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The Cretaceous Tetori biota in Japan and its evolutionary significance for terrestrial ecosystems in Asia

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Abstract

Cretaceous nonmarine deposits are widely distributed on the Asian continent and include various kinds of zoo- and phyto-assemblages. The Tetori Group is one of the most important Mesozoic terrestrial deposits in East Asia, and for this reason its geology, stratigraphy, and biota have been studied intensively by our group for more than a decade. We present the main results herein.

We confirm that formations as lithostratigraphic units are the best geological correlation tools for the Tetori Group and the best tools for a geological mapping of the group. Although subgroups have previously been used for correlation, proper designation and evaluation of subgroups is required if they are to be used effectively, and we show that previous geological correlation of the Tetori Group has been confused by inappropriate definition of these subgroups. We located fossil localities including reported zoo- and phyto-assemblages in the framework of formations correlated by our stratigraphy. The occurrence of zoo-assemblages was probably controlled by environments (i.e., most are in situ), but phyto-assemblages were mostly transported and rapidly buried by high-energy river systems. Although two distinct dinosaur faunas and four floras have been named for the zoo- and phyto-assemblages in the Tetori Group, in reality there is only one Tetori Dinosaur Fauna and one Tetori Flora, as proved by careful correlation. Two types of zoo-assemblages co-occur in the Tetori Group: vertebrate species whose ancestors flourished in the Jurassic (as found in China), and their descendants from the Late Cretaceous. As the latter modern type of assemblage is more abundant than the former, changeable environments at the continental margin probably accelerated evolution of more modern species.

We can employ nonmarine molluscan species as geological correlation tools in some cases, i.e., when their taxon ranges are well-confirmed by independent evidence. However, because freshwater molluscan species and terrestrial vertebrate species had many opportunities to move to optimum habitat as environments changed through time on the Cretaceous Asian continent, their correlation potential is uncertain. Many nonmarine molluscan species from the Japanese and Chinese Cretaceous had their stratigraphic occurrences controlled by changing environments.

Keywords: Cretaceous; Tetori Group; Geological correlation tool; Nonmarine chronological indices; Terrestrial ecosystem

1. Introduction

In the Early Cretaceous Epoch, the evolution of Japanese terrestrial ecosystems is thought to have been largely controlled by continental rifting and accompanying environmental changes (Obata, 1993; Barrera and Johnson, 1999). Lower Cretaceous nonmarine deposits are widely distributed on the Asian continent and yield various kinds of fossils such as fish, amphibians, reptiles, dinosaurs, mammals, bivalves, gastropods, insects, ostracodes, conchostracans, and terrestrial plants. Because it represents one of the world's best records, the Lower Cretaceous nonmarine biota in Asia

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is especially important for understanding zoo- and phyto-assemblage changes through time.

The Tetori Group is one of the most important Mesozoic terrestrial deposits in East Asia, with common zoo- and phyto-taxa throughout the region. It is especially suitable for analyzing relations between environmental changes, and zoo- and phyto-assemblage changes, caused by the development of the Tetori Basin (Fig. 1). Establishing a stratigraphic scheme for the Tetori Group is indispensable for these analyses. However, in previous studies, regional formation names of the Tetori Group were given separately for sequences in each of three unconnected local regions: the Kuzuryugawa, Mt. Hakusan, and Jinzu regions. Matsukawa et al. (2003a) synthesized a coherent stratigraphic sequence throughout the whole area of the Mt. Hakusan region, which can be considered the main "type" section for the Tetori Group, and the geological map was revised to reveal the correct distribution of formations based on geological correlation between these separate areas. Matsukawa et al. (2003c) reported that the Tetori Group in the Kuzuryugawa region is divided into five formations and that these formations are correlative with seven formations in the main "type" section for the group in the Mt. Hakusan region. In addition, Ito and Matsukawa (2002) showed that the depositional environment and basin development of the Tetori Group can be placed in a sequence-stratigraphic framework.

In this paper, we present a stratigraphy of the Tetori Group in both the Kuzuryugawa and Mt. Hakusan regions and evaluate zoo- and phyto-fossil assemblages horizons in a coherent

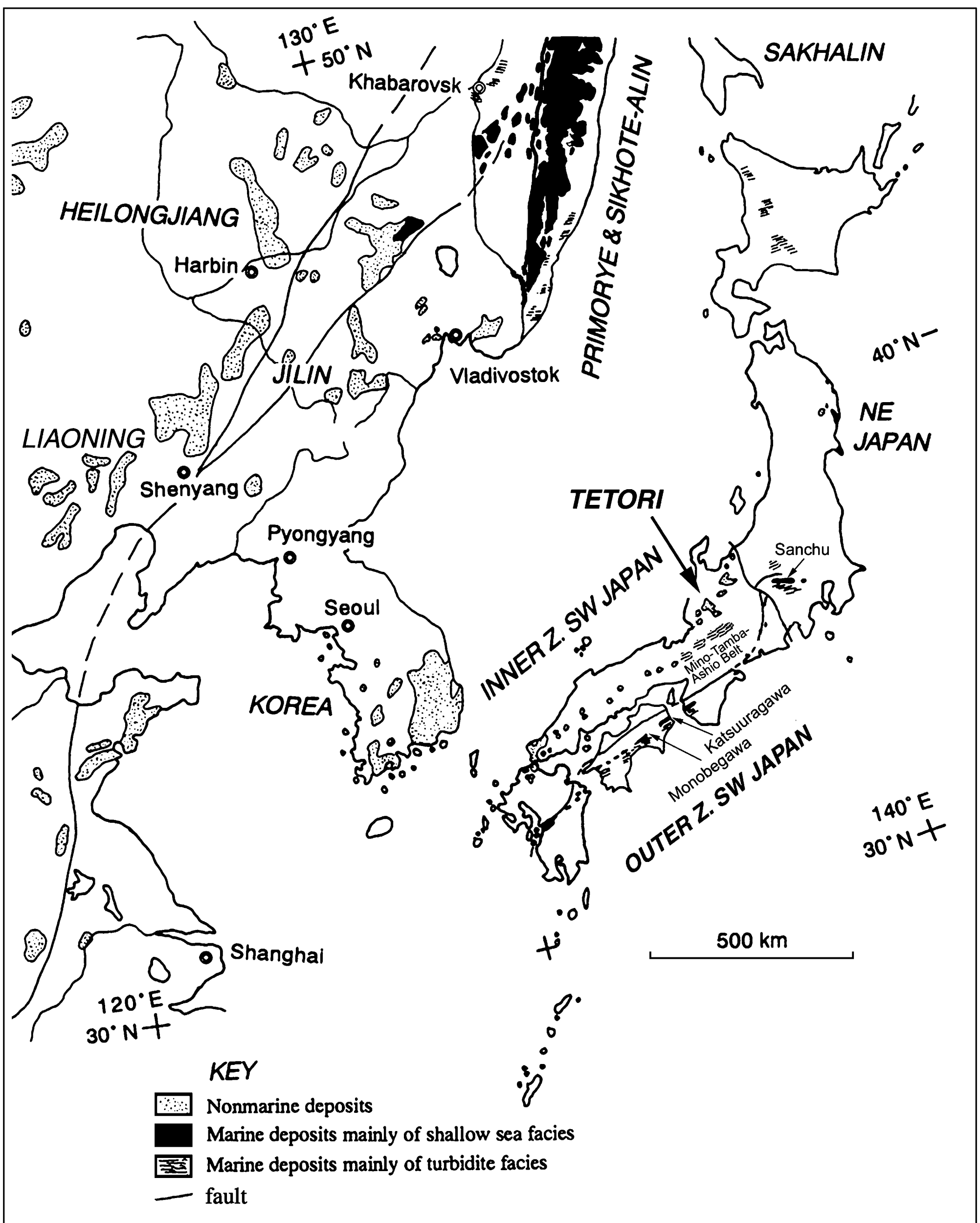

Fig. 1. Locations of Lower Cretaceous exposures in East Asia.

stratigraphic framework throughout the whole area. Furthermore, we describe characteristics of the zoo- and phyto-fossil assemblages and discuss the evolutionary significance of terrestrial paleoecosystems in the Tetori Group. We also evaluate nonmarine mollusks as chronological indices.

2. Geological setting, age, and stratigraphy of the Tetori Group

2.1. History of stratigraphic studies of the Tetori Group

The sedimentary successions of the Tetori Basin were originally defined as the Tetori Series in reference to Japanese Middle Jurassic strata by Yokoyama (1889). Later, Oishi (1933) gave the name Tetori Group for the successions and divided the sequence along the Itoshirogawa River in the Kuzuryugawa region into the Yambara Conglomerate, Izuki Formation, and Nochino Sandstone. The rock stratigraphic unit concept of Oishi (1933) was followed by Maeda (1950, 1951), and later Maeda (1952b, 1957a,b) divided the group into three subgroups named Kuzuryu, Itoshiro, and Akaiwa in ascending order. Still later, Maeda (1961) proposed many formation names for stratigraphic units in each area in each region. As a result, more than 40 formation names were used in three separate regions. Since Maeda (1961) proposed his stratigraphic divisions and geological maps, his scheme of group and subgroup level divisions has been followed, although new stratigraphic divisions were proposed by some stratigraphers (e.g., Kawai, 1961; Omura, 1973; Ishikawa Prefecture Board of Education, 1978).

To eliminate the use of different formation names for correlative units in the same region, Matsukawa et al. (2003a) redefined lithostratigraphic units of the Tetori Group and proposed unified definitions and nomenclature for these strata in the Mt. Hakusan region. They then presented a geologic map based on a coherent stratigraphic sequence throughout that region (Fig. 2). Matsukawa et al. (2003c) revised stratigraphic divisions at the formation level, and in the Kuzuryugawa region they formalized their stratigraphic definitions with the aid of geological mapping. They also demonstrated geological correlations of the Tetori Group between the Mt. Hakusan and Kuzuryugawa regions.

2.2. Stratigraphic relations and geological age

The Tetori Group sits on the Jurassic accretionary complex named the Mino Terrane, Hida Gneiss (160–410 Ma; Nakajima, 1997), and Unazuki Schist (200–230 Ma; Nakajima, 1997) (Sohma and Kunugiza, 1993). The basal contacts of the group with these basement rocks are defined by faults or unconformities. The Tetori Group is unconformably overlain by Maastrichtian nonmarine deposits and by younger volcanic rocks. Locally, the basal part of the group was intruded by Late Cretaceous and younger plutonic and volcanic rocks. The age of the group has been estimated as Bathonian to Albian on the basis of faunal characteristics (ammonites, bivalves, dinosaurs) and fission-track and K-Ar dating of some volcanic ash beds intercalated in the group (Matsukawa and Ido, 1993; Matsukawa et al., 2003a,c). In particular, the Kuwajima, Okurodani, and Izuki formations, which contain rich zoo- and phyto-assemblages, are regarded as the Valanginian to Barremian in age.

2.3. Brief note on the lithology of the Tetori Group

The Tetori Group is distributed in three separate regions, the Kuzuryugawa, Mt. Hakusan, and Jinzu regions. Both the Kuzuryugawa and Mt. Hakusan regions contain the main "type" sections of the group and bear rich zoo- and phyto-fossils. The Jinzu region, however, consists mainly of conglomerates and has few fossils. So, both the Kuzuryugawa and Mt. Hakusan regions are better than the Jinzu region for understanding environmental changes and paleoecosystem reconstruction based on zoo- and phyto-assemblage analyses.

2.4. Stratigraphy of the Tetori Group in the Kuzuryugawa region

In the Kuzuryugawa region, the Tetori Group can be divided into eight formations: the Shimoyama, Tochimochiyama, Kaizara, Yambarazaka, Yambara, Ashidani, Izuki, and Nochino formations, in ascending order (Figs. 3, 4).

The definitions, synonyms, type sections, stratigraphic relationships with underlying formations, distribution, thicknesses, and descriptions of lithology and stratigraphy of the Tochimochiyama, Izuki, and Nochino formations are given in Matsukawa et al. (2003c). Lithologic characteristics for all eight formations are briefly reviewed here.

2.4.1. Shimoyama Formation

The Shimoyama Formation consists of conglomerates. This formation was named by Maeda (1950) and was described as conglomerate-rich deposits.

2.4.2. Tochimochiyama Formation

The Tochimochiyama Formation is composed mainly of medium- to fine-grained arkosic sandstone.

2.4.3. Kaizara Formation (revised herein)

Definition. The formation (named by Maeda, 1950) consists primarily of black muddy sandstone rich in ammonites and marine bivalves.

Synonyms. Kaizara Formation of Maeda (1950), Kaizara Shale of Kawai et al. (1957), Middle Formation of the Kuzuryu Subgroup of Yamada et al. (1989), lower part of the Kaizara Formation of Matsukawa et al. (2003c).

Type section. Kaizara, Izumi village, Fukui Prefecture.

Distribution. Lower Itoshiro, Horadani, Taniyama, Suidani, Amagashiradani rivers.

Thickness. 320 m.

Lithology and stratigraphy. The formation consists of black muddy sandstone that overlies arkosic sandstone of the underlying Tochimochiyama Formation. The lithological change between the formations is abrupt.

