A peer-reviewed version of this preprint was published in PeerJ on 1 April 2019.

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Miranda LS, Collins AG. 2019. Eyes in Staurozoa (Cnidaria): a review. PeerJ 7:e6693 https://doi.org/10.7717/peerj.6693

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Eyes in Staurozoa (Cnidaria): a review

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The presence of dark pigment spots associated with primary tentacles (or structures derived from them, i.e., rhopalioids) in Staurozoa was recently overlooked in a study on the evolution of cnidarian eyes (defined as a “region made of photoreceptor cells adjacent to pigment cells”, irrespective of image formation, i.e., including all photoreceptive organs). Review of old and recent literature on Staurozoa shows that dark pigment spots are present in virtually all species of *Manania*, as well as some species of *Haliclystus*, *Stylocoronella,*and probably *Calvadosia*. Based on our review, we support the hypothesis that these dark spots may be related to synchronous spawning, and that rhopalioids have both adhesive and sensorial functions. Observations summarized here suggest a possible ninth independent origin of eyes in Cnidaria, within a lineage of benthic medusae. Alternatively, documented similarity across Cubozoa, Scyphozoa, and Staurozoa – with eyes being topologically associated with primary tentacles in each of these taxa – could indicate shared homology and a single origin of eyes in this clade known as Acraspeda. Information on Staurozoa, one of the least studied groups within Cnidaria, is often neglected in the literature, but correctly recognizing the characters of this classis crucial for understanding cnidarian evolution.

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Eyes in Staurozoa (Cnidaria): a review

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PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.27362v1 | CC BY 4.0 Open Access | rec: 19 Nov 2018, publ: 19 Nov 2018

Abstract

The presence of dark pigment spots associated with primary tentacles (or structures derived from them, i.e., rhopalioids) in Staurozoa was recently overlooked in a study on the evolution of cnidarian eyes (defined as a "region made of photoreceptor cells adjacent to pigment cells", irrespective of image formation, i.e., including all photoreceptive organs). Review of old and recent literature on Staurozoa shows that dark pigment spots are present in virtually all species of *Manania*, as well as some species of *Haliclystus*, *Stylocoronella,* and probably *Calvadosia*. Based on our review, we support the hypothesis that these dark spots may be related to synchronous spawning, and that rhopalioids have both adhesive and sensorial functions. Observations summarized here suggest a possible ninth independent origin of eyes in Cnidaria, within a lineage of benthic medusae. Alternatively, documented similarity across Cubozoa, Scyphozoa, and Staurozoa – with eyes being topologically associated with primary tentacles in each of these taxa – could indicate shared homology and a single origin of eyes in this clade known as Acraspeda. Information on Staurozoa, one of the least studied groups within Cnidaria, is often neglected in the literature, but correctly recognizing the characters of this class is crucial for understanding cnidarian evolution.

Introduction

In a recent article, Picciani et al. (2018) proposed that eyes (defined as a "region made of photoreceptor cells adjacent to pigment cells", irrespective of image formation, i.e., including all photoreceptive organs) originated at least eight times in Cnidaria, even in the absence of a central nervous system. Their study was mainly based on a review of the literature on the presence of eyes for adult medusae (their table S1) in light of an extensive molecular phylogeny for Cnidaria.

