# New data for *Isoxys* of the Balang Fauna (Cambrian Stage 4), South China

Shuai Liu, Jin Peng, Rongqin Wen & Boyan Liang

*Isoxys* Walcott, 1890 is a large bivalved arthropod taxon, commonly occurring in the Cambrian Series 2–3. Here, we report on a new group of *Isoxys* from the Balang Fauna (Cambrian Stage 4) of Guizhou, South China. It is composed of five species: *Isoxys acutangulus* (Walcott, 1908), *I. auritus* (Jiang, 1982), *I. jianheensis* sp. nov., *I. globulus* sp. nov., and *Isoxys* sp. *Isoxys* first appeared in the Chengjiang Biota (Cambrian Stage 3) located in the shallow-water Yangtze Platform in Yunnan, South China, and ranged to the Guanshan Biota (Cambrian Stage 4) above the Chengjiang Biota. The Balang Fauna of Guizhou Province is located in the transitional slope area of the deeper-water environments and is equivalent to the Guanshan Biota in age. The discovery of *Isoxys* in the Balang Fauna suggests that the genus, originally present in the shallow platform of Yunnan, migrated eastward to the deeper water shelf of Guizhou during the early Cambrian (Stage 4), becoming suited to a new ecological environment. The *Isoxys* assemblage of the Balang Fauna not only adds new taxa record for this genus but also provides new information for its palaeoecology, evolution, and geographic distribution. • Key words: *Isoxys*, Balang Fauna, Balang Formation, Cambrian, Guizhou, South China.

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The large bivalved arthropod *Isoxys* Walcott, 1890 is a common taxon in the Burgess Shale-type biotas of the global Cambrian Series 2–3 and has a wide palaeogeographic distribution. It is known to occur in North America (Walcott 1908, Campbell & Kauffman 1969, Simonetta & Delle Cave 1975, Conway Morris *et al.* 1987, Butterfield & Nicholas 1994, Williams *et al.* 1996, Briggs *et al.* 2008, García-Bellido *et al.* 2009b, Peel 2010, Stein *et al.* 2010), Australia (Daily 1956, Glaessner 1979, García-Bellido *et al.* 2009a), Europe (Richter & Richter 1927, Vannier *et al.* 2005), Russia (Ivantsov 1990, 2005), and China (Jiang 1982; Hou 1987; Luo *et al.* 1999, 2006, 2008; Steiner *et al.* 2005; Zhao *et al.* 2005, 2011; Wang *et al.* 2010; Liu & Lei 2013; Wen *et al*. 2015). It is characterized by prominent antero- and posterodorsal spines on a dorsal shield and double near-half-oval carapaces in outline (Fig. 1A). Based on the collection from the lower Cambrian Chilhowee Group in Tennessee, United States, *Isoxys* was first described by C. D. Walcott in 1890 as the type species *Isoxys chilhoweanus*. Subsequently, Walcott (1908) described *Anomalocaris acutangulus* from the Mt. Stephen Trilobite Beds (Canada). However, after specimens of *Anomalocaris acutangulus* were re-examined and compared with characteristics of *Isoxys*, *Anomalocaris acutangulus* was redesignated as *Isoxys acutangulus* (Walcott, 1908), meanwhile, another species, *I. longissimus* from the Burgess Shale, was described by Simonetta & Delle Cave (1975). Since then, more species and localities for *Isoxys* have been continually reported all over the world; many studies have recognized soft anatomy, such as visual organs, limbs, and posterior tagmosis morphology (Shu *et al.* 1995, Vannier & Chen 2000, García-Bellido *et al.* 2009b, Vannier *et al.* 2009, Stein *et al.* 2010, Fu *et al.* 2011, Schoenemann & Clarkson 2011, Huang & Wang 2015). In addition, some researchers have provided information on the ontogeny and dimorphism of some species (Fu *et al.* 2014). Up until now, more than 17 species have been described.

The affinities of *Isoxys* have been controversial, especially its high-level taxonomic position. The reason for this is the lack of soft anatomic information, *i.e.* most specimens are preserved as isolated dorsal shields, often referred to as carapaces (Stein *et al.* 2010). Walcott (1890) placed *Isoxys* among small crustaceans based on its isolated dorsal shields. Generally, the cephalosome of crustaceans has 2 pairs of large anterior appendages; *Isoxys*, however, only has 1 pair of great appendages, which distinguishes it from crustaceans. Meanwhile, some scholars have placed

*Isoxys* within Branchiopoda (Luo *et al.* 1999). However, Branchiopoda also have 2 pairs of large appendages, as they are crustaceans.

Despite the debates, *Isoxys* was placed within the "great-appendage" arthropods as a sister taxon of the anomalocaridid (Vannier *et al.* 2009). However, this hypothesis is challenged by the appendage segmentation of *Isoxys*, which differs from that of other "great-appendage" taxa (Fu *et al.* 2011). Another view is that all species of *Isoxys* may not be congeneric (Stein *et al.* 2010, Fu *et al.* 2011). Some researchers have evaluated their morphology and coded these taxa in extensive cladistics analyses, indicating that many species of *Isoxys* belong to the most basal arthropod taxa (Bergström *et al.* 2008, Legg *et al.* 2012, Legg & Vannier 2013, Legg & Caron 2014). The discovery of soft part of *Isoxys* has prompted a reconsideration of the affinities of this group; however, additional knowledge and evidence of the great appendages, especially the proximal parts, are needed to resolve the systematic position of *Isoxys* (García-Bellido *et al.* 2009b). In this paper, the higher-level affiliations of the arthropod genera are still left open.

*Isoxys* has a wide geographic distribution in the Cambrian of South China, aside from the Chengjiang and Guanshan Biotas of Yunnan (Hou 1987, Luo *et al.* 1999, Vannier & Chen 2000). It also occurs in the Niutitang, Balang, and Kaili Biotas of Guizhou (Steiner *et al.* 2005, Zhao *et al.* 2005, Peng 2009). Although *Isoxys* from Guizhou has not been systematically studied, specimens of *Isoxys* are illustrated or recorded in some documents (Steiner *et al.* 2005; Zhao *et al.* 2005, 2011; Peng 2009). Here, we report on a new group of *Isoxys* from the Balang Fauna. The Balang Fauna is a Burgess Shale-type Biota from the Cambrian Series 2 of Guizhou (Peng *et al.* 2005) that includes representatives of 8 major groups, such as porifer-chanceleoriids, sponges, cnidarians, brachiopods, priapulids, mollusks, arthropods, and echinoderms, as well as many algae and trace fossils (Peng 2009). Since the Balang Formation has a wide distribution in Guizhou, 9 localities of the Balang Fauna have been found (Peng 2009; Ma *et al.* 2011; Peng *et al.* 2012a, b; Zhao *et al.* 2015; Shen *et al.* 2016). *Isoxys* from the Balang Fauna was first recognized as only one species, *I. auritus*, in one locality, based on a specimen with a counterpart in the Jiaobang section of the Balang Formation near Jiaobang Village, Jianhe County (Peng 2009, Peng *et al.* 2012b). A new collection from the Lazizhai section of the Balang Formation near Lazizhai Village, Jianhe County, contains more than 300 specimens of *Isoxys*, which display a diverse

