Naked chancelloroids from the lower Cambrian of China show evidence for sponge-type growth

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Abstract

Chancelloriids are an extinct group of spiny Cambrian animals of uncertain phylogenetic position. Despite their sponge-like body plan, their spines are unlike modern sponge spicules, but share several features with the sclerites of certain Cambrian bilaterians, notably halkieriids. However, a proposed homology of these “coelosclerites” implies complex transitions in body plan evolution. A new species of chancelloriid, Allonnia nuda, from the
lower Cambrian (Stage 3) Chengjiang Lagerstätte is distinguished by its large size and sparse spination, with modified apical sclerites surrounding an opening into the body cavity. The sclerite arrangement in *A. nuda* and certain other chancelloriids indicates that growth involved sclerite addition in a subapical region, thus maintaining distinct zones of body sclerites and apical sclerites. This pattern is not seen in halkieriids, but occurs in some modern calcarean sponges. With scleritome assembly consistent with a sponge affinity, and in the absence of cnidarian- or bilaterian-grade features, it is possible to interpret chancelloriids as sponges with an unusually robust outer epithelium, strict developmental control of body axis formation, distinctive spicule-like structures and, by implication, minute ostia too small to be resolved in fossils. In this light, chancelloriids may contribute to the emerging picture of high disparity among early sponges.

**Keywords:**
Chancelloriids; Porifera; Cambrian explosion; biomineralization; exceptional preservation; metazoan phylogeny

1. Introduction

The Cambrian fossil record famously preserves a variety of animals that lie outside the range of modern (crown-group) phyla. The application of cladistic techniques in phylogenetic reconstruction has led to the incorporation of many of these “problematic” fossils into the stem groups of higher taxa [1]. Others, however, are resistant to phylogenetic placement, either because of a simple lack of preserved, identifiable homologies [2] or because of their genuinely perplexing character combinations [3]. In the latter category are chancelloriids, an extinct group of Cambrian animals known from exceptionally preserved whole-body fossils in Burgess Shale-type Lagerstätten, and as disarticulated skeletal elements (sclerites) in assemblages of small shelly fossils (SSFs). In overall body form, chancelloriids resemble sponges in having a spiny sac-like body with radial symmetry, an apical opening, and a basal attachment stalk or bulb [4] and unsurprisingly were initially classified as sponges [5]. Since then, however, it has been shown that their hollow, external sclerites with basal foramina are fundamentally distinct in their structure and mode of formation from modern sponge spicules [6]. Instead, the sclerites of chancelloriids resemble those of the mollusc-like bilaterian
Halkieria and related taxa, and the similarities extend to fine-scale microstructural characteristics including a fibrous biomineral component (interpreted as aragonitic in life), an organic outer layer, and pustulose ornamentation [7]. A proposed homology of these “coelosclerites” is the basis for the hypothesized clade Coeloscleritophora [6].

Accepting the homology of coelosclerites poses major challenges for reconciling character evolution among such disparate groups as chancelloriids and halkieriids. Either chancelloriids have lost an unprecedented number of bilaterian characters in a transition to a sessile condition, or coeloscleritophorans record the establishment of the bilaterian body plan from a radial, chancelloriid-like animal [8] – though much later than expected (unless biomineralization originated more than once in the group) and with multiple losses of coelosclerites among bilaterians [7]. These difficulties have led some researchers to question the phylogenetic value of coelosclerites, leaving the chancelloriids in phylogenetic limbo [9,10], or as sponges with convergently evolved spicule-like structures [11,12]. Recently, a direct link has been proposed between chancelloriids and certain Cambrian protomonaxonid sponges, based on similarities in body surface texture, body shape and a proposed shared sclerite structure [13] – although it has not been demonstrated that protomonaxonid spicules exhibit the non-accretionary, foramen-bearing hollow structure that is so characteristic of chancelloriid sclerites. Clearly, additional homologies are needed to test the phylogenetic affinities of chancelloriids.

