doi:10.3969/j.issn.1673-9736.2019.04.06
Article ID: 1673-9736(2019)04-0280-09

Araucarian cone-scale complexes, newly found in Aptian Kitadani Formation of Tetori Group in Fukui Prefecture, Central Japan

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Abstract: This study reports on two forms of Araucarian cone-scale complexes from the Aptian Kitadani Formation of the Tetori Group in Fukui Prefecture, Central Japan. One of these has been identified as a new fossil species: *Araucarites kitadaniensis* Yabe et Yukawa sp. nov. This is the first known occurrence of Araucarian macrofossils from the Tetori Group, indicating that this group was substantially diverse during that time period. This finding concurs with previous palynological investigations at the site, supporting the hypothesis that Araucarian plants began to diversify during Aptian global warming.

Keywords: Araucarian cone-scale complexes; *Araucarites kitadaniensis* Yabe et Yukawa sp. nov.; Aptian; Early Cretaceous; Japan

0 Introduction

The Araucarian conifer is one of seven extant conifer families consisting of three extant genera: *Araucaria* Juss., *Wollemia* Jones, Hill et Allen, and *Agathis* Salisb. They show a typical Gondwanan distribution pattern; the first two genera are confined to the southern hemisphere, while *Agathis* Salisb. is distributed throughout Indomalaya and Australasia (Kershaw & Wagstaff, 2001). Fossil records indicate that this family derived from voltzialean conifers in the latest Permian or Early Triassic (Stewart & Rothwell, 1993). *Araucaria* and closely related organ genera appeared prior to the breakup of the Pangea supercontinent in the Early Jurassic and thus could have dispersed globally in the warm Mesozoic climate and moved toward high latitude areas. However, they disappeared from the northern hemisphere around the end of the Mesozoic (Kunzmann, 2007a).

In East Asia, fossil representatives of the family are relatively minor elements known to appear in the Late Triassic, but the acme of diversification can be seen in the Late Cretaceous. Several extant and extinct sections of the genus have been recorded in East Asia in this time period (Stockey, 1994; Ohsawa *et al.*, 1995). In contrast, however, East Asian records of the Early Cretaceous are quite limited (Dijkstra & van Ameron, 1999) and it is extremely difficult to trace the history of diversification processes in this area because the appearances of extant sections of the genus are still not well understood. In this study, we report new forms of Araucarian cone-scale complexes collected from the Lower Cretaceous Tetori Group in Central Japan, which was located at the eastern edge

Received 12 October 2019, accepted 8 November 2019
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of the middle latitude of the Eurasian continent at the time of deposition. After a description of the specimens, we briefly discuss their phytogeographic and phylogenetic implications.

1 Geologic setting

The fossil site, called "Kitadani Dinosaur Quarry", is situated in the northern part of Katsuyama City, Fukui Prefecture, Central Japan (Fig. 1); the Lower Cretaceous Kitadani Formation of the Tetori Group crops out at this location. The Tetori Group is a major fossil-bearing strata of vertebrates, invertebrates, and plants (Kimura *et al*., 1978; Matsukawa *et al*., 2006; Sano *et al*., 2008; Sano & Yabe, 2017) and is distributed throughout the Hokushin'etsu and Hida areas of Honshu Island, Central Japan (Maeda, 1961). The group is subdivided into the Itoshiro (lower) and Akaiwa (upper) subgroups (Sano, 2015; Yamada, 2017; Yamada & Sano, 2018), and the Kitadani Formation occurs at the uppermost part of the group in the Takinamigawa area (Maeda, 1958). The site is well-known for yielding non-marine molluscs (Maeda, 1958), plants (Yabe *et al*., 2003; Yabe & Kubota, 2004; Terada & Yabe, 2011; Legrand *et al*., 2013), and charophytes (Kubota, 2005), as well as various terrestrial and freshwater vertebrate fossils, including dinosaurs (Azuma & Currie, 2000; Hirayama, 2002; Kobayashi & Azuma, 2003; Azuma & Shibata, 2010; Lee *et al*., 2010; Shibata & Azuma, 2015; Miyata *et al*., 2016; Tsukiji *et al*., 2019).