46 Their analyses covered all of the cnidarian classes, including Staurozoa (i.e., stalked jellyfishes,
47 Figure 1), which was characterized as lacking eyes (Picciani et al., 2018).
48 Picciani et al. (2018) considered eyes absent in Staurozoa based on a simple statement by
49 Mayer (1910 p. 520: "eyes [...] are absent in Stauromedusae"). Nevertheless, Picciani et al.
50 (2018) correctly included an exception for the genus *Stylocoronella* Salvini-Plawen 1966. Polyps
51 of *Stylocoronella riedli* Salvini-Plawen 1966 and *Stylocoronella variabilis* Salvini-Plawen 1987
52 possess dark pigment spots on the oral side of the calyx, at the inner bases of the tentacles
53 (Salvini-Plawen, 1966; Blumer et al., 1995; Kikinger & Salvini-Plawen, 1995). Based on
54 histological studies, these pigment spots were interpreted as being ocelli (Salvini-Plawen, 1966).
55 This function was later corroborated by an ultrastructure study (Blumer et al., 1995), which
56 demonstrated that the dark pigment spots are light-sensitive organs, with characteristics (e.g.,
57 photoreceptive cilia) that were hypothesized as unique for *Stylocoronella* and unknown within
58 other metazoans. The dark pigment spots are, in a somewhat modified arrangement, retained in
59 the medusa stage (Blumer et al., 1995; Kikinger & Salvini-Plawen, 1995). The stauromedusa
60 stage of *S. riedli* has "numerous tiny pigment spots in the basal area of the capitate tentacles and
61 four larger perradial ones at the subumbrellar margin", which were also presumed to be ocelli
62 (Kikinger & Salvini-Plawen, 1995). However, there are no molecular sequences for
63 *Stylocoronella* species, so the presence of these ocelli was disregarded in the analyses of eye
64 origins within Cnidaria (Picciani et al., 2018). On the other hand, Picciani et al. (2018) included
65 two species of *Manania* Clark 1863: *Manania gwilliami* Larson & Fautin 1989 and *Manania*
66 *uchidai* (Naumov 1961) (their Table S1) in their phylogeny, and both possess dark pigment spots
67 (=eyes, *sensu* Picciani et al., 2018) associated with rhopalioids (= anchors) (Naumov, 1961;
68 Larson & Fautin, 1989). Therefore, Picciani et al. (2018) neglected literature on Staurozoa and

our aim is to review it, particularly for the genus *Manania* Clark 1863, and discuss the evolutionary implications of correctly coding this character in Staurozoa.

Survey methodology

For recent papers reviewing the global diversity and natural history of stalked jellyfishes (Miranda et al., 2017), and their systematics (Miranda et al., 2016), we compiled and reviewed literature containing every original description (51), occurrence, and morphological description of staurozoan species to our knowledge (see Miranda et al., 2016; Miranda et al. 2017, and respective online resources). For this study, we updated our list for any new additions to the literature and searched for any detail that could speak to the possibility of eye-like structures using the terms “black”, “dark”, “pigment”, “eye”, “spot” in English, French, and German in the accumulated literature on Staurozoa.

Results

The genus *Manania* Clark 1863 (family Haliclystidae)

Currently, the genus *Manania* comprises seven valid species. Virtually all of them have evidence of dark pigment spots in adult stauromedusae.

Manania auricula (Fabricius 1780) and *Manania hexaradiata* (Broch 1907)

There is not a clear mention of dark pigment spots associated with rhopalioids for these two species in the literature. However, see Figure 1 (C–E) showing a specimen identified as *M. auricula* from Svalbard with dark pigment spots associated with rhopalioids. Additionally, there are doubts regarding the validity of *M. hexaradiata*. Mayer (1910) considered *M. distincta* (see

below) closely allied to *M. hexaradiata*. Uchida (1929) proposed that *M. hexaradiata* seemed a "young specimen of a medusa closely allied to, if not identical with" *M. distincta*.

Manania distincta (Kishinouye 1910)

The first unequivocal mention on the dark pigment spots in *Manania* in the literature was provided by Kishinouye (1910) in his description of *M. distincta*: "the eight primary tentacles are transformed into small, cylindrical bodies. They are erect, hollow inside, and not adhesive. They are black at base and along the axial median line. They serve probably as a sensory organ standing in relation to light".

Manania atlantica (Berrill 1962)

Berrill (1962) mentioned that, at the base of each rhopalioid of *M. atlantica*, there is a "small spherical ocellus, apparently only a pigment spot".

Manania uchidai (Naumov 1961)

Different records in the literature of *M. distincta* are actually *M. uchidai* (Figure 1, A–B), as proposed by Naumov (1910). Uchida & Hanaoka (1933) mentioned that at the axial base of the rhopalioids of *M. uchidai* (as *M. distincta*) "there exists a blackly pigmented spot which probably serves as an organ standing in relation to light" and that "on the axial side of these tentacles [= rhopalioids] there is a sensory organ for light which is blackly pigmented and composed of exceedingly narrow cells arranged in a row". Hanaoka (1935) added that "on the axial side of primary tentacles [=rhopalioids]" of *M. uchidai* (as *M. distincta*) "there is a sensory organ for light, which is blackly pigmented". Uchida (1929), also for *M. uchidai* misidentified as

M. distincta, highlighted that "in my specimen the pigment has probably faded away on account of preservation, or has not yet appeared owing to its being young". Later, Hirano (1986) observed that "the axial base of each primary tentacle (= rhopalioids)" was "provided with a black spot".

