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Revision of the triprojectate and oculate angiosperm pollen record in Japan, with new data from the Maastrichtian of the Hakobuchi Formation, Yezo Group, in the Hobetsu area, Hokkaido

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Abstract. Angiosperm pollen grains of the triprojectate and oculate groups are widely distributed in Upper Cretaceous strata of the Northern Hemisphere, being used as biostratigraphic markers from their high diversification rate. Most reports from northeastern Asia, however, concern terrestrial deposits, and the rich record existing in Japan from marine sequences, with a well-established bio-magnetostratigraphy, appears critical for correlating their range among the Circum Pacific region. Here we propose a revision of Japanese reports of these groups, constraining their diversity to 17 genera and 91 species. A selected array of 15 species of well-preserved triprojectate pollen was further obtained from an abundant sporo-pollen assemblage of a hadrosaurian dinosaur *Kamuysaurus japonicus*-bearing bone bed in the outer shelf deposits of the Upper Cretaceous Hakobuchi Formation, Yezo Group, recently discovered in the Hobetsu area of Mukawa Town in Hokkaido, Japan; the assemblage co-occurs with the ammonoid *Pachydiscus* (*Neodesmoceras*) *japonicus* belonging to the *Nostoceras hetonaiense* zone, supporting an early Maastrichtian age.

Keywords: Japan, Palynostratigraphy, Triprojectate pollen, Upper Cretaceous, Yezo Group

Introduction

Within the Upper Cretaceous palynostratigraphy of the Northern Hemisphere, pollen belonging to the oculate and triprojectate groups have proved to be reliable stratigraphic index fossils because of their wide varieties of sculpture patterns and high diversification rate (e.g. Srivastava, 1970; Takahashi, 1981, 1982; Nichols and Sweet, 1993; Nichols, 1994). Their chronostratigraphic ranges are well calibrated from radiometric dating, magnetostratigraphy, and ammonoid biostratigraphy of marine and non-marine strata of North America and Asia (e.g. Eberth and Deino, 2005; Cobban *et al.*, 2006; Li *et al.*, 2011; Yoshino *et al.*, 2017; Braman, 2018). In particular, the Campanian to Maastrichtian sequence of the mainly non-marine Horseshoe Canyon (e.g. Srivastava, 1970) and St. Mary River (e.g. Jerzykiewicz and Sweet, 1988) formations, the marine Bearpaw Formation (e.g. Jerzykiewicz *et al.*, 1996) and other formations outcropping in Alberta (Canada) and Montana (USA) have rich pollen assemblages. Recent U–Pb dating with magneto-cyclostratigraphy of the terrestrial succession in the Songliao Basin, China further calibrated the palynostratigraphy including oculate and triprojectate groups (Li *et al.*, 2011; Wu *et al.*, 2014; Yoshino *et al.*, 2017).

Triprojectate pollen (i.e., tridemicolpate pollen with a polar axis and most commonly three equatorial projections [Funkhouser, 1961; Krutzsch, 1970; Stanley, 1970]) is reported from the late Turonian to the Oligocene, and is mostly diversified in Campanian to Maastrichtian sediments, being mainly cosmopolitan but also showing provincialism for some species (Braman, 2013). In Asia, it is the dominant component of many palynofloras of Siberia, Far East Russia, Northeast China, and Japan. Botanical

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affinities of this group are still unclear due to the lack of *in situ* material associated with floral remains, but some authors suggested affinities to the Santalales (Funkhouser, 1961; Krutzsch, 1970) or the Apiales (Stanley, 1970) based on morphological similarities to extant pollen grains of these orders, and a possible polyphyletic origin was proposed by Farabee (1990). Angiosperm plants producing triprojectate pollen (or the "Triprojectacites-type") grew under humid climate conditions (Sweet, 1990) and preferred a marshy paludal environment (Srivastava, 1973).

Oculate type pollen (or the "Oculata-type") was designated by Chlonova (1962) to include pollen showing an elliptical shape and bilateral symmetry, with one pair of apertures formed on opposite sides of the grain. Only dispersed pollen was reported for this type and no similar pollen is known from extant plants (Chlonova, 1967; Leffingwell *et al.*, 1970; Wiggins, 1976). Therefore, its botanical affinity is not yet clarified. It includes the three genera *Azonia* Samoilovitch *in* Samoilovitch and Mtchedlishvili (1961), *Wodehouseia* Stanley, 1961, and *Singularia* Samoilovitch *in* Samoilovitch and Mtchedlishvili (1961), and ranges from the late Santonian to Paleocene of North America, Canada, Greenland, Russia, China and Japan, being most common and widely distributed during the Maastrichtian (e.g. Samoilovitch and Mtchedlishvili, 1961; Stanley, 1961; Wiggins, 1976; Takahashi, 1984).

Bio-magnetostratigraphy is well established in Japan compared to adjacent areas, and palynostratigraphy would provide an additional tool for dating terrestrial strata of Asia with still debated age. In particular, the rich triprojectate and oculate pollen record existing in marine formations of northern Japan appears critical for correlating records from eastern Asia and North America. However, many of these pollen records are from pioneering works, while many nomenclatural modifications were applied to the two groups since then. Geological age of strata including these grains has also been modified.

We propose in this paper a major revision of the triprojectate and oculate pollen records of Japan, and discuss its consequences for the biostratigraphic significance of these groups in the Circum-Pacific region. We further add new well-preserved pollen data obtained from calcareous nodules of a hadrosaurian dinosaur *Kamuysaurus japonicus*-bearing bone bed of the Hakobuchi Formation, Yezo Group. This assemblage co-occurs with the ammonoid *Pachydiscus* (*Neodesmoceras*) *japonicus* belonging to the *Nostoceras hetonaiense* zone tentatively correlated with the early Maastrichtian, however, possibly late Campanian according to the uncertainty of magnetostratigraphy and radiometric age. We use triprojectate species of the palynoflora to confirm the age of the *K. japonicus*-bearing bone bed in the *Nostoceras hetonaiense* zone.

Localities and ages of triprojectate and oculate pollen used for palynostratigraphic compilation

Marine formations yielding triprojectate and oculate pollen used for establishing the palynostratigraphic framework of the present revision are distributed in Northeast Honshu and Hokkaido. In Northeast Honshu, reports exist from the Uge Member of the Taneichi Formation (Takahashi and Sugiyama, 1990), assigned to the Santonian from the inoceramid *Sphenoceramus sanrikuensis* (Matsumoto and Sugiyama, 1985); the Tamagawa Formation of the Kuji Group (Miki, 1972, 1977; Umetsu and Kurita, 2007), assigned to the Turonian on the basis of 90.51 ± 0.54 Ma of U–Pb age of intercalated tuff beds (Uno *et al.*, 2018), and correlation with the ammonoid (Futakami *et al.*, 1987; Toshimitsu *et al.*, 1995) and inoceramid (Toshimitsu *et al.*, 1995) assemblages of the Kunitan Formation.

In Hokkaido, pollen records are obtained from the following hemipelagic to shallow marine successions bearing molluscan fossils: the Turonian Tenkaritoge Formation, Santonian–Campanian Haborogawa Formation, Coniacian Nishichirashinai Formation, Campanian Omagari and Osoushinai formations, and Campanian–Maastrichtian Hakobuchi Formation of the Yezo Group (Sato, 1961; Takahashi, 1964, 1965; Miki, 1977; Tanaka and Hirano, 2008), and the Maastrichtian Hamanaka and Oborogawa formations, the Maastrichtian–Danian Akkeshi Formation, and the Paleocene Tokotan Formation of the Nemuro Group (Takahashi and Ueda, 1990; Takahashi, 1991a, b, c; Takahashi and Yamanoi, 1992), the Paleocene Kiritappu Formation (Takahashi, 1991c), and the Maastrichtian–Danian Katsuhira Formation (Takahashi and Yamanoi, 1992).

Geological setting

Kamuysaurus japonicus-*bearing bone bed.*—Calcareous nodules of the *Kamuysaurus japonicus*-bearing bone bed were obtained from the Hakobuchi Formation, representing the uppermost part of the Yezo Group. The Hakobuchi Formation consists of lower Campanian–Paleocene shallow marine sandstone and conglomerate facies (Takashima *et al.*, 2004). Matsumoto (1942) further divided the Hakobuchi Formation into five units (IVa–IVe). *Kamuysaurus japonicus* was found from the middle part of the IVb unit of the Hakobuchi Formation, at the upstream of the Shirafunezawa Creek, in northern Hobetsu area (Figure 1; location of the outcrop, 42°50′48″N, 142°7′20″E), and large-scaled joint excavation was held in 2013 and 2014 by the Hobetsu Museum, Mukawa Town, and Hokkaido University (Kobayashi *et al.*, 2019). The IVb unit is considered as having been

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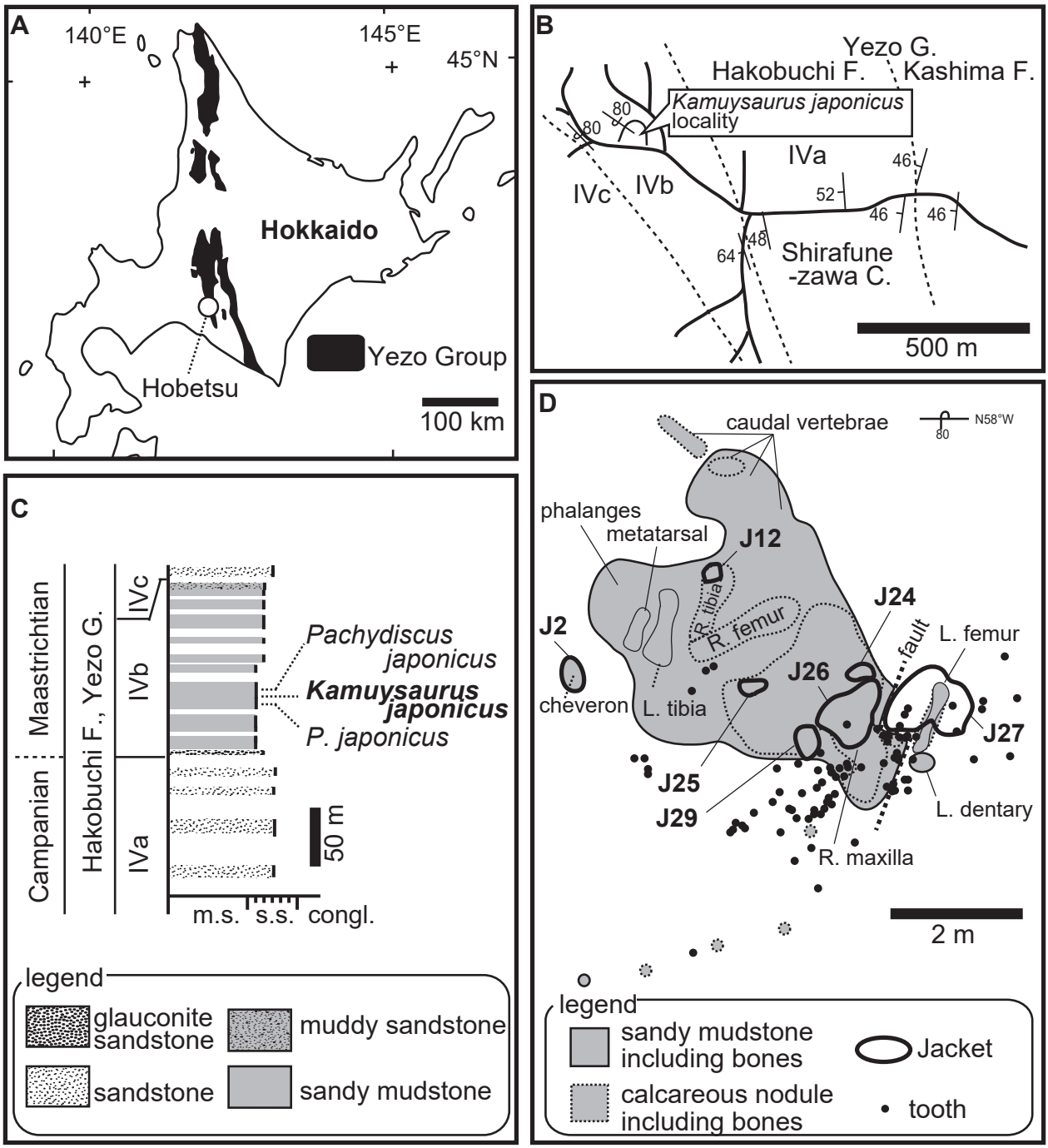

Figure 1. Location map and geology of *Kamuysaurus japonicus* excavation site. **A**, distribution map of the Yezo Group in Hokkaido; **B**, geological map of Shirafune-zawa creek, northern Hobetsu area; **C**, columnar section of the IVb unit of the Hakobuchi Formation, Yezo Group; **D**, *Kamuysaurus japonicus*-bearing bone bed from an downward view, with location of the seven jacket samples (modified after Kobayashi *et al.*, 2019).

deposited in an outer shelf environment based on the presence of glauconite sandstone and the absence of any hummocky cross-stratification (Kusuhashi *et al.*, 2017; Kobayashi *et al.*, 2019). Some marine bivalves (e.g. *Nannonavis*, *Nucula* and *Inoceramus*), gastropods, shark teeth, and fish scales were found at the locality. Moreover, *Pachydiscus* (*Neodesmoceras*) *japonicus*, an index of the *Nostoceras hetonaiense* zone, was recovered about

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5 m below and 3 m above the *K. japonicus*-bearing horizon (Kobayashi *et al.*, 2019). The age of the *Nostoceras hetonaiense* zone has been considered as early Maastrichtian, but a possibility could not be completely ruled out that it may start from late Campanian based on magnetostratigraphy (Kodama, 1990) and U–Pb ages (Shigeta *et al.*, 2017a, b). Kodama (1990) identified Chron 32n2n to 32n1n for the *Nostoceras hetonaiense* zone in the Izumi Group in Southwest Japan, striding the Campanian/Maastrichtian boundary. For U–Pb radiometric dating, 73.0 ± 1.8 Ma and 70.5 ± 1.1 Ma are reported from the ash beds below and above *Gaudryceras izumiense* zone, one zone above the *Nostoceras hetonaiense* zone of Etanpakku Formation in the Soya Hill area, Hokkaido, Japan (Shigeta *et al.*, 2017a). Additionally, the *Didymoceras awajiense* zone, three zones below the *Nostoceras hetonaiense* zone, reports a U–Pb age of 72.4 ± 0.8 Ma from a volcanic ash layer (Shigeta *et al.*, 2017b). Thus, a part of the *Nostoceras hetonaiense* zone may be older than the age assigned to the Campanian/Maastrichtian boundary (72.2 ± 0.2 Ma; Gale *et al.*, 2020).

