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Late Kungurian conodonts of the pelagic Panthalassa from seamount-capping limestone in Ogama, Kuzuu, Tochigi Prefecture, Japan

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Abstract

Biostratigraphy of conodonts is widely used for age assignment of Permian strata. In this paper, we report conodonts that occurred from the limestone of the Nabeyama Formation deposited on a pelagic seamount in the Panthalassa, which is an oceanic realm where Permian conodont data are scarce compared to other oceanic realms.
Samples collected from the lower part of the Nabeyama Formation yielded *Mesogondolella idahoensis* (Youngquist, Hawley and Miller) and *Sweetognathus hanzhongensis* (Wang), which indicate a late Kungurian age. Previous studies and fusulinids obtained in this study indicate the studied samples belong to the *Parafusulina yabei* biozone. Therefore, the *Parafusulina yabei* Zone includes the uppermost Kungurian. *Mesogondolella idahoensis* and *Sweetognathus hanzhongensis* are respectively regarded as cool and warm water species. Hence, the distribution of cool and warm water conodont species may have overlapped in the pelagic Panthalassa during the late Kungurian.

Key words: conodont, fusulinid, Nabeyama Formation, Panthalassa, Permian

**Introduction**

The study of Permian conodonts began in the western North America as early as the 1930s (Branson, 1932). In the following decades, the Great Basin region was the centre of Permian conodont research (Youngquist *et al*., 1951; Clark and Ethington, 1962; Wardlaw and Collinson, 1979). Studies in the Great Basin lead to the establishment of the rough framework of conodont biozones for the Permian (Clark and Behnken, 1971; Clark *et al*., 1979). The pioneer work in western North America were followed by studies in Europe (Bender and Stoppel, 1965), southern Urals (Chernykh and Reshetkova, 1987), South China (Ching, 1960; Wang, 1978; Wang and Wang, 1981),
the Arctic region (Bender and Stoppel, 1965; Szaniawski and Malkowski, 1979; Sobolev and Nakrem, 1996), Iran (Teichert et al., 1973), Japan (Igo and Koike, 1966, Igo, 1981) and elsewhere. Based on the global-scale data of conodont biostratigraphy, correlation of regional biozones were attempted, resulting in the proposal of biozones that are traceable across the globe (Kozur, 1995). At present, conodonts are recognised as one of the most useful taxa for biostratigraphic division of the Permian System, so much so that all the Stage and substage boundaries of the Permian ratified to date are based on conodonts (Henderson et al., 2012; Henderson, 2016).

While the accumulation of knowledge on Permian conodonts has led to refinements in taxonomy and improvements in the resolution of biozones in the well-studied regions, some regions have been left behind from the progress. One such region is Japan, where Permian strata occur most typically as allochthonous rocks within accretionary complexes (e.g., Isozaki et al., 1990, 2010). Such strata potentially provide precious biostratigraphic and biogeographic records of the pelagic Panthalassa that occupied a large part of the surface of the Earth (Figure 1.1).

In Japan, Permian conodonts have been reported from seamount-capping limestones (Hayashi, 1971; Sobajima, 1972; Makino, 1976; Ishida, 1977, 1985; Matsuda, 1980; Igo, 1981, 1989; Igo and Hisada, 1986; Shen et al., 2012) and deep-sea bedded chert (Toyohara, 1976, 1977; Ishida, 1977, 1979, 1985; Kitao, 1996; Nishikane et al., 2011) within the Jurassic accretionary complexes. In particular, the seamount-capping limestones yield abundant specimens of conodonts, based on which a biostratigraphic framework for the Permian was built (Igo, 1981). However, the taxonomy of Permian
conodonts has gone under significant revision since this framework was constructed.

For example, platform conodonts previously assigned to the genus *Gondolella* (as in Clark and Mosher, 1966), were split into *Mesogondolella*, *Jinogondolella* and *Clarkina* (Kozur, 1989; Mei and Wardlaw, 1994). Unfortunately, only a limited number of specimens were illustrated by previous studies on Permian conodonts in Japan.

Therefore, it is important that new conodont specimens are obtained and described from Panthalassic seamount-capping carbonates.

