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The arrangement of possible muscle fibres in the Ediacaran taxon *Haootia quadriformis*

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Haootia quadriformis from Newfoundland, Canada, is one of the most unusual impressions of a soft-bodied macro-organism yet described from the late Ediacaran Period. Interpreted as a metazoan of cnidarian grade [1], the body impression of *H. quadriformis* possesses features interpreted as fibrous structures that represent possible evidence for muscular tissue. Evidence both in support of and against a relationship between *H. quadriformis* and the Staurozoa, one of the cnidarian groups to which *Haootia* was compared in Liu *et al.* [1], is outlined by Miranda *et al.* [2]. Our intention in our original paper was to illustrate the staurozoan body plan for comparative purposes, rather than suggest homology or direct ancestry. Nevertheless, fresh insights from workers with expertise in the biology of extant cnidarians are welcomed.

We are pleased that the main points of our paper find support from the biological community: that recently discovered *Haootia quadriformis* probably preserves the impressions of muscle fibres in a macrofossil characterized by tetra-radial symmetry, and that these structures are consistent with a cnidarian body plan [2]. Histological images provided by Miranda *et al.* [2], plus their accompanying discussion, present a clear picture of muscular arrangements within modern stauromedusae. We concur that *Haootia* shows both similarities and differences with respect to stauromedusans.

Miranda *et al.* [2] suggest that the organization of musculature described by us (see [1], fig. 3b) within the body of *Haootia* appears inconsistent with that observed in modern staurozoan taxa. While the argument for the presence of a radial (longitudinal) muscle arrangement is well reasoned (see [2], fig. 1s), a revisiting of the type material to determine the orientation of fibrous structures in *Haootia* leads us to conclude that they are essentially as published in our original paper. The paratype specimen (see [1], fig. 1f) has fibres from potential coronal muscles that extend in arcs almost to the base of the calyx, with no clear preservation of radial fibres running perpendicular to these. We would argue that this phenomenon contradicts the suggestion that coronal muscle may have been restricted to the margins of the *Haootia* body [2].

The arrangement of musculature inferred by Liu *et al.* [1] does not preclude the presence of additional radial muscle bundles within the body of the organism. The holotype of *H. quadriformis* contains evidence for superposition of fibrous structures. We can clearly discern that the body sheet/calyx drapes parallel fibres observed in the stalk/peduncle, and that subsidiary branches appear to extend beneath the body (figure 1). In such cases, the fibres beneath the calyx are not expressed in the fossilized impression and are inferred to lie beyond the plane of preservation. It is therefore possible that both coronal and radial musculature were present in the calyx of *Haootia* (just as both are present in the arms of modern stauromedusae [2]), but only the outermost set is recorded in the cast of the body tissues so beautifully preserved in the *Haootia* impression.

If one were to adopt a stauromedusan analogue for *Haootia*, the inferred coronal musculature would be in the 'calyx' rather than the radial disc. This

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The accompanying comment can be viewed at http://dx.doi.org/10.1098/rspb.2014.2396.

We dedicate this manuscript to our co-author, mentor and friend Martin Brasier, who contributed so much to this field.

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Figure 1. The disc, stalk and body of the *Haootia quadriformis* holotype. Image taken at The Rooms Provincial Museum, St John's. Note that although the outline of the stalk/peduncle can be seen beneath the body/calyx, the longitudinal fibres running along its length cannot be easily traced (white arrow). Similarly, fibres radiating from the smallest subsidiary branches are typically not seen to continue beneath the body (e.g. cross-hatched arrow). It is thus plausible that additional muscle bundles, perhaps in different arrangements from those preserved, were present in the original *Haootia* organism, but do not lie in the plane of preservation. Scale bar, 10 mm. (Online version in colour.)

proposed muscular arrangement (see [1], fig. 3*b*) would argue against a free-swimming mode of life, and adds support to a benthic mode of life for *Haootia*. We therefore take great interest in the suggestion that this arrangement of muscles is consistent with an organism capable of producing powerful body contractions, potentially involved in a pulsing feeding strategy [2]. We must keep in mind that some, or maybe most, Ediacaran body plans and feeding strategies may have been specifically adapted to Ediacaran conditions. Possible behavioural ecologies such as surface detritus feeding, which would be feasible for an organism with so flexible a body, still await analysis.

The hypothetical models of muscle fibre arrangement proposed both by ourselves [1] and Miranda *et al.* [2] require further testing against the fossil material. The remarkably preserved holotype specimen of *Haootia* has now been collected (under permits issued by the Department of Tourism, Culture and Recreation, Government of Newfoundland and Labrador) and is housed at The Rooms Provincial Museum, St. John's, Newfoundland (specimen NFM F-994). While the fidelity of preservation restricts elements of the interpretation of this key fossil, the opportunity to apply controlled lighting conditions to the specimen following its removal from the outcrop offers the potential for further analysis (e.g. figure 1). We are confident that well-informed discussion of analogue taxa such as that offered by Miranda *et al.* will lead to a more complete understanding of *Haootia*, and its evolutionary significance. Similarly detailed consideration of the physiology of other extant cnidarian clades would be greatly beneficial for palaeontologists working on candidate early cnidarians.

We would like to add in support of our discussion of *Haootia* that strata of similar age in Newfoundland also contain rare fossilized surface locomotion trails that are considered to have formed by contractile activities associated with a cnidarian body plan [3–6]. We have hitherto found no evidence that the basal disc of *Haootia* could contract or move, but having two independent lines of evidence for the presence of organisms with contractile tissues in the Ediacaran makes a more compelling case for the presence of cnidarian-grade organisms [1]. While we recognize the potential importance of a fossil cnidarian ancestor from somewhat well-dated strata for understanding the phylogeny of the Cnidaria, we would caution against the uncritical extension of such interpretations to other Ediacaran taxa. The preservation and morphology of many late Ediacaran macrofossils make them difficult to interpret, and further work is required before we can be confident in our understanding of these ancient and evolutionarily important organisms.

Data accessibility. Additional images are available from the Dryad Digital Repository: doi:10.5061/dryad.8m2q8.

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