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Avitograptus species (Graptolithina) from the Hirnantian (uppermost Ordovician) Anji Biota of South China and the evolution of *Akidograptus* and *Parakidograptus*

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Abstract.—The latest Ordovician to earliest Silurian graptolite *Avitograptus avitus* is important in the biostratigraphy of the Ordovician–Silurian boundary interval. Two additional species of *Avitograptus* are described from the sponge-dominated Anji Biota of the Upper Ordovician Wenchang Formation (*Metabolograptus persculptus* Biozone) of Zhejiang Province, South China. One species, *Avitograptus akidomorphus* new species, is new; the other, *Avitograptus acanthocystus* new combination, which was previously placed in *Climacograptus*, is herein assigned to *Avitograptus*. The former species may represent the ancestral akidograptid because it is identical in thecal form to *Akidograptus*, but differs in the development of the proximal end. The evolutionary changes from *Avitograptus avitus* to *Akidograptus* and *Parakidograptus* involved distal movement of the origins of th1^1 and th1^2, thecal elongation, and greater outward inclination of the thecal walls.

UUID: http://zoobank.org/81c433a0-9069-48d2-ae72-1267400cbf77.

Introduction

The base of the Silurian System is marked by the first appearance of the graptolite *Akidograptus ascensus* Davies, 1929 (Williams, 1988; Melchin and Williams, 2000; Rong et al., 2008) at 1.6 m above the base of the Birkhill Shale Formation at the global stratotype section and point (GSSP) at Dob's Linn, Scotland, UK. This species and the related *Parakidograptus acuminatus* (Nicholson, 1867) have extremely wide geographical distributions in lower Silurian rocks (Štorch, 1996; Rong et al., 2008). In some places, both *Akidograptus* Davies, 1929 and *Parakidograptus* Li and Ge, 1981 appear simultaneously (e.g., Štorch et al., 2019).

Avitograptus avitus (Davies, 1929) has long been hypothesized to be ancestral to *Akidograptus* and *Parakidograptus* (Davies, 1929; Melchin et al., 2011), although this has been disputed (Williams, 1983; Zalasiewicz and Tunnicliff, 1994). Plausible intermediates between *Av. avitus* and akidograptines have not yet been described. In this paper, we describe two species of *Avitograptus* from the uppermost Ordovician of South China that represent morphological intermediates between *Av. avitus* and akidograptines.

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Geological setting

The graptolites described in this paper were collected from a mudstone interval within the sandstone-dominated Upper Ordovician Wenchang Formation in the area around the Fushi Reservoir, Anji County, Zhejiang Province, China (Fig. 1). The specimens were obtained from three localities: Shuangshe, spelled "Shuanshe" by Botting et al. (2017a) (30°36.544′N, 119°27.156′E), Tianjiashan 3 (30°35.807′N, 119°26.080′E), and Zhuwukou (30°36.507′N, 119°22.712′E). Shuangshe is a roadside section beside the Fushi Reservoir, Zhuwukou is a roadside section, and Tianjiashan 3 is a short section along a farm track. Graptolites were collected from distinct beds at Shuangshe and Zhuwukou, but specimens from Tianjiashan 3 were not separated by bed. The mudstone interval is ~6 m thick at Shuangshe, but can be as much as 10 m thick at other sites within the area (Botting et al., 2017a). The graptolite assemblage and succession is consistent at all sites within the area. In addition to graptolites, the mudstone interval contains abundant, diverse, exceptionally preserved sponges (Botting et al., 2017a, b, 2018a). The only other fossils discovered at Shuangshe, Tianjiashan 3, and Zhuwukou were rare orthoconic nautiloids.

The graptolite fauna of the mudstone interval (Figs. 2–4) includes *Avitograptus acanthocystus* (Fang et al., 1990; Figs. 3.5, 3.8, 3.12, 3.13, 4.3, 4.5, 4.8, 4.11) n. comb., *Av.*

