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Pterophyllum pachyrachis (Bennettitales) from the Upper Jurassic to Lower Cretaceous Tetori Group, Fukui Prefecture, Central Japan

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Abstract. We designate the lectotype of *Ptilophyllum pachyrachis* Oishi (1940), collected from the Upper Jurassic (Tithonian) to Lower Cretaceous (Berriasian) Ashidani Formation of the Tetori Group exposed in Mochiana, Ohno City, Fukui Prefecture, Central Japan. We further propose a reclassification of this species to the genus *Pterophyllum*. We found that Oishi's (1940) syntypes included one *Ptilophyllum* specimen that reflected Eurosinian-type vegetation, contrary to the widely accepted idea that typical Siberian-type vegetation flourished in the Tetori Group region during the Tithonian to Berriasian.

Keywords: Bennettitales, Early Cretaceous, Late Jurassic, *Pterophyllum*, *Ptilophyllum pachyrachis*, Tetori Group

Introduction

Ptilophyllum pachyrachis was established as a new species in the genus *Ptilophyllum* (Bennettitales) by Oishi (1940) based on four syntypes collected from Mochiana, Kamianama Village (presently Ohno City), Fukui Prefecture, Central Japan. The exact location of the type locality was not provided, but is considered to be included in the Upper Jurassic (Tithonian) to Lower Cretaceous (Berriasian) Ashidani Formation of the Tetori Group (*sensu* Yamada and Sano, 2018) (Figure 1; Fujita, 2002; Sato and Yamada, 2005; Yamada and Uemura, 2008; Yamada, 2017). Kimura and Ohana (1987) later proposed a reclassification of this species to *Pterophyllum pachyrachis* (Oishi) Kimura and Ohana without designating a lectotype; although they cited Oishi's 1940 monograph, they did not specify the page or plate where the basionym appeared. Therefore, their proposal is invalid under Article 41.5 of the International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) (Turland *et al.*, 2018).

We recently reexamined syntypes of *Ptilophyllum pachyrachis* Oishi (1940) deposited at the Hokkaido University Museum and found that they included both *Pterophyllum* and *Ptilophyllum* species. In this paper, we formally propose a transfer of *Ptilophyllum pachyrachis* Oishi to the genus *Pterophyllum*, with lectotypification and some changes to specific diagnostic characteristics and further re-describe one syntype as an uncertain species of the genus *Ptilophyllum*. We also reevaluated the paleophytogeographical significance of Oishi's (1940) findings, which had been previously overlooked.

Material and methods

Plant-bearing beds in Mochiana (Figure 1) had been assigned to the Ochiai Formation (Maeda, 1961), but these were reassigned to the lower part of the Ashidani Formation in later studies (Fujita, 2002; Sato and Yamada, 2005; Yamada and Uemura, 2008). The Ashidani Formation is composed of conglomerates, sandstones and mudstones of non-marine origin, while the upper part consists of marine facies (the Kamihambara Formation) in the East of Izumi area where Mochiana is located (Fujita, 2002; Figure 2). The Late Jurassic (Tithonian) to Early Cretaceous (Berriasian) age is inferred for the Ashidani Formation based on ammonoids collected from the Kamihambara Formation (Sato and Yamada, 2005; Yamada, 2017; Figure 2).

Syntypes of *Ptilophyllum pachyrachis* are leaf impressions preserved on mudstone in which cuticular layers had been lost through diagenetic processes (Figure 3).

