THESIS

Paleozoic palynostratigraphy and vegetational changes in the South Kitakami Belt of Northeast Japan

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March 2024

Abstract

The study of Paleozoic (538.8–251.9 Ma; Ma: million years ago) microfloras in Eastern Asia is uncomplete and it only restricted to some definite regions. In Japan, only a very few attempts were done to study its Paleozoic micro- and macrofloras. This is mainly due to the complexity of the Paleozoic geology in Japan and the unresolved problematic origin of its terranes. Palynology is considered as a valuable tool to investigate Paleozoic sediments and rocks, especially in areas which have been subjected to high tectonic activity, making it hard to find and study plant macrofossils. As a result, there is an obvious lack of understanding about the Paleozoic terrestrial floras of Japan. This thesis aims to introduce the first comprehensive paleopalynological study on Paleozoic sediments and rocks from various regions of Japan, corresponding to the period of establishment of the oldest terrestrial ecosystems on Earth. The results are based on the study on four areas in Japan, from which were collected more than one hundred rock samples distributed in different tectonic belts. In particular, I focused on Silurian (443.8–419.2 Ma) to Permian (298.9–251.9 Ma) rocks of the South Kitakami Belt in Northeast Japan, where a variety of fossils are reported, together with unstudied Paleozoic plant materials. Part of the material obtained was unfortunately of high thermal maturity and highly coalfield (black and opaque) because of the highly tectonic activity, making very difficult to study, thus identification was chiefly based on SEM imaging. I will present here my results based on the obtained from best-preserved material, and propose a first outline for Paleozoic palynostratigraphy of Japan.

In the South Kitakami Belt, I obtained tabular remains and sporomorph types from the Silurian Kawauchi Formation, providing the first discovery of terrestrialization in Japan. The Devonian (419.2–358.9 Ma) Nakazato Formation yielded some cryptospores and diverse spores, tabular remains, and fragments of vascular tissues indicating the expansion into the hinterland of herbaceous plants including rhyniophytes, zosterophyllophytes, and lycophytes. The first representatives of pteridosperms and progymnosperms were obtained from the Carboniferous (358.9–298.9 Ma) Hikoroichi Formation. Monilophyte spores and pteridosperm pollen then dominate assemblages from the Permian Kanokura Formation, along with occasional conifer pollen, aligning with microfloras reported from the Cathaysian realm. This dictates that studied formations of the South Kitakami Belt, which were inferred from marine invertebrate fossils, developed near the South China block (Northeast Gondwana) during the Paleozoic.

Aim of the thesis

The current study aims at understanding the status and nature of Paleozoic micro- and macrofloras in Japan, focusing in the three areas, i.e., the South Kitakami Terrane in Northeast Honshu, the Hida-Gaien Terrane in central Honshu, and the Kurosegawa Terrane in Kyushu and western Shikoku, where are reported Paleozoic fossil-bearing sediments. I discuss the past location of Japan during the Paleozoic and propose a reconstruction of its paleovegetation and paleoecosystems.

The general concluding points and remarks of this thesis are as follows:

1. I obtained the oldest plant microremains of Japan from the Silurian sediments of the Kawauchi Formation of the South Kitakami Belt, most probably belonging to algal parent plants.
2. The first reliable terrestrial plant fossils were obtained from the Devonian Nakazato Formation of the South Kitakami Belt, represented by rich assemblages of miospores, associated with abundant plant fragments including masses of conducting cells, tabular remains and cuticles. The palynological assemblage consists of two species of cryptospores and 14 species of trilete spores, suggesting an Early Devonian (Pragian-Emsian) age, confirming it represents the oldest terrestrial flora recorded from Japan. Miospores permit to propose for the first time a reconstruction of a paleovegetation dominated by rhyniophytes and zosterophyllophytes, along with trimerophytes. Furthermore, the composition of the miospore assemblage indicates proximity of the South Kitakami sediments with the South China block during the Early Devonian.
3. Studied samples from the Carboniferous Hikoroichi Formation and Permian Kanokura Formation of the South Kitakami Belt revealed some sporomorphs and probable plant fragments, including pteridosperm and conifer pollen.
4. Samples from the Hida-Gaien Belt of central Honshu were carbonized but moderately well preserved. However they were very poor in both number and diversity.
5. I could not obtain reliable palynomorph from samples from the Kurosegawa Belt in southwest Japan.
6. This first attempt of Paleozoic palynological study on various areas of Japan revealed plant microfossils from two of the three studied areas (i.e., the South Kitakami and

Hida-Gaien belts). Microfossils were mostly highly coalified; however, SEM imaging permitted their identification. These results are very promising for further palynological studies on Paleozoic sediments of Japan.

Contents

General introduction:
Geography, climate and floral evolution during the Paleozoic period

Ecophysiological strategies indicating the early terrestrialization process occurred during the Middle Ordovician (470.0–458.4 Ma; Figure 1), based on evidence from cryptospores, i.e., miospore obligated tetrads, with supposed affinities to the hepatics and mosses, reflecting non-vascular vegetation. The Silurian period (443.8–419.2 Ma; Figure 1) witnessed the early stages for the colonization of land (Melchin *et al.*, 2020). The first trilete spores appear during the early Silurian (Gray, 1985; Strother and Foster, 2021). Then, late Silurian to Early Devonian (419.2–393.3 Ma; Figure 1) is considered to be a key-period for understanding the process of terrestrialization and early diversification of embryophytes, and one of the most exciting periods in land plant history (Richardson, 1996; Fürst-Jansen *et al.*, 2020) (Figure 2). Four major phases in the evolution of land plant have been recognized during the Paleozoic (Figure 1): an Eotracheophytic flora was dominated by basal eutracheophytes and rhyniophytoids from the Silurian to Early Devonian (Lochkovian), followed by an early Eophytic Flora dominated by zosterophylls in the Early Devonian, a transitional late Eophytic Flora dominated by lycopsids and cladoxylopsids from the Middle Devonian (393.3–382.7 Ma; Figure 1) to earliest Carboniferous, and a Palaeophytic Flora dominated by the first seed plants in the Late Devonian (382.7–372.2 Ma; Figure 1) to earliest Carboniferous (Capel *et al.*, 2021).

Plants rapidly adapted to terrestrial conditions, and the Early Devonian in particular witnessed major innovations in plants with the birth of the first terrestrial ecosystems (Kenrick and Crane, 1997; Edwards and Richardson, 2004). The Lochkovian was characterized by an extinction of primitive rhyniophytes towards a proliferation and diversification of ecologically and physiologically better adapted forms of the zosterophylls and lycophytes, with in particular an increase in plant size and complexity of branching (e.g., Lang, 1937; Fanning *et al.*, 1992; Edwards *et al.*, 2014), and a diversification and increased production of spores (e.g., Traverse, 2007; Morris and Edwards, 2014). They will permit the formation of soil and later appearance of the first trees, noted from the late Emsian (Cladoxylopsida) to early Givetian (progymnosperms) in the Spitzbergen, Norway (Schweitzer, 1999), resulting in the rise and expansion of forests from the Middle Devonian, with a worldwide distribution (Gensel, 2021; Capel *et al.,* 2022).

Then, the Carboniferous (coal age) (358.9–298.9 Ma; Figure 1) is marked by cold temperate and humid climatic conditions, leading to a wide development of coal swamps related to lycopods, ferns, pteridosperms, *Cordaites*, and sphenopsids (Phillips *et al*., 1974; Césari and Gutiérrez, 2000). This period is particularly characterized by the appearance of the tree habit of lycopsids, bearing secondary xylem and phloem, and periderm as a major support tissue; lycopsids also developed differentiated gas-diffusion system associated with appendages and lateral branches as well as leaf cushions, and megaspore-sporangial dispersal units (Phillips and DiMichele, 1992). Lycopsids plants might have reached a peak during the Carboniferous because their habit changed from herbaceous to arborescent (Thomas, 1978; Balme, 1995). Then, conifer *Cordaites* became dominant by the late Pennsylvanian (Late Carboniferous) (Jasper *et al*., 2010).

During the Permian (298.9–251.9 Ma; Figure 1), the supercontinent Pangea completed its assembly and moved northwards (Figure 3). Climate became warmer with seasonally dry to probable xeric conditions in tropical Pangaea during early Permian (van Hoof *et al*., 2013; Agnihotri *et al*., 2017; Wagner *et al*., 2019). The Permian period is marked by a distinctive level of floral differentiation, caused by the separation of the Laurasia, Gondwana and other continents (Utting and Piasecki, 1995). An "Angara Flora" containing herbaceous sphenophytes and conifer *Cordaites* is distributed from the Urals to Siberia and the Pacific; an "Euramerica flora" dominated by lycopsids extends from the U.S.A and eastern Canada to western Europe; a "Cathaysia flora" characterized by arborescent lycopods, sphenophytes, and *Gigantopteris* is recognized in China, Korea, Japan, Vietnam, Laos, Thailand, Indonesia, Malaysia, and northern Saudi Arabia; a "Gondwana flora", dominated by *Glossopteris*, is reported from South America, Africa, Madagascar, southern Tibet, New Guinea, Australia, and Antarctica (Ziegler, 1990; Utting and Piasecki, 1995; Bernardi *et al.*, 2017) (Figure 4). At this period, Asia is considered as a composite continent formed by accretion of crustal blocks; contemporaneous Japan was supposed to be located near the Equator and then separated from the Asian continent (McElhinny *et al*., 1981) (Figure 3). Permian was marked by a great ice age and ended with the Earth's greatest extinction (Henderson *et al*., 2020).

Mudrock was preserved in alluvium and increased during the Paleozoic, incorporating these land plants (McMahon *et al*., 2023). Despite several previous palynological studies dealt on Paleozoic material worldwide, some regions and periods were more extensively studied than others, and recent works pointed out that there existed a bias of sampling in the palaeobotanical record (Capel *et al*., 2021), as is the case for Japan, and Southeast Asia as recently shown in Vietnam (Legrand *et al.*, 2021).

Focusing on the critical period of the early stages when plants colonized emerged continents, this thesis aims to contribute to fill this gap by studying unexplored areas for palynological studies of Japan. In the following chapters, I propose a reconstruction of the first terrestrial ecosystems which appeared on the lands of Proto Japan. The microfossil assemblages are also compared to those reported from Laurussia, Gondwana, and the South and North China blocks to infer the origin of their parent plants and get new elements to discuss about the location of Proto Japan during the Paleozoic.

Chapter 1: Paleozoic geological and palaeobotanical context of Japan

The oldest shallow marine sediments known in Japan are from the Ordovician (Isozaki, 2011). Proto-Japan was grown from Paleozoic orogenic components to form a mature arc-trench system. It is hypothesized that regional rifting occurred near the Paleo-Tethys along the eastern margin of Eurasia to form present-day Japanese islands (Isozaki, 2023). The pre-Cenozoic rocks of the Japanese islands, i.e. rocks from Paleozoic to Cretaceous ages, were formed by accretionary complex (Ehiro *et al.*, 2016) (Figure 5). Six major periods clearly represent the geologic setting of Japan, i.e. (1) the Cambrian to Middle Devonian, (2) Late Devonian to Carboniferous, (3) Permian to Middle Triassic, (4) Late Triassic to Early Cretaceous, (5) Late Cretaceous to Paleogene, and (6) Neogene to Quaternary (Wakita *et al.*, 2018).

Thus, the geologic setting of Japan for pre-Mesozoic ages is very complex due to the extensive tectonic activities (Wakita *et al.*, 2018) (Figure 3), as we will see in this chapter.

I.1. Formation of Japan

The accretionary history of Japan is uncertain until the Middle Devonian (Wakita *et al.*, 2018), and older paleogeographic configurations of Japan and eastern Asia have been intensively studied, in continuous works (e.g. Isozaki, 1996, 2019; Maruyama *et al.*, 1997; Ehiro and Kanisawa, 1999; Isozaki *et al.*, 2010, 2011; Kasahara *et al.*, 2010; Uno *et al.*, 2011; Cocks and Torsvik, 2013; Wakita, 2013; Wakita *et al.*, 2018; Tanaka *et al.*, 2018), the general view of the position change of Japan during the Paleozoic ages is illustrated in Figure 3.

The geological history of Japan started with the breakup of the Rodinia super continent, at about 750 Ma, and the Paleo-Pacific oceanic plate began to be subducted beneath the continental margin of the South China Block (Wakita, 2013). The previous trails to the understanding of Japan have some conflict and the most accepted scenario was covered by Isozaki *et al.* (2010) and accepted in the paleogeographic work by Cocks and Torsvik (2013) that the Paleozoic rocks of Japan were deposited as accretionary prisms and island arcs of the Cathaysian margin of South China, the complexity of theses accretionary is illustrated in Figure 5. Williams *et al.* (2014) proposed a configuration based on the fossil results that Japan was formed under the marine settings during the Silurian-Devonian ages (Figures 6, 7).

It is hypothesized that the birth of Japan resulted from rifted continental margin of the Yangtze craton (South China) around 750-700 Ma (Maruyama *et al.*, 1997). Japan is thought to have formed along the eastern continental margin of Asia, in remarkable orogenic belts (Taira, 2001). However, origin of Japan is not clear, and other studies suggested that Japanese Islands might have formed as part of the oceanic plate subduction since about 500 Ma, accelerated when the North and South China blocks separated from Gondwana during the Devonian (Wakita, 2019). The first bed rocks of Japan would have formed as terranes near the margin of Gondwana during the Paleozoic. Consequently, all the Paleozoic rocks of Japan would have deposited as accretionary prisms and island arcs off the Cathaysian margin of South China (Cocks and Trovisk, 2013).

The position of Japan during the early Paleozoic ages was reconstructed based on a tectonic setting (Miller, 1970; Uyeda and Kanamori, 1979; Ehiro and Kanisawa, 1999; Isozaki *et al.*, 2010; Yamamoto, 2010; Cocks and Torsvik, 2013; Isozaki, 2019) (Figure 3). The linking between Japan and adjacent Asian mainland was then proposed on the extending process of the Paleozoic belts (Maruyama *et al.*, 1997). Ishikawa *et al.* (2011) proposed a configuration in which the land of Japan was formed as small sills to form an oceanic basin. A marked change occurred when Japan began to be subjected to the subduction of oceanic plates from the paleo-Pacific side of Gondwana (Maruyama *et al.*, 1997). Kasahara *et al.* (2010) proposed that orogenic belts of Japan were born near the South China craton after breakup of the Proterozoic supercontinents Rodinia and Laurentia to represent that Japan was linked to the North and South Chinas before the tectonic separation. Proto-Japan was changed from a passive margin to represent an active Pacific-type margin around 500 Ma and has grown oceanward for *ca.* 500 km with the successive oceanic subduction from the Pacific side (Kasahara *et al.*, 2010).

I.2. Evolution of Japan during the Paleozoic

The Kurosegawa Belt in southwest Japan (Figure 5) is considered as a southern extension of the South Kitakami Belt, forming the South Kitakami – Kurosegawa Arc (Umeda 1996a; Ehiro and Kanisawa, 1999; Ehiro, 2000). Cocks and Torsvik (2013) reconstructed an origin of this island arc within the southern hemisphere, with its drifting to northern tropics by the late Ordovician. Palaeomagnetic data obtained from the Kurosegawa Belt indicate paleolatitudes of 5–15° North during the Silurian and Early Devonian (Shibuya *et al.*, 1983). The Silurian–Devonian coral, brachiopod, gastropod and trilobite faunas reported from the South Kitakami Belt show similarities to those from eastern Australia, South China and Central Asia (Hamada, 1959; Minato and Kato, 1977; Kaneko, 1990; Kato, 1990; Zhou & Campbell, 1990; Tazawa and Chen, 2001; Tazawa, 2002; Hua-Zhang and Cook, 2003; De Jong *et al.*, 2006; Williams *et* *al.*, 2014), which were amalgated in northeastern Gondwana before the opening of the Palaeo-Tethys ocean (Duan *et al.*, 2012). Ages of detrital zircons from the South Kitakami Belt further suggest close relationships with the South China Block until the Middle Devonian (Wakita *et al.*, 2018). The South Kitakami Belt would have formed and developed along the continental margin of northeastern Gondwana (Figure 3), then in an island arc setting nearby the north of the South China block after its break-up from Gondwana and opening of the Palaeo-Tethys Ocean from the Late Devonian (Kawamura and Kawamura, 1989; Ehiro and Kanisawa, 1999; Duan *et al.*, 2012; Cocks and Torsvik 2013; Ozawa *et al.*, 2015). Post-Devonian palaeobiogeographic, faunal and floral data still suggest a location of the South Kitakami Belt at or near the eastern margin of South China until the Early Cretaceous (Kimura, 1987, 2000; Ehiro and Kanisawa, 1999; Ehiro, 2001).

The continental crust of the Northern part of Japan was proposed to have been subjected to highly thermal tectonism especially for the rocks from the Ordovician to the Devonian ages (Ozawa *et al.*, 2015).

Recently, Suzuki *et al.* (2023) studied detrital zircon U–Pb of the Devonian–Carboniferous strata in the Hida Gaien belt, Southwest Japan, and suggested that these sediments were supplied from NE Gondwana along the western margin of the Paleo-Pacific Ocean.

I.3. Previous Paleozoic palaeobotanical studies in Japan

In Japan, Silurian to Devonian fossil-bearing sediments is mainly distributed in three areas (Figures 5–7): the Hikoroichi and Arisu areas of South Kitakami Terrane in Northeast Japan, the Fukuji area of the Hida Gaien Terrane in central Japan, and the Yokokurayama area of Shikoku and Gionyama area of the Kurosegawa Terrane of Kyushu in Southwest Japan (Kato *et al.*, 1980; Williams *et al.*, 2014; Isozaki, 2019). They yield a rich fauna dominated by corals but also including sponges, stromatoporoids, echinoderms, bryozoans, brachiopods, cephalopods, tentaculitids, bivalves, gastropods, trilobites, ostracods, conodonts, dendroid graptolites and radiolarians (e.g., Kato *et al.*, 1980; Williams *et al.*, 2014).

However, there exists only a few reports on terrestrial plant remains from the Paleozoic of Japan, pioneered by the description by Yabe and Endo (1920) of stems of *Calamites* from Yamaguchi Prefecture in Southwest Japan (Table 1). Oldest plant fossils are represented by macrofossils of *Cyclostigma*, *Leptophloeum* (Protolepidodendrales, Lycophyta) and *Aphyllopteris* (unclassified) from the Upper Devonian Tobigamori (Iwate Prefecture, Northeast Japan; Tachibana, 1950, 1959) and Naidaijin (Kumamoto Prefecture, Southwest

Japan; Kimura *et al.*, 1986) formations. Carboniferous plant fossils are represented by macrofossils (Asama, 1989) and earliest microfossils (Yang and Tazawa, 2000a) reported only from the Lower Carboniferous Hikoroichi Formation, and *Calamites* stems from the Onimaru Series (Endo and Mori, 1969), both outcropping in Iwate Prefecture. Assemblages become more diversified from the Permian, with a series of studies on macrofossils from the lower Permian Rodai (The "Maiya Flora" described from the Miyagi Prefecture; Endo, 1955; Asama, 1956, 1967, 1970, 1981; Ueda, 1963) and Sakamotozawa (The "Setamai Flora" described from the Iwate Prefecture; Asama and Murata, 1974) formations, and the upper Permian Kashiwadaira Formation (The "Takakurayama Flora" described from the Fukushima Prefecture; Yanagisawa, 1967; Asama, 1974) of Northeast Japan; microfossils were further reported from the Permian Tanba Belt (Kyoto Prefecture, central Japan; Takahashi and Yao, 1969) and the middle Permian Kanokura Formation (Iwate Prefecture; Yang and Tazawa, 2000b).

Algal macrofossils were also reported from the Carboniferous of Southwest and central Japan (Konishi, 1956; Endo and Horiguchi, 1957), and from the Permian of Southwest, central, and Northeast Japan (e.g., Konishi, 1952; Horiguchi, 1961; Ueda, 1963; Endo, 1966).

Chapter II: Geological setting and methods

This chapter covers geological setting of areas where I collected samples (Figures 8–12). Areas were selected from their fossiliferous content previously reported in Chapter I. In particular, I focused my study on the South Kitakami Belt as it represents one of the major Paleozoic deposits known in Japan. There, I collected samples from the Silurian into the Permian.

II.1. South Kitakami Belt

The South Kitakami Belt in Northeast Japan (Figures 5, 8) consists of early Paleozoic igneous and metamorphic basement rocks covered by shallow-marine sediments deposited from the late Ordovician to Lower Cretaceous (Umemura and Hara, 1985; Ehiro and Kanisawa, 1999; Isozaki *et al.*, 2011; Ehiro *et al.*, 2016). It was originally defined by Shimazu *et al.* (1970) and later by Ehiro and Suzuki (2003) and Ehiro *et al.* (2005). The South Kitakami Belt represents the southern half of the Kitakami Massif and the eastern marginal part of the Abukuma Massif, and it is composed of older basement rocks which are covered with shallow marine from Ordovician to the Lower Cretaceous strata (Ehiro and Kanisawa, 1999; Isozaki *et al.* 2011; Ehiro *et al.*, 2016). The South Kitakami Belt is characterized by Ordovician ultramafic to mafic rocks and shallow marine continental shelf deposits. Silurian and Devonian sediments are mainly outcropping in the Hikoroichi and Arisu areas of Iwate Prefecture. In the Hikoroichi area, they are represented by the Kawauchi, Ohno and Nakazato formations in ascending order.

II.1.1. Kawauchi Formation

In the Hikoroichi region, the Kawauchi Formation (Figure 13) is composed of up to 300 m of limestone and mudstone with basal arkose bed (Suzuki and Minato, 1958). It is regarded to unconformably overlie the Hikami Granite (Murata *et al.*, 1974; Tachibana, 1976), and is unconformably overlain by radiolarian mudstone of the Takainari Formation (Suzuki and Minato, 1958; Tachibana, 1976). The upper Silurian Kawauchi Formation was subjected to several paleontological works on trilobites (Sugiyama, 1941; Kobayashi and Hamada, 1974; Tachibana, 1981), corals, stromatoporoids and brachiopods (Sugiyama, 1940; Kato, 1982), bryozoans (Sakagami, 1970), conodonts (Männik *et al.*, 2018) which permitted to assign the formation a Wenlock (Sheinwoodian) to mid-Ludlow age (Kobayashi and Hamada, 1976; Männik *et al.*, 2018).

I collected eleven samples for palynological analysis from limestones and dark colored shale of the Kawauchi Formation, at the Kusayamizawa locality (GPS coordinates: 39º06'47"N, 141º40'26"E) assigned to the Wenlock (Sheinwoodian) from its trilobite fauna (Sugiyama, 1941; Tachibana, 1981; Kobayashi and Hamada, 1974) (Figures 11, 13).

II.1.2. Nakazato Formation

The Nakazato Formation (first named "Nakazato Group" by Yabe and Sugiyama, 1937) conformably overlies the Ohno Formation and is probably unconformably overlain by the Tobigamori Formation (Suzuki and Minato, 1958; Kato *et al.*, 1980) (Figure 14). It is estimated to be more than 750 m in thickness, consisting predominantly of volcaniclastic rocks (Minato *et al.*, 1974). The Nakazato Formation yields a rich shallow marine fauna: trilobites (Yabe and Sugiyama, 1937; Sugiyama and Okano, 1941; Sugiyama, 1944; Okubo, 1950, 1951, 1956; Kobayashi, 1957, 1977; Kobayashi and Hamada, 1974, 1977; Minato *et al.*, 1979; Kaneko, 1984, 1985, 1990), corals (Murata, 1972; Minato *et al.*, 1979; Kato *et al.*, 1980; Niko, 2019), brachiopods (Minato and Kato, 1977; Minato *et al.*, 1979; Copper *et al.*, 1982; Tazawa, 1988, 2002; Tazawa and Chen, 2001; Chen and Tazawa, 2003), cephalopods (Niko, 1989), and gastropods (Kase and Nishida, 1986; Hua-Zhang and Cook, 2003). A placoderm fish was also reported by Okura and Masuda (2002). The formation has been divided into four members, i.e., the N1 to N4 members in ascending order (Minato *et al.*, 1979) (Figure 14). The N3 Member, from which samples of the present study were collected, consists of an alternance of sandstone and mudstone. It is the member bearing the richest fossil assemblage, and it is assigned to the Emsian to Givetian (Figure 1) from trilobites (Kobayashi, 1977; Kobayashi and Hamada, 1977; Minato *et al.* 1979) and radiolarians (Umeda, 1996b), and from correlation by trilobites (Kaneko, 1990; Zhou and Campbell, 1990), gastropods (Pan and Cook, 2003) and brachiopods (Tazawa and Chen, 2001; Tazawa, 2002) with the Emsian Zhusileng and the Eifelian Yikewusu formations of Inner Mongolia, North China. Kaneko (2007) furthermore constrained the trilobite-bearing strata of the N3 Member to the latest Emsian (Lower Devonian) to earliest Eifelian (Middle Devonian).

I collected 22 samples from the Devonian Nakazato Formation (Figures 14, 15) in the Hikoroichi area of the South Kitakami Belt, outcropping along the upper stream of the Higuchizawa river, around 5 km northwest of Ofunato City, Iwate Prefecture, Northeast Japan

(Higuchizawa locality, GPS coordinates: 39º06'59"N, 141º40'20"E). Pictures to the field trip are illustrated in Figure 16, and detailed position of the collected samples in Figure 15. Brachiopods, corals and bryozoans were observed on the field in many horizons when collecting the samples along with trilobites including *Rhinophacops* suggesting age of the Emsian/Eifelian boundary (Kaneko, 2007).

I also took samples from the Kuronborozawa locality (Figure 11) (GPS coordinates: 39º06'16"N, 141º39'46"E), where trilobite fauna has been described (e.g., Kaneko, 2007), but could not obtain any palynomorph from there. It will thus not be detailed in this thesis.

II.1.3. Hikoroichi Formation

The Hikoroichi Formation was first introduced by Minato and Okubo (1948) as the "Hikoroichi Series". The Hikoroichi Formation is distributed western part of the southern Kitakami Mounains, near the vicinity of Hikoroichi, Ofunato City, Northeast Japan (Okubo, 1951; Sakagami, 1962; Minato *et al.*, 1979). The lithostratigraphy of the Hikoroichi Formation was described by Onuki (1956), and its stratigraphic setting established by Minato (1950). In the Hikoroichi area, the Hikorochi Formation overlies with angular unconformity the Nakazato Formation and is conformably overlain by the Onimaru Formation (Tazawa, 1984) (Figure 17). The Hikoroichi Formation is composed of sandstones with a basal conglomerate and intercalations of shale, acidic to intermediate tuffs and limestone. It is about 560 m in total thickness. A rather thick (40-90 m), greyish green, dacitic to andesitic tuff is developed at the middle horizon, about 250 to 300 m above the base of the formation. A rich fossiliferous content of corals, bryozoans, brachiopods, pelecypods, trilobites, crinoids (e.g., Minato and Kato, 1977; Kobayashi and Hamada, 1980; Tazawa, 1984) suggests a late Visean (early Carboniferous) age for the formation (Tazawa, 1984).

The area studied was greatly covered by vegetation (Figure 18A, B). The Hikoroichi locality (GPS coordinates: 39º06'44"N, 141º39'34"E) where the samples were collected was very consolidated, with rocks very hard (Figure 11). Sampled horizons were rich in corals, brachiopods, bryozoans, with rare trilobites (Figure 18C, D).

II.1.4. Kanokura Formation

The Southern Kitakami Mountains represents the type areas for the Japanese Permian (Choi, 1970). Stratigraphy and fossils of the Kamiyasse area have been widely studied (Tazawa, 1976), and Permian shallow marine sediments of this area were divided into the Sakamotozawa, Kanokura, and Toyoma formations in ascending order (Tazawa, 1976; Ehiro and Misaki, 2004). The Kanokura Formation rests conformably on the Sakamotozawa Formation.

The Kanokura Formation is about 1,100 m in thickness and divided into four members, i.e., the KN1 Member consisting of shales with layers of sandstone and conglomerate, the KN2 Member consisting of sandstones and limestones, the KN3 Member consisting of limestones with layers of conglomerate, sandstone, and shale, and the KN4 Member consisting of shales with layers of sandstone and limestone, in ascending order (Figure 19). Fusulinoideans, corals, molluscs brachiopods, as well as a microflora have been reported from the Kanokura Formation (e.g., Minato *et al*., 1978). In particular, the brachiopods (Tazawa and Takaizumi, 1987) and microflora (Yang and Tazawa, 2000b) reported from the KN1 Member of the formation suggest a middle Permian age.

I collected fifteen mudstone samples from the Imo locality (GPS coordinates: 38º59'54"N, 141º31'17"E) of the Kanokura Formation (Figure 11), corresponding to the creek #43 of Misaki and Ehiro (2004). I could observe fusulinid foraminifers including middle Permian index fossil *Monodiexodina matsubaishi*, brachiopods including *Leptodus* sp., trilobites, corals, bryozoans, bivalves, and crinoids from the sampled horizons. Limestones of the outcrop were rich in marine fossils including brachiopods, fusulinid foraminifers and trilobites. I collected samples in the fusulinids-bearing limestone and black mudstone (Figure 20C).

II.1.5. Nishikori Formation

The Nishikori formation, outcropping in the Maiya area of Miyagi Prefecture, Northeast Japan, is regarded to be the equivalent of the fossiliferous Kanokura Formation developed around Kesennuma, Miyagi Prefecture (Ueda, 1963). The Nishikori Formation consists of bedded limestone with intercalations of sandstone and black shale. It is conformably overlain by the Higashifukakaya Formation. The Nishikori Formation yields fusulinaceans, corals, bryozoans, brachiopods and trilobites, and abundant plant fossils belonging to the Cathaysian flora such as *Cathaysiopteris*, *Sphenopteris*, *Odontopteris*, *Pecopteris*, *Taeniopteris* and *Cordaites* (Asama, 1956, 1967). U–Pb dating for detrital zircon of tuffaceous sandstone from the Nishikori Formation indicated 287 and 301 Ma (lower Permian) (Okawa *et al*., 2013; Li and Takeuchi, 2021).

II.2. Hida Gaien Belt

The Paleozoic-Mesozoic Hida Gaien Belt, which belongs to the Inner Zone of SW Japan (Figure 9), was described by Tsukada *et al.* (2004). It represents one of the three oldest exposure rocks in Japan and is also considered as one of the most structurally complex areas in Japan (Kurihara and Sashida, 2000). It is regarded as a suture zone between the continental mass of the Hida Belt and the middle Paleozoic (Silurian to Carboniferous) oceanic crust of the Mino Belt (Horikoshi, 1972). The Hida Gaien Belt contains moderately metamorphosed Paleozoic and Mesozoic strata consisting of Ordovician mafic to ultramafic rocks, Ordovician to Permian clastic, volcaniclastic and carbonate rocks, 300-400 Ma metamorphic rocks with blueschists, serpentinites and the Mesozoic to Cenozoic covers (Komatsu, 1990; Tazawa, 2004). The continental orogenic recorded in the Hida Gaien Belt was proposed to be of landwards erosion during Pacific (Cordilleran) -type orogenesis (Ehiro *et al.*, 2016). The Hida Belt is divided into the Moribu and Fukuji formations based on its lithological variations (Ehiro *et al.*, 2016).

II.2.1. Fukuji Formation

The Fukuji Formation consists of 75-250 m of limestones with thin beds of dark mudstone (Figure 21), sandstones, and felsic tuff (Adachi and Ezaki, 2007). It unconformably overlies the Yoshiki Formation (Manchuk *et al.*, 2013). Kuwano (1987) divided the Fukuji Formation into five lithological members, i.e., the Lower Shaly Member, Lower Carbonate Member, Middle Shaly Member, Upper Carbonate Member, and Upper Shaly Member. The Middle Shale Member of the formation was suggested to have been deposited in a shallow marine lagoonal setting (Tanaka *et al.*, 2018). The Fukuji Formation is fossiliferous and contains brachiopods, conodonts (Kuwano, 1987), corals (Kamei, 1955; Niko, 2003, 2005, 2006; Tsukada, 2005), gastropods (Kase *et al.*, 1985), cephalopods (Niko, 1990, 1991, 1993, 1996) tentaculids, trilobites (Kobayashi, 1988), ostracods (Kuwano, 1987; Tanaka *et al.*, 2018), leperditicopids (Hamada, 1959; Tanaka *et al.*, 2012), scolecodonts (Vandenbroucke *et al.*, 2019) and a bivalved arthropod (Tanaka *et al.*, 2013). Conodont and ostracod assemblages suggested an Early Devonian (Lochkovian to Emsian) age to the Fukuji Formation (Kuwano, 1987).

Fifteen samples were collected for palynological analysis from the Fukuji Formation, at three localities (Figure 12): the Fukuji Onsen locality (Fossil boardwalk outcrop, GPS coordinates: 36º13'25"N, 137º31'45"E; Mountain trail entrance outcrop, GPS coordinates:

36º13'21"N, 137º31'42"E), the Ichinotani locality (GPS coordinates: 36º13'12"N, 137º31'18"E), and the Hitoegane locality (GPS coordinates: 36º14'27"N, 137º32'14"E). I observed brachiopods, trilobites, corals, and rare plant fragments in collected horizons (Figure 22).

II.3. Kurosegawa Belt

The Kurosegawa Belt expands for over 600 km through southwestern Japan (Figure 10), in southwest Honshu, Shikoku and Kyushu islands. It is distributed in a SW-NE oriented narrow belt extending from the Chichibu Terrane to the north, and the Sanbosan to the South (Hada *et al.*, 1979). It predominantly consists of a serpentinite-matrix mélange, with lesser amounts of mud-matrix mélange (Aitchison *et al.*, 1991). The Middle Paleozoic strata in central Shikoku are represented by the Siluro-Devonian Yokokurayama Group, divided into the Gomi, Fukata, Ichiyama, Joryu, Nakahata and Ochi formations in ascending order (Umeda, 1998). The Kurosegawa Belt in southwest Japan is considered as a southern extension of the South Kitakami Belt, forming the South Kitakami – Kurosegawa Arc (Umeda 1996a; Ehiro and Kanisawa, 1999; Ehiro, 2000).

II.3.1. Joryu Formation

The Joryu Formation outcrops at Okanaru, Seiyo City, Ehime Prefecture. It is divided into a lower conglomerate member and upper more heterogeneous member comprising acidic tuff, mudstone, sandstone, and conglomerate (Umeda, 1998). Corals, radiolarians (Kurihara *et al.*, 2009), and trilobite (Kobayashi and Hamada, 1974) are reported. A late Silurian (Přídolí) age was suggested from the radiolarian assemblage (Kurihara *et al.*, 2009).

I made palynological analysis from two samples of the Joryu Formation from the trilobite-bearing shale bed, and coral-rich limestone of the Okanaru locality, which were shared by Dr. Rie Hori, Ehime University.

II.3.2. Naidaijin Formation

The Naidaijin Formation was described for its lithological description by Kimura *et al.* (1986). Its type locality is located along the pass of Tenshu Mountain near Tomochi Town, Shimomashiki District, Kumamoto Prefecture, central Kyushu (Saito *et al.*, 2005).

The formation is up to 290 m in thickness, and is composed of mudstone, sandstone, conglomerate, and welded tuffs (Miyamoto and Tanimoto, 1993). It conformably overlies the Gionyama Formation (Saito *et al.*, 2005; Ehiro *et al.*, 2016).

The Lower Member of the Naidaijin Formation yields a rich trilobite assemblage (Murata *et al.*, 1997; Kaneko, 2007) which, combined with a radiometric age from detrital zircons (Stocker *et al.*, 2018), indicate a Middle Devonian (Emsian to Givetian) age. The Upper Member of the Naidaijin Formation has been assigned to the Famennian (Late Devonian) by Miyamoto and Tanimoto (1993) for yielding brachiopods (Yanagida *et al.*, 1987) and plant fossil *Leptophloem rhombicum* (Hirata, 1966), and correlation with the Tobigamori Formation of the South Kitakami Belt (Tachibana, 1952), and Rosse Formation of the Hida-Gaien Belt (Tazawa *et al.*, 2000).

Five samples from the brachiopods and *Leptophloem rhombicum*-bearing beds of the Upper Member of the Naidaijin Formation were shared by Dr. Toshifumi Komatsu, Kumamoto University, to check their palynological content.

II.4. Methods for the palynological analysis

Microfossils were extracted following the methods of Legrand *et al.* (2021). Samples were crushed into small pieces (Figure 23), then immersed in cold 50% hydrofluoric acid for 24 hours, followed by a treatment in hot 36% hydrochloric acid until reaching the boiling point. After sieving, the fraction with a diameter between 10 and 125 μm was oxidized with 69% nitric acid in a boiling water bath (Figure 23). The organic residue was concentrated by centrifugation and mounted on slides with Canada balsam. Palynomorphs were observed under a differential interference contrast microscope (DM 2500, Leica, Wetzlar, Germany). The position of palynomorphs on the slide was recorded using an England Finder graticule (Pyser Optics, Edenbridge, England). Microfossils for scanning electron microscope (SEM) observation were mounted on aluminum stubs, coated with platinum using a magnetron sputter (JUC-5000, JEOL, Tokyo, Japan), and observed under a SEM (JSM-IT100, JEOL, Tokyo, Japan). Classification of miospores follows the scheme of *Sporae dispersae* defined by Pflug (1953), Potoni and Kremp (1954, 1955), Potoni (1956, 1958,1960, 1966, 1970a, b, 1975), and Dettmann (1963). Classification of tubular remains follows the artificial classification proposed by Burgess and Edwards (1991). Samples and residues are housed in the Palynological collections of the Department of Geosciences, Faculty of Science, Shizuoka University, Japan.

