Articulated *Wiwaxia* from the Cambrian Stage 3 Xiaoshiba Lagerstätte

Jie Yang[1], Martin R. Smith[2], Tian Lan[1], Jin-bo Hou[1] & Xi-guang Zhang[1]

[1]Key Laboratory for Palaeobiology, Yunnan University, Kunming 650091, China, [2]Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EQ, UK.

Wiwaxia is a bizarre metazoan that has been interpreted as a primitive mollusc and as a polychaete annelid worm. Extensive material from the Burgess Shale provides a detailed picture of its morphology and ontogeny, but the fossil record outside this lagerstätte is scarce, and complete wiwaxiids are particularly rare. Here we report small articulated specimens of *Wiwaxia foliosa* sp. nov. from the Xiaoshiba fauna (Cambrian Stage 3, Hongjingshao Formation, Kunming, south China). Although spines are absent, the fossils' sclerites – like those of *W. corrugata* – are symmetrically arranged in five distinct zones. They form rows across the body, and were individually added and shed throughout growth to retain an approximately symmetrical body shape. Their development pattern suggests a molluscan affinity. The basic body plan of wiwaxiids is fundamentally conserved across two continents through Cambrian Stages 3–5 – revealing morphological stasis in the wake of the Cambrian explosion.

The cataphract lophotrochozoan *Wiwaxia* was first described from isolated sclerites[1]. These distinctive and widespread scales have been recognized from a range of palaeoenvironmental settings from the early to middle Cambrian (Stage 3–Guzhangian) of western Canada, Utah, Russia, China, eastern Europe, and Australia, establishing wiwaxiids as a key component of Cambrian ecosystems[2-11].

Despite this broad geographical occurrence, articulated *Wiwaxia* specimens are only known from the Burgess Shale[12] and two partial specimens from Kaili[10,13]. The hundreds of complete Burgess Shale specimens denote a scale-covered organism with a creeping foot, distinctive mouthparts, and two series of long dorsal spines[12,14,15]. Sclerites are arranged in four distinct zones on each side of the body, with an additional anterior sclerite zone. The sclerites were initially likened to the fleshy scales (elytra) of certain annelid worms[16] – but annelid elytra and *Wiwaxia* sclerites differ fundamentally in distribution, shape, and construction[5,12]. The flattened chaetae (paleae) of other annelids are more promising homologues[5,17] – yet paleae always occur as part of a biramous unit, paired with a 'normal' seta. Elements that were putatively interpreted in this role have since been recognized as components of an unrelated organism[18]; indeed, *Wiwaxia* sclerites do not form pairs but occur in 'bundles'[15].

On balance, the growth, distribution and microstructure of *Wiwaxia* sclerites do not bear out an annelid affinity; they instead suggest a relationship with aculiferan molluscs[15]. *Wiwaxia*'s radula-like mouthparts uphold a molluscan affinity[12,14,19]; their proposed interpretation as an annelid jaw[5,17,20] is not consistent with their detailed anatomy[14]. The presence of a creeping foot in *Wiwaxia*[15] and the likely molluscan affinity of closely-related *Odontogriphus*[14,21,22] provide further grounds to ascribe *Wiwaxia* to Mollusca, even if the precise nature of this relationship remains ambiguous.

Whereas the disparate array of isolated sclerites suggests that *Wiwaxia* was highly diverse[3,7], articulated specimens represent just two species, *W. taijiangensis* and *W. corrugata*, distinguished based on their sclerites' dimensions and ornament[10,15]. Here we report a third species of *Wiwaxia*, represented by articulated specimens from thinly bedded mudstones near the base of the Hongjingshao Formation (Cambrian Series 2, Stage 3), Xiaoshiba, Kunming.

