



First report of *Wiwaxia* from the Cambrian Chengjiang Lagerstätte

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Keywords:	Maotianshan shale, Cambrian Series 2, Mollusca, halwaxiids, Cambrian explosion, China

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4 First report of *Wiwaxia* from the Cambrian Chengjiang Lagerstätte
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38 **Abstract**

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40 The robust spines and sclerites of the early to middle Cambrian ‘mollusc’ *Wiwaxia* are
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42 ubiquitous in suitably-preserved deposits – but are strikingly absent from the
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44 Chengjiang Lagerstätten (Cambrian Stage 3, Yunnan Province, southwest China).
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47 Here we provide the first record of *Wiwaxia* sclerites from this rich deposit, extending
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49 the record of the genus to earliest Cambrian Series 2. This reinforces the cosmopolitan
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51 distribution of this iconic Cambrian lophotrochozoan and demonstrates the strong
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53 faunal continuity that unites distant Cambrian Lagerstätten.
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Keywords: Maotianshan shale, Mollusca, halwaxiids, Cambrian explosion, China

1. Introduction

Since the first discovery of its isolated sclerites (Matthew, 1899), *Wiwaxia* has established itself among the iconic Burgess Shale problematica. Until recently, its affinity was considered unresolvable (Eibye-Jacobsen, 2004); an interpretation as a mollusc – whether at a crown-group or stem-group level (Scheltema & Ivanov 2002; Scheltema *et al.* 2003; Caron *et al.* 2006, 2007; Conway Morris & Caron, 2007) – had competed with alternative positions in the annelid crown group or stem group (Walcott, 1911; Butterfield, 1990, 2003, 2006, 2008; Conway Morris & Peel, 1995), or in the stem group to Annelida + Brachiopoda (Conway Morris & Caron, 2007). Membership of an extinct phylum with remote affiliation to the molluscs had also been proposed (Bengtson & Conway Morris, 1984; Conway Morris, 1985). A position among Mollusca was finally established through the identification of radula-like mouthparts, a creeping ventral foot and an Aculiferan-like scleritome – even if *Wiwaxia*'s exact position within the molluscs remains unresolved (Smith, 2012, 2014).

Despite the phylogenetic uncertainty, the morphology of *Wiwaxia*'s dorsal imbricating scleritome is well constrained by hundreds of articulated specimens from the Burgess Shale (Walcott, 1911; Conway Morris, 1985; Smith, 2012, 2014), complemented by a handful of further individuals from Utah (Conway Morris *et al.* **in press**) and two localities in South China (Sun *et al.* 2014; Yang *et al.* 2014). The *Wiwaxia* scleritome comprised eight rows of overlapping scale-like sclerites,

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4 punctuated (in adults) by two rows of elongate dorsal spines. Sclerites are arranged in
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6 four distinct zones on either side of the body (**ventral, lower lateral, upper lateral**
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8 **and dorsal), with a distinct zone of sclerites arming the anterior of the body.**

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11 Leaf-like, the sclerites comprise a smooth proximal root that opens out into an oval,
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13 siculate or spinose blade; this blade has a reinforced margin and edge-parallel ribs,
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15 and sometimes bears a pustular ornament (Butterfield & Harvey, 2012; Smith, 2014).

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18 Elongate internal chambers indicate that they were secreted by microvilli, suggesting
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20 a chitinous original composition (Butterfield, 1990; Smith, 2014). This recalcitrant
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22 carbonaceous construction gives the sclerites a strong preservation potential in
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24 suitable taphonomic regimes, either as Burgess Shale-type macrofossils or as **robust**
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26 **acid-extracted microfossils (Small Carbonaceous Fossils, see Butterfield and**
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28 **Harvey 2012).**