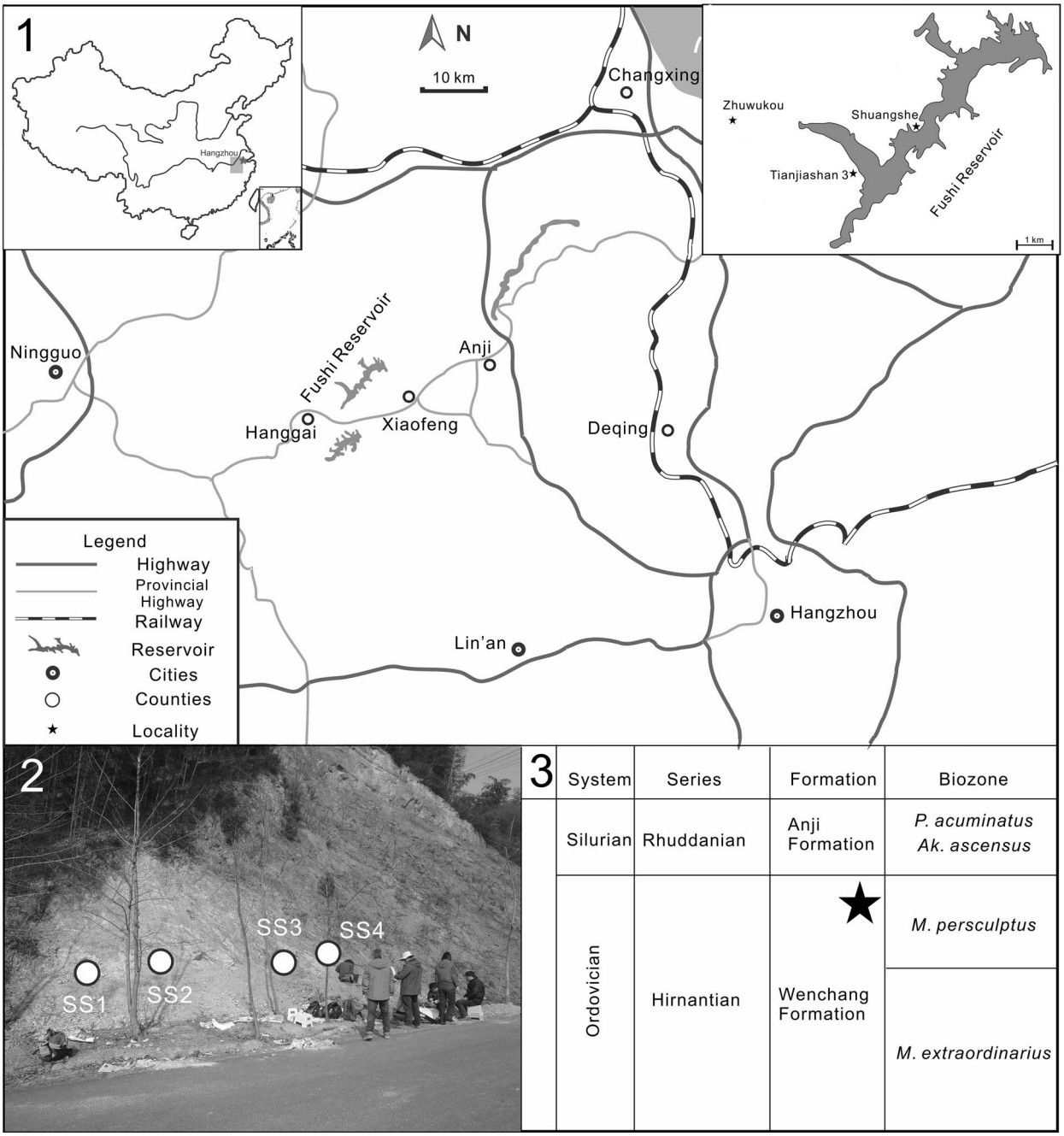

Figure 1. (**1**) Location of the study area within China, of Fushi Reservoir within Anji County, and of the Shuangshe, Tianjiashan 3, and Zhuwukou localities relative to Fushi Reservoir. (**2**) Photograph showing the Shuangshe section. The white circles mark the beds from which the graptolite material described in this study was collected. (**3**) Stratigraphy of the Wenchang Formation. The black star indicates the approximate position of the study interval within the *M. persculptus* Biozone.

akidomorphus n. sp. (Figs. 3.6, 3.7, 4.1, 4.2), *Av. avitus* (Davies, 1929; Figs. 3.2, 4.4), *Metabolograptus persculptus* (Elles and Wood, 1907; Fig. 4.9), *M. parvulus* (Lapworth, 1900; Fig. 3.3), *M. wangjiawanensis* (Mu and Lin, 1984; Fig. 4.6), *Neodiplograptus modestus* (Lapworth in Armstrong, Young, and Robertson, 1876; Fig. 4.7), *Ne. shanchongensis* (Li, 1984; Fig. 3.1), *Normalograptus angustus* (Perner, 1895; Fig. 3.10), *No. minor* (Huang, 1982; Fig. 4.10), *No. mirnyensis* (Obut and Sobolevskaya in Obut, Sobolevskaya, and Nikolaev, 1967; Fig. 3.4), *No.*? *zhui* (Yang, 1964; Fig. 3.9), and some other taxa. A full description of the graptolite fauna will be published separately. Most of these species occur in the latest Ordovician *M. persculptus* and earliest Silurian *Akidograptus ascensus* and *Parakidograptus acuminatus* biozones (Chen et al., 2005; Loydell, 2007; Zalasiewicz et al., 2009). *Normalograptus minor* primarily occurs in the *M. persculptus* Biozone (Chen et al., 2005; Melchin, 2008; Štorch et al., 2019), but has also been reported from the *Akidograptus ascensus* Biozone of Yunnan Province, China (Zhang et al., 2014, p. 41). Similarly, *Normalograptus*? *zhui* has been reported from the lower

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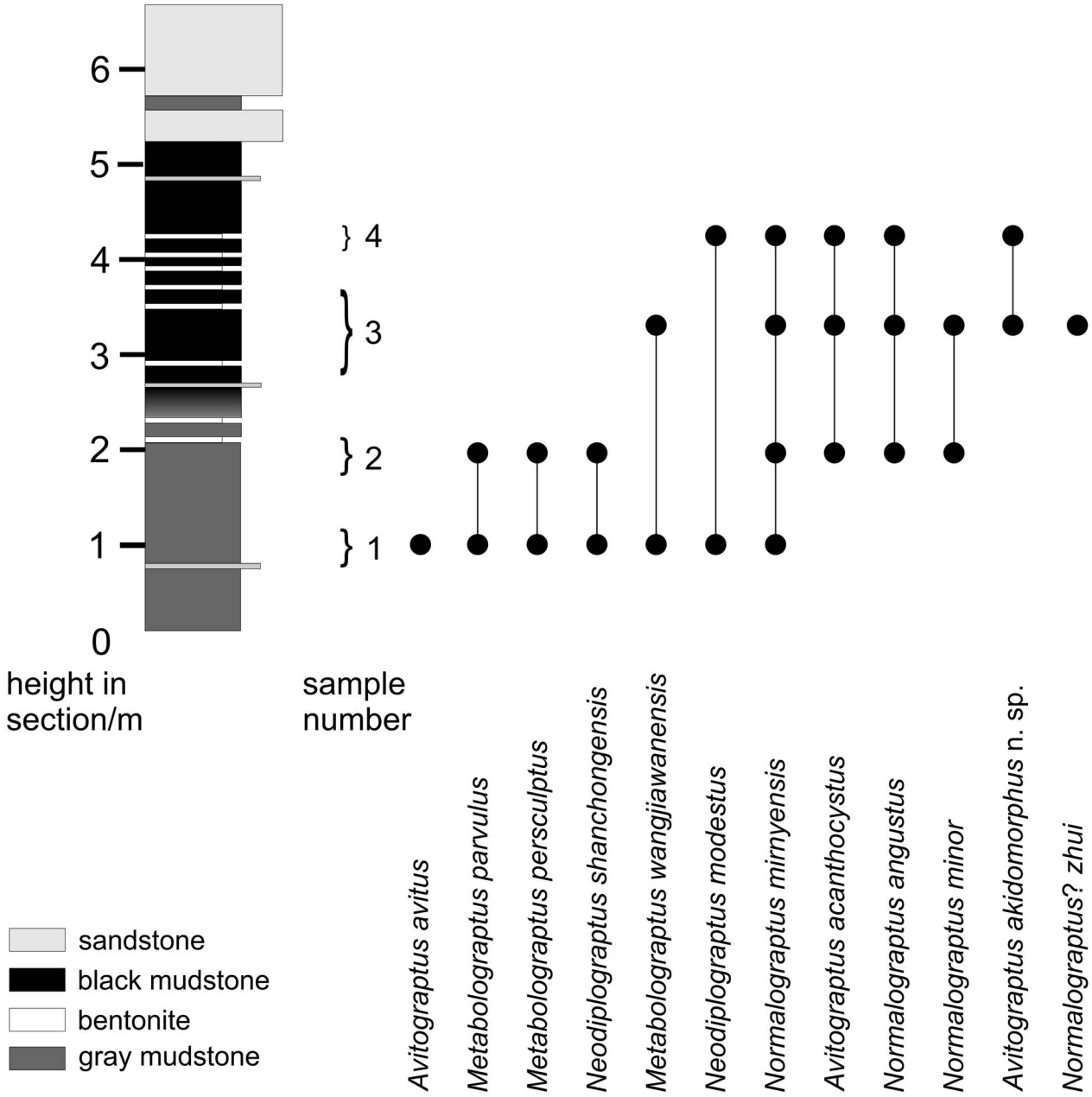

Figure 2. Log showing the stratigraphic distribution of selected graptolites in the Shuangshe section.

