular) and Cdh1 antibody2:domain1 were raised in rats; Cdh1 antibody3:domain3 (intracellular) was raised in a rabbit. All three custom Cdh1 antibodies show the same staining result. Monoclonal Cdh3 antibody1 and Cdh3 antibody2 were generated against different Cdh3 peptides and result in the same staining pattern.

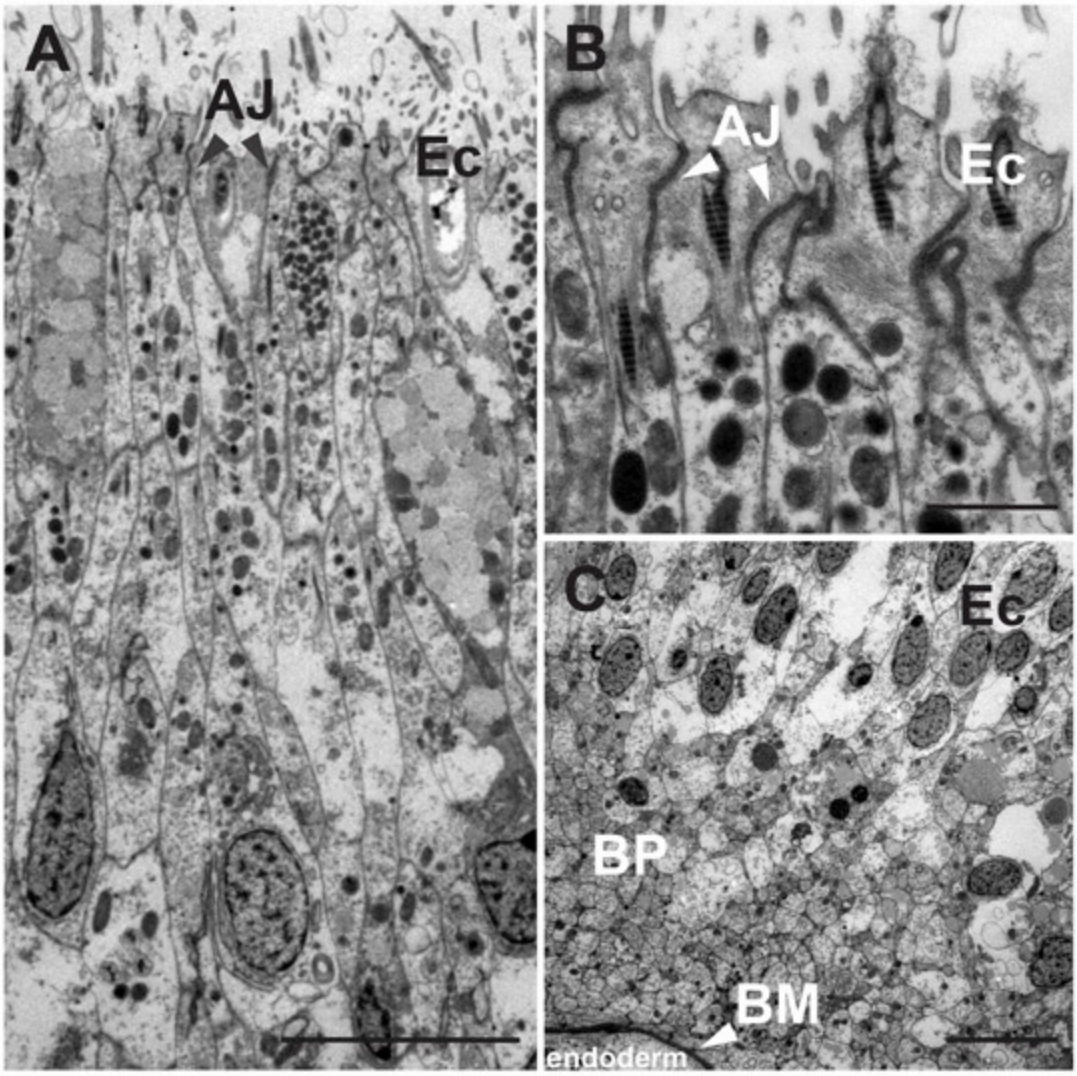


Fig. S5. TEM of the ectoderm of the apical organ. (A,B) Apical side of the ectodermal cells of the apical organ. (C) Basal side of the apical organ ectoderm. AJ apical junctions; Ec ectoderm; BP basal protrusions; BM basal membrane Scale bar A,C: 5 µm. Scale bar B: 1 µm.