The Chengjiang biota of Yunnan Province, South China [14], has yielded exceptionally preserved, fully articulated chancelloriid specimens, some currently assigned to Allonnia phrixothrix [15] of which A. junyuani [16] is a junior synonym [4], and Allonnia erjiensis [17]. In addition, the Chengjiang species Nidelric pugio [18] is based on a single specimen of a chancelloriid-like animal with unique, single-rayed sclerites. Specimens have also been reported which are characterised by a low density of proportionally small sclerites [15,16,19]. Here, we describe from the Chengjiang biota new specimens that clarify the presence of a distinct new species, Allonnia nuda, which is notable for its weak (sometimes absent) spination and large body size. Based on comparisons between the apical morphology of A. nuda with taxa from the Burgess Shale, we present a revised model of chancelloriid growth which compares closely to that of some extant calcareous sponges, offering a new character for testing hypotheses of chancelloriid relationships.

2. Systematic palaeontology
Phylum uncertain
Order Chancelloriida Walcott, 1920[5]
Family Chancelloriidae Walcott, 1920[5]
Genus *Allonnia* Doré and Reid, 1965[20]

Type species. *Allonnia tripodophora* Doré and Reid, 1965 (based on isolated sclerites).

Diagnosis. After Yun et al. 2017[17] (emended from Bengtson and Collins 2015[4]): ‘Chancelloriid with a sac-like and radially symmetrical body, an orifice on the apex, and a tapering basal end. Body surface is ornamented with upward-pointing 3+0 type sclerites, and the apical orifice is surrounded by modified single-element sclerites forming an apical tuft.’

*Allonnia nuda* sp. nov. (figures 1,2 and electronic supplementary material, figure S1, S2a)

Synonymy list:
? Chancelloriid new species, Chen et al. 1996[19], figs 93, 94
*Allonnia* sp., Bengtson and Hou 2001[15], fig. 9

Etymology. Latin, *nuda*, bare, naked; alluding to the small sclerite size and the tendency to lose sclerites, leaving a “naked” body surface.

Material. YKLP 13501a,b (holotype), plus five additional specimens, YKLP 13502, 13503, 13504, 13506, and 13507 housed in the Yunnan Key Laboratory for Palaeobiology, Yunnan University, Kunming, China.

Locality and stratigraphy. The specimens are from the Chengjiang biota, which mainly occurs in the *Eoredlichia-Wutingaspis* trilobite biozone of the Yu’anshan Member, Chiungchussu Formation in eastern Yunnan Province, China. This biozone falls within the local Chinese Nangaoan Stage, equivalent to the Cambrian unnamed Stage 3, Series 2. YKLP 13501, 13502, 13504 & 13506 are from the Mafang section, and YKLP 13503 is from the Jianshan section, both of which are in the Haikou area (see ref. 14).

Diagnosis. A large species of *Allonnia* characterised by apically-directed sclerites that are small in proportion to the body, and sparsely distributed (up to ~5 per cm²) or absent over
much of the body surface. Apical tuft with modified, single-rayed sclerites. Smooth or very finely wrinkled integument, without discernible platelets.

Description. The holotype (figures 1a,h, 2) is the most complete specimen, and the only one to preserve the apical end. It is elongate, 160 mm long by up to 37 mm wide, except where a rounded bulge on one margin locally extends the width to 44 mm. Aside from this bulge, the specimen is parallel-sided for much of its length but tapers apically into a narrow cone, and seems also to taper towards the base (though here it is folded); the basal-most part, at the edge of the slab, is missing. Its margins are defined in places by a c. 1.5 mm-wide dark line (“crease”), presumably resulting from the compaction of the body wall. Over most of the body surface, the sclerites are inconspicuous, being small (< 2 mm long and with an inflated base ~ 0.5 mm wide) and sparsely distributed (~0–3 per cm²). Most sclerites expose only two rays, but a third ray is apparent where the sclerite base is exposed, and a 3+0 structure probably typifies all the body sclerites (cf. figure 1e–g). A contrasting region of densely-packed sclerites occurs at the apex, where the majority of sclerites consist of a single ray with a more broadly triangular profile (figure 2). The integument is unornamented at the preserved level of resolution, except for low-relief ring-shaped structures (“doughnuts”) c. 1.6–1.8 mm in diameter, with a central depression of c. 0.5 mm in diameter, and visible using low-angled light (figure 1h); they occur at densities of up to c. five per cm², counting only those in matching positive or negative relief. The holotype specimen is preserved as a flattened composite surface [15] in most places, although a region of three-dimensional sediment fill defines an ovoid region extending into the body from the apex, presumably representing post-mortem sediment ingress through an orifice into a body cavity.

