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ARTICLE

VERTEBRATE DIVERSITY OF THE EARLY CRETACEOUS TETORI BIOTA FROM JAPAN, THE STATE OF THE ART

Shin-ichi SANO

Fukui Prefectural Dinosaur Museum
51-11, Terao, Muroko, Katsuyama, Fukui 911-8601, Japan

ABSTRACT

The comprehensive list of vertebrate skeletal fossils (excluding ichnofossils) from the Early Cretaceous Tetori Group is provided. Numbers of species of selected vertebrate taxonomic groups of the Tetori Group are compared with those from several famous Late Jurassic–Early Cretaceous *Lagerstätten* to evaluate the vertebrate diversity of the Tetori Biota. Vertebrate fauna of the Tetori Group is characterized by the presence of a tritylodont synapsid, that of both diversified choristoderes and a crocodyliform, remarkably high diversity of the testudines, moderate diversity of mammals, squamates and dinosaurs, and possible low diversity of fish. Most of the vertebrate taxonomic groups recognized in other fauna/biotas are present in the Tetori Biota. The vertebrate diversity of the Tetori Biota can be considered to be comparable to those of the Late Jurassic–Early Cretaceous *Lagerstätten* at present, and is expected to be higher in the near future. Further investigation and comparison of vertebrate diversities in almost coeval strata in several regions in East and Southeast Asia probably provide the useful information to reveal the paleo(bio)geographical and palaeoclimatic reconstruction in Asia, and also the evolution of the Mesozoic terrestrial ecosystem.

Key words : vertebrates, diversity, Tetori Group, Early Cretaceous, Central Japan, East Asia, terrestrial ecosystem, palaeobiogeography

佐野晋一（2017）手取層群の脊椎動物相はどのぐらい多様なのか．福井県立恐竜博物館紀要 16：1–15.
手取層群の脊椎動物相を概観すべく，論文等で報告された脊椎動物の体化石のリストを作成した．手取層群の脊椎動物相は，トリティロドン類の存在，ワニ類と比較的多様なコリストデラ類の両方の存在，カメ類の顕著な多様性，哺乳類，有鱗類，恐竜類の多様性，魚類の多様性が小さいことによって特徴づけられる．手取層群の脊椎動物化石の各グループの種数を，後期ジュラ紀～前期白亜紀の幾つかの著名なラガシュテッテンと比較した結果，手取生物群には他のラガシュテッテンに知られるほとんど全てのグループが存在しており，かつ，現在知られている種数も他地域のものにほぼ匹敵する規模に達することがわかった．今後，東・東南アジア各地のほぼ同時代の地層から知られる脊椎動物相の多様性を比較することにより，アジアにおける当時の古（生物）地理や古気候の復元，さらには中生代陸上生態系の進化の解明に貢献できるものと期待される．

INTRODUCTION

The presence of rich terrestrial vertebrate fauna has been recognized in the Early Cretaceous Tetori Group (Oishi, 1933a, b) in northern Central Japan, and its importance to reveal the evolution of Mesozoic terrestrial ecosystem in East Asia attracts much attention recently (e.g., Manabe et al., 2000; Matsuoka et al., 2002; Matsukawa et al., 2006; Sano and Yabe, 2017). However, most previous studies mainly focused on the faunas in each area/formation (e.g., Evans et al., 1998; Matsuoka, 2000a; Matsuoka et al., 2002) or on each taxonomic group (e.g., Matsumoto et al., 2015; Evans and Matsumoto, 2015; Shibata et al., 2017), and the whole diversity of the Tetori Biota (Matsukawa et al., 2006) has not been fully understood. In this paper, almost all available data of the vertebrate skeletal fossils from the Tetori Group is summarized to evaluate the potential vertebrate diversity of the Tetori Biota in comparison with those of the Jehol Biota in northeastern China and other Late Jurassic–Early Cretaceous *Lagerstätten*.

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Corresponding author―Shin-ichi SANO
E-mail: ssano＊dinosaur.pref.fukui.jp

GEOLOGICAL OUTLINE

The Early Cretaceous Tetori Group is sporadically distributed in the Hakusan Region in the western part of the Hida Belt (Fig. 1), which is considered to be a fragment of continental block, possibly a part of the North China Block, or the Jiamushi (or Jiamusi) Block in the eastern margin of the Central Asian Orogenic Belt before the Miocene opening of the Japan Sea (e.g., Jin and Ishiwatari, 1997; Kim et al., 2007; Arakawa et al., 2000; Kunugiza et al., 2010; Zhao et al., 2013; Takahashi et al., 2017). The Tetori Group is divided into two depositional stages: DS2 and DS3 (Sano, 2015). In DS2 (Berriasian–late Hauterivian), the brackish environment is dominant with intercalation of shallow marine environment in some horizons, whereas a fluvial environment prevailed without any marine/brackish horizons in DS3 (Barremian–Aptian).

Vertebrate skeletal fossils have been described or figured mainly from the Itsuki Formation in the Itoshiro area; the Mitarai, Okurodani and Amagodani formations in the Shokawa area; the Taie Formation in the Hida-Furukawa area; the Kuwajima, Akaiwa and Kitadani formations in the Shiramine and Takinamigawa areas; the Kowashimizu Formation in the Asuwa area (Figs. 1 and 2). Depositional stage and age, and stratigraphical relationships of vertebrate fossil-bearing formations of the Tetori Group are summarized in Figure 2 (See Sano (2015) for details). Among vertebrate fossil localities in the Tetori Group, KO-2 in the lowermost part of the Okurodani Formation corresponds to upper part of DS2 (possibly assigned to late Hauterivian or earlier, but later than Berriasian in age), Kasekikabe in the uppermost part of the Kuwajima Formation lower part of DS3 (Barremian), and the Kitadani Dinosaur Quarry in the lower part of the Kitadani Formation upper part of DS3 (Aptian) (Sano and Yabe, 2017). However, since similar vertebrate taxa including same genera have been known from KO-2 and Kasekikabe, and the last occurrence of brackish molluscs, meaning the transition from DS2 to DS3, is recognized within the Kuwajima and Okurodani formations, it is supposed that the strata of these two fossil localities are probably not so different in age (Sano and Yabe, 2017).