Chapter III: Results

Most samples from the South Kitakami Belt were productive and contained spores and plant fragments, excepting the Nishikori Formation, although these were carbonized and often fragmented or deformed due to a low-grade metamorphism. The palynological content obtained from each formation will be explained in this chapter. The palynofacies of the studied rocks from the South Kitakami Belt are illustrated in Figure 24 and Plates I and II..

III.1. South Kitakami Belt

III.1.1. Kawauchi Formation

Microfossils obtained from the Kawauchi Formation were very few and highly coalfield (black and opaque) (Plate I D, F). I could observe some grains with a miospore-like shape under light microscopy (Plates I A, F, II D), but I could not confirm identifications as no grain could be observed under the SEM. These miospore-like grains are triangular with rounded corners, apparently smooth, 42 μm in diameter, and look like primitive trilete spores.

Rounded palynomorphs without ornamentation appear larger and brown color, 40 μm in diameter, probably corresponding to acritarchs, were also observed (Plates I C, II A, B). There are numerous rounded palynomorphs with opaque color, 18-20 μm in diameter were observed in numerous counting (Plate I D).

Several tissues of unknown origin and some tubular remains were obtained, observed with both LM and SEM (Plate I J; Plate II E). The tabular remains are all characterized by a smooth wall without any apparent structure, around 40 to 70 μm in diameter, some showing a slight curvature some observed with opaque conditions and other single record of brown color.

Singles crystals and framboids of pyrite (Plate II F), as well as small spherules of unknown origin (Plate II C), were also observed. The results of the Silurian are presented in Plates I and II.

III.1.2. Nakazato Formation

All samples from the Nakazato Formation contained spores and plant fragments, although these were carbonized and often fragmented or deformed due to a low-grade metamorphism (Plate III). The dispersed spore assemblages were all very similar in composition among observed samples. Palynomorphs appeared dark gray to opaque under the light microscope and all species-level identifications were confirmed with SEM observations. Most abundant and well-preserved palynomorphs were obtained from horizons 2021.12.10–20 and –21 (Table 3). The microfossil assemblage is composed of two marker species of cryptospores and distinctive of 15 species represent trilete spores, associated with abundant plant fragments including mass of conducting cells, tabular remains and cuticles (Plates III, IV). Cryptospores are represented by monads or loosely attached dyads of *Laevolancis* sp. (Plate IV) and fused permanent dyads (pseudodyads) of *Pseudodyadospora petasus* Wellman and Richardson (Plate IV). The trilete spore assemblage is dominated in number and diversity by retusoid laevigate spores of cf. *Retusotriletes* (*Retusotriletes* cf. *triangulatus* (Streel) Streel [Plate IV], cf. *Retusotriletes* spp. [Plate III]), crassitate spores of *Ambitisporites* (*Ambitisporites avitus* Hoffmeister [Plates III, IV], *Ambitisporites.* sp. [Plate IV]), and trilete laevigate spores of *Calamospora atava* (Plate IV), *Deltoidospora* (*Leiotriletes*) *priddyi* (Plate IV). While ornamented spores are not commonly found, they nonetheless display a striking range of diversity. These include apiculate spores of *Aneurospora xujiachongensis* (Plate III) and *Apiculiretusispora plicata* (Plates III, IV), granulate spores of *Granulatisporites muninensis* Allen (Plate IV), verrucate spores of *Verrucosisporites polygonalis* Lanninger (Plate IV), reticulate spores of *Dictyotriletes emsiensis* (Allen) McGregor (Plate III) and *Brochotriletes foveolatus* Naumova (Plate IV), conate-baculate spores of *Apiculiretusispora* sp. (Vigran) Allen (Plate IV), and spores of *Dibolisporites* showing characteristic compound sculptural projections consisting of baculae, coni and spinae (*Dibolisporites* cf. *echinaceus* (Lanninger) McGregor [Plate IV], *Dibolisporites* sp. [Plate III]).

I counted 158 spores on one slide from horizon 2021.12.10-21 (Figure 15), although the opaque nature of the spores does not permit precise identifications. The count reveals a composition of approximately 63% laevigate spores (possibly assigned to *Retusotriletes*, *Ambitisporites*, *Deltoidospora*, or *Calamospora*), 11% verrucate spores (*Verrucosisporites*), 9% granulate or apiculate spores (*Apiculiretusispora* or *Granulatisporites*), 15% conate/baculate/foveolate spores (*Aneurospora*, *Dictyotriletes*, *Brochotriletes*, *Dibolisporites*, or *Geminospora*), and 2% dyads (*Pseudodyadospora* or *Laevolancis*). Among the numerous plant fragments observed in preparations, we could recognize smooth aseptate tubes of *Laevitubulus tenuis* Burgess and Edwards (Plate III) and a variety of water-conducting cells (Plate III). Wall fragments with numerous minute rounded perforations of various size are widely observed in pro-tracheophytes (Kenrick and Crane, 1991) which are similar to hydroid walls of some extant bryophytes (Ligrone *et al.*, 2000). On the other hand, tracheids characterize vascular plants. Tracheids with annular thickenings (Plate V), classified as "G-type tracheids" (Kenrick and Crane, 1991), are commonly observed in basal tracheophytes such as zosterophyllophytes and lycophytes (Kenrick and Crane, 1991), and known no later than the Lochkovian (Edwards, 2003). Tracheid elements with uniseriate bordered pits (Plates III, V) are observed in some late Early Devonian trimerophytes like *Psilophyton* (Hartman and Banks, 1980). Besides, the investigated samples also yield numerous opaque plant fragments and cuticles of unknown origin. No aquatic palynomorphs were observed. They were possibly destroyed during the fossilization process because of their generally less resistant structure, especially by the low-grade metamorphism as noted above. However, I could observe several scolecodonts (Plate III).

III.1.3. Hikoroichi Formation

Microfossils obtained from the Hikoroichi Formation were few in number and coalfield (dark brown to black colored) but in moderately good preservation state with some grains non fragmented. They were observed using both LM and SEM (Plates VI and VII). The microfossil assemblage, of insecure identification, is composed of trilete spores which may correspond to ?*Calamospora* sp., *Deltoidospora* sp., *Densosporites* sp., *Punctatisporites* sp., ?*Verrucosisporites* sp., pseudosaccate trilete spore ?*Spelaeotriletes* cf. *owensii,* and monolete spore ?*Monoletes* cf. *ellipsoides*. Some cuticle fragments of unknown origin, and smooth tubular remains were also observed.

III.1.4. Kanokura Formation

The assemblage is composed of trilete spores poor in number and diversity, but with a good state of preservation, dark brown in color (Plate VIII). I could identify some small rounded punctate spores of *Punctatisporites* sp., triangular granulate spores of *Granulatisporites* sp., rounded triangular verrucate spores of *Verrucosisporites* sp., baculate spores of *Baculatisporites* sp. The pseudosaccate trilete spore *Spelaeotriletes* cf. *owensii* was also observed under the SEM. Some plant fragments were also present and picked for SEM observation.

III.2. Hida Gaien Belt

III.2.1. Fukuji Formation

Microfossils obtained from the Fukuji Formation were few in number and coalfield (dark brown to black colored) but in moderately good preservation state with many grains non fragmented. They were observed using both LM and SEM (Plates XI, XII).

The microfossil assemblage, of insecure identification, is composed of trilete spores of probable *Deltoidospora* sp., *Retusotriletes* cf. *triangulatus* and *Retusotriletes* sp., along with some acritarchs.

Many cristals and framboids of pyrite were observed together with miospores.

III.3. Kurosegawa Belt

I could not obtain any reliable miospore from the Kurosegawa Belt (Joryu and Naidajin formations), but only some wood fragments with tracheids, possibly belonging to *Leptophloem rhombicum* yielded in the same bed, were observed in the palynological preparations. These two formations will not be detailed in the results.

III.4. Description of palynomorphs

Anteturma Cryptosporites (Richardson *et al.,* 1984) Richardson, 1988 emend. Steemans, 2000
Naked cryptospore unfused dyads (true dyads)
Genus ***Laevolancis*** Burgess and Richardson, 1991
Type species.— Laevolancis divellomedia (Chibrikova) Burgess and Richardson, 1991

***Laevolancis* sp.**
Plate IV B

Description.— Hilate cryptospore, in monads or loosely attached dyads. Amb circular to subcircular, 21–24 µm in diameter. An equatorial crassitude 3–4 µm wide delimits a circular hilum collapsed. Exine laevigate, unfolded.

Occurrence.— Nakazato Formation.

Remarks. —Laevolancis and other hilate laevigate cryptospores are reported *in situ* from the latest Silurian and Early Devonian rhyniophytoids sporangia (e.g., Lang, 1937; Fanning *et al.*, 1991; Edwards *et al.*, 1994; Wellman *et al.*, 1998a), as summarized in Steemans and Wellman (2018).

Naked fused cryptospore dyads (pseudodyads)

Genus ***Pseudodyadospora*** Johnson, 1985

Type species.— Pseudodyadospora laevigata Johnson, 1985

Pseudodyadospora petasus Wellman and Richardson, 1993

Plate IV A

1993 *Pseudodyadospora petasus* Wellman and Richardson, p. 168, 169, pl. 2, figs. 1–7.

Occurrence.— Nakazato Formation.

Remarks.—This species has worldwide distribution, reported from the Middle Ordovician to Lower Devonian (Abuhmida and Wellman, 2017). Its dyads were reported *in situ* from *Fusitheca fanningiae* Wellman *et al* (1998) for which they proposed rhyniophytoid affinities (Wellman *et al.*, 1998b).

Anteturma Proximegerminantes Potonié, 1970a

Turma Triletes Reinsch emend. Dettmann, 1963

Suprasubturma Acavatitriletes Dettmann, 1963

Subturma Azonotriletes Lüber emend. Dettmann, 1963

Infraturma Laevigati (Bennie and Kidston, 1886) Potonié, 1956

Genus ***Calamospora*** Schopf *et al.*, 1944

Type species.—Calamospora hartungiana Schopf *et al.*, 1944

Calamospora atava (Naumova, 1953) McGregor, 1964

Plate IV E

1953 *Leiotriletes atavus* Naumova, p. 22, 103, pl. 1, fig. 8; pl. 16, fig. 3.

1964 *Calamospora atava* (Naumova, 1953) McGregor, p. 6, 7, pl. 2, fig. 17.

1964 *Phyllothecotriletes microgranulatus* Vigran, p. 8, pl. 1, figs. 7, 8.

1971 *Leiotriletes insuetus* Umnova, p. 135, pl. 2, figs. 1, 2.

Occurrence.— Nakazato Formation.

Remarks.—This species is reported worldwide from the Emsian to Frasnian. Spores similar to this species were isolated from Early Devonian specimens of the rhyniophyte *Hostimella globosa* Lang (Lang, 1926), the trymerophytes *Psilophyton princeps* Lang (Lang, 1931; Hueber and Banks, 1967) and *Trimerophyton robustius* Hopping (Hopping, 1956), and the zosterophyllophytes *Sawdonia acanthotheca* P. G. Gensel, H. N. Andrew and W. H. Forbes (Gensel *et al.*, 1975; Gensel, 1980) and *S. ornata* Hueber (McGregor, 1973; Allen, 1980).

?*Calamospora* sp.

Plate VI C, F

Description.—Amb circular, around 45 μm in diameter, with small laesurae.

Occurrence.— Hikoroichi Formation.

Distribution.—Genus *Calamospora* ranges from the Paleozoic to Cretaceous (Archangelsky and Villar de Seoane, 1994).

Remark.—*Calamospora* is usually associated with Equisetales (including calamitaceans, Sphenophyllales and Noeggerathiales), and is similar with *in situ* spores observed in Carboniferous *Calamites* and *Sphenophyllum* (Good, 1977).

Genus ***Deltoidospora*** Miner, 1935

Type species.— Deltoidospora hallii Miner, 1935

Deltoidospora (***Leiotriletes***) ***priddyi*** (Berry, 1937) McGregor, 1973

Plate IV F

1937 *Zonales-sporites priddyi* Berry, p. 156, fig. 2
1955 *Leiotriletes priddyi* (Berry, 1937) Potonié and Kremp, p. 38.
1973 *Deltoidospora priddyi* (Berry, 1937) McGregor, p. 16, pl.1, figs. 6, 7.

Occurrence.— Nakazato Formation.

Remark.—It is distributed widely and ranges from the upper Silurian to Mesozoic (McGregor, 1973). A number of species assigned to *Leiotriletes* are similar to *D. priddyi* (McGregor, 1964, 1973), but they are often distinguished according to their stratigraphic range, i.e., Paleozoic (*Leiotriletes*) or Mesozoic (*Deltoidospora*). We combine them here as suggested by McGregor (1973). Devonian spores of *Leiotriletes* were observed in *Zosterophyllum llanoveranum* Croft and Lang, and are associated with zosterophyllopsids or rhyniopsids (Gensel, 1980; Balme, 1995).

Deltoidospora **(*Leiotriletes*) sp.**

Plate XI A, B

Description.—Trilete spore, triangular, laesurae distinct.

Occurrence.— Fukuji Formation.

Distribution.—Genus *Deltoidospora* is distributed widely and ranges from the upper Silurian to Mesozoic (McGregor, 1973).

Remark.—Devonian spores of *Leiotriletes* are associated with zosterophyllopsids or rhyniopsids (Balme, 1995).

?*Deltoidospora* **(*Leiotriletes*) sp.**

Plate VI I

Description.— Trilete spore, triangular, laevigate, opaque.

Occurrence.— Hikoroichi Formation.

Distribution.—Genus *Deltoidospora* is widely distributed and ranges from the upper Silurian to Mesozoic (McGregor, 1973).

Remark.—Carboniferous *Deltoidospora* was produced by Filicophytes.

Genus ***Punctatisporites*** Ibrahim 1933

Type species.— Punctatisporites punctatus Ibrahim 1933

Punctatisporites **sp.**

Plate VIII A-D

Description.—Spore, amb circular, trilete indistinct.

Occurrence.— Kanokura Formation.

Distribution.—Genus *Punctatisporites* ranges from the Paleozoic to Neogene.

Remark.—Punctatosporites is associated to Filicophytes, possibly Sphenophyllales (Libertín *et al.*, 2008).

?***Punctatisporites*** **sp.**

Plate VI G, J

Description.— Spore, triangular, trilete distinct, laesurae not reaching the equator.
Occurrence.— Hikoroichi Formation.
Distribution.—Genus *Punctatisporites* ranges from the Silurian to Cenozoic (Menendez and Azcuy, 1969).
Remark.—Punctatosporites is associated to Filicophytes, possibly Sphenophyllales (Libertín *et al.*, 2008).

Infraturma Retusotrileti Streel, 1964

Genus ***Retusotriletes*** Naumova, 1953 emend. Streel, 1964

Type species.— Retusotriletes simplex Naumova, 1953

Retusotriletes **cf.** ***triangulatus*** (Streel, 1964) Streel, 1967

Plates IV J, XI H-J

1964 *Phyllothecotriletes triangulatus* Streel, p. 5, pl. 1, figs. 3–5.
1967 *Retusotriletes triangulatus* (Streel, 1964) Streel, p. 24.
2006 *Retusotriletes* cf. *triangulatus* (Streel, 1964) Streel, 1967, in Wellman, p. 175, pl. 10, figs. i–k.

Occurrence.— Nakazato Formation, Fukuji Formation.
Remarks.—It is widely reported in the Devonian, particularly the Lower-Middle Devonian strata (Breuer and Steemans, 2013). Morphological characteristics of specimens are consistent with those of *Retusotriletes triangulatus*, however their opacity prevents any observation of the typical triangular thickening needed to confirm species. *Retusotriletes triangulatus* is known from the trimerophyte *Psilophyton dawsonii* Banks *et al.* (Banks *et al.*, 1975).

cf. ***Retusotriletes*** **spp.**

Plates III A, B, XI D-F,L

Description.—Trilete microspore. Amb subtriangular to subcircular, 22–39 µm in diameter. Laesurae straight, extending from 4/5 to full distance to the equator. Exine laevigate, about 1 µm thick.

Occurrence.— Nakazato Formation, Fukuji Formation.

Remarks.—Most common taxa in the assemblage. cf. *Retusotriletes* spp. show a trilete mark reaching to the equator, longer than that observed in *R.* cf. *triangulatus.*

Infraturma Apiculati (Bennie and Kidston, 1886) Potonié, 1956
Genus *Apiculiretusispora* (Streel, 1964) Streel, 1967
Type species.— *Apiculiretusispora brandtii* Streel, 1964

***Apiculiretusispora* sp.**

Plates III F, IV G

Description.—Microspore with an amb rounded subtriangular, 38–42 µm in diameter. The laesurae are not observed. Exine densively covered with grana and small coni and spinae, less than 1 µm high.

Remarks.—Spores almost identical to *A. plicata* were found from the rhyniophytes *Cooksonia crassiparietilis* Yurina (McGregor, 1973), *Rhynia gwynne-vaughanii* Kidston and Lang (Bhutta, 1987), the trymerophytes *Pertica dalhousii* Doran *et al.* (Doran *et al.*, 1978), *P. varia* Granoff *et al.* (Granoff *et al.*, 1976), *Psilophyton crenulatum* Doran (Doran, 1980).

Genus ***Dibolisporites*** Richardson, 1965
Type species.— Dibolisporites echinaceus (Eisenack, 1944) Richardson, 1965

Dibolisporites* cf. *echinaceus (Eisenack, 1944) Richardson, 1965

Plate IV O, P

1944 *Trilites echinaceus* Eisenack, p. 113, pl. 2, fig. 5.
1965 *Dibolisporites echinaceus* (Eisenack) Richardson, p. 568, pl. 89, figs. 5, 6.
1965 *Dibolisporites* cf. (al. *Retusotriletes*) *gibberosus* (Naumova) var. *major* (Kedo) Richardson, p. 569, pl. 89, figs. 4.
1965 *Bullatsporites bullatus* Allen, p. 703, pl. 96, figs. 5–7.

1970 *Dibolisporites mammatus* Brideaux and Radford, p. 34, pl. 1, fig. 6.

Occurrence.— Nakazato Formation.

*Remarks.—*The specimens observed correspond in their morphological characteristics to *Dibolisporites echinaceus*, but are smaller than usually noted for this species; spores with a similar size were reported by Wellman *et al.* (2012) from the Pragian–lower Emsian Xujiachong Formation in South China. This species is reported from the Pragian to Givetian. This genus could be related to Cladoxylopsida (Balme, 1995). *Dibolisporites echinaceus* is also recorded from the Middle Devonian *Calamophyton bicephalum* Leclercq and Andrews (Bonamo and Banks, 1966).

Dibolisporites sp.

Plate III D

*Description.—*Amb rounded subtriangular to subcircular, 30 μm in diameter. Laesurae are not observed. Surface densely ornamented with compound projections 1 to 2 μm high, consisting in baculae, coni and spinae surmounted by small spinae or pilae.

Occurrence.— Nakazato Formation.

Remarks.—Dibolisporites sp. shows typical ornamentation of this genus, and is distinct from *D.* cf. *echinaceus* by its smaller size. However, it is left in open nomenclature from the opacity of specimens.

Genus ***Granulatisporites*** Ibrahim, 1933 emend. Potonié and Kremp, 1954

Type species.— Granulatisporites granulatus Ibrahim, 1933

Granulatisporites* cf. *muninensis Allen, 1965

Plate IV H

1965 *Granulatisporites muninensis* Allen, p. 693, 694, pl. 94, figs. 3–5.

Occurrence.— Nakazato Formation.

*Remarks.—*It has a worldwide distribution, widely reported from the upper Silurian to middle Tournaisian (Lower Carboniferous) (Askew and Wellman, 2019). This spore has been reported from the rhyniophyte *Rhynia gwynnevaughanii* (Bhutta, 1987).

***Granulatisporites* sp.**

Plate VIII G, L

Description.—Spore, amb triangular, granulate ornamentation.
Occurrence.— Kanokura Formation.
Distribution.—Genus *Granulatisporites* ranges from the Silurian to early Eocene
Remark.—Granulatisporites is associated to Filicophytes (Balme, 1995).

Subinfraturma Verrucati Dybová and Jachowicz, 1957

Genus ***Verrucosisporites*** Ibrahim, 1933 emend. Smith, 1971

Type species.— Verrucosisporites verrucosus (Ibrahim, 1932) Ibrahim, 1933

Verrucosisporites* cf. *polygonalis Lanninger, 1968

Plate IV I

1954 Spore type H6’ in Radforth and McGregor, p. 613, pl. 2, fig. 51.
1954 Spore type H7’ in Radforth and McGregor, p. 613, pl. 2, fig. 52.
1966 *Verrucosisporites* sp., McGregor and Owens, pl. 1, fig. 34, pl. 2, figs. 20, 22, 34.
1968 *Verrucosisporites polygonalis* Lanninger, p. 128, pl. 22, fig. 19.
1973 *Verrucosisporites ?polygonalis* Lanninger, 1968, in McGregor, p. 37, 38, pl. 4, figs. 16, 17, 19, 25, 26.
1976 *Verrucosisporites platyverruca* Lu and Ouyang, p. 30, 31, pl. 3, figs. 1, 2.

Occurrence.— Nakazato Formation.
Remarks.—It is mostly reported worldwidely from the Pragian–Emsian, while there are a few records from the Eifelian in the Middle East (e.g., Breuer and Steemans, 2013). This genus is possibly born by Lycopsida (Balme, 1995).

***Verrucosisporites* sp.**

Plate VIII E, F, I

Description.—Spore triangular, ornamented with verrucae/grana. Trilete mark indistinct.
Occurrence.— Kanokura Formation.

*Distribution.—*Genus *Verrucosisporites* ranges from the Devonian to Miocene (Barreda and Palamarczuk, 2000).

Remark.—Verrucosisporites is associated to Filicophytes (Balme, 1995).

?*Verrucosisporites* sp.

Plate VI H

Description.— Spore triangular, opaque.

Occurrence.— Hikoroichi Formation.

*Distribution.—*Genus *Verrucosisporites* ranges from the Devonian to Miocene (Barreda and Palamarczuk, 2000).

*Remark.—*Carboniferous *Verrucosisporites* was possibly produced by Lycopsida (Balme, 1995).

Subinfraturma Baculati Dybová and Jachowics, 1957

Genus **Baculatisporites** Pflug and Thomson in Thomson and Pflug, 1953

Type species.—Baculatisporites primarius (Wolff, 1934) Pflug and Thomson in Thomson and Pflug, 1953

Baculatisporites sp.

Plate VIII H, J-K

*Description.—*Trilete spore triangular, baculate.

Occurrence.— Kanokura Formation.

*Distribution.—*Genus *Baculatisporites* ranges from the Paleozoic to Pleistocene (Mautino and Anzótegui, 2000).

Remark.—Baculatisporites is associated to Filicophytes (Balme, 1995)

Infraturma Murornati Potonié and Kremp, 1954

Genus ***Brochotriletes*** Naumova, 1939 ex Ishchenko, 1952

Type species.—Brochotriletes magnus Ishchenko, 1952

Brochotriletes cf. *foveolatus* Naumova, 1953

Plate IV M

1953 *Brochotriletes foveolatus* var. *minor* Naumova, p. 58, pl. 7, fig. 23.
1953 *Brochotriletes foveolatus* var. *major* Naumova, p. 59, pl. 7, fig. 24.
1961 *Perforosporites robustus* Scott and Rouse (pars), p. 978.
1963 *Brochotriletes perforatus* (Luber) Naumova, in Shepeleva, fig. 9.
1967 *Brochotriletes* sp. in McGregor, pl. 1, fig. 3.
1967 *Perforosporites robustus* Scott and Rouse, in Beju, pl. 1, figs. 23, 24.
1967 *Perforosporites* sp. 1 in Beju, pl. 1, figs. 25, 26.
1973 *Brochotriletes*? *foveolatus* Naumova, in McGregor, p. 39, pl. 4, figs. 20, 23.

Occurrence.— Nakazato Formation.
Remarks.—It is reported worldwidely from the Lower to Upper Devonian (McGregor, 1973).

Genus ***Dictyotriletes*** Naumova, 1953 ex Ishchenko, 1952

Type species.— Dictyotriletes bireticulatus (Ibrahim, 1933) Potonié and Kremp, 1955

***Dictyotriletes* sp.**

Plate III E

1965 *Reticulatisporites emsiensis* Allen, p. 705, pl. 97, figs. 9–11.
1967 ?*Dictyotriletes* sp. in Richardson, pl. 4, fig. c.
1973 *Dictyotriletes emsiensis* (Allen, 1965) McGregor, p. 42, 43, pl. 5, fig. 15.
1976 *Dictyotriletes* cf. *D. emsiensis* (Allen, 1965) McGregor, 1973, in McGregor and Camfield, p. 21, pl. 3, figs. 5, 6.

Description.—Microspore with an amb rounded, 45 μm in diameter. Exine doubly reticulate, with large polygonal lumina 8–12 μm, each again finely reticulate with lumina 1 μm. Muri slightly projecting at the amb, appearing as coni around 1.5 μm high.
Occurrence.— Nakazato Formation.
Remarks.—The genus may be related to Cladoxylopsida plants (Balme, 1995).

Subturma Zonotriletes Waltz, 1935 (in Luber and Waltz, 1938)

Infraturma Crassiti Bhardwaj and Venkatachala, 1961

Genus ***Ambitisporites*** Hoffmeister, 1959

Type species.—Ambitisporites avitus Hoffmeister, 1959

Ambitisporites avitus Hoffmeister, 1959

Plate III C

1959 *Ambitisporites avitus* Hoffmeister, p. 332, pl. 1, figs. 1–8.

1969 *Ambitisporites* cf. *avitus* Hoffmeister, 1959, in Richardson and Lister, p. 228, pl. 40, fig. 2.

Occurrence.— Nakazato Formation.

Remarks.—It has a worldwide distribution and is widely reported from the lower Silurian to Lower Devonian (Emsian) (Breuer and Steemans, 2013). The genus is suggested to have an affinity to Rhyniales (Balme, 1995). *Ambitisporites* spores have been observed *in situ* from sporangia of *Cooksonia pertoni* Lang (Fanning *et al.*, 1988).

Genus ***Aneurospora*** (Streel, 1964) Streel, 1967

Type species.—Aneurospora goensis Streel, 1964

Aneurospora **spp.**

Plates III G, IV C, K, L, N

Occurrence.— Nakazato Formation.

Description.—Small trilete microspore. Amb rounded triangular, 20 to 40 μm in diameter. The laesurae are straight, narrow, extending to an equatorial crassitude around 1 μm wide. Exine smooth to finely punctate on the proximal face, and densely ornamented with grana and coni 1.5–2 μm high on the distal face.

Remarks.—The genus could be shed by plants of Rhyniopsida (Rhyniales), Lycopsida (Protolepidodendrales) or Progymnospermopsida (Aneurophytales) (Balme, 1995). Spores of *Asteroxylon mackiei* Kidston and Lang (Drepanophycales, Lycopsida) were compared to *Aneurospora goensis* (Allen, 1980). *Aneurospora goensis* is identical with spores recovered in large numbers from *Aneurophyton germanicum* Kräusel and Weyland of the Aneurophytales (Streel, 1964).

Genus ***Densosporites*** Berry *emend.* Butterworth *et al.* in Staplin and Jansonius, 1964

Type species.—Densosporites covensis Berry 1937

?***Densosporites*** **sp.**

Plate VI D

*Description.—*Spore triangular, apparently thickly zonate.

Occurrence.— Hikoroichi Formation.

*Distribution.—*Genus *Densosporites* ranges from the Paleozoic to Pleistocene.

Remark.—Densosporites is associated with herbaceous lycopods (Chaloner, 1958).

Genus ***Spelaeotriletes*** Neves and Owens 1966

Type species.—Spelaeotriletes triangulus Neves and Owens 1966

?***Spelaeotriletes*** **cf.** ***owensii*** Loboziak and Alpern, 1978

Plate VI B

cf. *Spelaeotriletes owensi* Loboziak and Alpern 1978, pp. 60-61, pl. 2, figs. 15-17.

*Description.—*Spore circular, pseudosaccate.

Occurrence.— Hikoroichi Formation, Kanokura Formation.

*Distribution.—*Genus *Spelaeotriletes* is reported from the Visean-Serpukhovian of Northern Gondwanan (Playford *et al.*, 2008). *Spelaeotriletes owensii* ranges from the early to late Carboniferous (Clayton, 1995).

Remark.—Spelaeotriletes is of exclusively Gondwanan occurrence (Playford *et al.*, 2001). The lack of *in situ* material prevents sure parent plant affiliation, but Playford *et al.* (2001) suggested affiliation to the true ferns (Pterophyta) and/or the lycopods (Lycopodophyta).

Anteturma Variegerminantes Pot a

Turma Plicates (Naumova, 1937, 1939) Potoni , 1960

Subturma Monocolpates (Monosulcites) et Zonocolpates Potoni , 1970b

Genus ***Monoletes*** **(**Ibrahim, 1933) Schopf *et al.*, 1944

Type species.—Monoletes ovatus Schopf, 1935

?***Monoletes*** **cf.** ***ellipsoides*** **(Ibrahim, 1933) Schopf, 1938**

Plates VI E, VII A, B

1932 *Sporonites ellipsoides* Ibrahim in R. Potoni , p. 449, pl. 17, fig. 29.
1932 *Sporonites ellipsoides* Ibrahim, Neues Jahrbuch f. Min. etc. Beil. Bd. 67, p. 449, pi. 17, fig. 29.
1933 *Monoletes*, *Laevgatosporites ellipsoides* Ibrahim, Diss. Tech. Hochschule I Berlin, p. 40, pi. 4, fig. 29.
1934 *Monoletes*, *Punctatosporites ellipsoides* Ibrahim, Loose Arbeiten aus dem Inst. f. Palaobot. etc., Bd. 4, p. 158, pi. 7, fig. 35.
1934 *Monoletes Laevigatosporites*; *Sporites ellipsoides* Ibrahim, Wicher Arbeiten aus dem Inst. f. Palaobot. etc., Bd. 4, p. 185.
1938 *Monoletes ellipsoides* (Ibrahim 1932) Schopf, p. 45, pl. 1, fig. 14, pl. 6, figs. 5, 6.
1954 *Schopfipollenites ellipsoides* (Ibrahim 1932) R. Potoni and Kremp, p. 180.

Description.—Monolete spore with an amb elongate.
Occurrence.— Hikoroichi Formation.
Distribution.—Genus Monoletes is worldwidely distributed from the Upper Mississippian to Pennsylvanian (Playford *et al*., 2008). *Monoletes ellipsoides* is restricted to the Pennsylvanian (Millay *et al*., 1978).
Remark.—Monoletes is associated to Pteridospermales. Taylor (1978) suggested this pollen grains may represent a type transitional between wind and insect pollination.

Anteturma Trichomiformis Burgess and Edwards, 1991
Turma Tubiformis Burgess and Edwards, 1991
Infraturma Laevimurali Burgess and Edwards, 1991
Genus ***Laevitubulus*** Burgess and Edwards, 1991
Type species.—Laevitubulus tenuis Burgess and Edwards, 1991

Laevitubulus tenuis **Burgess and Edwards, 1991**

Plates I G-I, III I

1978 “unbranched tubular elements”, Pratt *et al.,* p. 131, pl. 2, figs 5-8.
1982 “black tube” in Edwards, p. 242, fig. 78.
1983 “larger smooth tubes” in Edwards *et al.,* p. 30.

1984 “tube type 4” in Al-Ameri, p. 384, pl. 2, fig. 7.
1991 *Laevitubulus tenuis* Burgess and Edwards, p. 47, figs. 1–4.

Occurrence.— Kawauchi Formation, Nakazato Formation.

*Remarks.—*It is worldwidely reported, generally abundant throughout the Silurian and Devonian (Burgess and Edwards, 1991; Edwards and Wellman, 1996). Its affinity is unknown.

Chapter IV: Discussion

IV.1. Paleozoic palynostratigraphy

The study of the Paleozoic palynology is considered the most effective tool for the rocks remarked with complex lithology. The studied outcrops of the Paleozoic rocks of Northeast Japan bear promising taxa to construct a palynostratigraphy for the Paleozoic (Figure 27). In this study, the results from the Silurian are represented by rare record of triangular palynomorphs associated with tabular remains. The results from the Devonian to Permian contain palynomorphs and some plant fragments. In particular, the studied samples from the Devonian outcrops are promising because I collected theses samples from rocks rich in marine fossils, permitting to construct a detailed palynostratigraphy for the Devonian of the Nakazato Formation.

IV.1.1. Silurian: Kawauchi Formation

The outcrop studied at the Kusayamizawa locality of the Kawauchi Formation, was assigned to the Wenlock (Sheinwoodian) from its trilobite fauna (Sugiyama, 1941; Kobayashi and Hamada, 1974; Tachibana, 1981).

Composition

The Kawauchi Formation contains a rich fossil fauna comprising trilobites, corals, stromatoporoids, brachiopods, bryozoans, conodonts (Sugiyama, 1940, 1941; Tachibana, 1967, 1981; Sakagami, 1970; Kobayashi and Hamada, 1974; Kato, 1982; Männik *et al.*, 2018). However, no plant report exists.

Paleovegetation

Laevigate trilete miospore-like grains were observed. Trilete spores appear from the Middle Ordovician as the product of dissociation of tetrads, first confined to southern Gondwana (Steemans *et al.*, 2009) before spreading worldwide. By the Late Silurian (Wenlock), trilete spores proliferate in terms of abundance, taxonomic diversity, and morphological disparity, presumably as the vascular plants underwent an adaptive radiation (e.g., Gray, 1985, 1991; Richardson, 1996).

Among microfossils, I also obtained acritarchs and tubular remains of *Laevitubulus tenuis* (Plate III). Acritarchs represent the resting cysts of phytoplanktonic algal protists. They are the dominant component of marine organic-walled microfossils in the Palaeozoic (Vecoli and Le Hérissé, 2004). Oldest *Laevitubulus* in uppermost Ordovician sedimentary deposits of the Anglo-Welsh Basin and is generally abundant in Silurian to Devonian deposits (Burgess and Edwards, 1991).

The presence of some framboid pyrite crystals is most probably representative of anoxic conditions during the sedimentation.

IV.1.2. Lower Devonian: Nakazato Formation

Samples were collected at the Higuchizawa locality outcropping along the upper stream of the Higuchizawa river in the Hikoroichi area, from the N3 Member of the Nakazato Formation. The outcrop yielded rich trilobite fauna including *Rhinophacops* suggesting latest Emsian to earliest Eifelian age (Kaneko, 2007).

The Nakazato Formation yields a rich shallow marine fauna, but no plant report exists so far. The palynoassemblage in this study thus represents the oldest terrestrial flora in Japan.

Age

I attempted an age confirmation from the palynoassemblage recovered. Lower to Middle Devonian dispersed spore assemblages are mostly documented from Laurussia and Gondwana. For Laurussia, standard miospore biozonations were first established by Richardson and McGregor (1986) for the Silurian and Devonian (Lochkovian) of the Old Red Sandstone deposits of the Welsh Borderland, UK, and adjacent basins. Then, the standard was emended and completed by Burgess and Richardson (1991) and Richardson (1992, 1996). Streel *et al.* (1987) and Steemans (1989) also modified Richardson and McGregor's (1986) biozones for the Devonian of the Ardenne-Rhenish regions and Western Europe. For northwestern Gondwana, standard miospore biozonations were established by Breuer and Steemans (2013) in Saudi Arabia and Libya.

The palynomorph assemblage from the N3 Member of the Nakazato Formation is characterized by the presence of biform sculpture (*Dibolisporites*) and abundance of *Apiculiretusispora*, *Dictyotriletes emsiensis* and *Verrucosisporites polygonalis*. Therefore, it is most similar to the *V. polygonalis-D. emsiensis* Assemblage Zone (*sensu* Richardson and McGregor, 1986) or PoW Oppel Zone (*sensu* Streel *et al.*, 1987 and Steemans, 1989) which correspond to the Pragian to early Emsian (Figure 25). Consistent with this comparison, I could not obtain *Emphanisporites*, *Camarazonosporites* and *Acinosporites* from the N3 Member, which characterize younger zones. In the scheme of Breuer and Steemans (2013), the Nakazato assemblage could be compared to the upper Pragian *Synorisporites papillensis*-*Cymbohilates baqaensis* assemblage zone in the dominance of simple laevigate spores, presence of cryptospores, and absence of any monolete spores which are characteristic of the younger zone (Figure 25).

