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Coprolites from the upper Osawa Formation (upper Spathian), northeastern Japan: Evidence for predation in a marine ecosystem 5 Myr after the end-Permian mass extinction

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ABSTRACT

Lower Triassic marine deposits, which can potentially provide important information on the diversity and trophic structure of marine ecosystems following the end-Permian mass extinction, are rarely exposed in the world. Given the sparse body fossil record from the Lower Triassic, non-body fossil evidences, such as trace fossils for example, may provide additional windows on fossil ecosystems. Herein, the authors recently found dark, amorphous lumps of various sizes, ranging from a few millimetres to approximately 7 cm in maximum dimension, from the offshore marine deposit of upper Osawa Formation (Spathian, Lower Triassic) in the South Kitakami Terrane of northeast Japan. Compared with the surrounding siliciclastic sediments, the lumps are rich in phosphate and organic carbon, and poor in silicates. Shape, mode of occurrence, bone inclusion and geochemical signatures of these lumps confirm that these are coprolites, produced not by benthic sediment feeders, but most likely by nektonic animals. Bone inclusion also suggests that carnivorous fish and/or marine reptiles, constituting the higher part of the food chain, produced at least a part of the specimens. Despite the low diversity of the known fossil vertebrates from the Osawa formation, coprolites first shed light on the predator–prey interactions in the marine ecosystem in South Kitakami Terrane 5 Myr after the end-Permian mass extinction.

1. Introduction

It is well known that the end-Permian mass extinction deeply impacted marine ecosystems, with 92% of Late Permian marine species becoming extinct (Knoll et al., 2007). Marine animal groups such as trilobites, brachiopods and crinoids that dominated in the Permian were largely replaced during the Triassic by groups such as bivalves, gastropods, decapod crustaceans, echinoids, and scleractinian corals (Sepkoski, 1984). Marine reptiles (ichthyosaurs, sauropterygians, thalattosaurs and prolacertiformes) became part of the marine ecosystem after the Permian–Triassic event, adding a new group of top predators to the ecological pyramid (Massare, 1987; Mazin, 2001; Walker and Brett, 2002; Hu et al., 2010). Chen and Benton (2012) suggested that the marine food web with top predators was first recovered in the Anisian (Middle Triassic); however, the presence of large predatory marine animals such as fishes and ichthyosaurs in the Lower Triassic is evident from the fossil record (McGowan and Motani, 2003; Błażejowski, 2004; Scheyer et al., 2014).

The process of biotic recovery from the end-Permian mass extinction is also a matter of interest. In the traditional view, the full recovery in guilds and taxonomic diversity from the mass extinction did not occur until after the Early Triassic: specifically, it took more than 5 Myr to complete (Schubert and Bottjer, 1995; Kirchner and Weil, 2000). Nonetheless, recent studies have shown that the marine biotic recovery was temporally and geographically complex, allowing faster recovery within 2 Myr depending on particular groups or settings, based on detailed analysis of particular localities and re-examination of the definition of recovery (Twitchett et al., 2004; Twitchett, 2006; Brayard et al., 2009; Hofmann et al. 2011; Song et al., 2011; Scheyer et al., 2014). Completeness of Early Triassic marine fossil records is low, and possibly influenced by lower population sizes (Twitchett, 2001) and geological megabiases (Benson et al., 2010). Therefore, new perspectives on the investigation of this important geological interval are necessary to more accurately reconstruct the marine palaeoecosystems of the Early Triassic.

The Osawa Formation (Olenekian, Lower Triassic) of the South Kitakami Terrane (Fig. 1A–B) is a part of a marine unit named Inai Group, which is widely distributed across northeastern Japan. The lower part of the Inai Group represents a deepening-upward sequence. An older, fluvial to shallow-marine deposit (Hiraiso Formation) transitions into deeper water facies of the Osawa Formation. The upper part of the Osawa Formation was deposited in a continental slope to basin plain setting, as evidenced by laminated mudstones intercalated with turbidite sandstones (Kamada, 1993; Kawakami and Kawamura 2002; YN personal observation). The upper part of the Osawa Formation is

