Title: *Shishania* is a chancelloriid and not a Cambrian mollusk

Authors: Jie Yang[1]†, Wei Li[1], Ai-lin Chen[2]†, Kun-sheng Du[2], Xiao Peng[1], Yu Wang[1], Xi-guang Zhang[1]*, Martin R. Smith[3]*

Affiliations:

[1]Institute of Paleontology, Yunnan University; Chenggong, Kunming, China.

[2]Research Center of Paleobiology, Yuxi Normal University; Yuxi, China.

[3]Department of Earth Sciences, Durham University; Durham, UK.

*Corresponding author. Email: xgzhang@ynu.edu.cn (X.G.Z.); martin.smith@durham.ac.uk (M.R.S.).

†These authors contributed equally to this work.

Abstract: The Cambrian evolutionary radiation is noted for its profusion of bizarre and unfamiliar body forms, many of which illuminate the early ancestry of major animal groups. The spine-covered fossil *Shishania aculeata* (Cambrian Stage 4, Yunnan, China) has been interpreted as intermediate between mollusks and their lophotrochozoan ancestors. Our new material challenges this interpretation. We propose taphonomic explanations for apparent molluscan features, and instead identify prominent anatomical similarities to coeval chancelloriids from nearby strata. Our reinterpretation of *Shishania* as an early-diverging chancelloriid helps to consolidate a model for the early evolution of this enduringly problematic group of sponge-like metazoans.

Main Text:

Alongside the extant animal phyla, the Cambrian explosion gave rise to short-lived taxa whose distinctive body plans did not endure. One such organism is *Shishania aculeata*, a morphologically simple animal adorned with hollow spines, known from flattened compression fossils in Fumin, Yunnan (*1*). A fibrous microstructure in *S. aculeata* sclerites hints at the presence of microvilli, secretory cells responsible for sclerite formation in Lophotrochozoa (*2*, *3*). *Shishania* has been interpreted as exhibiting a ventral foot, which would unite it with the sclerite-covered *Wiwaxia* (*4*, *5*) and indicate phylogenetic proximity to Cambrian mollusks such as *Odontogriphus* (*6*, *7*). On the other hand, *Shishania* lacks the gills and robust radulae that prominently characterize *Wiwaxia* and *Odontogriphus* (*6*, *8*); and the sclerites of *Shishania* are strikingly different to those of *Wiwaxia* in shape, hollowness and microstructure.

Hollow conical sclerites, sometimes with an intriguingly similar fibrous microstructure (*9–12*), are also evident in certain Cambrian chancelloriids (*13*, *14*). Chancelloriids – sessile, sac-like, centimeter-scale Problematica – are found in most Burgess Shale-type Lagerstätten (*13–20*). Their disarticulated sclerites frequently occur in mineralized 'small shelly' fossil assemblages (*9*, *21–24*), and their non-mineralized carbonaceous equivalents (*25–27*), from the Fortunian (lowermost Cambrian) to the Jianghsanian (mid-Furongian, upper Cambrian) (*28*). Chancelloriids somewhat resemble sponges in exhibiting an axially symmetric sac-like body plan with a prominent apical aperture (*15*); and in lacking differentiated internal organs or mesenteries (*29*). Their integument is embedded with hollow sclerites (*30*) that exhibit a sophisticated microstructure (*9*); individual elements are typically fused into multi-element rosettes (*13*, *28*, *31*). A ring of radially-oriented sclerites often forms a distinct 'apical tuft' around the orifice (*29*).

The phylogenetic affinity of chancelloriids is difficult to constrain, as their spartan morphology could be primitively or secondarily simplified. Their sclerites (*32*) and pattern of growth (*29*) resemble sponges, but also exhibit structural similarities with the sclerites of halkieriids – lophotrochozoans that somewhat resemble polyplacophoran mollusks (*33*, *34*), and which have been suggested to have brachiopod affinities (*35*, *36*).

Here we compare new specimens of *Shishania aculeata* (Fig. 1, A to P) from the Cambrian Series 2, Stage 4 (*Megapalaeolenus* zone) Wulongqing Formation in Luquan, Yunnan Province, with co-occurring specimens of the chancelloriid *Nidelric gaoloufangensis* (Figs. 1, Q to R and fig. S2). Our material suggests that the perceived dorsoventral differentiation of *Shishania* is an artefact of the folding and twisting of the organism, compounded by the splitting of the fossils through an open central cavity. We therefore propose that *Shishania* is not a mollusk, but is more likely a chancelloriid.

Systematic paleontology

Chancelloriida Walcott, 1920 (*16*)

Shishania Zhang et al. 2024 (*1*)

Type species: *Shishania aculeata* Zhang et al. 2024 (*1*)

Holotype: YKLP (Yunnan Key Laboratory for Palaeobiology) 11500

Additional referred material: YKLP 12482–12484.

Horizon and locality: All material is from the *Megapalaeolenus* Zone (*18*) of the Wulongqing Formation. We complement the type material from an unspecified site in Fumin County, Yunnan, southern China (*1*), with new specimens from the nearby Xinglongcun locality (*10*), in Luquan County (Fig S1; Supplementary Text S1).

Emended diagnosis: Radially arranged metazoan with hollow subovoid body, lacking obvious attachment structure. Body covered with hollow conical sclerites, projecting outwards. Sclerite bases with concentric or helical ornamentation. Sclerites with weak transverse ornamentation. Apical tuft composed of modified sclerites, directed upward.

Description: *S. aculeata* is a hollow and flexible bag-shaped organism covered with hollow conical spines of similar size, distributed irregularly but evenly. A terminal fringe of elongated spines forms a central apical tuft, which presumably surrounded an orifice (Fig. 1A and fig. S3, E and G). Uneven splitting surfaces variously expose the outer and inner surfaces of the integument. The spines occur on the outer surface. When compacted parallel to their axis, these preserve as dome-like spine bases with a concentric or helical ornament (Fig. 1, D and F and fig. S3H). When compressed laterally, the spines display a triangular outline, without obvious surface ornament (Fig. 1, E and F). Vertical compaction is most common in central regions of a specimen (e.g. Fig. 1, A, B, H and K), with lateral compaction common towards the margins (e.g. Fig. 1, E, H and J), consistent with the spines originally radiating outwards from the organism. Certain spines exhibit substantial relief (Fig. 1A and fig. S3E), denoting a robust constitution. The inner surface of the integument exhibits fine pit-like depressions (Fig. 1, B, C, G, K, O and P) corresponding to the attachment sites of spines on the outer surface.