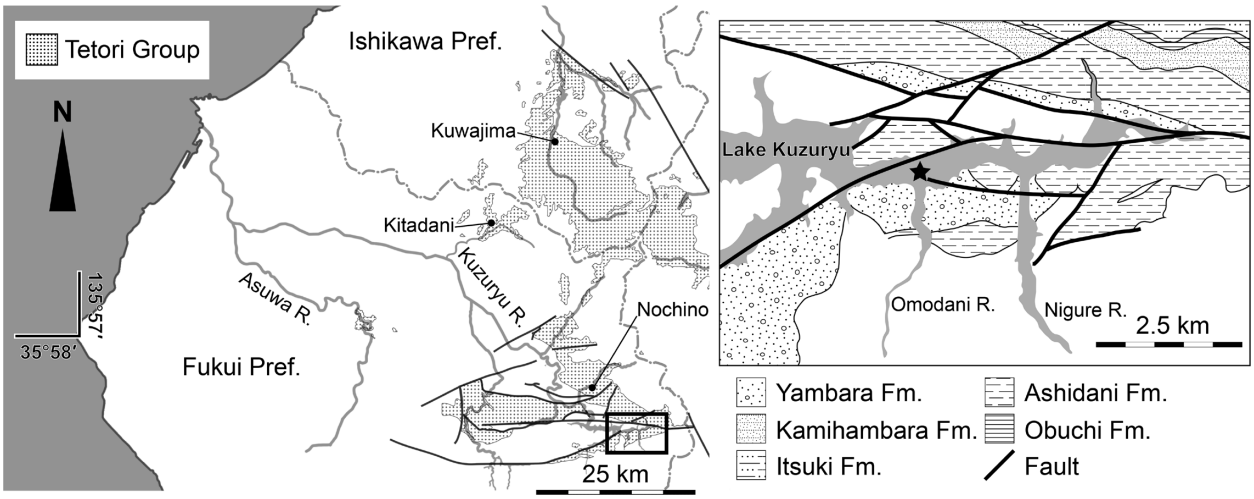

Figure 1. Distribution of the Tetori Group [based on Maeda (1961) and Yamada and Sano (2018)] around the type locality of *"Ptilophyllum" pachyrachis*. The inset map shows a geological map [based on Fujita (2002)] of the boxed area shown in the small-scale map. The type locality, Mochiana (indicated with a star in the inset map), is now submerged below Lake Kuzuryu. The locations of Kuwajima, Kitadani, and Nochino are also indicated.

