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Biogeographical and biostratigraphical significance of a new Middle Devonian phacopid trilobite from the Naidaijin Formation, Kurosegawa Terrane, Kyushu, southwest Japan

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Abstract. A newly discovered trilobite from the Naidaijin Formation in the Kurosegawa Terrane of southwest Japan is referred to *Toxophacops* (*Atopophacops*) *fujiwara* sp. nov. The trilobite occurs in strata 2 m below a level with detrital zircons that yield an age of 383.9 ± 4.4 Ma that is likely Givetian (late Mid-Devonian). Elsewhere, Early to Mid-Devonian trilobite species of *T.* (*Atopophacops*) and *T.* (*Toxophacops*) have been recorded from the Nakazato Formation of the South Kitakami Terrane of northeast Japan, and from the Zhusilenghaierhan region of western Inner Mongolia, North China. The new trilobite species extends the geographical range of the phacopid subfamily Echinophacopinae, and supports the affinities of some Devonian Japanese trilobites with those of north China. The occurrence of *Toxophacops* in the Lower Member of the Naidaijin Formation, combined with other trilobite evidence, confirms a clear biostratigraphical distinction between the Lower Member (upper Lower and Middle Devonian) and Upper Member (Upper Devonian) of the Naidaijin Formation.

Key words: detrital zircon geochronology, Devonian, Japan, Kurosegawa, Kyushu, Trilobita

Introduction

Trilobites have been studied extensively in Japan from the upper Emsian to Eifelian (upper Lower and lower Middle Devonian) 'N3 Member' of the Nakazato Formation of Takainari-yama in the South Kitakami Terrane of northeast Japan (Sugiyama and Okano, 1941; Sugiyama, 1944; Okubo, 1951; Kobayashi, 1957; Kaneko, 1984, 1985, 1990), and the Lower Devonian Fukuji Formation in the Fukuji and Oise areas of the Hida Gaien Terrane, in central Honshu (Kobayashi and Igo, 1956; Okazaki, 1974; Kobayashi and Hamada, 1977; Kobayashi, 1988a, 1988b). The only formal record of phacopid trilobites is of *Phacops okanoi* Sugiyama, 1944 and *Reedops nonakai* Okubo, 1956 in the Nakazato Formation, each of which have been subsequently assigned to *Toxophacops* (*Atopophacops*) and *Toxophacops* (*Toxophacops*) by Zhou and Campbell (1990) and Kaneko (2007), respectively. Devonian trilobites from the Kurosegawa Terrane of southwest Japan have not been given formal taxonomic descriptions. However, Murata *et al*. (1997) previously reported *Taxophacops nonakai* (*sic*) and *Phacops pustliceps* (*nom. nud.*) from the Naidaijin Formation, and Kaneko (2007) figured *Toxophacops nonakai* and Phacopidae sp. A from the type locality of the Naidaijin Formation (Figure 1).

The Kurosegawa Terrane is a predominantly Paleozoic, structurally disrupted composite terrane within the Mesozoic melange zone known as the Chichibu Belt (Ehiro *et al*., 2016). It forms a narrow E–W striking zone through the islands of Kyushu and Shikoku and extending into the Kii Peninsula of Honshu, but its maximum width never

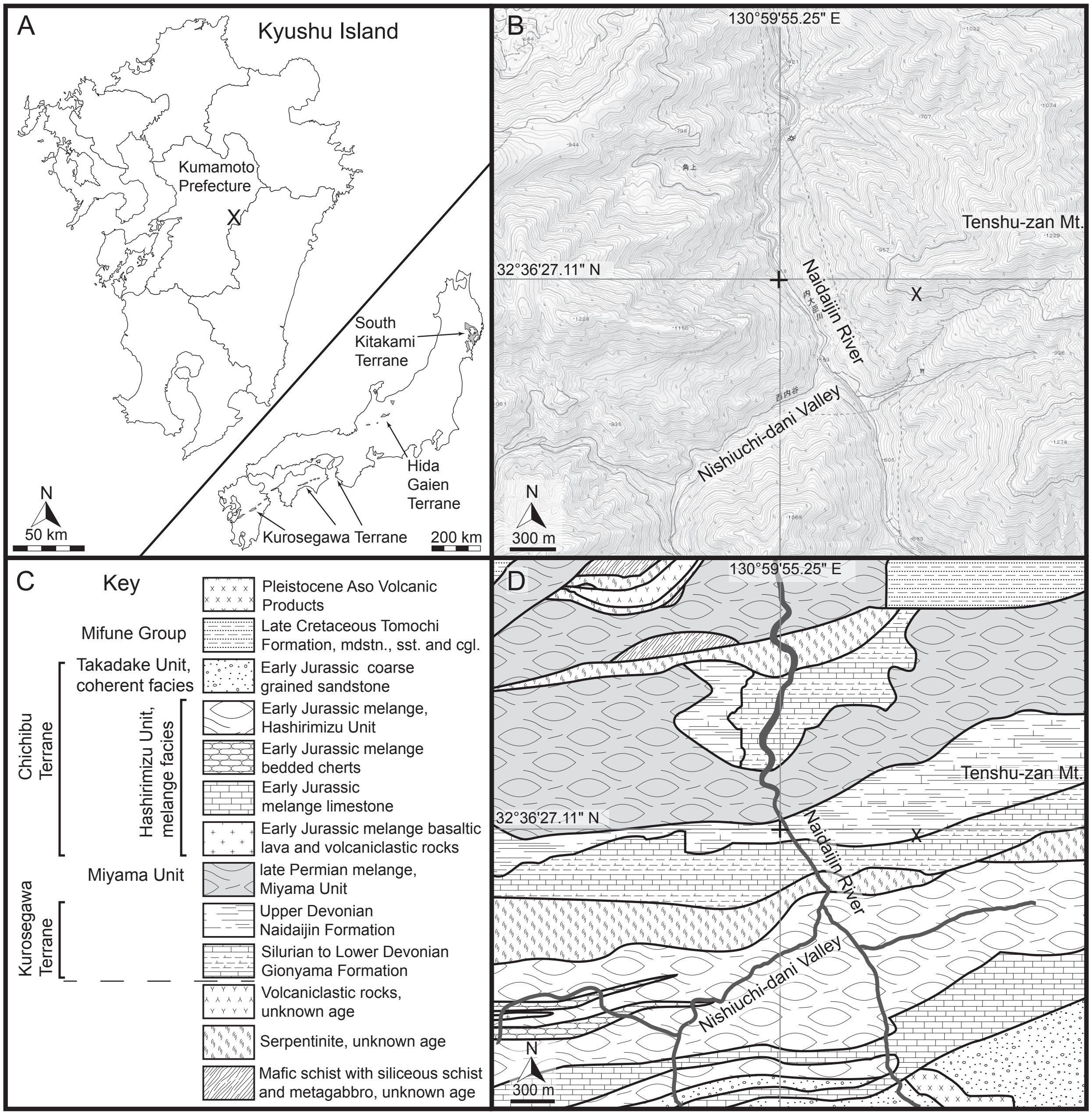

Figure 1. Geographical location of the Naidaijin Formation. **A,** location within Kyushu Island (and the Kurosegawa Terrane of southwest Japan, inset). **B,** geographical location of the type section at Tenshu-zan (Tenshu Mountain) near Tomochi Town, Shimomashiki District, Kumamoto Prefecture, central Kyushu, Japan (highlighted with an 'x'), and the section described herein on the eastern slope of Memaruyama (Memaru Mountain), along the valley of the Naidaijin River, near Tomochi Town, Shimomashiki District, Kumamoto Prefecture, central Kyushu, Japan (highlighted with a '+') (after the 1:25,000 scale topographic map published by the Geospatial Information Authority of Japan, Ministry of Land, Infrastructure, Transport and Tourism, Japan). **C, D,** geological map showing extent of the Naidaijin Formation, and its context within the local geology (based on Saito *et al*., 2005). The abbreviations 'mdstn.', 'sst.' and 'cgl.' have been used for mudstone, sandstone and conglomerate respectively.

exceeds 10 km. Thick successions of commonly fossiliferous, volcanic arc-derived sedimentary rocks and carbonates can be found throughout its outcrop. In Kyushu, the Silurian to Lower Devonian Gionyama Formation (Figure 1) comprises much of the sedimentary succession of the local Kurosegawa Terrane and is rich in marine invertebrate fossils (Kido, 2010; Kido and Sugiyama, 2011 and references therein). Silurian trilobites such as *Coronocephalus kobayashii*, have been described by Hamada (1959) and Kobayashi and Hamada (1974) from the Gionyama Formation, but hitherto there has been no systematic description of trilobites from the overlying Devonian Naidaijin Formation. Previously, fossils described from the Naidaijin Formation comprise mainly plant material of Late Devonian age (Kimura *et al.*, 1986).