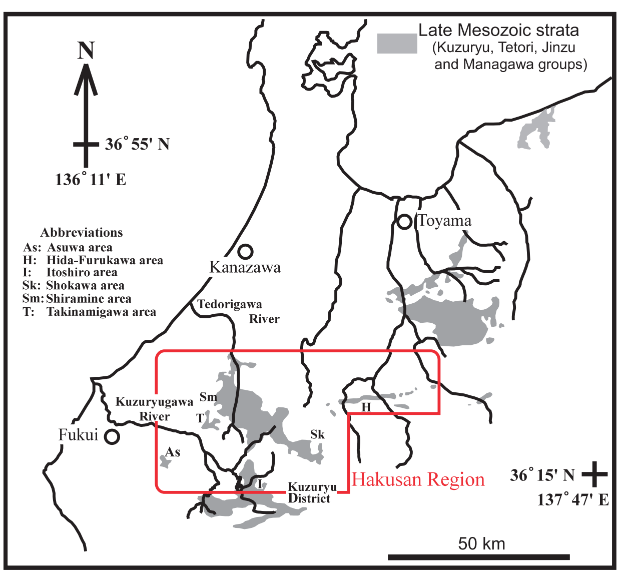

FIGURE 1. Index map showing the distribution of the Early Cretaceous Tetori Group in northern Central Japan. The Kuzuryu and Tetori groups are distributed in the Hakusan Region, though the former shows a narrow distribution only in the Itoshiro area (modified from Maeda (1961b) and Fujita (2003)).

The stratigraphy of three other vertebrate skeletal fossil localities is briefly mentioned here, because it was not discussed in Sano (2015) and Sano and Yabe (2017). An unidentified theropod tooth was recovered from a grey mudstone float in East of Shiramine Village in the Shiramine area (Tanimoto et al., 2009; Utsunomiya, 2009). Co-occurrence of a bivalve *Nippononaia tetoriensis* and a gastropod with a tooth in the float suggests this float was most probably derived from the Tetori Group. Yanagidani, the type and only known locality of *N. tetoriensis* in the Shiramine area (Maeda, 1962), is located close to the fossil discovery site. Thus the fossil-bearing float is supposed to be originated from the stratum at Yanagidani, or nearby locality/horizon. Based on the stratigraphical interpretation of the stratum at Yanagidani in Matsuura (2001), original authors considered the dinosaur fossil was derived from the Akaiwa Formation. However, Sano and Yabe (2017) discussed this fossil-bearing stratum can be correlated with the lower part of the Kuwajima Formation (upper part of DS2), and the latter interpretation is accepted here.

Several vertebrate remains including a new squamata *Tedorosaurus asuwaensis* have been described or figured from the Sakaidera Alternation of the Tetoti Group in the Asuwa area (Shikama, 1967, 1969; Yasuno, 2004, 2005). Yasuno (2005) figured freshwater and brackish water bivalves: *Nippononaia tetoriensis*, *Megasphaerioides okurodaniensis*, *Myrene* sp., *Tetoria* sp., and a shark tooth *Hybodus* sp. from this stratum, and compared this fossil bivalve assemblage with those of the Okurodani Formation and the lower part of the Kuwajima Formation in Yanagidani, and discuss the possible correlation of the fossil-bearing stratum to the upper part of the Itoshiro Subgroup of the "Tetori Group" (Maeda, 1961b). Yamada et al. (2008) revised the stratigraphy of the Tetori Group in this area, redefining the Kowashimizu Formation, which now includes the Sakaidera Alternation of Maeda (1961a), and assigned it to the Itoshiro Subgroup. These recent stratigraphical views are accepted here, and the vertebrate fossil-bearing formation in this area probably corresponds to the upper part of DS2.

Manabe (1999) described an isolated premaxillary tooth of a tyrannosauroid from the Jobu Formation of the "Itoshiro Subgroup of the Tetori Group" (Yamada et al., 1989) in the Kamihambara area, in the eastern part of Kuzuryu District. Sano (2015) proposed the idea that this fossil-bearing stratum is separated from the Tetori Group, and assigned to the Managawa Group in the Hida Gaien Belt. Furthermore, the age of the fossil-bearing stratum is still controversial. Thus this record is not included in the discussion of this paper. Vertebrate fossil records from the Kuzuryu Group (= DS1 of Sano (2015)) (e.g., a possible plesiosaur tooth (Board of Education of Toyama Prefecture, 2003) and fish scales (Yasuno, 1994, 1995)) are also excluded.

