









RESEARCH ARTICLE

The paleobiogeographical significance of the Silurian and Devonian trilobites of Japan

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Abstract

Six major groups of trilobites from the Silurian and Devonian of Japan are evaluated for their paleobiogeographical signature. Silurian illaenids and scutelluids show four generic-level and at least two species-level links with the Australian segment of the Gondwana paleocontinent; encrinurids also indicate two generic-level links with Australia and also the South China paleocontinent; whilst Devonian phacopids, and possibly proetids, suggest at least two generic-level links with the North China paleocontinent. These different patterns may reflect the fragmentary biostratigraphical record of Japanese trilobites, but they also appear to reflect paleoenvironmental parameters associated with lithofacies, and paleoecology. Thus, Japanese assemblages of proetids and phacopids occurring in deep-water clastic lithofacies have counterparts in similar settings in North China, and Japanese scutelluids and illaenids are strongly associated with shallow marine carbonate lithofacies that are similar to those of their occurrences in Australia. Japanese encrinurids occur in carbonate rocks indicative of shallow marine settings in the Kurosegawa Terrane, and they demonstrate a consistent paleobiogeographical affinity with Australia and South China. Larval ecology cannot be directly assessed for Japanese trilobite groups. However, proetids have consistently been shown to have planktonic protaspides, whereas illaenids, scutelluids, and encrinurids have benthic protaspides. Planktonic protaspides would have a greater propensity for distribution in ocean currents than benthic ones, and therefore may be of more limited paleobiogeographical utility. The combined data from the six different groups indicates that the complex paleobiogeographical patterns of the Japanese trilobite assemblages need to be interpreted with caution, and similarity of taxa does not necessarily denote paleogeographical proximity to other regions.

KEYWORDS

biogeography, biostratigraphy, Devonian, Japan, lithofacies, Silurian, trilobites

1 | INTRODUCTION

The Silurian and Devonian marine sedimentary successions of Japan comprise those of the South Kitakami Terrane (SKT) of north-eastern Honshu, the Hida Gaien Terrane (HGT) of central Honshu, and the Kurosegawa Terrane (KT), which extends from the Kii Peninsula in southwest Honshu to the islands of Shikoku and Kyushu (Figure 1). Strata in each of these terranes contain locally abundant fossil invertebrate faunas including brachiopods, cephalopods, ostracods and trilobites (see Williams, Wallis, Oji, & Lane, 2014 for an overview of Japanese lower Paleozoic stratigraphy). Trilobites have been reported

from each of these terranes (see Table 1), with the most diverse faunas reported from the Silurian Fukata Formation (approximately 32 species), and the Devonian Fukuji Formation and its lateral equivalent the Kamianama Formation (together ~ 22 species).

In this paper we focus on six groups of Japanese trilobites that have recently undergone taxonomic revision, and which are interpreted to have a range of paleoecologies. Recent revision of the Illaenidae and Scutelluidae (Holloway & Lane, 1998, 2012, 2016) has demonstrated links between the trilobite faunas of Japan and Australia. It should be noted that the composition and delimitation of the families Illaenidae and Scutelluidae remain contentious, particularly so far as their effaced (illaenimorph)



FIGURE 1 Position of the South Kitakami, Hida Gaien, and Kurosegawa terranes of Japan. The extent of the outcrop of each terrane is represented by areas with dark grey shading. Open circles denote areas containing trilobite-bearing rocks within each terrane, solid circles represent cities, and dashed lines highlight the three terranes

taxa are concerned (Holloway & Lane, 1998, 2012, 2016; Lane & Thomas, 1980; Whittington, 1999). Of the taxa belonging to those families dealt with in this paper, *Bumastella*, *Rhaxeros* and *Lalax* are assigned to the Illaenidae and *Japonoscutellum*, *Illaeoscutellum*, *Kosovopeltis* and *Borenoria* to the Scutelluidae, following Holloway and Lane (1998, 2012, 2016). Revision of Encrinuridae by Holloway (1994), Ramsköld (1986), Strusz (1980), and Zhang (1983) suggests links between Australia, Japan, and South China. Additionally, revision of the Phacopidae by Kaneko (1990, 2007), Stocker et al. (2018), and Zhou and Campbell (1990) has demonstrated links between the KT and SKT as well as with the North China paleocontinent. However, a recent review of the Proetidae and Aulacopleuridae of Japan (Stocker et al., 2018), considered both of these groups to be endemic at the species level, even between the Japanese terranes, though proetids suggested links with North China at the genus-level. These studies represent trilobite groups occurring in a range of lithofacies, and with a range of paleoecologies.

In this paper we evaluate the significance of the distribution patterns of Japanese trilobites from the Silurian and Devonian. We consider whether geography, lithofacies or ecology provides the strongest influence on the biogeographical patterns of the Japanese Silurian and Devonian trilobite faunas and assess whether biogeographical patterns changed over time.

2 | BIOSTRATIGRAPHICAL RANGES OF THE SILURIAN AND DEVONIAN TRILOBITES OF JAPAN

The trilobite material used in this study has been collected at different times, and by different authors over the past century (e.g. Kobayashi, 1988a, 1988b, 1988c; Kobayashi & Hamada, 1974, 1976, 1977, 1985, 1987; see summary in Williams et al., 2014). As a result, piecing together the stratigraphical ranges of the different taxa relies on a detailed assessment of the trilobite literature, of geological maps of the various regions (e.g. see Stocker et al., 2018), and analysis of the most up-to-date literature on paleontological and radiometric dates for the region. Seven formations are trilobite-bearing (Figure 2). Here we summarize the data and approach we have used to assemble a composite trilobite biostratigraphy based on the six groups studied.

Graptolite biostratigraphy underpins the international correlation for rocks of Silurian and Early Devonian age, and provides a stratigraphical resolution in the Silurian of less than 1 million years for some biozones (Zalasiewicz et al., 2009). Palynological biozonations based on chitinozoans provide similar resolution (e.g. Steeman et al., 2016). However, the Japanese succession is so far devoid of graptolites, and biostratigraphically significant chitinozoans have only now been reported (Vandenbroucke et al., 2018). The biostratigraphical

TABLE 1 Summary of Silurian and Devonian Japanese trilobites and their paleobiogeographical connections

Terrane	Trilobite group	Total diversity		Terrane endemic taxa		Japan endemic taxa		Localized taxa and relevant terrane(s)		Pandemic taxa		Major biogeographical links			
		Genera	Species	Genera	Species	Genera	Species	Genera	Species	Genera	Species	Japanese terranes	Other terranes		
South Kitakami	Encrinuridae	2	2	0	2	0	0	2 (South China, Australia)	0	0	0	0	Batocara also occurs in the HGT and the KT. <i>Coronoccephalus</i> also occurs in the KT and possibly in the HGT.	Coronoccephalus is diverse in South China and Australia.	
		1	1	0	0	1	1	0	0	0	0	0	<i>Kobayashipeltis paucispinosa</i> also occurs in the KT.	None	
		4[1]	1[5]	0	0	0	1	1 (North China)	0	1	0	0	0	Dechenellids are also diverse in North China. <i>Otodechenella</i> suggests links with North China.	
Hida Gaian	Phacopidae	2[1]	3[1]	0	0	0	1[1]	2 (North China)	1 (North China)	0	0	0	<i>Toxophacops</i> (Atopophacops) <i>nonakai</i> and Phacopidae sp. A of Kaneko (2007) also occur in the KT.	Sub-family Echinophacopininae found in North China and Japan only. <i>Rhinophacops</i> and <i>Toxophacops</i> only found in Japan and North China. <i>R. schizoloma</i> Found in both above regions.	
		1[2]	1[2]	0	1	0	[2]	1 (Australia, South China)	0	1	0	0	0	<i>Batocara</i> and <i>Coronoccephalus</i> also occur in the SKT and the KT.	<i>Batocara</i> is diverse in Australia and also occurs in South China
		4	4	1	4	0	0	0	0	2	0	0	0	0	None
Aulacopleurida	Proetida	2	8	0	8	0	0	1 (North China, Siberia)	0	1	0	0	0	0	<i>Gaminella</i> is diverse in Siberia, but also found in North China
		1	1	0	1	0	0	0	0	1	0	0	0	0	None