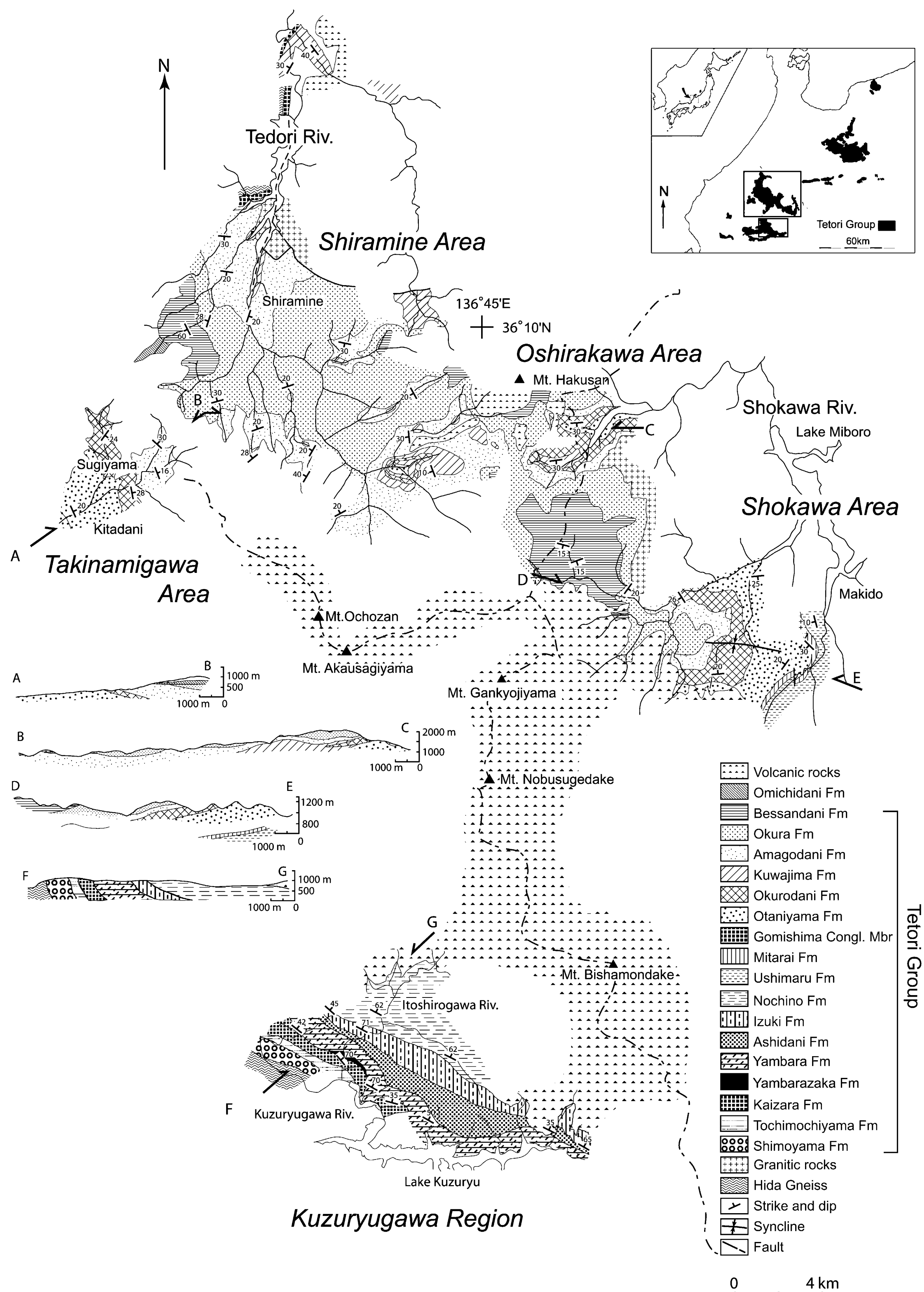

Fig. 2. Geological map and geological sections of the Tetori Group in both Kuzuryugawa and Mt. Hakusan region. Compiled from Matsukawa et al. (2003a,c).

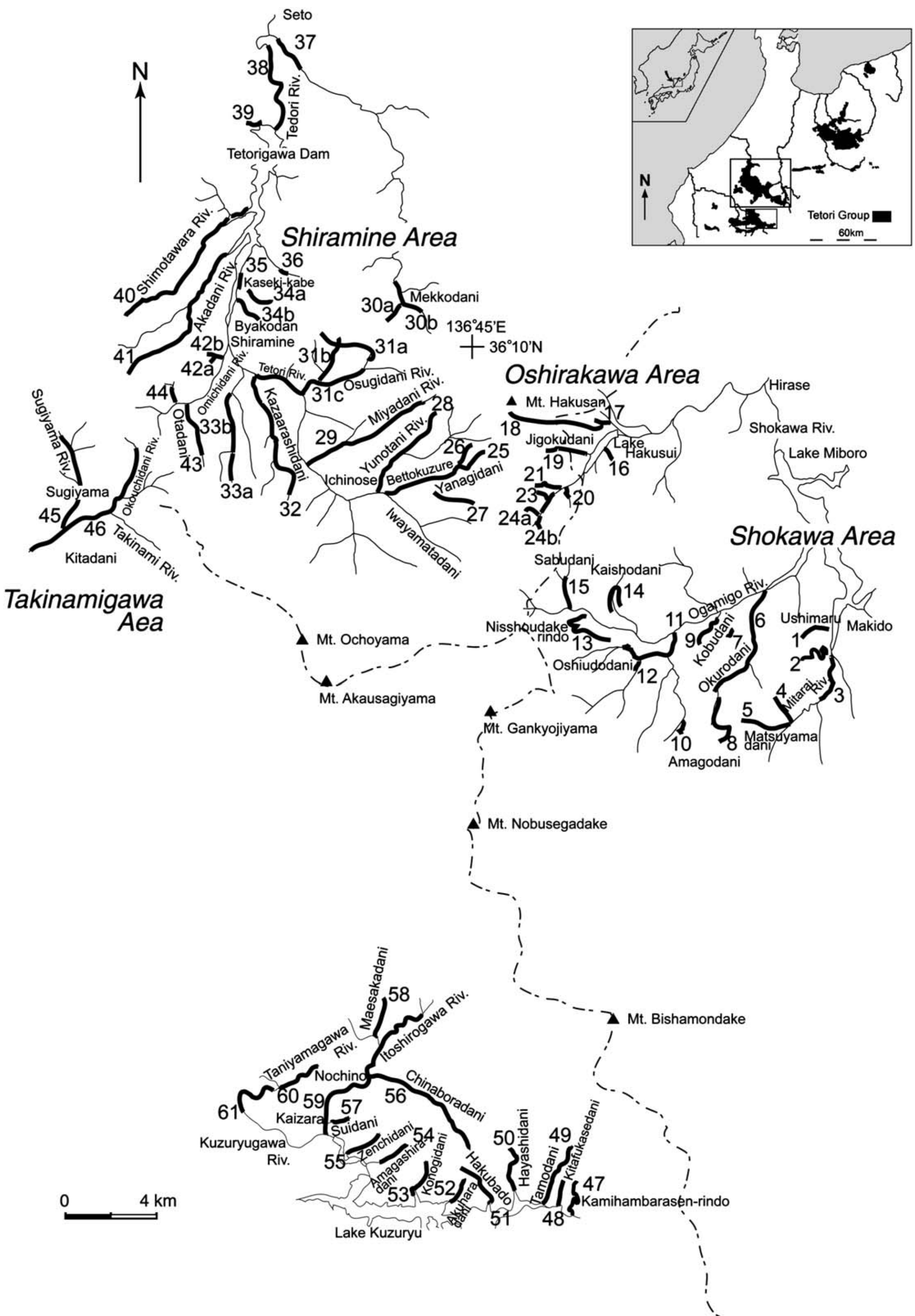

Fig. 3. Map showing locations of the routes along which columnar sections of the Tetori Group were measured in both Kuzuryugawa and Mt. Hakusan regions. Compiled from Matsukawa et al. (2003a,c).

Fossils. Ammonite and marine bivalve specimens are common. From the occurrence of specimens of *Neuqueniceras yokoyamai*, *Oxycerites* cf. *sulaensis*, and *Kranaosphinctes matsushimai*, the formation is assignable to the late Bathonian and early Callovian (Sato, 1962; Sato and Westerman, 1985).

2.4.4. Yambarazaka Formation (revised herein)

Definition. The formation consists of alternating beds of sandstone and mudstone. This formation was named by Maeda (1950) and was described as sandstone and mudstone deposits.

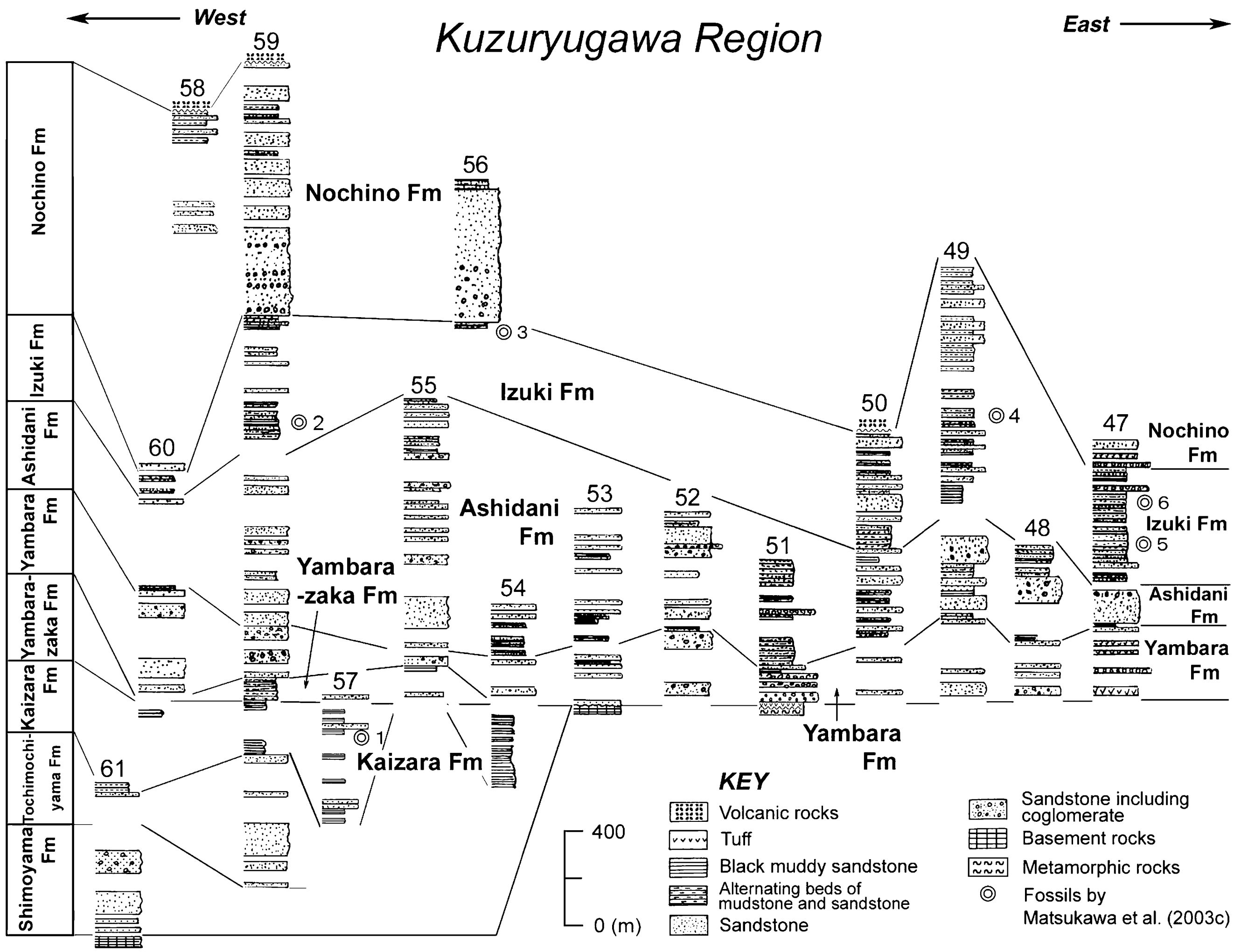

Fig. 4. Individual columnar sections of the Tetori Group in Kuzuryugawa region. Revised from Matsukawa et al. (2003c).

Synonyms. Yambarazaka Formation of Kawai et al. (1957), Upper Formation of Kuzuryu Subgroup of Yamada et al. (1989), upper part of the Kaizara Formation of Matsukawa et al. (2003c).

Type section. Kaizara, Izumi village, Fukui Prefecture.

Distribution. Lower Itoshiro, Suidani, and Zenchidani rivers.

Thickness. 120 m.

Lithology. The Formation is composed primarily of alternating beds of sandstone and mudstone that conformably overlies black muddy sandstone of the Kaizara Formation. The lithological change from the underlying Kaizara Formation is abrupt.

Fossils. The occurrence of specimens of *Kranaosphinctes matsushimai* suggests that the formation is correlative with the Oxfordian.

2.4.5. Yambara Formation (revised herein)

Definition. The formation (named by Maeda, 1950) consists of conglomerates and arkosic sandstone including pebble conglomerates.

Synonyms. Dosaiyama conglomerates member of Kawai et al. (1957), Lower Formation of the Itoshiro Subgroup of Yamada et al. (1989), lower part of the Yambara Formation of Matsukawa et al. (2003c).

Type section. Kaizara, Izumi village, Fukui Prefecture.

Distribution. The formation is distributed throughout the entire Kuzuryugawa region: lower Itoshiro, Taniyama, Zenchidani, upper Amagashiradani, Konogidani, Akuharadani, Hakubado, Hayashidani, Tamodani, Kitafukasedani, and Kamihambarasenrindo rivers.

Thickness. 240 m. The formation thins gradually to the east.

Lithology. The formation is made up of conglomerates at the type section that change laterally to sandstone including pebbles sized conglomerates. The conglomerates consist mainly of poorly sorted gravels including sandstone clasts up to 1 m in diameter.

2.4.6. Ashidani Formation (revised herein)

Definition. The formation (named by Maeda, 1950) is composed of medium-grained arkosic sandstone with sporadic pebble-sized gravels and thin alternating beds of sandstone and mudstone and includes coal seams.

Synonyms. Obuchi Formation of Maeda (1950), Lower Formation of the Itoshiro Subgroup of Yamada et al. (1989), main part of the Yambara Formation of Matsukawa et al. (2003c).

Type section. Yambara dam, Izumi village, Fukui Prefecture.

Distribution. The formation is distributed throughout the entire Kuzuryugawa region: lower Itoshiro, Taniyama, upper Amagashiradani, Konogidani, Akuharadani, Hakubado, Hayashidani, Tamodani, Kitafukasedani, and Kamihambarasenrindo rivers.

Thickness. 1200 m. The formation thins gradually to the east.

Lithology. The formation consists mainly of medium-grained arkosic sandstone at the type section and of alternating beds of sandstone, mudstone, and conglomerates in the eastern part.

2.4.7. Izuki Formation

The Izuki Formation includes alternating beds of sandstone and mudstone with common coal seams, brackish-water bivalves including corbiculoids, and marine pectinids and *Inoceramus maedae* (which Fujita et al., 1998, identified as *Inoceramus* cf. *maedae*). This formation was named by Oishi (1933), although he did not write the name in English characters. Kobayashi and Suzuki (1937) first named the Izuki Shale (in English) for alternating beds of sandstone and mudstone with corbiculoids. Maeda (1952b) used the name Itsuki Formation without giving a reason for this changed designation. Evidently, the formation name originates from the locality name Itsuki, but preferably the name should be the Izuki Formation as designated by Kobayashi and Suzuki (1937), based on nomenclatural priority. Recently, Matsukawa et al. (2003c) redefined the formation giving its stratigraphy, synonyms, type section, stratigraphic relationship with the underlying formation, distribution, thickness, and lithology.

2.4.8. Nochino Formation (revised herein)

Definition. The formation (named by Oishi, 1933) consists of medium- to coarse-grained arkosic sandstone with sporadic pebble-sized gravels and thin alternating beds of sandstone and mudstone.