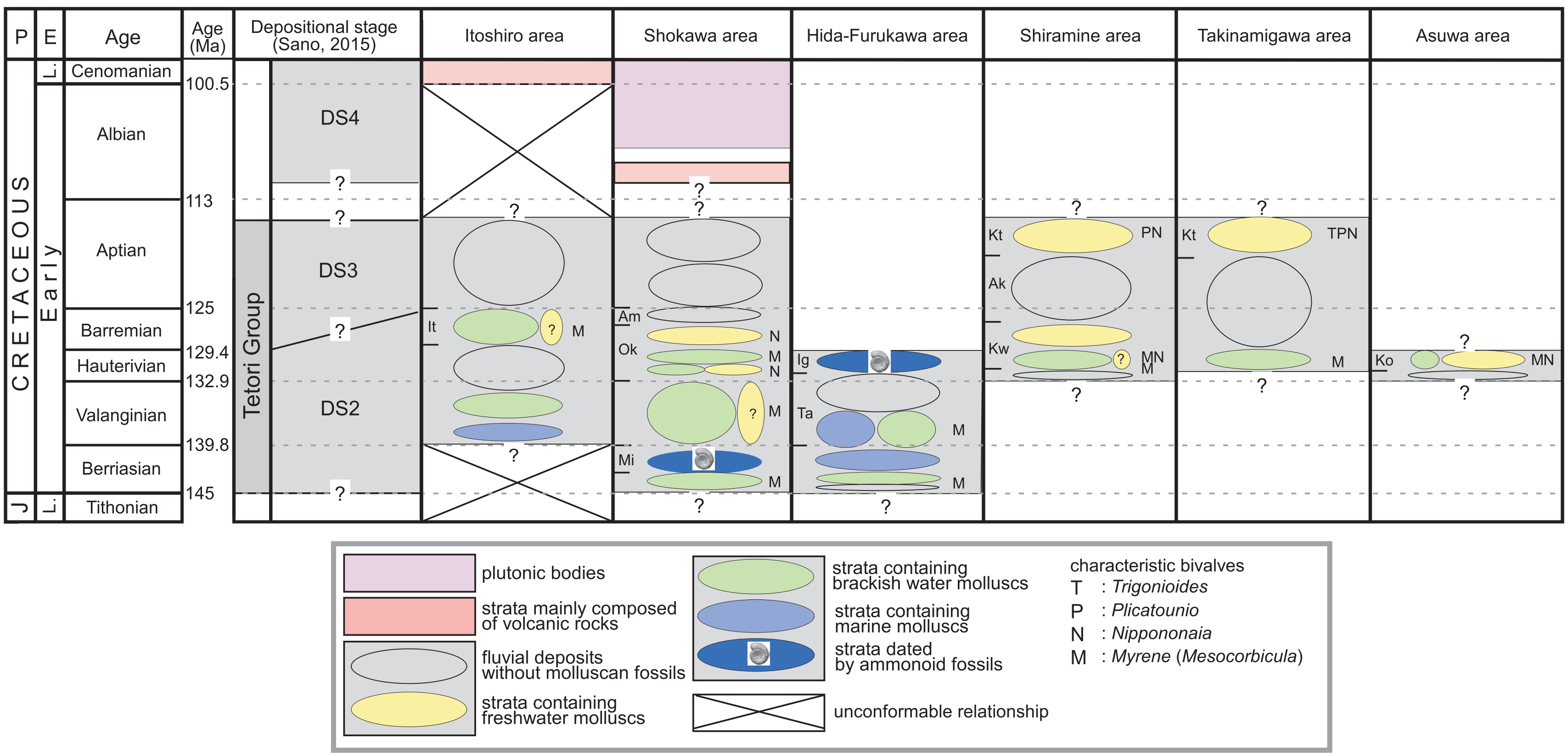

FIGURE 2. Depositional stages, stratigraphic distribution of marine and brackish horizons, and the occurrences of characteristic bivalves in the Tetori Group (modified from Sano and Yabe (2017)). Stratigraphy and molluscan fossil occurrences in the Tetori Group: Maeda (1952b, 1957) for the Itoshiro area; Maeda (1952a) and Matsukawa and Nakada (1999) for the Shokawa area; Matsukawa et al. (2007) for the Hida-Furukawa area; Maeda (1958, 1962), Tamura (1990), Isaji (1993) and Sano et al. (2008) for the Shiramine and Takinamigawa areas; Yasuno (2004, 2005) andYamada et al. (2008) for the Asuwa area; see text and Sano (2015) for details. Ammonoid data: Sato et al. (2003, 2008) for the Mitarai Formation in the Shokawa area; Matsukawa and Fukui (2009) for the Inagoe Formation in the Hida-Furukawa area. Abbreviation: It–Itsuki Formation in the Itoshiro area; Mi–Mitarai Formation, Ok–Okurodani Formation, Am–Amagodani Formation in the Shokawa area; Ta–Taie Formation, Ig–Inagoe Formation in the Hida-Furukawa area; Kw–Kuwajima Formation, Ak–Akaiwa Formation, Kt–Kitadani Formation in the Shiramine and Takinamigawa areas; Ko–Kowashimizu Formation in the Asuwa area. The numerical ages are based on International Commission on Stratigraphy (ICS) (2015).

VERTEBRATE DIVERSITY OF THE TETORI GROUP

Methods

To evaluate the vertebrate diversity of the Tetori Group, only the skeletal fossils (excluding ichnofossils, such as footprints and eggshells) formally described in scientific papers are surveyed. Indeterminate material is also included in the list, if at least its higher level (generally Order) classification is mentioned in the description. However, in case almost all the information of selected taxonomic groups from the Tetori Group is summarized in the review papers (e.g., Hirayama, 2006 for testudines; Shibata et al., 2017 for dinosaurs), some undescribed taxa mentioned in these papers are also included in the list with original references (usually abstracts for the scientific meeting). Although a crocodyliform from the Tetori Group has not been formally described yet (Kobayashi, 1998), this record has been frequently mentioned in the palaeobiogeographical and palaeoclimatic discussions (e.g., Amiot et al., 2011; Matsumoto et al., 2015; Sano and Yabe, 2017), and thus is included in the list. Such uncertain records are shown with asterisk.

Since systematic revision of each taxon is beyond the scope of this paper, its original taxonomic assignment is generally followed, but higher taxonomic names are sometimes revised according to their recent usage (e.g., Pantrionychia Joyce et al., 2004). The change of the names applied for the same specimens or species are carefully surveyed, and related references are mentioned in one same row of the list.