The Naidaijin Formation was first proposed as a discrete lithological unit by Miyamoto and Tanimoto (1986). The type locality, as designated by the Geological Survey of Japan (Saito *et al*., 2005), lies along a small pass on Tenshu-zan (Tenshu Mountain) near Tomochi Town, Shimomashiki District, Kumamoto Prefecture, central Kyushu. The formation forms an ENE–WSW trending lenticular body 3 km long and 0.5 km wide, and is composed mainly of mudstone, sandstone, conglomerate and welded tuffs: it has a maximum thickness of 170 m in the eastern part and 290 m in the west (Miyamoto and Tanimoto, 1993), and conformably overlies the Silurian to Lower Devonian Gionyama Formation (Saito *et al*., 2005; Ehiro *et al*., 2016). The Naidaijin Formation has been correlated with the Ochi Formation of Yokokurayama, Shikoku, based on the co-occurrence of the plant *Leptophloem rhombicum* (Hirata, 1966). This species is also found in Frasnian to Fammenian (Upper Devonian) rocks in several parts of China (Li and Cai, 1977), as well as Europe, Asia, Africa and Australia (Edwards and Berry, 1991) where the biostratigraphic age is well constrained (see Tazawa *et al*., 2000, p. 733, fig. 7 for a summary of its distribution). *Leptophloem rhombicum* occurs alongside brachiopods in the Tobigamori Formation of the South Kitakami Terrane (Tachibana, 1952) and in the Rosse Formation of the Hida Gaien Terrane (Tazawa *et al*., 2000); brachiopods including *Cyrtospirifer tobigamoriensis* Noda and Tachibana, 1959 from the Tobigamori Formation, have been dated as Late Devonian (Yabe and Noda, 1933; Tachibana, 1952; Noda and Tachibana, 1959), and in the case of Tachibana's study they occur close to the boundary with the Carboniferous, suggesting from their stratigraphical context a Fammenian age. *Cyrtospirifer tobigamoriensis* also occurs in conjunction with plant fossils in the Naidaijin Formation (Yanagida *et al*., 1987). The plant fossil biostratigraphy provides the only measure of the relative age of the Naidaijin Formation, which has been reported as Fammenian (Miyamoto and Tanimoto, 1993), although Saito *et al.* (2005) referred to it as Mid- to Late Devonian. Trilobites were described by Murata *et al.* (1997), and subsequently by Kaneko (2007), from the Naidaijin Formation, and the following species also occur in the Emsian to Givetian Nakazato Formation of the South Kitakami Terrane in northeast Honshu: *Toxophacops* (*Atopophacops*) *nonakai*, *Kobayashipeltis paucispinosa* (Okubo, 1951), *Dechenella* (*Dechenella*) *minima* Okubo, 1950 and *Acanthopyge* (*Jasperia*) *duplicispinata* Kaneko, 1984. *Nipponocalymene hamadai* Kaneko 1985 is the only species that also occurs in the Hida Gaien Terrane, where it appears in an allochthonous limestone block within the Upper Devonian Rosse Formation (Kaneko, 2007). This strongly suggests that the Naidaijin Formation, as currently conceived, incorporates strata of both late Early and Mid- and Late Devonian age.

In this paper we present the first Devonian trilobite species formally described from the Kurosegawa Terrane, and assess its biogeographical and biostratigraphical importance in relation to northeast Japan and north China. In addition, we present a radiometric age from U–Pb and LA-ICP-MS analysis of detrital zircons from a sandstone bed directly above the horizon bearing *Toxophacops* (*Atopophacops*) *fujiwara* sp. nov., which provides an upper age limit to the trilobite bed (Figure 2, see horizons '75 m' for the trilobites, and '77 m' for the zircons).

Material and methods

The trilobite material is housed in the Oxford University Museum of Natural History (OUMNH DY.3 to OUMNH DY.14). The trilobites used in this study were collected from an exposure of dark grey mudstones ('75 m' horizon) in the Lower Member of the Naidaijin Formation (Figures 2, 3) from the eastern slope of Memaruyama (Mount Memaru), along the valley of the Naidaijin River. Poorly preserved fragmentary trilobites were also collected from another mudstone bed approximately one metre below (Figure 2, '74 m' horizon). The trilobite-bearing mudstones contain organic-rich material and pyrite, as well as fossil, bryozoans, brachiopods, ostracods and pelmatozoan debris. Twelve trilobite specimens, possibly belonging to three taxa, have been collected from the upper, '75 m' horizon. These comprise two cephala (one with part and counterpart), six pygidia, and two thoracopyga assignable to *Toxophacops* (*Atopophacops*) *fujiwara* sp. nov., one thoracopygon that is indeterminate, and one incomplete scutelluid pygidium, most likely *Kobayashipeltis paucispinosa*. Only the phacopid *T.* (*A.*) *fujiwara* is taxonomically described in this paper. Fragments of trilobite material from the lower, '74 m' horizon (Figure 2) are too poorly preserved to identify specifically.

The trilobites were prepared using a Burgess Vibrotool with gramophone needle, and manually with needles in a pin-vice, before being painted black with a fine coating of Pébéo extra fine gouache opaque paint (T7, 13 series 2, 'Black Lake'). Silicone casts of internal and external moulds were created using Provil Novo Putty,

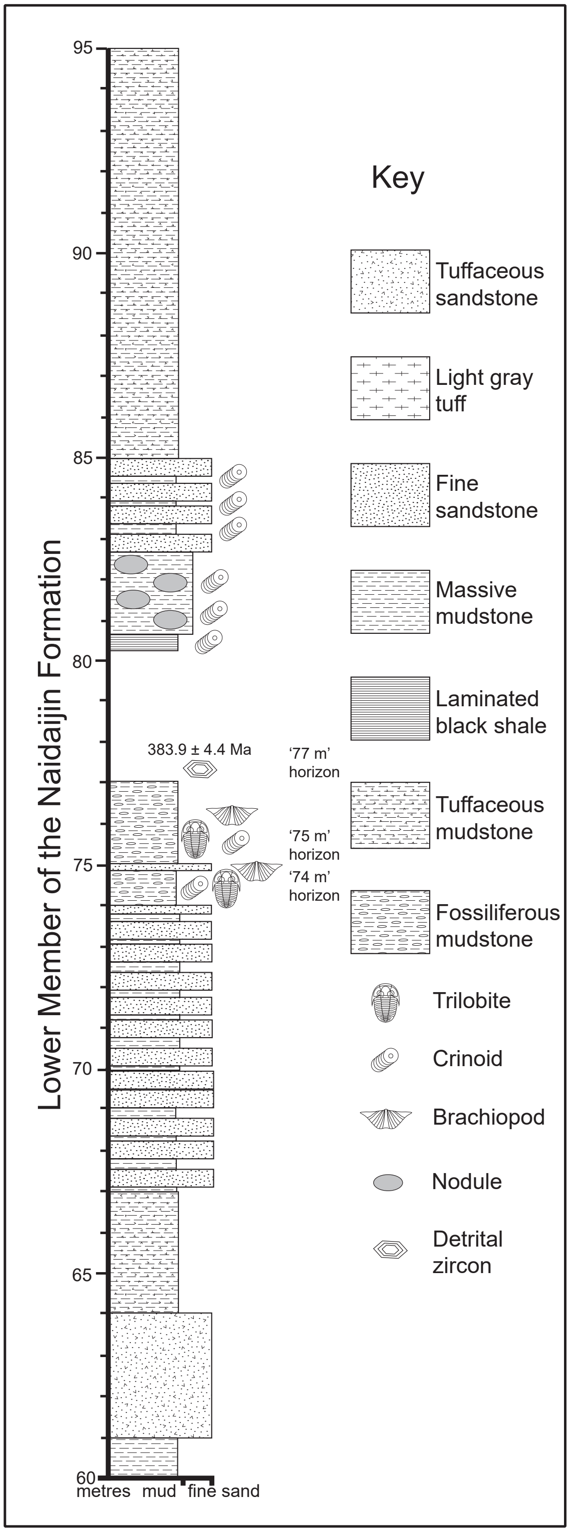

Figure 2. Lithological log of the Lower Member of the Naidaijin Formation, eastern slope of Memaruyama, along the valley of the Naidaijin River. Position of trilobite-bearing horizons ('74 m' and '75 m' levels) indicated with trilobite symbols, and the position of the sandstone bed with zircons at the '77 m' horizon.

