

First occurrence of the Cambrian arthropod *Sidneyia* Walcott, 1911 outside of Laurentia

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Original Article

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Abstract

The arthropod *Sidneyia* Walcott, 1911 is a remarkable animal of the Burgess Shale biota (Cambrian Miaolingian, Wuliuan; British Columbia, Canada), which has not been confidently reported from other Cambrian Konservat-Lagerstätten. Here we report the discovery of *Sidneyia* cf. *inexpectans* from the Wuliuan Mantou Formation of North China, which substantially expands the known palaeogeographical distribution of this genus. Our discovery suggests that *Sidneyia* had much greater dispersal ability than hitherto thought. It also confirms the presence of exceptionally preserved fossils in the Wuliuan Mantou Formation, one of the rare Burgess Shale-type deposits of North China.

1. Introduction

As one of the most remarkable arthropods from the Burgess Shale (Cambrian Miaolingian, Wuliuan; British Columbia, Canada), the morphology (e.g. Walcott, 1911; Bruton, 1981; Stein, 2013; Zacaï *et al.* 2016; Bicknell *et al.* 2018b), phylogeny (e.g. Lerosey-Aubril *et al.* 2017) and palaeoecology (e.g. Zacaï *et al.* 2016; Bicknell *et al.* 2018a) of *Sidneyia* Walcott, 1911 have been studied extensively. However, the known palaeogeographical distribution of this arthropod was particularly limited. More than a hundred years after its original description, *Sidneyia* remained known only from its type locality, the Burgess Shale in British Columbia (Bruton, 1981; Caron *et al.* 2010, 2014; Zacaï *et al.* 2016), and claimed additional occurrences within Laurentia (e.g. Briggs & Robison, 1984; Briggs *et al.* 2008; Peel, 2017) have all proved incorrect or insufficiently documented. In the present paper, we describe a nearly complete specimen of *Sidneyia* from the middle Cambrian (Miaolingian, Wuliuan) Mantou Formation at Weifang, Shandong Province, North China that is nearly identical to the type species *S. inexpectans*. This discovery extends the known geographical distribution of *Sidneyia* beyond North America, indicating that it had a larger palaeogeographical distribution than was previously thought.

Miaolingian Burgess Shale-type Lagerstätten are essentially known from Laurentia, such as the Marble Canyon, Spence Shale, and Wheeler, Marjum and Weeks formations (e.g. Caron *et al.* 2014; Robison *et al.* 2015; Lerosey-Aubril *et al.* 2018; Kimmig *et al.* 2019). The only notable exception is the Kaili Formation in South China (Zhao *et al.* 2011). This stresses the need for searching for Miaolingian Burgess Shale-type Lagerstätten in other terranes. Previous studies have documented the presence of exceptionally preserved fossils in the Upper Shale Member of the Mantou Formation, North China (Resser & Endo, 1937; Liu *et al.* 2012; Sun *et al.* 2015; Wang *et al.* 2018), which is further confirmed by the discovery of *Sidneyia* cf. *inexpectans* here. In addition, exceptional preservation has been recorded in the Lower Shale Member of the Mantou Formation (Lin, 1995; Huang, 2012; Huang *et al.* 2012; Zhu *et al.* 2014), making the Mantou Formation a potential Lagerstätten assembly.

2. Geological setting and fossil locality

The Mantou (alternate spelling ‘Manto’) Formation is widely distributed in North China and was originally characterized as consisting of brick-red shale (Willis *et al.* 1907; Xiang *et al.* 1999). In Shandong Province, the Mantou Formation is subdivided into the Shidian Member (argillaceous dolostone and shale), the Lower Shale Member, the Honghe Member (sandstone) and the Upper Shale Member (Zhang & Liu, 1996).

There is a well-established trilobite biostratigraphy for the Cambrian of Shandong Province, where the Mantou Formation spans the interval extending from the *Redlichia chinensis* Zone (lower Lungwangmiaoan, corresponding to the lower part of Cambrian Stage 4) to the *Bailiella lantenoisi* Zone (uppermost Hsuchuangian, corresponding to the uppermost Wuliuan) (Zhang & Liu, 1996; Yuan *et al.* 2012). In many parts of Shandong Province, the Mantou Formation comprises 13 trilobite biozones.