The fossil material, but not the matrix, is characterized by a microstructure of multiple laminae of micron-scale fibers (Fig. 1, L to N, and fig. S5). The fibers are slightly inclined relative to the body axis; in places, overlying laminae exhibit distinct orientations (Fig. 1M and fig. S5C). The microstructure continues without interruption across the body integument and the hosted spines (Fig. 1, M and N and fig. S5, B to I), suggesting a diagenetic origin – perhaps replacing original tissue or filling voids produced by its decay (cf. *37–39*).

Remarks: The spines are preserved in the same manner as those in the co-occurring chancelloriid *Nidelric gaoloufangensis* (Fig. 1 Q and R; Supplementary Text S2), which also displays vertically compressed, concentrically ornamented spines in its medial region (Fig. 1Q and fig. S2, A to D), hollow, laterally compressed spines at its margins (Fig. 1 R and fig. S2 A, D and I to M), pit-like spine attachment impressions on its inner surface (Fig. 1 R) and an apical tuft (Fig. 1Q and fig. S2 A, B, F and G). Equivalent preservation also characterizes chancelloriids in other deposits (*11*, *29*).

Discussion: Zhang et al. (*1*) interpret *Shishania* as dorsoventrally differentiated, with sclerites covering an undifferentiated dorsal surface, but absent on the ventral surface. The ventral surface is interpreted as comprising lateral regions of unarmored girdle, separated by mantle cavities from a medial foot (summarized in fig. 3L in (*1*)). Our new material provides a more complete picture of how the taphonomic processes of burial and irregular splitting can result in incomplete preservation and substantial deformation (fig. S3). Evidence for an unarmored girdle region comes only from prominently incomplete specimens; on close inspection, spines can be seen in supposedly unarmored regions of the figured type material (e.g. fig. 1G in (*1*) and fig. 3 H to K in (*1*)). Geometric analysis of YKLP 11502 indicates that the interpreted ventral girdle regions are unlikely to correspond to the original margins of the organism (fig. S4). A similar situation

likely characterizes specimens such as YKLP 11303 and 11526 (fig. S4 in (*1*)). We thus interpret this purported girdle region as a taphonomic artefact.

The region interpreted as a 'foot' by Zhang et al. seems to correspond to the passage of the plane of splitting through the central cavity of the organism. In YKLP 11504 (Fig. 3, A to C in (1)), 11535 (fig. S3, A to C in (1)) and 11527 (Fig. 1G and fig. S5 in (1)), areas interpreted as the 'foot' bear pit-like impressions of spine bases, identifying them as the inner surface of the scleritome. Conversely, the interpretation of YKLP 11527 as a folded, laterally preserved specimen seems to imply that the internal surface of the dorsal mantle is displayed at the anterior limit of the specimen (fig. S3B in (*1*)); however, laterally preserved spines demonstrate that this region corresponds to the outer surface of the integument (fig. S3D in (*1*)). In YKLP 11505 (fig S3, G–J in (*1*)), the presence of laterally-preserved spines on the ventral surface belies the claim that the ventral surface lacks sclerites, and suggests rather that the preservational quality of this specimen makes it difficult to discriminate spines from the integument, as also occurs within between certain regions of our specimens (e.g. Fig. 1 B and H) due to heterogeneous preservation. Taken together, it is more parsimonious to interpret these specimens as different taphonomic expressions of compression and fracturing in a bag-like organism with an undifferentiated outer integument – consistent with the equivalent morphological and taphonomic expression of the co-occurring chancelloriid *Nidelric* (Fig. 1, Q and R; Supplementary Text S3).

Zhang et al. (*1*) interpret the fibrous microstructure as evincing microvillar sclerite secretion. Three-dimensionally preserved microvillar canals have not been reported in setae of Cambrian brachiopods or annelids. The microvillar canals in Burgess Shale *Wiwaxia* (*4*) represent pyrite casts of parallel microvillar canals that were consistent in width and aligned with the growth direction of the sclerite. Since *S. aculeata* fibers vary in width; do not infill cavities; vary in orientation between laminae; and are not always parallel to the axis of sclerites, we dismiss a microvillar interpretation. A diagenetic origin best accounts for the continuity of the microstructural fabric across sclerite boundaries, and its common inclination to the body axis on the front and rear integument surfaces. We are not aware of equivalent microstructures in this or other Burgess Shale-type deposits; an acicular microstructure in *Hallucigenia* sclerites from the Wulongqing Formation (fig. 7J in *37*) is not obviously equivalent. Most Wulongqing Formation specimens are strongly weathered, and the common occurrence of pyrite framboids (*40*, *41*) suggests that original microstructure may have been lost. As such, we cannot determine whether the microstructure represents a distinct diagenetic signature of *Shishania* tissue, or is a more widespread taphonomic feature of unweathered material from these deposits.

Conclusion: Our new material does not uphold the interpretation of *Shishania aculeata* as a stem-group mollusk. Whilst *Wiwaxia* and *Odontogriphus* do affirm the origin of mollusks from scleritomous organisms with a ventral foot (*4–6*, *8*, *36*), our reinterpretation removes the hollow sclerites of *S. aculeata* as a potential link between early mollusks and the hollow sclerites of halkieriids, which we prefer to interpret as tommotiid-like organisms (*35*, *36*). Instead, *Shishania* is best interpreted as a chancelloriid closely affiliated to, or even synonymous with, *Nidelric* (*13*). Its single, unfused spines are potential precursors to the fused multipronged spines of established chancelloriids (*11*, *13*), perhaps via the paired spines of *Dimidia* (*28*). Substantial flexibility in the shape of the organism, also documented in *N. pugio* (*13*), supports suggestions (*15*) that chancelloriids expanded and contracted their central cavity to facilitate fluid circulation. The particularly irregular form of *Shishania* suggests increasingly refined organismal control of fluid circulation through chancelloriid evolution, perhaps facilitated by the acquisition of a holdfast.

The confirmation of a chancelloriid affinity for *Shishania* illuminates the potential origins of this enigmatic group, consistent with an evolutionary transition from an irregular bag-shaped organism to the more gracile, sponge-like habit of derived chancelloriids characterized by multi-element spicules.

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Acknowledgments: We thank B. R. Pratt for comments on taphonomy of mineralization of fossil sclerites, T.-Y. Yuan for assistance with SEM photography, X.-Y. Yang, Q.-H. Guo and C.-L. Li for fossil collection, and T.-S. Li and T.-D. Li for long-term assistance in fieldwork.