Terrestrial strata of Japan yielding triprojectate and oculate pollen.—In Northeast Honshu, reports exist from the Kasamatsu Formation of the Futaba Group (Takahashi, 1964), assigned to the late Coniacian from its stratigraphic position between the Ashizawa and Tamayama formations, which yield inoceramids (Matsumoto *et al.*, 1982); the Sawayama Formation of the Kuji Group (Miki, 1972, 1977; Umetsu and Kurita, 2007), tentatively assigned to the early Campanian from its pollen assemblage; and the Yokomichi Formation (Tanai *et al.*, 1978), assigned to the late Campanian from the report of a fission-track zircon dated as 71.2 + 4.4 Ma from the upper part of the formation (Kato *et al.*, 1986).

In Central Japan, triprojectate pollen has been reported from non-marine sequences of the Miyadani-gawa Formation (Kasahara and Shimono, 1974; Takahashi, 1980; Takahashi and Shimono, 1982), the Omichidani Formation (Takahashi, 1991d; Nichols *et al.*, 2010) and the Asuwa Formation (Sazawa *et al.*, 2020). The Miyadani-gawa Formation should intercalate within volcanic rocks of 72–70 Ma (Hoshi *et al.*, 2016), however, the exact relationship between the Miyadani-gawa Formation and latter volcanic rocks is not clear. All these strata have an uncertain age and were assigned to the Maastrichtian from their plant macro- and microfossil assemblages.

Thus, the Sawayama, Miyadani-gawa, Omichidani and Asuwa formations will not be included in stratigraphic considerations of the present study, but mentioned in appendix for their palynoflora. Recently, triprojectate pollen was also recovered from a terrestrial sequence of the Himenoura Group in South Japan (Legrand *et al.*, 2018), assigned to the Maastrichtian based on U–Pb radiometric dating on zircons of 70.0 ± 0.5 Ma (Miyake *et al.*, 2018).

Material and methods

The material used in this study consists of sandy mudstone collected from jackets used during the excavation of *Kamuysaurus japonicus* (Kobayashi *et al.*, 2019), and provided by the Hobetsu Museum, Mukawa town, Japan. Jackets are burlap bandages soaked in plaster for encasing and tightly binding together excavated bones with the surrounding rock matrix and permitting their secured transportation. Samples were collected from seven jackets (J2, J12, J24, J25, J26, J27, J29) stored at the Hobetsu Museum, which covered the chevron (J2), right metatarsus (J12), dorsal vertebrae (J24), scapula (J25), left femur (J27), and skull (J26, J29) of *K. japonicus*. We collected some samples from the downside part of these jackets, labeled as J24D, J25D, and J29D (Figure 1).

Method for pollen extraction follows Legrand *et al.* (2013). Pollen grains were observed using a Leica DM2500 Differential Interference Contrast Microscope equipped with a Leica Flexacam C1 Camera, and a JEOL JSM-6010LA Scanning Electron Microscope. Position of the specimen on the slide was recorded using an England Finder graticule (Pyser Optics, Edenbridge, England). Slides were housed in the collection of the Hobetsu Museum, Mukawa town, Japan. We follow nomenclatural and classification systems revised by Wiggins (1976) for the oculate group, and the latest taxonomic modifications and new combinations proposed by Braman (2013) for the triprojectate group. Species rejected and junior synonyms follow Braman (2013); we further consider *Aquilapollenites conatus nipponicus* Miki, 1977 and *Wodehouseia parva* Miki, 1977 reported from the Hakobuchi Formation (Miki, 1977) as *nomina nuda* because of the lack of any description or illustration. *Aquilapollenites miyajiense* (Takahashi and Shimono) Braman, 2013, *Integricorpus kokufuense* (Takahashi and Shimono) Braman, 2001, *Parviprojectus triauritus* (Takahashi) Braman, 2013, *Triprojectus nemuroensis* (Takahashi, 1991a) Braman, 2013, *Triprojectus proprius* (Takahashi and Shimono) Braman, 2013, *Scollardia nortoni* Srivastava, 1966 are listed but were considered as uncertain identifications by Braman (2013) and Srivastava and Braman (2013). Species reported in open nomenclature are listed as their original genus.

After the revision, taxa from Japanese strata include 16 genera and 86 triprojectate species, and one genus and five oculate species (Figure 2, Appendix 1), with 17 species endemic to Japan. Moreover, 15 genera and 60 triprojectate species and one genus and four oculate species have a stratigraphic significance (Figure 2).

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		Northeast Honshu				Hokkaido					
		Turonian	late Con.	Santonian	late Camp.	Turonian	Coniacian	Santonian	Campanian		
		Kuji Gr	Futaba Gr			Yezo Group					
		Tamagawa Fm	Kasamatsu Fm	Taneichi Fm (Uge Member)	Yokomichi Fm	Tenkaritoge Fm	Nishichirashinai Fm	Haborogawa Fm		Omagari Fm	Osoushinai Fm
Triprojectate pollen	*Accuratipollis enodatus* Chlonova, 1961 (reported as *"Fibulapollis enodatus"*)			●☆							
	Accuratipollis evanidus Chlonova, 1961 (reported as *"Aquilapollenites evanidus"* (not validly published), *"Fibulapollis evanidus"* or *"Kurtzipites evanidus"* (not validly published))	○☆		●☆	●		○			○	○
	Aquilapollenites manifestus (Takahashi and Shimono, 1982) Braman, 2013 (former *"Pentapollenites manifestus"*)										
	Aquilapollenites quadrilobus Rouse, 1957 emend. Srivastava and Rouse, 1970						○★				-
	Aquilapollenites cf. *quadrilobus in* Takahashi and Yamanoi (1992)										
	Aquilapollenites tripterum (Takahashi *in* Takahashi and Shimono, 1982) Braman, 2013 (former *"Hemicorpus tripterum"*)										
	Bratzevaea cf. *striatella in* Takahashi and Yamanoi (1992)										
	Cranwellia rumseyensis Srivastava, 1966										
	Cranwellia striata (Couper, 1953) Srivastava, 1966										
	Fibulapollis mirificus (Chlonova, 1957) Chlonova, 1961 (former *"Kurtzipites mirificus"*, also reported as *"Pentapollenites minus"* (junior synonym))										
	Fibulapollis pusillus Takhashi *in* Takahashi and Shimono (1982)										
	Integricorpus clarireticulatus Samoilovitch, 1964										
	Laevicorpus minimus (Chlonova, 1961) Braman, 2013 (former *"Mancicorpus minimus (non minimum)"*)										
	Mancicorpus anchoriforme Mtchedlishvili *in* Samoilovitch and Mtchedlishvili (1961)										
	Orbiculapollis globosus (Chlonova, 1957) Chlonova, 1961										
	Orbiculapollis lucidus Chlonova, 1961 (reported as *"Orbiculapollis minutus"* (junior synoym))										
	Orbiculapollis moderatus Takahashi *in* Takahashi and Shimono, 1982										
	Parviprojectus borealis (Takahashi, 1964) Braman, 2013 (former *"Aquilapollenites borealis"*)										
	Parviprojectus fusiformis (Tschudy, 1969) Braman, 2013 (reported as *"Integricorpus fusiforme"* (not validly published))										
	Parviprojectus cf. *mirabilis* (Srivastava, 1968) Braman, 2013 (former *"Aquilapollenites* cf. *mirabilis"*)										
	Parviprojectus procerus (Samoilovitch, 1964) Braman, 2013 (former *"Aquilapollenites procerus"*)										
	Parviprojectus reticulatus Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961 (former *"Integricorpus mtchedlishvilii"*, also reported as *"Aquilapollenites reticulatus* Stanley, 1961*"* (junior synonym))										
	Parviprojectus cf. *reticulatus in* Takahashi and Yamanoi (1992) (former *"Integricorpus* cf. *mtchedlishvilii"*)										
	Parviprojectus rigidus (Tschudy and Leopold, 1971) Braman, 2013 (former *"Aquilapollenites rigidus"*)						-	-		-	-
	Parviprojectus aff. *rombicus* (Samoilovitch, 1964) Braman, 2013 (former *"Aquilapollenites* aff. *rombicus"*)										
	Parviprojectus triauritus (Takahashi, 1964) Braman, 2013 (former *"Aquilapollenites triauritus"*)										
	Pentapollenites dongtaiensis Zhou *in* Song *et al*., 1981 (reported as *"Integricorpus dongtaiensis"* (not validly published))										
	Pentapollenites yezoensis Takahashi, 1964		●								
	Pseudoaquilapollenites cf. *bertillonites* (Funkhouser, 1961) Braman, 2013 (former *"Integricorpus* cf. *bertillonites"*)										
	Pseudoaquilapollenites conatus (Norton, 1965) Liu, 1983 (former *"Aquilapollenites conatus"*)										
	Pseudoaquilapollenites melior (Takahashi and Shimono, 1982) Braman, 2013 (former *"Aquilapollenites melior"*)										
	Pseudoaquilapollenites melioratus (Takahashi *in* Takahashi and Shimono, 1982) Braman, 2013 (former *"Aquilapollenites melioratus"*)										
	Pseudoaquilapollenites cf. *melioratus in* Takahashi and Yamanoi (1992) (former *"Aquilapollenites* cf. *melioratus"*)										
	Pseudoaquilapollenites mirus (Takahashi *in* Takahashi and Shimono, 1982) Braman, 2013 (former *"Aquilapollenites mirus"*)										
	Pseudoaquilapollenites pachypolus (Martin, 1968) Braman, 2013 (former *"Aquilapollenites striatus"* and *"Integricorpus* cf. *striatus* (non *striatum*)*"*)										
	Pseudoaquilapollenites quadrinus (Takahashi, 1964) Braman, 2013 (former *"Aquilapollenites quadrinus"*)										
	Reticorpus tenue (Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961) Braman, 2013 (former *"Hemicorpus tenue"*)										
	Reticorpus trapeziforme (Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961) Braman 2013 (former *"Hemicorpus trapeziforme"*)										
	Scollardia nortoni Srivastava, 1966										

Figure 2. Summary of the stratigraphic distribution of triprojectate and oculate pollen record of Japan. Pollen grains illustrated in related reports are indicated with a star, white in case of grains identifiable on the picture, or black in case of grains poorly recognizable on the picture because of a poor state of preservation and/or badly oriented and/or with a picture in a low resolution or bad quality. Abbreviations: Con., Coniacian; Camp., Campanian; Maastr., Maastrichtian; Fm, Formation.