Manania gwilliami Larson & Fautin 1989

Larson & Fautin (1989) described that each rhopalioid of *M. gwilliami* has a "small, dark pigment spot near margin".

Manania handi Larson & Fautin 1989

In this unpublished thesis, Gwilliam (1956) described the species *Manania prasinus*, mentioning that "the adaxial side of the primary tentacles [= rhopalioids] bears a dark pigment fleck". Later, the species was formally described by Larson & Fautin (1989) as *M. handi*, with a "dark spot on adaxial side of each primary tentacle [= rhopalioids] near margin".

Recently, Westlake & Page (2017) showed that the pigment spot at the base of the rhopalioids of *M. handi* is associated with a greatly increased "concentration of FMRFamide-IR neuronal cell bodies".

The genus *Haliclystus* Clark 1863 (family Haliclystidae)

Haliclystus is the more diverse genus within Staurozoa, with 13 valid species (Miranda et al., 2017), but the presence of dark pigment spots in this genus is more elusive. Naumov (1961) mentioned that the rhopalioids of *Haliclystus* are sometimes supplied with a pigmented eyespot. Gwilliam (1956), while describing *Haliclystus* species, observed that "there are no conspicuous

pigment stripes other than the dark pigmented band on the subumbrellar side of the anchor [= rhopalioid] peduncle".

More specifically, Clark (1878; see also his figures 27 and 32) observed, for *Haliclystus auricula* Clark 1863, "dark patch of color so noticeable at the proximal bases of tentacular groups, and which remind one of eye-spots" and dark spots associated with rhopalioids. Then, Clark (1878) clearly inferred the existence of a nervous system in *H. auricula* based on the presence of "eye-spots" found in rhopalioids: "We speak of these eye-spots because they occupy a position at the proximal side of the base of the anchors homologous with that in which a more highly developed and even well defined optical apparatus is to be found in other Acalephae. In our Lucernarian it amounts to a mere accumulation of pigment, in unusual quantity, in a small circle, among the interstices of the prismatic cells of a specially thickened wall […]. The boss-like protuberance of the wall at these spots, conjoined with the conspicuous coloring matter imbedded in it down to half its depth, give it strong claims to some special functional status, or to a typical representation of what finds its full development in other Acalephs. The accumulation of pigment matter at any point concentrates light there rather than any other force capable of being taken note of by a nervous centre. Neither odor nor sound would be affected by it, nor does it seem possible that taste could be seated at a point so distant from the digestive system. That it is after all a mere foreshadowing, or a mimetism, of a more efficient organ of vision becomes strongly probable when we learn that these spots lose their distinctness, or disappear altogether, by the time the animal measures one-half an inch across the umbrella. When the latter is about one-fifth of an inch across […] the spots have attained to their greatest definiteness, and from that period onward they gradually become obliterated; not so much, though, by fading out as by the increase of pigment all around them, until they lose their distinctness for want of contrast".

Clark (1878) added that "they are then probably to be set down rudimentary oculiferous tentacles situated within the line along which the anchors are disposed. Now in all Acalephae the eye, so called, stands in close proximity to the margin of the umbrella". In addition, Clark (1878) mentioned that "we find it [pigment matter] holding exactly the same relation to the prismatic cells […], i.e., forming a dark casing or envelope about them, as the pigment does to the facets of the eyes of Articulata" and concluded "we have all that can be brought forward in favor of their functional characters as elements of an optical apparatus". Therefore, it seems that the dark pigment spots associated with rhopalioids in *Haliclystus* disappear during the development, but their rhopalioids might still have knots of FMRFamide- immunoreactive neurons in adult stauromedusae (Westlake & Page, 2017).

In addition, but with less precision, Ling (1939) mentioned that *Haliclystus inabai* (Kishinouye 1893) has "anchors [= rhopalioids] brown with brown spot in center".