The presence of sandy conglomerate in the upper part of the Honghe Member, together with the presence of bidirectional trough cross-stratified layers and halite pseudocrystals in the Shidian Member, suggests that the Mantou Formation may represent a tidal flat environment (Zhang & Liu, 1996). However, because the Mantou Formation represents an extended period of sedimentation, the depositional environments of this deposit were probably diverse. Additionally, the dark shale and global agnostoids in the uppermost part of the Mantou Formation (Sun, 1989; Sun *et al.* 2018) correspond to the global eustatic flooding surface at the base of the *Ptychagnostus gibbus* Zone (Babcock *et al.* 2015).

The new material described in this paper was collected from the Upper Shale Member of the Mantou Formation (*Bailiella lantenoisi* Zone) in the Longgang section near the town of Shanwang (Longgang village), Linqu County, Shandong Province (Fig. 1). Burgess Shale-type fossils occur in three distinct fossiliferous beds called, in ascending order, Beds A, B and C. *Sidneyia* was found in Bed A along with the trilobites *Proasaphiscus lui* (Chang, 1959), *Ptychagnostus sinicus* Lu, 1957, *Peronopsis rotundatus* Ergeliev, 1980 and *Pe. taitzuhoensis* Lu, 1957. Bed A also contains other fossils, including algae, brachiopods, the bivalved arthropods *Tuzoia manchuriensis* Resser & Endo in Resser, 1929 and *Isoxys* sp., worm-like animals and possible Hurdiidae (unpublished). Bed B has yielded the trilobites *Bailiella lantenoisi* (Mansuy, 1916) and *Pe. rotundatus*, the bivalved arthropod *T. manchuriensis*, sponges, cancelloriids and worm-like animals. Lastly, Bed C has yielded the trilobites *Pr. yabei* Resser & Endo in Kobayashi, 1935 and *Lioparia bassleri* Resser & Endo, 1937, the bivalved arthropod *T. manchuriensis*, brachiopods and hyolithids.

The occurrence of two global agnostoid trilobites, *Pt. sinicus* and *Pe. rotundatus*, in the Upper Shale Member allows biostratigraphical correlation of the *Bailiella lantenoisi* Zone with the *Ptychagnostus gibbus* Zone (top of the Wuliuan) (Zhang, 1986; Peng, 2009; Yuan *et al.* 2012; Sun *et al.* 2018). *Pt. praecurrens* (Westergård, 1936) in the Burgess Shale (Rasetti, 1967) belongs to the *Ptychagnostus praecurrens* Zone (Sundberg, 1994), which lies below the *Ptychagnostus gibbus* Zone. Therefore, *Sidneyia* cf. *inexpectans* from the Upper Shale Member of the Mantou Formation is younger than *S. inexpectans* from the Burgess Shale.

3. Material and methods

The single specimen of *Sidneyia* cf. *inexpectans* described in this paper is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China (NIGPAS 170198). Photographs were taken under crossed-polarized light using a Nikon D810 camera fitted with a Nikon AF-S Nikkor 105 mm lens. Images were processed using Photoshop™ to adjust tone, contrast and brightness. Morphological terminology used in this paper mainly follows Bruton (1981), Stein (2013) and Zacaï *et al.* (2016). Measurements were made parallel to or normal to the sagittal line, directions of which are referred to as sagittal (sag.) / exsagittal (exs.) and transverse (tr.), respectively.

4. Description

Single nearly complete specimen flattened parallel to bedding, which consists of a long, oval-shaped exoskeleton measuring 82.5 mm long (sag.) and 51.1 mm wide (tr.). Exoskeleton smooth and complete, but for the tailspine, which is represented by a single uropod only (i.e. telson and second uropod missing) (Fig. 2a, b).