Results

Geological setting. The recently discovered Xiaoshiba lagerstätte within the lower part of the Hongjingshao Formation is characterized by a series of yellow-green or purple-red sandstones, siltstones and shales, occasionally interbedded with yellow, thin-bedded mudstones. It overlies the Yu'anshan Formation (which hosts the Chengjiang lagerstätte), and contains three trilobite genera that also occur in the Chengjiang fauna (*Kuanyangia*, *Yunnanocephalus* and *Chengjiangaspis*) and one (*Hongshiyanaspis*) that does not. These taxa are found in the upper Qiongzhusian *Eoredlichia–Wutingaspis* Zone[24], although their extensive and poorly-
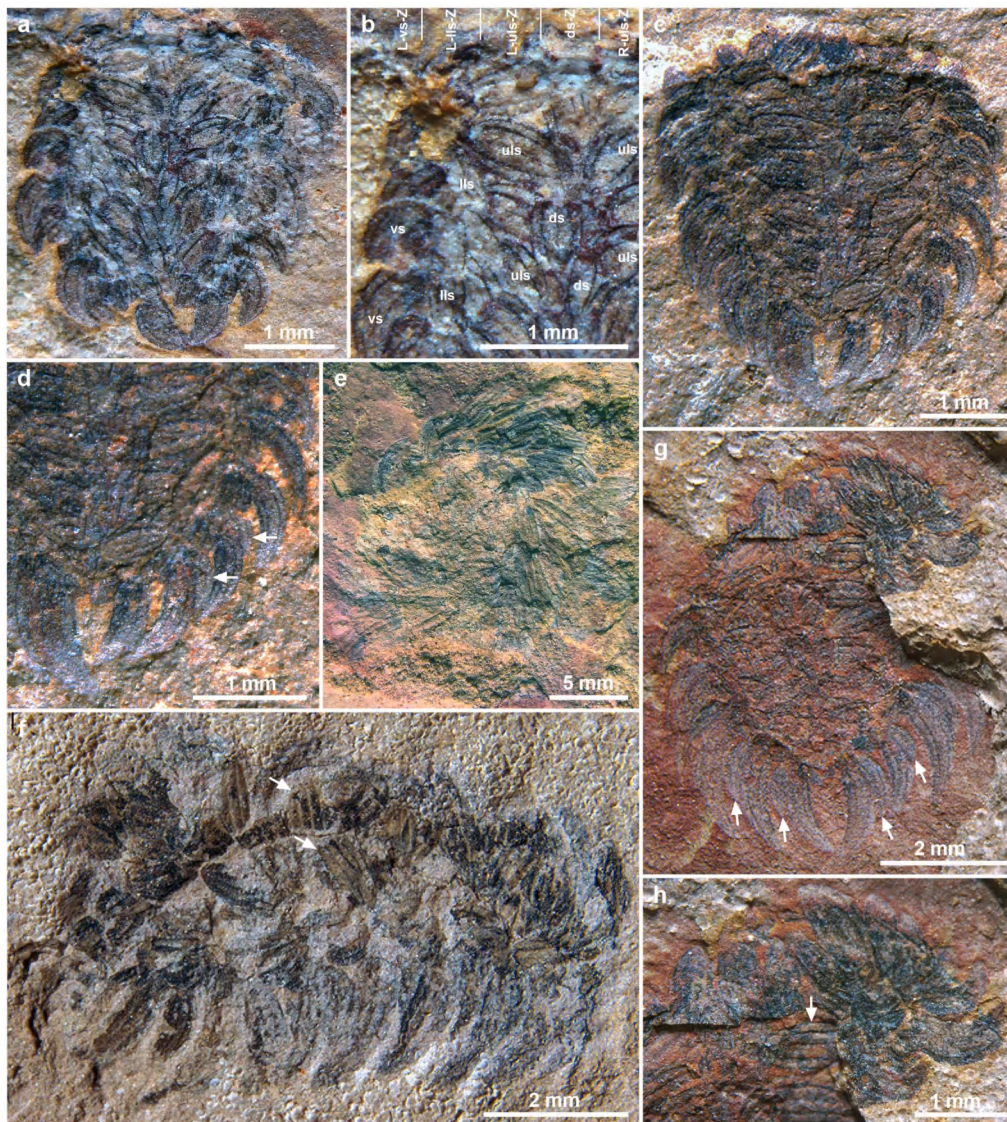
Figure 1 | Wiwaxia foliosa sp. nov. from the early Cambrian (Stage 3) of southern China. (a) YKLP 12121, ventral view of complete specimen. (b) details of the left upper part of (a), showing the symmetrically arranged dorsal sclerites with no more than five ribs, including the marginal ribs. The approximate extent of the transverse sclerite zones is illustrated. Abbreviations: ds, dorsal sclerite; uls, upper lateral sclerite; lls, lower lateral sclerite; vs, ventro-lateral sclerite; L, left; R, right; Z, zone. (c) YKLP 12120 (holotype), ventral view of complete specimen. (d) details of (c), showing incipient ventral sclerites (arrowed) and elongated siculate ventral sclerites, which are not symmetrical about the body's midline. (e) YKLP 12125, lateral view, fully enrolled specimen. (f), YKLP 12124, dorsal surface, showing some sclerites with six ribs (arrowed). (g) YKLP 12122, ventral view of partly-enrolled specimen with anterior portion on higher layer within rock; incipient sclerites arrowed. (h), details of (g), showing sclerite with six ribs (arrowed).

