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A review of the vertebrate fossil assemblage from the Lower Jurassic Nishinakayama Formation in the Ischimachi district of Toyota Town, Yamaguchi Prefecture, Japan

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Abstract: The Lower Jurassic Nishinakayama Formation in the Ishimachi district of Toyota Town in the Toyora region of Shimonoseki City, Yamaguchi Prefecture has yielded a small but important assemblage of vertebrate fossils from shallow-marine rocks. This vertebrate fossil assemblage includes the body fossils of teleost fish (Leptolepidiformes?), crocodylomorphs (Crocodylomorpha), and turtles (Testudinata), but no vertebrate trace fossils have yet been identified. The crocodylomorph and turtle specimens, together with a turtle shell fragment from the Kuruma Group in the Toyama Prefecture, represent the oldest records of their respective clades within Japan, and the turtle specimen is particularly significant because it is the only articulated Early Jurassic turtle known from marine strata. Although limited, the vertebrate fossil assemblage of the Nishinakayama Formation is internationally significant because it is both comparable with other Early Jurassic vertebrate fossil assemblages worldwide and among the only records of Early Jurassic tetrapod fossils in Japan.

Key words: Vertebrate palaeontology, Early Jurassic, Toyora Group, Toarcian Ocean Anoxic Event.

INTRODUCTION

The shallow marine Lower to Middle Jurassic sediments of the Toyora Group are exposed in the vicinity of Toyota Town in Shimonoseki City, Yamaguchi Prefecture, Japan (Fig. 1), and these strata represent one of the best Toarcian palaeoenvironmental records from northwestern Panthalassa (Izumi *et al*., 2012, in press). The Toarcian is characterized by an interval of marked global environmental change and an associated turnover of marine invertebrate faunas; however, it is unclear how vertebrate animals were affected by these changes, if at all. To better understand this, it is necessary to critically assess the global fossil record of Early Jurassic vertebrates.

Within the Toyora Group, vertebrate fossils are known only from the Nishinakayama Formation in the Ishimachi District of Toyota Town (Fig. 2), and the material from the Nishinakayama Formation represents one of the only significant records of Lower Jurassic tetrapod vertebrate body fossils in Japan. The Nishinakayama Formation is important because it is the only stratigraphic unit in East Asia from which a stable carbon-isotope perturbation associated with the Toarcian ocean anoxic event has been identified (Izumi *et al*., 2012, 2018a, b; Kemp & Izumi, 2014; Them *et al*., 2017). Furthermore, it is the only stratigraphic unit in East Asia to have yielded articulated vertebrate body fossils of definitively Toarcian age. Although the Lower Jurassic Lower Lufeng Formation in the Yunnan Province of southwestern China has yielded a diverse assemblage of

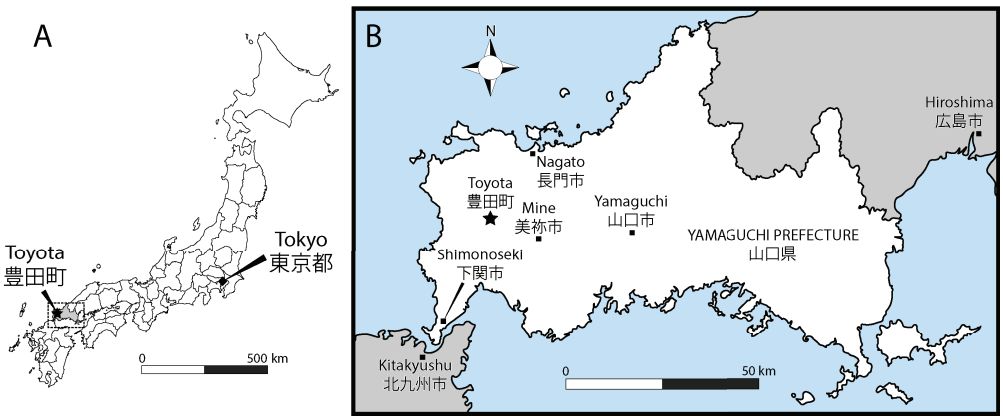

Figure 1. Geographic location of the study area (Ishimachi district, Toyota Town) within (A) Japan and (B) Yamaguchi Prefecture.

well-preserved vertebrate body fossils, including reptiles (e.g., Young, 1941; Luo & Wu, 1994; Barrett & Xu, 2005; You *et al*., 2014), those strata are likely Hettangian to Pliensbachian in age based on biostratigraphic correlation (Luo & Wu, 1995). It is possible that the Lower Lufeng Formation may be as young as Toarcian in age based on magnetostratigraphy (Huang *et al*., 2005); however, that age assignment is not supported by other methods of stratigraphic correlation.

Despite the inherent significance of the vertebrate fossils from the Nishinakayama Formation, vertebrate palaeontological research focused on this formation is scarce, particularly over the past two decades. This is partially owing to the relatively limited nature of exposures of the Nishinakayama Formation; however, despite the limited outcrop exposure and rarity of vertebrate fossils, several potentially significant vertebrate fossils have been reported from the formation beginning during the 1980s (e.g., Tanabe *et al*., 1982; Manabe & Hasegawa, 1998; Hasegawa *et al*., 1998; Nakada & Matsuoka, 2012). Herein, we summarize the published record of vertebrate fossils from the Nishinakayama Formation, provide new observations on the taxonomy of these fossils based on recent phylogenetic systematics, and compare the vertebrate fossil assemblage of the Nishinakayama Formation to other Early Jurassic vertebrate fossil assemblages both within Japan and globally.