Investigation of conodont biostratigraphy in pelagic seamount-capping limestone deposited in central Panthalassa can also aid the establishment of an integrated conodont-fusulinid biostratigraphy. Fusulinid biostratigraphy has traditionally been used for biostratigraphic division of Panthalassic seamount-capping limestones of Japan (e.g., Toriyama, 1967). However, fusulinid biozones are not readily correlated with the international standard Geological Time Scale (Leven, 2003). Recently, correlation of fusulinid biozones with conodont and radiolarian biozones and magnetic polarity reversals were established for the Permian in South China (Shen et al., 2018). Igo (1981) presented parallel biozonation of conodonts and fusulinids in the Panthalassic seamount-capping limestone in Japan, but the conodont biostratigraphic framework needs to be brushed up, as mentioned earlier.

This study reports conodonts obtained from the Panthalassic seamount-capping limestone of the Nabeyama Formation in Ogama, Sano City, Tochigi Prefecture, Japan. The Nabeyama Formation in the Kuzuu area has been a target of many biostratigraphic and tectonostratigraphic studies (see also **Geological setting**). The age of the Nabeyama
Formation was previously studied based on conodonts and fusulinids. Fujimoto (1961) dated the Nabeyama Formation as middle Permian based on fusulinids. Hayashi (1971) reported the occurrence of Carboniferous conodonts from this formation, but Hisayoshi Igo (1972) and Hisaharu Igo (1981) insisted that the “Carboniferous” species in Hayashi (1971) were Permian species. Subsequently, Igo (1981) assigned the Nabeyama Formation to the middle Permian based on conodonts, and Kobayashi (2006) also implied a middle Permian age based on fusulinids. Herein, we reassess the age of the Nabeyama Formation based on our new conodont specimens. The biogeographic significance of the conodonts is also discussed.

**Geological setting**

The samples treated in this study are limestone samples obtained in a valley east of Ogama in the northern part of Sano City, Tochigi Prefecture, Kanto District, Japan (36°29′18″N 139°33′54″E). The studied limestone belongs to the Nabeyama Formation (defined by Yoshida, 1956), which is a part of the Kuzuu Complex (Kuzu Complex *sensu* Kamata, 1996, 1997) of the Tamba–Mino–Ashio Belt (also known as the Mino–Tamb–Ashio Belt). The Tamba–Mino–Ashio Belt is mostly composed of Jurassic accretionary complexes (Yamakita and Otoh, 2000; Isozaki *et al.*, 2010; Kojima *et al.*, 2016) (Figure 1.2). The Jurassic accretionary complexes of the Tamba–Mino–Ashio Belt mainly comprise Carboniferous to Middle Jurassic oceanic rocks (ocean floor basalt, deep-sea chert, hemipelagic siliceous mudstone, seamount basalt and
seamount-capping carbonate), and Jurassic to lowermost Cretaceous trench-fill terrigenous clastic rocks (mudstone and sandstone). The Carboniferous to Middle Jurassic oceanic rocks were deposited in the pelagic Panthalassa several thousand kilometres from the nearest continent (Figure 1.1), after which they traveled to a subduction zone along the palaeo-continent and formed a part of the accretionary complexes by the tectonic movement of the oceanic plates (Matsuda and Isozaki, 1991; Wakita and Metcalfe, 2005; Isozaki et al., 2010).

The Kuzuu Complex is the southernmost part of the Tamba–Mino–Ashio Belt in the Kanto District of east Japan (Figure 2). Our studied samples belong to the limestone of the Nabeyama Formation (Yoshida, 1956; Fujimoto, 1961). The Nabeyama Formation conformably overlies the Izuru Formation that is composed mainly of basaltic volcanic and volcaniclastic rocks (Yoshida, 1956; Fujimoto, 1961; Kamata, 1996). The Nabeyama and Izuru formations together form a thrust sheet (Yanagimoto, 1973), which is named as tectonostratigraphic “Unit 2” of the Kuzuu Complex (Kamata, 1996, 1997). The Izuru and Nabeyama formations are considered to be derived from a seamount in the pelagic Panthalassa (Kamata, 1996).

