

# A new eocrinoid from the Guanshan Biota (Cambrian Series 2, Stage 4), with implication of the development of different attachment modes in early Cambrian

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Received 26 February 2021; received in revised form 29 July 2021; accepted 4 August 2021

Available online 12 August 2021

## Abstract

Eocrinoids are scarce in the Guanshan Biota (Cambrian Series 2, Stage 4), Yunnan Province, southwest China. Here, we introduce a new gogiid: *Kunmingeocrinus cupuliformis* n. gen. n. sp. which is characterized by a short stalk and a well-developed attachment disc. Preservation may indicate a weakly biomineralized body for the new taxon. Morphological similarities between the new taxon and other eocrinoids with attachment discs from Cambrian Lagerstätten of Guizhou Province (Series 2, Stage 4 and Miaolingian, Wuliuan) might suggest a similar mode of life. The eocrinoids from the Guanshan Biota possibly utilized different attachment modes.

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**Keywords:** Echinodermata; Eocrinoidea; attachment disc; Cambrian Lagerstätten

## 1. Introduction

Eocrinoids, with more than 20 genera, are a group of primitive echinoderms which are mainly found in Cambrian and Ordovician strata from Europe, North America, Siberia, Australia, North Africa and China (Robison, 1965; Ubags, 1968; Sprinkle, 1973, 1976, 1992; Zhao et al., 1994, 2007; Parsley and Zhao, 2006, 2010; Lin et al., 2008; Zamora et al., 2013; Allaire et al., 2017; Deline et al., 2020). Articulated eocrinoids have been described from the Cambrian Kaili (Miaolingian, Wuliuan) and Balang (Series 2, Stage 4) biotas of southwest China (e.g., Zhao

et al., 2007, 2011), the Wuliuan Mantou Formation of northeast China (Huang, 2012), and the Furongian Guole Formation of south China (Chen and Han, 2014). These occurrences have greatly expanded the paleogeographic and geochronologic distributions of eocrinoids.

Compared with those from Guizhou Province, Cambrian articulated eocrinoids from Yunnan Province are scarce in abundance and diversity. *Wudingeocrinus rarus* Hu and Luo in Luo et al., 2008 was the first and the only eocrinoid hitherto known from the Guanshan Biota in Yunnan Province (Luo et al., 2008; Hu et al., 2013). In this study, we describe and discuss a new eocrinoid genus and species, which is different from *Wudingeocrinus* in some morphological aspects, notably with a short stalk and a well-developed attachment disc. The new material not only

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provides additional data on the early evolution of echinoderms, but also shows that eocrinoids from the same biota had possibly developed different attachment modes.

## 2. Material and methods

All described fossils come from the Gaoloufang section (102.80539°E, 24.95916°N), Kunming, Yunnan Province, southwest China. *Wudingeoocrinus rarus* Hu and Luo in Luo et al., 2008 (specimens YKLP 13388 and YKLP 13389) was collected in 2013 and the new form (specimens YKLP 13387 and CJHMD 00035) was collected in 2020. All specimens were prepared using a needle under a Nikon SMZ 800N microscope, revealing parts covered by matrix. Digital photographs were taken using a Canon EOS 5D SR camera with a Canon MP-E 65 mm (1–5×) macro lens, under cross-polarized light and processed in Adobe Photoshop CS 5. Line drawings were made using Adobe Illustrator CS 5. Terminology follows Parsley and Zhao (2006) and Lin et al. (2008). YKLP 13387, YKLP 13388 and YKLP 13389 are housed at the Yunnan Key Laboratory

for Palaeobiology, Yunnan University (YKLP), and CJHMD 00035 is housed at the Chengjiang Fossil Museum of the Management Committee of the Chengjiang Fossil Site World Heritage, China.

## 3. Systematic palaeontology

Phylum Echinodermata Klein, 1734  
Subphylum Blastozoa Sprinkle, 1973  
Class Eocrinoidea Jaekel, 1918  
Order Gogiida Broadhead, 1982  
Family Eocrinidae Jaekel, 1918 emend.

*Kunmingeoocrinus* n. gen.

**Etymology:** From the city of Kunming, Yunnan Province, southwest China, where the specimens were collected.

**Type species:** *Kunmingeoocrinus cupuliformis* n. gen. n. sp.

**Diagnosis:** Eocrinoid composed of brachioles, a theca, a stalk and an attachment disc. At least six brachioles, coiled. Theca sac-like or in an inverted-cone shape, plates polygonal (irregular in the holotype and mostly hexagonal