Cephalic shield broadly (tr.) semi-elliptical in outline, slightly deformed (ventrally curved?) on the left side, measuring 12.0 mm long (sag.) and 35.4 mm wide (tr.). Presence of numerous wrinkles near anterior margin indicating post-depositional compression of shield into sediment plane in forward tilted posture (Fig. 2e, g). Lateral notches (ln in Fig. 2b, g) preserved on right side of cephalic shield accounting for one-third of total length (exs.) of cephalic shield and measuring c. 4.1 mm long (sag.). Anterior margin of cephalon steeply sloping, while smooth posterior margin partially overlaps first thoracic tergite. Present beneath dorsal shield, and exposed by exfoliation of dorsal shield (Fig. 2e, g), possibly a wide frontal margin previously observed extending ventrally (Bruton, 1981; Stein, 2013), but other structures such as appendages or eyes cannot be excluded (fm? in Fig. 2b, e).

Thorax consisting of nine partially overlapping tergites (tt in Fig. 2b), with anterior margin of each tergite exposed owing to compaction of exoskeleton. Thorax 52.9 mm long (sag.), with maximum width of 49.2 mm between thoracic tergites 4 and 5 and minimum width of 31.1 mm (width of posteriormost thoracic tergite). Thoracic tergites 1–4 narrow, with average length (sag.) 7.3 mm; first and shortest thoracic tergite 6.5 mm long (sag.), last five thoracic segments averaging 8.2 mm long (sag.) (length data for thoracic tergites include portion covered by adjacent tergite). First four thoracic tergites widening and lengthening (tr.) posteriorward; thoracic tergites 5–9 gradually narrowing (tr.). Impressions of exopodites of appendages present on both sides of each thoracic tergite (pa in Fig. 2b). Posterolateral margins of thoracic tergites bearing spines (sp in Fig. 2d).

Abdomen consisting of three overlapping abdominal segments and a separate tail fan (Fig. 2a–c, f), and measuring 17.6 mm long (sag.). Abdominal segments relatively long, with segment 1 measuring 9.2 mm long (sag.), segment 2 measuring 6.6 mm long (sag.) and segment 3 measuring 12.4 mm long (sag.) (foregoing data include covered portion). Anterior margins of abdominal segments represented by two lines, which indicates shape of the abdominal segment is cylindrical. Posterior margin of third abdominal segment exhibits several pairs of spines, one of which is larger than other (sp in Fig. 2a, b, f). Single uropod preserved to the left of third abdominal segment measures 12.2 mm in length.

Impressions of appendages present on both sides of each thoracic tergite, with portion of each impression preserving exopodites (pa in Fig. 2b). Endopodite fragments present near abdomen (ap in Fig. 2b, d, e).

5. Discussion

In the new specimen from North China, the length-to-width ratio is close to 0.33, as in *S. inexpectans* from the Burgess Shale reported by Bruton (1981). In addition, the new specimen is hardly distinguishable from *S. inexpectans* from the Burgess Shale in other measurements and in the outline of the exoskeleton (Bruton, 1981). Certain details, such as the fact that the posterolateral margins of the thoracic tergites bear spines (sp in Fig. 2d), and that the last abdominal segment exhibits several pairs of spines (sp in Fig. 2b, f), are also identical to the type species (Bruton, 1981). Therefore, even though the morphologies of the tail fan and appendages are incompletely shown, the new specimen is not significantly different from the type species in the exoskeleton. Because only one specimen has been collected so far, it is appropriate to assign this specimen to *Sidneyia* as a conformis of the type species *S. inexpectans*. A more accurate taxonomic assignment needs more material from the fossil horizon.

