



Discussion on ‘*Tabelliscolex* (Cricocosmiidae: Palaeoscolecoidomorpha) from the early Cambrian Chengjiang Biota and the evolution of seriation in Ecdysozoa’ by Shi *et al.* 2021 (JGS, jgs2021-060)

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Supplementary material: Code necessary to reproduce analyses from the paper is available at <https://doi.org/10.6084/m9.figshare.16419522>

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Summary

Exceptionally preserved fossils are key to reconstructing the origin of the modern animal body plans in the Cambrian radiation. The Panarthropod phyla Euarthropoda, Onychophora and Tardigrada have roots in a ‘lobopodian’ grade typified by broadly cylindrical organisms with sclerotized dorsal plates and paired ventral projections. A similar anatomical configuration has been taken to link certain palaeoscolecoid worms with the earliest ecdysozoans. Shi *et al.* (2021a) contend that these similarities evolved convergently, and that palaeoscolecids are priapulid relatives with little bearing on the panarthropod evolution.

Here we show that this conclusion holds only under a particular treatment of inapplicable character states with known shortcomings. When inapplicable tokens are handled more rigorously, palaeoscolecids are most parsimoniously reconstructed as stem-group panarthropods with homologous dorsal plates and ventral projections – highlighting the degree to which the treatment of inapplicable data can influence fundamental evolutionary conclusions. As the position of palaeoscolecids depends so strongly on the underlying methodology, and is highly uncertain under a Bayesian approach, we consider it premature to exclude the possibility that panarthropods evolved from a grade of palaeoscolecids with dorsal plates and ventral projections.

Introduction

Palaeoscolecids are a widespread Palaeozoic group of armoured subcylindrical worms whose phylogenetic position has attracted much debate. Their regionalized pharyngeal armature and posterior hooks recall those of priapulans (Harvey *et al.* 2010; Smith 2015; Smith *et al.* 2015), but the possibility that such features may have been present in the ancestral ecdysozoan (Smith and Caron 2015) permits relationships elsewhere among the moulting animals, whether close to the nematomorphs, recognizing similarities in cuticle structure (Hou and Bergström 1994; Wills *et al.* 2012); as sister to the panarthropods (Dzik and Krumbiegel 1989; Han *et al.* 2007a); or close to the root of Superphylum Ecdysozoa (Budd 2001).

Precise anatomical observations of additional fossil material, such as the valuable description of new cricocosmiid specimens by Shi *et al.* (2021a), are needed in order to resolve this uncertainty. *Tabelliscolex* and its close relatives *Cricocosmia* and *Tylotites* have previously been linked to lobopodians on the basis of their phosphatized dorsal sclerites (Han *et al.* 2007a, b), which potentially correspond to net-like sclerites in an equivalent position on early-diverging lobopodians such as *Microdictyon*, *Onychodictyon* and *Cardiodictyon* (Ramsköld and Chen 1998).

Shi *et al.* (2021a) describe serially repeated projections that lie ventrally opposite these dorsal plates. These structures fit neatly into the appealing, if speculative, framework proposed by Dzik and Krumbiegel (1989), in which lobopodians evolved from a palaeoscolecoid-like ancestor *via* the extrusion of ventral legs opposite dorsal plates. This scenario rests on the assumption that plates in lobopodians and palaeoscolecids are homologous, and could imply that newly described ventral projections represent precursors to the lobopod limbs of lobopodians.

Shi *et al.* (2021a) display commendable caution by testing this model in a phylogenetic framework, combining characters from two established phylogenetic datasets to test palaeoscolecoid relationships within a modern framework of ecdysozoan evolution, encompassing recent fossil finds and conceptual advances (Wills *et al.* 2012; Smith and Ortega-Hernández 2014; Smith and Caron 2015; Yang *et al.* 2015; Zhang *et al.* 2016; Howard *et al.* 2020).

This combined dataset is characterized by a high proportion of character states that cannot logically be coded; 7155 of 17 005 entries are marked as ‘inapplicable’. As an example, a taxon without sclerites cannot be meaningfully coded for the sub-character ‘sclerite ornamentation’ (character 86, Shi *et al.* 2021b), as neither of the two states ‘net-like’ or ‘scaly’ applies.