The limestone of the Nabeyama Formation is divided into three parts: the lower, middle and upper parts (Yoshida, 1956; Fujimoto, 1961; Kobayashi, 1979). Fujimoto (1961) and Yanagimoto (1973) classified these three parts as members of the Nabeyama Formation, but Kobayashi (1979) noted that this stratigraphic division is not valid, because the dolomitisation of the middle part is secondary, and is also recognisable in the lower and upper parts. We will follow Kobayashi (1979) and refrain from using the
members defined by Fujimoto (1961) and Yanagimoto (1973). The lower part of the Nabeyama Formation is mainly composed of black, dark grey or grey well-bedded limestone that is frequently dolomitised and includes chert nodules (Figure 3; Fujimoto, 1961; Kobayashi, 1979). The middle part is dominated by light grey, grey or dark grey massive dolostone (Figure 3; Fujimoto, 1961; Kobayashi, 1979). The upper part is mainly composed of light grey, grey, dark grey or black massive limestone that is frequently dolomitised and includes chert nodules (Figure 3; Fujimoto, 1961; Kobayashi, 1979).

The Izuru Formation has been dated as middle Permian by fusulinids (Kobayashi, 2006). The Nabeyama Formation has been dated as middle Permian by conodonts (Igo, 1981; Koike et al., 1974), fusulinids (Fujimoto, 1961; Igo, 1964; Kobayashi, 1979, 2006) and brachiopods (Tazawa et al., 2016). Fusulinids are the most thoroughly studied index fossils in the Izuru and Nabeyama formations, and three biozones of the middle Permian have been established: the *Parafusulina nakamigawai*, *Parafusulina yabei* and *Parafusulina tochigiensis* zones in ascending order (Kobayashi, 2006). The Nabeyama Formation is overlain unconformably by a limestone conglomerate that yields conodonts of middle Permian to late Triassic age (Conodont Research Group, 1972, 1974; Yanagimoto, 1973; Koike et al., 1974) and middle to late Permian fusulinids (Figure 3; Igo and Igo, 1977; Kobayashi, 1979). This conglomerate is thought to be correlative with cave deposits that occur within the Nabeyama Formation (Kobayashi, 1979).

In Ogama, the lower to middle part of the Nabeyama Formation is exposed (OG in
Figure 3; Kobayashi, 1979). Here, the *Parafusulina yabei* and *Parafusulina tochigiensis* fusulinid biozones have been recognised (Figure 3; Kobayashi, 2006). The locality we studied is exactly the same as that studied by Tazawa *et al.* (2016) (note that the locality is mislocated in their paper), and is apparently a lateral extension of the strata within the *Parafusulina yabei* Zone of Kobayashi (2006) (Figures 3 and 4). This is further supported by the finding of *Parafusulina yabei* Hanzawa from this locality by Tazawa *et al.* (2016).

**Methods**

We conducted a field survey at the Ogama locality and collected limestone samples for extraction of conodonts. We also observed the lithology of the limestone for comparison with the lithostratigraphic section drawn by Kobayashi (1979). The collected limestone samples were treated by 4.8 wt% formic acid. Conodonts were picked up from the residue and photographed with a scanning electron microscope (SEM: Keyence-VF8800) and an optical stereoscopic microscope at the University of Tokyo. For observation of fusulinids, we made thin sections of the limestone and observed them under a microscope through transmitted light.

**Results**

In the studied locality in Ogama, outcrops of limestone occur structurally above outcrops of sandstone (Figure 4). The distribution of these two lithofacies is consistent
with the geological map by Kobayashi (1979, 2006) (Figure 4). Two lithostratigraphic sections were observed in the limestone outcrops: Section 1 and Section 2 in structurally ascending order (Figure 4). The top of Section 1 corresponds approximately with the base of Section 2 according to the orientation of the bedding plane. Both sections are composed of well-bedded or weakly bedded dark grey fossiliferous limestone (Figures 5 and 6.1). Black chert nodules are present in the middle to upper part of Section 1 and the upper part of Section 2.