Institutional Abbreviations

FPDM, Fukui Prefectural Dinosaur Museum (福井県立恐竜博物館); GMNH, Gunma Museum of Natural History (群馬県立自然史博物館); MMHF, Mine Museum of History and Folklore (美祢市歴史民俗資料館); NU, Niigata University (新潟大学)

GEOLOGIC SETTING

The Nishinakayama Formation is a stratigraphic unit within the Lower to Middle Jurassic Toyora Group, which crops out around the towns of Toyota and Kikugawa in the western Yamaguchi Prefecture of southwestern Japan (Kobayashi, 1926; Takahashi *et al*., 1965). The Toyora Group is a package of siliciclastic continental shelf sedimentary strata with sporadic horizons of volcanic tuffs (Tanabe *et al*., 1982). Outcrop of the Toyora Group is distributed across two districts of the Tabe Basin separated by the NW-SE-trending Tabe Fault. These districts are the Ishimachi (northern) district and the Tabe (southern) district. The study area comprises the northern Ishimachi District along distributary channels of the Koya River where the Nishinakayama Formation is primarily exposed along incised valleys and streambeds (Fig. 2).

In the study area of the Ishimachi district, the Toyora Group unconformably overlies the metamorphosed pre-Jurassic rocks of the Nagato Tectonic Zone (Kawamura, 2010) and itself comprises Lower to Middle Jurassic (Sinemurian to Bathonian)

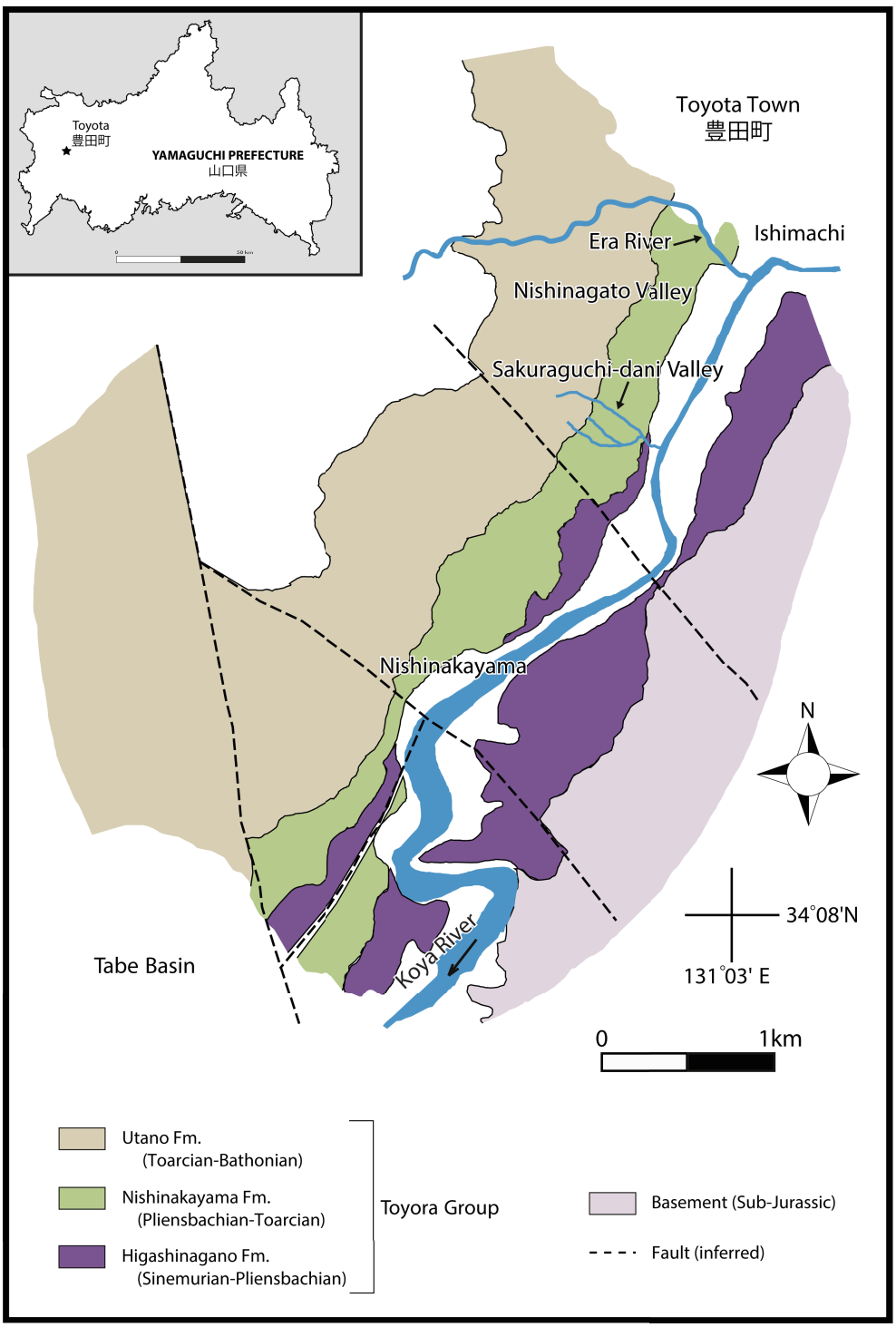

Figure 2. Geologic map of the study area in the Ishimachi district of Toyota Town, Shimonoseki City, Yamaguchi Prefecture. Vertebrate fossil-bearing localities discussed within are highlighted by name. Modified after Nakada and Matsuoka (2011) and Izumi *et al*. (2012).