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		Hokkaido								
		Camp.	Maastrichtian				Paleocene		Maastr.	Danian
		Yezo Group			Nemuro Group					
		Hakobuchi Fm	Nishibetsu	Hamanaka, Oborogawa Fms	Akkeshi Fm	Tokotan Fm	Kiritappu Fm	Katsuhira Fm		
Triprojectate pollen	*Accuratipollis enodatus* Chlonova, 1961 (reported as *"Fibulapollis enodatus"*)									
	Accuratipollis evanidus Chlonova, 1961 (reported as *"Aquilapollenites evanidus"* (not validly published), *"Fibulapollis evanidus"* or *"Kurtzipites evanidus"* (not validly published))	-								●☆
	Aquilapollenites manifestus (Takahashi and Shimono, 1982) Braman, 2013 (former *"Pentapollenites manifestus"*)					●☆	●			●☆
	Aquilapollenites quadrilobus Rouse, 1957 emend. Srivastava and Rouse, 1970	○☆	●							
	Aquilapollenites cf. *quadrilobus in* Takahashi and Yamanoi (1992)									●☆
	Aquilapollenites tripterum (Takahashi *in* Takahashi and Shimono, 1982) Braman, 2013 (former *"Hemicorpus tripterum"*)									●☆
	Bratzevaea cf. *striatella in* Takahashi and Yamanoi (1992)									●☆
	Cranwellia rumseyensis Srivastava, 1966	-	(-)	●						●☆
	Cranwellia striata (Couper, 1953) Srivastava, 1966			●★		●☆	●☆	●☆	●☆	●☆
	Fibulapollis mirificus (Chlonova, 1957) Chlonova, 1961 (former "*Kurtzipites mirificus*", also reported as *"Pentapollenites minus"* (junior synonym))					●☆	●☆			
	Fibulapollis pusillus Takhashi *in* Takahashi and Shimono (1982)					●☆	●☆		●☆	●☆
	Integricorpus clarireticulatus Samoilovitch, 1964									●☆
	Laevicorpus minimus (Chlonova, 1961) Braman, 2013 (former *"Mancicorpus minimus (non minimum)"*)									●
	Mancicorpus anchoriforme Mtchedlishvili *in* Samoilovitch and Mtchedlishvili (1961)									●☆
	Orbiculapollis globosus (Chlonova, 1957) Chlonova, 1961		●		●	●☆	●☆		●☆	●
	Orbiculapollis lucidus Chlonova, 1961 (reported as *"Orbiculapollis minutus"* (junior synoym))					●☆	●☆	●☆	●☆	●☆
	Orbiculapollis moderatus Takahashi *in* Takahashi and Shimono, 1982								●☆	●
	Parviprojectus borealis (Takahashi, 1964) Braman, 2013 (former *"Aquilapollenites borealis"*)	-☆	-							
	Parviprojectus fusiformis (Tschudy, 1969) Braman, 2013 (reported as *"Integricorpus fusiforme"* (not validly published))								●☆	
	Parviprojectus cf. *mirabilis* (Srivastava, 1968) Braman, 2013 (former *"Aquilapollenites* cf. *mirabilis"*)			●★						
	Parviprojectus procerus (Samoilovitch, 1964) Braman, 2013 (former *"Aquilapollenites procerus"*)								●☆	
	Parviprojectus reticulatus Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961 (former "*Integricorpus mtchedlishvili*", also reported as *"Aquilapollenites reticulatus* Stanley, 1961*"* (junior synonym))	○	-			●☆				
	Parviprojectus cf. *reticulatus in* Takahashi and Yamanoi (1992) (former *"Integricorpus* cf. *mtchedlishvili"*)								●☆	●☆
	Parviprojectus rigidus (Tschudy and Leopold, 1971) Braman, 2013 (former *"Aquilapollenites rigidus"*)	-								
	Parviprojectus aff. *rombicus* (Samoilovitch, 1964) Braman, 2013 (former *"Aquilapollenites* aff. *rombicus"*)	○								
	Parviprojectus triauritus (Takahashi, 1964) Braman, 2013 (former *"Aquilapollenites triauritus"*)	-☆								
	Pentapollenites dongtaiensis Zhou *in* Song *et al*., 1981 (reported as *"Integricorpus dongtaiensis"* (not validly published))									●☆
	Pentapollenites yezoensis Takahashi, 1964	-☆								
	Pseudoaquilapollenites cf. *bertillonites* (Funkhouser, 1961) Braman, 2013 (former *"Integricorpus* cf. *bertillonites"*)					●☆	●☆			
	Pseudoaquilapollenites conatus (Norton, 1965) Liu, 1983 (former *"Aquilapollenites conatus"*)								●☆	●☆
	Pseudoaquilapollenites melior (Takahashi and Shimono, 1982) Braman, 2013 (former *"Aquilapollenites melior"*)					●☆	●☆			
	Pseudoaquilapollenites melioratus (Takahashi *in* Takahashi and Shimono, 1982) Braman, 2013 (former *"Aquilapollenites melioratus"*)					●☆				
	Pseudoaquilapollenites cf. *melioratus in* Takahashi and Yamanoi (1992) (former "*Aquilapollenites* cf. *melioratus*")									●☆
	Pseudoaquilapollenites mirus (Takahashi *in* Takahashi and Shimono, 1982) Braman, 2013 (former *"Aquilapollenites mirus"*)								●☆	●☆
	Pseudoaquilapollenites pachypolus (Martin, 1968) Braman, 2013 (former *"Aquilapollenites striatus"* and *"Integricorpus* cf. *striatus* (non *striatum*)*"*)	-	-			●				●
	Pseudoaquilapollenites quadrinus (Takahashi, 1964) Braman, 2013 (former *"Aquilapollenites quadrinus"*)		○			●☆			●	
	Reticorpus tenue (Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961) Braman, 2013 (former *"Hemicorpus tenue"*)									●☆
	Reticorpus trapeziforme (Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961) Braman 2013 (former *"Hemicorpus trapeziforme"*)					●☆				●☆
	Scollardia nortoni Srivastava, 1966						●			

Figure 2. *Continued.*

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		Northeast Honshu				Hokkaido					
		Turonian	late Con.	Santonian	late Camp.	Turonian	Coniacian	Santonian	Campanian		
		Kuji Gr	Futaba Gr			Yezo Group					
		Tamagawa Fm	Kasamatsu Fm	Taneichi Fm (Uge Member)	Yokomichi Fm	Tenkaritoge Fm	Nishichirashinai Fm	Haborogawa Fm		Omagari Fm	Osoushinai Fm
Triprojectate pollen	*Triprojectus attenuatus* (Funkhouser, 1961) Braman, 2013 (former "*Aquilapollenites attenuatus* ", also reported as "*Aquilapollenites asper* Mtchedlishvili, 1961" "*Aquilapollenites matsumotoi* Takahashi, 1964" or "*Aquilapollenites parvus* Takahashi, 1970" (junior synonyms))										
	Triprojectus cf. *attenuatus in* Takahashi and Ueda (1990) (reported as "*Aquilapollenites* cf. *parvus*")										
	Triprojectus aucellatus (Srivastava, 1969) Braman, 2013 (former "*Aquilapollenites aucellatus* ", also reported as "*Aquilapollenites pseudoaucellatus* Takahashi and Shimono, 1982" (junior synonym))										
	Triprojectus drumhellerensis (Srivastava, 1969) Braman, 2013 (former "*Aquilapollenites drumhellerensis*")										
	Triprojectus hakobuchiensis (Sato, 1961) Braman, 2013 (former "*Aquilapollenites hakobuchiensis*")										●
	Triprojectus cf. *hamulatus in* Takahashi (1991b) (reported as "*Fibulapollis* cf. *hamulatus*")										
	Triprojectus latialatus (Takahashi *in* Takahashi and Shimono, 1982) Braman, 2013 (former "*Aquilapollenites latialatus*")										
	Triprojectus latilobus (Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961) Braman, 2013 (also reported as "*Aquilapollenites amplus* Stanley, 1961" (junior synonym))										
	Triprojectus miser (Takahashi *in* Takahashi and Shimono, 1982) Braman, 2013 (former "*Pentapollenites miser*")										
	Triprojectus nemuroensis (Takahashi, 1991a) Braman, 2013 (former "*Aquilapollenites nemuroensis*")										
	Triprojectus cf. nemuroensis in Takahashi and Yamanoi (1992) (reported as "*Aquilapollenites cf. nemuroensis* ")										
	Tripojectus normalis (Takahashi and Shimono, 1982) Braman, 2013 (former "*Pentapollenites normalis*")										
	Tripojectus cf. *normalis in* Takahashi and Yamanoi (1992) (repoted as "*Pentapollenites* cf. *normalis* ")										
	Tripojectus ovalis (Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961) Stanley, 1970 (reported as "*Aquilapollenites colvillensis* Tschudy, 1969" (junior synonym))										
	Triprojectus pudicus (Srivastava, 1969) Braman, 2013 (former "*Aquilapollenites pudicus*")										
	Triprojectus rectus (Tschudy, 1969) Braman, 2013 (former "*Aquilapollenites rectus*")										
	Triprojectus cf. *sentus in* Takahashi and Yamanoi (1992)										
	Triprojectus subspinulosus Braman, 2013 (former "*Aquilapollenites* cf. *spinulosus*")										
	Triprojectus subtilis (Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961) Braman, 2013 (former "*Aquilapollenites subtilis*")										
	Triprojectus turbidus (Tschudy and Leopold, 1971) Braman, 2013 (former "*Aquilapollenites turbidus*")										
	Triprojectus cf. *turbidus in* Miki (1977)										
Oculate pollen	*Wodehouseia asper* (Samoilovitch *in* Samoilovitch and Mtchedlishvili, 1961) Wiggins, 1976 (reported as "*Wodehouseia aspera*")										
	Wodehouseia edmontonicola Wiggins, 1976										
	Wodehouseia gracile (Samoilovitch *in* Samoilovitch and Mtchedlishvili, 1961) Pokrovaskaya, 1966 (reported as "*Wodehouseia gracilis*")										
	Wodehouseia spinata Stanley, 1961										

Species in open nomenclature

Triprojectate pollen	*Aquilapollenites* sp. *in* Sato, 1961										
	Aquilapollenites sp. a *in* Takahashi, 1964										
	Aquilapollenites sp. b *in* Takahashi, 1964										
	Aquilapollenites sp. c *in* Takahashi, 1964										
	Aquilapollenites sp. d *in* Takahashi, 1964										
	Aquilapollenites sp. B *in* Miki, 1977						(-)			●	
	Aquilapollenites sp. C *in* Miki, 1977										
	Aquilapollenites sp. D *in* Miki, 1977										
	Aquilapollenites sp. E *in* Miki, 1977										
	Aquilapollenites sp. F *in* Miki, 1977										
	Aquilapollenites sp. G *in* Miki, 1977										
	Aquilapollenites sp. H *in* Miki, 1977										
	Aquilapollenites sp. indet. *in* Miki, 1977										-
	Aquilapollenites sp. *in* Takahashi and Ueda, 1990										
	Aquilapollenites sp. *in* Takahashi, 1991a										
	Aquilapollenites sp. *in* Takahashi, 1991b										
	Aquilapollenites sp. *in* Takahashi, 1991c										
	Aquilapollenites sp. a *in* Takahashi and Yamanoi, 1992										

Figure 2. *Continued.*

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		Hokkaido								
		Camp.	Maastrichtian				Paleocene		Maastr.	Danian
		Yezo Group			Nemuro Group					
		Hakobuchi Fm		Nishibetsu	Hamanaka, Oborogawa Fms	Akkeshi Fm	Tokotan Fm	Kiritappu Fm	Katsuhira Fm	
Triprojectate pollen	*Triprojectus attenuatus* (Funkhouser, 1961) Braman, 2013 (former "*Aquilapollenites attenuatus* ", also reported as "*Aquilapollenites asper* Mtchedlishvili, 1961" *"Aquilapollenites matsumotoi* Takahashi, 1964" or "*Aquilapollenites parvus* Takahashi, 1970" (junior synonyms))	○☆	○	●★		●☆	●☆	●☆	●☆	●☆
	Triprojectus cf. *attenuatus in* Takahashi and Ueda (1990) (reported as "*Aquilapollenites* cf. *parvus*")				●	●☆				
	Triprojectus aucellatus (Srivastava, 1969) Braman, 2013 (former "*Aquilapollenites aucellatus* ", also reported as *"Aquilapollenites pseudoaucellatus* Takahashi and Shimono, 1982" (junior synonym))					●	●			
	Triprojectus drumhellerensis (Srivastava, 1969) Braman, 2013 (former *"Aquilapollenites drumhellerensis"*)								●☆	
	Triprojectus hakobuchiensis (Sato, 1961) Braman, 2013 (former *"Aquilapollenites hakobuchiensis"*)	+☆	●				●			
	Triprojectus cf. *hamulatus in* Takahashi (1991b) (reported as *"Fibulapollis* cf. *hamulatus"*)						●☆		●☆	●☆
	Triprojectus latialatus (Takahashi *in* Takahashi and Shimono, 1982) Braman, 2013 (former *"Aquilapollenites latialatus"*)				●					
	Triprojectus latilobus (Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961) Braman, 2013 (also reported as "*Aquilapollenites amplus* Stanley, 1961" (junior synonym))									●☆
	Triprojectus miser (Takahashi *in* Takahashi and Shimono, 1982) Braman, 2013 (former *"Pentapollenites miser"*)					●☆				●☆
	Triprojectus nemuroensis (Takahashi, 1991a) Braman, 2013 (former *"Aquilapollenites nemuroensis"*)					●☆	●☆			●☆
	Triprojectus cf. nemuroensis in Takahashi and Yamanoi (1992) (reported as "*Aquilapollenites cf. nemuroensis* ")								●☆	
	Tripojectus normalis (Takahashi and Shimono, 1982) Braman, 2013 (former *"Pentapollenites normalis"*)				●	●☆				●☆
	Tripojectus cf. *normalis in* Takahashi and Yamanoi (1992) (repoted as "*Pentapollenites* cf. *normalis*")									●☆
	Tripojectus ovalis (Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961) Stanley, 1970 (reported as *"Aquilapollenites colvillensis* Tschudy, 1969" (junior synonym))									●☆
	Triprojectus pudicus (Srivastava, 1969) Braman, 2013 (former *"Aquilapollenites pudicus"*)									●☆
	Triprojectus rectus (Tschudy, 1969) Braman, 2013 (former *"Aquilapollenites rectus"*)	○	-							
	Triprojectus cf. *sentus in* Takahashi and Yamanoi (1992)									●☆
	Triprojectus subspinulosus Braman, 2013 (former *"Aquilapollenites* cf. *spinulosus"*)						●☆			●☆
	Triprojectus subtilis (Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961) Braman, 2013 (former *"Aquilapollenites subtilis"*)									●☆
	Triprojectus turbidus (Tschudy and Leopold, 1971) Braman, 2013 (former *"Aquilapollenites turbidus"*)									●☆
	Triprojectus cf. *turbidus in* Miki (1977)	○								
Oculate pollen	*Wodehouseia asper* (Samoilovitch *in* Samoilovitch and Mtchedlishvili, 1961) Wiggins, 1976 (reported as *"Wodehouseia aspera"*)									●☆
	Wodehouseia edmontonicola Wiggins, 1976						●☆		●☆	
	Wodehouseia gracile (Samoilovitch *in* Samoilovitch and Mtchedlishvili, 1961) Pokrovaskaya, 1966 (reported as *"Wodehouseia gracilis"*)					●☆	●☆			●☆
	Wodehouseia spinata Stanley, 1961		○						●☆	●☆