Results

The comprehensive list of vertebrate skeletal fossils from the Tetori Group is provided in Table 1. It should be noted that the number of species in each taxonomic group is tentative, and can be changed (probably larger) during the course of future studies. Two elasmobranch and five neopterygian fish, including two new taxa: *Sinamia kukurihime* and *Tetoriichthys kuwajimaensis* (Yabumoto, 2008, 2014), are recognized. At least two amphibians including Anura and Caudata are present. One new tritylodontid synapsid *Montirictus kuwajimaensis* (Matsuoka et al., 2016), and seven mammals, including four new taxa: *Symmetrolestes parvus*, *Hakusanobaatar matsuoi*, *Tedoribaatar reini* and *Hakusanodon archaeus* (Tsubamoto et al., 2004; Rougier et al., 2007; Kusuhashi, 2008), were described. Among 13 testudines, only one new taxon *Kappachelys okurai* (Hirayama et al., 2013) was formally described at present. A new lizard *Tedorosaurus asuwaensis* is the first vertebrate fossil recovered from the Tetori Group (Shikama, 1967, 1969), though its identification is still uncertain (Evans and Matsumoto, 2015). After this discovery, 10 squamates, including 6 new taxa: *Kaganaias hakusanensis*, *Kuwajimalla kagaensis*, *Sakurasaurus shokawensis*, *Asagaolacerta tricuspidens*, *Kuroyuriella mikikoi* and *Hakuseps imberis* (Evans and Manabe, 1999a, 2008; Evans et al., 2006; Evans and Matsumoto, 2015), were described, though other taxa were also probably present (Evans and Manabe, 1999a). The presence of all three known choristoderan morphotypes (short-necked longirostrine, short-necked brevirostrine and long-necked brevirostrine) were recognized in the Tetori Group (Matsumoto et al., 2015), and one new long-necked taxon *Shokawa ikoi* was proposed (Evans and Manabe, 1999b). One crocodyliform, possibly four pterosaurs, and one avis are present. Dinosaurs excluding aves represent possibly 10 theropods, two sauropods and possibly six ornithischians. Among them, two theropods: *Fukuiraptor kitadaniensis* and *Fukuivenator paradoxus* (Azuma and Currie, 2000; Azuma et al., 2016), one sauropod: *Fukuititan nipponensis* (Azuma and Shibata, 2010), and three ornithischians: *Albalophosaurus yamaguchiorum*, *Fukuisaurus tetoriensis* and *Koshisaurus katsuyama* (Kobayashi and Azuma, 2003; Ohashi and Barrett, 2009; Shibata and Azuma, 2015) were described as new taxa. In summary, vertebrate skeletal fossils from the Tetori Group is composed of about 68 taxa in total, among which 22 taxa are newly described.

COMPARISON WITH VERTEBRATE DIVERSITIES OF THE LATE JURASSIC–EARLY CRETACEOUS *LAGERSTÄTTEN*

Methods

Numbers of species of selected vertebrate taxonomic groups from several famous Late Jurassic–Early Cretaceous *Lagerstätten* are compared with those of the almost coeval Tetori Group to evaluate the vertebrate diversity of the Tetori Biota (Table 2, Fig. 3). Six *Lagerstätten*: the Yanliao Biota (Middle–Late Jurassic, 166–159 Ma) in northeastern China, the Solnhofen Fauna (Late Jurassic) in southern Germany, the Las Hoyas Fauna (Upper Barremian) in Spain, the Wealden Fauna (Barremian–earliest Aptian) in southern United Kingdom, the Jehol Biota (Early Cretaceous, 131–120 Ma) in northeastern China, and the Santana Fauna (Early Cretaceous) in Brazil are selected, and their vertebrate diversities are compared using similar data sets published in Zhou and Wang (2010, 2017) and Sweetman (2016), though detailed genera and species lists were published only for the Wealden and Jehol fauna/biotas. Fish in Table 2 and Figure 3 represents total number of species of an agnathan, elasmobranchs, and neopterygians. The data of the Solnhofen Fauna is very different from other faunas, because of its outstanding diversity of fish, the presence of rich marine reptiles, such as ichthyosaurs, sphenodonts, crocodyliforms, which have not been recognized in other faunas, and the absence of amphibians and mammals, and thus is not shown in Figure 3.

Results

Most of the vertebrate taxonomic groups recognized in other faunas are present in the Tetori Biota, except marine reptiles, such as ichthyosaurs and plesiosaurs (Table 2). Total number of species in the Tetori Biota (68 species) is more than that of the Yanliao Biota (40 species), and comparable to those of the Las Hoyas (63 species) and Santana (69 species) faunas, and less than those

TABLE 1. The comprehensive list of vertebrate skeletal fossils (excluding ichnofossils) from the Early Cretaceous Tetori Group. Taxon names in bold represent the new taxa from the Tetori Group. The asterisk denotes the taxa, which has not been described formally. Abbreviation: Ak–Akaiwa Formation; Am–Amagodani Formation; Ta–Taie Formation; It–Itsuki Formation; Ko–Kowashimizu Formation; Kt–Kitadani Formation; Kw-u–upper part of the Kuwajima Formation; Kw-l–lower part of the Kuwajima Formation; Mi–Mitarai Formation; Ok–Okurodani Formation.

