Fossilized gut of the trilobite *Lioparia bassleri* and the distribution of exceptional preservation in the Cambrian Stage 4–Drumian Manto Formation of North China

Pingli Wang, Oldřich Fatka, Zhixin Sun, Petr Budil & Jian Gao

The preservation of digestive structures of trilobites is not unique but recognition and reporting about these remains are rare. Here we describe a specimen of *Lioparia bassleri* Resser & Endo, 1937, recently collected from the Weifang Biota in the Manto Formation (Cambrian, Miaolingian, Shandong, North China). This exceptionally preserved specimen displays the remains of the digestive system in the cephalon as well as in thoracic and pygidial parts of the body. The morphology of the remains of soft parts preserved in the specimen agrees with a simple digestive tract which included a simple gut tube in the thorax and pygidium associated with four pairs of cephalic gut diverticulae in the glabella. The morphology of the digestive tract of *L. bassleri* compares favourably with earlier observations on trilobites that had gut diverticulae. The preservation of the digestive system in the studied trilobite confirms that the depositional environment of the Manto Formation was favourable to soft-tissue preservation. Earlier papers on trilobites with preserved soft parts from China are summarized. Exceptional preservation of sponges, palaeoscolecids, radiodonts, bivalved arthropods, trilobites, and echinoderms in the Manto Formation is briefly discussed. • Key words: trilobites, digestive system, Weifang Biota, soft-tissue preservation, Manto Formation, mid-Cambrian, China.

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Trilobites form an important part of the Palaeozoic fossil record, but knowledge about their non-mineralized parts, including the digestive system, is still very scanty. Babcock (2003), Lerosey-Aubril *et al.* (2011) and Robison & Babcock (2011) reviewed all earlier data on the gut of trilobites. Some 25 species having guts preserved were newly reported in Robison & Babcock (2011). English & Babcock (2007) provided information on digestive tracts preserved in Ordovician trilobite material that was overlooked in previous years. Even with the addition of the paper of Lerosey-Aubril *et al.* (2011), not all species were reviewed, but in total, those papers account for, directly or by way of reference, about 50 species. Additional information on Cambrian species from Utah that have preserved guts was recently published also by Robison *et al.* (2015). However, the information on exceptionally preserved trilobites has increased in the last years due to intensive study of several Ordovician and particularly Cambrian Lagerstätten (*e.g.* Robison & Babcock 2011; Lerosey-Aubril *et al.* 2011, 2012a, b, 2017; Eriksson & Terfelt 2012; Fatka *et al.* 2013a, b, 2015; Zhu *et al.* 2014; Gutiérrez-Marco *et al.* 2017; Hopkins *et al.* 2017). Remains of the digestive system in Cambrian trilobites have been known from almost ten Konservat-Lagerstätten of four major areas – Laurentia, Baltica, West Gondwana and East Gondwana.

The aim of the present paper is to describe and illustrate an exceptionally preserved specimen of the trilobite *Lioparia bassleri* recently collected from the Manto Formation, North China (Sun & Yuan, 2015). This spe-

Figure 1. Distribution of Cambrian rocks within the North China Plate and geographic position of the western suburb of Weifang – the discovery site of *Lioparia bassleri* with digestive structures discussed in text.

cimen was mentioned in a preliminary abstract by Wang *et al.* (2014).