shallow marine siliciclastic deposits of the Higashinagano Formation (Sinemurian-Pliensbachian), Nishinakayama Formation (Pliensbachian-Toarcian), and Utano Formation (Toarcian-Bathonian), listed in ascending stratigraphic order. These strata have been interpreted to represent transgressive, inundative, and regressive phases of a major sedimentary cycle, respectively (Hirano, 1971). The Nishinakayama Formation comprises silty shale, mudstone, and sandstone horizons which were deposited in a shallow marine environment with terrestrial influence (Tanabe *et al.*, 1982; Kemp & Izumi, 2014). The formation in this region is approximately 300 meters in maximum stratigraphic thickness, and multiple informal lithostratigraphic nomenclatural schemes for dividing it have been used over the past several decades. Hirano (1971, 1973a, 1973b) divided the Nishinakayama Formation into a lower Nm member and an upper Na Member; Tanabe *et al*. (1982) divided it into Na, Nb, and Nc members, listed in ascending stratigraphic order; and Nakada and Matsuoka (2011, 2012) utilized the divisions of Hirano (1971, 1973a, 1973b) but renamed those divisions the Sakuraguchidani Mudstone Member (="Nm member") and the Ischimachi Sandstone and Mudstone Member (="Na member"). Herein, we will utilize the lithostratigraphic framework of Tanabe *et al*. (1982) unless otherwise noted. In ascending stratigraphic order, the Nishinakayama Formation *sensu* Tanabe *et al*. (1982) comprises the Na member (silty shale, ~90 m thick), Nb member (dark silty shale with intercalated fine-grained sandstone and laminated black shales, ~160 m thick), and Nc member (alternating sandstone and mudstone, ~20-60 m thick). The "Nb member" is relatively well-exposed in the region surrounding Toyota Town, primarily in valleys formed by both permanent rivers and ephemeral mountainside streams; however, continuous exposures are rare. It is also the most fossiliferous member of the Nishinakayama Formation in the Ishimachi district, and it is from this interval that the vertebrate fossils discussed herein originated. The uppermost "Nc member" is considered a barren interval for macrofossils, and no ammonite biozones have been established within it. The Toyora Group is unconformably overlain by the Cretaceous Kwanmon (=Kanmon) Group in the Ishimachi district.

The Toyora Group in the Ishimachi district is characterized by abundant marine macrofossils such as ammonites, whereas it is predominantly characterized in the Tabe district by the presence of abundant plant fossils and a relative lack of marine fossils (Yamada & Ono, 2005). As a result of this, the biostratigraphy is better established in the Ishimachi district. The biostratigraphic framework of the Toyora Group in the Ishimachi district was first established by Hirano (1971, 1973a, b), and that framework was recently revised for the Sakuraguchi-dani section by Nakada and Matsuoka (2011). The biostratigraphic framework recognized by Hirano (1973b) comprises three ammonite biozones within the "Nb member" of the Nishinakayama Formation. In ascending stratigraphic order, those are the *Fontanelliceras fontanellense*, *Protogrammoceras nipponicum*, and *Dactylioceras helianthoides* zones.

Nakada and Matsuoka (2011) recognized four ammonite assemblage biozones within the "Nb member" of the Nishinakayama Formation in the Sakuraguchi-dani valley section. In ascending stratigraphic order, those ammonite biozones are the *Canavaria japonica*, *Paltarpites paltus*, *Dactylioceras helianthoides*, and *Harpoceras inouyei* zones. The *Canavaria japonica* Zone is only exposed along the southern branch of the Sakuraguchi-dani valley and is characterized by the occurrence of *Canavaria japonica* and the Pliensbachian index taxon *Amaltheus margaritatus*. The same morphotype of *Amaltheus margaritatus* occurs in Tethyan marine deposits of northwestern Europe, which supports correlation between the *Canavaria japonica* Zone of Japan with the *Pleuroceras apyrenum* Subzone of Europe (Meister, 1988). Nakada and Matsuoka (2011) placed the boundary between the Pliensbachian and Toarcian stages at the base of the *Paltarpites paltus* Zone; however, the contact between the *Canavaria japonica* and *Paltarpites paltus* zones is ambiguous owing to a paucity of ammonite fossils from that interval. The biostratigraphic framework of Nakada and Matsuoka (2011) has not yet been established beyond the Sakuraguchi-dani section.

In the Sakuraguchi-dani valley section of the Ishimachi district, a ~3‰ negative organic stable carbon isotope excursion ($\delta^{13}C_{org}$) spanning ~30 m within the "Nb member" was recognized via $\delta^{13}C_{org}$ isotope ratio mass spectrometry (IRMS) analysis,

which was interpreted as a diagnostic expression of the Toarcian ocean anoxic event (Izumi *et al*., 2012; Kemp & Izumi, 2014; Izumi *et al*., 2018a, b). That interpretation was supported by ammonite biostratigraphy. The negative carbon isotope excursion observed in the Sakuraguchi-dani valley section occurs within the *Paltarpites paltus* and *Dactylioceras helianthoides* Zone of Nakada and Matsuoka (2011) within the lower Toarcian Stage (Izumi *et al*., 2018a, b) and was chemostratigraphically correlated to lower Toarcian sections in Europe.

MATERIALS AND METHODS

The published record of vertebrate fossils from the Nishinakayama Formation is summarized herein. Comments pertaining to MMHF specimens are made on the basis of firsthand observations by the authors unless otherwise noted by a citation. Additionally, the turtle (MMHF 5-00001) and crocodylomorph (MMHF-5-00002) specimens are briefly reassessed in a modern phylogenetic systematic context.