Synonyms. Nochino conglomerate of Kawai et al. (1957), Chinaboradani Formation of Maeda (1957a), Akaiwa sandstone of Maeda (1961), Kitadani alternation of Maeda (1961), Nochino Formation of Matsukawa et al. (2003c).

Type section. Nochino, Izumi village, Fukui Prefecture.

Distribution. Itoshiro, Taniyama, Maesakadani, Chinaboradani and Kamihambarasenrindo Rivers.

Thickness. 1100 m.

Lithology and stratigraphy. The succession of the formation at the type section consists of medium to coarse-grained arkosic sandstone with sporadic pebble-sized gravels, massive arkosic sandstone and arkosic sandstone with thin alternating beds of sandstone and mudstone in ascending order. The basal part of the arkosic sandstone rests unconformably upon the underlying alternating beds of sandstone and mudstone of the Izuki Formation. The lithological change between the formations is abrupt and its boundary is distinct.

Fossils. Ornithopod tracks were reported from alternating beds of sandstone and mudstone in the lower part of the formation at Chinaboradani River (Kukihara et al., 2003).

2.5. Stratigraphy of the Tetori Group in the Mt. Hakusan region

In the Mt. Hakusan region, the Tetori Group is subdivided into eight formations: the Ushimaru, Mitarai, Otaniyama, Kuwajima, Okurodani, Amagodani, Okura, and Bessandani formations, in ascending order (Matsukawa et al., 2003a). Definition, synonyms, type sections, stratigraphic relationships with underlying formations, distribution, thicknesses, and descriptions of lithology and stratigraphy are given in Matsukawa et al. (2003a). Lithologic characteristics are briefly summarized here; see also Fig. 5.

2.5.1. Ushimaru Formation

The Ushimaru Formation consists of a lower black mudstone bearing brackish-water mollusks and an upper fine- to medium-grained sandstone. The formation is exposed in the eastern part of the region.

2.5.2. Mitarai Formation

The Mitarai Formation consists of monotonous black mudstone with cephalopods and marine bivalves and contains a thin tuff layer. This formation is only 50 m thick and is narrowly distributed in the extreme eastern part of the region. From the occurrence of specimens of the ammonites *Delphinella* cf. *obtusenodosa*, *Berriasella* sp., and others, the formation is considered Tithonian to Berriasian in age (Sato et al., 2003). The marine bivalve assemblage including *Inoceramus maedae* and *Chlamys mitaraiensis* can be compared with that from the Upper Jurassic to Lower Cretaceous in Spitsbergen and Siberia (Hayami, 1959, 1960).

2.5.3. Otaniyama Formation

The Otaniyama Formation consists primarily of arkosic sandstone, frequently intercalated in thin mudstone layers. In particular, thin layers of alternating sandstone and mudstone beds, muddy sandstone, and granule conglomerate are intercalated in the upper part of the formation in the eastern part of the region, and a conglomerate bed consisting of boulder- to granule-sized gravels, named the Gomishima Conglomerate Member, is distributed in the extreme western part of the region. Marine, brackish-water, and freshwater mollusks occur throughout the formation (Matsukawa and Nakada, 1999; Kumon and Umezawa, 2001).

2.5.4. Kuwajima Formation

The Kuwajima Formation is predominantly composed of alternating beds of mudstone and sandstone. This formation is mainly distributed in the western part of the region. Various kinds of fossils such as fishes, amphibians, reptiles, dinosaurs, mammals, bivalves, gastropods, insects, and terrestrial plants occur in the formation.

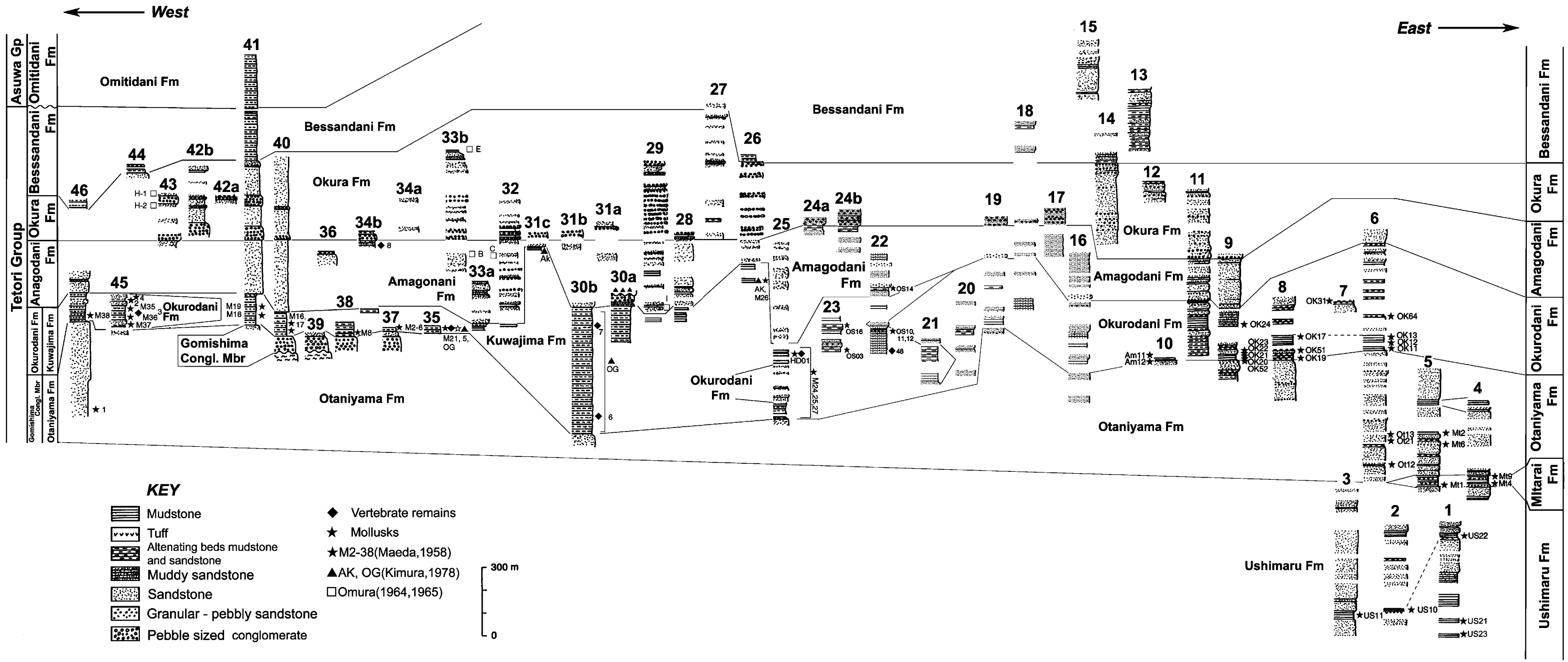

Fig. 5. Individual columnar sections of the Tetori Group in Mt. Hakusan region. Revised from Matsukawa et al. (2003a).

2.5.5. Okurodani Formation

The Okurodani Formation comprises alternating beds of mudstone and sandstone; fine-grained sandstone; muddy sandstone; and thin, black mudstone beds. Nonmarine mollusks and vertebrate remains, including dinosaurs, and terrestrial plants, are intercalated in the black mudstone and fine-grained sandstone beds.

The Okurodani and Kuwajima formations are present in both the eastern and western parts of the region. They are lateral equivalents of one another, differing in lithology.

2.5.6. Amagodani Formation

The Amagodani Formation consists primarily of coarse-grained arkosic sandstone and thin layers of conglomerate. The conglomerate beds consist of pebble- to granule-sized orthoquartzite gravels.

2.5.7. Okura Formation

The Okura Formation includes pebble- to boulder-sized gravels of conglomerate and arkosic coarse-grained sandstone. The formation is widely distributed in the entire region, although conglomerate beds change in thickness and clast size.

2.5.8. Bessandani Formation

The Bessandani Formation consists of alternating beds of sandstone and mudstone and coarse-grained arkosic sandstone. Schizaeaceous spores including *Cicatricosisporites* and unidentified sculptured spores occur in the mudstone beds.

3. Discussion of geological correlation among the three regions

3.1. What is the best tool for geological correlation between nonmarine formations in the Tetori Basin?

Although the Tetori Group is continuously exposed in the Mt. Hakusan region, which includes the main "type" section for the group, four different lithostratigraphic divisions have been proposed in each of the four areas within the region (Maeda, 1952a, 1958, 1961). However, a coherent correlation between these areas showing the accompanying lateral lithologic changes has not previously been demonstrated. Some stratigraphic divisions were carefully proposed following Maeda's studies, but until recently no one had constructed a coherent stratigraphy based on geological correlation throughout the entire Mt. Hakusan region (Table 1). Furthermore, biostratigraphic, and paleomagnetic studies have been proposed

Table 1
Different views on the stratigraphic sequence of the Tetori Group in Mt. region

Region	Shiramine						Oshirakawa			Shokawa	
Stratigraphic division	Nagao in Osishi (1933)	Maeda (1958)	Kawai (1961)	Omura (1965)	IBE (1978)	Matsukawa et al. (2003a)	Maeda (1958)	Matsukawa et al. (1999)	GDRC (1993)	Maeda (1952a)	Matsukawa & Nakada (1999)
		Kitadani alternation	Myogatani Fm	Myodani Fm	Myodani Fm	Bessandani Fm	Akaiwa sandstone	Bessandani Fm	Bessandani Fm	Bessandani Fm	Bessandani Fm
	Akaiwa sandstone	Akaiwa sandstone upper	Akaiwa Fm	Akaiwa Fm	Akaiwa Fm sandstone Mbr	Okura Fm	Okura conglomerate	Okura Fm		Okura Fm	Okura Fm
		Akaiwa sandstone lower			Akaiwa Fm Alternation Mbr	Amagodani Fm	Futamatadani alternation	Amagodani Fm	Amagodani Fm	Amagodani Fm	Amagodani Fm
	Kuwajima Fm	Kuwashima alternation Mbr	Oguchi Fm: Kuwajima alternation	Kuwajima Fm	Kuwajima Fm	Kuwajima / Okurodani Fm	Kuwashima alternation	Okurodani Fm	Okurodani Fm	Okurodani Fm	Okurodani Fm
	Gomishima conglomerate	Gomishima congl. Mbr	Oguchi Fm: Gomishima conglomerate	Gomijima Fm	Gomishima Fm	Otaniyama Fm	Kagidani sandstone	Otaniyama Fm	Otaniyama Fm	Otaniyama Fm	Otaniyama Fm
							Jigokudani shale		Jigokudani Fm		
						Gomishima congl. Mbr	Hidagoe sandstone and shale		Okurayama Fm		
										Mitarai Fm	Mitarai Fm
										Akahoke Fm	Ushimaru Fm
										Ushimaru Fm	

IBE: Ishikawa Board of Education

GDRC: Gifu Dinosaur Research Commission

Stratigraphic correlation is not implied. From Matsukawa et al. (2003a).

without re-examination of the stratigraphic framework (Kimura, 1961, 1978, 1980, 1987; Kimura and Sekido, 1976b, 1978; Azuma, 1991, 2003; Hirooka et al., 2002; Fujita, 2003; Yabe et al., 2003).

To resolve this problem, Matsukawa et al. (2003a) measured many individual columnar sections to establish lithostratigraphic correlations throughout the whole region. They divided the Tetori Group into eight lithostratigraphic units in the Shokawa area in the Mt. Hakusan region. This includes the complete stratigraphic sequence of the group in the region. Then they traced these units one by one in the Oshirakawa, Shiramine, and Takinamigawa areas. In particular, they used three main units: thick, predominantly conglomeratic and arkosic sandstone beds of the Okura Formation; underlying thick arkosic sandstone beds of the Amagodani Formation; and an overlying unit of thick sandstone beds and alternating beds of sandstone and mudstone in the Bessandani Formation. These key units are widely distributed throughout the Mt. Hakusan region. As a result, the Tetori Group in the Mt. Hakusan region can be divided into eight formations in ascending order: the Ushimaru, Mitarai, Otaniyama (including the Gomishima Conglomerate Member), Kuwajima/Okurodani, Amagodani, Okura, and Bessandani formations. Thus, the group was shown to consist of a coherent stratigraphic sequence throughout the whole region and the geological map was revised to reveal the correct distribution of nine lithostratigraphic units (Matsukawa et al., 2003a).

3.2. Is the stratigraphic unit ''subgroup'' useful as a geological correlation tool in the Tetori Group?

It has been proposed that the Tetori Group is divided into three subgroups, the Kuzuryu, Itoshiro, and Akaiwa subgroups (Maeda, 1958, 1961). Hitherto, regional formation names of the Tetori Group were given separately for sequences in each of the areas in the regions. Furthermore, some stratigraphic divisions at the formation level were proposed without careful geological correlation within the group. Subgroup nomenclature had been used for geological correlation between areas within the regions and between the regions by several authors (e.g., Kimura, 1978; Takeuchi and Takizawa, 1991; Chang and Park, 2003; Fujita, 2003; Yabe et al., 2003). Although this apparently is sometimes a useful tool for correlation at the subgroup level, this method is not always functional because Kawai (1961), Omura (1973), and Matsukawa et al. (2003a) used different criteria from those used for the subgroups of Maeda (1958, 1961). For instance, concerning the dinosaur-bearing Kitadani Formation, Maeda (1953, 1958, 1961), Azuma (1991), Azuma and Currie (2000), Kobayashi and Azuma (2003), and Tsukano (1969) placed it in the Akaiwa Subgroup, but Kawai (1961) classified the formation in the Itoshiro Subgroup. Matsukawa et al. (2003a) showed that the Kitadani Formation is a synonym of the Okurodani Formation, while Maeda (1961) assigned to the Itoshiro Subgroup. This shows that a valid classification of subgroups is required for any useful geological correlation in the Tetori Group and this, in turn, requires correct correlation of the formations within the subgroup, as shown by the Kitadani-Okurodani example.

Although lithological correlation should use formations as the fundamental lithologic unit, the subgroup correlation has not always been founded on lithology. Thus, the subgroup correlation leads more easily to mistakes than lithological correlation at the formation level. The proper designation and evaluation of subgroups is required if the subgroup is to be used for geological correlation. Until now geological correlation of the Tetori Group has been confused by inappropriate definitions of subgroups.