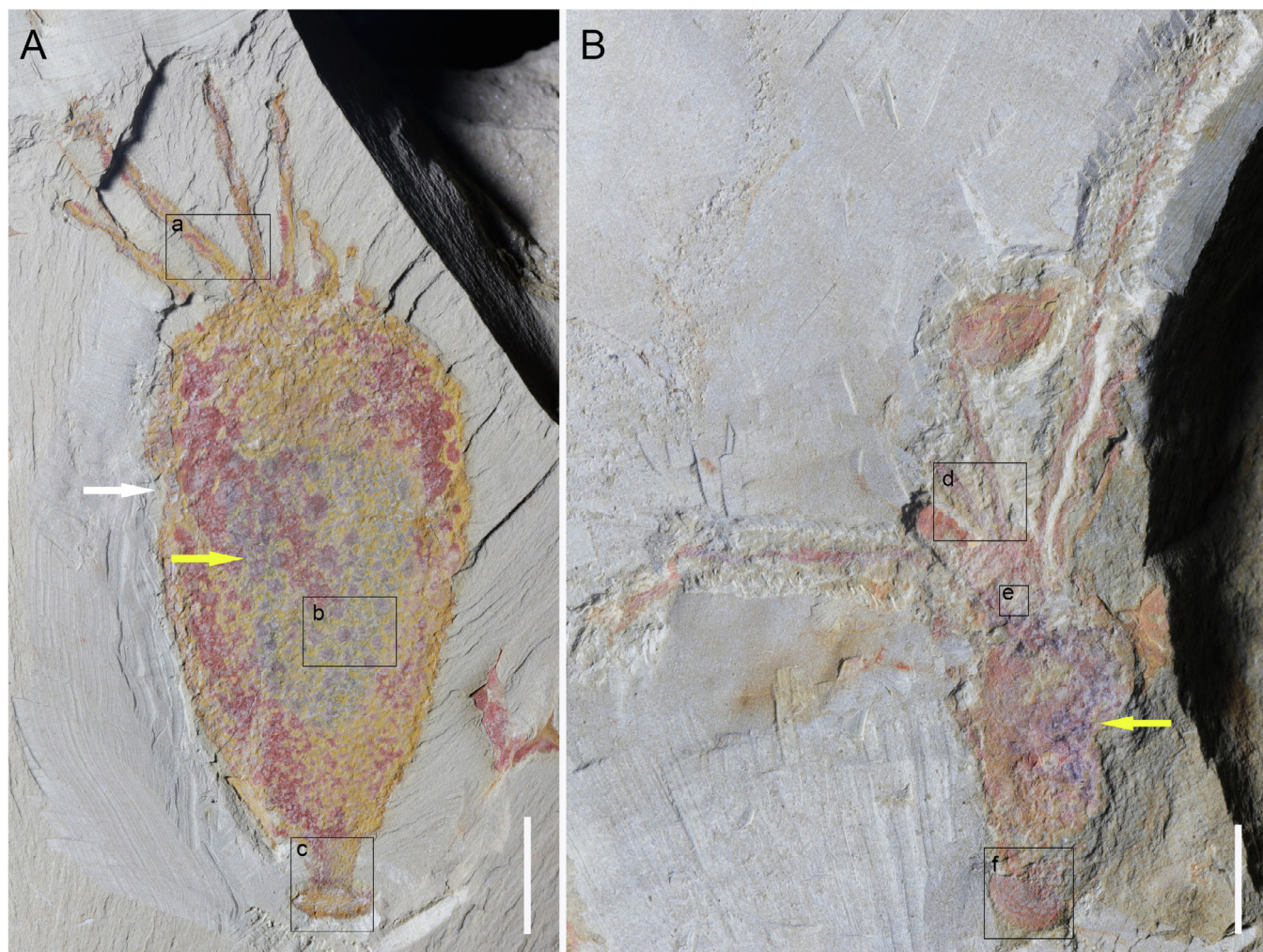


Fig. 1. *Kunmingeoocrinus cupuliformis* n. gen. n. sp. (A) Overall profile of CJHMD 00035; white arrow points to a notch-like structure on the left margin of the theca; yellow arrow points to the black coelom. (B) Overall profile of YKLP 13387; yellow arrow points to the black coelom. Scale bar = 5 mm.



in the paratype). Stalk short and polyplated. Attachment disc large and flat, having seven circlets of polygonal platelets.

**Remarks:** *Kunmingeocrinus* n. gen. (Fig. 1) differs from *Wudingeocrinus* Hu and Luo in Luo et al., 2008 (Fig. 4), the first-known eocrinoid from the Guanshan Biota, mostly in the stalk morphology and presence of a basal attachment disc. *Wudingeocrinus* has a slim and elongated stalk, the length of which could be as twice that of the theca (Wu et al., 2017, fig. 1A), while the stalk of the new genus is rather short (Figs. 1, 4). A well-developed and polyplated attachment disc is present in the new genus (Figs. 1, 4), but absent in *Wudingeocrinus*.

Three genera with four species of Gogiida have been documented from the Cambrian Series 2, Stage 4 and Miaolingian, Wuliuan, Guizhou Province: *Sinoeocrinus* lui Zhao et al., 1994, *Globoeocrinus globulus* Zhao et al., 2008 from the Kaili Biota; *Guizhoueocrinus yui* Zhao et al., 2007 and *Globoeocrinus zhaoyuanlongensis* Yang et al., 2015 from the Balang Fauna. *Kunmingeocrinus* n. gen. is assigned to the order Gogiida based on overall profile, including bra-

chioles, theca, stalk and attachment disc. It is the first representative of gogiid discovered from the Guanshan Biota (Cambrian Series 2, Stage 4), Yunnan Province.

In the detailed morphologies of brachioles, theca, stalk and attachment disc, *Kunmingeocrinus* shows the following differences from *Sinoeocrinus*, *Globoeocrinus* and *Guizhoueocrinus*: brachioles of *Sinoeocrinus* are not clearly coiled; theca plates are regularly arranged on the theca surface; the size of theca plate relative to that of theca is much larger than that of *Kunmingeocrinus*; an anal pyramid is present on *Sinoeocrinus*, but absent from *Kunmingeocrinus*; the stalk of *Sinoeocrinus* is much elongated and the size of stalk plate relative to that of stalk is larger than that of *Kunmingeocrinus*; compared to that of *Kunmingeocrinus*, the attachment disc of *Sinoeocrinus* is smaller in size (Zhao et al., 2011, figs. 206–209); the theca of *Globoeocrinus* is spherical in shape and covered by regularly arranged plates; compared to *Kunmingeocrinus*, the size of theca relative to that of the body is much smaller, while the size of theca plates relative to that of the theca is bigger (Zhao et al., 2011, figs. 210–214); the stalk of *Guizhoueocrinus* is