Funding:

National Natural Science Foundation of China grant 42162002 (JY)

National Natural Science Foundation of China grant 42262004 (ALC)

National Natural Science Foundation of China grant 41730318 (XGZ)

Leverhulme Trust Research Project Grant 2019-223 (MRS)

Author contributions:

Conceptualization: XGZ, MRS, JY, WL

Methodology: JY, WL, KSD, YW, XP

Investigation: JY, ALC, KSD, YW, XP, WL

Visualization: XGZ, JY, WL, XP

Funding acquisition: JY, XGZ

Project administration: XGZ, JY, ALC

Supervision: XGZ, ALC

Writing – original draft: XGZ, MRS

Writing – review and editing: MRS, XGZ

Competing interests: Authors declare no competing interests.

Data and materials availability: All data are available in the main text and the supplementary materials. All figured specimens housed in the collections of the Institute of Paleontology, Yunnan University (YKLP) can be accessed by contacting Guo-li Zi <guolizi1986@163.com>; accession numbers can be found in the Materials and Methods in the Supplementary Materials.

Supplementary Materials

Materials and Methods

Supplementary Text S1 to S3

Figs. S1 to S5

References (*42–45*)

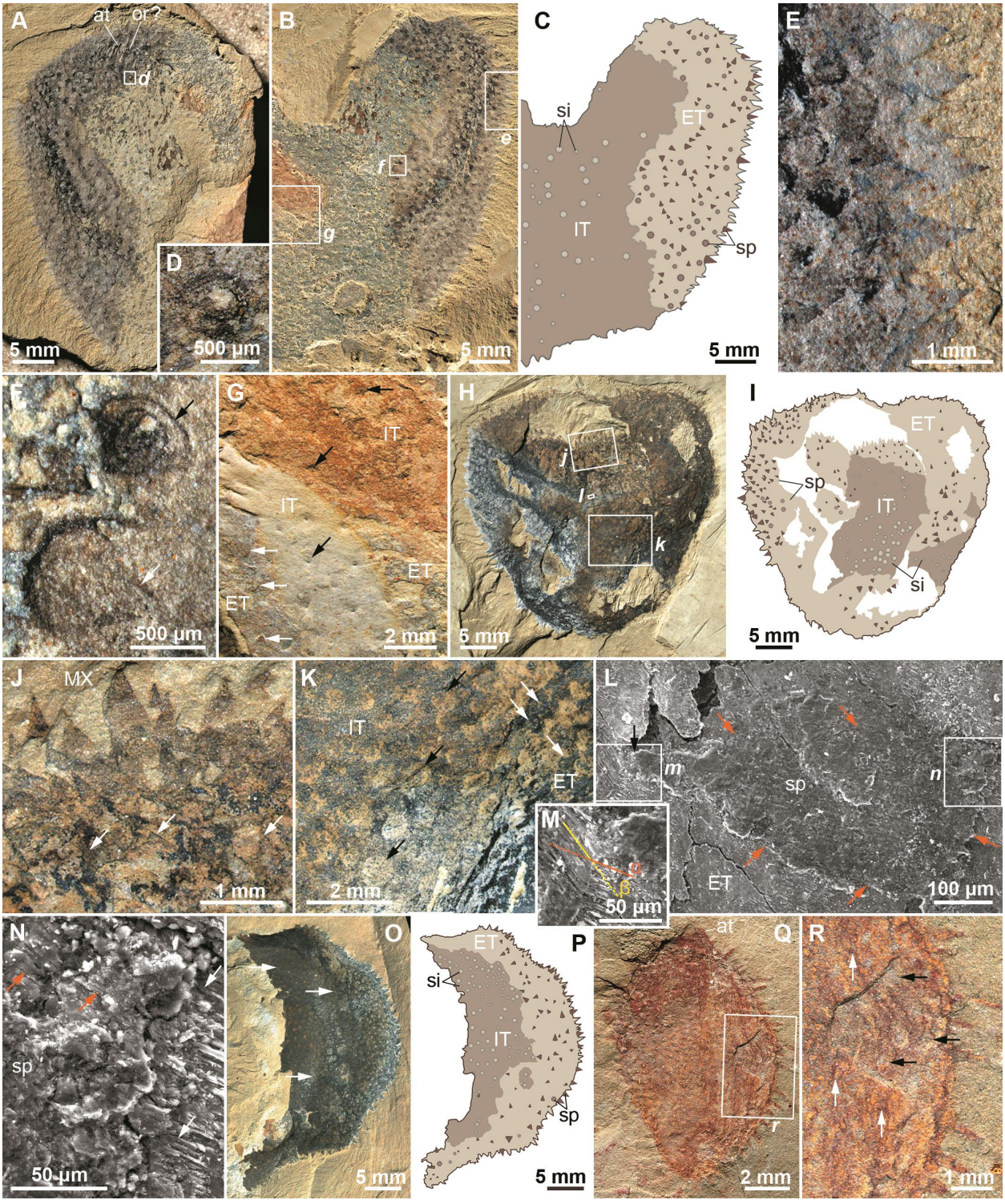

Fig. 1. Microstructure and body configuration of chancelloriids *Shishania* and *Nidelric* from Cambrian Stage 4 of Yunnan. (**A** to **G**), YKLP12482: (**A**) YKLP 12482a, part, showing outer surface with densely ornamented conical spines and apical tuft which may conceal an orifice; (**B**) YKLP 12482b, counterpart, showing external spiny layer and internal body integument with spine attachment points; (**C**) Interpretative drawing of (B); (**D**) Enlargement of area ***d*** in (A) showing spine base with concentric ornamentation; (**E**) Close-up of area ***e*** in (B)

showing spines at the body margin. (**F**) Enlargement of area ***f*** in (B). Black arrow indicates a spine compressed parallel to its axis, with concentric basal ornament; white arrow indicates a laterally preserved spine with triangular outline. (**G**) Close-up of area ***g*** in (B) showing flattened spines on the external scleritome (white arrows) and depressions on the internal integument (black arrows). (**H** to **N**) YKLP 12483: (**H**) dorsal view; (**I**) Interpretative drawing; (**J**) Close-up of area ***j*** in (H) showing spines (white arrows) centrally situated in the fragment; (**K**) Close-up of area ***k*** in (H) showing spines (white arrows) on the outer integument surface and depressions (black arrows) on the inner integument surface; (**L**) Scanning electron micrograph of area ***l*** in (H); showing laterally preserved sclerite (orange arrows) with apex (black arrow) pointing to west. (**M**), Enlargement of area ***m*** in (L) showing two oblique orientations of fibrous microstructure (α and β); (**N**), Fine fibers, 0.3–0.8 μm in diameter, evident in spine (orange arrows) and integument (white arrows) (**O**) YKLP 12484, partial specimen displaying internal and external integument. (**P**) Interpretative drawing of (O). (**Q**) YKLP 12485, *Nidelric gaoloufangensis* with apical tuft at the body apex, bearing thin, long and radially extending spines. (**R**) Close-up of area ***r*** in (Q) showing flattened spines (white arrows) on the external body scleritome, and circular depressions (black arrows) on the internal integument surface. Abbreviations: at, apical tuft; ET, external body integument; IT, internal body scleritome; or, orifice; si, spine impressions; sp, spines.