The genus *Stylocoronella* Salvini-Plawen 1966 (family Lucernariidae)

Dark pigment spots in the two species of *Stylocoronella* have been examined in detail (Salvini-Plawen, 1966; Blumer et al., 1995; Kikinger & Salvini-Plawen, 1995) in both stauropolyp and stauromedusa stages. Polyps of *S. riedli* and *S. variabilis* possess dark pigment spots on the oral side of the calyx, at the inner bases of the tentacles (Salvini-Plawen, 1966; Blumer et al., 1995; Kikinger & Salvini-Plawen, 1995). The stauromedusa stage of *S. riedli* has "numerous tiny pigment spots in the basal area of the capitate tentacles and four larger perradial ones at the subumbrellar margin", which were presumed to be ocelli (Kikinger & Salvini-Plawen, 1995). The stauromedusa stage of *S. variabilis* does not have four perradial pigment spots (Kikinger & Salvini-Plawen, 1995).

The genus *Calvadosia* Clark 1863 (family Kishinouyeidae)

The genus *Calvadosia* is the second most diverse in Staurozoa, with 11 valid species (Miranda et al., 2017). However, we found few mentions in the literature that could indicate (with imprecision) the presence of dark pigment spots in this genus. Kishinouye (1902) observed that the primary tentacles of *Calvadosia nagatensis* (Oka 1897) are absent and "in place of them we see a dark pigment for each". Ling (1937) described that a "semi-triangular purplish area is seen in each of the eight marginal notches in close contact with the primary tentacles" for *Calvadosia cruciformis* and a "semi-triangular purplish streak present at bottom of every marginal notch" for *Calvadosia tsingtaoensis*, that faded away gradually after specimens are preserved.

Conclusions

During the metamorphosis of a stauropolyp into an adult stauromedusa, the eight primary tentacles (four interradial and four perradial) can have four fates: 1) they disappear by resorption (e.g., *Lucernaria*, *Craterolophus*, and some *Calvadosia*); 2) they metamorphose into adhesive rhopalioids (e.g., *Manania* and *Haliclystus*); 3) they remain as primary tentacles but with a modified shape (e.g., some *Calvadosia*); 4) they change their shape (filiform to capitate), migrate and cluster together with the secondary tentacles (e.g., *Stylocoronella*) (see Miranda et al., 2016). Based on our review, all dark pigment spots in Staurozoa are associated with the primary tentacles (or with the region where they used to be, e.g., *Stylocoronella* and *Calvadosia*) or with structures derived from them, the rhopalioids (e.g., *Manania* and *Haliclystus*).

Rhopalioids in adult stauromedusae are derived via metamorphosis of the eight primary tentacles of stauropolyps (see Miranda et al., 2016). Because the rhopalia of Cubozoa and Scyphozoa are also derived via metamorphosis of primary cubopolyps and scyphopolyps, respectively, rhopalioids and rhopalia are hypothetically homologous (Thiel, 1966). However, whereas the rhopalia is clearly a sensory structure (Katsuki & Greenspan, 2013), an adhesive rather than sensorial function thought to be associated with the benthic habit of staurozoans is often attributed to the rhopalioids of stauromedusae (Larson, 1988; Miranda et al., 2017).

We recently hypothesized that rhopalioids are a synapomorphy of the family Haliclystidae, which includes the genera *Manania*, *Haliclystus*, *Depastromorpha*, *Depastrum*, and *Halimocyathus* (Miranda et al., 2016). The shape of rhopalioids, information frequently used in the taxonomy of the group, varies across the family (Miranda, Morandini & Marques, 2009; Kahn et al., 2010; Miranda et al., 2016). Dark pigment spots associated with the eight rhopalioids have been observed in virtually all species of *Manania* and in at least some species of *Haliclystus*. We found no records of dark pigment spots for the genera *Depastromorpha*, *Depastrum*, and *Halimocyathus* in the literature, but this information could be overlooked, since the dark spots disappear after preservation (Uchida, 1929) and their presence can vary during development (Clark, 1878).

Unlike the pigment spots in *Stylocoronella* (Blumer et al., 1995), the ultrastructure of dark pigment spots in *Manania* and *Haliclystus* have never been analyzed, potentially raising doubt about a sensorial function. However, recent evidence (Westlake & Page, 2017) supports the idea of photo reception by these organs in both genera. Westlake & Page (2017) analyzed the neuromuscular morphology of two stauromedusae, *Manania handi* (Larson & Fautin 1989) and *Haliclystus "sanjuanensis"* (*nomen nudum*), using whole mount immunohistochemistry with

229 antibodies against FMRFamide and α-tubulin to label neurons. Comparative observations on
230 cnidarians indicate that photoreceptive organs are consistently associated with the expression of
231 these markers (see Westlake & Page, 2017). Interestingly, they observed that the "transformed
232 primary tentacles" of *M. handi* had a greatly increased "concentration of FMRFamide-
233 immunoreactive neurons at their base" associated with the dark pigment spots, which they
234 concluded to be "consistent with their homology with rhopalia" of cubomedusae and
235 scyphomedusae (Westlake & Page, 2017).