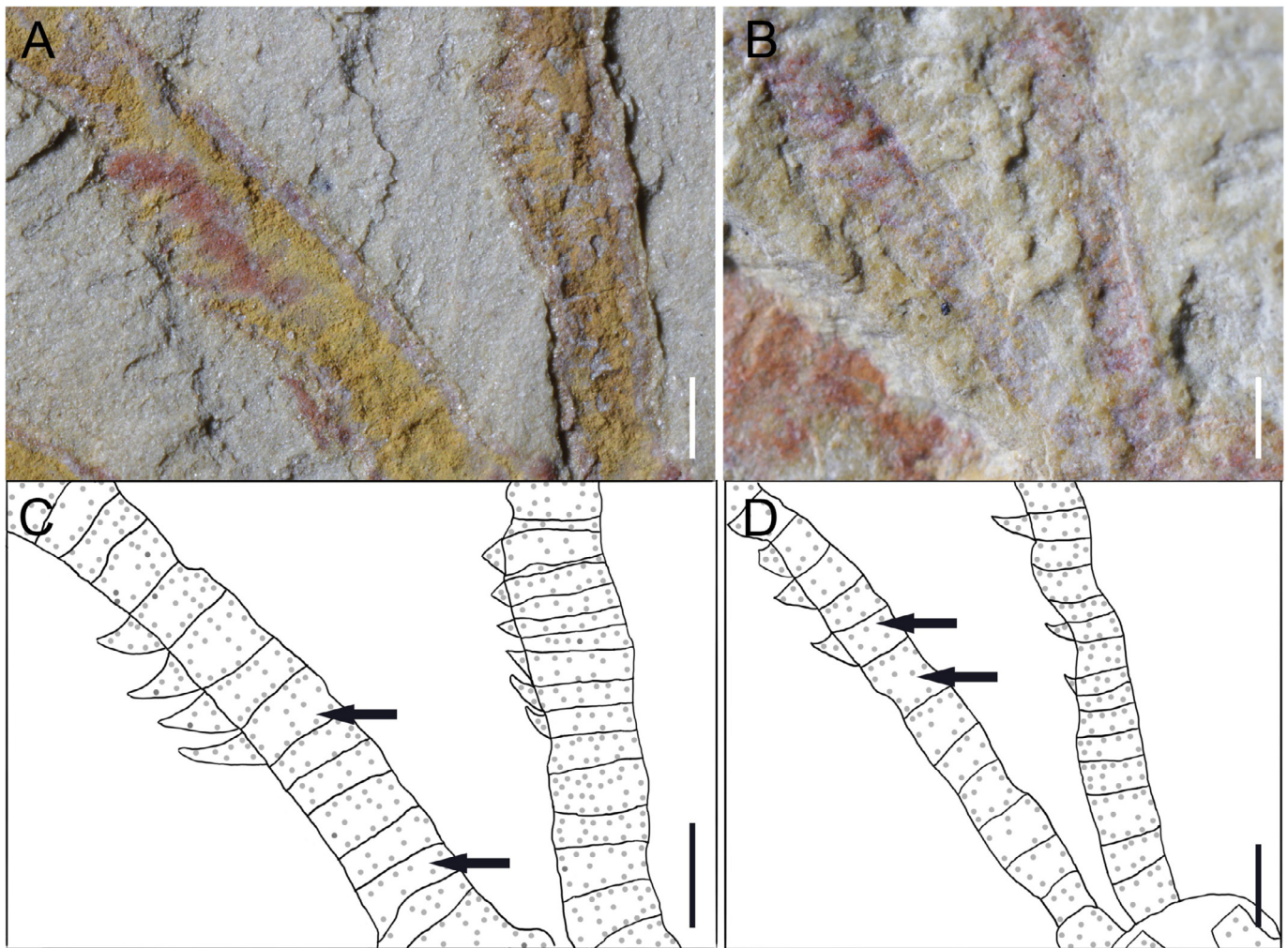


Fig. 2. *Kunmingeocrinus cupuliformis* n. gen. n. sp. (A) Detail of brachioles in CJHMD 00035 (position marked by frame a in Fig. 1A). (B) Detail of brachioles in YKLP 13387 (position marked by frame d in Fig. 1B). (C) Interpretive line drawing of (A); black arrows point to the plates on one brachiole. (D) Interpretive line drawing of (B); black arrows point to the plates on one brachiole. Scale bar = 0.5 mm.



