Journal of Micropalaeontology, **33**, 2014, 179–192. http://dx.doi.org/10.1144/jmpaleo2014-012

Phylogenetic model of *Follicucullus* lineages (Albaillellaria, Radiolaria) based on high-resolution biostratigraphy of the Permian Bancheng Formation, Guangxi, South China

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ABSTRACT – High-resolution sampling was performed on four Permian sections in Guangxi Province, South China (Gujingling, Sanpaoling, Guoyuan and Yutouling sections). We report abundant and well-preserved Guadalupian–Lopingian radiolarian assemblages, with 25 species belonging to three genera of the order Albaillellaria. Among them, the most abundant genus is *Follicucullus* with 17 species: *F. bipartitus, F. charveti, F.* sp. cf. *F. charveti, F. dilatatus, F. falx, F.* sp. cf. *F. falx, F. guangxiensis, F. hamatus, F. monacanthus, F.* sp. cf. *F. monacanthus, F. orthogonus, F.* sp. cf. *F. orthogonus, F. porrectus, F. scholasticus, F.* sp. cf. *F. scholasticus, F. ventricosus* and *F.* sp. cf. *F. ventricosus*. On the basis of composite stratigraphic ranges, this study suggests four Interval Zones in ascending order, namely F. monacanthus, F. porrectus, F. scholasticus and F. charveti Interval Zones. We provide a phylogenetic model for *Follicucullus* based on their morphological affinities and stratigraphic distribution. The genus *Follicucullus* originated from *Pseudoalbaillella fusiformis*, with *F. monacanthus* as the forerunner species from which two contemporary species then radiated: *F. dilatatus* and *F. porrectus. Follicucullus porrectus* is a long-lasting species, it is abundant in our material and several *Follicucullus* lineages originated from it. In terms of evolution it is considered to be the ancestor of a number of *Follicucullus* species.

SUPPLEMENTARY MATERIAL: Systematic palaeontology of *Follicucullus* is available at http://www.geolsoc.org.uk/SUP18772

KEYWORDS: *Permian, Radiolaria,* Follicucullus, *taxonomy, phylogenetic model, interval biozones*

INTRODUCTION

The radiolarian genus *Follicucullus*, known from the Guadalupian–Lopingian (Permian) and the Lower Triassic, is very interesting to palaeontologists because of its simple morphology, relatively rapid evolution and worldwide distribution. It was originally described from the Guadalupian of the Delaware Basin (Texas, USA), where two species were recognized: *F. scholasticus* (type-species) and *F. ventricosus* (Ormiston & Babcock, 1979). Six new species were later described from the Guadalupian and/or Lopingian of Japan: *F. monacanthus* (Guadalupian; Ishiga *et al.*, 1982*b*), *F. bipartitus, F. charveti, F. falx, F. hamatus* and *F. orthogonus* (Guadalupian–Lopingian; Caridroit & De Wever, 1984). The species *F. dilatatus, F. lagenarius* and *F. porrectus* were established by Rudenko (in Belyanskiy *et al.*, 1984) and, more recently, *F. guangxiensis* was described from the Wuchiapingian (Lower Lopingian) of the Guangxi Province, China (Wang *et al.*, 2012).

Caridroit & De Wever (1986) discussed the phylogeny of *Follicucullus* species in the Lopingian and documented the position of most members in a phylogenetic tree. They recognized two lineages: (i) *F. scholasticus* giving rise to *F. furca* and *F. bipartitus*, the latter evolving further up into *F. hamatus*; (ii) *F. ventricosus* giving rise to *F. orthogonus* and *F. charveti*, the latter evolving further up into *F. falx*. Based on morphology, Ishiga (1991) and Feng & Liu (1993) studied the relationships of *F. scholasticus* (Ormiston & Babcock, 1979), *F. ventricosus* and *F. latior* (Feng & Liu, 1993) and suggested the existence of three evolutionary lineages associated with each of these species. The relationship between genera *Pseudoalbaillella* and *Follicucullus* was later established by De Wever *et al.* (2001) on the basis of morphological affinities. Xia *et al.* (2005) illustrated three main lineages of *Follicucullus* (the divergence of *F. monacanthus* from a *Pseudoalbaillella* stock, the *F. bipartitus–F. scholasticus–F. porrectus* lineage, and the *F. porrectus–F. ventricosus–F. charveti–F. falx* lineage). However, these proposed lineages need to be revised because several *nomen nudum* species are depicted. More recently, the conclusions reached by Wang *et al.* (2012) differ slightly from those of Caridroit & De Wever (1986), as they recognize three lineages: (i) *F. scholasticus* giving rise to *F. porrectus* (Rudenko in Belyanskiy *et al.,* 1984), *F. furca* (Cardroit & De Wever, 1986) and *F. hamatus* (Cardroit & De Wever, 1984), and the latter to *F. bipartitus*, (ii) *F. porrectus* giving rise to *F. guangxiensis* and *F. ventricosus*; (iii) *F. ventricosus* giving rise to *F. charveti, F. falx*, and *F. orthogonus*. However, phylogenetic relationships within these three evolutionary lineages are still in dispute, mostly because key intermediate morphotypes have not yet been documented. In addition, regarding the *Follicucullus*-based biostratigraphy, three Assemblage Zones are known for the Guadalupian–Lopingian interval: these are, in chronological order, the F. monacanthus, F. scholasticus and F. bipartitus–F. charveti Assemblage Zones (Ishiga *et al.*, 1982*a*; Ishiga, 1990). However, the full biostratigraphic potential of *Follicucullus* evolutionary lineages has not yet been exploited, and will benefit from the definition of evolutionary bioevents that will constrain the lower and upper limits of Interval Zones.

To improve phylogenetic and biostratigraphic knowledge of Guadalupian–Lopinginan radiolarian diversity and evolution, four sections situated in the Xiaodong area, southern Guangxi, China, were carefully studied and sampled (Fig. 1). We report here abundant and diverse assemblages from Guadalupian to Lower Lopingian units recording the complete evolution of the genus

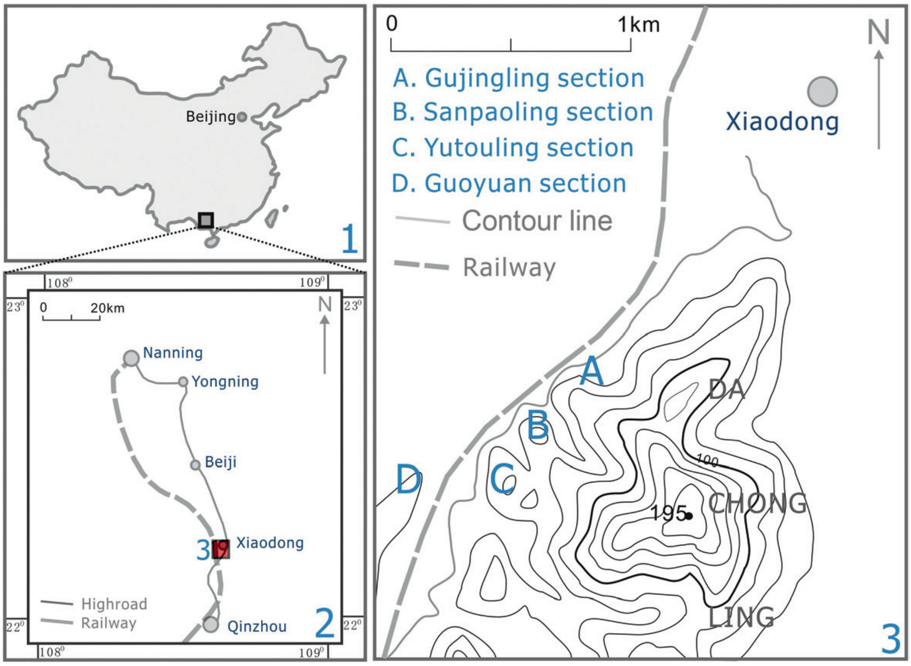

Fig. 1. Maps of the studied area: (**1**) geographical map of China; (**2**) enlargement of the Southern Guangxi area – the square illustrates the studied locality; (**3**) detailed topographic map of the four sections sampled for this work (see Fig. 2).