Species in open nomenclature

Triprojectate pollen	*Aquilapollenites* sp. *in* Sato, 1961	-☆								
	Aquilapollenites sp. a *in* Takahashi, 1964	-☆								
	Aquilapollenites sp. b *in* Takahashi, 1964	-☆								
	Aquilapollenites sp. c *in* Takahashi, 1964	-☆								
	Aquilapollenites sp. d *in* Takahashi, 1964	-☆								
	Aquilapollenites sp. B *in* Miki, 1977									
	Aquilapollenites sp. C *in* Miki, 1977		○							
	Aquilapollenites sp. D *in* Miki, 1977		○							
	Aquilapollenites sp. E *in* Miki, 1977		-							
	Aquilapollenites sp. F *in* Miki, 1977	●								
	Aquilapollenites sp. G *in* Miki, 1977	-								
	Aquilapollenites sp. H *in* Miki, 1977		●							
	Aquilapollenites sp. indet. *in* Miki, 1977		-							
	Aquilapollenites sp. *in* Takahashi and Ueda, 1990					●				
	Aquilapollenites sp. *in* Takahashi, 1991a					●☆				
	Aquilapollenites sp. *in* Takahashi, 1991b						●			
	Aquilapollenites sp. *in* Takahashi, 1991c							●☆		
	Aquilapollenites sp. a *in* Takahashi and Yamanoi, 1992								●☆	

Figure 2. *Continued.*

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		Northeast Honshu				Hokkaido					
		Turonian	late Con.	Santonian	late Camp.	Turonian	Coniacian	Santonian	Campanian		
		Kuji Gr	Futaba Gr			Yezo Group					
		Tamagawa Fm	Kasamatsu Fm	Taneichi Fm (Uge Member)	Yokomichi Fm	Tenkaritoge Fm	Nishichirashinai Fm	Haborogawa Fm		Omagari Fm	Osoushinai Fm
Triprojectate pollen	*Aquilapollenites* sp. b *in* Takahashi and Yamanoi, 1992										
	Aquilapollenites sp. c *in* Takahashi and Yamanoi, 1992										
	Aquilapollenites sp. d *in* Takahashi and Yamanoi, 1992										
	Aquilapollenites sp. e *in* Takahashi and Yamanoi, 1992										
	Aquilapollenites sp. f *in* Takahashi and Yamanoi, 1992										
	Aquilapollenites sp. g *in* Takahashi and Yamanoi, 1992										
	Aquilapollenites sp. h *in* Takahashi and Yamanoi, 1992										
	Aquilapollenites sp. i *in* Takahashi and Yamanoi, 1992										
	Aquilapollenites sp. j *in* Takahashi and Yamanoi, 1992										
	Aquilapollenites spp. *in* Tanaka and Hirano, 2008							○★	○		-
	? *Aquilapollenites* sp. *in* Takahashi, 1964										
	? *Aquilapollenites* sp. a *in* Takahashi, 1991a										
	? *Aquilapollenites* sp. b *in* Takahashi, 1991a										
	? *Aquilapollenites* sp. *in* Takahashi and Yamanoi, 1992										
	Azonia sp. *in* Tanaka and Hirano, 2008										
	Cranwellia sp. *in* Takahashi, 1991a										
	Cranwellia sp. *in* Takahashi and Yamanoi, 1992										
	Cranwellia sp. *in* Tanaka and Hirano, 2008					-★	○			○	-
	Fibulapollis sp. a *in* Takahashi, 1991a										
	Fibulapollis sp. b *in* Takahashi, 1991a										
	Fibulapollis sp. c *in* Takahashi, 1991a										
	Fibulapollis sp. a *in* Takahashi and Yamanoi, 1992										
	Fibulapollis sp. b *in* Takahashi and Yamanoi, 1992										
	? *Fibulapollis* sp. *in* Takahashi, 1991a										
	Hemicorpus sp. a *in* Takahashi and Yamanoi, 1992										
	Hemicorpus sp. b *in* Takahashi and Yamanoi, 1992										
	Hemicorpus sp. c *in* Takahashi and Yamanoi, 1992										
	? *Hemicorpus* sp. *in* Takahashi, 1991a										
	Integricorpus sp. a *in* Takahashi, 1991a										
	Integricorpus sp. b *in* Takahashi, 1991a										
	Integricorpus sp. *in* Takahashi, 1991c										
	Integricorpus sp. *in* Takahashi and Yamanoi, 1992										
	? *Kurtzipites* sp. a *in* Takahashi, 1991a										
	? *Kurtzipites* sp. b *in* Takahashi, 1991a										
	Mancicorpus sp. *in* Takahashi, 1970										
	Orbiculapollis sp. *in* Takahashi and Ueda, 1990										
	Orbiculapollis sp. a *in* Takahashi and Yamanoi, 1992										
	Orbiculapollis sp. b *in* Takahashi and Yamanoi, 1992										
	Orbiculapollis spp. *in* Tanaka and Hirano, 2008								○	○★	-
	Pentapollenites sp. a *in* Takahashi and Yamanoi, 1992										
	Pentapollenites sp. b *in* Takahashi and Yamanoi, 1992										
	Pentapollenites sp. c *in* Takahashi and Yamanoi, 1992										
	Pentapollenites sp. d *in* Takahashi and Yamanoi, 1992										
	Pentapollenites sp. *in* Takahashi, 1991a										
	Pentapollenites sp. *in* Takahashi, 1991c										
	? *Pentapollenites* sp. a *in* Takahashi, 1991a										
	? *Pentapollenites* sp. b *in* Takahashi, 1991a										
	? *Pentapollenites* sp. c *in* Takahashi, 1991a										
	? *Pentapollenites* sp. d *in* Takahashi, 1991a										
	? *Pentapollenites* sp. *in* Takahashi and Yamanoi, 1992										
	? *Pseudointegricorpus* sp. *in* Takahashi, 1991a										
	Triprojectus sp. a *in* Takahashi and Yamanoi, 1992										
	Triprojectus sp. b *in* Takahashi and Yamanoi, 1992										
Oculate pollen	*Wodehouseia* sp. *in* Takahashi and Ueda, 1990										
	Wodehouseia sp. *in* Takahashi and Yamanoi, 1992										

Figure 2. *Continued.*

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		Hokkaido								
		Camp.	Maastrichtian				Paleocene		Maastr.	Danian
			Yezo Group		Nemuro Group					
			Hakobuchi Fm	Nishibetsu	Hamanaka, Oborogawa Fms	Akkeshi Fm	Tokotan Fm	Kiritappu Fm	Katsuhira Fm	
Triprojectate pollen	*Aquilapollenites* sp. b *in* Takahashi and Yamanoi, 1992								●☆	
	Aquilapollenites sp. c *in* Takahashi and Yamanoi, 1992								●☆	
	Aquilapollenites sp. d *in* Takahashi and Yamanoi, 1992									●☆
	Aquilapollenites sp. e *in* Takahashi and Yamanoi, 1992									●
	Aquilapollenites sp. f *in* Takahashi and Yamanoi, 1992									●☆
	Aquilapollenites sp. g *in* Takahashi and Yamanoi, 1992									●☆
	Aquilapollenites sp. h *in* Takahashi and Yamanoi, 1992									●☆
	Aquilapollenites sp. i *in* Takahashi and Yamanoi, 1992									●☆
	Aquilapollenites sp. j *in* Takahashi and Yamanoi, 1992									●☆
	Aquilapollenites spp. *in* Tanaka and Hirano, 2008	++★								
	? *Aquilapollenites* sp. *in* Takahashi, 1964	-								
	? *Aquilapollenites* sp. a *in* Takahashi, 1991a						●			
	? *Aquilapollenites* sp. b *in* Takahashi, 1991a						●☆			
	? *Aquilapollenites* sp. *in* Takahashi and Yamanoi, 1992									●☆
	Azonia sp. *in* Tanaka and Hirano, 2008	○★								
	Cranwellia sp. *in* Takahashi, 1991a					●☆				
	Cranwellia sp. *in* Takahashi and Yamanoi, 1992								●☆	
	Cranwellia sp. *in* Tanaka and Hirano, 2008									
	Fibulapollis sp. a *in* Takahashi, 1991a					●☆				
	Fibulapollis sp. b *in* Takahashi, 1991a					●☆				
	Fibulapollis sp. c *in* Takahashi, 1991a				●☆					
	Fibulapollis sp. a *in* Takahashi and Yamanoi, 1992									●
	Fibulapollis sp. b *in* Takahashi and Yamanoi, 1992									●
	? *Fibulapollis* sp. *in* Takahashi, 1991a						●			
	Hemicorpus sp. a *in* Takahashi and Yamanoi, 1992								●☆	
	Hemicorpus sp. b *in* Takahashi and Yamanoi, 1992								●☆	
	Hemicorpus sp. c *in* Takahashi and Yamanoi, 1992									●
	? *Hemicorpus* sp. *in* Takahashi, 1991a					●☆				
	Integricorpus sp. a *in* Takahashi, 1991a					●				
	Integricorpus sp. b *in* Takahashi, 1991a					●☆				
	Integricorpus sp. *in* Takahashi, 1991c							●☆		
	Integricorpus sp. *in* Takahashi and Yamanoi, 1992								●☆	
	? *Kurtzipites* sp. a *in* Takahashi, 1991a						●			
	? *Kurtzipites* sp. b *in* Takahashi, 1991a						●			
	Mancicorpus sp. *in* Takahashi, 1970			●★						
	Orbiculapollis sp. *in* Takahashi and Ueda, 1990						●			
	Orbiculapollis sp. a *in* Takahashi and Yamanoi, 1992									●☆
	Orbiculapollis sp. b *in* Takahashi and Yamanoi, 1992									●☆
	Orbiculapollis spp. *in* Tanaka and Hirano, 2008	○★								
	Pentapollenites sp. a *in* Takahashi and Yamanoi, 1992								●☆	
	Pentapollenites sp. b *in* Takahashi and Yamanoi, 1992									●☆
	Pentapollenites sp. c *in* Takahashi and Yamanoi, 1992									●
	Pentapollenites sp. d *in* Takahashi and Yamanoi, 1992									●
	Pentapollenites sp. *in* Takahashi, 1991a					●☆				
	Pentapollenites sp. *in* Takahashi, 1991c							●☆		
	? *Pentapollenites* sp. a *in* Takahashi, 1991a					●				
	? *Pentapollenites* sp. b *in* Takahashi, 1991a					●				
	? *Pentapollenites* sp. c *in* Takahashi, 1991a					●☆				
	? *Pentapollenites* sp. d *in* Takahashi, 1991a					●☆				
	? *Pentapollenites* sp. *in* Takahashi and Yamanoi, 1992									●☆
	? *Pseudointegricorpus* sp. *in* Takahashi, 1991a					●☆				
	Triprojectus sp. a *in* Takahashi and Yamanoi, 1992								●☆	
	Triprojectus sp. b *in* Takahashi and Yamanoi, 1992									●☆
Oculate pollen	*Wodehouseia* sp. *in* Takahashi and Ueda, 1990					●				
	Wodehouseia sp. *in* Takahashi and Yamanoi, 1992								●☆	●☆

- rare (less than 0.5%)
○ few (0.5-3.0%)
+ common (3.0-10%)
++ abundant (more than 10%)
● Reported without numerical information
☆ grain illustrated
★ grain illustrated but poorly recognizable on the picture

Figure 2. *Continued.*

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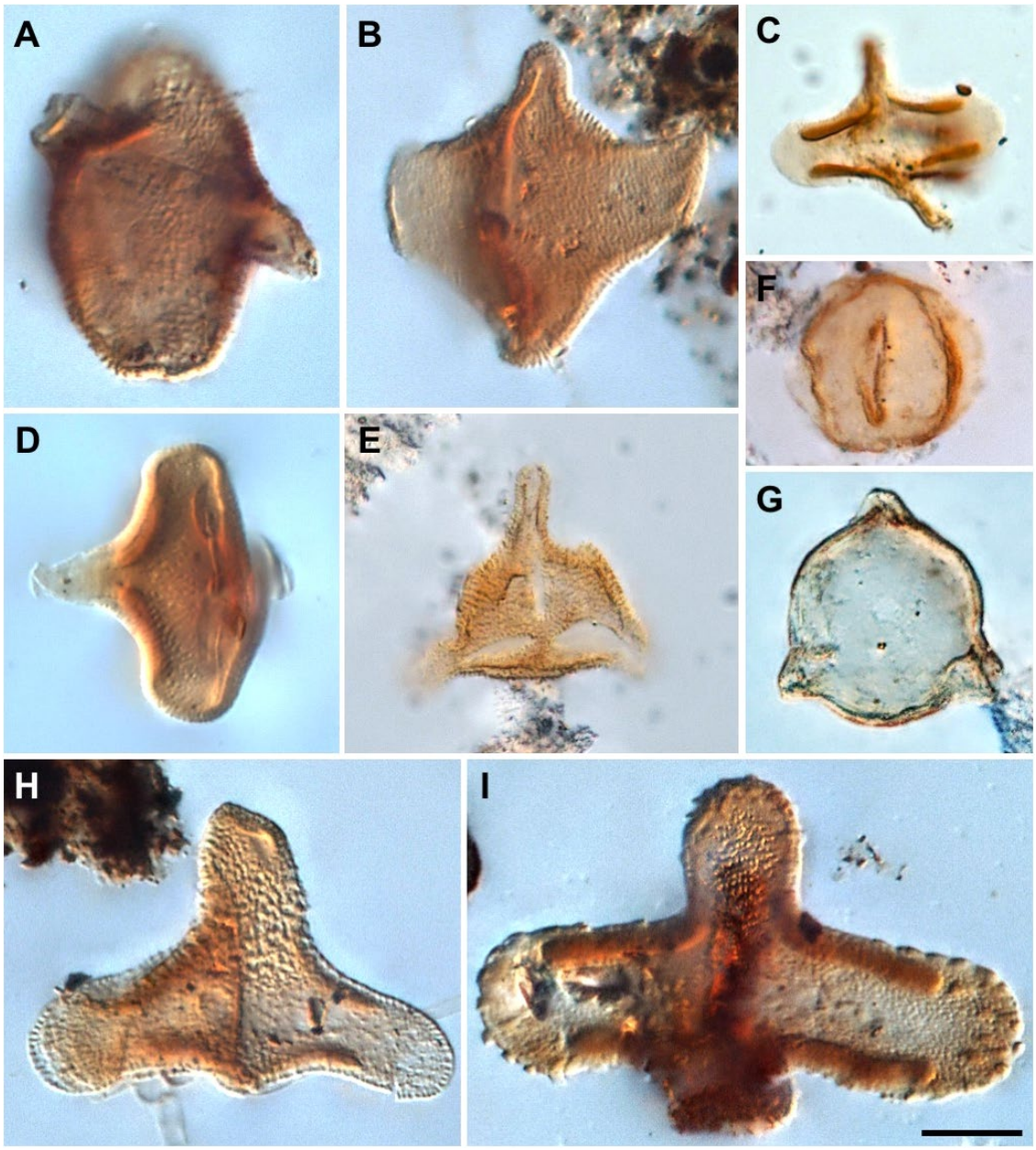

Figure 3. Triprojectate pollen obtained from the Hakobuchi Formation, observed under the Differential Interference Contrast Microscope; slide number, and position of pollen using an England Finder, are indicated in brackets. **A,** *Integricorpus kokufuense* (equatorial view, J25Db, T59); **B,** *Pseudoaquilapollenites melior* (equatorial view, J29Db, J66/2); **C,** *Pseudoaquilapollenites melioratus* (equatorial view, J25Dc, X5/1); **D, E,** *Parviprojectus reticulatus* (D, equatorial view, J25Db, T65/1; E, polar view, J12a, S23/1); **F, G,** *Orbiculapollis globosus* (F, equatorial view, J2a, R47/2; G, polar view, J12a, D38/3); **H,** *Reticorpus delicatus* (equatorial view, J25Db, L66/2); **I,** *Triprojectus attenuatus* (equatorial view, J25Db, Z62/2). Scale bar, 10 μm.