TABLE 1 (Continued)

Terrane	Trilobite group	Total diversity		Terrane endemic taxa		Japan endemic taxa		Localized taxa and relevant terrane(s)		Pandemic taxa		Major biogeographical links	
		Genera	Species	Genera	Species	Genera	Species	Genera	Species	Genera	Species	Japanese terranes	Other terranes
Kurosegawa	Encrinuridae	4	8	0	8	0	[1]	2 (South China, Australia)	0	2	0	<i>Batocara</i> also occurs in the SKT and HGT. <i>Coronocephalus</i> also occurs in the SKT and possibly the HGT. <i>Encrinurus nodai</i> may also be present in the HGT.	<i>Coronocephalus</i> is diverse in South China and Australia. <i>Batocara</i> is diverse in Australia and also occurs in South China.
	Scutelluidae	4[2]	9[2]	0	6[2]	1	1	2 (Australia)	1 (Australia)	2	0	<i>Japonoscutellum</i> also occurs in the HGT, <i>Kobayashipeltis paucisinosae</i> also occurs in the SKT.	<i>Borenoria</i> and <i>Illaeoscutellum</i> only occur in Australia and Japan. <i>Japonoscutellum japonicum</i> also occurs in Australia. <i>J. laticephalum</i> may be conspecific with <i>J. magnum</i> from Australia and Chu-iji terrane (Kazakhstan).
	Proetida	6[1]	7[3]	1	5[2]	0	1	1 (South China)	0	4[1]	0	<i>Dechenella minima</i> also occurs in the SKT, <i>Latiproetus</i> may be present in the SKT	<i>Latiproetus</i> is a common genus in South China.
	Phacopidae	2[1]	3[1]	0	2	0	1[1]	1 (North China)	0	1	0	<i>Toxophacops</i> (<i>Atopophacops nonakai</i> and <i>Phacopidae</i> sp. A of Kaneko (2007)) also occur in the SKT.	Echinophacopinae is a sub-family diverse in North China and Japan only. <i>Toxophacops</i> is only found in Japan and North China.
	Iliaenidae	4	6	0	5	0	0	2 (Australia)	1 (Australia)	2	0	No iliaenids found in other Japanese terranes.	<i>Bumastella</i> , <i>Rhaxeros</i> and <i>Lalax</i> are all diverse in Australia. <i>Bumastella spicula</i> also occurs in Australia.

Additional taxa (in square brackets) refer to those which are here left in open nomenclature or considered to be of uncertain affinity. The term 'Japanese endemic taxa' is used for those that occur in more than one of the Japanese terranes; the term 'Localized taxa' is used for those taxa that have biogeographical links with other non-Japanese terranes.

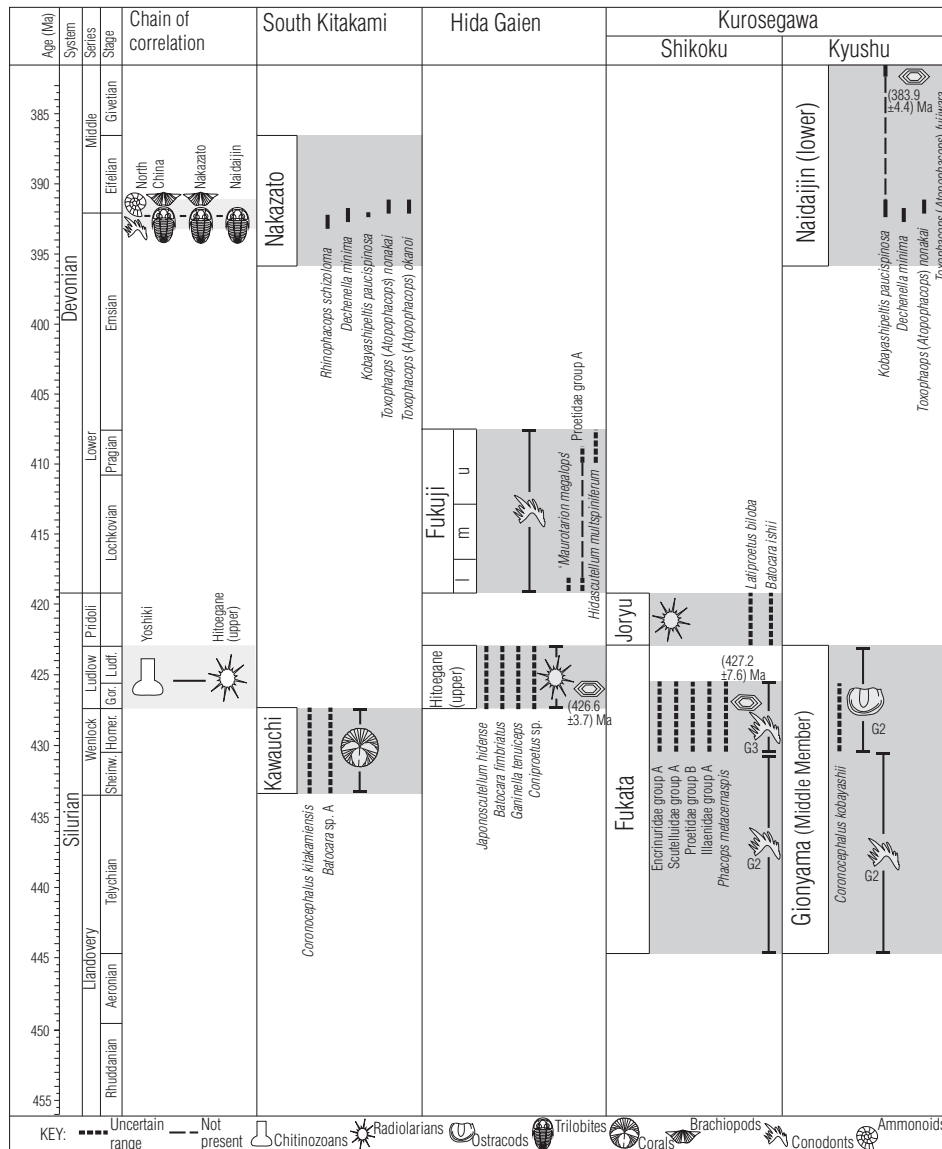


FIGURE 2 Temporal distribution of trilobites recorded across seven formations in the South Kitakami, Hida Gaien, and Kurosegawa terranes of Japan. Silurian stages are the Homerian, Sheinwoodian, Gorstian, and Ludfordian. Proetidae group A comprises the following species of the genus *Ganinella* (sensu Stocker et al., 2018): *G. fukujiensis*, *G. oisensis*, *G. antijuba*, *G. angustus*, *G. latipolus*, and *G. longiconus*. Proetidae group B comprises the following species: *Interproetus* sp. A, *Eremiproetus? magnicerviculus*, *Eremiproetus? subcarinatus*, *Coniproetus subovalis*, *Gomiites granulatus*, and *Gomiites latiaxis*. Encrinuridae group B comprises the following species: *Batocara yokokurensis*, *Batocara mamelon*, *Encrinurus stenorrhachis*, *Batocara tosenensis*, *Encrinurus nodai*, and *Staurocephalus trichonin*. Scutellulidae group A comprises the following species of the genus *Japonoscutellum*: *J. japonicum*, *J. laticephalum*, *J. puteatum*, *J. angusticostatum*, *J. primigenium*, as well as *Kosovopeltis fungiformis*, *Kosovopeltis? geniculata*, *'Japonoscutellum' tumidum* (see Holloway & Lane, 2012), *Borenoria trinodosa* and *Iliaenoscutellum platiceps*. Iliaenidae group A comprises the following species: *Bumastella spicula*, *Rhaxeros subquadratus*, *Rhaxeros shinoharai*, *Lalax kattoi*, *Lalax sakoi*, and *Bumastus agmakros*