Follicucullus, from its appearance to disappearance. Radiolarian abundance and diversity are very high in these localities, and many intermediate forms between distinct *Follicucullus* species have been recovered. These morphotypes provide the opportunity to put forward a novel phylogenetic model for this genus. They also provide key data to clarify and specify the *Follicucullus*-based biostratigraphy.

STRATIGRAPHIC SETTING, MATERIAL AND METHODS

In southeastern Guangxi, the Bancheng Formation is composed of grey-yellow and brown-grey thinly bedded siliceous rocks, muddy siliceous rocks, siliceous shales and mudstones (Bureau of Geology and Mineral Resources of Guangxi Autonomous Region, 1997). The Bancheng Formation belongs to the Qinzhou allochthon and contains Late Carboniferous–Lopingian radiolarian fossils (e.g. Wang *et al.*, 1998; Ito *et al.*, 2013).

The Guadalupian–Lopingian series of the Bancheng Formation was sampled in four sections (Gujingling, Sanpaoling, Guoyuan and Yutouling) located in the Dachongling region, south of Xiaodong town, 28 km north of Qinzhou city, Guangxi Province, China (Fig. 1). All samples were processed with hydrofluoric acid (concentration 4%); productive samples yielded well-preserved and very abundant radiolarian specimens. In the scope of our discussion, we list only the species of *Follicucullus* and *Pseudoalbailella*; the complete faunal list of the studied sections is work in progress. The systematic descriptions and discussion of all species of *Follicucullus* found in these four sections are given at the end of this article.

The Gujingling (GJL) section is about 26 m thick, subdivided into 16 units. In the lower part (8.57 m; unit 1 to base of unit 5) there are thinly bedded red to yellow-red silty cherts, with occasional thinly bedded mudstones. The middle part (1.81 m; unit 5) comprises thickly bedded siltstones with abundant clay minerals. The upper part (15.31 m; units 6 to 16) consists of red to yellow-red cherts and yellow to yellow-brown siliceous siltstones, with occasional layers of tuff and mudstone. Some 154 samples were collected, of which 143 were productive and yielded four *Pseudoalbaillella* and nine *Follicucullus* species (Fig. 2A).

The Sanpaoling (SPL) section is about 20 m thick, subdivided into 8 units. The lower part (about 7.8 m; unit 1 to base of unit 4) comprises thinly bedded red to yellow-red silty cherts, with several small folds. In the middle part (8.78 m; unit 4 to middle part of unit 6) are siliceous mudstones with clay materials interbedded with yellow to reddish thin-bedded silty cherts. The upper part (2.4 m; top part of unit 6 to unit 8) comprises grey to yellow thinly bedded cherts. Some 147 samples were selected, of which 130 were productive; 11 *Follicucullus* species were identified (Fig. 2B).

The Guoyuan (GY) section is 23 m thick, subdivided into 2 units. The section comprises yellow moderate to thickly bedded silty cherts with occasional yellow thinly bedded tuff layers. All of the 27 samples were productive and yielded 11 *Follicucullus* species (Fig. 2C).

The Yutouling (YTL) section is comprised of 7 units, with a total thickness of *c.* 27.8 m. The lower and middle parts (*c.* 20 m; unit 1 to base of unit 4) are thick to medium-bedded yellow-purple-red silty cherts, interbedded with some thin-bedded silty cherts. In the upper part (7.2 m; top of unit 4 to base of unit 7), there are thinly bedded grey-yellow-purple silty cherts. The uppermost part (*c.* 0.5 m; top of unit 7) is composed of siliceous mudstone with clay and tuff materials. Among the 103 samples collected, 33 were productive and yielded nine *Follicucullus* species (Fig. 2D).

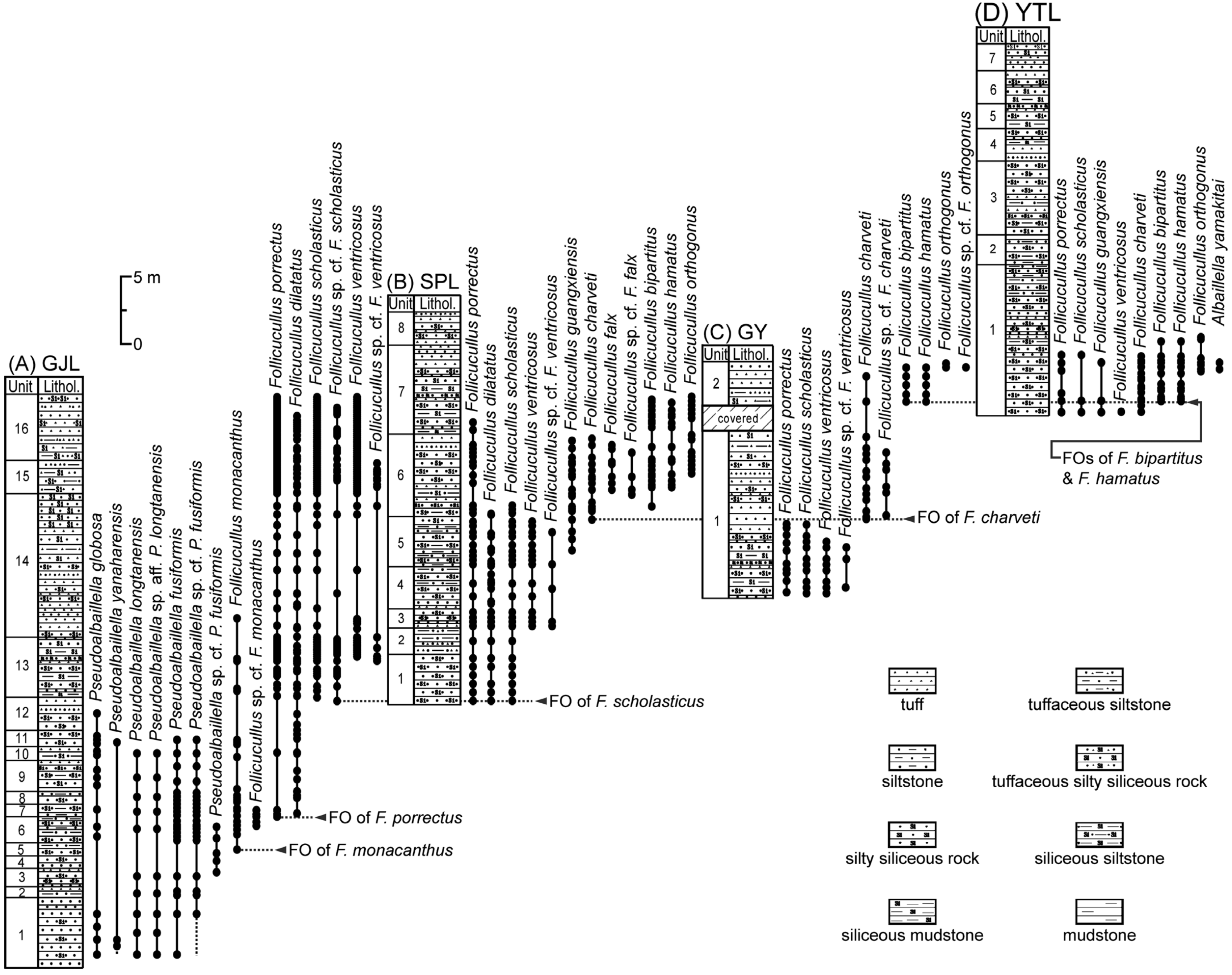

Fig. 2. Lithostratigraphic columns of the four sections studied here and stratigraphic position of the radiolarian fauna described. (**A**) Gujingling section (GJL); (**B**) Sanpaoling section (SPL); (**C**) Guoyuan section (GY); (**D**) Yutouling section (YTL). All sections comprise the Bancheng Formation of the Qinzhou allochthon.