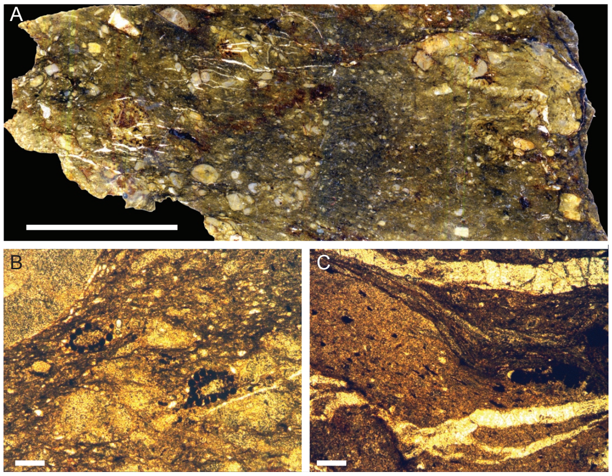

Figure 3. Bioclastic mudstone yielding *Toxophacops* (*Atopophacops*) *fujiwara* sp. nov. at the '75 m' horizon. **A,** trilobite-bearing mudstone containing organic material and pyrite, as well as bryozoans, ostracods, brachiopods and pelmatozoan debris; **B,** matrix of trilobite-bearing mudstone containing microfossils; **C,** organic matter found commonly in the mudstone. Scale bars are 40 mm in A, 0.2 mm in B, C. Thin section cut from the matrix surrounding sample OUMNH DY.11. Deposited in Oxford University Museum of Natural History as OUMNH DY.11/p.

and coloured black with the pigment 'Liquid Black 6025 Masterbatch' by Silmix Ltd. Samples were whitened with ammonium chloride before photographing with Leitz 'Aristophot' apparatus mounted with a Canon EOS 5D camera and Leica 12 mm Summar lens. Photographs of eyes (Figure 4) were produced using focus-stacking techniques in Adobe Photoshop CC 2015.5, to increase the depth of field at higher magnification.

For the zircon analysis (see Appendix 1), the rock samples were scrubbed and washed in an ultrasonic bath for ten minutes to avoid zircon contaminants. The zircon grains were handpicked from heavy fractions that were separated from the rock samples by standard crushing and heavy-liquid techniques. Zircon grains from the samples, the zircon standards FC1 (1099.9 Ma; Paces and Miller, 1993) and OT4 (191.1 Ma; Horie *et al.*, 2013), and the glass standard NIST SRM610 were mounted in an epoxy resin and polished until the surface was flattened with the center of the embedded grains exposed. Backscattered electron and cathodoluminescence images of zircon grains were taken using scanning electron microscope-cathodoluminescence (SEM-CL) equipment, JSM-6610 (JEOL) and a CL detector (SANYU electron), installed at the National Museum of Nature and Science, Japan. The images were used to select the sites for analysis. U–Pb dating of these samples was carried out using LA-ICP-MS that was composed of NWR213 (Electro Scientific Industries) and Agilent 7700x (Agilent Technologies)

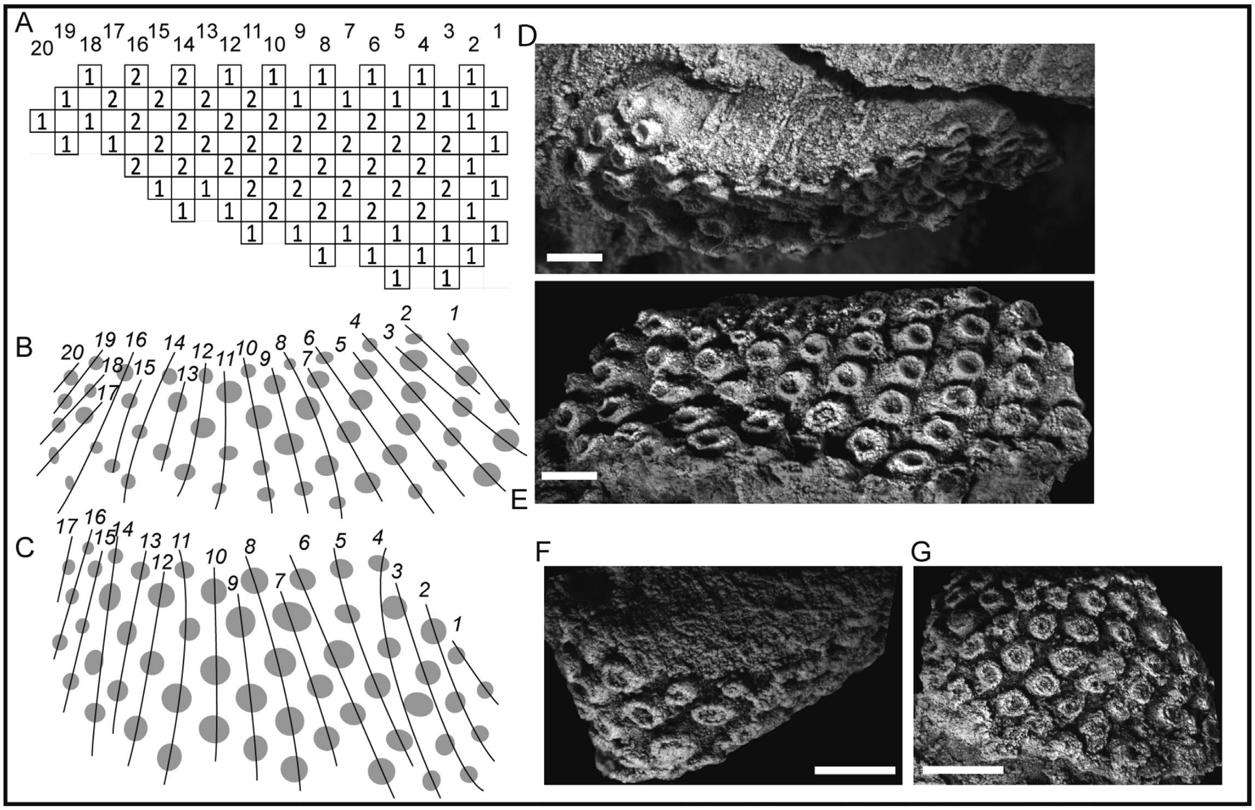

Figure 4. Trilobite eye map for *Toxophacops* (*Atopophacops*) *fujiwara* sp. nov. **A,** lens count in population (based on Clarkson and Tripp, 1982, figure 6); **B,** lens map of almost complete right eye of OUMNH DY.4a (based on the methodology of Clarkson, 1966, text-fig 2c, f); **C,** lens map of almost complete right eye of OUMNH DY.3; **D, E,** right eye of OUMNH DY.4a in dorsal and lateral views; **F, G,** right eye of OUMNH DY.3 in dorsal and lateral views. Scale bars represent 2 mm.

installed at the National Museum of Nature and Science, Japan. The experimental conditions and the analytical procedures followed for the measurements were after Tsutsumi *et al.* (2012). The spot size of the laser was 25 μm. A correction for common Pb was made on the basis of the ^{208}Pb/^{206}Pb and Th/U ratios (^{208}Pb correction; e.g. Williams, 1998) and the model for common Pb compositions proposed by Stacey and Kramers (1975). ^{206}Pb* indicates radiometric ^{206}Pb. The data of secondary standard OT4 zircon obtained during analysis yielded a weighted mean age of 189.9±3.6 Ma (95% conf.; $n = 5$; MSWD = 0.64). MSWD is an acronym of 'mean square weighted deviation', which is calculated from the square root of chi-square value.

Systematic paleontology

Morphological terminology follows that used in the Treatise on Invertebrate Paleontology, Part O (Whittington and Kelly, 1997) and Eldredge (1972, 1973). Length is typically used to describe sagittal/exsagittal measurements, and width to describe transverse measurements; where this is not obvious the abbreviations 'sag.', 'exsag.' or 'tr.' are used to clarify. The terms thoracopygon (plural thoracopyga) is used throughout to indicate a pygidium with attached thorax (e.g. Crônier and Tsmeyrek, 2011). Subfamily level trilobite systematics follow Zhou and Campbell (1990).

Order Phacopida Salter, 1864
Suborder Phacopina Struve and Moore, *in* Moore, 1959
Family Phacopidae Hawle and Corda, 1847
Subfamily Echinophacopinae Zhou and Campbell, 1990
Genus ***Toxophacops*** Zhou and Campbell, 1990

Type species.—*Toxophacops* (*Toxophacops*) *costata* Zhou and Campbell, 1990 (p. 80, pl. 3, figs 7–14) from the Zhusileng Formation (upper Emsian, upper Lower Devonian), Zhusilenghaierhan Region, western Inner Mongolia, China.

Diagnosis.—Cephalon without marginal spines; glabella slightly overhanging the anterior border; axial furrow shallow; preglabellar furrow present. Lateral preoccipital lobes present but weak. Eyes very large, and high. Vincular furrow reduced or absent medially; lateral vincular notches weak or absent. Hypostomal suture transverse medially, slightly deflected backwards at abaxial extremities. Pygidium subtriangular with 11–12 axial rings plus terminal piece; rings with a median tubercle; 12–14 pleural ribs; posterior margin arched; border poorly defined. Glabellar tubercles variably sized, usually smooth but occasionally with granules on their crests; cephalic marginal tubercles weak or absent (emended after Zhou and Campbell, 1990, p. 69).