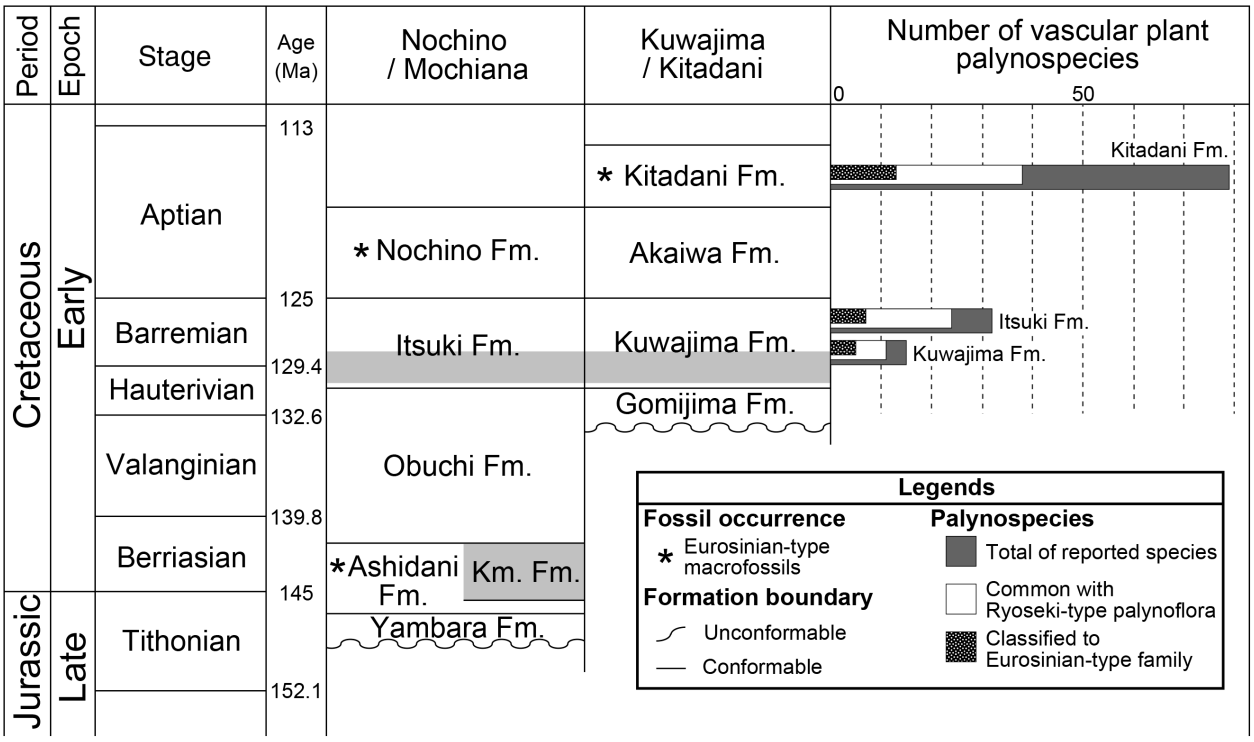

Figure 2. Stratigraphies of the Tetori Group showing localities of Eurosinian-type plant fossils compiled from Yamada and Uemura (2008), Sano (2015), and Yamada (2017). Plant macrofossils of the Nochino and Kitadani formations are based on Sakai *et al*. (2020) and Yabe and Shibata (2011), respectively. The number of vascular plant palynospecies were compiled based on Legrand *et al*. (2021). Shading indicates periods of marine transgression (Sato and Yamada, 2005; Sano, 2015; Yamada, 2017). Fm., Formation; Km. Fm., Kamihanbara Formation.