VERTEBRATE BODY FOSSILS

Actinopterygii

The earliest mention of fossil actinopterygiian fish from the Nishinakayama Formation was made by Tanabe *et al*. (1982), who noted the presence of specimens tentatively referred to the teleost clade Leptolepiformes within the *Protogrammoceras nipponicum* and *Dactylioceras helianthoides* ammonite zones of Hirano (1973b); however, no further data were provided for those specimens. Tanabe (1991) also noted the presence of fossil fish scales in the *Protogrammoceras nipponicum* Zone from the Ishimachi and Sakuraguchi-dani Valley localities and in the *Dactylioceras helianthoides* Zone from the Nishinagato Valley locality. Additionally, Tanabe (1991) noted a specimen referred to *Leptolepis?* sp. from the Nishinagato Valley locality in the *Dactylioceras helianthoides* Zone. Again, no further data were provided for those specimens. The observations of Tanabe (1991) followed the ammonite biostratigraphy established by Hirano (1973b).

Nakada and Matsuoka (2012) reported a partial fish skeleton (NU-MV0001; see Nakada & Matsuoka, 2012: Fig. 4) from the Sakuraguchi-dani Mudstone Member of the Nishinakayama Formation in the northern branch of the Sakuraguchi-dani Valley locality. The Sakuraguchi-dani Member, which roughly correlates to the "Nb member," is characterized by laminated black silty mudstones (Nakada & Matsuoka, 2011), and the horizon which yielded NU-MV0001 is further characterized by parallel lamination, pyrite granules, ammonoid fossils, and fossil wood fragments (Nakada & Matsuoka, 2012: horizon 23-1). The specimen was collected from the *Harpoceras inouyei* Zone of the revised ammonite biostratigraphy of the Nishinakayama Formation established by Nakada and Matsuoka (2011). NU-MV0001 comprises a 15 mm portion of the postcranial skeleton including vertebrae, ribs, and a caudal fin, and it is preserved in the same slab as an individual of the ammonite *Fuciniceras nakayamense* (Nakada & Matsuoka, 2012).

In addition to the published record of fossil actinopterygiian fish from the Nishinakayama Formation, previously unpublished teleost specimens are reposited at the Mine Museum of History and Folklore in Mine City, Yamaguchi Prefecture. One specimen tentatively referred to *Leptolepis* (MMHF 5-00003; Fig. 3A) comprises the anterior end of an individual including the skull, pectoral girdle, and a portion of the vertebral column. This specimen was collected in Ishimachi, Toyota Town. Two other specimens (MMHF 5-00004; MMHF 5-00005) comprise partial postcranial skeletons tentatively referred to Leptolepiformes. MMHF 5-00004 (Fig. 3B) was collected in Ishimachi, Toyota Town by a Mrs. or Mr. Shiraishi. MMHF 5-00005 (Fig. 3C) was discovered in the Nishinakayama Quarry in Kikugawa Town by Mr. Kenro Hironaka. No further locality or occurrence data are documented for any of these specimens. The anatomy of the fish fossils from the Nishinakayama