Discussion.—Toxophacops is a non-spinose representative of Echinophacopinae. The genus was subdivided into three subgenera by Zhou and Campbell (1990): *Toxophacops* (*Toxophacops*)*, Toxophacops* (*Atopophacops*) and *Toxophacops* (*Zhusilengops*)*.* Species of *Toxophacops* occur in the Yikewusu Formation (Eifelian, lower Middle Devonian), and the Zhusileng Formation (Emsian, upper Lower Devonian) of the Zhusilenghaierhan Region, western Inner Mongolia. They are also present in the upper Emsian to Eifelian successions of the South Kitakami and Kurosegawa terranes of northeast and southwest Japan, respectively.

Subgenus *Toxophacops* (*Atopophacops*) Zhou and Campbell, 1990

Type species.—Toxophacops (*Atopophacops*) *apiculata* Zhou and Campbell, 1990 (p. 82, pl. 5, figs. 1–10) from the Yikewusu Formation (Eifelian, lower Middle Devonian), Zhusilenghaierhan Region, western Inner Mongolia, China.

Other species.—Toxophacops (*Atopophacops*) *cornigera* Zhou and Campbell, 1990 and *Toxophacops* (*Atopophacops*) *lepida* Zhou and Campbell, 1990*,* both from the Eifelian Yikewusu Formation, Zhusilenghaierhan Region, western Inner Mongolia. *Toxophacops* (*Atopophacops*) sp. indet. was also discussed by Zhou and Campbell (1990) from the uppermost part of the Zhusileng Formation, but this record is based on two poorly preserved specimens. *Toxophacops* (*Atopophacops*) *nonakai* (Okubo, 1956) is reported from the upper Emsian to Eifelian N3 Member of the Nakazato Formation of Takainari-yama in the South Kitakami Terrane, northeast Japan.

Diagnosis.—Axial furrows divergent at 55–65° in front of intercalating ring. Vincular furrow continuous from the anterior to the lateral parts, with absence of strong ridge on the inner side anteriorly, and weak notches often present. Visual surface with up to 21 files with between 56 and 136 lenses in total (see Table 1 for comparison). Pygidium with 9–11 pleural furrows (emended from that of Zhou and Campbell (1990, p. 70), to accommodate the new species described here).

Discussion.—Toxophacops (*Atopophacops*) displays the following differences from *Toxophacops* (*Toxophacops*): vincular furrow more continuous; eye with fewer lenses in each file; pygidium generally broader, with posterior margin less truncated and less dorsally upturned; and fewer pygidial pleural furrows (9–11 rather than 12–14).

Zhou and Campbell (1990) considered that *Toxophacops* (*Atopophacops*) may have arisen through evolution of *T.* (*Toxophacops*) species*,* owing to its occurrence in slightly younger strata of the Yikewusu Formation. The evolutionary changes include the glabella overlapping the anterior margin, an anterior glabellar furrow close to the margin, separation of the occipital and S1 apodemes to allow formation of a lateral occipital lobe, and the well delineated intercalating ring.

Toxophacops* (*Atopophacops*) *fujiwara Stocker, Tanaka, Derek Siveter and Lane sp. nov.

Figures 4–6

Etymology.—After the Fujiwara clan, established in AD 669 by Emperor Tenji for Japan's first 'Naidaijin' (Inner Minister) Nakatomi no Kamatari.

Holotype.—Internal mould of a cephalon, OUMNH DY.3 (Figure 5A) from the Givetian, Lower Member of the Naidaijin Formation, eastern slope of Memaruyama (Mount Memaru), along the valley of the Naidaijin River, near Tomochi, Shimomashiki District, Kumamoto Prefecture, central Kyushu (Figures 1, 2).

Other material.—An incomplete internal mould of a cephalon, OUMNH DY.4a, with counterpart OUMNH DY.4b, and silicone mould OUMNH DY.4/p; a laterally compressed, mostly internal mould of a pygidium, OUMNH DY.5; a large, tectonically sheared, internal mould of a pygidium, OUMNH DY.6; an incomplete external mould of a thoracopygon, OUMNH DY.7, with silicone mould OUMNH DY.7/p; an incomplete internal mould of a thoracopygon, OUMNH DY.8; an incomplete internal mould of a pygidium with axis and right pleural lobe, OUMNH DY.10; an incomplete internal mould of a pygidium, OUMNH DY.11; a small external mould of a pygidium, OUMNH DY.12 (on the same block as OUMNH DY.11), with a silicone mould OUMNH DY.12/p; and a laterally compressed, internal mould of a pygidium, OUMNH DY.13. All are topotypes from the '75 m' horizon.

Diagnosis.—Cephalon with large tubercles and relatively small eyes for the genus, with up to 56 lenses in 13 dorsoventral files, with a maximum of 7 lenses per file. Elongate subtriangular pygidium with 9–10 axial rings

Table 1. Comparison between the eyes of key phacopid species discussed in this paper. *Toxophacops* (*Atopophacops*) *fujiwara* sp. nov. (highlighted in bold) has the smallest number of lenses of the named species. In the first column for locality: Z = Zhusileng, Inner Mongolia; Y = Yikewusu, Inner Mongolia; NZ = Nakazato, northeast Japan; N = Naidaijin, southwest Japan.

Species	locality	Files	Maximum in a file	Maximum total lenses
Toxophacops (*Toxophacops*) *costata*	Z	22	10	166
Toxophacops (*Atopophacops*) *apiculata*	Y	21	8	136
Toxophacops (*Atopophacops*) *cornigera*	Y	21	8	133
Toxophacops (*Atopophacops*) *lepida*	Z	21	6	85
Toxophacops (*Atopophacops*) sp.	Z	21	6	91
***Toxophacops* (*Atopophacops*) *fujiwara* sp. nov.**	**N**	**20**	**4**	**55**
Toxophacops (*Atopophacops*) *okanoi*	NZ	17	11	157
Toxophacops (*Atopophacops*) *nonakai*	N, NZ	17	11	160
Toxophacops (*Zhusilengops*) *ejinensis*	Z	23	10	190
Toxophacops (*Zhusilengops*) sp.	Y	21	10	164
?*Phacops robusta*	Z	12	7	56

plus a terminal piece, and 7–8 pleural ribs.

Description.—Cephalon poorly preserved but with subpentagonal outline, almost as long as wide, weakly convex (sag., trans.); anterior arch prominent. Axial furrow deep; diverging at around 50–60° from occipital lobe, slightly convex abaxially inside the palpebral area due to inflated intercalating ring, with maximum divergence in line with the anterior margin of the visual surface. Glabella 30% longer than wide, occupying 68% of the cranidial width, with an almost circular preoccipital glabellar outline, and a flat dorsal surface. Occipital furrow deep, shallowing medially in line with inflated intercalating ring. Occipital ring long and highly convex (sag.), approximately 20% as long as wide, occupying 17% of glabellar length, and 53% of glabellar width; lateral occipital nodes absent. Preoccipital ring with well defined, small, lenticular lateral lobe roughly half as long (sag.) as wide and depressed relative to the rest of the intercalating ring, and occupying 18% of its width. S1 expanding forwards medially to isolate the prominent median lobe of the intercalating ring, occupying 42% of the ring's width. S2 absent. S3 weakly impressed in front of an inverted bell-shaped, inflated composite L2 and L3, medially bounded by the intercalating ring of 1P. Posterior border furrow deep and broad (exsag.), with steeper posterior slope; posterior border slightly narrower (exsag.) than occipital ring with a gently convex (sag.) dorsal surface. Lateral border furrow poorly preserved. Palpebral furrow shallow exsagittally; palpebral area large, moderately convex, 40% as wide as long, slightly lower than the glabella in lateral view. Eye large relative to the cephalon, occupying 50% of the total length of the glabella and almost reaching the lateral border furrow; visual surface containing up to 20 dorsoventral files, with up to 4 lenses per file, giving up to 55 lenses, with an average diameter of about 0.5 mm (Figure 4).

Thorax only partially preserved. Pleural furrows deep and long (tr.).

Pygidium semielliptical, roughly 65% as long as wide; 37% as high as wide, with convex anterior margin defined by posteriorly curved first ribs; moderately arched in posterior view. Deep, straight, moderately tapering axial furrows shallowing slightly at posterior margin. Narrow, highly arched axis occupying just under half of maximum pygidial width; comprises 9–10 transverse axial rings, the first the shortest (sag.), plus a terminal piece. Pleural lobes carry 7–8 ribs, with deep pleural furrows with rounded bases; interpleural furrows indistinct, faintly visible on the first two ribs. Lateral border poorly preserved, lacking a border furrow.

