

Palaeoscolecids from the Balang Fauna of the Qiandongian (Cambrian Series 2), Guizhou, China

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Abstract – *Wronascolex* is a taxon of palaeoscolecids. It is commonly represented by isolated button-like microfossils or compressed individuals, which are found worldwide in strata ranging from the Cambrian Series 2 to Series 3. The earliest representative of *Wronascolex* is known from the Sink Formation of the lower Cambrian of the Siberian Platform. Other species occur in Burgess Shale-type biotas of Cambrian age from Australia, Spain and North America. New palaeoscolecid material from the Balang Fauna of the Cambrian Series 2 of eastern Guizhou represents a new species of *Wronascolex*, *W. geyiensis* sp. nov., and extends the geographic and stratigraphic distribution of *Wronascolex*, as well as providing additional evidence for understanding its morphology based upon correlation of body configuration and cuticular ornaments.

Keywords: *Wronascolex geyiensis* sp. nov., Balang Fauna, Cambrian, Guizhou, South China.

1. Introduction

Palaeoscolecids are macroscopic, soft-bodied fossils that are relatively common in the Cambrian shales. They are defined by an elongate, annulated, cylindrical body with a cuticle consisting of numerous, tiny, individual button-shaped plates and platelets and often compose an important component of Burgess Shale-type biotas (Robison, 1969; Conway Morris, 1977; Glaessner, 1979; Hou & Bergström, 1994; Zhao *et al.* 1994; Ivantsov & Wrona, 2004; Hu *et al.* 2008, 2012). Specimens are also known from phosphate deposits, where isolated button-shaped microfossils or three-dimensional trunk fragments occur (Müller, 1973; Gedik, 1977; Müller & Hinz-Schallreuter, 1993; Harvey, Dong & Donoghue, 2010; Topper *et al.* 2010; Butterfield & Harvey, 2012). This group's recognized range extends from the lower Cambrian to the Lower Silurian (Ulrich, 1878; Whittard, 1953; Glaessner, 1979; Mikulic, Briggs & Klussendorf, 1985; Conway Morris & Robison, 1986; Conway Morris, 1977; Kraft & Mergl, 1989; Hinz *et al.* 1990; Müller & Hinz-Schallreuter, 1993; Zhang & Pratt, 1996; Ivantsov & Wrona, 2004). The phylogenetic placement of the palaeoscolecids has been a longstanding problem. Palaeoscolecids have been variously assigned to the Oligochaeta within the Annelida (Whittard, 1953; Robison, 1969; Conway Morris, 1977; Glaessner, 1979) or said to have an affinity with nematomorphs (Hou & Bergström, 1994; Ivantsov & Wrona, 2004), as well as closer affinities with nematodes and priapulids (Kraft & Mergl, 1989; Müller & Hinz-Schallreuter, 1993). Although there are many controversies surrounding

their taxonomy, most authors agree that palaeoscolecids fall within Cycloneuralia, which are most likely stem-group priapulids (Zhang & Pratt, 1996; Conway Morris, 1997; Wills, 1998; Huang, Vannier & Chen, 2004; Huang, Chen & Vannier, 2006; Harvey, Dong & Donoghue, 2010). Recently, this group has attracted more attention, with new finds contributing new taxonomic data and expanding the known geographic range of the group (Duan, Dong & Donoghue, 2012; Hu *et al.* 2012; Butterfield & Harvey, 2012; García-Bellido, Paterson & Edgecombe, 2013; Wang *et al.* 2014). The Balang Fauna, a Burgess Shale-type biota from the lower Cambrian of China (Peng *et al.* 2005), also yields representatives of this group (Peng *et al.* 2010; Peng, Zhao & Sun, 2012). These fossils are primarily known from the very fossiliferous Geyi Section of the Balang Formation in Geyi Town, Taijiang County, where the section contains the best examples of the Balang Fauna (Peng, Zhao & Sun, 2012). These fossils display a cylindrical body with clear annulations densely separated by intersegment furrows and possessing a cuticle consisting of numerous, tiny, individual button-shaped plates on each annulation. Based on SEM (scanning electron microscope) micrographs of the button-shaped plates on the surface cuticle of the annulations (Figs 3, 4), the characters of the plates are similar to those of *Wronascolex*. These specimens represent a new species of *Wronascolex*, *W. geyiensis* sp. nov. Newly discovered articulated specimens expand the geographic and stratigraphic distribution of *Wronascolex* and provide additional evidence for understanding the genus's body configuration, ecology and taphonomy.

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2. Geological setting and stratigraphy

The Balang Formation is primarily limited to a Cambrian outcrop belt in eastern Guizhou Province and western Hunan Province (Zhou *et al.* 1979; Yin, 1987, 1996; see Fig. 1). The lower part of the Balang Formation is composed of grey-greenish to yellow-greenish clayey shale, while the upper part is composed of light grey calcareous shale and silty shale with intercalations of thin-bedded argillaceous carbonates. In general, the Balang Formation represents a shallowing-upwards sequence. The formation ranges widely in thickness from 100 m to more than 658 m (Yin, 1987). Typically, the Balang Formation is more than 600 m thick in central eastern Guizhou and more than 300 m thick in northern Guizhou. In eastern Guizhou the overlying Tsingshutung Formation is dominated by green-greyish thin-bedded limestone, while in Nangao, Danzhai area, the lithofacies of the overlying Wuxun Formation is dominated by green-greyish and silty calcareous shale. The underlying Bianmachong Formation is mainly composed of grey-black mudstone, but it changes to yellow-greyish shale southwards (Yin, 1987). The previous biostratigraphic framework was described as a single genus-level assemblage zone (Zhou & Yuang, 1980; Yin, 1987), considered first to represent up to four species-level zones (Yuan, Zhao & Li, 2001; Yuan, Zhao & Yang, 2006), but subsequent work recognized only one species-level assemblage zone (Peng, 2009; Peng *et al.* 2010; Peng, Zhao & Sun, 2012). Most recently, a single species-level zone, that is the *Arthrocephalus chauveaui* Zone, has been proposed (Yan *et al.* 2014). *A. chauveaui* Bergeron, 1889 and *Changaspis elongata* Lee in Chien, 1961 are known from the lower Cambrian Henson Gletscher Formation of Greenland; the latter was described as *Lancastria plana* by Blaker & Peel (1997, pp. 118–22, figs 69/2, 3, 70, 71/4, 5). In addition, *A. (Arthrocephalites) jishouensis* Zhou in Zhou *et al.* 1977, which is common in the Balang Formation, was assigned to *Hailiplaktos jishouensis* by Blaker & Peel (1997, figs 64/5–7). However, according to correlation using three genera of corynexochid trilobites, the Balang Formation and part of the Henson Gletscher Formation are equivalent in age. The Balang Formation is early Cambrian to late Tsanglangpuan in age, equivalent to the Qiangdongian early Duyunian of the Cambrian stratigraphic system in slope facies (Peng & Babcock, 2001). According to the criteria for correlation in South China, the Balang Formation is equivalent to the Wulongqing Formation of Yunnan Province in age (Luo *et al.* 2008; Peng *et al.* 2010; Peng, Zhao & Sun, 2012). The Balang Formation contains abundant *R. (Pteroredlichia) chinensis* Walcott, 1905, and is correlative with the lower part of the Ordian of the Cambrian of Australia (Öpik, 1970; Nedin, 1995). The Balang Fauna occurs in the middle to upper part of the formation at seven newly identified localities (Peng, Zhao & Sun, 2012; Ma *et al.* 2011). The Balang Formation at the very fossiliferous Geyi Section is 375.4 m thick at exposures near Geyi Town, Taijiang County,