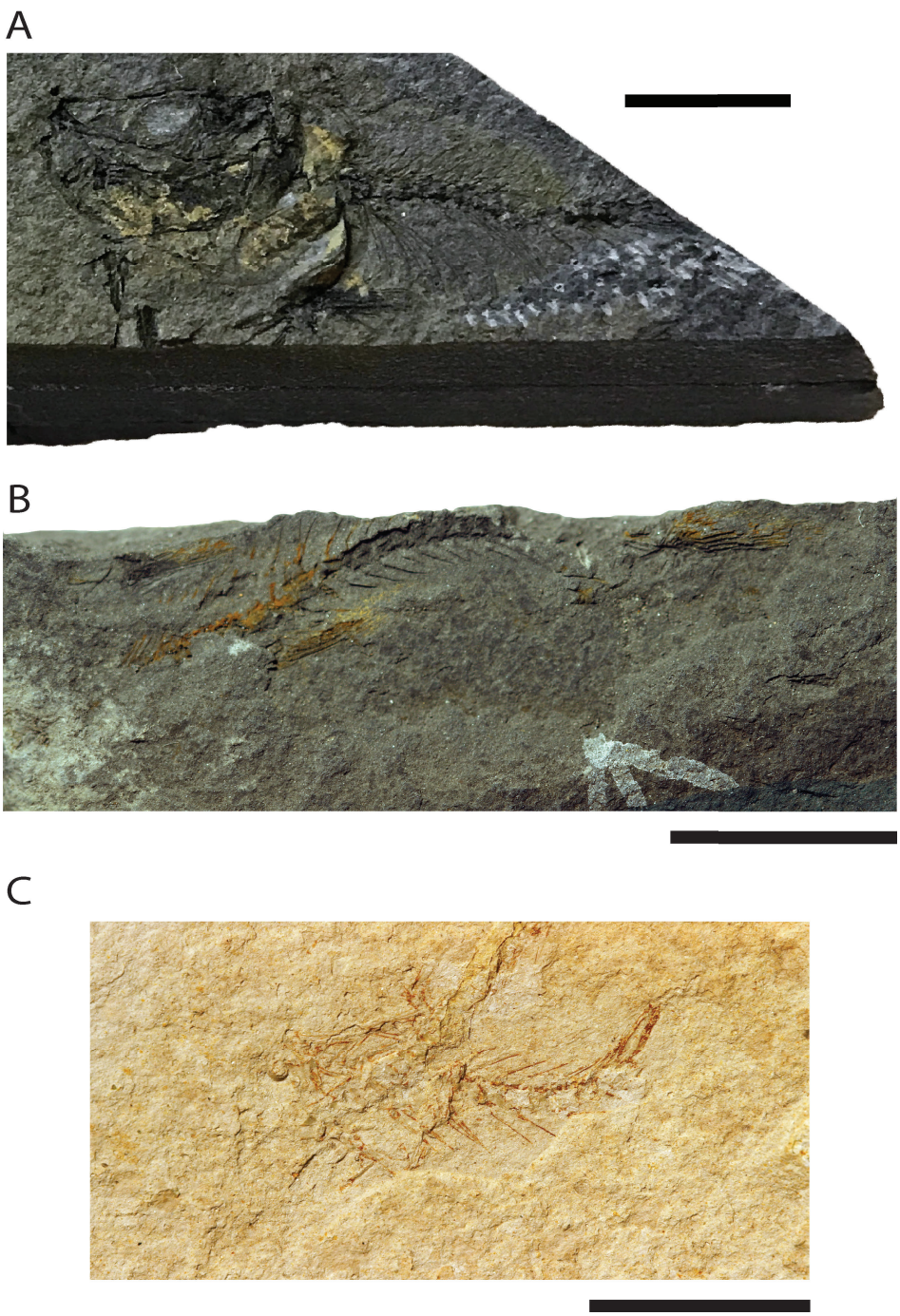

Figure 3. Fossil teleost actinopterygian fish from the Lower Jurassic Nishinakayama Formation, Toyota Town, Yamaguchi Prefecture, Japan. A, Leptolepiformes? (MMHF 5-00003). B, Leptolepiformes? (MMHF 5-00004). C, Leptolepiformes? (MMHF 5-00005). Scale bars equal 10 mm.

Formation is superficially consistent with leptolepiform teleosts; however, further detailed study of these specimens is required before their taxonomy may be rigorously tested, and they are herein tentatively referred to Leptolepiformes.

Crocodylomorpha

A single crocodylomorph specimen (MMHF 5-00002; Fig. 4) has been reported from the Nishinakayama Formation (Manabe & Hasegawa, 1998). MMHF 5-00002 was collected as an isolated slab near the Era River in Toyota Town, but more detailed locality data are not available for the specimen. The crocodylomorph specimen comprises associated caudal and trunk (i.e., dorsal) vertebrae, the distal portion of the left tibia, the distal portion of the left fibula, the left tarsus, the left pes, and several postcranial osteoderms from a single individual. The specimen is preserved mostly as external molds of bones on a part and counterpart of a split slab of mudstone, and a specimen of the ammonite *Harpoceras inouyei* is preserved on the same slab. Given that *Harpoceras inouyei* is only known to occur within the "Nb member" of the Nishinakayama Formation (Nakada & Matsuoka, 2011), it follows that the MMHF 5-00002 slab itself originated from the "Nb member."

Manabe and Hasegawa (1998) tentatively referred MMHF 5-00002 to Atoposauridae, a clade of crocodylomorphs long considered important components of Mesozoic ecosystems; however, they emphasized the tentative nature of their assignment of the specimen to Atoposauridae and the need for further study of the specimen. Recent phylogenetic revisions by Tennant *et al*. (2016) have rendered Atoposauridae a much more taxonomically and chronostratigraphically exclusive clade restricted to the Upper Jurassic of Europe. Manabe and Hasegawa (1998) noted similarities between MMHF 5-00002 and *Alligatorellus beaumonti*, an atoposaurid from the Upper Jurassic of France, including anteroposteriorly elongated caudal centra, elongated metatarsals, and morphologically comparable osteoderms; however, these features are widespread among crocodylomorphs, and the specimen has not yet been referred to a taxon on the basis of apomorphies (e.g, Bell *et al*., 2004; Nesbitt & Stocker, 2008) or placed into a rigorous phylogenetic analysis.

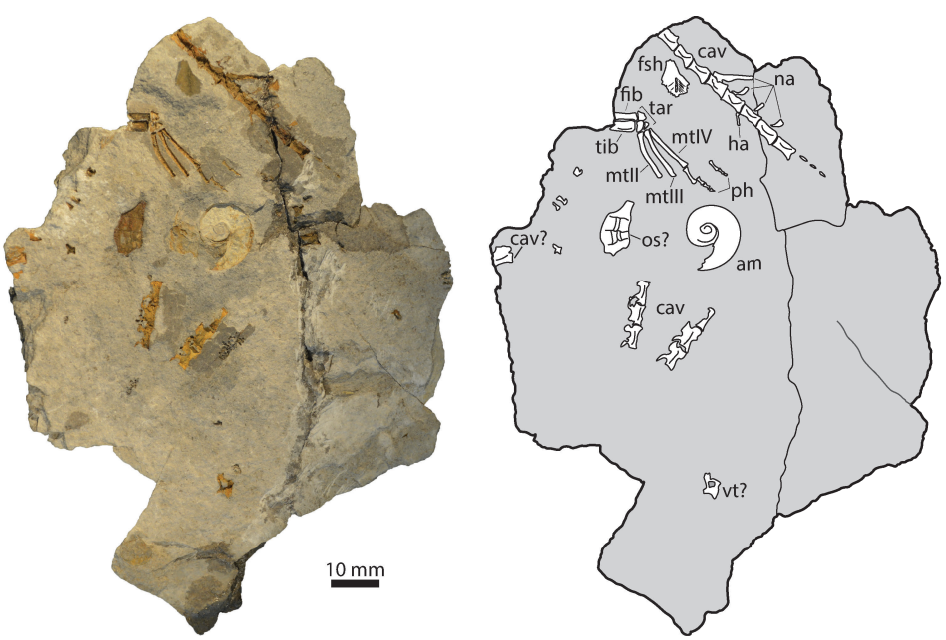

Figure 4. Fossil crocodylomorph (Crocodylomorpha, MMHF 5-00002) from the Lower Jurassic Nishinakayama Formation, Toyota Town, Yamaguchi Prefecture, Japan. Photograph and line drawing. **Abbreviations**: **am**, ammonite fossil; **cav**, caudal vertebrae; **fib**, fibula; **fsh**, fish fossil; **ha**, haemal arch; **mt**, metatarsal; **na**, neural arch; **os**, osteoderm; **ph**, phalanges; **tar**, tarsals; **tib**, tibia; **II-IV**, digit number.