Classification	References	Formations (Localities)
Elasmobranchii : two species		
Hybodus sp.	Kitaura et al., 1974; Yamada, 1990; Ohe, 1990; Yasuno, 2005	Mi, Ta, Ko
unidentified elasmobranch teeth*	Kitaura et al., 1974	Mi
Neopterygii: five species including two new taxa		
Lepidotes sp.	Yabumoto, 2005	Kw-u (Kasekikabe)
Sinamia kukurihime	Yabumoto, 2014, 2017	Kw-u (Kasekikabe)
Pachycormidae, gen. et sp. indet.	Yabumoto, 2005	Kw-u (Kasekikabe)
Tetoriichthys kuwajimaensis	Yabumoto, 2008	Kw-u (Kasekikabe)
Teleostei, order, fam., gen. et sp. indet.	Yasuno, 1995, 2004; Azuma, 2003; Yabumoto, 2005	It, Ko, Kw-u (Kasekikabe), Kt
Amphibia: two species		
Anura	Evans and Manabe, 1998, Matsuoka, 2000b; Matsuoka et al., 2002; Ikeda et al., 2016	Ok (KO-2), Kw-u (Kasekikabe)
Caudata	Evans and Manabe, 1998	Ok (KO-2)
Synapsida (Tritylodontidae): one species (new taxon)		
Montirictus kuwajimaensis	Setoguchi et al., 1999; Matsuoka, 2000c; Matsuoka et al., 2002, 2016	Kw-u (Kasekikabe)
Mammalia: seven species including four new taxa		
Symmetrolestes parvus	Tsubamoto et al., 2004	Kt
Hakusanobaatar matsuoi	Kusuhashi, 2008	Kw-u (Kasekikabe)
Tedoribaatar reini	Kusuhashi, 2008	Kw-u (Kasekikabe)
Eobaataridae, gen. et sp. indet.	Miyata et al., 2016	Kt (Dinosaur Quarry)
Hakusanodon archaeus	Rougier et al., 2007	Kw-u (Kasekikabe)
“Amphilestidae” gen. et sp. indet.	Kusuhashi and Tsubamoto, 2010	Kw-u (Kasekikabe)
?Triconodontidae, gen. et sp. indet.	Miyata et al., 2016	Kt (Dinosaur Quarry)
Testudines: 13 species including one new taxon		
Sinochelyidae, gen. et sp. indet. (right frontal)*	Hirayama, 1996, 2006	Ok (KO-2)
Sinemydidae, gen. et sp. indet. (hyoplastron with fontanels and carapace fragments)*	Hirayama, 1996, 2004, 2006	Ok (KO-2)
Sinemydidae, gen. et sp. indet.	Hirayama, 2000, 2005, 2010; Hirayama et al., 2000	Kw-u (Kasekikabe)
Sinemydidae?, gen. et sp. indet.	Hirayama, 2002	Kt (Dinosaur Quarry)
Xinjiangchelyidae, gen. et sp. indet.---possibly one taxon	Hirayama, 1996, 2000, 2004, 2005, 2006, 2010; Hirayama et al., 2000	Ok (KO-2), Kw-u (Kasekikabe)
Xinjiangchelyidae, gen. et sp. indet.	Hirayama, 2002, 2006	Kt (Dinosaur Quarry)
Pan-trionychia, fam., gen. et sp. indet. (complete skeleton?; carapace fragments)*	Hirayama, 1996, 2000, 2004, 2006; Yasuno, 2004, 2005	Ok (KO-2), Ko
Pan-trionychia, fam., gen. et sp. indet.---at least two taxa	Hirayama, 2000, 2005, 2010; Hirayama et al., 2000	Kw-u (Kasekikabe)
Adocus sp.	Hirayama, 2002	Kt (Dinosaur Quarry)
Basilemys sp.	Hirayama, 2002	Kt (Dinosaur Quarry)
Kappachelys okurai	Hirayama et al., 2013; Nakajima et al., 2017	Ak
Trionychidae, gen. et sp. indet.	Hirayama, 2002; Nakajima et al., 2017	Kt (Dinosaur Quarry)
Squamata: 11 species including seven new taxa		
Tedorosaurus asuwaensis	Shikama, 1967, 1969; Evans and Matsumoto, 2015	Ko
Kaganaias hakusanensis	Evans et al., 2006	Kw-u (Kasekikabe)
Kuwajimalla kagaensis	Evans and Manabe, 2008	Kw-u (Kasekikabe)
Sakurasaurus shokawensis	Evans and Manabe, 1999a	Ok (KO-2)
Sakurasaurus sp.	Evans and Manabe, 2009	Kw-u (Kasekikabe)
Asagaolacerta tricuspidens	Evans and Matsumoto, 2015	Kw-u (Kasekikabe)
Kuroyuriella mikikoi	Evans and Matsumoto, 2015	Kw-u (Kasekikabe)
Hakuseps imberis	Evans and Matsumoto, 2015	Kw-u (Kasekikabe)
Second bicuspid form (Morphotype A)	Evans and Matsumoto, 2015	Kw-u (Kasekikabe)
Myrmecodaptria-like Morphotype B	Evans and Matsumoto, 2015	Kw-u (Kasekikabe)
Morphotype C	Evans and Matsumoto, 2015	Kw-u (Kasekikabe)
Choristodera: three species including one new taxon		
Monjurosuchus sp.	Matsumoto et al., 2007	Ok (KO-2), Kw-u (Kasekikabe)
Shokawa ikoi	Evans and Manabe, 1999b; Matsumoto et al., 2002	Ok (KO-2)
Neochoristodera indet.	Matsumoto et al., 2015	Kw-u (Kasekikabe)
Crocodyliform: one species		
Goniopholididae, gen. et sp. indet. (nearly complete skeleton)*	Kobayashi, 1998; Azuma, 2003	Kt (Dinosaur Quarry)
Pterosauria: four species		
Ornithocheiridae, gen. et sp. indet.	Unwin and Matsuoka 2000; Matsuoka et al., 2002	Kw-u (Kasekikabe)
Gnathosaurinae, gen. et sp. indet.	Unwin and Matsuoka 2000; Matsuoka et al., 2002	Kw-u (Kasekikabe)
Dsungariptreridae, gen. et sp. indet.	Unwin et al., 1996	Am
Dsungariptreroidea?, gen. et sp. indet.	Unwin and Matsuoka 2000; Matsuoka et al., 2002	Kw-u (Kasekikabe)
Theropoda: 10 species including two new taxa		
Fukuiraptor kitadaniensis	Azuma and Currie, 2000; Currie and Azuma, 2006	Kt (Dinosaur Quarry)
tyrannosauroid tooth*	Manabe, 2005; Ohashi, 2010	Kw-u (Kasekikabe)
Fukuivenator paradoxus	Azuma et al., 2016	Kt (Dinosaur Quarry)
ornitomimosaurian unguals*	Azuma et al., 2013; Shibata et al. 2017	Kt (Dinosaur Quarry)
oviraptorosaurian ungual	Manabe et al. 2000; Manabe and Barrett, 2000; Matsuoka et al., 2002; Ohashi, 2010	Kw-u (Kasekikabe)
Dromaeosauridae, gen. et sp. indet.	Azuma and Currie, 2000; Currie and Azuma, 2006	Kt (Dinosaur Quarry)
dromaeosaurid tooth*	Manabe, 2004	Ok (KO-2)
dromaeosaurid? teeth	Manabe and Barrett, 2000; Matsuoka et al., 2002; Ohashi, 2010	Kw-u (Kasekikabe)
theropod teeth	Manabe and Barrett, 2000; Matsuoka et al., 2002; Ohashi, 2010	Kw-u (Kasekikabe)
theropod tooth*	Tanimoto et al., 2009	Kw-l
Aves: one species		
Enantiornithes	Unwin and Matsuoka 2000; Matsuoka et al., 2002	Kw-u (Kasekikabe)
Sauropoda: two species including one new taxon		
Fukuititan nipponensis	Azuma and Shibata, 2010, Saegusa and Tomida, 2011	Kt (Dinosaur Quarry)
Titanosauriformes, gen. et sp. indet.	Barrett et al., 2002; Saegusa and Tomida, 2011	Kw-u (Kasekikabe)
Ornithischia: six species including three new taxa		
Albalophosaurus yamaguchiorum	Ohashi and Barrett, 2009	Kw-u (Kasekikabe)
Ornithischia indet.	Ohashi, 2011; Barrett and Ohashi, 2016	Ok, Kw-u (Kasekikabe)
Fukuisaurus tetoriensis	Kobayashi and Azuma, 2003 ; Shibata and Azuma, 2015	Kt (Dinosaur Quarry)
Koshisaurus katsuyama	Shibata and Azuma, 2015	Kt (Dinosaur Quarry)
Styracosterna indet.	Hasegawa et al., 1995; Barrett and Ohashi, 2016	Kw-u (Kasekikabe)
"iguanodontian teeth"	Hasegawa et al., 1995	Ok (KO-2, another locality), Am

