

Research



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Evolutionary biology

Flight, symmetry and barb angle evolution in the feathers of birds and other dinosaurs

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There has been much discussion over whether basal birds (e.g. *Archaeopteryx* and *Confuciusornis*) exhibited active flight. A recent study of barb angles has suggested they likely could not but instead may have exhibited a gliding phase. Pennaceous primary flight feathers were proposed to show significant shifts in barb angle values of relevance to the inference of flight in these extinct taxa. However, evolutionary trends in the evolution of these barb angle traits in extant volant taxa were not analysed in a phylogenetic frame. Neither the ancestral crown avian condition nor the condition in outgroup dinosaurs with symmetrical feathers were assessed. Here, we expand the fossil sample and reanalyse these data in a phylogenetic frame. We show that extant taxa, including strong flyers (e.g. some songbirds), show convergence on trailing barb angles and barb angle asymmetry observed in Mesozoic taxa that were proposed not to be active fliers. Trailing barb angles in these Mesozoic taxa are similar to symmetrical feathers in outgroup dinosaurs, indicating that selective regimes acted to modify primarily the leading-edge barb angles. These trends inform dynamics in feather shape evolution and challenge the notion that barb angle and barb angle ratios in extant birds directly inform the reconstruction of function in extinct stem taxa.

1. Introduction

The evolutionary origin of avian flight is long debated [1–5]. Understanding the evolution of functional traits present in extant avian wings and feathers remains key. While there is evidence that feathers evolved prior to flight, which fossilizable feather or wing structures may imply the presence of a wing used in active flight remains debated [6]. Compared to wing shape, the variation in, and functional significance of flight feather vane geometry are less well understood, though previous studies have yielded key insights into vane anatomy, the function of vane morphology and structural variations among flight feathers (e.g. [4,7–10]). Consequently, it is still largely unknown how the vane geometry (vane shape) of ancient birds are comparable anatomically and functionally to those of extant birds [11,12].

Variation in feather vane geometry has been described with reference to barb–rachis angle, and comparisons of this angle in the leading and trailing edge of flight feathers. This angle is measured where the barbs contact the rachis in proximal, central and distal parts of primary flight feathers [2]. Together with barb length, the leading and trailing angles determine vane width asymmetry [8,13]. Consequently, feathers with different barb angles may gain different feather geometries, which may influence how the feathers respond to aerodynamic forces [4]. However, the relationship between flight

feather geometry and the potential flight functions has rarely been investigated in a quantitative frame [4,14].

Recently, Feo *et al.* [4] investigated the relationship between barb geometry and aerodynamic function in asymmetrical flight feathers. They proposed that early Mesozoic stem taxa like *Archaeopteryx* and *Confuciusornis* are distinctly different from modern birds in having lower trailing vane barb angles and suggested that a modern capacity for powered flight may not have been developed in these taxa [2]. Pap *et al.* [14], with a larger data size, found that barb angle values vary along the wing length and flight feather length within extant birds. They also identified the effect of flight style on barb angle using a phylogenetic comparative approach. However, the proposed relationship between barb angle and flightedness was tested neither in a phylogenetic nor a 'traditional' non-phylogenetic statistical frame [4]. The influence of phylogeny on the assessment of the inferred ancestral condition for barb angle in extant taxa and within Avialae was not explored. The ancestral outgroup barb angle condition was still unknown. The sample of extinct stem birds was also limited.

Here, we reassess in a phylogenetically informed statistical frame the evolution of leading and trailing barb angles across birds to reconstruct the ancestral state of this character for Aves, shedding new light on the macroevolutionary trends in these characteristics. We also further test the hypothesis that barb angles in the flight feathers vary systematically with flightedness and flight style, including an increased sample of extinct stem avialan specimens. Understanding the relationship between barb angle, flightedness and flight style will influence conclusions about the functional performance of flight feathers in extinct taxa.

