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THE TETORI-TYPE FLORA, REVISITED: A REVIEW

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ABSTRACT

This paper reviews the study of the Tetori-type floras, with a major emphasis on the Tetori Flora, the plant fossil assemblages from the Tetori Group distributed in the Hokuriku region, Central Japan, and discusses the climatic changes inferred from them.

The Tetori Flora recovered from the Lower Cretaceous Itoshiro and Akaiwa subgroups, upper two subgroups of the Tetori Group, is subdivided into three stratofloras, the Oguchi (Hauterivian), Akaiwa (Hauterivian to late Barremian), and Tamodani (late Barremian) floras, in ascending order. The Oguchi Flora is characterized by "older Mesozoic elements" and shows similarity in floristic composition and physiognomy with those of Siberia. Climatic condition in which the Oguchi Flora flourished is interpreted as temperate and moderate humid. The Akaiwa and Tamodani floras also shows similarity with the Oguchi and coeval floras of Siberia; however, they include several thermophilic species, such as *Cyathocaulis naktongensis*, *Brachyphyllum* sp., and *Nilssonia* sp. cf. *N. schaumburgensis*, and there is a little but distinct change in floristic composition and physiognomy. These facts as well as carbonate nodules from the strata bearing the Akaiwa and Tamodani floras suggest the warmer and dryer climatic condition than that of the Oguchi Flora.

Comparison of the Tetori Flora with those of coeval strata in Southwest Japan, Korea, China, and Siberia reveals that similar climatic changes are recognized in eastern Eurasia except for southern Primorye. It seems that changes of the Tetori Flora reflect the climatic fluctuations of eastern Eurasia possibly during Hauterivian to Barremian.

Key words: Tetori-type floras, Tetori Flora, phytogeography, climatic change, Early Cretaceous, eastern Eurasia

矢部　淳・寺田和雄・関戸信次（2003）手取型植物群の再検討：その現状と課題．福井県立恐竜博物館紀要 2：23–42.

ユーラシア東部地域における白亜紀前期の詳しい古気候条件とその変化を明らかにするため，手取層群の上半部にあたる，白亜紀前期の石徹白・赤岩亜層群から報告された手取植物群を中心に，最近蓄積されつつある新しいデータを加味して，手取型植物群の既存の研究を再検討した．その結果，Kimura（1975a）によって示された尾口・赤岩・田茂谷植物群に有意な組成，葉相観の変化があることが明らかとなった．尾口植物群からは温暖で適度な湿度のある環境が示唆されたのに対し，赤岩・田茂谷植物群は尾口植物群のものよりも暖かく乾燥した環境を示唆した．手取植物群と同時期にあたる，西南日本および韓国の植物化石群集の組成変化やユーラシア大陸内部の植物地理区の変化は，手取植物群から推測される気候変化とよく一致することから，白亜紀前期（Hauterivian–Barremian）のユーラシア東部地域では，広域にわたって気候の温暖化・乾燥化が起こったことが示唆された．

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INTRODUCTION

Distribution of fossil plants is one of the most reliable tools for a better understanding of terrestrial climatic conditions through geologic times (Francis and Frakes, 1993). A considerable number of studies have been made on the Mesozoic phytogeography of Eurasia, because it is generally considered that Eurasian continent is an ideal area to provide a view of latitude-related climatic conditions as well as continental−marine climates (Spicer et al., 1996).

Latitudinally divided two paleophytogeographic provinces have generally been recognized in eastern Eurasia during the later Mesozoic (Vakhrameev, 1966, 1971; Kimura, 1979, 1980, 1984a, 1984b; Wu, 1995; Deng and Chen, 2001) (Fig. 1). Northern province called the Siberian-Canadian Region (Vakhrameev, 1978), Northern Phytogeographic Province (Wu, 1995), or Tetori-type floras (Kimura, 1979) was considered to represent temperate and humid climatic condition. Southern province was called the Euro-Sinian Region (Vakhrameev, 1978), Southern Phytogeographic Province (Wu, 1995), or Ryoseki-type floras (Kimura, 1979). This province was interpreted to represent subtropical conditions with continuous dry season, on the basis of anatomical character of plants (e.g. Ohana and Kimura, 1995a), presence of evaporites (Ziegler et al., 1993) and red beds (Wu, 1995). Most of researchers recognize the mixture of elements of each province around the boundary (Kimura, 1987; Cao, 1994, 1999; Li and Liu, 1994; Sun et al., 1995; Saiki et al., 2001). It can be ascribed to the fact that there was no distinct division in the original vegetation that would enable biomes to be clearly delineated (Spicer et al., 1993, 1996; Saiki and Wang, in press). There is fairly general agreement in the boundaries proposed between the northern and southern phytogeographic regions distributed in Eurasian continent, whereas opinions are divided on the treatment of Early Cretaceous floras from the Tetori Group, inner side of Japan.

The Tetori Flora, a main objective of this review, is a representative of the Late Jurassic to Early Cretaceous Tetori-type floras (e.g. Kimura, 1984, 1987). Over a century a considerable number of studies have been made on the Tetori Flora, but no one have described climatic changes which occurred in the realm where the Tetori Flora flourished. The purpose of this paper is to understand the climatic condition in which the Tetori Flora flourished and floristic changes in eastern Eurasia during the Early Cretaceous. We begin with a review of previous studies about the Tetori Flora and the Tetori-type floras. Then we report some thermophilic species recently discovered from the Tetori Group, which is a key to infer the climatic condition. Next we discuss the subdivision of the Tetori Flora, which was once proposed by Kimura (1975a). Finally, we discuss the climatic changes inferred from the Tetori Flora, and consider whether they are recognized in plant fossil assemblages from coeval strata in the eastern Eurasia.

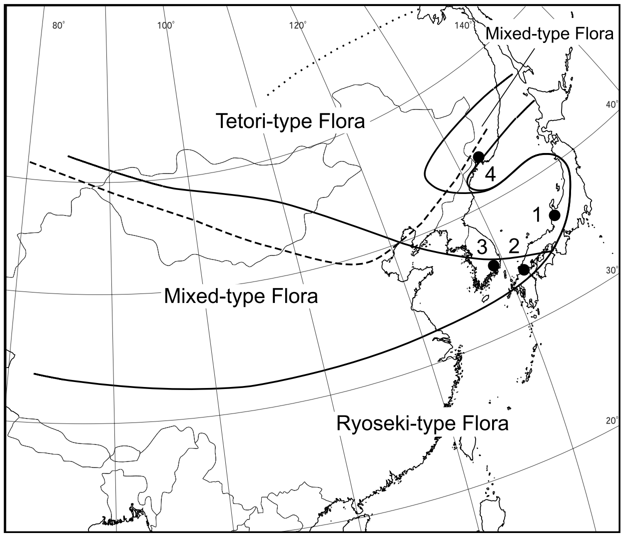

FIGURE 1. Early Cretaceous phytogeographic provinces of eastern Eurasia (modified from Kimura, 1987). Solid line indicates paleophytogeographic division of Kimura (1987). Broken line indicates the boundary between the Siberian-Canadian (north) and Euro-Sinian (south) regions of Vakhrameev (1991). Vakhrameev (1991) subdivided the Siberian-Canadian Region into two provinces (dotted line): the Lena Province in the north and the Amur Province in the south. Black circles represent localities of Early Cretaceous floras mentioned in the text. **1**: Hida region (Tetori Group), **2**: Kanmon region (Toyonishi and Kwanmon groups), **3**: Gyeongsang region (Gyeongsang Supergroup), **4**: Southern Primorye (Nikan and Suchan groups). Note that the upper two subgroups of the Tetori Group yield some thermophilic species and their floras are assigned to the mixed-type floras of Kimura (1987). Plant fossil assemblages from Berriasian and Valanginian strata, underlying the Nikan and Suchan groups, were assigned to the Ryoseki-type floras (Ohana and Kimura, 1995a).

THE TETORI FLORA AND THE TETORI-TYPE FLORAS: A BRIEF OVERVIEW

Plant fossils from the Tetori Group is called the Tetori Flora (Tateiwa, 1925), which exclusively consists of vegetative and reproductive organs of ferns and gymnosperms without any unequivocal angiosperm remains. Petrified woods are also found throughout the group, which comprises only one species *Xenoxylon latiporosum* (Ogura et al., 1951; Suzuki and Terada, 1992; Terada et al., 2002). They are mostly fragmented, but some of them are preserved *in situ* as the stumps to represent fossil forests (Maeda, 1955). A considerable number of studies have been made on the plant megafossils (e.g. Shimakura, 1934; Oishi, 1940; Kimura, 1958a), whereas there were only a few works on the plant microfossils in the Tetori Flora (Umetsu, 2002; Umetsu and Matsuoka, 2002).

The first paleobotanical work on the Tetori Flora was done by Geyler (1877). Geyler studied plant fossils collected from the Tetori Group in Shiramine Village, Ishikawa Prefecture, and correlated them to the Middle Jurassic floras of Siberia.

