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ARTICLE

REPORT OF *CLAVATIPOLLENITES HUGHESII* FROM THE KITADANI FORMATION: FIRST ANGIOSPERM RECORD FROM THE LOWER CRETACEOUS OF INNER JAPAN

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ABSTRACT

The early Aptian Kitadani Formation of the Tetori Group, which outcrops at the “Kitadani Dinosaur Quarry” located in Katsuyama City, Fukui Prefecture, is well known for its rich floral and vertebrate fossil assemblages. The authors previously reported a diverse palynoflora from the lower part of the quarry composed of spores, gymnosperm pollen grains, freshwater algae and one epiphyllous fungus, but barren of any angiosperm pollen grain. We report here eumagnoliid angiosperm pollen attributable to *Clavatipollenites hughesii* Couper from the middle to upper part of the quarry. It represents the first convincing angiosperm fossil record for the Lower Cretaceous of the Inner Zone of Japan.

Key words: *Clavatipollenites hughesii*, early angiosperms, Kitadani Formation, Lower Cretaceous, Japan.

ルグラン ジュリアン・寺田和雄・湯川弘一・西田治文（2019）北谷層から内帯日本の下部白亜系において初となる被子植物化石 *Clavatipollenites hughesii*. 福井県立恐竜博物館紀要 18：21–30.

手取層群北谷層（下部 Aptian）は福井県勝山市の「北谷恐竜発掘現場」に露出し，植物や脊椎動物化石を多く産出する．我々は以前，発掘現場の下部から胞子や裸子植物花粉，淡水性緑藻類，葉上寄生菌類などの多様なパリノフロラを報告したが，これまで被子植物花粉は未発見だった．今回，発掘現場の上部から真正モクレン類の *Clavatipollenites hughesii* Couper を発見した．これは内帯日本の下部白亜系から初の被子植物化石記録である．

INTRODUCTION

Angiosperm fossils of the Lower Cretaceous period are scarce in Japan. The oldest angiosperm record is a pollen grain reported from the late Barremian of the Nishihiro Formation, Monobegawa Group, Wakayama Prefecture (Legrand et al., 2014), belonging to the Outer Zone of Japan. Other reports of angiosperms are permineralized remains such as a seed of Trimeniaceae (Yamada and Kato, 2008; Yamada et al., 2008) and wood (Takahashi and Suzuki, 2003), both from the Albian of the Yezo Group, Hokkaido. Monosulcate, tricolpate and chotomosulcate pollen have also been reported from the late Barremian-early Aptian Pechikunnai Formation of the Sorachi Group, Hokkaido (Tanaka and Hirano, 2009), but this diverse angiosperm assemblage suggests much younger age than authors thought (Legrand et al., 2014).

No angiosperm report exists from the Lower Cretaceous of the Inner Zone of Japan. With regard to the Upper Cretaceous of the Inner Zone of Japan, the oldest angiosperm fossils are leaves reported from the Coniacian-Campanian Upper Formation of the Mifune Group in Kumamoto Prefecture (Matsuo, 1993). Leaves were reported in the Izumi Group from the Upper Campanian in Sanuki City, Kagawa Prefecture (Kimura and Ohana, 1995) and from the Maastrichtian in Kada-cho, Wakayama Prefecture (Matsuo, 1966) and Awaji Island, Hyogo Prefecture (Iwaki and Maeda, 1989). Leaves and pollen grains were reported from the Maastrichtian of the Asuwa Formation in Fukui Prefecture (Matsuo, 1962; Sazawa et al., in press) and Omichidani Formation in Fukui and Ishikawa Prefectures (Matsuo, 1960,

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1970; Nichols et al., 2010). Soda (1955) and Oyama (1962) also reported some angiosperm leaves recovered from an horizon inserted between volcanic rocks of the Upper Cretaceous Sugitani Formation in Okayama Prefecture.