Guizhou Province, where the Balang Fauna assemblage occurs in the middle and upper parts of the formation. Here, we describe the palaeoscolecid *W. geyiensis* sp. nov. so far known only from the Geyi Section, where it is associated with other components of the Balang Fauna, e.g. *Guizhouocrinus yui* Zhao, Parsley & Peng, 2007; *Naoroia taijianensis* Peng, Zhao & Sun, 2012; *Tuzoia canadaensis* Resser, 1929; the trilobites *R. (Pteroredlichia) chinensis*, *A. chauveaui*, *A. (Arthrocephalites) xinzhaiheensis* Chien & Lin in Lu *et al.* 1974 and *C. elongata*, etc. (Fig. 1).

3. Material and methods

More than 50 specimens were collected from grey-greenish mudstone of the Geyi Section of the Balang Formation. They often form tiles on slabs of shale or mudstone. Some specimens are preserved as moulds, but many possess a black, fine, linear intestinal tract. Specimens typically split uniformly between two sides of the cuticle. Thus, both sides (part and counterpart) of the specimens preserve the gross morphology of the body. The cuticular structures are apparent on the inside of the specimens; thus, the dark holes in the SEM observations indicate protuberate nodes (Fig. 4d–h). Fifteen nearly complete specimens (without introvert and pharynx) and some cuticular fragments were selected for SEM analysis; three specimens (counterparts) were coated with gold prior to imaging. Analysis was completed at the scanning electron microscope (SEM) laboratories of the Nanjing Institute of Geology and Palaeontology CAS (using a ZEISS-SUPRA 40VP). Further observation was conducted using a VHE photomicrographic system: specimens were photographed in natural light as well as in lamplight. The nomenclature applied in this study follows Conway Morris & Robison (1986), Conway Morris (1997), Kraft & Mergl (1989) and Müller & Hinz-Schallreuter (1993). All described specimens are deposited in the Palaeontological Museum of Guizhou University, Guiyang, China (GU); the prefix GY assigned to specimens indicates the Geyi Section.

3.a. Systematic palaeontology

Phylum PRIAPULIDA Delage & Hérouard, 1897
 Class PALAEOSCOLECIDA Conway Morris & Robison, 1986
 Family PALAEOSCOLECIDAE Whittard, 1953
 Genus *Wronascolex* Ivantsov & Zhuravlev, 2005

- 1969 *Palaeoscolex* Whittard; Robison, pp. 1171–2, pl. 138, figs 1, 2.
 1979 *Palaeoscolex* Whittard; Glaessner, pp. 25–7, fig. 3.
 1986 *Palaeoscolex* Whittard; Conway Morris & Robison, p. 14
 1991 *Palaeoscolex* Whittard; Robison, fig. 6–5.
 2004 *Palaeoscolex* Whittard; Ivantsov & Wrona, pp. 6–12, figs 3–8.