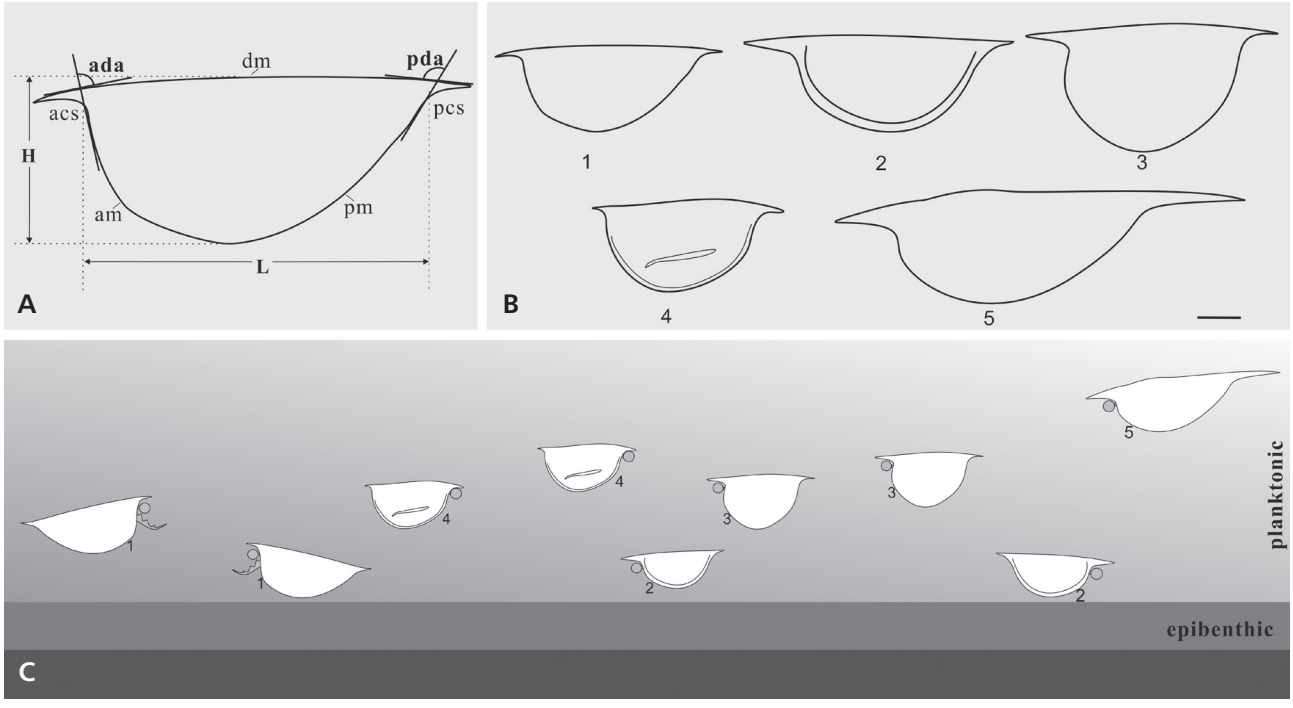


**Figure 1.** *Isoxys* species from the Balang Fauna of Guizhou, South China. • A – drawing showing the morphological terminology of a valve of *I. acutangulus* (Walcott 1908) corresponding to Fig. 4A. Abbreviations of morphologic terms mostly follow Vannier *et al.* (2009) and Fu *et al.* (2014): acs = anterior cardinal spine; ada = angle between anterior spine axis and anterior margin; am = anterior ventral margin; dm = dorsal margin; L = valve length (exclusive cardinal spines); H = valve height; pcs = posterior cardinal spine; pda = angle between posterior spine axis and posterior margin; pm = posterior ventral margin. • B – outline of the 5 studied species of *Isoxys*. Abbreviations: 1 = *I. acutangulus* (Walcott 1908); 2 = *I. auritus* (Jiang, 1982); 3 = *I. jianheensis* sp. nov.; 4 = *I. globulus* sp. nov.; 5 = *I.* sp. Scale bar represents 5 mm. • C – presumed reconstructions and possible position in the water column of the 5 species of *Isoxys*.

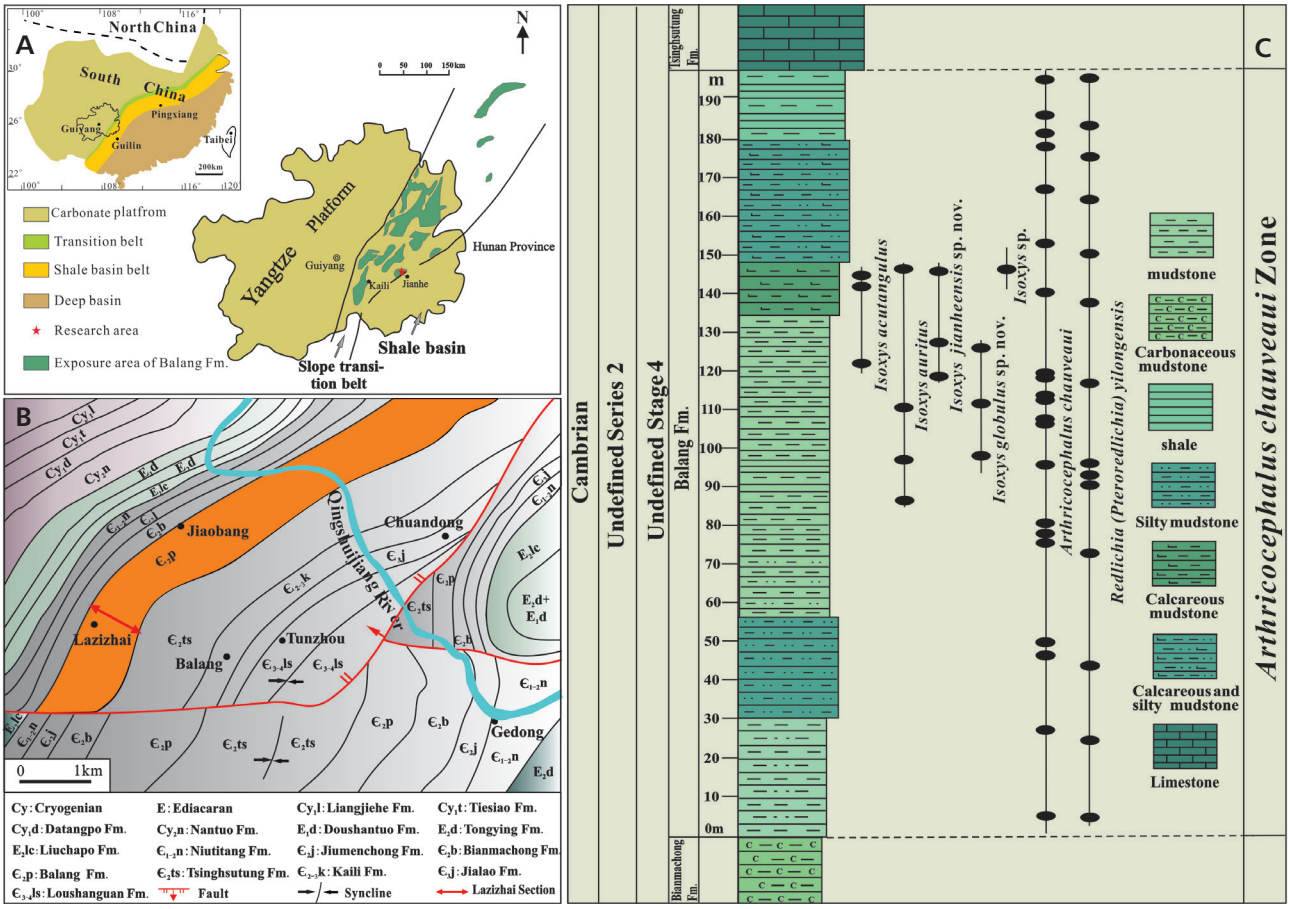


**Figure 2.** A – geographic extension of the Balang Formation (green shades). • B – geological map of the Gedong Region, Jianhe Country, Guizhou Province (after Zhao *et al*. 2001), and location of the Lazizhai section of the Balang Formation. • C – stratigraphy of the Lazizhai section (Balang Formation) and distribution of *Isoxys* species and some trilobites.

assemblage, including five species: *Isoxys acutangulus* (Walcott, 1908), *I. auritus* (Jiang, 1982), *I. jianheensis* sp. nov., *I. globulus* sp. nov., and *Isoxys* sp. (see Fig. 1). It is known that *I. acutangulus* first appeared in the Burgess Shale Biota of Canada (Walcott 1908, Simonetta & Delle Cave 1975), and this species from the Balang Fauna extends its geographic range. *I. auritus* is a common species in the Chengjiang Biota from the shallow-water platform of Yunnan. The discovery of this species of the Balang Fauna indicates that species originally present in the shallow-water platform migrated eastward to the deep-water area of Guizhou, adapting to a new ecological setting. The *Isoxys* assemblage from the Balang Fuana not only adds new records but also provides some new information regarding its palaeoecology, evolution, and geographic distribution.