Glabellar sculpture comprises large subcircular tubercles; occipital ring, palpebral lobe, palpebral area and lateral cephalic borders lack tubercles; pygidial pleurae with sparse granules.

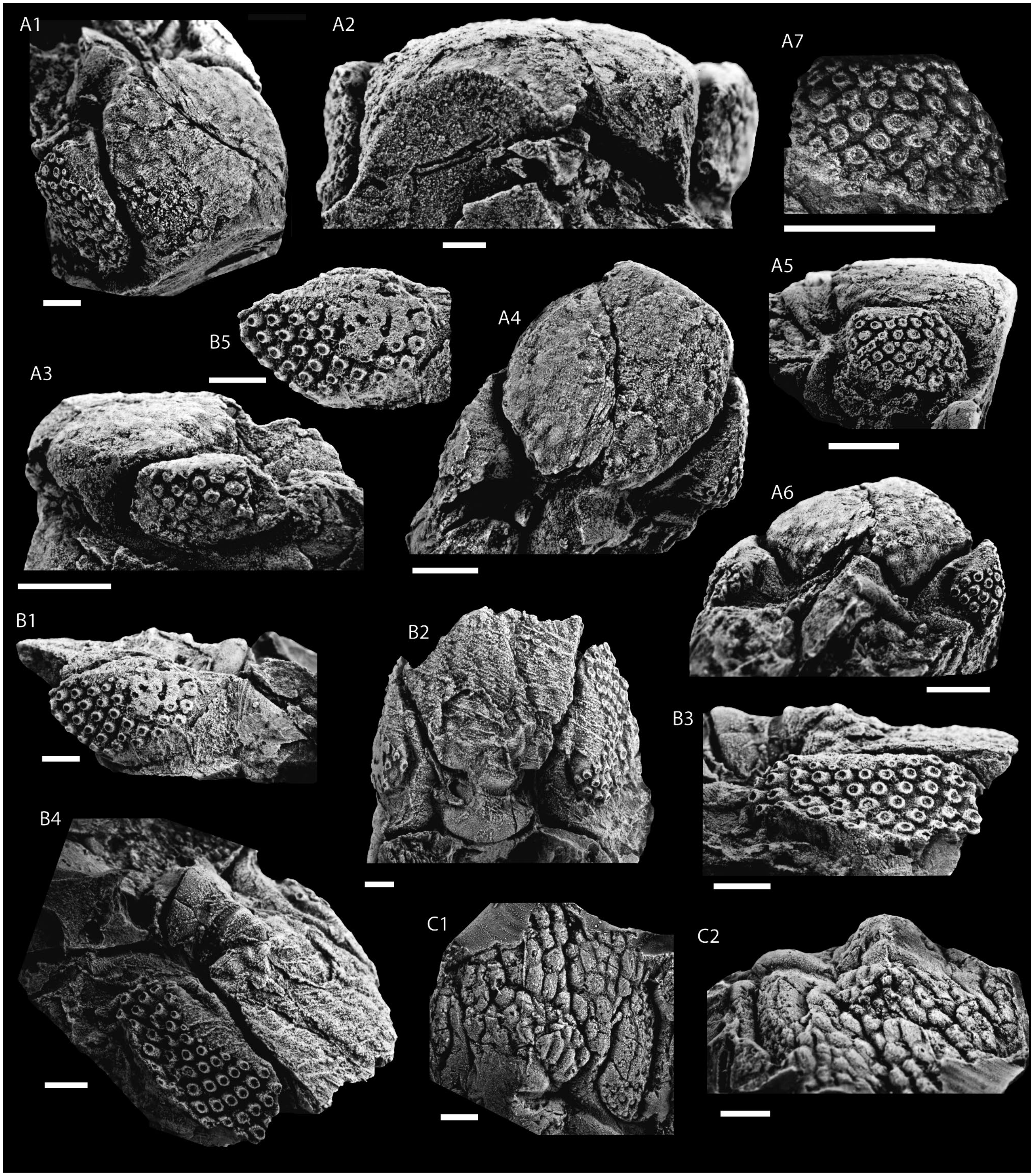

Figure 5. *Toxophacops* (*Atopophacops*) *fujiwara* sp. nov. from the Lower Member of the Naidaijin Formation. **A,** holotype, internal mould of cephalon OUMNH DY.3; A1, antero-dorsal view; A2, frontal view; A3, left lateral view; A4, dorsal view; A5, right lateral view; A6 posterior view; A7, close-up of right eye, right lateral view; **B,** an incomplete internal mould of a cephalon OUMNH DY.4a; B1, left lateral view; B2, dorsal view; B3, right lateral view; B4, antero-dorsal view; B5, left lateral view of left eye; **C,** silicone cast OUMNH DY.4/p (cast of external mould of cephalon OUMNH DY.4b, counterpart of OUMNH DY.4a); C1, dorsal view; C2, frontal view illustrating irregular flattening of the glabella. All scale bars represent 5 mm.

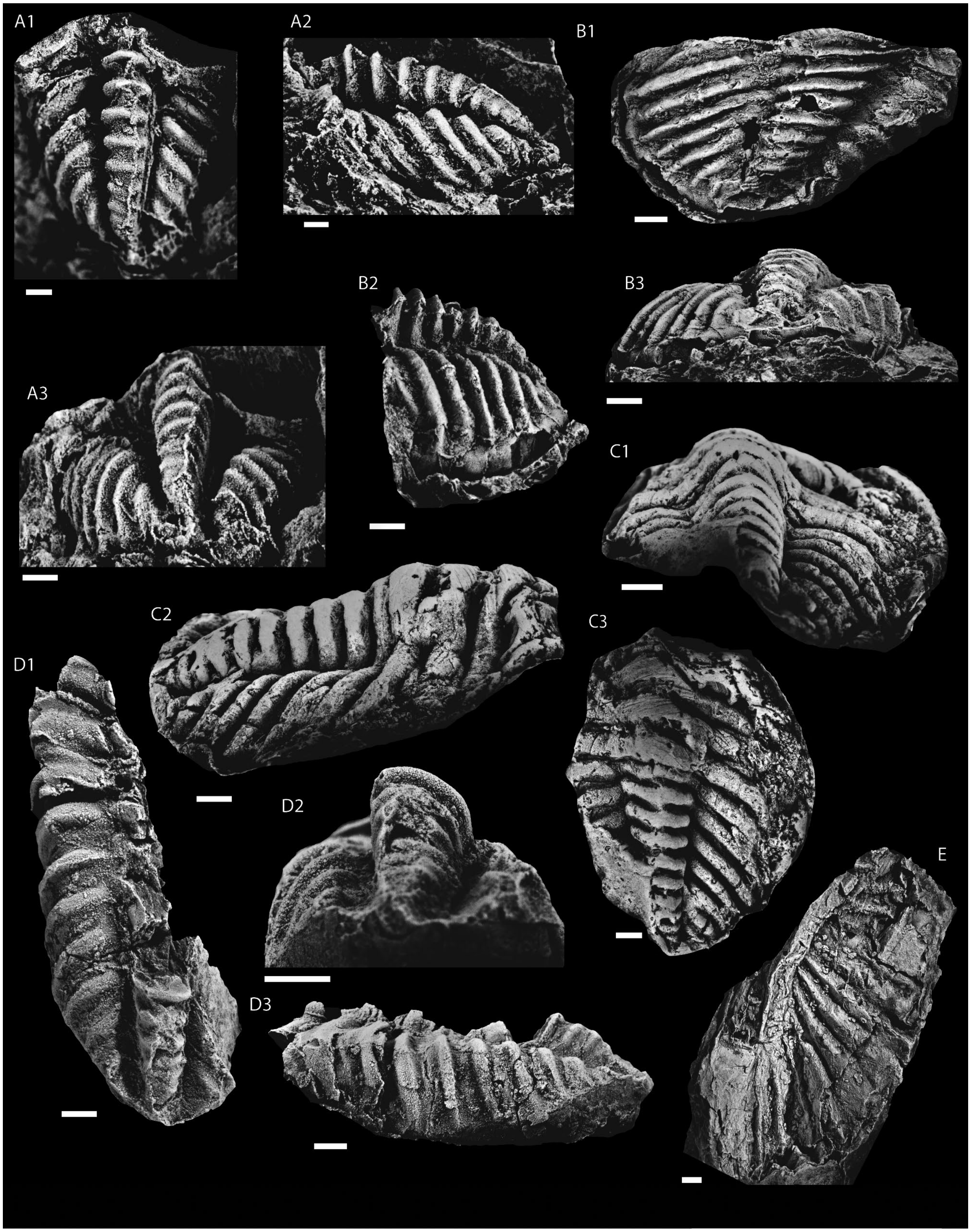

Figure 6. Trilobites from the Lower Member of the Naidaijin Formation. **A–D,** *Toxophacops* (*Atopophacops*) *fujiwara* sp. nov.; A, internal mould of a laterally compressed pygidium OUMNH DY.5; A1, dorsal view; A2, left lateral view; A3, posterior view; B, tectonically sheared internal mould of a pygidium OUMNH DY.6; B1, dorsal view; B2, left lateral view; B3, posterior view; C, silicone cast OUMNH DY. 7/p (cast of external mould of an incomplete thoracopygon, OUMNH DY.7); C1, posterior view; C2, right lateral view; C3, dorsal view; D, incomplete internal mould of a thoracopygon OUMNH DY.8; D1, dorsal view; D2, posterior view; D3, left lateral view; **E,** *Kobayashipeltis paucispinosa* (Okubo, 1951), internal mould of incomplete pygidium OUMNH DY.9 in dorsal view. All scale bars represent 5 mm.