In Asia, Gao (1981) and Tian *et al.* (2011) proposed spore assemblage zones based on palynofloras reported in South China (Figure 25). However, it should be noted that ages of these zones were determined by palynostratigraphical comparisons to the Laurussian and Gondwanan standards because other biostratigraphically informative fossils are absent in these regions. Gao (1981) defined eight Devonian spore assemblage zones for South China. Among them, the Nakazato assemblage could be compared to the Assemblage zone IV mainly known from Longhuashan (= Xujiachong) Formation of Yunnan for which the late Pragian to early Emsian age was inferred, because our assemblage contains *Retusotriletes triangulatus*, *Ap. plicata*, *V.* sp., and *D.* cf. *emsiensis*. Tian *et al.* (2011) further defined spore assemblage zones for the upper Silurian to Lower Devonian of southwest China from the first appearance datum (FAD) of characteristic species in this region, such as *Ambitisporites dilutus*, *Synorisporites verrucatus* and *Verrucosisporites polygonalis*. The Nakazato assemblage closely resembles the youngest assemblage in this scheme, i.e., the *V. polygonalis*-*Dibolisporites wetteldorfensis* assemblage zone. This zone was recognized within a horizon of the Xujiachong Formation, which is assigned to the Pragian stage. It is most characterized by the first appearance datums (FADs) of *Dib. eifeliensis* and *V. polygonalis*.

Cryptospores appeared in the Ordovician-Silurian and have a long stratigraphic range (Steemans *et al.*, 2009). Cryptospore dyads, loose dyads and hilate monads nearly vanished in the upper Lochkovian, although there are a few reports from the Middle and Upper Devonian strata (Richardson, 2007). The two species (*Pseudodyadospora petasus* and *Laevolancis* sp.) yielded in the Nakazato Formation are recorded in the Silurian to Lower Devonian deposits of many regions over Laurussia and Gondwana. In post-Lochkovian strata, *P. petasus* is reported from the Pragian-early Emsian of South China (Wellman *et al.*, 2012), while *Laevolancis* species from the Emsian of Laurussia (Russia: Chibrikova, 1959; England: Molyneux, 2006), northwestern Gondwana (Saudi Arabia: Molyneux and Al-Hajiri, 2000; Spain: Wellman *et al.*, 2023), and early Frasnian of northeastern Gondwana (Australia: Balme, 1988). These data imply that the Nakazato assemblage is not younger than the early Frasnian. The trilete spores obtained from the Nakazato Formartion (*Leiotriletes*), *Apiculiretusispora, Granulatisporites* were reported worldwide from the upper Silurian and Lower Devonian (McGregor, 1973; Breuer and Steemans, 2013). Besides, ornamented species greatly diversified during the Devonian, in particular, a proliferation of foveolate (*Brochotriletes*) and regularly verrucate (*Verrucosisporites)* species (Richardson and McGregor, 1986; Richardson, 1996). The appearance of species characterized by biform elements (*Dibolisporites*) happened no later than the late Lochkovian, as well expressed in the fact that following species are used as stratigraphic markers of the post-Lochkovian age: *D. emsiensis* (Lochkovian to Eifelian), *V. polygonalis* (Pragian to Eifelian), *B. foveolatus* (Lochkovian to Frasnian) and *Calamospora atava* (Emsian to Frasnian) (Richardson and McGregor, 1986; Streel *et al*., 1987; Breuer and Steemans, 2013).

In summary, spore zonations established in Gondwana and Laurussia indicate a late Pragian age for the Nakazato assemblage, while those in Laurussia suggest a Pragian–early Emsian age. The Nakazato assemblage shares similarities with assemblages in China, which are considered to be Pragian in age (Tian *et al.*, 2011) or late Pragian-Emsian in age (Gao, 1981) (indicated by grey lines in Figure 25). On the other hand, based on trilobite and radiolarian assemblages, the N3 Member of the Nakazato Formation has been assigned an Emsian to Givetian age (Kobayashi, 1977; Kobayashi and Hamada, 1977; Minato *et al.*, 1979; Umeda, 1996b). Trilobite biostratigraphy further narrows down the age of the N3 Member to the latest Emsian–earliest Eifelian (Kaneko, 2007). Therefore, my palynostratigraphic results suggest a slightly older age than those based on marine index fossils. This may imply that relict vegetations from older Laurussia and Gondwana thrived in the Nakazato Formation area. It is also possible to hypothesize that there was a time lag in the appearance and disappearance of indices between the Nakazato area and other regions, although exact position is not clarified where the Nakazato Formation was deposited (Figure 25).

Vegetation

The assemblage recovered from the Nakazato Formation is dominated by cryptospores (*Laevolancis* sp., *Pseudodyadospora petasus*) and spores (*Ambitisporites avitus*, *Granulatisporites* cf. *muninensis*) with possible affinities to the rhyniophytes (Bhutta, 1987; Fanning *et al.*, 1991; Balme, 1995; Wellman *et al.*, 1998a, b). Although exact affinity should be clarified in future, there are many palynomorphs which could be shed from either of the rhyniophytes, zosterophyllophytes, trimerophytes (*Calamospora atava*, *Deltoidospora*

(*Leiotriletes*) *priddyi*, *R.* cf. *triangulatus*, cf. *R.* spp., *Apiculiretusispora* cf. *plicata*) (McGregor, 1973; Allen, 1980; Gensel, 1980; Bhutta, 1987; Balme, 1995). *Verrucosisporites* cf. *polygonalis* and *Aneurospora* spp. may have been produced by lycopsids (Allen, 1980; Balme, 1995). Cladoxylopsida are also represented by *Dibolisporites* cf. *echinaceus*, *D.* sp. and *Dictyotriletes* sp. (Balme, 1995). Water-conducting structures recovered from the Nakazato Formation probably belonged to rhyniophytes and/or zosterophyllophytes, lycophytes, trimerophytes.

These data reflect a vegetation consisting of only herbaceous plants which possibly lived in proximity to freshwater areas. The abundance of laevigate spores represented by *Retusotriletes* suggests that the zosterophyllophytes constituted major vegetation in the backland of the Nakazato Formation because *Zosterophyllum yunnanicum* Hsü (1966) and *Huia gracilis* Wang and Hao (2001) bear *R.* sp. and *R.* cf. *triangulatus* (Hsü, 1966; Cai and Schweitzer, 1983; Hao, 1985; Wang and Hao, 2001; Wang *et al.*, 2002; Wang, 2007), respectively. Their spores should have been easily transported by the rivers towards the Palaeo-Tethys Ocean and trapped in shallow marine sediments of the South Kitakami Belt. The abundance of spores and plant fragments found in the Nakazato assemblage could suggest that the entrapment site was located near the living habitats of these plants (Figure 26).

IV.1.3. Lower Devonian: Fukuji Formation

The Fukuji Formation is considered Lower Devonian (Lochkovian to Emsian) from its conodont and ostracod assemblages (Kuwano, 1987).

Composition and age

Only a poor assemblage could obtain from preparations, composed of miospores tentatively identified as *Deltoidospora* (*Leiotriletes*) sp., *Retusotriletes* cf. *triangulatus* and *Retusotriletes* sp. All taxa were also observed in the Nakazato Formation, that we assigned to a similar Pragian to Emsian age.

The frequent presence of the pyrite crystals with high number of framboid pyrite may indicate natural combustion before sedimentation.

Vegetation

Genera *Deltoidospora* (*Leiotriletes*) and *Retusotriletes* are usually associated with rhyniophytes, zosterophyllophytes or trimerophytes during the Devonian. They reflect a vegetation consisting of herbaceous plants distributed along freshwater areas.

IV.1.4. Lower Carboniferous: Hikoroichi Formation

Fossil fauna suggested a late Visean (early Carboniferous) age for the formation (Tazawa, 1984).

Composition

The palynological study of samples from the Carboniferous Hikoroichi Formation revealed an assemblage composed by six spore and one pollen taxa. No aquatic element was observed.

A comparison with the microflora previously reported by Yang and Tazawa (2000a) from the HK2 Member of the formation confirms close similarities with our assemblage. All genera identified in this work were reported by Yang and Tazawa (2000a), excepting pollen genus *Monoletes*.

Age

Retusotriletes cf. *crassus* ranges from the Carboniferous (Clayton and Lobozial, 1985). *Spelaeotriletes owensii* range is restricted to the Carboniferous (Clayton, 1995). *Calamospora* ranges from the Devonian to Triassic. *Monoletes* cf. *ellipsoides* range is restricted to the Carboniferous (Millay *et al*., 1978). *Punctatisporites* ranges from Paleozoic to Neogene. The common occurrence of taxa composing the assemblage is consistent with an early Carboniferous age.

The Carboniferous assemblage obtained in this study is bearing some Cathyasian elements according to Utting and Piasecki (1995). However, the opacity of sporomorphs did not permit species identification, preventing any further discussion. Genera obtained are widely reported from the early Carboniferous (e.g., Clayton and Lobozial, 1985).

Vegetation

Among spores obtained, *Calamospora* is usually associated with Equisetales (including calamitaceans, Sphenophyllales and Noeggerathiales), and is similar with *in situ* spores observed in Carboniferous *Calamites* and *Sphenophyllum* (Good, 1977). *Verrucosisporites* was possibly produced by Lycopsida (Balme, 1995), and *Densosporites* by herbaceous lycopods (Chaloner, 1958). According to distribution of world palynofloras by Utting and Piasecki (1995), the Permo-Carboniferous Caythasian palynofloral province was characterized by the presence of genera *Laevigatosporites*, *Limitisporites*, and *Densosporites.* In particular, Gao (1985) defined Cathaysian Carboniferous and Lower Permian assemblages in North China from the presence of genera *Laevigatosporites*, *Punctatosporites*, *Florinites*, *Limitisporites, Alisporites*, *Lycospora* and *Densosporites*.

Spelaeotriletes is of exclusively Gondwanan occurrence (Playford *et al*., 2001). The lack of *in situ* material prevents sure parent plant affiliation, but Playford *et al*. (2001) suggested affiliation to the true ferns (Pterophyta) and/or the lycopods (Lycopodophyta).

Deltoidospora was produced by herbaceous fern spores. *Punctatosporites* is also associated to Filicophytes, possibly Sphenophyllales (Libertin *et al*., 2008).

The only pollen genus observed, *Monoletes*, is associated to pteridosperms. Taylor (1978) suggested this pollen grains may represent a type transitional between wind and insect pollination.

I summarized my results and previous works, with botanical affinities of taxa, in Tables 5 and 6. The micro- and macrofloral assemblages recovered from the Hikoroichi Formation are coherent, the microflora being richer in the number of taxa. The paleoflora is dominated by taxa with affinities to the Lycopodiales, Equisetales and Filicales. Pteridosperms and Progymnosperms appear for the first time in Japanese sediments, each represented by one to two taxa.

IV.1.5. Permian: Kanokura Formation

A middle Permian age has been suggested for the Kanokura Formation inferred from its brachiopod fauna (Tazawa and Takaizumi,1987) and microflora (Yang and Tazawa, 2000b).

Composition

The palynological assemblage from the middle Permian Kanokura Formation is composed of five spore taxa. No aquatic element was observed.

Punctatisporites ranges from the Paleozoic to Neogene; *Granulatisporites* ranges from the Silurian to Early Eocene; *Verrucosisporites* ranges from the Devonian to Carboniferous; *Baculatisporites* ranges from the Middle Devonian to Neogene. The range of taxa composing the assemblage is consistent with a middle Permian age. The assemblage is not diversified but adds significant new data to the previously described palynoflora by Yang and Tazawa (2000b).

Vegetation

All taxa obtained are associated with ferns (four taxa) or maybe lycopsids (one taxon). No pollen grain was observed in this study, while pollen is represented by three species of pteridosperms and gymnosperms in the microflora reported by Yang and Tazawa (2000b). My results are coherent to previous works and add new taxa to the microflora. I summarized my results and previous works, with botanical affinities of taxa, in Tables 7 and 8.

IV.2. Paleovegetational changes during the Paleozoic

My palynological study records for the first-time possible apparition of terrestrial plants, which are characterized by trilete spores, from the late Silurian (Wenlock). The first reliable spore record is from the Early Devonian, reflecting a vegetation consisting of herbaceous plants distributed along freshwater areas. Assemblages are dominated by rhyniophytes, zosterophyllophytes, and trimerophytes, with a few lycophytes and cladoxylophytes.

Carboniferous vegetation radically changes, becoming dominated by the newly appeared Equisetales and Filicales. Lycophytes and cladoxylophytes diversify, while rhyniophytes, zosterophyllophytes and trimerophytes are not present anymore. Pollen is observed for the first time, represented by a few species with affinities to the pteridosperms and progymnosperms. Permian is marked by the diversification of Filicales and pollen-producing plants, represented by pteridosperms and conifers. The botanical affinities are illustrated in Tables 4, 6, 8, and 10.

IV. 3. Paleophytogeographic significance of the results for the past location of Japan

The paleogeographic configurations of Japan and eastern Asia have been intensively studied (e.g., Isozaki, 1996, 2019; Maruyama *et al*., 1997; Ehiro and Kanisawa, 1999; Isozaki *et al.*, 2010, 2011; Kasahara *et al*., 2010; Uno *et al*., 2011; Cocks and Torsvik, 2013; Wakita, 2013; Wakita *et al*., 2018; Tanaka *et al.*, 2018). Despite these efforts, the accretionary history of Japan is not still clearly understood for Middle Devonian and older times (Wakita *et al*., 2018).

The Kurosegawa Belt in southwest Japan is considered as a southern extension of the South Kitakami Belt, which constituted the South Kitakami – Kurosegawa Arc (Umeda 1996a; Ehiro and Kanisawa. 1999; Ehiro, 2000). Cocks and Torsvik (2013) hypothesized that this island arc originated in the Southern Hemisphere, and that it drifted to northern tropics by the Late Ordovician to accommodate paleomagnetic and paleontological observations. Palaeomagnetic data obtained from the Kurosegawa Belt indicate paleolatitudes of 5–15° N during the Silurian and Early Devonian (Shibuya *et al.*, 1983). The Silurian–Devonian coral, brachiopod, gastropod and trilobite faunas reported from the South Kitakami Belt show similarities to those from eastern Australia, South China and Central Asia (Hamada, 1959; Minato and Kato, 1977; Kaneko, 1990; Kato, 1990; Zhou and Campbell, 1990; Tazawa and Chen, 2001; Tazawa, 2002; Hua-Zhang and Cook, 2003; De Jong *et al.*, 2006; Williams *et al.*, 2014). These lands were amalgamated to form the northeastern part of Gondwana before the opening of the Palaeo-Tethys Ocean (Duan *et al.*, 2012). Hinterland analysis based on ages of detrital zircons suggests that the South Kitakami Belt was close to the South China Block before the Middle Devonian (Wakita *et al.*, 2018). Therefore, the South Kitakami Belt is considered to be developed as an island arc near the north of the South China block which was located in the northeastern Gondwana (Figure 26).

It has already been pointed out that the Silurian to Devonian fauna and flora of the South Kitakami Belt have affinities with those of coeval northern East Gondwana (Figure 26). For example, tabulate coral taxa yielded from the Kawauchi Formation are abundant in coeval strata of Australia and South China (e.g., Hamada, 1960; Kato, 1990)

The Nakazato palynoflora predominantly consists of cosmopolitan taxa but demonstrates the closest similarities to those of South China (Figure 26), in alignment with the paleogeographic history stated above. In particular, the palynoflora reported from the Xujiachong Formation (Lu and Ouyang, 1976; Gao, 1981 as the Longhuashan Formation; Tian *et al.*, 2011; Wellman *et al.,* 2012) shows strong similarities in its composition: eight of the 14 identified species, and all spore genera obtained of the Nakazato assemblage excepting *Laevolancis* and *Granulatisporites*, are reported from the Xujiachong Formation. In addition, *Laevolancis* is reported from Lochkovian strata of the Cuifengshan Group in which the Xujiachong Formation is included (Tian *et al.*, 2011). The dominance of laevigate spores in the Nakazato palynoassemblage (63%) is also true for those of the Xujiachong Formation in which *Retusotriletes* represents 28–78.5% (Tian *et al.*, 2011) or 49.5– 80% (Wellman *et al.*, 2012). Abundance of granulate or apiculate spores is also shared between the Nakazato palynoassemblage (9%) and those in the Xujiachong Formation: 14.5–20.5% (Tian *et al.*, 2011) or 12.5–38% (Wellman *et al.*, 2012) of *Apiculiretusispora*. Gao (1981) also noted that *Retusotriletes* and *Apiculiretusispora* account for 40–60% of the assemblage in the

Longhuashan Formation (*syn.* Xujiachong Formation), while these spores occupy about 70% in the Nakazato palynoassemblage.

The microfloral results obtained from the Fukuji, Hikoroichi and Kanokura formations do not permit reliable comparisons to discuss about relations with adjacent regions. However, the Hikoroichi Formation yields various corals and brachiopods showing affinities with those of northeastern Gondwana (Okawa *et al*., 2013). Asama (1985) further noted that the Early Permian Maiya Flora described from Nishikori (or Rodai) Formation belonged to the Cathaysian Floristic Province, distributed in China and Korea. Those previous works together with my new data support the paleogeographic inference that Japan was formed and developed near the northeastern margin of Gondwana during the Paleozoic (Figure 26).

Conclusions

This thesis proposed the first comprehensive study on Paleozoic microfloras of Japan, at the period when plants colonized the land and first terrestrial ecosystems developed. The results were based on materials collected from the Silurian to Permian strata of the three major areas with fossil-bearing sediments in Japan, i.e., the South Kitakami Belt in Northeast Japan, Hida-Gaien Belt in central Japan, and the Kurosegawa Belt in southwest Japan. The Hida-Gaien Belt only provided poor assemblages, and I could not obtain any reliable palynomorph from the Kurosegawa Belt. However, the South Kitakami Belt revealed for the first time microfloral assemblages. The late Silurian Kawauchi Formation yields probable trilete spores of terrestrial plants along with rare tubular remains; the Lower Devonian Nakazato Formation yielded a rich assemblage, representing the oldest vegetation of Japan. The microflora is dominated by rhyniophytes, zosterophyllophytes, and/or trymerophytes, with some lycopsids and cladoxylopsids. The common range of taxa suggests a Pragian to Emsian age. The microflora has furthermore great similarities to those of the South China agreeing with the hypothesis that Proto Japan was formed and developed near the northeastern margin of Gondwana. The Hikoroichi Formation revealed an assemblage composed by six spore with affinities to the Lycophytes and Filicophytes, and one pteridosperm pollen taxa, consistent with an early Carboniferous age. The middle Permian Kanokura Formation yielded five spore taxa, which were not reported in previous palynological studies. All taxa obtained are associated with ferns (four taxa) or maybe lycopsids (one taxa).

I trace for the first time the evolution of vegetations in Japan from the late Silurian to Permian and propose a first outline for Paleozoic palynostratigraphy.

Acknowledgements

I am very grateful to Professor Akihisa Kitamura for his outstanding guidance and his critical guiding during this study besides his great help to me to start my research studies in Shizuoka University after my contract was ended at the Botanical Gardens of Osaka City University. I deeply thank Dr. Julien Legrand for his help and support for each single step of this study and for several and multiple discussions. I seriously thank Professor Toshihiro Yamada for his valuable discussion on the early land plants and his understanding of the linking between the living and fossilized lycopsids plants and for his help for me to be here in Japan. I am thankful for Professor Toshifumi Komatsu for his help in the field trip and for his experience in the study of the Paleozoic of Japan, beside the discussion to study the Devonian of Japan, and many discussions at the Laboratory in Shizuoka University. Further, I strongly appreciate the great role done by Professor Yamada and Professor Kitamura with help from Dr. Legrand to help me to transfer from Osaka City University to Shizuoka University, and also the fourteen month I studied with Professor Yamada at the Botanical Gardens. It was a great time for me as a training to understand the plant science as living and fossilized.

I appreciate and thank all the members of the Museum of Natural and Environmental History, Shizuoka, Japan, for permitting the SEM observation. I thank Ofunato City and Takayama City for permitting the field research. I would like to offer my sincerest gratitude to Shizuoka University for the financial support which covered all my research activities including the field trips and attendance at the international conferences in Tokyo during the study of the PhD.

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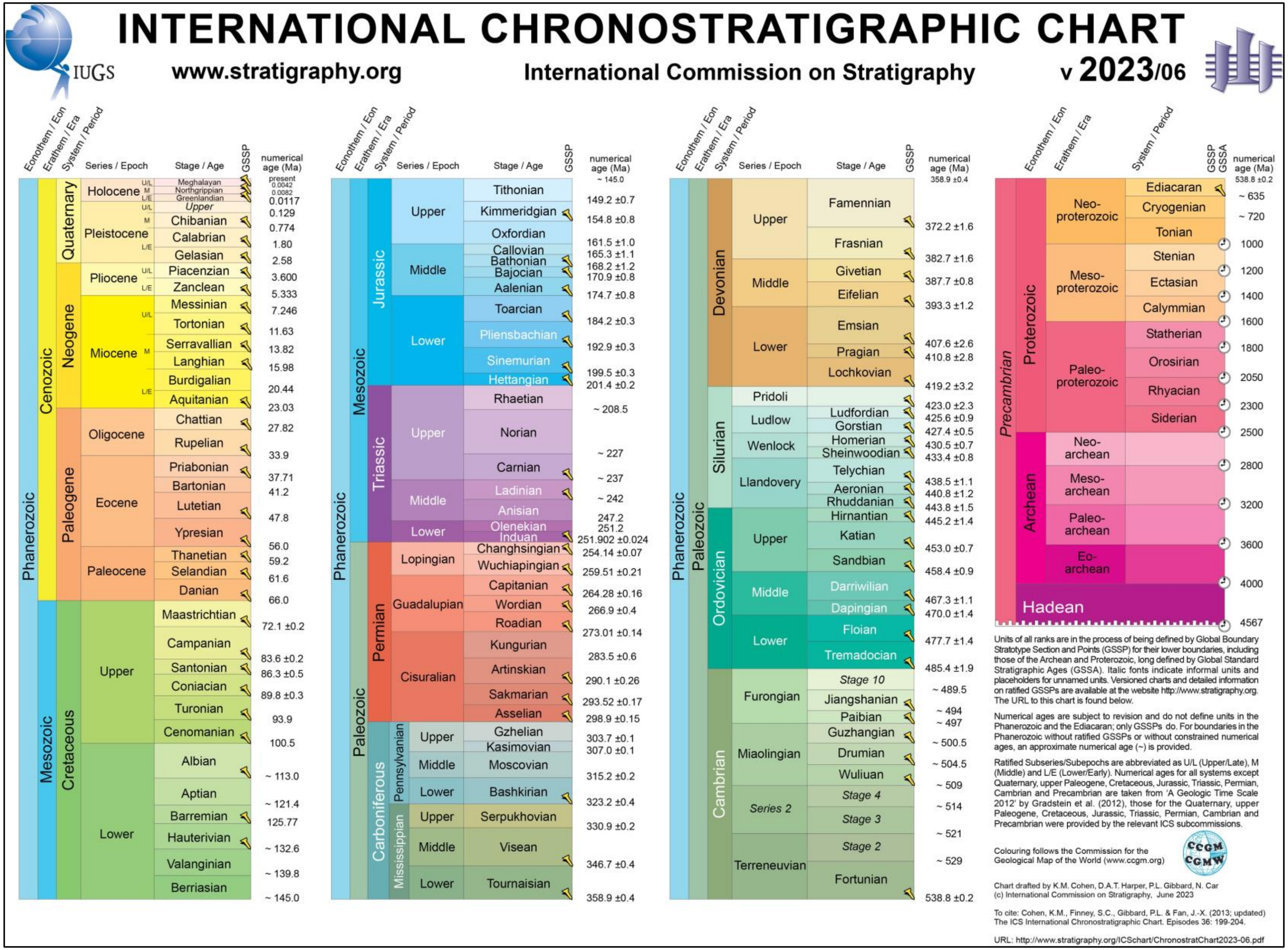


INTERNATIONAL CHRONOSTRATIGRAPHIC CHART

IUGS www.stratigraphy.org International Commission on Stratigraphy v 2023/06

Eonothem / Eon	Erathem / Era	System / Period	Series / Epoch	Stage / Age	GSSP	numerical age (Ma) present
Phanerozoic	Cenozoic	Quaternary	Holocene U/L	Meghalayan	✓	0.0042
			M	Northgrippian	✓	0.0082
			L/E	Greenlandian	✓	0.0117
			Pleistocene U/L	*Upper*		0.129
			M	Chibanian	✓	0.774
			L/E	Calabrian	✓	1.80
				Gelasian	✓	2.58
		Neogene	Pliocene U/L	Piacenzian	✓	3.600
			L/E	Zanclean	✓	5.333
			Miocene U/L	Messinian	✓	7.246
				Tortonian	✓	11.63
			M	Serravallian	✓	13.82
				Langhian	✓	15.98
			L/E	Burdigalian		20.44
				Aquitanian	✓	23.03
		Paleogene	Oligocene	Chattian	✓	27.82
				Rupelian	✓	33.9
			Eocene	Priabonian	✓	37.71
				Bartonian		41.2
				Lutetian	✓	47.8
				Ypresian	✓	56.0
			Paleocene	Thanetian	✓	59.2
				Selandian	✓	61.6
				Danian	✓	66.0
	Mesozoic	Cretaceous	Upper	Maastrichtian	✓	72.1 ±0.2
				Campanian	✓	83.6 ±0.2
				Santonian	✓	86.3 ±0.5
				Coniacian	✓	89.8 ±0.3
				Turonian	✓	93.9
				Cenomanian	✓	100.5
			Lower	Albian	✓	~ 113.0
				Aptian		~ 121.4
				Barremian	✓	125.77
				Hauterivian	✓	~ 132.6
				Valanginian		~ 139.8
				Berriasian		~ 145.0

Eonothem / Eon	Erathem / Era	System / Period	Series / Epoch	Stage / Age	GSSP	numerical age (Ma) ~ 145.0
Phanerozoic	Mesozoic	Jurassic	Upper	Tithonian		149.2 ±0.7
				Kimmeridgian	✓	154.8 ±0.8
				Oxfordian		161.5 ±1.0
			Middle	Callovian		165.3 ±1.1
				Bathonian	✓	168.2 ±1.2
				Bajocian	✓	170.9 ±0.8
				Aalenian	✓	174.7 ±0.8
			Lower	Toarcian	✓	184.2 ±0.3
				Pliensbachian	✓	192.9 ±0.3
				Sinemurian	✓	199.5 ±0.3
				Hettangian	✓	201.4 ±0.2
		Triassic	Upper	Rhaetian		~ 208.5
				Norian		~ 227
				Carnian	✓	~ 237
			Middle	Ladinian	✓	~ 242
				Anisian		247.2
			Lower	Olenekian		251.2
				Induan	✓	251.902 ±0.024
	Paleozoic	Permian	Lopingian	Changhsingian	✓	254.14 ±0.07
				Wuchiapingian	✓	259.51 ±0.21
			Guadalupian	Capitanian	✓	264.28 ±0.16
				Wordian	✓	266.9 ±0.4
				Roadian	✓	273.01 ±0.14
			Cisuralian	Kungurian		283.5 ±0.6
				Artinskian	✓	290.1 ±0.26
				Sakmarian	✓	293.52 ±0.17
				Asselian	✓	298.9 ±0.15
		Carboniferous Pennsylvanian	Upper	Gzhelian		303.7 ±0.1
				Kasimovian		307.0 ±0.1
			Middle	Moscovian		315.2 ±0.2
			Lower	Bashkirian	✓	323.2 ±0.4
		Mississippian	Upper	Serpukhovian		330.9 ±0.2
			Middle	Visean	✓	346.7 ±0.4
			Lower	Tournaisian	✓	358.9 ±0.4

Eonothem / Eon	Erathem / Era	System / Period	Series / Epoch	Stage / Age	GSSP	numerical age (Ma) 358.9 ±0.4
Phanerozoic	Paleozoic	Devonian	Upper	Famennian	✓	372.2 ±1.6
				Frasnian	✓	382.7 ±1.6
			Middle	Givetian	✓	387.7 ±0.8
				Eifelian	✓	393.3 ±1.2
			Lower	Emsian	✓	407.6 ±2.6
				Pragian	✓	410.8 ±2.8
				Lochkovian	✓	419.2 ±3.2
		Silurian	Pridoli		✓	423.0 ±2.3
			Ludlow	Ludfordian	✓	425.6 ±0.9
				Gorstian	✓	427.4 ±0.5
			Wenlock	Homerian	✓	430.5 ±0.7
				Sheinwoodian	✓	433.4 ±0.8
			Llandovery	Telychian	✓	438.5 ±1.1
				Aeronian	✓	440.8 ±1.2
				Rhuddanian	✓	443.8 ±1.5
		Ordovician	Upper	Hirnantian	✓	445.2 ±1.4
				Katian	✓	453.0 ±0.7
				Sandbian	✓	458.4 ±0.9
			Middle	Darriwilian	✓	467.3 ±1.1
				Dapingian	✓	470.0 ±1.4
			Lower	Floian	✓	477.7 ±1.4
				Tremadocian	✓	485.4 ±1.9
		Cambrian	Furongian	*Stage 10*		~ 489.5
				Jiangshanian	✓	~ 494
				Paibian	✓	~ 497
			Miaolingian	Guzhangian	✓	~ 500.5
				Drumian	✓	~ 504.5
				Wuliuan	✓	~ 509
			Series 2	*Stage 4*		~ 514
				Stage 3		~ 521
			Terreneuvian	*Stage 2*		~ 529
				Fortunian	✓	538.8 ±0.2

Eonothem / Eon	Erathem / Era	System / Period	GSSP GSSA	numerical age (Ma) 538.8 ±0.2
Precambrian Proterozoic	Neo-proterozoic	Ediacaran	✓	~ 635
		Cryogenian		~ 720
		Tonian	◷	1000
	Meso-proterozoic	Stenian	◷	1200
		Ectasian	◷	1400
		Calymmian	◷	1600
	Paleo-proterozoic	Statherian	◷	1800
		Orosirian	◷	2050
		Rhyacian	◷	2300
		Siderian	◷	2500
Archean	Neo-archean		◷	2800
	Meso-archean		◷	3200
	Paleo-archean		◷	3600
	Eo-archean		◷	4000
Hadean			◷	4567

Units of all ranks are in the process of being defined by Global Boundary Stratotype Section and Points (GSSP) for their lower boundaries, including those of the Archean and Proterozoic, long defined by Global Standard Stratigraphic Ages (GSSA). Italic fonts indicate informal units and placeholders for unnamed units. Versioned charts and detailed information on ratified GSSPs are available at the website http://www.stratigraphy.org. The URL to this chart is found below.

Numerical ages are subject to revision and do not define units in the Phanerozoic and the Ediacaran; only GSSPs do. For boundaries in the Phanerozoic without ratified GSSPs or without constrained numerical ages, an approximate numerical age (~) is provided.

Ratified Subseries/Subepochs are abbreviated as U/L (Upper/Late), M (Middle) and L/E (Lower/Early). Numerical ages for all systems except Quaternary, upper Paleogene, Cretaceous, Jurassic, Triassic, Permian, Cambrian and Precambrian are taken from 'A Geologic Time Scale 2012' by Gradstein et al. (2012), those for the Quaternary, upper Paleogene, Cretaceous, Jurassic, Triassic, Permian, Cambrian and Precambrian were provided by the relevant ICS subcommissions.

Colouring follows the Commission for the Geological Map of the World (www.ccgm.org)

Chart drafted by K.M. Cohen, D.A.T. Harper, P.L. Gibbard, N. Car
(c) International Commission on Stratigraphy, June 2023

To cite: Cohen, K.M., Finney, S.C., Gibbard, P.L. & Fan, J.-X. (2013; updated) The ICS International Chronostratigraphic Chart. Episodes 36: 199-204.

URL: http://www.stratigraphy.org/ICSchart/ChronostratChart2023-06.pdf

Figure 1. International Chronostratigraphic Chart (v 2023/09) (International Commission on Stratigraphy; https://stratigraphy.org/chart).

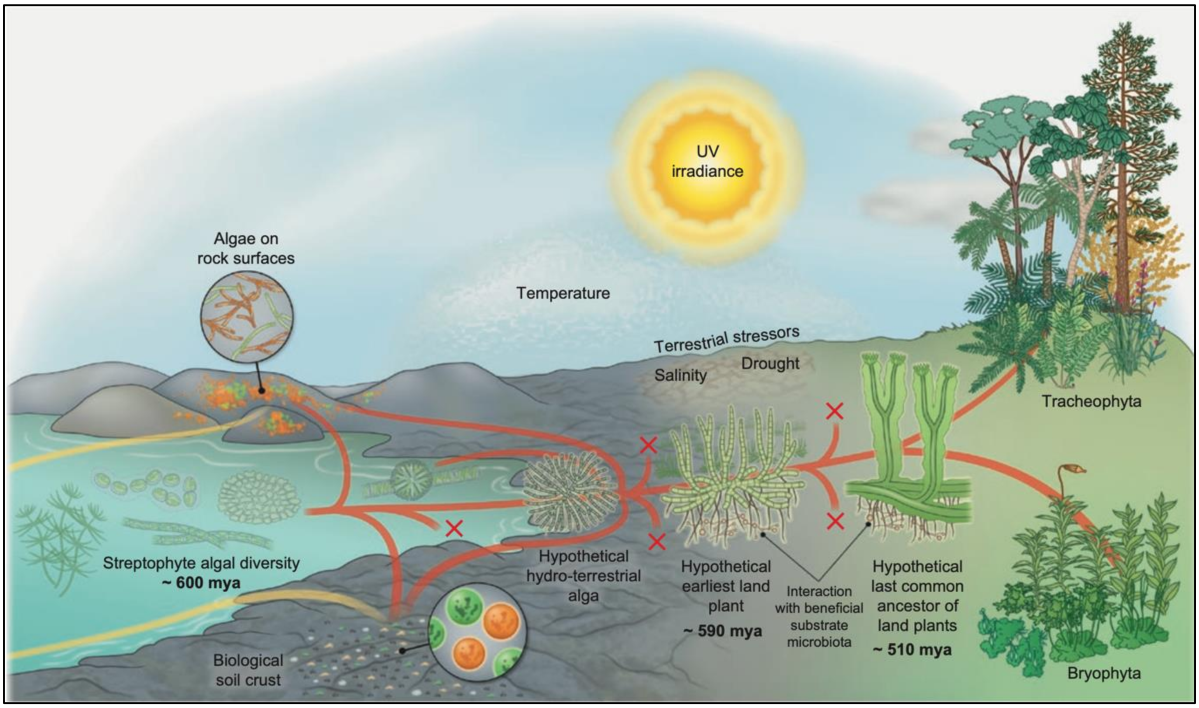
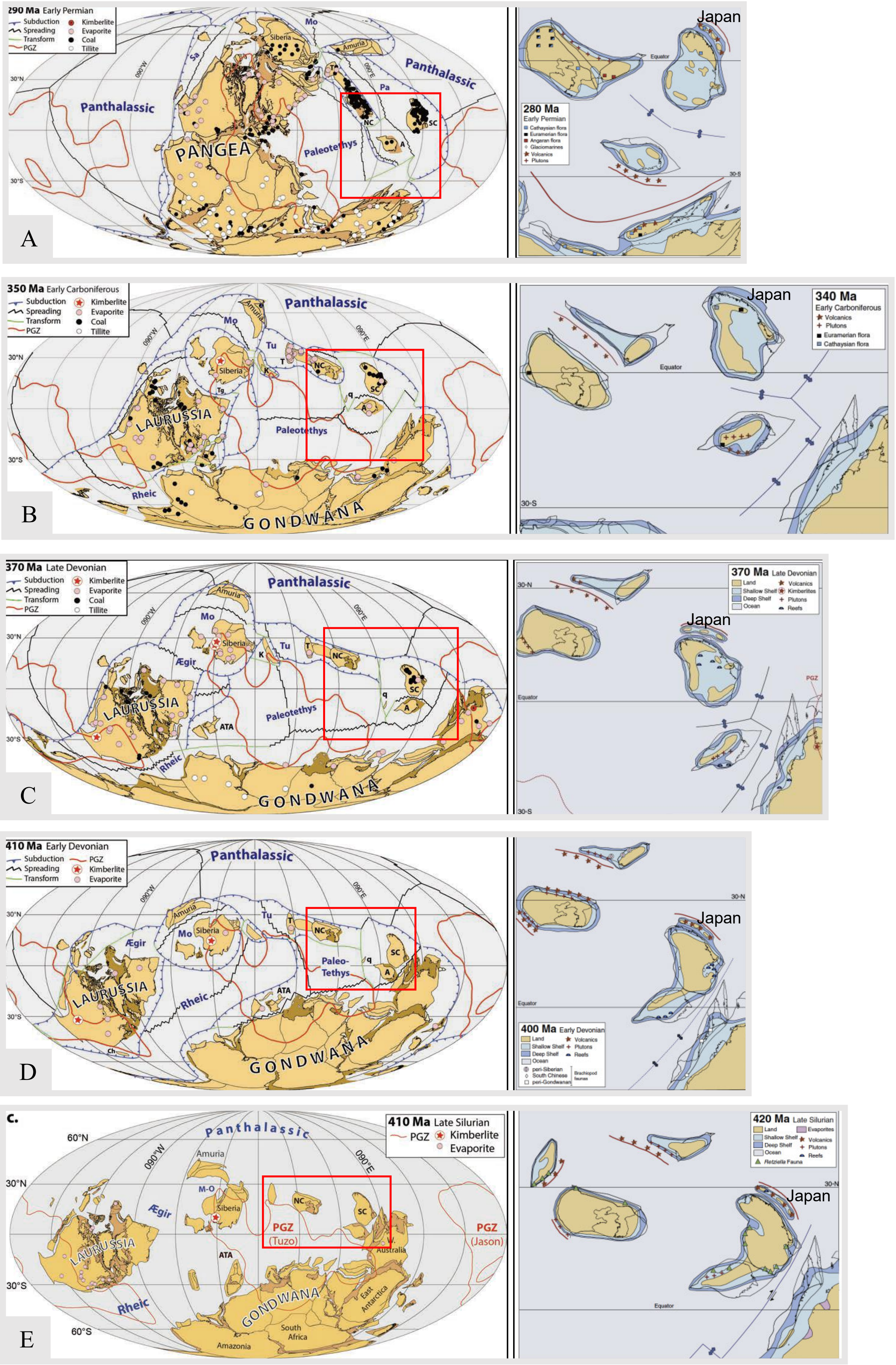
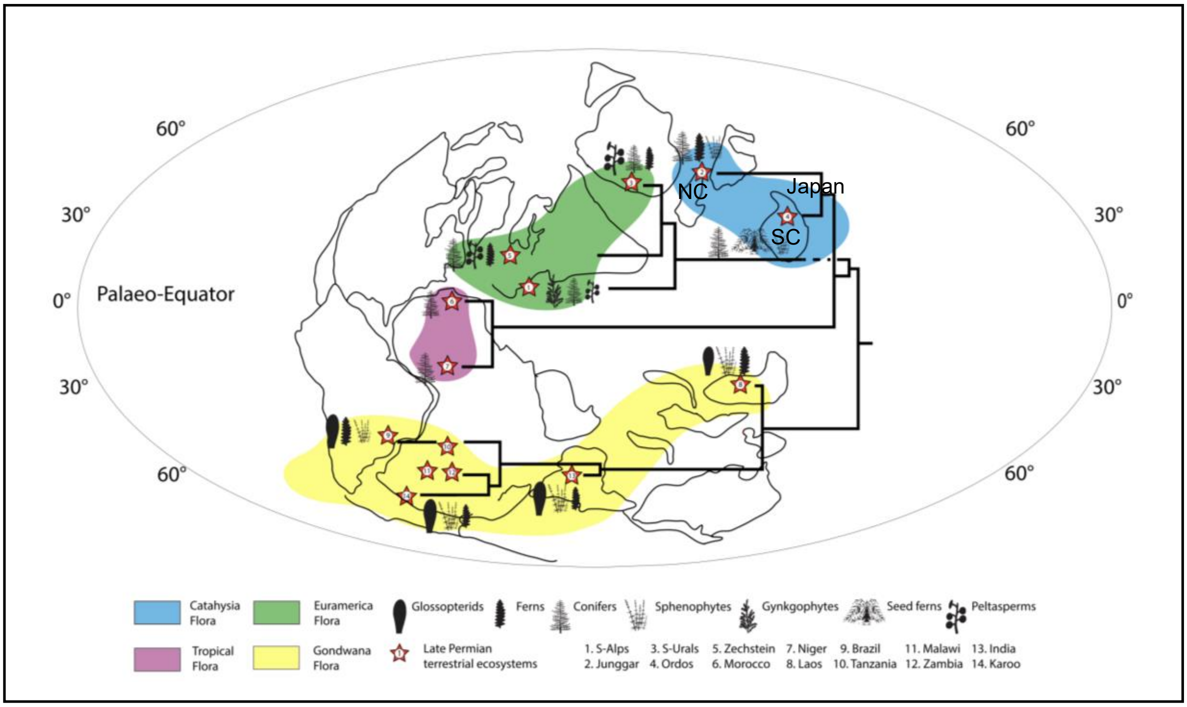


Figure 2. Evolutionary scenario for the terrestrialization process of plants (Fürst-Jansen *et al.*, 2020).