assignment of different formations also depends on the interpretation of shelly faunas, or on the intermittent and serendipitous occurrence of biostratigraphically significant conodonts and radiolarians (e.g. Aitchison, Hada, Ireland, & Yoshikura, 1996; Kurihara, 2003a, 2003b, 2004, 2007; Kurihara, Sato, & Tazawa, 2005; Manchuk et al., 2013; Männik et al., 2018; Tsukada & Koike, 1997; Umeda, 1998a, 1998b). The biostratigraphical and sometimes absolute ages of Japanese trilobites are here constrained by a combination of previously published microfossil biostratigraphy and zircon geochronology (Figure 2), enhanced by the new research on chitinozoans (Vandenbroucke et al., 2018), conodonts

(Männik et al., 2018) and ostracods (Siveter, Tanaka, Williams, & Männik, 2018).

3 | STRATIGRAPHY OF THE TRILOBITE-BEARING FORMATIONS OF JAPAN

3.1 | South Kitakami Terrane

The Kawauchi Formation of the Hikoroichi area of Iwate Prefecture, Honshu, comprises strata of the Silurian Wenlock and Ludlow series based on biostratigraphical data from corals, conodonts and trilobites

(Kato et al., 1980; Kido & Sugiyama, 2011; Kobayashi, 1988c; Kobayashi & Hamada, 1974). The 'Encrinurus bed' of the Kawauchi Formation sensu Sugiyama (1940) is considered to represent the lower to middle Ludlow (Kobayashi & Hamada, 1976). Conodonts reported from this formation (Harashinaï (1981) suggest the lower Sheinwoodian Stage of the Wenlock Series (Männik et al., 2018), though only a selected few taxa were illustrated by Harashinaï (1981).

The N3 Member is a formal stratigraphic unit of the upper Nakazato Formation, also in the Hikoroichi area, is correlated by trilobites (Kaneko, 1990; Zhou & Campbell, 1990), and gastropods (Pan & Cook, 2003) with the Zhusileng Formation of Inner Mongolia, North China, where ammonoids and conodonts indicate the Emsian Stage. Brachiopods from another horizon within the N3 Member (Tazawa, 2002) correlate with the Eifelian Yikewusu Formation in the same region of North China, therefore effectively constraining the age of the N3 Member to Emsian–Eifelian by a chain of correlation. Kaneko (2007, p. 6, Figure 5) shows trilobites of the N3 Member straddling the boundary between the Emsian and Eifelian stages.

3.1.1 | Hida Gaïen Terrane

The Hitoegane Limestone member is not a formal stratigraphic unit (see Williams et al. 2014) within the upper part of the Hitoegane Formation in the Hitoegane area of Gifu Prefecture, Honshu has yielded a diverse trilobite fauna suggesting either the middle or upper Ludlow Series (Kobayashi, 1988a, 1988b; Kobayashi & Hamada, 1987), and a coral fauna indicative of the Ludlow (Niko, 2004). Radiolarians from tuffaceous clastic rocks of the upper Hitoegane Formation suggest an age range from the Ludlow to Early Devonian, but the relationship of the tuffaceous clastic rocks to the Hitoegane Limestone member is uncertain. Felsic tuffs in radiolarian-barren rocks intercalated between these radiolarian-bearing clastic strata provide a mean radiometric age of (426.6 ± 3.7) Ma (Manchuk et al., 2013), which would indicate the Gorstian Age of the Ludlow Epoch.

New research on chitinozoans (Vandenbroucke et al., 2018) has refined the biostratigraphy of the Yoshiki Formation, also of the Hitoegane area, and established a biostratigraphical tie with the Ludlow Series (Gorstian or lower Ludfordian Stage) of the type Silurian in the Welsh Borderland. Approximate equivalence between the upper Hitoegane and Yoshiki formations is suggested by their similar radiolarian assemblages (*Futobari solidus*–*Zadrappolus tenuis* Zone), though this assemblage is long-ranging in the upper Silurian to lowest Devonian (Kurihara, 2007).

Silurian strata have been reported at the Hakubado locality, Izumi Village, Ohno County in the Kuzuryu Lake–Upper Ise river area of Fukui Prefecture (Ohno, Okazaki, & Hirano, 1977) and Kobayashi and Hamada (1987) reported '*Encrinurus cf. similis*' that might suggest a Wenlock age similar to the Fukata Formation, where *E. similis* was first described (*E. similis* was synonymized with *E. nodai* from the same locality by Edgecombe & Ramsköld, 1996).

The Devonian Fukuji Formation of the Fukuji area of Gifu Prefecture, Honshu, contains ostracods and conodonts that indicate Lower Devonian, Lochkovian to Emsian stages (Kuwano, 1987). The Kamiyama Formation in the Kuzuryu Lake–Upper Ise river area of Fukui Prefecture is Lower to Middle Devonian based on radiolarians (Kurihara, 2003b, 2004; Niko & Senzai, 2010), and the common occurrence of the trilobites *Gravicalymene yamakoshii*, *Hidascutellum*

multispiniferum, and *Crotalocephalina (Pilletopectis) japonica* suggests a correlation with the Fukuji Formation (Kobayashi & Hamada, 1977).

3.1.2 | Kurosegawa Terrane

The Silurian Fukata Formation of the Yokokurayama Group, Kochi Prefecture, Shikoku has been biostratigraphically dated using conodonts, cephalopods and trilobites that collectively indicate the upper Wenlock or lower Ludlow (Kobayashi & Hamada, 1985; Kuwano, 1976, 1980); however, see Männik et al. (2018) for uncertainties with the conodont data. The Silurian Joryu Formation of Ehime Prefecture, Shikoku has been dated as Pridoli based on radiolarians (Kurihara, 2009).

The Silurian Gionyama Formation of Miyazaki Prefecture, Kyushu was divided by Hamada (1959) into four lithostratigraphic and biostratigraphic units, termed 'Members G1 to G4' in ascending stratigraphic order. Subsequent work (e.g. Kido & Sugiyama, 2007, 2011) has shown this subdivision to be untenable. Kido and Sugiyama (2007) divided the Gionyama Formation into Lower, Middle, and Upper members whose lithostratigraphical relationships to each other are complex and may in part be structural. The Silurian Middle Member of the Gionyama Formation (sensu Kido & Sugiyama, 2011; equivalent to part of the 'G2' and 'G3' limestones of Hamada, 1959) has been dated from outcrop using conodonts (Männik et al., 2018), and these indicate the lower Wenlock (Sheinwoodian Stage). This horizon is from a black limestone conglomerate about 6 m below the trilobite-bearing nodules evaluated herein (Figures 3 and 4). Ostracods in the same conglomerate suggest the Wenlock or lower Ludlow Series (Siveter et al., 2018). It should be noted, however, that these ostracods and conodonts are recovered from pebbles within a conglomerate, and therefore provide only a maximum age. Conodonts recovered from a loose boulder nearby, and likely also from the Middle Member, are indicative of the upper Llandovery (Männik et al., 2018).