Discussion.—Toxophacops (*Atopophacops*) *fujiwara* sp. nov. is most similar to *T.* (*A.*) *lepida* Zhou and Campbell, 1990 in the following features: its small size; highly medially arched occipital ring lacking occipital lobes; a medially forwards directed S1, isolating a strong well developed preoccipital ring; reduced, depressed lateral preoccipital lobes; a flat, wide glabella, with large tubercles and smaller interspersed second-order tubercles; a relatively smaller number of eye lenses (see Table 1); a subtriangular pygidial outline and narrow, highly arched pygidial axis; strong, deep pleural furrows; a lack of interpleural furrows; 9 pygidial axial rings plus a terminal piece, and 7–8 pleural ribs. Of these differences one of the clearest is the significantly lower number of lenses in the eye of *T.* (*A.*) *fujiwara* (see Table 1: 55 in 20 dorsoventral files, with at maximum 4 lenses per file) in comparison with those in *T.* (*A.*) *lepida* (85 lenses in 21 dorsoventral files containing up to 6 lenses per file).

Dimorphism (and trimorphism) is a well known phenomenon that affects lens counts of phacopid trilobite species (e.g. Clarkson, 1966). However, there are insufficient specimens of *Toxophacops* (*Atopophacops*) *fujiwara* to assess the presence of dimorphism.

Devonian Phacopina have previously been described from the South Kitakami Terrane of northeast Honshu (Sugiyama and Okano, 1941; Kaneko, 1990; Tazawa and Kaneko, 1987). *Phacops okanoi* Sugiyama, 1944 from that region may be referable to *Toxophacops* (*Atopophacops*), though the absence of a pygidium currently precludes a precise subgeneric assignment. *Phacops okanoi* differs from *T.* (*A.*) *fujiwara* in the much higher number of lenses in the eye, with 157 lenses in 17 dorsoventral files which contain up to 11 lenses in each file (see Table 1).

Toxophacops (*Atopophacops*) *nonakai* occurs in the Nakazato Formation in the South Kitakami Terrane, at a stratigraphical level considered to be at the boundary between the Emsian and Eifelian stages (Lower-Middle Devonian boundary, Kaneko, 1990, 2007), whilst Murata *et al.* (1997) previously reported *Taxophacops nonakai* (*sic*) and *Phacops pustliceps* (*nom. nud.*) from the Naidaijin Formation, and Kaneko (2007) figured *T. nonakai* and Phacopidae sp. A from the type locality of the Naidaijin Formation. The latter resembles *T.* (*A.*) *fujiwara* in the number of lenses in the eye and the large tubercles on the glabella, but it differs by the presence of an incised S2. Kaneko (2007) compared Phacopidae sp. A to the species described as ?*Phacops robustus* by Zhou and Campbell (1990), which has a similar number of files and lenses as *T.* (*A.*) *fujiwara*, and a similar glabellar sculpture.

Paleoenvironmental setting of *Toxophacops* (*Atopophacops*) *fujiwara* sp. nov.

Within the Lower Member of the Naidaijin Formation, the trilobite-bearing horizon is a sandy mudstone (Figure 3) in a succession rich in volcaniclastic material, tuffaceous sandstones and mudstones. Marine fossils including brachiopods, pelmatozoan debris and ostracods cooccur with the trilobites, and pelmatozoan debris also occurs in adjacent mudstones (Figure 2). The trilobites occur as non-fragmented detached cephala and pygidia as well as thoracopyga. The disarticulated nature of many of the fossils suggests a thanatocoenosis, though it is not clear how far the material has been transported. Alternatively the disarticulated trilobite sclerites could indicate exuviae. However, there is insufficient material to confirm either hypothesis.

Biostratigraphical significance of the trilobites

The occurrence of trilobites in the Naidaijin Formation is summarised in Figures 2 and 7, including the level ('75 m' horizon) in the Memaruyama section with *Toxophacops* (*Atopophacops*) *fujiwara* sp. nov. This level also includes an incomplete pygidium that is most likely referable to *Kobayashipeltis paucispinosa* (Figure 6E). Trilobite-bearing horizons in the Naidaijin Formation at the type Tenshu-zan section, a few kilometres from Memaruyama, comprise *T.* (*A.*) *nonakai*, *K. paucispinosa*, *Dechenella* (*Dechenella*) *minima, Acanthopyge* (*Jasperia*) *duplicispinata* and *Nipponocalymene hamadai*. Kaneko (2007) suggested these trilobites are of late Emsian to early Eifelian age.

Several of the trilobites of the Tenshu-zan section are also recorded from the N3 Member of the Nakazato Formation of the South Kitakami Terrane in northeast Japan (Figure 7). The Nakazato Formation has been accorded a late Emsian to Eifelian age based on interregional trilobite and brachiopod biostratigraphy (Sugiyama, 1942; Okubo, 1956; Minato and Kato, 1977; Minato *et al.*, 1979; Copper *et al.*, 1982; Kaneko, 1984, 1985, 1990, 2007; Tazawa, 1988; Chen and Tazawa, 2003). The trilobite *Nipponocalymene hamadai* is also recorded from the Rosse Formation of the Hida Gaien Terrane in central Japan (Kaneko, 2007), but from an allochthonous limestone block within Upper Devonian mudstones containing the plant *Leptophloem* and the brachiopod *Cyrtospirifer* (Tazawa *et al*., 2000). The allochthonous block may be of late Early or early Middle Devonian age (cf. Tazawa *et al*., 2000).

The trilobite *Rhinophacops schizoloma* Kaneko, 1990 is also present in the Nakazato Formation at stratigraphical horizons with the widespread late Early and early Middle Devonian Japanese trilobite fauna listed above. *R.*