236 Surprisingly, a similar, but less pronounced, knot of FMRFamide- immunoreactive
237 neurons is present at the base of the rhopalioids of *H. "sanjuanensis"*, although the species lacks
238 a pigment spot in this area (although, as we pointed out, there are changes during development in
239 *Haliclystus*). This result might help explain the observed expression of opsin genes in species of
240 *Haliclystus* (Picciani et al., 2018), but raises interesting questions about the expression of
241 medusozoan opsin genes reported by Picciani et al. (2018) in staurozoan species whose adult
242 stauromedusae apparently lack both rhopalioids and dark pigment spots, such as *Lucernaria*
243 *quadricornis* Müller 1776 and *Craterolophus convolvulus* (Johnston 1835).

244 Although the dark pigment spots in *Manania* species were often associated with
245 hypotheses of light perception, Westlake & Page (2017) mentioned that *M. handi* showed no
246 immediate response to changes in light intensity. However, they highlighted that many
247 stauromedusae spawn in response to light (see Otto, 1976; Otto, 1978; Miranda et al., 2017)
248 despite having no obvious pigment spots, and hypothesized that "light sensitive neurons in
249 staurozoans may detect light to trigger synchronous spawning, rather than to modify immediate
250 behavior" (Westlake & Page, 2017).

In conclusion, the presence of dark pigment spots (or ocelli) in Staurozoa suggests that rhopalioids in stauromedusae can have both adhesive and sensorial functions. The reasons related to the wide occurrence of these structures in species of *Manania* needs further investigation. The homology of dark pigment spots in Staurozoa is questionable, since the genera *Manania*, *Haliclystus*, *Stylocoronella*, and (possibly?) *Calvadosia* do not form a monophyletic group (Miranda et al., 2016). However, in all these genera, the dark pigment spots were associated with primary tentacles, their region (perradial/interradial) or structures derived from them. Therefore, based on our review and on the phylogenetic topology obtained by Picciani et al. (2018), in which Staurozoa formed a sister group relationship to the remaining medusozoans, the presence of these structures in Staurozoa could indicate at least a ninth independent origin of eyes in Cnidaria. Alternatively, the observations reviewed here highlighting eyes associated with structures derived from primary tentacles (rhopalioids/rhopalia) might indicate shared homology of eyes across Cubozoa, Scyphozoa, and Staurozoa, which were recently shown to form a clade based on phylogenomic data (Kayal et al., 2018). In short, correctly coding this character in Staurozoa, a lineage of benthic medusae, has profound consequences for understanding the evolution of eyes and nervous systems in Cnidaria.

Acknowledgements

We thank Marina Nunes for discussions on cnidarian eye evolution, Yayoi Hirano for information on *Manania* taxonomy, and Maciej Mańko for kindly allowing us to use his images of *Manania auricula* (Figure 1, C–E).

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Figure legend

Figure 1: Dark pigment spots associated with rhopalioids in species of *Manania*. (A) General view of *Manania uchidai*. (B) View of calyx margin of *M. uchidai*, with rhopalioids and dark pigment spots associated with rhopalioids. (C) General view of *Manania auricula*. (D) View of calyx of *M. auricula* with arrows pointing to dark pigment spots associated with rhopalioids. (E) Arrow pointing to dark pigment spot associated with rhopalioid in *M. auricula*. Abbreviations: am, arm; cl, calyx; dp, dark pigment spot; pe, peduncle; rh, rhopalioid; st, secondary tentacles. Scale bar: A, C, D=0.5 cm; B=0.25 cm; E=0.1 cm. Photo credits: A–B, A.G.C.; C–E, courtesy of Maciej Mańko.