Submitted Manuscript: Confidential
Template revised July 2024

Supplementary Materials for

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Jie Yang, Wei Li, Ai-lin Chen, Kun-sheng Du, Xiao Peng, Yu Wang, Xi-guang Zhang, Martin R. Smith

Corresponding author: Xi-guang Zhang, xgzhang@ynu.edu.cn (X.G.Z.); Martin R. Smith, martin.smith@durham.ac.uk (M.R.S.).

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Materials and Methods

Provenance

The Cambrian Stage 4 (local Changlangpuan stage) Wulongqing Formation encompasses the majority of known metazoan taxa of the Guanshan Biota. The formation spans two consecutive biozones: the lower *Palaeolenus* zone is overlaid by the *Magapalaeolenus* zone, dated to 510–515 million years ago (*18*), occurring widely in Kunming and surrounding areas such as Chenggong, Fumin, Wuding, Malong and Yiliang (*18*). Within the Guanshan fossil assemblage, articulated chancelloriids with single-ray sclerites (Ref. *18*, fig. 64) have been identified as *Nidelric gaoloufangensis* (*14*), which also occur in our collections. All figured specimens are housed in the collections of the Institute of Paleontology, Yunnan University (YKLP) and can be freely accessed by contacting Guo-li Zi <guolizi1986@163.com>.

Of the 23 specimens (YKLP 12482-12504, including 17 *Shishania aculeata* and 6 *Nidelric gaoloufangensis*) studied herein, 21 were collected by Jie Yang, Wei Li, Xiao Peng, and Yu Wang, except one (YKLP 12483) collected by Kun-sheng Du and one (YKLP 12484) by Ai-lin Chen during fieldwork from 2019 to 2023. All specimens come from the sequence defined by the *Megapalaeolenus* zone within Wulongqing Formation at the Xinglongcun section in Luquan, Yunnan, cooccurring with some 'hermit' shell-dwelling priapulans (*42*), as well as many other shelly invertebrates.

Methods

Specimens were prepared manually with a needle to remove matrix concealing the fossils with the aid of high magnification using a Nikon SMZ800 or 1500 stereomicroscope. Photographs were captured with crossed polarizers using a Nikon D3X fitted with a Nikon AF-S Micro Nikkor 105 mm lens, and a Leica M205-C stereomicroscope with a Leica DFC 500 digital camera. Digital photographs were processed in Adobe Photoshop CS6 and interpretative drawings were made with CorelDRAW X8.

Supplementary Text

1. Locality and biostratigraphy

All of our specimens were obtained from the Xinglongcun section in Luquan. Past studies on this section, which has focused primarily on palaeoscolecids (*43*), have not indicated the exact stratigraphic position of the fossil assemblage. In turn, Zhang et al., 2024 (*1*) do not give detailed information about the exact locality of the *Shishania aculeata* within Fumin county. Nevertheless, the Fumin is geographically adjacent to Luquan and Kunming, and the type locality of *S. aculeata* yielded by the Cambrian Stage 4 (*Megapalaeolenus* zone) Wulongqing Formation must be somewhere close to the Xinglongcun section since our recent field survey indicates that all examined Cambrian strata in Fumin are exposed within a small region, as depicted in the geological map (fig. S1). The paleontological and paleobiogeographical data indicate these Cambrian Age 4 fossils belonging to the same biota.

2. Systematic description

Phylum and Class uncertain
Order Chancelloriida Walcott, 1920 (*16*)
Family Chancelloriidae Walcott, 1920 (*16*)

Genus *Nidelric* Hou *et al.*, 2014 (*13*)
Type species: *Nidelric pugio* Hou *et al.*, 2014 (*13*).
Revised Diagnosis: Species of *Nidelric* bearing single-element spines projecting outward; body profile subovoid, spines projecting outward and gently curved with a non-flaring base.
Remarks: Based on its small size and general morphological characters (e. g. the modified apical spines, thin and elongated spines densely on the body surface), the single specimen assigned to chancelloriids in ref. (*18*) is an early growth stage individual of *Nidelric*. In particular these chancelloriids show a reddish color, regarded as imparted by iron oxide (*13*), as is the case for our material. Repeated occurrences of *Nidelric* from the same horizon (Cambrian Stage 4 Wulongqing Formation) within Kunming and adjacent counties, including our new material, establish *Nidelric* as a distinctive chancelloriid lineage of the Guanshan biota.