Trilobites with soft parts from China have been documented in more than ten contributions. Gut structures in *Eoredlichia intermedia* were studied by Shu *et al.* (1995) and Hou *et al.* (2009) from the Chengjiang Lagerstätte; these data were partially reinterpreted by Lerosey-Aubril *et al.* (2011). From this Konservat-Lagerstätte, a specimen of *Kuanyangia* (*Sapushania*) *bella* with incomplete anterior part of the alimentary structures was figured by Chen *et al.* (1996), Chen & Zhou (1997) and Chen (2004); Zhang *et al.* (2003, text-fig. 7d) figured a juvenile naraoid similar to *Primicaris larvaformis*. Yuan *et al.* (2002) and Lin (2007) described gut structures in *Olenoides paraptus* from the Kaili Lagerstätte of Guizhou. From the same Lagerstätte, Zhao *et al*. (2005, pl. 3, fig. 4) figured a specimen of *Oryctocephalus indicus* with distinct remains of a gut canal preserved in the thorax and pygidium. Structures described by Lin (2007) were reinterpreted by Lerosey-Aubril *et al.* (2011). Specimens of *Redlichia mai*, *Redlichia noetlingi* and *Palaeolenus lantenoisi* with preserved remains of the gut from the Guangshan Lagerstätte were figured by Hu *et al.* (2013). More recently, Hopkins *et al.* (2017) studied the digestive system in several exceptionally preserved specimens of *Palaeolenus lantenoisi* and *Redlichia mansuyi*, all from the Guanshan Biota of Yunnan; a comprehensive list of Cambrian, Ordovician and Devonian trilobite taxa with part of digestive system was compiled in this contribution.

All these previously described examples are from South China (also see summary of early–middle Cambrian fossil Konservat-Lagerstätten in Zhang *et al.* 2008). In contrast, in North China, soft-bodied fossils have been sparsely reported, mostly from the Cambrian Manto Formation (Fig. 1), which has yielded the new specimen described herein.

Geological setting and associated fossils

The Manto Formation. – (Mantou Formation of some authors). The Manto Formation (Cambrian Series 2–Miaolingian) was named by Blackwelder (1907) from the stratotype section at Mantoushan, Zhangxia Town, Changqing County, Shandong Province (Fig. 1). Later the unit was subdivided into the Manto, Maochuang (= Maozhuang) and Hsuchuang (= Xuzhuang) formations (Lu & Dong 1952) and this modified concept was accepted for decades. More recently, Zhang (1996) and Xiang *et al.* (1999) restored the original concept of Blackwelder (1907) to simplify this definition, which we follow in this contribution.

The Manto Formation is widely distributed, being identified in 11 provinces of North China (Xiang *et al.* 1999). This lithostratigraphic unit is characterized by purple, brownish-red or yellowish-green shales, with intercalated beds of limestone, dolostone or sandstone. It has been interpreted to represent a warm, arid tidal-flat and lagoonal facies (Xiang *et al.* 1999). The Manto Formation is transgressive, and its lower and upper boundaries are conspicuously diachronous.

In most places, for example in the interior and northeast areas of the North China Plate, the Manto Formation overlies the Changping Formation. The Zhushadong Formation underlies the Manto Formation at the southwestern plate margin. In some areas, the Manto Formation overlies the Huoshan Formation (near the southwest plate margin) or the Houjiashan Formation (south plate margin), or rests on the Precambrian (interior and northwestern plate areas). Lower levels of the Manto Formation are dominated by variegated shale or pelitic dolostone which contrasts with the limestone or dolostone that comprises underlying strata. The boundary between the Manto Formation and the overlying Changhia Formation can also be easily recognized by the siliciclastic rock below the boundary and the limestone above (Xiang *et al.* 1999).

Weifang Biota. – In the upper part of the Manto Formation, soft-bodied fossils were discovered by one of the authors (Zhixin Sun) in a western suburb of Weifang, Shandong, in 2009. A well-exposed, about 6-metres-thick sequence of calcareous purple-reddish shale, dark brown shale and yellowish-green shale intercalated with grey medium- to thick-bedded limestone is accessible at this outcrop. This assemblage of exceptionally preserved fossils was recently named the Weifang Biota by Sun & Yuan (2015).

The Weifang Biota actually comprises two distinct assemblages. The lower assemblage belongs to the *Bailiella–Lioparia* Biozone and correlates with the upper part of Cambrian Stage 5 (the Wuliuan), according to Yuan *et al.* (2012). The upper assemblage, composed of most of the exceptionally preserved fossils yet found, occurs