Geyler's notion was developed by Yokoyama, who established the "Tetori Series" as a representative of the Middle Jurassic stage in Japan (Yokoyama, 1889). Oishi (1933a) examined the composition of plant fossil assemblages as well as stratigraphy of plant-bearing strata in the Tetori Group and concluded that there were no distinct divisions in floristic composition. On the basis of mixture of the element of Middle Jurassic and Early Cretaceous (Wealden) floras, he assigned the Tetori Flora to the Late Jurassic (Oishi, 1933a; 1933b). Oishi (1940) subsequently proposed three distinct vegetative series in the Mesozoic System of Japan and adjacent regions from the viewpoint of plant evolution; namely *Dictyophyllum*, *Onychiopsis*, and Angiosperm series, in ascending order. He further subdivided the *Onychiopsis* Series into the Tetori, Ryoseki, and Monobegawa series, in upward sequence. The Tetori Series was defined with the plant fossils from the Tetori Group, and was regarded to represent the Upper Jurassic, whereas the Ryoseki Series, which was defined with those from the Outer zone of Japan, was assigned to the Lower Cretaceous. Plant-bearing strata dealt with Oishi (1933a, 1940) and previous studies were confined to the lower and middle subgroups of the Tetori Group in a present sense, whereas Kimura studied those from the whole sequence of the Tetori Group and examined the precise stratigraphic position of fossil plants (Kimura, 1958b, 1961, 1975a; Kimura and Sekido, 1976b, 1978). As a consequence, Kimura (1975a) divided the Tetori Flora into four stratofloras, the concept of which was initially proposed by Samylina (1974): the Kuzuryu Flora for fossil plants from the Kuzuryu Subgroup, the Oguchi Flora for those from the Itoshiro Subgroup, the Akaiwa and Tamodani floras for those from the Akaiwa Subgroup.

Kimura (1958b, 1961) firstly proposed the Mesozoic phytogeography in Japan. He pointed out that the difference in floristic composition between plant fossil assemblages from the Tetori and Ryoseki series should be ascribed not to the difference of geologic age, but to that of paleophytogeographic conditions, because the plant fossil assemblage from the Tochikubo Formation, Somanakamura Group, outer side of northeast Japan, which was previously assigned to the Ryoseki Series by Oishi (1933b, 1940), were assigned to Late Jurassic (Oxfordian–Kimmeridgian) on the basis of ammonites from the underlying strata (Masatani, 1950). Further, he considered that plant fossil assemblages from the Itoshiro and Akaiwa subgroups (Oguchi, Akaiwa and Tamodani Floras) could be correlated to the Early Cretaceous floras of Siberia. On the basis of geologic age of the Kitadani Formation that represents the uppermost part of the Tetori Group, Kimura (1973) assigned the Oguchi, Akaiwa and Tamodani floras to early Neocomian, late Neocomian, and Aptian, respectively. He further suggested the similarity of fossil plants from the "Tetori Series" with those in Siberia and northern China; and those from "Ryoseki Series" with those in southern Primorye, southern China and Southeast Asia. This led him to establish the Tetori-type and Ryoseki-type floras, both of which range from Late Jurassic to Aptian (Kimura, 1979). He proposed the complex pattern of distribution between the Tetori-type and Ryoseki-type floras, especially in Japanese Islands and southern Primorye. The peculiarity of the boundary between these floras are regarded to relate to the sinistral strike-slip displacement along the eastern margin of Eurasian continent occurred during the mid-Cretaceous (Otoh, 1998; Otoh and Sasaki, 1998).

Kimura (1984b) summarized his concept of paleophytogeography of Japan and eastern Eurasia, although he modified it in 1987, where he distinguished the Mixed-type flora from both Tetori-type and Ryoseki-type floras. The Mixed-type flora occurs between the areas of both Tetori-type and Ryoseki-type floras in southwestern Japan, northeastern China, southern Korea and southern Primorye (Fig. 1). Further, Kimura (1987) described that the composition of the Tetori-type and Ryoseki-type floras were "completely" different with no common species and were relatively uniform throughout the Late Jurassic to the Early Cretaceous (Ohana and Kimura, 1995a). On the other hand, Ohana and Kimura (1995b) and Kimura et al. (1996) pointed out that a marked environmental change caused the northward invasion of the Ryoseki-type element to bring the emergence of the Mixed-type floras, though they did not mention what kind of environmental change had occurred.

Kimura (1987) illustrated the floristic composition of the Tetori-type and Ryoseki-type floras as follows: The Tetori-type flora is characterized by the predominance of osmundaceous and dicksoniaceous ferns, bennettitaleans such as *Otozamites*, *Neozamites*, and *Dictyozamites*, cycadaleans such as *Ctenis*, *Nilssonia*, and *Tetoria*, ginkgoaleans, czekanowskialeans, several kinds of *Podozamites* and conifers with needle-like leaves. On the contrary, the Ryoseki-type flora (e.g. Kimura and Hirata, 1975) is characterized by the predominance of gleicheniaceous and matoniaceous ferns, bennettitaleans such as *Zamites* and *Ptilophyllum*, small-sized *Nilssonia* leaves and conifers with scale-like leaves. In the Ryoseki-type flora, dicksoniaceous ferns and ginkgoaleans are quite rare; and czekanowskialeans and leaves safely assignable to *Podozamites* have not been found.

GEOLOGIC SETTING

The Tetori Group sporadically distributed in the Hida region, inner-side of Southwest Japan (Fig. 2). The Tetori Group has been subdivided into three subgroups as Kuzuryu, Itoshiro, and Akaiwa, in ascending order (e.g. Maeda, 1961c; Fujita, 2002a, b; Kusuhashi et al., 2002). The distribution of Kuzuryu Subgroup is confined to the Kuzuryu, Makito and Arimine areas. It unconformably underlies the Itoshiro Subgroup in the Kuzuryu and Arimine areas, whereas in the Makito area it is conformably overlain by the Itoshiro Subgroup. The Kuzuryu Subgroup comprises non-marine strata in its lower part and yields abundant fossil plants, whereas in the upper part, it consists of marine strata with bivalves and ammonites, which indicate Callovian and Oxfordian in age (Sato et al., 1963). On the other hand, the Itoshiro and Akaiwa subgroups consist mainly of non-marine coarse clastic rocks, which yield abundant fossil plants (Fig. 3). Geologic ages of both subgroups have been presumed as Late Jurassic to Early Cretaceous, though no index fossil has been recognized. During the past few decades, marine molluscan fossils were recovered from the Lower Formation (Yamada et al., 1989) or the Kamihambara Formation (Fujita, 2002a) of the Itoshiro Subgroup (e.g. Fujita et al., 1998). Goto (2001) reported an ammonite fossil from the upper part of this subgroup, which indicates late Hauterivian to early Barremian. Non-marine and brackish bivalve faunas of the Itoshiro and Akaiwa subgroups are thought to be important for regional stratigraphic correlation (e.g. Maeda, 1962; Tamura, 1990; Isaji, 1993). Fujita (2002a) suggested the probable reference of the Itsuki Formation to Hauterivian to Barremian on the basis of the occurrence of brackish bivalve, *Myopholas* sp. cf. *M. semicostata*. Kozai et al. (2001, 2002) assigned the non-marine bivalve fauna of the Kuwajima and coeval formations to Hauterivian and that of the Kitadani Formation to late Barremian. Consequently, geologic age of the Kuzuryu Subgroup is regarded as Middle to Late Jurassic, although its lower limit is still unknown. The upper part of the Itoshiro Subgroup is dated as Hauterivian and the Akaiwa Subgroups is assigned to Hauterivian to Barremian.

Stratigraphic correlation of the Tetori Group among areas remains matter for debate. Figure 3 shows a tentative correlation of the Itoshiro and Akaiwa subgroups, which are the main objectives of this review, among five areas mainly based on Fujita (2002b).

In the case of the Akaiwa Subgroup, correlation among areas is difficult because of the scarcity of molluscan fossils except in the Kitadani Formation. The Akaiwa Subgroup of the Kuzuryu area comprises the Nochino and Chinaboradani formations, in ascending order. The Kitadani Formation distributed in the Takinami and Tedori River areas (Fig. 3C, D) are regarded as an equivalent to the Chinaboradani Formation from the presence of tuffaceous rocks in each formation (Maeda, 1961c). Thus, the underlying Akaiwa Formation of the Tedori River and Takinami River areas is comparable to the Nochino Formation. On the basis of the similarity of lithology, the Bessandani Formation in the Makito area is generally correlated to the Akaiwa Formation in the Tedori River area (Maeda, 1961c). However, its geologic age remains to be proved as noted by Fujita (2003). On the other hand, the Minamimatadani and overlying Wasabu formations in the Arimine area (Fig. 3E) were assigned to the Akaiwa Subgroup (Kawai and Nozawa, 1958). The plant fossil locality 15 shown in Figure 3E represents that of the "Ohyama dinosaur footprint site" in the Ohyama Town, Toyama Prefecture. The stratigraphic position of the strata exposed in this locality is controversial, because this area is bounded by series of NE–SW trend faults in the type section of the Tetori Group in the Arimine area, and lithology of the strata is similar to both the Wasabu and Inotani formations. It was assigned to the Inotani Formation of the Itoshiro Subgroup by Matsukawa et al. (1997a), whereas Toyama Dinosaur Footprint Research Committee (1997) regarded it as the Wasabu Formation of the Akaiwa Subgroup. The Board of Education of Toyama Prefecture (in press) recently correlated it to the Wasabu Formation on the basis of lithology and fission-track dating of tuffaceous rock from the outcrop. We here follow this opinion.

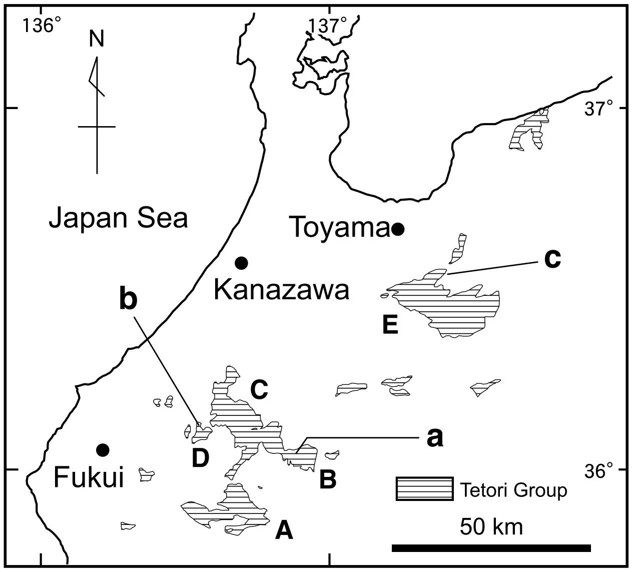

FIGURE 2. Map showing the distribution of the Tetori Group and plant fossil localities mentioned in the text. **A–E**: Areas shown in Fig. 3, **a–c**: Localities of thermophilic plants (**a**: *Cyathocaulis naktongensis*, **b**: *Brachyphyllum* sp., **c**: *Nilssonia* sp. cf. *N. schaumburgensis*).