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34 The distinctive shape and robust constitution of *Wiwaxia* sclerites has led to their
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36 recognition in a worldwide suite of deposits representing platform to outer shelf
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38 environments from Cambrian Series 2 to 3 (Fig. 1; Conway Morris, 1985; Butterfield,
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40 1994; Zhao *et al.* 1994; Ivantsov *et al.* 2005; Fatka *et al.* 2011; Sun *et al.* 2014; Yang
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42 *et al.* 2014). Thus, although articulated specimens are only known from **four** sites
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44 (Conway Morris 1985; Zhao *et al.* 1994; Sun *et al.* 2014; Yang *et al.* 2014; **Conway**
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46 **Morris *et al.* in press**), isolated sclerites extend the range of *Wiwaxia* to North
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48 America (Mount Cap, Stephen, Earlie, Pika, Spence Formation; Matthew, 1899;
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50 Walcott, 1911; Conway Morris, 1985; Conway Morris & Robison, 1988; Butterfield,
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52 1994; Harvey & Butterfield, 2011; Butterfield & Harvey, 2012), South China
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4 (Tsinghsutung, Kaili Formation; Zhao *et al.* 1994, 1999; Harvey *et al.* 2012; Sun *et al.*
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6 2014), Australia (Emu Bay Shale, Monastery Creek Formation; Porter, 2004), Siberia
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8 (Sinsk Formation; Ivantsov *et al.* 2005), and the Czech Republic (Buchava Formation;
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10 Fatka *et al.* 2011). Nevertheless, *Wiwaxia* has not been reported from Chengjiang,
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12 even though this is among the richest and best sampled Cambrian Lagerstätten (Zhao
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14 *et al.* 2012, 2014) and has a broadly equivalent ecological and taxonomic composition
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16 to the Burgess Shale biota, where *Wiwaxia* is known from hundreds of specimens
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18 (Conway Morris, 1985; Smith, 2014). Here, we fill this surprising gap in *Wiwaxia*'s
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20 distribution with a report of associated sclerites from Chengjiang.
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28 **2. Materials and methods**

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30 Our material was collected from the mudstone-dominated Maotianshan Shale

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32 Member of the Yu'anshan Formation, Cambrian Series 2, Stage 3,

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34 *Eoredlichia-Wudingaspis* Zone (Chen *et al.* 1996; Zhu *et al.* 2001), at the Mafang

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36 section, Haikou, Yunnan, southwest China (24°46'20" N, 102°35'10" E). Detailed

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38 locality information and fossil taphofacies were presented by Zhao *et al.* (2009).

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40 The material was prepared using a blade and is deposited in the Nanjing Institute of

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42 Geology and Palaeontology, Chinese Academy of Sciences, China (NIGPAS).

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44 Photographs were taken under dark field illumination using a Zeiss Discovery V20

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microscope system.

56 **3. Description**

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The material consists of part and counterpart of a single slab of fine-grained mudstone

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4 (NIGPAS160801a/b) preserving compressions of four aligned bundles of sclerites on
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6 a single bedding surface (Fig. 2). **It exhibits characteristic Chengjiang-type**
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8 **preservation (Zhu *et al.* 2005); its originally carbonaceous components are**
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10 **reflected by weathered aluminosilicate films associated with superficial iron**
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12 **oxides.**

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16 **The sclerite bundles** contain one to four sclerites of similar size, around 8 mm
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18 long and 0.8–1.6 mm wide; sclerites within a bundle are closely aligned such that
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20 their tips and bases are almost adjacent. **Sclerites appear to vary in curvature and**
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22 **width between bundles, with the aspect ratio varying from 6:1 to approximately**
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24 **10:1. This apparent variation may reflect differences in the obliquity of the**
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26 **sclerites' burial angle, or result from post-mortem deformation.** Each sclerite
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28 proceeds from a narrow root to a gently curved blade that tapers to a pointed apex
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30 with an angle of $\sim 20^\circ$. Longitudinal ribs adorn the blade, although these are difficult
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32 to distinguish from sclerite margins. Individual sclerites can only be discriminated by
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34 identifying their tips: four sclerites are evident in the first bundle, four in the second,
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36 one in the third, and four in the fourth. These counts may represent underestimates;
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38 sclerites with occluded tips cannot be identified, and if additional sclerites exist, their
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40 margins are difficult to distinguish from ribs.
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49 The identity of this material as *Wiwaxia* sclerites is indicated by the sclerites'
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51 outlines, longitudinal ribbing, smooth root, and limited three dimensional relief
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53 (indicating an originally **robust** carbonaceous composition). Their close association
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55 indicates that they were linked by connective tissue (presumably decayed) when they
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4 were buried.