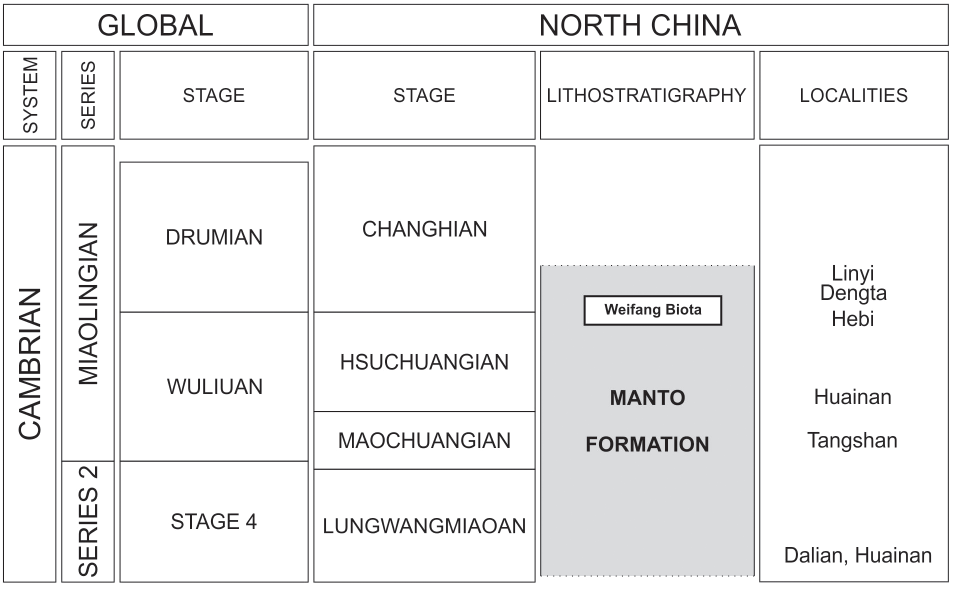

Figure 2. Stratigraphy of the Cambrian in North China with the stratigraphic position of the localities discussed in the text and the position of the Weifang Biota (stratigraphy modified from Peng 2009). As the Manto Formation is diachronous and there are still uncertainties about correlation between regional stages and global stages, the range of the Manto Formation, especially the upper boundary is tentative.

immediately above the *Bailiella–Lioparia* Biozone. *Proasaphiscus yabei* and *Lioparia bassleri* found in this upper assemblage are known to occur together with *Ptychagnostus sinicus* in the North China Plate (Wang *et al.* 1954, Lu 1957, Guo *et al.* 1996, Yuan *et al.* 2012). *Ptychagnostus sinicus* was considered by Sun (1989) and Peng (2009) to be synonymous with the index agnostid species *Ptychagnostus intermedius*, which occurs in the *Triplagnostus* (or *Ptychagnostus*) *gibbus* to *Acidusus* (or *Ptychagnostus*) *atavus* biozones (Robison 1982, 1984). Accordingly, the upper assemblage of the Weifang Biota is most probably of early Drumian age (Fig. 2).

Preliminary analysis of the material collected so far documents a mixture in the Weifang Biota of biomineralized and non-biomineralized animals along with algae. Abundant articulated trilobites of the species *Bailiella* sp., ?*Eosoptychoparia hoboi* (= *Elrathia hoboi*), *Honanaspis honanensis*, *Lioparia bassleri*, *Proasaphiscus yabei* and *Psilaspis changchengensis* are associated with the large bivalved arthropod *Tuzoia manchuriensis* (see Sun *et al.* 2015). The associated fauna includes a three-dimensionally preserved hyolith conch with operculum and helens, another hyolith conch with possible remains of gut structures, as well as brachiopods and problematic fossils. Internal and external moulds of one trilobite specimen are preserved with possible digestive structures.

Results

Description

Partially damaged internal and external moulds of a complete articulated exoskeleton of *Lioparia bassleri* are preserved in yellowish-green shale. The original calcareous cuticle of the exoskeleton was lost during diagenesis; both internal and external moulds are composed of the rock matrix (clay minerals) with iron oxides. The specimen is about 32 mm long (sag.), 21 mm in width (tr) and oriented parallel to the bedding. The exoskeleton has eleven thoracic segments, suggesting a holaspid growth stage. All parts of the dorsal exoskeleton are intact, the hypostome is not visible, the rostral plate is exposed in front of the glabella (RP in Fig. 3B), and the cephalic shield is slightly warped and cracked.