constrained stratigraphic ranges limit their practical utility. Additionally, the Canglangpuian index trilobite *Zhangshania* has been found about eight metres above the horizon yielding the Xiaoshiba lagerstätte – which is therefore of late Qiongzhusian (Cambrian Series 2, Stage 3) age, rather than early Canglangpuian as previously ascribed[25]. Biostratigraphically, the Hongjingshao Formation is diachronous in the Kunming area.

Systematic palaeontology. Family Wiwaxiidae Walcott, 1911 (nom. corr. Howell 1962[26]).

Genus *Wiwaxia* Walcott, 1911.

Type species. *Wiwaxia corrugata* (Matthew, 1899), Cambrian Stage 5 *Ogygopsis* Shale, Stephen Formation, Field, Canada.

Wiwaxia foliosa sp. nov.

Fig. 1a–h.

Etymology. *foliosus* (Latin), many leaves, alluding to the leaf-like arrangement of sclerites.

Holotype. YKLP (Key Laboratory for Paleobiology, Yunnan University) 12120 (Fig. 1c, d), an articulated and almost-complete specimen.

Type locality. Xiaoshiba section, near the bottom of the Hongjingshao Formation, about 8 meters below the Canglangpu Stage *Zhangshania* Zone (Cambrian Stage 3), near Xiaoshiba village, eastern Kunming, Yunnan.

Material. Six specimens (YKLP 12120–12125, see Supplementary Text online) from the type locality.

Measurements. The smallest specimen (YKLP 12121) is 3.7 mm long and 3.5 mm wide (Fig. 1a); the largest complete specimen (YKLP 12124) is 8.7 mm long, but is not preserved in a position that allows its full width to be accurately measured (Fig. 1f).