The five additional specimens we have examined and referred to *A. nuda* extend the size range of this species, and vary in the extent of sclerite coverage. YKLP 13502a,b represents a mid-body portion, 96 mm long by up to c. 50 mm wide (figure 1b, d–g). Neither base nor apex is preserved. The specimen extends beyond the slab basally, and apically disappears into the sediment, creating a transverse section that reveals a thin “wall” (up to 1 mm thick in oblique section) surrounding a sediment-filled cavity. The sclerites resemble those of the holotype in morphology, size, and the density of their coverage (up to ~ five per cm²). A faint body-surface granulosity is expressed locally (see electronic supplementary material, figure S2a).

YKLP 13506 a,b (figure 1c) and YKLP 13504 (electronic supplementary material, figure S1a) represent mid-portions of large specimens, respectively 120 mm long by 70 mm
wide, and 190 mm long by 60 mm wide, the latter with prominent longitudinal folds. Both specimens lack obvious sclerites, but are identifiable as *A. nuda* by their outlines, their smooth or, in places, finely wrinkled textures, and characteristic marginal creases. YKLP 13503a,b represents a portion of a specimen more than 120 mm long and up to 65 mm wide with a sparse scattering of sclerites (electronic supplementary material, figure S1b). It is unusual in having a blunt end that seems to be neither an apical nor a basal terminus, and in having sclerites oriented perpendicular to the long axis. We interpret this specimen as a folded fragment of a larger individual. YKLP 13507 is a largely incomplete specimen preserving only a small length of one margin, in association with two diagnostic sclerites (electronic supplementary material, figure S1c). The minimum preserved width (measuring perpendicular to the margin, and to sclerite ray orientation) is 115 mm, suggestive of a very large body size for this individual.

Remarks: The available specimens are variable in overall morphology, but are united by sclerites, where present, of a consistent size, structure and distribution. Specimens without sclerites exhibit a characteristic outline and/or expression of a marginal crease that is typical of both *A. nuda* and co-occurring specimens of *A. phrixothrix*. We interpret the ring-shaped “doughnut” structures to be the sites of former sclerite attachment, based on their size and distribution (matching in their density the densest non-apical sclerite arrays). Comparable structures were found to be associated with the sclerite bases in *Nidelric pugio* [18], and partly three-dimensionally preserved chancelloriids occur in which sclerites are mounted on short projections of the body wall [21], further supporting our interpretation. The “bulge” preserved in the holotype could represent a distinct body region, or perhaps a site of early-stage budding – or it might simply be an artefact of twisting and folding of the body wall. It is unique among known chancelloriiid specimens, making it hard to test between these alternative interpretations.

The holotype represents a medium-sized individual. Assuming the same length to width ratio (L:W ~4.3) in the specimen with the largest preserved body width (70 mm; YKLP 13506) predicts a body length of more than 30 cm. Applying the same calculation to the largest incomplete fragment (minimum width 115 mm, YKLP 13507) predicts a body length of around 50 cm. In other species of *Allonnia*, L:W values of up to 4.75 are known, though are typically less than this (c. 3.0–3.6) for smaller, more club-shaped specimens [4]. Even taking a conservative scaling value of 3.0 for the largest *Allonnia* fragments suggests lengths
of more than 30 cm, substantially larger than the 20 cm maximum size that has previously been reported for chancelloriids [4,16,22].

Among the three other species of Allonnia known from articulated scleritomes, *A. phrixothrix*, which co-occurs with *A. nuda* in the Chengjiang biota, has larger sclerites (with rays up to 8 mm long) and a prominent, commonly rhombic or pustulose surface ornamentation [15,16, and see electronic supplementary material, figure S2]. Juvenile specimens assignable to *A. phrixothrix* exhibit larger sclerites than adult *A. nuda* (supplementary electronic material, figure S3). *Allonnia erjiensis*, also from the Chengjiang biota, has sclerites with rays up to 5 mm long that are densely distributed across the body surface (>35 per cm², vs 20 per cm² in *A. phrixothrix* [16]). *Allonnia tintinopsis* from the middle Cambrian Burgess Shale has moderately long sclerite rays (up to 3.8 mm) that are distributed evenly across the body surface [4].