The internal mould of the cephalon has both left and right librigenae only partly preserved. The anterior and lateral cephalic parts are broken off in the external mould. Except for four anterior thoracic segments, all other thoracic pleurae are broken off distally on the left side of the internal mould. On the external mould, the axis is very slightly damaged by an oblique fracture, and the left side of the axial and proximal parts of the third to eleventh segments are peeled off.

The left postero-lateral part of the pygidium is missing on the internal mould (Fig. 3A). The external mould of the pygidium is undamaged but part of the doublure is embedded in the matrix. A tiny *Gordia*-type ichnofossil is preserved near the right postero-lateral margin of the pygidium (Fig. 3B).

The specimen exhibits brown to black markings under the axial lobe of the cephalon, thorax and pygidium (Fig. 3), which are interpreted as remains of the gut. A large polylobate dark marking occurs under the slightly vaulted glabella (GL in Fig. 3B) and the adaxial part of the right fixigena (Fig. 3A, C). A longitudinal dark marking of variable width is visible on the external and internal moulds along the axis of all thoracic segments

(G in Fig. 3B, E). On the internal mould, the darker area reaches nearly fifty percent of the axial width in the five anteriormost thoracic segments, as well as in the anterior part of the pygidium. A slightly narrower marking is seen in the more completely preserved external mould of the pygidium; this marking gently narrows posteriorly. It is not apparent whether this marking reaches the posterior tip of the pygidial axis (Fig. 3F). There are no distinctive sedimentary particles visible within the dark marking.

Interpretation

We interpret the above described dark marking preserved under the axis of this specimen as remains of a relatively simple digestive tract. Four pairs of distinct lobes developed in the cephalon are regarded as evidence of four pairs of cephalic diverticulae (Dc1 to Dc4 in Fig. 3B). The anteriormost four or five thoracic segments might also preserve diverticulae, but the outline of the dark marking is not clear there. Posteriorly, the gut might be restricted to a simple tube devoid of diverticulae (G in Fig. 3B, E).

The slightly asymmetrical position of the assumed digestive tract presumably resulted from a post-mortem deformation of soft parts with respect to the dorsal exoskeleton. During this deformation, the alimentary canal and the other attached organs would have been shifted from their sagittal position.

Ichnofossils associated with exceptionally preserved fossils have been reported from several Cambrian Konservat-Lagerstätten (Babcock & Peel 2007, Wang *et al.* 2009, Lin *et al.* 2010, Mángano 2011, Mikuláš *et al.* 2012). The occurrence of a *Gordia*-type ichnofossil in the studied specimen of *L. bassleri* indicates an oxygenated sea bottom (see Lin *et al.* 2010, p. 253).

Discussion – Exceptional preservation in the Manto Formation

The Manto Formation has recently yielded bivalved arthropods, palaeoscolecids, articulated echinoderms and sponges, anomalocaridids and trilobites with soft parts, which attests to the presence of exceptional preservation in the Cambrian of North China. So far, most studies have been undertaken by Diying Huang (Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences) and his team, who have emphasized a great potential for more exceptionally preserved specimens to be discovered in the Manto Formation.

Bivalved arthropods. – Resser (1929) reported the occurrence of a non-mineralized arthropod *Tuzoia* at Dengta (Figs 1, 2), Liaoning Province, northern margin of the North China Plate. It is associated with the trilobites *Proasaphiscus yabei*, *Lioparia bassleri* and *Lioparia walcotti*, a lingulid brachiopod *Lingulella tangshihensis*, and a hyolithid *Hyolithes carinferus*. More recently, Sun *et al*. (2015) described *Tuzoia manchuriensis* from the same locality as the specimen of *Lioparia bassleri* with digestive structures described herein.

Wang *et al.* (2010) described a new species of *Isoxys*, *I. shandongensis*, from the upper part of the Manto Formation at Linyi, Shandong Province (Figs 1, 2). This locality also yielded abundant articulated trilobites (mainly *Maotunia*), sponges, chancelloriids, hyoliths, brachiopods and non-trilobite arthropods. In North China, *Maotunia* is considered to occur in the Changhian Regional Stage (Yuan *et al.* 2012), and the fauna at Linyi is considered to be of Drumian Age (Fig. 2).