Rhuddanian of Hunan Province, China (Chen et al., 2012). *Metabolograptus persculptus* appears to be confined to the *M. persculptus* Biozone (Chen et al., 2005; Loydell, 2007). Although *M. persculptus* occurs only in the lower part of the mudstone interval at Shuangshe (Fig. 2), there are no unambiguously Silurian elements in the fauna; thus, we assign the assemblage to the *Metabolograptus persculptus* Biozone (Hirnantian, Upper Ordovician). Koren' et al. (2003) recognized a distinct *Avitograptus avitus* Faunal Interval containing (with other elements) *No. minor* and *Av. avitus* immediately above the *M. persculptus* Biozone in Sweden. We hence correlate the Anji assemblages with the middle to upper *M. persculptus* Biozone on the basis of the occurrence of both *No. minor* and *Av. avitus*.

South China was located at or near the equator during the Late Ordovician (Cocks and Torsvik, 2013; Zhan et al., 2015). During the latest Hirnantian, the study area was located in a deep-water basinal area between the Cathaysian landmass to the present-day south and graptolitic shales deposited in relatively shallower water to the present-day north (Botting et al., 2018b). The shallower-water Yangtze platform was located to the present-day west (Botting et al., 2018b). The main sediment input to the area was from the Cathaysian landmass (Botting et al., 2018b). The graptolite- and sponge-bearing mudstone interval within the sandstones of the Wenchang Formation represents an interval of sea-level rise (Botting et al., 2017a).

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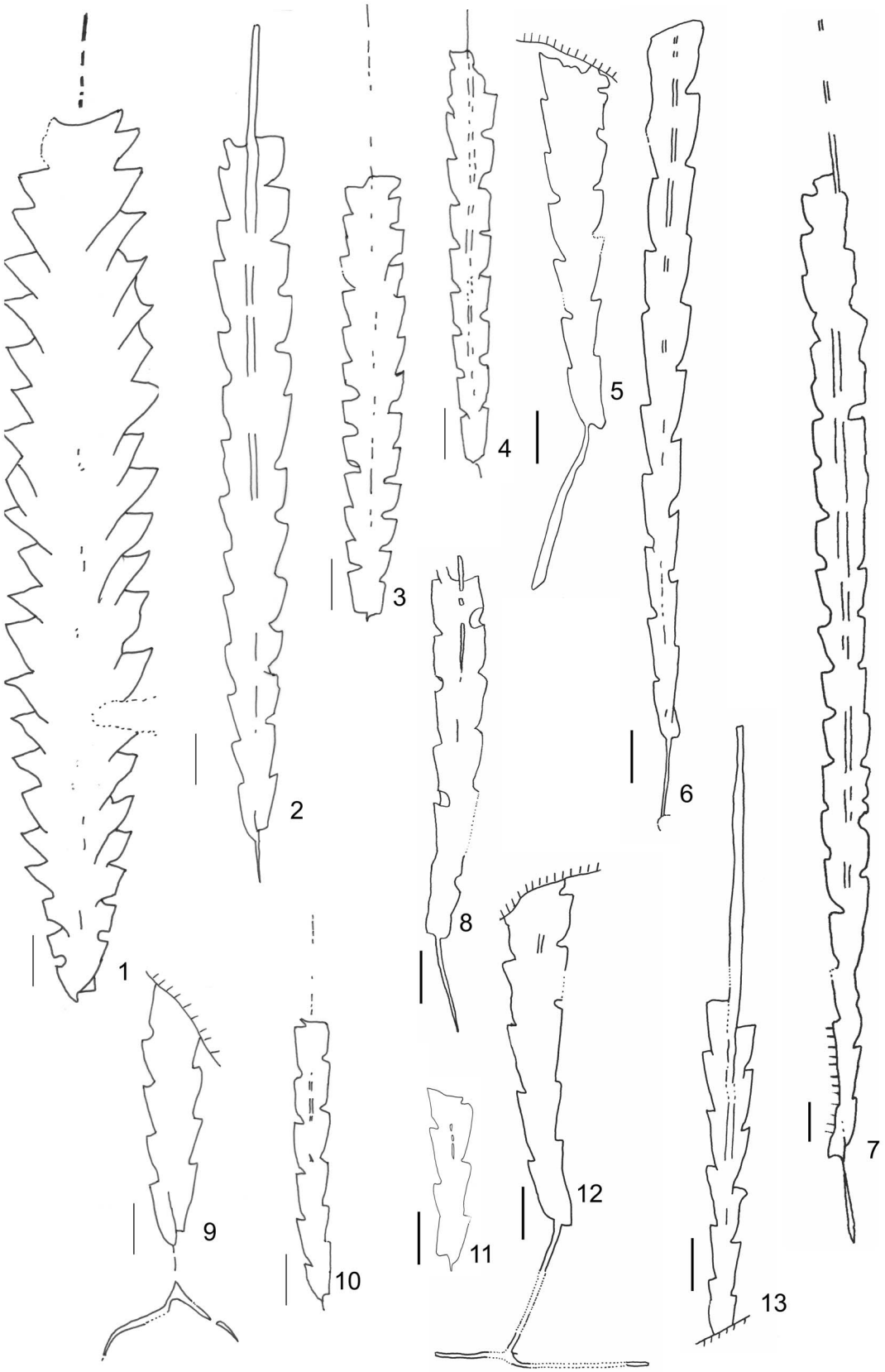

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Figure 3. Camera lucida drawings of graptolite taxa from Shuangshe, Wenchang Formation, *Metabolograptus persculptus* Biozone. (**1**) *Neodiplograptus shanchongensis*, NIGP 170578, Shuangshe bed 2; (**2**) *Avitograptus avitus*, NIGP 170568, Shuangshe bed 1; (**3**) *Metabolograptus parvulus*, NIGP 170579, Shuangshe bed 2; (**4**) *Normalograptus mirnyensis*, NIGP 170580, Shuangshe bed 2; (**5, 8, 11, 12**) *Avitograptus acanthocystus* n. comb., (**5**) NIGP 170575, Shuangshe bed 4, (**8**) NIGP 170572, Shuangshe bed 3, (**11**) NIGP 170571, Shuangshe bed 3, (**12**) NIGP 170573, Shuangshe bed 3; (**6, 7**) *Avitograptus akidomorphus* n. sp., (**6**) paratype, NIGP 170569, Shuangshe bed 3, (**7**) paratype, NIGP 170361, Shuangshe bed 3, note that the proximal end of this specimen is slightly damaged (location of damage indicated by short horizontal lines), resulting in th1[2] being obscured; (**9**) *Normalograptus*? *zhui* NIGP 170581, Shuangshe bed 3; (**10**) *Normalograptus angustus* NIGP 170582, Shuangshe bed 3; (**13**) *Avitograptus acanthocystus*? n. comb., NIGP 170574, Shuangshe bed 3. All scale bars represent 1 mm.