We obtained two limestone samples from the middle part of Section 2 (2013-12 and 2014-236; Figure 5). We also obtained two samples from limestone floats that lay in front of the outcrop of the base of Section 2 (2014-188 and 2014-215; Figure 4). Treatment of these samples with formic acid yielded conodonts along with brachiopods, ichthyoliths, foraminifera, bryozoans, ostracods, trilobite fragments and placoid scales, some of which were silicified. A total of 41 conodont elements were obtained by dissolving 97 kg of limestone. A large part of the extracted conodont specimens was broken, but some were valid for taxonomic investigation (Figures 7 and 8). The conodonts were uniformly of black colour corresponding to conodont alteration index (CAI) 5 of Epstein et al. (1977) (Figure 9). The surface of the conodont skeletons is generally well-preserved, exemplified by the preservation of honeycomb structures on the platform of segminiplanate elements (Figures 7 and 8). Obvious evidence indicating reworking such as abrasion was not found. Both the outcrop samples and the float samples yielded *Mesogondolella idahoensis* (Youngquist, Hawley and Miller), *Mesogondolella* sp. and *Sweethognathus hanzhongensis* (Wang) (Figures 7 and 8). Thus,
the conodont assemblages from the middle part of Section 2 and the floats are identical.

It is noteworthy that some of our specimens retain the basal bodies of conodont elements, which are relatively fragile tissues that occupy the basal part of the element (Donoghue, 1998). Basal bodies of conodonts are fragile due to having less densely mineralised structures and are also easily broken off from the rest of the element: the more resistant crown (Donoghue, 1998; Souquet and Goudemand, 2019). Therefore, the basal bodies of conodonts are rarely preserved and poorly described. In our samples, some specimens of *Mesogondolella* retain the basal bodies as white to transparent tissues (Figure 9). It is rather surprising that the fragile basal bodies were found in conodonts from sedimentary rocks that have experienced considerable thermal maturation and tectonic deformation during subduction-accretion.

We also observed fusulinids from the sample obtained from Section 2. Observation of thin sections confirmed the presence of *Parafusulina yabei* Hanzawa (Figure 6.2). Since the range of *Parafusulina yabei* defines the *Parafusulina yabei* Zone of Kobayashi (2006), our finding assures that the sampled horizon is within this fusulinid biozone (Figures 3). This is consistent with the results of Tazawa *et al.* (2016) as well as the position and lithofacies of the studied section (Figures 3, 4 and 5).

**Discussion**

**Age**

Here, we will discuss the age of our samples based on the specimens obtained in this
Mesogondolella idahoensis (Youngquist, Hawley and Miller) is a widely distributed species found from western USA (Youngquist et al., 1951; Mytton et al., 1983; Behnken et al., 1986; Wardlaw and Collinson, 1986; Lambert et al., 2007), Svalbard (Szaniawski and Malkowski, 1979; Nakrem, 1991), central Tibet (Yuan et al., 2016), South China (Wang, 1994; Zhang et al., 2010; Sun et al., 2017) and Japan (Igo, 1981). Based on a global compilation of conodont occurrences, the range of M. idahoensis falls within the late Kungurian (latest Cisuralian; latest early Permian) (Henderson, 2016). Sweetognathus hanzhongensis (Wang) has been reported from Shaanxi (Wang, 1978), Guangxi (Mei et al., 2002; Sun et al., 2017) and Guizhou (Mei et al., 1999) of South China, Oman (Kozur and Wardlaw, 2010) and Tunisia (Angiolini et al., 2008). Based on a compilation of these data, the range of S. hanzhongensis is from the Kungurian–Roadian (Cisuralian–Guadalupian) boundary to the late Capitanian (latest Guadalupian; latest middle Permian) (Henderson, 2016). According to high-resolution investigations in Guangxi (Sun et al., 2017) and Guizhou (Mei et al., 1999), S. hanzhongensis begins to occur below the first occurrence (FO) of Jinogondolella nankingensis (Ching), which is a marker for the Cisuralian–Guadalupian boundary (i.e., the Kungurian–Roadian boundary) (Henderson et al., 2012). Thus, the range of S. hanzhongensis is from the latest Kungurian to late Capitanian. The co-occurrence of M. idahoensis and S. hanzhongensis narrows the age of our samples to the latest Kungurian (latest early Permian). Our age assignment is consistent with the brachiopod-based age by Tazawa et al. (2016). Comparison with fusulinid-based age assignment is a little
more complicated, as noted below.