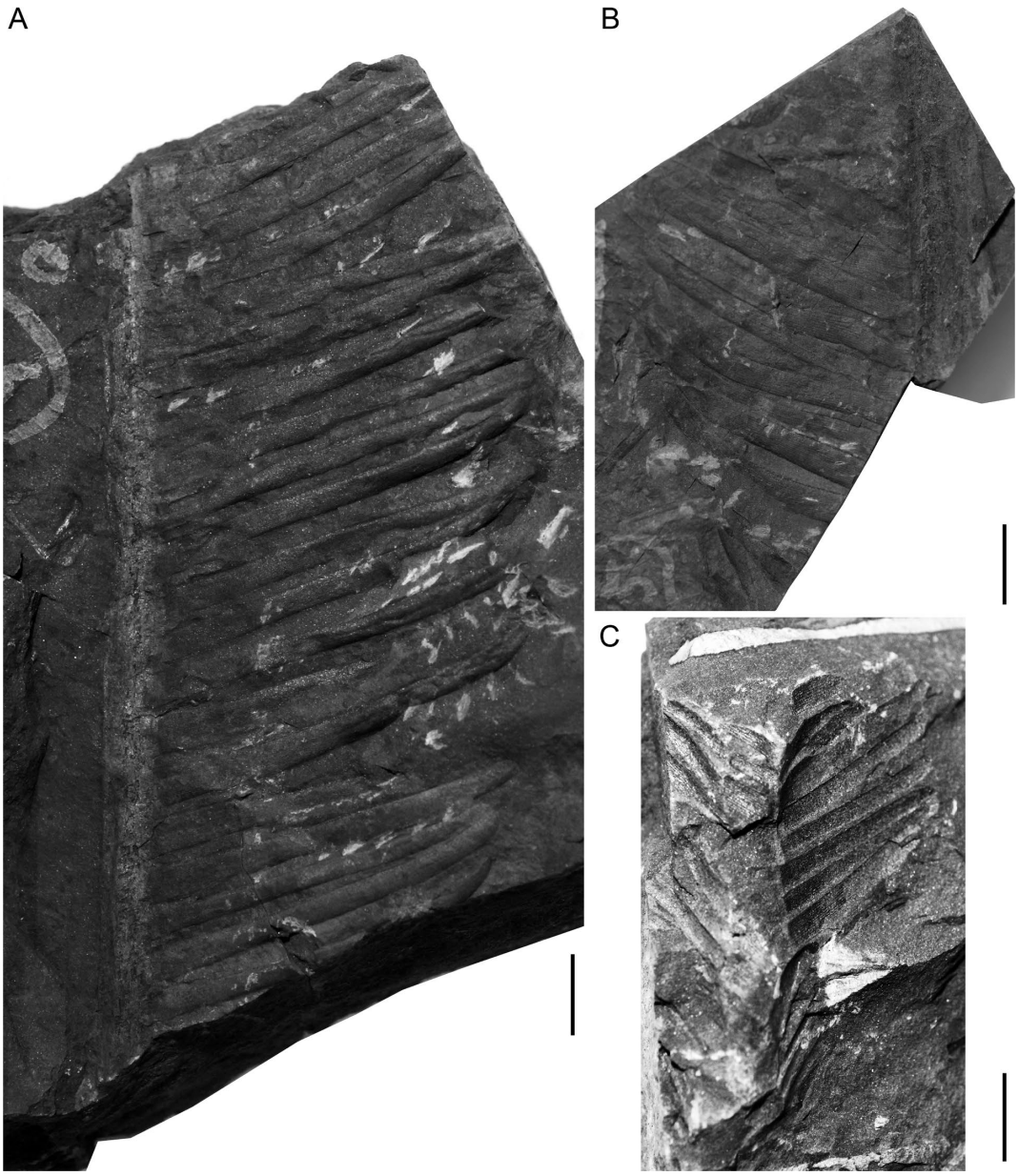

Figure 3. *Pterophyllum pachyrachis* (A, B) and *Ptilophyllum* sp. (C). **A,** lectotype (UHR8485B); **B,** UHR8485C; **C,** UHR8485D. Scale bars = 1 cm.

We photographed them by D200 digital camera equipped with AI AF Micro-Nikkor 60 mm f/2.8D lens (Nikon, Tokyo, Japan) under incandescent light.

Systematic palaeobotany

Class Bennettitopsida
Order Bennettitales Engl., 1892
Family uncertain
Genus ***Pterophyllum*** Brongn., 1825 emend. J. Watson and Sincock, 1992

Type species.—Pterophyllum filicoides (Schlotheim, 1822) Zeiller, 1906.