Many plant fossils have been reported from the upper part of the Itoshiro Subgroup: the Itsuki Formation (e.g. Kimura, 1975a) in the Kuzuryu area (Fig. 3A); the Okurodani (e.g. Kimura et al., 1978) and Amagodani (Kunimitsu and Nakashima, 1987) formations in the Makito area (Fig. 3B); the Kuwajima Formation (e.g. Kimura and Sekido, 1961; Matsuo and Omura, 1968) in the Tedori River area (Fig. 3C). Plant fossils from the Akaiwa Formation and its equivalents were described by Kimura (1975a) and Kimura and Sekido (1976b, 1978), those from the Chinaboradani Formation and its equivalents were reported by Matsuo and Omura (1966) and Kimura and Horiuchi (1979). There are some reports on the occurrence of plant fossils elsewhere. We will not deal with them here, because in most cases they do not have any descriptions and figures so that identifications cannot be verified.

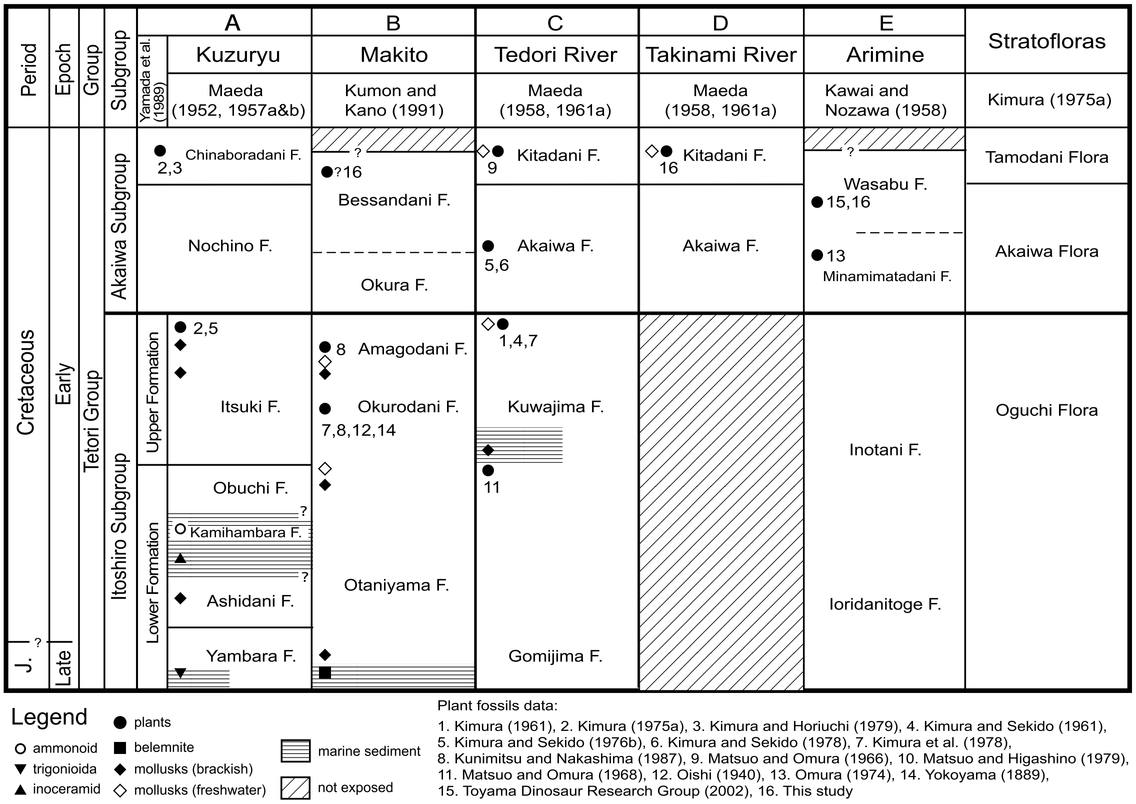

FIGURE 3. Stratigraphic correlation of the Itoshiro and Akaiwa subgroups of the Tetori Group (modified from Fujita, 2002b), showing stratigraphic positions of plant megafossil assemblages. Numbers next to black circle indicate the papers dealt with these assemblages. Possible stratigraphic position of some thermophilic species in the text is presented with no. 16. The one shown in the Bessandani Formation is a stem of fossil tree fern collected as a float. Note that the Bessandani Formation was generally correlated to the Akaiwa Formation, but its upper limit remains matter for debate (Fujita, 2003).

OCCURRENCE OF THERMOPHILIC SPECIES

To avoid confusion, we use the term "thermophilic" which was used by Vakhrameev (1991) for the species that are considered to live under a tropical or subtropical climatic condition. Some thermophilic species have been reported in the Tetori Flora already (e.g. Kimura, 1973; Matsuo and Omura, 1966; Omura, 1974). Nobody, however, paid much attention to their occurrences in the paleophytogeographic studies due to lack of descriptions and even figures in most cases. Followings are several thermophilic species recently discovered and/or reported.

Cyathocaulis naktongensis Ogura (Fig. 4)

A petrified stem of fossil tree fern was recently discovered as a float in Kobu-tani of the Ogamigo Valley, Shokawa, Gifu Prefecture (Makito area: Figs. 2, 3). It was safely identified as *Cyathocaulis naktongensis* Ogura (Terada et al., 2001). *C. naktongensis* is a tree fern belonging to the family Cyatheaceae. This species was firstly described by Ogura (1927) from the materials collected from the Nagdong Formation of the Sindong Group (South Korea) and the Nishihiro Formation (Wakayama, Kinki, Outer zone of Southwest Japan) (see Matsumoto, 1953; Hirayama and Tanaka, 1956). Nishida and Tanaka (1982) reported some specimens of this species from the Sebayashi Formation, Sanchu district, Kanto Mountains, the Outer zone of Japan.

There is hitherto no record of cyatheaceous ferns in the Tetori-type floras, whereas they are abundant in the Ryoseki-type floras. Thus, Kimura and Ohana (1997) regarded them as a representative of the Ryoseki-type floras. It has been considered that possible tree fern in the Tetori Flora should be the dicksoniaceous ferns, such as *Coniopteris*, *Dicksonia*, and *Birisia*; all of which are abundant in the Tetori Flora and the Tetori-type floras (Kimura and Ohana, 1997), though no evidence of stems has been reported. Deng (2002) recently suggested that dicksoniaceous ferns found in the North Phytogeographic Province of China (Wu, 1995), an analogue of

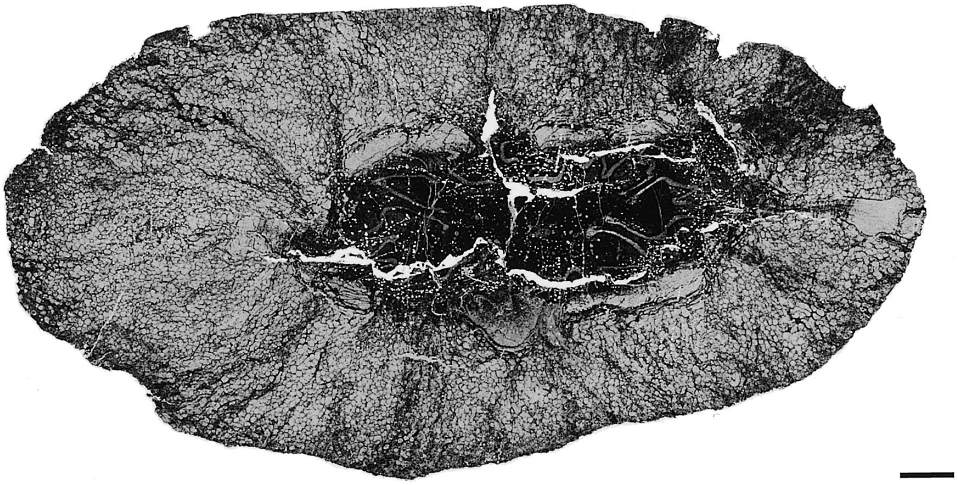

FIGURE 4. Cross-section of the stem of *Cyathocaulis naktongensis* Ogura, from Kobu-tani of the Ogamigo Valley, Shokawa, Gifu Prefecture (Makito area). SBEGpb0056. Scale bar represents 10 mm.

the Tetori-type floras and Siberian-Canadian Region, were small to large creeping rhizomatous ferns. This agrees well with the study of Vakhrameev (1971), which suggested that there was no evidence of tree fern stems in the Siberian-Canadian Region. Therefore discovery of *Cyathocaulis naktongensis* is the first evidence of tree fern in the Tetori Flora, though leaves connected to that stem remain to be proved.