Although fairly incomplete, MMHF 5-00002 possesses a limited number of character states that are consistent with a referral to Crocodylomorpha. The specimen possesses four or fewer phalanges on pedal digit IV, which is diagnostic of Crocodylomorpha under accelerated transformation (“ACCTRAN”) parsimony parameters (Nesbitt, 2011: Character 396-1). Furthermore, MMHF 5-00002 possesses a compact metatarsus (at least half as wide as long), which is unambiguously diagnostic of a more exclusive clade comprising (*Sphenosuchus* + Crocodyliformes) within Crocodylomorpha (Nesbitt, 2011: Character 382-1). Given both the geographically and temporally restricted nature of the revised Atoposauridae *sensu* Tennant *et al.* (2016) and the combination of apomorphic taxonomically informative morphological features preserved in MMHF 5-00002, a referral to Crocodylomorpha rather than Atoposauridae is therefore perhaps the most conservative taxonomic assignment possible for MMHF 5-00002 at this time. Regardless, MMHF 5-00002 represents the oldest record of a fossil archosaur in Japan, and further study of the specimen will elucidate the evolution and distribution of crocodylomorphs during the Early Jurassic in East Asia.

Testudinata

Fujinaga (1990) reported a single turtle specimen comprising an associated skull, shell, and forelimb (MMHF 5-00001; Fig. 5) from the Nishinakayama Formation near the mouth of the Era River in Toyota Town. MMHF 5-00001 was collected as an isolated slab of mudstone, which was split into a part and counterpart to expose the skeleton. MMHF 5-00001 was described in more detail by Hasegawa *et al*. (1998), who formally referred it to Testudines but noted that further preparation of the specimen was necessary before a detailed description or further taxonomic assignment could be given. A specimen of the ammonoid *Cleviceras chrysanthemum* is preserved on the same slab, and Cleviceras chrysanthemum is only known to occur within the “Nb member” of the Nishinakayama Formation (Nakada & Matsuoka, 2011), so it is most likely that the MMHF 5-00001 slab originated from the “Nb member.”

MMHF 5-00001 preserves at the least a skull, cervical vertebrae, a partial right forelimb comprising the zeugopodial and autopodial elements, a carapace, and plastral elements from an individual partially articulated turtle skeleton; however, the specimen is split into part and counterpart through the carapace, and the entire skeleton is not exposed. The skull and cervical vertebrae remain too poorly exposed for detailed description. The zeugopodium and autopodium of the right forelimb are seemingly complete, preserving the ulna, radius, carpus, and manus. The ulna and radius are 8 mm in length, and articulate with one another via a ridge on the ulna. At least eight flattened carpal elements are preserved. The manus is not elongated and modified into a paddle or flipper. The phalanges are taphonomically offset from their respective metacarpals, but Hasegawa *et al*. (1998) estimated a phalangeal formula of 2-3-3-3-3 for the digits of the manus.

Hasegawa *et al*. (1998) estimated the complete carapace to be 70 mm in length and 62 mm in width. The nuchal is broad and ventrally flat. There appear to be seven neural osteoderms and eight costal osteoderm pairs (= “coastal” osteoderms in Hasegawa *et al*, 1998). Nine peripheral osteoderms are exposed; however, the exact number of peripheral osteoderms present in the carapace remains unknown. Hasegawa *et al*. (1998) noted the presence of large fontanelles between the costal and peripheral osteoderms. Of the plastron, Hasegawa *et al*. (1998) tentatively identified two elements as the entoplastron and a fragment of the plastron tentatively identified as the hypoplastron. The entoplastron is a cruciform element 15 mm in length with a prominent keel on one side. The tentative hypoplastron fragment was identified only based on its position relative to the carapace, and it is too incomplete to describe its morphology.

Recent phylogenetic revisions of early turtle relationships have rendered the clade Testudines (i.e., the crown group of living turtles) more taxonomically exclusive in the time since the original publication of MMHF 5-00001 (e.g., Joyce, 2007; Anquetin, 2012; Joyce *et al*., 2016). The fossil record of Testudines begins in the Upper Jurassic, and all known Lower Jurassic turtles belong to the clade Testudinata outside of Testudines. Hasegawa *et al*. (1998) noted superficial similarities between the