Nidelric gaoloufangensis Zhao et al. 2018 (*14*)
Fig. 1, Q and R, and fig. S2
Holotype: YN-GLF-PAL-17 (ref. *14*, fig. 9.1) found in Cambrian Series 2, Stage 4, *Palaeolenus* zone, Wulongqing Formation, Gaoloufang section, Kunming, Yunnan Province, China.
Diagnosis: Small species of *Nidelric* bearing single-element spines; body profile subovoid with elongated spines, including a tuft-like arrangement at the pole; spine surfaces smooth or covered with fine tubercles.
Description: Body is subovoid, about 11 to 24 mm in height. The greatest width ranges from 4 to 11 mm. The integument bears slender spines, 1 to 2 mm long, typically around 0.5 mm wide at the base. The spine surface may be smooth, or ornamented with fine tubercles. A possible apical tuft is indicated by the arrangement of spines at the pole. The presence of an orifice has not been determined.
Remarks: *N. gaoloufangensis* is distinguished from the type species by having elongate and morphologically simpler spines without a broad base. All of our specimens referred to *N. gaoloufangensis* resemble those found by Zhao et al. (*14*), showing a subovoid body ornamented with long, thin spines. The apical orifice is invisible, but at the pole deformed sclerites form a tuft-like structure extending subparallel to the growth axis. Although the single-element spines determined from the type species *N. gaoloufangensis* have not yet been firmly observed in our material (for possible candidates, see fig. S2, F and G), the overall similarity supports their designation to this species, particularly as no other taxa reported from the Kunming–Luquan–Fumin district are similar.
N. gaoloufangensis is similar to *Shishania aculeata* in general body configuration: a bag-shaped body scleritome densely covered with spines, bearing an elongated tuft-like structure. The former differs from the latter by having relatively thin, long spines, which are often ornamented with fine tubercles (fig. S2, J, L and M). The discovery expands the biostratigraphic range of this species from the *Palaeolenus* zone upward to the *Megapalaeolenus* zone. The rather subtle morphological distinction between *N. gaoloufangensis* and *S. aculeata* suggests that the two taxa may be co-generic, but we prefer to retain separate genera, noting that future discoveries of better-preserved material may allow a more rigorous taxonomic treatment of the material.
Occurrence: Cambrian Series 2, Stage 4, Wulongqing Formation, *Palaeolenus* zone and *Magapalaeolenus* zone in Kunming–Luquan–Fumin district, Yunnan Province, China.

3. Geometrical and morphometric analyses

We regard the configuration of spines as a key mechanism for distinguishing the internal and external surfaces of the body integument. The presence of spines or dome-like spine bases on a complete or fragmentary specimen identifies the visible surface as external, whereas the presence of depressions or pits left by spine bases denote the internal integument surface. This simple evaluation criterion resolves all flatted specimens of *Shishania aculeata* as comprising two layers, with the upward-facing external layer overlying the internal surface of a separate downward-facing layer (Figs. 1, A to K, and O and P).

Fossil specimens belonging to the same species are often characterized by certain unique traits, whilst exhibiting similar body profiles, ontogenetic changes notwithstanding (*44, 45*). On this basis, comparing the somewhat damaged specimen (YKLP 12483) with another (YKLP 12482) that displays relatively complete outline (fig. S3, E and F) makes it clear that its anterior and posterior portions of YKLP 12483 are missing (fig. S3D).

Likewise, this basic morphological feature could be applied to clarify the descriptions and speculations for *Shishania aculeata* collected from Fumin, where the holotype specimen (YKLP 11500) is nearly complete and based on the measurement (*1*), it shows a L1/W1 ratio of 1.27—a constant parameter applicable for evaluation the completeness and deformation of other specimens. Specimen (YKLP 11502) is argued to be "preserved in an oblique, lateral view" (*1*), differing from that of many co-occurring others. However, with a low relief it has also been flattened on the bedding surface. Even so, specimen YKLP 11502 was depicted to have had its ventral girdles bilaterally preserved on the basis of fluorescence analysis (*1*). However, this severely distorted body scleritome notably exhibits a quite different L2/W3 ratio of 2.10—much higher than that determined from YKLP 11500. The great deviation, based on geometrical and morphometric analyses, may indicate YKLP 11502 with a meandering margin has been damaged or folded before being finally buried, the original body should be much wider than what we can see from the fragmentary specimen with neither side of its lateral body scleritome preserved (fig. S4). As a result, the missed portion gives no place for housing the presumed ventral girdles. The hypothesis of a ventral girdle present in *S. aculeata* is defined by fluorescence results, which relied on analysis of elemental maps (figs. 1, E and F, and 3, J and K in (*1*)), seem doubtful, especially as applying for determining the presence of a real sclerite structure.

Figs. S1 to S5

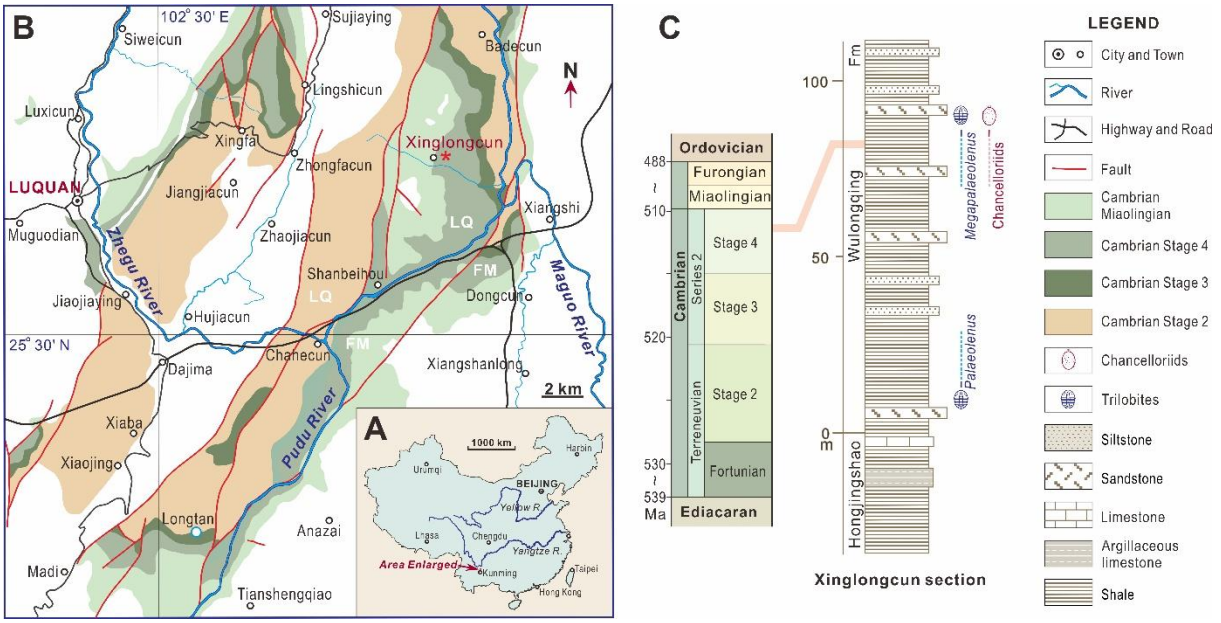

Fig. S1. Locality maps and stratigraphical succession of the Cambrian Stage 4 Xinglongcun section in Luquan, Yunnan. (**A**) The studied area in southern China. (**B**) Geological map showing the main explored Cambrian strata explored in Luquan and Fumin counties which are separated by the Pudu river: Luquan (LQ) is on the northwestern bank, whereas the Fumin (FM) on the southeastern. Asterisk indicates the Xinglongcun section. (**C**) Chancelloriids reported in this study occurring within trilobite *Magapalaeolenus* zone, which is stratigraphically above the *Palaeolenus* zone.