The Lower Member of the Devonian Naidaijin Formation of Kumamoto Prefecture, Kyushu is dated via a chain of correlation with trilobites of the Nakazato Formation (see above). Detrital zircons from a sandstone bed 2 m above the trilobite-bearing horizon evaluated herein have yielded a radiometric age of (383.9 ± 4.4) Ma that is likely Givetian (late Mid-Devonian; Stocker et al., 2018).

4 | JAPANESE PALEOGEOGRAPHY DURING THE EARLY AND MID-PALEOZOIC

As highlighted by Williams et al. (2014) the biogeographical patterns of Japanese Ordovician to Devonian faunas are ambiguous, with links suggested with all of the major paleocontinents in the eastern peri-Gondwanan region. Several competing paleogeographical reconstructions of this region for the early- and mid-Paleozoic exist, based on a combination of faunal and other data (see below for examples), but the position of Japan relative to the Gondwana, North China, or South China paleocontinents remains controversial with, for example, Cocks and Torsvik (2013) concluding that the paleontology of Japan is of limited biogeographical utility. They chose to place Japan as a unified island arc terrane off the margin of South China (Figure 5).

By contrast, Metcalfe (2006), who also noted that the position of Japan is at best speculative, suggested a position adjacent to eastern South China on the margin of the Australian part of Gondwana for the

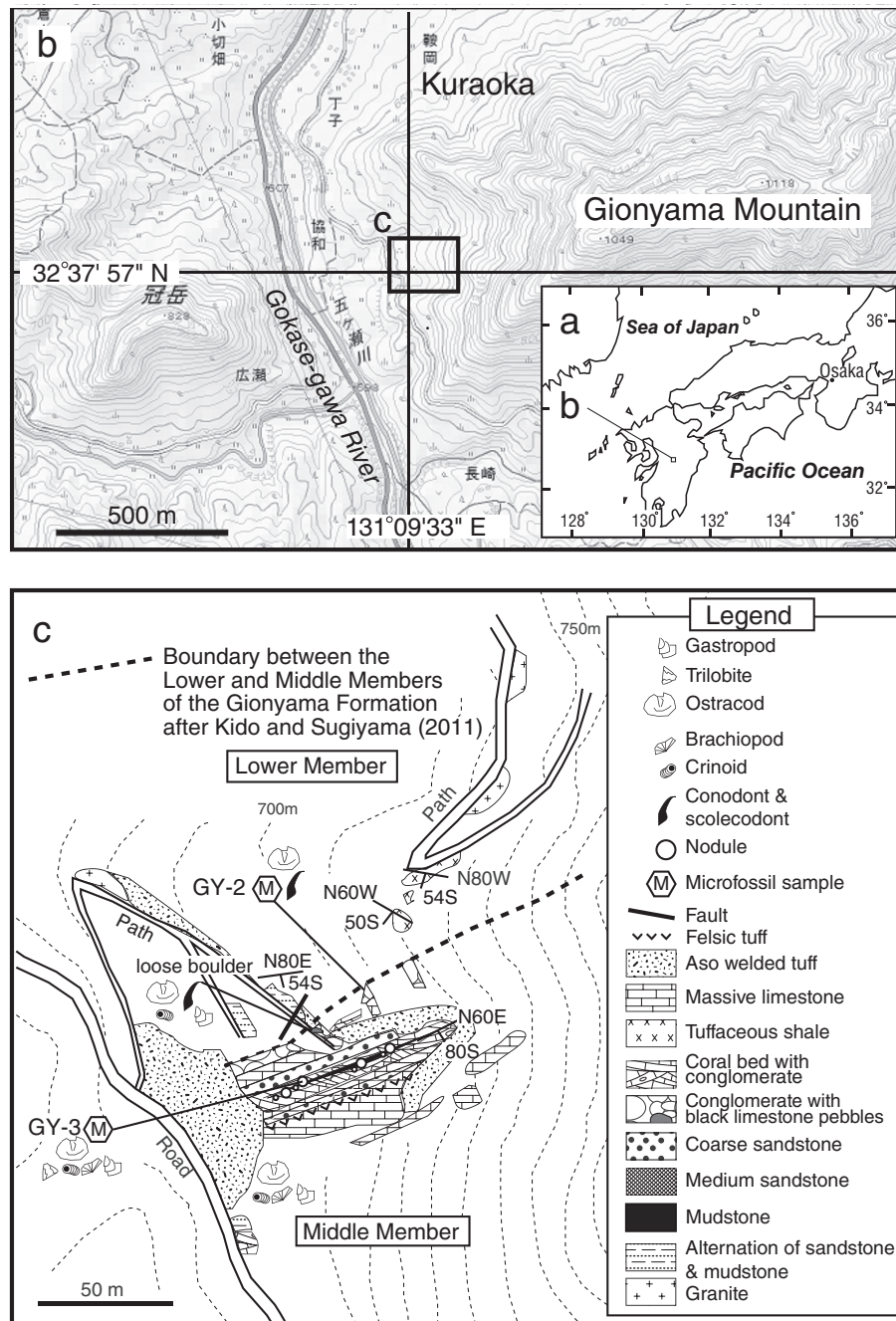


FIGURE 3 Locality map for biostratigraphically diagnostic conodont samples at Gionyama, Kuraoka, Miyazaki Prefecture, central Kyushu Island. In map 'c', the position of the scolecodont/conodont/ostracod-bearing black limestone GY-2, sampled from outcrop within the Middle Member (sensu Kido & Sugiyama, 2011) is marked, as is the loose boulder (GY-1). Sample GY-3 of this figure contains ostracods described by Siveter et al. (2018), but no conodonts. For the stratigraphical position of samples GY-2 and GY-3 see Figure 4

KT (Hisada, Arai, & Negoro, 1994; Saito, 1992), and an origin along the North China paleocontinent for the SKT (Yoshida & Machiyama, 2004). Metcalfe (2006, p. 27, Table 1) summarized the multidisciplinary data that his reconstructions were based on, which included (but were not limited to) data from paleobiogeographic constraints, paleoclimatology, paleomagnetic data, detrital zircon provenance, and the positions of volcanic intrusions. In the reconstruction presented by Metcalfe (2006, p. 39, Figure 6) South China is over the paleo-equator, with Tarim to the north-northwest, and North China to the northwest of Tarim. This is in contrast to Cocks and Torsvik (2013, p. 57, Figure 11) who presented North China far to the west of South China, and Tarim even further west. In contrast,

Tazawa (2002) suggested an origin along the northern or eastern margin of the North China paleocontinent for all three of the Japanese terranes discussed here (see also Tazawa, 1993, 2000, 2001, 2004).

5 | PALEOBIOGEOGRAPHICAL AFFINITY OF JAPANESE SILURIAN AND DEVONIAN TRILOBITES

The diversity of trilobites of each of the six groups studied here, along with their paleobiogeographical affinities, is represented in Table 1.