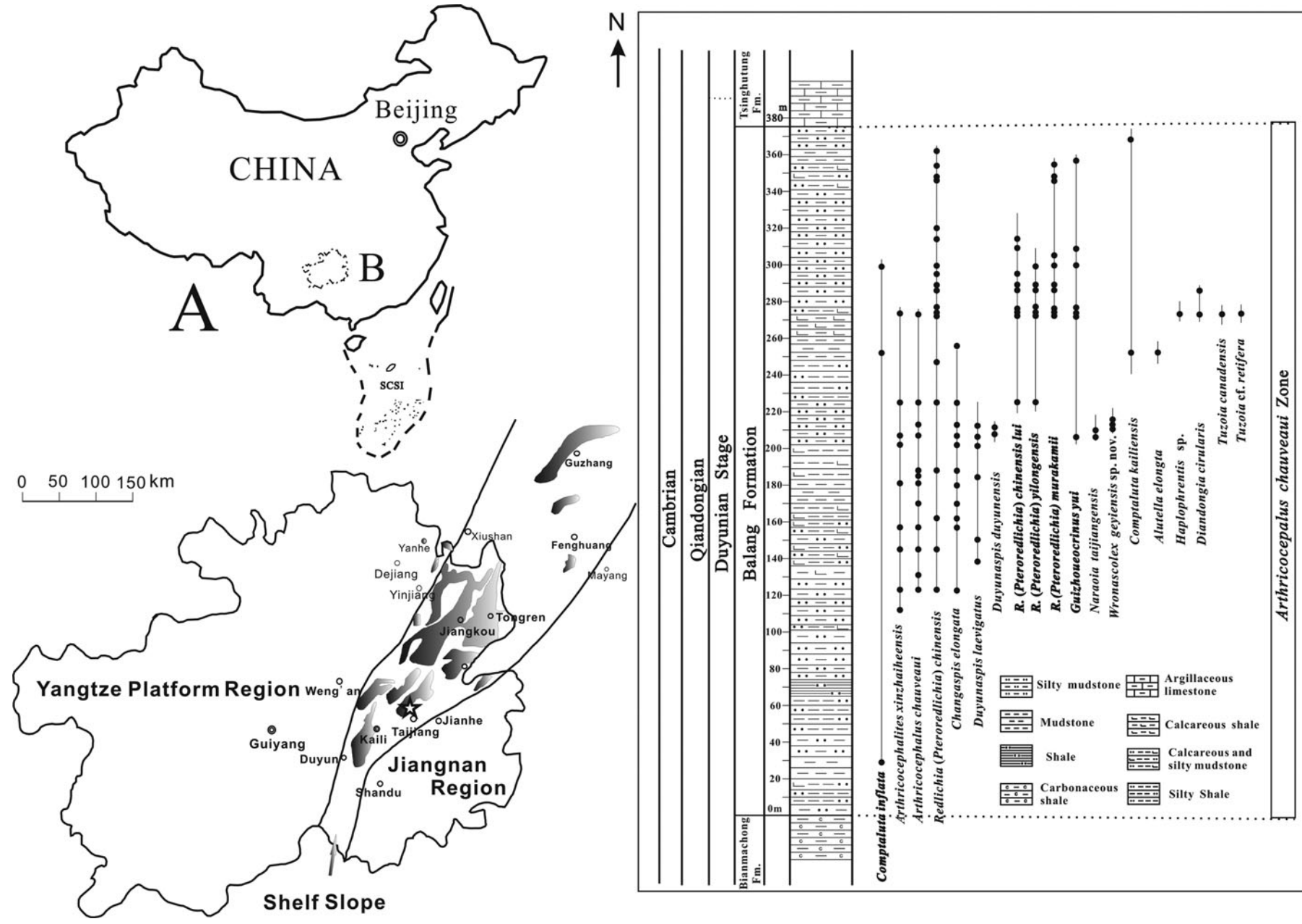


Figure 1. Map of the geographic distribution of the Cambrian Balang Formation (shaded area; five-pointed star represents fossil locality), Guizhou Province, South China and distribution of key fossils within the Geyi Section of the Balang Formation.

- 2005 *Wronascolex* Ivantsov & Zhuravlev, pp. 64–7, pl. XVI, fig. 5., pl. XVII, fig. 6, pl. XVIII, figs 1, 2, pl. XIX, figs 1, 2
- 2005 *Palaeoscolex* Whittard; García-Bellido & Aceñolaza, pp. 470–1, pl. 1, figs 3, 4
- 2011 *Palaeoscolex* Whittard; García-Bellido & Aceñolaza, pp. 534–6, fig. 3A–D.
- 2013 *Wronascolex* Ivantsov & Zhuravlev; García-Bellido, Paterson & Edgecombe, pp. 781–3, tables 1, 2.

Type species. *Palaeoscolex lubovae* (Ivantsov & Wrona, 2004)

Diagnosis. Elongate and slender worm, trunk cylindrical, with fine annulations, each annulation armed with rows of circular to sub-circular sclerites, each small sclerite or plate ornamented by a single ring of 4–10 nodes and an occasional central node. Outer margins of plates armed with a ring-like sculptured band with radial lines. Introvert armed with scalids and posterior end with simple paired caudal hooks; intestine simple and straight.

Discussion. The typical character of *Wronascolex* is the possession of circular to sub-circular plates in additional rows alternately arranged on the annulations of the trunk. Previously, most palaeoscolecids from Burgess Shale-type biotas were recognized as *Palaeoscolex* (Robison, 1969; Conway Morris, 1977; Glaessner, 1979; Hou & Sun, 1988; Ivantsov & Wrona, 2004), such as the type species of *Wronascolex*, *Palaeoscolex lubovae* (Ivantsov & Wrona, 2004) from the Siberian Platform, *P. antiquus* Glaessner, 1979 from Australia, *P. ratcliffei* Robison, 1969 from North America and *P. sinensis* Hou & Sun, 1988 from China. According to the precise diagnosis of *Palaeoscolex* (see Whittard, 1953; Conway Morris, 1997), this genus, in addition to possessing a long, slender cylindrical body covered by an annulated cuticle, possesses two rows of plates on each annulation, respectively, near the intersegment furrow, and a space between the two plate rows filled by numerous microplates; per row of plates near the furrow, there are 1–2 rows of platelets; and in particular, a 7–12 node array is present on the upper surface of the plates forming a circular to slightly elongated single ring (Conway Morris, 1997). With reference to characters of the detailed configuration, *Palaeoscolex*, first described (*P. lubovae*; Ivantsov & Wrona, 2004, p. 6, figs 3, 4) from the lower Cambrian Sinsk Formation of the Siberian Platform and placed in Nematelminthes, was reassigned to *Wronascolex lubovae* within the cephalorhynchids by Ivantsov & Zhuravlev (2005). *P. sinensis* from the lower Cambrian Yu'an-shan Formation of Yunnan, China was reassigned to *Mafangscoclex sinensis* by Hu (2005). Recently, *P. antiquus* Glaessner, 1979 from Australia, *P. ratcliffei* Robison, 1969 from North America and *P. cf. P. ratcliffei* Robison, 1969 from Spain were reassigned to relative species under *Wronascolex* or *Wronascolex?* (García-Bellido, Pater-

