Paterimitra pyramidalis Laurie, 1986, the first tommotiid discovered from
the early Cambrian of North China

Bing Pan^{a, b}, Glenn A. Brock^c, Christian B. Skovsted^d, Marissa J. Betts^e, Timothy P. Topper^f,
Guo-Xiang Li^{a, *}

^a *State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and
Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China*

^b *University of Science and Technology of China, Hefei 230026, China*

^c *Department of Biological Sciences, Macquarie University, NSW 2109, Australia*

^d *Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden.*

^e *Palaeoscience Research Centre, School of Environmental and Rural Science, University of
New England, Armidale, NSW, Australia.*

^f *Palaeoecosystems Group, Department of Earth Sciences, Durham University, Durham, UK.*

^{*} *Corresponding author.*

E-mail: bpan@nigpas.ac.cn (B. Pan), glenn.brock@mq.edu.au (G.A. Brock),
christian.skovsted@nrm.se (C.B. Skovsted), marissa.betts@une.edu.au (M.J. Betts),
timothy.topper@durham.ac.uk (T.P. Topper), gxli@nigpas.ac.cn (G.X. Li)

ABSTRACT

The eccentrothecimorph tommotiid *Paterimitra pyramidalis* Laurie, 1986, was
previously only known from lower Cambrian rocks of the Northern Territory and South
Australia. Herein, we document the first occurrence of *P. pyramidalis* from the Xinji
Formation in the Shuiyu section at Ruicheng County, Shanxi Province, located at the
southwestern margin of the North China Platform. This represents the first report of a

tommotiid taxon from lower Cambrian strata of the North China Platform. All three sclerite types that characterise the scleritome of *P. pyramidalis* have been recovered and are described, permitting definitive identification to species level. The discovery of *P. pyramidalis* from the North China Platform not only greatly extends the palaeogeographic range of this distinctive tommotiid taxon, but also supports planktotrophic development of larvae in *Paterimitra* as a stem group brachiopod. The discovery of *P. pyramidalis* supports a Cambrian, Epoch 2, late Age 3 to early Age 4 age for the shelly fossil fauna from the Xinji Formation and indicates a close palaeogeographic position between the North China Platform and Australian East Gondwana during the early Cambrian.

Key words: Tommotiida, *Paterimitra*, North China, Cambrian Epoch 2, biostratigraphy, palaeobiogeography

1. Introduction

The eccentrothecimorph tommotiids *Paterimitra pyramidalis* Laurie, 1986, *Eccentrotheca helenia* Skovsted, Brock, Topper, Paterson and Holmer, 2011 and *Kulparina rostrata* Conway Morris and Bengtson in Bengtson et al., 1990 are critical taxa for interpreting the timing of character assembly and bivalved body plan evolution in organophosphatic brachiopods (Skovsted et al., 2009, 2011, 2015; Larsson et al., 2014). Identical mineralogical composition, external ornamentation and distinctive organic polygonal ultrastructure shared between *P. pyramidalis* and early Cambrian paterinid brachiopods such as *Askepasma* Laurie, 1986 (Balthasar et al., 2009; Topper et al., 2013) and *Salanygolina* Ushatinskaya, 1987 (Holmer et al., 2009, 2011) led Larsson et al. (2014) to suggest a homologous relationship between these taxa. The bivalved brachiopod shell evolved through successive stages of sclerite reduction, specialisation and tube shortening from an

Eccentrotheca-like stem group ancestor through intermediary forms such as *Paterimitra pyramidalis* and *Micrina etheridgei* Laurie, 1986 (Holmer et al., 2008; Skovsted et al., 2008, 2009, 2011, 2015; Larsson et al., 2014).

The original description of *Paterimitra pyramidalis* by Laurie (1986) from the Todd River Dolostone, Amadeus Basin in central Australia was based on 10-12 specimens of a large pyramidal sclerite type, subsequently recognised as the S1 sclerite by Skovsted et al. (2009). Large collections comprising more than 1400 isolated sclerites from rocks of the Hawker Group in the Arrowie Basin, South Australia have revealed that this taxon bore three sclerite morphotypes, the S1, S2 and L sclerites (Skovsted et al., 2009, figs. 1, 2; Larsson et al., 2014, fig. 2). Significantly, partially articulated scleritome composites indicate that *P. pyramidalis* secreted a cone-shaped skeleton consisting of a single pair of conjoined bilaterally symmetrical S1 and S2 sclerites, and an unresolved number of laterally compressed L sclerites fused around the distal margin of the open cone formed by the S1-S2 composite. An organic, pedicle-like structure for epifaunal attachment is interpreted to have emerged through the foramen-like posterior opening formed between the S1 and S2 sclerites. The cone-like scleritome is assumed to have housed a filter-feeding lophophorate organism (see Larsson et al., 2014, fig. 21 for reconstruction). Similar fixed epifaunal scleritomes have been demonstrated for *Eccentrotheca helenia* (Skovsted et al., 2011) and *Kulparina rostrata* (Skovsted et al., 2015).

Like many tommotiids, *Paterimitra pyramidalis* had been regarded as an East Gondwanan endemic (Skovsted et al., 2011, 2015; Larson et al., 2014). Here we describe *P. pyramidalis* from the Xinji Formation in the Shanxi Province, greatly extending the palaeogeographic range of this taxon. This is the first tommotiid ever reported from the North China Platform, which has significant implications for understanding stem group brachiopod larval dispersal patterns, biostratigraphic correlation between Australia and North China, and

for testing a wide range of contradictory interpretations regarding the palaeogeographic position of the North China Platform and Cambrian East Gondwana.

