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A new assemblage of plant mesofossils (late Turonian–middle Santonian; Upper Cretaceous) from the Tamagawa Formation, Kuji Group, in northeastern Japan

MASAMICHI TAKAHASHI[1], PATRICK S. HERENDEEN[2], FABIANY HERRERA[2], REN HIRAYAMA[3], HISAO ANDO[4], KAZUHISA SASAKI[5] AND PETER R. CRANE[6,7]

[1]*Department of Environmental Sciences, Niigata University, 8050, 2-cho, Ikarashi, Nishi-ku, Niigata 950-2181, Japan (e-mail: masamichi@env.sc.niigata-u.ac.jp)*
[2]*Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, Illinois 60022, USA*
[3]*School of International Liberal Studies, Waseda University, 1-7-14, Nishiwaseda, Shinjuku-ku, Tokyo 169-0051, Japan*
[4]*Department of Earth Sciences, Faculty of Science, Ibaraki University, 2-1-1, Bunkyo, Mito 310-8512, Japan*
[5]*Kuji Amber Museum, 19-156-133, Kokujicho, Kuji, Iwate 028-0071, Japan*
[6]*Yale School of the Environment, Yale University, 195, Prospect Street, New Haven, Connecticut 06511, USA*
[7]*Oak Spring Garden Foundation, 1776, Loughborough Lane, Upperville, Virginia 20184, USA*

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Abstract. A preliminary description is provided of a new assemblage of small, three-dimensional and charcoalified mesofossils from the Tamagawa Formation (late Turonian–middle Santonian; Upper Cretaceous) of the Kuji Group in northeastern Japan. The new mesofossils yield excellent structural details and include well-preserved circinate shoots of ferns together with conifer leafy-shoots, seeds and probable pollen cones, and variety of angiosperm fruits and seeds, including fruits of Cornales and seeds of Nymphaeales. The new mesofossil assemblage is complementary to the previously published macrofossil flora from the Kuji Group.

Key words: charcoalified, Cretaceous, Kuji Group, late Turonian–middle Santonian, mesofossils, Tamagawa Formation

Introduction

Since the early classic papers by Friis and Skarby (1981, 1982), numerous paleobotanical studies of small three-dimensionally preserved flowers, fruits and seeds (mesofossils) recovered by bulk sieving techniques from Cretaceous sediments, have greatly enhanced our understanding of the pattern of angiosperm diversification through the first 70 million years of their evolutionary history. The bulk of the angiosperm mesofossil record has been recovered from Cretaceous sediments collected in eastern North America, central Portugal, and southern Sweden (Atkinson *et al.*, 2018; Friis and Pedersen, 2012; Friis *et al.*, 2013a, b, 2015, 2017a, b, 2018a, b, c, d, e, 2019; Herendeen *et al.*, 2017; Martínez *et al.*, 2016; Mendes and Friis, 2018; Mendes *et al.*, 2014; Schönenberger *et al.*, 2012). In contrast, the mesofossil record from Asia is much less extensive, and so far angiosperm mesofossils have been recovered only from Kazakhstan and Japan (Frumin and Friis, 1996, 1999; Frumin *et al.*, 2004; Takahashi *et al.*, 1999a, b, 2001a, b, 2002, 2007, 2008a, b, 2014, 2017).

In Japan, current knowledge of Cretaceous angiosperms is derived from a variety of permineralized angiosperm flowers and fruiting structures recovered from the Upper Cretaceous (Coniacian-Santonian) Yezo Group of Hokkaido (Nishida, 1985, 1991, 1994; Nishida and Nishida, 1988; Nishida *et al.*, 1996). In addition, a mesofossil assemblage from the Kamikitaba locality (Ashizawa Formation, early Coniacian, *ca.* 89 Ma) of the Futaba Group of northeastern Honshu in Japan preserves a mesofossil flora that includes three-dimensional angiosperm flowers, as well as several kinds of angiosperm fruits and seeds. The fossils recovered include flowers or fruits of *Futabanthus* (Annonaceae, Takahashi *et al.*, 2008b), *Esgueiria* (Combretaceae, Takahashi *et al.*, 1999b), *Hironoia* (Cornaceae, Takahashi *et al.*, 2002), *Archaefagacea* (Fagaceae, Takahashi *et al.*, 2008a), *Lauranthus*, *Microlaurus* (Lauraceae, Takahashi *et al.*, 2001a, 2014), and *Archaestella* (Trochodendraceae, Takahashi *et al.*, 2017).