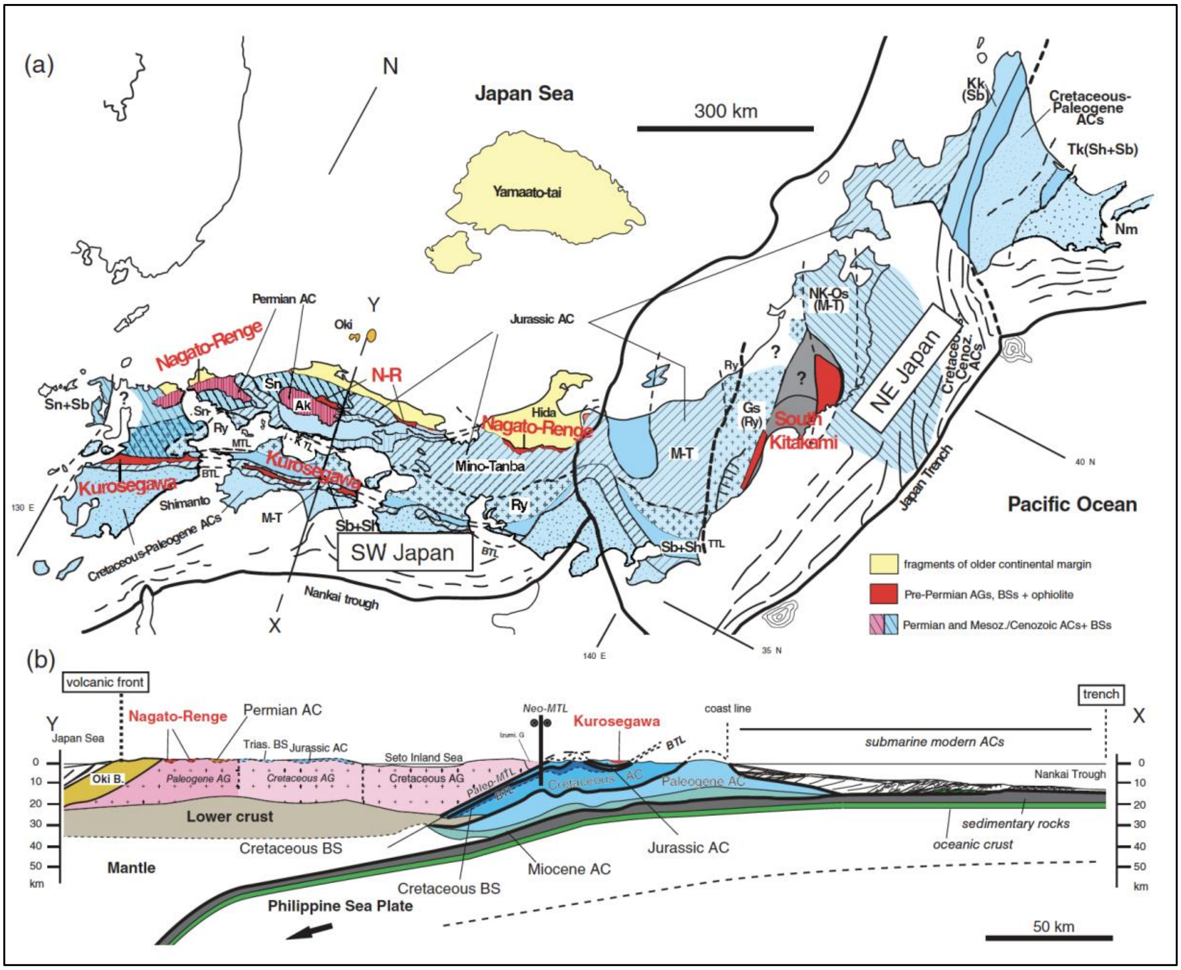
NC: North China
SC: South China

Figure 3. Tectonic evolution of Japan (modified from Cocks and Torsvik, 2013; Torsvik and Cocks, 2016) .



NC: North China
SC: South China

Figure 4. Late Permian terrestrial floras (Bernardi *et al.*, 2017).



AC, accretionary complex; AG, arc granitoid; BS, blueschist; AK, Akiyoshi; BTL, butsuzo tectonic line; Gs, Gosaisho; I-KTL, Ishigaki-Kuga tectonic line; Kk, Kamuikotan; M-T, Mino-Tanba; MTL, Median tectonic line; Nk-Os, North Kitakami-Oshima; Nm, Nemuro; Ry, Ryoke; Sb, Sanbagawa; Sn, Sangun; Tk, Tokoro; TTL, Tanakura tectonic line.

Figure 5. The distribution of Paleozoic rocks in Japan (Isozaki, 2019).

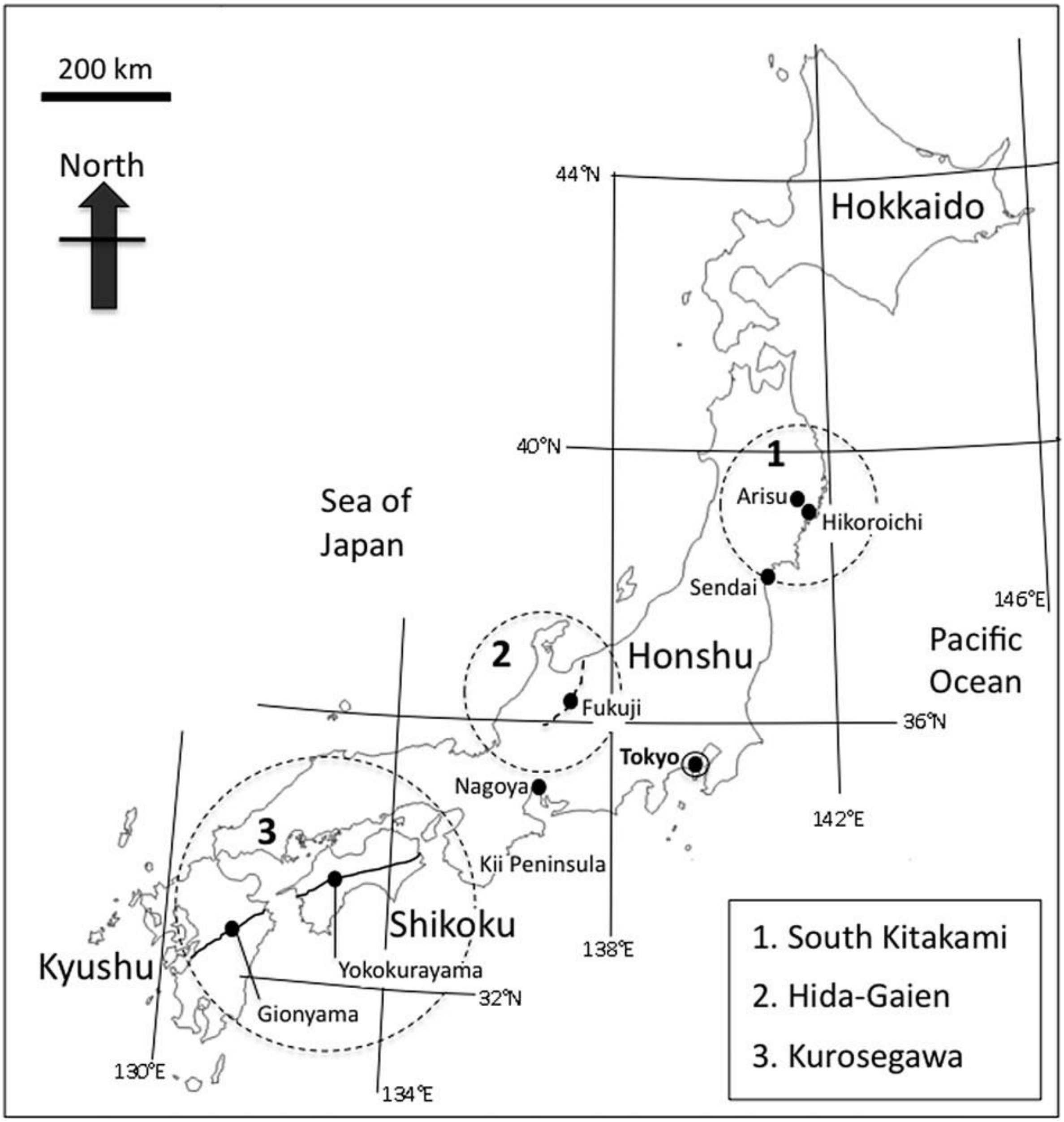
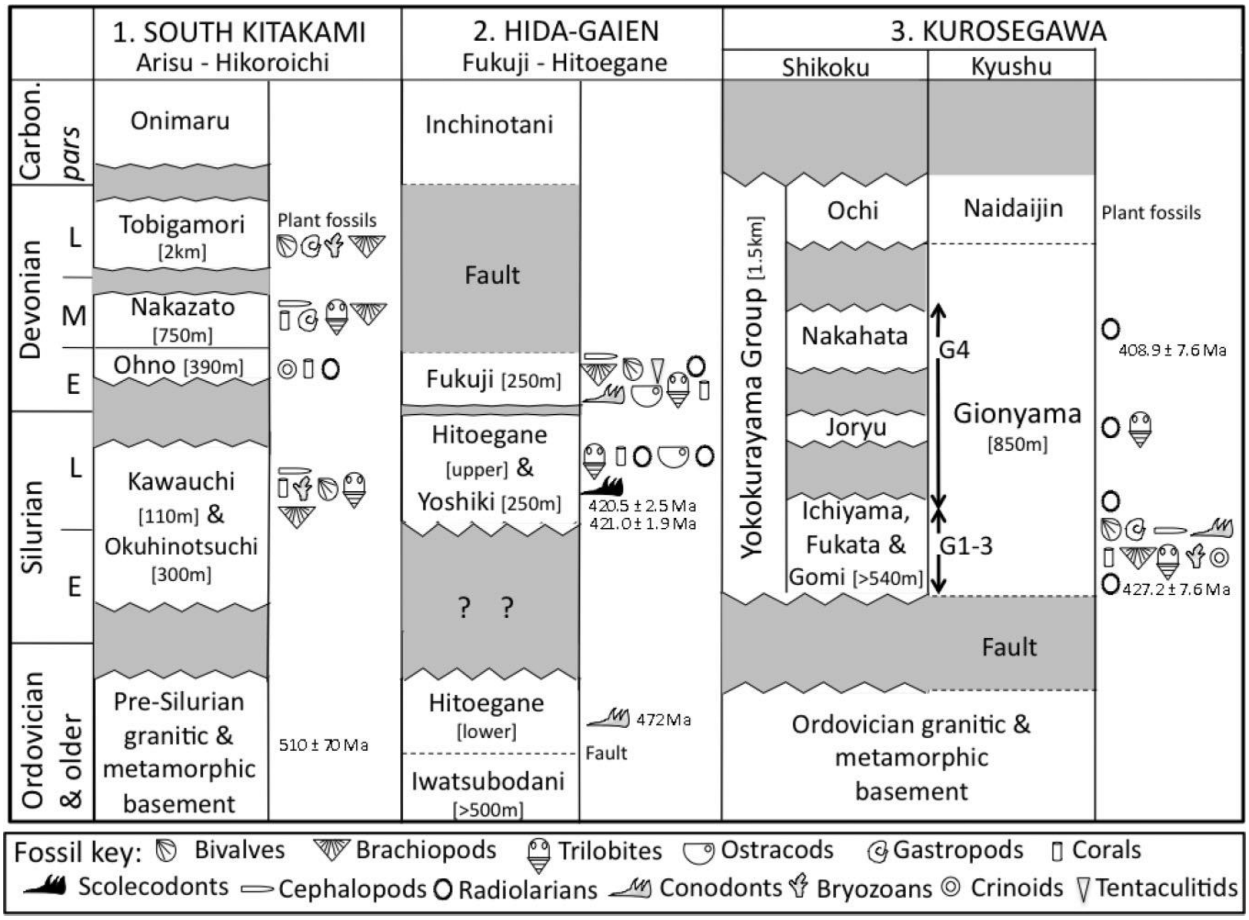


Figure 6. Map showing the geographical location of the three major fossil-bearing terranes of Ordovician, Silurian and Devonian rocks in Japan (Williams *et al*., 2014).



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MI. P: Miyagi Prefecture

Figure 8. Location of the Silurian to Devonian outcrops (in red) in the South Kitakami Belt of Iwate Prefecture, northeast Japan (Stocker, 2021).

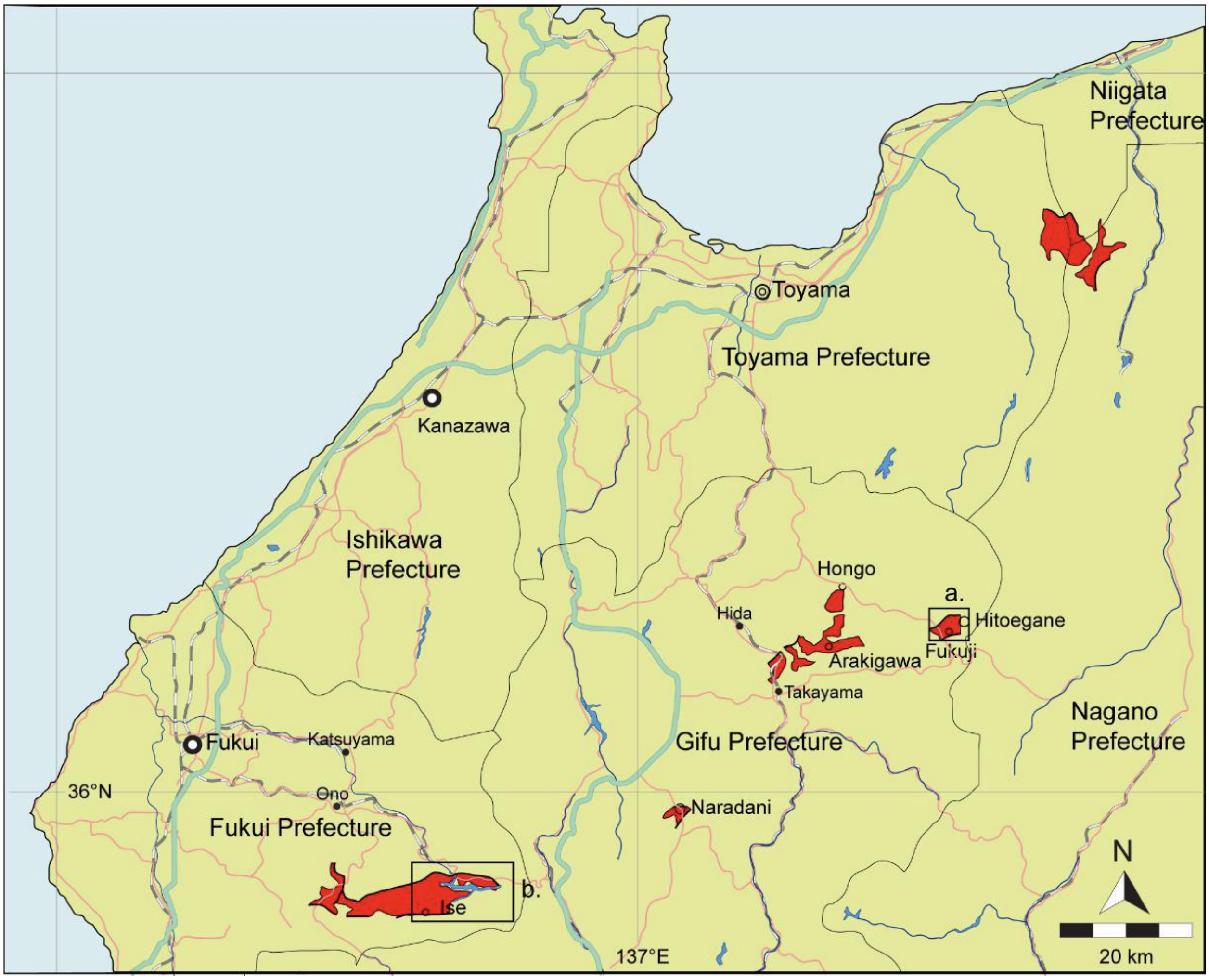

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Figure 10. Location of the Silurian and Devonian outcrops (in red) in the Kurosegawa Belt in southwestern Japan (Stocker, 2021).

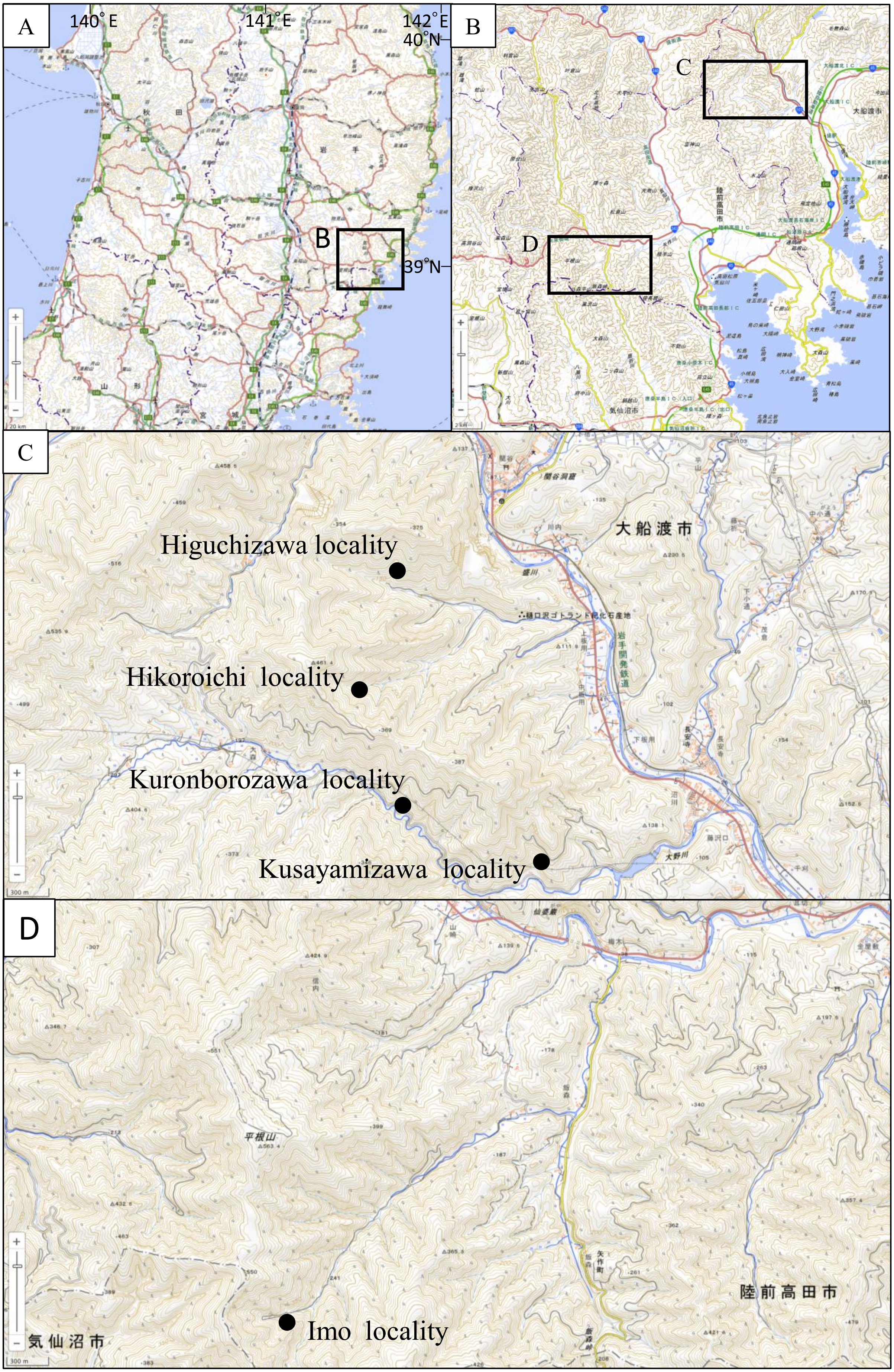


Figure 11. Topographical maps of sampled locality in the South Kitakami Belt (maps from Geographical Survey Institute; https://maps.gsi.go.jp).

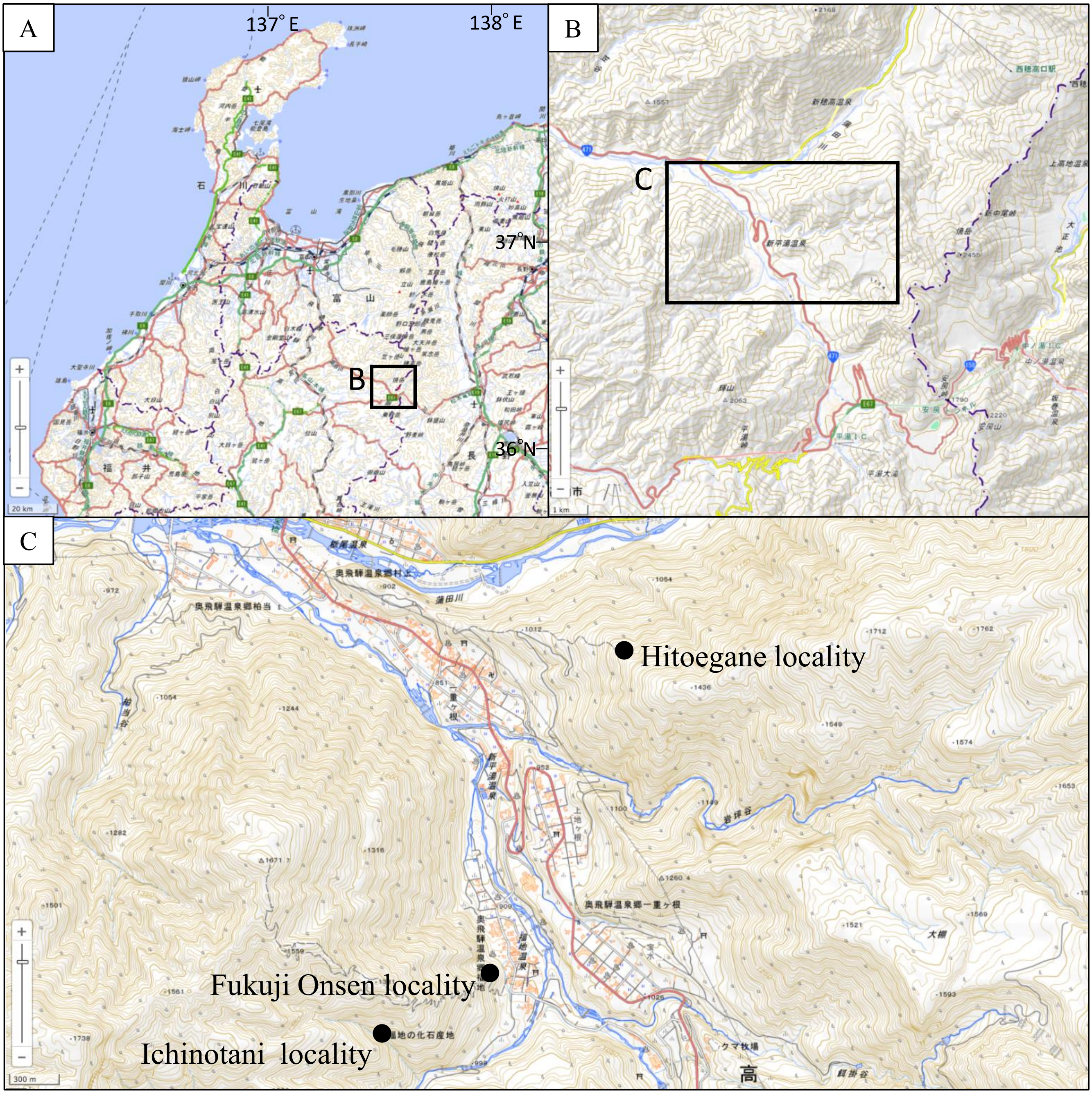


Figure 12. Topographical maps of sampled locality in the Hida-Gaien Belt (maps from Geographical Survey Institute; https://maps.gsi.go.jp).

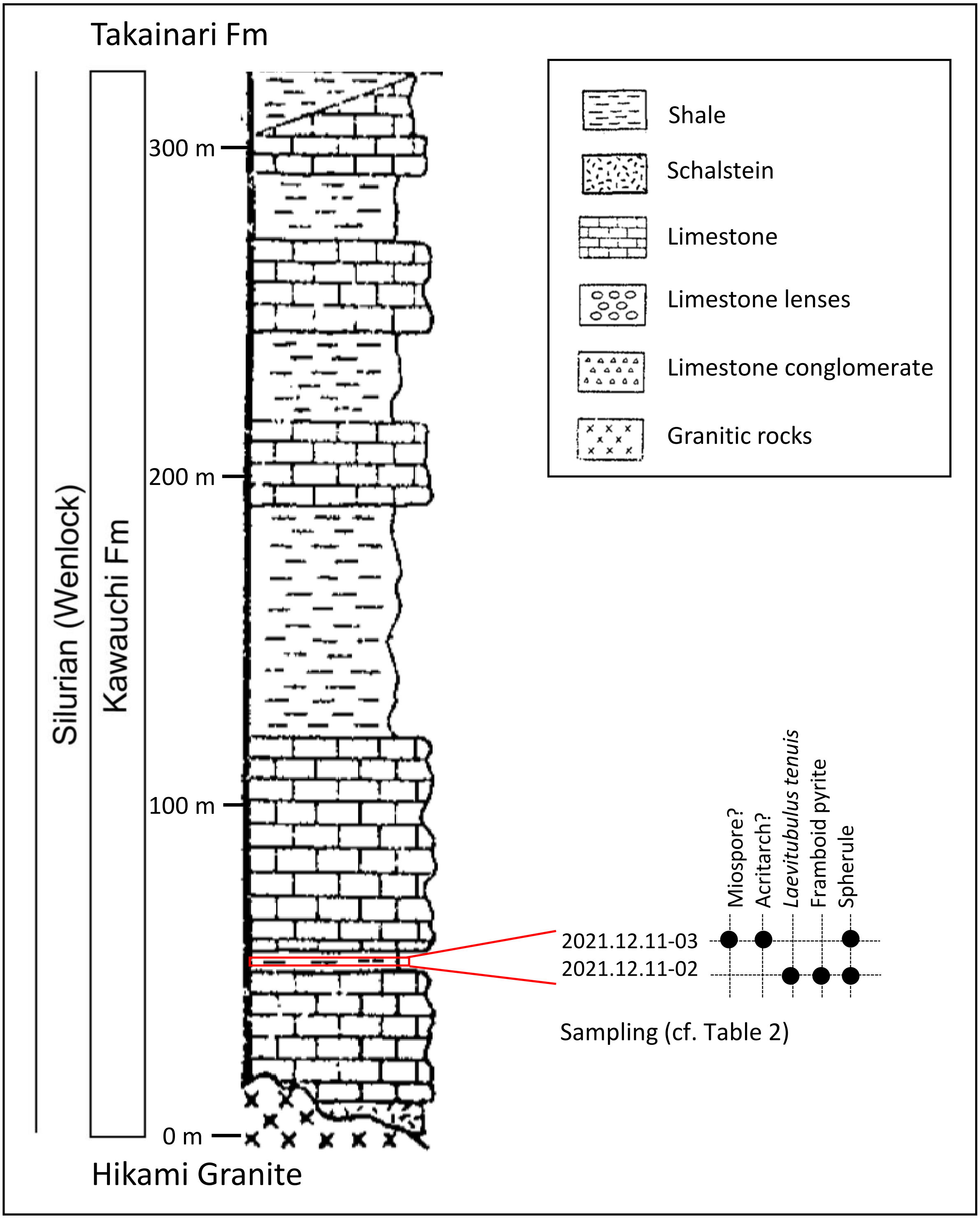


Figure 13. Generalized stratigraphic column of the Silurian Kawauchi Formation across various localities in the Hikoroichi area (modified from Hamada, 1959).

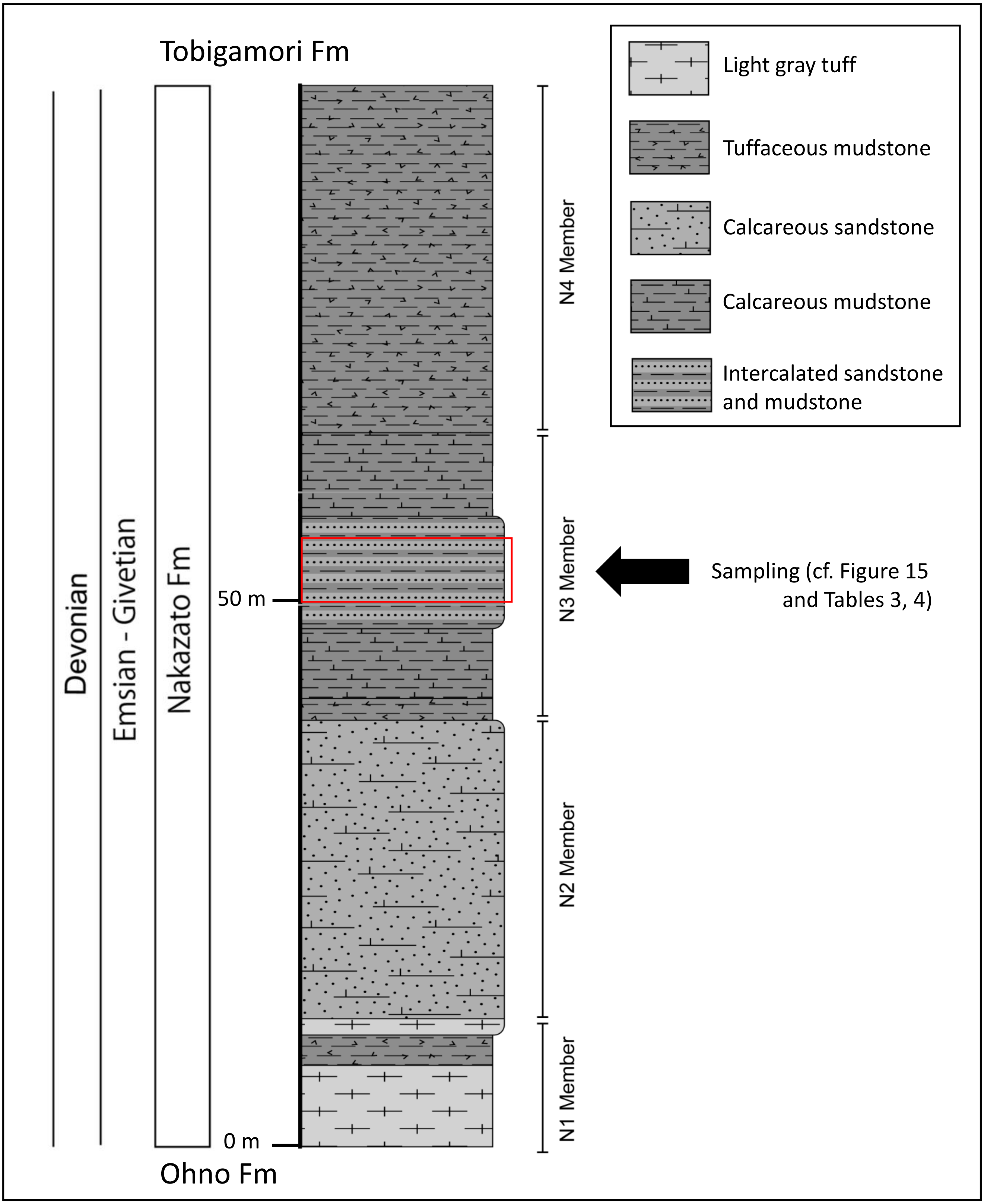
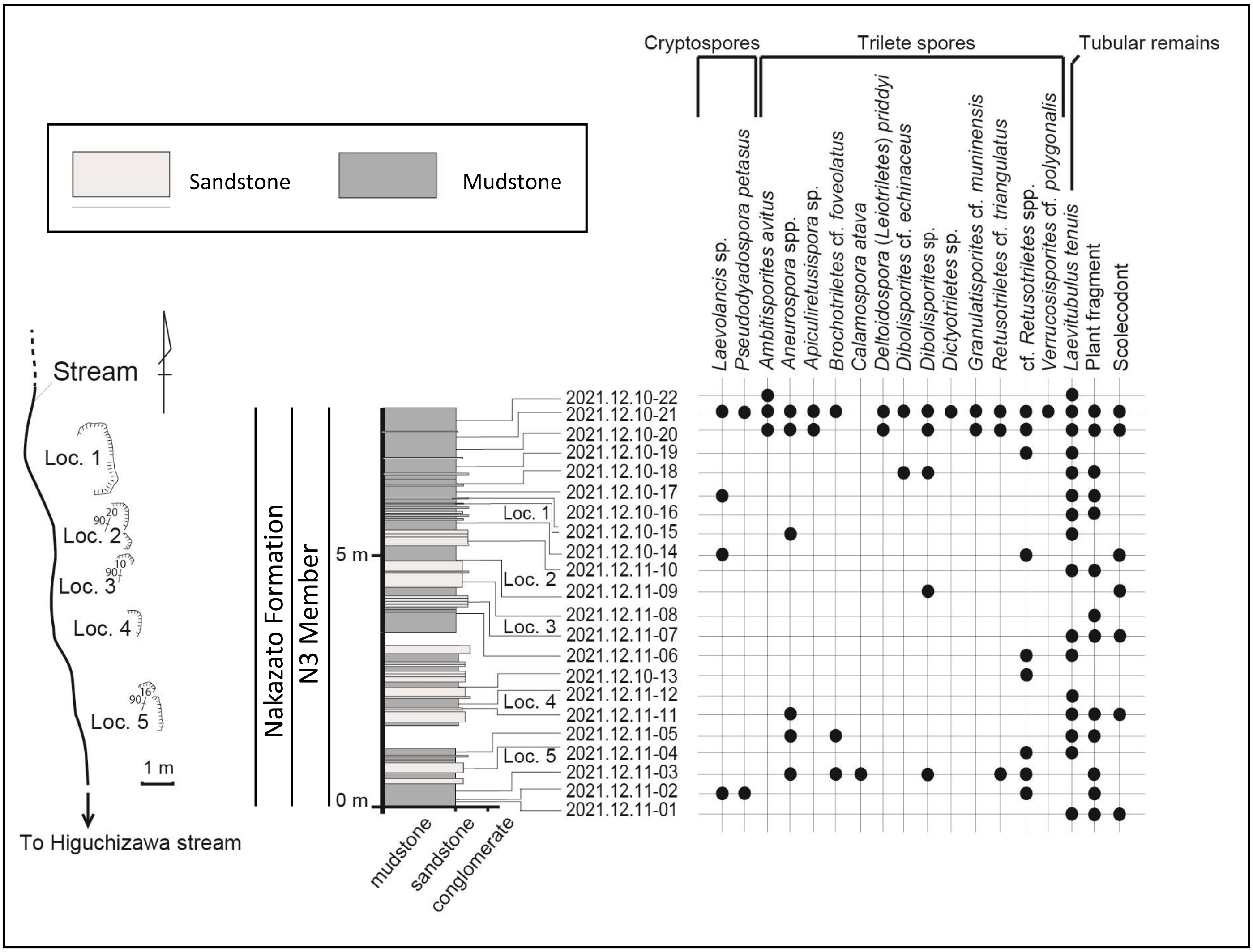


Figure 14. Generalized stratigraphic column of the Nakazato Formation (modified from Okubo, 1950; Stocker, 2021).