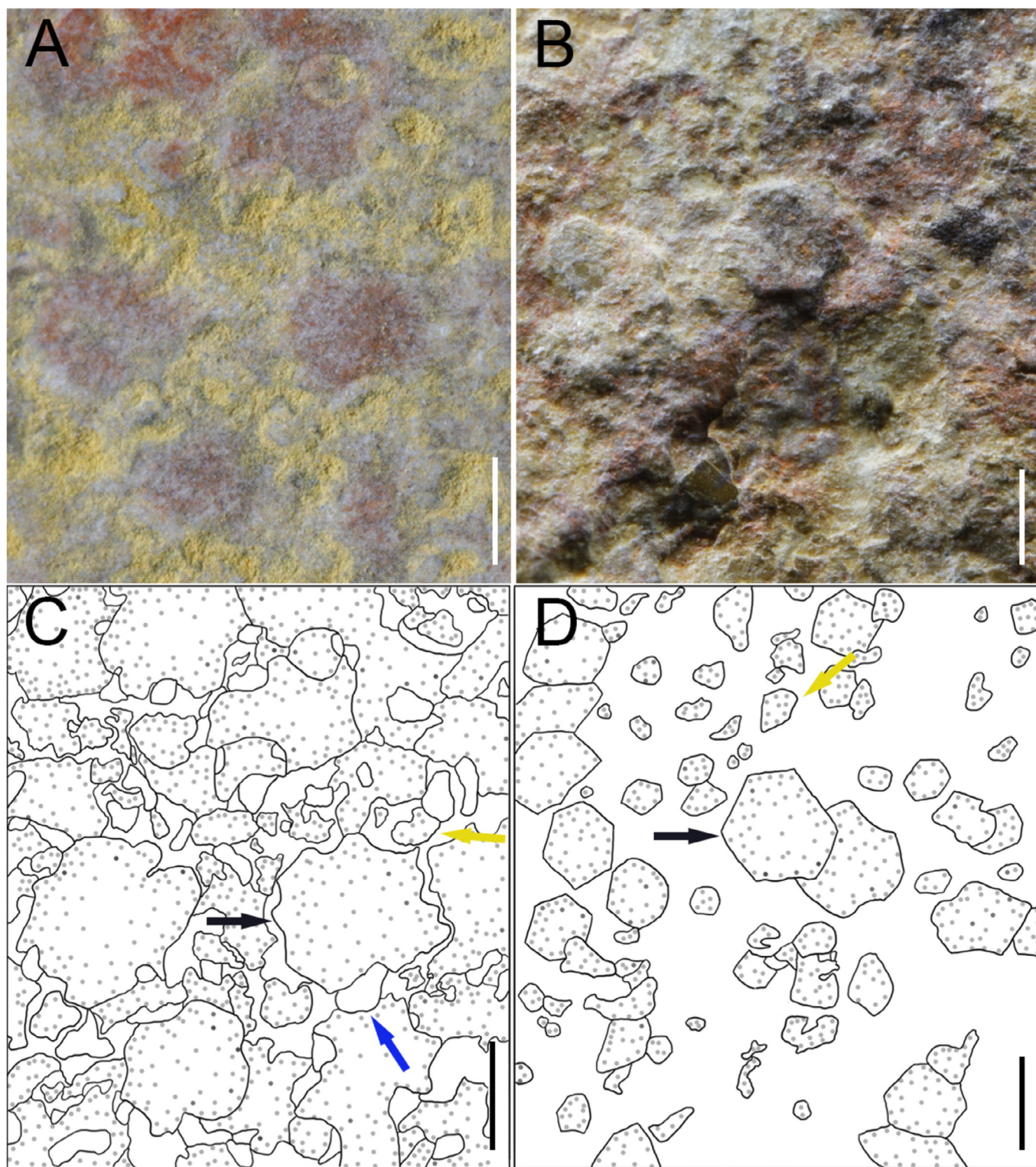


Fig. 3. *Kunmingeocrinus cupuliformis* n. gen. n. sp. (A) Detail of the theca plates in CJHMD 00035 (position marked by frame b in Fig. 1A). (B) Detail of the theca plates in YKLP 13387 (position marked by frame e in Fig. 1B). (C) Interpretive line drawing of (A); black arrow points to a polygonal theca plate; blue arrows point to an epispire; yellow arrows point to a fragmentary theca plate. (D) Interpretive line drawing of (B); black arrow points to a hexagonal theca plate; yellow arrow point to a fragmentary theca plate. Scale bar = 0.5 mm.

much elongated, and the attachment disc is much smaller; furthermore, the size of theca plates relative to that of theca is bigger (Zhao et al., 2007, figs. 5–7).

*Kunmingeocrinus cupuliformis* n. sp.  
(Figs. 1–4)