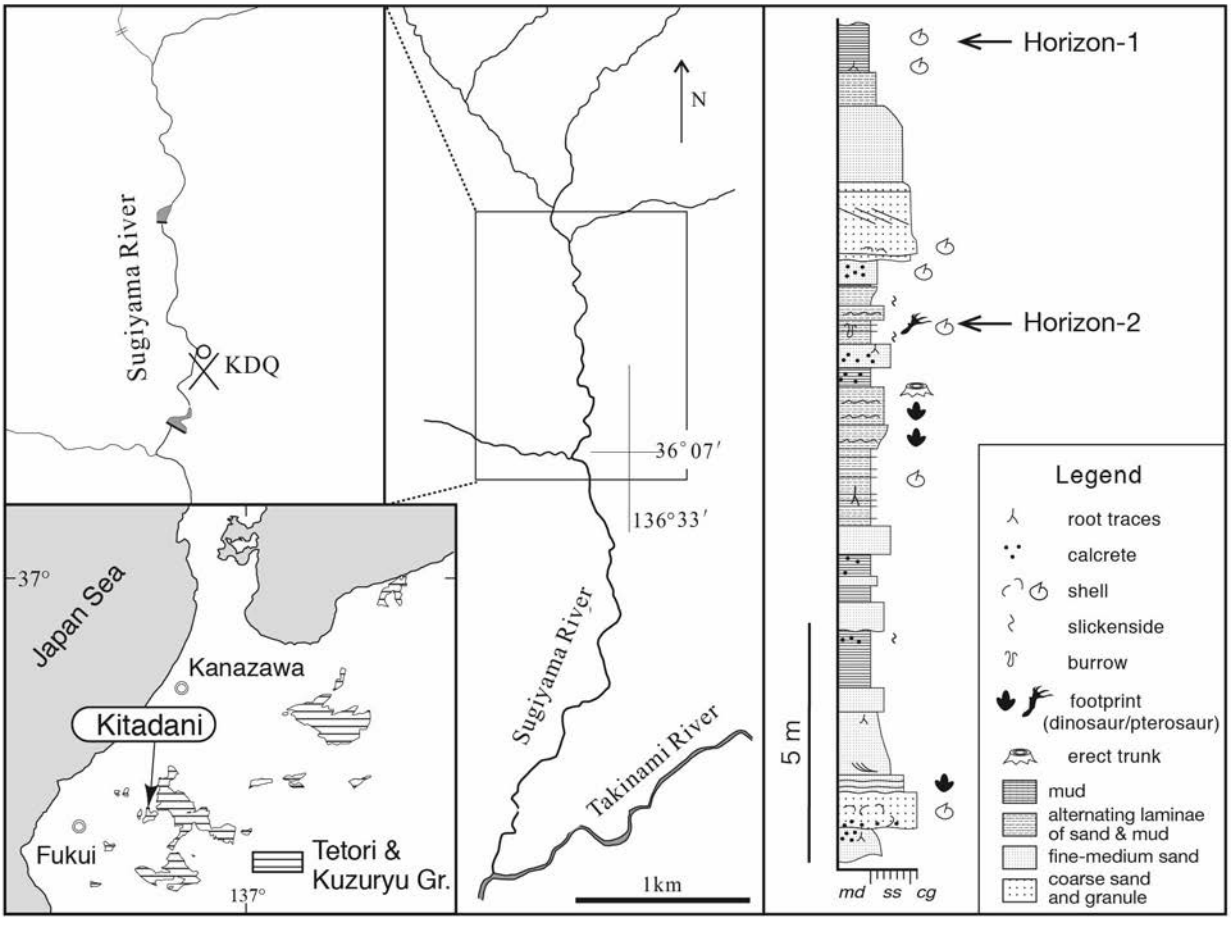


Fig. 1 Index map of the fossil locality (Kitadani Dinosaur Quarry: KDQ) and partial columnar section of the outcrop