	Cryptospores		Trilete spores													Tubular remains		
	Laevolancis sp.	*Pseudodyadospora petasus*	*Ambitisporites avitus*	*Aneurospora* spp.	*Apiculiretusispora* sp.	*Brochotriletes* cf. *foveolatus*	*Calamospora atava*	*Deltoidospora* (*Leiotriletes*) *priddyi*	*Dibolisporites* cf. *echinaceus*	*Dibolisporites* sp.	*Dictyotriletes* sp.	*Granulatisporites* cf. *muninensis*	*Retusotriletes* cf. *triangulatus*	cf. *Retusotriletes* spp.	*Verrucosisporites* cf. *polygonalis*	*Laevitubulus tenuis*	Plant fragment	Scolecodont
2021.12.10-22			●													●		
2021.12.10-21	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●
2021.12.10-20			●	●	●			●		●		●	●	●		●	●	●
2021.12.10-19														●		●		
2021.12.10-18									●	●						●	●	
2021.12.10-17	●															●	●	
2021.12.10-16																●	●	
2021.12.10-15				●												●		
2021.12.10-14	●													●				●
2021.12.11-10																●	●	
2021.12.11-09										●								●
2021.12.11-08																	●	
2021.12.11-07																●	●	●
2021.12.11-06														●		●		
2021.12.10-13														●				
2021.12.11-12																●		
2021.12.11-11				●												●	●	●
2021.12.11-05				●		●										●	●	
2021.12.11-04														●		●		
2021.12.11-03				●		●	●			●			●	●			●	
2021.12.11-02	●	●												●			●	
2021.12.11-01																●	●	●

Figure 15. Route map (left) and columnar section (right) of the Higuchizawa locality in the Nakazato Formation. Loc. 1, trilobite-bearing layer; Loc. 2, tuffaceous sandstone (N20°E, 90°); Loc. 3, tuffaceous sandstone (N10°E, 90°); Loc. 4, trilobite-bearing layer; Loc. 5, muddy sandstone (N16°E, 90°).

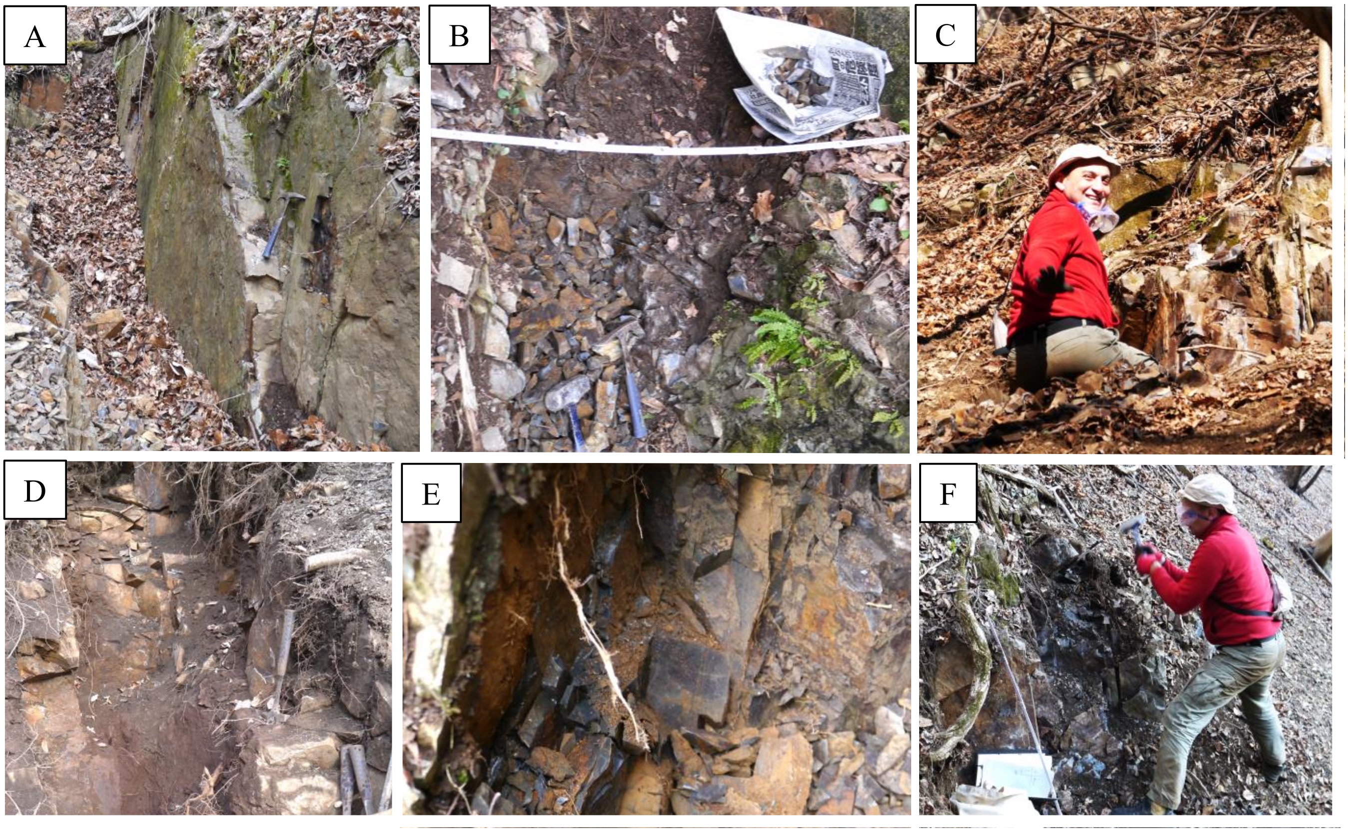
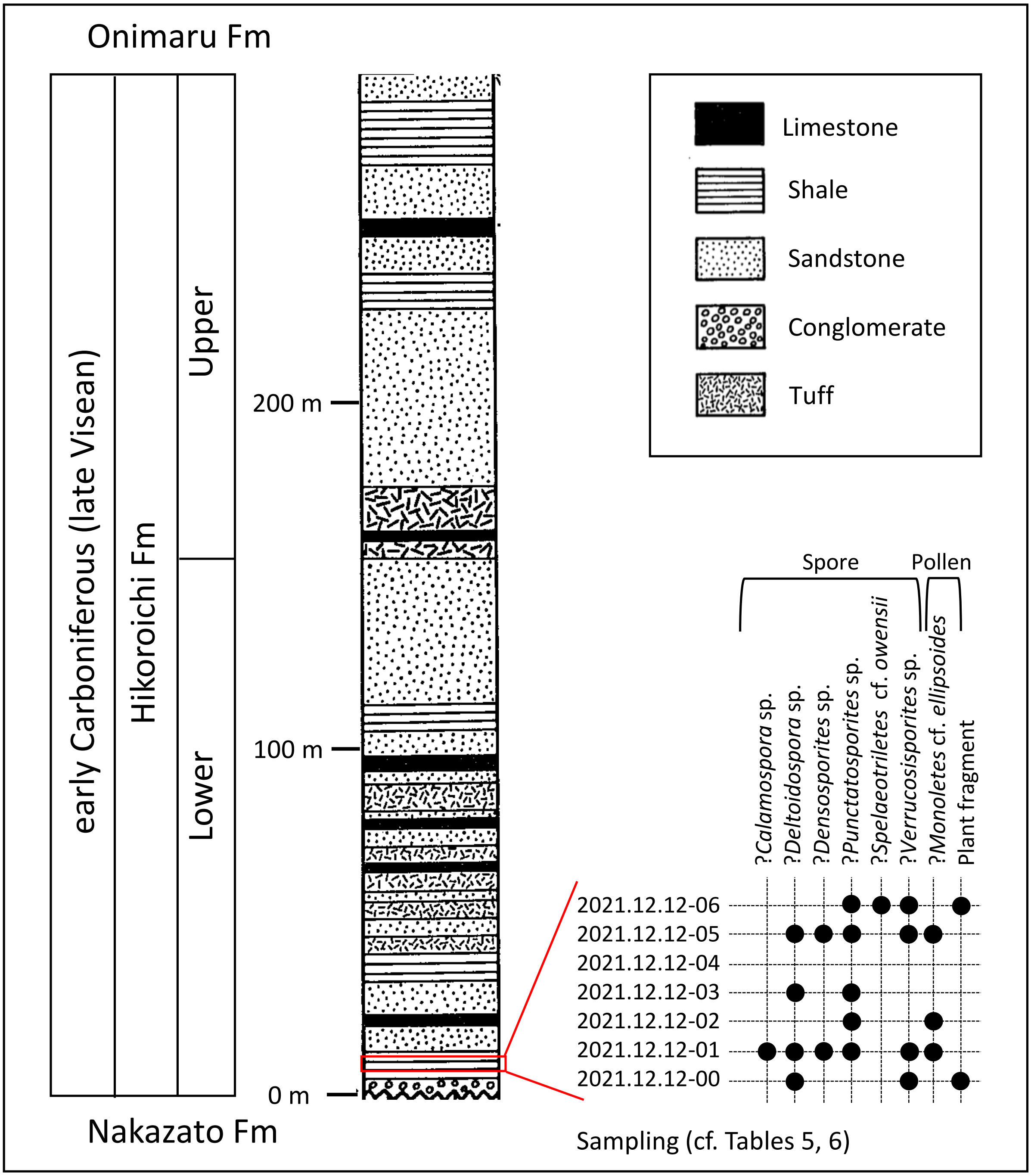


Figure 16. Pictures of the field (2021.12.11) in the Devonian Nakazato Formation of the South Kitakami Belt, Iwate Prefecture, Northeast Japan. A, B. Loc. 1. C. Loc. 3. D, E. Loc. 4. F. Loc. 5 (see Figure 15 for details on localities position).



	Spore						Pollen	
	?*Calamospora* sp.	?*Deltoidospora* sp.	?*Densosporites* sp.	?*Punctatosporites* sp.	?*Spelaeotriletes* cf. *owensii*	?*Verrucosisporites* sp.	?*Monoletes* cf. *ellipsoides*	Plant fragment
2021.12.12-06				●	●	●		●
2021.12.12-05		●	●	●		●	●	
2021.12.12-04								
2021.12.12-03		●		●				
2021.12.12-02				●			●	
2021.12.12-01	●	●	●	●		●	●	
2021.12.12-00		●				●		●

Figure 17. Generalised stratigraphic column of the Hikoroichi Formation (modified from Tazawa, 1984).

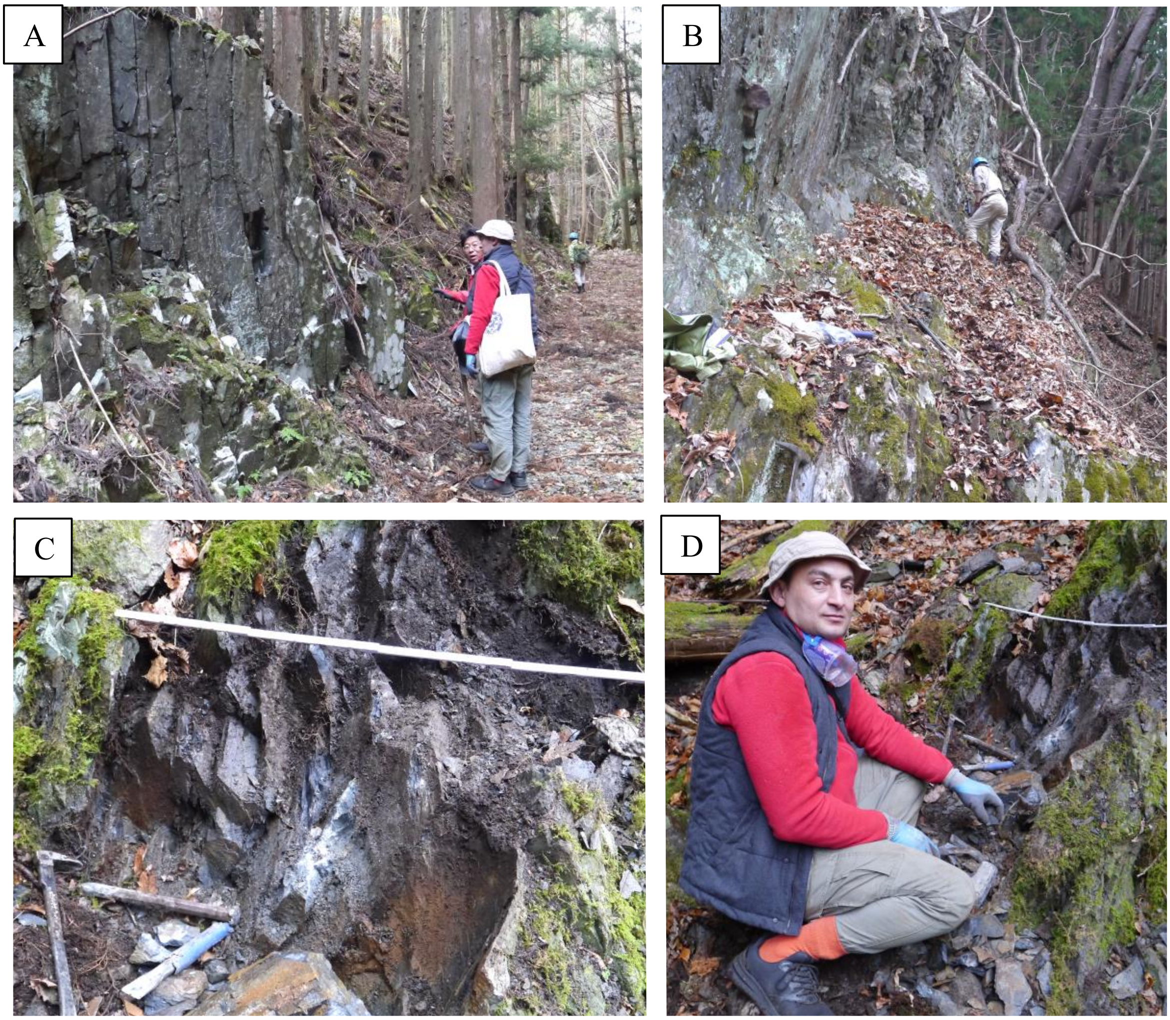


Figure 18. Pictures of the field in the Carboniferous Hikoroichi Formation (2021.12.12) of the South Kitakami Belt, Iwate Prefecture, Northeast Japan. A. Examination of rocks around the sampling locality. B. Examination of rocks at horizon 2021.12.12-04. C, D. Collecting material on horizon 2021.12.12-00.

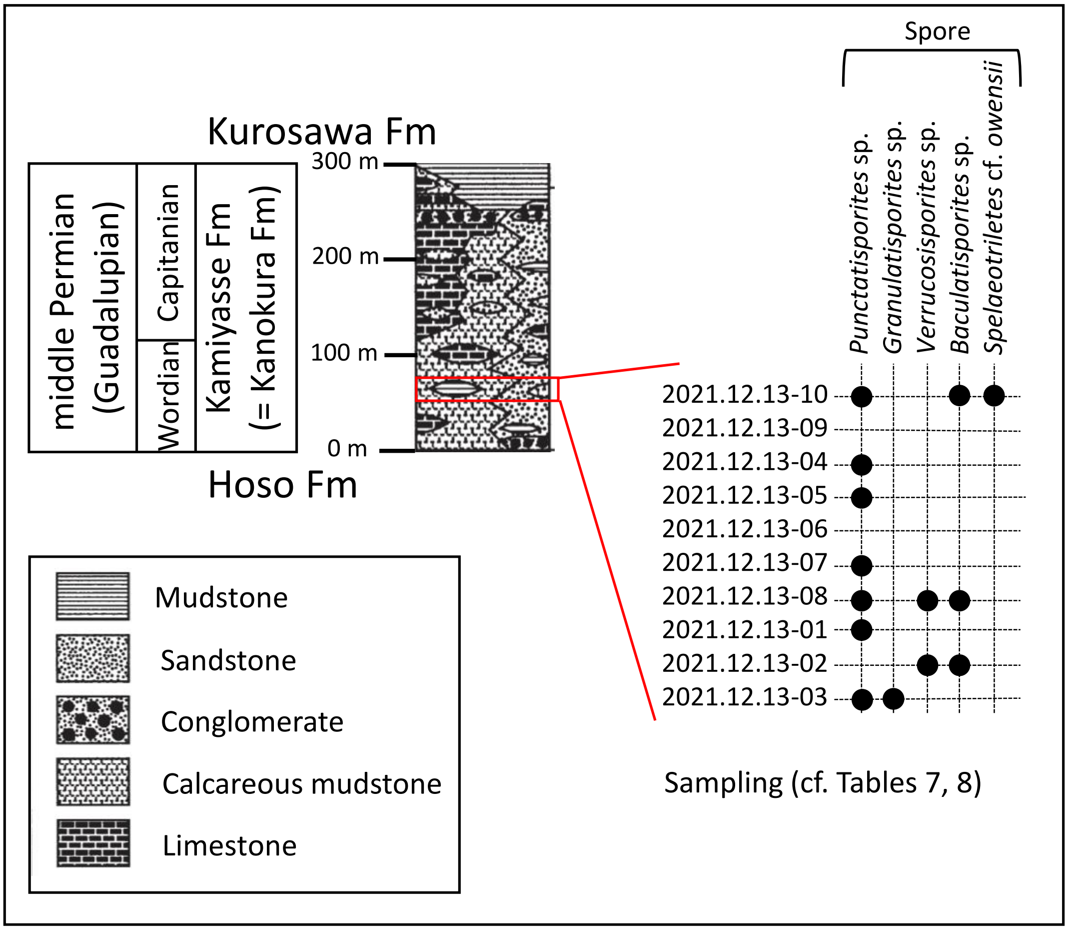


Figure 19. Generalised stratigraphic column of the Kanokura Formation (modified from Misaki and Ehiro, 2004).

Figure 20. Pictures of the field in the Permian Kanokura Formation of the South Kitakami Belt (2021.12.13), Iwate Prefecture, Northeast Japan. A, B. Collecting material at horizon 2021.12.13-04. C. Close-up picture of horizon 2021.12.13-04.

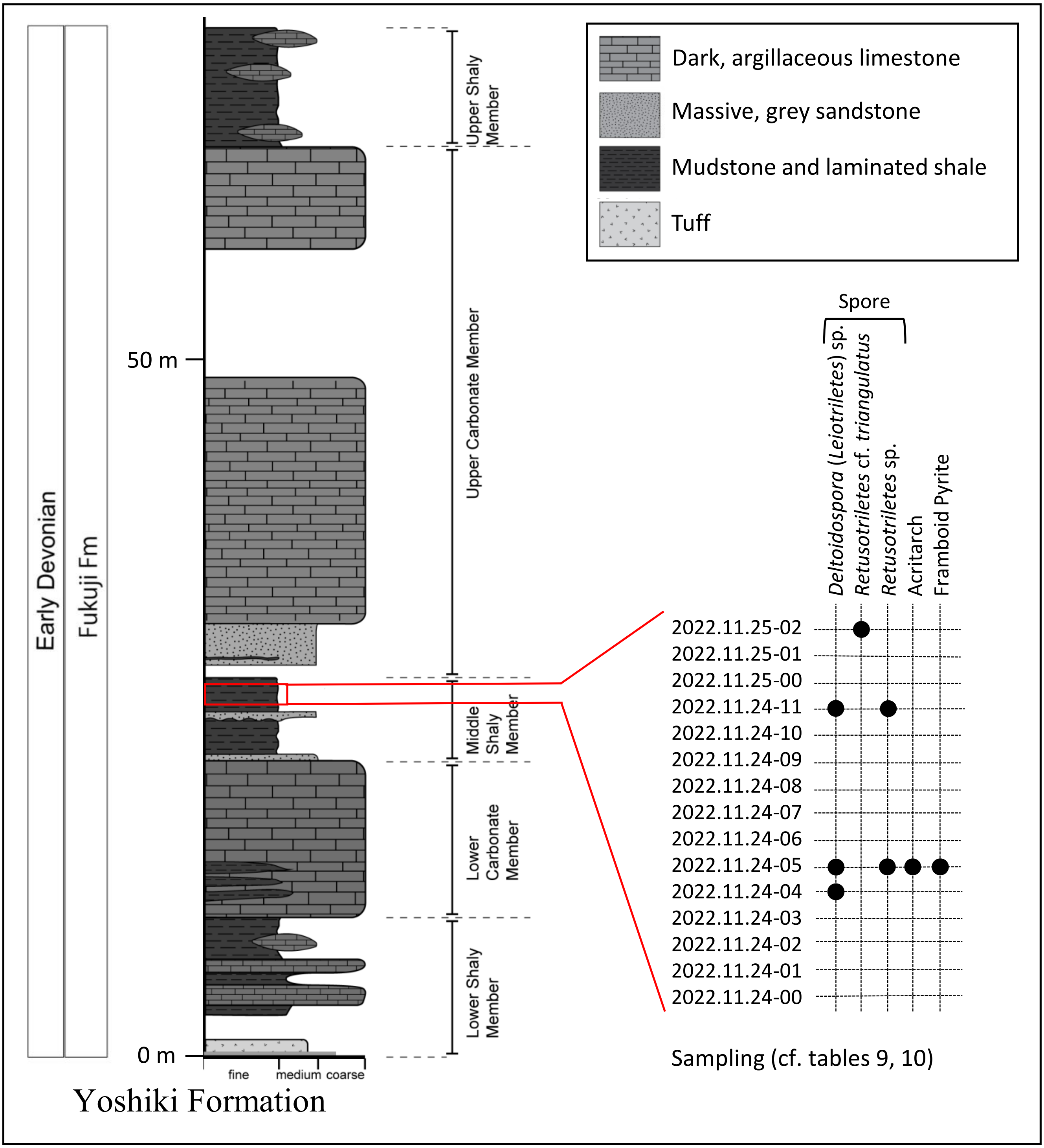


Figure 21. Stratigraphic column of the Fukuji Formation (modified from Kuwano, 1987; Stocker, 2021).

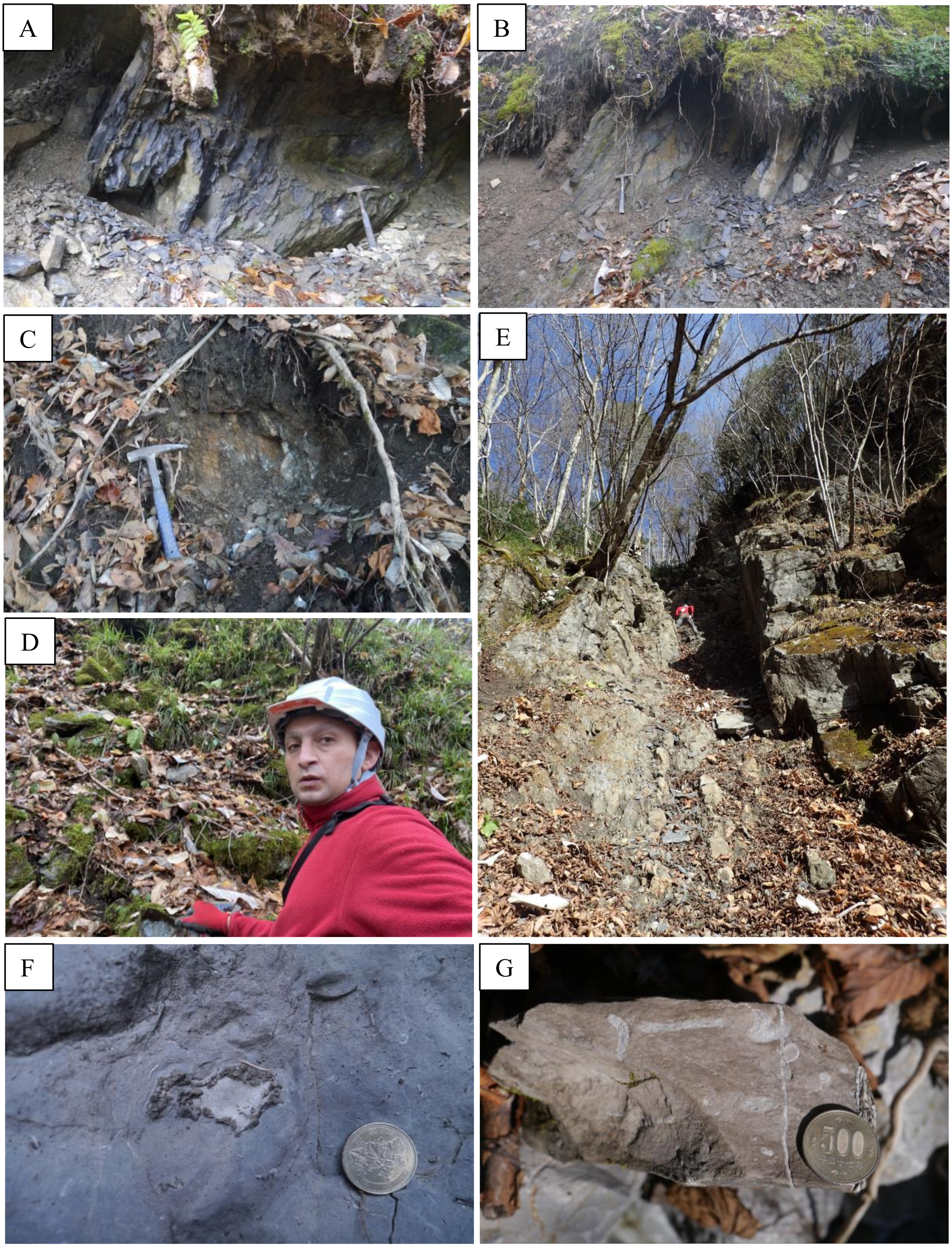


Figure 22. Pictures of the field in the Devonian Fukuji Formation of the Hida-Gaien Belt, Gifu Prefecture, central Japan. A, B. Fukuji Onsen locality (A. Fossil boardwalk outcrop. B. Mountain trail entrance outcrop). C, D. Hitoegane locality. E-G. Ichinotani locality (E. Collecting samples for Palynology. F. *Favosites* sp. G. Corals).

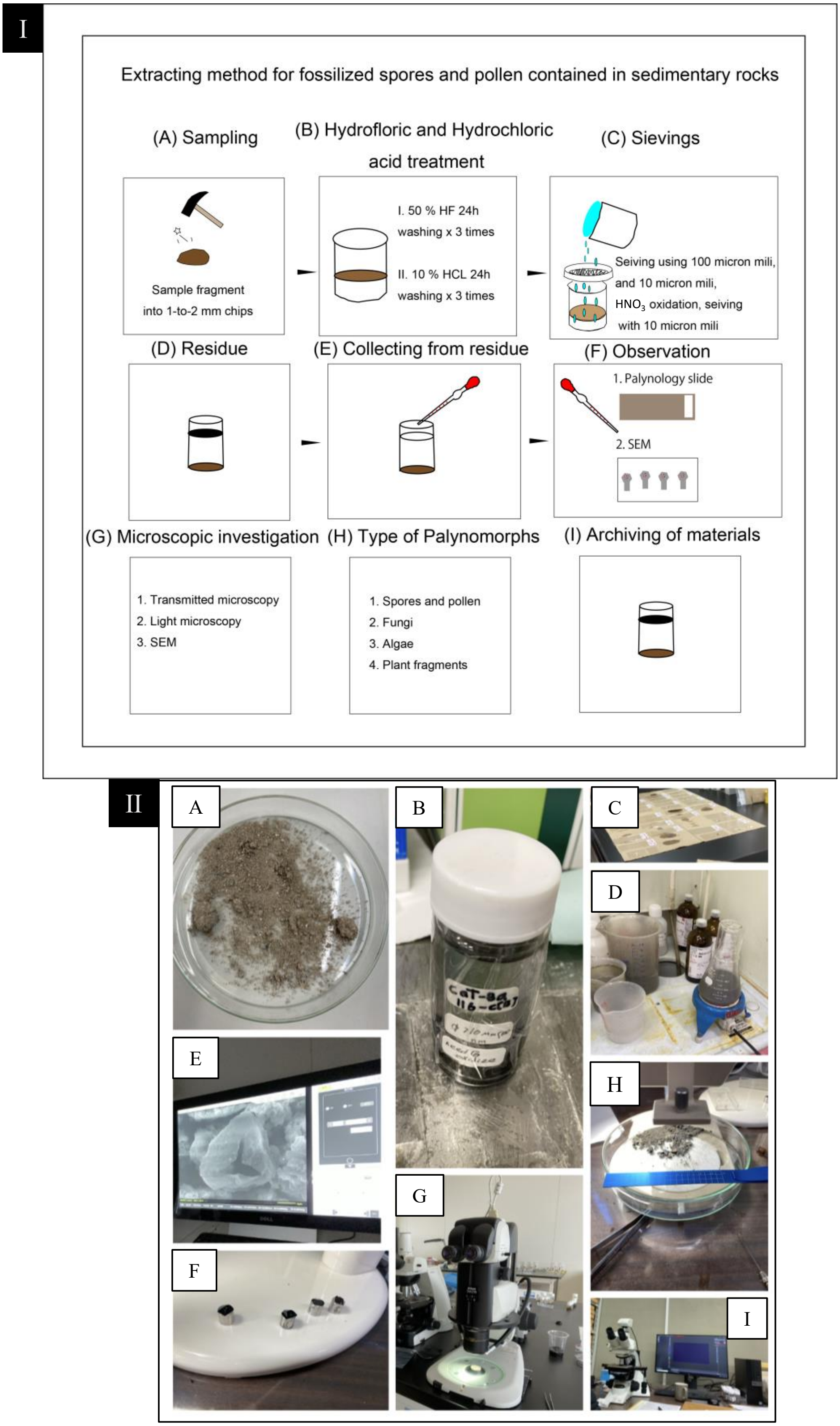


Figure 23. Sketch (I) and pictures (II) of the palynological analysis method. II, A. Fragments of rock sample. B. Residue for study. C. Slides for LM observation. D. Acid treatments in the draft chamber. E. SEM investigation and observation of marker spore *Ambitisporites avitus* from the Devonian Nakazato Formation. F. Preparing samples for SEM. G. Microscopic investigation. H. Investigation of rock sample under light microscopy for microfossil isolation and plant fragment isolation. I. LM investigation.

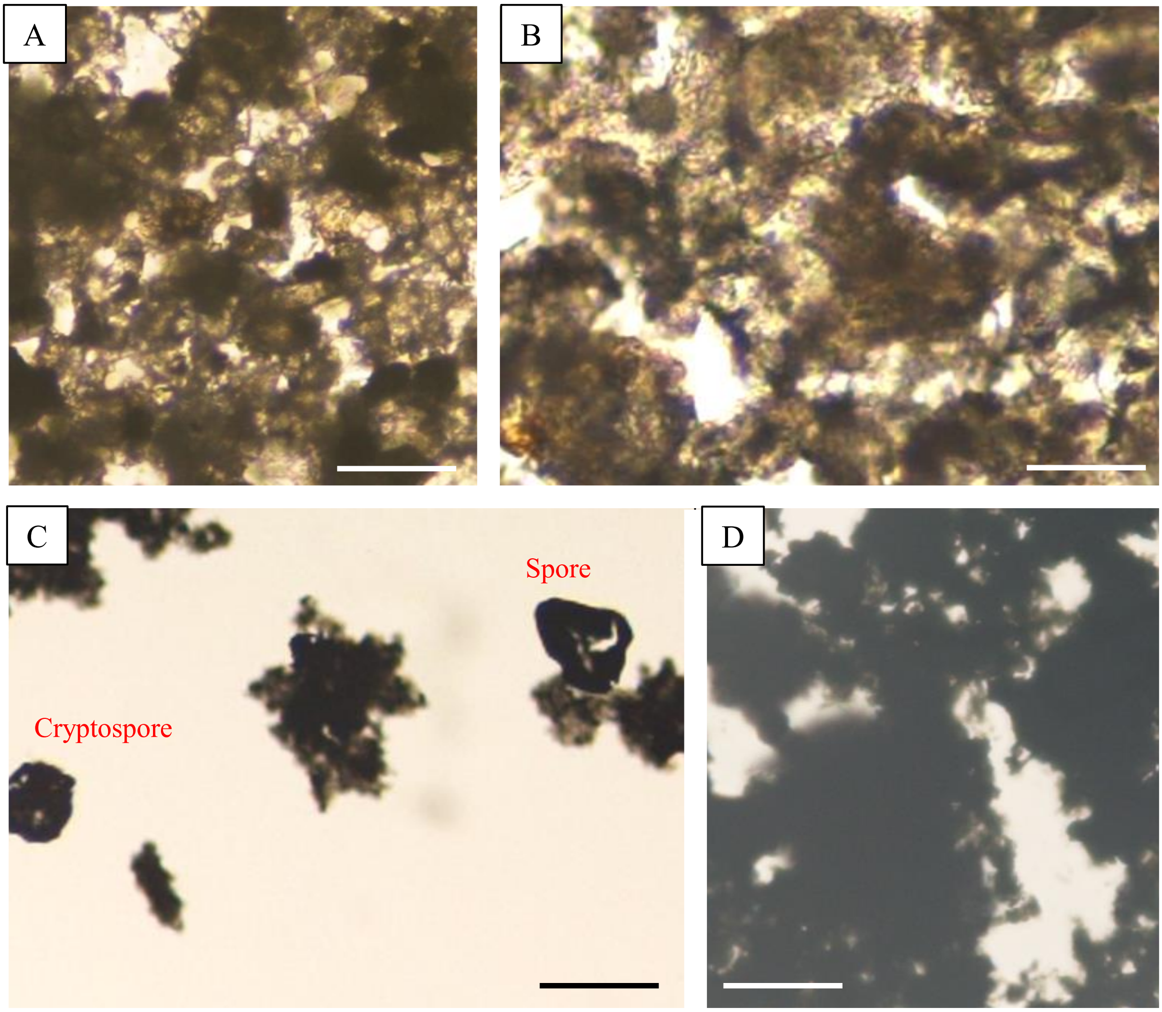


Figure 24. Examples of palynological facies from studied formations. A. Permian Kanokura Formation. B. Carboniferous Hikoroichi Formation. C. Devonian Nakazato Formation. D. Silurian Kawauchi Formation. Scale bar, 50 µm.