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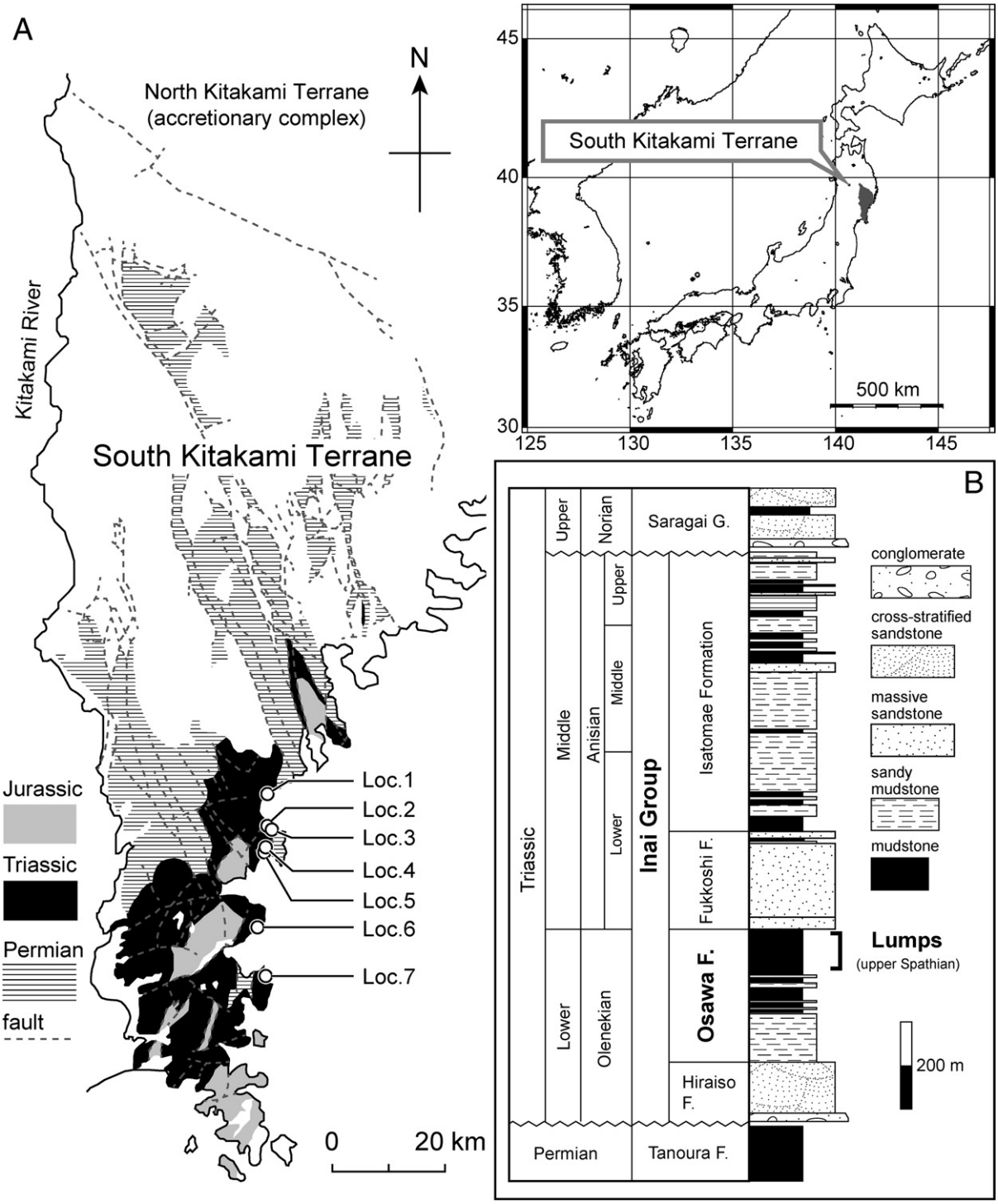

Fig. 1. Geological setting of the South Kitakami Terrane and occurrence of the studied coprolite specimens. A. Geological map of the South Kitakami Terrane, with reference to the distribution of Permian to Jurassic systems (modified from Yoshida and Machiyama, 2004). Seven localities yielding amorphous lumps are indicated by blank circles. B. Generalized geological column of the Triassic in the South Kitakami Terrane (modified from Kamada, 1993; Kamada and Takizawa, 1992), shown with a range of horizons yielding lump specimens.

dated as Spathian (late Olenekian) (Fig. 1B) because of the presence of ammonoid genera *Columbites*, *Subcolumbites* and *Keyserlingites*, which are found in the original stratotype of the Spathian substage in the Canadian Arctic, as well as in Spathian strata of the western USA (Bando and Shimoyama, 1974; Ehiro, 1993; Guex et al., 2010; Ogg, 2012). Hence, stratigraphically the Osawa Formation is one suite of marine deposits that may provide information on a marine palaeoecosystem of the Early Triassic age. The Osawa Formation yields macrofossil species including plant debris (Kon'no, 1973), bivalves and brachiopods (Murata, 1973), in addition to small-sized ammonoids. However, regarding high trophic-level carnivorous animals, only two species, namely a hybodontid shark (Kato et al., 1995) and a basal ichthyosaur *Utatsusaurus hataii* (Shikama et al., 1978), have been reported.

2. Amorphous lumps from the Osawa Formation

In our field investigation, the authors newly found amorphous lumps from laminated mudstone of the upper part of the Osawa