son & Edgecombe, 2013). *Palaeoscolex* is presently recognized only from Ordovician strata (Whittard, 1953; Kraft & Mergl, 1989; Conway Morris, 1997; García-Bellido, Paterson & Edgecombe, 2013). Based on detailed SEM photographs from fossil material (Ivantsov & Zhuravlev, 2005; Hu, 2005; García-Bellido, Paterson & Edgecombe, 2013), we agree that the reassignment of these genera is valid. But morphologic characters, in particular, the plates on the annulations of the three genera *Palaeoscolex*, *Wronascolex* and *Hadimopanella*, are actually different (Gedik, 1977, pl. V5; Conway Morris, 1997; Ivantsov & Zhuravlev, 2005). We argue that both plate-types for *Wronascolex* and *Palaeoscolex* were separately defined as *Hadimopanella*-type plates and *Milaculum*-type plates (García-Bellido, Paterson & Edgecombe, 2013). *Hadimopanella* is only known from isolated small sclerite fossils as a form genus; the node array on the upper surfaces of its sclerites shows variation from no rings with 1–4 nodes to 7–30 nodes forming complicated node arrays (Gedik, 1977; Boogaard, 1983, p. 337, fig. 3). *Milaculum* Müller, 1973 is another isolated small sclerite fossil known from small sclerites described as slightly larger than those of *Hadimopanella* (Gedik, 1977; Boogaard, 1983, p. 337, fig. 3). The sclerite form is described as elongate and oval with the node array variation on the upper surface (Müller, 1973; Boogaard, 1988) only somewhat similar to the plates of *Palaeoscolex* (Conway Morris, 1997). *Wronascolex* had been suggested to have a wide geographic distribution, being found in North America, Australia, Spain and China (García-Bellido, Paterson & Edgecombe, 2013). New fossil material from the Balang Formation confirms *Wronascolex*'s occurrence in China. The type species of *Yunnanoscolex*, *Y. magnus* Hu *et al.* 2012, also from China, was recognized to have plates similar to *W. spinosus* by García-Bellido, Paterson & Edgecombe (2013). The placement of this genus, however, is not straightforward, although it was reassigned to *Wronascolex*. Before, only a single taxon, *P. spinosus?*, was reported from the Guanshan Biota of the Wulongqing Formation of Huize, Yunnan, China. The assignment of this taxon was based on two SEM photographs from one specimen (Liu *et al.* 2012, p. 128). The stratigraphic position of this taxon is equivalent to that of *Y. magnus*. In fact, the characters of the plates and the node array of *P. spinosus?* on the upper surface of the plates closely resemble those of *Y. magnus*. This indicates that *Wronascolex* does not occur in Yunnan, China. According to SEM micrographs of single button-shaped plates on the cuticle annulations of the Balang worm trunk (Figs 3, 4), the characters of the plates are similar to those of the type species of *Wronascolex*, *W. lubovae*. Specifically, each annulation on the trunk having *c.* 6–7 rows of alternating plates and a single ring with 4–7 nodes in a petal-shaped array and no central node on the upper surface of the plates distinguishes specimens from the Balang Formation from those of related species of *Wronascolex*, providing additional species-level taxonomic information for this genus.