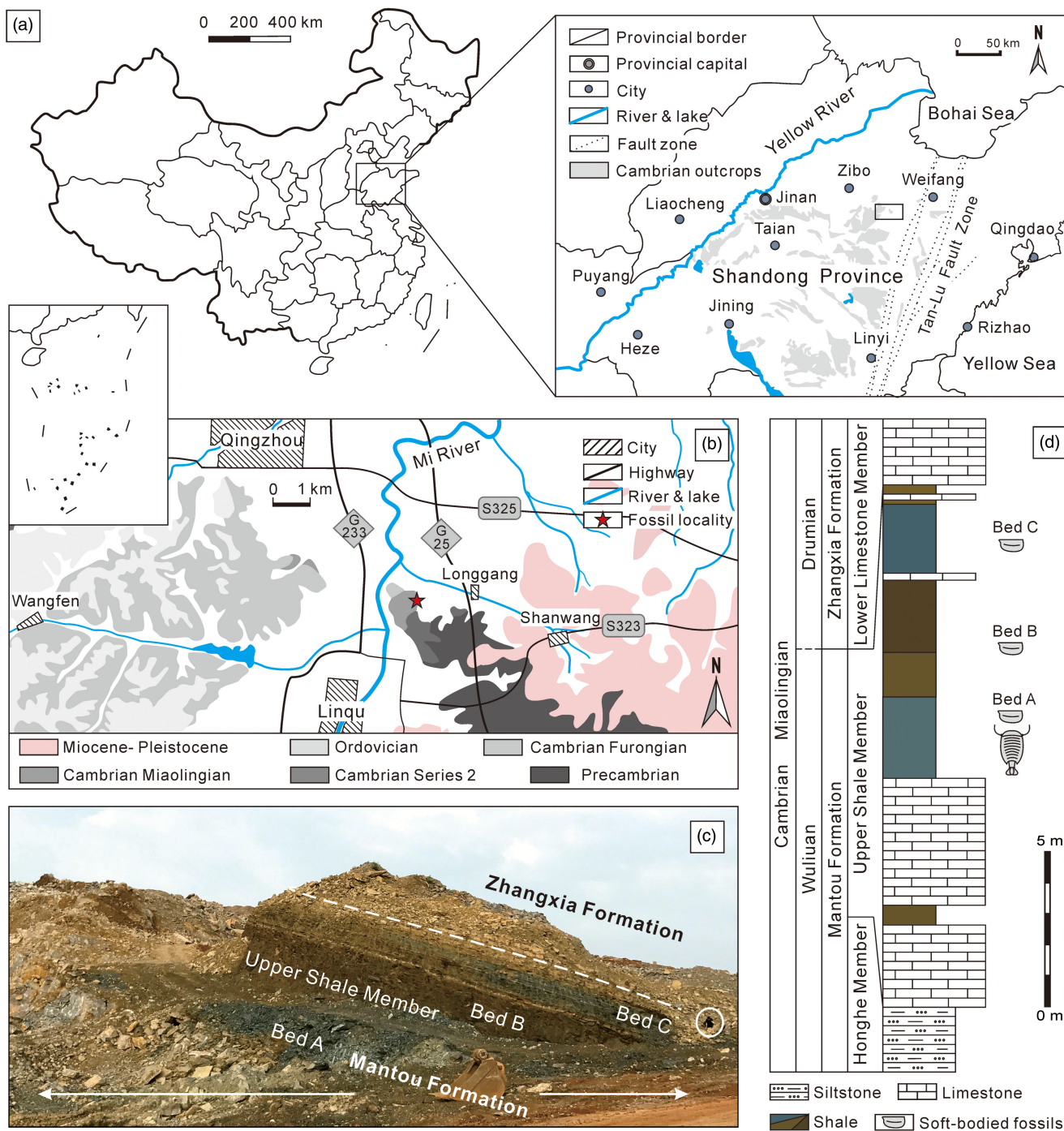


Fig. 1. Location and geological setting of the Longgang Section. (a) Regional map. (b) Simplified geological map of the area near the Longgang Section. (c) Upper Shale Member, Mantou Formation in the Longgang section, viewed from the south. Note the circled person for scale. (d) Stratigraphic column of the Upper Shale Member and fossil horizons in the Longgang Section. The alternate spelling of Zhangxia is ‘Changhia’.

Although Stein (2013) revised the length-to-width ratio of the cephalic shield of *S. inexpectans* from 0.33 to 0.5 (Stein, 2013), this reinterpretation may be problematic (R. Lerosey-Aubril, pers. com. 2019). Zacaï *et al.* (2016, fig. 2) illustrated a specimen with a short (sag.) cephalic shield preserved in lateral orientation, and this preserved orientation is incompatible with a taphonomic shrinking of the cephalic shield. Therefore, a short cephalic shield is more likely to represent the original morphology, and Bruton’s ratio data remain a more precise description of *S. inexpectans* (Bruton, 1981).