2. Material and methods

(a) Dataset

Measurements of barb angles for the 60 species of extant volant birds and 13 species of secondarily flightless birds used were collected by Feo *et al.* [4] (electronic supplementary material, table S1). For each extant species, the trailing and leading vane angles of the outermost primary at 50% from the feather tip were used in all analyses. Barb angle asymmetry was calculated as the difference between the trailing vane and the leading vane (trailing–leading) [4].

We measured primaries from 16 specimens of 10 Mesozoic stem taxa comprising taxa recovered as part of Avialae as well as non-avialan taxa (*Microraptor gui* and *Caudipteryx zoui*) (electronic supplementary material, table S2). Feathers of Mesozoic taxa were studied from high-resolution digital photographs of prepared fossils taken by the authors and, where direct reassessment was not possible, from the literature [15–18]. For each Mesozoic species, we measured barb angle of primaries at 50% of total vane length from the tip of the feather (electronic supplementary material). The values for outer primary feathers were used when multiple feathers were available as they showed the greatest degree of vane asymmetry [8,19] and also because they are comparable for all extant and fossil data.

(b) Phylogenetic signal and ancestral state reconstruction

Pagel's λ [20] and Blomberg's K [21] were performed in R v. 3.0.1 [22] using the Phytools package (function `phylosig` [23]) to assess phylogenetic signal of barb angles. Mesquite (v. 2.75 [24]) was

used to map barb angles onto the reference phylogeny. Each character was traced onto the tree using the 'reconstruct ancestral state' module of Mesquite with weighted squared change parsimony [25].

One thousand time-calibrated trees for the possible phylogenetic affinities of these 73 birds were sampled from the posterior distribution of Jetz *et al.* [26] (<http://www.birdtree.org>). These trees use the Hackett *et al.* [27] topology as a backbone. A majority rules consensus tree was built by Mesquite [24]. The consensus tree was further resolved following recent phylogenetic hypotheses for passerines and rails [28,29]. For Mesozoic taxa, we generated a fossil subtree with the timePaleoPhy function in paleotree [30] based on published fossil ages and branch [1,31] (summarized in electronic supplementary material, table S3). We grafted this time-calibrated tree of extinct taxa to the Aves tree with the `bind.tip` function in Phytools.

(c) Statistical analysis

To see if feather geometry (represented by barb angle values in the middle of the outer primary) was significantly different between any two flight styles, ANOVAs on phylogenetic generalized least-squares (PGLS) models were conducted in R using the `procD.pgls` function in Geomorph package (residual randomization permutation procedure) [32] and pairwise comparison was made in RRPP package [33]. Phylogenetic generalized least-squares (PGLS) were also performed in R package Caper [34] to assess the relationship between trailing vane barb angle and barb angle asymmetry. We categorized flight styles for living birds as those defined by Bruderer *et al.* [35]. Fossils and flightless taxa were categorized as distinct flight styles in this study. Measurements were log transformed to obtain a normal distribution of residuals.

3. Results

(a) Phylogenetic signal and ancestral state reconstructions

Feather geometry as described by leading and trailing barb angles does not show strong phylogenetic signal (leading vane angle $K=0.93$, $\lambda=0.82$; trailing vane angle $K=0.19$, $\lambda=0.34$; angle difference $K=0.19$, $\lambda=0.41$). Further pGLS tests show that trailing vane barb angle values and angle asymmetry values are significantly related ($r^2=0.84$, $p<0.001$) and this pattern can also be seen in the ancestral state reconstructions (figures 1 and 2).

Within extant birds, the well-nested passerines included in this study show reduced trailing vane barb angles and angle asymmetry relative to other extant taxa, while galloanseres show reduced leading vane barb angles (figures 1 and 2; electronic supplementary material, figure S1). Other clades show higher asymmetry values. While the mean barb angle asymmetry difference for Aves was 24.84, within Columbimorphae it was 32.52. In Caprimulgimorphae and Coraciimorphae comparatively high values were also seen (37.33 and 32.11, respectively).