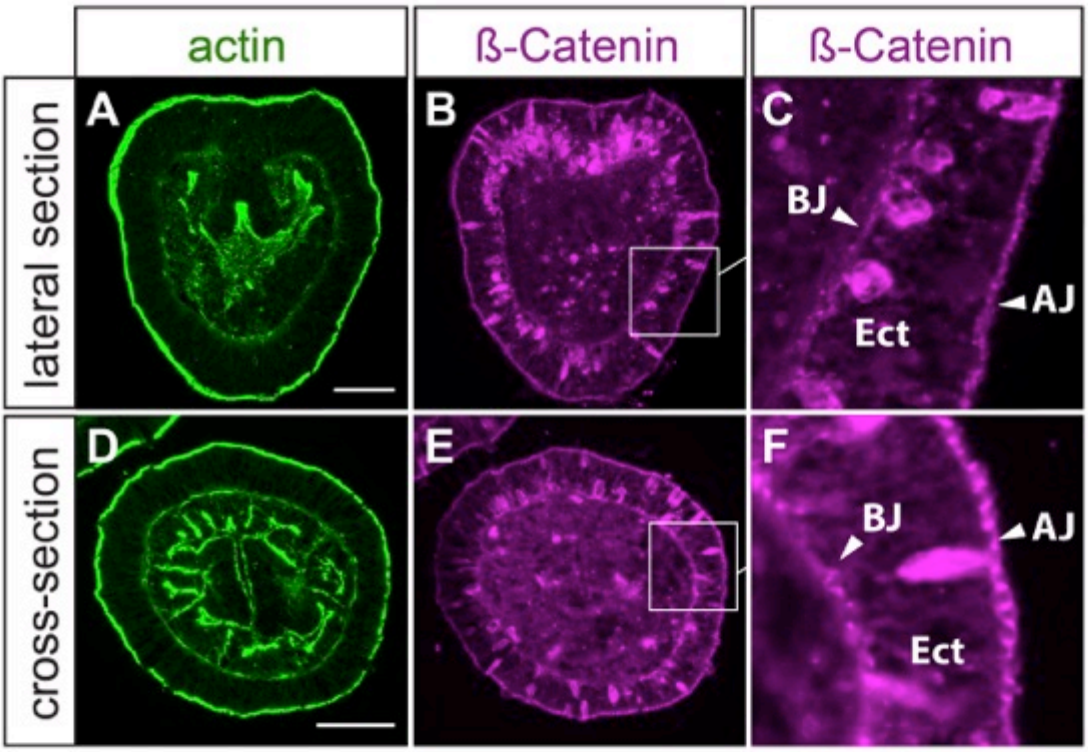


Fig. S6. β-Catenin is localized to the apical and basal adhesion junctions of the body wall ectoderm. β-Catenin antibody and phalloidin staining of vibratome sections of the 4 day old planula to exclude a possible penetration problem of the β-Catenin antibody. Please note that in vibratome sections, the β-Catenin antibody detects the basal junction in the ectoderm, but has a tendency to show unspecific staining in nematocytes and other subcellular structures. Scale bar 50 μm.