Pterophyllum pachyrachis (Oishi, 1940) T. Yamada and Nishino, *comb. nov.*

Figures 3A, 3B, 4A

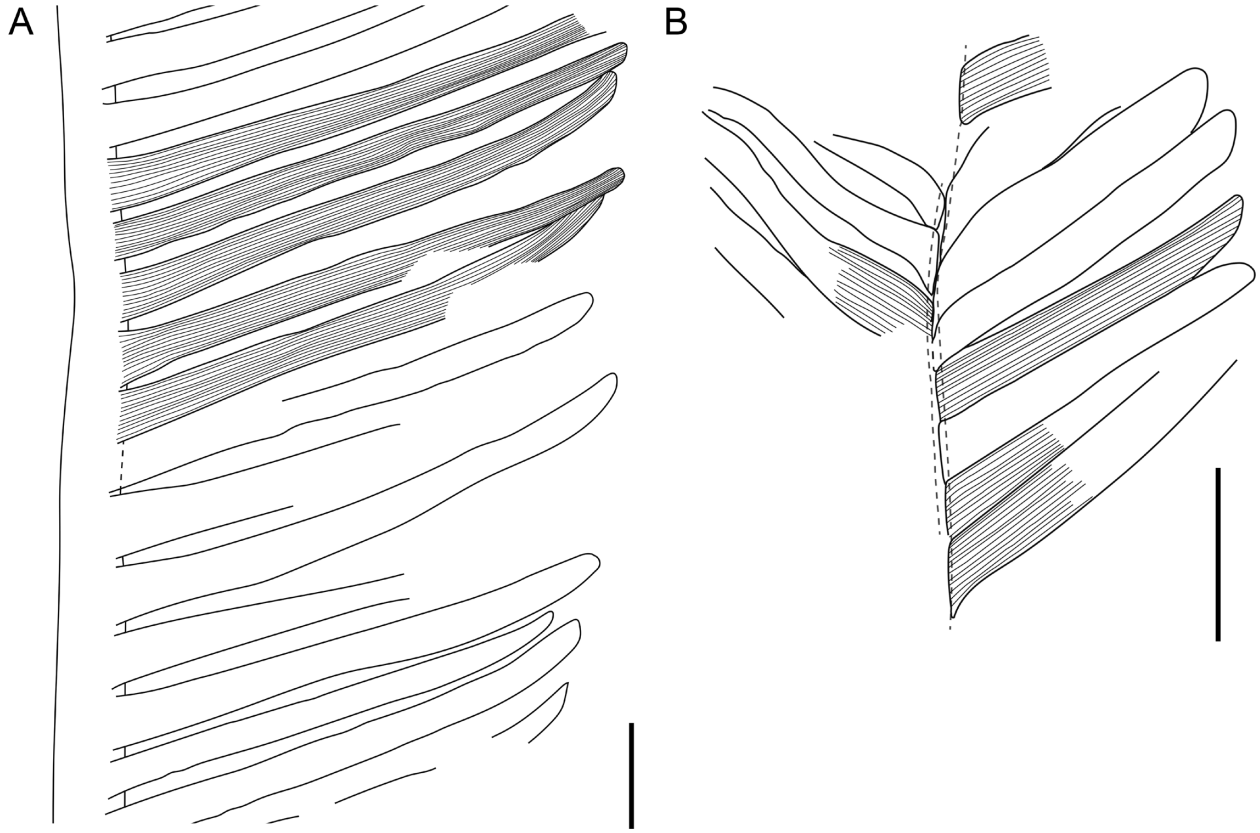

Figure 4. Line drawings of *Pterophyllum pachyrachis* (A) and *Ptilophyllum* sp. (B). **A,** lectotype (UHR8485B); **B,** UHR8485D. Scale bars = 1 cm.

Ptilophyllum pachyrachis. Oishi, 1940, J. Fac. Sci. Hokkaido Imp. Univ., Ser. 4, Geol. 5, p. 346–347, pl. 34, figs. 1 (UHR8485A), 2 (UHR8485B), 3 (UHR8485C); *non* pl. 33, fig. 1 (UHR8485D).

Lectotype.—The Hokkaido University Museum, UHR8485B (designated here; Figures 3A, 4A).

Other specimens examined.—UHR8485A, C (Figure 3B).

Emended diagnosis.—Leaf large, linear, narrowing gradually towards the proximal portion; rachis stout, smooth; leaflets long and narrow, parallel-sided, straight or slightly falcate, set closely, subacute at the apex, those in the proximal portion slightly broader and obtuse at the apex, and attached to the upper-lateral surface of the rachis at a wide angle or nearly at a right angle; leaflet bases expanding both proximally and distally, separated from those on the other side by the upper surface of the rachis; veins fine, parallel, approximately 33 in the interval of 10 mm.

Remarks.—UHR8485A–C are large leaves with a thick rachis, whereas UHR8485D is a small leaf with a thin rachis. UHR8485A–C should be classified as a species of genus *Pterophyllum* due to having leaflets with expanded apical and basal bases which insert into the upper-lateral side of the rachis (Watson and Sincock, 1992). By contrast, UHR8485D should be assigned to genus *Ptilophyllum* due to having leaflets with contracted distal and slightly decurrent proximal bases which are attached to the upper surface of the rachis (Watson and Sincock, 1992; Rees and Cleal, 2004; see below for detailed descriptions).