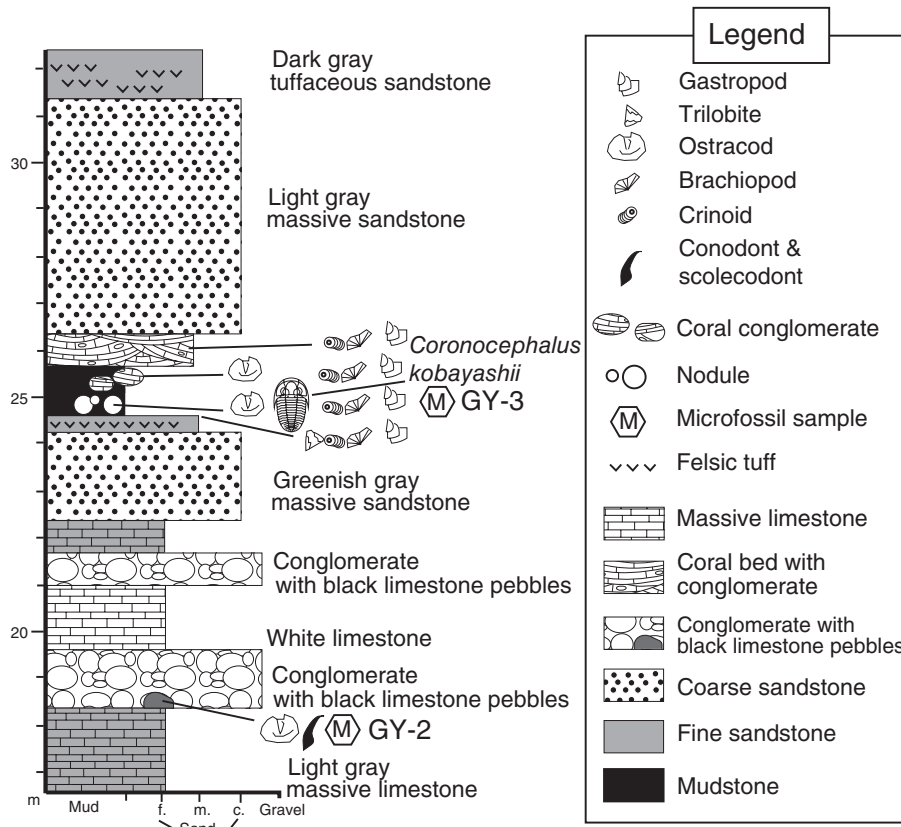


FIGURE 4 Stratigraphical column showing the position of the biostratigraphically diagnostic conodont bearing sample GY-2 see (Männik et al. 2018) from outcrop at Gionyama (see Figures 2 and 3), in relation to the trilobite species *Coronoecephalus kobayashii*. Sample GY-2 also yields scolecodonts, and ostracods (see Vandenbroucke et al., 2018; Siveter et al., 2018). A younger conglomeratic horizon (GY-3) yields ostracods but no conodonts. The abbreviations ‘f.’, ‘m.’, and ‘c.’ refer to fine, medium, and coarse grained sandstone, respectively

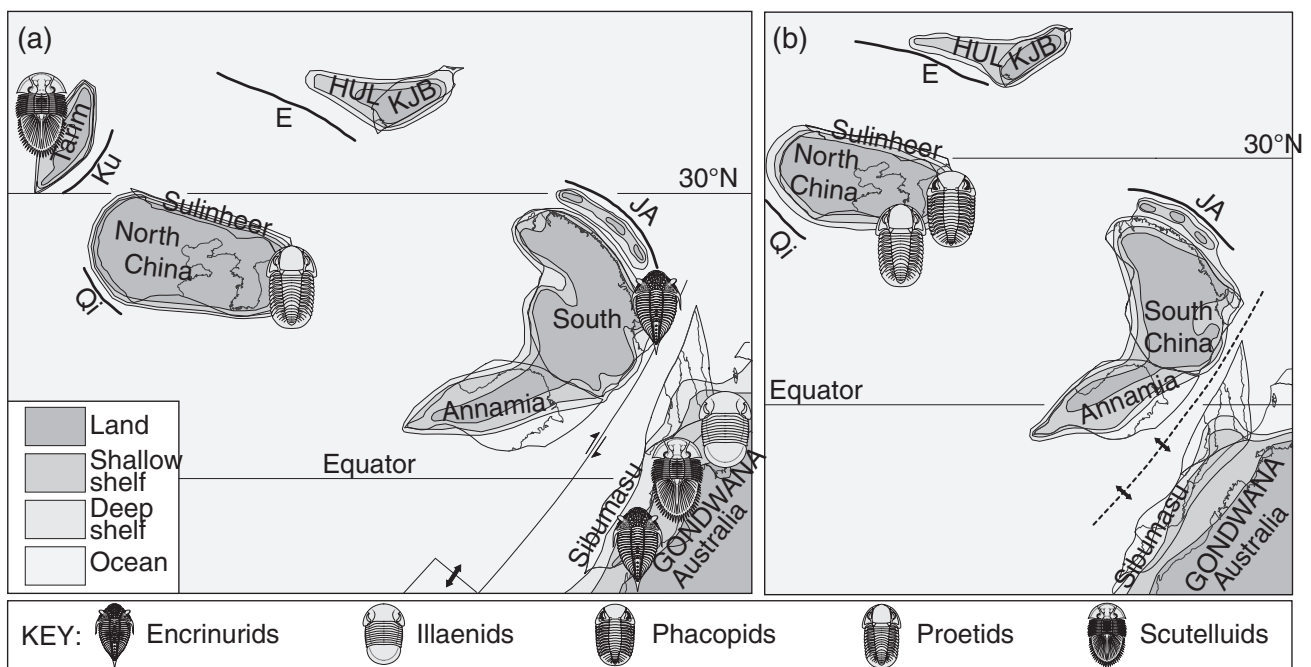


FIGURE 5 Paleogeographical position of the Japanese Arc (JA) during the late Silurian and Early Devonian, following the reconstruction of Cocks and Torsvik (2013), with trilobite groups that show links to different regions. (a) Late Silurian. (b) Devonian. Major plate margins are represented by the following lines: Dashed line with diverging arrows for a spreading margin, solid line with opposing half arrows for a strike-slip margin, and bold solid line for subduction zone. The following abbreviations apply: E, Enshoo Arc Trilobite symbols courtesy of Dr. Sam Gon III; HUL, Huutag Uul-Songliao; KJB, Khanka-Jiamusu-Bureya; Ku, arcs now in the Kunlun Terrane; Qi, arcs now in the Qaidam–Qilian Terrane

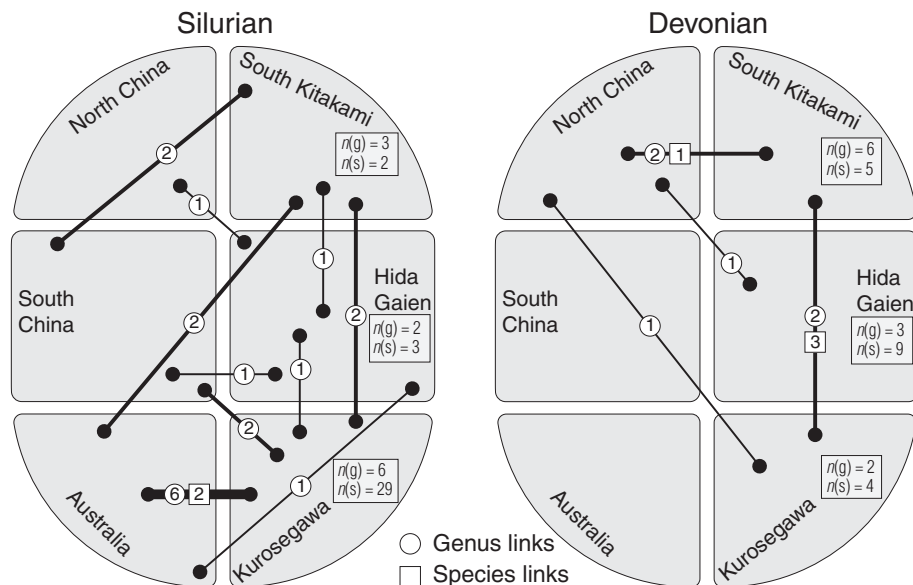


FIGURE 6 Paleobiogeographical connections of trilobite genera and species between the three Japanese terranes and with other regions. Coarser lines equate to a greater number of generic links. Pandemic taxa have been excluded from the analysis, and the total number of taxa analysed is given as ' $n(g)$ ' and ' $n(s)$ ' for genera and species respectively. Sizes and positions of terranes are schematic, and not to scale

Figure 6 summarizes the paleobiogeographical links for the Silurian and Devonian between each of the Japanese terranes and other regions, and Figure 7 illustrates a representative sample of Silurian and Devonian trilobites from the three terranes.