When first established in the Izuru and Nabeyama formations, the *Parafusulina nakamigawai* Zone and the middle part of the *Parafusulina tochigiensis* Zone were respectively correlated to the early middle Permian (Kubergandian in the Tethyan Scale) and the middle middle Permian (Murgabian in the Tethyan Scale) (Kobayashi, 2006). This means that the *Parafusulina yabei* Zone, which lies between the *Parafusulina nakamigawai* and *Parafusulina tochigiensis* zones, is within the middle Permian. However, correlation with the global standard Geological Time Scale (Henderson *et al.*, 2012) was not determined, which can now be attempted based on conodonts from our samples and previous studies (Igo, 1981).

The co-occurrence of *M. idahoensis* and *S. hanzhongensis* in our samples indicate that the age of the *Parafusulina yabei* Zone includes the latest Kungurian. Previously, *M. idahoensis* has been found to occur with *Diplognathodus lanceolatus* Igo from the lower part of the Nabeyama Formation in Yamasuge in Kuzuu (Igo, 1981; see Figure 2 for location). The latter species is identical to *S. hanzhongensis* (see Plate 9 Figures 1–5, 7, 8, 13 of Igo, 1981), and is here considered as a junior synonym of *S. hanzhongensis*. This is concordant with the fact that the stratigraphic range of both “*D. lanceolatus*” and *S. hanzhongensis* overlap in their lower part with the range of *M. idahoensis* (in the uppermost Kungurian). Because the horizons in Yamasuge span a large part of the *Parafusulina yabei* Zone of Kobayashi (2006) (compare Text-fig. 4 of Igo, 1981 and “YS” in Figure 3 of this paper), much of the *Parafusulina yabei* Zone is probably of latest Kungurian age. The upper part of the Nabeyama Formation in Nagaami, which is
assigned to the *Parafusulina tochigiensis* Zone of Kobayashi (2006), yields “*D. lanceolatus*” but lacks *M. idahoensis* (Igo, 1981). Therefore, the *Parafusulina tochigiensis* Zone may be of Guadalupian age (Henderson, 2016).

**Biogeography**

Our samples are characterised by the co-occurrence of *M. idahoensis* and *S. hanzhongensis*. As mentioned above, the co-occurrence of the two species in the lower part of the Nabeyama Formation can also be observed in the illustrations of Igo (1981) (respectively treated as *Neogondolella idahoensis* and *Diplognathodus lanceolatus* in his paper). According to Igo (1981), some horizons from the Yamasuge area in Kuzuu, which are roughly correlative with the studied section in Ogama (Figure 2), yield abundant specimens of both “*D. lanceolatus*” and *M. idahoensis*. Although the specimens obtained in our study are not numerous, they seem to represent major constituents of a typical latest Kungurian conodont fauna recorded in the Nabeyama Formation.

Outside Japan, the co-occurrence of *M. idahoensis* and *S. hanzhongensis* has been reported from South China (Sun *et al*., 2017), but not from other geographic areas. Apart from Japan and South China, almost all of the localities of *M. idahoensis* are in Svalbard that was located in northern high latitudes (Szaniawski and Malkowski, 1979; Nakrem, 1991) and the northwestern Pangaean margin, where the northern gyre of the Panthalassa would have brought cold waters from the north (Youngquist *et al*., 1951; Mytton *et al*., 1983; Behnken *et al*., 1986; Wardlaw and Collinson, 1986; Lambert *et al*.,
An exception is central Tibet that was positioned in southern mid latitudes (Yuan et al., 2016). Hence, this species is regarded to represent cool water province of the north Panthalassa and Boreal Ocean (Mei and Henderson, 2001; Henderson and Mei, 2007), while it also inhabited parts of cool waters of the southern hemisphere. In contrast, Kungurian species of Sweetognathus are abundant only in equatorial regions, and therefore are regarded as warm water taxa (Mei and Henderson, 2001; Mei et al., 2002). In particular, *S. hanzhongensis* are limited to South China, Oman and Tunisia, which were all positioned in low latitudes (Wang, 1978; Mei et al., 2002; Angiolini et al., 2008; Kozur and Wardlaw, 2010; Sun et al., 2017). Thus, a fauna that includes *M. idahoensis* and *S. hanzhongensis* as main constituents, such as that suggested for the Nabeyama Formation and perhaps South China, is irregular in terms of conodont provincialism. It is possible that the pelagic Panthalassa and South China was a biogeographic province where cool water taxa and warm water taxa coexisted during the latest Kungurian, and further research on faunal compositions will shed light on the significance of these provinces.