The stratigraphic position of *Cyathocaulis naktongensis* from the Tetori Group is difficult to determine, because this fossil was found as a float, and possible hosted strata range from the Itoshiro to Akaiwa subgroups. Stratigraphic positions of *Cyathocaulis naktongensis* in other areas are surveyed here. Although geology of the Sanchu district is complicated, *Cyathocaulis* specimens were found from the lower member of the Sebayashi Formation of Matsukawa (1977), where the Sebayashi-type non-marine bivalve fauna occur. According to Kozai et al. (2001, 2002), the Sebayashi and Nagdong formations are characterized by the Sebayashi-type non-marine bivalve fauna, and are dated as late Barremian. Geologic age of the Nishihiro Formation was dated as late Barremian to Aptian from ammonites recovered from the underlying Arida Formation as well as the correlation of coeval strata distributed in the Outer zone of Japan (Matsumoto et al., 1982). Consequently, *Cyathocaulis*-bearing strata distributed in the Outer zone of Japan and Korea are presumably range from late Barremian to Aptian. Taking into account the stratigraphy of the Makito area, it seems reasonable to suppose that *C. naktongensis* from the Ogamigo Valley was derived from the upper part of the Akaiwa Subgroup exposed in the upstream of the Ogamigo Valley. This specimen is stored in the Shokawa Village Board of Education (SBEGpb0056) and will be described in a separate paper.

Brachyphyllum sp. (Fig. 5)

Leafy branch of *Brachyphyllum* sp. shown in Figure 5 was discovered from black-colored mudstone in the Kitadani Formation, distributed along the Sugiyama River, a tributary of the Takinami River (Takinami River area: Figs. 2, 3). Locality of this specimen is 1 km upstream of the Kitadani Dinosaur Quarry (Goto et al., 2002). It is stratigraphically close to the level bearing *Nippononaia ryosekiana*, reported by Isaji (1993).

The leafy branch axes are covered by close helices of adnate leaves. Leaves are covered their lower part with short free parts of the lower leaves. The free part of leaf is shorter than width of its basal cushion. All of these external features agree well with the definition of *Brachyphyllum* (e.g. Ohana and Kimura, 1993; Stewart and Rothwell, 1993). This genus is a representative of the Ryoseki-type floras (Kimura and Ohana, 1997), and is firstly reported from the Tetori-type flora. Although the systematic position of *Brachyphyllum* has not been settled yet, it is suggested to relate to xeric condition (Spicer et al., 1993). This specimen is stored in the Fukui Prefectural Dinosaur Museum (FPDM-P30) and will be described in a separate paper.

Nilssonia sp. cf. *N. schaumburgensis* (Dunker) Nathorst

Toyama Dinosaur Research Group (2002) reported and figured the occurrence of one *Nilssonia* species, which is similar to *N. schaumburgensis*, from the “Ohyama dinosaur footprint site” in the Arimine area (Toyama Dinosaur Research Group, 2002, pl. 11, fig. 5: OBET001; fig. 6: OBET002). These specimens are stored in Motokosaka Branch, Board of Education of Ohyama Town.

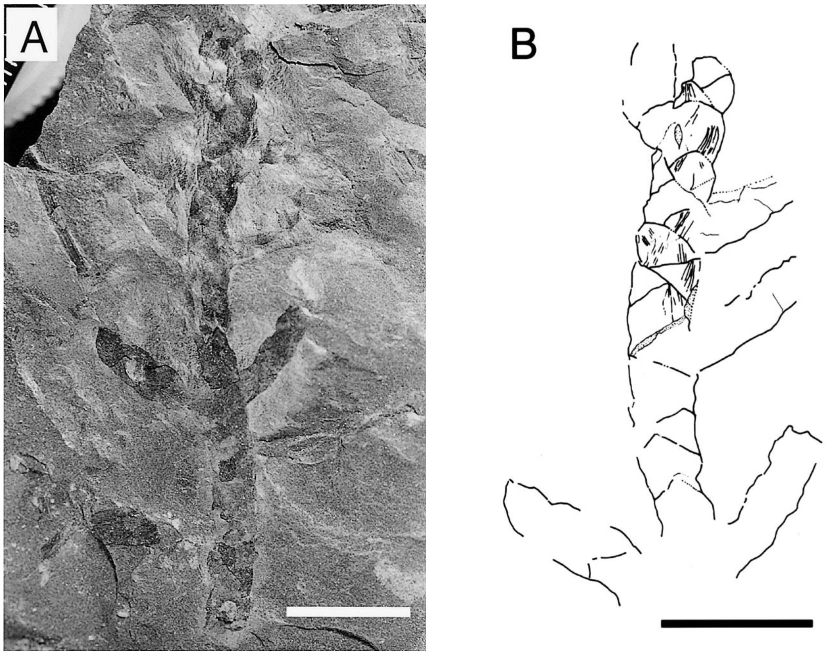

FIGURE 5. Compressed leafy branch of *Brachyphyllum* sp. from about 1 km upstream of Kitadani Dinosaur Quarry, along the Sugiyama River, Katsuyama, Fukui Prefecture (Takinami River area). FPDM-P30. Scale bar represents 10 mm.

One of the authors of present paper (A.Y.) had a chance to observe these specimens. They are characterized by a long and narrow leaf with thick texture; although base and apex of leaf is missing, it seems to be more than 10 cm long and 1 cm wide; surface of lamina is convex upwards; laminae covers entirely the upper surface of rachis; veins are prominent, diverged from the rachis at right angles to the margin without forking; concentration of veins is about 30 per cm*. These characters are in good agreement with the definition of *N. schaumburgensis* (e.g. Kimura and Ohana, 1988), which is one of the characteristic elements of the Ryoseki-type floras (Kimura and Ohana, 1997). *N. schaumburgensis* was once reported and described from the Minamimatadani Formation of the Arimine area (Arimine Flora: Omura, 1974, p. 135, pl. 8, figs. 1, 2). No attention, however, has ever been paid to that report.

REVISED SUBDIVISION OF THE TETORI FLORA

Kimura (1975a) divided the Tetori Flora into four stratofloras: the Kuzuryu Flora for fossil plants from the Kuzuryu Subgroup; the Oguchi Flora for those from the Itoshiro Subgroup; the Akaiwa and Tamodani floras for those from the Akaiwa Subgroup. Kimura (1958b, 1959) studied 6 plant fossil assemblages from the Kuzuryu Subgroup (Kuzuryu Flora), and described 27 species, of which 18 species are common in the Oguchi Flora. Most of these assemblages were collected and reported by previous authors and probably range from the lower to upper part of the Kuzuryu Subgroup. Exact stratigraphic positions were not clear in some cases. The Kuzuryu Flora comprises small number of species and is not sufficient enough to discuss the character. Further, stratigraphic position of each locality is far remote to the subsequent stratofloras in the Tetori Flora. Thus, we are not concerned here with the Kuzuryu Flora.

Oguchi Flora

This flora was established based on plant fossils from the Kuwajima Formation (or the Oguchi Formation: Kawai, 1961) and its equivalents collected from Shiramine (Kaga Flora: Yokoyama, 1889; Kimura et al., 1978, Matsuo and Sekido, 2000) and Mekkodani (Kimura, 1961, 1991; Kimura and Sekido, 1965, 1966, 1967, 1972a, 1972b, 1974, 1975, 1976a; Kimura et al., 1978) in the Tedori River area, and Ogamigo in the Makito area (Yokoyama, 1889; Oishi, 1940; Kimura et al., 1978) (Fig. 3). The Togadani Flora in Tedori River area proposed by Matsuo and Omura (1968) was regarded as a constituent of the Oguchi Flora (Kimura et al., 1978). Plant fossil assemblage from the Okurodani Formation (Loc. OG: Kunimitsu and Nakashima, 1987; Gifu-ken Dinosaur Research Committee, 1993) is probably the same level as those of the Ogamigo locality mentioned above (Oishi, 1933a). That from the Amagodani Formation (Loc. OK: Kunimitsu and Nakashima, 1987; Gifu-ken Dinosaur Research Committee,

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* Note that magnification of photographs shown in plate 11 of Toyama Dinosaur Research Group (2002) is erroneous. Fig. 5 should be in 2.7 and fig. 6, in 2.1 magnifications.

TABLE 1. Systematic list and the occurrence of fossil plants in the Oguchi, Akaiwa and Tamodani floras. **A**: Modified from Kimura et al. (1978) and Kimura (1987). Note that plant fossils reported from locs. C, D and E of Kimura (1975a) was assigned to the Oguchi Flora. Those described by Omura (1974) were not included. **B**: Thermophilic species discovered from the Tetori Flora.