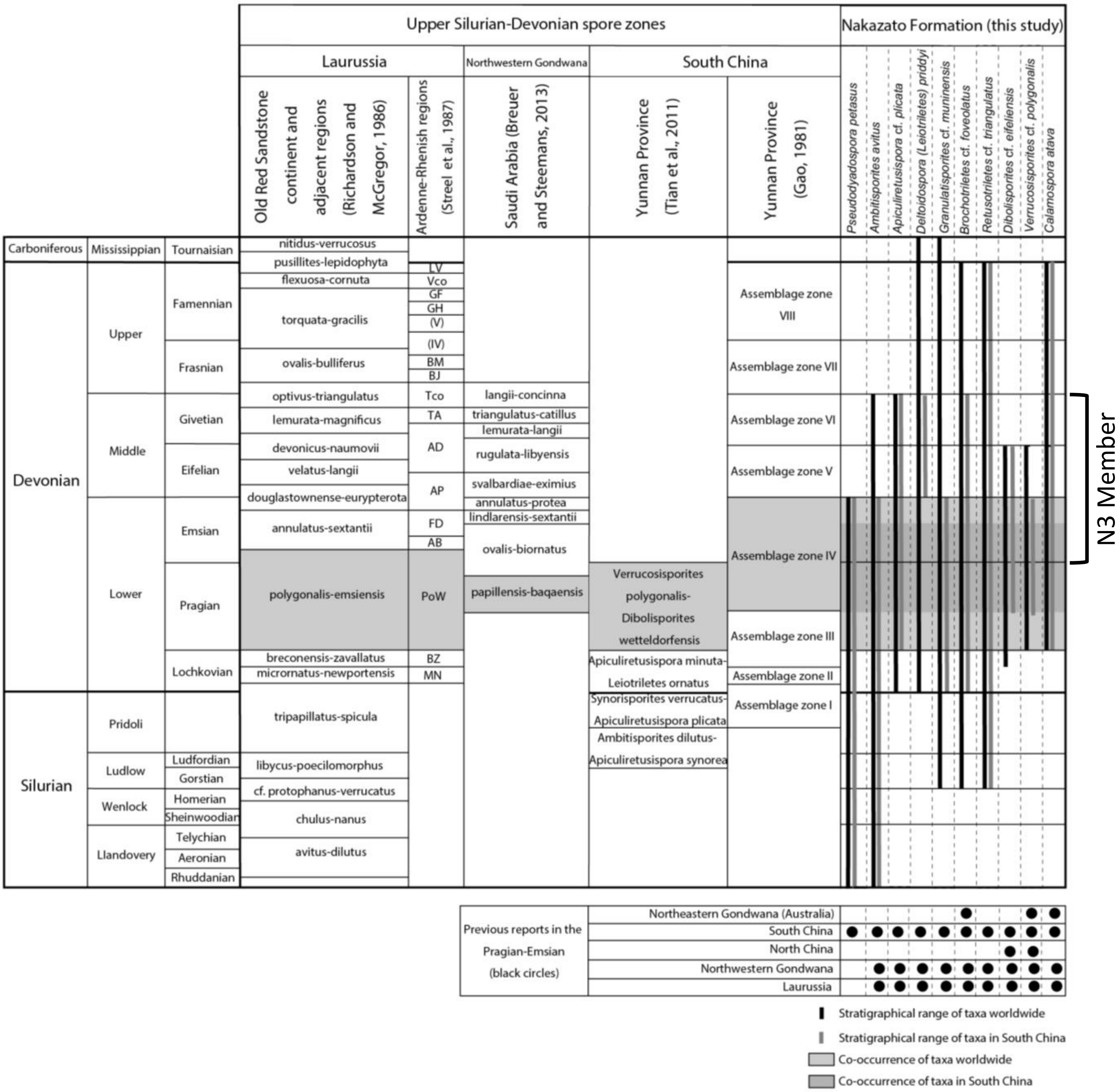


Figure 25. Stratigraphical range of taxa from the Nakazato Formation, with correlation with upper Silurian-Devonian standard spore zones of Laurussia, northwestern Gondwana and South China (left part), and previous reports in the Pragian-Emsian (lower part).

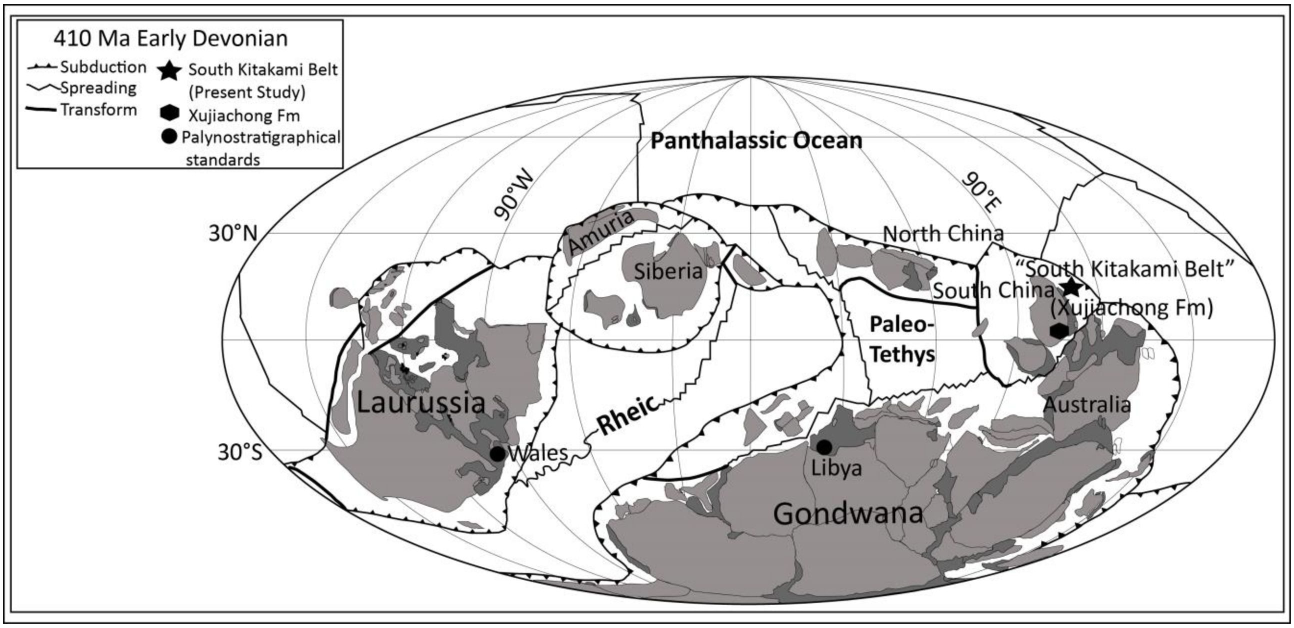


Figure 26. World paleomap during the Early Devonian, with location of the Laurussia and northwestern Gondwana palynostratigraphical standards, Xujiachong Formation, and presumed location of the South Kitakami Belt (modified from Torsvik and Cocks, 2016).

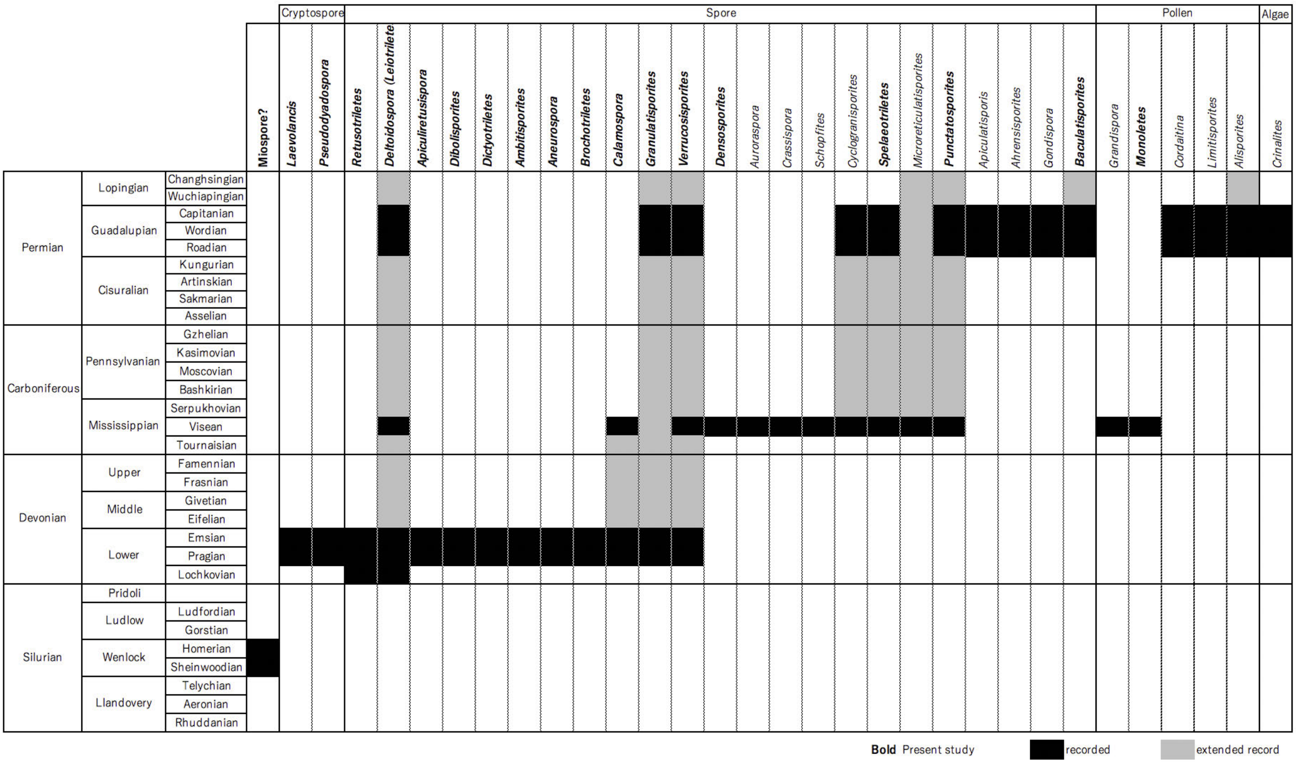


Figure 27. Palynostratigraphy established for the Paleozoic of Japan.

Table 1. Previous palaeobotanical studies in Japan, with results of this study (in bold).

NORTHEAST JAPAN

Age		Formation	Plant fossil	Location	Reference
Permian	upper	Kashiwadaira Fm	*Gigantopteris nicotianaefolia*, *Bicoemplectopteris hallei*, *Taeniopteris* sp., *Pecopteris* sp., *Odontopteris subcrenulata*, *Psygmophyllum*? sp., *Cordaites*? sp.	Iwaki City, Fukushima Pref.	Yanagisawa, 1967; Asama, 1974
	middle	Kanokura Fm (KNI Member) (Kamiyasse Fm)	*Ahrensisporites* cf. *thorsteinssonii*, *Apiculatisporis* sp., ***Baculatisporites*** **sp.**, *Cyclogranisporites* sp., *Gondispora* cf. *obstaculifera*, and ***Granulatisporites*** **sp.**, *Leiotriletes ulutus*, ***Punctatisporites*** **sp.**, ***Spelaeotriletes*** **cf. *owensii***, ***Verrucosisporites*** **sp.**, *Alisporites* sp., *Limitisporites* sp., *Cordaitina* cf. *vulgaris*, *Crinalites* cf. *sabiensis*	Kamiyasse area, southern Kitakami	Yang and Tazawa, 2000b; **this study**
	lower	Sakamotozawa Fm	*Taeniopteris setamaiensis, T. motoiwaensis*	Sumita village, Iwate Pref.	Asama and Murata, 1974
	lower	Nishikori Fm (Rodai Fm)	*Sphenophyllum* cf. *oblongifolium*, *Sphenophyllum thonii* var. *minor*, *Pecopteris* toyomaensis, *P. yabei*, *Sphenopteris tenuis*, *S*. sp., *Callipteridium koraiense*, *Odontopteris subcrenulata*, O. yongwolensis, Cyclopteris sp., Aphlebia sp., *Cathaysiopteris* (=*Gigantopteris*) *whitei*, *Taeniopteris latecostata*, *Taeniopteris* cf. *schenkii*, *T. paradensissima*, *T. thailandica*, *T. latecostata*, *T. nystroemii*, *T. mayaensis*, *T. setamaiensis*, *T. laciniata*, *T. arakawae*, *T. oishii*, *T. linearifolia*, *T*. sp., *Cordaites japonicus, C. palmaeformis*, *C. principalis*, *C. (Noeggerathiopsis) aralcawae*, *Zamiopteris glossopteroides*, *Zamiopteris uedae*, *Psygmophyllum flabellatum, P. mayaensis*, *Parasphenophyllum thonii* var. *minor, Trizygia oblongifolia*, *Paratrizygia maiyaensis, P. uedae*	Maiya Town, Tome-gun, Miyagi Pref.	Asama, 1956, 1967, 1970, 1981
Carboniferous	lower	Onimaru Series	*Calamites* sp.	Rikuzen-Takata City, Iwate Pref.	Endo and Mori, 1969
	lower	Hikoroichi Fm, HK3 member	*Psedusporochnus* sp., *Rhodeopteridium* sp.?, *Sublepidodendron*? *wusihense*, *Lepidodendron* sp., *Archaeocalamites scrobiculatus*	Ofunato City, Iwate Pref., Kitakami mountains	Asama *et al.*, 1989
	lower	Hikoroichi Fm, HK2 member	*Auroraspora* cf. *macra*, *Calamospora* sp., **?*Calamospora* sp.**, *Crassispora trychera*, *Cyclogranisporites* sp., **?*Deltoidospora* sp.**, *Densosporites* sp., **?*Densosporites* sp.**, *Grandispora* cf. *echinata*, *Leiotriletes* cf. *incomptus*, *Microreticulatisporites araneum*, *Punctatisporites irrasus*, *P. minus*, *P. planus*, **?*Punctatosporites* sp.**, *Schopfites* sp., *Spelaeotriletes crustatus*, **?*Spelaeotriletes* cf. *owensii***, *S*. cf. *pretiosus*, *Verrucosisporites* sp., **?*Verrucosisporites* sp.**, **?*Monoletes* cf. *ellipsoides***	Ofunato City, Iwate Pref., Kitakami mountains	Yang and Tazawa, 2000a; **this study**
Devonian	Upper	Tobigamori Fm ("Nakakura Fm")	*Leptophloeum* cfr. *australe*, *Cyclostigma* sp.	Nagasaka-mura and Takozu-mura, Higashiiwai-gun, Iwate Pref.	Tachibana, 1950, 1959
	Lower	**Nakazato Fm**	***Laevolancis*** **sp.**, ***Pseudodyadospora petasus***, ***Retusotriletes*** **cf. *triangulatus***, ***Apiculiretusispora*** **cf. *plicata***, ***Apiculiretusispora*** **sp.**, ***Dibolisporites*** **cf. *eifeliensis***, ***Dibolisporites*** **sp.**, ***Dictyotriletes*** **sp.**, ***Ambitisporites avitus***, ***Calamospora atava***, ***Deltoidospora (Leiotriletes) priddyi***, ***Aneurospora*** **spp.**, ***Brochotriletes*** **cf. *foveolatus***, ***Granulatisporites*** **cf. *muninensis***, ***Verrucosisporites*** **cf. *polygonalis***, ***Laevitubulus tenuis***, **Plant fragments**	**Ofunato City, Iwate Pref., Kitakami mountains**	**This study**
Silurian	**upper**	**Kawauchi Fm**	**Miospore?**, ***Laevitubulus tenuis***	**Ofunato City, Iwate Pref., Kitakami mountains**	**This study**

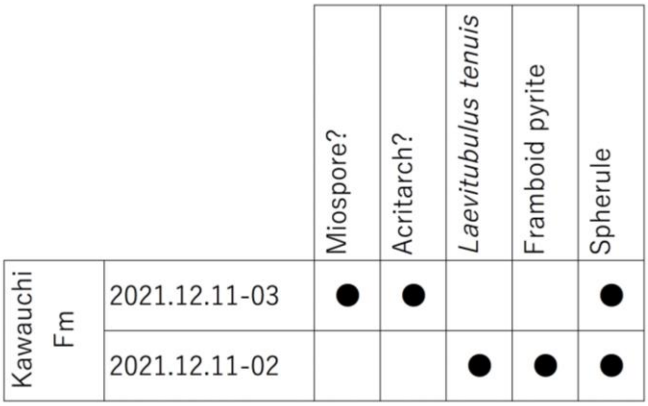
CENTRAL JAPAN

Permian		Tanba Belt	?*Araucariacites gloriosus*, ?*Florinites* sp. (?Cordaitales), *Reticulatasporites foraminulatus*, *Tasmanites tanbaensis* (microplankton)	Kyoto Pref.	Takahashi and Yao, 1969
Devonian	Upper	Rosse Fm	*Leptophloeum rhombicum*	Gifu Pref.	Tazawa et al., 2000
	Lower	**Fukuji Fm**	***Deltoidospora (Leiotriletes)*** **sp.**, ***Retusotriletes*** **cf. *triangulatus***, ***Retusotriletes*** **sp.**	**Gifu Pref.**	**This study**
paleozoic (undetermined)		Chichibu Fm	stems of *Calamites*		Yabe and Endo, 1920

SOUTHWEST JAPAN

Devonian	Upper	Naidaijin Fm ("Yuzuriha Fm")	*Cyclostigma* sp., *Leptophloeum rhombicum*, *Aphyllopteris*? sp.	Naidaijin, Kumamoto Pref., Kyushu	Kimura *et al.*, 1986

Table 2. Occurrence of microfossils obtained from the Silurian Kawauchi Formation of the South Kitakami Belt.



		Miospore?	Acritarch?	*Laevitubulus tenuis*	Framboid pyrite	Spherule
Kawauchi Fm	2021.12.11-03	●	●			●
	2021.12.11-02			●	●	●

Table 3. Occurrence of microfossils obtained from the Devonian Nakazato Formation of the South Kitakami Belt.

				Cryptospore		Spore													Tubular remain		
				Laevolancis sp.	*Pseudodyadospora petasus*	*Retusotriletes* cf. *triangulatus*	*Apiculiretusispora* cf. *plicata*	*Apiculiretusispora* sp.	*Dibolisporites* cf. *eifeliensis*	*Dibolisporites* sp.	*Dictyotriletes* sp.	*Ambitisporites avitus*	*Calamospora atava*	*Deltoidospora* (*Leiotriletes*) *priddyi*	*Aneurospora* spp.	*Brochotriletes* cf. *foveolatus*	*Granulatisporites* cf. *muninensis*	*Verrucosisporites* cf. *polygonalis*	*Laevitubulus tenuis*	Plant fragment	Scolecodont
Nakazato Fm	Kuronborozawa locality		2021.12.14-01																		
			2021.12.13-13																		
			2021.12.13-12																		
			2021.12.13-11																		
	Higuchizawa locality	Loc. 1	2021.12.10-22									●							●		
			2021.12.10-21	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●
			2021.12.10-20		●	●	●			●		●		●	●		●		●	●	●
			2021.12.10-19			●													●		
			2021.12.10-18						●	●									●	●	
			2021.12.10-17	●															●	●	
			2021.12.10-16																●	●	
			2021.12.10-15												●				●		
			2021.12.10-14	●			●														●
			2021.12.11-10																●	●	
		Loc. 2	2021.12.11-09							●											●
			2021.12.11-08																	●	
		Loc. 3	2021.12.11-07																●	●	●
			2021.12.11-06				●												●		
		Loc. 4	2021.12.10-13				●														
			2021.12.11-12																●		
			2021.12.11-11												●				●	●	●
		Loc. 5	2021.12.11-05												●	●			●	●	
			2021.12.11-04				●												●		
			2021.12.11-03			●	●			●			●		●	●				●	
			2021.12.11-02	●	●		●													●	
			2021.12.11-01																●	●	●

Table 4. Botanical affinities of microfossils from the Devonian Nakazato Formation of the South Kitakami Belt.

Phylum		Microflora
Rhyniophyta	cryptospores	*Laevolancis* sp.
		Pseudodyadospora petasus
	spores	*Ambitisporites avitus*
		Granulatisporites cf. *muninensis*
Rhyniophyta, Zosterophyllophyta, or Trimerophyta		*Calamospora atava*
		Deltoidospora (*Leiotriletes*) *priddyi*
		Retusotriletes cf. *triangulatus*
		cf. *Retusotriletes* spp.
		Apiculiretusispora cf. *plicata*
Lycophyta		*Verrucosisporites* cf. *polygonalis*
		Aneurospora spp.
Cladoxylophyta		*Dibolisporites* cf. *eifeliensis*
		Dibolisporites sp.
		Dictyotriletes sp.
Unknown	tubular remain	*Laevitubulus tenuis*

Table 5. Occurrence of microfossils obtained from the Carboniferous Hikoroichi Formation of the South Kitakami Belt.

		Spore						Pollen	Plant fragment
		?*Calamospora* sp.	?*Deltoidospora* sp.	?*Densosporites* sp.	?*Punctatosporites* sp.	?*Spelaeotriletes* cf. *owensii*	?*Verrucosisporites* sp.	?*Monoletes* cf. *ellipsoides*	
Hikoroichi Fm	2021.12.12-06				●	●	●		●
	2021.12.12-05		●	●	●		●	●	
	2021.12.12-04								
	2021.12.12-03		●		●				
	2021.12.12-02				●			●	
	2021.12.12-01	●	●	●	●		●	●	
	2021.12.12-00		●				●		●

Table 6. Botanical affinities of microfossils from the Carboniferous Hikoroichi Formation of the South Kitakami Belt.

Phylum	Order	Microflora	Macroflora
Lycophyta	Lycopodiales	*Auroraspora* cf. *macra* *Crassispora trychera* **?*Verrucosisporites* sp.** *Verrucosisporites* sp. *Densosporites* sp. **?*Densosporites* sp.**	*Lepidodendron* sp. *Sublepidodendron*? *wusihense*
Cladoxylophyta	Pseudosporochnales		*Pseudosporochnus* sp.
Monilophyta	Equisetales	**?*Calamospora* sp.** *Calamospora* sp. *Microreticulatisporites araneum* *Schopfites* sp	*Archaeocalamites scrobiculatus*
	Filicales	**?*Deltoidospora* sp.** *Leiotriletes* cf. *incomptus*	
	Unknown	**?*Punctatosporites* sp.** *Punctatisporites irrasus* *Punctatisporites minus* *Punctatisporites planus*	
Lycophyta or Monilophyta		*Cyclogranisporites* sp. **?*Spelaeotriletes* cf. *owensii*** *Spelaeotriletes crustatus* *Spelaeotriletes* cf. *pretiosus*	
Pteridospermatophyta		**?*Monoletes* cf. *ellipsoides***	*Rhodeopteridium* sp.?
Progymnospermophyta		*Grandispora* cf. *echinata*	

Bold: species obtained in this study

Table 7. Occurrence of microfossils obtained from the Permian Kanokura Formation of the South Kitakami Belt.

		Spore				
		Punctatisporites sp.	*Granulatisporites* sp.	*Verrucosisporites* sp.	*Baculatisporites* sp.	*Spelaeotriletes* cf. *owensii*
Kanokura Fm	2021.12.13-10	●			●	●
	2021.12.13-09					
	2021.12.13-04	●				
	2021.12.13-05	●				
	2021.12.13-06					
	2021.12.13-07	●				
	2021.12.13-08	●		●	●	
	2021.12.13-01	●				
	2021.12.13-02			●	●	
	2021.12.13-03	●	●			

Table 8. Botanical affinities of microfossils from the Permian Kanokura Formation of the South Kitakami Belt.

Phylum	Order	Microflora
Lycophyta	Lepidodendrales	*Gondispora* cf. *obstaculifera*
Monilophyta	Filicales	*Apiculatisporis* sp. ***Baculatisporites* sp.** ***Granulatisporites* sp.** *Leiotriletes ulutus* ***Punctatosporites* sp.** ***Verrucosisporites* sp.**
Lycophyta or Monilophyta		*Ahrensisporites* cf. *thorsteinssonii* *Cyclogranisporites* sp. ***Spelaeotriletes* cf. *owensii***
Pteridospermatophyta	Corystospermales or Peltaspermales	*Alisporites* sp.
Coniferophyta	Coniferales	*Cordaitina* cf. *vulgaris*
Pteridospermophyta or Coniferophyta		*Limitisporites* sp.
Algae	Unknown	*Crinalites* cf. *sabiensis*

Bold: species obtained in this study

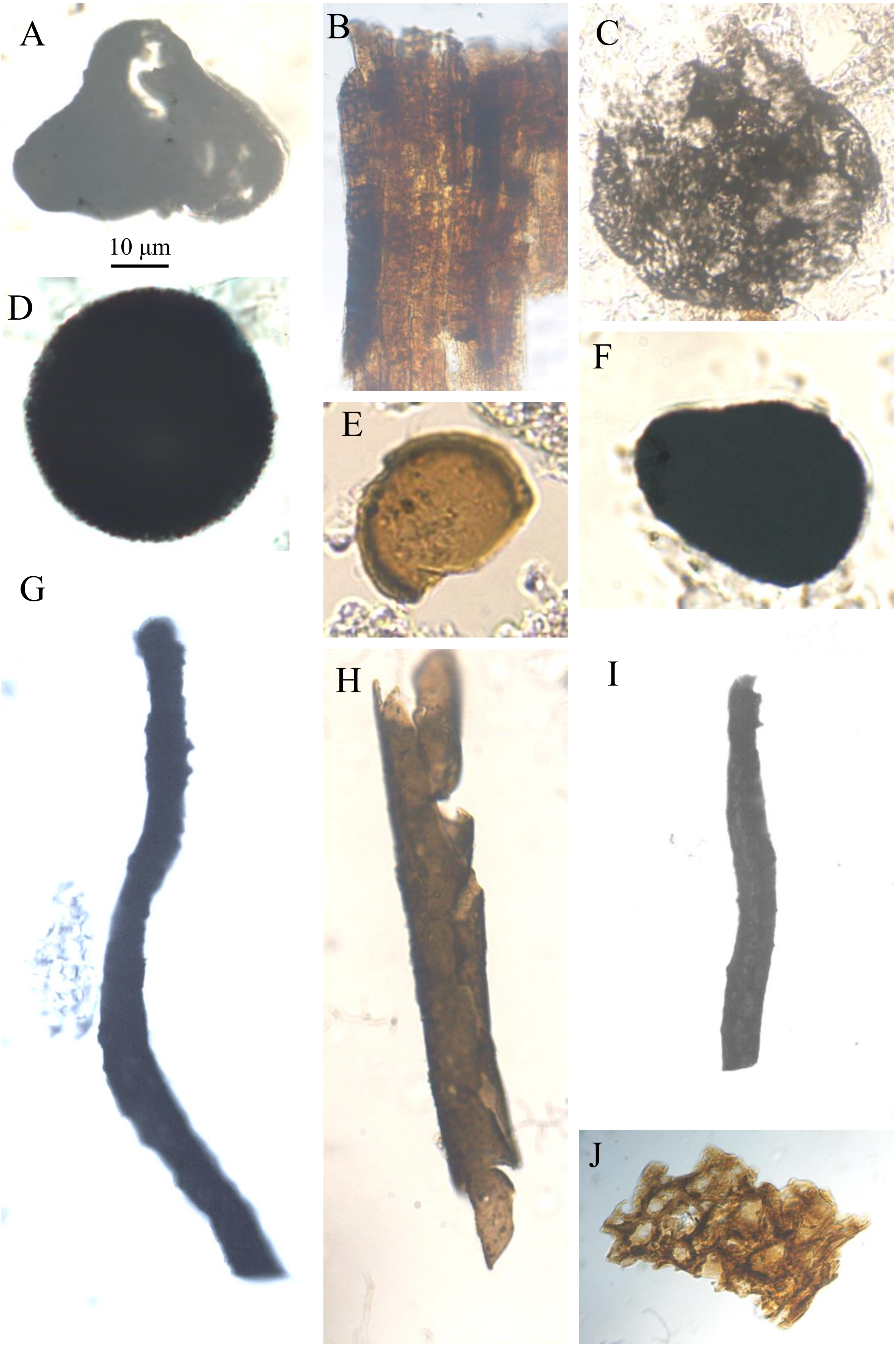
Table 9. Occurrence of microfossils obtained from the Devonian Fukuji Formation of the Hida-Gaien Belt.

				Spore				
				Deltoidospora（*Leiotriletes*）sp.	*Retusotriletes* cf. *triangulatus*	*Retusotriletes* sp.	Acritarch	Framboid Pyrite
Fukuji Fm	Hitoegane locality		2022.11.25-02		●			
	Ichinotani locality		2022.11.25-01					
			2022.11.25-00					
	Fukuji Onsen locality	Mountain trail entrance	2022.11.24-11	●		●		
			2022.11.24-10					
			2022.11.24-09					
			2022.11.24-08					
		Fossil boardwalk	2022.11.24-07					
			2022.11.24-06					
			2022.11.24-05	●		●	●	●
			2022.11.24-04	●				
			2022.11.24-03					
			2022.11.24-02					
			2022.11.24-01					
			2022.11.24-00					

Table 10. Botanical affinities of microfossils from the Devonian Fukuji Formation of the Hida-Gaien Belt.

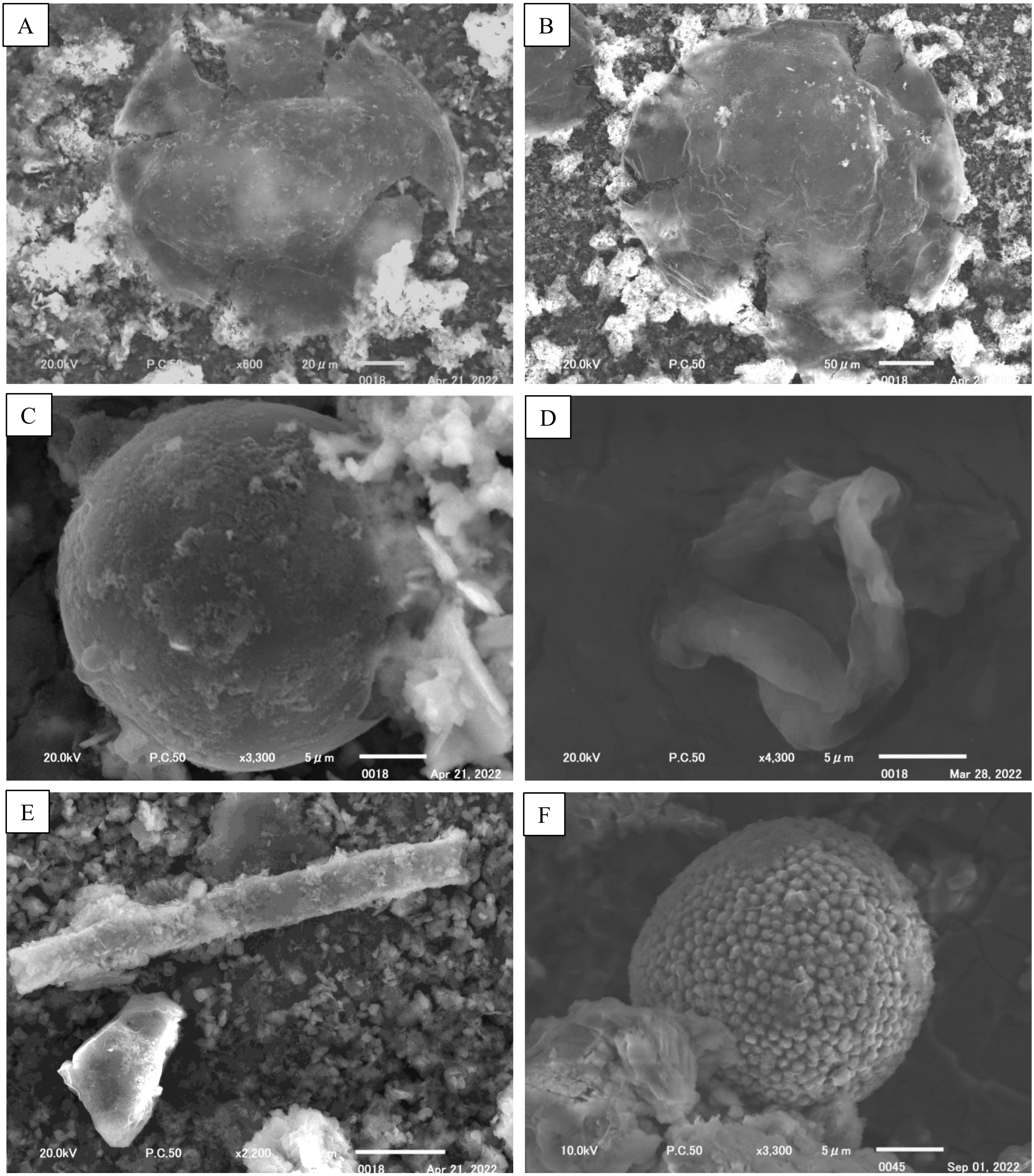
Rhyniophyta, Zosterophyllophyta, or Trimerophyta	Spores	*Deltoidospora*（*Leiotriletes*）sp.
		Retusotriletes cf. *triangulatus*
		Retusotriletes sp.

Plate I



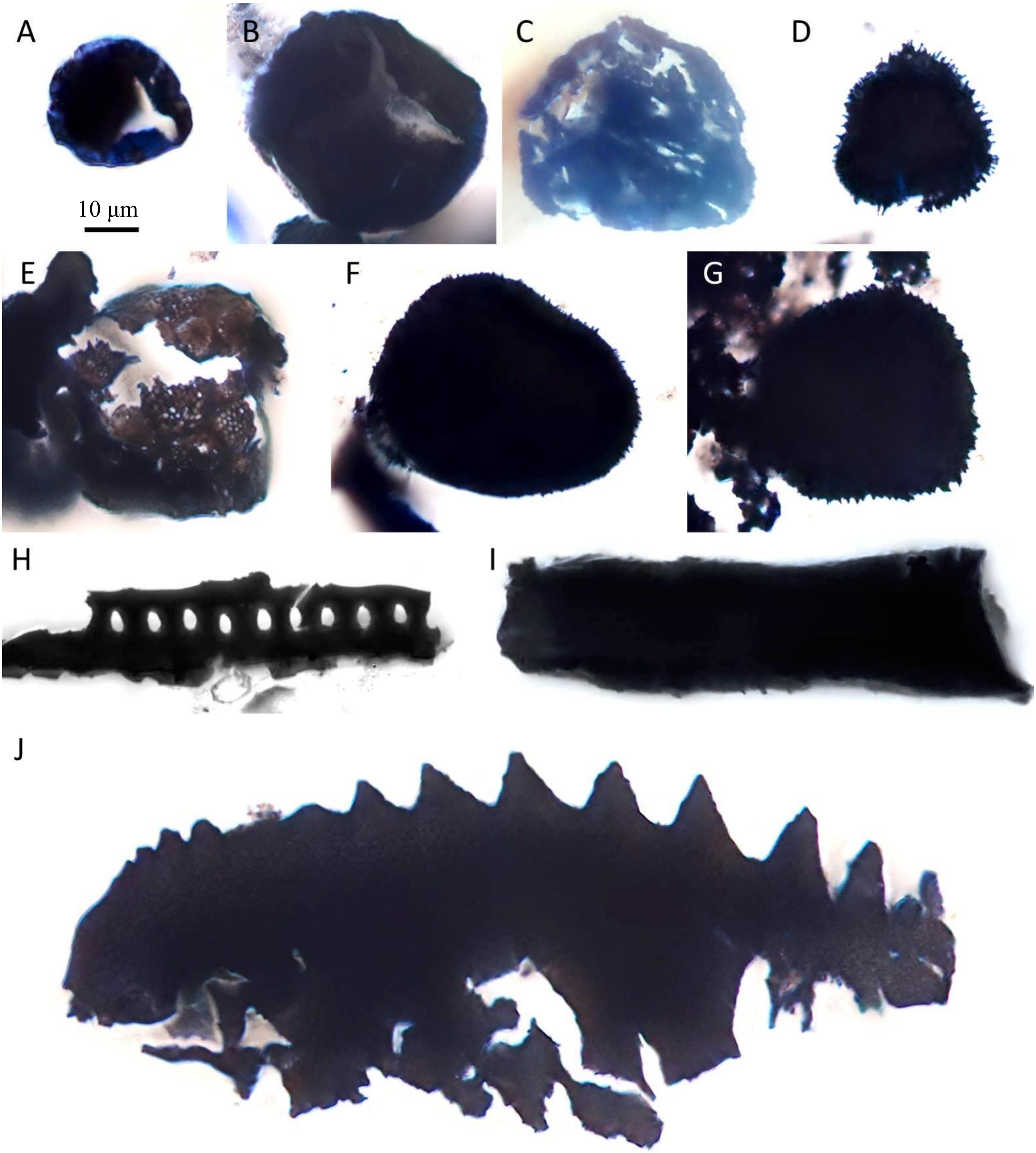
LM pictures of palynomorphs from the Silurian Kawauchi Formation. A, F. Triangular miospore? (A, 2021.12.1209; F, 2021.12.11.leg-2-4). B. Sheet tissue. C. Acritarch?, 2021.12.1202; EF R27. D. rounded palynomorph, 2021.12.11, leg-2-4. E, Fungus. G-I. *Laevitubulus tenuis* (G, 2021.12.1209; H, 2021.12.1202). J. Sheet tissue. Scale bar, 10 µm.