(b) The relationship between feather geometry and flight capability/styles

Within extant taxa, no significant difference is recovered when barb angle values of flightless species are compared to those of volant species using ANOVA on PGLS models (leading, $F=2.67$, $p=0.12$; trailing, $F=2.62$, $p=0.14$; angle difference, $F=3.55$, $p=0.08$). This result statistically supports

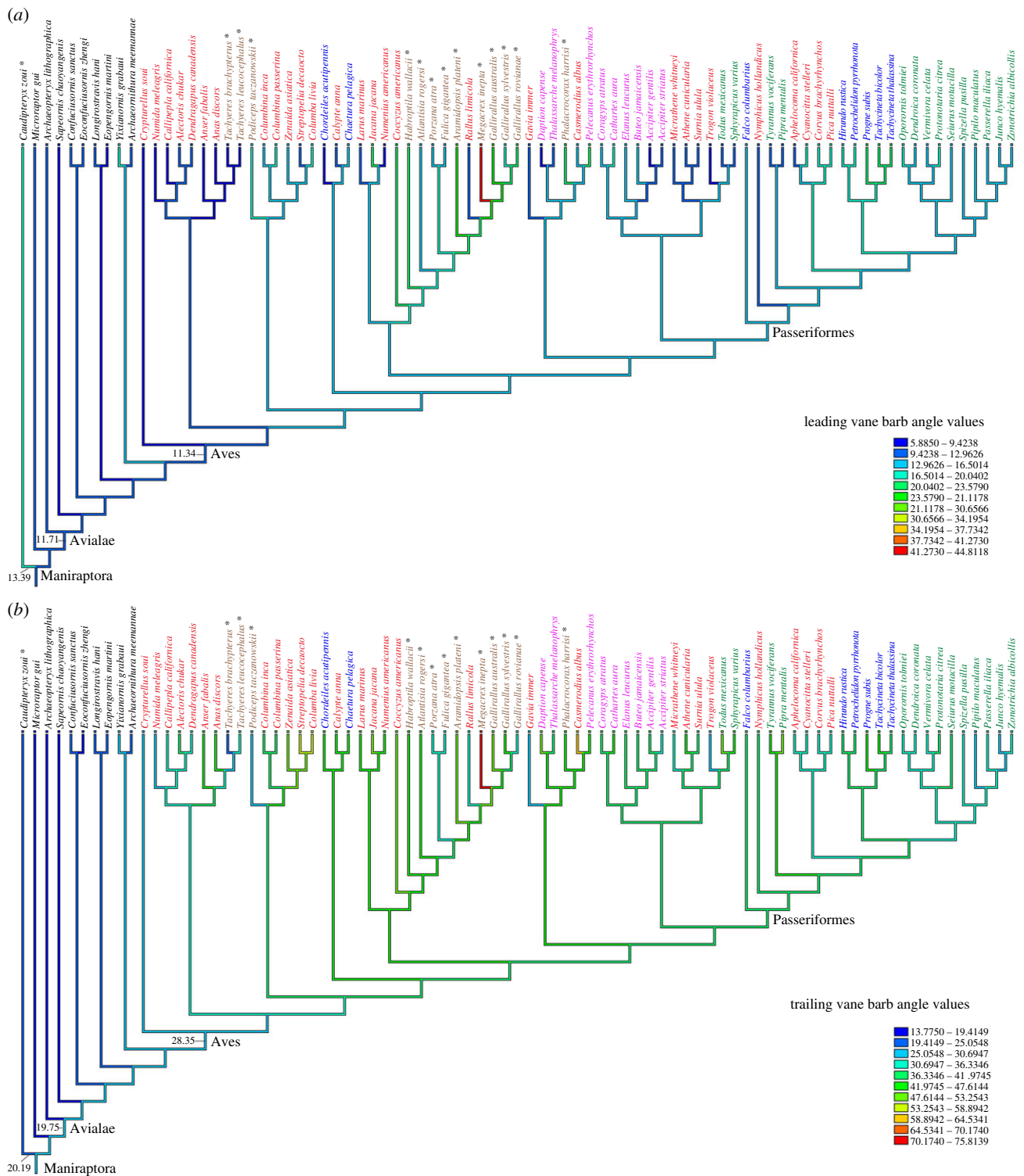


Figure 1. Ancestral state reconstruction for leading (a) and trailing (b) vane barb angles. Taxa are coloured with different flight styles. Red, continuous flapping ‘CF’; blue, flapping and soaring ‘FS’; purple, flapping and gliding ‘FG’; green, passerine type flight ‘PT’; brown, flightless ‘FL’; black, Mesozoic fossil taxa. * non-volant taxa. Leading and trailing barb angle values for Aves and Avialae and *Caudipteryx* are labelled.

the study of Feo *et al.* [4], which did not report outcomes of statistical tests (e.g. PGLS) for differences between flightless and volant taxa or by flight style. For extant taxa, trailing vane barb angle values do not significantly vary among four previously described flight style groups [35] ($F = 0.64$, $p = 0.39$), while leading vane barb angle ($F = 5.31$, $p = 0.03$) and barb angle asymmetry values ($F = 10.55$, $p = 0.01$) are only significantly different between ‘continuous flappers’ and ‘passerine type flyer’ (figures 1 and 2). This result partly agrees with the studies of Feo *et al.* [4] and Pap

et al. [14], where trailing vane barb angle was also found clearly associated with flight styles.

In Mesozoic stem avialan taxa, leading vane barb angles are not significantly different from those of extant birds ($F = 3.6$, $p = 0.06$). However, trailing vane barb angle ($F = 23.11$, $p = 0.005$) and barb angle asymmetry ($F = 43.81$, $p = 0.005$) are recovered as significantly smaller than those of extant birds. Further pairwise tests show that trailing vane barb angle and barb angle asymmetry of extinct Mesozoic stem avialan taxa are only significantly different from those