(A)

	O	A	T		O	A	T
Algites ? sp.	○			*D. imamurae* Oishi	○		
Thallites yabei (Kryshtofovich) Harris	○			*D. ishikawaensis* Kimura et Sekido	○		
Equisetites ushimarensis (Yokoyama) Oishi	○			*D. kawasakii* Tateiwa	○		
E. sp.		○		*D. reniformis* Oishi	○		
Todites nipponicus Kimura et Sekido	○			*D. tetoriensis* Kimura et Sekido	○		
Osmudopsis distans (Heer) Kimura et Sekido	○	○		*D. yamazakii* Kimura et Sekido	○		
O. sp. cf. *O. efimoviae* Samylina			○	*D.* sp. cf. *D. cordatus* (Kryshtofovich) Prynada		○	
O. sp.			○	*D.* sp. cf. *D. obliquus* Samylina		○	
Osmunda ? sp.			○	*D.* sp. A	○		
Clathropteris sp.	○			*D.* sp. B	○		
Hausmannia (*Protorhipis*) sp.	○			*Pterophyllum* sp.	○		
Klukia okamigoensis Kimura et Sekido	○			*Neozamites elongatus* Kimura et Sekido	○		
Gleichenites hakusanensis (Kimura et Sekido) Kimura et Sekido	○			*Ctenis burejensis* Prynada	○		
G. ishikawaensis Kimura et Sekido	○			*C.* sp. cf. *C. formosana* Vachrameev	○		
G. nipponensis Oishi	○	○	○	*C. nipponica* Kimura et Sekido	○		
G. porsildi Seward		○	○	*Nilssonia kotoi* (Yokoyama) Oishi	○	○	
G. yamazakii Kimura et Sekido	○			*N. lobatidentata* Vassilevskaja	○	○	
G. sp. cf. *G. sphenopteris* (*Gleichenia* ?) *erecta* Bell	○			*N.* ex gr. *orientalis* Heer	○		
Coniopteris bicrenata Samylina	○			*N. schmidtii* (Heer) Seward		○	
C. burejensis (Zalessky) Seward	○	○		*N.* sp. A	○		
C. saportana (Heer) Vachrameev		○		*N.* sp. B	○		
C. vachrameevi Vassilevskaja	○			*N.* sp.			○
Coniopteris sp. cf. *C. arctica* (Prynada) Samylina			○	*Nilssoniocladus nipponensis* Kimura et Sekido	○	○	
C. sp. A	○			*Tetoria endoi* Kimura et Sekido	○	○	
Birisia alata (Prynada) Samylina	○			*Butefia* ? sp.		○	
B. onychioides (Vassilevskaja et Kara-Mursa) Samylina	○		○	*Cycadites sulcatus* Kryshtofovich et Prynada	○		
Eboracia ishikawaensis Kimura et Sekido	○			*Ginkgo* ex gr. *digitata* Brongniart	○	○	
E.nipponica Kimura et Sekido	○			*G.* ex gr. *huttoni* Sternberg	○	○	
E. tetoriensis Kimura et Sekido	○			*G. paradiantoides* Samylina		○	
Dicksonia ishikawaensis Kimura et Sekido	○			*G.* ex gr. *sibirica* Heer	○	○	
Asplenium dicksonianum Heer			○	*Ginkgoidium nathorsti* Yokoyama	○	○	
Adiantopteris ginkgoifolia Kimura et Sekido	○			*Ginkgoidium* ? sp.			○
A. sewardi (Yabe) Vassilevskaja	○	○		*Eretmophyllum tetoriense* Kimura et Sekido	○		
A. toyoraensis (Oishi) Vassilevskaja		○		*Sphenobaiera* ? sp.			○
A. sp.			○	*Pseudotorellia* sp. A	○		
Cladophlebis ex gr. *denticulata* (Brongniart) Fontaine	○		○	*Pseudotorellia* sp. B	○	○	
C. hamasakai Kimura et Sekido	○			*Czekanowskia* sp.	○	○	
C. hukuiensis Oishi	○			*Phoenicopsis* sp.	○		
C. laxipinnata Prynada	○			*Arctobaiera* ? sp.		○	
C. ex gr. *williamsoni* (Brongniart) Brongniart	○	○		*Leptostrobus* sp.		○	
C. sp. cf. *C. pseudolobifolia* Vachrameev			○	*Podozamites angustifolius* (Eichwald) Heer	○	○	
Onychiopsis elongata (Geyler) Yokoyama	○	○	○	*P. eichwaldi* Schimper			○
Raphaelia diamensis Seward	○	○		*P.* ex gr. *lanceolatus* (Lindley et Hutton) Braun	○	○	
R. sp. A		○		*P. reinii* Geyler	○	○	
R. sp. B		○		*Elatocladus* sp. A		○	
Sphenopteris kochibeana (Yokoyama) Oishi			○	*E.* sp. B		○	
S. sp. A.	○			*E.* sp. C		○	
S. sp. B	○			*E.* sp. D		○	
S. sp. C	○			*E.* sp. E	○		
S. sp. D	○			*E.* sp. F	○		
S. sp. E	○			*Pityophyllum lindstroemi* Nathorst	○	○	○
S. sp. F	○			*Conites* sp.			○
Arctopteris sp.			○	*Protodammara* sp.		○	
Jacutopteris sp.			○	*Xenoxylon latiporosum* (Cramer) Gothan	○	○	
Ctenozamites sp.	○			*Taeniopteris emarginata* Oishi	○		
Sagenopteris sp.		○		*T. richthofeni* (Schenk) Sze	○		
Otozamites endoi Kimura	○			*T.* ex gr. *vittata* Brongniart	○		
O. pseudoanglica Kimura et Sekido	○			*Carpolithus* spp.		○	
Dictyozamites auriculatus Kimura et Sekido	○			unclassified seeds	○		
				Total number of species (*Carpolithus* and unclassified seeds were excluded)	82	41	21

(B)

	O	A	T
Cyathocaulis naktongensis Ogura			○
Ptilophyllum pecten ? (Phillips) Morris		○	
Nilssonia sp. cf. *N. schaumburgensis* (Dunker) Nathorst		○	
Brachyphyllum sp.			○

O: Oguchi Flora, A: Akaiwa Flora, T: Tamodani Flora

1993) and middle part of the "Tamodani Formation" (Kimura, 1958a, 1975a) in the Kuzuryu area is here assigned to this stratoflora. The "Tamodani Formation" (Kimura, 1975a) or "Tamodani Group" (Kimura and Horiuchi, 1979) has been used informally without any definition. It is comparable to the Itsuki, Nochino and Chinaboradani formations of Maeda (1957a). Judging from the lithofacies and the locality map shown in Kimura (1975a) as compared with Maeda (1957b) and Fujita (2002a), stratigraphic positions of localities of his "Akaiwa Flora" in the Kuzuryu area (Locs. C, D and E: Kimura, 1975a) correspond to the upper part of the Itsuki Formation. Plant fossils from those localities comprise 7 species, of which 6 species are common in the Oguchi Flora (*sensu* Kimura et al., 1978). The other one, *Pseudotorellia* sp. B, is distinct but similar to *P*. sp. A described in the Oguchi Flora. Therefore, we disagree with Kimura's opinion that floristic composition of Tamodani localities and that of the Tedori River area (Bettokuzure) is similar enough to establish a stratoflora.

According to Kimura (1987), this flora comprises 39 genera and 82 species (Table 1). The most conspicuous plant is dicksoniaceous fern with 11 species, followed by *Dictyozamites* (9 species), ginkgoaleans with czekanowskialeans (9 species), and *Nilssonia* (6 species: including *Nilssoniocladus*). *Gleichenites* is also a common element represented by 5 species. Form-genus *Sphenopteris* and *Cladophlebis* consist of 6 and 5 species, respectively.

The localities of the Oguchi Flora are stratigraphically confined to the upper part of the Itoshiro Subgroup (Fig. 3), which is characterized by Tatsukawa-type non-marine bivalve fauna (Kozai et al. 2001, 2002). Thus, geologic age of the Oguchi Flora can be assigned to Hauterivian.

Akaiwa Flora

This flora was defined by Kimura (1975a), on the basis of the plant fossils from the Tedori River area (Bettokuzure and Osugidani: Kimura and Sekido, 1976b, 1978) and middle part of the "Tamodani Formation" in the Kuzuryu area (Kimura, 1958a, 1975a) (Fig. 3). Fossil localities in the Tedori River area correspond with the lower part of the Akaiwa Formation (Ishikawa Prefectural Board of Education, 1978). As mentioned above, we excluded those of the Kuzuryu area from the constituents of the Akaiwa Flora. Plant fossils from the Minamimatadani Formation (Arimine Flora: Omura, 1974) and those from Yunotani of the Tedori River area (Matsuo and Higashino, 1979) should be correlative with this flora. Plant fossils from the "Ohyama dinosaur footprint site" (Toyama Dinosaur Research Group, 2002) are here treated as constituents of this stratoflora.

The Akaiwa Flora comprises 26 genera and 41 species (Table 1). The most dominant is ginkgoaleans with czekanowskialeans, comprising 9 species. Dicksoniaceous ferns, *Nilssonia*, and coniferous leafy shoot *Elatocladus* comprise 4 species. It includes a possible Ryoseki-type element, *Nilssonia* sp. cf. *N. schaumburgensis* (Omura, 1974; Toyama Dinosaur Research Group, 2002). Matsuo and Higashino (1979) figured *Ptilophyllum pecten*?, which is also an element of the Ryoseki-type flora, recovered from the lower course of the Yunotani River, Ishikawa Prefecture, though further study is necessary to confirm its taxonomic position.

Geologic age of the Akaiwa Flora has not been settled yet. The age of the Kuwajima Formation that underlies the Akaiwa Formation is Hauterivian. The Kitadani Formation that conformably overlies the Akaiwa Formation is dated as late Barremian by non-marine bivalve fauna (Kozai et al., 2001, 2002). Thus, the Akaiwa Flora is not older than Hauterivian and not younger than late Barremian.

Tamodani Flora

This flora was established based on plant fossils from the uppermost part of the "Tamodani Formation" (Kimura, 1975a) and the Chinaboradani Formation (Kimura and Horiuchi, 1979) distributed along the Itoshiro River (Kuzuryu area). Judging from figures shown in Kimura (1975a) as well as lithofacies of fossil-bearing strata described, localities F, G, and H of the "Tamodani Formation" might be correlative with the Chinaboradani Formation (Maeda, 1957a, 1957b). Plant fossils from the Kitadani Formation of the Tedori River area (Myodani flora: Matsuo and Omura, 1966) are also included in this flora (they used "the Myodani Formation" of Kawai, 1961). The Kitadani Formation of the Takinami River area yields a number of leaves and seeds, although they have not been described yet (Goto et al., 2002). Plant fossil assemblages of each locality are different in composition, however, as noted by Kimura and Horiuchi (1979), they are correlated stratigraphically by the dominance of acidic tuff or tuffaceous rocks. A tree fern stem, *Cyathocaulis*, from the Makito area is here treated as an element of the Tamodani Flora (Fig. 3-B) tentatively.