2. Materials and methods

All isolated sclerites of *Paterimitra pyramidalis* from the Xinji Formation are more or less fragmentary, but micro-ornament and other diagnostic characters are generally well preserved. Many specimens are encrusted with adhering quartz grains. Whilst some grains have been carefully removed, it is not possible to remove all of them without the risk of damaging the specimens. In total, 22 specimens have been recovered including 6 fragments of S1 sclerites, 1 S2 sclerite and 15 L sclerites.

All samples were treated in 6% acetic acid. Selected specimens were placed on pin-type stubs, gold coated and photographed using the Scanning Electron Microscopy facility (LEO 1530VP) at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS), Nanjing. All illustrated specimens are housed and cataloged at storage facilities of NIGPAS.

3. Geological setting

3.1 Locality and stratigraphy

All specimens of *Paterimitra pyramidalis* are derived from the Xinji Formation, located at Ruicheng County, Shanxi Province. (Fig. 1A). The Xinji Formation represents the lowermost Cambrian strata in this region, disconformably overlying Precambrian strata. The Xinji Formation consists of siliciclastic rocks intercalated with carbonates, and mainly crops out on the southwestern to southern margin of the North China Platform (Liu et al., 1991, 1994). The thickness of the Xinji Formation decreases from south to north, along the southern margin of the North China Platform (Liu, 1986; Liu et al., 1991; Yan et al., 1993). In the

Shuiyu section, the Xinji Formation disconformably overlies Precambrian strata; either the Luoquan Formation, or the Longjiayuan Formation (Palaeoproterozoic or Mesoproterozoic, gray dolostones) (Fig. 1B). A karst surface is developed between the Luoquan Formation and the Longjiayuan Formation. The Xinji Formation at the Shuiyu section is about 39.8 m thick, and can be subdivided into two parts: The lower part, which is dominated by grey-black phosphatic conglomerates, purple-red shale and phosphatic sandstone, and the upper part, which consists of red quartz sandstone intercalated with argillaceous dolostone (Bureau of Geology and Mineral Resources of Shanxi Province, 1989). The basal 10.7 m of the section was sampled for shelly fossils since the upper part of the section is covered by alluvium and vegetation. There are abundant trace fossils in the lowermost rocks, and the trace fossil assemblage belongs to a typical *Cruziana* ichnofacies (Miao and Zhu, 2014), indicating a subtidal environment for the basal Xinji Formation at the Shuiyu section. The brachiopod *Kutorgina sinensis* Rong in Lu 1979 had been reported from the lower part of this section (Lu, 1979, pl. V, figs. 9-11). *Paterimitra* was collected from a strongly weathered bed of calcitic phosphatic quartz siltstone, located 3.4-3.8 m above the base of the Xinji Formation (Fig. 1B).

3.2. Biostratigraphy

The Xinji Formation and the coeval Houjiashan Formation along the southern margin of North China Platform have both yielded a trilobite fauna with low diversity, consisting of *Estaingia* (*Bergeroniellus*) *lonanensis* Hsiang in Lu et al., 1965 (Luonan County and Huoqiu County), *Estaingia* (*Hsuaspis*) *houchiuensis* Chang in Hsiang, 1963 (in Luonan County and Huoqiu County), and *Redlichia* cf. *R. nanjiangensis* Zhang and Lin in Lee, 1978 (in Queshan County) (Zhang and Zhu, 1979; Zhang et al., 1979; Miao, 2014). Based on the trilobite assemblage, the Xinji Formation was correlated with the *Drepanuloides* Biozone of the middle Tsanglangpuan stage (Cambrian Stage 4) on the Yangtze Platform (Zhang et al., 1979;

Zhang and Zhu, 1979; He et al., 1984; He and Pei, 1985; Miao, 2014). The *Estaingia* trilobite assemblage from the Xinji Formation and the Houjiashan Formation of North China was also correlated with the *Pararaia janeae* trilobite Zone (Stage 4) assemblage of South Australia by Miao (2014).

In South Australia, *Redlichia* occurs in Stage 3 (*Pararaia bunyeroensis* Zone in Paterson and Brock, 2007; *Dailyatia odyseï* Zone of Betts et al., 2016) rather than only in Stage 4 as in South China. In addition, *Estaingia* is known from late Stage 3 to early Stage 4 in South China (Zhang et al., 1957; Dai and Zhang, 2012; Zhang et al., 2016), rather than being restricted to Stage 4 as in South Australia. The opposing distributions of *Estaingia* and *Redlichia* in South China and South Australia suggests more detailed sampling is required to accurately determine the stratigraphic ranges of these trilobite taxa in both terranes. As the base of Stage 4 has not been formally defined, it remains possible that both *Redlichia* and *Estaingia* could co-occur in Cambrian late Stage 3 which would mean the trilobite assemblage from the Xinji Formation could also be late Stage 3.