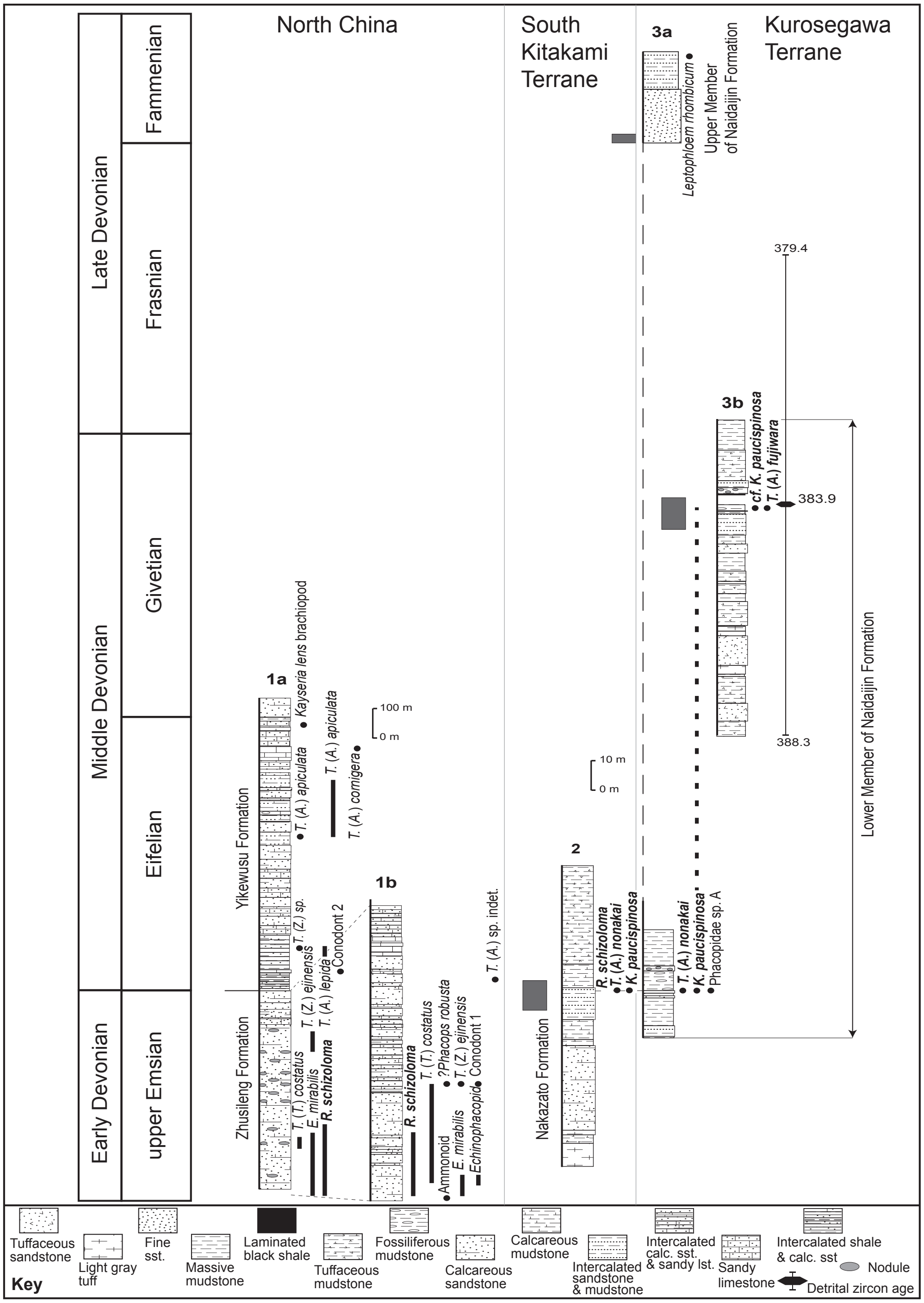

Figure 7. Correlation of key trilobite-bearing strata in the upper Emsian to Givetian (Devonian) interval between Japan and north China. Chain of correlation from the Memaruyama section of the Lower Member of the Naidaijin Formation, Kurosegawa Terrane, Kyushu, Japan (3b); to the Upper Member of the Naidaijin Formation at the type section in Tenshu-zan, less than 1 km to the east (3a) of the type section (see Figure 1); to the Nakazato Formation, South Kitakami Terrane, northeast Japan (2), and on to the Zhusileng and Yikewusu formations, Zhusilenghaierhan region, Inner Mongolia (see Figure 9 for locations). Logs 1a, 1b adapted from Zhou and Campbell (1990), log 2 compiled from data in Okubo (1950). 'Conodont 1' is *Pandorinellina steinhornensis steinhornensis* (Ziegler, 1959), 'conodont 2' is *Icriodus corniger* Wittekindt, 1966. For the Japanese logs (2, 3a, b), due to a large difference in scale, the thicknesses relative to the Chinese logs (1a, b) are represented by a gray box to the left of each log. Confirmed biostratigraphical ranges of trilobites are represented by thick black lines, and inferred ranges are represented by dashed lines. Trilobite species that are key links in the chain of correlation are marked by bold species names (see Figure 8 for greater clarification). The 100 m scale refers to logs 1a and b, and the 10 m scale to logs 2, 3a and 3b. Error on the age of the detrital zircons is represented to the right of log 3b (dates 388.3 to 379.4 Ma).

schizoloma also occurs in the Zhusileng Formation of the Zhusilenghaierhan Region of Inner Mongolia (Zhou and Campbell, 1990). The ammonoid *Anarcestes* (*Anarcestes*) *praecursor* Frech, 1897 and the conodont *Pandorinellina steinhornensis steinhornensis* (Ziegler, 1959) occur in the Zhusileng Formation, indicating a late Emsian age (Zhang and Ruab, 1983; Zhang, 1985). The appearance of the conodont *Icriodus corniger* at the base of the overlying Yikewusu Formation signals an early Eifelian age. The brachiopods *Kayseria lens* (Schnur, 1851) and *Reticulariopsis* Fredericks, 1916 define the upper unit of the Yikewusu Formation as late Eifelian (Zhang, 1985).

Data from detrital zircons in the Memaruyama Section 2 m above the trilobite-bearing ('75 m') horizon with *Toxophacops* (*Atopophacops*) *fujiwara* and cf. *Kobayashipeltis paucispinosa* suggest a maximum age of 383 Ma±4.4 Ma (see Appendix 1a–c) for this part of the Naidaijin Formation. This radiometric age would indicate a likely Givetian age, but given the 4.4 million-year uncertainty, this could also be as young as earliest Frasnian and therefore Late Devonian (Frasnian boundary at 382.7 Ma, according to Becker *et al*., 2012). Therefore, through a chain of interregional correlation of the trilobites (Figure 7) the Lower Member of the Naidaijin Formation appears to span the late Emsian to Givetian stages with the Tenshu-zan section recording strata of late Emsian and Eifelian age, and the Memaruyama section including strata of Givetian age, or possibly a little younger.

There is apparently no gap in sedimentation between the trilobite- and zircon-bearing horizons in the Memaruyama section (Figure 1), and no additional fossil data to suggest this is a condensed interval, with a significant biostratigraphical difference between the horizons. This suggests that the widespread phacopid trilobite fauna of the North China Plate and Japanese terranes may include a succession of species which have overlapping biostratigraphical ranges (Figures 7, 8), the overlaps being of correlative value. Thus, *Rhinophacops schizoloma* appears to be typical of late to latest Emsian rocks, *Toxophacops* (*Atopophacops*) *nonakai* more typical of the Eifelian, *Kobayashipeltis paucispinosa* ranging through the Eifelian and Givetian, and *T.* (*A.*) *fujiwara*, apparently typical of the Givetian (Figure 8).

Overall, a late Early and Middle Devonian age for the Lower Member of the Naidaijin Formation is strongly suggested by the trilobites and radiometric age. This is older than the Late Devonian age of the Upper Member based on floral and brachiopod assemblages (Kimura *et al*., 1986; Yanagida *et al*., 1987), which is most likely Fammenian. Nevertheless, poor exposure in the type and other sections obscures the geological boundary between the Lower and Upper members, so the nature of the lithological contact cannot be discerned.

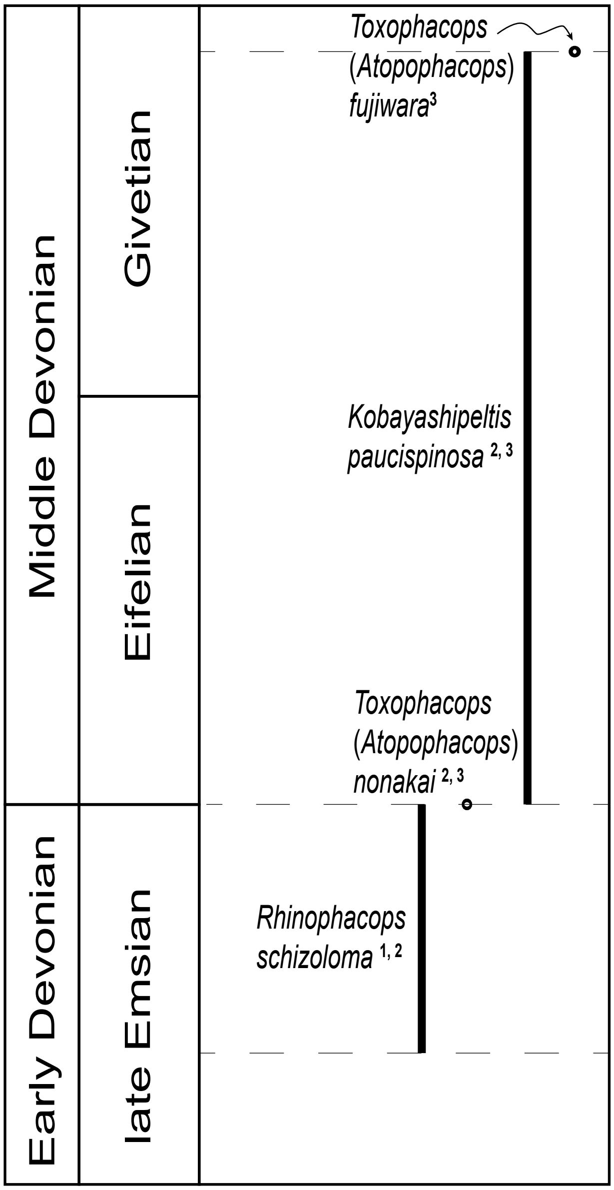

Figure 8. Biostratigraphical ranges of key phacopid species that are useful for subdividing the upper Emsian through to Givetian stratigraphy of Japan (based on the chain of correlation in Figure 7). The geographical distribution of the key trilobite taxa is indicated by: 1, Zhusileng Formation, Mongolia; 2, Nakazato Formation, South Kitakami Terrane, north-eastern Japan; 3, Naidaijin Formation, Kurosegawa Terrane, Kyushu, Japan.