The authors previously reported a diverse palynological assemblage from samples collected in the lower part of the early Aptian locality known as the "Kitadani Dinosaur Quarry" (Azuma, 2003) of the Kitadani Formation, Tetori Group, Inner Zone of Japan (Legrand et al., 2013). The plant assemblage already reported from the Kitadani Formation is characterized by the abundance of Filicopsida together with common Bennettitales and Coniferales (Kimura, 1975; Kimura and Horiuchi, 1979; Yabe et al., 2003; Yabe and Kubota, 2004; Terada and Yabe, 2011; Yabe and Shibata, 2011; Sano and Yabe, 2017), whereas the palynoflora is dominated by palynomorphs of spore-producing plants, mostly Filicopsida (Schizaeales, Cyatheales, and Osmundales) and gymnosperm pollen, primarily of Coniferales and Bennettitales, Cycadales or Pentoxylales (Legrand et al., 2013). However, neither the macro- nor microfossil assemblages yielded any angiospermous remain.

The fourth excavation project held by the Fukui Prefectural Dinosaur Museum started in 2013, revealing unstudied horizons in the middle to upper part of the quarry from which we took fresh samples (Legrand et al., 2016). Among them, two samples revealed angiosperm pollen of *Clavatipollenites hughesii* Couper (1958), that we report in this paper. Detailed palynological assemblages of these two horizons will be summarized and discussed together with those from other horizons in a later paper.

GEOLOGICAL SETTING

The Tetori Group (*sensu stricto*) outcrops in the Hokushinetsu and Hida districts of central Japan (Maeda, 1961) and is divided, in the Takinamigawa area, into the Akaiwa and Kitadani Formations in ascending order (Maeda, 1958). The Kitadani Formation crops out along the Sugiyama River, northeastern part of Katsuyama City, Fukui Prefecture. It constitutes the uppermost part of the Tetori Group, where it conformably overlies the Akaiwa Formation and is unconformably overlain by the Maastrichtian Omichidani Formation.

The Kitadani Formation has been assigned to the early to mid-Aptian in age based on the molluscan (Isaji, 1993; Kozai et al., 2002), ostracod (Cao, 1996) and charophyte (Kubota, 2005) biostratigraphy and on geological correlations with coeval strata distributed in the basin (Sano, 2015; Sano and Yabe, 2017). It probably deposited in a meandering river and fluvio-lacustrine environment (Legrand et al., 2013; Suzuki et al., 2015).

MATERIALS AND METHODS

The two samples were collected from the "Kitadani Dinosaur Quarry" in 2013. Sample "2013.10.02-01" was collected from the mudstone intercalated between sandstone layers in the middle part of the quarry close to the third step dug during the fourth excavation project (Fig. 1). Suzuki et al. (2015) interprets this deposit as alternation of mudstone and sandstone subfacies (AMS) of abandoned channel-fill facies (Suzuki et al., 2015: Fig. 5a). Sample "2013.06.11-12" was taken in a block of siltstone excavated during the same year from an unknown horizon of the middle to upper part of the quarry.

We followed Legrand et al. (2013) for palynomorph isolation as well as for classification system. In the name of specimens, the letter after sample number corresponds to the slide number, followed by the position of the grain on the slide using an England Finder graticule. The grains were observed under a Leica DMRD Differential Interference Contrast Microscope equipped with a Leica MC170HD Camera, and a Confocal Laser Scanning Microscope Zeiss LSM510.

DESCRIPTION AND DISCUSSION

All angiosperm pollen grains obtained from the two samples belong to *Clavatipollenites hughesii* (Fig. 2) and they represent about 0.5% in number in both palyno-assemblages. The state of preservation of palynomorphs was slightly better in sample 2013.06.11-12. The preparations cited in present paper are housed in the Collection of the Fukui Prefectural Dinosaur Museum.

Some problems remain for defining genus *Clavatipollenites* (Friis et al., 2011), and *Clavatipollenites hughesii* may also include several morphological types (Hugues et al., 1979). We describe the pollen type found from the Kitadani Formation below.