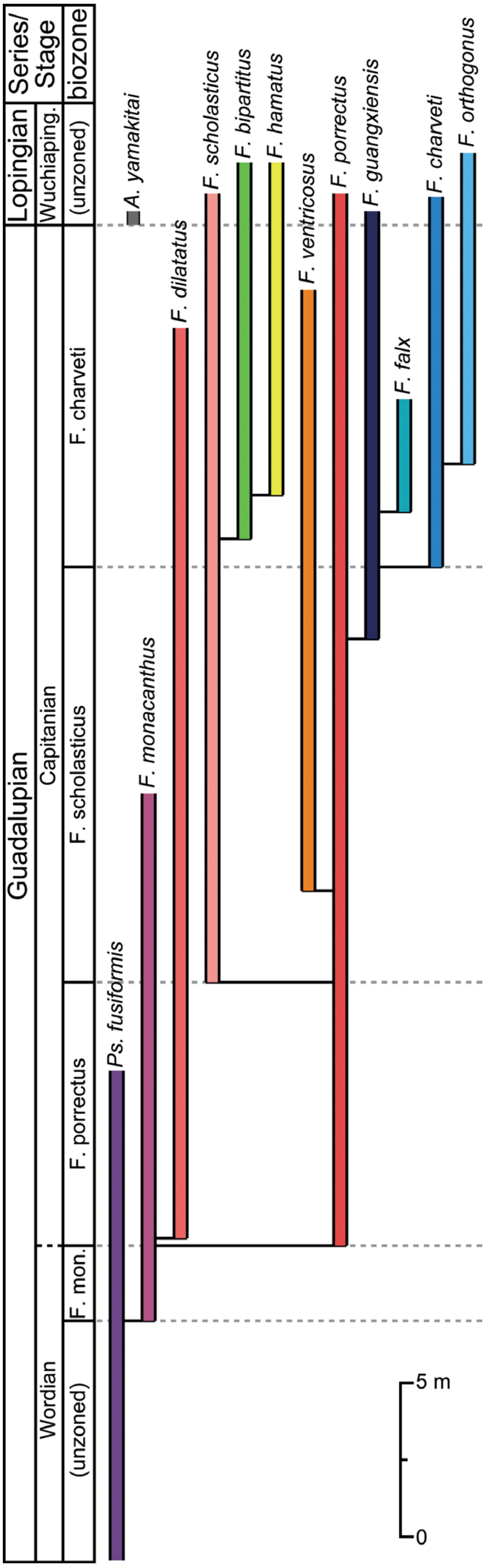

Fig. 3. Composite stratigraphic range and deduced phylogeny of *Follicucullus* species.

STRATIGRAPHIC AND FAUNAL CORRELATIONS OF *FOLLICUCULLUS*

The sections were compared based on the first occurrences (FOs) of specific species, as well as the presence of species occurring continuously through a section. The Gujingling (GJL) and Sanpaoling (SPL) sections can be correlated based on the FO of *F. scholasticus*; the Sanpaoling and Guoyuan (GY) sections were compared based on the FO of *F. charveti*; and the Guoyuan and Yutouling (YTL) sections were compared based on the FOs of *F. bipartitus* and *F. hamatus* (Fig. 2). The composite stratigraphic range of *Follicucullus* species and related *Pseudoalbaillella* species was reconstructed as shown in Figure 3, with consideration of the stratigraphic order of bioevents and morphological similarities.

The composition of *Follicucullus* species is nearly the same in each examined section, but some significant differences are also recognizable. For example, despite the continuous occurrence of *Follicucullus* in the GJL section, *F. guangxiensis* was not detected in this sequence. The upper part of the GJL section overlaps with the lower part of the SPL section based on biostratigraphy, but *F. monacanthus* was not found in the SPL section. In the GY section, *F. dilatatus* was absent.

BIOZONES AND BIOSTRATIGRAPHY

Based on the stratigraphic ranges of *Follicucullus* species, four Interval Zones are suggested for the Late Guadalupian (Wordian and Capitanian), in chronological order: the F. monacanthus, F. porrectus, F. scholasticus and F. charveti Interval Zones (Fig. 4).

Follicucullus monacanthus Interval Zone

Definition. The base of the zone is defined by the FO of *F. monacanthus* and the top is marked by the base of the succeeding zone, the FO of *F. porrectus* (Fig. 3).

Type section. Unit 5 to unit 6 of the GJL section.

Bioevents of *Follicucullus*. FO of *F. monacanthus*.

Remarks. The abundance and diversity of *Pseudoalbaillella* are higher in this Interval Zone than those of *Follicucullus*, with *Follicucullus monacanthus, Ps. fusiformis, Ps. globosa, Ps.* cf. *longicornis* and *Ps. longtanensis* being prevalent. The F. monacanthus Interval Zone is correlated with the Jinogodolella asserata and the lower part of the Jinogodolella postserrata conodont zones, as recorded in the Hubei province, China (Kuwahara *et al.*, 2008) and, therefore, they can be correlated with the Wordian and the earliest Capitanian (Henderson *et al.*, 2012).

Distribution. SW Japan (Ishiga, 1986*a*, *b*, 1990; Kawai & Takeuchi, 2001); Hubei, Anhui, Jiangsu, Guizhou, and Guangxi provinces, China (Wang *et al.*, 1994, 2006; Yu, 1996; Kuwahara *et al.*, 1997, 2007; Yao *et al.*, 2004; Yao & Kuwahara, 2004; Sun & Xia, 2006; Kametaka *et al.*, 2009; this work); Grindstone Terrane of Central Oregon (Blome & Reed, 1992); North Thailand (Sashida & Salyapongse, 2002; Wonganan & Caridroit, 2006); East Russia (Suzuki *et al.*, 2005).

Age. Capitanian (late Guadalupian) (Fig. 4).

Follicucullus porrectus Interval Zone

Definition. The base of the zone is defined by the FO of *F. porrectus* and the top is marked by the base of the succeeding zone, the FO of *F. scholasticus* (Fig. 3).

Type section. Unit 7 to unit 12 of the GJL section.

Bioevents of *Follicucullus*. FO of *F. porrectus*; FO of *F. dilatatus*.

Remarks. *Follicucullus japonicus* (Ishiga, 1991) is a junior synonym of *F. porrectus* Rudenko in Belyanskiy *et al.*, 1984. The abundance and diversity of *Pseudoalbaillella* are lower than in the F. monacanthus zone, but *Follicucullus* species are equally few. The occurring species are *F. porrectus, F. dilatatus, F. monacanthus, Ps. fusiformis, Ps. globosa, Ps.* cf. *longicornis* and *Ps. longtanensis*. The F. porrectus zone is equivalent to the Ps. scalprata m. rhombothoracata zone described in Malaysia (Jasin, 1997). According to Ishiga (1986*a*, 1991) the FO of *F. japonicus* occurs approximately midway through the previously described F. monacanthus zone. Consequently, the F. japonicus zone defined by Ishiga (1991) is correlated with the lower part of the F. porrectus zone in this study (Fig. 4).

Distribution. Malaysia (Jasin, 1997); North Thailand (Sashida & Salyapongse, 2002; Wonganan & Caridroit, 2006); Central Japan (Kawai & Takeuchi, 2001); East Russia (Suzuki *et al.*, 2005); Guangxi, China (this work).

Age. Capitanian (late Guadalupian) (Fig. 4).