Diagnosis. Sclerites unornamented, bearing a single order of ribs. Ribs few in number, typically four per sclerite. Dorsal sclerites symmetrical. Spines absent in specimens under 8 mm in length.
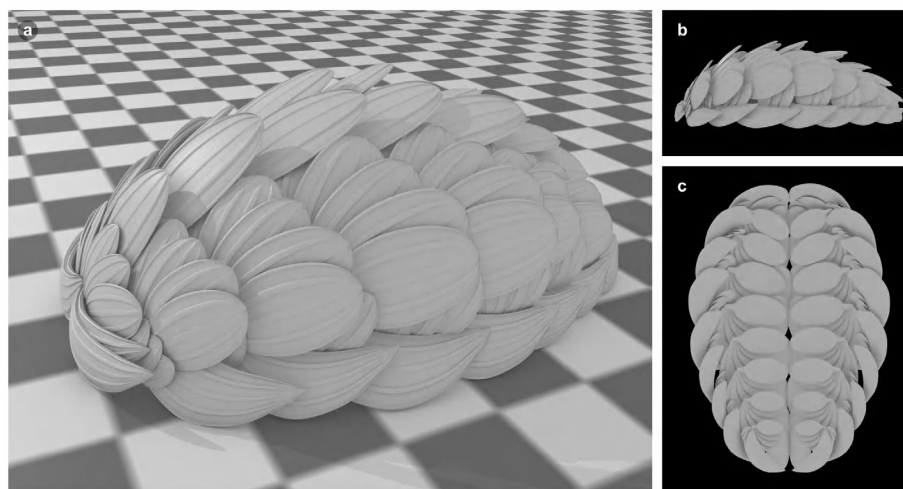
Figure 2 | Three-dimensional reconstruction of *Wiwaxia foliosa* sp. nov. (a) perspective view; checkerboard represents 1 mm; (b) lateral view, indicating partially-erect nature of sclerites; (c) ventral view, indicating broad sweep of dorsal sclerites and elongate nature of ventral sclerites.

Description. The body is oval in outline (dorsal view) and covered by an imbricate scleritome comprising eight transverse rows (Fig. 2). Prominent dorsal sclerites are aligned along the anterior-posterior axis and form a symmetrical paired series about the sagittal plane. Upper-lateral sclerites are a similar shape; they are arranged in fan-like bundles that radiate from a central attachment point and are slightly erect from the body surface, becoming more so in enrolled specimens. The lower-lateral sclerites are rounded, relatively small, and often obscured by other sclerites; their tips are dorsally inclined. Ventro-lateral sclerites are elongate and sickle-shaped; their tips point posteriad. The anterior zone contains symmetrical and sickle-shaped sclerites. Each sclerite bears four to six equally-pronounced ribs. In each sclerite zone, most sclerites are a similar size, but occasional sclerites are smaller and apparently incomplete (Fig. 1d). Sclerite length increases at the same rate as body length, whereas sclerite width increases slightly more slowly (see Supplementary Table S1 online).

Remarks. In terms of shape, aspect ratio and sclerite distribution, the material closely resembles juvenile specimens of *W. corrugata* from the Burgess Shale[15]. In the latter case, however, sclerites are generally flush with the body, somewhat obscuring the distinction between separate sclerite zones; here, the distribution of sclerites is more regimented and separate bundles are readily recognized even in fully articulated specimens. The aspect of the upper-lateral sclerites is also distinctive; in the new material, bundles are arranged such that the outermost sclerite is the most lateral, whereas in *W. corrugata*, the outermost sclerite is closest to the midline. This allows the bundles in *W. foliosa* to spread more broadly and to overlap the lower-lateral sclerites.

Since the largest articulated specimen is under 9 mm long, it is not possible to determine whether the absence of spines is organic, or ontogenetic (as in *W. corrugata*).

Discussion

Preservation. Whereas the Burgess Shale fossils are typically preserved in random orientations, the majority of Chengjiang fossils are preserved in a mechanically stable orientation, indicating that they settled under the force of gravity[27] rather than in turbulent flow. The same is true of the Xiaoshiba fauna; indeed most of the new *Wiwaxia* specimens are preserved parallel to the bedding plane in approximately dorso-ventral aspect. The exception is the rolled-up specimen YKLP 12125 (Fig. 1e), indicating that the enrolled organism was stable on its side. The enrolled position cannot have arisen through gravitational settling, but rather implies the presence of an enrolling

muscle. Enrolling musculature is present in chitons and juvenile aplacophorans, but not in conchiferan molluscs or other lophotrochozoans[28,29].