Fossil seeds assigned to *Symphaenale* (Nymphaeaceae) have also been recovered from another mesofossil assemblage, Gokurakuzawa locality, (Tamayama Formation, Santonian, *ca.* 85 Ma) in the Futaba Group (Takahashi *et al.*, 2007).

In this study, a preliminary description is provided of a new assemblage of plant mesofossils from sediments of the Kuji Group exposed about 350 km north of the Futaba Group along the Pacific coast of northeastern Japan that includes small, three-dimensional and charcoalified mesofossils.

The Kuji Group has yielded abundant fossil leaves (Tanai, 1979) from the Tamagawa and Sawayama formations, and has yielded a palynoflora similar to that from the Futaba Group, but with the important addition of *Aquilapollenites* pollen in the Kuji assemblages (Miki, 1972, 1977; Umetsu and Kurita, 2007). Takahashi *et al.* (2001b) have described fossil megaspores from the Tamagawa Formation. The new mesofossils described here include well-preserved circinately coiled fern shoots (fiddleheads), conifer leafy-shoots, seeds and pollen cones, and a variety of angiosperm fruits and seeds. This preliminary report highlights the potential for future discoveries of informative fossil material, including well-preserved angiosperm flowers, from the Tamagawa Formation of the Kuji Group exposed in a part of Japan where sediments potentially rich in mesofossils have not been fully explored.

Materials and methods

The Kuji Group includes the Tamagawa, Kunitan and Sawayama formations in ascending order (Ando, 1997). Arimoto *et al.* (2018) suggested that the age of the Kuji Group ranges from the middle Turonian to the middle Campanian based on the $\delta^{13}C$ wood chemostratigraphy and U-Pb radiometric analysis of intercalating tuff layers. The Tamagawa Formation, the lowermost of the three formations in the Kuji Group, consists of a non-marine and shallow marine sedimentary succession, characterized by alluvial fan conglomerates with lacustrine mudstones, fluvial sandstone and mudstone, and estuary to shoreface sandstones (Ando, 1997). Outcrops of the Tamagawa Formation comprise a sequence of sandy to subordinately silty clastic sediments deposited in fluvial to shallow-marine environments (Ando, 1997; Umetsu and Kurita, 2007; Umetsu *et al*., 2013). The deposits are regarded as of middle Turonian–middle Campanian age (from 92.6 ± 0.6 Ma to 79.1 ± 1.2 Ma) based on the U-Pb radiometric dating of intercalating tuff layers and carbon isotope chemostratigraphy (Arimoto *et al*., 2018).

The plant mesofossil assemblage was isolated from a black carbonaceous, poorly-sorted sandy mudstone from the upper part of the Tamagawa Formation that is exposed along the sea cliff at Tamagawa, Noda village, Iwate Prefecture, in northeastern Honshu (lat. 40° 5′ 12.1776″ N, long. 141° 49′ 42.8082″ E). The samples were collected by MT in 2016–2018 from a horizon corresponding to the carbonaceous mudstone recorded at 230 m at the Tamagawa section (column 1 of fig. 3 of Arimoto *et al*., 2018). This layer is broadly correlated to a vertebrate bone bed in the Osawada section, that includes well-preserved terrestrial fossils of turtles (*Adocus*), crocodilomorphs, and dinosaurs (Hirayama *et al*., 2010; Umetsu *et al*., 2013; column 2 on fig. 3 of Arimoto *et al*., 2018). Arimoto *et al.* (2018) estimated the depositional age of the dinosaur-bearing bone bed of the Tamagawa Formation in the Kuji Group to be the early - middle Santonian (85.9 ± 0.7 Ma). On the other hand, Hirayama *et al.* (2021) estimated the age of the same bone bed of the Tamagawa Formation to be the late Turonian (90.51 ± 0.54 Ma) based on U-Pb dating for zircon grains of an intercalating tuff bed.