TABLE 2. Numbers of species of selected vertebrate taxonomic groups of the Tetori Biota are compared with those from several famous Late Jurassic–Early Cretaceous *Lagerstätten*.

Biota/Fauna	Country	Age	fish	Amphibia	Tritylodontidae	Mammalia	Testudines	Ichthyosauria	Sphenodontidae
Tetori	**Japan**	**Hauterivian–Aptian**	**7**	**2**	**1**	**7**	**13**	**0**	**0**
Santana	Brazil	Early Cretaceous	30	2	0	0	6	0	0
Jehol	China	Early Cretaceous	15	8	0	17	4	0	0
Wealden	UK	Barremian–earliest Aptian	19	9	0	6	3	0	0
Las Hoyas	Spain	Upper Barremian	20	8	0	4	3	0	0
Solnhofen	Germany	Late Jurassic	107–130	0	0	0	8–10	2–4	6–8
Yanliao (=Daohugou)	China	Middle–Late Jurassic	2	6	0	11	0	0	0

Biota/Fauna	Squamata	Plesiosauria	Choristodera	Crocodylomorpha	Pterosauria	Dinosauria	Aves	total	References
Tetori	**11**	**0**	**3**	**1**	**4**	**18**	**1**	**68**	**This study**
Santana	0	0	0	2	25	4	0	69	Zhou and Wang (2010)
Jehol	5	0	7	0	24	38	53	171	Zhou and Wang (2017)
Wealden	14	1	0	10	8	36	4	110	Sweetman (2016)
Las Hoyas	8	0	0	9	1	7	3	63	Zhou and Wang (2010)
Solnhofen	4	0	0	8–10	16–19	2	2–3	155–190	Zhou and Wang (2010)
Yanliao (=Daohugou)	2	0	0	1	13	5	-	40	Zhou and Wang (2017)

