

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>

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., rhopaloids) 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 rhopaloids 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.

1 **Eyes in Staurozoa (Cnidaria): a review**

2

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23 **Abstract**

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

39

40 **Introduction**

41 In a recent article, Picciani et al. (2018) proposed that eyes (defined as a “region made of
42 photoreceptor cells adjacent to pigment cells”, irrespective of image formation, i.e., including all
43 photoreceptive organs) originated at least eight times in Cnidaria, even in the absence of a central
44 nervous system. Their study was mainly based on a review of the literature on the presence of
45 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 gwilliamii* 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 rhopaloids (= anchors) (Naumov, 1961;
68 Larson & Fautin, 1989). Therefore, Picciani et al. (2018) neglected literature on Staurozoa and

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

71

72 **Survey methodology**

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

81

82 **Results**

83 **The genus *Manania* Clark 1863 (family Haliclystidae)**

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

86

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

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

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

94

95 *Manania distincta* (Kishinouye 1910)

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

101

102 *Manania atlantica* (Berrill 1962)

103 Berrill (1962) mentioned that, at the base of each rhopaloid of *M. atlantica*, there is a
104 “small spherical ocellus, apparently only a pigment spot”.

105

106 *Manania uchidai* (Naumov 1961)

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

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

119

120 *Manania gwilliami* Larson & Fautin 1989

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

123

124 *Manania handi* Larson & Fautin 1989

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

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

132

133 **The genus *Haliclystus* Clark 1863 (family Haliclystidae)**

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

138 pigment stripes other than the dark pigmented band on the subumbrellar side of the anchor [=
139 rhopaloid] peduncle”.

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

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

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

173

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

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

184

185 **The genus *Calvadosia* Clark 1863 (family Kishinouyeidae)**

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

195

196 **Conclusions**

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

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

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

223 Unlike the pigment spots in *Stylocoronella* (Blumer et al., 1995), the ultrastructure of
224 dark pigment spots in *Manania* and *Haliclystus* have never been analyzed, potentially raising
225 doubt about a sensorial function. However, recent evidence (Westlake & Page, 2017) supports
226 the idea of photo reception by these organs in both genera. Westlake & Page (2017) analyzed the
227 neuromuscular morphology of two stauromedusae, *Manania handi* (Larson & Fautin 1989) and
228 *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).

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

267

268 **Acknowledgements**

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

272

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351

352 **Figure legend**

- 353 Figure 1: Dark pigment spots associated with rhopaloids in species of *Manania*. (A) General
354 view of *Manania uchidai*. (B) View of calyx margin of *M. uchidai*, with rhopaloids and dark
355 pigment spots associated with rhopaloids. (C) General view of *Manania auricula*. (D) View of
356 calyx of *M. auricula* with arrows pointing to dark pigment spots associated with rhopaloids. (E)
357 Arrow pointing to dark pigment spot associated with rhopaloid in *M. auricula*. Abbreviations:
358 am, arm; cl, calyx; dp, dark pigment spot; pe, peduncle; rh, rhopaloid; st, secondary tentacles.
- 359 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
360 Maciej Mańko.

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.