Plant mesofossils were isolated by sieving from unconsolidated sediment samples. The samples were disaggregated in water, then cleaned and rinsed using standard techniques (e.g., Friis *et al.*, 2011; Takahashi *et al.*, 1999a). The mesofossil specimens were examined with a Hitachi S-4300 field emission SEM. Some specimens were photographed (LM) using a Canon Rebel camera with 100 mm macrolens attached to a stack-shot system, and digital images were merged using Helicon Focus software.

The specimens illustrated in this article are deposited in the paleobotanical collections of the National Science Museum (NSM-PP), Tsukuba, 305-0005 Japan.

Results

Ferns

Ferns are represented in the collection by about seven specimens of charcoalified, tightly curled, circinate shoots (fiddleheads), approximately 2–4 mm in diameter. The shoots have trichomes (Figure 1A). The systematic affinities of the fiddleheads are uncertain, although the specimens are similar in size and trichomes to the fiddleheads of the filmy fern, *Hymenophyllum iwatsukii* (Hymenophyllaceae) from the Khukhteeg Formation (Aptian–Albian; Lower Cretaceous) at Tevshiin Govi in Mongolia (Herrera *et al.*, 2017). Tanai (1979) reported megafossils of fronds of Osmundaceae, Schizaeaceae, and Gleicheniaceae from the Tamagawa Formation of the Kuji Group. Other pteridophytes recovered from the Tamagawa Formation include abundant megaspores of *Molaspora* (Marsileales), *Erlansonisporites* (Selaginellales), as well as forms assigned to *Verrutriletes*, *Bacutri-*