4. Correlation of the Tetori Group between Mt. Hakusan and Kuzuryugawa regions

Based on lithostratigraphic and biostratigraphic characteristics, formations of the Tetori Group in the Mt. Hakusan region can be correlated with those in the Kuzuryugawa region, as follows: (1) on the basis of ammonites, the succession from the Kaizara to Yambarazaka formations (Kuzuryugawa region) is assigned to Bathonian-Oxfordian through Callovian, and the Mitarai Formation (Mt. Hakusan region) is assigned to Tithonian–Berriasian; (2) transgressive facies are recognizable in the Izuki Formation (Kuzuryugawa region) and in the succession from the Ushimaru to Mitarai formations (Mt. Hakusan region); (3) both the Izuki Formation and the succession of the Ushimaru and Mitarai formations have a sequence of corbiculoid assemblages in their lower parts and a marine bivalve assemblage including *Inoceramus maedae* and pectinids in their upper parts; (4) thick arkosic sandstone facies predominate in the Nochino Formation (Kuzuryugawa region) and in the succession from Amagodani through Bessandani formations (Mt. Hakusan region); and (5) schizaeaceous spores including *Cicatricosisporites* and unidentified sculptured spores occur in both the Bessandani and Nochino formations. Therefore, the Izuki Formation is correlative with the Ushimaru and Mitarai formations, and the Nochino Formation is correlative with the Amagodani, Okura, and Bessandani formations (Fig. 6).

5. Paleoenvironment of the Tetori Group

Ito and Matsukawa (2002) determined the sedimentary depositional environments of the Tetori Group using facies analysis. The succession from the Shimoyama to Yambarazaka formations is the lower part of the Tetori Group. During the time of their deposition, the Japanese Islands were situated at the eastern margin of the Asian continent. Lower Cretaceous strata show a simple array of sedimentary facies and represent deposition in continental, back-arc, fore-arc, and trench settings (Stage 1 in Fig. 7). This setting is fundamentally the same in the Middle to Late Jurassic (Matsukawa et al., 1997, 1998). The Tetori Basin at that time was undergoing initial subsidence and incipient sedimentation caused by subduction of the Izanagi plate beneath the Eurasia plate along the eastern margin of the Asian continent (e.g., Isozaki and Maruyama, 1991; Maruyama et al., 1997; Matsukawa et al.,

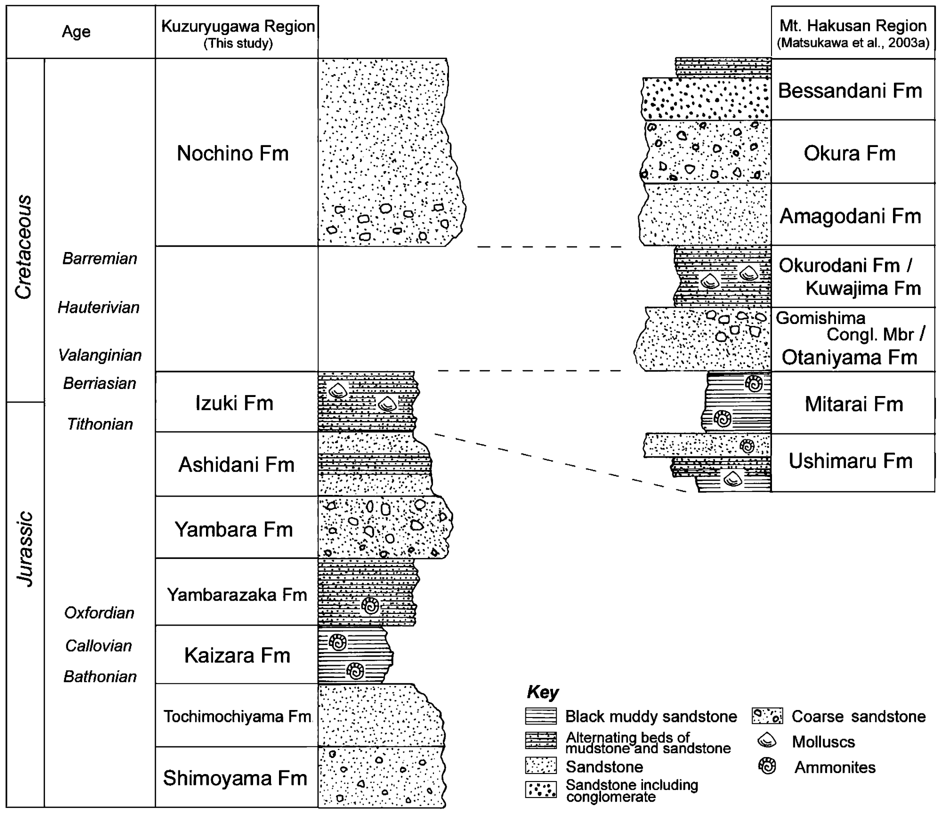

Fig. 6. Geological correlation of the Tetori Group between the Mt. Hakusan and Kuzuryugawa regions. Revised from Matsukawa et al. (2003c).

1997, 1998), although the subsidence mechanisms in an intra-arc setting are still controversial (e.g., Smith and Landis, 1995). As a result, the Tetori Basin faced the paleo-Pacific, and a land area existed on the western and southern flanks of the basin as a part of the eastern margin of the Asian continent. This interpretation is supported by the development of alluvial fan deposits and overlying gravelly braided-river deposits with evidence of northeastern current directions, represented by successions from the Shimoyama to Tochimochiyama formations in the Kuzuryugawa region, and by the forming of inner shelf, delta front, shoreface, and delta plain environments in the succession from the Kaizara to Yambarazaka formations (Ito and Matsukawa, 2002). This means that the succession from the Shimoyama to Yambarazaka formations was a transgressive phase. Based on both Boreal and Tethyan Callovian to Oxfordian ammonites (Sato, 1962), the region was influenced by currents from both high latitude and equatorial regions (Matsukawa et al., 1997, 1998).

The Yambara Formation (composed of alluvial fan deposits) shows regression, and the successions from the Ashidani to Izuki formations in the Kuzuryugawa region (consisting of sandy braided-river, lacustrine delta, and delta plain deposits) and the Ushimaru and Mitarai formations in the Mt. Hakusan region (consisting of estuary, bay-head delta, shoreface, and inner shelf deposits) indicate a second transgression (Stage 2 in Fig. 7). From the occurrence of three molluscan assemblages and the sequence of occurrence of nonmarine bivalves including *Myrene* (*Mesocorbicula*) *tetoriensis* and marine pectinid bivalves and *Inoceramus maedae*, the transgressive phase is recognizable in the type section of the Izuki Formation and in its eastern outcrops (Matsukawa et al., 2003c). This concurs with the sequence of occurrence of nonmarine molluscan assemblages and ammonites in the Ushimaru and Mitarai formations. The succession from the Otaniyama (including the Gomishima Conglomerate Member) to the Kuwajima/Okurodani formations is continuously recognizable in the Mt. Hakusan region, but there is a barren interval with unconformable relationship in their correlative formations in the Kuzuryugawa region. The northern distribution of the Tetori Group in the Mt. Hakusan region indicates an expansion and northward shifting of the basin and an uplift in the Kuzuryugawa region. This was interpreted as caused by the duplication of Jurassic to early Early Cretaceous accretionary complexes and accompanying strike-slip movement (Matsukawa et al., 1997, 1998). The duplication led to eastward shifting of development of the fore-arc basins along a new trench, and also caused uplift of the former fore-arc basin and changed it to intra-arc basin. During this time, the Tetori Basin was interpreted as changing into an intra-arc basin (Matsukawa et al., 1997, 1998). Northward, westward, and eastward paleocurrents in deltaic and alluvial fan deposits and overlying gravelly and sandy braided-river deposits suggest a hinterland on the southern, western, and eastern flanks of the basin (Ito and Matsukawa, 2002). The conglomerates, composed of Permo-Triassic radiolarian chert clasts originated from the Mino-Tamba-Ashio Belt in the uppermost part of the Otaniyama Formation; they also indicate a probable uplift of

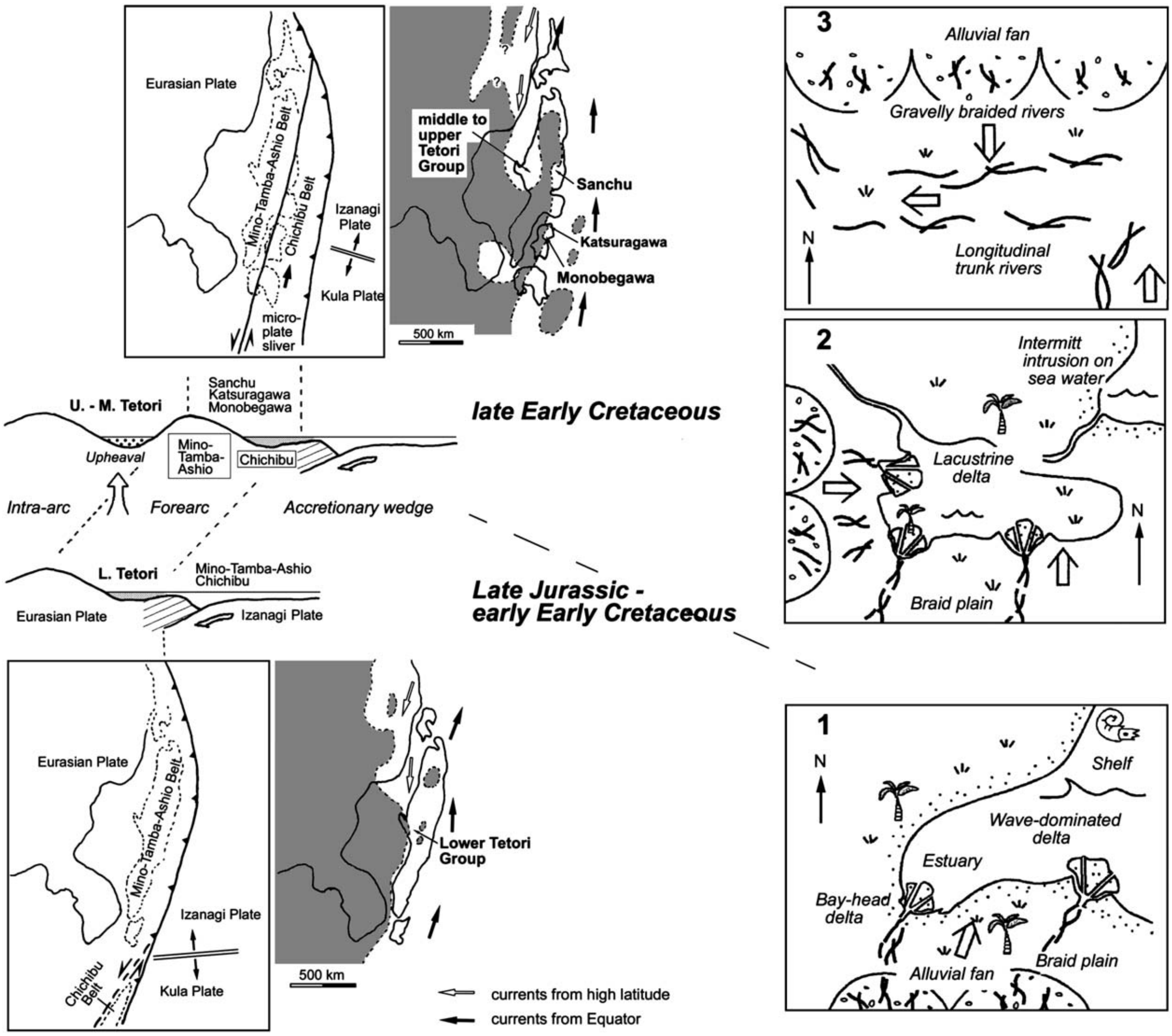

Fig. 7. Geological basin developments in East Asia during depositional time of the Tetori Group (left) and cartoon of deposition environments of the Tetori Group (right). Revised from Matsukawa et al. (1998) and Ito and Matsukawa (2002).

the eastern hinterland of the Tetori Basin (Matsukawa and Takahashi, 1999).

The successions from the Okura to Bessandani formations in the Mt. Hakusan region and from the Nochino Formation in the Kuzuryu region are characterized by alluvial fan to gravelly and sandy braided-river deposits (Stage 3 in Fig. 7). The Tetori Basin was interpreted as being filled with proximal sediments eroded from the Okura and Nochino formations, revealing southward and northward paleocurrent directions, and also distal sediments eroded from the Bessandani Formation with westward paleocurrent indicators (Matsukawa and Nakada, 1999; Ito and Matsukawa, 2002).

6. Characteristics of the biota

Various kinds of fossils such as fish, amphibians, reptiles, dinosaurs, mammals, bivalves, gastropods, insects, ostracodes, conchostracans, and terrestrial plants occur in the Tetori Group. This is one of the richest Early Cretaceous terrestrial biotas in the world.

6.1. Stratigraphic horizons of zoo- and phyto-fossil assemblages

Based on geological correlation between four areas in the Mt. Hakusan region, Matsukawa et al. (2003b) discussed and evaluated zoo- and phyto-fossil assemblages as chronological and ecological indices placed in a geologically meaningful framework. As a result, terrestrial vertebrates and freshwater bivalves are seen to occur mainly in the Kuwajima and Okurodani formations, deposited in flood-plain and lacustrine environments. Similarly, the rich terrestrial plant fossils also are mostly found in the Kuwajima and Okurodani formations. The very limited occurrence of these fossils in other fluvial formations suggests that these occurrences are controlled by environmental and/or preservational factors.

In this section, we discuss and evaluate zoo- and phytofossil assemblages (Fig. 8) as chronological and ecological indices in both the Mt. Hakusan and Kuzuryugawa regions, and we show the evolutionary significance of terrestrial paleoecosystems in the Tetori Group.

Fig. 8 shows fossil localities including reported zoo- and phyto-assemblages. We can locate these fossil localities in reference to the formations correlated by Matsukawa et al. (2003a,c); see Fig. 9. All zoo-assemblages reported by previous studies came from the Ushimaru to Okura formations as designated by Matsukawa et al. (2003a) in the Mt. Hakusan region, and also from the Tochimochiyama to Nochino formations as designated by Matsukawa et al. (2003c) in the Kuzuryugawa region. The successions from the Ushimaru to Okura formations and from the Shimoyama to Nochino formations mainly indicate shallow marine to deltaic and flood-plain environments. Zoo-assemblages originated in these shallow marine, deltaic, and flood-plain environments, not in high-energy fluvial-channel deposits. However, phyto-assemblages are found in all formations in the Mt. Hakusan region. Thus, it appears that only leaves having hard and thick tissues had a chance to be buried in sandstone deposits representing high energy-flow environments.