Fitch (1971) parsimony and the Mk model (Lewis 2001) treat these inapplicable states as though they were simply uncertain, an approach that is known to materially affect the identification of optimal topologies (Maddison 1993; Brazeau *et al.* 2019). By way of example, a transition between ‘net-like’ and ‘scaly’ dorsal sclerites might be inferred in an ancestor that lacks sclerites. The inference of an evolutionary step that could not logically have occurred may add to an overall parsimony score that would

otherwise be optimal. Workable solutions to the problem – each with their own strengths and limitations – have recently been proposed (De Laet 2005; Brazeau *et al.* 2019; Tarasov 2019; Goloboff *et al.* 2021; Hopkins and St. John 2021).

Methods

We explore the impact of inapplicable data on the results of Shi *et al.* (2021) by reanalysing their morphological matrix using four methods: Bayesian inference and maximum likelihood under the Mk model (Lewis 2001); standard Fitch (1971) parsimony; and the ‘inapplicable-aware’ parsimony algorithm of Brazeau *et al.* (2019) (‘BGS’).

The first three methods seek to replicate and extend the results of Shi *et al.* (2021); we follow these authors’ methodology, making appropriate selections for unspecified analytical parameters.

For Bayesian inference, we conduct three independent runs of six chains in MrBayes 3.2.7a (Ronquist *et al.* 2012), sampling every 10 000 generations for 6 000 000 generations, discarding the first 25% of samples as burn-in. We use the Mk model with gamma-distributed rate variation across characters (Lewis 2001), and a Dirichlet prior distribution on branch lengths (Rannala *et al.* 2012; Zhang *et al.* 2012). Convergence between runs is indicated by minimum estimated sample sizes > 1800 and potential scale reduction factors = 1.000 for the tree length and alpha parameters.

We calculate the maximum likelihood tree using IQ-tree 1.6.12 (Nguyen *et al.* 2015). ModelFinder (Kalyaanamoorthy *et al.* 2017) identifies the Mk model (Lewis 2001), with a four-category gamma model of rate heterogeneity and a correction for ascertainment bias, as the most appropriate model under the Bayesian information criterion. Correspondingly, the five invariant sites are removed prior to analysis. This model estimates 188 parameters from 174 variable sites, meaning that branch length estimates – and consequently reconstructed tree topologies – are likely to be unreliable (Burnham and Anderson 2002). We further note that IQ-tree treats partially ambiguous states (e.g. {0, 2}) as fully ambiguous (i.e. ?).

To identify optimal trees under the Fitch (1971) parsimony implementation, we use TNT 1.5 (Goloboff *et al.* 2008a) with each of the implied weighting (Goloboff 1993) concavity constants 2, 3, 4.5, 7, 10, 15, 22, 34, 51, 76, 114 and ∞ (i.e. equal weights), without extended implied weighting (Goloboff 2014). We stop tree search, using the parsimony ratchet and tree drifting heuristics (Goloboff 1999; Nixon 1999), once the optimal score is hit 1000 times.

Finally, we apply the ‘Morphy’ (Brazeau *et al.* 2017) implementation of the BGS inapplicable treatment (Brazeau *et al.* 2019) using the R (R Core Team 2021) package ‘TreeSearch’ (Smith 2018, 2021), which conducts tree search using the parsimony ratchet heuristic (Nixon 1999). Implied weighting scores are calculated using the formula $e/(e+k)$ (Goloboff 1993), where e is the extra score associated with each character (i.e. the ‘Morphy’ score minus the minimum score possible), and k is the concavity constant. At each concavity constant, we run the search until tree score has not improved for 18 consecutive ratchet iterations, retaining up to 171 most parsimonious trees for each analysis.

Because six characters in the Shi *et al.* (2021a) matrix contain 6–13 sub-characters, and 14 sub-characters are contingent on more than one character, the TNT implementation of the Goloboff *et al.* (2021) algorithm (which supports a maximum of five sub-characters) cannot be used. The BGS algorithm, whilst approximate and imperfect (Brazeau *et al.* 2019; Goloboff *et al.* 2021), is the only inapplicable-aware phylogenetic method that supports arbitrarily many contingent sub-characters, and for which a computationally tractable implementation is presently available. This allows us to analyse the Shi *et al.* (2021a) matrix without modification, simplifying the interpretation of our results.