Results

Well-preserved palynomorphs were obtained from all seven samples of the Hakobuchi Formation, with the best state of preservation observed in jackets J2, J12, and J25. Among them, we could identify six genera and 15 species of triprojectate pollen that we describe below. Pollen of genus *Triprojectus* is most abundant and diversified with eight species: *Triprojectus attenuatus* (Funkhouser) Braman, 2013 (Figures 3I, 5E), *T. blandus* Braman, 2013 (Figures 4A, 5C), *T. elegans* (Zhao) Braman, 2013 (Figure 4B), *T. granatus* (Zhou) Braman, 2013 (Figure 4C),

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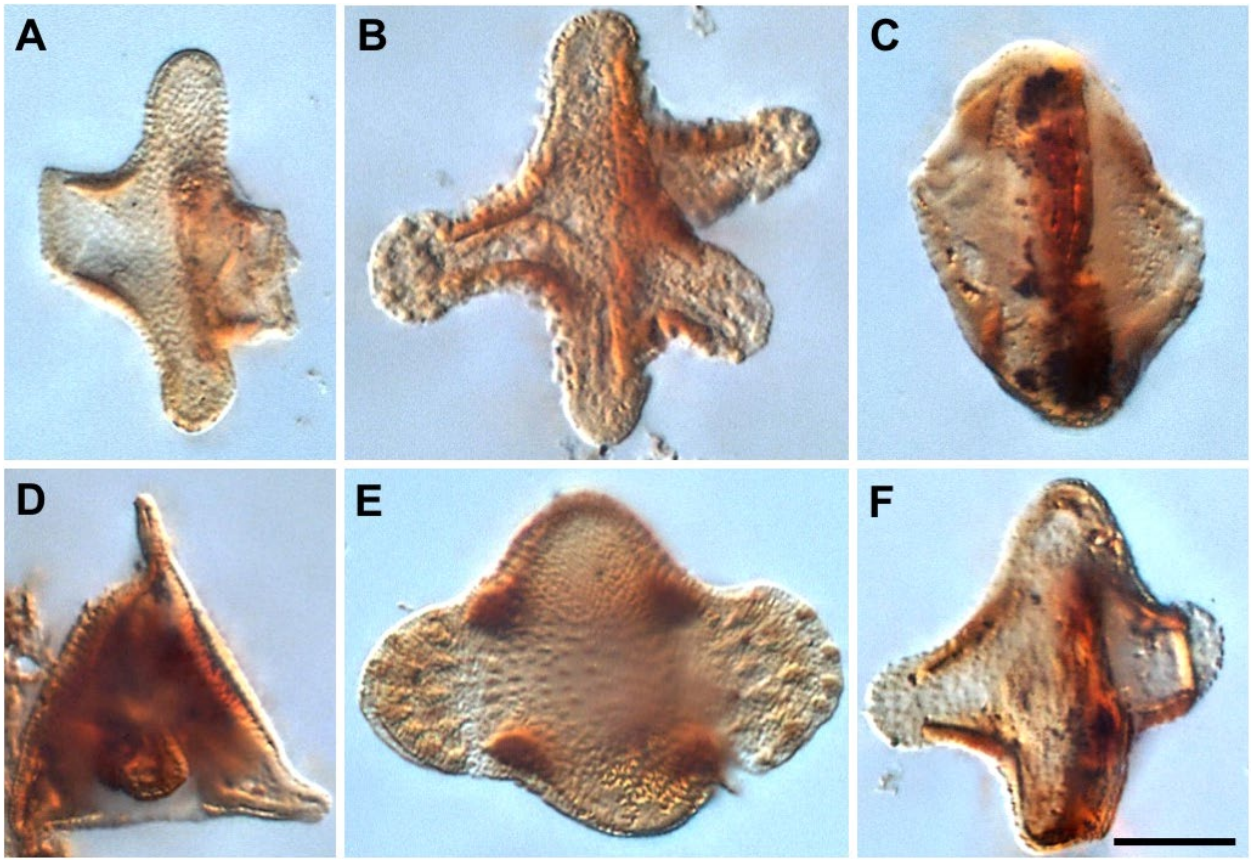

Figure 4. Triprojectate pollen obtained from the Hakobuchi Formation, observed under the Differential Interference Contrast Microscope; slide number, and position of pollen using an England Finder, are indicated in brackets. **A,** *Triprojectus blandus* (equatorial view, J25Db, M67/2); **B,** *Triprojectus elegans* (equatorial view, J24Db, O70/1); **C,** *Triprojectus granatus* (equatorial view, J25Db, X63); **D,** *Triprojectus hakobuchiensis* (polar view, J24Db, D54/2); **E,** *Triprojectus normalis* (equatorial view, J25Db, S68/4); **F,** *Triprojectus turbitus* (equatorial view, J25Db, G33). Scale bar, 10 μm.

T. hakobuchiensis (Sato) Braman, 2013 (Figures 4D, 5I), *T. miser* (Takahashi) Braman, 2013 (Figure 5D), *T. normalis* (Takahashi and Shimono) Braman, 2013 (Figures 4E, 5B), and *T. turbitus* (Tschudy and Leopold) Braman, 2013 (Figure 4F). Genus *Parviprojectus* is represented by *P. reticulatus* Mtchedlishvili, 1961 *in* Samoilovitch and Mtchedlishvili (1961) (Figure 3D, E). *Pseudoaquilapollenites* is represented by the three species *Ps. melior* (Takahashi and Shimono) Braman, 2013 (Figures 3B, 5G), *Ps. melioratus* (Takahashi) Braman, 2013 (Figure 3C) and *Ps. mirus* (Takahashi) Braman, 2013 (Figure 5H). *Integricorpus kokufuense* (Figures 3A, 5A), *Orbiculapollis globosus* (Chlonova) Chlonova, 1961 (Figure 3F, G) and *Reticorpus delicatus* (Stanley) Braman, 2013 (Figures 3H, 5F) are also present.

Systematic descriptions

Genus ***Integricorpus*** Mtchedlishvili *in* Samoilovitch and Mtchedlishvili (1961) emend. Braman, 2013

Type species.—*Integricorpus bellum* Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961.

Integricorpus kokufuense (Takahashi and Shimono) Braman, 2001

Figures 3A, 5A

Occurrence.—J2, J12, J25D (few; six specimens).

Description.—Isopolar pollen grain with three equatorially situated projections, and one polar projection on each apocolpium. Pole broad with rounded apex. Equatorial projections triangular in equatorial view. Three long narrow meridional colpi across equatorial projections, reaching the polar regions. Exine fissure surrounding equatorially central body and projections in their middle part. Ornamentation of central body reticulate, the reticulum becoming finer and striate along the equatorial exine

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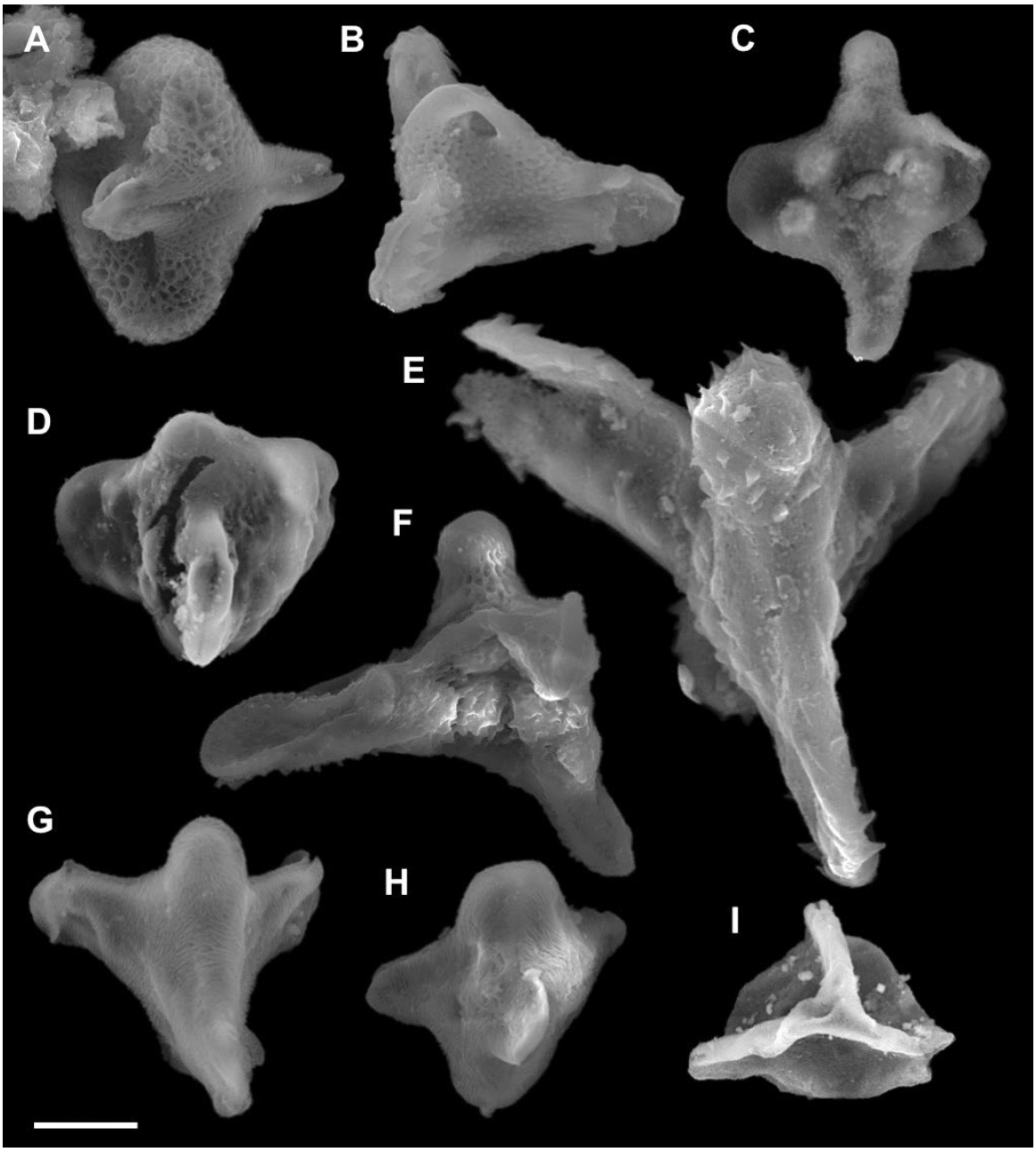

Figure 5. Triprojectate pollen obtained from jacket J25D of the Hakobuchi Formation, observed under the Scanning Electron Microscope. **A,** *Integricorpus kokufuense*; **B,** *Triprojectus normalis*; **C,** *Triprojectus blandus*; **D,** *Triprojectus miser*; **E,** *Triprojectus attenuatus*; **F,** *Reticorpus delicatus*; **G,** *Pseudoaquilapollenites melior*; **H,** *Pseudoaquilapollenites mirus*; **I,** *Triprojectus hakobuchiensis.* Scale bar, 10 μm.

fissure; equatorial projections smooth to finely punctate. Polar axis: 30–34 μm; equatorial axis: 25–33 μm. Exine: 0.5–1 μm.

Distribution.—*Integricorpus kokufuense* is only reported from the Miyadani-gawa Formation of Central Japan (Takahashi and Shimono, 1982).

Genus ***Orbiculapollis*** Chlonova, 1961

Type species.—*Orbiculapollis globosus* (Chlonova) Chlonova, 1961.

Orbiculapollis globosus (Chlonova) Chlonova, 1961

Figure 3F, G

Occurrence.—J2 (rare), J12 (few) (seven specimens).

Description.—Isopolar pollen grain with three equa-

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torially situated projections. In polar view, polar body subrounded, with equatorial projections very short of a triangular shape. In equatorial view, apical projections rounded with their base extending half of the length of the grain. Polar axis: 18–20 μm; equatorial axis: 21–24 μm. Exine thin, psilate, 1 μm.