In the Arrowie Basin of South Australia, *Paterimitra pyramidalis* has a long stratigraphic range, occurring in the *Kulparina rostrata* Zone, *Micrina etheridgei* Zone, and lower-mid *Dailyatia odyseï* Zone (Laurie, 1986; Bengtson et al., 1990; Skovsted et al., 2009; Larsson et al., 2014; Betts et al., 2016, 2017). In the Xinji Formation, a suite of abundant and diverse small shelly fossils have previously been described, including cancelloriid sclerites, sponge spicules, hyoliths, *Pojetaia runnegari* Jell, 1980, *Mackinnonia rostrata* Zhou and Xiao, 1984, *Stenotheca drepanoida* He and Pei in He et al., 1984, *Pelagiella madianensis* Zhou and Xiao, 1984, *Cupithea holocyclata* Bengtson in Bengtson et al., 1990, *C. costellata* Xiao and Zhou, 1984, *Yochelcionella chinensis* Pei, 1985, *Cambroclavus absonus* Conway Morris in Bengtson et al., 1990, *Apistoconcha* cf. *apheles* Conway Morris in Bengtson et al., 1990, and *Microdictyon* sp. (He et al., 1984; He and Pei, 1985; Pei, 1985; Feng et al., 1994; Li et al.,

2014; Pan et al., 2015, 2017, 2018; Li et al., 2016, 2017; Skovsted et al., 2016; Yun et al., 2016). Most of these fossils have been reported from the *Dalmanella odyseae* Zone (Cambrian Stage 3–4) in South Australia (Bengtson et al., 1990; Gravestock et al., 2001; Topper et al., 2009; Betts et al., 2016, 2017). This, in conjunction with trilobite occurrences, indicates that the Xinji Formation equates to a Cambrian Epoch 2, late Age 3 to early Age 4, which is also suggested by the hyolith assemblage (Pan et al., 2017). However, more detailed biostratigraphic work, and formal international definition of the Cambrian Stage 3-4 boundary is required before confident international correlation can be attempted.

4. Description and Comparison

Skovsted et al. (2009) and Larsson et al. (2014) provided comprehensive illustration of partially articulated skeletal composites of *Paterimitra pyramidalis* which demonstrated a coniform scleritome comprised of three morphologically distinct organophosphatic sclerite types. Each scleritome consists of a pair of bilaterally symmetrical sclerites, the S1 sclerite and the smaller S2 sclerite, plus an unresolved number of compressed, arched and twisted L sclerites (see Larsson et al., 2014, figs. 2, 21). *Paterimitra* sclerites are distinguished by the characteristic reticulate external micro-ornament which consists of regular polygonal compartments up to 5 µm in maximum diameter. The inner surface of each sclerite is covered by a network of hemispherical pustules or polygonal depressions. The isolated specimens from the Xinji Formation in the Shuiyu section are rare (total of 22 sclerites), but all 3 sclerite types are present from the same stratigraphic level (Fig. 1B). The S1, S2 and L sclerites are often fragmentary, but are well preserved and the overall shape, dimensions, growth of concentric lamellae and external reticulation of the micro-ornament, are essentially identical to the Australian material (Fig. 2). A few specimens even preserve the tiny spherical grains within some cellular compartments of the reticulate external ornament (compare Fig. 2P

herein with Larsson et al., 2014, fig. 3C). All sclerite types of *P. pyramidalis* from Australia are highly variable in morphology (Larsson et al., 2014) and the preserved specimens from North China all fall within this range of variability.

4.1. S1 sclerites

The S1 sclerites from the Xinji Formation are all fragmentary, but together preserve nearly all diagnostic features (Fig. 2A-F). The specimens display the typical subpyramidal shape with a rounded apex and height range from 500 to 850 μm , which falls within the 200 to 1700 μm height range of the Australian material (Larsson et al., 2014, p. 422). The most complete specimen (Fig. 2A) preserves the lateral plates and major part of the anterior sinus that characterises this sclerite. NIGPAS167943 is a fragmentary S1 sclerite that preserves part of the anterior and complete lateral plate (Fig. 2C). One fragment partially preserves the subapical flange (Fig. 2E, F). Unusually, the longitudinal margin forming the junction between the posterior margin and the lateral plate forms a distinctive sequential series of folded “pleats” that is unlike any other S1 sclerite from Australia (arrows in Fig. 2A). The polygonal external micro-ornament is well preserved in all specimens (Fig. 2B) and compares very closely to the micro-ornament of Australian specimens (Larsson et al., 2014, fig. 3B-C).

4.2. S2 sclerite

A single S2 sclerite has been recovered from the Xinji Formation thus far. This specimen (Fig. 2G-I) is well preserved, with a length of 530 μm and a width of 510 μm . It has the typical acutely triangular and slightly saddle-shaped outline, and bilateral symmetry very similar to the material from Australia (cf. Larsson et al., 2014, fig. 5A-I). This sclerite has 5 concentric laminae (compared to 7-8 laminae in larger Australian specimens) and so is likely to represent a subadult sclerite (Fig. 2G-I). This would also explain the incipient development

of the posterior “upturned flange” in Xinji specimen. The subrectangular protegulum is located in the central area of the shell (Fig. 2I).

4.3. L sclerites

The L sclerites from the Xinji Formation display the typical high, laterally compressed form (Fig. 2J-P), with moderate twisting in apical view (Fig. 2K, L) almost identical to the sclerites from South Australia (Larsson et al., 2014, figs 6A-J). Sclerites range in length from 612-668 μm which falls well within the range of 400-1600 μm in the Australian specimens. All sclerites have a single elongate apex (Fig. 2K) and moderately to strongly curved basal margin forming a distinct arcuate shape (Fig. 2L). One specimen preserves tiny spherical grains (compare Larsson et al., 2014, fig. 18F) on the outer surface (Fig. 2P).