Systematic Palynology

Anteturma VARIEGERMINANTES Potonié, 1970
Turma MONOCOLPATES (MONOSULCITES) and ZONOCOLPATES
Iversen and Troels-Smith, 1950
Infaturma RETICULATI Pons, 1988
Genus *CLAVATIPOLLENITES* Couper, 1958
CLAVATIPOLLENITES HUGHESII Couper, 1958

Type species.—*Clavatipollenites hughesii* Couper, 1958, p. 159–160, Pl. 31, Fig. 19–22.

Material examined.— 2013.06.11-12a, B29/4, 2013.10.02-01a, S52.

Description.—Grain subspherical, 23 μm in diameter. Pollen monosulcate; sulcus broad, from 4 μm at the ends to 7 μm wide in its middle part, and almost extending to the whole length of the grain; microreticulum irregularly polygonal of lumina around 0.4 μm wide (0.35 to 0.7), smooth, with muri about 0.5 μm high. Exine thin, about 0.5 μm thick.

Distribution.—*Clavatipollenites hughesii* was firstly described by Couper (1958) from the Wealden (Barremian) of England. The oldest reports are from the late Hauterivian of Morocco (Gübeli et al., 1984) and Israel (Brenner, 1996), and

FIGURE 1. Location of the horizon which yielded sample "2013.10.02-01" (picture taken on August 19th, 2014).

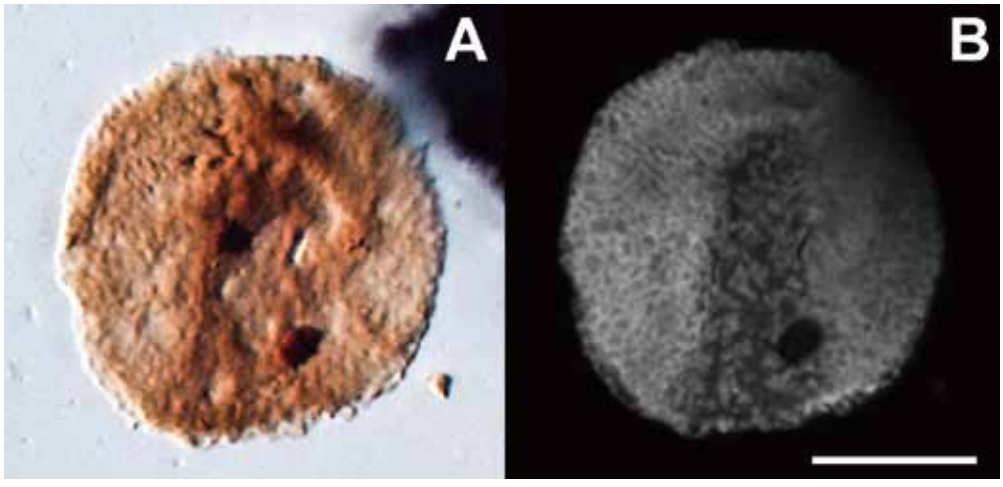

FIGURE 2. *Clavatipollenites hughesii* observed under the light (**A**) and confocal laser scanning (**B**) microscopes (2013.06.11-12a, B29/4). Scale bar: 10 µm.

the species is found worldwide from the Barremian to Maastrichtian lowland sediments.

In Asia, the oldest report of *Clavatipollenites hughesii* is from the Barremian Qingshila Formation of the Jehol Group of Western Liaoning in North East China (Yu, 1990). It is then reported from the Aptian of the Lumuwan Group of Hainan in southernmost China (Dong et al., 1991), the Aptian Changcai Formation of eastern Jilin (Yu and Miao, 1983) and the Aptian Dongning Formation of eastern Heilongjiang (Kovaleva et al., 2017) in North East China, the Barremian-Aptian Longpan Formation in North Korea (Jiang and Yang, 1996), and the Barremian-Aptian (age uncertain because of a lack of any marine intercalation or other stratigraphic marker; Vakhrameev, 1991) Zazinskaya Formation of the Transbaikal region in Russia (Markevitch, 1994; Vakhrameev and Kotova, 1977). In younger strata, it is reported from the Aptian-Albian Fuxin Formation of

TABLE 1. Previous reports of *Clavatipollenites hughesii* and other species of the *Clavatipollenites* genus in the Lower Cretaceous of Asia.