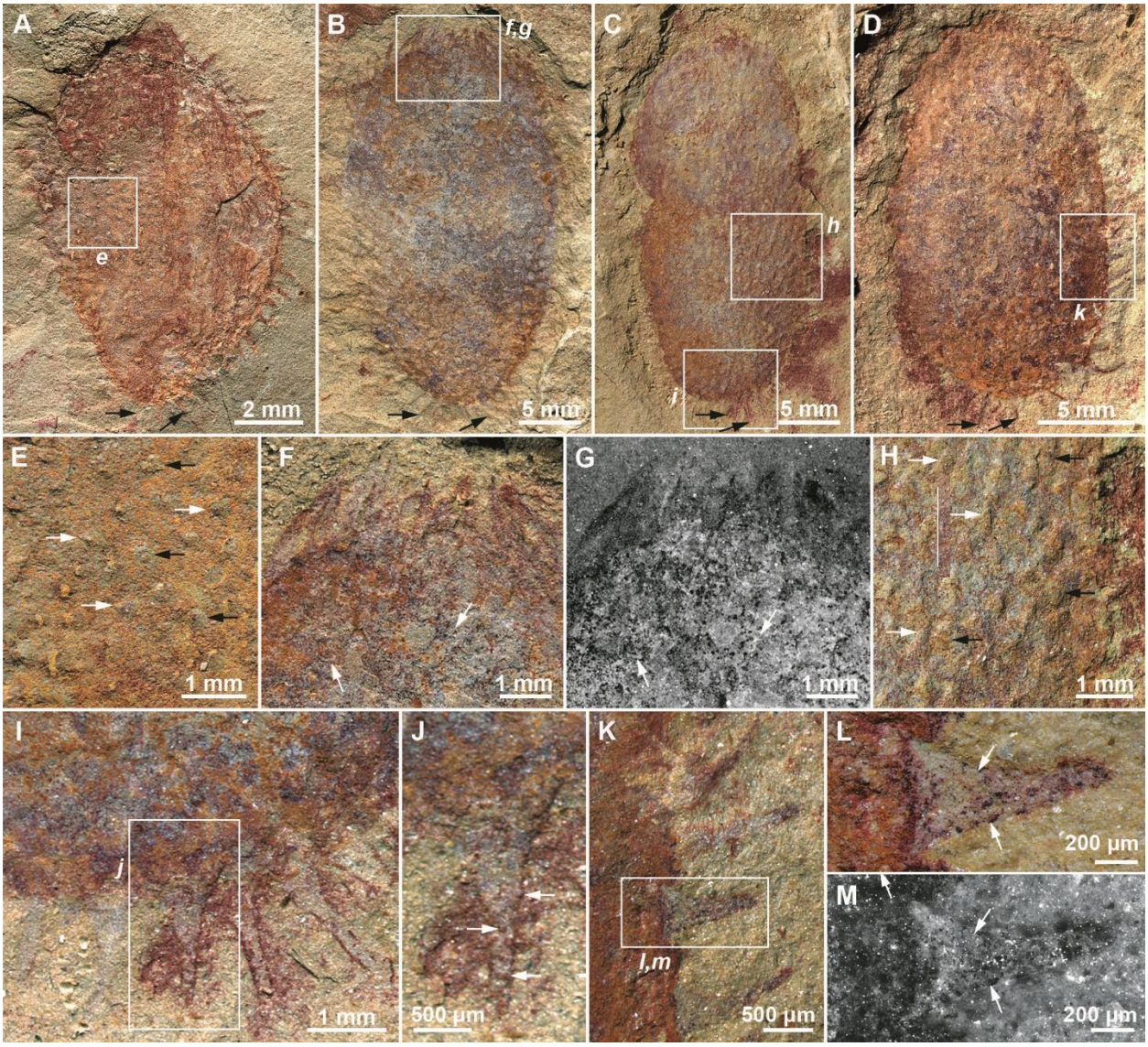

Fig. S2. Chancelloriid *Nidelric gaoloufangensis* from the Cambrian Stage 4 of Yunnan. (**A** to **D**) YKLP 12485-12488, compressed individuals, each with radially extending spines (arrows) situated on the rear body surface, and parallel to slightly convergent apical tuft at the body apex; lots of rounded spine bases centrally located together with a few fallen spines. (**E**), Close-up of area ***e*** in (A) showing spines (white arrows) fallen on the external body integument, and spine bases (black arrows). (**F** and **G**) Normal light and fluorescence images of area ***f*** in (A) showing spines (white arrows) and spine bases (black arrows). (**G**) Close-up of area ***g*** in (B) showing possible apical tuft and multi- (or single-) element spines (arrows). (**H**) Close-up of area ***h*** in (C) showing fallen spines (white arrows) and spine bases (black arrows). (**I**) Close-up of area ***i*** in (D) showing the radially extending spines. (**J**) Close-up of area ***j*** in (I) show fine tubercles on spine surface (arrows) (**K**) Close-up of area ***k*** in (D) showing spines along lateral margin. (**L** and **M**) Close-up of area ***l***, ***m*** in (K) showing fine tubercles on spine surface (arrows).