According to Kimura (1987), 17 genera and 19 species have been recognized in the Tamodani Flora (Table 1). Dicksoniaceous and osmundaceous ferns, and ginkgoaleans are the dominant elements with 3 species, followed by *Gleichenites* with 2 species. Some fern genera characteristic to the Early Cretaceous floras of the Siberian-Canadian Region, such as *Arctopteris* and *Jacutopteris*, characterize the Tamodani Flora. Both species have not been recognized in the Oguchi and Akaiwa floras. *Osmunda*-like ferns and *Asplenium* were regarded as "younger elements" of late Early Cretaceous (Kimura and Horiuchi, 1979). Plant fossil assemblages of the Kitadani Formation of the Takinami River area are characterized by: rarity of ferns represented by *Onychiopsis* and *Gleichenites*, abundance of cycadales and conifers represented by cones and shoots. Some Ryoseki-type elements, such as *Cyathocaulis naktongensis* and *Brachyphyllum* sp., were recovered very recently as noted previously. Matsuo and Omura (1966) listed *Zamiophyllum* sp. in the Myodani flora,

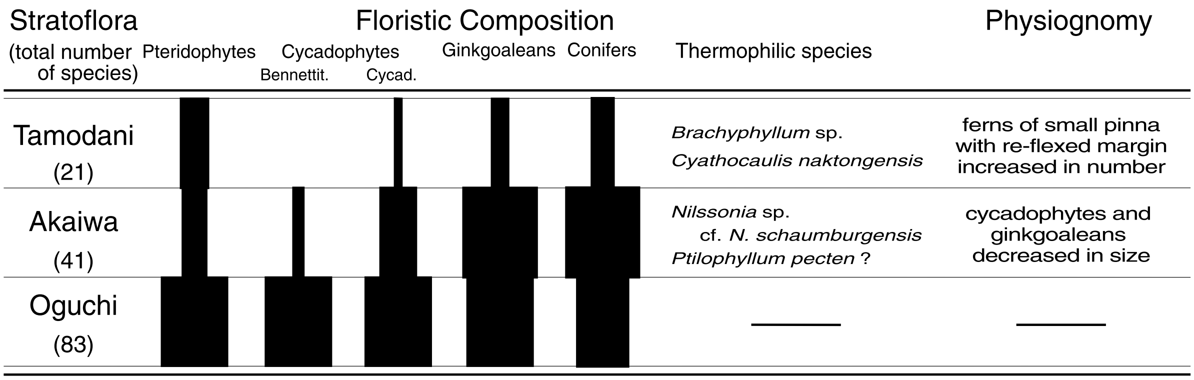

FIGURE 6. Stratigraphic changes of species number of selected taxonomic groups, and foliar physiognomy among three stratofloras in the Tetori Flora. Each column indicates relative abundance compared with the number of species in the Oguchi Flora (Table 1). Bennettit.: Bennettitales, Cycad.: Cycadales.

which is considered as a Ryoseki-type element.

Geologic age of the Tamodani Flora is presumed from that of the Kitadani Formation; molluscan fossils of this formation belong to the Sebayashi-type non-marine bivalve fauna, which is dated as late Barremian (Kozai et al., 2002).

DIFFERENCES IN COMPOSITION AND PHYSIOGNOMY AMONG THE STRATOFLORAS

Kimura and Sekido (1976b) noted that floristic composition of the Oguchi and Akaiwa Floras was similar, but the latter was characterized by rarity of ferns and cycadophytes. Difference in leaf physiognomy between the Oguchi and Akaiwa floras is more obvious than in composition. On the other hand, the Tamodani Flora is rather distinct in its floristic composition compared with other two floras (Kimura and Horiuchi, 1979).

Foliar physiognomy is regarded to relate to climate (Givnish, 1979; Chaloner and McElwain, 1997), and is generally used for climate reconstruction in angiosperms of Late Cretaceous and Tertiary (e.g. Wolfe, 1979; Herman and Spicer, 1997). On the basis of statistical analysis of non-angiosperm fossils reported in eastern Eurasia, Spicer et al. (1993) suggested that these fossils also exhibited a weak, poorly differentiated phytogeographic pattern linked most strongly to precipitation, and that this relationship was reflected in foliar physiognomy. Here we summarize stratigraphic changes of floristic composition and foliar physiognomy of the Oguchi, Akaiwa, and Tamodani floras, from the descriptions in previous section as well as published papers (Fig. 6).

Floristic composition

Because each flora was collected from more than two localities, difference in composition can be attributed mainly to the difference of their age, reflecting the evolutionary history of floras and/or changes in distribution of species in response to climate. Comparison among three Early Cretaceous floras in the Tetori Flora reveals that there is a decrease in the number of genus and species. This trend is more obvious in the number of species than in genus. It implies that this trend more or less reflects the difference of fossil preservation, depositional environments, and probably number of specimen collected. Floristic composition of each flora shows high degree of similarities as discussed below. The reason for comparing presence or absence of each taxonomic group among three floras than relative abundance is to avoid an influence of these conditions (Fig. 6). In other words, relative abundance of each taxonomic group in particular flora tends to reflect local depositional environment. Thus, we will draw more attention to presence or absence of each taxonomic group to discuss differences of floras.

There are typical Tetori-type elements, such as dicksoniaceous ferns, *Nilssonia* (with broad leaf), ginkgoaleans, *Pityophyllum* and *Podozamites*, in three floras, although the number of species decreased upward. Common genera between the Oguchi and subsequent floras are 21 (80.7%: Akaiwa Flora) and 11 (64.7%: Tamodani Flora), respectively. Among new genera recognized in the Akaiwa Flora, it is possible to say that *Leptostrobus* sp. is a reproductive organ related to *Czekanowskia* found in the Oguchi Flora. On the other hand, 6 new genera are recognized in the Tamodani Flora. Regarding the pteridophytes, the "younger elements" (Kimura and Horiuchi, 1979), such as *Osmunda*-like ferns and *Asplenium* are firstly appeared in the Tamodani Flora. *Arctopteris* and *Jacutopteris* have been considered as representatives of Early Cretaceous floras of the Siberian-Canadian Region (Kimura, 1975a). Relative abundance of pteridophytes apparently increases in the Tamodani Flora. Coeval assemblage from the Kitadani Formation is, on the contrary, characterized by rarity of ferns as mentioned previously. It suggests that abundance of pteridophytes in the Tamodani Flora in the Kuzuryu area does reflect vegetation close to the place of deposition. Kimura used the term "cycadophytes" to indicate the species belonging to both cycadales and bennettitales (or cycadeoidales), because the distinction of those two groups is sometimes difficult without cuticular analysis. We followed here a treatment of Kimura et al. (1978): dividing both groups tentatively based on external morphology. Kimura (1987) pointed out that cycadophytes tend to reduce its number in the Akaiwa and Tamodani floras in contrast to the Oguchi Flora. Judging from the plant fossil composition of the Kitadani Formation mentioned above, however, cycadales are also abundant in the Tamodani Flora. On the contrary, bennettitales are disappeared in the Tamodani Flora. Conifers are relatively rare in number of species and those except for *Podozamites* are also rare in number of specimens (Kimura, 1975; Kimura and Sekido, 1976). Taking into account the abundance of conifers in the Kitadani Formation, it is likely that percentage of conifers increased upward to the Tamodani Flora. In addition, the occurrence of thermophilic species is confined to the Akaiwa Flora (*Nilssonia* sp. cf. *N. schaumburgensis* and *Ptilophyllum pecten*?) and the Tamodani Flora (*Cyathocaulis naktongensis* and *Brachyphyllum* sp.).

Physiognomy

According to Kimura (1973, 1975a) and Kimura and Sekido (1976b), those three floras in the Tetori Flora show distinct differences in foliar physiognomy as follows. Compared with the Oguchi Flora, *Nilssonia* leaves reduced in size, and leaves with marginal teeth or sinuses increased in number in the Akaiwa Flora. Reduction of leaf size is also obvious in ginkgoaleans except *Ginkgoidium* whose leaves increased in size. Ferns of the Oguchi Flora show similarity with those of the Siberian floras and are characterized by pinnules of large size. On the contrary, ferns in the Akaiwa and Tamodani Floras are characterized by small-sized pinnules with re-flexed margin (Kimura, 1973, 1975b).

CLIMATIC CONDITIONS INFERRED FROM THE TETORI FLORA

The Tetori Flora is characterized by many elements common in the coeval floras of Siberian-Canadian Region as suggested by Kimura (1987) and Vakhrameev (1991). There are, however, some disparities between the Tetori Flora and those in the Siberian-Canadian Region in the common presence of *Onychiopsis*, gleicheniaceous ferns, and *Dictyozamites*; and in the absence of such cycadalean species, as *Heilungia* and *Aldania* in the former. These facts led to the conclusion that the Tetori-type floras represent southern marginal facies of the Siberian-Canadian Region (Kimura, 1987) or an ecotone between the Euro-Sinian and Siberian-Canadian regions (Vakhrameev, 1991; Cao, 1999). Kimura and his co-workers suggested that the climatic condition in which the Tetori-type floras flourished was temperate and moderate humid (e.g. Ohana and Kimura, 1995a; Kimura, 2000b). Similarity of floristic composition among the stratofloras in the Tetori Flora implies roughly a similar climatic condition. However, as described in the previous section, there is a little but distinct change recognized in floristic composition and foliar physiognomy within the Akaiwa and Tamodani floras so that their interpretation should be confined to the Oguchi Flora.