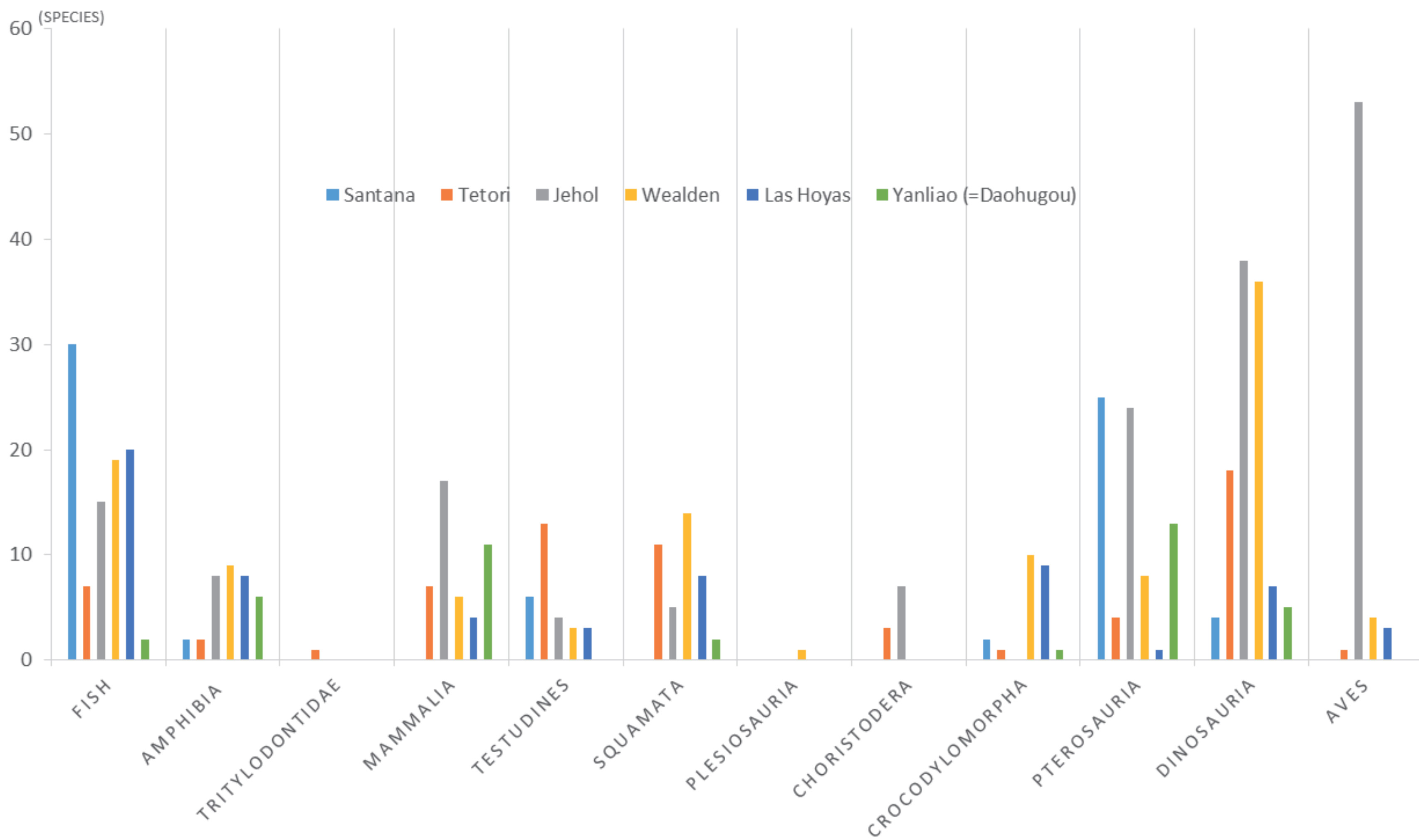

FIGURE 3. Comparison of the species diversity of the Tetori Biota with those of several famous Late Jurassic–Early Cretaceous *Lagerstätten*.

of the Solnhofen (155–190 species), Wealden (110 species) and Jehol (171 species) fauna/biotas. In general, the diversity of fish shares the significant part of the vertebrate diversity of each fauna. In the tetrapod diversity, only the Wealden (91 species) and Jehol (156 species) faunal biotas exceed the Tetori Biota (61 species). Thus the vertebrate diversity of the Tetori Biota can be considered to be comparable to those of the Late Jurassic–Early Cretaceous *Lagerstätten*.

Most striking faunal element of the Tetori Biota is a tritylodont synapsid, which has not been known in other fauna/biotas. Furthermore, choristoderes have been known only from the Jehol and Tetori biotas. It should be noted that choristoderes and a crocodyliform coexist only in the Tetori Biota, though these two faunal groups occur in different formations of the Tetori Group (Matsumoto et al., 2015). Remarkable higher diversity of the testudines is also another characteristic feature of the Tetori Biota. Mammals, squamates and dinosaurs are moderately diverse in the Tetori Biota. It should be noted that the squamate diversity of the Tetori Biota is much higher than that of the Jehol Biota, though generally the diversity of each vertebrate taxonomic group: e.g., mammals, pterosaurs, dinosaurs, and aves, is remarkably higher in the Jehol Biota than in the Tetori Biota. Low diversity of fish in comparison with other fauna/biotas may be additional characteristic feature of the Tetori Biota.

Compositions of dinosaur assemblages are different in almost coeval Tetori, Jehol and Wealden fauna/biotas. In the Tetori Biota, the dinosaur fauna is composed of possibly six ornithischians, two sauropods and possibly 10 theropods. On the other hand, 12 ornithischians, two sauropods and 24 theropods have been known in the Jehol Biota; 11 ornithischians, 15? sauropods and 11 theropods in the Wealden Fauna (Sweetman, 2016). Striking differences among three fauna/biotas are the high diversity of theropods in the Jehol Biota and that of sauropods in the Wealden Fauna. Besides them, Tetori dinosaur assemblage shows the comparable diversity with those of the Wealden and Jehol fauna/biotas.

Discussion

Vertebrate diversities of each fauna/biotas was probably affected by many biases, such as evolutionary history, habitat, palaeoecology, palaeobiogeography, research history and/or activities of selected taxa; palaeoclimatic conditions and their temporal changes, depositional environments and taphonomical conditions of the fossil-bearing strata, and so on. For examples, outstanding diversity of fish and pterosaurs in the Santana Fauna, those of mammals, pterosaurs in the Yanliao and Jehol biotas, those of dinosaurs (especially theropods) and aves in the Jehol Biota are most probably caused by the extensive studies of these taxonomic groups in these fauna/biotas (e.g., Kellner and Campos, 1999; Unwin and Martill, 2007; Zhou and Wang, 2010, 2017). Consequently, total species number of pterosaurs, theropods and aves in the Jehol Biota is over 100, and nearly 60 percent of total species number of whole vertebrates. In the Wealden Fauna, its long (almost 200 years) research history probably contributes its high vertebrate diversity.

Most of vertebrate skeletal fossils of the Tetori Biota have not yet been intensively studied especially in their systematic assignment, although some taxa, such as neopterygii, squamates and choristoderes, have (see Table 1). Thus the detailed comparison among the Tetori Biota and other fauna/biotas needs await further taxonomic works. However, some characteristic features of the Tetori Biota are briefly discussed here.

The low diversity of the fish fauna in the Tetori Biota may be explained in palaeoenviromental and taphonomical meanings by that a fluvial environment prevailed in the vertebrate fossil rich formations of the Tetori Group (e.g., Sano and Yabe, 2017), since the fish diversity is usually higher in large lakes than rivers (e.g., Joyce et al., 2005). In addition, the preservation potential of the biotas is also probably higher in the large lacustrine environments, where the Yanliao and Jehol biotas are preserved (e.g., Pan et al., 2013; Zhou and Wang, 2017), than the fluvial environments (e.g., Allison et al., 2008).

Remarkably high diversity of the testudines in the Tetori Biota owes mainly to the abundance of the Pantrionychia (e.g., Hirayama, 2006), which has been absent in the Wealden Fauna (Sweetman, 2016), and very rare (only one specimen) in the Jehol Biota (Zhou and Wang, 2017). These data support the hypothesis that the centre of origin of this taxon group existed in the eastern margin of East Asia and/or Central Asia in the Early Cretaceous (e.g., Hirayama et al., 2013; Nakajima et al., 2017).