Materials and methods

The specimens described in this study are preserved flattened in mudstone as black or brown films representing the remains of the original skeletal material. In some cases the periderm has weathered sufficiently to allow some details of the internal structure, such as the presence of a median septum, to be visible. The mudstone was originally black and in many samples has weathered to a whitish color.

Specimens were photographed using a Leica M125 microscope with a Leica DFC450C (Leica, Wetzlar, Germany). Measurements of graptolite specimens follow those of Štorch et al. (2011, fig. 13) and Loydell (2007, text-fig. 7). Thecal spacing is given as two-thecae repeat distances (2TRD; Howe, 1983). The term "tubarium" is used to describe the graptolite remains, rather than "rhabdosome," following usage in the current version of the Treatise on Invertebrate Paleontology (Maletz et al., 2014a).

Repository and institutional abbreviation.—All material is deposited in the Nanjing Institute of Geology and Palaeontology, Nanjing, China (NIGP).

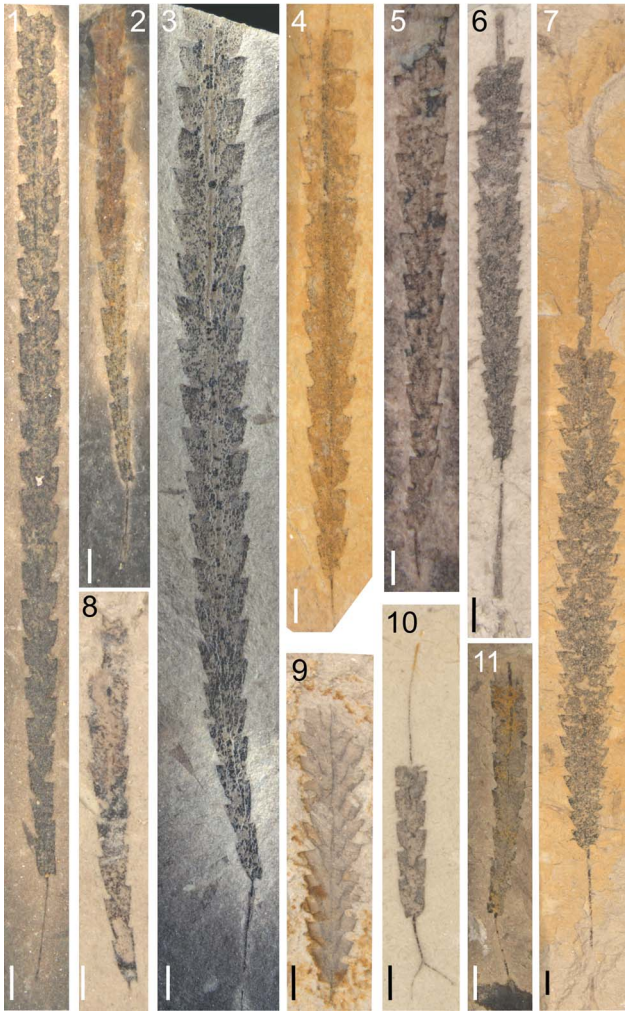

Figure 4. Photographs of graptolites from Shuangshe, Zhuwukou and Tianjiashan 3, Wenchang Formation, *Metabolograptus persculptus* Biozone. (**1, 2**) *Avitograptus akidomorphus* n. sp., (**1**) holotype, NIGP 170360, Shuangshe bed 3, (**2**) paratype, NIGP 170569, Shuangshe bed 3; (**3, 5, 8, 11**) *Avitograptus acanthocystus* n. comb., (**3**) NIGP 170577, Zhuwukou, (**5**) NIGP 170576, Tianjiashan 3, (**8**) NIGP 170570, Shuangshe bed 2, (**11**) NIGP 170572, Shuangshe bed 3; (**4**) *Avitograptus avitus*, NIGP 170567, Shuangshe bed 1; (**6**) *Metabolograptus wangjiawanensis*, NIGP 170583, Shuangshe bed 1; (**7**) *Neodiplograptus modestus*, NIGP 170584, Shuangshe bed 1; (**9**) *Metabolograptus persculptus*, NIGP 170585, Shuangshe bed 2; (**10**) *Normalograptus minor*, NIGP 170586, Shuangshe bed 2. All scale bars represent 1 mm.

Systematic paleontology

The high-level taxonomic classification used in this study is that of Maletz (2014, 2017); diplograptid taxonomy follows Melchin et al. (2011).

Superfamily Monograptoidea Lapworth, 1873
Family Dimorphograptidae Elles and Wood, 1908, emend. Melchin et al., 2011
Genus *Avitograptus* Melchin et al., 2011

Type species.—*Glyptograptus* (?) *avitus* Davies, 1929, from Dob's Linn, southern Scotland, UK, by original designation.

Other species.—*Climacograptus acanthocystus* Fang et al., 1990; *Avitograptus akidomorphus* n. sp.; *Avitograptus* aff. *avitus* of Melchin et al. (2011).

Emended diagnosis.—Development presumed Pattern J (Melchin et al., 2011, p. 289). Th1[1] upturned at level of sicular aperture, or slightly below or above level of sicular aperture, th1[2] arising from low within the upward-grown portion of th1[1]. Thecae slightly to moderately inclined; geniculate proximally, geniculate or almost straight distally. First thecal pair elongated relative to subsequent thecae. Full median septum.

Remarks.—Because isolated material is not available for any taxon assigned to this genus (Melchin et al., 2011), the developmental pattern is not known with certainty, but seems likely to be Pattern J. The flattened specimens of *Avitograptus akidomorphus* n. sp. and of *Av. acanthocystus* n. comb. described herein are consistent with a pattern J development. The position of upturn of th1[1] appears to be variable in the species described herein and in material of *Avitograptus* from Dob's Linn (Melchin et al., 2011, p. 295).