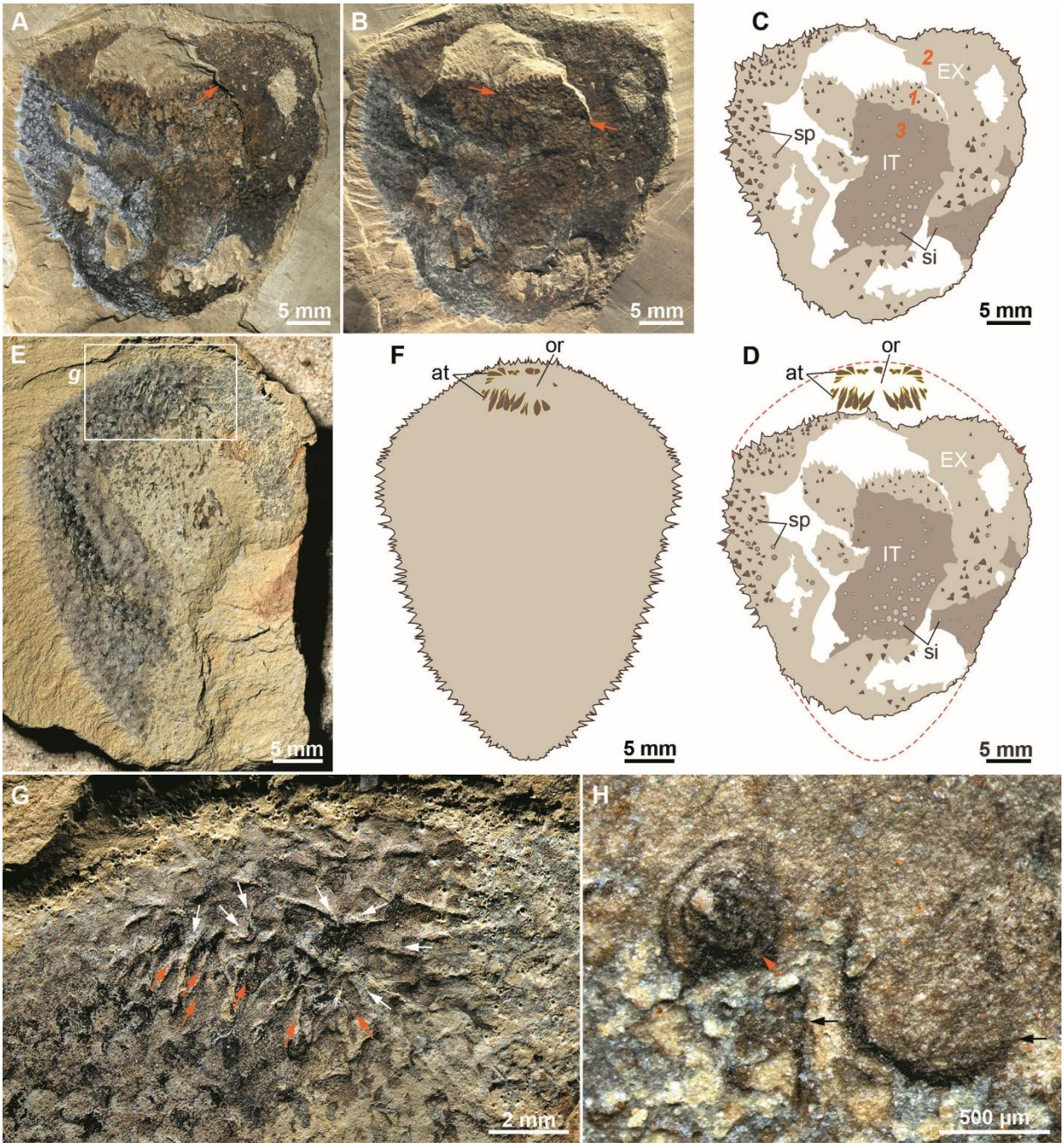

Fig. S3. Fragment reconstruction of *Shishania aculeata*. (**A** to **D**) YKLP 12483, dorsal view of a fragmentary specimen: (**A**) The shadow caused by light from the northeast (arrow) makes it clear that fragment 1 is beneath fragment 2; (**B**) The boundary between fragment 1 and fragment 3 (arrows) is revealed by light from the north; (**C**) interpretative drawing; (**D**) reconstruction in showing the missed parts of the body scleritome, including possibleapical tuft. (**E** to **G**) YKLP 12482: (**E** and **F**) dorsal view showing body profile and microstructures, which helps the reconstruction in (D); (**G**) Close-up of area ***g*** in (E) showing modified spines (orange arrows) and other apical spines (white arrows) pointing inwards to an obscured orifice. (**H**) YKLP 12482b, enlargement of area ***f*** in Fig. 1B showing a concentric or helical ornament (orange arrow)

on a vertically compressed spine situated beside two laterally flattened spines (black arrows). Abbreviations as in Fig.1.