6.2. Usefulness of nonmarine molluscan assemblages as ecological indicators

Freshwater and brackish-water bivalves occur at more than 30 horizons in the Tetori Group. Matsukawa and Ido (1993) classified five assemblages of nonmarine bivalves from these strata as follows: (1) Ostreidae gen. et sp. indet.–*Myrene* (*Mesocorbicula*) *tetoriensis* Assemblage, (2) *Myrene* (*Mesocorbicula*) *tetoriensis* Assemblage, (3) *Tetoria* (*T.*) *yokoyamai* Assemblage, (4) *Sphaerium* sp. Assemblage, and (5) *Plicatounio* (*P.*) *naktongensis*–*Trigonioides* (*Wakinoa*) *tetoriensis* Assemblage. They showed that these assemblages reflect certain grades of environments from brackish- to freshwater, and the species composition of an assemblage varies with salinity. Based on comparison with recent allied species and their assemblage occurrences in many areas, Matsukawa and Nakada (1999) indicated presumed salinity ranges for these species, using the Venice system (Oertli, 1964): e.g., Ostreidae gen. et sp. indet. was mesohaline and brachyhaline, *Myrene* (*Mesocorbicula*) *tetoriensis* was oligohaline and mesohaline, and *Unio*? *ogamigoensis* and *Viviparus onogoensis* were freshwater and oligohaline. They recognized that the Ushimaru Formation, during transgression, reflects more repeated environmental changes than the succession of the Otaniyama to Okurodani formations in the Mt. Hakusan region during regression (Fig. 10). Thus, we see repetition of numerous minor cycles of transgression and regression in the transgression phase, but smooth environmental changes in the regression phase.

In the Izuki Formation of the Kuzuryugawa region, four assemblages, excluding the *Plicatounio* (*P.*) *naktongensis*–*Trigonioides* (*Wakinoa*) *tetoriensis* Assemblage, are also recognizable, and the assemblage changes from the lower to upper horizons show fluvial mouth bar to lacustrine deposits (Matsukawa and Ito, 1995). This is consistent with the stratigraphic assemblage changes indicated by the occurrences of the *Sphaerium* sp. Assemblage to the Ostreidae gen. et sp. indet.–*Myrene* (*Mesocorbicula*) *tetoriensis* Assemblage through the *Tetoria* (*T.*) *yokoyamai* Assemblage and the *Myrene* (*Mesocorbicula*) *tetoriensis* Assemblage.

Although these assemblages are useful for environmental analyses, they have only been recognized in the Tetori Group. During the time of deposition of the upper part of the Tetori Group, the basin is interpreted to be uplifted, with the gulf mouth of the basin moved northward in the Primorye and Sikhote-Alin areas of Russian Far East (Matsukawa et al., 1997, 1998). Thus, these nonmarine bivalve assemblages were expected to move into the Russian Far East, but different bivalve assemblages occupied the region instead (Matsukawa et al., 1997).

Plicatounio (*P.*) *naktongensis* and *Nagdongia soni*, which are species of the *Plicatounio* (*P.*) *naktongensis*–*Trigonioides* (*Wakinoa*) *tetoriensis* Assemblage, are also found in the flood-plain deposits of the Asian continent. *Plicatounio* (*P.*) *naktongensis* is reported from the Wakino Subgroup, Japan; the Yeonghuadon and Hasandong formations in Korea; the Xiachengzhi Formation of Heilongjiang in northeastern China; the Zhoujiawan Formation of Ganzu in northwestern China; the Dongjian Formation of Hulan in central China; the Matoushan, Mahgang and Nanxin formations of western Yunnan in southern China; and the Jiaguan Formation of Sichuan in southwestern China (Sha Jingeng, pers. comm. 2003). Although the classification of *Nagdongia* as a junior synonym of the genus *Nakamuranaia* is still controversial (e.g., Guo, 1986; Tamura, 1990), *Nagdongia soni* is reported from the Yeonghuadon and Hasandong formations in Korea (Yang, 1975) and *Nakamuranaia chingshanensis* occurs in the Chingshan Formation. However, both *Trigonioides* (*Wakinoa*) *tetoriensis* and *Nippononaia tetoriensis* of the *Plicatounio* (*P.*) *naktongensis*–*Trigonioides* (*Wakinoa*) *tetoriensis* assemblages are only reported from the Tetori Group. *Nippononaia ryosekiana* of this assemblage is also recorded in the Sebayashi Formation, Japan (Hayami and Ichikawa, 1965; Matsukawa, 1977). This means that *Plicatounio* (*P.*) *naktongensis* and *Nagdongia soni* had high adaptability, but *Trigonioides* (*Wakinoa*) *tetoriensis*, *Nippononaia tetoriensis*, and *N. ryosekiana* were not as adaptable to certain environments. This is comparable to Holocene nonmarine bivalves including unionids and corbiculoids, which are distributed only where optimum conditions prevail because elsewhere chemical conditions of lakes, ponds, and rivers are too variable.

6.3. Vertebrate assemblages

Vertebrate remains including bones, teeth, egg shells, and tracks are reported from localities 5–8 and HD01 in the Shiramine area; locality 3 in the Takinamigawa area; localities 13 and 48 in the Oshirakawa area; localities OK31 and 34 in the Shokawa area; and localities T-10–T-14, T-I1, T-I2,

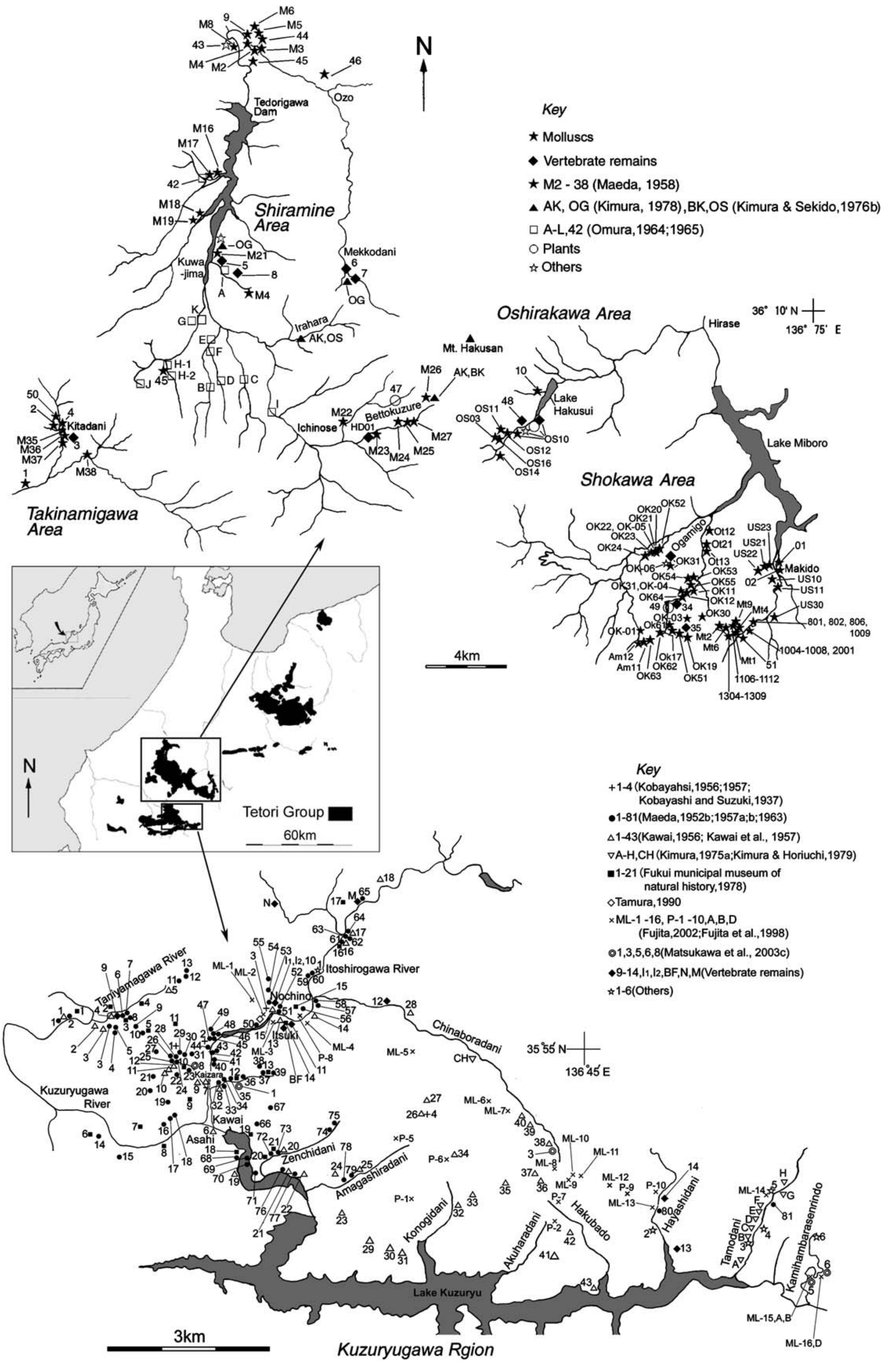

Fig. 8. Map showing all reported fossil localities in the Tetori Group.

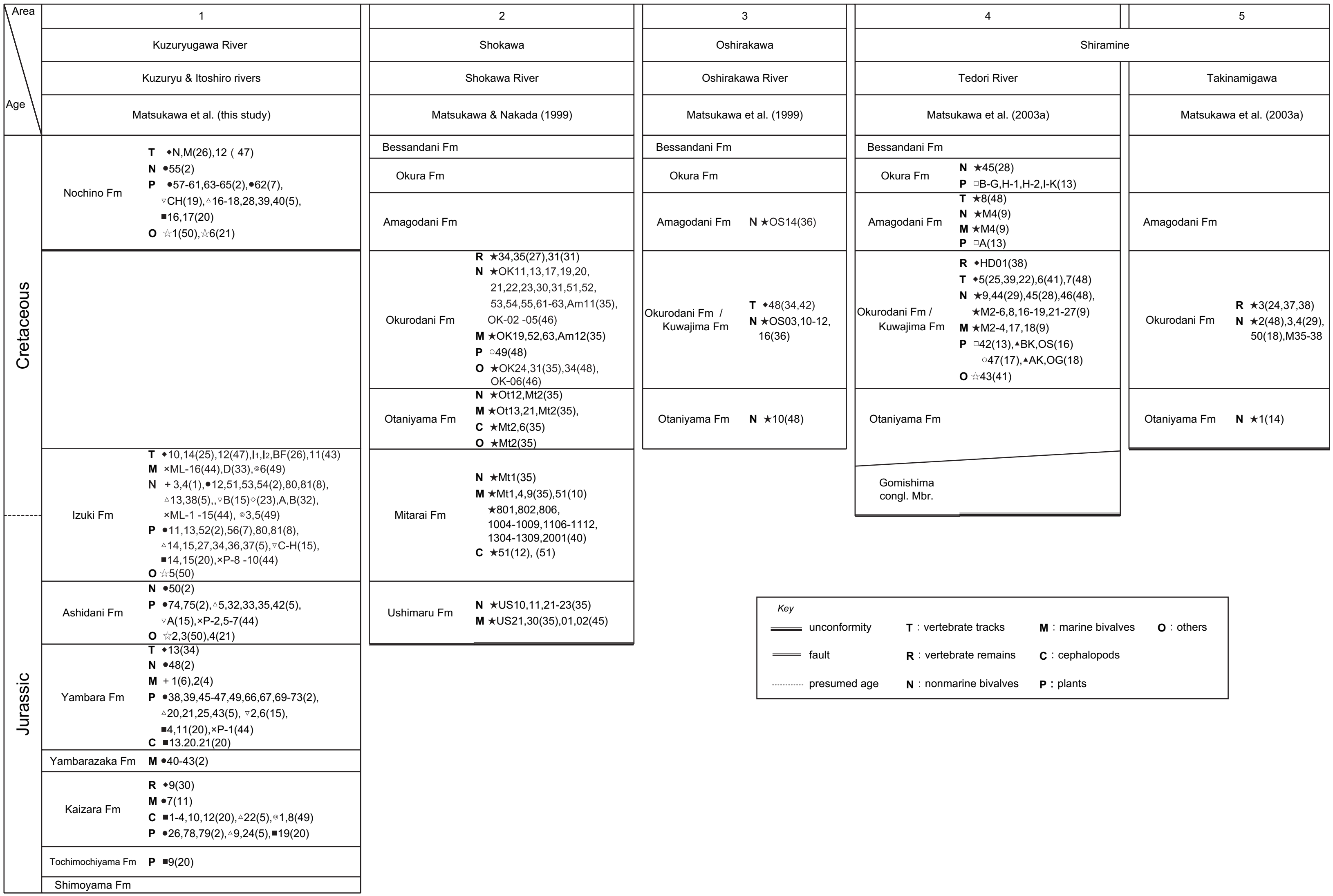

Fig. 9. Evaluation of stratigraphical occurrence of reported fossils based on our stratigraphic scheme. 1, Kuzuryugawa region. 2−5, Mt. Hakusan region (references: (1) Kobayashi and Suzuki, 1937; (2) Maeda, 1952b; (3) Kawai, 1956; (4) Kobayashi, 1956; (5) Kawai et al., 1957; (6) Kobayashi, 1957; (7) Maeda, 1957a; (8) Maeda, 1957b; (9) Maeda, 1958; (10) Hayami, 1959; (11) Maeda, 1963; (12) Sato and Kanie, 1963; (13) Omura, 1964, 1965; (14) Tsukano, 1969; (15) Kimura, 1975a; (16) Kimura and Sekido, 1976a; (17) Ishikawa Prefecture Board of Education, 1978; (18) Kimura, 1978; (19) Kimura and Horiuchi, 1979; (20) Fukui municipal museum of natural history, 1978; (21) Saida, 1987; (22) Manabe et al., 1989; (23) Tamura, 1990; (24) Azuma, 1991; (25) Azuma and Takeyama, 1991; (26) Azuma et al., 1992; (27) Gifu Dinosaur Research Committee, 1993; (28) Isaji, 1993; (29) Matsukawa and Ido, 1993; (30) Yasuno, 1994; (31) Cook et al., 1998; (32) Fujita et al., 1998; (33) Lockley and Matsukawa, 1998; (34) Manabe, 1999; (35) Matsukawa and Nakada, 1999; (36) Matsukawa et al., 1999; (37) Azuma and Currie, 2000; (38) Hirayama, 2000; (39) Shiramine Village Board of Education, 2000; (40) Komatsu et al., 2001; (41) Matsuoka et al., 2001; (42) Shikano et al., 2001; (43) Azuma et al., 2002; (44) Fujita, 2002; (45) Komatsu et al., 2002; (46) Komatsu et al., 2003; (47) Kukihara et al., 2003; (48) Matsukawa et al., 2003b; (49) Matsukawa et al., 2003c; (50) Umetsu and Matsuoka, 2003; (51) Sato et al., 2003; consultations: (a) Sato, 1962; (b) Fukui municipal museum of natural history, 1991; (c) Hirayama, 2002; (d) Yabumoto, 2002).