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The three species described herein are a little like *Rhaphidograptus* Bulman, 1936, in that the dorsal margin of the sicula is completely obscured and the ventral margin is partly covered by th1[1]. However, *Avitograptus* is biserial, whereas *Rhaphidograptus* is uni-biserial. In addition, the new material differs from *Rhaphidograptus* in the thecal form: *Rhaphidograptus* has climacograptid (strongly geniculate) thecae; the new species have sigmoidally curved thecae either throughout the tubarium or in the distal portion. Some species of the uni-biserial genus *Dimorphograptus* Lapworth, 1876 have a similar thecal form to *Avitograptus*, but *Dimorphograptus* is uniserial proximally, whereas *Avitograptus* is entirely biserial (Maletz, 2017). In addition, th1[1] of *Dimorphograptus* consistently turns upward above the aperture of the sicula (Melchin, 1998), rather than slightly below, at, or slightly above the sicular aperture as in *Avitograptus*.

Avitograptus can be distinguished from *Akidograptus* and *Parakidograptus* by the development of the proximal end. In *Avitograptus*, th1[1] turns upwards below, at, or slightly above the aperture of the sicula, whereas in *Akidograptus* and *Parakidograptus* th1[1] consistently turns upward markedly above the sicular aperture. Distinguishing species of *Avitograptus* from species of *Akidograptus* or *Parakidograptus* thus is only possible in material in which the proximal end is preserved.

Avitograptus avitus (Davies, 1929)
Figures 3.2, 4.4

1929 *Glyptograptus*? *avitus* Davies, p. 8, fig. 2l.
1962 *Glyptograptus* (?) *avitis* [sic]; Packham text-fig. 7a.
1983 *Glyptograptus*? *avitus*; Williams, p. 625, text-fig. 7l.
?1983 *Glyptograptus*? *avitus*; Williams, p. 625, pl. 66, figs 8–10; text-fig. 7h–k, 9a–d, 10a–c.
1988 *Glyptograptus*? *avitus*; Rickards, fig. 1f.
?1994 *Glyptograptus*? *avitus*; Zalasiewicz and Tunnicliff, p. 704, text-fig. 5m.
?non *Climacograptus avitus*; Li, p. 92, pl. 1, figs 3–5; text-fig. 1b–d.
1999
?aff. *Glyptograptus* aff. *avitus* Underwood et al., fig. 5Y, Z.
1998
2003 *Normalograptus avitus*; Koren' et al., fig. 3.16, 3.17, 3.28, 3.32.
?2003 *Normalograptus avitus*; Masiak et al., fig. 4h, 7g.
2005 *Normalograptus avitus*; Chen et al., pl. 1 fig. 11, pl. 2, fig. 9, text-fig. 7D, G, J–L.
?2007 *Normalograptus avitus*; Chen et al., text-figs 3N, O, 4I, J.
2011 *Avitograptus avitus*; Melchin et al., fig. 6B.
2017 *Avitograptus avitus*; Maletz, fig. 5.1a.

Holotype.—SM A10019 (Sedgwick Museum, Cambridge) from the Lower Birkhill Shales, Dob's Linn, Scotland, UK (Davies, 1929, fig. 2l).

Occurrence.—*Avitograptus avitus* has primarily been described from the UK (e.g., Davies, 1929; Zalasiewicz and Tunnicliff, 1994; Zalasiewicz et al., 2009), China (e.g., Chen et al., 2005), and questionably from North Africa (Underwood et al., 1998). There have been a few reports from Europe (e.g., Koren' et al., 2003; Masiak et al., 2003; Maletz et al., 2014b) and North America (Goldman et al., 2011; Loxton, 2017), but the species has not yet been recorded in Australia.

Description.—Tubarium straight, expanding gradually. Dorsoventral width 0.9 mm at th1, 1.4–1.5 mm at th5, 1.6 mm distally (Table 1). Thecae glyptograptid with rounded genicula and small apertural excavations. Supragenicular walls slightly inclined outward relative to tubarium axis. Median septum slightly undulating and present from at least aperture of th2[1]. Th1[1] grows downward along virgella. Both nema and virgella long, straight, and unbranched, extending in the same direction as the tubarium axis. 2TRD large throughout tubarium (1.6–2.1 mm proximally, at least 2 mm in the rest of the tubarium).

Materials.—NIGP 170567, 170568 from Shuangshe bed 1.

Remarks.—The virgella bifurcates close to the tubarium in some material assigned to this species by other authors (e.g., Zalasiewicz and Tunnicliff, 1994), but such branching was not observed in our material. Specimens with a bifurcating virgella identified as *Av. avitus* by Williams (1983) were assigned to *Av.* aff. *avitus* by Melchin et al. (2011); previously, Koren' et al. (2003) had assigned similar material to *No. avitus* (sensu Williams, 1983).

Avitograptus acanthocystus (Fang et al., 1990) new combination
Figures 3.5, 3.8, 3.11–3.13, 4.3, 4.5, 4.8, 4.11

1990 *Climacograptus acanthocystus* Fang et al., p. 64 (Chinese text), p. 128 (English text), pl. 12, figs 12–14.

Holotype.—Specimen number 50529, Department of Earth Sciences, Nanjing University, from the *Diplograptus bohemicus* Biozone (= *M. extraordinarius* Biozone), Lishuwo Formation, Wuning, Jiangxi Province, China (Fang et al., 1990, pl. 12, fig. 14).

Diagnosis.—*Avitograptus* with gently curved proximal end and thecae with rounded genicula. Supragenicular walls slightly inclined relative to tubarium axis proximally, often becoming parallel to tubarium axis distally. Ventral margin of sicula entirely obscured by th1[1]; dorsal margin partly covered by th2[1].

Occurrence.—This species is only known from Hirnantian strata, having been reported from the *Diplograptus bohemicus* Biozone (equivalent to the *M. extraordinarius* Biozone) to the *Climacograptus anjiensis* Biozone (equivalent to the *M. persculptus* Biozone) of the Lishuwo Formation, Wuning, Jiangxi Province, China (Fang et al., 1990) and the *M. persculptus* Biozone of the Wenchang Formation, Fushi Reservoir area, Anji County, Zhejiang Province, China.

Description.—Tubarium with gentle proximal curvature, widening from 0.6–0.9 mm across th1 pair to 0.8–1.4 mm at th5 pair to 1.5–1.8 mm at th10 to 2.5 mm distally (Table 2). Median septum straight and present from at least the level of the middle of th4 (Fig. 4.3). The specimen tentatively assigned to this species (NIGP 170574) has a median septum

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Table 1. Measurements of specimens of *Avitograptus avitus* (Davies, 1929) n. comb. Sicula dorsal length = length of exposed portion of dorsal margin of sicula, measured parallel to tubarium axis; aperture distance = distance from aperture of sicula to aperture of th1[1], measured parallel to tubarium axis; 2TRD = two-thecae repeat distance; DV width = dorsoventral width. All measurements in millimeters.