5. DISCUSSION

The larval shells have been documented in both the well preserved S1 and S2 sclerites of *Paterimitra pyramidalis* from Australia (Holmer et al., 2011; Larsson et al., 2014). The larval shell of the S1 sclerites is defined by a 300-500 μm wide, major growth disturbance with the same outline as the adult sclerite (Holmer et al., 2011, fig. 2A, C, J; Larsson et al., 2014, fig. 8A, C, D). The anterior side of the larval shell has an open semicircular indentation which is covered by the anterior plate, and a smooth dome through later ontogeny. The posterior side is adjacent to the saddle-shaped protegulum (which is about 100 μm in width and length) eventually forming the subapical flange (Holmer et al., 2011, fig. 2A, C–E, H, J; Larsson et al., 2014, fig. 8A, C–F). According to the definition of Holmer et al. (2011), the larval shell in S2 sclerites is acutely triangular (150-200 μm), with a similar shape to the adult sclerites, and an up-turned flange. The poorly defined crescent-shaped protegulum is located at the posterior side of the larval shell and has a shallow posterior indentation (Holmer et al., 2011,

fig. 2B, F–G, K–L). However, based on the investigation of ~~the~~ many more S2 sclerites, Larsson et al. (2014) considered that the protegulum defined by Holmer et al. (2011) probably represents shell deformation of a subsequent growth increment along the posterior margin of S2 sclerites. Larsson et al. (2014) suggested that the protegulum is a rounded or rectangular plate smaller than the larval shell and situated near the center of the larval shell. The S2 sclerite from North China also supports this interpretation.

The larval shell of the *Paterimitra* S1 sclerite is closely comparable to the transversely elongate ventral larval shell of the organophosphatic stem group rhynchonelliform taxon *Salanygolina* Ushatinskaya, 1987. The protegulum and incipient subapical flange in *Paterimitra* also compare with the posterior projection of the pseudodeltidium of the ventral larval shell in *Salanygolina* (Holmer et al., 2011; Larsson et al., 2014). Thus, *Paterimitra* likely belongs within the stem of the rhynchonelliforms (Holmer et al., 2011). This led Holmer et al. (2011) to propose that *Paterimitra* larvae were bivalved and possibly planktotrophic, which would have facilitated dispersal between juxtaposed palaeocontinents. The discovery of *P. pyramidalis* in North China and the well-preserved larval shell in the sclerites also supports this hypothesis.

Sclerites of *Paterimitra* are common constituents in shelly fossil assemblages recovered from lower Cambrian rocks in the Arrowie and Stansbury basins of South Australia. These units represent various carbonate-dominated facies including restricted lagoonal systems and inshore open carbonate shelf environments, with high abundance of biohermal build-ups (Skovsted et al., 2009; Larsson et al., 2014). *Paterimitra* was an important member of these carbonate ecosystems, with adult life habit interpreted as a sessile filter feeder that attached to hard substrates via a soft pedicle-like structure (Skovsted et al., 2009; Larsson et al., 2014). The wide distribution and high abundance of *Paterimitra* sclerites in a range of lower Cambrian carbonate depositional facies from south and central Australia (Laurie, 1986;

Bengtson et al., 1990; Gravestock et al., 2001; Skovsted et al., 2009; Larsson et al., 2014; Betts et al., 2016, 2017) (Fig. 3) reinforces their dispersal ability along epeiric platforms. Furthermore, the discovery of *Paterimitra* from North China may also suggest *Paterimitra* could cross oceanic barriers. The exclusive occurrence of *Paterimitra* at the southern margin of North China and the eastern margin of Australia may also suggest close palaeogeographic proximity of these regions in the early Cambrian.

The exact palaeogeographic position of the North China Platform has long been controversial. It has been variously placed along the margin of Western Gondwana bordering today's north-eastern India based on detrital zircon age distributions and polymerid trilobite biogeography (McKenzie et al., 2011), or as an independent continent in either close juxtaposition to the north of Australia (Brock et al. 2000; Golonka, 2011) or located thousands of kilometres to the east of Australia in the Palaeo-Pacific Ocean based on palaeomagnetic interpretation (Li and Powell, 2001; Li et al., 2013; but see Torsvik and Cocks 2013a, b; 2017 for completely different interpretations of APWP data for North China). According to Zircon U-Pb and Hf isotopic data, Han et al. (2016) suggested that the North China craton likely collided with the northern Australia margin of East Gondwana at ca. 500 Ma. North China could also have been located close to the north or north-eastern margin of Australian East Gondwana based on the palaeogeographic distribution and comparison of early Cambrian fossil assemblages (Burrett et al., 1990; Brock et al., 2000; Wrona, 2003, 2004; Li et al., 2016; Yun et al., 2016). The occurrence of *Paterimitra pyramidalis* along with a suite of other co-occurring shelly fossil taxa (Betts et al., 2016, 2017), hyoliths (Skovsted et al. 2016; Pan et al., 2017), helcionelloid and bivalved molluscs (Zhou and Xiao, 1984; He and Pei, 1985; Pei, 1985; Feng et al., 1994), *Apistoconcha* (Li et al., 2014), cambroclavids (Li et al., 2016) and *Microdictyon* (Pan et al., 2018) along the southern margin of the North China Platform reinforces the close palaeobiogeographic links

between the southern margin of the North China platform and the north-eastern margin of Australian East Gondwana (Fig. 3). The alternative interpretation, that North China was close to South China and India along the northern margin of West Gondwana is difficult to resolve based on the simple fact that these shelly fossil taxa listed above have never been found in either region. This faunal distribution pattern strongly suggests geographic proximity between Australia and North China Platform during the early Cambrian. A relatively narrow oceanic barrier would best account for the high levels of endemism, species-level similarity and larvae dispersal patterns of these Cambrian shelly fossil taxa. The next step will be to undertake a broad scale quantitative palaeobiogeographic analysis of available data to test the validity of these interpretations. .