Follicucullus scholasticus Interval Zone

Definition. The base is defined by the FO of *F. scholasticus* and the top by the base of the succeeding zone, the FO of *F. charveti* (Fig. 3).

Type section and type horizons. Unit 1 to unit 5 of the SPL section.

Bioevents of *Follicucullus*. FO of *F. scholasticus*; FO of *F. ventricosus*; last occurrence (LO) of *F. monacanthus*.

Remarks. *Follicucullus* is abundant but not very diverse in this Interval Zone; *F. porrectus* is particularly abundant, while the species *F. scholasticus, F. dilatatus, F. monacanthus, F. guangxiensis* and *F. ventricosus* are common. The zone is correlated with the F. scholasticus–F. ventricosus Assemblage Zone of Wang *et al.* (2006).

Distribution. SW Japan (Ishiga, 1986*a*, *b*, 1990; Kuwahara & Yao, 2001; Yamanaka, 2001; Yao *et al.*, 2001); East and South China (Wang *et al.*, 1994, 2006; Kuwahara *et al.*, 1997, 2007; Yao & Kuwahara, 2004; Yao *et al.*, 2004; Sun & Xia, 2006; this study); Grindstone Terrane of Central Oregon (Blome & Reed, 1992); East Russia (Suzuki *et al.*, 2005).

Age. The Follicucullus scholasticus Interval Zone is correlated with the Lepidolina kumaensis fusulina zone in the Mino belt, SW Japan (Ishiga, 1982). The L. kumaensis Zone is dated as late Capitanian (Leven, 1996; Kotylar, 2008; Kasuya *et al.*, 2012), although sporadic occurrences of *L. kumaensis* are known from the Lopingian in the South Kitakami Belt (Choi, 1970), Primorye region of Russia (Kotylar *et al.*, 2007) and South China (Rui, 1983). Because the underlying F. charveti Interval Zone is dated to the latest Capitanian, the F. scholaticus Interval Zone is assigned here to the Middle–Late Capitanian (Fig. 4).

Follicucullus charveti Interval Zone

Definition. The base is defined by the FO of *F. charveti* and the top by the base of the succeeding zone, the FO of *Albaillella yamakitai* (Fig. 3).

Type section and type horizons. *Albaillella yamakitai* occurs only in the YTL section, but the FO of *F. charveti* is unclear in the YTL section. These two species occur throughout the YTL section. Therefore, this study does not define a type section and type horizons for the F. charveti Interval Zone.

Bioevents of *Follicucullus*. FO of *F. charveti*; FO of *F. bipartitus*; FO of *F. falx*; FO of *F. hamatus*; FO of *F. orthogonus*; LO of *F. falx*; LO of *F. dilatatus*.

Remarks. Species *F. charveti, F. bipartitus, F. scholasticus, F. ventricosus, F. guangxiensis* and *F. orthogonus* are common The F. charveti zone described here corresponds to the F. charveti zone of Sun & Xia (2006), the F. charveti–F. bipartitus Assemblage Zone of Ishiga (1986*a*, *b*, 1990), the F. charveti–F. bipartitus–F. orthogonus Assemblage Zone of Wang *et al.* (2006) and to the lower part of the F. charveti–Albaillella yamakitai Assemblage Zone of Kuwahara *et al.* (1997, 1998, 2003, 2007), Yao *et al.* (2001, 2004), Kuwahara & Yao (2001) and Yao & Kuwahara (2004).

Distribution. SW Japan (Ishiga, 1986*a*, *b*, 1990; Kuwahara & Yao, 2001; Yao *et al.*, 2001); East and South China (Wang & Li, 1994; Wang *et al.*, 1994, 2006; Kuwahara *et al.*, 1997, 2003; Yao & Kuwahara, 2004; Yao *et al.*, 2004; Sun & Xia, 2006; this work); East Russia (Suzuki *et al.*, 2005).

Age. The F. charveti Interval Zone is defined below the FO of *A. yamakitai* whose datum is recognized below the basal Wuchiapingian (the base of the Lopingian) (Nishikane *et al.*, 2010). Consequently, the F. charveti Interval Zone is assigned to the latest Capitanian (Fig. 4).

PHYLOGENETIC MODEL OF *FOLLICUCULLUS*

Origin of *Follicucullus*

As with the intermediate forms between *Pseudoalbaillella* and *Follicucullus* reported by De Wever *et al.* (2001), two specimens with transitional characters were found in our material (Pl. 1, figs 7 and 12). The specimen shown in Plate 1, figure 7 can still be classified as *Pseudoalbaillella*, although its symmetrical pseudothoracic flaps have degenerated into two little inflations. Some important characters of *F. monacanthus*, for example the projection on only one side of the pseudothorax, are present on the subsequent specimens (Pl. 1, fig. 12). In spite of these features, the

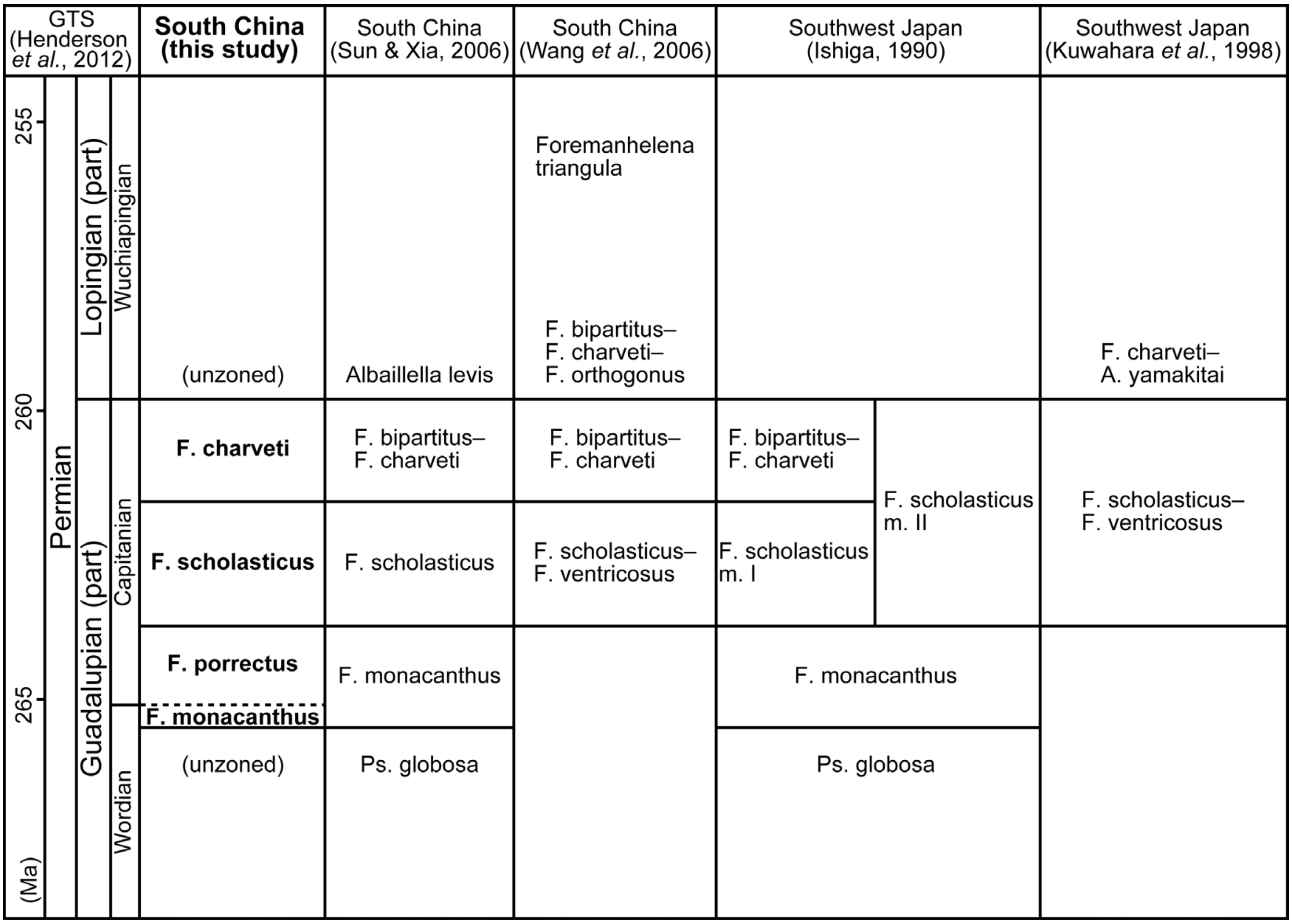

Fig. 4 . Correlation of radiolarian biozones in the Guadalupian and Lopingian. Data from Ishiga (1990), Kuwahara *et al*. (1998), Wang *et al*. (2006), Sun & Xia (2006) and Henderson *et al*. (2012).