We explore differences between analytical methods by constructing a tree space (Hillis *et al.* 2005; Smith *in press a*) on a subset of 20 most parsimonious trees from each parsimony analysis, 100

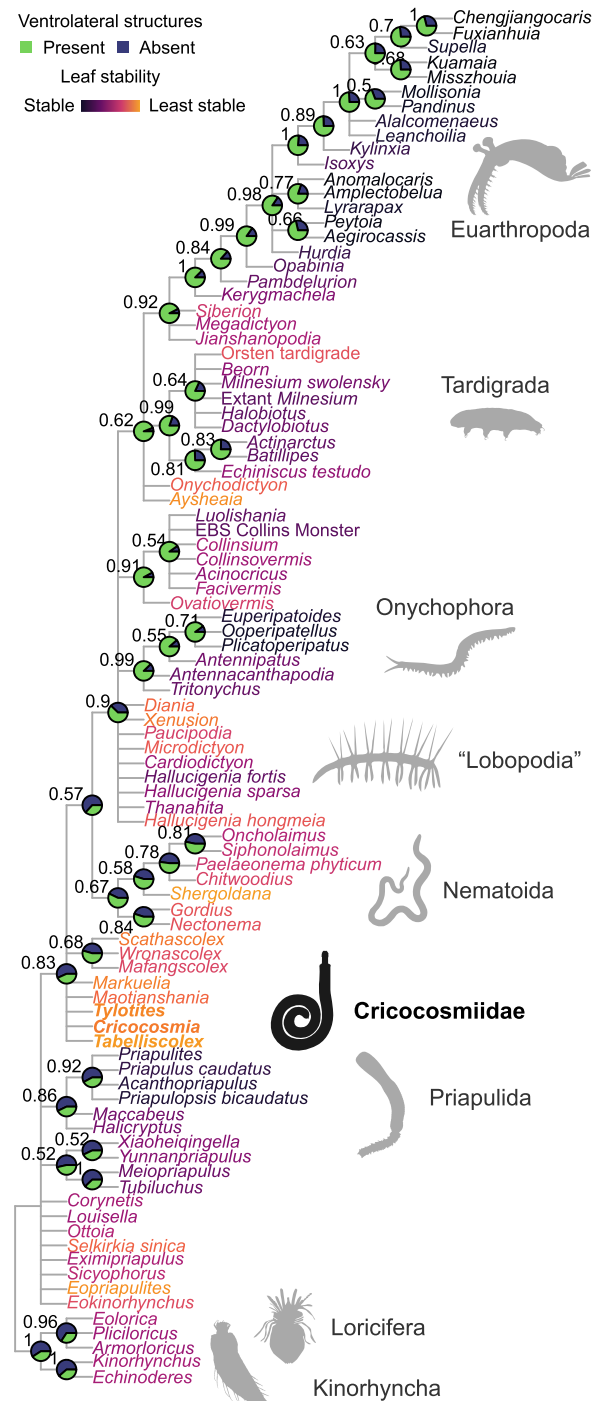


Fig. 1. Summary of Bayesian posterior trees. Cricocosmiids (bold) are among the least stable taxa in Bayesian analyses, but are most likely to fall as sister to a clade comprising nematoids and panarthropods. The presence of paired ventral structures in the common ancestor of these taxa is not resolved by probabilistic methods. Tree represents the majority-rule consensus of the posterior distribution after removing the rogue taxon *Acosmia*, and is arbitrarily rooted on Loricifera + Kinorhyncha. Taxa are coloured according to their relative instability (Smith *in press b*): darker text denotes taxa that occupy a consistent position in all sampled trees. Edges are labelled with the posterior probability of the associated bipartition split; pie charts at nodes denote the reconstructed probability that serially repeated paired ventral structures (char. 77, Shi *et al.* 2021b) were present at each ancestral node.

trees from the posterior distribution of each of MrBayes run, and the single most likely tree.

We define our tree space based on quartet distances between unrooted trees (Estabrook *et al.* 1985; Sand *et al.* 2014; Smith 2019b), which map faithfully into two dimensions *via* principal coordinates analysis (Gower 1966) (trustworthiness \times continuity > 0.9) (Venna and Kaski 2001; Kaski *et al.* 2003). The minimum spanning tree (Gower and Ross 1969), which shows the shortest graph connecting all trees, highlights distortions in the mapping (Smith *in press a*). We verified that the results of tree space analysis are robust to the choice of distance metric by repeating the analysis using the clustering information distance (Smith 2020).