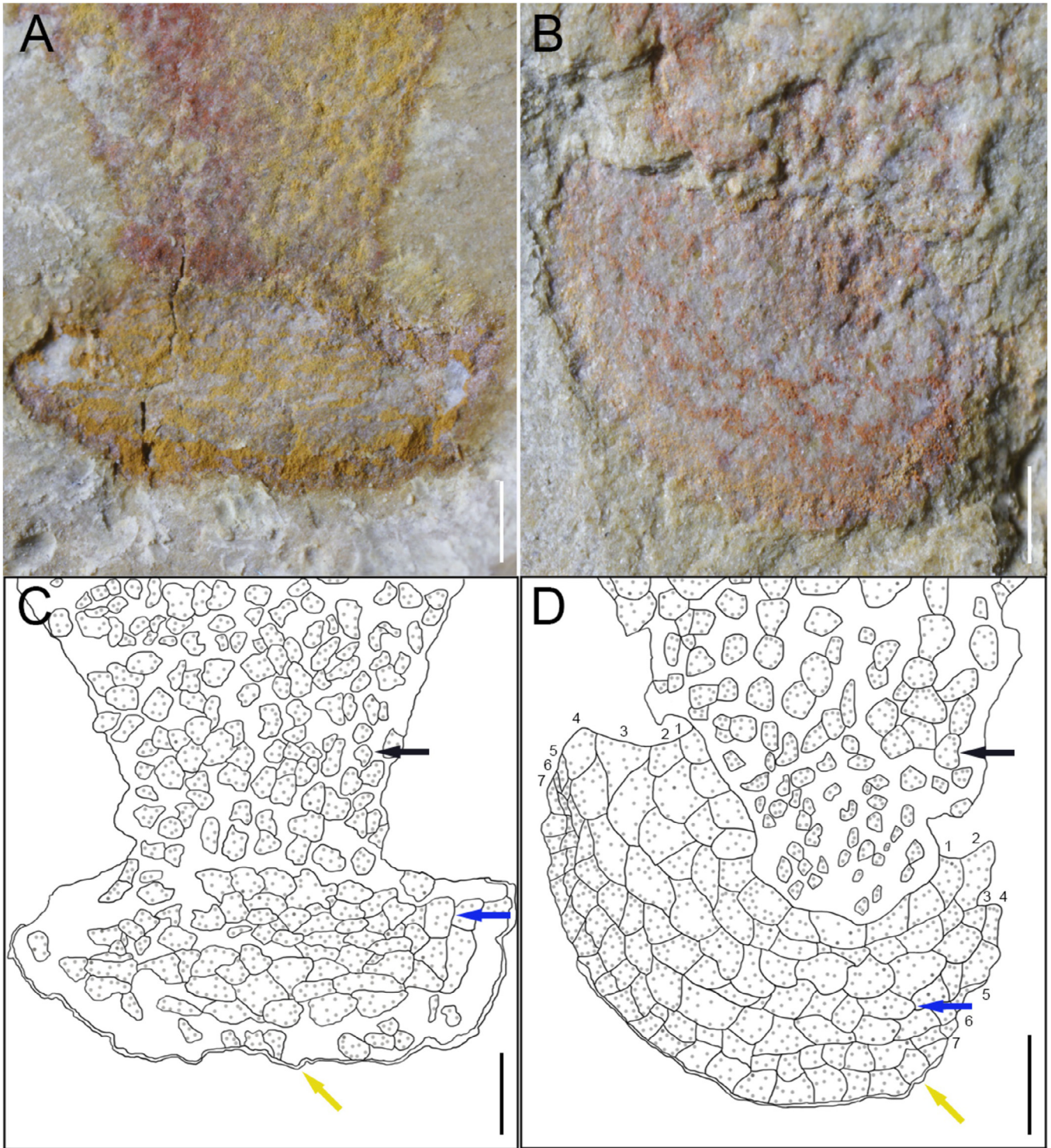


Fig. 4. *Kunmingeocrinus cupuliformis* n. gen. n. sp. (A) Detail of the stalk and attachment disc in CJHMD 00035 (position marked by frame c in Fig. 1A). (B) Detail of the stalk and attachment disc in YKLP 13387 (position marked by frame f in Fig. 1B). (C) Interpretive line drawing of (A); black arrow points to a polygonal imprint of a stalk plate; blue arrow points to a polygonal ornament on the attachment disc; yellow arrow points to the possible transitional zone. (D) Interpretive line drawing of (B); black arrow points to a polygonal imprint of a stalk plate; blue arrow points to a polygonal ornament on the attachment disc; yellow arrow points to the possible transitional zone; 1–7 indicate the seven circles of polygonal ornaments on the attachment surface. Scale bar = 5 mm.

**Etymology:** From the Latin word *cupuliformis*, cup-shaped, referring to the overall profile of this species.

**LSID:** urn:lsid:zoobank.org:pub:136A27F3-75D1-4A4F-B278-3DF453BFFD94.

**Holotype:** CJHMD 00035. The holotype was collected in Cambrian Series 2, Stage 4, Wulongqing Formation, *Palaeolenus* biozone, Gaoloufang section, Kunming City, Yunnan Province, southwest China.

**Paratype:** YKLP 13387. Its location and horizon are the same with the holotype.

**Diagnosis:** As for genus (monotypic).

**Description:** The new eocrinoid has a cup-shaped body, composed of, from top to base, brachioles, theca, stalk and attachment disc (Fig. 1). The holotype measures ca. 22 mm in height (excluding brachioles) and 14 mm in maximum width (on upper part of theca), while the paratype is ca. 11 mm in height and ca. 5 mm in maximum width. At least six unbranched and coiled brachioles with tiny brachiolar plates can be recognized (Fig. 2). Theca is sac-like or inverted cone-shaped, with upper surface slightly arched. Theca plates are polygonal: sprocket-shaped in the holotype (Fig. 3A, C) and mostly hexagonal in paratype (Fig. 3B, D). Epispires and fragments of theca plates are present in the holotype, and only fragments of theca plates are present in the paratype (Fig. 3). Black patch (Fig. 1) covering middle part of theca is interpreted as coelom (as in *Wudingeocrinus rarus*, e.g., Wu et al., 2017, fig. 5). Stalk is short, subcylindrical in profile (Figs. 1, 3). The width of the stalk is about one-fifth of maximum width of theca, and the height is 1/11 of that of body (excluding brachioles). There are imprints of polygonal plates (Fig. 4) on the stalk surface, but no clear pattern is discernible. Attachment disc is suboval, situated at base of stalk (Fig. 4). The width is ca. three-fifths of maximum width of theca, and the heights are 1/22 and 1/11 of body height in the holotype and paratype respectively. Circlets (seven in paratype) of tiny polygonal ornaments are discernible on attachment disc surface (Fig. 4), interpreted as imprints of platelets (cf. those described in *Globoeocrinus globulus* Zhao et al., 2008; e.g., fig. 2.3 in Zhao et al., 2008 and fig. 6.6 in Yan et al., 2010). Margin of attachment disc is fringed by yellow stripe (Fig. 4), which possibly corresponds to the transitional zone discerned in *Globoeocrinus globulus* (Yan et al., 2010, fig. 4), based on location and morphology.

**Remarks:** The holotype shows a curve on the left margin of the theca, forming a notch-like structure (Fig. 1A), but no crack can be observed nearby; the stalk and the attachment disc of the holotype and paratype are preserved deflected from the longitudinal midline of the theca, particularly in the paratype (Fig. 1B). Both suggest that the main body of *Kunmingeocrinus cupuliformis* n. gen. n. sp. is weakly biomineralized.