It should also be noted that different specimens of *S. inexpectans* may have different numbers of abdominal segments. Walcott (1911) and Simonetta (1963) described what is now called the ‘abdomen’ as two segments, Bruton (1981, p. 633) noted that some specimens have three abdominal segments and in recent years investigators have stated that there are two such segments in their studied sample (Zacaï *et al.* 2016). In the presence of detailed descriptions and photographs of specimens, it is hard to conclude that Bruton’s observations were incorrect. The abdomen

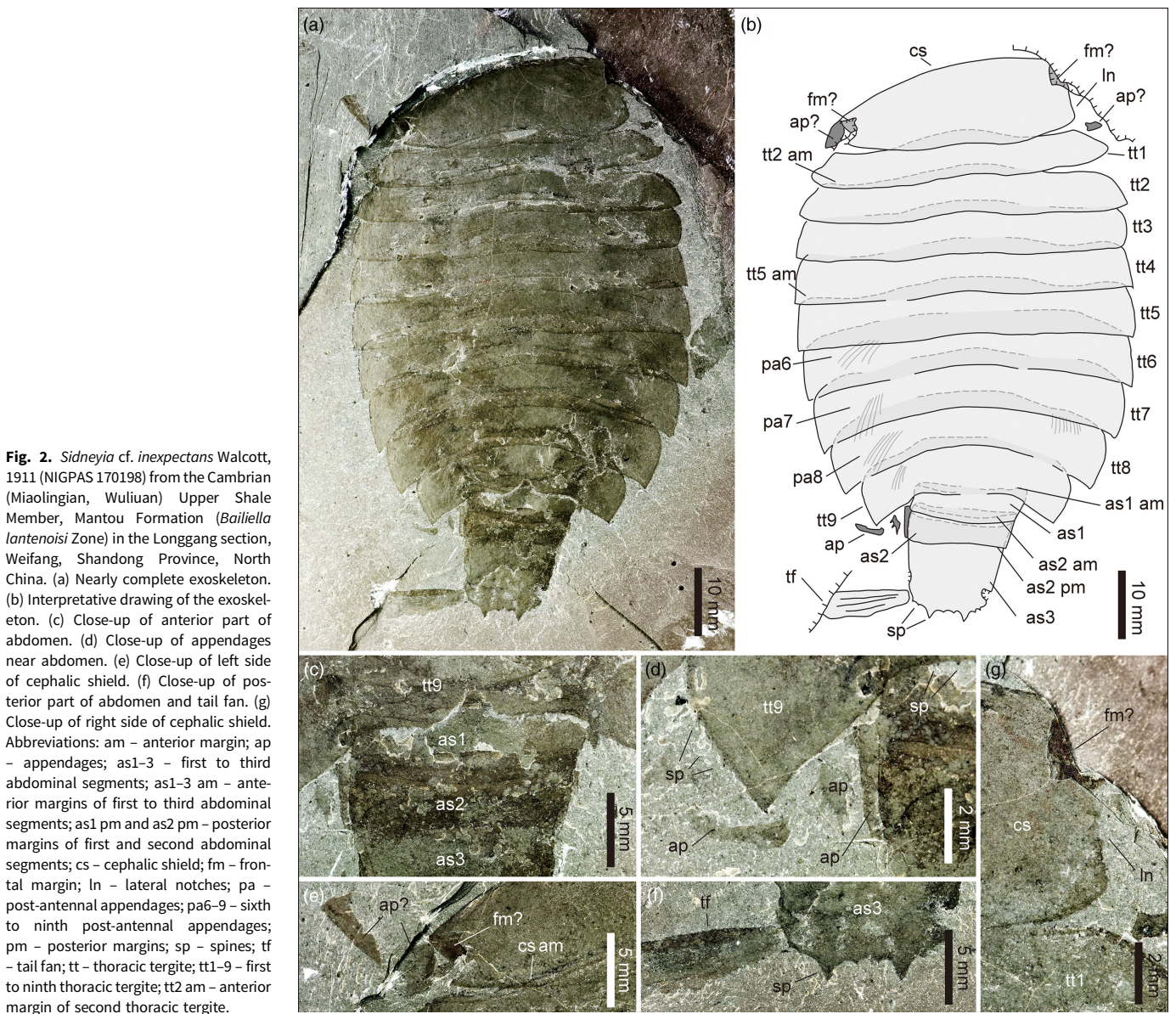


Fig. 2. *Sidneyia cf. inexpectans* Walcott, 1911 (NIGPAS 170198) from the Cambrian (Miaolingian, Wuliuan) Upper Shale Member, Mantou Formation (*Bailiella lantenoisi* Zone) in the Longgang section, Weifang, Shandong Province, North China. (a) Nearly complete exoskeleton. (b) Interpretative drawing of the exoskeleton. (c) Close-up of anterior part of abdomen. (d) Close-up of appendages near abdomen. (e) Close-up of left side of cephalic shield. (f) Close-up of posterior part of abdomen and tail fan. (g) Close-up of right side of cephalic shield. Abbreviations: am – anterior margin; ap – appendages; as1–3 – first to third abdominal segments; as1–3 am – anterior margins of first to third abdominal segments; as1 pm and as2 pm – posterior margins of first and second abdominal segments; cs – cephalic shield; fm – frontal margin; In – lateral notches; pa – post-antennal appendages; pa6–9 – sixth to ninth post-antennal appendages; pm – posterior margins; sp – spines; tf – tail fan; tt – thoracic tergite; tt1–9 – first to ninth thoracic tergite; tt2 am – anterior margin of second thoracic tergite.

of *S. inexpectans* probably consists of two or three segments. The new specimen from North China exhibits three of them (Fig. 2c).