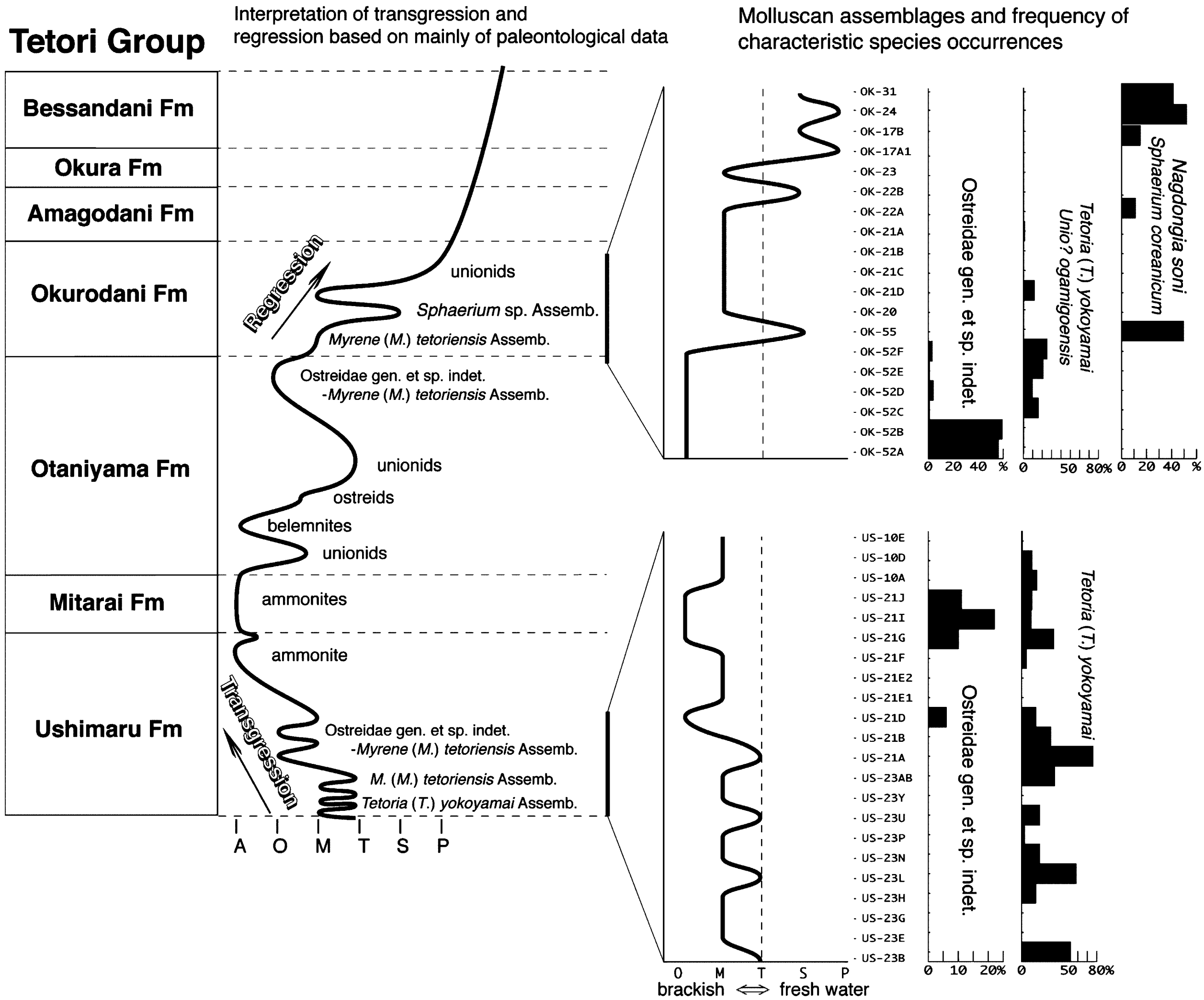

Fig. 10. Environmental changes based on paleontological interpretation of the Tetori Group in Mt. Hakusan region. A, Ammonites; O, Ostreidae gen. et sp. indet.—*Myrene* (*Mesocorbicula*) *tetoriensis* Assemblage; M, *Myrene* (*Mesocorbicula*) *tetoriensis* Assemblage; T, *Tetoria* (*Tetoria*) *yokoyamai* Assemblage; S, *Sphaerium* sp. Assemblage; P, *Plicatounio* (*Plicatounio*) *naktongensis*—*Trigonioides* (*Wakinoa*) *tetoriensis* Assemblage. Revised from Matsukawa and Nakada (1999).

T-BF, T-N, T-M in the headwaters of the Kuzuryugawa region (Figs. 8, 9) (Manabe et al., 1989; Azuma, 1991; Azuma and Takeyama, 1991; Azuma et al., 1992; Gifu Dinosaur Research Committee, 1993; Matsukawa and Obata, 1994; Cook et al., 1998; Evans and Manabe, 1999; Manabe, 1999; Shiramine Village Board of Education, 2000; Azuma, 2003; Kukihara et al., 2003). They occur in the Kuwajima/Okurodani formations, which represent lateral facies equivalents (Fig. 9). Thus, the Shiramine Dinosaur and Katsuyama Dinosaur Faunas proposed by Azuma (1991) should be named merely as a single Tetori Dinosaur Fauna (Matsukawa et al., 2003b). They do not represent two faunas on the basis of different stratigraphic settings as proposed by Azuma (1991). Slightly different faunal compositions within the Tetori Dinosaur Fauna probably reflect different habitats of flood plains and delta plains with rivers and lakes (Matsukawa et al., 2003b), and may also represent local differences in preservation patterns.

Terrestrial turtles are recorded from localities OK31 and OK34 in the Shokawa area; from locality 3 in the Takinamigawa area; and localities 5–7 and HD01 in the Shiramine area (Figs. 8, 9) (Hirayama, 2000). They belong to the Kuwajima and Okurodani formations. Hirayama (2002) reported the occurrence of terrestrial turtles at a locality in the Okura Formation in the Shiramine area.

Marine and freshwater fish fossils are also reported from the Kuwajima and Okurodani formations (Yabumoto, 2000, 2002). They belong to types known in both marine and freshwater habitats since the time of the middle to Late Jurassic Kaizara Formation (Yasuno, 1994) (Figs. 8, 9).

Dinosaur tracks occur in the Okurodani, Kuwajima, and Amagodani formations in the Oshirakawa, Shiramine, and Takinamigawa areas and in the Izuki and Nochino formations in the Kuzuryugawa region (Matsukawa et al., 2003c). Some ichnotaxa from the Tetori Group are similar to ichnotaxa from the Cretaceous deposits in Korea and northeastern China. They are characterized by ornithopod- and gracile-toed theropod-dominated communities from fluvio-lacustrine environments. This supports ichnofaunas in both areas belonging to the same ichnofacies and possibly to the same paleogeographic province (Matsukawa et al., 1995, 1997).

Diverse occurrences of vertebrates are recognizable. Terrestrial vertebrates occur only in mudstone and alternating beds of sandstone and mudstone from flood-plain environments, but aquatic vertebrates came from both flood-plain deposits and fluvial-channel deposits. This probably reflects both transportation effects and habitat preference.

6.4. Plant assemblages

Various rich plant fossil assemblages occur in the Tetori Group. Hitherto, Yokoyama (1889), Oishi (1933), Maeda (1952a,b, 1957a,b), Kawai (1956), Kawai et al. (1957), Kimura (1958a,b, 1959, 1961, 1975a,b, 1978, 1979, 1980, 1987), Kimura and Sekido (1961, 1965, 1966, 1967, 1972a,b, 1974, 1975, 1976a,b, 1978), Omura (1964, 1965), Kimura and Horiuchi (1979), and Fukui Municipal Museum of Natural History (1978) have reported plant fossil localities in the Mt. Hakusan and Kuzuryugawa regions. These localities in the Mt. Hakusan region occur in the Kuwajima and Okurodani formations, except for the locality of Yunotani in Oishi (1933), which is in the Amagodani Formation (Matsukawa et al., 2003c). Thirteen fossil localities were reported by Omura (1964, 1965). Two localities (A and 42) among the 13 are from the Kuwajima Formation, three localities (B, C and I) are in the Amagodani Formation, and another eight (D, E, F, G, H-1, H-2, J and K) are in the Okura Formation (Figs. 5, 9). Thus, the plant fossil localities named Ozo, Mekkodani, Kuwashima (=Kuwajima), Okamigo, Bettokuzure, and Irahara described by Kimura (1961, 1975a,b, 1978, 1980, 1987) and Kimura and Sekido (1965, 1966, 1972a,b, 1976a,b, 1978) are in the Kuwajima and Okurodani formations (Figs. 5, 8, 9) (Matsukawa et al., 2003b). However, plant fossil localities in the Kuzuryugawa region are in the Tochimochiyama through Nochino formations.

The Tetori Flora was previously divided into four components: the Kuzuryu, Oguchi, Akaiwa, and Tamodani floras, based on the stratigraphic differences (Kimura, 1975a). Exact localities for plant assemblages of the Kuzuryu Flora have not been recorded in some cases, and the composition is made up of a small number of species. The occurrences in both the Oguchi and Akaiwa floras reported in a series of Kimura's papers are from the Kuwajima Formation and its equivalent the Okurodani Formation. Although seven localities are reported as the Tamodani Flora by Kimura (1975a), one locality (A) is in the Ashidani Formation, and six localities (C-H) are in the Izuki Formation. Furthermore, plant specimens from the Chinaboradani Formation reported as the Tamodani Flora are in the Nochino Formation (Figs. 8, 9). Thus, the terms Oguchi, Akaiwa, and Tamodani floras are invalid classifications based on false assumptions of stratigraphic differences, and can be abandoned in favor of the term the Tetori Flora (Matsukawa et al., 2003b,c). There are only slightly different specific compositions in the assemblages named as the Oguchi, Akaiwa, and Tamodani floras. This probably reflects local vegetation in the Tetori Basin (Matsukawa et al., 2003b), or local preservational factors.

Yabe et al. (2003) followed Kimura's floral classification and discussed climatic changes based on the Tetori Flora. They considered plant fossil dates and differentiated: (1) the Kuzuryugawa region with the Izuki Formation (Kimura, 1975a; Kimura and Sekido, 1976b) and the Chinaboradani Formation (Kimura, 1975a; Kimura and Horiuchi, 1979); (2) the Shokawa area in the Mt. Hakusan region with the Okurodani Formation (Yokoyama, 1889; Oishi, 1940; Kimura, 1978; Kunimitsu and Nakashima, 1987) and the Amagodani Formation of Kunimitsu and Nakashima (1987), and their probable Bessandani Formation; (3) the Shiramine area in the Mt. Hakusan region with the Kuwajima Formation (Kimura, 1961, 1975a; Matsuo and Omura, 1968; Kimura, 1978) and the Akaiwa Formation of Kimura and Sekido (1976b, 1978), and their Kitadani Formation; and (4) the Takinamigawa area in the Mt. Hakusan region with the Kitadani Formation (Yabe et al., 2003). Although they did not show the fossil localities on their map, we can place their localities on our stratigraphic columns based on their references (Figs. 8, 9). Thus, the Chinaboradani Formation referred to by Maeda (1952b, 1957a,b) is a synonym of the Nochino Formation; the Okurodani, Amagodani, and Bessandani formations of Kumon and Kano (1991) are in the same succession as the Okurodani to Amagodani formations and the Bessandani Formation; the Kuwajima Formation of Maeda (1958, 1961) is either the Kuwajima or Okurodani Formation; the Akaiwa and Kitadani formations in the Shiramine area (Maeda, 1958, 1961) are synonyms of the succession from the Amagodani to Okura formations; the Kitadani Formation in the Takinamigawa area (Maeda, 1961) is a synonym of the Okurodani Formation. Hence, their fossil localities can be classified in the Ashidani, Izuki, and Nochino formations in the Kuzuryugawa region and in the Kuwajima Formation and its equivalents the Okurodani Formation, and the Amagodani, Okura, and Bessandani formations in the Mt. Hakusan region. Based on Kimura (1975a,b, 1978) and Kimura and Horiuchi (1979), the Kuwajima Formation and its equivalent the Okurodani Formation bear 115 species and is the richest assemblage in the Tetori Flora, and the Izuki and Nochino formations have 22 and nine species, respectively. Although certain four and one species from the Izuki and Nochino Formations, respectively, are not common to an assemblage of the Kuwajima Formation, they are included in assemblages of Siberia and Arctic regions. This means that plant assemblages from the Izuki, Kuwajima, Okurodani, and Noichino formations have the same composition as the Tetori Flora, which is similar to floras in Siberia.

Three terrestrial floras are recognized during late Mesozoic time in East Asia (Kimura and Hirata, 1975; Kimura, 1984, 1987): (1) the Tetori-type flora, which is characterized by dominant osmundaceous and dicksoniaceous ferns, bennettitaleans such as *Otozamites*, *Neozamites*, *Tetoria*, ginkgoaleans, czekanowskialeans, several kinds of *Podozamites*, and conifers with needle-like leaves; (2) the Ryoseki-type flora, which is characterized by a predominance of gleicheniaceous and matoniaceous ferns, bennettitaleans such as *Zamites* and *Ptilophyllum*, small-sized *Nilssonia* leaves, and conifers with scale-like leaves; and (3) the Mixed-type flora, which is distinguished from both Tetori-type and Ryoseki type floras. They are interpreted as being a distributed mix of southern Ryoseki-type flora, northern Tetori-type flora, and their intermediate Mixed-type flora (Kimura, 1987; Ohana and Kimura, 1995a,b; Kimura et al., 1996). The Tetori-type flora is similar to floras in Siberia, and the Ryoseki-type flora is similar to those in Indo-European paleofloristic areas (Kimura, 1979, 1980, 1984). The difference between the two floras has been interpreted as the result of geographic separation of land with different climates during the Late Jurassic and Early Cretaceous in Japan. Both floras occupied areas that were far apart in comparison with their present geographic positions. The Tetori-type flora was influenced by a temperate and moderately humid climate, whereas the Ryoseki-type indicates a subtropical or tropical and arid climate (Kimura, 1979, 1980, 1987). Ohana and Kimura (1995a,b) and Kimura et al. (1996) indicated that the Mixed-type flora came into existence by the northward invasion of the Ryoseki-type elements. This is interpreted as being caused by the predominance of warm, northward-moving currents from the Equator during the Hauterivian and Barremian transgression (Ito and Matsukawa, 2003). Some plants characteristic of the Ryoseki-type flora are mixed with Tetori-type floristic assemblages in the Izuki Formation (=Tamodani and Chinaboradani formations; Kimura, pers. comm. 1991, in Matsukawa and Obata, 1994). Warmer and drier climatic conditions are indicated by the Tetori Flora, labeled as the Akaiwa and Tamodani floras (Yabe et al., 2003). These localities are in the Ashidani, Izuki, and Nochino formations in the Kuzuryugawa region and in the Kuwajima and Okurodani formations in the Mt. Hakusan region. Climatic change started during the middle depositional phase of the Tetori Group correlative with the Kimmeridgian or Tithonian. Furthermore, the variable distribution of humid and warm floras in the Tetori region probably reflects altitude differences and local climatic conditions.