Morphological datasets often include taxa with a poorly constrained phylogenetic position, removal of which allows additional groupings to be resolved in a consensus tree (Wilkinson 1994, 1996). We evaluate the stability of leaves within the posterior distribution of trees in order to identify rogue taxa using the heuristic approaches of Smith (*in press b*).

To evaluate the evolutionary implications of different tree topologies, we reconstruct ancestral states using the BGS algorithm (parsimony trees) and maximum likelihood (Bayesian trees), using the R packages ‘ape’ and ‘TreeSearch’ (Paradis and Schliep 2019; Smith 2021).

Results

Our Bayesian analysis reproduces the results presented by Shi *et al.* (2021a). Analysis of the Bayesian posterior tree sample identifies *Acosmia* (Howard *et al.* 2020) as a rogue taxon whose variable position between posterior trees reduces the resolution of the majority-rule consensus tree. A majority-rule summary of the Bayesian posterior after removing *Acosmia* from each tree topology

(Fig. 1) thus yields additional phylogenetic information (Smith *in press b*). Most pertinently, the posterior tree sample suggests (with $p > 0.7$) that cricocosmiids belong in the stem group of a clade comprising nematoid worms and panarthropods, which are likely ($p > 0.6$) to be sister taxa.

Despite the tendency of phylogenetic analyses to overestimate Bayesian posterior probabilities, particularly in the presence of ambiguous (or inapplicable) data (Suzuki *et al.* 2002; Erixon *et al.* 2003; Yang and Rannala 2005; Lemmon *et al.* 2009), the results of this analysis are inconclusive as to whether the common ancestor of cricocosmiids and panarthropods had serially repeated paired ventral structures (char. 77, Shi *et al.* 2021b; Fig. 1); indeed, this character is reconstructed with a degree of uncertainty at all nodes. Dorsal epidermal specializations (char. 79, Shi *et al.* 2021b) are reconstructed as absent at this ancestral node with $p = 0.8$.

Trees identified as optimal under the maximum likelihood and parsimony criteria fall at or beyond the fringes of the area of tree space sampled by the Bayesian posterior distribution (Fig. 2; Supplementary Data). Their high distance from the more central and densely sampled regions of the Bayesian posterior distribution indicates that these trees do not correspond to the most plausible trees under the Mk model.

Even if the most likely tree has a low likelihood of being exactly correct ($p = e^{-2390.0492}$), it can in principle serve as a point estimate of the most likely tree topologies in situations where a single bifurcating tree is desired (Brown *et al.* 2017). In this case, however, the large distances between the maximum likelihood tree and the majority of the Bayesian sample (Fig. 2) indicate that it inadequately represents the distribution of plausible trees and the associated phylogenetic uncertainty.

Parsimony analysis under the Fitch algorithm replicates the results of Shi *et al.* (2021a), though our extended searches recover