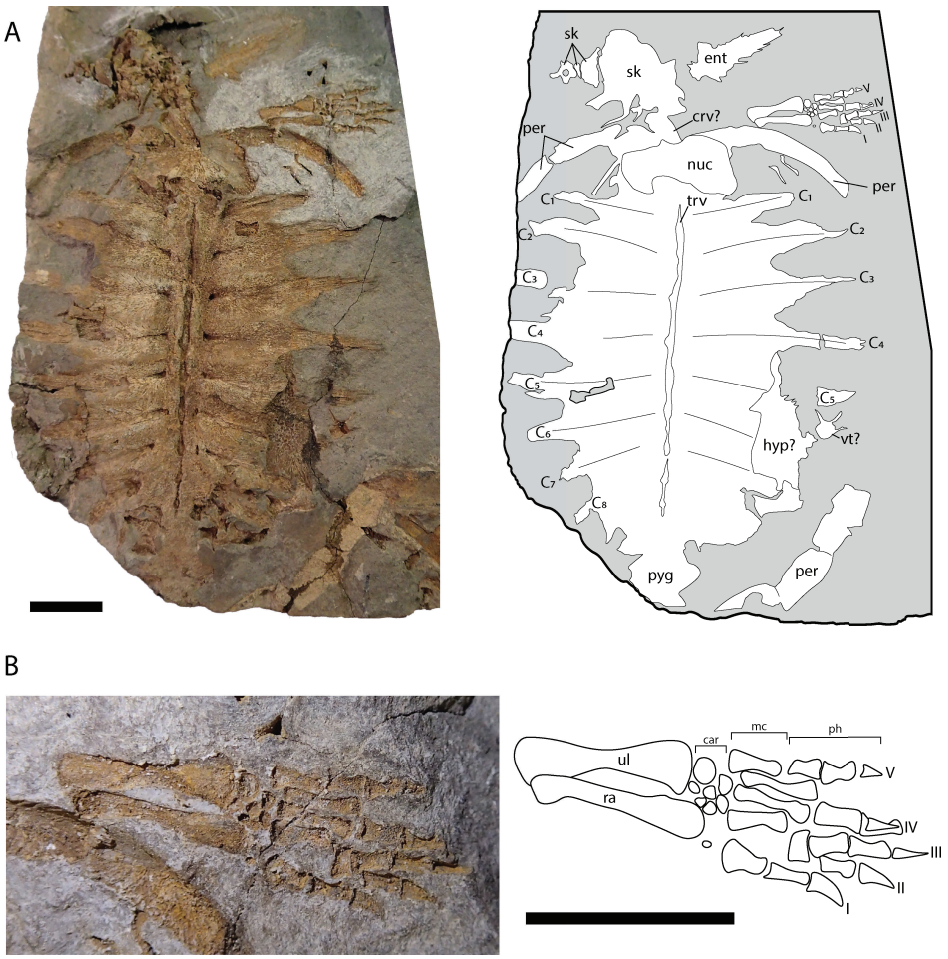

Figure 5. Fossil turtle (Testudinata, MMHF 5-00001) from the Lower Jurassic Nishinakayama Formation, Toyota Town, Yamaguchi Prefecture, Japan. (A) Photograph and line drawing of part slab and (B) close up photograph and line drawing of partial forelimb from part slab. **Abbreviations**: **car**, carpals; **crv**, cervical vertebrae; **C#**, costal plate of carapace; **ent**, entoplastron; **hyp**, hypoplastron; **mc**, metacarpals; **per**, peripheral plate of carapace; **ph**, phalanges; **pyg**, pygal plate of carapace; **ra**, radius; **sk**, skull; **trv**, trunk vertebrae; **ul**, ulna; **vt**, vertebra; **I-V**, digit number. Scale bars equal 10 mm.

carapace of MMHF 5-00001 and Toxochelyidae; however, Toxochelyidae is a derived clade of sea turtles within Testudines known only from the Cretaceous, and MMHF 5-00001 lacks other diagnostic features of *Toxochelys*, so any similarities present between the two are likely the result of evolutionary convergence rather than shared ancestry. Pending further study of the anatomy and phylogeny of MMHF 5-00001, a referral to Testudinata is the most conservative assignment possible at this time. Although a fragment of turtle shell has been reported from the Lower Jurassic Kuruma Group in central Japan (Sonoda *et al*., 2015), MMHF 5-00001 represents the oldest relatively complete fossil record of turtles in Japan, and given the rarity low taxonomic diversity of turtle fossils from the early Mesozoic (i.e., the Triassic and Early Jurassic), further study of this specimen has great potential for elucidating the early evolution of turtles.

DISCUSSION

Aside from the Toyora Group, only the brackish to shallow-marine Lower to Middle Jurassic Kuruma Group which crops

out in the Toyama, Nagano, and Niigata prefectures (e.g., Goto & Tazaki, 1996) has also produced significant vertebrate fossil material from Lower Jurassic strata in Japan. Perhaps the earliest reference to vertebrate material from the Kuruma Group was a teleost fish skull tentatively referred to the genus *Leptolepis* (Oe & Chiba, 1988). Subsequent discoveries of vertebrate fossils from the Kuruma Group include chondrichthyan teeth (Takakuwa & Hasegawa, 1992); plesiosaurid teeth (Tanimoto and Okura, 1989; Takakuwa & Hasegawa, 1992); and dinosaur trackways (Hatakeyama, 1995; Matsukawa *et al*., 2005). Most recently, Sonoda *et al*. (2015) reported a partial isolated costal osteoderm plate of a turtle (FPDM-V9543), a ganoid fish scale (FPDM-V9544), and several other indeterminate bone fragments. Putative vertebrate coprolites have also been discovered from the Kuruma Group (pers. obs.); however, these remain unpublished. Additionally, an acrodontid chondrichthyan tooth was reported from the marine Lower Jurassic Iwamuro Formation near Numata City, Gunma Prefecture (GMNH-PV 2406; Takakuwa & Gunma Fossil Club, 2011).