characters considered typical for *Pseudoalbaillella* (i.e. globular pseudothorax) are not totally obliterated. Similar specimens are also recognized from the literature: *F. monacanthus* in De Wever *et al.* (1988, pl. 1, fig. D). Ishiga (1991, p. 111) also noticed the affinity between *Follicucullus* and *Pseudoalbaillella*: 'The possession of the wing even though it is an asymmetric one, suggests connection of *Pseudoalbaillella* and *Follicucullus* probable ancestor of *F. monacanthus* is *Pseudoalbaillella* sp. cf. *P. fusiformis*'. De Wever *et al.* (2001) also pointed out the shape and size similarities of *F. monacanthus* and *Ps. fusiformis*: both have an apical cone, a pseudothorax and pseudoabdomen, and a flap on the pseudothorax. *Follicucullus monacanthus* primarily differs from *Ps. fusiformis* in having only one pseudothoracic flap, as opposed to the pair of symmetrical flaps of *Ps. fusiformis*. Hence, *Follicucullus* may have originated from *Pseudoalbaillella* through the species *Ps. fusiformis* that gave rise to *F. monacanthus*.

Position of *F. porrectus* and *F. dilatatus* in the phylogenetic model of *Follicucullus*

In our samples, *F. porrectus* and *F. dilatatus* occur almost at the same level and earlier than *F. scholasticus.* They are similar in shape with a long apical cone, a pseudothorax, an apertural spine and a very short slightly curved pseudoabdomen. The

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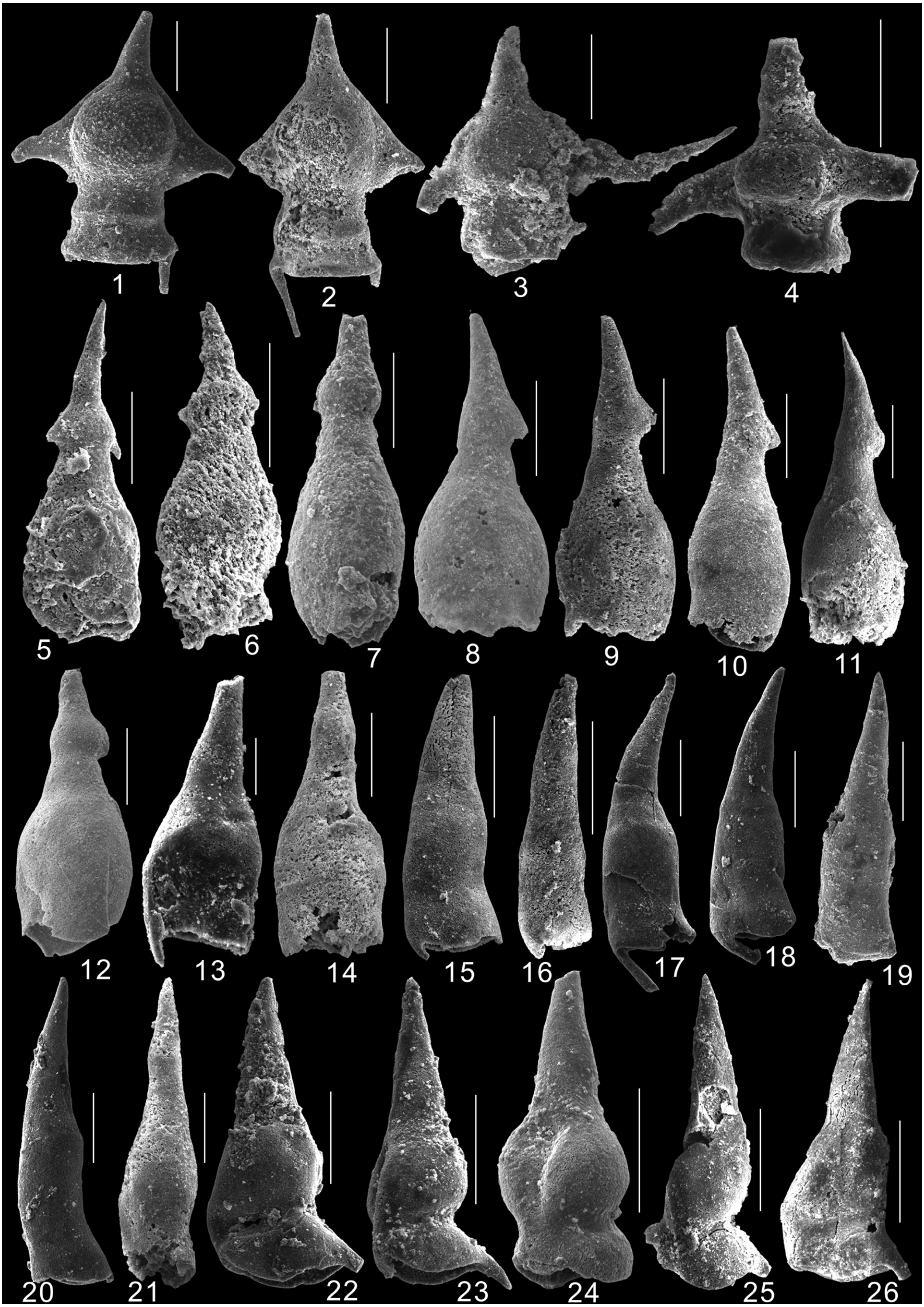
Explanation of Plate 1. figures 1–26. Guadalupian radiolarians from the Xiaodong Town, southern Guangxi, China. The sample number and SEM photo number are given for each illustrated specimen. Scale bar 100 µm for all specimens, unless otherwise specified: **1, 2,** *Pseudoalbaillella globosa* Ishiga & Imoto in Ishiga *et al.,* 1982*b* (1: sample GJL1-3/003, 2: sample GJL1-3/005); **3,** *Pseudoalbaillella yanaharensis* Nishimura & Ishiga, 1987 (sample GJL11-5/015); **4,** *Pseudoalbaillella* sp. cf. *F. longicornis* Ishiga & Imoto, 1980 (sample GJL1-8/001); **5, 6,** *Pseudoalbaillella fusiformis* Holdsworth & Jones, 1980 (5: sample GJL6-3/00, 6: sample GJL1-5/001); **7,** *Pseudoalbaillella* sp. cf. *P. fusiformis* Holdsworth & Jones, 1980 (sample GJL8-1/008); **8–11,** *Follicucullus monacanthus* Ishiga & Imoto in Ishiga *et al.,* 1982*b* (8: sample GJL11-4/004, 9: sample GJL11-6/002, 10: sample GJL11-5/00, 11: sample GJL11-6/004); **12,** *Follicucullus* sp. cf. *Follicucullus monacanthus* Ishiga & Imoto in Ishiga *et al.,* 1982*b* (sample GJL8-5/004); **13,** *Follicucullus dilatatus* Rudenko in Belyanskiy *et al.,* 1984 (sample YTL1-1/017); **14,** *Follicucullus* sp. cf. *F. dilatatus* Rudenko (sample GJL11-5/012); **15–20,** *Follicucullus porrectus* Rudenko in Belyanskiy *et al.,* 1984 (15: sample SPL3-1/025, 16: sample SPL3-3/001, 17: sample GY1-1/027, 18: sample GY1-1/022, 19: sample GY1-1/023, 20: sample GY1-1/019); **21,** *Follicucullus* sp. cf. *F. porrectus* Rudenko (sample GJL11-8/001); **22–24,** *Follicucullus ventricosus* Ormiston & Babcock, 1979 (22: sample GY1-1/008, 23: sample GY1-1/018, 24: sample GY1-1/020); **25, 26,** *Follicucullus* sp. cf. *ventricosus* Ormiston & Babcock, 1979 (25: sample SPL3-1/026, 26: sample SPL3-1/012).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only difference is the smoother contour and slender shell of *F. porrectus*. Two transitional specimens are similar to *F. porrectus* (Pl. 1, fig. 21) and *F. dilatatus* (Pl. 1, fig. 14). However, they possess a slight projection on the apical cone similar to a degenerated pseudothoracic flap of *F. monacanthus*. It suggests a parallel relationship between *F. porrectus* and *F. dilatatus*, both of them deriving from *F. monacanthus*. *Follicucullus scholasticus* appeared slightly earlier than *F. ventricosus*. *Follicucullus scholasticus* has a smoother and slender shell while *F. ventricosus* has a strongly swollen pseudothorax, a sinus on the pseudothorax and a clear constriction between the pseudothorax and pseudoabdomen. Some specimens with intermediate forms between *F. porrectus* and *F. scholasticus* (Pl. 1, fig. 16) and between *F. porrectus* and *F. ventricosus* (Pl. 1, fig. 26) were also found, suggesting that they all originate from *F. porrectus*.