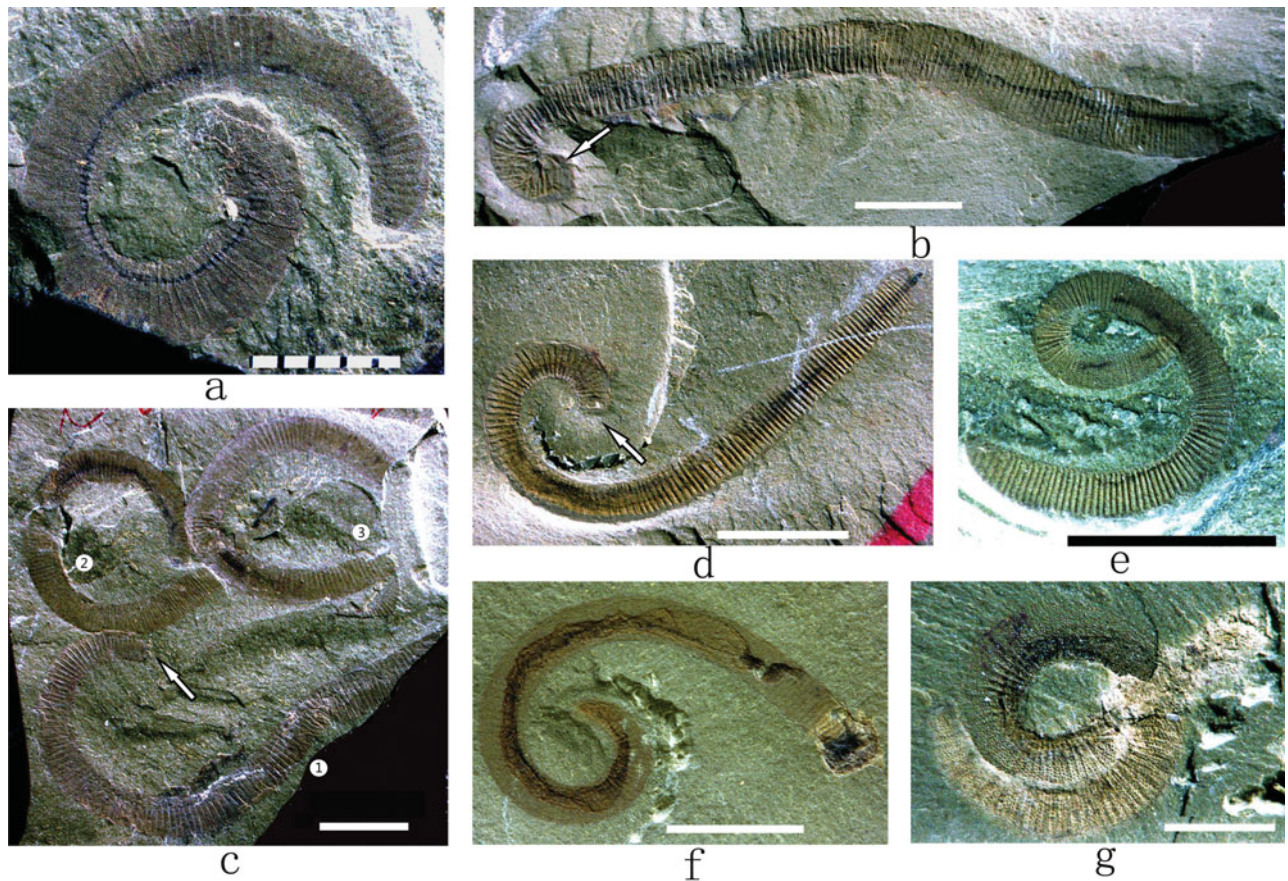


Figure 2. (Colour online) *Wronascolex geiyensis* sp. nov. Multiple individuals from the Cambrian Balang Fauna, Geyi Town, Taijiang County, eastern Guizhou. (a) A coiled specimen showing the general habitus and intestine (GY-203.4-3). (b) A nearly straight specimen, paratype (GY-208-3), with preserved posterior end and intestine; white arrow indicates caudal hooks. (c) A specimen with three coiled individuals (GY-203.4-6a), holotypes, type individual labelled with number 1 (GY-203.4-6a-1). (d) A nearly complete juvenile with posterior end preserved; white arrow indicates caudal hooks (GY-201-1). (e) A nearly complete juvenile, (GY-203.4-7). (f) A coiled nearly complete juvenile with complete posterior end (GY-203.4-1). (g) A coiled nearly complete juvenile with complete posterior end, paratype (GY-203.4-5b). Scale bars represent 2 mm in (g), and 5 mm in others.

Occurrence. North America, Spain, Russia, China; Cambrian Series 2 to Series 3.

Wronascolex geiyensis sp. nov.

Figures 2–4

Etymology. The name of the species derives from the name of the place where the fossil was first discovered in the Balang Formation of Geyi Town, Taijiang County, Guizhou Province, China.

Holotype. A slab with three coiled individuals (GY-203.4-6a, b), type individual located below individual GY-203.4-6a-1 (see Fig. 2c), and detailed configuration of small sclerites (plates) on the surface of the body as seen by SEM photographs (Fig. 3f–j).

Paratypes. Paratype-1: a half-complete specimen with aboral terminate and dark straight intestinal tract, GY-208-3 (Fig. 2b); paratype-2: a coiled individual with aboral terminate, juvenile specimen (part and counterpart), GY-203.4-5a,b (Figs 2g, 3a), and detailed configuration of small plates on the surface of the body as seen in SEM photographs (Fig. 3b–e); paratype-3, an adult individual fragment, GY-195-1, and detailed

configuration of small plates on the surface of the body as seen in SEM photographs (Fig. 4a–h).

Material. A total of 53 specimens preserved in slabs of shale, including juvenile and adult individuals, among which 20 specimens are nearly complete with trunk and aboral terminations, and five specimens are known from both parts and counterparts; others are fragments. All collected from the Geyi Section of the Balang Formation, near Geyi Town, Taijiang County.

Diagnosis. Body medium large, elongate, slender, about 14 times longer than wide; introvert poorly and incompletely preserved; cylindrical trunk densely covered with annulations, numbering approximately 128; each annulation with *c.* 6–7 rows of inlaying alternately arranged plates; single ring with petal-shaped array with 4–7 nodes (normally with six nodes); no central node on the surface of the plates, only one plate pattern. Number of plates and rows on each annulation unequal. Size of plates unequal; diameter of the plates ranges from 30–60 μm . Plates are rounded, the outer margin armed with a ring-like sculptured band with radial lines. Terminal end armed with simple