Some previous studies on Chengjiang chancelloriids have discussed (but not formally named) specimens with small, sparsely distributed sclerites. Among these, a specimen figured as *Allonnia* sp. (fig. 9 in ref. 15) appears to be conspecific with *A. nuda*. The “Form B” specimens of *Allonnia* discussed but not figured in ref. 16 await more detailed description, as does a specimen with small but more densely arranged sclerites (figs 93, 94 in ref. 19).

3. Discussion

The discovery of *Allonnia nuda* substantially expands the known disparity of chancelloriids to include very large forms with weak or absent spination. The spectrum of sparsely spiny to spine-less specimens, coupled with the evidence from the ring-shaped scars and otherwise well-preserved integument and body outline in spine-less body regions and individuals, suggest that the sclerites were shed (or became detached) during life, rather than through decay. Interestingly, one specimen of *Archiasterella coriacea* from the Burgess Shale (figured in ref. 4, fig. 42) exhibits a bald mid-section. This suggests that chancelloriids more generally may have been prone to sclerite loss – although this specimen may simply represent a rare preservational variant or damaged individual, since it occurs within a population with more regular scleritomes. In contrast, the recurrent morphology of *A. nuda* combined with its clear distinction in sclerite size from co-occurring chancelloriids suggests that it is a separate taxon, rather than an ecophenotypic or taphonomic variant, or a teratological form. As a group, chancelloriids are noted for their characteristic sclerites, but *A. nuda* reveals that there are also poorly spinose forms that have previously been overlooked. It also questions whether
the absence of chancelloriid sclerites in the post-Cambrian record reliably indicates the timing of the group’s extinction.

Chancelloriid architecture, growth and affinities: The sparse spination of *A. nuda* allows an unprecedented view among chancelloriiids of the underlying body. Even so, no additional body organs, orifices, or integumentary differentiation can be discerned; neither is there evidence of additional internal morphology where the body has been partially infilled, or fortuitously cross-sectioned by the angle of rock-splitting. All evidence supports previous reconstructions of the chancelloriid body as a thin-walled sac with a single apical orifice. There is no trace of a gut or other internal organs, functional or vestigial, which would reasonably be expected in a secondarily sessile bilaterian [7,12], especially given the widespread preservation of such features in the Chengjiang Lagerstätte [14]. There are no mesenteries such as divide the body cavity in actinarian cnidarians, nor any oral tentacles, which are crucial for feeding in almost all cnidarians except for some derived atentaculate infaunal anemones with exterior nematocysts [23]. The simplicity of the chancelloriid body plan is not simply a result of character loss through decay, but is supported by preserved characters including a single orifice and axial (radial) symmetry. This architecture narrows the range of viable hypotheses for both the phylogenetic placement and trophic ecology of chancelloriiids.

In addition, new characters for testing between competing hypotheses of affinity come from a full consideration of chancelloriid scleritome construction, which provides evidence for the underlying growth pattern of the chancelloriid body. It has been noted that smaller sclerites occur near the base of the body in several species [4,21], and a detailed analysis of sclerite size distribution in *Allonnia tintinopsis* found that the largest sclerites are positioned near the apex, while those of the basal region are the same size in large and small individuals [4] (see also electronic supplementary material, figure S3). This pattern suggests that body growth and sclerite addition were focussed at the apical end, because individual sclerites show no evidence of accretionary size increase (they could not grow), and if they had been shed and replaced during life, larger individuals would not be expected to retain small basal sclerites. In contrast, the similarly non-accretionary sclerites of *Halkieria*, a bilaterally symmetrical “coeloscleritophoran”, and also *Wiwaxia*, whatever its precise relationships, are uniformly larger in larger-bodied individuals, suggesting a pattern of shedding and replacement of sclerites [24,25].
Our observations from *A. nuda* support previous inferences about chancellorid growth. Although the sclerites do not exhibit a clear size gradient across the body, perhaps because of their small size combined with differential exposure along the plane of splitting, they occur more densely at the apical end. Also, the “doughnut” scars suggest that once lost, sclerites were not replaced, assuming this happened in life rather than post mortem. However, a simple model of apical growth does not account for the modified sclerites that surround the apical orifice (figure 2).