6. CONCLUSIONS

Paterimitra pyramidalis Laurie, 1986 is reported from the early Cambrian Xinji Formation from the southern margin of the North China Platform, the first occurrence of the taxon outside of Australia. All three sclerite types (S1, S2 and L) are described and illustrated, and are clearly conspecific to *P. pyramidalis* from Australia. *Paterimitra* has a stratigraphic range which intersects the *Kulparina rostrata* Zone (latest Stage 2) to the lower-mid *Dalmanella odyseae* Zone (Stage 3–4) in Australia (Betts et al., 2016, 2017). The co-occurrence of *P. pyramidalis* (along with a range of other shelly fossil species) in South Australia and the Xinji Formation in North China indicates a late Stage 3 rather than definite Stage 4 age for these faunas, though additional trilobite data from both regions would determine the age more securely. The new discovery also supports the hypothesis that *P. pyramidalis* potentially produced planktotrophic larvae, also suggested by larval and adult shell morphology, which is similar to that of the brachiopod *Salanygolina*. Occurrence of *P. pyramidalis* in both terranes supports the view that during the early Cambrian, the southern margin of North China

Platform was closely juxtaposed to the north-eastern margin of Australian (East Gondwana), being separated only by a narrow ocean.

Acknowledgements

This work was supported by grants from the National Natural Science Foundation of China (41372021), the Chinese Academy of Sciences (XDB10010101, XDB18000000 and XDB18030304) and Swedish Research Council (VR2016-04610). We thank Maoyan Zhu, Lanyun Miao and Zhaonian Wu (Nanjing) for their field guidance and assistance. GAB gratefully acknowledges funding from the Chinese Academy of Science President's International Fellowship Initiative (PIFI) to fund his two months stay at the Nanjing Institute of Geology and Palaeontology when this manuscript was written.

The authors wish to thank Lars E. Holmer (Uppsala) and two anonymous reviewers for constructive comments and suggestions for the enhancement of the manuscript.

References

- Balthasar, U., Skovsted, C.B., Holmer, L.E., Brock, G.A., 2009. Homologous skeletal secretion in tommotiids and brachiopods. *Geology* 37 (12), 1143–1146.
- Bengtson, S., Conway Morris, S., Cooper, B.J., Jell, P.A., Runnegar, B.N., 1990. Early Cambrian fossils from South Australia. *Memoirs of the Association of Australasia Palaeontologists* 9, 1–364.
- Betts, M.J., Paterson, J.R., Jago, J.B., Jacquet, S.M., Skovsted, C.B., Topper, T.P., Brock, G.A., 2016. A new lower Cambrian shelly fossil biostratigraphy for South Australia. *Gondwana Research* 36, 163–195.

324 Betts, M.J., Paterson, J.R., Jago, J.B., Jacquet, S.M., Skovsted, C.B., Topper, T.P., Brock,
 325 G.A., 2017. Global correlation of the early Cambrian of South Australia: Shelly fauna of
 326 the *Dalmanella odyseae* Zone. *Gondwana Research* 46, 240–279.

327 Brock, G., Engelbrechtsen, M., Jago, J., Kruse, P., Laurie, J., Shergold, J., Shi, G., Sorauf, J.,
 328 2000. Palaeobiogeographic affinities of Australian Cambrian faunas. *Memoir of the*
 329 *Association of Australasian Palaeontologists* 23, 1–61.

330 Bureau of Geology and Mineral Resources of Shanxi Province, 1989. Regional Geology of
 331 Shanxi Province. Beijing, Geological Publishing House, 116–120. (In Chinese).

332 Burrett, C., Long, J., Stait, B., 1990. Early-Middle Palaeozoic biogeography of Asian terranes
 333 derived from Gondwana. *Geological Society, London, Memoirs* 12, 163–174.

334 Dai, T., Zhang, X.L., 2012. Ontogeny of the trilobite *Eostaingia sinensis* (chang) from the
 335 lower Cambrian of south china. *Bulletin of Geosciences* 87(1), 151–158.

336 Feng, W.M., Qian, Y., Rong, Z.Q., 1994. Study of monoplacophora and gastropoda from
 337 lower Cambrian Xinji Formation in Yexian, Henan. *Acta Micropalaeontologica Sinica*
 338 11 (1), 1–19. (In Chinese with English abstract)

339 Golonka, J., 2011. Phanerozoic palaeoenvironment and palaeolithofacies maps of the Arctic
 340 region. *Geological Society, London, Memoirs* 35, 79–129.

341 Gravestock, D.I., Alexander, E.M., Demidenko, Y.E., Esakova, N.B., Holmer, L.E., Jago,
 342 J.B., Lin, T.-R., Melnikova, N., Parkhaev, P.Y., Rozanov, A.Y., Ushatinskaya, G.T.,
 343 Zang, W.L., Zhegallo, E.A., Zhuravlev, A.Y., 2001. The Cambrian biostratigraphy of the
 344 Stansbury Basin, South Australia. *Transactions of the Palaeontological Institute of the*
 345 *Russian Academy of Sciences* 282, pp. 1–341.