Specimen	Tubarium length	Sicula dorsal length	Aperture distance	Length of th1[2]	2TRD th2	2TRD th5	2TRD th10	Distal 2TRD	DV width th1	DV width th5	DV width th10	Distal width
NIGP 170567	15.2	0.3	0.7	0.9	2.1	2.1	2.4	2.5	0.9	1.4	1.6	1.6
NIGP 170568	8.5	0.2	0.9	1.0	1.6	2.0	—	—	0.9	1.5	—	—

visible throughout the preserved portion of the tubarium. Thecae with rounded genicula; supragenicular walls slightly inclined relative to tubarium axis proximally, often becoming parallel to tubarium axis distally. Thecal apertures generally horizontal. Apertural excavations shallow proximally. Thecae widely spaced: 2TRD 1.8–2.4 mm at th2[1], 2.0–2.8 mm at th5[1], 2.3–2.5 mm at th10[1], 2.5 mm distally (Table 2). Virgella, when preserved, long and robust. In one specimen (NIGP 170575), the virgella is initially in the same line as the axis of the tubarium (for a distance of 0.4 mm), then bends and widens, forming a spatulate structure that is 2.9 mm long (Fig. 3.5). In another specimen (NIGP 170573), the virgella bifurcates to form two horizontal branches 2.5 mm from the sicular aperture (Figs. 3.11, 4.11). Nema not preserved in most specimens. In the specimen tentatively assigned to this species (NIGP 170574), the nema is robust. Details of sicula not visible. Th1[1] covers the ventral margin of the sicula, extending slightly below the sicular aperture in two specimens (NIGP 170571, 170572) and growing upward from the level of the aperture in the other specimens. Dorsal margin of sicula free for 0.5–0.9 mm. Distance from sicular aperture to th1[1] aperture 0.8–1.3 mm.

Materials.—NIGP 170570 from bed SS2 at Shuangshe, NIGP 170571–170573 from bed SS3 at Shuangshe, NIGP 170575 from bed SS4 at Shuangshe, NIGP 170576 from Tianjiashan 3, and NIGP 170577 from Zhuwukou. NIGP 170574 from bed SS3 at Shuangshe lacks the extreme proximal end and is questionably assigned to this species.

Remarks.—In the holotype of the species, the virgella widens to form what Fang et al. (1990) called an "acanthocyst". Only one of the Anji specimens displays this feature (Fig. 3.5); other specimens have a long, relatively thin virgella, which branches in one specimen (Figs. 3.11, 4.11). Because the virgella varies within the population, it cannot be used as a species-defining characteristic. Elaboration of the virgella appears to be common in akidograptines (Štorch, 1983) and *Avitograptus*, although not all individuals exhibit this feature. For example, Williams (1983) illustrated specimens of *Av. avitus* (identified as *Av.* aff. *avitus* by Melchin et al., 2011) with a bifurcating virgella with horizontal branches, and Zalasiewicz and Tunnicliff (1994) reported a specimen with downward-pointing branches. The specimens of *Akidograptus ascensus*, *Ak. cuneatus*, and *Parakidograptus acuminatus* from Uzbekistan figured by Koren' and Melchin (2000) all display branching virgellae.

Avitograptus acanthocystus n. comb. can be readily distinguished from other avitograptid and normalograptid species. It is similar to *Av. avitus* in thecal form, but can be distinguished by the curvature of the proximal end, the greater 2TRD, and the greater dorsoventral width. *Avitograptus acanthocystus* n. comb. differs from *Av. akidomorphus* n. sp. in its more pronounced proximal curvature, the lack of sharp geniculation on the proximal thecae, and the greater dorsoventral width. *Normalograptus minor*, which characteristically bears a branching virgella, has a more slender tubarium and lower thecal spacing than *Av. acanthocystus* n. comb. In addition, the tubarium of *No. minor* is straight proximally rather than curved. *Normalograptus rhizinus* (Li and Yang in Nanjing Institute of Geology and Mineral Resources, 1983) has a spatulate virgella and proximal dorsoventral width values similar to those of *Av. acanthocystus* n. comb., but the former has a straight tubarium and a smaller distal width.

Table 2. Measurements of specimens of *Avitograptus acanthocystus* (Fang et al., 1990) n. comb. for which the proximal end is available. Sicula dorsal length = length of exposed portion of dorsal margin of sicula, measured parallel to tubarium axis; aperture distance = distance from aperture of sicula to aperture of th1[1], measured parallel to tubarium axis; 2TRD = two-thecae repeat distance; DV width = dorsoventral width. All measurements in millimeters.

Specimen	Tubarium length	Sicula dorsal length	Aperture distance	Length of th1[2]	2TRD th2	2TRD th5	2TRD th10	Distal 2TRD	DV width th1	DV width th5	DV width th10	Distal width
NIGP 170570	10.0	0.6	1.2	0.9	2.4	2.8	—	—	0.7	0.8	—	—
NIGP 170571	3.1	0.8	1.3	0.9	2.1	—	—	—	0.7	—	—	—
NIGP 170572	6.4	0.7	0.9	—	2.2	2.3	—	—	0.9	1.3	—	—
NIGP 170573	5.7	0.9	1.1	1.2	2.3	—	—	—	0.6	—	—	—
NIGP 170575	6.9	0.5	—	—	2.0	2.0	—	—	0.7	1.2	—	—
NIGP 170576	13.9	0.7	0.8	0.8	1.8	2.1	2.3	—	0.7	1.0	1.5	—
NIGP 170577	25	0.7	1.1	0.9	2.3	2.5	2.5	2.5	0.6	1.4	1.8	2.5

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Table 3. Measurements of *Avitograptus akidomorphus* n. gen. n. sp. Sicula dorsal length = length of exposed portion of dorsal margin of sicula, measured parallel to tubarium axis; aperture distance = distance from aperture of sicula to aperture of th1[1], measured parallel to tubarium axis; 2TRD = two-thecae repeat distance; DV width = dorsoventral width; x = data not measurable. All measurements in millimeters.

Specimen	Tubarium length	Sicula dorsal length	Aperture distance	Length of th1[2]	2TRD th2	2TRD th5	2TRD th10	Distal 2TRD	DV width th1	DV width th5	DV width th10	Distal DV width
NIGP 170569	13.2	0.6	1.0	1.2	2.5	2.8	x	x	0.4	0.8	—	—
NIGP 170360	24.9	0.7	1.0	1.1	2.3	2.3	2.1	2.2	0.6	0.9	1.2	1.2
NIGP 170361	21.7	—	1.1	1.1	2.0	2.3	2.4	2.5	x	0.8	1.1	1.2

Avitograptus akidomorphus new species
Figures 3.6, 3.7, 4.1, 4.2

?1980 *Glyptograptus* aff. *avitus* Davies, 1929; Koren' et al., p. 140, pl. XL, fig. 10, text-fig. 41.
?2007 *Normalograptus rhizinus*; Chen et al., text-figs 3U, 4N.

