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DECLARATION OF INTERESTS

The authors declare no competing interests.

SUPPLEMENTAL INFORMATION

Supplemental information including one figure, one table, experimental procedures, author contributions, and one video can be found with this article online at https://doi.org/10.1016/j.cub.2025.12.002.

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Letter

Mollisonia is probably not an arachnid

Samuel J. Bolton[1,*], Markus Friedrich[2], and Prashant P. Sharma[3]

In a recent publication in *Current Biology*, Strausfeld *et al*.[1] describe the neuroanatomy of the Cambrian arthropod *Mollisonia symmetrica*, in which they infer a recurved brain (cerebrum), a condition found in some modern arachnids. However, beyond the proposed neuroanatomical key trait, little of the fossil's body plan organization bears any resemblance to that of any arachnid. Strausfeld *et al*.[1] complement their description with a phylogenetic analysis that recovers *Mollisonia* as sister to Arachnida. This placement stands in contrast to a previous morphological analysis that recovered *Mollisonia* as a stem-group chelicerate[2], a position that has also been questioned[3,4]. Moreover, the new analysis by Strausfeld *et al*.[1] failed to recover the monophyly of both Arachnopulmonata (including spiders and scorpions) and Tetrapulmonata (spiders and allied orders). Notably, the latter is one of the most robust chelicerate clades, supported by over four decades of morphological and molecular analyses[5,6].

Equally important, the analysis of Strausfeld *et al*.[1] is compromised by the narrow sampling of both characters and taxa. Within Arachnida, only a single taxon was included from outside of Arachnopulmonata (Solifugae: *Eremobates*), making the failure to recover monophyletic Tetrapulmonata all the more problematic. Their results suggest Solifugae are nested within Tetrapulmonata, whereas they have been recovered as early branching chelicerates in phylogenomic analyses[5,6]. Solifugae lack book lungs and chelicerae with dorsally positioned movable digits (apoteles), disfavoring a placement within Tetrapulmonata.

An important weakness of the matrix utilized by Strausfeld *et al*.[1] is that most characters (85/115) pertain to details of brain anatomy and innervation patterns. The incorporation of non-independent characters from a single character system has the well-known effect of biasing the tree toward a specific outcome (in this case, placing *Mollisonia* near the arachnids). Moreover, some character states coded as present or absent for fossil taxa by Strausfeld *et al*.[1] cannot be observed by any empirical means for Cambrian species (e.g., "Genetically fixed number of neurons"; "Undergoes molting development"). The danger of stacking a matrix with characters drawn from a preferred character system is that it suppresses the testability of the hypothesis that a focal trait (e.g., a recurved cerebrum) has evolved more than once. A phylogenetic analysis biased in this manner is a recapitulation of single-character systematics ("two taxa have my trait of interest, so they must form a clade").

Phylogenetic analysis aside, Strausfeld *et al*.[1] largely base the arachnid affiliation of *Mollisonia* on the interpretation of a recurved cerebrum, which we find unconvincing. Some of their conclusions are based on the application of digital blurring and a mirror composite. By softening or removing edges, blurring risks creating the illusion of form and shape where there is too much noise to provide reliable information. Many of the boundaries proposed by the authors are not evident to us. For example, the fan-shaped arrangement of neuromeres that is present on each side of the head in spiders is clearly absent in *Mollisonia* (Figure 1C in Strausfeld *et al*.[1]) on the left-hand side (hence the need for a mirror composite) while not at all obvious on the right-hand side, and possibly an effect of taphonomic distortion.

Even if the interpretation of a recurved cerebrum were correct, it is more accurate to describe the cerebrum of arachnids as upwardly curved relative to the rest of the synganglion (Figure 1A). In this arrangement, the neuromeres are generally closely positioned to their associated appendages and sensorial structures. For the same reason, the cerebrums of mandibulates also curve upwards, anteriorly, accommodating the dorsal positions of the eyes and antennae (e.g. Figure 2 in[7]). Within Chelicerata, upward curvature of the