In addition to specimens from the Burgess Shale, several questionable specimens have been identified as *Sidneyia*. Among them, *Sidneyia* sp. from the Kinzers Formation (Resser & Howell, 1938, pl. 13, fig. 3) was incorrectly assigned to *Sidneyia* (Bruton, 1981; Briggs *et al.* 2008). A couple of appendages from the Wheeler Formation in Utah have been tentatively assigned to the genus by Briggs & Robison (1984), but this interpretation was rejected by Stein (2013). Another species, *Sidneyia sinica* Zhang & Shu in Zhang *et al.* 2002, was described from the Chengjiang biota, but the assignment of this fossil was rejected by Briggs *et al.* (2008), Stein (2013) and Lerosey-Aubril (2015). Additionally, *Sidneyia* sp. from the Spence Shale (Briggs *et al.* 2008) is incomplete, and no preserved characters in this fossil allow a confident assignment to this genus. *Sidneyia?* sp. from the Sirius Passet biota (Peel, 2017) is similar to the type species in general outline of the body, but except for this, data supporting a convincing assignment

to the genus are still unavailable. In other words, *Sidneyia* was only confidently known from the Burgess Shale (Fig. 3). Accordingly, the discovery of *Sidneyia* from the Mantou Formation is both the first well-supported occurrence outside the Burgess Shale and its first occurrence of the genus outside Laurentia.

The palaeogeographical location of North China during the Cambrian Period is far from resolved, various hypotheses having been proposed: on the margin of Western Gondwana (McKenzie *et al.* 2011), in the oceanic region between Gondwana and Siberia (Torsvik & Cocks, 2017), north of Australia (Brock *et al.* 2000; Golonka, 2011), on the north or northeastern margin of East Gondwana (e.g. Burrett *et al.* 1990; Li *et al.* 2016; Yun *et al.* 2016; Pan *et al.* 2018) or thousands of kilometres to the east of Australia in the Palaeo-Pacific Ocean (e.g. Li & Powell, 2001; Li *et al.* 2013). Despite these different hypotheses, extensive palaeontological and geological data have supported that North China had strong biogeographic links with Australia, which was situated on the East Gondwana margin during early and middle Cambrian