Plate II



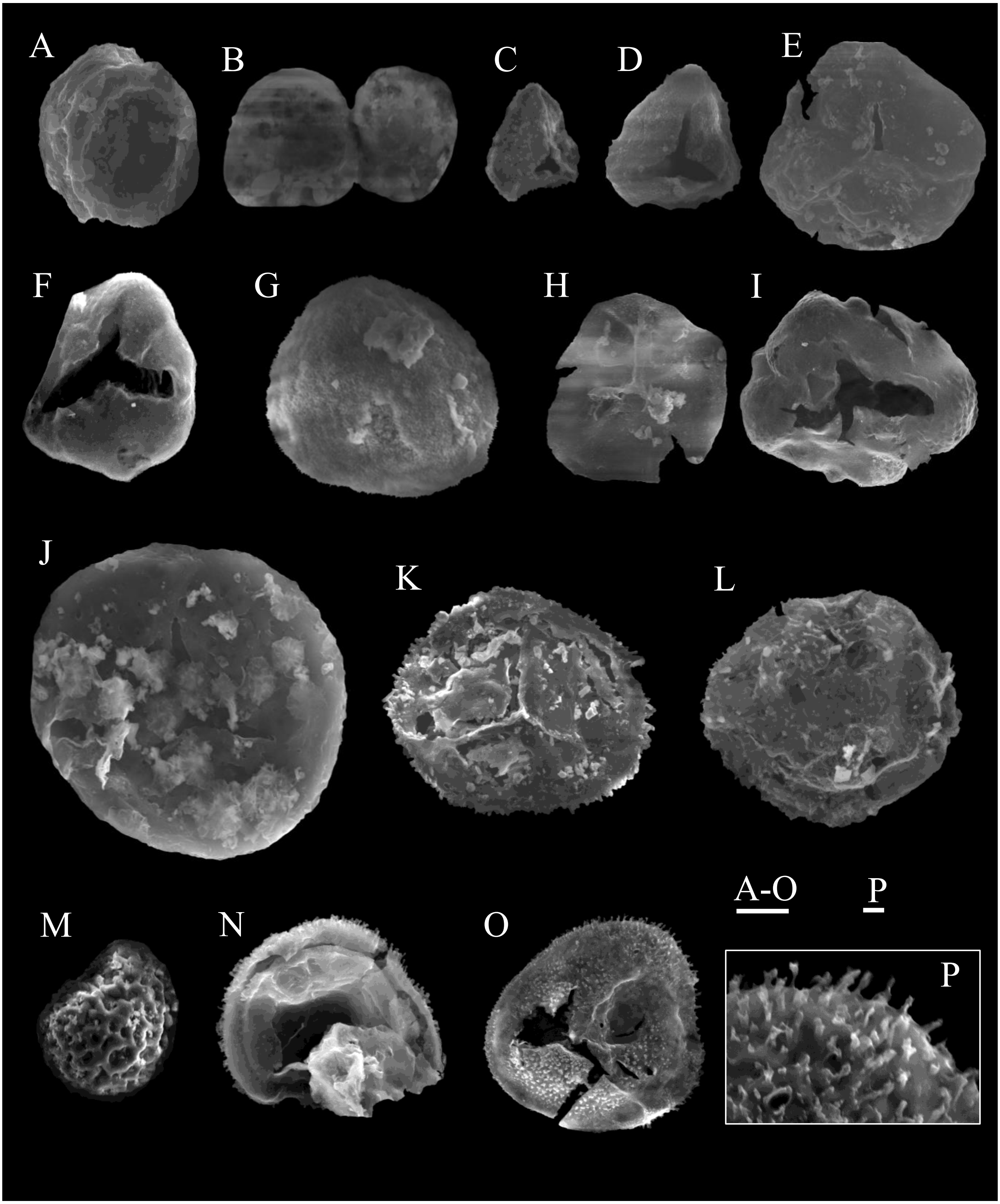
SEM pictures of palynomorphs from the Silurian Kawauchi Formation. A-B. Acritarch?, 2021.12.11.02. C. spherules, 2021.12.11.03. D. Triangular miospore?, 2021.12.11.06. E. *Laevitubulus tenuis*, 2021.12.11.08. F. Framboid pyrite.

Plate III



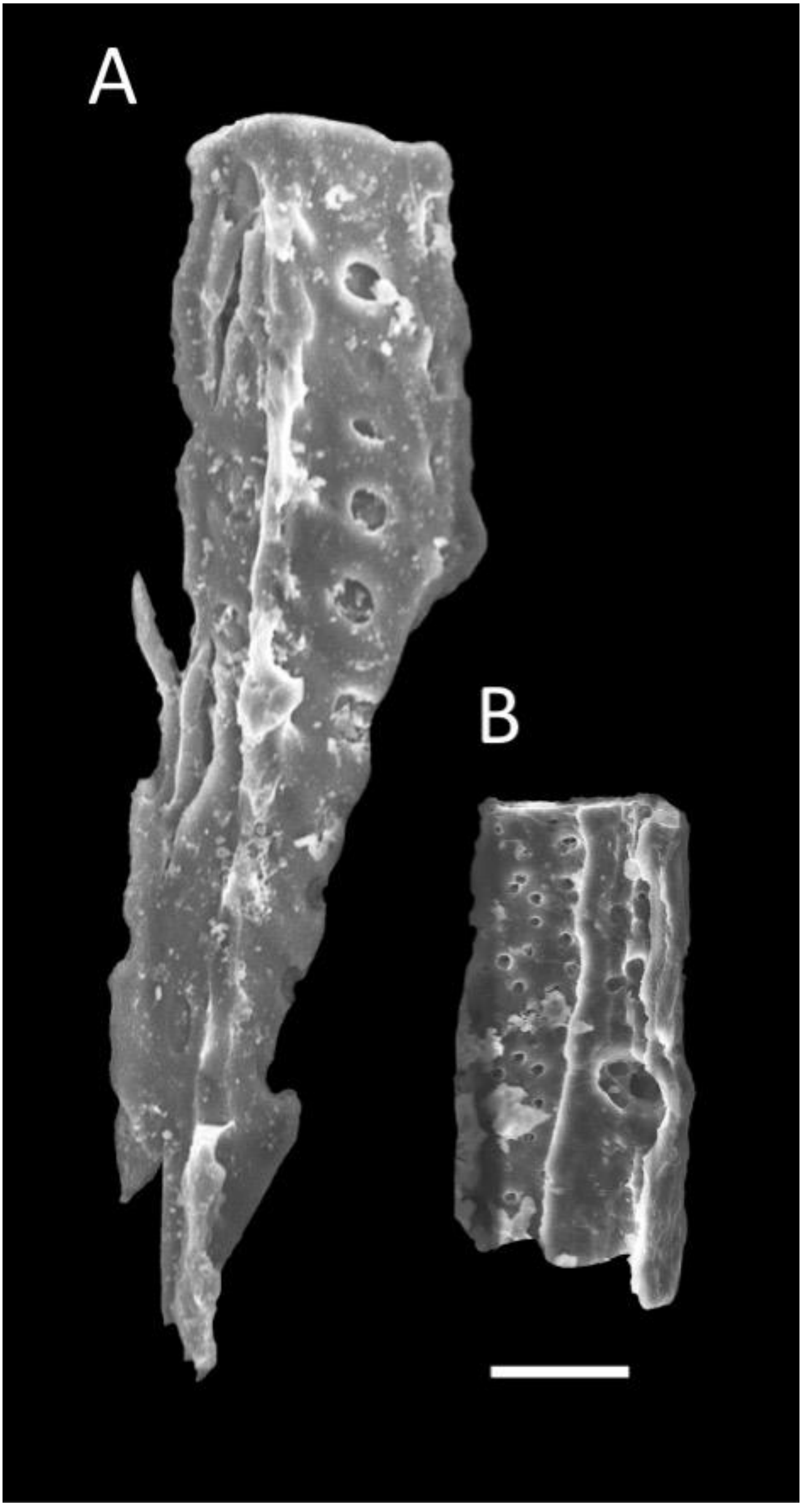
Trilete spores (A–G), plant fragments (H–I) and scolecodont (J) from the Nakazato Formation photographed under the Differential Interference Contrast Microscope. A, B, cf. *Retusotriletes* spp. (A, 2021.12.10-20a, P57/3; B, 2021.12.10-21a, C42/2); C, *Ambitisporites avitus* (2021.12.10-22a, M53); D, *Dibolisporites* sp. (2021.12.10-21a, L39/2); E, *Dictyotriletes* sp. (2021.12.10-21a, O50/4); F, *Apiculiretusispora* sp. (2021.12.10-21a, O47/2); G, *Aneurospora* sp. (2021.12.10-21a, T59/3); H, Conducting tissue (2021.12.10-20a, F45/2); I, *Laevitubulus tenuis* (2021.12.10-21a, Y49); J, Scolecodont (2021.12.10-21a, W60/1). Scale bar, 10 μm.

Plate IV



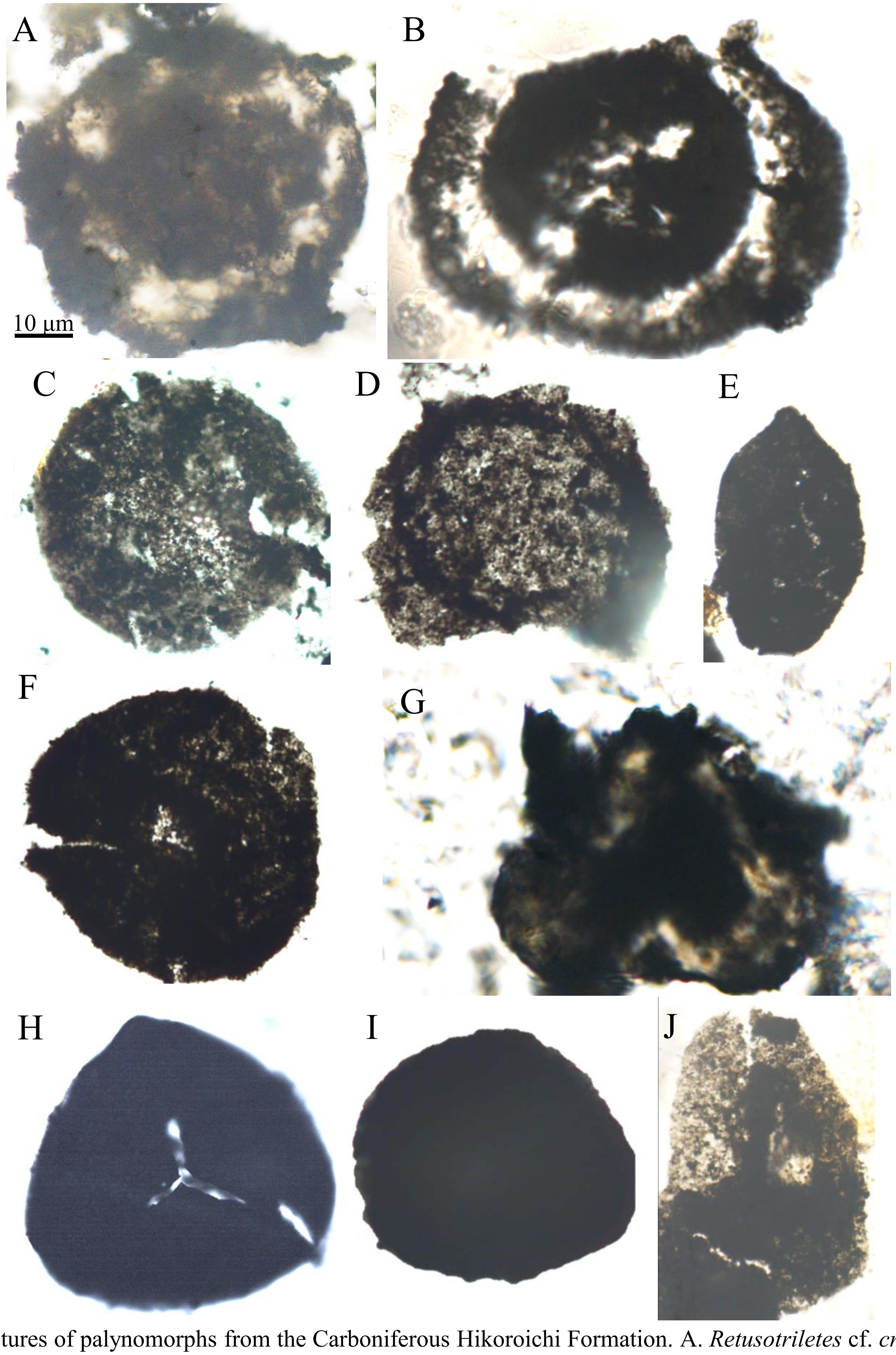
Cryptospores (A, B) and trilete spores (C–O) from the Nakazato Formation observed under the Scanning Electron Microscope. A, *Pseudodyadospora petasus* (2021.12.11-02); B, *Laevolancis* sp. in loosely attached dyad (2021.12.11-02); C, K, L, N, *Aneurospora* spp. (C, 2021.12.10-20; K, L, 2021.12.11-03; N, 2021.12.10-21); D, F, *Deltoidospora* (*Leiotriletes*) *priddyi* (D, 2021.12.10-20; F, 2021.12.10-20); E, *Calamospora atava* (2021.12.11-03); G, *Apiculiretusispora* sp. (2021.12.10-20); H, *Granulatisporites* cf. *muninensis* (2021.12.10-20); I, *Verrucosisporites* cf. *polygonalis* (2021.12.10-21); J, *Retusotriletes* cf. *triangulatus* (2021.12.11-03); M, *Brochotriletes* cf. *foveolatus* (2021.12.11-03); O, P, *Dibolisporites* cf. *echinaceus* (2021.12.10-18). Scale bar, 10 μm (A–O), 1 μm (P).

Plate V



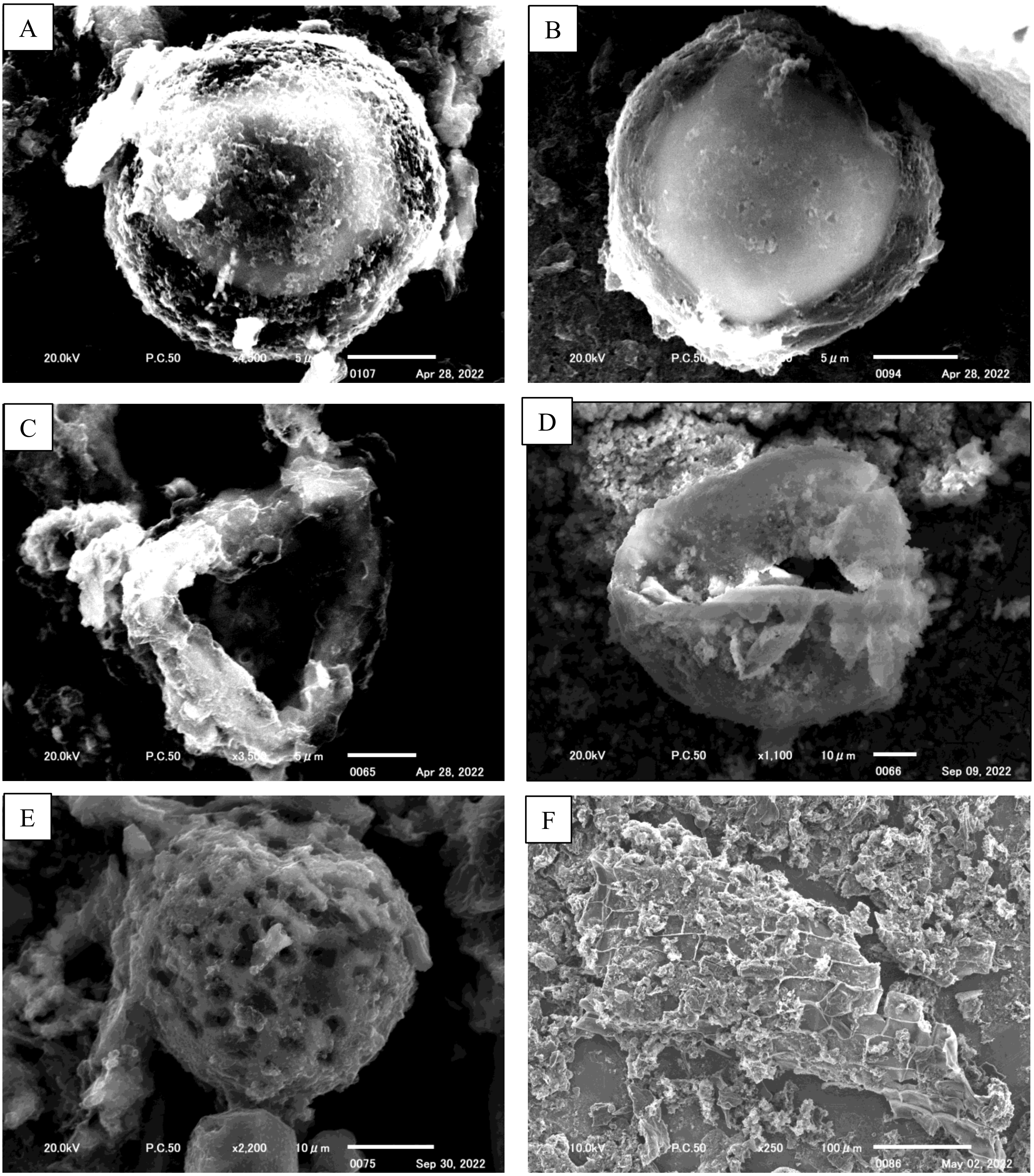
Longitudinal view of vascular tissues from the Nakazato Formation observed under the Scanning Electron Microscope. A, tracheary element with uniseriate pitting (2021.12.10-21); B, wall fragment of a water-conducting tube showing randomly distributed minute pores of various size (2021.12.11-03). Scale bar, 10 µm.

Plate VI



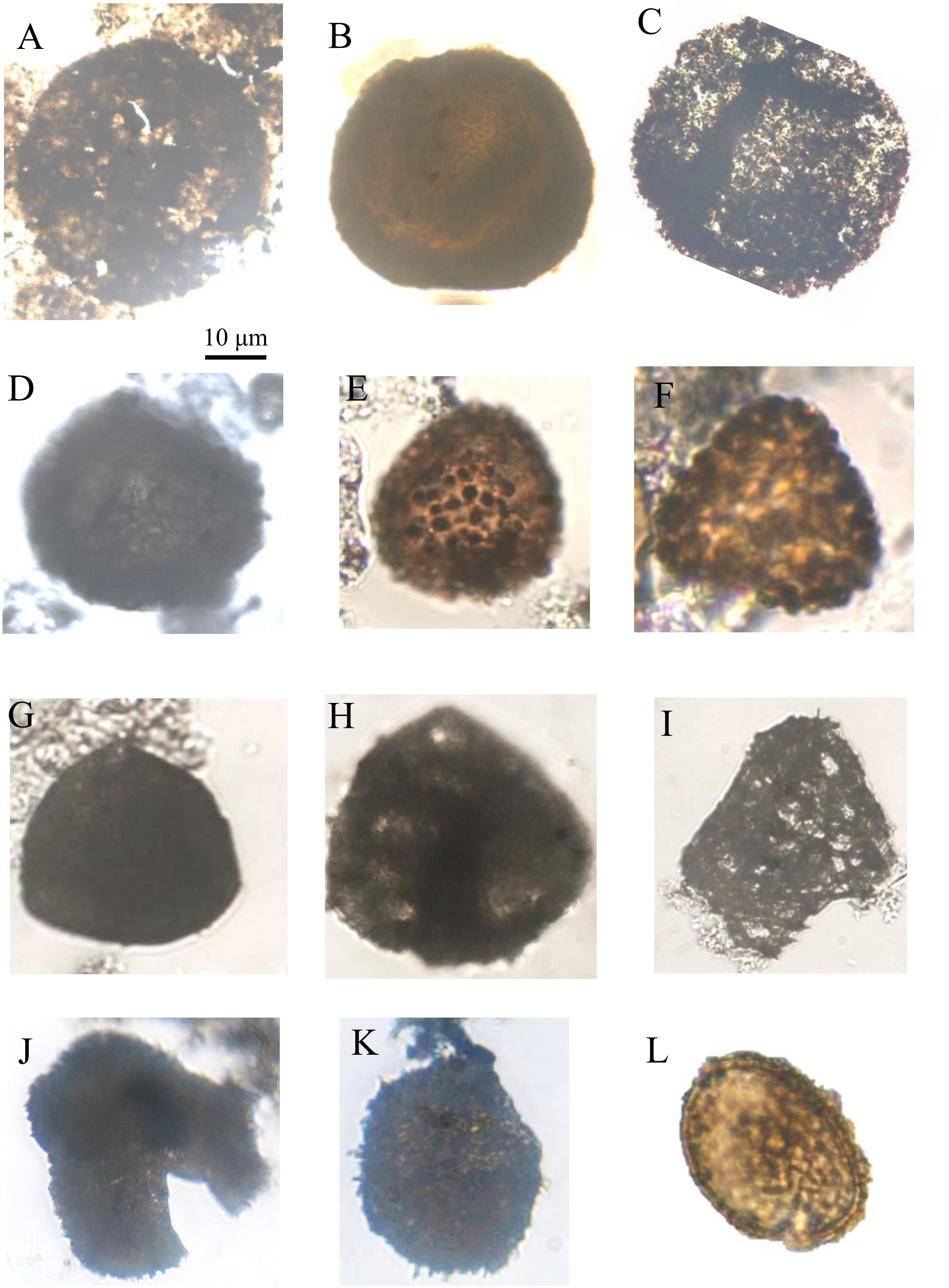
LM pictures of palynomorphs from the Carboniferous Hikoroichi Formation. A. *Retusotriletes* cf. *crassus*, 2021.12.122.06. B. ?*Spelaeotriletes* cf. *owensii*, 2021.12.12.06. C. ?*Calamospora* sp., 2021.12.12.01c, Ef: C22-4. D. *Densosporites* sp., 2021.12.12.05e, Ef: S44. E. ?*Monoletes* cf. *ellipsoides*, 2021.12.12.01b, Ef: S40-2. F.? *Calamospora* sp., 2021.12.12, 01e, Ef: V30. G. ?*Punctatisporites* sp., 2021.12.12.06. H. *Verrucosisporites* sp., 2021.12.12.01C, Ef: P54-4. I. ?*Deltoidospora* sp., 2021.12.12.06e, Ef: T49-2. J. ?*Punctatisporites* sp., 2021.12.12.01e. Scale bar, 10 µm.

Plate VII



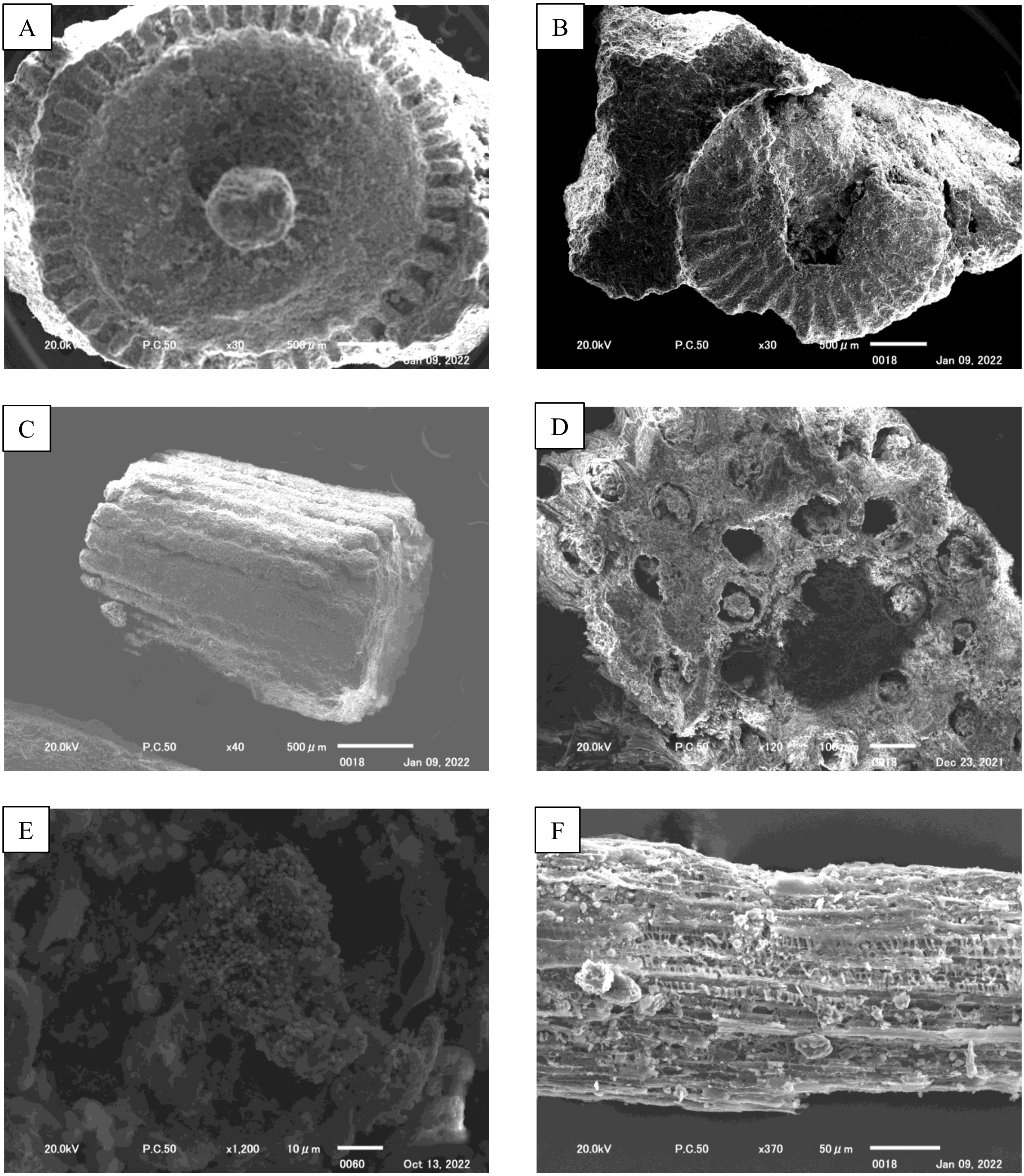
SEM pictures of palynomorphs from the Carboniferous Hikoroichi Formation.
A-B. ?*Spelaeotriletes* cf. *owensii*, 2021.12.12.02. C-D. ?*Deltoidospora* sp., 2021.12.12.
E, rounded palynomorph. F. Cuticle fragment, 2021.12.1205.

Plate VIII



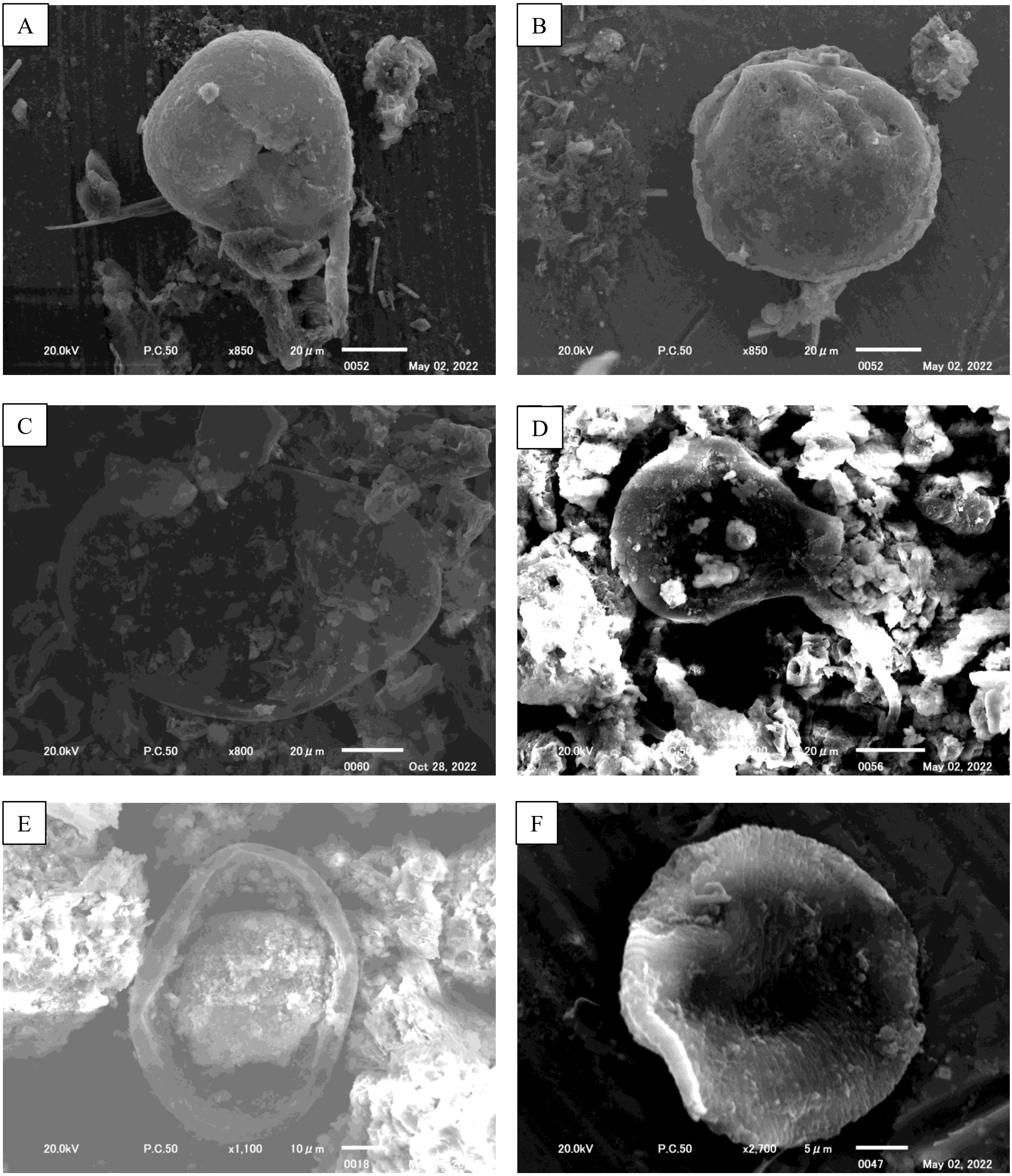
LM pictures of palynomorphs from the Permian Kanokura Formation. A-D. *Punctatisporites* sp. (A. Nishikori Fm-5-1; B, 2021.12.13.011b, Ef: N53; D, 2021.12.13.-8G). E-F, I. *Verrucosisporites* sp. (E, 2021.12.13.03-d-3; F, 2021.12.13.03-a-2; I, 2021.12.13.03-d-3). G, L. *Granulatisporites* sp. (G, 2021.12.13.011g, Ef: V42-2, L, 2021.12.13.03-d-3). H, J-K. *Baculatisporites* sp. (H, 2021.12.13.02e, Ef: W44-1). Scale bar, 10 μm.

Plate IX



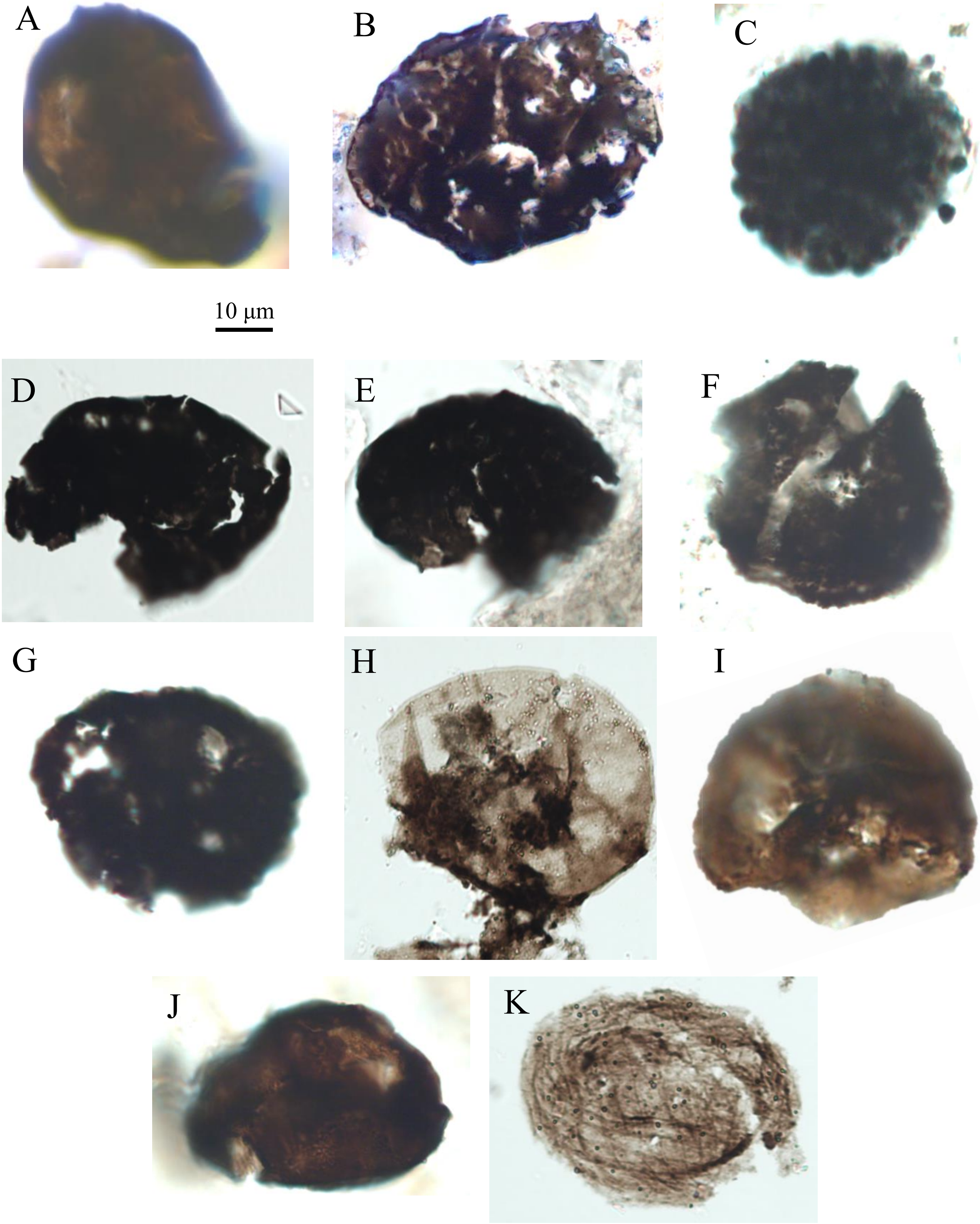
SEM pictures of microfossils from the Permian Kanokura Formation. A-D. Coral fragments. E. Pyrite crystals. F. Plant fragment showing detailed biostructures.

Plate X



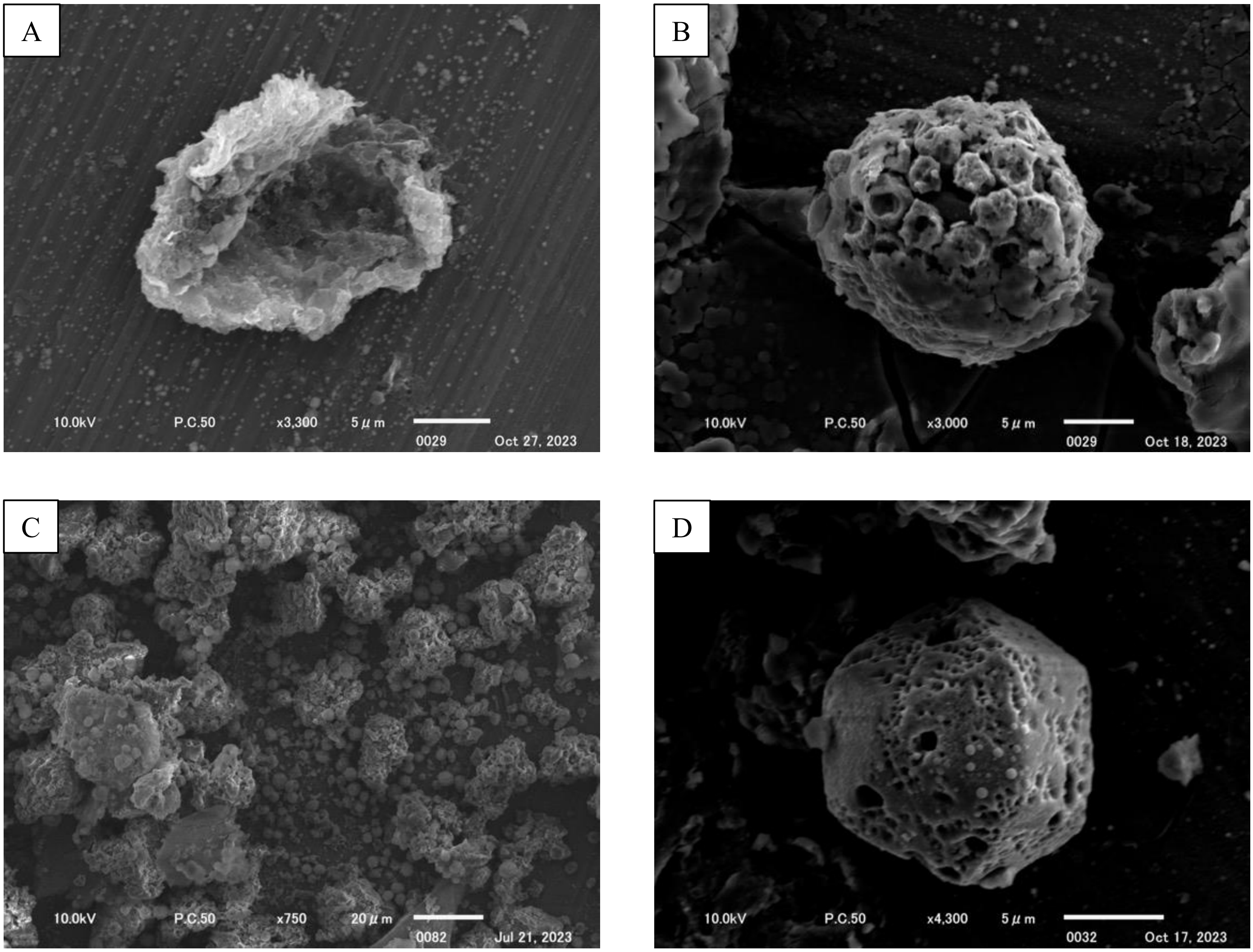
SEM pictures of palynomorphs from the Permian Kanokura Formation. A-D. Fungi.
E. *Spelaeotriletes* cf. *owensii.* F. Rounded striate palynomorph.