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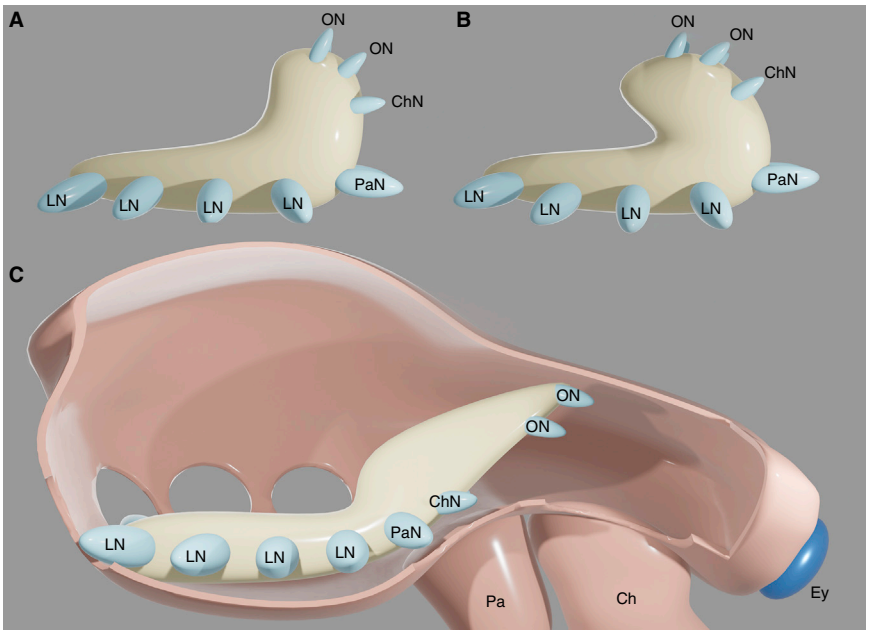

Figure 1. Three-dimensional schematic representations of the synganglion in Arachnida.
(A) Synganglion with upwardly curved cerebrum (anterior region), based on *Centruroides* (Scorpiones)[9]; (B) synganglion with recurved cerebrum, based on *Hadrurus* (Scorpiones)[9]; (C) synganglion with forward-slanting cerebrum, based on *Marpissa* (Araneae)[10]. Ch, chelicera; ChN, cheliceral nerve; Ey, eye; LN, leg nerve; ON, ocular nerve; Pa, palp; and PaN, palpal nerve.

cerebrum is not unique to arachnids, as it is also present in Pycnogonida[8]. In some arachnids, the curvature is great enough to result in the recurved organization described by Strausfeld *et al*.[1] (Figure 1B). The shape and orientation of the cerebrum is nevertheless variable, as exemplified by the pronounced differences among extant scorpions[9] (Figure 1A,B). Some spiders have a forward-slanting cerebrum that causes the synganglion to more closely resemble a linear rather than recurved form[10] (Figure 1C). This accommodates the anterior positioning of the eyes. Therefore, given the considerable variation in synganglion morphology, this trait strikes us as too variable to justify rearrangements of basal chelicerate relationships.

Moreover, taphonomic processes may make it virtually impossible to confidently distinguish a recurved cerebrum from one that is upwardly curved. The two states are not very different, and an upwardly curved cerebrum could be readily compressed into a recurved form. Upward curvature of the cerebrum may even be plesiomorphic for crown-group Arthropoda, given its presence in Mandibulata. The linear arrangement of the synganglion in *Limulus* could represent an apomorphy, considering its placement within Arachnida in phylogenomic analyses[5,6].

In conclusion, rather than provide a compelling case for placing *Mollisonia* within Chelicerata, the interpretation of Strausfeld *et al*.[1] has highlighted uncertainty in the position of this taxon, as well as in the composition of Chelicerata. This underscores the difficulty of reliably resolving relationships among stem euarthropods. If *Mollisonia* is the sister group of arachnids, as Strausfeld *et al*.[1] claim, one is left with the notion that numerous non-neural character systems used in morphological matrices of Cambrian arthropods are so unreliable that they cannot be used to infer relationships — rendering the practice of placing fossils impossible. However, given the inability by Strausfeld *et al*.[1] to recover even very strongly supported relationships (e.g., Tetrapulmonata), it is more likely that their phylogenetic matrix is not suited to its purpose; nor (giving their neuroanatomical interpretation the benefit of the doubt) does their analysis rigorously test the possibility that recurved cerebrums evolved more than once over 550 million years of evolution.

AUTHOR CONTRIBUTIONS

S.J.B. wrote the original draft. P.P.S. and M.F. made edits.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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