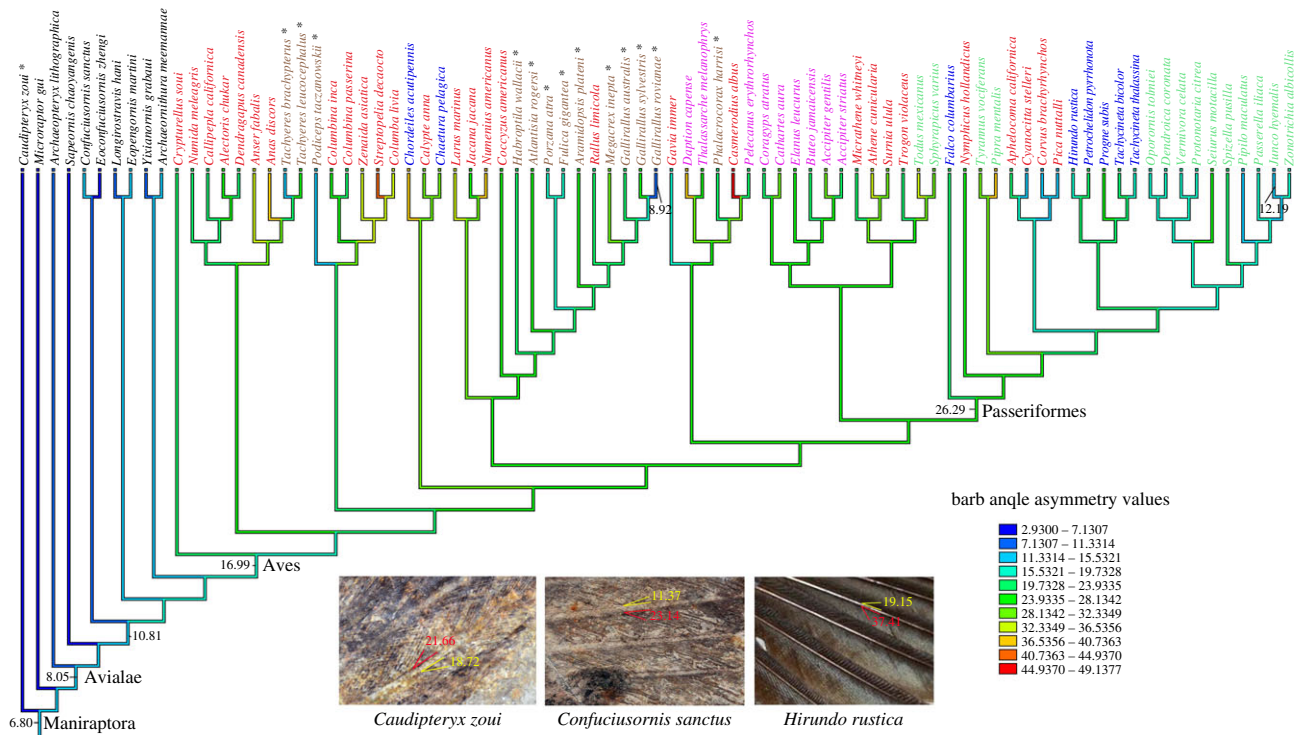


Figure 2. Ancestral state reconstruction for barb angle asymmetry. Taxa are coloured with different flight styles. Red, continuous flapping ‘CF’; blue, flapping and soaring ‘FS’; purple, flapping and gliding ‘FG’; green, passerine type flight ‘PT’; brown, flightless ‘FL’; black, Mesozoic fossil data. * non-volant taxa. The most parsimonious ancestral asymmetry values are labelled at the split of *Caudipteryx*, *Archaeopteryx*, *Confuciusornithidae*, the base of Aves and Passerines. The lowest values in the flightless Aves (*Gallirallus rovineae*) and flighted Aves (*Junco hyemalis*) are labelled. Insets show feathers of *Archaeopteryx* and crown bird (*Hirundo rustica*) with leading and trailing angle measured.

of Bruderer *et al.*’s [35] ‘Continuous Flapping’ group ($Z = 2.54$, $p = 0.03$; $Z = 3.54$, $p = 0.01$); they are not significantly different from other flight style groups including that comprising all passerines ($Z = 1.67$, $p = 0.085$; $Z = 1.48$, $p = 0.09$) or flightless species ($Z = -0.93$, $p = 0.82$; $Z = 1.86$, $p = 0.06$). Extinct ornithurines, enantiornithines and *Confuciusornis* all have trailing barb angles and barb angle asymmetry (figure 2; electronic supplementary material, figure S3) significantly larger than comparatively stemward avian taxa like *Archaeopteryx* and *Sapeornis* ($F = 74.1$, $p = 0.005$; $F = 82.55$, $p = 0.005$). Comparisons show that the trailing barb angle values in non-volant maniraptoran *Caudipteryx* are similar to those in avialan stem taxa (figure 1b). Leading-edge values of *Caudipteryx* are distinct from most stem avialans (figure 1a) but overlap with those seen in some Aves.

4. Discussion

Feo *et al.* [4] provided a unique dataset to assess the evolution of primary feather geometry. Taking this dataset into a phylogenetic and statistical frame with the addition of a larger sample of extinct taxa further informs the evolution of these feather shape traits. Our results agree with those of Feo *et al.* [4] that a small leading vane barb angle is ubiquitous across a phylogenetically and functionally diverse sample of asymmetrically vaned flight feathers in both extant volant birds and Mesozoic stem taxa. As smaller barb angles have been hypothesized to increase vane rigidity in primary feathers to withstand aerodynamic forces in flight [7,8], this reveals that a fundamental aerodynamic adaptation has developed and persisted since the Late Jurassic [4].