5.1 | Silurian links with the Australian segment of East Gondwana

Illaenidae and Scutelluidae (Holloway & Lane, 1998, 2012) from the Silurian Fukata Formation of the KT show four species links, through *Bumastella spicula*, *Borenoria trinodosa*, *Japonoscutellum japonicum* and *J. magnum* (Table 1), with the Molong and Mirabooka Formations of the Australian Benambra Terrane. The illaenids *Bumastella* and *Rhaxeros*, and scutelluid genera *Borenoria* and *Illaenoscutellum* are also only found in Australia and the KT of Japan.

Similarities between Silurian encrinurids of the Benambra Terrane of Australia and the KT and HGT of Japan were suggested by Strusz (1980), who included the Japanese *Encrinurus* species *E. ishii*, *E. mamelon*, *E. tosenensis*, and *E. yokokurensis* from the KT, and *E. fimbriatus* from the HGT, in the 'mitchelli-Plexus', species of which were subsequently assigned to *Batocara* (see Edgecombe & Ramsköld, 1992; Holloway, 1994). Another species from the SKT has been assigned to *Batocara* as part of our study. The encrinurid *Batocara* is common in Australia, and also occurs in the Fukata Formation of the KT, and the upper Hitoegane Formation of the HGT. Species of *Coronocephalus* occur in the Benambra Terrane of Australia and the Silurian Gionyama and Kawauchi Formations of the KT and SKT, respectively; the genus may also occur in the upper Hitoegane Formation of the HGT (see below).

5.2 | Silurian links with South China

As noted above, species of the encrinurid *Batocara* are common in Australia, but also occur in the South China paleocontinent as well as the

Fukata Formation of the KT, the upper Hitoegane Formation of the HGT, and the Kawauchi Formation of the SKT. There are no species-level links between these terranes, however. Species of *Coronocephalus* are diverse throughout the South China paleocontinent, and also occur in Australia and the Gionyama and Kawauchi Formations of the KT and SKT, respectively. Again, there are no species-level links between any of these terranes.

5.3 | Silurian links with North China

Proetids from the upper Hitoegane Formation in the HGT suggest generic links with North China. *Ganinella tenuiceps* is found in the upper Hitoegane Formation. There are several Silurian species of *Ganinella* in Siberia, and the genus has representatives in North China. However, *Ganinella* may be a biogeographically widespread genus (see below).

5.4 | Devonian links with North China

At least two species of the proetid genus *Ganinella*, *G. fukujiensis* and *G. oisensis*, occur coevally in the Fukuji and Kamianama Formations of the HGT. *Ganinella* is a common Siberian genus, which also occurs in North China, but it may be widespread, with closely related genera such as *Lacunoporaspis* having a global distribution; relationships between these closely related genera, however, are difficult to resolve at present, and require a detailed phylogenetic analysis (see Stocker et al., 2018).

Devonian phacopids of the KT and SKT of Japan (Kaneko, 1990, 2007; Stocker et al., 2018) show strong generic links, and one species link with North China (Kaneko, 1990, 2007; Zhou & Campbell, 1990). The sub-family Echinophacopinae, including *Toxophacops* and *Rhinophacops*, are only found in the Zhushilenghaierhan region of Inner Mongolia, North China, and the KT and SKT of Japan. The species *Rhinophacops schizoloma* is also only found in the SKT and North China.

The Devonian proetids from the Nakazato Formation also indicate generic links with North China, with *Dechenella*, *Otodechenella*, and *Paradechenella* occurring in both regions (Kaneko, 2007), although

Dechenella has a global distribution. *Otodechenella* is only found in the Zhusilenghaierhan region of Inner Mongolia, North China, and the SKT of Japan.

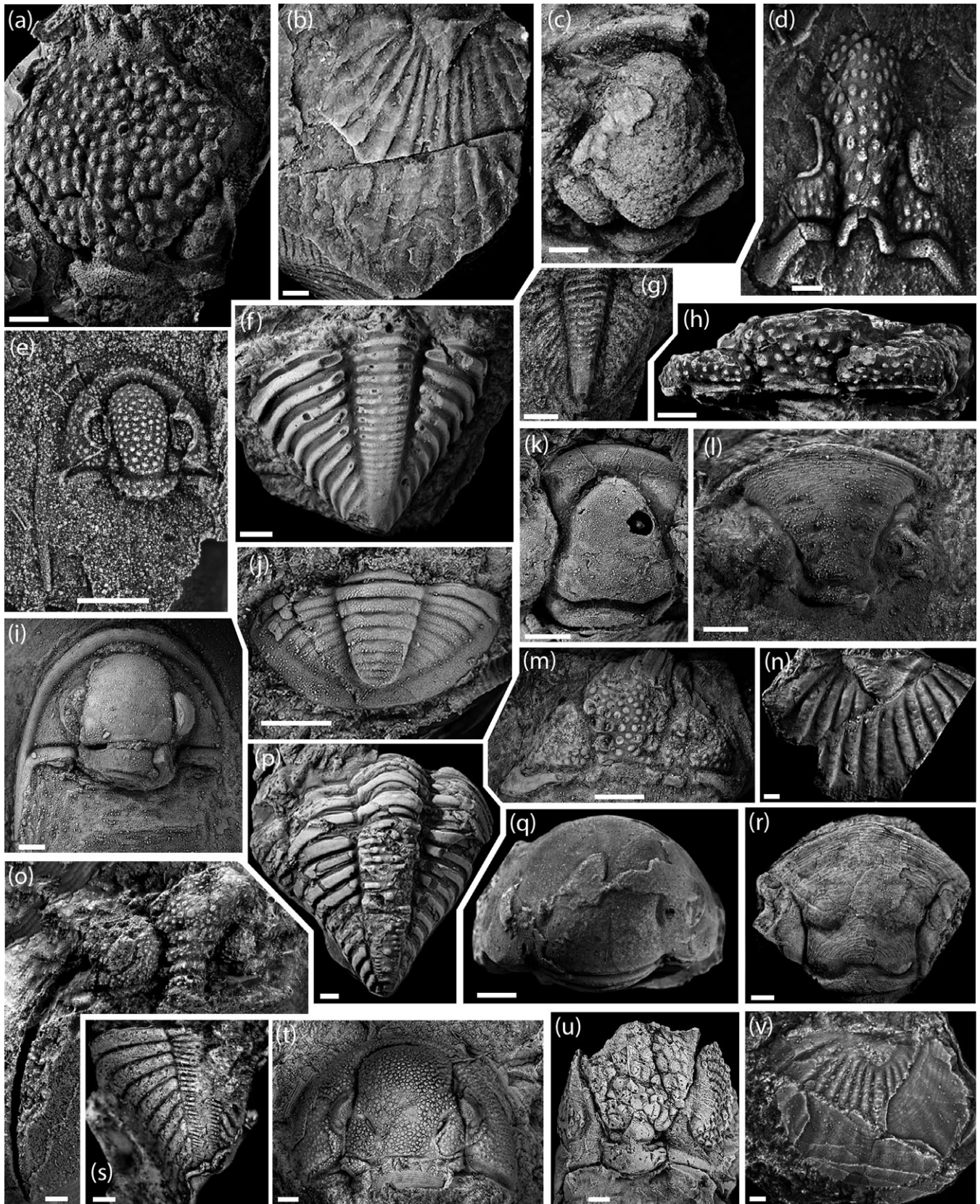


FIGURE 7 Legend on next page.