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6 The parallel preservation of multiple bundles recalls a transverse row of
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8 sclerites (cf. Smith, 2014, fig. 5B). Under this interpretation, the four bundles
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10 correspond to the four zones of body sclerites. However, the absence of the
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12 fan-like splaying typically associated with non-ventral sclerites (e.g. Fig. 2e)
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14 militates against this interpretation, as do the extreme difference between the
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16 length:width ratio of the second and third bundle of sclerites (c. 8) and the
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18 smaller values in the non-ventral sclerites of *W. corrugata* (1.8 ± 0.5) and *W.*
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20 *foliosa* (1.82 ± 0.3) (Fig. 3a). (Detailed measurements from *W. herka* are not
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22 available.)
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29 More promisingly, the fossil might correspond to iterated bundles of ventral
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31 sclerites. This interpretation accounts for the curvature present in all sclerites,
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33 the regular spacing of the four bundles, each bundle's limited splaying. The
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35 length:width ratio of each bundle fits the profile of the ventral sclerites of
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37 *W. corrugata* and (assuming a similar trend with increasing sclerite size)
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39 *W. foliosa* (Fig. 3b), the latter species being only currently known from
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41 diminutive (juvenile?) specimens. (Due to oblique preservation, particularly in
42
43 the first two sclerite bundles, measurements of sclerite width are likely
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45 underestimates.) We therefore interpret our material as an articulated series of
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47 ventral *Wiwaxia* sclerites of indeterminate species.
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55 4. Discussion