#### 4. Discussion

The holotype of *Kunmingeocrinus cupuliformis* n. gen. n. sp. is two times longer and ca. three times wider than the

paratype. Numerous epispires can be observed clearly on the theca surface of the holotype, while epispires are absent in the paratype. Compared to the holotype, the attachment disc of the paratype is bigger relative to the size of the body. All these characteristics suggest that the holotype is at a mature ontogenetic stage, while the paratype represents a juvenile stage, which correspond respectively to the epispire bearing phase and the pre-epispire bearing phase proposed by Nohejlová and Fatka (2016).

Specimens of articulated eocrinoids are rather scarce in Cambrian Lagerstätten of Yunnan Province, but relatively abundant in Guizhou Province (Zhao et al., 1994; Parsley and Zhao, 2006; Yan et al., 2010; Parsley, 2012). The relevant research findings from Guizhou Province, we believe, could be used to discuss the eocrinoids from the Guanshan Biota. Previously reported specimens showed that *Globoeocrinus globulus* Zhao et al., 2008 could attach directly to the sediment (e.g., fig. 4.2 in Zhao et al., 2008 and fig. 3.7 in Yan et al., 2010) or to hard objects lying on the sediment, such as the trilobite fragments (Yan et al., 2010, fig. 3.5) or branchiopod shells (Yan et al., 2010, fig. 3.3). *Kunmingeocrinus cupuliformis* was attached directly to the sediment (Fig. 1), but the platelets on the attachment disc are clearly smaller and arranged more intensively than the theca plates. Similar morphologies were also found in *Globoeocrinus globulus*, and thus the possibility of *Kunmingeocrinus cupuliformis* being attached to hard substrates cannot be excluded. Parsley and Prokop (2004) proposed that eocrinoids could extrude ‘biogluue’ to help anchor their bodies, which was supported to some extent by a transitional zone between the matrix and the attachment disc, first noted by Yan et al. (2010, fig. 4). A possible transitional zone can also be discerned on the specimens described here (Fig. 4), and morphological similarities may indicate a similar function had been developed by *Kunmingeocrinus cupuliformis* from Cambrian Series 2, Stage 4.

Yan et al. (2010) described and discussed the holdfasts of Cambrian eocrinoids (Series 2, Stage 4 and Miaolingian, Wuliuan) from Guizhou Province, and divided them into two categories based on the size of the attachment disc relative to the stalk: a long stalk with a small attachment disc and a short stalk with a relatively big attachment disc. Representatives of the former are *Sinoeocrinus lui* Zhao et al., 1994 from the Kaili Biota (Cambrian Miaolingian, Wuliuan) and *Guizhoueocrinus yui* Zhao et al., 2007 from the Balang Biota (Cambrian Series 2, Stage 4), whereas the latter is represented by *Globoeocrinus globulus* from the Kaili Biota. Yang et al. (2015) described a species of *Globoeocrinus* from the Balang Biota, which was the first report of an eocrinoid with a short stalk and big attachment disc from Cambrian Series 2, Stage 4 of Guizhou Province. This suggests that Cambrian eocrinoids (Series 2, Stage 4) from Guizhou Province had already developed different kinds of holdfast. According to the criteria proposed by Yan et al. (2010), *Kunmingeocrinus* n. gen. falls into the second category, while the holdfast of *Wudingeocrinus* from the



same biota is an elongated stalk which tapers distally, and no attachment disc can be discerned (Hu et al., 2013). The stalk of *Wudingeocrinus* is often covered by matrix (Fig. 5) (Wu et al., 2017, fig. 1A) and the extension of the stalk is preserved deeper into the matrix than the theca and brachioles during preparation of the specimens. This might be the result of rapid deposition, with the individual trapped in turbidity or storm currents after a short distance of transportation, or from *in situ* smothering of a living individual by suspended mud. Alternatively, this may indicate that *Wudingeocrinus* implants its stalk into the sediment rather

than attaches its body to the sediment surface. Some specimens show that the long stalk of *Wudingeocrinus* was obviously bent (Fig. 5) or even cracked (Wu et al., 2017, fig. 8A) during entombment, which indicates a relatively high rigidity of the stalk. A stalk with high rigidity would be fragile and vulnerable to breakage by water currents. Therefore, we suggest that *Wudingeocrinus* might embed most of its stalk into the sediment, by which the adhesion to adjacent sediment could be promoted to resist the drag forces generated by currents. Eocrinoids from the Guanshan Biota have possibly developed different attachment modes: one



Fig. 5. *Wudingeocrinus rarus* Hu and Luo in Luo et al., 2008. (A) YKLP 13388; white arrow points to the long stalk; scale bar = 10 mm. (B) YKLP 13389; white arrows point to the bent stalk; scale bar = 5 mm.