5.5 | Intra-Japanese terrane links

In the Silurian there are no species links between the three terranes (Figure 6). '*Encrinurus cf. similis*', reported by Kobayashi and Hamada (1987) from the Silurian of Hakubado in the HGT, is too poorly preserved to compare with material of *Encrinurus* from the KT. The encrinurid genus *Batocara* occurs in all three Japanese terranes, but is more species diverse in the Fukata Formation of the KT, and the encrinurid genus *Coronocephalus* occurs in the Kawauchi Formation of the SKT, the Gionyama Formation of the KT, and possibly the upper Hitoegane Formation of the HGT (*Encrinurus cf. kitakamiensis* of Kobayashi and Hamada (1987)). The scutelluid genus *Japonoscutellum* occurs in the Fukata Formation of the KT and the upper Hitoegane Formation of the HGT. The proetid genus *Coniproetus* also occurs in the Fukata and upper Hitoegane formations, but it is a globally distributed taxon. Illaenids only occur in the KT.

In the Middle Devonian phacopids and proetids of the Naidaijin Formation of the KT and the Nakazato Formation of the SKT of Japan (Kaneko, 1990, 2007; Stocker et al., 2018) show species-level links between these two terranes; the phacopid species *Toxophacops (Atopophacops) nonakai*, the proetid *Dechenella minima*, and the scutelluid *Kobayashipeltis paucispinosa* also occur in the Naidaijin and Nakazato Formations (Kaneko, 2007) of the KT and SKT terrane, respectively. *Kobayashipeltis* is endemic to these two Japanese terranes.

5.6 | Summary

In a general sense then, the Silurian trilobites of all three terranes suggest closest links with the South China and East Gondwanan regions (Figure 6; Table 1). *Ganinella* in the HGT is the only common link with North China during the Silurian. By contrast, Devonian trilobites consistently show strongest affinities with those of North China, including material from all three Japanese terranes examined here.

In terms of intra-Japanese terrane connections, in the Silurian there are no species-level biogeographical links between the three terranes (Figure 6). The strongest generic links between all three terranes are represented by the encrinurids *Batocara* and *Coronocephalus*, both of which also occur in South China and Australia.

In the Devonian there are strong specific and generic links between the SKT and KT (Figure 6), but similar links with the HGT are only suggested by limited material of a calymenid species, *Nipponocalymene hamadai* which occurs in the Rosse Formation, as well as the Nakazato and Naidaijin Formations (Kaneko, 2007); the trilobite fauna from the Fukuji Formation (HGT) is very different from that of the other two terranes.

Some groups, e.g. the proetids from the Fukata Formation of the KT, appear to be more endemic than other trilobite groups with which they co-occur, such as scutelluids, illaenids and encrinurids. The Devonian proetids from the upper Hitoegane and Fukuji Formations of the HGT appear to indicate generic links with North China and Siberia, whereas other co-occurring trilobite groups (Calymenidae, Cheiruridae, Lichida) have demonstrated generic links with the South China paleocontinent (Kaneko, 2007; Wang, Boucot, Rong, & Yang, 1987) and in the case of Lichida also with Australia (Sherwin & Meakin, 2010). This suggests that factors in addition to paleogeography are at play. In the following section, we examine the significance of lithofacies relationships and ecology in this context.

6 | PALEOENVIRONMENTAL AND PALEOECOLOGICAL CONTROLS ON TRILOBITE DISTRIBUTION

6.1 | Lithofacies

The Silurian and Early Devonian trilobite-bearing lithofacies of Japan are dominated by shallow marine carbonate rocks, but in the Devonian the trilobite lithofacies are characteristically deeper-water siliciclastics (see Figure 8). The taxa from all three Japanese terranes in the Silurian suggest links with Australia and South China, where carbonate lithofacies contain similar faunas, whereas in the Devonian the Japanese trilobites show clear links with North China. Given the change of predominant lithofacies between the Silurian and Devonian (carbonate to siliciclastic), this may suggest some degree of environmental control on trilobite distribution that has also been noted for other invertebrate faunas of Japan (Williams et al., 2014). Thomas (1979) suggested that

FIGURE 7 Representative Silurian and Devonian Japanese trilobites: (a–d,g), South Kitakami terrane; (e,f,j–l,n) Hida Gaien terrane; (i,m,o–v) Kurosegawa terrane. (a) *Rhinophacops cf. schizoloma* Kaneko, 1990 cephalon (OCM.G000588). (b) *Kobayashipeltis paucispinosa* (Okubo, 1951), holotype pygidium (PA08001). (c) *Dechenella minima* Okubo, 1951, holotype cranidium (PA8006). (d) *Batocara* sp. A, cranidium (OCM.G000638). (e) '*Maurotarion megalops*' (Kobayashi & Hamada, 1977), juvenile cephalon (OUMNH.DY.15). (f) *Batocara fimbriatus* Kobayashi & Hamada, 1974, pygidium (PA18108). (g) *Dechenella cf. minima*, pygidium (OCM.G000578). (h) *Batocara* sp., cranidium (OCM.G00627). (i) *Interproetus* sp. A, cephalon (SGMX1-11). (j) *Ganinella oisensis* (Kobayashi & Hamada, 1977), pygidium (NUM-Fa218). (k) *Ganinella fukujiensis* (Kobayashi & Hamada, 1977), paratype cranidium (PA8963). (l) *Japonoscutellum hidense* (Kobayashi & Hamada, 1987), holotype cranidium (PA18095). (m) *Batocara yokokurensis* (Kobayashi & Hamada, 1974), holotype cranidium (KPFM618). (n) *Japonoscutellum hidense*, pygidium (PA18096). (o) *Coronocephalus kobayashii*, holotype cranidium (PA07280). (p) *Batocara yokokurensis*, thoracopygon (SGMX1-15). (q) *Bumastella spicula* (Kobayashi & Hamada, 1974), juvenile cephalothorax (KPFM15155). (r) *Japonoscutellum japonicum* Kobayashi & Hamada, 1974, holotype cranidium (PA07353). (s) *Coronocephalus kobayashii*, paratype pygidium (PA7294). (t) *Gomiites latixis* (Kobayashi & Hamada, 1986), holotype cephalon (PA18078). (u) *Toxophacops (Atopophacops) fujiwara*, composite image of part and counterpart of topotype cephalon (OUMNH.DY4a,b). (v) *J. japonicum*, paratype pygidium (PA7354). (a–c,g) from the Devonian (Emsian to Eifelian) Nakazato Formation, Hikoroichi, Iwate Prefecture, Honshu; (d,h) from the Silurian (Wenlock) Kawauchi Formation Hikoroichi, Iwate Prefecture, Honshu Island; (e,j,k) are from the Devonian (Lochkovian to Emsian) Fukuji Formation, Okuhida-onsen-gou, Takayama City, Gifu Prefecture, Honshu Island; (f,l,n) from the Silurian (Ludlow) upper Hitoegane Formation, Kamitakara-mura, Yoshiki-gun, Gifu Prefecture, Honshu Island; (u) from the Devonian (Emsian to Givetian) Lower Member of the Naidaijin Formation, Shimomashiki District, Kumamoto Prefecture, central Kyushu Island, Japan; (o,s) are from the Silurian (Wenlock, Sheinwoodian) Gionyama Formation, Kuraoka, Miyazaki Prefecture, central Kyushu Island; (i,m,p,q,r,t,v) from the Silurian Fukata Formation of Yokokurayama, Ochi, Kochi Prefecture, Shikoku Island. All specimens are in dorsal view. Scale bars represent 2 mm