The Kitadani Formation at the quarry is considered to have been formed in a meandering fluvial system (Yabe & Shibata, 2011). The formation comprises the point bar, the abandoned channel fill, and the

over bank facies (Suzuki *et al.*, 2015). Plant fossils have been recovered from each of these units, including swamp vegetation reconstructed by Yabe and Shibata (2011), which is dominated by *Brachyphyllum*. It has been suggested that the deposit formed during the Aptian based on biostratigraphic studies of freshwater bivalves (Isaji, 1993), ostracodes (Cao, 1996), and charophyte gyrogonites (Kubota, 2005), as well as through regional stratigraphic correlations (Sano, 2015).

2 Materials and methods

Each of the fossil specimens discussed in this paper were collected from the Kitadani Formation, which was exposed at the Kitadani Dinosaur Quarry during excavation projects conducted by the Fukui Prefectural Museum between 1989 to 1999 and the Fukui Prefectural Dinosaur Museum in 2000 and beyond. The relevant specimens—FPDM-P-1556, 1557, and 1558—occurred in homogeneous, structureless mudstone (Horizon-1) together with bivalves, fish bones, turtle shells, and charophyte gyrogonites (Fig. 1). This sediment has been interpreted as a deposit of organic structureless mudstone subfacies of abandoned channel-fill facies (Suzuki *et al.*, 2015: Fig. 5a). Specimen FPDM-P-1559 was situated within fine alternating beds of mudstone and fine-grained sandstone (Horizon-2) (Fig. 1). The horizon is relatively rich in plant fossils, including *Brachyphyllum* and *Podozamites* (Yabe & Shibata, 2011) (Fig. 2) as well as insects and trace fossils of pterosaurs, birds, and non-avian dinosaurs (Lee *et al.*, 2010).

After collection, the specimens were cleaned and fragments of carbonized materials were collected to make cuticular slides. These were photographed using a Pentax K-3II digital camera with a 35 mm Pentax-DA macro lens. Sketches were created using Adobe Draw software. Due to the especially delicate preservation state of cuticles, we observed the epidermal features of the specimen without using standard chemical treatment; instead, we made direct observations using a Zeiss Axio Scope. A1 fluorescence microscope equipped with an Axiocam 105 digital camera. All the specimens and slides used in this study are stored at Fukui Prefectural Dinosaur Museum (FPDM-P).

3 Systematic paleontology

Family Araucariaceae

Genus *Araucarites* C. Presl in Sternberg, 1838

***Araucarites kitadaniensis* Yabe et Yukawa, sp. nov.**

(Fig. 2)

Synonym: *Araucarites* sp., Krassilov, 1967, p. 183, pl. 63, figs. 7, 8.

Holotype: FPDM-P-1556-1, 2 (Fig. 2-1, 4)

Paratypes: FPDM-P-1557 (Fig. 2-2), 1558 (Figs. 2-3, 5)

Type locality: Horizon-1 of the "Kitadani Dinosaur Quarry", Kitadani, Katsuyama City, Fukui Prefecture, Central Japan

Stratigraphic Horizon: The Kitadani Formation of the Tetori Group (possibly mid-Aptian) (Fig. 1)

Etymology: From the name of fossil locality.