However, our results do not support the conclusion made by Feo *et al.* [4] that ‘possibly a modern capacity for powered

flight, evolved crownward of *Confuciusornis*.’ The barb angle difference supposed to be indicative of the lack of powered flight ability shows nearly the opposite trend in living birds: the difference in the stem Mesozoic birds taxa is most closely approached by clades of highly manoeuvrable extant fliers and is not seen in taxa like chickens. Additionally, barb angle asymmetries seen in stem avialans, which were previously interpreted as indicating that these taxa may not have been active fliers [2], are seen in volant Aves; for example, within songbirds (figure 2). Asymmetry values in *Confuciusornis* ranged from 11 to 14 (electronic supplementary material, table S1), while in the extinct *Yixianornis* that is thought to have flown this value was 11.29 and in the extant passerine (*Junco hyemalis*) it was 12.19 ([2]; figure 2). On the other hand, extant flightless species do not show statistically significantly different barb angles and barb angle asymmetry from volant extant taxa, which suggests that most secondarily flightless species sampled still retain functionally asymmetric primaries, as suggested by Feo *et al.* [4]. These results strongly indicate that barb angle asymmetry alone is not a reliable measure of flight capability in extant or stem taxa. Flight is a complex phenotype, and any attempts to estimate the flight capabilities of an extinct organism from the values for any single metric including, but not limited to feather asymmetry, barb angle or limb bone proportions should be viewed with appropriate caution.

Through new comparisons with feathers in the clearly non-volant outgroup *Caudipteryx*, the plesiomorphic condition for a primary feather is indicated to show trailing barb angles approximately in the 21° range (figure 2). Similar values are seen in paravians *Anchiornis huxleyi* (LPMB00169; 19.5) and *Caihong juji* (PMoL-B00175; 23.3), and these species are not generally inferred to have the identical form of aerial

locomotion as that in Aves. Mesozoic stem avialans show similar trailing vane barb values to this outgroup condition, while crown avian taxa show larger angles (figure 1b; electronic supplementary material, table S1). Thus, we propose that the trailing barb angle was not an abrupt modification in taxa shortly after the gain of aerial locomotion in its first form, but a gradual response to selective pressures acting on the form of the feather over a longer duration.

Leading-edge barb angle values differ between *Caudipteryx* and stem Paraves and avialans, suggesting that a decrease in this angle from 19° to 7°–10° may characterize early asymmetric feathers. However, a reversal toward a larger leading vane angle is seen in some crown birds (figure 1a). Barb angle characteristics of asymmetric feathers seen in living birds today may not be *requisite* of flight but a modified response to its acquisition and associated novel selective pressures acting on the forelimb.

Indeed, within extant birds, barb angles vary markedly by clade. We found no correlation of feather geometry (vane barb angles) with previously described flight style categories [30], consistent with recent studies [14,36]. Feather geometry, like wing geometry [24], is suggested to evolve comparatively early in major clades during the radiation of living birds and to relatively rarely shift within clades even as flight behaviour changes. Thus, our results do not fit a model where feather geometry is highly plastic and evolves

readily or abruptly with flight loss or gain, or with changes in flight style within clades.

The influence of the variability of barb angle traits within a single individual may be important [10], but was not investigated here owing to the limitations of the available fossil data. More and better fossil samples with more complete feathers and wings are needed to explore how among-feather variation in barb angles and feather asymmetry may evolve. Further data on feather microstructure (e.g. of barbules [37] and hooklets) and feather development will enable a better understanding of potential parameters constraining the evolution of feather barb geometry.

Data accessibility. Data are available in the electronic supplementary material.

Authors' contributions. X.W. and J.A.C. designed the study and analysed the data. H.K.T. help measured the samples. X.W. and J.A.C. wrote the manuscript, and all authors contributed to and approved the final version of the paper and agree to be held accountable for the content herein.

Competing interests. We declare we have no competing interests.

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