346 Han, Y.G., Zhao, G.C., Cawood, P.A., Sun, M., Eizenhöfer, P.R., Hou, W.Z., Zhang, X.R.,
 347 Liu, Q., 2016. Tarim and North China cratons linked to northern Gondwana through
 348 switching accretionary tectonics and collisional orogenesis. *Geology* 44, 95–98.

349 He, T.G., Pei, F., 1985. The discovery of bivalves from the lower Cambrian Xinji Formation
350 in Fangcheng county, Henan province. *Journal of Chengdu College of Geology* 1, 61–68.
351 (In Chinese with English abstract)

352 He, T.G., Pei, F., Fu, G.H., 1984. Small shelly fossils from the lower Cambrian Xinji
353 Formation in Fangcheng County, Henan Province. *Acta Palaeontologica Sinica* 23 (3),
354 350–357. (In Chinese with English abstract)

355 Hsiang, L., 1963. Trilobita, *In* Academy of Geological Sciences, Ministry of Geology ed.,
356 Fossil Atlas of Qinling Mountains. Beijing, China Industry Press, 27.

357 Holmer, L.E., Stolk, S.P., Skovsted, C.B., Balthasar, U., Popov, L.E. 2009. The enigmatic
358 Early Cambrian *Salanygolina*—a stem group of rhynchonelliform chileate brachiopods?
359 *Palaeontology* 52, 1–10.

360 Holmer, L.E., Skovsted, C.B., Brock, G.A., Valentine, J.L., Paterson, J.R., 2008. The early
361 Cambrian tommotiid *Micrina*, a sessile bivalved stem group brachiopod. *Biology Letters*
362 4 (6), 724–728.

363 Holmer, L.E., Skovsted, C.B., Larsson, C., Brock, G.A., Zhang, Z., 2011. First record of a
364 bivalved larval shell in Early Cambrian tommotiids and its phylogenetic significance.
365 *Palaeontology* 54, 235–239.

366 Jell, P.A., 1980. Earliest known bivalve on Earth—A new Early Cambrian genus from South
367 Australia. *Alcheringa* 4, 233–239.

368 Larsson, C.M., Skovsted, C.B., Brock, G.A., Balthasar, U., Topper, T.P., Holmer, L.E., 2014.
369 *Paterimitra pyramidalis* from South Australia: scleritome, shell structure and evolution
370 of a lower Cambrian stem group brachiopod. *Palaeontology* 57, 417–446.

371 Laurie, J.R., 1986. Phosphatic fauna of the Early Cambrian Todd River Dolomite, Amadeus
372 Basin, Central Australia. *Alcheringa* 10, 431–454.

- 373 Lee, S., 1978. Trilobite, *In* Southwest Institute of Geological Sciences, ed., Palaeontological
374 Atlas of Southwest China, Sichuan Volume, Part 1, from Sinian to Devonian. Beijing,
375 Geological Publishing House, 180. (In Chinese)
- 376 Li, G.X, Zhang, Z.F., Hua, H., Yang, H.N., 2014. Occurrence of the enigmatic bivalved fossil
377 *Apistoconcha* in the lower Cambrian of southeast Shaanxi, North China Platform.
378 Journal of Paleontology 88 (2), 1–8.
- 379 Li, L.Y., Zhang, X.L., Yun, H., Li, G.X, 2016. New occurrence of *Cambroclavus absonus*
380 from the lowermost Cambrian of North China and its stratigraphical importance.
381 Alcheringa 40 (1), 45–52.
- 382 Li, L.Y., Zhang, X.L., Yun, H., Li, G.X., 2017. Complex hierarchical microstructures of
383 Cambrian mollusk *Pelagiella*: insight into early biomineralization and evolution.
384 Scientific reports 7, 1935.
- 385 Li, Z.X., Powell, C.McA., 2001. An outline of the palaeogeographic evolution of the
386 Australasian region since the beginning of the Neoproterozoic. Earth-Science Reviews
387 53, 237–277.
- 388 Li, Z.X., Evans, D.A., Halverson, G.P., 2013. Neoproterozoic glaciations in a revised global
389 palaeogeography from the breakup of Rodinia to the assembly of Gondwanaland.
390 Sedimentary Geology 294, 219–232.
- 391 Liu, Y.H, 1986. The lower Cambrian Xinji Formation in Hennan Province. Henan Geology 4
392 (4), 28–35. (In Chinese)
- 393 Liu, Q., Ma, L., Zhu, Y., Jin, R., Dai, W., Chen, Y., Fan, X., Zhang, T., Zhang, Z., 1994.
394 Lithofacies palaeogeography and gypsum deposits of the lower Cambrian of North
395 China platform. Beijing, Geologic Publishing House, 1–144. (In Chinese)
- 396 Liu, Y.H., Wang J.P., Zhang, H.Q., Du, F.J., 1991. The Cambrian and Ordovician Systems of
397 Henan Province. Beijing, Geological Publishing House, 1–225. (In Chinese)

398 Lu, Y.H., Zhang, W.T., Zhu, Z.L., Qian, Y., Xiang, L.W., 1965. The trilobites of China.
399 Beijing, Science Press, 85.

400 Lu, Y.H., 1979. Sedimentary Mineral of the Cambrian from China and Biology-Environment
401 Cybernetics. Beijing: Geology Publishing House, 1–76 (In Chinese).