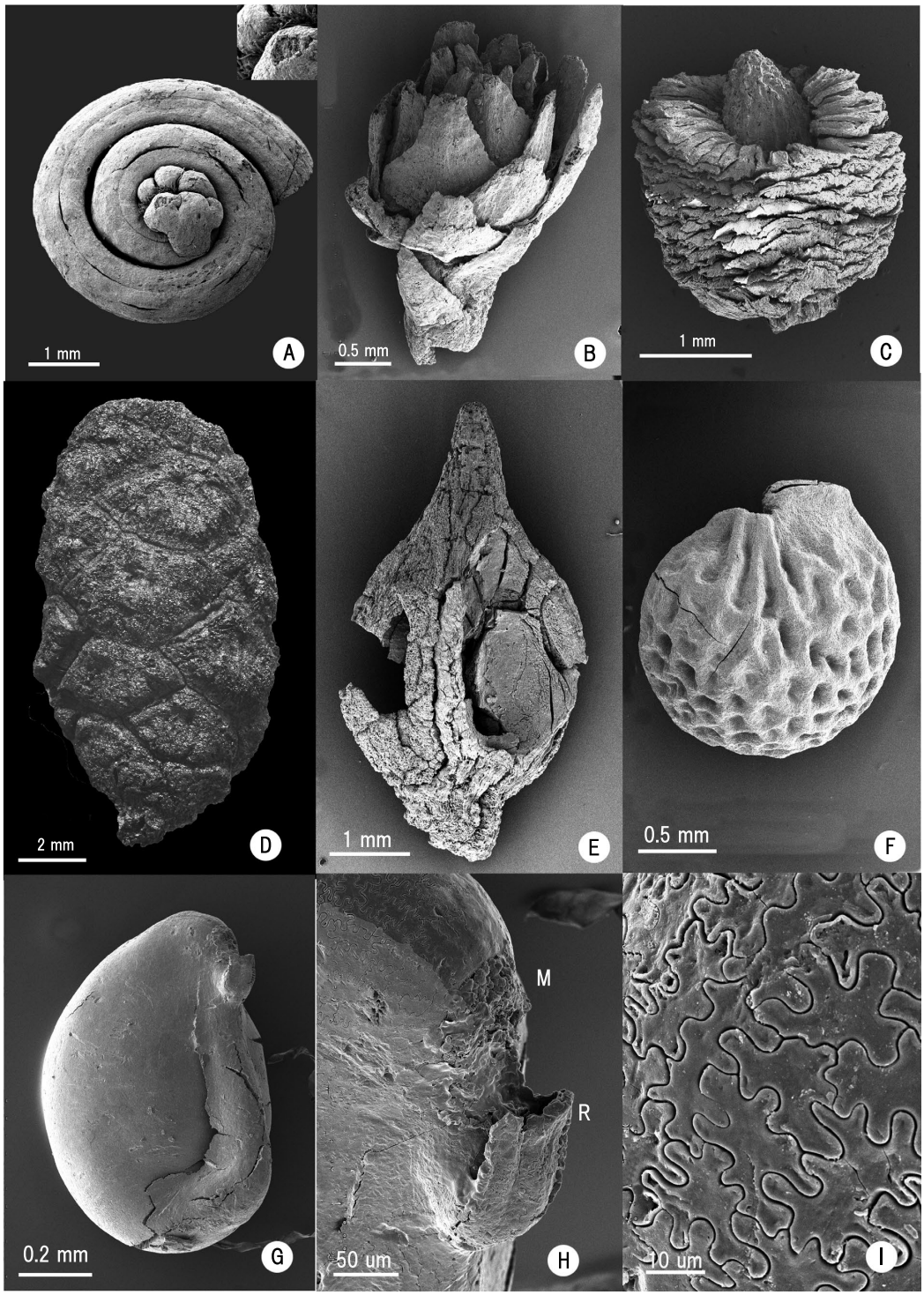

Figure 1. Mesofossils from the Tamagawa Formation (Kuji Group). **A,** Charcoalified circinnately curled fern fronds (fiddleheads) showing pinnules; Inset, trichomes, NSM-PP 12140; **B,** Conifer leafy shoot with terminal buds, NSM-PP 12141; **C,** Seed cone type 1, NSM-PP 12142; **D,** Seed cone type 2, NSM-PP 12143; **E,** cf. *Hironoia fusiformis* Takahashi *et al.* (Cornales), NSM-PP 12144; **F,** Fruit (Endocarp), lateral view of specimen with leathery outer layer (exocarp) missing, showing reticulate surface of the inner sclerotic layer, NHM-PP 12145; **G–I,** cf. *Symphaenale futabensis* Takahashi *et al.* (Nymphaeales), NHM-PP 12146; G, Seed in lateral view showing micropyle hilum and raphe; H, Detail of microphyle (M) and raphe (R); I, Seed surface showing the digitate outlines of the columnar sclerenchyma that comprise the exotesta sclerenchyma.

letes and *Trileites* (Takahashi *et al.*, 2001b).

Conifers

Conifers are abundant in the assemblage and are represented by about 30 leafy shoots with terminal vegetative buds, as well as pollen cones, seed cones and seeds (Figure 1B–D). The leafy shoots have spirally arranged acicular scale-like leaves with acute apices (Figure 1B), and terminal rounded shoot apices (Figure 1B). The buds range from 2.0–2.2 mm in width, and 1.3–1.8 mm in length. The leafy buds appear similar to those present in Cupressaceae (Schulz *et al*., 2005).

Seed cone type 1 is represented in the collection by a single specimen (Figure 1C). The cone is ovoid-oblong, 2.0–2.3 mm long, 1.5 mm wide, with numerous helically arranged bract-scale complexes. The complexes are linear-lanceolate, 0.5–0.6 mm long and 0.2–0.3 mm wide. At the base the scales are subtruncate (Figure 1C). Apices of the bract-scale complexes are abraded and poorly preserved. The seeds are unknown.