Holotype.—NIGP170360 (Fig. 4.1) from bed SS4 at Shuangshe, Fushi Reservoir, Anji County, Zhejiang Province, South China. Wenchang Formation, *Metabolograptus persculptus* Biozone, Hirnantian, Upper Ordovician.

Diagnosis.—*Avitograptus* with strongly geniculate proximal thecae and weakly geniculate distal thecae. Tubarium straight, dorso-ventral width 0.4–0.6 mm at th1, maximum dorso-ventral width 1.2 mm. Ventral margin of sicula entirely obscured by th1[1]; dorsal margin partly covered by th2[1]. Complete median septum.

Occurrence.—Only known with certainty from the type locality. The specimen of Koren' et al. (1980) that is questionably assigned to this species is from the *P. acuminatus* Biozone (lower Silurian) of Kazakhstan. The specimen of Chen et al. (2007) that is questionably identified herein as *Av. akidomorphus* n. sp. is from the Tangjia section (*M. extraordinarius* or *M. persculptus* Biozone; exact horizon not stated) of Lin'an County, Zhejiang Province, ~45 km south of Fushi Reservoir.

Description.—Tubarium slender, very slightly curved proximally, widening from 0.4–0.6 mm across th1 to 0.8–0.9 mm at th5 to a maximum of 1.2 mm distally (Table 3). Proximal thecae (th2–4) with pronounced geniculum, geniculum less pronounced in distal thecae. Apertures horizontal or slightly introverted. Thecal walls slightly inclined relative to tubarium axis proximally, becoming parallel distally. Thecae widely spaced: 2TRD 2.0–2.5 mm at th2[1], 2.3–2.8 mm at th5[1]. Distal 2TRD measurements are not available for the specimen with the greatest 2TRD value at th5 (NIGP 170569), but in the other two specimens 2TRD values are 2.1–2.4 mm at th10[1] and 2.1–2.4 mm distally. Median septum complete, very slightly undulating. Exact point of origin of th1[1] cannot be determined, but presumed to be low on the sicula (the ventral margin of the sicula is entirely covered). Th1[1] extends slightly below (Fig 4.1) or grows up from (Fig. 4.2) the level of the sicular aperture. Distance from aperture of sicula to aperture of th1[1] 1.1 mm. Sicula partly obscured by th1[2], so sicula length cannot be determined.

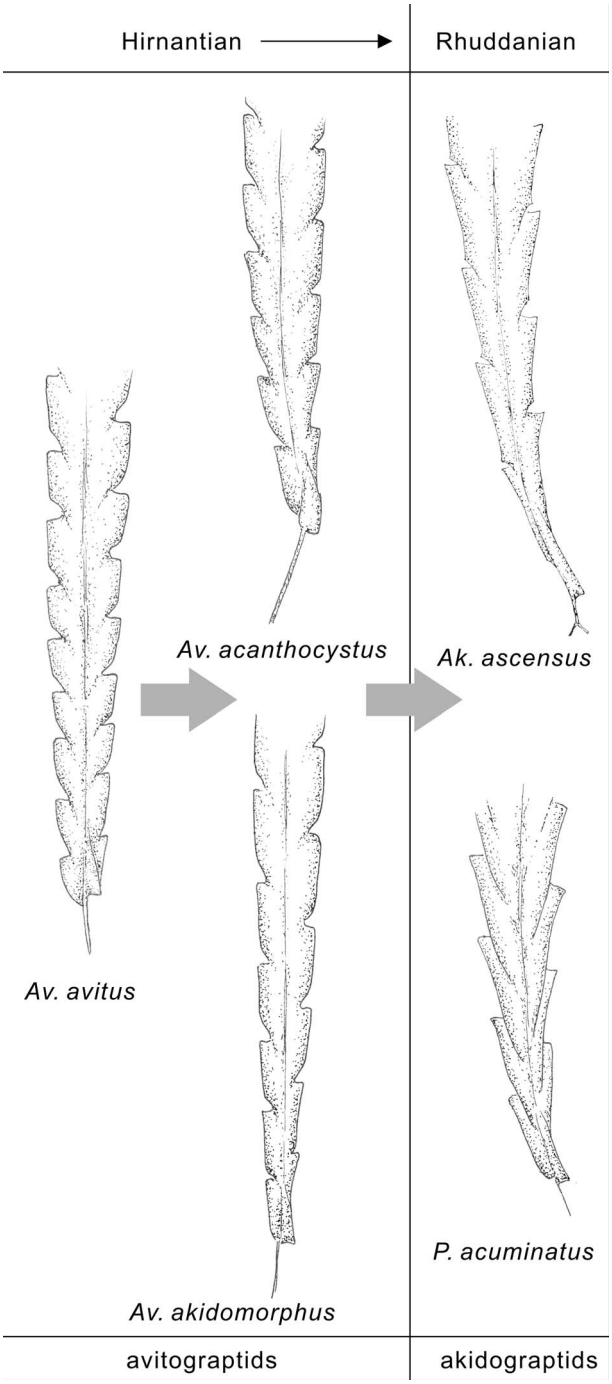

Figure 5. Schematic evolution of akidograptids from *Avitograptus* during the Hirnantian–Rhuddanian boundary interval. The figure indicates grades of change rather than exact relationships. *Av.* = *Avitograptus*, *Ak.* = *Akidograptus*, *P.* = *Parakidograptus*.

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Dorsal margin of sicula free for 0.6–0.7 mm. Virgella robust, at least 2.1 mm long, projecting at a slight angle from the tubarium. In specimen NIGP 170361, the virgella is thickened; in specimen NIGP 170569, it appears to bifurcate 1.4 mm from the sicula. Only one specimen (NIGP 170361) preserves the nema, which extends beyond the last thecae and is quite slender.

Etymology.—From Greek *akis*, thorn, and *morphe*, shape, reflecting the slender, pointed shape of the tubarium, and the similarity of the species to *Akidograptus*.

Materials.—Paratypes NIGP170361 (Fig. 3.7) and NIGP 170569 (Figs. 3.6, 4.2) from bed SS3 at Shuangshe.

Remarks.—This species is similar to species of *Akidograptus* in terms of thecal shape and slight tubarium curvature, but differs in the details of the proximal end. As stated above in the discussion of the genus, in *Akidograptus* the entire dorsal margin of the sicula and a portion of the ventral margin are free, and in *Parakidograptus* the ventral margin is also free, but the dorsal margin is partly obscured by th1^2. In contrast, in *Av. akidomorphus* n. sp., the ventral margin of the sicula is entirely covered by th1^1. Thus, *Av. akidomorphus* n. sp. cannot be assigned to *Akidograptus* or *Parakidograptus*, and is instead placed in *Avitograptus*.