Distribution.—This species is reported worldwide from the late Campanian to Eocene (Braman, 2013). It ranges from the Maastrichtian to Paleocene in Japan, and is reported from the Hakobuchi Formation (Takahashi, 1964 as "*Trivestibulopollenites* sp."; Takahashi, 1970), the Hamanaka, Oborogawa, Akkeshi formations (Takahashi and Ueda, 1990; Takahashi, 1991a), the Tokotan Formation (Takahashi, 1991b), and the Katsuhira Formation (Takahashi and Yamanoi, 1992) of Hokkaido. It is also reported from the Omichidani Formation of Central Japan (Takahashi, 1991d).

Genus ***Parviprojectus*** Mtchedlishvili *in* Samoilovitch and Mtchedlishvili emend Braman, 2013

Type species.—*Parviprojectus reticulatus* Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961.

Parviprojectus reticulatus Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961

Figure 3D, E

Occurrence.—J2, J25D (few; five specimens).

Description.—Isopolar pollen grain with three equatorially situated projections, and one polar projection on each apocolpium. Pole broad with rounded to conical apex. Equatorial projections triangular in equatorial view. Three long narrow meridional colpi across equatorial projections, reaching the polar regions. Ornamentation of central body reticulate, in some specimens striate in polar regions; equatorial projections smooth to finely punctate. Exine thickening between the poles and the equatorial projections; exine thinner at the extremity of equatorial projections. Polar axis: 28–47 μm; equatorial axis: 27–35 μm. Exine: 0.5 μm.

Distribution.—This species is reported worldwide from the late Campanian to late Eocene (Braman, 2013), and has been reported in Japan from the Campanian to Maastrichtian of the Hakobuchi Formation (Miki, 1977). It is also reported from the Miyadani-gawa Formation (Takahashi and Shimono, 1982).

Genus ***Pseudoaquilapollenites*** Liu, 1983

Type species.—*Pseudoaquilapollenites striatus* Liu, 1983.

Pseudoaquilapollenites melior (Takahashi and Shimono) Braman, 2013

Figures 3B, 5G

Occurrence.—J12 (rare), J25D (few), J29D (rare) (four specimens).

Description.—Subisopolar pollen grain with three equatorially situated projections, and one polar projection on each apocolpium. Pole with conical apex. Equatorial projections broad rounded. Colpi extending full length of equatorial projections and for a short distance on polar projections. Ornamentation of central body and equatorial projections finely striate; striae branched arranged polewards. Polar axis: 29–33 μm; equatorial axis: 27–32 μm. Exine: 0.5–1 μm.

Distribution.—*Pseudoaquilapollenites melior* is only known from Japan, reported from the middle Maastrichtian upper Akkeshi Formation at Ochiishi Bay (Takahashi, 1991a) and the Paleocene (possibly Danian; Naruse *et al.*, 2000) Tokotan Formation (Takahashi and Ueda, 1990). In the Akkeshi Formation, *Ps. melior* is obtained possibly from the Danian because the first appearance of this species well above the stratigraphic ranges of "lower Maastrichtian" ammonoid *Gaudryceras hamanakense* and *Pachydiscus flexuosus*, and inoceramid *Sphenoceramus hetonaianus* (Matsumoto *et al.*, 1979; Matsumoto and Yoshida, 1979; Naruse *et al.*, 2000). It is also reported from the Miyadani-gawa (Takahashi and Shimono, 1982) and Omichidani (Takahashi, 1991d) formations of Central Japan.

Pseudoaquilapollenites melioratus (Takahashi) Braman, 2013

Figure 3C

Occurrence.—J25D (rare; one specimen).

Description.—Isopolar pollen grain with three equatorially situated projections, and one polar projection on each apocolpium. Pole with conical apex. Equatorial projections broad rounded. Exine between the poles and the equatorial projections thickened. Ornamentation of central body and equatorial projections finely striate; striae branched arranged polewards. Polar axis: 20 μm; equatorial axis: 23 μm. Exine: 0.5 μm.

Distribution.—*Pseudoaquilapollenites melioratus* is only reported from Asia (Zhou, 1986). In Japan, it is known from the Maastrichtian Akkeshi Formation (Takahashi and Ueda, 1990; Takahashi, 1991a) and the Danian of the Katsuhira Formation of Hokkaido (Takahashi and Yamanoi, 1992). It is also reported from the Miyadani-gawa Formation of Central Japan (Takahashi and Shimono, 1982).

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Pseudoaquilapollenites mirus (Takahashi) Braman, 2013

Figure 5H

Occurrence.—J25D (rare; two specimens).

Description.—Isopolar pollen grain with three equatorially situated projections, and one polar projection on each apocolpium. Central body cylindrical with rounded polar apex. Equatorial projections short with a broad base and rounded apex, triangular in equatorial view. Colpi extending full length of equatorial projections and for a short distance on polar projections. Ornamentation of central body and equatorial projections finely striate; striae branched arranged polewards. Polar axis: 25–28 μm; equatorial axis: 25–26 μm. Exine: 0.5 μm.

Distribution.—Pseudoaquilapollenites mirus is only known from Japan, reported from the Maastrichtian to Danian of the Katsuhira Formation of Hokkaido (Takahashi and Yamanoi, 1992). It is also reported from the Miyadani-gawa Formation of Central Japan (Takahashi and Shimono, 1982).

Genus ***Reticorpus*** (Krutzsch) Braman, 2013

Type species.—Reticorpus delicatus (Stanley) Braman, 2013.

Reticorpus delicatus (Stanley) Braman, 2013

Figures 3H, 5F

Occurrence.—J2 (common), J12 (few), J25D (few), J27-10 (few), J29D (rare) (26 specimens).

Description.—Anisopolar pollen grain with three equatorially situated projections, and one polar projection on each apocolpium. In equatorial view, equatorial projections and major polar projection of approximately equal size (around 18 μm in length and 12 μm in width), with rounded apex. Equatorial projections slightly inclined toward minor polar projection. Minor polar projection short, protruding very slightly. Exine between the poles and the equatorial projections thickened. Ornamentation of polar projections reticulate; on the major polar projection, reticulate finer toward the apex until becoming psilate on the apex. Ornamentation of equatorial projections scabrate; exine thinner at the apex of equatorial projections. Polar axis: 22–30 μm; equatorial axis: 35–43 μm. Exine: 0.5 μm.

Distribution.—This species is reported worldwide in the Maastrichtian (Braman, 2013), known in Japan from the Omichidani Formation (Takahashi, 1991d) and the Asuwa Formation (Sazawa *et al.*, 2020).

Genus ***Triprojectus*** Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961

Type species.—Triprojectus dispositus Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961.

Triprojectus attenuatus (Funkhouser) Braman, 2013

Figures 3I, 5E

Occurrence.—J2 (common), J12 (few), J24D (few), J25D (common), J26-4 (few), J27-10 (few), J29D (few) (36 specimens).

Description.—Isopolar pollen grain with three equatorially situated projections, and one polar projection on each apocolpium. Polar projections short with apex rounded. Equatorial projections broad, wider and longer than the polar projections; exine thinner at the apex of equatorial projections. Exine between the poles and the equatorial projections thickened (width: 2–4 μm). Surface punctate, with punctuations of a regular size (around 1 μm in diameter) uniformly separated. Spinae (size up to 4 μm long and 3 μm wide) present on apices of polar and equatorial projections, and in a band along the equatorial axis widening in the central part of the grain; spinae of the equatorial projections oriented towards the polar axis. Polar axis: 33–55 μm; equatorial axis: 45–75 μm. Exine: 1–1.5 μm.

Distribution.—This species is reported worldwide from the Campanian to Paleocene (Braman, 2013), and has been reported in Japan from the Campanian to Maastrichtian of the Hakobuchi Formation (Takahashi, 1964, 1970; Miki, 1977) and the Paleocene Kiritappu Formation of Hokkaido (Takahashi, 1991c). It is also reported from the Omichidani (Takahashi, 1991d) and Asuwa (Sazawa *et al.*, 2020) formations of Central Japan.

Triprojectus blandus Braman, 2013

Figures 4A, 5C

Occurrence.—J2, J25D (rare; two specimens).

Description.—Isopolar pollen grain with three equatorially situated projections, and one polar projection on each apocolpium. Polar projections cylindrical with sides straight to slightly concave and apex rounded. Equatorial projections short, broad at the base, with rounded to truncated apex. Exine thickened extending from a short distance along polar projections to the 2/3 length of equatorial projections (width: 1 μm). Ornamentation granulate on equatorial projections and equatorial portion of polar body; polar projections reticulate, with psilate apex. Polar axis: 32–39 μm; equatorial axis: 23–42 μm. Exine: 0.5 μm.

Distribution.—Triprojectus blandus is reported only

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from the late Campanian of the Kanguk Formation in Ellef Ringnes Island, Canadian Arctic Islands (Braman, 2013), although its exact distribution is not described. This study represents the first report from Japan.

Triprojectus elegans (Zhao) Braman, 2013

Figure 4B

Occurrence.—J2 (rare), J24D (rare), J25D (few) (four specimens).

Description.—Isopolar pollen grain with three equatorially situated projections, and one polar projection on each apocolpium. Equatorial view cross-shaped. Exine between the poles and the equatorial projections thickened (width: 1 μm). Equatorial and polar projections of approximately equal size (around 14 μm in length and 9 μm in width). Polar body cylindrical with rounded apices. Equatorial projections straight to slightly concave-sided. Ornamentation granulate to spinate; exine thinner at the apex of equatorial projections. Polar axis: 33–43 μm; equatorial axis: 29–39 μm. Exine: 0.5–1 μm.

Distribution.—Triprojectus elegans is only reported from the Maastrichtian of Far East Russia (Bugdaeva, 2001) and the Mingshui Formation of the Songliao Basin, North East China (Zhao, 1987; Gao *et al.*, 1999; Song *et al.*, 1999), but detailed stratigraphic position is not described. The Mingshui Formation is assigned to the Maastrichtian by magnetostratigraphic and radiometric dating (Scott *et al.*, 2012; Wan *et al.*, 2013). This study represents its first report from Japan.

Triprojectus granatus (Zhou) Braman, 2013

Figure 4C

Occurrence.—J2 (few), J25D (rare), J27-10 (rare) (four specimens).

Description.—Isopolar pollen grain with three equatorially situated projections, and one polar projection on each apocolpium. Equatorial view oblate to diamond-shaped. Exine between the poles and the equatorial projections thickened (width: 2 μm), straight to slightly concave/convex. Polar projections rounded. Equatorial projections short; colpi extending full length of equatorial projections and for a short distance on polar projections. Ornamentation of central body and equatorial projections densely granulate (grana 0.5–1 μm in diameter). Polar axis: 26–33 μm; equatorial axis: 25–27 μm. Exine: 1–2 μm.

Distribution.—Triprojectus granatus is only reported from the Maastrichtian of Jiangsu, China (Zhou *et al.*, 2009). This study represents its first report from Japan.

Triprojectus hakobuchiensis (Sato) Braman, 2013

Figures 4D, 5I

Occurrence.—J2 (few), J24D (few), J25D (common), J27-10 (few) (20 specimens).

Description.—Isopolar pollen grain with three equatorially situated projections, and one polar projection on each apocolpium. In equatorial view, polar projections conical with rounded apex; equatorial projections with straight sides and apex rounded. In polar view, triangular-shaped with straight to slightly convex sides, and relatively long and narrow extremities. Short narrow meridional colpi across the apex of equatorial projections. Exine between the poles and the equatorial projections thickened, then exine thinner from the middle to extremities of equatorial projections. Ornamentation finely reticulate, slightly granulate around the apex of equatorial projections. Polar axis: 24–35 μm; equatorial axis: 29–39 μm. Exine: 0.5–1 μm.

Distribution.—Triprojectus hakobuchiensis is only reported from the Campanian Omagari Formation and the Campanian-Maastrichtian Hakobuchi Formation (Sato, 1961; Takahashi, 1967; Miki, 1977), and the Paleocene Tokotan Formation (Takahashi, 1991b) of Hokkaido.

Triprojectus miser (Takahashi) Braman, 2013

Figure 5D

Occurrence.—J25D (rare; one specimen).

Description.—Small isopolar pollen grain with three equatorially situated projections, and one polar projection on each apocolpium. Polar projections poorly developped, with rounded to tapered apex. Equatorial projections well-developped, with broad base and rounded apex. Colpi short narrow across the apex of equatorial projections. Ornamentation smooth to finely punctate; apex of polar projections smooth. Polar axis: 27 μm; equatorial axis: 29 μm. Exine: 1–1.5 μm.

Distribution.—Triprojectus miser is only reported from the Maastrichtian Akkeshi (Takahashi, 1991a) and Danian of the Katsuhira (Takahashi and Yamanoi, 1992) formations of Hokkaido. It is also reported from the Miyadani-gawa (Takahashi and Shimono, 1982) and Omichidani (Takahashi, 1991d) formations of Central Japan.

Triprojectus normalis (Takahashi and Shimono) Braman, 2013

Figures 4E, 5B

Occurrence.—J2 (abundant), J12 (few), J24D (few), J25D (common), J26-4 (rare), J27-10 (common), J29D (few) (56 specimens).