## Geological setting

The Balang Formation is exposed in eastern Guizhou Province and western Hunan Province, China, located in the transitional slope belt between the Cambrian Yangtze Platform and Jiangnan Basin (Zhou *et al.* 1979; Yin 1987, 1996; see Fig. 2A). The lithology of the formation varies but is dominated by greenish-grey shale and calcareous mudstone shale with intercalations of thin-bedded argillaceous carbonates. The thickness of this formation varies greatly throughout the emergence strata, from 100 m to more than 658 m (Yin 1987). The formation overlies the black shale of the Bianmachong Formation (Cambrian Stage 3) and underlies interbedded shale carbonates and shales of the Tsinghsutung (also published as Qingxudong) Formation (Cambrian Stage 4). In general, the Balang Formation represents a shallowing upward sequence toward its contact overlaying the Tsinghsutung Formation (Peng *et al.* 2012c).

The biostratigraphic framework of the Balang Formation was first described by Zhou *et al.* (1980), with trilobites indicative of the *Arthricocephalus* Zone in the lower Balang Formation and trilobites indicative of the *Arthricocephalites-Changaspis-Balangia* Assemblage Zone in the upper Balang Formation. Subsequently,

Yin (1987) modified the name of the upper biozone as the *Arthricocephalites-Changaspis* Assemblage Zone. Since then, the work has been revised several times. It has been described from 1 genus-level assemblage zone (Yin 1996) up to 3 or 4 species-level zones (Yuan *et al.* 2001, 2002, 2006) and 1 species-level assemblage zone (Peng 2009, Qin *et al.* 2010). Most recently, Yan *et al.* (2014) included the entire Balang Formation as a single species-level zone, that is, the *Arthricocephalus chauveaui* Zone. The Balang Formation is equivalent to the Qiandongian early Duyunian of the Cambrian stratigraphic system of China in slope facies (Peng & Babcock 2001). According to the criteria for correlation in South China, the Balang Formation is equivalent in age to the Wulongqing Formation in Yunnan Province (Luo 1994, Luo *et al.* 2008, Peng *et al.* 2010). *Arthricocephalus chauveaui* Bergeron, 1899, *Changaspis elongata* Lee *in* Chien, 1961 and *Arthricocephlites intermidum* Zhou *in* Lu *et al.* 1974, which are common in the Balang Formation (Shen *et al.* 2016), are known from the lower Cambrian Henson Gletscher Formation of Greenland (Blaker & Peel 1997). However, according to correlation using three genera of corynexochid trilobites, the Balang Formation and part of the Henson Gletscher Formation are equivalent in age (Peng *et al.* 2016). Moreover, the Balang Formation contains abundant *Redlichia* (*Pteroredlichia*) *chinensis* (Walcott 1905) and correlates with the lower part of the Ordian of the Cambrian of Australia (Öpik 1970, Nedin 1995), and consequently correlates with that of the Guanshan Fauna and Emu Bay Shale Fauna (Nedin 1995, Hu *et al.* 2008, Luo *et al.* 2008, Peng *et al.* 2010).

The Lazizhai section of the Balang Formation near Lazizhai Village, Jianhe County, Guizhou Province, China, is a very fossiliferous unit. Here, the formation is 192 m thick and is exposed along a mountain ridge in which the Balang Fauna occurs in the middle and upper parts of the formation (Fig. 2B). Lithologically, the Balang Formation in this section can be divided into 2 members: the upper part is composed of greenish-yellow silty mudstone, and the lower part consists of greenish-grey siltstone, silty mudstone, and shale. The Balang Fauna occurs in the upper part (Fig. 2C). *Isoxys* specimens occur 95–150 m away from the bottom of the formation, associated with other components of the Balang Fauna, *Guizhoueocrinus yui* Zhao *et al.*, 2007; *Tuzoia sinensis* Pan, 1957; palaeoscolecids; and the trilobites *Redlichia* (*Pteroredlichia*) *chinensis* (Walcott, 1905); *Arthricocephalus chauveaui* Bergeron, 1899; and *Arthricocephalites xinzhaiheensis* Chien & Lin *in* Lu *et al.* 1974.

## Material and methods

All *Isoxys* specimens (Figs 3–7) described here are deposited in the Guizhou Research Center for Paleontology, Guizhou University, Guiyang, China. Specimens with the prefix JLS were collected from the Lazizhai section of the Balang Formation near Lazizhai Village, Jianhe County, Guizhou Province, China.

Specimens were examined and imaged using standard light microscopy, digital macrophotography [Canon Rebel Xsi (450D) with a Canon 60 mm f/2,8]. Digital macrophotographs were stacked and rendered using Photoshop and CorelDraw software.

## Systematic paleontology

Phylum Arthropoda von Siebold, 1848
Class, Order, and Family uncertain

**Genus *Isoxys* Walcott, 1890**

*Type species*. – *Isoxys chilhoweanus* Walcott, 1890.

*Diagnosis*. – Emended. Modified from Williams *et al.* (1996), Vannier & Chen (2000), and García-Bellido *et al.* (2009b). Bivalved arthropod. Unmineralized carapace, semicircle, bivalved carapace connected in dorsal line (valves conjoined by a narrow band of cuticle; absence of articulating hinge), dorsal line straight or slightly convex in mid-position, dorsal line extends in front-to-back orientation to form long anterior and posterior cardinal spines. Lateral view weakly preplete to postplete, valve surface smooth or ornament expressed as uniform microreticulation or longitudinal striae or granulose. No dorsal spine or marginal spine, ventral margin smooth, or a very narrow lateroventral marginal ridge, or narrow to broad doublure present. Some species have a pair of large spherical stalk eyes and a pair of uniramous frontal appendages. Segments of the body trunk are less clear. Each segment has a pair of biramous appendages, which appear to consist of a pair of short segmented endopods and longer paddle-like exopods fringed with setae.

*Occurrence*. – North America, Europe, Siberia, Greenland, Australia, and China; Cambrian Series 2–3.

***Isoxys acutangulus* (Walcott, 1908)**
Figure 3

1908 *Anomalocaris acutangulus* sp. nov.; Walcott, p. 13, pl. 2: 5.
1928 *Anomalocaris acutangula* Walcott, 1908. – Walcott, p. 320.
1975 *Isoxys acutangulus* (Walcott, 1908). – Simonetta & Delle Cave, p. 6, pl. 5: 6, pl. 54: 3, 4, 6–9 [*non* 1 (= *Burgessia bella*)].
1986 "shrimp". – Collins 1986, p. 37, fig. 4.

