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 1a and 3b]). 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. 3b]) is similar to that of extant stauromedusae: a calyx with marginal branches (arms) and a peduncle with pedal disc (figure 1a; [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 1b; [3]), similar to the impression found at the attachment area of *H. quadriformis* ([1, fig. 1e]). 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. 3b]) 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 1c,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. 56]; [10–12]), consistent with the benthic habit of stauromedusae [12,13]. The coronal muscle of a stauromeda is a narrow band, restricted to the calyx margin, either entire or regionally divided at the arms, depending on the species (figure 1c; [7]). Therefore, the hypothetical reconstruction of a series of muscles parallel to the calyx margin in *H. quadriformis* ([1, fig. 3b]) is not present in stauromedusae, 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 1e–g; [3,7]). When present, the longitudinal muscles of the peduncle are organized into four distinct interradial bands (intramesogleal or associated with gastric septa) (figure 1e,f) and are continuous with the four interradial muscle bands at the base of the calyx (figure 1h,i). While longitudinal striations along the peduncle of *H. quadriformis* ([1, fig. 1f]) 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...
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 (perradial 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 10–q). There are also thin fibres of longitudinal muscle associated with manubrium and perradii (figure 1r). Therefore, reconstruction of longitudinal muscles of the branches of H. quadriformis ([1, fig. 1d]) 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 stauromedusae and one that is not, thereby casting a stauromedusan interpretation for H. quadriformis in doubt. The hypothetical coronal muscular arrangement in Haootia ([1, fig. 3b]) 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. 3b]; [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. 3b]) could be misinterpreted, perhaps biased by a more clear understanding of the muscular arrangement in Scyphozoa and Cubozoa, which is predominantly circular ([1, fig. 56]; [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 1s). 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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