Origin of *F. falx*

The diagnostic character of *F. falx* is its hatchet-shaped ventral spine (Caridroit & De Wever, 1984). Its shape is close to that of *F. charveti*, suggesting that these two species have a clear affinity and that they are probably situated on an evolutionary continuum (Caridroit & De Wever, 1986). Some specimens from the SPL section led Wang *et al.* (2012) to introduce *F. guangxiensis*. This species is rather similar to *F. porrectus* but it possesses a strong horizontal spine on the ventral side of the pseudoabdomen, which seems to indicate a transitional morphotype between *F. porrectus* and *F. charveti*. Some transitional specimens display a nearly continuous morphological change from *F. guangxiensis* to *F. charveti* (Pl. 2, fig. 15). The pseudothorax of these transitional species inflated gradually to achieve an ovoid shape. A similar pattern is also recorded with the transitional specimens between *F. guangxiensis* and *F. falx*. With the exception of the change on the pseudothorax, the ventral spine is also gradually modified into a hatchet-shaped spine. Rather than evolutionary continuity, our data support the idea that the phylogenetic position of *F. falx* is parallel to that of *F. charveti*. Accordingly, we conclude that they all originated from *F. porrectus* through *F. guangxiensis*.

Phylogenetic model of *Follicucullus*

Our results slightly modify the current ideas of the *Follicucullus* phylogeny, as detailed previously. Some transitional specimens we present here indicate that *F. monacanthus* originated from *Ps. fusiformis*. Although their taxonomic nomination is still ambiguous (e.g. Wang *et al.*, 2012), it is the first time that *F. monacanthus* is recognized as the link between the genera *Pseudoalbailella* and *Follicucullus*. From *F. monacanthus* the radiation of two co-existing species took place: *F. porrectus* and *F. dilatatus*. *Follicucullus porrectus* appears as a common ancestor of many *Follicucullus* species, for example *F. hamatus* and *F. bipartitus* through *F. scholasticus, F. charveti* and *F. falx* through *F. guangxiensis* and *F. ventricosus*. *Follicucullus orthogonus* unquestionably originated from *F. charveti*. The details of the inferred phylogenic relationships of *Follicucullus* are shown in Figure 3.

CONCLUSIONS

(1) High-resolution stratigraphic distributions of various species of the genus *Follicucullus* were determined for the Guadalupian–Lopingian interval.
(2) Based on the stratigraphic ranges and phylogenetic relationships of *Follicucullus*, four *Follicucullus* interval lineage zones are suggested: the F. monacanthus, F. porrectus, F. scholasticus and F. charveti Interval Zones. Previously known Permian radiolarian zones are essentially assemblage zones without discrete definition of their bases and tops. This is the first time that Interval Zones are defined.
(3) The genus *Follicucullus* originated from *Ps. fusiformis*, and its oldest species is *F. monacanthus*. Two co-existing species radiated from *F. monacanthus: F. porrectus* and *F. dilatatus*. *Follicucullus porrectus* is very abundant and extends from the Guadalupian into the Lopingian, thus being the ancestor of several *Follicucullus* lineages

SYSTEMATIC PALAEONTOLOGY OF *FOLLICUCULLUS*

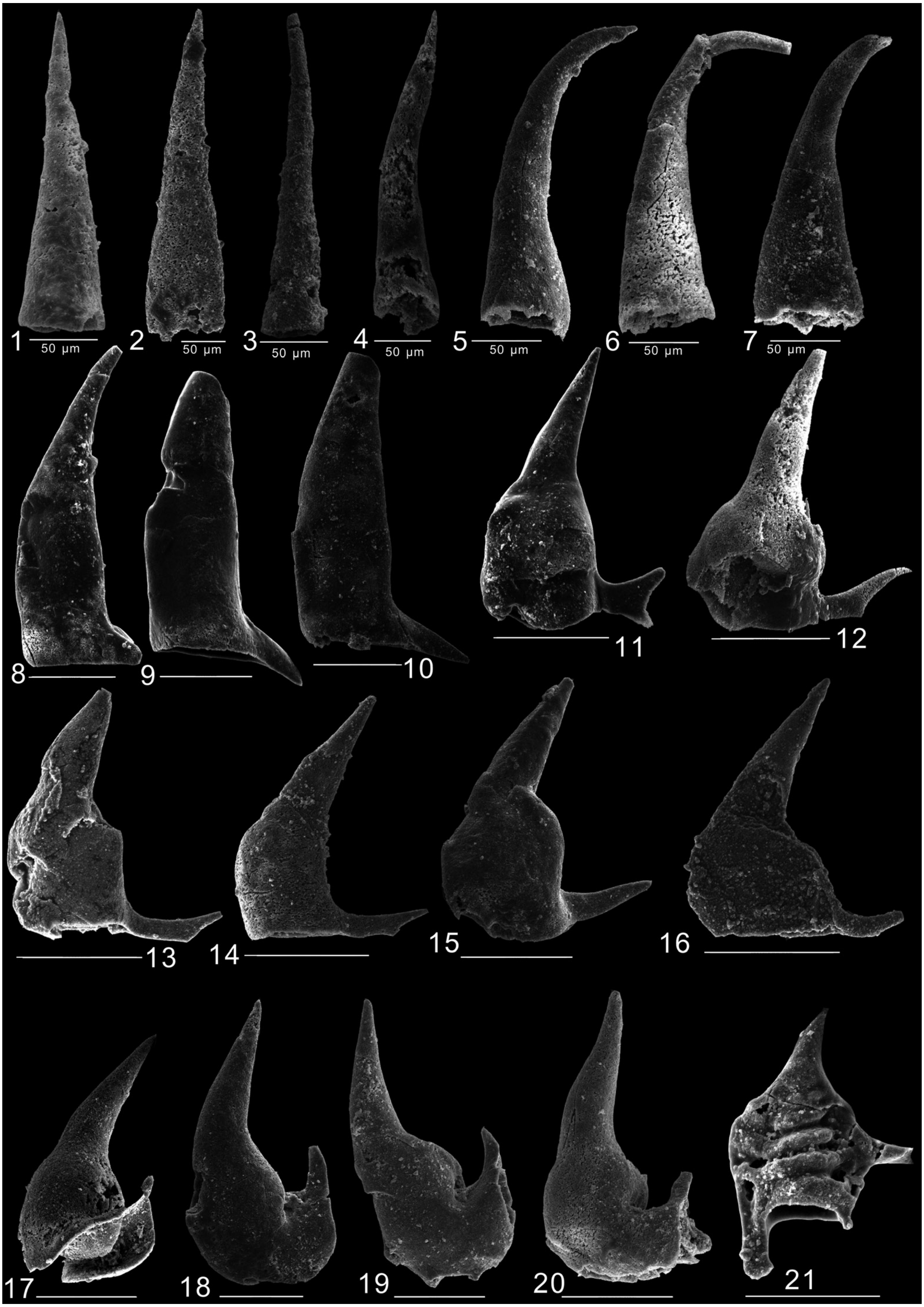
Full synonymy lists and associated literature can be found in the Supplementary material.