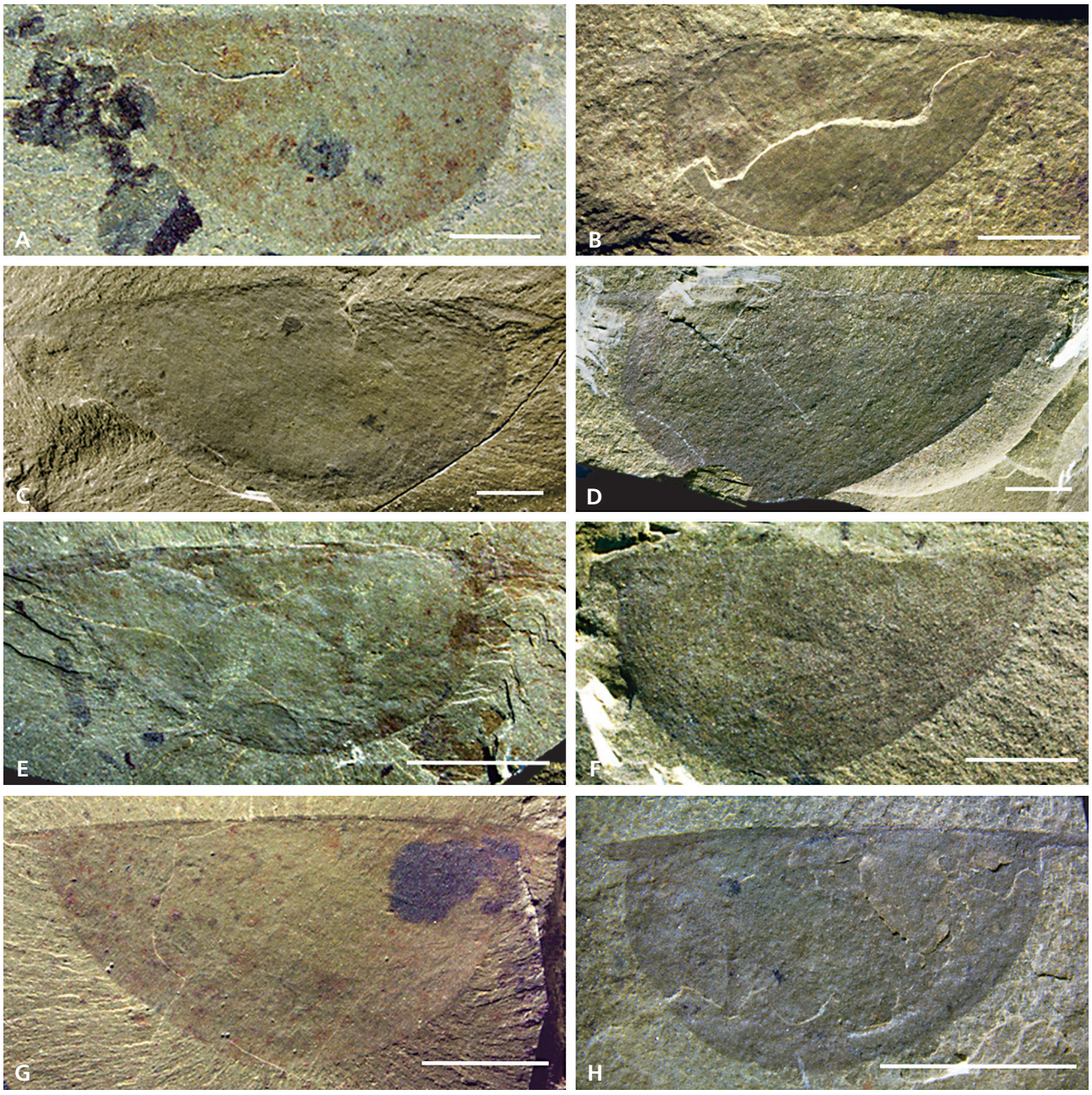


**Figure 3.** *Isoxys acutangulus* (Walcott, 1908), Lazizhai section, Balang Formation (Cambrian Stage 4) near Lazizhai Village, Jianhe County, Guizhou Province, China. All specimens are preserved only as hard shells without any soft parts. A – incomplete right valve with strong rostrum under acs, a thick-shell, surface layer partially falling off, JLS170-579; B – complete left valve with a thick shell, surface layer half falling off, JLS170-764; C – nearly complete right valve with strong rostrum under acs, JLS85-663; D – incomplete left valve with strong rostrum under acs, JLS170-1889; E – complete right valve with strong rostrum and cardinal spines, JLS170-682; F –incomplete left valve, JLS170-1755; G – complete right valve, JLS170-1528; H – complete left valve, juvenile individual, JLS170-680. Scale bars represent 5 mm.

1991 *Isoxys acutangulus* (Walcott, 1908). – Delle Cave & Simonetta, fig. 20f.
1991 "shrimp". – Delle Cave & Simonetta, fig. 23d.
1994 *Isoxys acutangulus* (Walcott, 1908). – Briggs *et al.*, p. 149, pl. 102.
2001 *Isoxys acutangulus* (Walcott, 1908). – Donovan & Lewis, fig. 1f.
2009b *Isoxys acutangulus* (Walcott, 1908). – García-Bellido *et al.*, p. 703, fig. 2.
2009 *Isoxys acutangulus* (Walcott, 1908). – Vannier *et al.*, p. 2570, fig. 2.

*Type species*. – The type material consists of 2 specimens from the Mt. Stephen Trilobite Beds, which occur within

the Campsite Cliff Shale Member, Burgess Shale Formation (Fletcher & Collins 1998). These are USNM 56521 (part and counterpart) and USNM 56521B. No holotype was designated in the original description by Walcott (1908: 13) (see García-Bellido *et al.* 2009b).

*Material*. – Over 120 specimens, most preserved as part and counterpart, 14 of them nearly complete, only 6 preserved the entire length of both cardinal spines; 25 of them preserved the anterior or posterior cardinal spines, other only preserved valve or partial valve.

*Diagnosis*. – *Isoxys* with strong amplete outline; relatively short, slightly droopy anterior cardinal spine; and very short posterior spine. Cardinal spines of each valve fold, joining to form a strong anterior and posterior rostrum; no lineated or reticulated micro-ornament on carapace (García-Bellido *et al.* 2009b).

*Description*. – Carapaces medium sized and semicircular, valve length ranges from 15.46 to 50.19 mm (excluding cardinal spines), and height from 8.78 to 26.16 mm. L:H ratio from 1.76 to 1.92. Anterior cardinal spine long and sharp with a thick base; the longest is 7 mm with a maximum thickness *ca*. 2.5 mm at the base. Posterior cardinal spine in short; the longest is 5 mm with a maximum thickness *ca*. 1.5 mm at the base. Greatest height located slightly anteriorly, near valve mid-length; anterior ventral margin more inflated than the posterior one (preplete outline). Ventral margin tapers regularly beyond the mid-length line toward the posterior cardinal spine. Carapace smooth.

*Remarks. – Isoxys acutangulus* differs from all congeneric species by its relatively short cardinal spines (see Vannier & Chen 2000), and does not show any lineated or reticulated microornament, as seen on *I. auritus* or *I. curvirostratus*. *I. acutangulus* is, so far, the species that displays the best-preserved soft-bodied features (*e.g.* visual and digestive organs, full series of appendages) (García-Bellido *et al.* 2009b). New specimens from the Balang Formation referred to this species have been examined. All preserved characteristics agree with the original material of *I. acutangulus* from the Stephen Formation (Cambrian Stage 5) of British Columbia, western Canada (see Vannier & Chen 2000, García-Bellido *et al.* 2009b, Vannier *et al.* 2009). However, the material from the Balang Formation lacks soft-parts, and individuals are generally larger than those from the Burgess Shale Biota. Perhaps this is because the species from Guizhou lived in an ecological environment different from that of British Columbia; or, we speculate that this species evolved by getting smaller.

*Occurrence*. – British Columbia, western Canada, the Stephen Formation (Cambrian stage 5); Lazizhai Village, Jianhe County, Guizhou Province, South China, the Balang Formation (Cambrian Stage 4).

***Isoxys auritus* (Jiang, 1982)**
Figure 4

1982 *Cymbia auritus*; Jiang *in* Luo *et al*., p. 265, 29, fig. 16.
1987 *Isoxys auritus* (Jiang, 1982). – Hou, pp. 286–292.
1995 *Isoxys auritus* (Jiang, 1982). – Shu *et al.*, pp. 333–342, figs 1–5.
1996 *Isoxys auritus* (Jiang, 1982). – Chen, p. 181, figs 240, 241.
1997 *Isoxys auritus* (Jiang, 1982). – Chen & Zhou, p. 65, fig. 94.
1999 *Isoxys auritus* (Jiang, 1982). – Luo *et al.*, pp. 13, 66, figs 1–4.
1999 *Isoxys auritus* (Jiang, 1982). – Hou *et al.*, p. 101, fig. 140.
2004 *Isoxys auritus* (Jiang, 1982). – Chen, p. 253, figs 392, 393.
2003 *Isoxys auritus* (Jiang, 1982). – Hou *et al.*, p. 116, figs 16.14, 16.15.
2011 *Isoxys auritus* (Jiang, 1982). – Schoenemann & Clarkson, pp. 223–230, figs 1–3.
2014 *Isoxys auritus* (Jiang, 1982). – Fu *et al.*, pp. 975–982, figs 2–7.