Plate XI



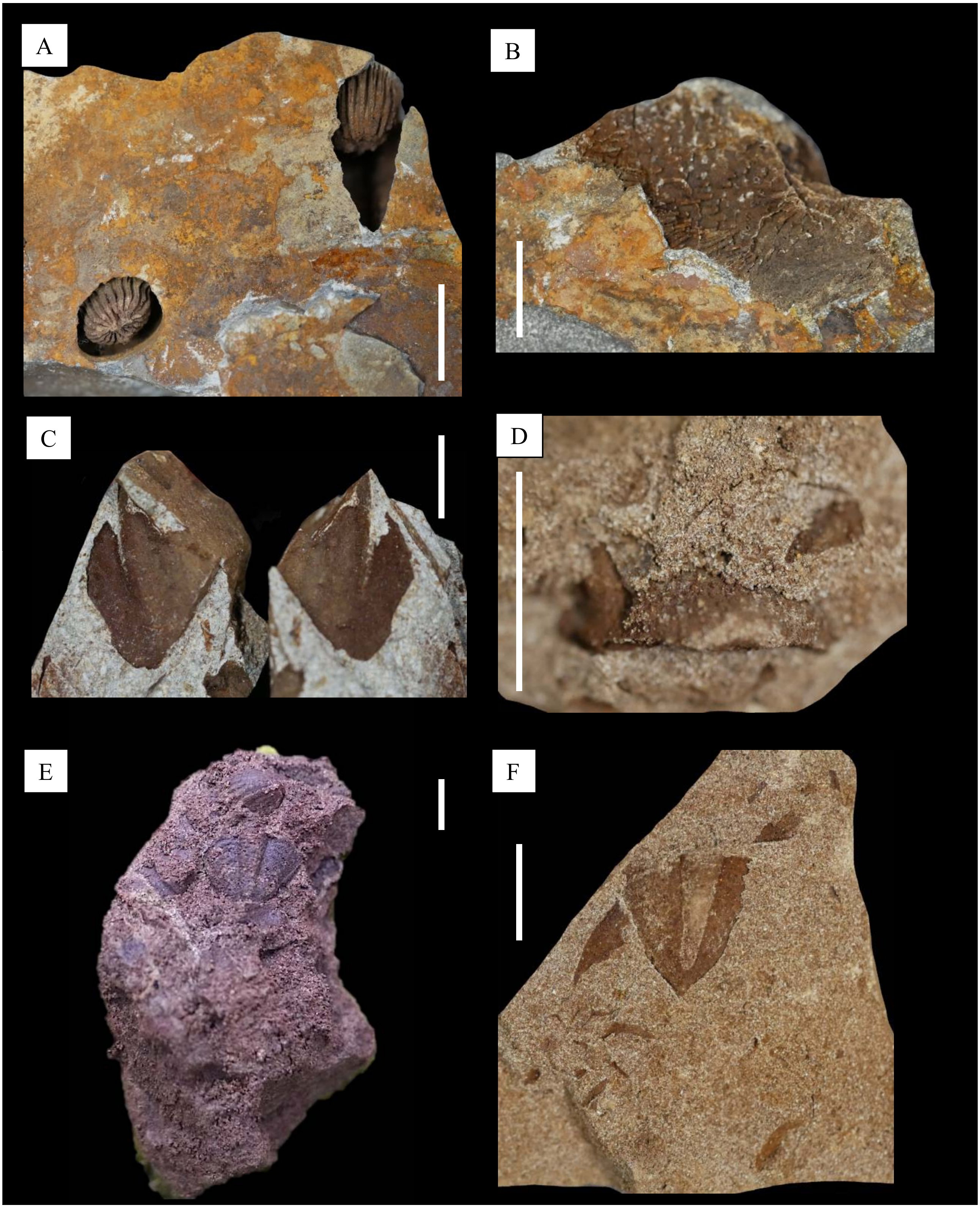
LM pictures of palynomorphs from the Devonian Fukuji Formation. A, B. *Deltoidospora* (*Leiotriletes*) sp. C. Framboid pyrite. D-G. *Retusotriletes* sp. H-J. *Retusotriletes* cf. *triangulatus*. K. Acritarch. Scale bar, 10 µm.

Plate XII



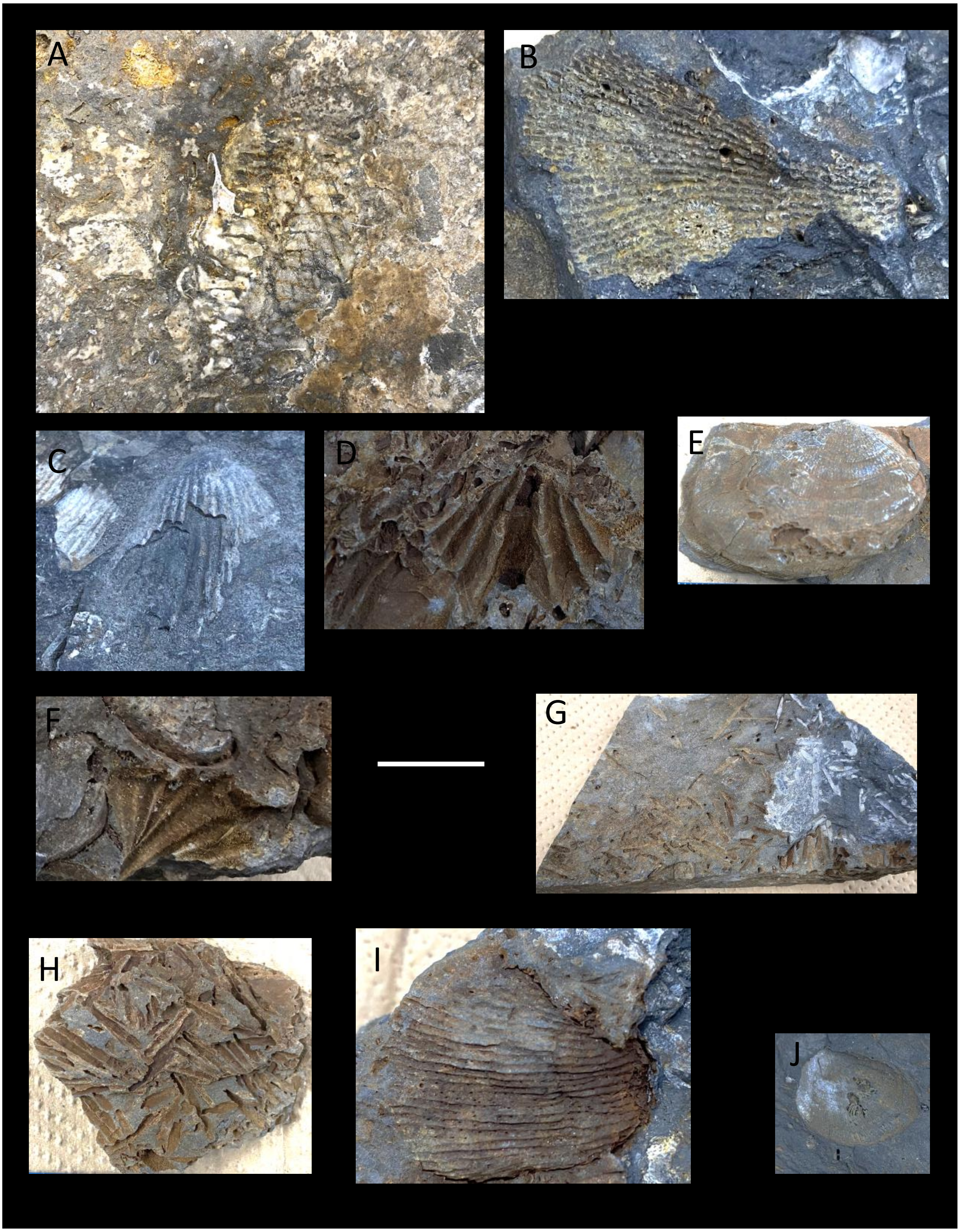
SEM pictures of microfossils from the Devonian Fukuji Formation. A, *Deltoidospora* (*Leiotriletes*) sp. B. Framboid pyrite. C, D. Crystals of pyrite.

Plate XIII



Example of macrofossils obtained from sampled horizons in the Devonian Nakazato Formation.
A. Corals (Loc. 1). B. Bryozoan (Loc. 1). C. Trilobite (Loc. 1). D-F. Trilobites (Loc. 4).
Scale bar, 1 cm.

Plate XIV



Example of macrofossils obtained from sampled horizons of the Permian Kanokura Formation. A. *Leptodus* sp. B. Bryozoan. C. *Planatrypa japonica.* D. *Pectorhyncha obtusiplicata*. E. *Orthotetes* sp. F. *Callispirina ornate.* G, H. *Monodiexodina matsubaishi*. I. *Fenestella crassistereoma.* J. *Rhipidomella* sp. Scale bar, 1 cm.

SHIZUOKA UNIVERSITY 静岡大学 創造科学技術大学院 Graduate School of Science and Technology, Shizuoka University

P14-2: APC2 (2023. 8. 3-7. JAPAN)

OLDEST TERRESTRIAL FLORA OF JAPAN OBTAINED FROM THE DEVONIAN NAKAZATO FORMATION OF THE SOUTH KITAKAMI BELT, NORTHEAST JAPAN

Ahmed MAHER (Graduate School of Science and Technology, Shizuoka University, Japan; Department of Geology, Faculty of Science, Al-Azhar University, Egypt), **Toshifumi KOMATSU** (Faculty of Advanced Science and Technology, Kumamoto University, Japan), **Toshihiro YAMADA** (Department of Earth and Planetary Sciences, Faculty of Science, Hokkaido University, Japan), **Julien LEGRAND** (Department of Geosciences, Faculty of Science; Graduate School of Science and Technology, Shizuoka University, Japan).

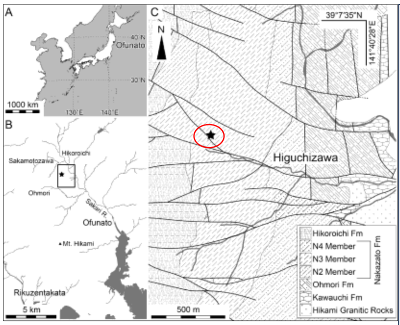
Silurian-Devonian is a crucial period for understanding the process of terrestrialization and early diversification of embryophytes. We conduct a wide palynological study for first time on Japanese Paleozoic sediments, and report here a well-preserved spore assemblage recovered from the Nakazato Formation outcropping in the Hikoroichi area of the South Kitakami Belt, Iwate Prefecture, NE Japan. The assemblage, which represents the oldest flora of Japan, is consistent with an Emsian-Eifelian age. It composed of cryptospores, probably produced by hepatics, and spores with affinities to the rhyniophytes and zosterophyllophytes, associated with abundant plant fragments including woods, tabular remains and cuticles. Most elements are cosmopolitan or widely distributed, but a comparison with previously reported microfloras from adjacent areas agrees with a probable location of the South Kitakami Belt close to the South China block during the Devonian.

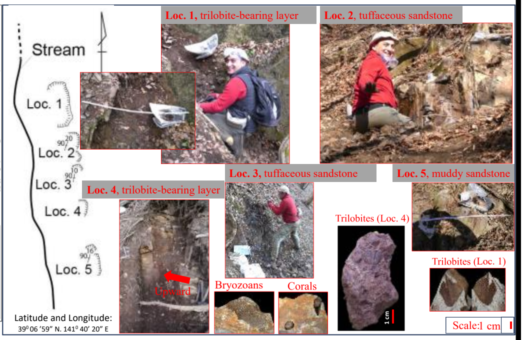
GEOLOGIC SETTING

In Japan, Silurian to Devonian fossil-bearing sediments are mainly distributed in three terranes: the South Kitakami Terrane in Northeast Japan, the Fukuji and Kuzuryu areas of the Hida Gaien Terrane in central Japan, and the Yokokurayama area of Shikoku and Gionyama area of Kyushu included in the Kurosegawa Terrane in Southwest Japan (Williams *et al*., 2014; Isozaki, 2019). These sediments yield a rich fauna dominated by corals and including sponges, stromatoporoids, echinoderms, bryozoans, brachiopods, cephalopods, tentaculitids, bivalves, gastropods, trilobites, ostracods, conodonts, dendroid graptolites and radiolarians (e.g., Kato et al., 1980). The South Kitakami Belt consists of early Paleozoic igneous and metamorphic basement rocks covered by shallow-marine sediments deposited from the late Ordovician to Lower Cretaceous (Isozaki *et al*., 2011).

MATERIAL AND METHODS

We collected 28 mudstone samples from the Nakazato Formation in the Hikoroichi area of the South Kitakami Belt, outcropping along the upper stream of the Higuchizawa river, around 5 km northwest of Ofunato City, Iwate Prefecture, Northeast Japan. Brachiopods and corals were observed on the field in many horizons when we collected the samples along with trilobites including *Rhinophacops* suggesting age of the Emsian/Eifelian boundary (Kaneko, 2007). Microfossils were extracted following the methods of Legrand *et al.* (2021).

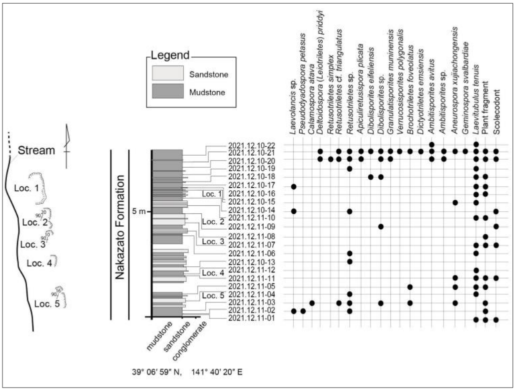




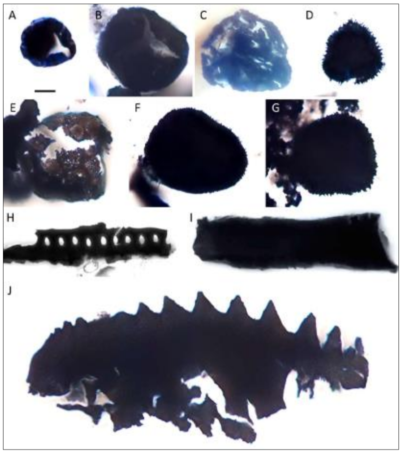
Location of the Nakazato Formation outcrop
(modified from Editorial Committee of TOHOKU, Part 2 of Regional Geology of Japan, 1989)

RESULTS

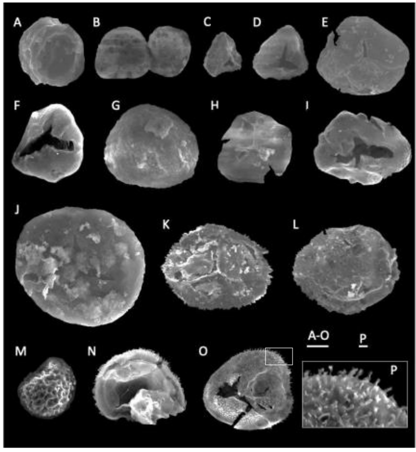
We obtained well-preserved palynomorphs composed of two species of cryptospores and 15 species of trilete spores, associated with abundant plant fragments including mass of conducting cells, tabular remains and cuticles. Most palynomorphs are abundant and diversified, represented by retusoid, apiculate, verrucate and reticulate spores, were obtained from horizons 2021. 12. 10-20 and -21.



Columnar section with sampling horizons and occurrence of palynomorphs



Trilete spores (A-G), plant fragments (H-I) and scolecodont (J) from the Nakazato Formation (2021.12.10-20 and -21) observed under the Differential Interference Contrast Microscope. A, *Retusotriletes simplex*; B, *Retusotriletes* sp.; C, *Ambitisporites avitus*; D, *Dibolisporites* sp.; E, *Dictyotriletes emsiensis*; F, *Apiculiretusispora plicata*; G, *Aneurospora xujiachongensis*; H, Conducting tissue; I, *Laevitubulus tenuis*; J, Scolecodont. Scale bar, 10 µm.

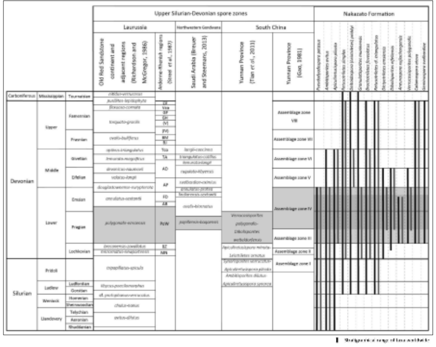


Cryptospores (A, B) and trilete spores (C-O) from the Nakazato Formation (2021.12.10-18, -20, -21; 2021.12.11-02, -03,) observed under the Scanning Electron Microscope. A, *Pseudodyadospora petasus*; B, *Laevolancis* sp. in loosely attached dyad; C, *Ambitisporites* sp.; D, *Ambitisporites avitus*; E, *Calamospora atava*; F, *Deltoidospora* (*Leiotriletes*) *priddyi*; G, *Apiculiretusispora plicata*; H, *Granulatisporites muninensis*; I, *Verrucosisporites polygonalis*; J, *Retusotriletes* cf. *triangulatus*; K, L, *Aneurospora xujiachongensis*; M, *Brochotriletes foveolatus*; N, *Geminospora svalbardiae*; O, P, *Dibolisporites eifeliensis*. Scale bar, 10 µm (A-N), 1 µm (O).

DISCUSSION

1- Age of the Nakazato Formation inferred from palynoflora

Spore zonations established in Gondwana and Laurussia indicate a late Pragian age for the Nakazato assemblage, while those in Laurussia suggest a Pragian–early Emsian age. The Nakazato assemblage shares similarities with assemblages in China, which are considered to be Pragian (Tian *et al*., 2011) or late Pragian-Emsian in age (Gao, 1981). On the other hand, based on trilobite and radiolarian assemblages, the N3 Member of the Nakazato Formation has been assigned an Emsian to Givetian age (Kobayashi and Hamada, 1977). Trilobite biostratigraphy further narrows down the age of the N3 Member to the latest Emsian–earliest Eifelian (Kaneko, 2007). It is possible to hypothesize that there was a time lag in the appearances and disappearances of indices between the Nakazato area and other regions.



Stratigraphical range of taxa from the Nakazato Formation, with correlation with upper Silurian Devonian standard spore zones of Laurussia, northwestern Gondwana and South China.

2- Vegetational characteristics of the Nakazato palynoassemblage

Hepatics	Cryptospores	*Pseudodyadospora petasus* *Laevolancis* sp.
Rhyniophytes	Trilete microspores	*Ambitisporites avitus* *Ambitisporites* sp. *Granulatisporites muninensis*
Trimerophytes		*Apiculiretusispora plicata* (1)
		Retusotriletes simplex *Retusotriletes* cf. *triangulates* (2)
Zosterophyllophytes		*Deltoidospora* (*Leiotriletes*) *priddyi* *Calamospora atava*
Unknown		*Geminospora svalbardiae*
		Brochotriletes foveolatus
		Dictyotriletes emsiensis
Lycopsids		*Verrucosisporites polygonalis* *Aneurospora xujiachongensis* (3)
Cladoxylopsida		*Dibolisporites eifeliensis* *Dibolisporites* sp. *Dictyotriletes emsiensis*

Zosterophyllophytes

Zosterophyllum reconstruction
(Steemans *et al*., 2012)

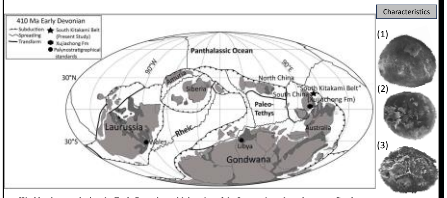
Rhyniophytes

Cooksonia reconstruction
(Steemans *et al*., 2012)

The data reflect a vegetation consisting of only herbaceous plants which possibly lived in proximity to freshwater areas. The abundance of laevigate spores represented by *Retusotriletes* suggests that the **zosterophyllophytes** constituted major vegetation in the backland of the Nakazato Formation. Their spores should have been easily transported by the rivers towards the Palaeo-Tethys Ocean and trapped in shallow marine sediments of the South Kitakami Belt. The abundance of spores and plant fragments found in the Nakazato assemblage could suggest that the entrapment site was located near the living habitats of these plants.

3- Paleophytogeographic significance of the Nakazato palynoassemblage

The Nakazato palynoflora predominantly consists of cosmopolitan taxa but demonstrates the closest similarities to those of South China. In particular, the palynoflora reported from the Xujiachong Formation shows strong similarities in its composition



World paleomap during the Early Devonian, with location of the Laurussia and northwestern Gondwana palynostratigraphical standards, Xujiachong Formation, and presumed location of the South Kitakami Belt
(modified from Torsvik and Cocks, 2016).

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CONCLUSION

The spore assemblage recovered from the N3 Member of the Nakazato Formation consists of 2 cryptospore and 16 spore species, and represents the oldest plant fossil assemblage reported from Japan. It indicates a vegetation predominantly composed of rhyniophytes, zosterophyllophytes, and/or trymerophytes, with some lycopsids and cladoxylopsids. The stratigraphic range of these taxa, along with the correlation of the assemblage with well-defined stratigraphic standards of Laurussia and northwestern Gondwana, suggests a Pragian-Emsian age slightly older than the latest Emsian to earliest Eifelian, as estimated by marine index fossils. This palynoassemblage closely resembles "contemporaneous" assemblages from South China.

ACKNOWLEDGEMENTS

The authors wish to thank Professor. Akihisa KITAMURA, Shizuoka University, for his valuable advices and continuous discussions during the study. The authors thank Ofunato City for permitting the field research; and the Museum of Natural and Environmental History, Shizuoka, Japan, for permitting the SEM observation.

Appendix 1. Poster for the 2nd Asian Palaeontological Congress, Tokyo (2023.08.03-07).

P14-2

Oldest terrestrial flora of Japan obtained from the Devonian Nakazato Formation of the South Kitakami Belt, Northeast Japan

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Abstract

Silurian-Devonian is a crucial period for understanding the process of terrestrialization and early diversification of embryophytes. Paleozoic fossil-bearing sediments of Japan, mainly distributed in NE, central and SW Japan, yield a rich marine fauna together with algae, however, there exists only a few studies on terrestrial flora. Oldest land plant fossils are represented by two lycopsids and an uncertain plant from the Upper Devonian Tobigamori (South Kitakami Belt, NE Japan) and Naidaijin (Kurosegawa Belt, SW Japan) formations. Macro- and microfossil reports increase in the Carboniferous and Permian deposits, particularly from the Miyagi and Iwate prefectures of NE Japan.

We conduct a wide palynological study on Japanese Paleozoic sediments, and report here a well-preserved spore assemblage recovered from the Nakazato Formation outcropping in the Hikoroichi area of the South Kitakami Belt, Iwate Prefecture, NE Japan. Samples were collected from mudstones assigned to the latest Emsian (Lower Devonian) to earliest Eifelian (Middle Devonian) from their trilobite, gastropod and brachiopod assemblage. We obtained a palynoflora composed of cryptospores, probably produced by hepatics, and spores with affinities to the rhyniophytes and zosterophyllophytes, associated with abundant plant fragments including woods, tabular remains and cuticles. The assemblage, which represents the oldest flora of Japan, is consistent with an Emsian-Eifelian age. Most elements are cosmopolitan or widely distributed, but a comparison with previously reported microfloras from adjacent areas agrees with a probable location of the South Kitakami Belt close to the South China block during the Devonian.

KEYWORDS: Devonian, microflora, Nakazato Formation, NE Japan.

Appendix 2. Proceeding for the 2nd Asian Palaeontological Congress, Tokyo (2023.08.03-07).

B18

上部白亜系蝦夷層群函淵層
ハドロサウルス産出層の古花粉学的研究[1]

馬場美邑・ルグラン ジュリアン（静岡大・理）[2]・
西村智弘（穂別博）[3]・池田昌之（東大・理）[4]

北海道南部むかわ町穂別に分布する蝦夷層群函淵層からハドロサウルス類の全身骨格化石が国内で初めて報告され，*Kamuysaurus japonicus* と記載された（Kobayashi *et al.*, 2019）．共産するアンモノイド *Pachydiscus*（*Neodesmoceras*）*japonicus* は，基底がカンパニアン／マーストリヒチアン（C/M）境界に対比されている *Nostoceras hetonaiense* 帯に属することから，ボーンベッドは下部マーストリヒチアンと推定された．しかし，古地磁気層序と U-Pb 放射年代によると，C/M 境界の位置は *N. hetonaiense* 帯の上下に対比される可能性もある．

本研究では，*K. japonicus* の地質年代を確認することと，周辺環境を解明するため，函淵層から採集した泥岩及び穂別博物館から提供されたジャケット試料の花粉分析を試みた．その結果，80 種以上の胞子・花粉化石が得られ，その中に，18 種の Triprojectate 花粉（極軸に３つの突起を持つ花粉）が含まれた．Triprojectate 花粉は白亜紀後期の北半球に広く分布し，生層序に利用されている．ジャケット試料からは，北米・カナダの年代が確定している種（*Parviprojectus reticulatus*, *Reticorpus delicatus*, *Triprojectus turbitus*）に加えて日本またはアジアのみで報告されている種（*Pseudoaquilapollenites melior*, *T. elegans*, *T. normalis*）が確認され，それらの共通レンジは，*K. japonicus* 産出層準がマーストリヒチアン下部であることを示唆する．

C/M 寒冷期における北米のハドロサウルス類の北上は降水量減少に起因したと推定されている．今回函淵層から得られた胞子・花粉群集では，湿潤環境を好むヘゴ目，ゼンマイ目などの多様なシダ植物の胞子が主体であり，ハドロサウルス類の生息域において北米同様に湿潤環境であることが重要であったと考えられる．尚，胞子・花粉群集の組成は，河口付近または海岸環境を示し，これまでハドロサウルス類に推定された生息域に矛盾しない．

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[1] Palynomorph assemblage associated with a hadrosaur from the Maastrichtian Hakobuchi Formation, Yezo Group, Hokkaido, Japan
[2] Miyu Baba, Julien Legrand (Shizuoka Univ.), [3] Tomohiro Nishimura (Hobetsu Mus.), [4] Masayuki Ikeda (Tokyo Univ.)

B19

Palynostratigraphy of the Permo-Carboniferous succession in two wells from the Gulf of Suez, Egypt[1]

Ahmed Maher (Shizuoka Univ.; Osaka City Univ.)[2]・Toshihiro Yamada (Osaka City Univ.)[3]・Julien Legrand (Shizuoka Univ.)[4]

The Gulf of Suez, located at the interface between the African and Arabian plates, is considered as one of the major grabens and oil-yield areas of the world, and results from the stretching and collapsing of the crust between these two provincial landmasses. A standard biozonation is well established for the Late Paleozoic of the Arabian plate (Oman, Iraq, Pakistan, Yemen), however, only a few palynological studies exist in areas of the Gulf of Suez; as a result, paleoenvironments and vegetational changes of this key period remain unclear, making difficult correlations between regions of northern Gondwana.

Here, we conducted palynological analyses on 49 boring samples of the Nubia Formation consisting of black shale and sandstone, collected from two wells (OCT-K1 and OCT.G5) in the Gulf of Suez. We identified 34 genera and 86 species of spores (lycophytes and diverse monilophytes: Marrattiidae, Equisetidae, Polypodiidae), gymnosperm pollen (Cordaitales, ginkgophytes, and rare bisaccate pollen of pteridosperms and conifers), along with a few acritarchs and fungal spores. Palynomorphs represent a "mixed palynoflora" with elements of both the Gondwanan and Laurasian provinces. Assemblages of well OCT.G5 are particularly rich in terrestrial palynomorphs and allow defining four palynozones, that can be correlated with biozones of Europe and Oman, and assigned to the Visean (lower Carboniferous; Phase I) to Sakmarian (lower Permian; Phase IV) in age. They revealed changes from lycopod swamp forests reflecting temperate and humid conditions through the Carboniferous, to a vegetation dominated by cordaitaleans flourishing under a warm and dry climate from the Permian.

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[1] エジプト・スエズ湾のボーリング調査に基づくペルム紀〜石炭紀の花粉層序
[2] マヘル アフメド（静大；大阪市大）・[3] 山田敏弘（大阪市大・院）・
[4] ルグラン ジュリアン（静大・理）

B20

初期陸上植物の微化石群集から解明する北部ベトナム
Si Ka 層の地質年代と古環境[1]

Julien Legrand（静大・理）[2]・山田敏弘（大阪市大・院）[3]・小松俊文（熊大・院・先）[4]・Mark Williams・Tom Harvey（Univ. Leicester）[5]・Tim De Backer・Thijs R. A. Vandenbroucke（Ghent Univ.）[6]・Phong Duc Nguyen（VIGMR）[7]・Hung Dinh Doan・Hung Ba Nguyen（VNMN）[8]

後期シルル紀〜前期デボン紀に起きた維管束植物の適応放散は，地球の生態系を激変させた大事変である．ところが，南中国・インドシナブロックでは，この時期の非海成・浅海成堆積物の年代を正確に把握できておらず，年代値が確実な古植物学データが極めて少ない．そこで本研究では，この時期の堆積物を含む北部ベトナムの Song Cau 層群 Si Ka 層で植物微化石の分析を行い，その年代を推定した．Si Ka 層は，タイグエン省からカオバン省，ハーザン省にかけて東西 100 km以上にわたって分布し，南中国の雲南省や広西省（＝Lianhuashan Fm）にも連続する．また，Si Ka 層からは，浅海性〜汽水性の魚類，巻貝，貝形虫や初期維管束植物が報告されている．

本研究では，ハーザン省ドンヴァン地域に分布するSi Ka層最上部から，胞子を含む植物微化石群集を得た．この群集は18種からなり，原始的なコケ植物の隠胞子（二集粒の*Dyadospora murusattenuata*, *Pseudodyadospora petasus*, 四集粒の*Cheilotetras caledonica*）に加え，リニア植物（*Ambitisporites avitus*, *Apiculiretusispora* sp., *Synorisporites verrucatus*）及びゾステロフィルム植物（*Retusotriletes* cf. *triangulatus*, *R. warringtonii*）の三溝型胞子，ネマトファイト植物の通導組織とクチクラを含む．

Si Ka層の植物微化石群集を，イギリスやリビアなどの模式的な花粉層序や，南中国の群集と比較した結果，Si Ka層の最上部は上部シルル系（ラドロー〜プリドリ）の堆積物であり，従来の解釈（下部デボン系）よりも古いことがわかった．これは，ベトナムを含む東南アジアで最古の植物微化石群集である．

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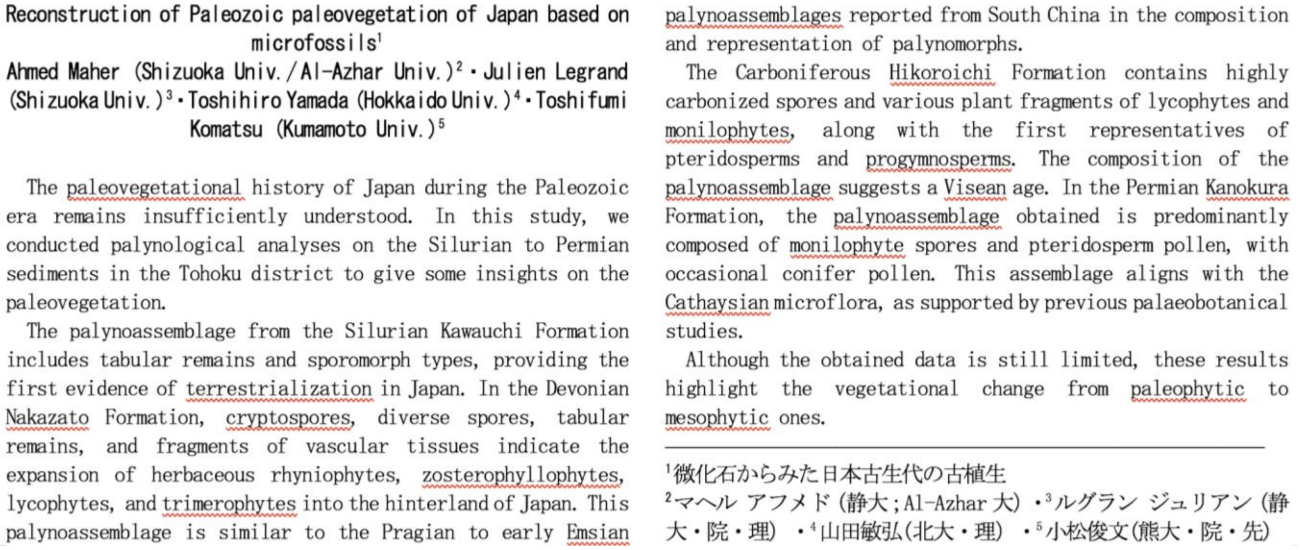
[1] Implications of an early land plant microfossil assemblage for the age and paleoenvironment of the Si Ka Fm, northern Vietnam.
[2] Julien Legrand (Shizuoka Univ.), [3] Toshihiro Yamada (Osaka City Univ.), [4] Toshifumi Komatsu (Kumamoto Univ.), [5] Mark Williams, Tom Harvey (Univ. Leicester), [6] Tim De Backer, Thijs R. A. Vandenbroucke (Ghent University), [7] Phong Duc Nguyen (VIGMR), [8] Hung Dinh Doan, Hung Ba Nguyen (VNMN)

Appendix 3. Abstract for the 2021 Annual Meeting of the Palaeontological Society of Japan (2021.07.02-04).



Reconstruction of Paleozoic paleovegetation of Japan based on microfossils[1]

Ahmed Maher (Shizuoka Univ. / Al-Azhar Univ.)[2] · Julien Legrand (Shizuoka Univ.)[3] · Toshihiro Yamada (Hokkaido Univ.)[4] · Toshifumi Komatsu (Kumamoto Univ.)[5]

The paleovegetational history of Japan during the Paleozoic era remains insufficiently understood. In this study, we conducted palynological analyses on the Silurian to Permian sediments in the Tohoku district to give some insights on the paleovegetation.

The palynoassemblage from the Silurian Kawauchi Formation includes tabular remains and sporomorph types, providing the first evidence of terrestrialization in Japan. In the Devonian Nakazato Formation, cryptospores, diverse spores, tabular remains, and fragments of vascular tissues indicate the expansion of herbaceous rhyniophytes, zosterophyllophytes, lycophytes, and trimerophytes into the hinterland of Japan. This palynoassemblage is similar to the Pragian to early Emsian palynoassemblages reported from South China in the composition and representation of palynomorphs.

The Carboniferous Hikoroichi Formation contains highly carbonized spores and various plant fragments of lycophytes and monilophytes, along with the first representatives of pteridosperms and progymnosperms. The composition of the palynoassemblage suggests a Visean age. In the Permian Kanokura Formation, the palynoassemblage obtained is predominantly composed of monilophyte spores and pteridosperm pollen, with occasional conifer pollen. This assemblage aligns with the Cathaysian microflora, as supported by previous palaeobotanical studies.

Although the obtained data is still limited, these results highlight the vegetational change from paleophytic to mesophytic ones.

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[1] 微化石からみた日本古生代の古植生

[2] マヘル アフメド（静大；Al-Azhar 大）・[3] ルグラン ジュリアン（静大・院・理）・[4] 山田敏弘（北大・理）・[5] 小松俊文（熊大・院・先）

Appendix 4. Abstract for the 173th Regular Meeting of the Palaeontological Society of Japan (2024.01.26-28).

Appendix 5. Accepted manuscript for *Paleontological Research*.