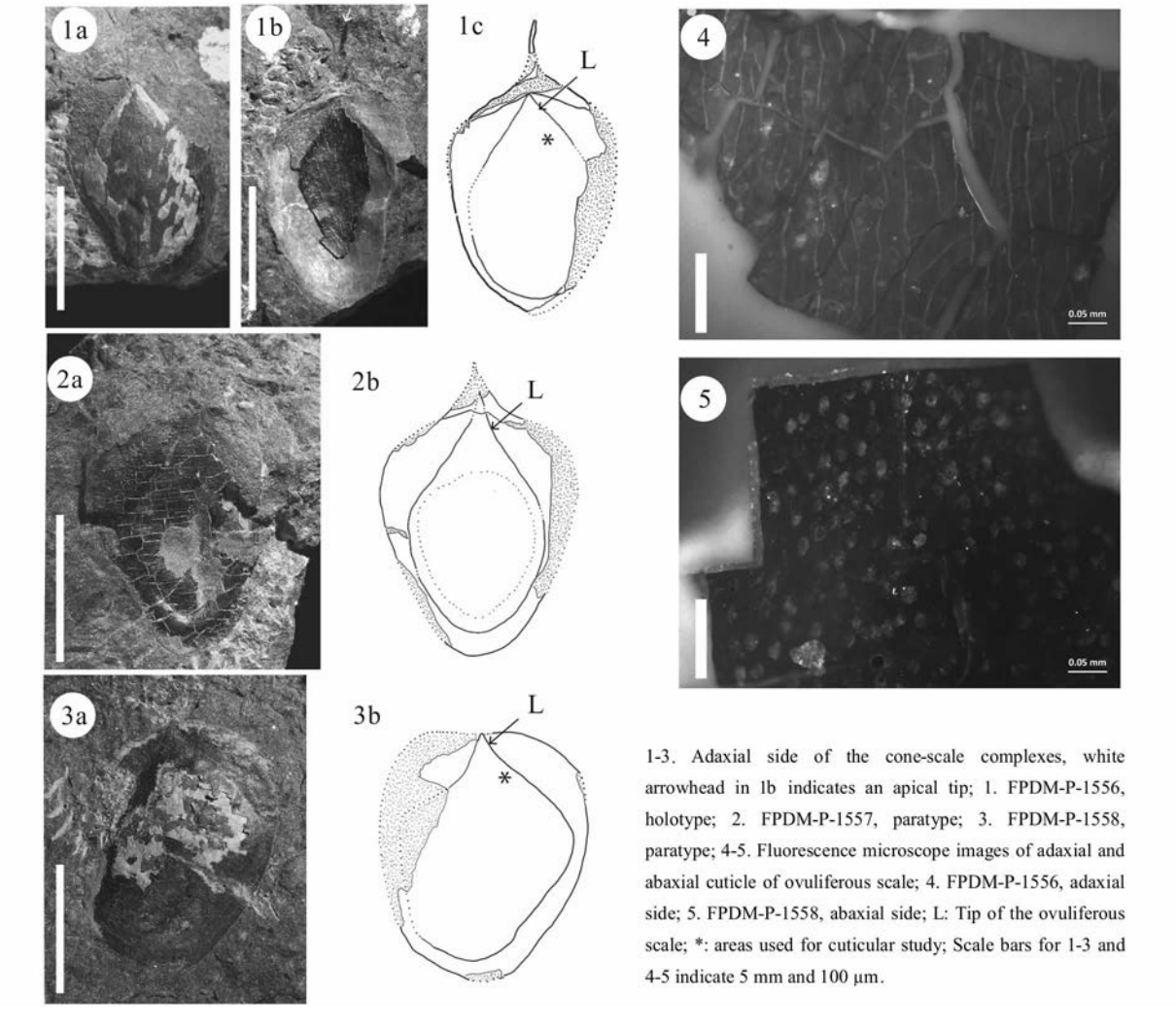
Diagnosis: Narrowly-winged cone-scale complex in wide-obovate shape measuring approximately 10 mm long by 6 mm wide. Base of the scale convex, obtuse; apex short acuminate with prolonged tip, ca. 2 mm long. Ventral side of seed-scale bearing a single seed medially. Embedded seed wide-obovate, covered with an ovuliferous scale. Ovuliferous scale wide-elliptic to wide-obovate with round base and short acuminate apex with unfused tip.

Description: Detached cone-scale complexes, 9.8–11.7 mm long, and 6.8–6.1 mm wide, narrowly winged, wide-obovate gloss form. Base of seed-scale convex, obtuse, probably truncate at very base. Apex acuminate with prolonged tip, as long as 2.2 mm. Ventral side of seed-scale bearing a single seed medially. Seed wide-obovate, embedded and covered with an ovuliferous scale, ca 5.0 mm long by 3.9 mm wide at broadest point. Ovuliferous scale wide-elliptic to wide-obovate with short acuminate apex and round base, measuring ca 8 mm long by 4.6–6.7 mm wide.