**Conclusions**

We obtained well-preserved specimens of *Mesogondolella idahoensis* (Youngquist, Hawley and Miller) and *Sweetognathus hanzhongensis* (Wang) from limestones of the *Parafusulina yabei* Zone of the Nabeyama Formation in Ogama, Kuzuu area, Tochigi Prefecture, Japan. The conodonts indicate a latest Kungurian age, which is consistent
with brachiopods reported from the same locality. The conodont data indicate that the
*Parafusulina yabei* fusulinid biozone includes, and is probably mostly correlated to the
latest Kungurian. Biogeographically, our data suggests that the conodont fauna of the
Nabeyama Formation may have been characterised by mixed cool water and warm
water taxa in the latest Kungurian.

**Systematic palaeontology**

Multielement taxonomy of Permian conodonts is still debated at the genus level
(Henderson and Mei, 2003). Therefore, only the synonym list for the P1 element is
presented. All specimens are deposited in the Kuzuu Fossil Museum.

- Class Conodonta Eichenberg, 1930
- Subclass Conodonti Sweet and Donoghue, 2001
- Order Ozarkodinida Dzik, 1976
- Superfamily Gondolellacea Lindström, 1970
- Family Gondolellidae Lindström, 1970
- Genus *Mesogondolella* Kozur

*Type species.*—*Gondolella bisseli* Clark and Behnken

*Remarks.*—*Mesogondolella* was defined for segminiplanate P1 elements with the
following features: a platform that is not reduced; no sculptures on the platform or only
weak serration on the anterior part of the platform; no free blade; a lower surface with
shallow V-shaped keel; a terminal basal cavity. Species with serrations on the anterior
part of the platform were separated to the genus *Jinogondolella* (Mei and Wardlaw, 1994). Consequently, *Mesogondolella* is restricted to species with an unornamented platform (Lambert et al., 2007). Multielement apparatus of species of *Mesogondolella* was proposed by Lambert et al. (2007).

*Mesogondolella idahoensis* (Youngquist, Hawley and Miller)

*Gondolella idahoensis* Youngquist, Hawley and Miller, 1951, p. 361, pl. 54, figs. 1–3, 14, 15; Clark and Mosher, 1966, p. 388, pl. 47, figs. 9–12.

*Neogondolella idahoensis* (Youngquist, Hawley and Miller). Clark et al., 1979, pl. 1, fig. 10; Szaniawski and Malkowski, 1979, p. 246–247, pl. 4, figs. 1–4, 6 (only), pl. 5, fig. 5?; Wang and Wang, 1981, p. 230, pl. 2, figs. 15, 23; Behnken et al., 1986, p. 179–181, figs. 4.12–16, 4.18; Wardlaw and Collinson, 1986, figs. 17.11, 12; Wang, 1994, p. 211, pl. 3, figs. 3–6 (only); Kozur, 1995, pl. 3, fig. 18.

*Mesogondolella idahoensis* (Youngquist, Hawley and Miller). Wardlaw, 2000, p.44, pl. 3-10, figs. 1–3; Lambert et al., 2007, pp. 215–216, figs. 4e, 6j.

*Mesogondolella idahoensis idahoensis* (Youngquist, Hawley and Miller). Henderson and Mei, 2003, pl. 2, fig. 15; Zhang et al., 2010, p. 152, figs. 3H, 3Q–3R.

*Mesogondolella? cf. idahoensis* (Youngquist et al.). Sun et al., 2017, pl. 5, fig. 4.