*Material*. – 52 specimens, 6 complete; the other 46 have partial valves preserved.

*Diagnosis*. – *Isoxys* with valves of medium size, ventral outline half-elliptical, anteriorly wide. Dorsal line straight or slightly domed at mid-length. Extended cardinal spines thin and elongate; anterior and posterior cardinal spines sub-equal in length. Ornaments on valves consist of fine lines and reticulations (after Hou *et al.* 2003 and Fu *et al.* 2014).

*Description*. – Valve are medium sized, elongate, and elliptical in outline. Length of valves ranges from 12.21 to 54.4 mm (excluding cardinal spines), and height from 5.96 to 26.48 mm; L:H ratio varies from 1.95 to 2.05. Greatest height located before mid-length (amplete outline). Dorsal hinge straight; the anterior cardinal spine could reach up to 8 mm, with a maximum thickness *ca*. 2.2 mm at the base. The posterior one is almost the same length with the anterior cardinal spine, with a maximum thickness *ca*. 1.8 mm at the base. Anterior ventral margin vaulted forward to some degree. The angle between the anterior spine axis and anterior margin (ada) is 74°–76°, and the angle between the posterior spine axis and posterior margin (pda) is 78°–80°. Some specimens present a doublure around the ventral margin. Carapace smooth.

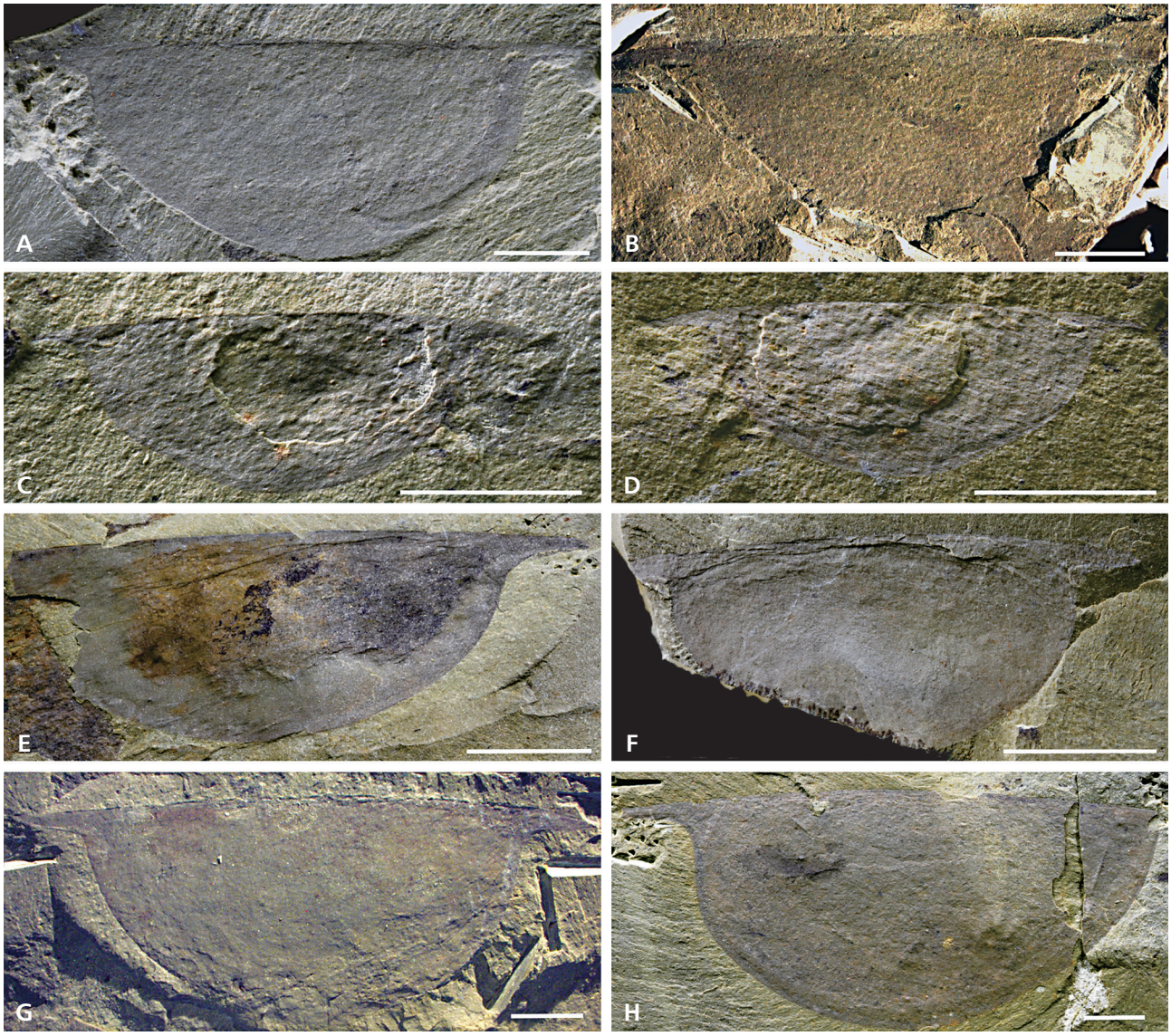


**Figure 4.** *Isoxys auritus* (Jiang, 1982), Lazizhai section, Balang Formation (Cambrian Stage 4) near Lazizhai Village, Jianhe County, Guizhou Province, China. A – complete left valve, lateral view, JLS170-537; B – nearly complete right valve with straight dorsal line, JLS170-614; C – complete right valve with asymmetric long acs and pcs, JLS77-6a; D – counterpart of C., JLS77-6b; E – complete right valve with more swollen anterior margin and small, short pcs, JLS170-989; F – incomplete right valve with part of postero-ventral missing, JLS160-134; G – complete right valve with obviously doublure, JLS160-2967; H – nearly complete left valve with strong and narrow ventral doublure, JLS85-110. Scale bars represent 5 mm.

*Remarks*. – Until now, *I. auritus* only occurred in the Chengjiang Biota. The new specimens from the Balang Fauna resemble the previously described materials from the Chengjiang Biota (*e.g.* Hou *et al.* 2003, Fu *et al.* 2011). The length of the valve exceeds 50 mm in some cases (excluding cardinal spines). These individuals are larger than those of the Chengjiang Biota. Disparities in individual sizes are probably attributable to the differing ecological factors of the localities. Because the Balang Formation was deposited in the relatively deep water of the outer shelf – as compared with the Heilinpu Formation (Chengjiang Biota), which was deposited in relatively shallow shelf environments (see Hou *et al.* 1999) or possibly because of ontogenetic age differences in the examined specimens (Fu *et al.* 2011), the ontogenetic morphology features of the carapace of *I. auritus* from the Balang Fauna belong to the preadult and adults stage, and there is a lack of fine lines or fine reticulation ornaments on the carapace. However, such ornament features are common among those of the Chengjiang Biota; perhaps these differences can be considered as sexual dimorphs (Fu *et al.* 2014). It is possible that the differences result in taphonomic bias.

Since the surfaces of the valves of the specimens from the Balang Fauna obviously lack sharpness, they are not comparable with those of the Chengjiang Biota.

*Occurrence*. – Kunming City, Yunnan Province, South China, the Maotianshan Shale of the Yu'anshan Member of the Helinpu Formation (previously Qiongzhusi Formation) (Cambrian Stage 3); Lazizhai Village, Jianhe County, Guizhou Province, South China, the Balang Formation (Cambrian Stage 4).