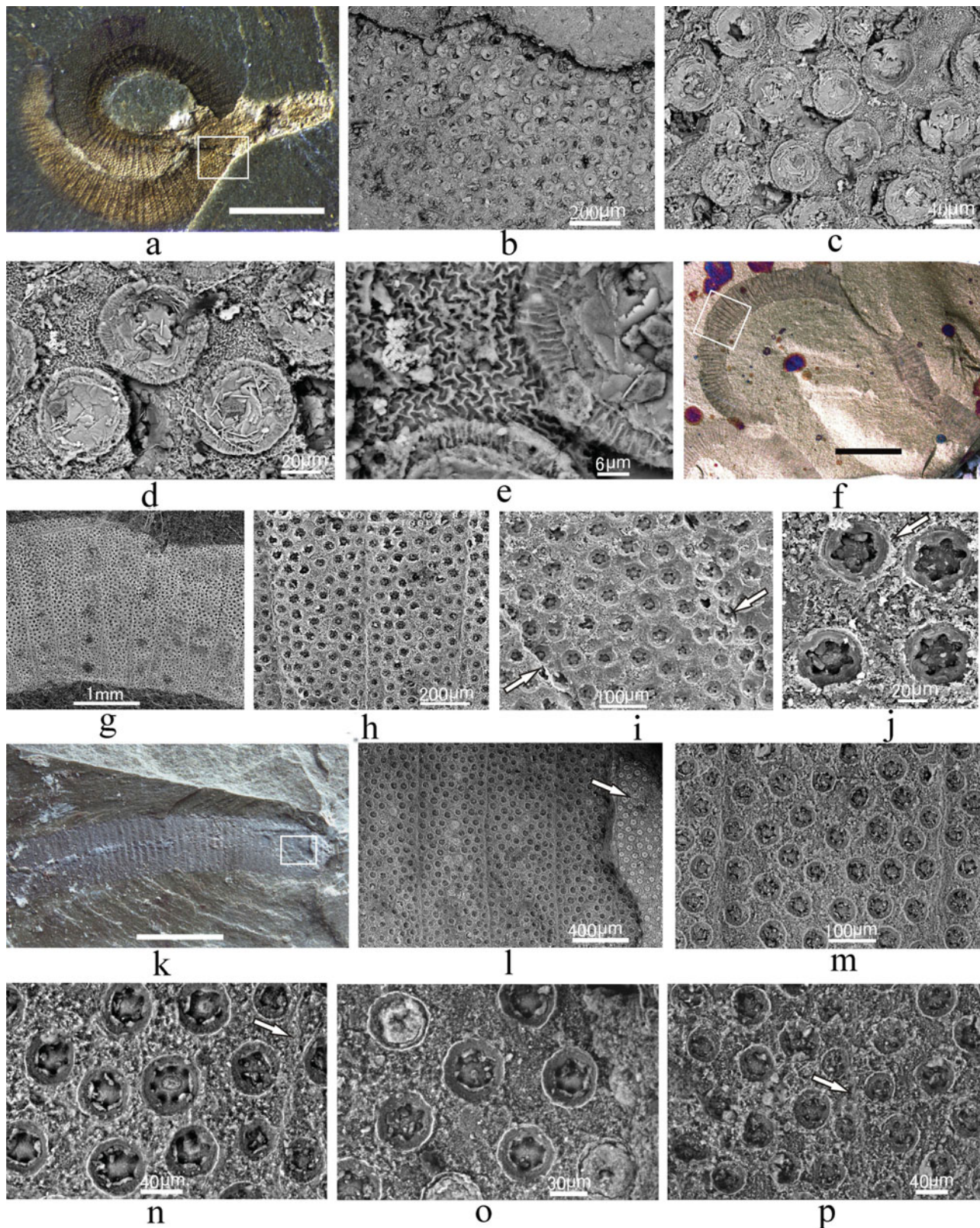


Figure 3. (Colour online) SEM micrographs of the cuticular characters of *Wronascolex geyiensis* sp. nov. from the Cambrian Balang Fauna, Geyi Town, Taijiang County, eastern Guizhou. (a) A coiled juvenile specimen with faint intestinal tract, paratype GY-203.4-5a. (b-e) Enlargement of square box in (a): (b) the fuzzy intersegment furrows and circular sclerites (plates); (c) the centre of the plates exhibit broken matrix caps; (d, e) the rimmed outer margin of the plate with a ring-like radially lined sculptured band; the space in between plates is occupied by fine wrinkles. (f) Partial fragment of a specimen of three associated individuals, the only counterpart specimen of the holotype (coated in gold), GY-203.4-6. (g-j) Enlargement of the square box in (f): (g) trunk with clear annulations and intersegment furrows, with *c.* 3 annulations per millimetre; (h) detail of two annulations and intersegment furrows, each annulation with about 6-7 rows of plates in alternating arrangement; (i) an annulation separated by two intersegment furrows (arrow points to position) with *c.* 6-7 rows of alternating plates; (j) detail of plates with five to six nodes, showing a dark hole; adjacent plates vary in both plate diameter and distance from each other. (k) A trunk specimen with aboral terminate, GY-198-4. (l-p) Enlargement of square

paired caudal hooks. Pharynx not preserved. Intestine is simple and straight, with an anal opening at posterior end.

Description. Body medium long, the longest individual being 46.7 mm (Fig. 2b); unclear boundary between trunk and introvert. Bodies are straight, bent or coiled; adult body over 3.0 mm in width, the widest individual is 3.3 mm (Fig. 2a–c), juvenile 1–1.8 mm wide (Fig. 2d–g). The length of the trunk in most specimens exceeds 40 mm (Fig. 2a–e) excluding the unpreserved introvert section. Most specimens show a coiled shape, which may result from rapid burial after death (Huang *et al.* 2014). Terminal end of the trunk armed with two simple caudal hooks (Fig. 2b–d). Bending of the straight trunk may result from burial of worms during locomotion (Huang *et al.* 2014). Some specimens are preserved with a dark intestine with an anal opening at the posterior end. The intestine is preserved on the ventral side in the coiled specimens. A specimen, near the ventral side, contains a clear dark intestine parallel to the coiled trunk, and the width of dark intestine is uniform (Fig. 2a). The holotype is a nearly complete bent individual with preserved posterior end (Fig. 2c, individual labelled 1), 42 mm long, with a trunk covered by dense annulations; *c.* 121 annulations may be discerned, *c.* 3 annulations per millimetre (Fig. 3g), with an estimated total number *c.* 126. Each annulation is separated by an intersegment furrow, and comprises a cuticle with *c.* 6–7 rows of alternately arranged circular plates; plates are tiny, button-shaped, in inlaying arrangement (Fig. 3h–j); rows of the array are irregular (Fig. 3h, i); spaces among plates are not equal and filled by fine wrinkles (Fig. 3i, j). Plates show an inlaying arrangement, adjacent rows varied in direction (Fig. 3h, i). The size of the plates mostly ranges from 30–60 μm in diameter (Fig. 3j). There is only one plate pattern per annulation. Paratypes 2 and 3 also show similar characters. Four to seven prominent nodes compose a single ring in a petal-shaped array on the plates, with no central node (Figs 3n–p, 4n–p); six prominent nodes are common (Figs 3j, n, o, 4h, q), while plates with four and seven prominent nodes are rare. When prominent nodes are removed, the positions of the nodes appear as dark points or blank spaces (Figs 3j, n, 4d–h). On the outer margin of each plate, near the base, lies a ring-like radially lined sculptured band (Figs 3c–e, n–o, 4q, s). The boundary between the two succeeding annulations in some specimens is not discernible; plates on the annulation near the intersegment furrow are slightly smaller in diameter (Figs 3h, i, m, n, p, 4k–m). In addition, the surface of the plates in some specimens is covered by thin matrix caps (Fig. 4f, k–m), which result from diagenetic secondary infilling. Juvenile spe-

cimens (Figs 2d–g, 3a–e) have plates slightly smaller than those of adult individuals, mostly ranging from 30 to 50 μm (Fig. 3c, d). They show the same morphologic characters as those of adult individuals in outline, differing only in that body diameter is less than 2 mm; the number of rows on each annulation is less than six (Fig. 3b). Based on observation and research, the worm body is divided into two types: (1) a coiled type: the aspect of the opening aperture is anterior and that of the coiling is posterior; the internal ring side is ventral and the outer ring side is dorsal (Fig. 2); (2) a straight or bent type: the part where the diameter of the body is large is anterior and that which is slightly smaller composes the end part, with a slight arch prominent on the dorsal side; the size of the plates located on the dorsal and ventral sides is almost identical, as are the sizes of the plates at the anterior and posterior ends (Fig. 4k, l).