Cuticle possibly obtained from ovuliferous scales

hypostomatic. Adaxial epidermis consists of longitudinally arranged, rectangular to polygonal ordinary cells, surrounded by smoothly undulating anticlinal cell wall, 68-123 μm long by 17-33 μm wide. Abaxial epidermis consists of rows of stomata which are intercalated with rows of ordinary cell. Stomatal apertures are probably oriented oblique to perpendicular to the stoma line. Detail of stoma not visible, but some measurable guard cells attaining 17-19 μm long by 9-11 μm wide.

Comparison: These detached, winged, cone-scale complexes can be readily identified with the genus *Araucaria*, given the medially-embedded single seed on the adaxial side and the presence of an ovuliferous scale. Cuticular structures, such as the elongated ordinaryl cell files with weakly undulate cell wall combined with an arrangement of stoma lines, also conform to the genus (Stockey, 1994). However, the size of the seed scale as well as the very narrow wings on both sides of the seed are features unique to this species. Detached cone-scale complexes that can be assigned to extant *Araucaria* have been named *Araucaria* Juss. or *Araucarites* C. Presl. Although there are taxonomic problems with using the name *Araucarites* (Kvaček, 1971; Kunzmann, 2007a), we tentatively use this name here following the treatment proposed by Zijlstra and Cittert (2000) for an organ genus for detached Araucarian cone-scale complexes. Based on our findings, we propose a new fossil species *Araucarites kitadaniensis* Yabe et Yukawa.



1-3. Adaxial side of the cone-scale complexes, white arrowhead in 1b indicates an apical tip; 1. FPDM-P-1556, holotype; 2. FPDM-P-1557, paratype; 3. FPDM-P-1558, paratype; 4-5. Fluorescence microscope images of adaxial and abaxial cuticle of ovuliferous scale; 4. FPDM-P-1556, adaxial side; 5. FPDM-P-1558, abaxial side; L: Tip of the ovuliferous scale; *: areas used for cuticular study; Scale bars for 1-3 and 4-5 indicate 5 mm and 100 μm.

Fig. 2 ***Araucarites kitadaniensis*** **Yabe et Yukawa sp. nov.**

Among fossil species reported so far, this species is most similar to *Araucarites minutus*, collected from the Sher River near Sehora in the Satpura Basin, Central India (Bose & Maheshwari, 1979: Early Cretaceous Age by Rajanikanth & Chinnappa, 2016), in its general shape, size, and short acuminate tip. However, *A. minutus* has a more cuneate shape, with straight sides and pointed shoulders at the distal end of the wing. Moreover, that species does not yield distinct ligules.

Only a few representatives of cone-scale complexes or cones with Araucarian affinities have been recorded from the Early Cretaceous strata in East Asia (Dijkstra & van Ameron, 1999). Oishi (1940) reported two specimens from the Tithonian-Berriasian Kiyosue Formation in Yamaguchi Prefecture, Western Japan, as *Araucarites cutchensis* Feistmantel. These are notably distinct from our species; they are two to three times larger and have distinct wings on both sides of the seed. Kimura and Ohana (1987) reported a fragmentary cone from the Lower Jurassic Nishinakayama Formation and compared it with the same species; however, that specimen probably belongs to another conifer family because it does not yield an embedded seed on each scale (Kimura & Ohana, 1997). One detached cone reported as *Araucarites* sp. from the Aptian Lipovtsy Formation (Krassilov, 1967) is the only representative that can truly be compared with our new fossil species. The specimen bears tiny cone-scales, ca. 8 mm long by 4 mm wide, with a wide obovate to elliptic shape with slightly convex sides and a short acuminate tip. It also appears to have distinct ovuliferous scales.