The absence of larger articulated specimens could result from the Bernoulli effect, where larger objects produce more lift and are thus – if their density is sufficiently low – prone to transport and disarticulation by currents. Such a process seemingly affects other fossils in Xiaoshiba; for instance larger components of the arthropod exoskeleton are routinely transported short distances from the carcass[25]. This effect may have caused larger *Wiwaxia* specimens to disarticulate whilst smaller specimens remained intact.

Currents may also have affected the preservation of sclerites in articulated specimens. Because each sclerite is individually attached to the body at the root, some degree of motion – especially in a partially decayed specimen – may have been possible. Furthermore, bundles or 'fans' of sclerites may have encountered turbulence and been reoriented as a unit.

Scleritome. In some cases, the corresponding sclerites on opposite sides of the body differ in size. The most extreme case is of ventral sclerites in YKLP 12120 where sclerites are around a third of the typical length. These smaller sclerites correspond in shape and width to the distal part of ventral sclerites, and presumably represent sclerites that were incompletely formed when the organism died. Their erratic occurrence indicates that sclerites did not grow synchronously throughout the body; rather, they must have grown to a fixed size, then remained for some time before being individually shed and replaced by a larger sclerite. Because the replacement sclerite, when fully secreted, would be larger than the one it replaced (in order to accommodate the growth of the organism), it would be larger than the opposite sclerite, thus breaking bilateral symmetry (Fig. 1a, c, g). This matches the growth mechanism observed in the spines of *W. corrugata*[15], indicating that the spines grew in the same manner as the body-covering sclerites.

It is also evident that larger individuals bear more sclerites than smaller ones; as with *W. corrugata*, the dorsal surface grows more rapidly than sclerite width (see Supplementary Table S1 online), meaning that more sclerites are required to cover the expanding area. Accordingly, sclerites are added to each bundle faster than they are shed, and the asynchronous addition of sclerites to bundles causes a further deviation from bilateral symmetry.

This uncoordinated growth mechanism has no equivalent in annelid worms, yet bears close relation to the situation in scleritome-bearing molluscs where sclerites grow to a fixed size and are

individually replaced[30–33]. This periodic deviation from bilateral symmetry adds further support for a molluscan affinity.

The presence of eight transverse rows in the *W. foliosa* scleritome indicates that this feature is integral to the wiwaxiid body plan, not just a quirk of *W. corrugata*. This upholds the suggested correspondence between transverse rows in *Wiwaxia* and aculiferans[15]. The relationship between *Wiwaxia*'s scleritome and its underlying metameres is ambiguous; the anterior sclerite zone may correspond to a transverse row or may have a separate origin, and the metameres may correspond to the rows of sclerites or to the gaps between them (as in aplacophorans[34]). Depending on the interpretation, *Wiwaxia* could therefore bear seven to eight (or possibly nine) metameres. This echoes the seven metameres in the aculiferan ground plan (to which polyplacophorans add an eighth late in development[29]) and the eight iterated units in tryblidid monoplacophorans[35]. Whether this makes *Wiwaxia* a stem- or crown-group mollusc depends on relationships within Mollusca, which remain contentious[36]; either way, the taxon is important for understanding the origin of molluscs' epidermal hard parts[19,23]. Interpreting the ancestral mollusc as a scleritome-bearing organism would account for the presence of microvillar 'chaetae' in early torted conchiferans (*Aldanella* and *Pelagiella*)[37,38]; more speculatively, it would allow the *Wiwaxia*-like scleritome borne by a hot-vent gastropod[39] to represent the reactivation of a dormant genetic machinery[15].