	Russia	Mongolia	North-West China
Albian	**Primorye region** Suchan Basin, Galenkovskaya Formation (Albian) **34 *Clavatipollenites hughesii* (Markevitch, 1994)** 35 *C. incisus* (Markevich, 1994) Partizansk Basin (early to mid-Albian) **34 *C. hughesii* (Volynets, 1998; Volynets et al., 2001)** 35 *C. incisus* (Volynets, 1998; Volynets et al., 2001) Razdolnaya River Basin, Lipovtsy Formation (Aptian-early Albian) **36 *C. hughesii* (Kovaleva et al., 2016; Volynets et al., 2016)** 37 *C. incisus* (Markevich, 1995) **Siberia** early Albian 38 *C. rotundus* (Chlonova, 1977)	Bayan-Erkhet area, Bayan-Erkhet Formation (Albian) **29 *C. hughesii* (Ichinnorov, 2003b)** 30 *C. rotundus* (Ichinnorov, 2003b) 30 *C.* sp. (Ichinnorov, 2003b) Shaazan Govi area, Khukhteeg Formation (Albian) 31 *C. rotundus* (Ichinnorov, 2003a; 2003b) 31 *C.* sp. (Ichinnorov, 2003a; 2003b) Choyr Basin, Khuren Dukh Formation (Aptian-Albian) 32 *C. rotundus* (Nichols et al., 2001, 2006; Tsolmon et al., 2014) Tevshiin Govi and Shivee-Ovoo areas, Tevshiin Govi Formation (Aptian-Albian) 33 *C.* sp. (Ichinnorov, 1999; 2003b)	**Gansu Province** Jiuquan Basin, Zhonggou Formation (early Albian) **26 *C. hughesii* (Zhang et al., 2015)** 27 *C.* sp. (Zhang et al., 2015) Miaogou Group (Lower Cretaceous) 27 *C.* sp. (Yu et al., 1982) **Xinjiang region** Junggar Basin, Lianmuqin Formation (Lower Cretaceous) 28 *C.* sp. (Song, 1986)
Aptian	**Transbaikal region** Zazinskaya Formation (Barremian-Aptian) **12 *C. hughesii* (Markevitch, 1994; Vakhrameev and Kotova, 1977)** 13 *C. incisus* (Markevitch, 1994; Vakhrameev and Kotova, 1977) 13 *C. rotundus* (Markevitch, 1994; Vakhrameev and Kotova, 1977)		**Gansu Province** Xinminpu Group, Hekou Formation (Neocomian) 11 *C.* sp. (Yu et al., 1982)
Barremian	**Siberia** Neocomian 4 *C. couperi* (Markova, 1971)	Tamutsag Basin, Damoguaihe Formation (Barremian) 3 *C.* sp. (Wang et al., 2014)	

the Jehol Group (Yu, 1990), the Barremian-early Albian Yimin Formation (Wan et al., 2005), the Hauterivian-Albian Saihan Tal Formation and the Albian Hadat Formation (Hua, 1991) of Inner Mongolia in North East China, the early Albian Zhonggou Formation of Gansu in North West China (Zhang et al., 2015), the Albian Bayan-Erkhet Formation in Mongolia (Ichinnorov, 2003b), and the Aptian-early Albian Lipovtsy Formation (Kovaleva et al., 2016; Volynets et al., 2016), the early to mid-Albian of the Partizansk Basin (Volynets, 1998; Volynets et al., 2001), and the Albian Galenkovskaya Formation (Markevitch, 1994) of the Primorye region in Russia.