Oishi (1940) compiled characters found in each syntype in the diagnosis of *Ptilophyllum pachyrachis*, thus all syntypes could be eligible for the lectotype. However, as the species epithet "*pachyrachis*" suggests, Oishi (1940) emphasized that "this species is characterized by the large size of the frond traversed by a very thick rachis." These core diagnostic characters are represented in UHR8485A–C, with a leaf form assignable to *Pterophyllum*. Accordingly, we have proposed *Pterophyllum pachyrachis* (Oishi) T. Yamada and Nishino *comb. nov.* by selecting UHR8485B (Oishi, 1940, pl. 34, fig. 2) as the lectotype.

Pterophyllum pachyrachis is similar to *Pterophyllum fontarianum* J. Watson and Sincock (1992) from the English Wealden and *Pterophyllum footeanum* (Feistmantel, 1879) Bose and Banerji (1981) from the

Early Cretaceous of India in having finely veined leaflets on thick rachis, but the leaflets of the latter two species are attached to the rachis at a smaller angle and in a less crowded manner. A thick rachis and slender leaflets are characteristic of the following species, but the veins are much sparser in these species than in *Pterophyllum pachyrachis*: *Pterophyllum thomasii* Harris (1952), *Pterophyllum fossum* Harris (1952), and *Pterophyllum cycadites* Harris and Rest (1966) from the Middle Jurassic of Yorkshire; *Pterophyllum validum* Hollick (1930) from the Upper Cretaceous of Alaska.

Sakai *et al.* (2018) considered "*Ptilophyllum pachyrachis* Oishi" as *Zamiophyllum buchianum* (Ettingshausen, 1852) Nathorst (1890) or *Zamites chosiensis* Kimura and Ohana (1985). However, none of Oishi's (1940) syntypes could be identified as a species of *Zamiophyllum* or *Zamites*, judging from the shape of the leaflet bases (Watson and Sincock, 1992). In addition, *Pterophyllum pachyrachis* differs from these species in having slender leaflets.

Genus ***Ptilophyllum*** Morris, 1840

Type species.—*Ptilophyllum acutifolium* Morris, 1840.

***Ptilophyllum* sp.**

Figures 3C, 4B

Ptilophyllum pachyrachis. Oishi, 1940, p. 346–347, pl. 33, fig. 1 (UHR8485D); *non* pl. 34, figs. 1 (UHR8485B), 2 (UHR8485A), 3 (UHR8485C).

Description.—Leaves > 3.4 cm long, 3.3 cm wide, linear; rachis thin, 1 mm wide; leaflets parallel-sided, straight, closely set, 2.4–3.2 mm wide, subacute at apex, and attached to the upper surface of the rachis at a wide to nearly right angle; leaflets bases on both sides of the rachis meeting at the longitudinal median line of the rachis; proximal base of the leaflets slightly decurrent; distal base of the leaflets somewhat contracted; veins distinct, parallel, 30–40 per 10 mm.

Remarks.—We could not observe epidermal features from UHR8485D, which are required for species-level classification within the genus *Ptilophyllum*. However, UHR8485D has longer leaflets than the other *Ptilophyllum* specimens reported from the Tetori Group and the strata underlying the Tetori Group: *Ptilophyllum caucasicum* Doludenko and Svanidze (1969) and *Ptilophyllum* sp. A from the Callovian Kaizara Formation (Yamada and Uemura, 2008); *Ptilophyllum* sp. from the Oxfordian Arimine Formation (Yamada, 2018); *Ptilophyllum* sp. from the Aptian Kitadani Formation (Yabe and Shibata, 2011). *Ptilophyllum* sp. B from the Kaizara Formation also has slender leaflets (Yamada and Uemura, 2008), but this species has substantially thicker lamina compared to UHR8485D.