6.5. Evolutionary significance of terrestrial paleoecosystem in the Tetori Group

Rich, well-preserved, freshwater and terrestrial fossils including terrestrial plants, charophytes, ostracodes, conchostracans, arthropods, insects, mollusks, fishes, amphibians, reptiles, dinosaurs, pterosaurs, avians, and mammals occur in the Jurassic-Cretaceous strata of Liaoning and Hebei provinces in northeast China. This biota is named the Jehol Fauna (Grabau, 1928), the Jehol Flora, and the Jehol Biota (Chen and Wu, 1998). In recent years, many ''feathered dinosaur'' specimens were reported from the biota and the hypothesis of avian origin and the evolution of birds from dinosaurs has been discussed extensively. Furthermore, the rich and well-preserved biota is a classic ''Lagerstatte'' and can be considered a window into Late Jurassic to Early Cretaceous terrestrial ecological evolution.

Three assemblages are recognized from the three different formations containing the Jehol Biota (Chen, 1988, 1999) (Fig. 11). The Yixian Formation as a representative of the second stage of assemblages, which yields K-Ar a radiometric age of 124.6 Ma, is interpreted as a refugium of Jurassic terrestrial relicts in East Asia, based on the occurrences of compsognathids, rhamphorhynchids, and primitive mammalians (Luo, 1999). However, this opinion was based on co-occurrences in the Valanginian-Barremian Kuwajima and Okurodani formations and the Tithonian-Berriasian Izuki formations in the Tetori Group, Japan, of the mammal-like reptiles tritylodontids, previously thought to be extinct in the Middle to Late Jurassic, and of the Oviraptorosauria, Therizinosauroidea, and tyrannosaurids, which flourished in the Late Cretaceous (Manabe et al., 2000). This is similar to the co-occurrences of *Psittacosaurus*, whose descendants as ceratopsids in the Late Cretaceous of North America and compsognathids, rhamphorhynchoids, and primitive mammalians in the Yixian Formation. Shorebird tracks are found in the Tsuchenji Formation, which underlies the Yixian Formation (Matsukawa et al., 2001; Lockley et al., 2003; Lockley et al., 2006). Thus, we agree with the interpretation of Manabe et al. (2000) that vertebrate species whose ancestors flourished in the Jurassic and their descendants in the Cretaceous showed considerable interchange in East Asian assemblages from China to Japan.

Characteristics of assemblages in the Tetori Group and Jehol Group (the latter including the Yixian Formation) are different. No conchostracans are recognized in the Tetori Group, and ostracodes are rare. By contrast they are abundant in the Jehol Group. Some species of plants and unionid bivalves, psittacosaurids, and shorebird tracks (resembling plover footprints) are common to both groups, however. The different biotas may have been caused by different environments and stability patterns between both groups. The Tetori Group was deposited in an unstable fluvio-lacustrine basin on the eastern margin of the Asian continent, but the Jehol Group represents a stable lacustrine basin on the Asian continent. Concerning vertebrate taxa whose ancestors flourished in the Jurassic Period, the six key taxa *Jeholodens*, *Zhangheotherium*, *Sinosauropteryx*, *Caudipteryx*, *Eosipterus*, and *Dendrorhynchoides* occur in the Yixian Formation of the Jehol Group (Luo, 1999), but only tritylodontids are known from the Kuwajima and its equivalent formations in the Tetori Group (Manabe et al., 2000). This suggests that vertebrate taxa whose ancestors flourished in the Jurassic Period were more suited to stable continental lacustrine environments rather than the changeable fluvial environment of the Tetori Group of the eastern margin of the Asian continent. This suggests that these taxa preferred more conservative environments. Therefore, inland continental lacustrine habitats may have been better as refugia for relict faunas than were the fluvial environments on the eastern margin of the Asian continent. On the other hand, pterosaurids, whose ancestors flourished in the Jurassic Period, occur in both the Kuwajima and its equivalent formations in the Tetori Group and the Yixian

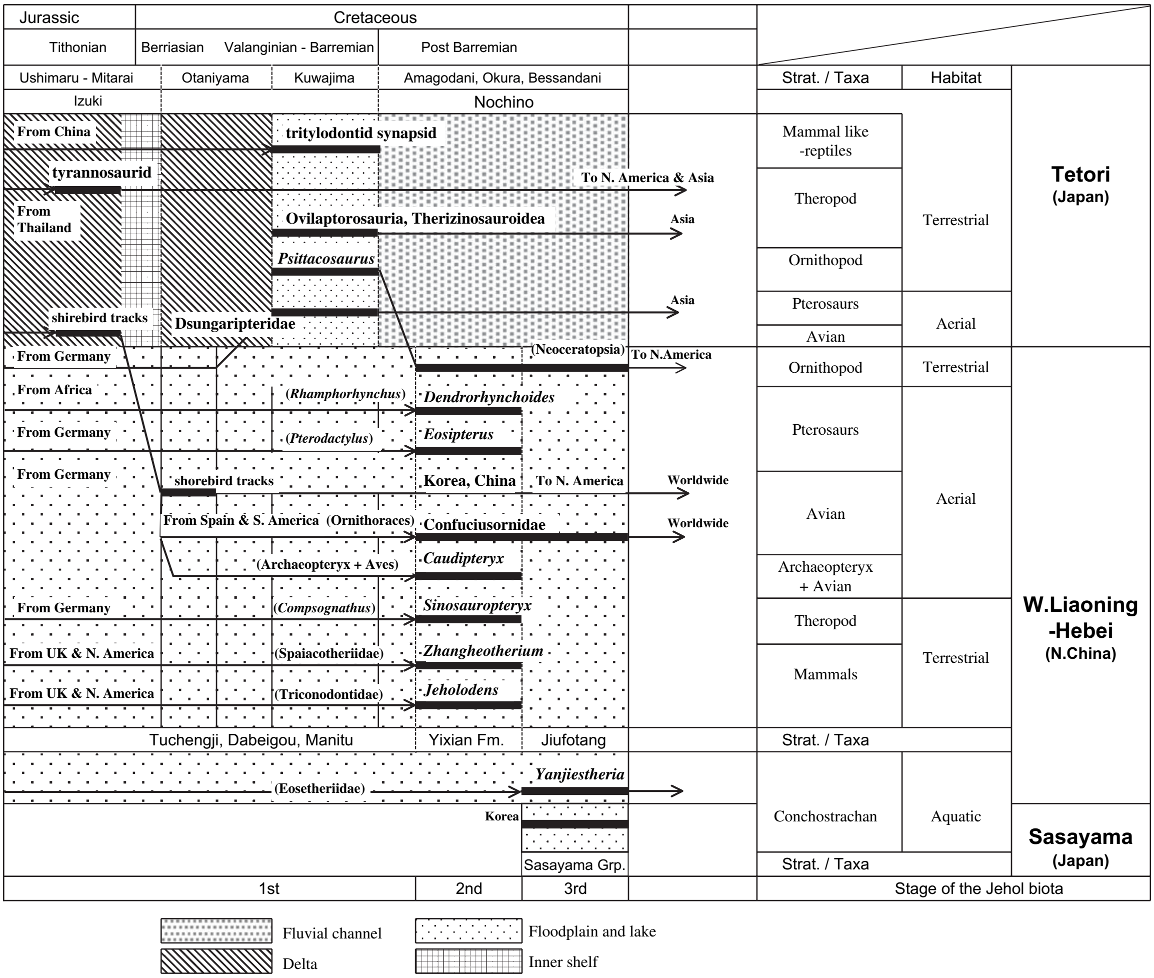

Fig. 11. Stratigraphic distributions of key taxa from the Yixian Formation (western Liaoning–Hebei, China) and the Tetori and Sasayama groups, southwest Japan with their close relatives from the Jurassic or Lower Cretaceous on other continents. Data from Chen (1988, 1999), Luo (1999), Manabe et al. (2000). Revised from Matsukawa et al. (2003a).

Formation of the Jehol Group. Birds also occur in both groups. This suggests that flying vertebrates were not restricted by environmental factors and could disperse easily.

The third sequence of assemblages in the Jehol biota can be identified in lacustrine deposits of the Jiufotang Formation and its equivalent formations. The assemblage in this third stage is characterized by new flying birds including *Cathayornis*, *Sinornis*, and *Chaoyangia*; fishes like *Lycoptera*; conchostracans like *Yanjiestheria*; and eoestherid conchostracans. This means that vertebrate taxa whose descendants flourished in the Cretaceous Period predominated in the assemblages of the Jehol biota. Conchostracans like *Yanjiestheria* and ostracodes occur in the Gyeongsang Group, Korea, and the Sasayama Group, southwest Japan. They are part of the Jehol biota (Chen, 1999). The upper part of the Tetori Group, deposited in alluvial fans and braided rivers, differs from the environment of the Jiufutang Formation and its equivalent formations, although the upper part of the group is correlative with both the Gyeongsang and Sasayama groups. These newcomer taxa were evidently not preserved in the Tetori Group, perhaps because of high-energy depositional environments.

7. Evaluation of nonmarine mollusks as chronological indices

7.1. What meanings can we take from the presence of nonmarine invertebrate and vertebrate species in terrestrial formations between marine formations?

Only fossil species recognized as reliable chronological indicators in well-dated sections can possibly be employed as chronological indices in the other sections. There are opposing opinions about the utility of nonmarine mollusks as chronological indices. They are: (1) that nonmarine mollusks may be considered a utilitarian chronological tool (Matsukawa, 1979; Tashiro and Kozai, 1984, 1986, 1994; Tanaka et al., 1984, 1998, 2000; Tashiro, 1985, 1986; Tanaka, 1989; Tashiro and Okuhira, 1993; Kozai and Ishida, 2003), and (2) that the appearance of nonmarine mollusks is controlled by paleoenvironmental conditions rather than by ‘‘evolutionary’’ appearance at a particular time as suggested by stratigraphic level (Matsukawa and Ito, 1995; Matsukawa et al., 1998).

The Upper Jurassic to Lower Cretaceous nonmarine strata of Japan have interfingering relationships with marine strata containing index species of ammonites and other marine invertebrates. Thus, Japanese Upper Jurassic to Lower Cretaceous marine deposits serve as links between nonmarine deposits in East Asia and Southeast Asia and the standard stage sections in Western Europe (Matsukawa and Obata, 1992; Matsukawa et al., 1998).

Fig. 12 shows the biostratigraphic distribution of nonmarine bivalve species in the main sections of both the outer and inner zones of southwest Japan. The distribution of some nonmarine bivalve species is interrupted by marine transgressions in sections of the outer zone of southwest Japan. We recognize the occurrence of common species, mainly corbiculoids, in the lower nonmarine formations, and many endemic species of corbiculoids in the upper nonmarine formations from the outer zone of southwest Japan. Common species of corbiculoids in the lower nonmarine formations have potential use as chronological indices, but many endemic species cannot be so employed. Each species of corbiculoids is interpreted as having been derived from the Arcticidae, because corbiculoid species could not expand to other brackish-water environments after speciation from marine species (Matsukawa and Nakada, 2003). Indeed, *Hayamina naumanni*, *Costocyrena otsukai*, *Isodomella shiroiensis*, and *Pulsidis antiqua* are distributed in almost every area in southwest Japan. This shows that these species were distributed by the late Hauterivian–early Barremian marine transgression. However, these species were extinct by the maximum marine transgression, and so not recognized afterwards. Based on the occurrence of Barremian ammonites in the marine transgressive formations, the lower nonmarine formations can be correlated with the upper Hauterivian–lower Barremian (Matsukawa, 1983; Obata and Matsukawa, 1984; Matsukawa et al., 1997, 1998). Thus, *Hayamina naumanni*, *Costocyrena otsukai*, *Isodomella shiroiensis*, and other species in the lower nonmarine formation can probably be used as a chronological index for the upper Hauterivian to lower Barremian.

Some nonmarine formations containing new species, including corbiculoids, occurred after the late Hauterivian to Barremian marine transgression. This indicates that endemic species moved in and developed when former inhabitant species failed to return to the same areas. We cannot reliably use these endemic species as chronological indices, even if these species are recognized in other younger nonmarine formations of the outer zone of southwest Japan or in its equivalent formations. To confirm that they are of contemporaneous age we would need other proof. These endemic species in the upper nonmarine formations of the outer zone of southwest Japan cannot be used as correlation tools and chronological indices because they have local geographic distributions and their true taxon ranges are unknown. Fujita (2002) suggested that the Izuki Formation is possibly correlative with the Hauterivian–Barremian because the bivalve species *Myopholas* sp. cf. *M. semicostata* occurs in the Ryoseki and Togawa formations in the outer zone of southwest Japan, and the Ryoseki Formation is then conformably overlain by the Monobe Formation, which bears Barremian ammonites (Tashiro, 1993; Tashiro et al., 1993). However, the taxon range of the bivalve species has not yet been demonstrated. Indeed, the Izuki Formation can be assigned to the Tithonian–Berriasian based on geological correlation with marine strata that contain the ammonite indices mentioned earlier in this paper.

Some ammonite species can be employed as chronological indices in the Tetori Group because their taxon ranges are recognized in the marine type sections in Europe. Non-ammonite invertebrate species cannot be used reliably as chronological indices if they can be dated by occurrences in formations between marine formations bearing reliable marine indices (e.g., ammonites, foraminifers). This is because there are few reliable examples of non-ammonite taxa (e.g., pollen, dinosaurs), whose ranges are well defined and restricted to intervals (zones) that have been used widely for biostratigraphic zonation. It is legitimate to date non-ammonite assemblages, but then to use them for correlation without good evidence for a temporally restricted global distribution is a dubious practice.