Paleobiogeographical significance of the phacopid trilobites

The paleobiogeographical relationships of the three early and middle Paleozoic terranes in Japan (Figure 9),

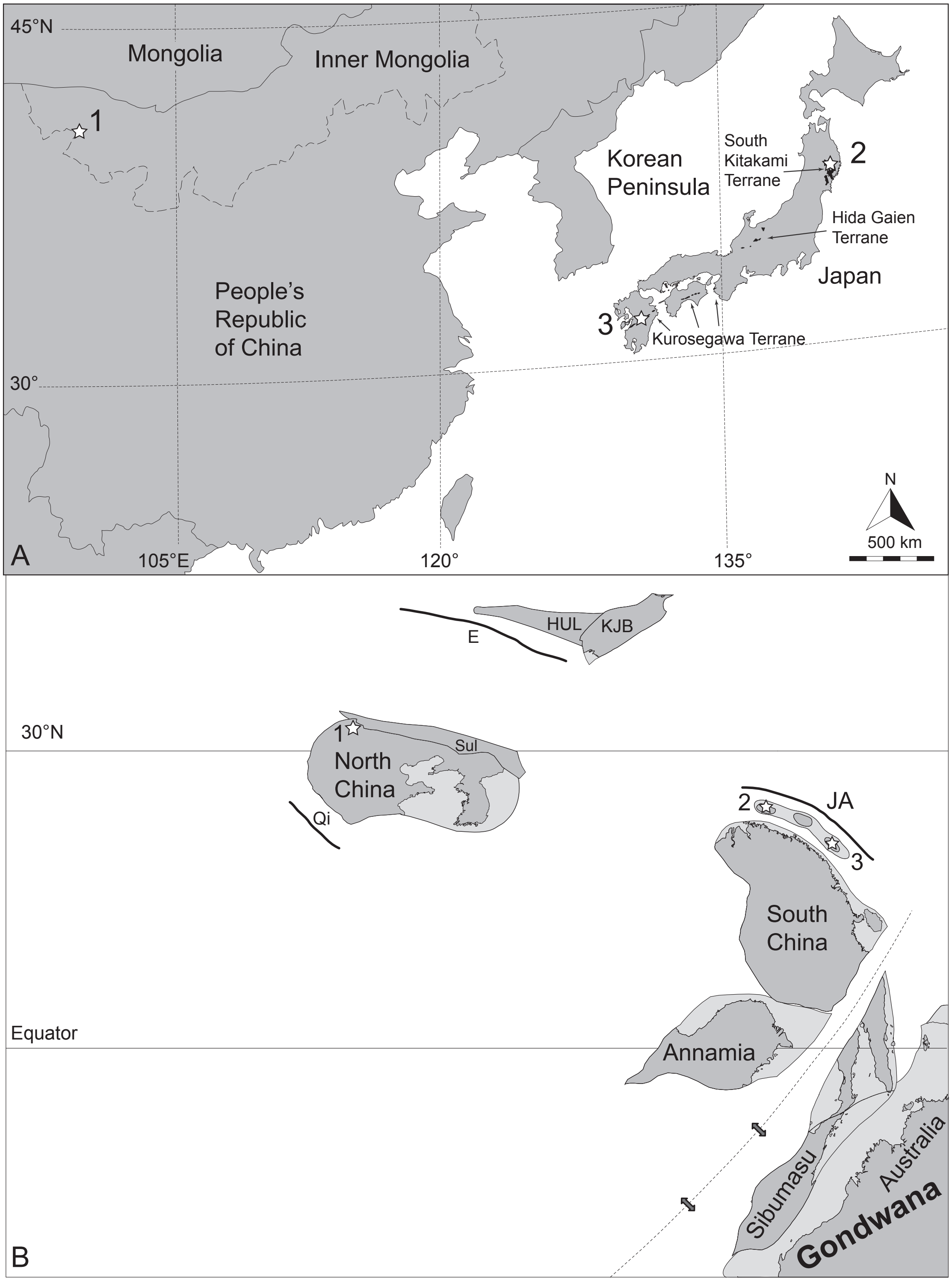

Figure 9. Biogeographical signature of *Toxophacops* (*Atopophacops*) Zhou and Campbell, 1990. **A,** modern geographical map showing distribution of fossil localities bearing *Toxophacops*. 1, Zhusileng and Yikewusu formations, Zhusilenghaierhan region, Inner Mongolia, China; 2, Nakazato Formation, Iwate Prefecture, South Kitakami Terrane, northeast Japan; 3, Naidaijin Formation, Kurosegawa Terrane, Kumamoto Prefecture, central Kyushu, southwest Japan. **B,** paleogeographical map of the late Early Devonian (Emsian) at 400 Ma, after Cocks and Torsvik (2013). E, Enshoo Arc; HUL, Hutag Uul-Songliao; JA, Japanese arcs; KJB, Khanka-Jiamusu-Bureya; Qi, arcs now in the Qaidam-Qilian Terrane; Sul, Sulinheer. Bold black lines are subduction zones.

both to each other and to other terranes in East Asia, provide conflicting paleogeographical evidence (summarised in Williams *et al*., 2014). The new trilobite data presented here contribute to this debate, but do not provide firm conclusions pending a full review of the entire Siluro-Devonian trilobite fauna of Japan. Nevertheless, species of *Toxophacops* (*Toxophacops*) appear to have been widely distributed between the North China Plate and at least two of the Japanese terranes during the early Late and Middle Devonian (Figures 7, 9).

Biogeographical links between the Devonian fossils of Japan and Inner Mongolia (North China Plate) are suggested by the co-occurrence of the phacopid trilobite species *Rhinophacops schizoloma* Kaneko, 1990 in the Nakazato Formation and the Zhusileng Formation (Kaneko, 1990; Zhou and Campbell, 1990). In addition, the typically Japanese trilobite species *Toxophacops* (*Atopophacops*) *nonakai* and *T.* (*Toxophacops*) *okanoi* are representatives of common subgenera of the Zhusileng and Yikewusu formations; the former occurs in both the South Kitakami and Kurosegawa terranes, the latter only within the South Kitakami Terrane (Kaneko, 2007). *Toxophacops* (*A.*) *fujiwara* sp. nov. from the Kurosegawa Terrane is also very similar to *T.* (*A.*) *lepida* from the Eifelian Yikewusu Formation, Zhusilenghaierhan region of Inner Mongolia, and also shows similarities to ?*Phacops robusta* Zhou and Campbell, 1990 from the same formation (Zhou and Campbell, 1990).

The phacopids as a group were thought to have reached their acme in the Early to Middle Devonian, reflected by their ability to occupy a variety of marine environments within warm climate zones (Chlupáč, 1983). Not restricted to specific facies, members of the group occur in both clastic and limestone lithologies. Their diversity and abundance in limestones were particularly notable at this time (Chlupáč, 1975, 1977), including their occurrence in the sedimentary successions of the South Kitakami and Kurosegawa terranes. However, by contrast, no phacopids have been reported from the Fukuji Formation of the Hida Gaien Terrane, despite this interval of the Devonian being characterized there by limestone-dominated facies. This absence of phacopid species from the Hida Gaien Terrane has previously been suggested to be of biogeographical significance (Kobayashi and Hamada, 1977; Kaneko, 1990; Zhou and Campbell, 1990), distinguishing this region from the South Kitakami Terrane of northeast Japan (Figures 1, 7). In this context it is notable that phacopids are also absent from the succession in south China during this interval (Zhou, 1987).

It has been suggested (e.g. Williams *et al*., 2014) that aside from representing real geographical proximity between terranes in this East Asian setting, mixed biogeographical signals could reflect differences between organisms with a wide or narrow dispersal capability. For example, those of deeper marine facies might have wider dispersal. Such facies controls on distribution are suggested by the fauna of the Lochkovian to Emsian Fukuji Formation of the Hida Gaien Terrane, in which shallow marine leperditiid arthropods from a possible lagoonal facies (Adachi and Ezaki, 2007) in the middle part of the formation suggest an affinity with South China (Tanaka *et al*., 2012; Wang and McKenzie, 2000; Wang, 2009), whilst an ostracod fauna of supposed deeper marine aspect (see Becker and Bless, 1990) from a black mudstone horizon in the upper part of the formation shows widespread affinities with species from the Carnic Alps, France, Spain and Germany (Kuwano, 1987). This highlights the potential facies control on biogeographical signals, in which deeper water faunas show a tendency towards greater biogeographical affinity with more distant regions from Japan than those in shallower marine settings.

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Author contributions

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