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Is *Haootia quadriformis* related to extant Staurozoa (Cnidaria)? Evidence from the muscular system reconsidered

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Haootia quadriformis was described from the lower Fermeuse Formation of the Bonavista Peninsula of Newfoundland (approx. 560 Ma) and its numerous regularly aligned impressions were interpreted as evidence of muscular tissue ([1, figs 1*a* and 3*b*]). Consequently, this fossil could represent the earliest preservation of metazoan musculature in the geological record.

Although Liu *et al.* [1] identified *H. quadriformis* as a cnidarian, the species was not decisively assigned to any particular class, but potentially within Medusozoa [1]. The fossil was predominantly compared to staurozoans (Cnidaria) based on an assertion of consistent ‘positioning of muscular fibres in the calyx of modern Staurozoa’ [1, p. 6]. Indeed, the hypothesized general morphology of the body of *H. quadriformis* ([1, fig. 3*b*]) is similar to that of extant stauromedusae: a calyx with marginal branches (arms) and a peduncle with pedal disc (figure 1*a*; [2–5]). Other possible correspondence not exploited by Liu *et al.* [1] is the presence of an invagination of the epidermis of the pedal disc resulting in an axial canal at the base of the peduncle of some stauromedusae (figure 1*b*; [3]), similar to the impression found at the attachment area of *H. quadriformis* ([1, fig. 1*e*]). Putative dissonant characters [1, p. 6] do not contradict the staurozoan hypothesis because they are encompassed within inter- and intraspecific variation in Staurozoa, like the supplementary number of arms [6], and the absence/presence of morphological features such as anchors, gonads and nematocyst clusters [2,4,7–9]. By contrast, detailed comparison of the reconstruction of the muscular organization in the calyx of *H. quadriformis* ([1, fig. 3*b*]) to that of living stauromedusae provides evidence against a close relationship between *Haootia* and Staurozoa.

The musculature of stauromedusae is organized in two muscular arrangements: coronal (circular) and longitudinal (radial) muscles (figure 1*c,d*; [3,4]), similar to Scyphozoa and Cubozoa [10,11]. The main muscular arrangement in Staurozoa is radial, and not circular as generally observed in active and free-swimming scyphomedusae and cubomedusae ([1, fig. S6]; [10–12]), consistent with the benthic habit of staurozoans [12,13]. The coronal muscle of a stauromedusa is a narrow band, restricted to the calyx margin, either entire or regionally divided at the arms, depending on the species (figure 1*c*; [7]). Therefore, the hypothetical reconstruction of a series of muscles parallel to the calyx margin in *H. quadriformis* ([1, fig. 3*b*]) is not present in staurozoans, nor would it be consistent with the behaviour of benthic stauromedusae, which do not vigorously open and close their calices (swimming movement).

Longitudinal muscles can be present or absent in the peduncle of stauromedusae, depending on species (figure 1*e–g*; [3,7]). When present, the longitudinal muscles of the peduncle are organized into four distinct interrational bands (intra-mesogleal or associated with gastric septa) (figure 1*e,f*) and are continuous with the four interrational muscle bands at the base of the calyx (figure 1*h,i*). While longitudinal striations along the peduncle of *H. quadriformis* ([1, fig. 1*f*]) could be interpreted as peduncular muscles, there is no clear evidence that there are four.

Longitudinal muscles from the base of the calyx to the stem of secondary tentacles have been observed in all studied species of stauromedusae (irrespective of