4. Comparison and discussion

García-Bellido, Paterson & Edgecombe (2013, p. 784, table 2) compiled taxonomic data for seven species of *Wronascolex* in a table. These species possess plate rows on each annulation that vary from one to four in number. *W. geviensis* sp. nov. is distinguished from other species of the genus by the presence of six to seven rows of alternating plates on each annulation, with *c.* 3 annulations per millimetre, only one plate pattern, and four to seven prominent nodes consisting of a single petal-shaped ring with no central node on the surface of the plates (Fig. 3d–h). The type species of *Wronascolex*, *W. lubovae* (Ivantsov & Wrona, 2004, p. 6, figs 3, 4; Ivantsov & Zhuravlev, 2005), possesses 5.5–8.3 annulations per millimetre, with four plate rows per annulation; a cylindrical body with a maximum width of 1.2 mm; and a single ring of 5–8 nodes in an array, and occasionally a central node, on the upper surface of each plate (García-Bellido, Paterson & Edgecombe, 2013, p. 784, table 2). The important disparity is the latter with the plates and platelets having two patterns. Both differences are obvious. Compared to *W. antiquus* (Glaessner, 1979) and *W. iacoborum* (García-Bellido, Paterson & Edgecombe, 2013 from the Emu Bay Shale of the Cambrian Series 2, Stage 4, Big Gully, Kangaroo Island, South Australia, *W. antiquus* is distinguished by plate morphology. Each plate on the upper promontory surface bears 3–6 nodes arranged in a single circle, occasionally with a central node, and each annulation contains only one row of large plates, with the diameter of the plates notably larger than that of the new species (García-Bellido, Paterson & Edgecombe, 2013, figs 3–5, p. 784, table 2); *W. iacoborum* is distinguished by the upper promontory surface of the

box in (k): (l) shows annulations, intersegment furrows and the plates' irregular array arrangement in *c.* 6–7 rows; arrow points to part belonging to a different layer of the specimen to be split, where the plates take on a conical convex shape; detail to be seen in (o); (m) an annulus with *c.* 6–7 rows of alternating plates; adjacent rows of alternating plates, plate diameter and distance from each other vary; (n, p) detail of plates with different sizes and five to seven nodes; near the intersegment furrow (arrow points to position), small sized plates with four or five nodes occur.