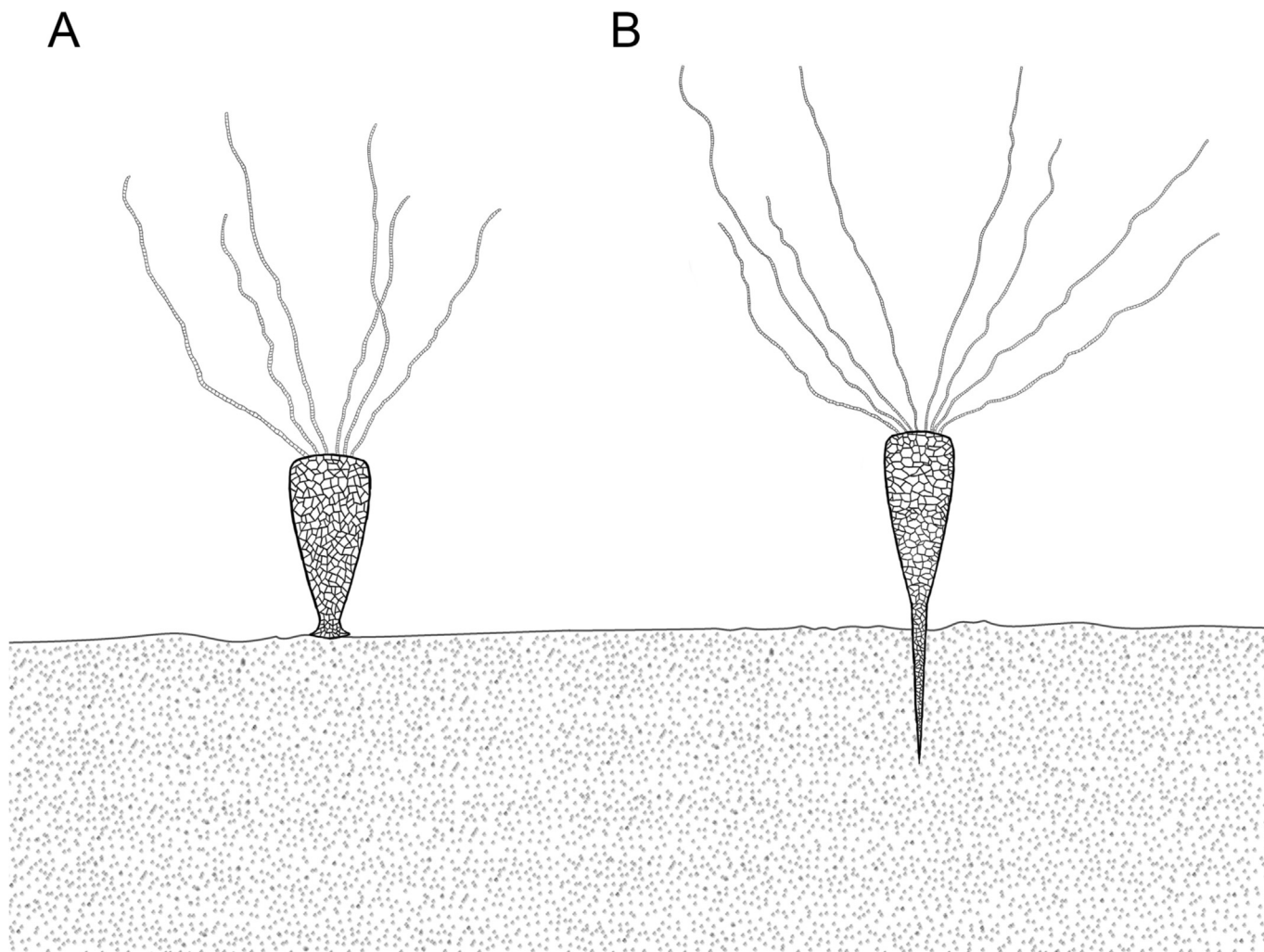


Fig. 6. Life reconstruction of eocrinoids from the Guanshan Biota. (A) *Kunmingeocrinus cupuliformis* n. gen. n. sp. (B) *Wudingeocrinus rarus* Hu and Luo in Luo et al., 2008.

attached itself directly to the sediment surface or hard objects lying on the sediment surface, the other attached by implanting its long stalk into the sediment (Fig. 6).

## 5. Conclusions

In this paper we describe a new Cambrian eocrinoid, *Kunmingeocrinus cupuliformis* n. gen. n. sp., based on two specimens from the Guanshan biota. The new taxon is weakly biomineralized, featured foremost by a short stalk terminated by a well-developed attachment disc. It supplements the attachment modes of eocrinoids from Cambrian Series 2, Stage 4 in the fossil record and leads to a better understanding of early evolution of echinoderms.

## Acknowledgements

This work was supported by the National Natural Science Foundation of China (Grant No. 42072019) and Strategic Priority Research Program of Chinese Academy of Sciences (Grant No. XDB26000000). We thank C.

Stocker and T. Clements for the comments and the language polishing. We thank National Mineral Rock and Fossil Specimens Resource Center, Fei Li and Zhong-Wei Li for the assistance during field work. We thank Qiang Ou and an anonymous reviewer for their careful reading of our manuscript and their insightful comments and suggestions.

## References

- Allaire, N., Lefebvre, B., Nardin, E., Martin, E.L.O., Vaucher, R., Escarguel, G., 2017. Morphological disparity and systematic revision of the eocrinoid genus *Rhopalocystis* (Echinodermata, Blastozoa) from the Lower Ordovician of the central Anti-Atlas (Morocco). *Journal of Paleontology* 91, 685–714.
- Broadhead, T.W., 1982. Reappraisal of Class Eocrinoidea (Echinodermata). In: Lawrence, J.M. (Ed.), *International Echinoderms Conference, Tampa Bay*. Balkema, Rotterdam, pp. 125–131.
- Chen, G.Y., Han, N.R., 2014. A new eocrinoid genus from the upper Cambrian of Guangxi, south China. *Acta Palaeontologica Sinica* 53, 290–301 (in Chinese, with English summary).
- Deline, B., Thompson, J.R., Smith, N.S., Zamora, S., Rahman, I.A., Sheffield, S.L., Ausich, W.I., Kammer, T.W., Sumrall, C.D., 2020.