Description.—The specimens obtained in our study are segminiplanate elements characterised by a markedly high and thick terminal cusp. The cusp is around 3 times higher than the posterior denticles. The cusp is weakly reclined to the posterior. The denticles are low and discrete in the posterior, and becomes higher and fused towards the anterior. The low posterior denticles are circular in cross section, while the higher anterior denticles are laterally compressed. The platform that runs the full length the element and is widest around mid-length. The platform tapers anteriorly, while its lateral margins are sub-parallel in the posterior half. The posterior end of the platform is a rounded square shape in upper and basal views. The keel has a wide v-shaped groove ending around a terminally located basal pit surrounded by a wide loop.

Remarks.—The features of our specimens agree well with those of *Mesogondolella idahoensis* (Youngquist et al.). Although the anterior denticles of *M. idahoensis* were originally described to be low and widely spaced (Henderson and Mei, 2003, Plate 2 Figure 15; holotype), forms with high, closely spaced and fused anterior denticles have been reported to occur alongside such forms (Behnken et al., 1986, Lambert et al., 2007, Figures 4d, e; Figures 4.14, 16; Wardlaw and Collinson, 1986, Figure 17.11). Hence, we regard that our specimens belong to *M. idahoensis*.

*Mesogondolella idahoensis* is similar to *Mesogondolella lamberti* Mei and Henderson in denticulation and platform morphology. *M. lamberti* was split from *M. idahoensis* as a new subspecies by Mei and Henderson (2002), then elevated to species status by Lambert et al. (2007). *M. idahoensis* can be separated from *M. lamberti* by having a larger cusp.
Mesogondolella siciliensis (Kozur) has a similar denticulation to M. idahoensis, but differs in that the cusp of the former is at most only slightly larger than the posterior denticles. Furthermore, the platform of the former is widest at the middle and tapers posteriorly, while that of the latter has sub-parallel lateral margins from the middle to the posterior.

Mesogondolella spp.

Figures 8.1, 8.2


Remarks.—These specimens differ from M. idahoensis in having very high and fused anterior denticles. The specimen illustrated in Figure 8.1 has a thick cusp, has a square posterior end in upper and basal views, and is strongly arched in lateral view. The specimen illustrated in Figure 8.2 has a similar cusp, but has a more rounded posterior end in upper and basal views, and is less arched in lateral view. Therefore, these two specimens may belong to different species, although the preservation is too poor to make a conclusion.

Genus Sweetognathus Clark

Type species.—Spathognathodus whitei Rhodes

Remarks.—Sweetognathus is represented by carminiscaphate P1 elements with pustulose ornamentation on a flat-topped carina that passes gradually into the anterior blade (Mei et al., 2002).
**Sweetognathus hanzhongensis** (Wang)

**Figures 8.3–8.5**


*Sweetognathus hanzhongensis* (Wang). Sun *et al.*, 2017, p. 60, pl. 3, fig. 15–18, pl. 7, figs. 9–10.


*Description.*—The specimens are carminiscaphate elements with an anterior blade of fused denticles and a posterior process that is formed above an expanded basal cavity. In lateral view, the anterior blade is the highest part of the element, and the upper margin decreases height gradually to the posterior end where it meets the basal margin. The carina on the posterior process is composed of a low and narrow row of pustulose nodes that continues to the posterior end. The anterior blade is composed of laterally compressed denticles that are fused to around 90% of its height. The anterior three denticles of the blade are subequal in height. The anterior blade and carina is connected by a narrow carinal ridge, which is positioned at the mid-length of the unit and above the anteriormost part of the basal cavity. In lateral view the length of this ridge is around three times the width of the carinal nodes. The basal cavity occupies around 60% of the
basal margin in lateral view. In upper and basal views, the basal cavity tapers both anteriorly and posteriorly. The upper surface of the basal cavity is unornamented.

**Remarks**—The characteristics of our specimens agree well with those of *Sweetognathus hanzhongensis* (Wang). The carinal ridge that connects the anterior blade with the posterior nodes is the key feature that differentiates this species from others. Note that Mei *et al.* (2002) regarded this species to be a geographical subspecies of *Sweetognathus iranicus*, and treated it as *S. iranicus hanzhongensis*.

*Sweetognathus iranicus* (Kozur) is similar, but differs from *S. hanzhongensis* in having discrete nodes instead of a ridge where the anterior blade connects with the posterior part of the carina. In addition, *S. iranicus* typically has laterally broader nodes on the carina.