***Isoxys globulus* sp. nov.**
Figure 5

*Holotype.* – Complete left valve with both anterior and posterior spines. Length: 18.33 mm (excluding cardinal spines), height: 12.1 mm (JLS85-99) (Fig. 5C).

*Paratypes*. – Paratype 1: Incomplete left valve showing anterior ventral margin and anterior cardinal spine; height: 21.88 mm (JLS77-85) (Fig. 5D). Paratype 2: Incomplete left valve showing posterior ventral margin and posterior cardinal spine; height: 25.21 mm (JLS78-3) (Fig. 5G).

*Type horizon and locality*. – Stage 4, Series 2 of Cambrian, Lazizhai Village, Jianhe County, Guizhou Province, South China.

*Material.* – 25 specimens; 1 complete, 4 almost complete and the other 20 incomplete with partial valves.

*Etymology.* – Derived from the Latin *globulus*, rounded.

*Diagnosis*. – Valve large, ventral outline nearly semicircle, slightly wider anteriorly, dorsal line straight, subequal lengths of acs and pcs. Greatest height close to mid-length (amplete outline); angle between anterior spine axis and anterior margin (ada) 90°–110°, and later one between posterior spine axis and posterior margin (pda) 100°–110°. Valve L:H ratio: 1.55–1.69. Both anterior and posterior ventral margins rounded; anterior margin more swollen; carapace surface is smooth.

*Description*. – Ventral outline nearly round, wider anteriorly, length ranges from 13.44 to 56.54 mm (excluding cardinal spines), and height from 7.93 to 33.45 mm; L:H ratio from 1.55 to 1.69. Dorsal line straight, lengths of acp and pcp subequal; however, lengths of the cardinal spines in both juvenile and adult stages vary from 31.3% to 19.6% of the total length, taking the length of the shield, ada 90°–110°, pda 100°–110°; anterior cardinal spine *ca*. 6–10 mm long, while posterior one varies from 5.5 to 10 mm in length. Over the ontogenetic stages, the position of greatest height changes from close to mid-length (amplete outline) to the anterior ventral margin (preplete outline). Anterior and posterior cardinal spines range from slender, short to thick and long, and broad at the base. The anterior ventral margin is vaulted more obviously than the posterior ventral margin. Carapace smooth.

*Remarks*. – *I. globulus* differs from all congeneric species through the characteristics of a bloated body and no lineated nor reticulated micro-ornaments. Meanwhile, acs and pcs are subequal in length, but both have a thick, broad base, which differs from *I. auritus*. *I. globulus* is, so far, the species displaying the largest valves, with a length of 56.54 mm (excluding cardinal spines) and a height of 33.45 mm. The features of the new species – a more rounded anterior ventral margin, smooth carapace without ornaments, anterior and posterior ventral margins nearly symmetrical, and larger-sized individuals – are clearly distinguished from those of other species of *Isoxys*.

*Occurrence.* – Lazizhai Village, Jianhe County, Guizhou Province, South China, the Balang Formation (Cambrian Stage 4).

***Isoxys jianheensis* sp. nov.**
Figure 6

*Holotype.* – Right-valve with part and counterpart; length: 17.65 mm, height: 11.47 mm (JLS170-2030a, b) (Fig. 6A, B).

*Paratypes.* – Paratype 1: Complete right valve showing clear posterior cardinal spine; length: 18.53 mm, height: 11.51 mm (JLS170-670) (Fig. 6C). Paratype 2: Carapace preserved in "butterfly" position. Dorsal view shows lateral ridge and obviously broad marginal doublure. Length: 18 mm, height: 9 mm (JLS160-141) (Fig. 6G).

*Type horizon and locality*. – Stage 4, Series 2 of Cambrian, Lazizhai Village, Jianhe County, Guizhou Province, South China.

*Material.* – 28 specimens; 3 complete, 3 almost complete, and 19 incomplete with partial valves.

*Etymology.* – From the name of Jianhe, Guizhou, China, where the Balang Fauna is located.

*Diagnosis.* – Valve medium sized, semi-oval in outline, subequally wide anteriorly and posteriorly and straight dorsal line. Maximum valve height located at mid-length (amplete outline). Valves armed with a droopy and broad-based anterior cardinal spine; posterior pine small, short, and pointing slightly upward. Ventral margin shows a broad doublure. Short lateral ridge located in the lower-middle part of the valve, forming a short line that does not reach the ventral margin toward the posterior ventral oblique

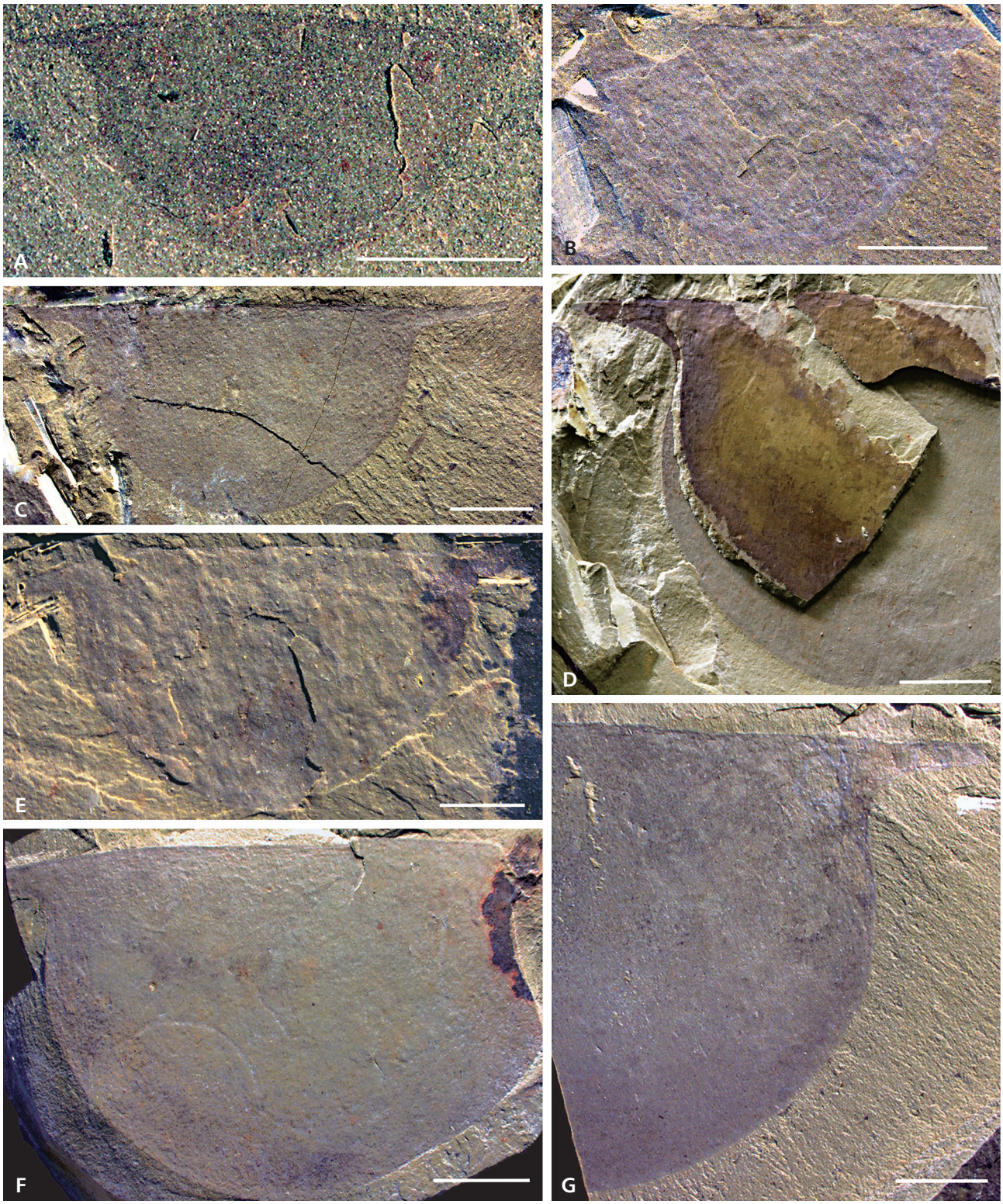


**Figure 5.** *Isoxys globulus* sp. nov., Lazizhai section, Balang Formation (Cambrian Stage 4) near Lazizhai Village, Jianhe County, Guizhou Province, China. A – juvenile left valve with a thick and pointed acs, JLS170-1704; B – incomplete right valve, JLS160-558; C – complete left valve, with ventral margin and asymmetric long acs and pcs in the dorsal line, holotype, JLS85-99; D – incomplete left valve with strong acs and enlarged anterior ventral margin, JLS77-85; E – nearly complete left valve with amplete outline, JLS85-773; F – incomplete left valve lacking cardinal spines, and line-like trace fossils on the valve surface, JLS85-193; G – incomplete left valve with posterior ventral margin and pcs, JLS78-3. Scale bars represent 5 mm.