Occurrence. The robust nature of *Wiwaxia* sclerites enhances their preservation potential and accounts for their broad occurrence as carbonaceous fossils, which provides a measure of wiwaxiid distribution through the Cambrian[3,4,7,40]. This record is complemented by sclerites preserved on bedding planes as the remnants of carbon films[2,9–11], and more unusually in three dimensions by phosphatization, as in the Cambrian Stage 5 of Australia[8] and the Cambrian Stage 3 Qiongzhusian Shuijingtuo Formation in southern China (unpublished material). Despite this wide distribution and good preservation potential, *Wiwaxia* has not yet been reported from the Chengjiang lagerstätte[41], an absence that has been suggested to represent either evolution, biogeography or ecology[42]. Our new material demonstrates that *Wiwaxia* had evolved by Chengjiang time, and was present in the region. The recalcitrance of *Wiwaxia* sclerites and the exceptional preservation in Chengjiang makes it difficult to attribute this absence to taphonomic factors. This provides further evidence that the described Chengjiang fauna was ecologically and environmentally distinct from the Burgess Shale[43]; furthermore, it indicates differentiation between the Chengjiang and Xiaoshiba lagerstätten despite their temporal and geographic proximity.

The new specimens extend the record of articulated *Wiwaxia* specimens – previously known from the Stage 4 Kaili biota and the Stage 5 Burgess Shale[12,13,15] – into Cambrian Stage 3. Differences between the known specimens represent trivial tweaks to the configuration or ornament of sclerites, rather than any meaningful change in body plan – the scleritome exhibits a striking degree of morphological stasis over this 15 million year period. Given this lack of disparity, the Stage 3–5 record of isolated wiwaxiid sclerites can reasonably be reconstructed as components of *Wiwaxia*-like scleritomes. *Wiwaxia* therefore joins a growing list of non-mineralised taxa whose morphology changed little from Stage 3 to Stage 5 (e.g. *Hallucigenia sparsa*[44], *Nectocaris*[45]), despite the elevated rate of evolution associated with the early Cambrian period[46].

Despite their similar body plan, the fossil records of wiwaxiids and halkieriids are more complementary than congruous. Halkieriids have a rich and extensive microfossil record (e.g. ref. 47), but are rarely found articulated[17], whereas articulated wiwaxiids are now known from a range of Burgess Shale-type sites, even though their isolated sclerites are rare even in the localities from which they are known[7].

Whether these mismatches between the microfossil and macrofossil records reflect biology or taphonomy, the presence of wiwaxiid sclerites (and absence of halkieriid sclerites) in other Burgess Shale-type deposits suggests that halkieriids – like many other constituents of the shelly fauna – were excluded from typical Burgess Shale-type faunas. Similarly, *Wiwaxia* is yet to be found in the Chengjiang lagerstätte. As such, environmental and ecological factors were clearly intrinsic to the shaping of Cambrian communities.

Conclusions. *Wiwaxia*'s eight sclerite rows are consistently evident in separate species, and recall the eight-fold metamerism of the polyplacophorans, aplacophorans and tryblidians – suggesting that this layout was a feature of the molluscan ground plan. Details of the scleritome and the way that it grew suggest that it had much in common with the aculiferan molluscs. Specifically, the piecewise replacement of individual sclerites produced a deviation from bilateral symmetry not seen in annelid worms.

Despite the diverse range of sclerite ornaments and outlines revealed by the small carbonaceous fossil record[3,4,41], this new material indicates that the underlying *Wiwaxia* body plan, once established, remained constant for some 15 million years – seeming to display only species-level variation. *Wiwaxia* was the most abundant and widespread scleritomorph organism in Burgess Shale-type assemblages, providing a common biological thread between these dispersed communities.

Methods

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Acknowledgments

Author contributions

J.Y. arranged fieldwork, J.Y., J.B.H. and T.L. collected material; X.G.Z. and J.Y. conceived the project; X.G.Z. and M.R.S. conducted research, M.R.S. wrote the paper with input from X.G.Z. and T.L.

Additional information

Supplementary information accompanies this paper at http://www.nature.com/scientificreports

Competing financial interests: The authors declare no competing financial interests.

How to cite this article: Yang, J., Smith, M.R., Lan, T., Hou, J.-B. & Zhang, X.-G. Articulated *Wiwaxia* from the Cambrian Stage 3 Xiaoshiba Lagerstätte. *Sci. Rep.* **4**, 4643; DOI:10.1038/srep04643 (2014).