Botanical affinities.—Pollen classified to *Clavatipollenites* could have been shed by a plant of the Chloranthaceae (Magnoliales). Among the extant Chloranthaceae, this genus is closely similar to pollen of *Ascarina lucida* distributed in New Zealand, Oceania in terms of morphology and wall ultrastructure (Couper, 1958; Doyle et al., 1975; Walker and Walker, 1984). *Clavatipollenites* grains were reported *in situ* from a carbonized anther closely similar to those of extant *Ascarina* from the Early Cretaceous (early Aptian) Baqueró Formation of Argentina (Archangelsky and Taylor, 1993). *Clavatipollenites hughesii* has also been reported *in situ* attached to the stigmatic area of the fossil fruit *Couperites mauldinensis* from the early Cenomanian of the Potomac Group, Maryland (Pedersen et al., 1991).

North-East China	South China	Korea	North Myanmar
Inner Mongolia	**Anhui Province**	**South-East Korea**	late Albian to early Cenomanian
Eren Basin, Hadat Formation (Albian)	Ehuling Formation (Lower Cretaceous)	Gyeongsang Basin, Iljik Formation (early Albian; Kang and Paik, 2013)	14 *C. rotundus* (Davies, 2001)
17 *C. hughesii* (Hua, 1991)	16 *C.* sp. (Li, 1979)	15 *C. minutus* (Choi, 1985; Yi et al., 1993)	
18 *C. minutus* (Hua, 1991)	lower Zhuxiang Formation (Lower Cretaceous)		
Eren Basin, Saihan Tal Formation (Hauterivian-Albian)	16 *C.* sp. (Wang et al., 1987)		
17 *C. hughesii* (Hua, 1991)			
18 *C.* sp. (Hua, 1991)			
Eren Basin, Bayanhua and Guyang formations (Lower Cretaceous)			
18 *C.* sp. (Wang et al., 1992)			
Hailar Basin, Yimin Formation (Barremian-early Albian)			
19 *C. hughesii* (Wan et al., 2005)			
20 *C.* sp. (Huang et al., 2004; Wan et al., 2005)			
Heilongjiang Province			
Songliao Basin, Denglouku Formation (Albian)			
21 *C.* sp. (Gao, 1982; Yan et al., 2017)			
Jilin Province			
Yanji, Dalazi Formation (Albian)			
22 *C.* sp. (Yu and Miao, 1983)			
Liaoning Province			
Jehol Group, Fuxin Formation (Aptian-Albian; Sha, 2007; Amiot et al., 2010)			
23 *C. hughesii* (Yu, 1990)			
24 *C. minutus* (Yu, 1990)			
24 *C.* sp. (Yu et al., 1986)			
Jiangsu Province			
Jurong Basin, Gecun Formation (late Aptian-late Albian)			
25 *C.* sp. (Zhou and Wang, 2001; Zhou et al., 2009)			
Unknown			
North China (Early Cretaceous)			
C. incisus (Yu, 1990)			
C. rotundus (Yu, 1990)			
North China (Late Barremian to Early Albian)			
C. ellipticus (Yu, 1990)			
Heilongjiang Province	**Hainan Province**	**North Korea**	
Dongning Formation (Aptian)	Baisha Basin, Lumuwan Group (Aptian)	Anchow Basin, Longpan Formation (Barremian-Aptian)	
7 *C. hughesii* (Kovaleva et al., 2017)	**6 *C. hughesii* (Dong et al., 1991)**	**5 *C. hughesii* (Jiang and Yang, 1996)**	
Chengzihe Formation (late Barremian to Aptian)			
8 *C.* sp. (Shang, 1997; Sun and Dilcher, 2002)			
Jilin Province			
Changcai Formation (Aptian)			
9 *C. hughesii* (Yu and Miao, 1983)			
Liaoning Province			
Jehol Group, Yixian Formation (Barremian-Aptian)			
10 *C.* sp. (Wang et al., 2000)			
Liaoning Province			
Jehol Group, Qingshila Formation (Barremian)			
1 *C. hughesii* (Yu, 1990)			
2 *C. minutus* (Yu, 1990)			