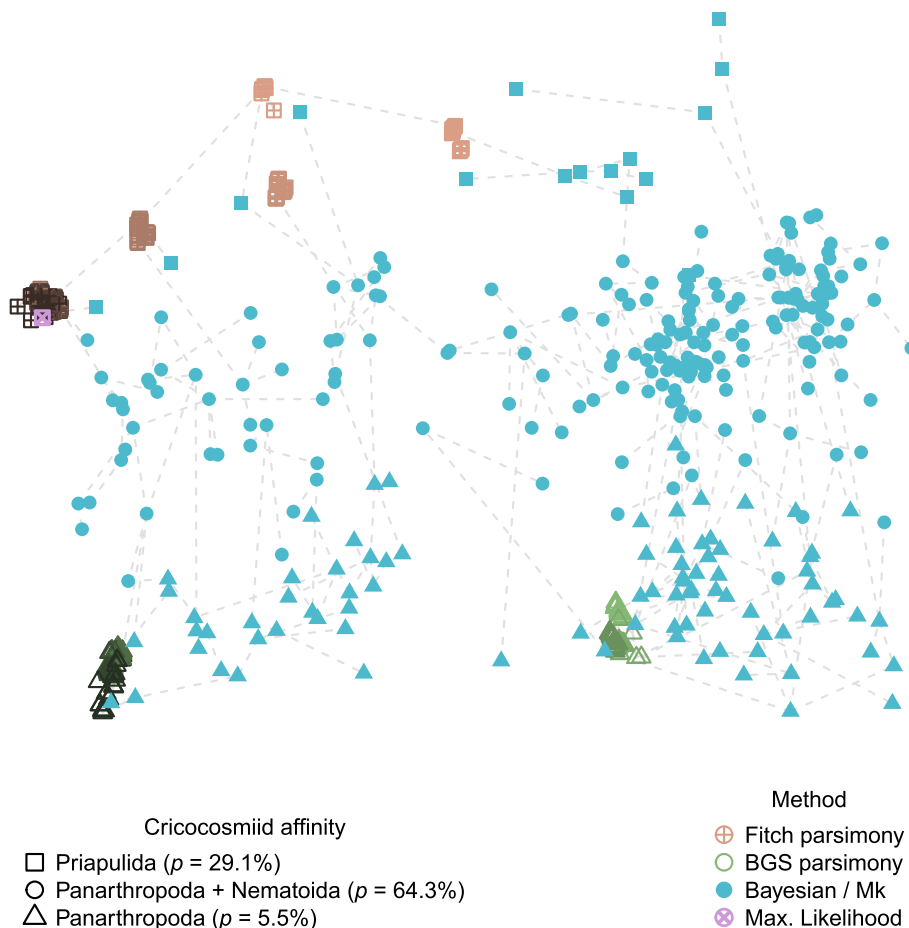


Fig. 2. Mapping of distances between trees recovered by different analyses. Fitch (1971) parsimony (+) and maximum likelihood (x) resolve cricocosmiids as sister to Priapulida (squares); BGS parsimony [Brazeau *et al.* (2019); open shapes] as sister to Panarthropoda (triangles); the Bayesian posterior sample [Lewis (2001); filled shapes] encompass both these possibilities as well as a position as sister to Panarthropoda + Nematoida (circles). p denotes the posterior probability of each topological hypothesis. Low (light shading) v. high (dark shading) concavity constants return a distinct set of trees in both parsimony treatments.