Choristoderes have been known only from the Jehol and Tetori biotas among seven fauna/biotas. It should be noted that all three known choristoderan morphotypes are present only in the Jehol and Tetori biotas in the world (Matsumoto et al., 2015). Absence of this group in the Santana Fauna is not surprising, because choristoderes are considered as the Laurasian taxa (e.g., Matsumoto et al., 2015). Its absence and the presence of crocodyliforms in the European and Yanliao fauna/biotas is supposed to be explained by the warmer climatic conditions in these regions than those in the Jehol and Tetori regions (Amiot et al., 2011; Matsumoto et al., 2015; Sweetman, 2016). The faunal change from the choristoderan occurrences without crocodilyforms to a crocodilyform occurrence without choristoderes in the Tetori Group, indicates the climatic change from cool to warm during the period (possibly Barremian to Aptian) when the Tetori Biota flourished (Yabe et al., 2003; Amiot et al., 2011; Matsumoto et al., 2015). It is notable that such an Early Cretaceous climatic change has not been recognized in the Jehol Biota (Sano and Yabe, 2017). On the contrary, the faunal change from the crocodylomorph occurrence without choristoderes in the Yanliao Biota to the choristoderan occurrences without crocodylomorphs in the Jehol Biota occurred in the northeastern China (Zhou and Wang, 2017). It is suggested that crocodylomorphs could expand their distribution to northeastern China in the Late Mesozoic, and their absence in the Jehol Biota should be explained by some palaeoclimatic or palaeogeographical conditions at that time, or their temporal changes around the Jurassic–Cretaceous transition (e.g., Xu et al., 2017).

CONCLUDING REMARKS

The study of the vertebrate fossils from the Tetori Group has a relatively long history, starting 50 years ago (Shikama, 1967), but active research have been conducted after the discovery of the dinosaurs about 30 years ago (Shibata et al., 2017, Table 1). As discussed above, the vertebrate diversity of the Tetori Biota can be considered to be comparable to those of the Late Jurassic–Early Cretaceous *Lagerstätten*, and provide the unique information of the vertebrate evolution and climatic change in East Asia.

The present vertebrate diversity of the Tetori Biota basically owes to the extensive studies of the vertebrate faunas from the two localities: KO-2 in the Shokawa area and Kasekikabe in the Shiramine area (e.g., Evans et al., 1998; Matsuoka, 2000a; Matsuoka et al., 2002). The recent studies of mammals and an avian eggshell from the Kitadani Dinosaur Quarry (Imai and Azuma, 2015; Miyata et al., 2016) clearly indicate the great potential of the microvertebrate studies in the Kitadani Formation. Further studies of ichnofossils, such as footprints and eggshells, may provide additional information of unrecognized vertebrate diversity of this biota (e.g., Matsukawa et al., 2005; Isaji and Matsushita, 2005; Isaji et al, 2006; Lee et al., 2010), as with the eggshell study of the Sasayama Group (Tanaka et al., 2016). Yoshimura and Matsuoka (2010) reported a testudine fossil from the Ushimaru Fomation in the Shokawa area, which underlies the Mitarai Formation. This record represents the earliest vertebrate record in the Tetori Group, and clearly suggests the lower part of DS2 of Sano (2015) can be also candidate for the future vertebrate palaeontological works. Furthermore, since brackish and marine molluscs were reported from many horizons/localities of DS2 of the Tetori Group (e.g., Sano, 2015; Koarai and Matsukawa, 2016), sometimes with shark teeth (e.g., Kitaura et al., 1974; Yamada, 1990), future discoveries of marine reptiles from the Tetori Group also can be supposed, as with the Wealden Fauna, where the occurrence of a plesiosaur was reported (Sweetman, 2016). Thus it is expected that more diverse vertebrate fauna should be recognized in the Tetori Biota in near future.

Some similarities and remarkable dissimilarities have been recognized in the vertebrate faunal and floral composition of the coeval Tetori and Jehol biotas, and thus possible palaeobiogeographical differentiation in East Asia is suggested (Sano and Yabe, 2017). Recently the rich Albian vertebrate fauna has been recognized from the Sasayama Group in the Tamba–Sasayama Region, southwestern Japan (Saegusa et al., 2008; Kusuhashi et al., 2013; Ikeda and Saegusa, 2013; Saegusa and Ikeda, 2014; Ikeda et al., 2015, 2016; Tanaka et al., 2016; Shibata et al., 2017), which is possibly correlated with DS4 of Sano (2015) in the Hakusan Region. Combination of the vertebrate diversities of the Tetori Biota and the faunal assemblage of the Sasayama Group possibly provides the information of the faunal change and/or evolution during the Early Cretaceous in the eastern margin of East Asia.

Palaeogeographical and palaeoclimatic conditions causing the strong provincialisms of dinosaurs and other biota in the Early Cretaceous in East and Southeast Asia attract much attention recently (e.g., Philippe et al., 2014; Amiot et al., 2015; Matsumoto et al., 2015; Shibata et al., 2017; Suarez et al., 2017). Further comparison of vertebrate diversities including microvertebrates in almost coeval strata in East and Southeast Asia: e.g., the Sindong and Hayang groups in South Korea (e.g., Lee et al., 2001; Yabumoto, et al., 2006), the Xinminbao Group in the Mazongshan Region in northwestern China (e.g., Tang et al., 2001), Xinlong Formation in the Napai Region in southern China (Mo et al., 2016), and the Khorat Group in northern Thailand (e.g., Buffetaut et al., 2006; Fernandez et al., 2009), with those of northeastern China (the Jehol Biota) and Japan (the Tetori Biota and the Tamba–Sasayama fauna), probably provides the useful information to reveal the palaeo(bio)geographical and palaeoclimatic reconstruction in Asia, and also the evolution of the Mesozoic terrestrial ecosystem.

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