*Diplognathodus lanceolatus* Igo from Panthalassic seamount capping limestones in Kuzuu and Mt. Ibuki in Japan has all the features of *S. hanzhongensis*, including a carinal ridge that connects the anterior blade with the posterior nodes. The stratigraphic distribution of *D. lanceolatus* is in the middle Permian, consistent with that of *S. hanzhongensis*. Therefore, we regard that *D. lanceolatus* is a junior synonym of *S. hanzhongensis*.

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**Figure captions**

**Figure 1.** 1, palaeogeographic map of the early Permian (Laya et al., 2013) and the depositional site of pelagic Panthalassic sediments in Japan. 2, distribution of the Jurassic accretionary complex of Japan, modified after Isozaki et al., (2010).

**Figure 2.** Geologic maps showing the geology of the Kuzuu area (Kamata, 1997). 1, surface distribution of the Tamba–Mino–Ashio Belt. 2, geologic map of the Ashio Mountains. 3, geologic map of the Kuzuu area and the location of the areas studied by Kobayashi (1979, 2006). OG: Ogama; TJ: Takajikko; NA: Nagaami; KS: Karasawa; YS: Yamasuge.

**Figure 3.** Lithostratigraphy and biostratigraphy of the Izuru and Nabeyama Formations. Lithostratigraphy after Kobayashi (1979). Fusilinid biostratigraphy is after Kobayashi (2006) and conodont biostratigraphy is after Igo (1981). See caption
for Figure 2 for abbreviation of the names of study areas.

**Figure 4.** Map showing the outcrops confirmed in this study (discrete outcrops in the northern part), the location of the studied sections, the location of the sampling point of the float samples (2014-188, 2014-215), and the geological map by Kobayashi (1979, 2006).

**Figure 5.** Stratigraphic columns of the studied sections. The samples from the outcrop (2014-12, 2014-236) were obtained from the horizon with the fossil occurrence mark.

**Figure 6.** 1, Outcrop photograph of the horizon from which samples 2014-12 and 2014-236 were obtained. The sample for observation of fusulinids was obtained from the point of the arrow. 2, photo micrograph of *Parafusulina yabei* Hanzawa from Section 2 observed in thin section through transmitted light.


1, palaeogeographic map of the early Permian (Laya et al., 2013) and the depositional site of pelagic Panthalassic sediments in Japan. 2, distribution of the Jurassic accretionary complex of Japan, modified after Isozaki et al., (2010).

81x140mm (300 x 300 DPI)
Geologic maps showing the geology of the Kuzuu area (Kamata, 1997). 1, surface distribution of the Mino-Tamba-Ashio Belt. 2, geologic map of the Ashio Mountains. 3, geologic map of the Kuzuu area and the location of the areas studied by Kobayashi (1979, 2006). OG: Ogama; TJ: Takajikko; NA: Nagaami; KS: Karasawa; YS: Yamasuge.

221x144mm (300 x 300 DPI)
Lithostratigraphy and biostratigraphy of the Izuru and Nabeyama Formations. Lithostratigraphy after Kobayashi (1979). Biostratigraphy after Kobayashi (2006). See caption for Figure 2 for abbreviation of the names of study areas.

170x234mm (300 x 300 DPI)
Map showing the outcrops confirmed in this study (discrete outcrops in the northern part), the location of the studied sections, the location of the sampling point of the float samples (2014-188, 2014-215), and the geological map by Kobayashi (1979, 2006).

714x578mm (72 x 72 DPI)
Stratigraphic columns of the studied sections. The samples from the outcrop (2014-12, 2014-236) were obtained from the horizon with the fossil occurrence mark.

77x113mm (300 x 300 DPI)
1, Outcrop photograph of the horizon from which samples 2014-12 and 2014-236 were obtained. The sample for observation of fusulinids was obtained from the point of the arrow. 2, photo micrograph of Parafusulina yabei Hanzawa from Section 2 observed in thin section through transmitted light.

712x782mm (72 x 72 DPI)

175x224mm (300 x 300 DPI)

175x193mm (300 x 300 DPI)

166x59mm (300 x 300 DPI)