Palaeoscolecids. – Lin (1995) established a new species of these stem-priapulid worms, *Palaeoscolex huainanensis*, collected from a purple shale in the lower part of the Manto Formation, Huainan, Anhui Province, southern margin of the North China Plate (Figs 1, 2). This species coexisted with *Redlichia* (*Pteroredlichia*) *chinensis*, *Redlichia triangularis* and *Leptoredlichia tumidolimbata*. Hence, the rock unit can be correlated to Cambrian Stage 4 (Peng 2009).

Echinoderms. – Huang (2012) discussed more than two hundred specimens of an unnamed eocrinoid from the amaranthine calcareous mudstone at Dalian, Liaoning Province (Figs 1, 2). They are associated with abundant trilobite fragments of *Redlichia murakamii* and with brachiopods. Eocrinoids have been widely reported from the Yangtze Platform in Yunnan and Guizhou provinces, but are usually rare in North China. The eocrinoid-bearing level belongs to the *Redlichia* (*Pteroredlichia*) *chinensis* Zone (Huang 2012), and therefore can be assigned to Cambrian Stage 4 (Peng 2009).

Anomalocaridids. – Huang *et al.* (2012) reported the discovery of an anomalocaridid frontal appendage from the purple-reddish shale of the Manto Formation at Tangshan, Hebei Province (Figs 1, 2). According to Huang *et al.* (2012), co-occurring trilobites, hyoliths and brachiopods indicate the *Luaspides huoshanensis* Zone corresponding to the Wuliuan Stage of the Miaolingian Series. Anomalocaridids are quite common in Cambrian faunas in South China, such as the Chengjiang, Niutitang, Guanshan and Kaili faunas, but are rare in North China.

Sponges. – Liu *et al.* (2012) described the articulated sponges *Diagoniella pera* and a possible *Protospongia* from the top of the Manto Formation, near Hebi, Henan