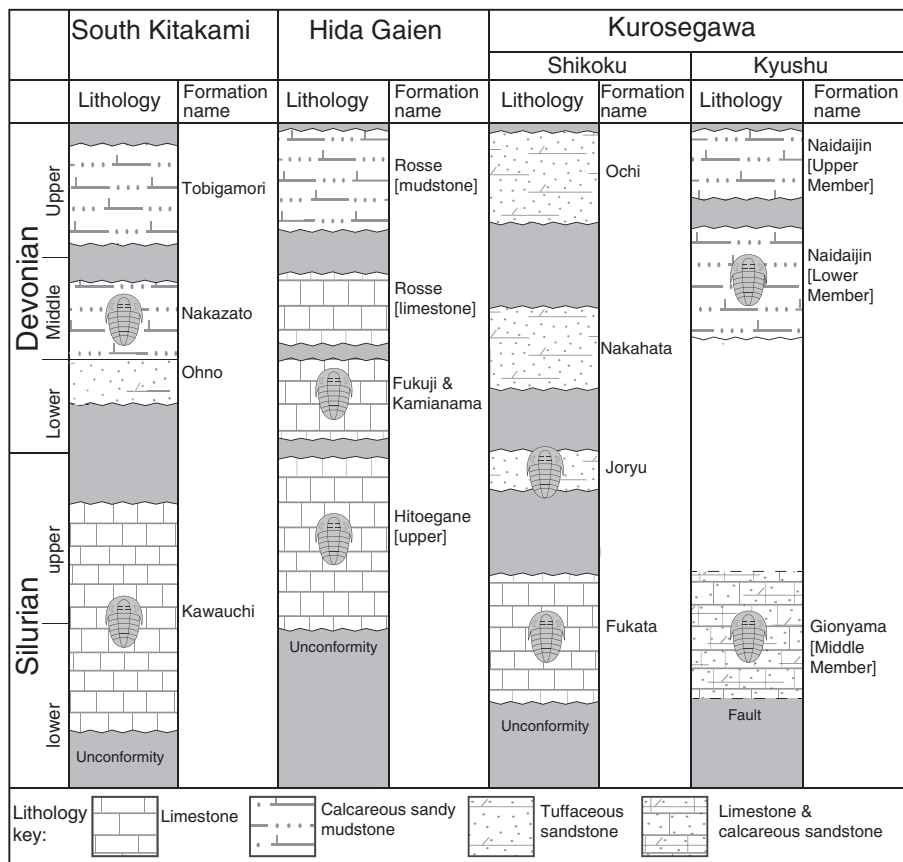


FIGURE 8 Lithology of each of the Japanese trilobite-bearing formations across the three terranes. Grey areas of the columns indicate uncertainty or gaps in the stratigraphy

in the Wenlock of the UK, trilobite distribution reflects original environmental variables, so that there is a close but not invariable correlation between the distribution of trilobite taxa and lithofacies. Some of the trilobite groups that occur in the Japanese formations, including some Proetida and Phacopidae, occur in both carbonate and clastic lithofacies. This is the case for the proetids of the carbonate dominated Fukuji and Kamianama Formations in the HGT and those in the siliciclastic dominated Nakazato Formation of the SKT, which nevertheless show consistent generic links with North China.

6.2 | Paleocology

Of the Japanese trilobite groups discussed here, the majority are interpreted to be predators/scavengers (Fortey & Owens, 1999), with only one, the proetids, being considered as detritivores (Fortey & Owens, 1999)

The Japanese scutelluids are in general somewhat restricted biogeographically, but with one species with a very broad distribution, *Japonoscutellum magnum*, which occurs in Australia, possibly Japan (Holloway and Lane (2012) suggested that *J. laticephalum* may be conspecific with *magnum*), and Kazakhstan. Illaenids are very restricted, with two genera and one species restricted to Australia and the KT of Japan. Japanese proetids are endemic to each terrane at the species-level, but some genera are globally distributed (*Coniproetus* and *Interproetus* for example), others have wide distributions across Asia and to Siberia (*Ganinella* for example), and some are more restricted

to South China and Australia (*Latiproetus*); there is only one endemic genus, *Gomiites*. Suggestions of other behavior relating to lifestyle have been offered for some of these groups. For example, scutelluids with flat exoskeletal morphologies have been interpreted as capable of swimming, using their large paddle-like pygidia (Chatterton, 1971; Feist & Lerosey-Aubril, 2008; Selwood, 1966), whereas some illaenids have been interpreted as burrowing into sediment. Proetids, however, have been interpreted in some cases as inhabiting sheltered cavities in the surface of reefs (Hughes & Thomas, 2011). These interpretations suggest that autecology has a variable effect on biogeography, but perhaps even more important is larval-stage ecology.

The majority of trilobite groups have been found to possess a calcified larval stage known as a protaspid. Protaspides have been shown to occupy either planktonic or benthic lifestyles of different duration (Chatterton & Speyer, 1989; Speyer & Chatterton, 1989). Groups with planktonic protaspides include proetids and phacopids, whereas encrinurids, scutelluids, and illaenids have been determined to have benthic protaspides. It is assumed that planktonic protaspides would be capable of more widespread distribution, and therefore such groups would be more geographically disparate than those with benthic protaspides.

7 | CONCLUSIONS

There are stronger paleobiogeographical links between the trilobites of the three Japanese terranes in the Devonian than in the Silurian. In

the Silurian, scutelluids and illaenids of the KT show strong overall generic- and species-level links with the Australian segment of eastern Gondwana, and encrinurids from all three Japanese terranes indicate generic-level links with the South China paleocontinent and the Australian segment of eastern Gondwana. A single proetid genus from the HGT suggests links with the North China paleocontinent, although this genus may in fact be pandemic. In the Devonian, phacopids indicate strong overall generic-level links between the KT and SKT and the North China paleocontinent, with a single species-level link between the Nakazato Formation of Iwate Prefecture and the Zhushileng Formation of Inner Mongolia. Proetids from the Early Devonian of the HGT and the Middle Devonian of the SKT, both suggest generic-level links with the North China paleocontinent. Of those genera and species with links to North China, the vast majority are from deeper-water siliciclastic facies, whereas genera with links to Australia and South China are all from shallow water carbonate facies. Scutelluids and illaenids are strongly restricted to limestone facies, and this may have an influence on links with Australia, where they occur in similar limestone facies. These data suggest that in the Silurian and Devonian of Japan, environmental setting may have exerted a strong influence on the biogeographical signal of trilobites, and thus inferences about paleogeography need to be made with caution.

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Declaration of conflicting interest

The authors declare that they have no competing interest.

Authors' contributions

MW devised the 'Assembling the Early Palaeozoic terranes of Japan' project. CPS, DJS, PDL and MW wrote the manuscript with input from all authors. CPS, TO and GT undertook fieldwork.

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