Discussion

Distribution of *Clavatipollenites* in East Asia during the Lower Cretaceous.—Previous reports of *Clavatipollenites hughesii* and other congeneric species in Asia are summarized in Table 1. According to these reports, a distribution of this species was restricted to the eastern margin of the Eurasian continent (Inner Japan; North Korea; North East China: Liaoning, Jilin and Heilongjiang; South China: Hainan) during the Barremian-Aptian, and then expanding to whole North China (Gansu and Inner Mongolia), Mongolia and the Primorye and Siberia regions of Russia during the Albian (Fig. 3). The presence of *Clavatipollenites hughesii* in the Kitadani Formation is concordant with the hypothesized paleophytogeography of this species.

Paleoecology.—Palynomorphs previously reported from the lower part of the "Kitadani Dinosaur Quarry" were composed of spores, gymnosperm pollen grains, freshwater algae and one epiphyllous fungus indicating a warm temperate and moderately humid climate, with locally drier conditions. Some of them suggested transportation and indicated an accumulation from various sources in the sedimentary basin (Legrand et al., 2013). Previous global reports of *Clavatipollenites* show a distribution in humid environments, so is the extant *Ascarina*. Among the earliest angiosperms, it has been suggested that plants producing *Clavatipollenites* would have flourished in shady, disturbed and