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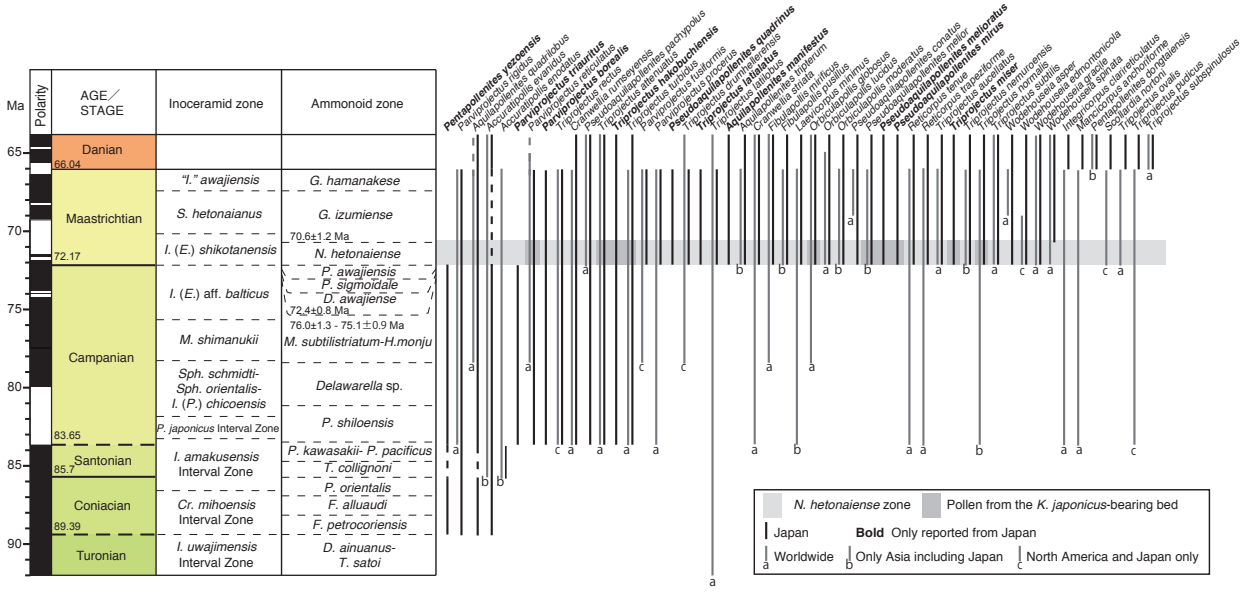

Figure 6. Stratigraphic distribution of triprojectate and oculate pollen species of Japan. Revised from Sato (1961), Takahashi (1964, 1965, 1970, 1980, 1991a, b, c, d), Shimada (1967), Miki (1972, 1977), Tanai *et al.* (1978), Takahashi and Shimono (1982), Takahashi and Sugiyama (1990), Takahashi and Ueda (1990), Takahashi and Yamanoi (1992), Tanaka and Hirano (2008), Nichols *et al.* (2010), Sazawa *et al.* (2020). Species only reported from Japan are written in bold. Inoceramid and ammonoid zones are mainly based on Toshimitsu *et al.* (1995). Turonian to lower Campanian inoceramid biozones are based on Hayakawa and Hirano (2013). U–Pb ages are from Shigeta *et al.* (2017a, b).

Description.—Isopolar pollen grain with three equatorially situated projections, and one polar projection on each apocolpium. Polar projections poorly developed, with rounded apex. Equatorial projections broad, short. Small thickened exine areas at the corner between the polar and equatorial projections (width: 2.5 µm). Colpi short narrow across the apex of equatorial projections. Ornamentation punctate to granulate; apex of polar projections punctate to psilate; on equatorial projections, prominent spinae oriented towards the polar axis, becoming larger towards apices (maximum length: 3.5 µm; width: 2.5 µm). Polar axis: 21–35 µm; equatorial axis: 24–42 µm. Exine: 1–1.5 µm.

Distribution.—This species is reported from the Campanian to Maastrichtian of Far East Russia (e.g. Markevich *et al.*, 1994) and the Kuril Islands (Markevich *et al.*, 2012), Helongjiang, China (Markevich *et al.*, 2011), and Japan, from the Maastrichtian Hamanaka, Oborogawa and Akkeshi formations (Takahashi and Ueda, 1990; Takahashi, 1991a), and Danian of the Katsuhira Formation (Takahashi and Yamanoi, 1992). It is also reported from the Miyadani-gawa (Takahashi and Shimono, 1982) and Omichidani (Takahashi, 1991d) formations of Central Japan.

Triprojectus turbitus (Tschudy and Leopold) Braman, 2013

Figure 4F

Occurrence.—J12 (rare), J25D (few), J27-10 (few) (five specimens).

Description.—Isopolar pollen grain with three equatorially situated projections, and one polar projection on each apocolpium. Equatorial view cross-shaped. Equatorial and polar projections of approximately equal size (length: 14–15 µm; width: 12 µm). Polar projections conical with apex rounded. Exine thickened extending from a short distance along polar projections to the 2/3 length of equatorial projections (width: 1.5–2 µm). Ornamentation granulate to spinate; spinae small on polar body, larger and oriented towards the polar axis at the apex of equatorial projections; apex of polar projections granulate to psilate. Exine thinner at the apex of equatorial projections. Polar axis: 30–33 µm; equatorial axis: 30–35 µm. Exine: 0.5–1 µm.

Distribution.—Triprojectus turbitus is mainly reported from the Campanian to Maastrichtian of North America (e.g. Tschudy and Leopold, 1971; Pearson *et al.*, 2001) and Canada (e.g. Evans *et al.*, 2012; Srivastava and Braman, 2013), and has been reported in Asia only from Central East Russia (Hofmann and Zetter, 2007; Hofmann *et al.*, 2008) and Japan, from the Danian of the

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Katsuhira Formation (Takahashi and Yamanoi, 1992) of Hokkaido. It is also reported from the Omichidani Formation of Central Japan (Takahashi, 1991d). *Triprojectus* cf. *turbitus* occurs in the Campanian of the Hakobuchi Formation (Miki, 1977).

Discussion

Appearance and diversification of triprojectate and oculate pollen in Japan.—The oldest triprojectate report in Japan is represented by *Cranwellia* sp. from the Turonian Tenkaritoge Formation of the Yezo Group (Tanaka and Hirano, 2008). Triprojectate pollen slightly increases during the Coniacian to Santonian, with the endemic *Pentapollenites yezoensis* Takahashi, 1964 reported from the late Coniacian Kasamatsu Formation of the Futaba Group (Takahashi, 1964), and *Accuratipollis evanidus* Chlonova, 1961, *Aquilapollenites quadrilobus* Rouse emend. Srivastava and Rouse, 1970, and *Parviprojectus rigidus* (Tschudy and Leopold) Braman, 2013 reported from the Coniacian Nishichirashinai Formation of the Yezo Group (Miki, 1977; Tanaka and Hirano, 2008). Only *Accuratipollis enodatus* Chlonova, 1961 newly appears from the Santonian and characterizes it; it is also reported from the Uge Member of the Taneichi Formation (Takahashi and Sugiyama, 1990) (Figure 6).

All above species, excepting *Accuratipollis enodatus*, are still present in the Campanian, further accompanied by *Cranwellia rumseyensis* Srivastava, 1966, *Parviprojectus reticulatus*, *Pseudoaquilapollenites pachypolus* (Martin) Braman, 2013, *Triprojectus attenuatus*, *T. rectus* (Tschudy) Braman, 2013, *T. turbidus* (Tschudy and Leopold) Braman, 2013, and the Japanese endemic species *Parviprojectus borealis*, *P. triauritus* (Takahashi) Braman, 2013, and *Triprojectus hakobuchiensis* in the Omagari, Osoushinai and Hakobuchi formations (Miki, 1977; Tanaka and Hirano, 2008).

Triprojectate and oculate groups drastically increase in diversity and abundance during the Maastrichtian, with 30 new species, while *Pentapollenites yezoensis* and *Parviprojectus triauritus* disappear. Triprojectate genera *Bratzevaea*, *Fibulapollis*, *Integricorpus*, *Laevicorpus*, *Orbiculapollis*, *Reticorpus*, and oculate genus *Wodehouseia* appear during the Maastrichtian (Figure 6).

Ten of the 41 triprojectate and oculate species reported from the Maastrichtian of Japan disappear during this period, while only seven new triprojectate species are reported from the Paleocene, including the new genera *Scollardia* and *Mancicorpus* respectively in the Tokotan (Takahashi and Ueda, 1990; Takahashi, 1991a) and Katsuhira (Takahashi and Yamanoi, 1992) formations.

In the Turonian to Danian distribution interval of triprojectate and oculate pollen in Japan, age diagnostic species for within one period appear to be few until the Campanian: none for the Turonian and Coniacian, *Accuratipollis enodatus* for the Santonian, *P. triauritus* for the Campanian.

On the other hand, six species are distributed in the Maastrichtian only, and seven species characterize the Danian (Figure 6).

Correlation of distributions around the Circum Pacific region.—During the Late Cretaceous, an epeiric sea separated North America into a Cordillera and the Western Interior, and it has been demonstrated that the Beringian isthmus, which connected Alaska and northeast Siberia since the mid-Cretaceous, permitted the geographic expansion of some floristic components, such as the triprojectate and oculate pollen-producing plants (Hofmann and Zetter, 2007). A provincialism and difference in the distribution of species may however have possibly occurred between the eastern and western sides of the Pacific region. Late Cretaceous pollen species reported from Japan are classified into three types in terms of their distributions (Figure 6): i.e., 1) worldwide distribution (Figure 6: a), 2) Asian distribution (Figure 6: b), 3) disjunct distribution between Japan and North America (Canada and United States) (Figure 6: c). For species only distributed in Asia, it can be noted a quite similar stratigraphic distribution between Japan and the continent. However, species only distributed in the United States and Canada outside Japan generally appear earlier in the United States/Canada (Figure 6). Provincialism of these plant groups is consistent with a westward expansion of floras via the Beringian isthmus in the Circum Pacific region during the Late Cretaceous (Graham, 2018). Similar westward dispersal is also known for some plant-eating animals, such as hadrosaurs, including *K. japonicus* and its relatives in Asia (Kobayashi *et al.*, 2019).

Wodehouseia spinata, considered as a stratigraphic marker for the late Maastrichtian (Nichols and Johnson, 2008), appears in Japan from the Maastrichtian in the Hakobuchi Formation of the Yubari area (Miki, 1977), which is slightly younger than the *K. japonicus*-bearing bed of the Hobetsu area (Kobayashi *et al.*, 2019), and in the Katsuhira Formation (Takahashi and Yamanoi, 1992). First occurrences (FOs) of *W. spinata* was *ca.* 69.2–68.4 Ma within Chron 31n in the Edmonton Group (Srivastava and Braman, 2013), and *ca.* 70.5 Ma in the orbitally-tuned Mingshui Formation of China (Wu *et al.*, 2014; Yoshino *et al.*, 2017), i.e., *ca.* 1 Myr earlier than in Canada, maybe due to uncertainty of pollen fossil records and/or dispersal of *W. spinata* from Asia to Canada. In Canada, FO of *W. spinata* is only a single specimen found within the Carbon-Thompson coal interval in the Whitemud Formation, to the southeast corner of Saskatchewan (Binda *et al.*, 1991). This species becomes abundant

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ca. 67 Ma in the Scollard Formation, upper part of the Edmonton Group (e.g. Srivastava and Braman, 2013). Considering the paleobiogeographic distribution, the appearance of *W. spinata* in Japan might be close to that in China.

We can guess that further successive palynological studies in other marine sections of the Yezo Group well dated from radiometric ages, magnetostratigraphy and index fossils, such as ammonoids and inoceramids, would provide additional age constraints for palynostratigraphy and plant biogeography, based on accurate correlations. In particular, because a palynological turnover is evident in East Asia across the Campanian–Maastrichtian cooling event, further high-resolution chronostratigraphic work is necessary to understand the botanical response at this period.

Comparison of our new data with previous ones on the Hakobuchi Formation.—Seventeen species of triprojectate and oculate pollen were previously reported from the Hakobuchi Formation (Sato, 1961; Takahashi, 1964, 1965, 1967, 1970; Shimada, 1967; Miki, 1977). Among the 15 species of triprojectate pollen described in this study, *Orbiculapollis globosus* (Takahashi, 1964), *Parviprojectus reticulatus* (Miki, 1977), *Triprojectus attenuatus* (Takahashi, 1964, 1970; Miki, 1977), *T. hakobuchiensis* (Sato, 1961; Takahashi, 1967; Miki, 1977) and *T.* cf. *turbitus* (Miki, 1977) were previously reported from the Hakobuchi Formation. They were noted as rare or few in the formation, excepted *T. hakobuchiensis* reported as common, in accordance with our results; we however also observed *T. attenuatus* as common in some samples. *Triprojectus normalis* is the most represented species in our assemblages and the only one that could be noted as abundant (more than 10% of the total assemblage), while it was not reported from the Hakobuchi Formation in previous studies.

Pseudoaquilapollenites melior, Ps. melioratus, Ps. mirus, Triprojectus miser and *T. normalis* are reported from the Nemuro Group (Takahashi and Ueda, 1990; Takahashi, 1991a) and/or the Katsuhira Formation (Takahashi and Yamanoi, 1992) of Hokkaido. *Integricorpus kokufuense* and *Reticorpus delicatus* were previously reported from Central Japan (Takahashi and Shimono, 1982; Takahashi, 1991d; Sazawa *et al.*, 2020) but are firstly found in Hokkaido, while *Triprojectus blandus, T. elegans*, and *T. granatus* are firstly reported from Japan. All those species, excepting *T. blandus*, were only reported from Japan, China or Russia, indicating a distribution in Asia wider than previously thought. In particular, *T. normalis* and *R. delicatus* are abundant and noted as dominant elements in some samples from the Hakobuchi Formation.

Geographical and stratigraphical distribution of pollen species obtained from the K. japonicus *bone bed.*—Among identified pollen species from the *K. japonicus-bearing* bone bed, we found cosmopolitan species (*Orbiculapollis globosus*, *Parviprojectus reticulatus*, *Reticorpus delicatus*, *Triprojectus attenuatus*) along with species mainly represented in Canada and North America (*Triprojectus turbitus*). These species only co-occur in the Maastrichtian based on reliable indices such as radiometric dating, magnetostratigraphy, and ammonite biostratigraphy (e.g. Eberth and Deino, 2005; Cobban *et al.*, 2006). All other species are distributed mainly or exclusively in Asia (Figure 6). *Triprojectus blandus, T. elegans* and *T. granatus* have never been found in Japanese strata until this study, while *Integricorpus kokufuense*, *Pseudoaquilapollenites melior*, *Ps. melioratus*, *Ps. mirus*, *Triprojectus hakobuchiensis* and *T. miser* seem to be endemic to Japan. Among taxa with an Asian distribution and stratigraphic significance, only *T. hakobuchiensis* is reported from the Campanian and Maastrichtian, while *Ps. melior*, *Ps. melioratus*, *Ps. mirus*, *T. elegans* and *T. granatus* have their range restricted from the Maastrichtian.