In respect of foliar physiognomy, it was observed in the preceding chapter that mean size of leaves tends to decrease in several groups in the Akaiwa Flora, and that some groups of ferns exhibit small pinnules with "re-flexed" margin in the Akaiwa and Tamodani floras. All of these characters may account for the decrease of water availabilities (e.g. Kimura, 1973). This is concordant with the occurrence of *Brachyphyllum* in the Tamodani Flora. The occurrence of carbonate nodules in the Akaiwa (Fujita, 1998) and Kitadani (Goto et al., 2002; Morikiyo and Sato, 2002) formations also suggests a drying condition (e.g. Retallack, 2001) in the age of the Akaiwa and Tamodani floras.

From the viewpoint of floristic composition, the following trends are obvious: decrease of number of genus and species, increase of conifers; and decrease and disappearance of bennettitales. Further, some thermophilic species, representatives of the Ryoseki-type floras, are recognized in the Akaiwa and Tamodani floras. That is, *Nilssonia* sp. cf. *N. schaumburgensis* and *Ptilophyllum pecten*? in the Akaiwa Flora, *Brachyphyllum* sp. and *Cyathocaulis naktongensis* in the Tamodani Flora. The occurrence of these species strongly suggests that climatic condition became warmer and dryer than that of the Oguchi Flora, when the Akaiwa and Tamodani floras flourished. Decrease of number of genus and species, and increase of conifers are probably ascribed to the increase of aridity mentioned above. Kimura (1975a) mentioned co-occurrence of *Arctopteris* and *Jacutopteris* in the Tamodani Flora and in the Siberian-Canadian Region of Vakhrameev (1991), and indicated that the Tamodani Flora might be close to those of the Siberian-Canadian Region. According to Vakhrameev (1991), *Arctopteris* species are common in the latter half of Early Cretaceous in the Siberian-Canadian Region. In the northern part of the Siberian-Canadian Region (Lena Province), they appear in late Neocomian and diversify in Albian. On the other hand, he pointed out that the distribution of some fern genera, such as *Onychiopsis* and *Birisia* common in the Tetori Flora, spread northward in response to warming during the Early Cretaceous. *Arctopteris* species are usually co-occurred with *Onychiopsis* and *Birisia* species mentioned above. This fact strongly suggests that distribution of these ferns expanded to the north in response to climate to became warmer and possibly dryer. Consequently, we conclude that "the Siberian elements" from the Tamodani Flora do not indicate

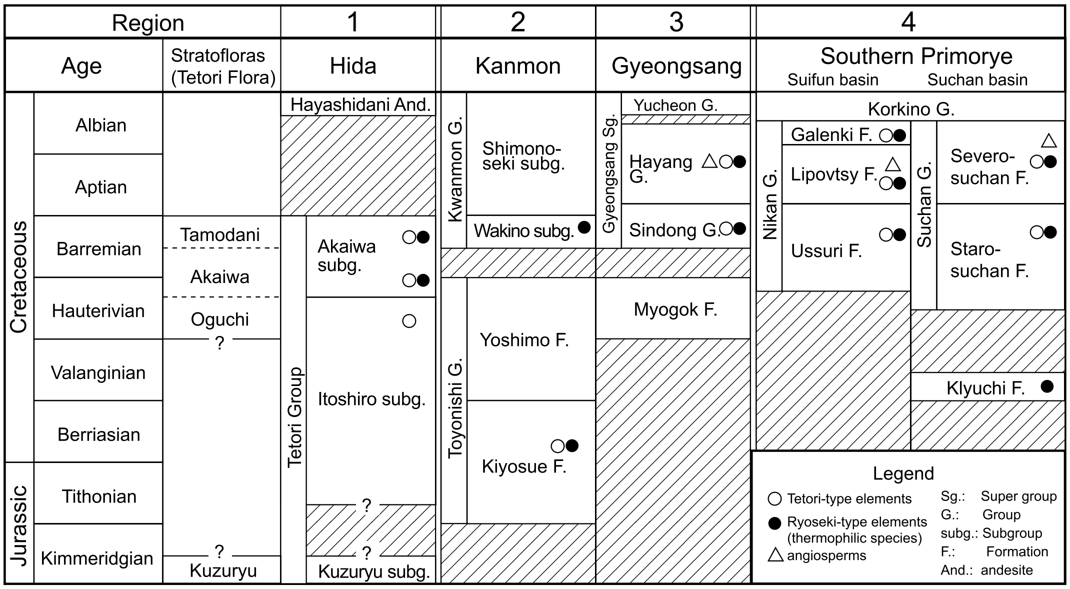

FIGURE 7. Stratigraphic correlation of the Upper Jurassic to Lower Cretaceous strata of the Hida, Kanmon, Gyeongsang, and Southern Primorye regions, showing the age of four stratofloras in the Tetori Flora, and the occurrence of the Tetori-type elements and thermophilic species in each region. For details of composition, see text. Occurrence of both elements in southern Primorye is after Kimura (1987) and Ohana and Kimura (1995a). First occurrences of angiosperm fossils seem to be confined in Aptian or Albian strata. The "Kuzuryu Flora" represents the plant fossils from the uppermost part (Yamada, 1988) of the Kuzuryu Subgroup reported by Maeda (1961b). Stratigraphy of each region is based on the following papers. Hida region: Maeda (1961c) and Tanase et al. (1994), Kanmon region: Okada and Sakai (2000) modified after Kozai et al. (2002), Gyeongsang region: Chang et al. (in press) and Sakai and Okada (1997) modified after Kozai et al. (2002), southern Primorye: Markevitch and Kanovalov (1999) and Matsukawa et al. (1997b).

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the contemporaneousness of the Tamodani Flora and those in the Siberian-Canadian Region, but reflect the climatic change took place during the Early Cretaceous. This is concordant with the climatic condition inferred from the floristic composition and foliar physiognomy.

EARLY CRETACEOUS CLIMATIC CHANGES IN EASTERN EURASIA BASED ON PLANT FOSSIL STUDIES

We recognized a warming and possibly drying trends from the floristic changes within the Tetori Flora. We here discuss whether similar floristic change is recorded in coeval strata. One from Southwest Japan and South Korea (Fig. 1, locs. 2 and 3), and another one in southern Primorye (Fig. 1, loc. 4) are mentioned here, because more than two stratigraphically different floras have been recognized in each area (Fig. 7). Further, we will briefly mention the climatic condition inferred from the plant fossil assemblages in China and Siberia.

Kanmon–Gyeongsang region

The Kanmon region, situated between the southwestern end of Honshu and northern Kyushu of Japan, yields abundant fossil plants, which are ranging from Late Triassic to Early Cretaceous. Basin of the Gyeongsang Supergroup (Chang, 1975) of South Korea is considered to have connected with that of the Kwanmon Group (Matsumoto, 1951) before the Japan Sea opened (e.g. Chang et al., 2000; Hisada et al., 2001). Thus, we examined the plant fossils from the Kwanmon Group and the Sindong Group of the Gyeongsang Supergroup together.

This region was previously included in the "Inner Zone Palaeophytogeographic Province" by Kimura (1979, 1980); however, the presence of some thermophilic species led him to assign to the area of the Mixed-type floras (Kimura, 1987). In this region, possible Neocomian flora is represented by that of the Kiyosue Formation of the Toyonishi Group and the Nagdong Formation of the Sindong Group (Fig. 7-2, 3). The one recently reported by Kenrick et al. (2000) seems correlative with that of the Nagdong Formation. Plant fossils from the Hayang Group, which overlies the Sindong Group, were reported by Tateiwa (1929), though they have not been described yet. According to Ohana and Kimura (1995b), this assemblage yields various angiosperms and the other elements show similarity to the Mixed-type floras.

The Kiyosue Formation constitutes the basal part of the Toyonishi Group, which is dated as the latest Jurassic or the earliest Cretaceous (Yamada and Kato, 2002). Plant fossil assemblage of the "Kiyosue Formation" was once described by

Oishi (1940). However, localities treated by Oishi (1940) were considered not to belong to the Kiyosue Formation but to the Middle Jurassic Utano Formation (Kimura and Ohana, 1987a). According to Takahasi (1973) and Kimura (1987), plant fossils from the Kiyosue Formation consist of 15 genera and 23 species. Kimura (1987) stated: "flora of the Kiyosue Formation is fundamentally of the Tetori-type, but includes several Ryoseki-type elements, as well as flora of the Lower Gyeongsang Group (Nagdong Formation), South Korea." Thermophilic plants recognized in the Kiyosue Formation are *Ptilophyllum*, *Zamites*, *Nilssonia* ex gr. *schaumburgensis*, and *Brachyphyllum* ex gr. *expansum* (Kimura, 1987). Most of them are found in the upper part of the Tetori Flora (the Akaiwa and Tamodani Floras).

The Nagdong Formation that represents the basal part of the Sindong Group yields abundant plant megafossils (Yabe, 1905, 1922; Tateiwa, 1929; Oishi, 1940). Geologic age of the Nagdong Formation is presumed as Barremian by fossil charophytes (Choi, 1989) and as late Barremian by non-marine mollusks (Kozai et al., 2001, 2002). As discussed by Kimura (1987, 2000a), plant fossil assemblage of the Nagdong Formation is fundamentally of the Tetori-type, but includes the following Ryoseki-type elements: *Ptilophyllum pecten*, *Naktongia yabei*, *Cyathocaulis naktongensis*, *Ciboticaulis tateiwai*, *Nilssonia* ex gr. *schaumburgensis*, *Frenelopsis* ex gr. *parceramosa*, *Brachyphyllum* ex gr. *expansum*, and *Cupressinocladus japonicus*.