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57 This is the first report of *Wiwaxia* from the Chengjiang biota, representing the earliest
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4 record of the taxon and further expanding its broad geographical range. Its apparent
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6 absence from the Chengjiang deposits was a long-standing puzzle, particularly given
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8 its prominence in multiple Burgess Shale-type through the Cambrian and the
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10 relatively high preservation potential of *Wiwaxia* sclerites in Burgess Shale-type
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12 biotas (Butterfield & Harvey, 2012). Evolution, biostratigraphy and ecology had been
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14 cited to account for its absence (Butterfield, 2003). We can now show that *Wiwaxia*
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16 had evolved and was present in the Chengjiang region by Cambrian Stage 3, adding it
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18 to a growing roster of species that were once considered endemic but are now
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20 recognized in both Lagerstätten: taxa such as *Primicaris* and *Misszhouia*, previously
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22 unique to Chengjiang, have recently been described in the Burgess Shale (Caron *et al.*
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24 2014), whereas taxa such as *Nectocaris* have been identified in Chengjiang after being
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26 considered unique to the Burgess Shale (Smith, 2013).
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34 *Wiwaxia* nevertheless remains a rare component of the Chengjiang fauna –
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36 particularly in view of the *c.* 500 articulated specimens known from the Burgess Shale
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38 (Smith, 2014). Ecology and taphonomy account for this discrepancy; the Chengjiang
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40 deposits **represent the relatively shallow-water settings of the continental**
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42 **platform** (Zhang *et al.* 2008), whereas the majority of Burgess Shale sites sample **a**
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44 **basinal setting representing deeper waters off the platform edge** (Caron *et al.*
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46 2010, 2014). What is more, substantial differences characterize contemporary Burgess
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48 Shale communities that are separated by trivial **spatial and stratigraphic** distances
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50 (Caron *et al.* 2010, 2014), emphasizing the prominent role of local-scale factors in
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52 controlling community composition. As such, *Wiwaxia* represents a striking example
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4 of faunal continuity between these two Lagerstätten, despite distinct environmental
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6 settings, a time difference of some 15 million years, and substantial geographic
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8 separation.
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20
21 **thank the anonymous reviewers for their constructive comments and improving**
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23 **the manuscript.**
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34 Figure 1. Distribution of *Wiwaxia*. (a) Stratigraphic distribution. (b) Palaeogeographic
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36 distribution (modified after McKerrow *et al.* 1992; Álvaro *et al.* 2003; Fatka *et al.*
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38 2011). Numbers in (a) correspond to those plotted in (b).
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46 **Figure 2. Sclerites of *Wiwaxia*. (a–d) from the lower Cambrian (Series 2, Stage 3)**
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48 **Maotianshan Shale Member, Yu'an Shan Formation (*Eoredlichia-Wudingaspis***
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50 **Zone) in the Mafang section, Haikou near Kunming, Yunnan Province; (e) from**
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52 **the middle Cambrian (Series 3, Stage 5) Burgess Shale. (a) Part**
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54 **(NIGPAS160801a). (b) Enlargement of boxed area, showing tips of constituent**
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4 sclerites in third bundle. (c) Counterpart (NIGPAS160801b). (d) Interpretative
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6 sketch of counterpart. (e) Semi-articulated scleritome from the Burgess Shale
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8 (Royal Ontario Museum 56965) illustrating variation in morphology between
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10 sclerite zones and splayed habit of upper lateral sclerite zone.
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16 **Figure 3. Comparison of sclerites from Chengjiang with those of other *Wiwaxia***
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18 **species. Aspect ratio of sclerites in first (1), second (2), third (3) and fourth (4)**
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20 **sclerite bundles in NIGPAS160801 compared to non-ventral (a) and ventral (b)**
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22 **sclerites of *Wiwaxia corrugata* (c, blue) and *W. foliosa* (f, orange). Width**
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24 **measurements from NIGPAS160801 may represent underestimates due to**
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26 **oblique preservation (see text).**
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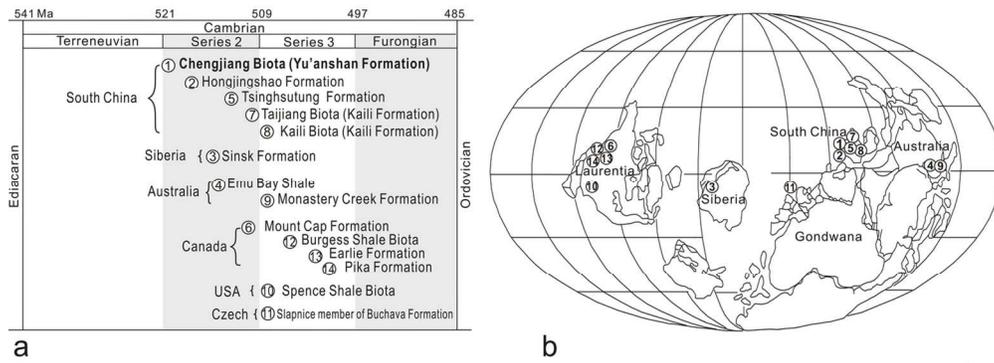


Figure 1. Distribution of *Wiwaxia*. (a) Stratigraphic distribution. (b) Palaeogeographic distribution (modified after McKerrow et al. 1992; Álvaro et al. 2003; Fatka et al. 2011). Numbers in (a) correspond to those plotted in (b).