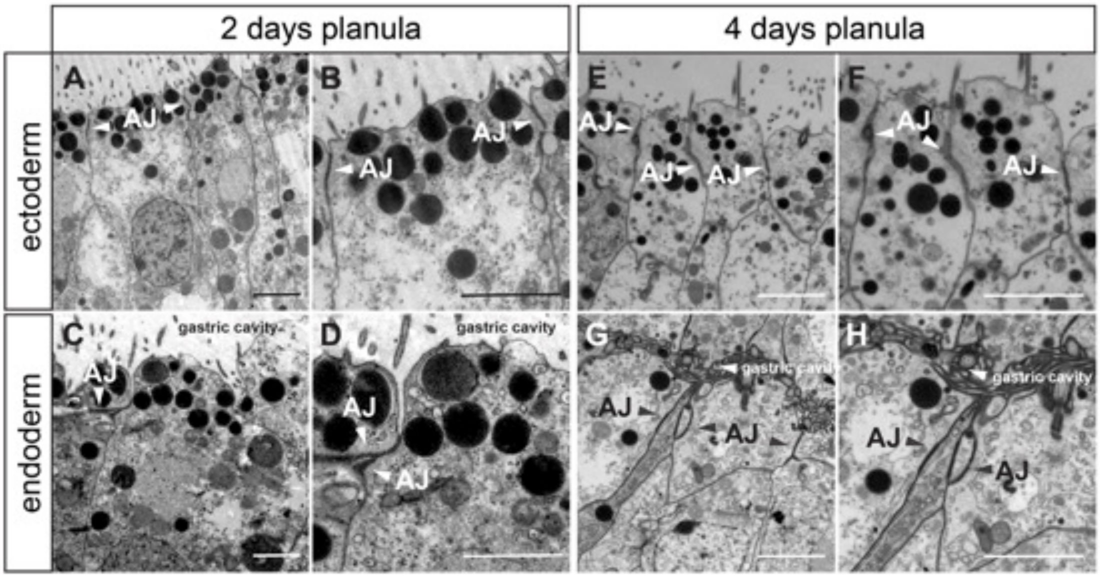


Fig. S7. TEM of the apical adherens junctions of the ectoderm and the endoderm. (A,B) ectoderm, 2 dpf planula; (C,D) endoderm, 2dpf planula; (E,F) ectoderm, 4 dpf planula; (G,H) endoderm, 4 dpf planula. Scale bar 2 µm.