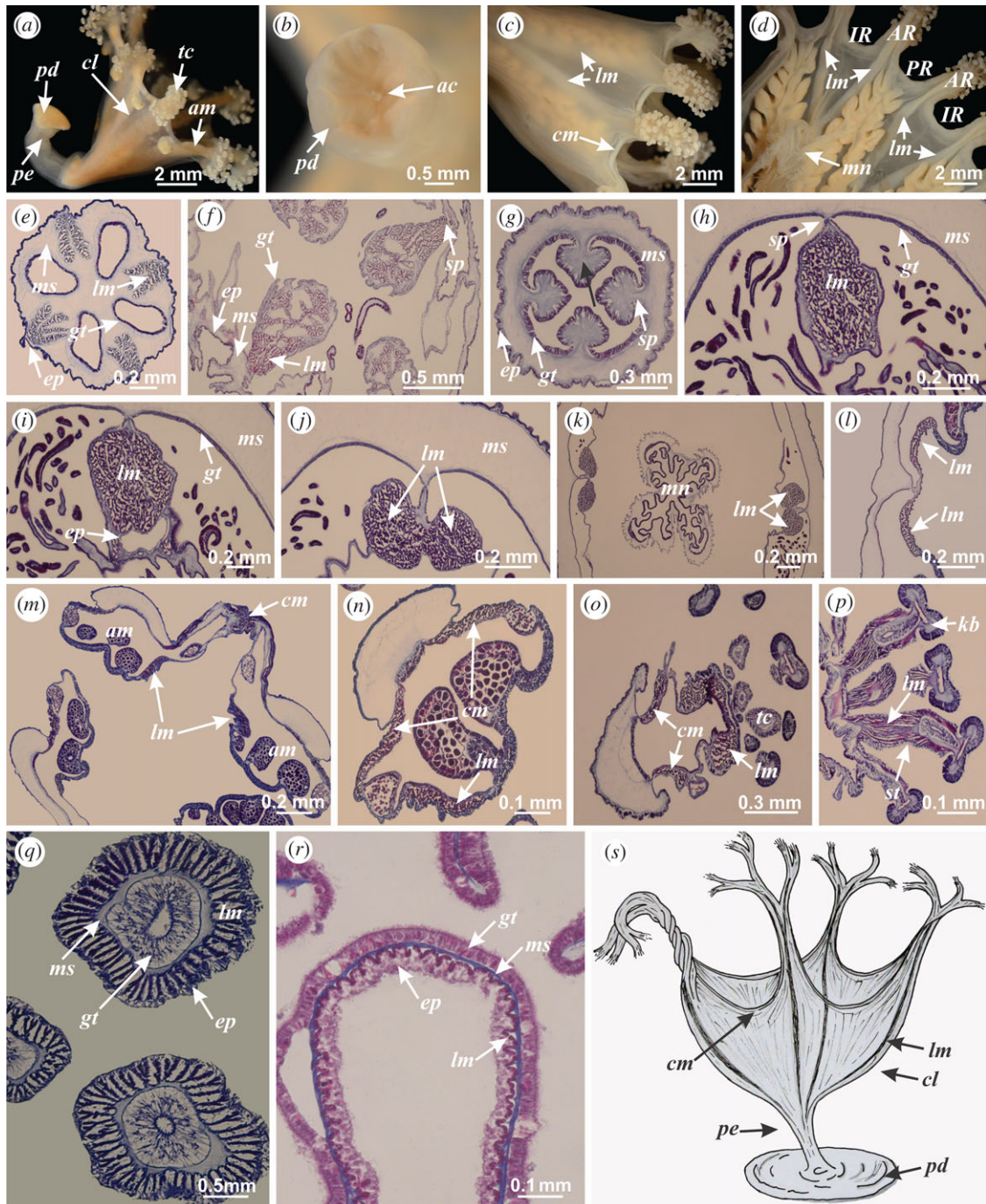


Figure 1. (a) *Halidystus tenuis*, general organization of stauromedusa. (b) *Kishinouyea nagatensis*, pedal disc with axial canal. (c) *Craterolophus convolvulus*, organization of musculature, exumbrellar view. (d) *Craterolophus convolvulus*, organization of musculature, subumbrellar view. (e) *Haliclystus tenuis*, intramesogleal interradial longitudinal muscles in peduncle. (f) *Lucernaria quadricornis*, interradial longitudinal muscles associated with septa. (g) *Kishinouyea corbini*, absence of interradial longitudinal muscles in peduncle (indicated by black arrow). (h) *Kishinouyea corbini*, interradial longitudinal muscle associated with septa at peduncle/calycal connection. (i) *Kishinouyea corbini*, interradial longitudinal muscle associated with septa at base of calyx. (j,k) *Kishinouyea corbini*, interradial longitudinal muscles divided into two sections at manubrium region. (l) *Halidystus tenuis*, interradial longitudinal muscle divided into two adradial bands at calyx margin. (m) *Haliclystus tenuis*, muscular organization at calyx/arms connection. (n) *Halidystus tenuis*, muscular organization of arm. (o) *Kishinouyea corbini*, longitudinal muscle of arm associated with secondary tentacles. (p,q) *Kishinouyea corbini*, longitudinal muscle of stem of secondary tentacles. (r) *Craterolophus convolvulus*, fibres of longitudinal muscle associated with manubrium. (s) *Haootia quadriformis*, alternative reconstruction of impressions interpreted as muscular fibres (mainly radially oriented, with coronal muscle restricted to a thin layer at calyx margin, modified from [1]). Histological sections: (e–o,q,r) cross sections; (p) longitudinal section (see methods in [5]). ac, axial canal; am, arm; AR, adradial; cl, calyx; cm, coronal muscle; ep, epidermis; gt, gastrodermis; IR, interradial; kb, knob of secondary tentacle; lm, longitudinal muscle; mn, manubrium; ms, mesoglea; pd, pedal disc; pe, peduncle; PR, perradial; sp, septum; st, stem of secondary tentacle; tc, secondary tentacle. (Online version in colour.)

the presence/absence of muscles in the peduncle) [3,4]. Gradually and towards the arms, the four interradial longitudinal bands of the calyx divide into two main sections (figure 1j–l), becoming eight adradial bands (figure 1l). At the calyx/arm connection, each one of these eight bands runs towards an

adradial arm (figure 1m,n). Therefore, a cross section of the arm of an animal with divided coronal muscle is composed of three main bands: two bands of coronal muscle (peradial and interradial) and one band of longitudinal muscle (figure 1n,o). The longitudinal muscle band is progressively divided into