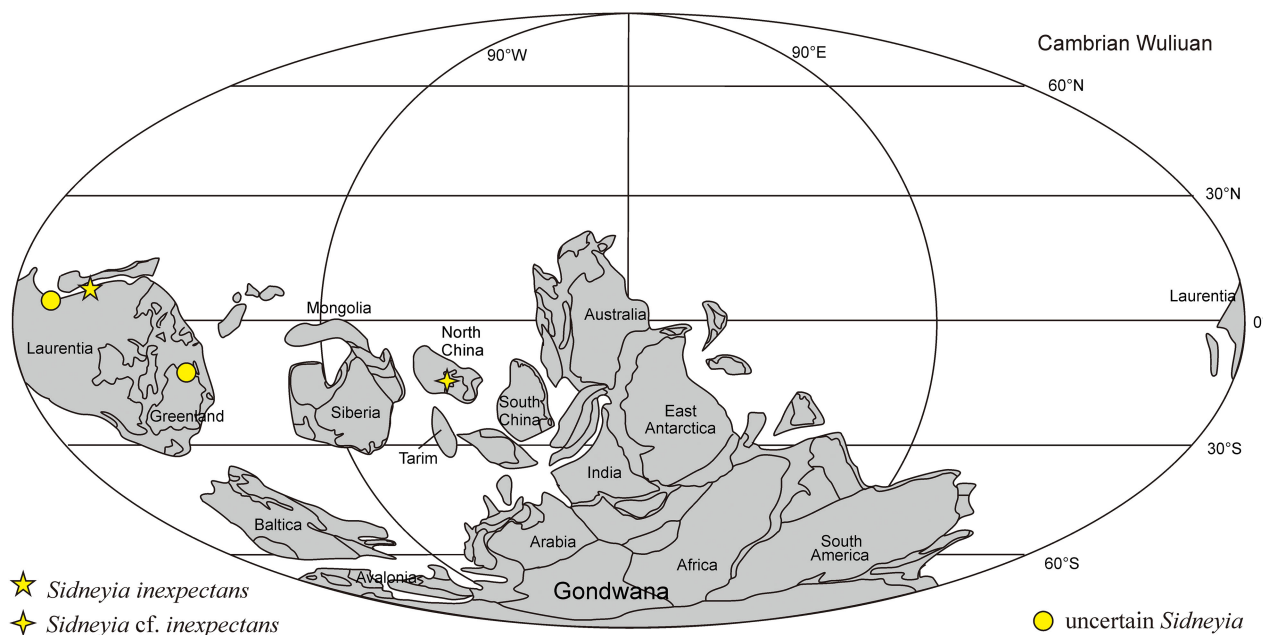


Fig. 3. (Colour online) Geographical distribution of *Sidneyia* Walcott, 1911 during the Cambrian Wuliuan period. The palaeogeographical reconstruction is based on true polar wander data (after Torsvik & Cocks, 2017).

times (e.g. Álvaro *et al.* 2013; Hally & Paterson, 2014). Given that North China is not close to North America in any of these palaeogeographical reconstructions, it can be concluded that *Sidneyia* was more widespread than previously thought.

6. Conclusions

Although only one specimen of *Sidneyia* has been collected from North China, its morphology allows a confident assignment to this genus, at least as a similar species to the type species *S. inexpectans*. The new *Sidneyia* specimen is younger than the type material from the Burgess Shale, but the temporal range of *Sidneyia* remains restricted to the Wuliuan. This is not only the first occurrence of *Sidneyia* outside Laurentia but also the first well-supported occurrence of this genus outside the Burgess Shale. The occurrence of *Sidneyia* on two distinct palaeocontinents greatly expands its known palaeogeographical distribution and provides evidence that *Sidneyia* was more widespread than previously thought. The reason why *Sidneyia* was previously believed to be a local species is that Burgess Shale-type Lagerstätten in the Cambrian Miaolingian were found mainly in Laurentia. The discovery of *Sidneyia* in North China raises the potential of discovering additional Burgess Shale-type fossils from North China.

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