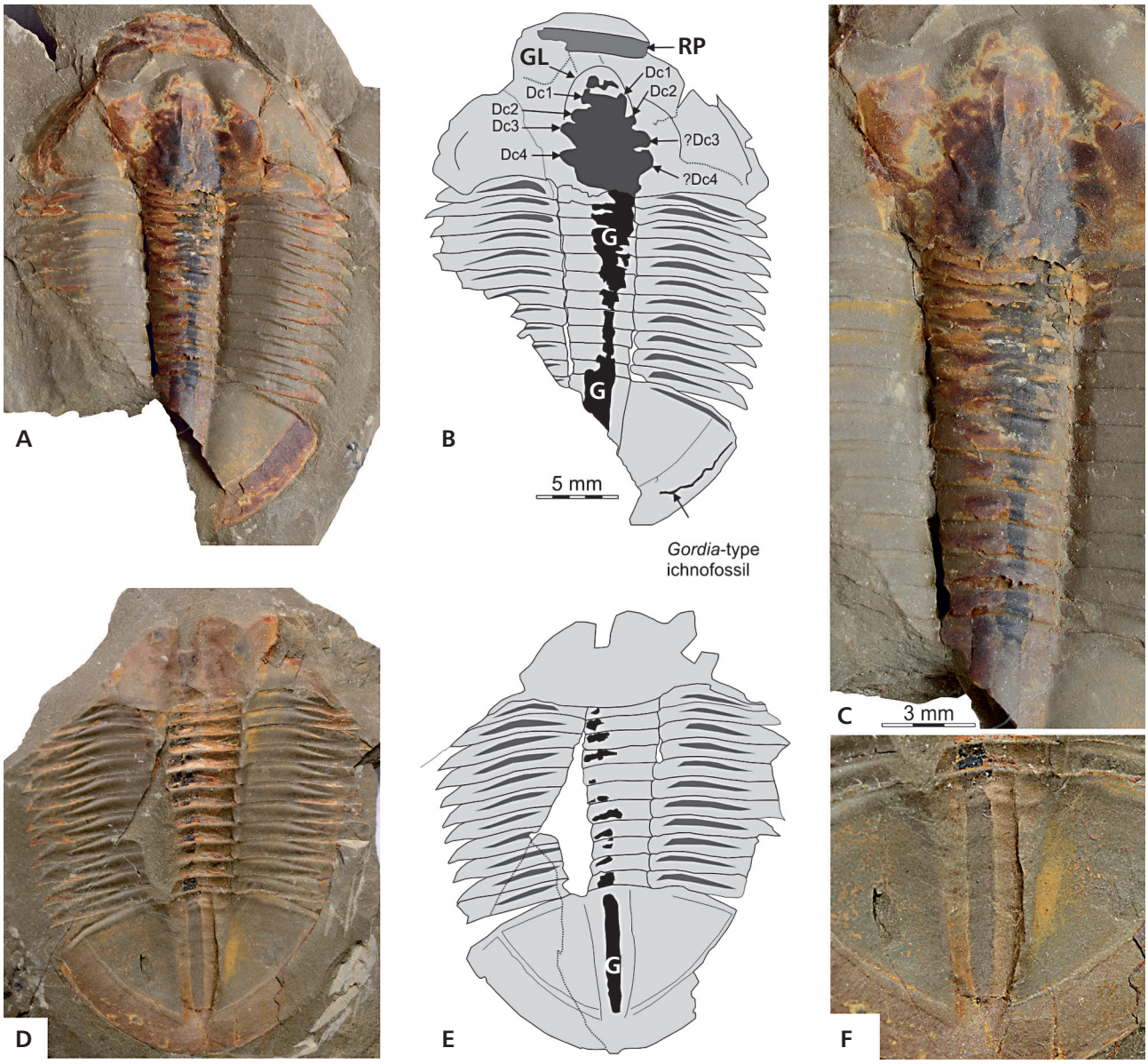

Figure 3. *Lioparia bassleri* Resser & Endo, 1937 with remains of the digestive system, middle Cambrian Manto Formation (Cambrian, Drumian Stage, Weifang Biota, Shandong, North China). Housed at the Shandong University of Science and Technology, under the number WF-WDS-0001a, b. • A – internal mould with assumed remains of digestive system; B – interpretative sketch; C – axial part of internal mould; D – external mould with remains of digestive system; E – interpretative sketch; F – axial part of external mould. Abbreviations: Dc – pairs of cephalic gut diverticulae; G – gut; GL – glabella; RP – rostral plate.

Province (Figs 1, 2). This was the first report of articulated sponges in North China. This locality also yields *Bailiella*, *Lioparia*, *Tuzoia*, hyoliths, chancelloriids and brachiopods. The *Bailiella–Lioparia* Zone is considered to be time-equivalent to the Wuliuan Stage of the Miaolingian Series (Peng 2009).

Trilobites with soft-parts. – An enrolled trilobite specimen with a partly preserved gut was tentatively assigned to *Jiumenia anhuiensis* by Zhu *et al.* (2014). It is associated with *Huaiaspis huainanensis* and *Zhongtiaoshanaspis huainanensis*. The exceptionally preserved specimen was collected in red shales with interbedded siltstones in the upper part of the Manto Formation (Miaolingian Series, Wuliuan Stage, Huainan, Anhui Province; Figs 1, 2). However, it comes from a different outcrop than the above mentioned palaeoscolecid. The three-dimensional preservation of the gut in this specimen was attributed to rapid burial, resulting in the physical protection of these delicate remains.

Conclusions

(1) The dark markings in the axial parts of the cephalon, thorax and pygidium observed in the exceptionally preserved specimen of *Lioparia bassleri* are interpreted as remains of a simple digestive tract composed of four pairs of cephalic gut diverticulae associated with a supposedly simple gut tube in the thorax and pygidium. Such morphology of the digestive tract agrees with the observation of Lerosey-Aubril *et al.* (2011, p. 180), who suggested that differentiation of a crop in trilobites was probably the result of secondary evolution.

(2) The occurrence of a *Gordia*-type ichnofossil in the studied specimen of *L. bassleri* indicates an oxygenated sea bottom at the time of burial.

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