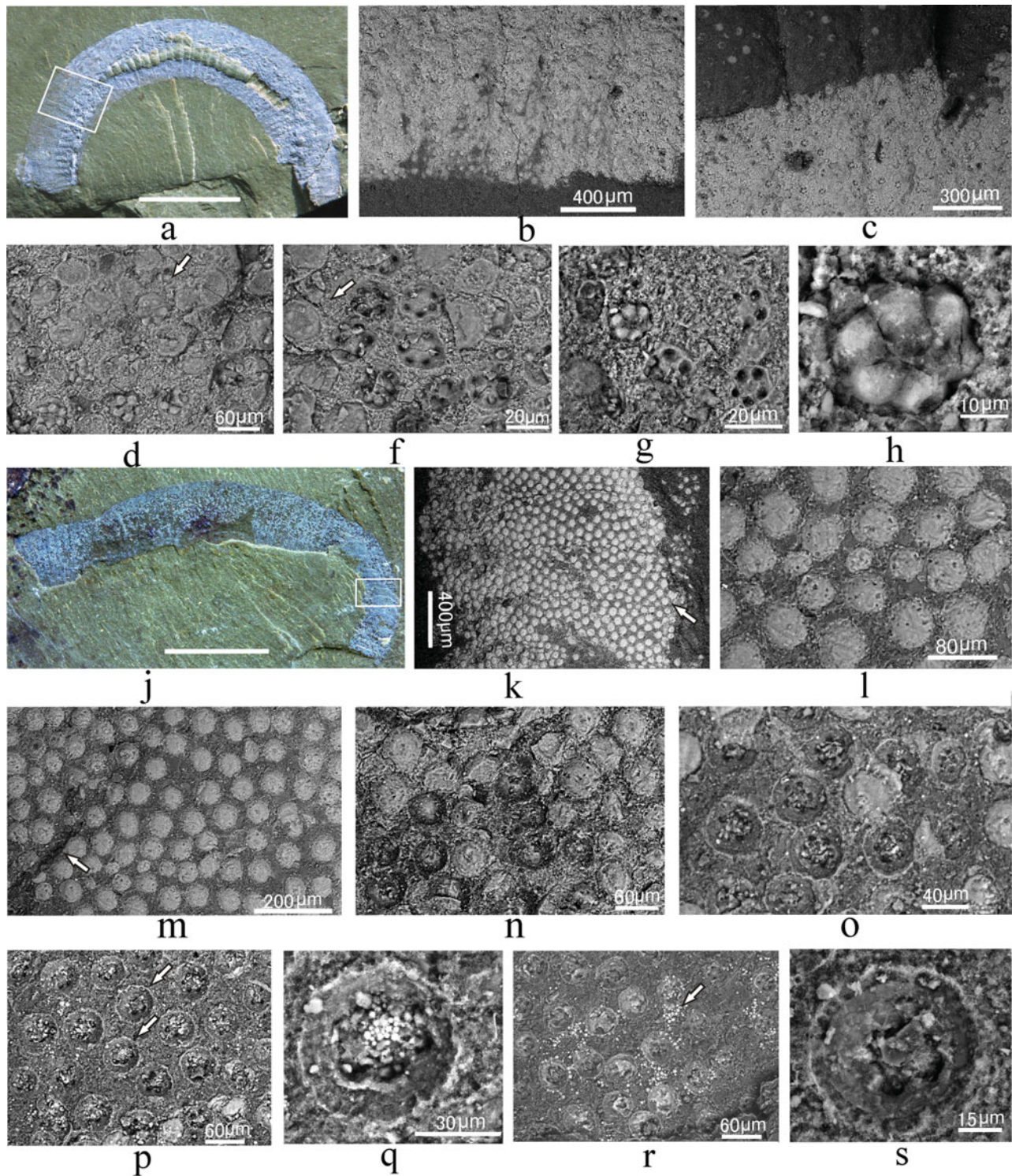


Figure 4. (Colour online) SEM photos showing the cuticular characters of *Wronascolex geyiensis* sp. nov. from the Cambrian Balang Fauna, Geyi Town, Taijiang County, eastern Guizhou. (a) A fragment of trunk with a whitish colour, with intestine filled with organic mud, paratype (GY-195-1); scale bar represents 5 mm. (b–h) Details of cuticular structures within the square box in (a): (b, c) the trunk cuticle with annulations, correlated to small plates; (d–f) the rounded small plates distributed on an annulation showing two states: plates with thin matrix caps or plates completely exposed, the latter plates with surface ornamentation of five to six smooth and ovate nodes in a petal-like array; after the nodes have fallen out the nodes appear as dark holes; on (d) the small arrow points to a plate with half-fallen out nodes, and on (f) the arrow points to a plate with a thin matrix cap; below the cap can be seen a faint trace of six nodes. (g, h) Detail of a plate with six nodes forming a petal-like single ring, and the fine wrinkles among plates. (j) The trunk specimen of an adult individual, GY-198-1, scale bar is 5 mm. (k–s) Enlargement of square box in (j). (k) Three annulations separated by intersegment furrows, with *c.* 6–7 rows of alternating plates per annulation with thin matrix caps; the arrow points to the intersegment furrow; (l–n) detail showing plates of two different sizes; adjacent plates vary considerably in size or inlaying arrangement; (o, p) detailed enlargement of partial plates, showing variation among plates in distance and in the inlaying arrangement of the plates; (q, s) enlargement of plates marked by the lower and upper arrows on (p), respectively; the two plates are in a convex position with a ring of nodes, forming a rim on the margin of the lower plate. On (q, r) the plates are in a convex position, with the arrow indicating a cluster of pyrite crystals in (r).

plates having five nodes arranged in a single ring, each annulation possessing two plate rows with a regular arrangement, and platelets and microplates between rows (see García-Bellido, Paterson & Edgecombe, 2013, figs 3–5, p. 784, tables 1, 2); this differs from the new species, which possesses *c.* 6–7 plate rows on each annulation, and no platelets. Specimens of *Wronascolex?* spec. 1 and *Wronascolex?* spec. 2 from the Murero Formation, Rambla de Valdemiedes, Murero, Spain (García-Bellido, Paterson & Edgecombe, 2013, p. 784, table 2), are larger, with each annulation containing three to four rows of large plates, the diameter of the plates ranging from 80–100 μm . Two species were described as *Wronascolex?*. The characters of *Wronascolex?* spec. 1 are a larger plate diameter, resulting in fewer plate rows on each annulated interval, and the number of nodes and the mode of arrangement on the upper surface of the plates being unclear (García-Bellido, Paterson & Edgecombe, 2013, p. 793, fig. 9). The characters of the plates and the arrangement of the nodes in *Wronascolex?* spec. 2 are similar to that of new species, but each annulation possesses three to four plate rows in regular arrangement, distinguishing it from the new species. *P. ratcliffei* Robison (1969) from the Spence Shale, Langston Formation, Utah, USA, has been re-assigned to *Wronascolex? ratcliffei* by García-Bellido, Paterson & Edgecombe (2013). The species not only has plates that are large in diameter, and four plate rows on each annulation, but also the space between the plates is filled by a tessellate pattern, a micro-net that is different from that of the new species. Another species, *W. spinosus* (Ivantsov & Wrona, 2004, p. 6, figs 3–4; Ivantsov & Zhuravlev, 2005) from the Sinsk Formation of the lower Cambrian of the Siberian Platform, exhibits a number of plate rows on each annulated interval and nodes arranged on a convex conical plate, and microplates among the plates, which are different from those of the new species, in particular, nodes with a pointed spine unlike the smooth, small oval shapes of the nodes of the new species (Fig. 3g, h). However, *Y. magnus* resembles the new species, but has neighbouring plates on succeeding rows spaced alternately. The plates are arranged quincunxially, the trunk is large, the size of the plates is small, with a loose arrangement on the annulations, and there is a single ring with 2–6 nodes on the upper surface of the plates, commonly five nodes in a quincunx arrangement, and four nodes forming a square (Hu *et al.* 2012). Large protuberances are irregularly present on the ventral side of the posterior segments, approximately 200–300 μm in diameter, though its individual large plates are arranged loosely and quincunx-like on each annulation; the size of the plates is small and ranges from 40–45 μm , with 2.5 annulations per 1 mm; plates are arranged in rows of less than five per annulation (Hu *et al.* 2012), resulting in poor preservation of the cuticle trunk, obviously different from the new species. Here, more than 30 specimens of Balang worm trunks are covered by dense and small sclerites. These sclerites or plates show different types of preservational states: one plate type

has a thin matrix cap (Figs 3b–d, 4k–m), the other type is completely exposed, the latter bearing surface ornaments with a petal-like array of five to six nodes on the plates (Fig. 4d, g, h). Dark holes are present where nodes are degraded. We speculate that these specimens representing worms with plates lacking the matrix caps and having degraded nodes (Fig. 3g, h, l–p) had been transiently exposed, after the matrix cap was removed, resulting in erosion and degradation of the node ring. Adult individuals show *c.* 6–7 plate rows per annulation (Figs 3g–i, l, m, 4k), while this number is fewer than six for juvenile individuals (Fig. 3b). We speculate that this trend may be ontogenetic, with increasing numbers of plate rows on each annulation during growth. The disparity in the size of the plates on the body annulations is not distinct; plates of smaller diameter are rare, perhaps forming only during transitions in growth, or are lost owing to taphonomic bias. Among all the nearly complete specimens, the introvert or anterior end are not preserved. This is likely owing to the softer cuticle of the pharynx with the longitudinally regular and irregular arrangement of many sclerites, so that non-mineralized sclerites are often not preserved. Some specimens are preserved with a dark line running the length of the trunk representing the intestine. This indicates that the worm ate organic mud that remained in the intestine. The dense small sclerites that covered the Balang worm not only protected the internal soft-body but also helped the worm to contract, facilitating locomotion and burrowing, while promontory nodes on the surface sclerites increased friction within the soft matrix. Future work may shed light on the ecology and taphonomy of this taxon. The new species not only expands the geographic and stratigraphic distribution of *Wronascolex*, but also provides additional evidence for understanding the genus's body configuration, ecology and taphonomy. *Wronascolex* is found globally in Cambrian strata ranging from Series 2 to Series 3.

Occurrence. Geyi Section of the Balang Formation, Taijiang County, Guizhou Province, China; Cambrian Series 2, Stage 4.

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