Miki (1977) suggested a change in spore and pollen assemblages across the Campanian/Maastrichtian boundary in northern Japan, however, the detailed stratigraphic position and their relation with molluscan biostratigraphy across the Campanian/Maastrichtian is not well constrained and needs to be confirmed. The palynofloral assemblage described from the Hakobuchi Formation in this study does not include species defined by Miki (1977) as definitively Campanian, but only species previously reported from the Campanian–Danian, Maastrichtian, Maastrichtian–Danian, or Danian. In the Hakobuchi Formation, *Parviprojectus reticulatus*, *Triprojectus attenuatus* and *T. hakobuchiensis* were previously reported across the Campanian–Maastrichtian (Sato, 1961; Takahashi, 1964, 1965, 1967; Shimada, 1967; Miki, 1977), and *Orbiculapollis globosus* from the Maastrichtian (Takahashi, 1964). In northern Japan, *T. attenuatus* is reported from the Campanian–Danian; *T. hakobuchiensis* and *P. reticulatus* from the Campanian–Maastrichtian; *Ps. melioratus* from the Maastrichtian; *T. miser*, *T. normalis*, *Ps. melior, Ps. mirus*, and *O. globosus* from the Maastrichtian–Danian; *T. turbitus* from the Danian (Figure 2). The triprojectate pollen assemblage obtained from the hadrosaur *Kamuysaurus japonicus*-bearing bone bed of the Hakobuchi Formation then appears consistent with the early Maastrichtian age previously proposed for the bone-bed by Kobayashi *et al.* (2019) on the basis of co-occurred ammonite *Pachydiscus* (*Neodesmoceras*) *japonicus*.

Conclusion

We revised records of triprojectate and oculate pol-

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len from Japan based on recent taxonomical updates of these groups: 16 genera and 86 species for the triprojectate group, and one genus and five species for the oculate group. Among them, 17 species are endemic to Japan. The record of the triprojectate and oculate groups in Japan extends from the Turonian to Paleocene, being most diversified during the Maastrichtian, and confirms age diagnostic species. Age ranges of Asian-endemic species are almost the same between continental Asia and Japan, while pollen species distributed disjunctly in Japan and North America tend to occur earlier in North America. This tendency implies a westward expansion of floras around the Circum Pacific region via the Beringian isthmus during the Late Cretaceous.

The triprojectate pollen assemblage obtained from the *Kamuysaurus japonicus*-bearing bone bed of the Hakobuchi Formation consists of six cosmopolitan species associated with nine Asian species. Three species reported from North America, as well as two species reported from Japan and China, have their distribution range well calibrated from cyclostratigraphic, magnetostratigraphic and radiometric data, that support an early Maastrichtian age. We can guess that further successive palynological studies in marine successions of Japan will provide additional age constraints, allowing direct correlation between marine and non-marine strata.

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Author contributions

J. L. initiated the study and was primarily responsible for the field survey and palynological analysis. M. B., M. I. and T. N. conducted the field investigation and contributed to the interpretation of the data. All authors contributed to the writing of the paper.

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Appendix 1. Stratigraphic distribution of triprojectate and oculate pollen record from Japanese terrestrial strata of uncertain age. Abbreviations: Camp., Campanian; Fm, Formation.

		Northeast Honshu	Central Honshu		
		early Camp.?	Maastrichtian ?		
		Kuji Group			
		Sawayama Fm	Miyadani-gawa Fm	Omichidani Fm	Asuwa Fm
	Accuratipollis evanidus Chlonova, 1961 (reported as *"Aquilapollenites evanidus"* (not validly published), *"Fibulapollis evanidus"* or *"Kurtzipites evanidus"* (not validly published))	○			
Triprojectate pollen	*Aquilapollenites aequus* Bolkhovitina, 1959				++☆
	Aquilapollenites alienum (Takahashi *in* Takahashi and Shimono, 1982) Braman, 2013 (former *"Hemicorpus alienum"*)		○★		
	Aquilapollenites manifestus (Takahashi and Shimono, 1982) Braman, 2013 (former *"Pentapollenites manifestus"*)		++☆	●☆	
	Aquilapollenites miyajiense (Takahashi and Shimono, 1982) Braman, 2013 (former *"Hemicorpus miyajiense"*)		○☆		
	Aquilapollenites quadrilobus Rouse, 1957 emend. Srivastava and Rouse, 1970		○☆	●☆	○☆
	Aquilapollenites tripterum (Takahashi *in* Takahashi and Shimono, 1982) Braman, 2013 (former *"Hemicorpus tripterum"*)		–☆		
	Bratzevaea amurensis (Bratzeva, 1965) Takahashi *in* Takahashi and Shimono (1982)		–☆	●	
	Bratzevaea striatella Takahashi *in* Takahashi and Shimono (1982)		–☆		
	Cranwellia rumseyensis Srivastava, 1966			●	
	Cranwellia striata (Couper, 1953) Srivastava, 1966		○☆	●	
	Fibulapollis pusillus Takhashi *in* Takahashi and Shimono (1982)		○☆	●☆	
	Integricorpus clarireticulatus Samoilovitch, 1964				
	Integricorpus fragile (Takahashi *in* Takahashi and Shimono, 1982) Braman, 2013 (former *"Pseudointegricorpus fragile"*)		–☆		
	Integricorpus kokufuense (Takahashi and Shimono, 1982) Braman, 2002 (former *"Pseudointegricorpus kokufuense"*)		++☆		
	Integricorpus protrusum (Takahashi and Shimono, 1982) Braman, 2002 (former *"Pseudointegricorpus protrusum"*)		++☆		–☆
	Laevicorpus albertensis (Srivastava, 1968) Braman, 2013 (former *"Mancicorpus albertensis (non albertense)"*)			●	
	Laevicorpus cf. *albertensis in* Takahashi and Shimono (1982) (former "*Mancicorpus* cf. *albertensis (non albertense)*")		–☆		
	Laevicorpus minimus (Chlonova, 1961) Braman, 2013 (former *"Mancicorpus minimus (non minimum)"*)		–		
	Orbiculapollis globosus (Chlonova, 1957) Chlonova, 1961			●	
	Orbiculapollis lucidus Chlonova, 1961 (reported as *"Orbiculapollis minutus"* (junior synoym))		○☆	●	
	Orbiculapollis moderatus Takahashi *in* Takahashi and Shimono, 1982		–☆		
	Orbiculapollis cf. *moderatus in* Takahashi (1991)			●☆	
	Parviprojectus venustus (Srivastava, 1968) Braman, 2013 (former *"Integricorpus* cf. *venustus* (*non venustum*)*"*)			●	
	Pseudoaquilapollenites delectus (Takahashi and Shimono, 1982) Braman, 2013 (former *"Aquilapollenites delectus"*)		–☆	●	
	Pseudoaquilapollenites melior (Takahashi and Shimono, 1982) Braman, 2013 (former *"Aquilapollenites melior"*)		○☆	●☆	
	Pseudoaquilapollenites cf. *melior* in Nichols *et al.* (2010) (reported as "*Aquilapollenites* sp. cf. *A. melior*"			●	
	Pseudoaquilapollenites melioratus (Takahashi *in* Takahashi and Shimono, 1982) Braman, 2013 (former *"Aquilapollenites melioratus"*)		○☆		
	Pseudoaquilapollenites mirus (Takahashi *in* Takahashi and Shimono, 1982) Braman, 2013 (former *"Aquilapollenites mirus"*)		–☆		
	Pseudoaquilapollenites quadrinus (Takahashi, 1964) Braman, 2013 (former *"Aquilapollenites quadrinus")*		–☆		
	Reticorpus collaris (Tschudy and Leopold, 1971) Braman, 2013 (former *"Aquilapollenites collaris"*)			●☆	
	Reticorpus delicatus (Stanley, 1961) Braman, 2013 (former "*Aquilapollenites delicatus*")			●	++☆
	Reticorpus senonicus (Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961) Braman, 2013 (former "*Mancicorpus senonicus*")				–☆
	Reticorpus tenue (Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961) Braman, 2013 (former *"Hemicorpus tenue"*)		++☆	●	
	Reticorpus trapeziforme (Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961) Braman 2013 (former *"Hemicorpus trapeziforme"*)		+☆	●	

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	Retroprojectus pseudosenonicus (Frederiksen, 1991) Braman, 2013 (former "*Mancicorpus pseudosenonicus*")			++☆
	Triprojectus aemulus (Takahashi and Shimono, 1982) Braman, 2013 (former *"Aquilapollenites aemulus"*)	+☆		
	Triprojectus attenuatus (Funkhouser, 1961) Braman, 2013 (former "*Aquilapollenites attenuatus*", also reported as "*Aquilapollenites asper* Mtchedlishvili, 1961" *"Aquilapollenites matsumotoi* Takahashi, 1964" or "*Aquilapollenites parvus* Takahashi, 1970" (junior synonyms))	–☆	●☆	○☆
	Triprojectus aucellatus (Srivastava, 1969) Braman, 2013 (former "*Aquilapollenites aucellatus*", also reported as *"Aquilapollenites pseudoaucellatus* Takahashi and Shimono, 1982" (junior synonym))	++☆		–☆
	Triprojectus augustus (Srivastava, 1969) Braman, 2013 (former "*Aquilapollenites augustus*", also reported as *"Aquilapollenites kasaharae* Takahashi and Shimono, 1982" (junior synonym))	○☆		
	Triprojectus cf. *augustus* in Takahashi (1991) (reported as "*Aquilapollenites* cf. *kasaharae*)		●★	
	Triprojectus hamulatus (Takahashi *in* Takahashi and Shimono, 1982) Braman, 2013 (former *"Fibulapollis hamulatus"*)	–☆		
	Triprojectus latialatus (Takahashi *in* Takahashi and Shimono, 1982) Braman, 2013 (former *"Aquilapollenites latialatus"*)	○☆		
	Triprojectus latilobus (Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961) Braman, 2013 (also reported as "*Aquilapollenites amplus* Stanley, 1961" (junior synonym))		●	
	Triprojectus longissimus (Takahashi and Shimono, 1982) Braman, 2013 (former *"Aquilapollenites longissimus*)	○★		
	Triprojectus miser (Takahashi *in* Takahashi and Shimono, 1982) Braman, 2013 (former *"Pentapollenites miser"*)	○☆	●☆	
	Tripojectus normalis (Takahashi and Shimono, 1982) Braman, 2013 (former *"Pentapollenites normalis"*)	++☆	●	
	Triprojectus proprius (Takahashi and Shimono, 1982) Braman, 2013 (former *"Aquilapollenites proprius"*)	–☆		
	Triprojectus proteus (Simpson, 1961 emend. Srivastava, 1975) Braman, 2013 (reported as *"Aquilapollenites brevialatus* Takahashi and Shimono, 1982" (junior synonym))	–☆	●★	
	Triprojectus songliaoensis (Gao and Zhao, 1976) Braman, 2013 (reported as *"Aquilapollenites doliiformis* Takahashi and Shimono, 1982" (junior synonym))	–☆		
	Triprojectus subtilis (Mtchedlishvili *in* Samoilovitch and Mtchedlishvili, 1961) Braman, 2013 (former *"Aquilapollenites subtilis"*)	++☆	●☆	
	Triprojectus turbidus (Tschudy and Leopold, 1971) Braman, 2013 (former *"Aquilapollenites turbidus"*)		●	
Oculate pollen	*Wodehouseia asper* (Samoilovitch *in* Samoilovitch and Mtchedlishvili, 1961) Wiggins, 1976 (reported as *"Wodehouseia aspera"*)	○☆		
Oculate pollen	*Wodehouseia gracile* (Samoilovitch *in* Samoilovitch and Mtchedlishvili, 1961) Pokrovaskaya, 1966 (reported as *"Wodehouseia gracilis"*)	+☆	●☆	
Oculate pollen	*Wodehouseia spinata* Stanley, 1961		●	○☆
Oculate pollen	*Wodehouseia stanleyi* Srivastava, 1966			–☆
Species in open nomenclature				
Triprojectate pollen	*Aquilapollenites* sp. a *in* Takahashi and Shimono (1982)	–☆		
Triprojectate pollen	*Aquilapollenites* sp. b *in* Takahashi and Shimono (1982)	–☆		
Triprojectate pollen	*Aquilapollenites* sp. *in* Nichols *et al.* (2010)		●☆	
Triprojectate pollen	*Cranwellia* sp. *in* Takahashi (1991d)		●☆	
Triprojectate pollen	? *Fibulapollis* sp. *in* Takahashi (1991d)		●☆	
Triprojectate pollen	*Hemicorpus* sp. *in* Takahashi and Shimono (1982)	–☆		
Triprojectate pollen	? *Hemicorpus* sp. *in* Takahashi and Shimono (1982)	–☆		
Triprojectate pollen	*Integricorpus* sp. *in* Takahashi (1991d)		●☆	
Triprojectate pollen	*Pseudointegricorpus* sp. *in* Takahashi and Shimono (1982)	–☆		
Triprojectate pollen	*Triprojectus* sp. *in* Takahashi and Shimono (1982)	–☆		
Oculate pollen	*Wodehouseia* sp. *in* Nichols *et al*. (2010)		●☆	

– rare (less than 0.5%)
○ few (0.5–3.0%)
\+ common (3.0–10%)
++ abundant (more than 10%)
● Reported without numerical information
☆ grain illustrated
★ grain illustrated but poorly recognizable on the picture

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