402 McKenzie, N.R., Hughes, N.C., Myrow, P.M., Choi, D.K., Park, T.-y., 2011. Trilobites and
403 zircons link north China with the eastern Himalaya during the Cambrian. *Geology* 39,
404 591–594.

405 Miao, L.Y., 2014. Biostratigraphy of the basal Cambrian Xinji Formation and the Houjiashan
406 Formation from the Southern North China Platform: University of Chinese Academy of
407 Sciences, 127. (Master thesis in Chinese with English summary)

408 Miao, L.Y., Zhu, M.Y., 2014. Trace fossils from the basal Cambrian Xinji Formation in
409 Southern North China Platform and its chronological significance: *Acta Palaeontologica*
410 *Sinica* 53(3), 274–289. (In Chinese)

411 Pan, B., Miao, L.Y., Yang, H.N., Li, G.X., 2015. Enigmatic tubular fossil *Cupithec*a from the
412 lower Cambrian Xinji Formation of Luonan, Shaanxi Province. *Acta*
413 *Micropalaeontologica Sinica* 32, 384–395. (In Chinese with English abstract)

414 Pan, B., Skovsted, C.B., Sun H.J., Li G.X., 2017. Hyoliths from the lower Cambrian along the
415 southern margin of the North China Platform and their biostratigraphic and
416 palaeogeographic significances, *in* Yang Q., Reitner J., Wang Y.D., Reich M. ed.,
417 Critical intervals in Earth history: Palaeobiological innovations, Abstract volume of the
418 2nd Joint Conference Palaeontological Society of China and the Paläontologische
419 Gesellschaft, 249–250.

420 Pan, B., Topper, T.P., Skovsted, C.B., Miao L.Y., Li G.X., 2018. Occurrence of *Microdictyon*
421 from the lower Cambrian Xinji Formation along the southern margin of the North China
422 Platform. *Journal of Paleontology* 92(1), 59–70.

423 Paterson, J.R., Brock, G.A., 2007. Early Cambrian trilobites from Angorichina, Flinders
 424 Ranges, South Australia, with a new assemblage from the *Pararaia bunyeroensis* Zone.
 425 Journal of Paleontology 81, 116–142.

426 Pei, F., 1985. First discovery of *Yochelcionella* from the lower Cambrian in China and its
 427 significance. Acta Micropalaeontologica Sinica 2 (4), 395–400. (In Chinese with English
 428 abstract)

429 Skovsted, C.B., Brock, G.A., Paterson, J.R., Holmer, L.E., Budd, G.E., 2008. The scleritome
 430 of *Eccentrotheca* from the Lower Cambrian of South Australia: Lophophorate affinities
 431 and implications for tommotiid phylogeny. Geology 36(2), 171–174.

432 Skovsted, C.B., Holmer, L.C., Larsson, C.M., Högström, A.E.S., Brock, G.A., Topper, T.P.,
 433 Balthasar, U., Stolk, S.P., Paterson, J.R., 2009. The scleritome of *Paterimitra*: an Early
 434 Cambrian stem group brachiopod from South Australia. Proceedings of the Royal
 435 Society B 276, 1651–1656.

436 Skovsted, C.B., Brock, G.A., Topper, T.P., Paterson, J.R., Holmer, L.E., 2011. Scleritome
 437 construction, biofacies, biostratigraphy and systematics of the tommotiid *Eccentrotheca*
 438 *helenia* sp. nov. from the Early Cambrian of South Australia. Palaeontology 54, 253–
 439 286.

440 Skovsted, C.B., Brock, G.A., Holmer, L.E., Topper, T.P., Larsson, C.M., 2015. Revision of
 441 early Cambrian tommotiid *Kulparina rostrata* from South Australia. Journal of
 442 Paleontology 89, 920–932.

443 Skovsted, C.B., Pan, B., Topper, T.P., Betts, M.J., Li, G.X., Brock, G.A. 2016. The operculum
 444 and mode of life of the lower Cambrian hyolith *Cupitheca* from South Australia and
 445 North China. Palaeogeography, Palaeoclimatology, Palaeoecology 443, 123–130.

446 Topper, T.P., Brock, G.A., Skovsted, C.B., Paterson, J.R., 2009. Shelly fossils from the lower
 447 Cambrian *Pararaia bunyeroensis* Zone, Flinders Ranges, South Australia. *Memoirs of*
 448 *the Association of Australasian Palaeontologists* 37, 199–246.

449 Topper, T.P., Holmer, L.E., Skovsted, C.B., Brock, G.A., Balthasar, U., Larsson, C.M., Stolk,
 450 S.P., Harper, D.A.T., 2013. The oldest brachiopods from the lower Cambrian of South
 451 Australia. *Acta Palaeontologica Polonica* 58, 93–109.

452 Torsvik, T.H., Cocks, L.R.M., 2013a. Gondwana from top to base in space and time.
 453 *Gondwana Research* 24, 999–1030.

454 Torsvik, T. H., Cocks, L. R. M., 2013b. New global palaeogeographical reconstructions for
 455 the Early Palaeozoic and their generation. *Geological Society, London, Memoirs* 38 (1),
 456 5–24.