Infrakingdom **Rhizaria** Cavalier-Smith, 2002, sensu emend. Cavalier-Smith, 2003
Phylum **Retaria** Cavalier-Smith, 1999
Class **Polycystina** Ehrenberg, 1839
Order **Albaillellaria** Deflandre, 1953, emend. Holdsworth, 1969
Superfamily **Follicuculoidea** Cheng, 1986
Family **Follicucullidae** Ormiston & Babcock, 1979, emend Kozur, 1981

Genus *Follicucullus* Ormiston & Babcock, 1979

Type species. *Follicucullus ventricosus* Ormiston & Babcock, 1979.

Explanation of Plate 2. figures 1–21. Guadalupian radiolarians from the Xiaodong town, south Guangxi, China. The sample number and SEM photo number are given for every illustration. Scale bar 100 μm for all specimens, unless otherwise specified: **1–3,** *Follicucullus scholasticus* Ormiston & Babcock, 1979 (1: sample GJL11-5/012, 2: sample SPL2-8/001, 3: sample SPL3-1/040); **4,** *Follicucullus* sp. cf. *F. bipartitus* Caridroit & De Wever, 1984 (sample SPL3-1/041); **5,** *Follicucullus bipartitus* Caridroit & De Wever, 1984 (sample SPL6-8/002); **6,** *Follicucullus* sp. cf. *F. hamatus* Caridroit & De Wever, 1984 (sample SPL6-8/002); **7,** *Follicucullus hamatus* Caridroit & De Wever, 1984 (sample SPL6-11/009); **8–10,** *Follicucullus guangxiensis* Wang in Wang *et al.,* 1992 (8: sample SPL5-1/039, 9: sample SPL5-1/035, 10: sample SPL5-1/015); **11,** *Follicucullus falx* Caridroit & De Wever, 1984 (sample SPL6-24/036); **12–14,** *Follicucullus* sp. cf. *F. falx* Caridroit & De Wever, 1984 (12: sample SPL6-24/029, 13: sample SPL6-24/063, 14: sample SPL6-24/056); **15, 16,** *Follicucullus charveti* Caridroit & De Wever, 1984 (15: sample GY1-1/031, 16: sample SPL6-24/030); **17,** *Follicucullus* sp. cf. *F. orthogonus* Caridroit & De Wever, 1984 (sample YTL1-1/030); **18–20,** *Follicucullus orthogonus* Caridroit & De Wever, 1984 (18: sample YTL1-1/034, 19: sample SPL6-22/035, 20: sample YTL1-1/035); **21,** *Albailella yamakitai* Kuwahara, 1999 (sample YTL1-1/025).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Follicucullus bipartitus Caridroit & De Wever, 1984
(Pl. 2, fig. 5)

1984 *Follicucullus bipartitus* Caridroit & De Wever: p.640, pl. 1, figs 1–3.

Material. Over 100 complete specimens from the SPL, GY and YTL sections.

Occurrence. SW Japan, North America, SE Asia and South China.

Stratigraphic range. Guadalupian–Lopingian.

Follicucullus charveti Caridroit & De Wever, 1984, emend Caridroit & De Wever, 1986
(Pl. 2, figs 15, 16)

1984 *Follicucullus (?) charveti* Caridroit & De Wever: p. 641, pl. 1, figs 15–22.

Material. Over 80 entire specimens from the SPL, GY and YTL sections.

Occurrence. SW Japan, North American, SE Asia, South China and New Zealand.

Stratigraphic range. Guadalupian–Lopingian.

Remarks. The specimens of this species vary between two morphological poles: the *charveti*-pole corresponding to specimens showing a thin and long apertural spine very similar to the holotype, while the *guangxiensis*-pole specimens display a less swollen pseudothorax and shorter apertural spine. Although the specimens of the *guangxiensis*-pole have apertural spines slightly different from the original description of *F. charveti*, they still cannot be assigned to *F. guangxiensis* because their apical cone is straighter and the pseudothorax is much less to not at all swollen.

Follicucullus dilatatus Rudenko in Belyanskiy *et al.,* 1984
(Pl. 1, fig. 13)

1984 *Follicucullus dilatatus* Rudenko in Belyanskiy *et al.*: p. 54, pl. 8, figs 6-7

Material. More than 180 entire specimens from the GJL section.

Occurrence. Worldwide.

Stratigraphic range. Guadalupian–Lopingian.

Remarks. *Follicucullus dilatatus* and *F. porrectus* mostly differ in the shape of their pseudothorax, which is larger in *F. dilatatus*. In our material, specimens defined as *F. dilatatus* show a continuous change from typical *dilatatus*- to *porrectus*-like morphology. The *porrectus*-like specimens belong to *F. dilatatus* because of their wider pseudothorax, much wider than in *F. porrectus*. They reveal an evolutionary trend from *F. porrectus* to *F. dilatatus*.

Follicucullus falx Caridroit & De Wever, 1984
(Pl. 2, fig. 11)

1984 *Follicucullus falx* Caridroit & De Wever : p.641, pl. 1, figs 4–6.

Material. More than 20 entire specimens from the Sanpaoling section.

Occurrence. North America and SW China.

Stratigraphic range. Guadalupian–Lopingian.

Follicucullus sp. cf. *Follicucullus falx* Caridroit & De Wever, 1984
(Pl. 2, figs 12–14)

Material. Seven entire specimens from the SPL section.

Occurrence. South China.

Stratigraphic range. Guadalupian–Lopingian.

Remarks. The specimens of this species cannot be assigned to *F. falx* because their spine is not bifide. They have a wider apertural spine than *F. charveti*, which is the initiation of the bifide spine of *F. falx*. Some of them resemble *F. guangxiensis* in their straight to slightly curved apical cone, slightly more inflated and shorter pseudothorax and aperture spines protruding horizontally.

Follicucullus guangxiensis Wang in Wang *et al.,* 2012
(Pl. 2, figs 8–10)

2012 *Follicucullus guangxiensis* Wang in Wang *et al.* :p.108, pl. 20, figs 8, 29, 30, pl. 21, figs 1, 2, 4–6.

Material. Twenty-four entire specimens from the SPL and YTL sections.

Occurrence. South China (Wang, 2012; this work).

Stratigraphic range. Upper Guadalupian–lowest Lopingian.

Follicucullus hamatus Caridroit & De Wever, 1984
(Pl. 2, fig. 7)

1984 *Follicucullus hamatus* Caridroit & De Wever: p. 642, pl. 1, figs 7–9.

Material. Forty-one entire specimens from the SPL, GY and YTL sections.