**Figure 6.** *Isoxys jianheensis* sp. nov., Lazizhai section, Balang Formation (Cambrian Stage 4) near Lazizhai Village, Jianhe County, Guizhou Province, China. A, B – part and counterpart of completely preserved right valve, with lateral ridge, broad marginal doublure and microornament on the surface of the valve, holotype, JLS170-2030a, b; C – complete right valve with strong acs and minor pcs, lateral ridge and microornament can be seen on the valve, paratype 1, JLS170-670; D –complete right valve with a thick shell, partial layer falling off in the mid- to posterior area of the ventral margin, lateral ridge, and asymmetrical cardinal spines, JLS160-260; E – incomplete ventral part with clear lateral ridge and compression lines as well as broad marginal doublure, JLS160-249; F – incomplete right valve lacking cardinal spines with clear lateral ridge and compression lines, JLS160-117; G – specimen in "butterfly" position, dorsal view with lateral ridge, broad marginal doublure, lacks acs and pcs, paratype 2, JLS160-141; H – juvenile right valve, with minute posterior cardinal spine and postplete outline, JLS160-886. Scale bars represent 5 mm.

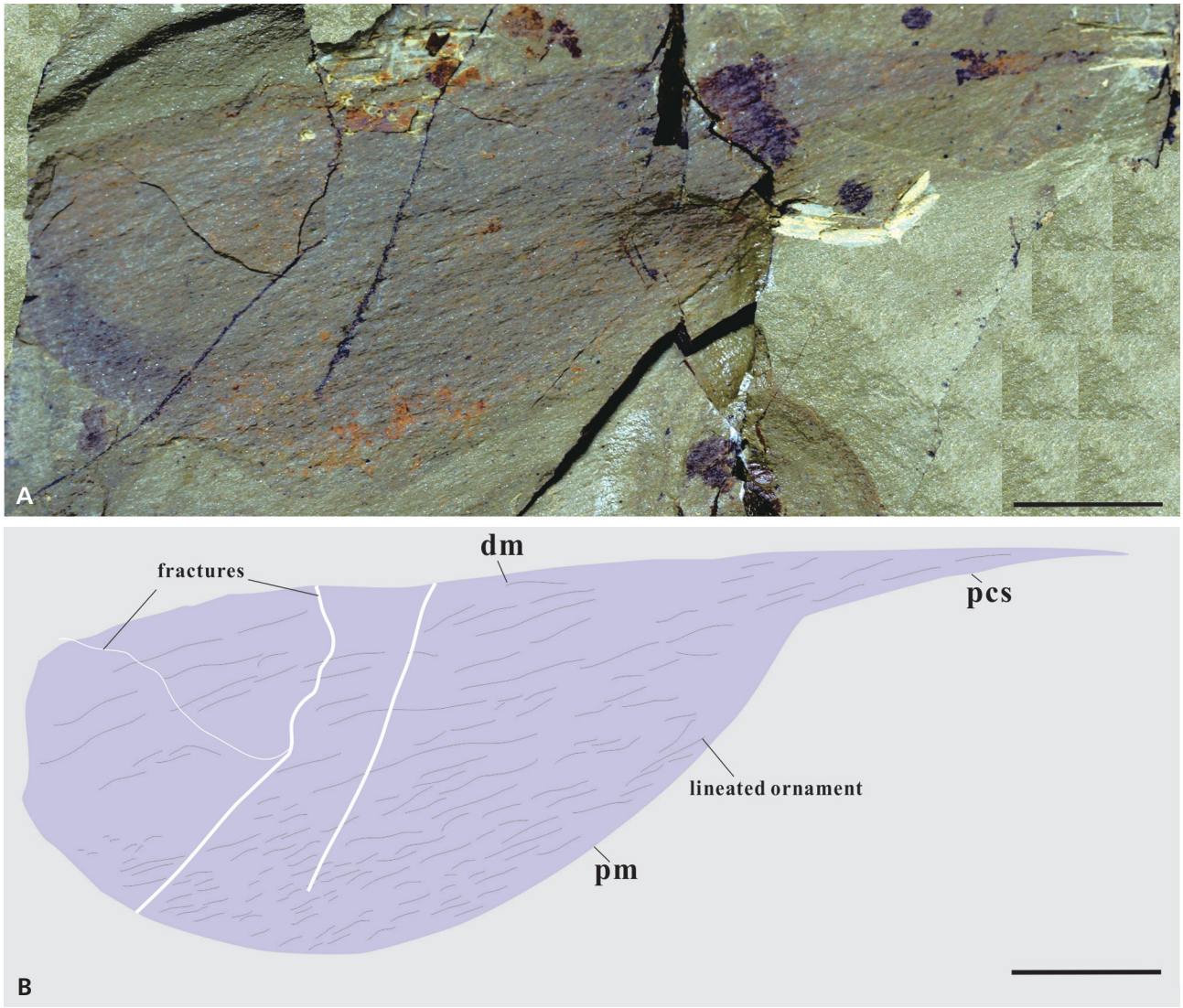


**Figure 7.** *Isoxys* sp., Lazizhai section, Balang Formation (Cambrian Stage 4) near Lazizhai Village, Jianhe County, Guizhou Province, China. A – incomplete left valve without anterior spine, posterior spine long and sharp, JLS170-1160; B – interpretative drawing of A. Scale bar represents 10 mm.

stretch. Position of the lateral ridge is located at the point of the valve vaulting. Faint microreticulated ornaments formed by adjacent hexagons on surface of valve.

*Description*. – Valve medium sized, semi oval outline, wide anterior ventral, almost equal posterior one. Length: 14.2–36.33 mm (excluding cardinal spines); height: 9.73–23.14 mm; L:H: 1.46–1.57. Dorsal margin nearly straight with gentle, dorsally directed flexure about one-third of the way from the anterior end. Anterior cardinal spine ranges from 3.0 to 6.0 mm in length, posterior one from 0.5 to 3.0 mm. Angle between the anterior spine axis and the anterior margin (ada) between 100° and 115°, and the pda between 120° and 135°. Surface of the valve covered by a microreticulated pattern. Reticulation varies, with a general diameter of about 1.4 mm. The reticulate pattern is ill-defined or obliterated on some specimens. Short lateral ridge in the lower-middle part of the valve forms a short line that does not reach the ventral margin toward the posterior ventral oblique stretch; lateral ridge located at the point of the valve vaulting.