457 Torsvik, T.H., Cocks, L.R.M., 2017. *Earth history and palaeogeography*. Cambridge
 458 University Press, 1–317.

459 Ushatinskaya, G.T. 1987. Unusual inarticulate brachiopods from the Lower Cambrian of
 460 Mongolia. *Paleontologicheskij Zhurnal* 2, 62–68. (In Russian)

461 Wrona, R., 2003. Early Cambrian molluscs from glacial erratics of King George Island, West
 462 Antarctica. *Polish Polar Research* 24, 181–216.

463 Wrona, R., 2004. Cambrian microfossils from glacial erratics of King George Island,
 464 Antarctica. *Acta Palaeontologica Polonica* 49, 13–56.

465 Xiao, L.G., Zhou, B.H., 1984. Early Cambrian hyolitha from Huainan and Huoqiu county in
 466 Anhui province. *Professional Papers of Stratigraphy and Palaeontology, Chinese*
 467 *Academy of Geological Sciences* 13, 141–151. (In Chinese with English abstract)

468 Yan, G.S, Zhang, E.H., Wang, D.Y., 1993. Evolution of North China-Type Cambrian
 469 sedimentary environments and trace fossils assemblage in Henan Province. *Sedimentary*
 470 *Facies and Palaeogeography* 13(3), 18–32. (In Chinese)

- 471 Yang, B., Steiner, M., Keupp, H., 2015. Early Cambrian palaeobiogeography of the Zhenba–
472 Fangxian Block (South China): Independent terrane or part of the Yangtze Platform?.
473 Gondwana Research 28(4), 1543–1565.
- 474 Yun, H., Zhang, X.L., Li, L.Y., Zhang, M.Q., Liu, W., 2016. Skeletal fossils and microfacies
475 analysis of the lowermost Cambrian in southwestern margin of North China Platform.
476 Journal of Asian Earth Sciences 129, 54–66.
- 477 Zhang, Z.F., Zhang, Z.L., Li, G.X., Holmer, L.E., 2016. The Cambrian brachiopod fauna from
478 the first-trilobite age Shuijingtuo Formation in the Three Gorges area of China.
479 Palaeoworld 25(3), 333–355.
- 480 Zhang, W.T., Zhu, Z.L., 1979. Notes on some trilobites from lower Cambrian Houjiashan
481 Formation in southern and southwestern parts of North China. Acta Palaeontologica
482 Sinica 18(6), 513–29. (In Chinese)
- 483 Zhang, W.T., Li, J.J., Qian, Y.Y., Zhu, Z.L., Chen, C.Z., Zhang, S.X. 1957. Cambrian and
484 Ordovician strata of East Gorges, Hubei. Bulletin of Sciences 5, 145–146.
- 485 Zhang, W.T., Zhu, Z.L., Yuan, K.X., Lin, H.L., Qian, Y., Wu, H.J., Yuan, J.L., 1979. The
486 boundary of the Cambrian-upper Precambrian in the southern and southwestern parts of
487 North China: Acta Stratigraphica Sinica 3(1), 51–56. (In Chinese)
- 488 Zhou, B.H, Xiao, L.G., 1984. Early Cambrian monoplacophorans and gastropods from
489 Huainan and Huoqiu Counties (Anhui Province). Professional Papers of Stratigraphy
490 and Palaeontology, Chinese Academy of Geological Sciences 13, 125–140. (In Chinese
491 with English abstract)

492

Figure captions

Fig. 1 Locality map and lithostratigraphic column of Shuiyu section. Abbreviations: LQ F., Luoquan Formation; LJY F., Longjiayuan Formation.

Fig. 2 *Paterimitra pyramidalis* Laurie, 1986 from the early Cambrian Xinji Formation, Shuiyu section, Ruicheng County, Shanxi Province. A-D, S1 sclerite. A, anterior-lateral view of the S1 sclerite fragment, NIGPAS167942. B, enlargement of A to show the polygonal ornament on the outer surface of S1 sclerite. C, anterior-lateral view of the S1 sclerite fragment, NIGPAS167943. D, lateral view of the S1 sclerite fragment, NIGPAS167944. E-F, possible subapical flange of S1 sclerite, NIGPAS167945. E, apical view. F, posterior view. G-I, S2 sclerite, NIGPAS1679426. G, lateral view. H, apical view. I, enlargement of central area of H to show the larval shell and protegulum of S2 sclerite. J-P, L sclerite. J-K, NIGPAS167947. J, lateral view. K, apical view. L-N, NIGPAS167948. L, basal view. M, enlargement of L to show the polygonal ornament. N, lateral view. O-P, NIGPAS167949. O, lateral-basal view. P, enlargement of O to show the tiny spherical grains ornament.

Fig. 3 The palaeogeographic map of early Cambrian to show the possible position of North China Platform and the approximate palaeogeographic distribution of *Paterimitra pyramidalis* Laurie, 1986 from North China and Australia (palaeogeographic map modified from Torsvik and Cocks, 2013b; Yang et al., 2015).

Fig. 1 Locality map and lithostratigraphic column of Shuiyu section. Abbreviations: LQ F., Luoquan Formation; LJY F., Longjiayuan Formation.

Fig. 2 *Paterimitra pyramidalis* Laurie, 1986 from the early Cambrian Xinji Formation, Shuiyu section, Ruicheng County, Shanxi Province.

Fig. 3 The palaeogeographic map of early Cambrian to show the possible position of North China Platform and the approximate palaeogeographic distribution of *Paterimitra pyramidalis* Laurie, 1986 from North China and Australia (palaeogeographic map modified from Torsvik and Cocks, 2013b; Yang et al., 2015).