The Wakino Subgroup of the Kwanmon Group unconformably overlies the Toyonishi Group. It is correlated to the Sindong Group of the Gyeongsang Supergroup of South Korea (e.g. Okada and Sakai, 2000). Plant fossils from the Kwanmon Group are not well understood. The only report with the description is Kimura et al. (1992) that reported *Cupressinocladus* sp. from the upper part of the Wakino Subgroup. Imamura and Kusumi (1951) mentioned the occurrence of *Elatocladus* sp. and "*Brachyphyllum*" sp. from the Yamaji Shale of the upper Inakura Formation, which is correlative with the upper part of the Wakino Subgroup. *Cupressinocladus* and *Brachyphyllum* are the element of the Ryoseki-type floras. Although composition of plant fossils is not sufficient to discuss floristic characters, it is consistent with that of the Nagdong Formation.

The occurrence of *Ptilophyllum pecten*, *Nilssonia* ex gr. *schaumburgensis*, and *Brachyphyllum* ex gr. *expansum* from the Nagdong Formation imply the similarity with that of the Kiyosue Formation. It is obvious that relative abundance of thermophilic plants indicates the warmer condition than that of the Kiyosue Formation. *Frenelopsis* is a well-known conifer belonging to the family Cheirolepidiaceae. This plant exhibits strong adaptation to xeric condition (Upchurch and Doyle, 1981). Consequently, flora of the Nagdong Formation indicates similarity but more arid and warmer condition than that of the Kiyosue Formation. Therefore, floristic change from the Kiyosue to Nagdong formation seems concordant with that in the Tetori Group.

Southern Primorye

There are several plant-bearing strata, of which the geologic age ranges from Berriasian to Albian, in the Suchan (Partizansk) and Suifun (Razdolnaya) Basins located in eastern and western part of southern Primorye (Fig. 7-4). They are generally correlated to Early Cretaceous floras in Japan (e.g. Vakhrameev, 1991).

The Lower Cretaceous strata distributed in the Suchan Basin, southeastern Primorye are divided into the Klyuchi, Starosuchan (Old-Suchan), Severosuchan (North-Suchan), Kangauz, and Romanovka formations, in ascending order (Markevich and Konovalov, 1999) (Fig. 7-4). The Starosuchan and Severosuchan formations constitute the Suchan Group, and the Kangauz and Romanovka formations constitute the Korkino Group, which is widely distributed in southern Primorye. According to Matsukawa et al. (1997b, Fig. 4), the Klyuchi Formation is of shallow-marine deposits and yields such index fossils as ammonites and buchiid bivalves, which are dated as Valanginian. On the other hand, the Starosuchan and Severosuchan formations are represented by non-marine facies, besides the upper part of the Severosuchan Formation that yields trigonioid fossils. On the basis of marine animals and palynostratigraphy (e.g. Markevitch, 1994), they assigned the Starosuchan Formation to Barremian and the Severosuchan Formation to the Aptian to the early Albian (Matsukawa et al., 1997b).

The Lower Cretaceous deposits distributed in the Suifun Basin, southwestern Primorye, are divided into the Nikan and overlying Korkino groups. The Nikan Group consists of the Ussuri, Lipovtsy and Galenki formations, all of which yields abundant fossil plants. The Ussuri Formation was stratigraphically correlated to the Starosuchan Formation of the Suchan basin, and the Lipovtsy and Galenki formations were correlated to the Severosuchan Formation (Markevich and Konovalov, 1999).

Plant fossil assemblages from the Klyuchi Formation and the Berriasian Taukhe Formation distributed in northeast of Suchan Basin (Krassilov, 1967, 1973), were correlated to the Ryoseki-type flora (Kimura, 1987). We, however, could not discuss its reliability, because the floristic composition is too small (8 and 10 species: Krassilov, 1967). Krassilov (1967) suggested the similarity of these assemblages with those of the inner-side of Japan. On the other hand, plant fossils from the Starosuchan and Severosuchan formations and their equivalents (Nikan flora: Krassilov, 1967) were assigned to the Mixed-type flora (Kimura, 1987). According to Ohana and Kimura (1995b), they are characterized by abundance of Ryoseki-type elements with few Tetori-type elements. Judging from the list shown in Krassilov (1967), the Ryoseki-type elements are much common in the floras of the Suifun basin than those of the Suchan basin.

Assuming that Kimura's description is reliable, we should say that change of floristic composition in those basins began with the Ryoseki-type and changes into the Mixed-type floras. This is opposite to that observed in the Tetori Group and the Kanmon–Gyeongsang region. Thus, another mechanism is required to explain this change. Tectonic reorganization along the eastern margin of Asia has been mentioned repeatedly to explain very close distribution of the Tetori-type and Ryoseki-type floras in Japan, and the Mixed-type and Ryoseki-type floras in Sikhote-Alin and northeastern China (Kimura, 1987; Otoh and Sasaki, 1998). Golozoubov et al. (1999) correlated the floras of the Suifun and Suchan basins to the Tetori-type and Ryoseki-type floras, respectively. They suggested that the Voznesenka and Sergeevka terranes, forming the basement of Early Cretaceous sediments of the Suifun and Suchan basins, migrated northward due to left lateral strike-slip displacement and the latter displaced for a much longer distance. We cannot support their opinion in respect of the correlation of floras; however, it is worth mentioning that tectonics might play an important role to explain floristic change from the Ryoseki-type to Mixed-type floras in southern Primorye.

Other regions in eastern Eurasia

The warming trend possibly during Hauterivian to Barremian was reported by Golovneva (1998), which dealt with floras distributed in the northeastern Russia. Sun et al. (1995) summarized the phytogeographic change of China during the Early Cretaceous that the transition of the elements of Southern Floristic Region (Euro-Sinian Region) into the Northern Floristic Region (Siberian-Canadian Region) gradually contributed to an establishment of broad mixed zone, particularly in the coastal areas of the northeastern China. They suggested the occurrence of a warm and arid climate during the late Early Cretaceous. On the other hand, Krassilov (1973) illustrated a detailed reconstruction of climate in eastern Asia as indicated by fossil floras of southern Primorye and the Bureya Basin. He reported a rise of temperature during the Late Jurassic up to the Berriasian, followed by a cooling in the Valanginian. Figure 3 of his paper, dealt with the flora of Bureya Basin, indicates the warming trend from the Barremian to Aptian (Hauterivian was not drawn). Kirillova et al. (2000) confirmed that a minor cooling trend mentioned by Krassilov (1973) coincided with Valanginian–Hauterivian regression. As a consequent, it is likely that a warming and drying trends recognized in the Tetori Flora reflects the occurrence of a warm and arid climate in the eastern Eurasia during the Hauterivian to Barremian.

FUTURE PROSPECTS

If we apply the definition of Kimura's Tetori-type, Mixed-type, and Ryoseki-type floras to the Tetori Flora, the Oguchi Flora is the Tetori-type, whereas the Akaiwa and Tamodani floras should be assigned to the Mixed-type flora. The emergence of the Mixed-type flora in the Hida region can be ascribed to the climatic changes discussed previously. All besides one locality of the Mixed-type flora in China have been regarded as Early Cretaceous (Kimura, 1987, fig. 2). Therefore, we may say that the recognition of the Mixed-type flora is important to understand climatic change during the Early Cretaceous. The Middle Jurassic Utano Flora (Kimura and Ohana, 1987a, b) of Kanmon region was assigned to the Mixed-type flora (Kimura, 1987). It should be important to study the Utano Flora in respect of the climatic changes.

Saiki and Wang (in press) examined the distribution of "climate indicator plants" previously reported from the Lower Cretaceous strata of China. They suggested that each taxon had a different distribution area and did not indicate any particular boundaries to be delineated. We agree with their opinion that floristic composition changes gradually through the continent. Detailed study of species distribution of "climate indicator plants" in time and space should be necessary to illustrate the climatic changes as well as floristic evolution in eastern Eurasia.

Although in the present paper we did not deal with the papers without any descriptions and/or figures of plant fossils, there are some reports on the occurrence of thermophilic plants from the Tetori Group in those papers (e.g. Kawai, 1961; Omura, 1973). It is debatable whether they indicate another warm episode during the period of the Tetori Flora. We should examine whether there are signals of climatic fluctuation within the Tetori Flora.

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* : in Japanese with English abstract
** : in Japanese with English summary
*** : in Japanese
\+ : in Russian
\++ : in Chinese with English summary

＜地名・地層名＞

Akaiwa	赤岩
Arimine	有峰
Bettokuzure	別当崩れ
Gyeongsang	慶尚
Inakura	稲倉
Itoshiro	石徹白
Kanmon	関門
Kobu-tani	コブ谷
Kwanmon Group	関門層群
Minamimatadani	南俣谷
Nishihiro	西廣
Ogamigo	尾上郷
Osugidani	大杉谷
Sanchu	山中
Shiramine	白峰
Sugiyama	杉山
Tedori	手取
Utano	歌野
Yambara	山原
Amagodani	アマゴ谷
Ashidani	葦谷
Chinaboradani	知那洞谷
Hasangdong	霞山洞
Inotani	猪谷
Itsuki	伊月
Kitadani	北谷
Kuwajima	桑島
Makito	牧戸
Myodani	明谷
Nochino	後野
Oguchi	尾口
Otaniyama	大谷山
Sebayashi	瀬林
Shokawa	荘川
Takinami	滝波
Tetori Group	手取層群
Wakino	脇野
Yucheon	楡川
Arida	有田
Bessandani	別山谷
Gomijima	五味島
Hayang	河陽
Ioridanitoge	庵谷峠
Kamihambara	上半原
Kiyosue	清末
Kuzuryu	九頭竜
Mekkodani	目付谷
Nagdong	洛東
Obuchi	大渕
Ohyama	大山
Ryoseki	領石
Shimonoseki	下関
Sindong	新洞
Tamodani	田茂谷
Toyonishi	豊西
Wasabu	和佐府
Yunotani	湯ノ谷