A differentiated apical tuft has been documented in various other chancelloriids, and is most clearly expressed in obliquely flattened specimens of *A. tintinopsis* from the Burgess Shale (figure 3b; see also figs 21, 22, 26 in ref. 4). In order to grow the body and add larger body sclerites from the apical end, but at the same time maintain a region of distinctly shaped sclerites surrounding the apical orifice, chancelloriids must have possessed a subapical (rather than apical [4]) zone of concentrated cell proliferation and sclerite addition, positioned between the two distinct sclerite zones (figure 3a). Some chancelloriid species are noted to have body sclerites of more mixed size (e.g., *Chancelloria eros* and *Archiasterella coriacea* [4]), implying either a more complex pattern of body sclerite addition, or the subapical addition of body sclerites of variable size. Either way, a subapical growth zone would still be required to maintain the apical tuft.

Comparable modes of growth are rare among metazoans. Various segmented animals have a sub-terminal growth zone, and polypoid cnidarians can exhibit cell proliferation in a mid-body or sub-tentacular zone [26]. However, among cylindrical, non-colonial animals which construct a ‘scleritome’, particular vase-shaped calcarean sponges provide a strong comparison. For example, the extant calcarean sponge *Sycon ciliatum* produces new filtratory chambers and specialized, elongate oscular-region spicules in ring-shaped zones just posterior to the osculum (figure 4) [27,28,29]. Although subsidiary growth and spicule addition can occur elsewhere in the body, notably at sites of budding, the pattern in *Sycon* contrasts with the often highly plastic growth and remodelling seen in sponges with more complex shapes or asymmetric body forms [30], and is more constrained than growth principally by overall body inflation that has been reconstructed for various Cambrian sponges [31].

*Sycon*-type growth in chancelloriids could represent either a synapomorphic, symplesiomorphic or convergent character, depending on the phylogenetic distribution of growth modes among calcareans, other sponges, and other metazoans. More generally, cylindrical body symmetry has been suggested to be plesiomorphic for metazoans [32],
although this result is sensitive to the topology of the tree, and growth modes are likely to be harder to establish for extinct groups that lack scleritomes. Clearly, however, the growth pattern of chancelloriiids falls within the range known from modern sponges, and suggests that the overall sponge-like habit could be underpinned by more than superficial similarities.

Chancelloriids as sponges: The arguments against chancelloriiids being sponges have been thoroughly rehearsed in the literature over the past forty years [4]. Even so, this hypothesis may still find more support than the alternatives. Chancelloriiids would be unusual among sponges for having a robust “integument”; but modern homoscleromorph sponges are notable for having true epithelia supported by basement membranes, an otherwise eumetazoan-like character [12]. Chancelloriid fossils do not preserve visible ostia (inhalant pores), which are vital to the working of a sponge-type water-canal system; but ostia in living sponges can be as small as 5 µm in diameter, arguably smaller than the resolution of preservation, and the fossils lack evidence for any known alternative feeding mode. Chancelloriiids do not exhibit budding or branching, unless this has gone unnoticed among clusters of specimens, or is indeed represented by the bulge in the holotype of *A. nuda*; but *Sycon* is able to maintain strict developmental control over body axis formation [29]. Accepting chancelloriiids as sponges almost certainly requires rejecting coelosclerite homology [7]; but biomineralization has arisen more than once in sponges, among calcified basal skeletons [33] and perhaps among spicules (e.g., in homoscleromorphs; discussed in ref. 13), and there are other examples of complex biomineralized tissues that are known to have arisen convergently, including the composite dentine/enamel-like tooth-like structures in conodonts and jawed vertebrates [34].

More broadly, the Cambrian fossil record has revealed an unexpected disparity among early sponges, with extinct combinations of spicule and skeleton characters that later became highly conserved [13,35,36], not least in the distinctive protonomonaxonids with robustly preserved body surfaces and unusual, perhaps open-based spicules that have been likened to chancelloriid sclerites [13]. At the same time, it has become clear that modern sponges share an extensive developmental genetic toolkit that was thought to have originated higher in the metazoan tree, and also show evidence for secondary gene loss [37,38]. It is not clear how an expanded developmental genetic repertoire in the ancestors of modern sponges might have been expressed phenotypically [38], and we should not necessarily expect Cambrian sponges to look more “animal-like” than modern representatives. Even so, chancelloriiids have the potential to shed light on the disparity, development and tissue complexity of early sponges,
and to test hypotheses from evolutionary developmental biology of body plan homologies among metazoans [39]. A sponge affinity for chancelloriids deserves renewed consideration.