To date, neither chondrichthyan nor plesiosaurid fossils have been identified from the Nishinakayama Formation; however, their eventual discovery would be unsurprising given the occurrence of both taxa in Lower Jurassic marine strata elsewhere both within Japan and globally. The presence of fish fossils referred to the genus *Leptolepis* from both the Nishinakayama Formation and the Kuruma Group is intriguing; however, none of these specimens have yet been described in enough detail to allow morphological or systematic comparison. The carapace of MMHF 5-00001 is not exposed such that individual costal plates can be directly compared to the material from the Kuruma Group, but together, these specimens represent the oldest record of turtles in Japan. No crocodylomorph fossils have been discovered from Lower Jurassic strata within Japan outside of the Nishinakayama Formation; however, their eventually discovery elsewhere would be unsurprising given the abundance of crocodylomorph taxa present in both non-marine and marine Lower Jurassic strata globally. The absence of vertebrate trace fossils within the Nishinakayama Formation is conspicuous given the shallow marine environment and the abundance of vertebrate trace fossils in the Kuruma Group; however, this lack of a vertebrate trace fossil record may be a result of limited outcrop and sampling rather than a natural indication of absence. The presence of dinosaur footprints within the Kuruma Group indicates that it was at least occasionally deposited at or near the interface between marine and non-marine depositional environments (Kumon *et al*., 1999). Although no dinosaur material has been identified from the Nishinakayama Formation, the ichnofossil record in the Kuruma Group indicates that dinosaurs were present in Japan by the Early Jurassic, and it would be conceivable to eventually discover the remains of dinosaurs from the Nishinakayama Formation. The abundance of terrestrial input in both the Nishinakayama Formation and the Kuruma Group strata and the resulting juxtaposition of both marine and non-marine fossils preserved within those strata is encouraging for further palaeontological exploration.

Despite an overall paucity of vertebrate fossils within the Nishinakayama Formation, the presence of teleost fish, crocodylomorphs, and turtles is consistent with other Early Jurassic assemblages worldwide. At present, Early Jurassic turtles are known only from non-marine deposits, including *Kayentachelys* from the Kayenta Formation in Arizona, U.S.A (Gaffney *et al*., 1987); Australochelys from the Elliot Formation in South Africa (Gaffney & Kitching, 1995); and Indochelys from the Kota Formation in India (Datta *et al*., 2000). In contrast to turtles, crocodylomorphs and teleost fish are somewhat more ubiquitous in both marine and non-marine Lower Jurassic strata worldwide (e.g., Simmons, 1965; Clark & Fastovsky, 1986; Arratia & Thies, 2001; Tykoski *et al*, 2002; Tykoski, 2005; Konwert & Stumpf, 2017; Ősi *et al*., 2018).

Interestingly, the cooccurrence of Early Jurassic testudinatans and crocodylomorphs is unique to non-marine deposits outside of Japan; however, the Nishinakayama Formation is itself unquestionably a shallow marine deposit (Hirano, 1973b; Tanabe *et al*., 1982; Tanabe, 1991). The superficial similarities between the vertebrate assemblages of the Nishinakayama Formation and non-marine Lower Jurassic strata elsewhere in the world is perhaps unsurprising given near-shore depositional environment of the Nishinakayama Formation and the high concentration of terrestrial matter preserved alongside marine fossils within the deposit, including plant fragments (e.g., Nakada & Matsuoka, 2011; Kemp & Izumi, 2014; Izumi *et al*., 2018a, in press). Both

the turtle and crocodylomorph specimens from the formation were initially interpreted as representing marine taxa (Hasegawa *et al*., 1998; Manabe & Hasegawa, 1998), but it is also possible that both are in fact allochthons washed out to sea prior to deposition and instead represent non-marine taxa. Further scrutiny of the anatomy of these two reptile specimens may allow a more rigorous evaluation and interpretation of their lifestyle.

CONCLUSIONS

The shallow marine strata of the Nishinakayama Formation preserve a limited but important Early Jurassic assemblage of vertebrate body fossils, and this is particularly true of tetrapod vertebrates. Although limited fragmentary and isolated plesiosaurid and testudinatan body fossils are known from the Lower to Middle Jurassic Kuruma Group in central Japan, the testudinatan and crocodylomorph specimens from the Nishinakayama Formation are the only articulated tetrapod skeletons of Early Jurassic age known in Japan. These specimens (MMHF 5-00001, Testudinata indet.; MMHF 5-00002, Crocodylomorpha indet.), together with the turtle shell fragment from the Kuruma Group, represent the oldest records of their respective clades within Japan, and the testudinatan specimen is particularly important because it is both relatively complete the only Early Jurassic turtle known from marine strata. The presence of teleost fish, testudinatans, and crocodylomorphs from strata deposited in northwestern Panthalassa is broadly comparable with other vertebrate fossil assemblages from Lower Jurassic strata worldwide and is thus consistent with age estimates assigned to the Toyora Group on the basis of ammonite biostratigraphy. Given the overall paucity of Early Jurassic vertebrate fossils in Japan, further study of the specimens discussed herein will certainly provide new insight about both the evolutionary and biogeographic histories of vertebrates in East Asia and the homogeneity of Early Jurassic vertebrate assemblages globally. This also encourages further palaeontological reconnaissance in the Nishinakayama Formation.

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豊田町石町の下部ジュラ系西中山層産の脊椎動物化石

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要約：山口県下関市豊田町石町の下部ジュラ系西中山層（海成層）は，小規模だが，重要な脊椎動物の化石を産出している．この脊椎動物の化石群集には魚類（Teleostei: Leptolepidiformes?），ワニ類（Crocodylomorpha）やカメ類（Testudinata）といった爬虫類の体化石がある．しかしながら脊椎動物の生痕化石は未だ確認されていない．西中山層のワニ類やカメ類と来馬層群のカメ類の甲羅の断片化石は，それぞれのクレードにおいて日本最古の化石記録である．西中山層のカメ類は，下部ジュラ系海成層のカメ類として関節状態の報告は唯一で，特に重要である．以上のことから化石は少数であるものの，西中山層の脊椎動物化石の群集は，世界のジュラ紀前期の脊椎動物群集と並ぶ国際的に重要な群集である．また日本におけるジュラ紀前期の四肢動物の化石の数少ない貴重な報告である．

キーワード：古脊椎動物学，ジュラ紀古世，豊浦層群，トアルシアン海洋無酸素事変．