63x23mm (600 x 600 DPI)

Proof For Review

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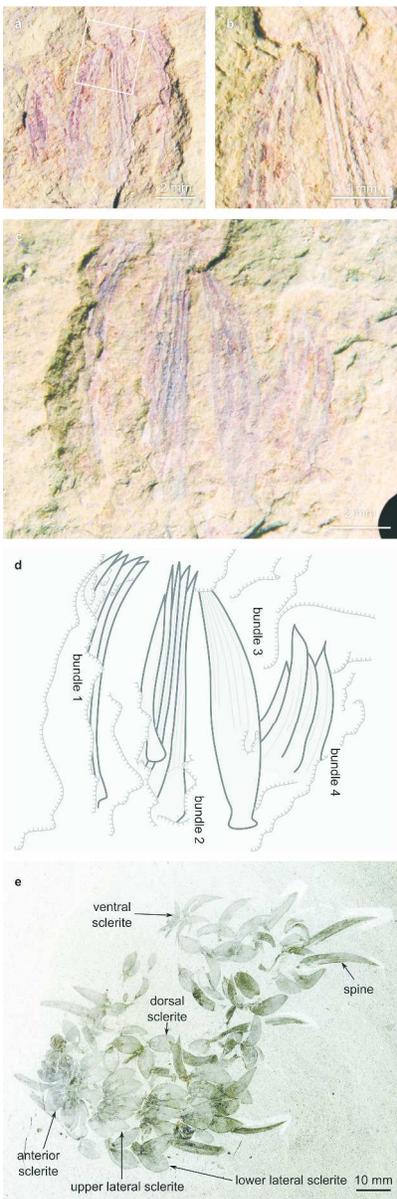


Figure 2. Sclerites of *Wiwaxia*. (a–d) from the lower Cambrian (Series 2, Stage 3) Maotianshan Shale Member, Yu'anshan Formation (Eoredlichia-Wudingaspis Zone) in the Mafang section, Haikou near Kunming, Yunnan Province; (e) from the middle Cambrian (Series 3, Stage 5) Burgess Shale. (a) Part (NIGPAS160801a). (b) Enlargement of boxed area, showing tips of constituent sclerites in third bundle. (c) Counterpart (NIGPAS160801b). (d) Interpretative sketch of counterpart. (e) Semi-articulated scleritome from the Burgess Shale (Royal Ontario Museum 56965) illustrating variation in morphology between sclerite zones and splayed habit of upper lateral sclerite zone.
234x707mm (600 x 600 DPI)

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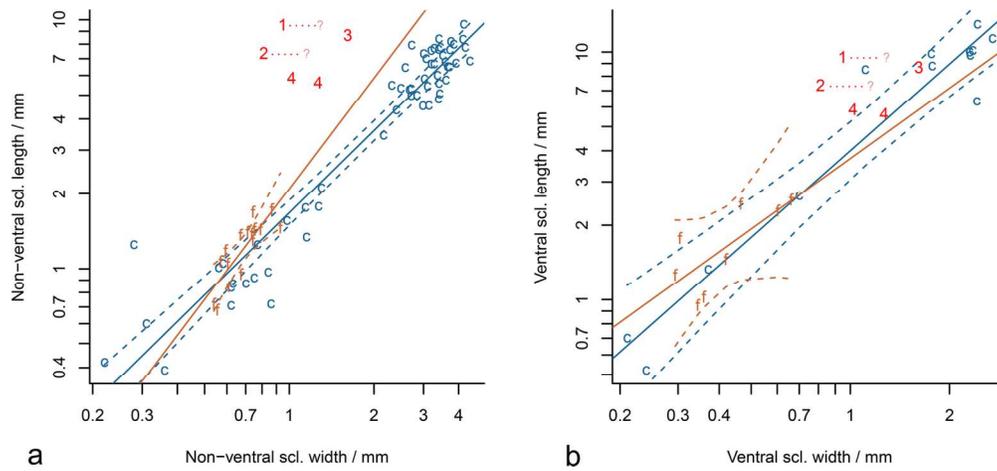


Figure 3. Comparison of sclerites from Chengjiang with those of other *Wiwaxia* species. Aspect ratio of sclerites in first (1), second (2), third (3) and fourth (4) sclerite bundles in NIGPAS160801 compared to non-ventral (a) and ventral (b) sclerites of *Wiwaxia corrugata* (c, blue) and *W. foliosa* (f, orange). Width measurements from NIGPAS160801 may represent underestimates due to oblique preservation (see text).
76x35mm (600 x 600 DPI)