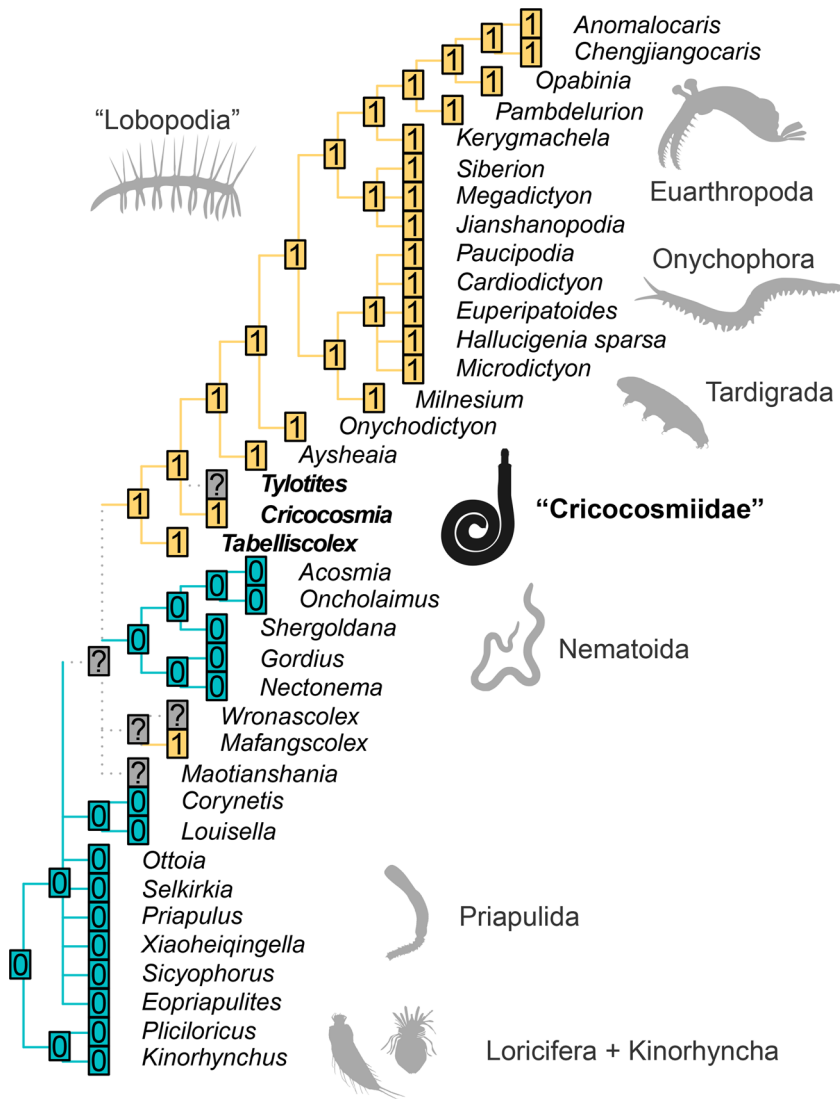


Fig. 3. Ecdysozoan relationships under the BGS (Brazeau *et al.* 2019) treatment of inapplicable data. Cricocosmiids (bold) are recovered as stem group panarthropods, with serially repeated paired ventral structures (char. 77, Shi *et al.* 2021b) reconstructed as homologous between these groups (0: absent; 1: present). Tree is strict consensus of all most parsimonious trees obtained under concavity constants from 10–114, rooted arbitrarily on Loricifera + Kinorhyncha. Some taxa omitted for clarity; full results in [Supplementary Data](#).

additional most-parsimonious trees ($k = 3$: 82 rather than four; equal weights: 4 981 rather than six; tree scores listed in [Supplementary Data](#)). Values of the concavity constant close to TNT's default of 3, which is understood to penalize homology too severely in many settings (Goloboff *et al.* 2008b, 2018; Smith 2019a), recover trees that are very different from those under more appropriate concavity constants (higher values; darker shades in Fig. 2), which in turn resemble those obtained under maximum likelihood and equal weights; the most prominent differences concern whether *Microdictyon* and similar taxa fall in the stem group to Panarthropoda or Onychophora ([Supplementary Data](#)).

BGS parsimony recovers very different trees to Fitch parsimony (Fig. 2; tree scores listed in [Supplementary Data](#)), again with strong differences between low concavity constants (in which *Acosmia* plots with kinorhynchs and loriciferans; [Supplementary Data](#)) and high ones (where *Acosmia* plots with nematoids; Fig. 3). All BGS trees recover the clade comprising panarthropods and lobopodians emerging from a paraphyletic 'Cricocosmiidae' (Fig. 3). The most parsimonious character reconstruction indicates that serially repeated paired ventral structures (char. 77, Shi *et al.* 2021b Fig. 3) and dorsal epidermal specializations (char. 79, Shi *et al.* 2021b) evolved in the common ancestor of *Tabelliscolex* and panarthropods, and are homologous between these groups. The potential homology of the paired ventral structures in *Mafangsclex* remains uncertain under the BGS algorithm.

Discussion

The central conclusion of Shi *et al.* (2021a) – that dorsal sclerotized plates and spinose ventral appendages evolved independently in lobopodians and cricocosmiids – is supported only when cricocosmiids are resolved as stem-group priapulans. Parsimony analyses only recover this situation under unsuitable treatments of inapplicable characters. Bayesian analysis, which cannot yet readily account for inapplicable characters, assigns a low posterior probability (5.5%) to a stem-group priapulid relationship.

Our reanalyses indicate that it is more parsimonious to reconstruct cricocosmiids in the stem group to Panarthropoda, and that this relationship – with the possible inclusion of the nematoids – is substantially more likely than any other. This view is consistent with the origin of panarthropods (and potentially nematoids) from within a palaeoscolecid grade, and the homology of their dorsal and ventral repeated structures (Dzik and Krumbiegel 1989). Nevertheless, in light of the strong impact of methodology on the relationships of the palaeoscolecids, and the considerable uncertainty in their super-phylum-level affinity indicated by Bayesian analyses, we feel that it is premature to offer a decisive statement on the potential homologies between serially repeated structures in lobopodians and palaeoscolecids.

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Author contributions MRS: formal analysis (lead), funding acquisition (lead), investigation (lead), methodology (lead), software (lead), visualization (lead), writing – original draft (lead), writing – review & editing (lead); AD: conceptualization (lead), writing – original draft (supporting), writing – review & editing (supporting)

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Data availability All data generated or analysed during this study are included in this published article (and its [supplementary information files](#)).

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