Occurrence. SW Japan, North America and South China.

Stratigraphic range. Guadalupian–Lopingian.

Follicucullus monacanthus Ishiga & Imoto in Ishiga *et al.,* 1982*b*
(Pl. 1, figs 8–12)

1982*b* *Follicucullus monacanthus* Ishiga & Imoto in Ishiga *et al.*: p. 642, pl. 4, figs 15–17, 21–23.

Material. Thirty-two entire specimens from the GJL section.

Occurrence. SW Japan, North America, Far East, SE Asia and South China.

Stratigraphic range. Guadalupian.

Remarks. The present species is assigned to *Follicucullus*. The number of wings is a generic criterion: *Pseudoalbaillella* is characterized by having two wings, which are absent in *Follicucullus. Follicucullus monacanthus* displays only a ventral wing and therefore seems transitional between *F. fusiformis*, which bears strong dorsal and ventral wings, and *F. porrectus*, bearing no wing. However, other morphological elements, such as pseudoabdomen, relate *F. monacanthus* more closely to *F. fusiformis*. Therefore, *F. monacanthus*, bearing a unique wing, should belong neither to *Follicucullus* nor to *Pseudoailbaillella* but to a different genus marked by a unique wing. It seems therefore more accurate to attribute this species to '*Para*'*follicucullus*. However, in the absence of a complete revision of this taxonomy, we have decided here to follow the traditional view and consider this species as belonging to the genus *Follicucullus*.

Follicucullus sp. cf. *Follicucullus monacanthus* Ishiga & Imoto in Ishiga *et al.,* 1982*b*
(Pl. 1, fig. 12)

Material. Five entire specimens from the GJL section.

Occurrence. South China.

Stratigraphic range. Guadalupian.

Remarks. This species is related to *F. monacanthus* in the shape of the wings and the projection on the apical cone. However, in *F. monacanthus* the wings are degenerated or absent and the pseudothorax is flat, weakly inflated.

Follicucullus orthogonus Caridroit & De Wever, 1984
(Pl. 2, figs 18–20)

1984 *Follicucullus orthogonus* Caridroit & De Wever : p. 276, pl. 1, figs 23–29.

Material. Forty-two entire specimens from the SPL, GY and YTL sections.

Occurrence. North America, South Japan, South China.

Stratigraphic range. Guadalupian–Lopingian.

Follicucullus sp. cf. *Follicucullus orthogonus*
Caridroit & De Wever, 1984
(Pl. 2, fig. 17)

Material. One entire specimen from the GY section.

Occurrence. South China.

Stratigraphic range. Guadalupian–Lopingian.

Remarks. The present specimen is consistent with *F. orthogonus* in most features: a straight or slightly curved apical cone, a moderately inflated pseudothorax, a pseudoabdomen with horizontal aperture and upturned aperture spines. However, our specimen has a peculiar aperture, which splits horizontally from the bottom. It may be a transitional species from *F. charveti* to *F. orthogonus*.

Follicucullus porrectus Rudenko in Belyanskiy *et al.,* 1984
(Pl. 1, figs 15–20)

1984 *Follicucullus porrectus* Rudenko in Belyanskiy *et al.*: p. 55, pl. 8, figs 3, 10.

Material. Some 319 entire specimens from the GJL, SPL, GY and YTL sections.

Occurrence. Worldwide.

Stratigraphic range. Guadalupian–Lopingian.

Remarks. Based on our material and on the literature, three morphotypes can be recognized for this species: (i) the first type is symmetrical, has sides of the apical zone that concave outwards, a bottleneck transition between the apex and pseudothorax, a slightly concave-outward pseudothorax and the transition between the pseudothorax and pseudoabdomen marked by a constriction; (ii) the second type is also symmetrical with straight divergent apical sides, a sharply angulated transition between the apex and pseudothorax, a straight pseudothorax and no constriction at the transition between pseudothorax and pseudoabdomen; (iii) the third type corresponds to the holotype of the species – it is asymmetrical, with the apex slightly concave outward on one side and more or less straight on the other, an angulated transition with the pseudothorax on one side, a straight pseudothorax and none to a slight constriction between the pseudothorax and pseudoabdomen. This third morphology is the most abundant. The first and third types are described in Belyanskiy *et al.*, 1984. In 1991, Ishiga described *F. japonicus*, proved later to be a synonym of *F. porrectus.* The holotype of *F. japonicus* is close to figures 4 and 5 illustrated in Belyanskiy *et al.*, 1984, which can be related to our third type.

For these three morphologies, those specimens that are longer and thinner with a smoother transition between the apical cone and pseudothorax are identified as *F. scholasticus*. However, specimens of the first type with a more elongated shape, a longer and thinner apical cone and a marked transition between the apical cone and pseudothorax are identified as *F. elongatus* by Spiller, 2002.

Follicucullus scholasticus Ormiston & Babcock, 1979
(Pl. 2, figs 1–3)

1979 *Follicucullus scholasticus* Ormiston & Babcock: pl. 1, figs 1–5.

Material. Some 269 entire specimens from the GJL, SPL, GY and YTL sections.

Occurrence. Worldwide.

Stratigraphic range. Guadalupian–Lopingian.

Remarks. This species displays important intraspecific variations in our material, ranging from wider specimens (Pl. 2, figs 1-2) to slimmer ones (Pl. 2, fig. 3).

Follicucullus sp. cf. *Follicucullus scholasticus* Ormiston & Babcock, 1979
(Pl. 1, fig. 12)

Material. Three entire specimens from the GJL section.

Occurrence. South China (this work).

Stratigraphic range. Guadalupian–Lopingian.

Remarks. The curved apical cone distinguishes this species from both *F. scholasticus* and F. *bipartitus* in being transitional between these two species: more curved than *scholasticus* but not sufficiently curved to be identified as *bipartitus*.

Follicucullus ventricosus Ormiston & Babcock, 1979
(Pl. 1, figs 22–24)

1979 *Follicucullus ventricosus* Ormiston & Babcock: pl. 1, figs 6–14.

Material. More than 250 entire specimens from the GJL, SPL, GY and YTL sections.

Occurrence. Worldwide.

Stratigraphic range. Guadalupian–Lopingian.

Follicucullus sp. cf. *Follicucullus ventricosus* Ormiston & Babcock, 1979
(Pl. 1, figs 25 and 26)

1981 *Follicucullus ventricosus* Ormiston & Babcock; Takemura & Nakaseko: pl. 34, fig. 7.

Material. More than 100 entire specimens from the GJL, SPL and GY sections.

Occurrence. South China (this work).

Stratigraphic range. Guadalupian.

Remarks. Some specimens differ from the holotype of *F. ventricosus* in having a longer pseudoabdomen and a weaker constriction between the pseudothorax and pseudoabdomen. This species can also be compared to *F. porrectus* both in the apical cone and pseudothorax, but the latter has a strong constriction between the pseudothorax and apertural skirt, and a longer skirt compared with the weak apertural skirt of *F. porrectus*.

ACKNOWLEDGEMENTS

This work was supported by NSFC (40839903), Ministry of Education of China (20110145130001), and 111 Project (Grant No. B08030). Lei Zhang was funded by the European ERASMUS MUNDUS External Windows programme for a year at the University Lille 1. The authors thank Wang Weijie and Zhao Duanchang for sample preparation, Wu Jun, Liu Guichun, Lei Yong, Yang Wenqiang and Marie-Beatrice Forel for their constructive suggestions during writing. The authors are deeply grateful to Suzuki Noritoshi (Tohoku University) and Paulian Dumitrica for critical comments and valuable suggestions which improved the paper considerably. This paper benefited from editing by Claire Allen of the British Antarctic Survey.

Manuscript received 30 April 2014
Manuscript accepted 30 April 2014
Scientific editing by Claire Allen

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