Based on the presence of distinct wings, and shortly acuminate ligular scale, our new species can be compared with the extant section *Eutacta* (Kunzmann, 2007b).

***Araucarites* sp.**

(Fig. 3)

Materials: FPDM-P-1559

Locality: Horizon-2 of the "Kitadani Dinosaur Quarry", Kitadani, Katsuyama City, Fukui Prefecture, Central Japan

Horizon: The Kitadani Formation of the Tetori Group (possibly mid-Aptian) (Fig.1)

Description: A single detached cone-scale complex was obtained. The overall shape of the scale is elliptic and wingless, measuring 25.4 mm long by 11.2 mm wide. Base of seed-scale is straight sided, narrow obtuse, probably truncate at very base. Tip of the scale is elongate, acute, straight- to concave-sided probably with pointed apex. Ventral side of the scale bearing a seed medially, which is covered with an ovuliferous scale. Seed embedded, obovate, 15.8 mm long by 8.0 mm wide at broadest point. Ovuliferous scale slightly shorter than cone-scale. Cuticle was not obtained due to its preservation state.

Remarks: The specimen has distinct features that are comparable with Araucarian cone-scale complexes, namely a seed scale bearing a single seed medially and covered by an ovuliferous scale. The specimen is distinct from *A. kitadaniensis* Yabe et Yukawa in size and general shape and in having an acute tip. The specimen is somewhat similar to *Araucaria fricii* from the Coniacian Březno Formation of the Czech Republic (Velenovský, 1893) and *A. pantiana* from the Early Cretaceous Bansa Formation of the South Rewa Basin in Central India (Bose & Maheshwari, 1973) in size, shape, and length/width ratio. However, the apical halves of these species are distinctly concave; moreover, they yield a much shorter ovuliferous scale tip than the current specimen.

Among the fossil and extant species described to date, no specimen shows features which are identical to those of this specimen. However, we only have a single specimen, and it has no cuticular information. While it appears that this is a new fossil species, more samples are needed before we can proceed with a definitive identification. The specimen may be compared with the extant section *Araucaria*, given its wingless bract and ovuliferous scale with relatively long tip (Kunzmann, 2007b). Alternatively, it may belong to any extinct section, because its seed scale tip is distinct from those seen in extant species.

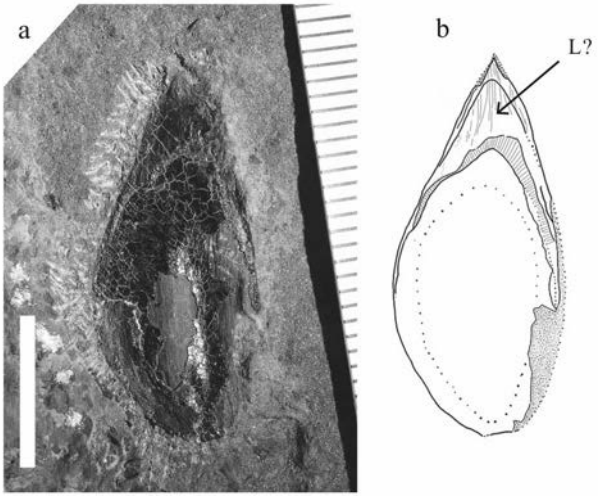


Fig. 3 ***Araucarites* sp., adaxial side, FPDM-P-1559. Scale bar = 1 cm**

4 Phytogeographic implications

In contrast to the relatively rich Araucarian macrofossil records in the Late Cretaceous (Stopes & Fujii, 1910; Stockey *et al.*, 1992, 1994; Kimura & Ohana, 1995; Ohsawa *et al.*, 1995), relatively few samples have been recorded from the Lower Cretaceous and earlier strata in East Asia. The presence/absence of the Araucariaceae and their abundance have been rarely discussed in the light of past climatic conditions (Krassilov, 1978).