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Figure 1

Dark pigment spots associated with rhopalioids in species of *Manania.*

(A) General view of *Manania uchidai*. (B) View of calyx margin of *M. uchidai*, with rhopalioids and dark pigment spots associated with rhopalioids. (C) General view of *Manania auricula*. (D) View of calyx of *M. auricula*with arrows pointing to dark pigment spots associated with rhopalioids. (E) Arrow pointing to dark pigment spot associated with rhopalioid in *M. auricula*. Abbreviations: am, arm; cl, calyx; dp, dark pigment spot; pe, peduncle; rh, rhopalioid; st, secondary tentacles. Scale bar: A, C, D=0.5 cm; B=0.25 cm; E=0.1 cm. Photo credits: A–B, A.G.C.; C–E, courtesy of Maciej Mańko.

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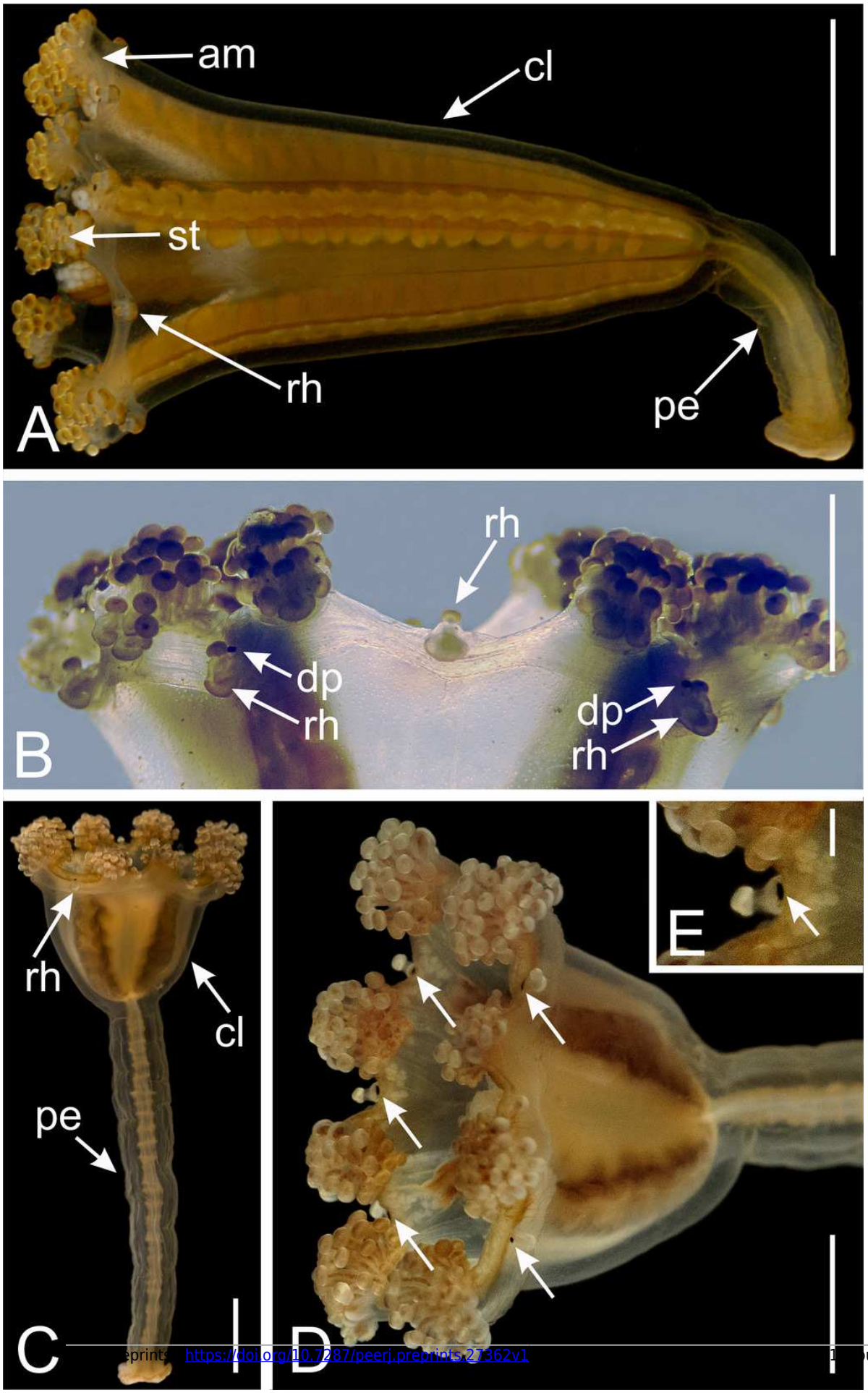
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