Discussion

The Siberian and Eurosinian floristic provinces existed in Eastern Asia from the Middle Jurassic to Early Cretaceous, with the former located north of the latter (Vakhrameev, 1987, 1991). Siberian-type vegetation was characterized by a variety of pteridophytes and macrophyllous gymnosperms, which favored a warm temperate climate (Vakhrameev, 1987, 1991). By contrast, microphyllous gymnosperms flourished in the Eurosinian province due to a seasonally dry climate (Vakhrameev, 1987, 1991). It has been suggested that typical Siberian-type vegetation dominated in the land of the Tetori Group during its period of deposition, i.e., from the Late Jurassic to the Early Cretaceous, whereas Ryoseki-type floras of the Eurosinian-type were coevally distributed in the Outer Zone of Japan along the Pacific coast (Kimura, 1987, 2000). However, Eurosinian-type plants were recently found in the Aptian portion of the Tetori Group, as well as with Siberian-type ones (Yabe *et al.*, 2003; Yabe and Kubota, 2004; Yabe and Shibata, 2011; Legrand *et al.*, 2013; Sakai *et al.*, 2020). Furthermore, Eurosinian-type coniferous pollen (e.g. Araucariaceae and Cheirolepidiaceae) has been found in the Barremian Kuwajima and Itsuki formations and palynoassemblages of these formations exhibit high similarities to those of the Ryoseki-type localities (Figure 2; Legrand *et al.*, 2021).

Oishi (1940) reported the occurrence of "*Ptilophyllum*" *pachyrachis* from a horizon that is now included in the Tithonian to Berriasian Ashidani Formation (Fujita, 2002; Sato and Yamada, 2005; Yamada and Uemura, 2008; Sano, 2015; Yamada, 2017; Figures 1, 2). Given that *Ptilophyllum* is a characteristic genus of Eurosinian-type vegetation (Vakhrameev, 1987, 1991; Kimura, 2000), this record suggests that the vegetation of the Tetori Basin included some Eurosinian-type plants from the earliest stage. The importance of this record was overlooked when this species was invalidly transferred to the genus *Pterophyllum* (Kimura and Ohana, 1987). Here, we highlight the importance of Oishi's (1940) finding by confirming that one of the collected specimens (UHR8485D) belongs to a *Ptilophyllum* species. The Tetori Basin was located adjacent to the southern border of the Siberian province (Yamada *et al.*, 2018), therefore, the vegetation of the Tetori Group may have been influenced by Eurosinian-type vegetation to some extent.

It has been argued that global warming from the Aptian onward triggered a northward migration of Eurosinian-type plants into the area of the Tetori Group (Sakai *et*

al., 2018, 2020), but this argument is inconsistent with a climatic reconstruction that a humid zone prevailed at the latitude of the Tetori Basin (Hasegawa *et al.*, 2012). Therefore, local topographic factors should also be taken into account to explain vegetation changes in this area, such as a rain shadow effect caused by high mountains (Yamada *et al.*, 2018). The "rediscovery" of *Ptilophyllum* provides another example wherein local topography is shown to have affected the vegetation of the Tetori Group. In the Tetori Group, marine transgressions occurred at least twice, i.e., in the Tithonian to Berriasian and the Hauterivian to Barremian (Sato and Yamada, 2005; Sano, 2015; Yamada, 2017). These transgressions coincided with the appearance of Eurosinian-type plants (Figure 2), which implies that marine transgression may have provided drying coastal environments suitable for Eurosinian-type plants.

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Author contributions

We declare that this ms is not published nor considered in other journals. No other person participated in this work as a "possible author". T. Y. designed this study. T. Y. and M. N. observed the syntypes and collected necessary data for the taxonomic revision. Both authors contributed to writing this manuscript.