To date, only two fossil records of the earliest Cretaceous are available in this context. Oishi (1940) reported two detached Araucarian cone-scale complexes from the Tithonian-Berriasian Kiyosue Formation in western Honshu, Japan. Krassilov (1982), meanwhile, described a new fossil species, *A. mongolica*, from a contemporaneous stratum in Mongolia (Shin-Khuduk Formation: Tithonian-Valanginian?) based on associated shoots, cones, and cone scales. No fossil records have been recognized in the late Neocomian. Araucariaceous fossils reappear in the Barremian-Aptian or Aptian periods, when a period of global warming began (Hasegawa *et al.*, 2012; Yamada *et al.*, 2018). Although still rare, they are found from relatively low to middle latitudes: Cao (1999) reported two detached cone-scale complexes as *Araucarites* sp. from the Aptian of Zhejiang Province, Southeast China. Further north, Sun *et al.* (2001) described a new fossil species of isolated cone, *A. minor*, from the Barremian-Aptian Yixian Formation in Northeast China. Krassilov (1967) also recorded isolated cones and cone scales from the Aptian Lipovtsy Formation in Suifun Basin, Russian Primorye, located in the same latitudes.

Similar floral successions have been recorded in the outer zone of Japan, where the southern phytogeographic province (i. e., the Euro-Sinian province of Vakhrameev, 1991) prevailed (Kimura, 1987). Recently, Legrand *et al.* (2011, 2014) examined palynofloras of the Barremian part of the Choshi Group and the Barremian-Aptian Nishihiro Formation of the Monobegawa Group, both in the outer zone of Japan. *Araucariacites* pollen are absent or rare in those areas. In contrast, the Aptian part of the Choshi Group has yielded several species of fossil woods with Araucarian affinities (Nishida, 1965; Nishida & Oishi, 1982; Nishida *et al.*, 1993).

The Tetori Group, located in the inner zone of Japan, is considered to belong to the northern phytogeographic province or the Siberian-Canadian province of Vakhrameev (1991) (Kimura, 1987). Legrand *et al.* (2013) described palynological assemblages of the Kitadani Formation at the same site as the present study and reported the presence of *Araucariacites australis* in all the horizons examined there. New Araucarian fossils described in this paper add further evidence that several species have appeared there at that time. Therefore, it can be said that the floral successions occurred simultaneously in both the outer and inner zones of Japan. The dispersed cone-scale complexes described in this paper are crucial to botanical identifications. As mentioned earlier, they are comparable with extant sections *Eutacta* and *Araucana* or with any extinct one in the genus *Araucaria*. They clearly show that substantial taxonomic diversities existed during the Aptian.

In Horizon-2 of the Kitadani Formation, conifer

shoots with appressed scale-like leaves identical to *Brachyphyllum* sp. are dominant; one of them occurred together with a cone scale reported here (FPDM-P-1559). Araucarian seed cones attached with *Brachyphyllum* shoots have been recorded in many cases (Kunzmann, 2007a). Ohsawa (2005) proposed a new extinct section, *Yezonia* (Stopes et Fujii) Ohsawa, H Nishida et M Nishida, based on permineralized Araucarian plants that bore *Brachyphyllum*-like foliage and *Eutacta*-like seed cones from the Upper Cretaceous of Hokkaido, Japan. Our materials from the Early Cretaceous might also show similar relationships to represent an extinct lineage as above.

Further comparisons of cuticular features of isolated organs, i. e. foliage identified as *Brachyphyllum* spp. and isolated cone-scale complexes, are necessary if we are to develop a better-rounded and more robust understanding of their sectional placement. This will contribute greatly to trace the diversification of Araucarian plants during Aptian global warming in the northern hemisphere.

Acknowledgements

This paper was prepared as a proceedings of the International Symposium held at Jiayin, NE China during Aug. 18–21 in 2019. We are indebted very much to organizing committee of the symposium and Jiayin Government for their help and support to AY for his trip to China. Thanks are also due to Dr Harufumi Nishida of Chuo University for his reading of our manuscript. The authors are grateful to all staff of the 4th Dinosaur Project of FPDM. Part of this work was financially supported by Fukui Prefectural Government.

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