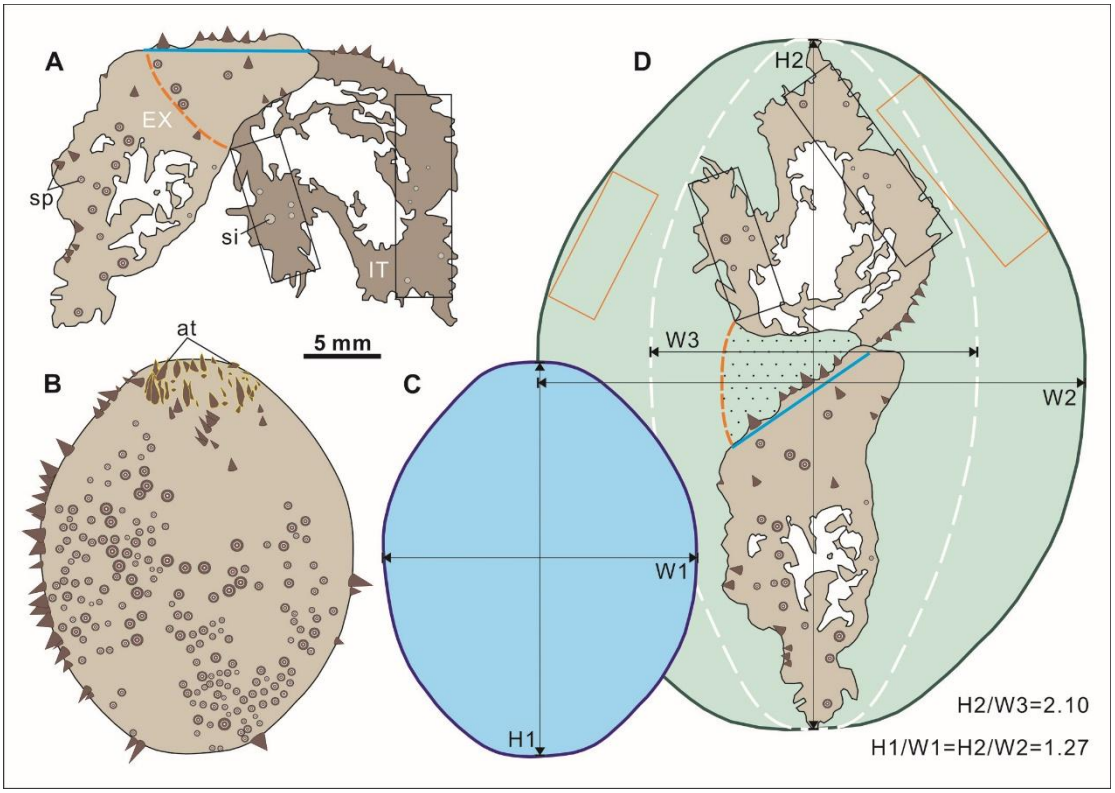

Fig. S4. Schematic reconstruction of specimens assigned to *Shishania aculeata* Zhang et al. 2024. (A) Interpretative drawing of YKLP 11502 (ref. (*1*), fig. 1e), showing twisted body scleritome, which, with assumed 'ventral girdle' (black rectangles), is approximately folded across the spiny scleritome (blue line), exhibiting the external and internal surfaces of the body integument (*1*). **(B)** Interpretative drawing of the holotype (YKLP11500) which shows an oval profile. **(C)** The Height/width (H1/W1) ratio of the oval profile should be constant between individuals of later growth stages. **(D)** The height (H2) of YKLP 11502 is measurable, with which the original width (W2) can be estimated (because H1/W1=H2/W2=1.27). Based on an estimated maximal profile of the fragmentary specimen (white dashed line), the preserved width (W3) becomes available. The body outline (the invisible part of IT concealed by EX is dotted) defined by H2/W3 clearly indicates that YKLP 11502 is seriously damaged, suggesting that the hypothesized ventral girdles (orange rectangles) are likely to denote post-mortem crumpling of the organism rather than original biological features. Abbreviations as in Fig. 1.

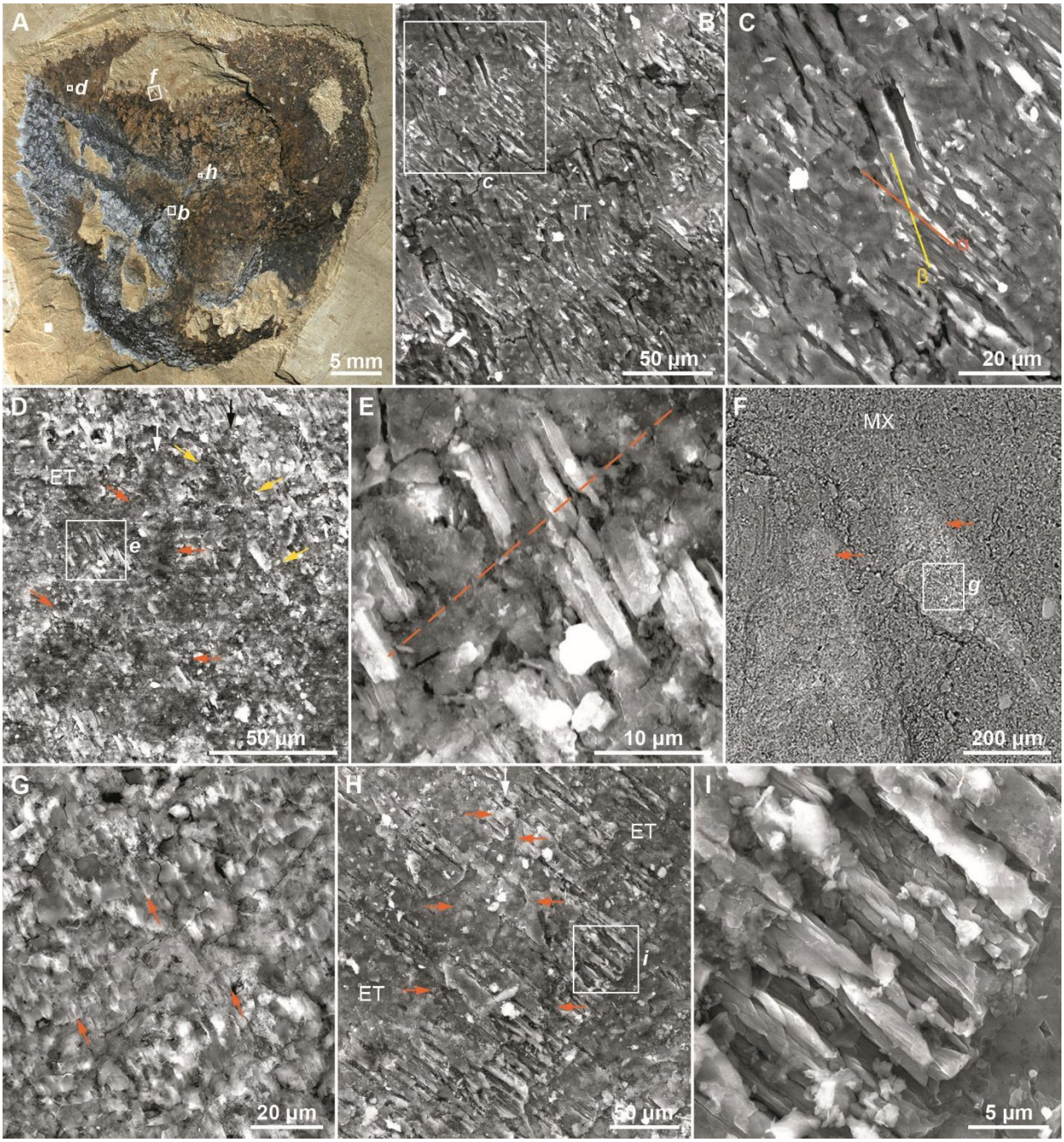

Fig. S5. Fibrous microstructure in *Shishania aculeata*. (**A**) YKLP 12483. (**B** to **I**) SEM images: (**B**) Close-up of area ***b*** in (A), showing linear structure on inner surface of integument; (**C**) Enlargement of area ***c*** in (B) with fiber lineations extending in two directions (marked by orange α and yellow β lines). (**D**) Close-up of area ***d*** in (A) showing two overlapping spines (marked by orange and yellow arrows correspondingly), and linear structure on outer surface across both spines and integument; (**E**) Enlargement of area ***e*** in (D) showing microfibers, which are present on both insides of the spine and integument (the spine surface is marked in dash line), extending in β direction. (**F**) Close-up of area ***f*** in (A) showing two flattened spines within matrix (MX), (**G**) Enlargement of area ***g*** in (F) showing incomplete preservation of fibers in spines (arrowed). (**H**) Close-up of area ***h*** in (A) showing linear structure on outer surface across both

integument and apical region of a possible flattened spine (arrows outline its lateral margins), (**I**) Enlargement of area ***i*** in (H) showing details of partially surviving fibers extending in α direction. Abbreviations as in Fig. 1.

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