*Remarks*. – The new species closely resembles *I. auritus*. Their similarities include the semi-oval outline, marginal doublure, microreticulate pattern, and similar ratio of valve length and height. However, the front broad ventral marginal doublure, the almost symmetrical anterior and posterior ventral, and the lateral ridge can distinguish from the latter. Especially, the characteristic of the lateral ridge in the new species is completely distinct from all species

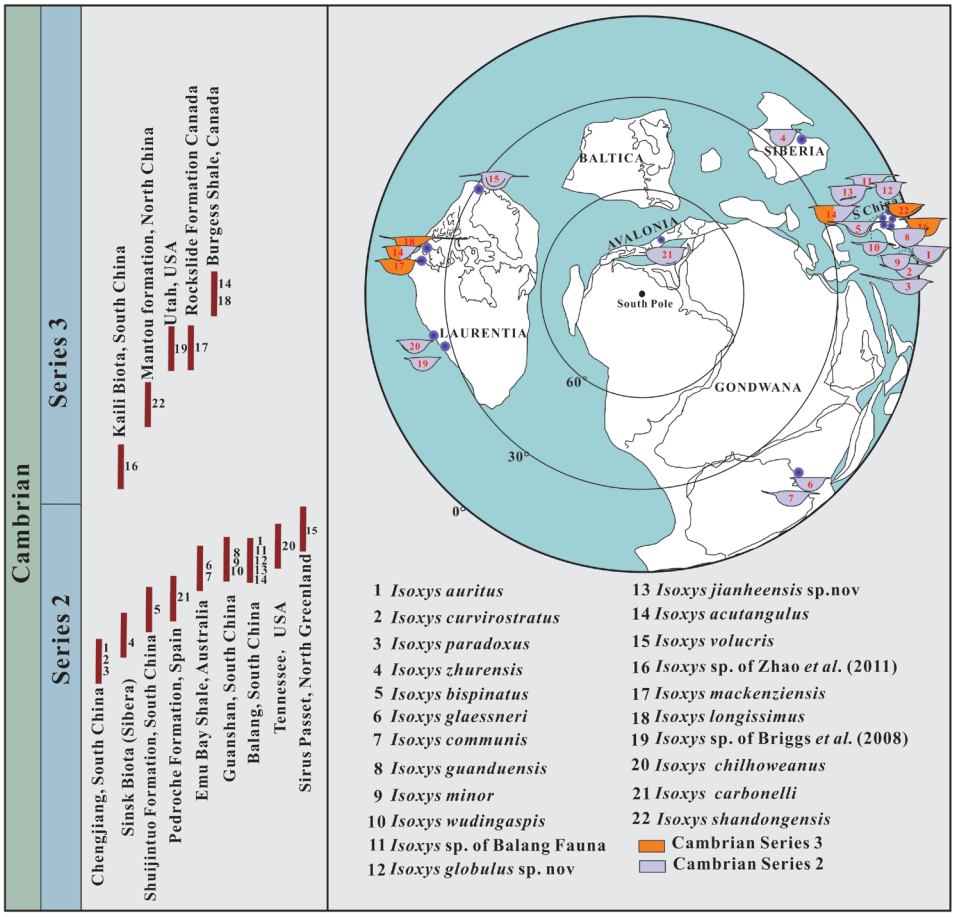


**Figure 8.** Global stratigraphic range of biotas containing *Isoxys*, Cambrian. Palaeogeographic distribution of all species of *Isoxys*; each taxon indicated by sequence number, corresponding to those beside the biotas. Map after McKerrow *et al.* (1992) and Cocks & Torsvik (2002)

of *Isoxys*. These valve features resemble the structure of *Tuzoia*. However, *Tuzoia* has relatively short anterior and posterior cardinal processes, marginal spines, lateral ridge long and straight located at mid-height to reach marginal spines on the poster ventral; its valve surface is covered by a reticulate pattern of fine ridges with small meshwork, including anterior and posterior cardinal processes, dorsal line, and even lateral ridge positions on each valve. The new species do the microfine on valve surface, the lack of marginal spines, and the short and slightly oblique lateral ridge, which can be clearly distinguishing from those of *Tuzoia*. Thus, *I. jianheensis* sp. nov. should be a species of *Isoxys* with a lateral ridge, belonging to a new taxon.

*Occurrence*. – Lazizhai Village, Jianhe County, Guizhou Province, South China, Balang Formation (Cambrian Stage 4).

***Isoxys* sp.**
Figure 7

*Material*. – One specimen incompletely preserved (JLS170-1160).

*Diagnosis*. – Valves large, elongated, near elliptical, broad anteriorly, straight dorsal line, greatest height before the mid-length of the valve, long posterior cardinal spine.

*Description*. – Incomplete specimen: left valve, nearly elliptical, broad anteriorly, straight dorsal line, greatest height before mid-length. Length: 43 mm (excluding cardinal spines), and height: 26 mm. The carapace is large, with a long, straight posterior cardinal spine, more than 21 mm fully extended. Anterior cardinal spine (acs) missing, so the total length of the valve exceeds 70 mm (only including posterior cardinal spines). Carapace shows micro-lineated ornament, perhaps caused by compaction.

*Remarks*. – *Isoxys* sp. and *I. paradoxus* have similar outlines, all with huge and long pcs. However, the length of the posterior cardinal spine of *I. paradoxus* is greater than that of the carapace, and the pcs length of *I.* sp. is only half the length of the valve, although acs information for *I.* sp. is unknown. *I.* sp. also differs from *I. longissimus* with its relatively short pcs; the length of the posterior cardinal spine of *I. longissimus* exceeds the length of the valve.

Thus, *I.* sp. can be easily distinguished from other species by its huge, and its possible microlined ornament.

*Occurrence*. – Lazizhai Village, Jianhe County, Guizhou Province, South China, the Balang Formation (Cambrian Stage 4).

## Discussion on stratigraphic range of Isoxys and its palaeogeographic distribution

*Isoxys* is a cosmopolitan genus. Its special morphological characteristics, including the features of its soft body parts, such as the uniformous series of exopodal paddles fringed with long setae and the relative reduction of the endopodal rami (Vannier & Chen 2000), and its wide distribution in the continental shelf, as well as in deep-water slope areas, suggest that it should be a swimming animal with dispersal capabilities similar to modern pelagic organisms (Williams *et al.* 1996, Vannier & Chen 2000, Vannier *et al.* 2009, Huang & Wang 2015). Based on palaeomagnetic data (McKerrow *et al.* 1992, Cocks & Torsvik 2002), all species of this genus reported occur in a range between 30° N and 30° S (Williams *et al.* 1996). Therefore, they are absent from the higher-latitude areas of the southern hemisphere, such as Baltica, Avalonia, and South America, which hints at some temperature control. Some species may have strong dispersal capabilities, such as *I. acutangulus* while others belong to endemic forms (see Fig. 8). The specimens from the Balang Fauna bring new data which provide a better understanding of palaeogeograpical distribution of *Isoxys*. *Isoxys* group from the Balang Fauna shares one taxon with the Chengjiang Biota (Cambrian Stage 3) and the Burgess Shale Biota (Cambrian Stage 5) respectively, the Balang Formation represents primarily fine-grained siliciclastic sedimentation of the Transitional Slope Belt between the shallow Yangtze (or South China) Platform and the Jiangnan Basin. Here, remains of *Isoxys* are preserved in deeper water deposits beyond the shelf margin. Globally, most other occurrences of the genus are in shallow-shelf to deep-shelf deposits. The remains are parautochthonous (Liu *et al*. 2017), they occurrence in the Balang Formation extends our knowledge of the geographic occurrence and paleoecology of this arthropod.

## Conclusion

*Isoxys* is a large bivalved arthropod with uncertain affinity that is well represented in strata of global Cambrian Series 2–3. The wide distribution of this group is possibly indicative of a swimming style. Assemblage of *Isoxys* described herein from the Balang Formation, Lazizhai Village, Jianhe County, Guizhou Province, China, includes five species: *Isoxys acutangulus* (Walcott, 1908), *I. auritus* (Jiang 1982), *I. jianheensis* sp. nov., *I. globulus* sp. nov., and *Isoxys* sp., which shares one taxon with the Chengjiang Biota (Cambrian Stage 3) and one with the Burgess Shale Biota (Cambrian Stage 5) and provides new essential information to a better understanding of the evolutionary pattern of these taxa in timeline, in terms of geographic distribution. The *Isoxys* species from the Balang Fauna are comparable with that of the equivalent Guanshan Biota. Observations of new taxa from the Balang Fauna open a new stratigraphic window on the diversity and early evolutionary history of this genus.

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