- Evolution and development at the origin of a phylum. *Current Biology* 30, 1672–1679.
- Hu, S.X., Zhu, M.Y., Luo, H.L., Steiner, M., Zhao, F.C., Li, G.X., Liu, Q., Zhang, Z.F., 2013. The Guanshan Biota. Yunnan Science and Technology Press, Kunming, 204 pp. (in Chinese, with English summary).
- Huang, D.Y., 2012. Eocrinoids from the Cambrian Mantou Formation of Dalian, Liaoning. *Chinese Science Bulletin* 57, 2933–2935.
- Jaekel, O., 1918. Phylogenie und System der Pelmatozoen. *Paläontologischen Zeitschrift* 3, 1–128.
- Klein, J.T., 1734. Naturalis disposition echinodermatum. Accessit lucubratiuncula de aculeis echinorum marinorum, cum spicilegio de belemnitis. Schreiber, Gedani, 79 pp.
- Lin, J.P., Auich, W.I., Zhao, Y.L., 2008. Settling strategy of stalked echinoderms from the Kaili Biota (middle Cambrian), Guizhou Province, South China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 258, 213–221.
- Luo, H.L., Fu, X.P., Hu, S.X., Li, Y., Hou, S.G., Liu, X.Y., Chen, L.Z., Li, F.J., Pang, J.Y., Liu, Q., 2008. Early Cambrian Malong Fauna and Guanshan Fauna from Eastern Yunnan China. Yunnan Science and Technology Press, Kunming, 134 pp. (in Chinese, with English summary).
- Nohejlová, M., Fatka, O., 2016. Ontogeny and morphology of Cambrian eocrinoid *Akadocrinus* (Barrandian area, Czech Republic). *Bulletin of Geosciences* 91, 141–153.
- Parsley, R.L., 2012. Ontogeny, functional morphology, and comparative morphology of lower (Stage 4) and basal middle (Stage 5) Cambrian gogiids, Guizhou Province, China. *Journal of Paleontology* 86, 569–583.
- Parsley, R.L., Prokop, R.L., 2004. Functional morphology and paleoecology of some Middle Cambrian echinoderms from Marginal Gondwana basins in Bohemia. *Bulletin of Geosciences* 79, 147–156.
- Parsley, R.L., Zhao, Y.L., 2006. Long stalked eocrinoids in basal Middle Cambrian Kaili Biota, Taijiang County, Guizhou Province, China. *Journal of Paleontology* 80, 1058–1071.
- Parsley, R.L., Zhao, Y.L., 2010. A new turban-shaped gogiid eocrinoid from the Kaili Formation (Kaili Biota), Balang County, Guizhou Province, China. *Journal of Paleontology* 84, 549–553.
- Robison, R.A., 1965. Middle Cambrian eocrinoids from western North America. *Journal of Paleontology* 39, 355–364.
- Sprinkle, J., 1973. Morphology and Evolution of Blastozoan Echinoderms. Harvard University Museum of Comparative Zoology Special Publication, 283 pp.
- Sprinkle, J., 1976. Biostratigraphy and paleoecology of Cambrian echinoderms from the Rocky Mountains. Brigham Young University Press Geology Studies 23, 61–73.
- Sprinkle, J., 1992. Radiation of Echinodermata. In: Lipps, J.H., Signor, P. W. (Eds.), *Origin and Early Evolution of the Metazoa*. Plenum Press, New York, pp. 375–398.
- Ubaghs, G., 1968. Eocrinoidea. In: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology*. Pt. S. Echinodermata 1(2). Geological Society of America and University of Kansas Press, Lawrence, pp. 455–495.
- Wu, D., Liu, Y., Zhao, T., Chen, H., Hou, X.G., 2017. The restudy of eocrinoids in the Guanshan Biota. *Acta Palaeontologica Sinica* 56, 1–9 (in Chinese, with English summary).
- Yan, X., Mao, Y.Q., Zhao, Y.L., Peng, J., Wu, M.Y., 2010. The holdfasts of eocrinoids in Cambrian, Guizhou Province. *Acta Palaeontologica Sinica* 49, 380–388 (in Chinese, with English summary).
- Yang, Z.C., Lin, J.P., Zhang, Y.P., Wu, Y.S., Meng, X.Y., 2015. A new eocrinoid fauna (Cambrian Series 2) from Guizhou Province, South China. *Palaeoworld* 24, 430–437.
- Zamora, S., Lefebvre, B., Álvaro, J.J., Clausen, S., Elicki, O., Fatka, O., Jell, P., Kouchinsky, A., Lin, J., Nardin, E., Parsley, R.L., Rozhnov, S., Sprinkle, J., Sumrall, C.D., Vizcaíno, D., Smith, A.B., 2013. Cambrian echinoderm diversity and palaeobiogeography. In: Harper, D.A.T., Servais, T. (Eds.), *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoir 38, 157–171.
- Zhao, Y.L., Huang, Y.Z., Gong, X.Y., 1994. Echinoderm fossils of Kaili Fauna from Taijiang, Guizhou. *Acta Palaeontologica Sinica* 33, 305–324 (in Chinese, with English summary).
- Zhao, Y.L., Parsley, R.L., Peng, J., 2007. Early Cambrian eocrinoids from Guizhou Province, South China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 254, 317–327.
- Zhao, Y.L., Parsley, R.L., Peng, J., 2008. Basal Middle Cambrian short-stalked eocrinoids from Kaili Biota, Guizhou Province, China. *Journal of Paleontology* 82, 415–422.
- Zhao, Y.L., Zhu, M.Y., Babcock, L.E., Peng, J., 2011. The Kaili Biota: Marine Organisms from 508 Million Years Ago. Guizhou Science and Technology Press, Guiyang, 251 pp. (in Chinese, with English summary).