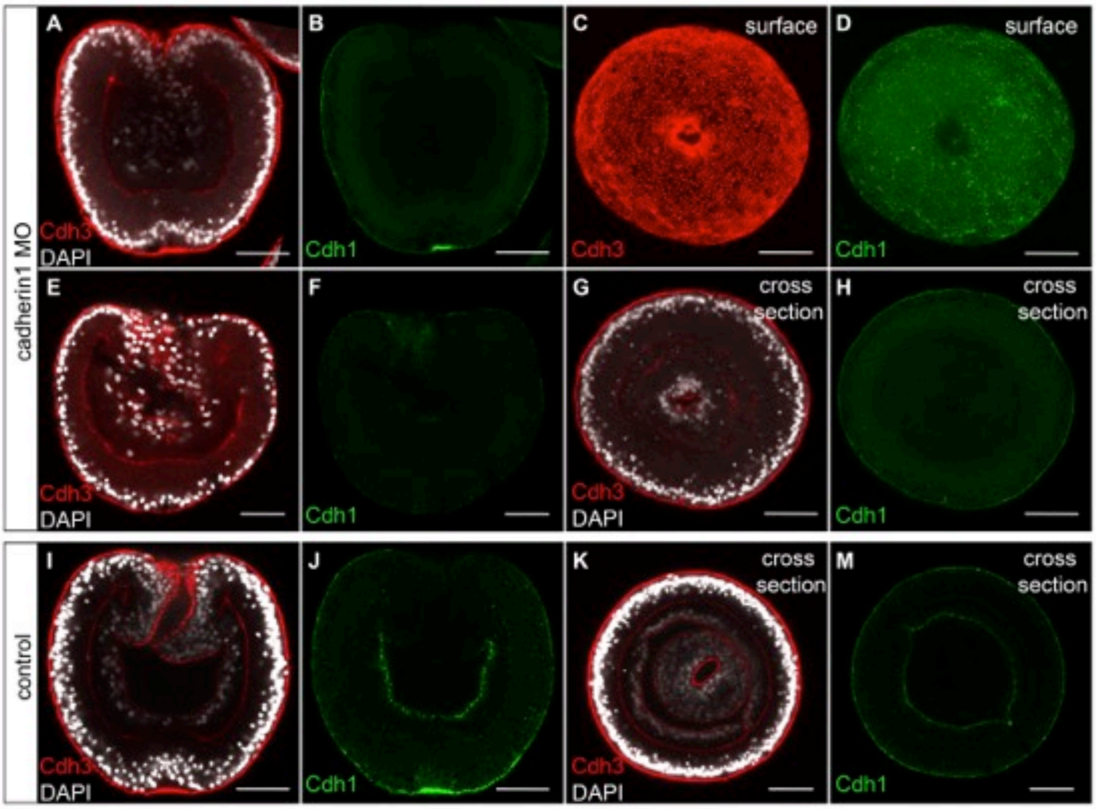
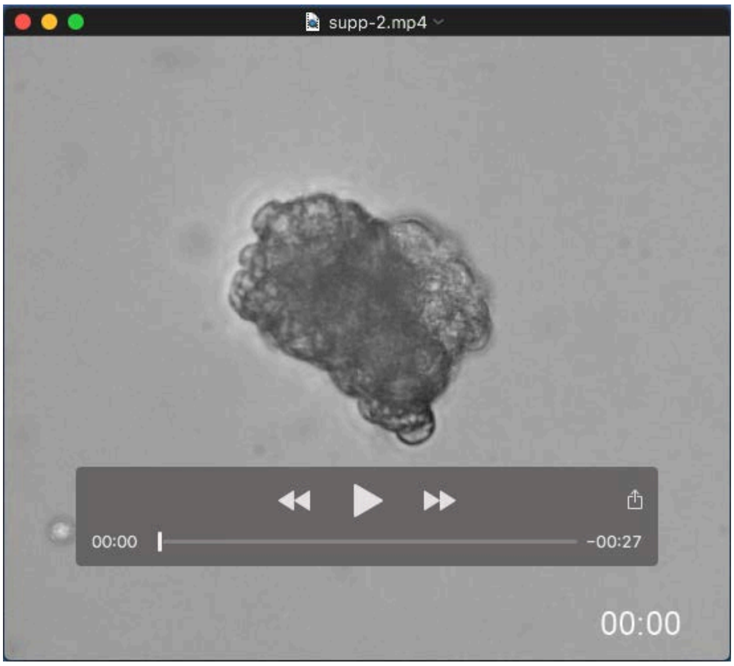
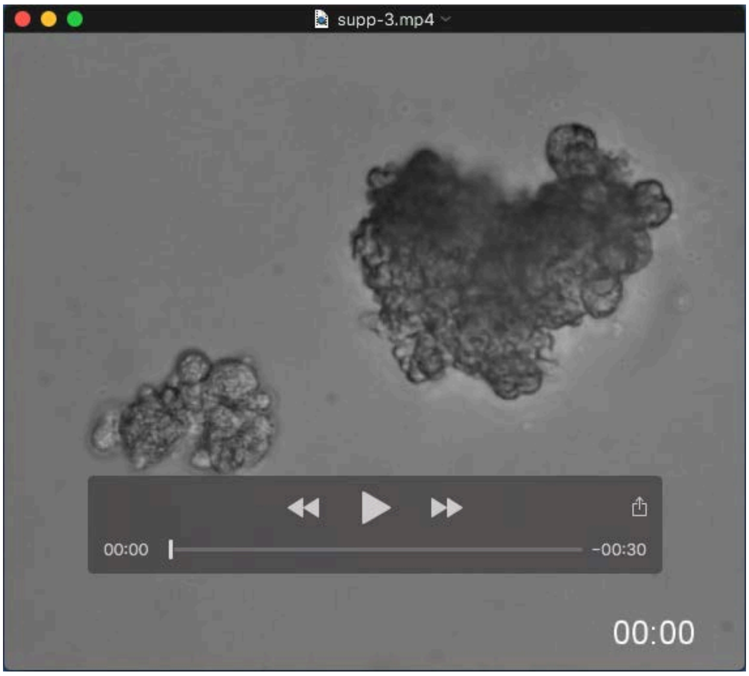


Fig. S8. Cdh1 and Cdh3 expression upon Cdh1 MO knockdown. (A-H) Cdh1 MO injected planula. (I-M) Uninjected control planula. Scale bar 50 µm.



Movie 1 Std MO aggregate development. Time indicates hours and minutes.



Movie 2 Cdh3 MO aggregate development. Time indicates hours and minutes.

Sequences for Phylogenetic analysis of Fig. 1 and Fig S1.

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