**Ethics.** No ethical approval was required for the research described here.

**Data accessibility.** All data used in this study are presented in the text and Supplementary Information.

**Authors’ contributions.** P.-Y.C. & X.-G.H. designed the study; P.-Y.C., T.H., M.W., D.S., D.S. and S.G. carried out the analysis; T.H. drafted the manuscript with contributions from all authors; all authors gave final approval for publication.

**Competing interests.** We have no competing interests.

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**References**


Figure captions

Figure 1. *Allonnia nuda* n. sp. from the lower Cambrian Chengjiang Lagerstätte. (*a,h*) Holotype, YKLP 13501; overview, apex at top (*a*) with box to locate the area magnified to show ring-shaped scars (*h*). (*b,d – g*) YKLP 13502; overview (*b*) with box to locate the area magnified to show the distribution of sclerites (*d*), and selected sclerites showing the typical two-ray aspect (*e,f*) and the rarer view exposing three ray-bases (*g*). The specimen is ‘sectioned’ at the top by the angle of rock splitting. (*c*) YKLP 13506, overview; the mid-section of a specimen that lacks sclerites. Scale bars: (*a – c*) are 2cm; (*d,h*) are 5 mm; (*e – g*) are 1 mm. Specimens in this and other figures were photographed dry, using low-angle light.

Figure 2. Apical end of the holotype of *Allonnia nuda*, YKLP 13501, to show the partial sediment infill through an orifice and differentiated, single-rayed apical sclerites. (*a*) photograph and (*b – d*) camera lucida drawings; (*c*) is a composite superimposing part and counterpart. Scale bars: (*a – c*) are 5 mm; (*d*) is 2 mm.

Figure 3. Reconstruction of *Allonnia nuda* n. sp. (*a*) and apical view of *A. tintinopsis* (*b*). The sub-apical growth zone (delimited by dashed lines) and directions of growth (arrows) in (*a*) are inferred from the distribution of sclerite types in *A. nuda* and other chancelloriid taxa, including *A. tintinopsis* (*b*; oblique view of apical tuft and orifice; traced from fig. 26 in ref. 4).

Figure 4. Growth of the extant calcarean sponge *Sycon ciliatum*. Overview (*b*) and longitudinal sections (*a,c*); fluorescence overlays from calcein disodium staining (green) show that spicule growth is concentrated around the osculum, forming new filtratory chambers and maintaining a ring of specialized, extra-long oscular diactines. Images courtesy of Oliver Voigt; for further details see ref. 27. Scale bars: (*a,c*) are 250 µm; (*b*) is 1 mm.

Electronic supplementary material

Figure S1. Additional specimens of *Allonnia nuda* n. sp. (*a*) YKLP 13504. (*b*) YKLP 13503. (*c*) YKLP 13507; specimen exposed on the uppermost surface (lower left-hand side of image); arrowhead indicates the short length of preserved body outline; arrows indicate the
position of the two preserved sclerites. Note that the prominent raised bumps in (a) and (c) are not sclerites but presumed sedimentary features. Scale bars: 2 cm.

Figure S2. A weakly expressed granular body-surface texture expressed locally in *Allonnia nuda* n. sp., specimen 13502a (a), the more strongly expressed reticulate and pustulose textures characteristic of the co-occurring Chengjiang chancelloriid *A. phrixothrix* (b – d); (b) is an overview image of the apical end of the specimen from which the detailed images (c, d) are magnified. Scale bars: (a, c, d) are 1 mm; (b) is 5 mm.

Figure S3. Juvenile chancelloriiids from the Chengjiang Lagerstätte. Both specimens display a prominent integument ornamentation typical of *Allonnia phrixothrix* but not known in *A. nuda*. The sclerite size-distribution suggests that larger sclerites were added during growth at the apical end. The smaller specimen (a) displays a bulb-shaped base that lacks sclerites, with increasingly larger sclerites positioned apically; the larger specimen (b) already has sclerites that are longer than those in much larger-bodied (decimetre-scale) *A. nuda*. Scale bars: 1 mm.
Electronic supplementary material:

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