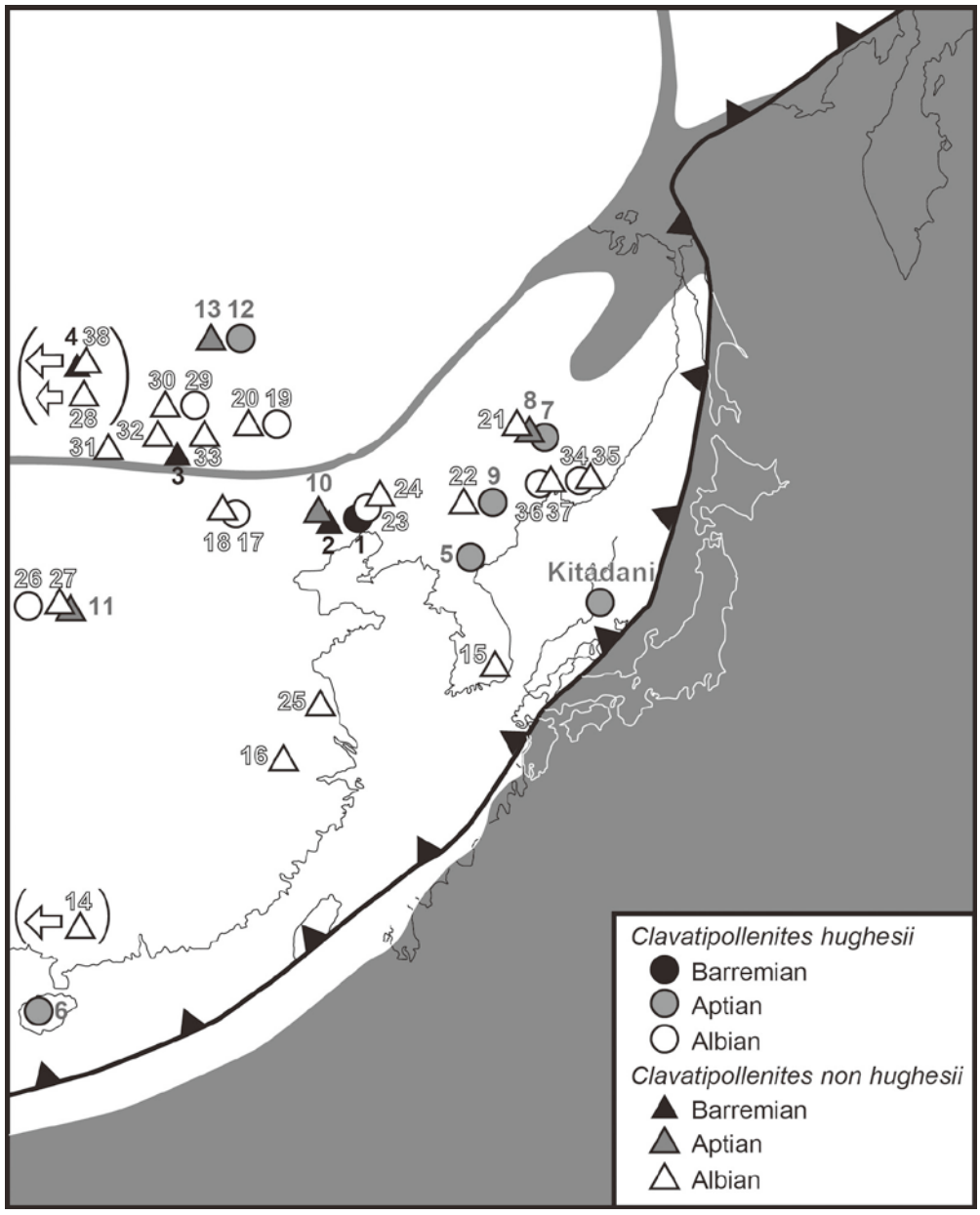

FIGURE 3. Distribution map of *Clavatipollenites hughesii* and other *Clavatipollenites* species in East Asia during the Lower Cretaceous. Localities number indicated in Table 1. Paleomap (black lines; white lines indicate the present position of Japan; bold line with triangles represents the subduction front) based on Maruyama et al. (1997).

wet habitats (Doyle and Hickey, 1976; Hickey and Doyle, 1977), and may have been wind- and occasionally insect-pollinated (Bernhardt and Thien, 1987, Crepet and Friis, 1987; Gottsberger, 1988; Feild and Arens, 2007; Friis et al., 2011).

The two samples of the quarry containing *Clavatipollenites hughesii* have a palynological composition close to those from other horizons (Legrand et al., 2013). However, these assemblages are markedly different from those by Legrand et al. (2013) in the relative abundance of Gnetalean pollen, particularily of *Gnetaceaepollenites* sp. (Legrand et al., in prep.). The extant species of the Gnetales, especially those of *Ephedra*, prefer a drying climate in which a wind-pollination is advantageous (Kubitzki, 1990). Therefore, paleoclimate inferred from *Clavatipollenites* seems contradictory to the abundant occurrences of the gnetalean pollen. However, similar co-occurrence has been reported in the Barremian-Aptian Yixian Formation of the Jehol Group in western Liaoning, China, where an early angiosperm *Archaefructus* (Sun et al., 2001) and Gnetalean fossils (Zhou et al., 2003; Rydin et al., 2006; Rydin and Friis, 2010) occur in fluvio-lacustrine sediments (Wang and Zheng, 2010). In addition, Crane and Lidgard (1989) suggested a

striking increase in Gnetalean diversity during the Early Cretaceous simultaneously with the initial angiosperm radiation. This contradiction would be reconciled if the Cretaceous gnetalean pollen is entomophilous and may not indicate dry conditions (Bolinder et al., 2015, 2016; Rydin and Hoorn, 2016).

CONCLUSION

Clavatipollenites hughesii is reported for the first time from the Lower Cretaceous of the Inner Zone of Japan, and the oldest appearance of the genus in Japan. *Clavatipollenites* is thought to be widely distributed in the eastern margin of the Eurasian Continent during the Aptian, but it has not been clarified if this scheme is applicable to Japan at that time period. Composition of the palyno-assemblage and the association of *C. hughesii* with relatively abundant Gnetalean pollen is very similar to the floral characteristics observed in the Yixian Formation, which also deposited in a fluvio-lacustrine environment.

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