diffuse bundles, running towards the stem of secondary tentacles (figure 1*o–q*). There are also thin fibres of longitudinal muscle associated with manubrium and perradii (figure 1*r*). Therefore, reconstruction of longitudinal muscles of the branches of *H. quadriformis* ([1, fig. 1*d*]) is consistent with that of modern stauromedusae.

In short, the hypothetical reconstruction of the muscular system of *H. quadriformis* contains two elements that are consistent with those of staurozoans and one that is not, thereby casting a staurozoan interpretation for *H. quadriformis* in doubt. The hypothetical coronal muscular arrangement in *Haootia* ([1, fig. 3*b*]) is not consistent with that of extant stauromedusae, but the reconstruction of longitudinal muscles in the branches and peduncle of *H. quadriformis* is similar to the organization observed in stauromedusae. A benthic lifestyle was proposed for *H. quadriformis* based on the evidence of a peduncle with pedal disc [1]. However, a benthic lifestyle does not seem to be consistent with the very well-developed coronal muscle organization hypothesized for the species ([1, fig. 3*b*]; [10]).

Fossil muscular impressions of Cambrian cnidarians, such as those of scyphomedusae, have an organization strikingly clear and similar to extant animals [14,15]. The impressions of *H. quadriformis* are considerably more complicated, probably because of its plane of preservation and possible superposition of morphological structures, making it difficult to reliably reconstruct muscular organization. Therefore, the proposed

reconstruction of the muscular organization of *H. quadriformis* ([1, fig. 3*b*]) could be misinterpreted, perhaps biased by a more clear understanding of the muscular arrangement in Scyphozoa and Cubozoa, which is predominantly circular ([1, fig. S6]; [10,11]). Interestingly, a major radial muscular arrangement, with coronal muscle restricted to the margin, is not inconsistent with the body fossil impressions of *H. quadriformis*. Therefore, we provide an alternative interpretation, with mainly radially oriented fibres, for consideration (figure 1*s*). This reconstruction must be properly assessed with direct comparison to the fossils because of their important status as the earliest tangible evidence of an animal muscular system. If the hypothetical muscular impressions are reconstructed accurately in the original paper [1], a different life habit—benthic with vigorous pulsation, perhaps as part of a feeding process—should be considered. This could have been a state from which a swimming detached descendant [15] could plausibly have arisen.

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