7.2. Evaluation of nonmarine molluscan assemblages

The Tetori Group in the inner zone of southwest Japan yields more than ten brackish- to freshwater molluscan species (Matsukawa and Ido, 1993; Matsukawa and Nakada, 1999). They occur in the Ushimaru Formation and in the succession of the Otaniyama and Okurodani formations interbedded with shallow marine Mitarai Formation in the Mt. Hakusan region. Five assemblages of nonmarine mollusks have been recognized: (1) Ostreidae gen. et sp. indet.–*Myrene* (*Mesocorbicula*) *tetoriensis* Assemblage, (2) *Myrene* (*Mesocorbicula*) *tetoriensis* Assemblage, (3) *Tetoria* (*T.*) *yokoyamai* Assemblage, (4) *Sphaerium* sp. Assemblage, and (5) *Plicatounio* (*P.*) *naktongensis*–*Trigonioides* (*Wakinoa*) *tetoriensis* Assemblage. These assemblages are typical of various grades of brackish- to freshwater environments, and the species composition of each assemblage varies with salinity (Matsukawa and Ido, 1993). The salinity ranges of nonmarine bivalve species from the Tetori Group were inferred by Matsukawa and Nakada (1999).

Fig. 12 shows the biostratigraphic distribution of nonmarine bivalve species in the Tetori Group section in the Mt. Hakusan region, on the inner zone of southwest Japan. *Myrene* (*Mesocorbicula*) *tetoriensis*, *Tetoria yokoyamai*, and other species occur in the nonmarine Ushimaru, Otaniyama, and Okurodani/Kuwajima formations above and below the marine Mitarai Formation in the Tetori Group of the Mt. Hakusan region. These species inhabited brackish- to freshwater environments; *Myrene* (*Mesocorbicula*) *tetoriensis* was interpreted as living in oligohaline to mesohaline waters, and *Tetoria yokoyamai* in freshwater to mesohaline settings (Matsukawa and Nakada, 1999). This means that these species emigrated from the Mt. Hakusan region and then came back to the same area after the marine transgression represented by the Mitarai Formation. From their long taxon ranges, these species cannot be used as correlation and chronological tools. Their appearances were likely controlled by environmental changes.

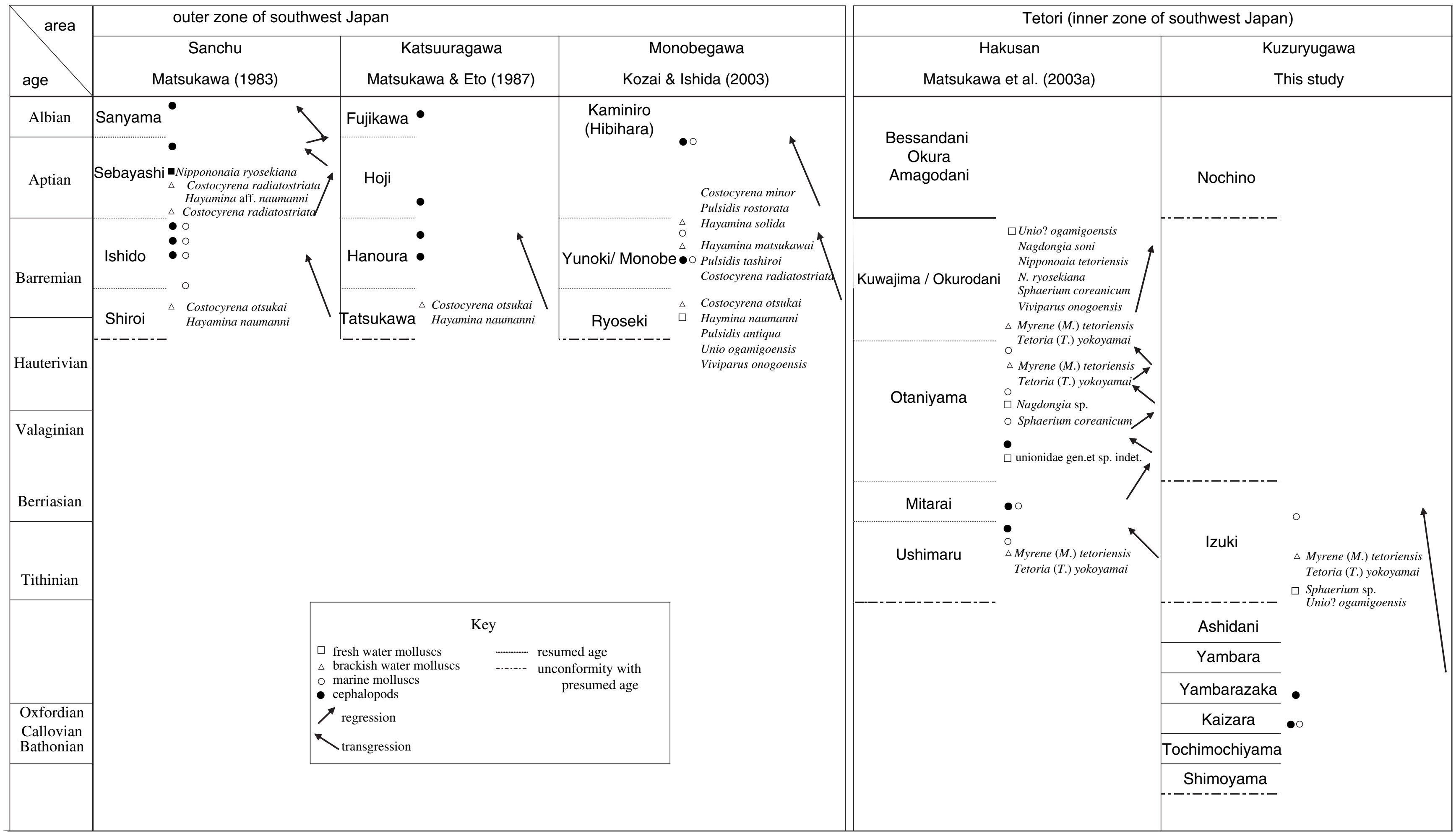

Fig. 12. Stratigraphy of Lower Cretaceous sections in both outer and inner zones of southwest Japan and stratigraphical occurrence of nonmarine molluscan species and transgressive–regressive phases (Matsukawa, 1983; Matsukawa and Eto, 1987; Kozai and Ishida, 2003; Matsukawa et al., 2003a).

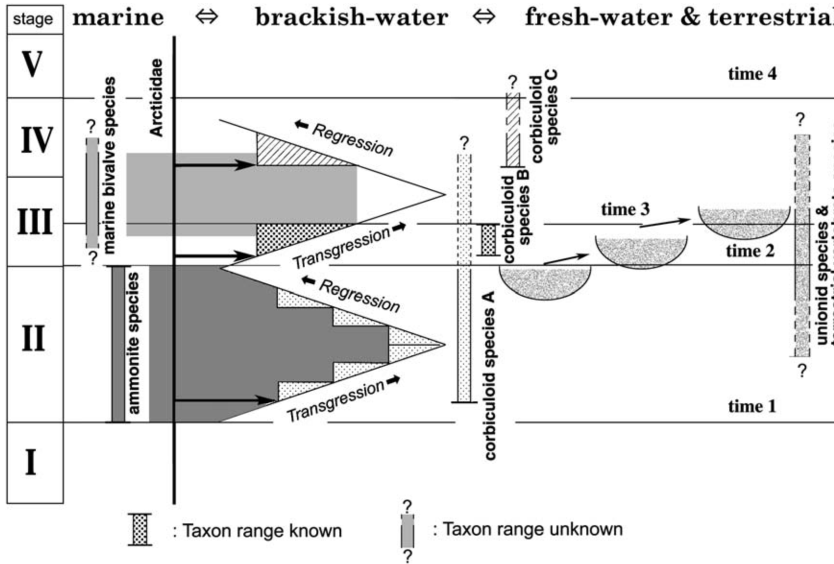

Fig. 13. Model for evaluation of nonmarine molluscan species and terrestrial vertebrate species as chronological indices.

Freshwater mollusks including *Plicatounio* (*P.*) *naktongensis*, *Trigonioides* (*Wakinoa*) *tetoriensis*, *Nippononaia tetoriensis*, *Unio*? *ogamigoensis*, *Nagdongia soni*, *N.* sp., *Sphaerium coreanicum*, *Viviparus onogoensis*, and *Micromelania*? *katoensis* occur in the Otaniyama, Okurodani, and Kuwajima formations (Matsukawa and Ido, 1993; Matsukawa and Nakada, 1999; Matsukawa et al., 2003b). *Nippononaia ryosekiana* was also reported by Isaji (1993) from the Okurodani and Okura formations (Matsukawa et al., 2003b). The environments represented by the formations bearing these mollusks were lacustrine to fluvial and surrounding flood-plain settings. This probably means that their appearances were also controlled by the environment.

Nippononaia ryosekiana has been interpreted to suggest Aptian age, because the Lower Member of the Sebayashi Formation bearing the species lies between marine formations dated as Barremian and Aptian (Matsukawa, 1979, 1983). Thus, the species has been employed as an Aptian index for the Tetori Group (Isaji, 1993), although no one has demonstrated its taxon range. In the Tetori Group, *N. ryosekiana* was reported from the Kitadani Formation, which is at the top of the group (Maeda, 1961). However, the Kitadani Formation is interpreted as a synonym of the Kuwajima Formation (Kawai, 1961) and the Okurodani Formation (Matsukawa et al., 2003b). Both the Kuwajima and Okurodani formations are possibly correlated to the Valanginian–Barremian, based on the Tithonian–Berriasian ammonite indices from the underlying Mitarai Formation (Sato et al., 2003), the taxon range of Iguanodontidae specimens, and a fission-track date (Matsukawa et al., 2003a). Based on the age of the Sebayashi and Kuwajima/Okurodani formations, the range of *Nippononaia ryosekiana* is likely from the Valanginian to the Aptian. However, the species only occurs at one horizon in each formation, and both formations are overlain by marine and fluvial-channel deposits. This means that the occurrence of the species was influenced by environmental change. The species had many chances to shift to optimum environments, and we cannot confirm its taxon range. Thus, we cannot use such species as correlation and chronological tools.

Freshwater molluscan species have many opportunities to move to optimum habitats, even if such habitats are later destroyed. This means that species taxon ranges are probably long and cannot be used as chronological indices. Many vertebrate species whose ancestors flourished in the Jurassic Period continued to exist in East Asia during the Early Cretaceous. For example, mammal-like reptiles such as tritylodontids and dicynodonts occur in the Cretaceous strata in the Tetori Group, Japan (Matsuoka, 2000), in the Rolling Downs Group, Australia (Thulborn and Turner, 2002), and in the mid-Cretaceous of western Siberia (Tatarinov and Matchenko, 1999). This suggests that terrestrial vertebrate species found suitable habitats in this region later than in other parts of the world (Fig. 13).

Recently, Kozai et al. (2005) tried to correlate Cretaceous nonmarine deposits between Japan and Korea based on nonmarine molluscan assemblages. However, they did not show taxon ranges of these species, and did not discuss their biostratigraphic or biogeographic distributions; therefore, their conclusions are questionable.

8. Conclusions

A coherent stratigraphy of the Tetori Group throughout the entire area in the type region was demonstrated by Matsukawa et al. (2003a,c). Geological correlation tools and the biological significance of zoo- and phyto-assemblages are here evaluated and discussed in the context of terrestrial ecosystems. We reach the following conclusions:

1. The formation as a lithostratigraphic unit is the best geological correlation tool for the Tetori Group, and the best tool for geological mapping of the group. Although the subgroup unit has frequently been used as a geological correlation tool, these usages have not always been

consistent. Thus subgroup names should not be casually used for geological correlation.

The Tetori Group in the Mt. Hakusan region is divided into eight formations, in ascending order, the Ushimaru, Mitarai, Otaniyama, Kuwajima/Okurodani, Amagodani, Okura, and Bessandani formations. The Tetori Group in the Kuzuryugawa region is subdivided into eight formations, in ascending order, the Shimoyama, Tochimochiyama, Kaizara, Yambarazaka, Yambara, Ashidani, Izuki, and Nochino formations. Based on ammonites, the Kaizara and Yambarazaka formations are Bathonian to Oxfordian in age and the Mitarai Formation is Tithonian to Berriasian in age. Because they are parts of the same transgressive succession, the Izuki Formation can be correlated to the Ushimaru and Mitarai formations. Based on their similar thick, arkosic sandstone facies, the Nochino Formation is correlative with the succession from the Amagodani to Bessandani formations.

2. All zoo-assemblages came from the Ushimaru to Okura formations in the Mt. Hakusan region and from the Tochimochiyama to Nochino formations in the Kuzuryugawa region. The zoo-assemblages come from shallow marine, deltaic, flood-plain, and lacustrine environments, but phyto-assemblages are found in high-energy fluvial-channel deposits. The occurrences of zoo-assemblages were controlled by environments, but phyto-assemblages could have resisted the high-energy river flow. These occurrences are controlled by environmental factors.
3. Terrestrial vertebrates including dinosaurs occur in the Kuwajima Formation and its equivalent the Okurodani Formation and in the underlying Izuki Formation. Although two faunal names are given for these two dinosaur assemblages from equivalent formations, the Tetori Dinosaur Fauna should be used as the only label for these assemblages.
4. The Tetori Flora was previously divided into four components: the Kuzuryu, Oguchi, Akaiwa, and Tamodani floras, based on stratigraphic occurrence. Our stratigraphic studies show that these do not occur as stratigraphically separate floras. The terms Kuzuryu, Oguchi, Akaiwa, and Tamodani floras can therefore be abandoned in favor of the term of the Tetori Flora. Ryoseki-type floral elements in the Tetori Group show warmer and dryer climatic condition, reflecting altitude and predominantly northward-flowing warm currents around East Asia and coming from the equator.
5. There are two types of zoo-assemblages in the Kuwajima and its coeval formations: vertebrate species whose ancestors flourished in the Jurassic, and their descendants from the later Cretaceous Period. The former Jurassic species predominate in the Yixian Formation, northeast China, rather than in the Kuwajima and its coeval formation of the Tetori Group, but later Cretaceous species are more abundant in the Kuwajima and its coeval formation. This suggests that more archaic faunas found refuge in inland continental regions. The Yixian Formation represents a lacustrine environment on the stable Asian mainland, but the Kuwajima and its coeval formation include fluvio-lacustrine environments of the unstable marginal area of the Asian continent. As the latter setting is more common than the former, changeable environments at the continental margin may have favored the evolution of more progressive.
6. We can only employ nonmarine molluscan species as geological correlation tools when their taxon ranges are well-confirmed over large regions. Freshwater molluscan species and terrestrial vertebrate species had many opportunities to change their local habitats on the Cretaceous Asian continent, and some nonmarine molluscan species from the Japanese Cretaceous had their distributions controlled by the environment. Thus, care should be exercised in using nonmarine mollusks for correlation.

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