Avitograptus akidomorphus n. sp. can be distinguished from *Parakidograptus praematurus* (Davies, 1929) by its lower width at th5 (>1 mm in *P. praematurus*, 0.8–0.9 mm in *Av. akidomorphus* n. sp.) and lower maximum width (1.5 mm in *P. praematurus*, 1.2 mm in *Av. akidomorphus* n. sp.; Davies, 1929; Štorch et al., 2019). The thecal spacing is lower in most specimens of *P. praematurus* than in *Av. akidomorphus* n. sp. In addition, in *P. praematurus*, th1^1 turns upwards slightly, but significantly, above the sicular aperture (see for example Zalasiewicz, 2007), whereas in *Av. akidomorphus* n. sp., th1^1 turns upwards at or slightly below the sicular aperture.

Avitograptus akidomorphus n. sp. is similar to *Av. avitus* in the proximal thecal shape, in the elongation of the proximal thecae, and in the low point of origin of th1^1. The new species differs in its more pronounced thecal geniculation, slight proximal curvature of the tubarium, and the smaller tubarium width and larger 2TRD values.

Avitograptus akidomorphus n. sp. is similar in overall appearance to some previously described species of *Akidograptus*. *Akidograptus longus* Huang and Lu, 1983, from the uppermost Ordovician or lower Silurian of Tibet, is strikingly similar to *Av. akidomorphus* n. sp. in overall form of the tubarium, but the two species can be distinguished on the basis of their proximal end development. In *Ak. longus*, th2^1 originates at the level of the middle of th1^2, leaving the dorsal margin of the sicula uncovered, whereas in *Av. akidomorphus* n. sp. th2^1 appears at about the level of the middle of th1^1 and partly covers the sicula. *Akidograptus macilentus* Chen and Lin, 1978 is also similar in overall appearance, but re-examination of the holotype (specimen NIGP36053) has shown that in that species the dorsal margin of the sicula is entirely uncovered (LAM personal observation, 2018). These similarities confirm the close relationship between *Av. akidomorphus* n. sp. and *Akidograptus* species.

The specimen described as *Glyptograptus* aff. *avitus* from the *Parakidograptus acuminatus* Biozone of Kazakhstan by Koren' et al. (1980) is similar to *Av. akidomorphus* n. sp., but a firm assignment is not possible because the proximal end is not preserved in the Kazakhstan material.

Climacograptus mirabilis Keller, 1956 from the *Pseudoclimacograptus scharenbergi* Biozone (Sandbian, Upper Ordovician) of Kazakhstan (Keller, 1956) is similar to *Av. akidomorphus* n. sp. in overall form; however, the two species can be readily distinguished by the slightly greater proximal tubarium width and lower 2TRD values of *C. mirabilis*. In the single *C. mirabilis* specimen illustrated by Keller (1956), the virgella has overgrown the sicular aperture, and so it is not possible to determine details of the proximal end development. Because only one specimen is illustrated, it is not possible to tell whether the virgellar overgrowth is a peculiarity of that specimen, or characteristic of that species. Such overgrowth is not present in the Anji material, so this may be another consistent difference between the species.

Discussion

Melchin et al. (2011) hypothesized that the genus *Avitograptus* (to which they assigned two species, *Av. avitus* and *Av.* aff. *avitus*) represents an evolutionary intermediate between *Normalograptus* and *Parakidograptus/Akidograptus*, following the earlier suggestion of Davies (1929) that *Av. avitus* gave rise to *Akidograptus* and *Parakidograptus*. The discovery of *Avitograptus akidomorphus* n. sp. and *Av. acanthocystus* n. comb. supports this hypothesis. The evolutionary changes between *Avitograptus avitus* and *Parakidograptus/Akidograptus* involved distal movement of the origin of th1^1 and th1^2 (resulting in the dorsal margin of the sicula being

Table 4. Measurements from the literature of holotype or topotype specimens of *Avitograptus avitus* (Davies, 1929) n. comb., *Akidograptus ascensus* Davies, 1929, *Parakidograptus acuminatus* (Nicholson, 1867), and *P. praematurus* Davies, 1929. Sicula dorsal length = length of exposed portion of dorsal margin of sicula, measured parallel to tubarium axis; aperture distance = distance from aperture of sicula to aperture of th1^1, measured parallel to tubarium axis; 2TRD = two-thecae repeat distance; DV width = dorsoventral width. All measurements in millimeters. Measurements of holotypes from: *Av. avitus*, Davies (1929, fig. 21) n. comb.; *Ak. ascensus*, Rigby (2000); *P. acuminatus*, Rong et al. (2008, fig. 1.3); *P. praematurus*, Zalasiewicz (2007). Measurements of *Av. avitus* topotype from Melchin et al. (2011, fig. 6B). Note that the holotype of *Av. avitus* is slightly tectonized longitudinally, resulting in a decrease in the dorso-ventral width (Williams, 1983) and possibly an increase in the 2TRD. All measurements in millimeters.

Species	Specimen	Sicula dorsal length	Aperture distance	Length of th1^2	2TRD th2	2TRD th5	DV width th1	DV width th5
Av. avitus	holotype	unclear	1.3	1.1	2.1	1.9	0.8	unclear
Av. avitus	topotype	0.42	1.3	1.2	2.1	2.0	0.6	1.0
Ak. ascenus	holotype	0.3	2.3	1.2	2.4	2.1	0.45	0.8
P. acuminatus	holotype	0.6	2.4	1.2	2.4	2.3	0.8	1.5
P. praematurus	holotype	0.05	1.3	1.0	2.0	—	0.65	—

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entirely uncovered and the ventral margin mostly uncovered), thecal elongation, and greater outward inclination of the thecal walls (shown schematically in Fig. 5). *Avitograptus akidomorphus* n. sp. and *Av. acanthocystus* n. comb. represent morphological intermediates between *Av. avitus* and both *Akidograptus* and *Parakidograptus* in several parameters (Table 4). For example, the distance from the aperture of the sicula to the aperture of th1[1], measured parallel to the tubarium axis, is 0.8–0.9 mm in Shuangshe *Av. avitus*, 1.0–1.1 mm in *Av. akidomorphus* n. sp., 0.8–1.2 mm in *Av. acanthocystus* n. comb., 2.3 mm in the holotype of *Akidograptus ascensus*, and 2.4 mm in the holotype of *Parakidograptus acuminatus*.

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