Seed cone type 2 is represented in the collection by a single specimen (Figure 1D). The seed cone type 2 is elongate-cylindric, 9.5 mm long, 6.0 mm wide, with 12–18 helically arranged tightly, persistent and imbricated bract-scale complexes. The apices of the ovuliferous scales are rhomboidal, 2.2–3.8 mm high and 3.8–5.0 mm wide, with an truncate apex (ovuliferous scale umbo). The specimen shows a peduncle that bears only small, thick, rudimentary bracts. The systematic affinity of the female cone is likely to the Cupressaceae (Schulz *et al*., 2005). A permineralized conifer seed cone, *Archicupressus*, has been recovered from the Yezo Group (Coniacian – Santonian) in Hokkaido (Ohsawa *et al*., 1992). *Archicupressus* is ellipsoid, 3.8 cm long and 1.7 cm in diameter, consisting of more than 12 bract-scale complexes. The permineralized seed cone from the Yezo Group is much larger than the seed cone type 2 from the Kuji Group.

Angiosperms

A preliminary survey of the angiosperms represented in the mesofossil assemblage has recovered five kinds of fruits and a single kind of dispersed seed.

Fruit type 1 is represented in the collection by 20 specimens (Figure 1E). The fruits are globose to elliptical, 4.0–4.2 mm long and 2.2–2.5 mm wide. The endocarps are trimerous, consisting of three fused carpels. The surface of the endocarp varies from smooth to corrugated. Each locule opens by a single dorsal valve that often becomes detached first at the apex of the endocarp (Figure 1E). The endocarp tapers gradually toward the apex and narrows at the base into a slender stalk. Fruit type 1 is similar to *Hironoia fusiformis* Takahashi *et al.* (Cornales) from the Kamikitaba assemblage (Takahashi *et al.*, 2002).

Fruit type 2 (endocarp) is represented in the collection by two specimens (Figure 1F). Both are flattened woody structures, *ca.* 1.7–2.0 mm in diameter. The outer layer is missing and exposes an inner sclerotic layer with a distinctive reticulate surface (Figure 1F). This type of endocarp is recovered frequently from the Kamikitaba assemblage (Takahashi *et al.*, 1999a, fig. 9A, B). The systematic affinity of these fruits is unknown. However, they are similar in general form to specimens described as *Sabia* (Sabiaceae) (Knobloch and Mai, 1986; Bodor *et al.*, 2012) or *Porosia* (Rutaceae) (Manchester and Kodrul, 2014).

Seed type 1 is represented in the collection by a single specimen (Figure 1G–I). The seed is anatropous, ovoid, and 1.2–1.5 mm long. The raphe enters the seed obliquely at a hilum that is adjacent to, but separated from the micropyle. The micropyle has a distinct plug with a papillate surface. The exotesta is composed of columnar palisade sclerenchyma cells with anticlinal walls that are strongly undulate. This seed is similar to *Symphaenale futabensis* Takahashi *et al*. (Nymphaeales) from the Tamayama Formation of the Futaba Group (Takahashi *et al*., 2007).

Discussion

The fossil flora of the Kuji Group

The Kuji Group has yielded abundant plant macrofossils preserved as impressions, and a comprehensive account of the leaf flora documented pteridophytes (*Gleichenites*, *Asplenium*, *Sachaliniea*, Osmundaceae, Schizaeaceae, Salviniaceae and *Cladophlebis*), gymnosperms (*Araucarites*, *Taxodium* and *Glyptostrobus*, *Metasequoia*, Cycadopsida, Nilssoniaceae, Cupressaceae), and angiosperms (Magnoliaceae, Lauraceae, Menispermaceae, Trochodendraceae, Platanaceae, Fagaceae, Dilleniaceae, Salicaceae, Sapindaceae, Vitaceae, Rhamnaceae, and Trapaceae [Tanai, 1979]). Only a subset of these plants occurs in the Tamagawa flora, from which 11 pteridophyte, six conifer and ten angiosperm species have been described (Tanai, 1979).

Miki (1977) showed that palynomorphs from the Tamagawa and Sawayama formations consist of 56% pteridophyte spores dominated by Schizaeaceous spores, 20% gymnosperm pollen dominated by Pinaceous winged and Taxodiaceous inaperturate pollen, and 26% angiosperm pollen dominated by tricolpate type and *Aquillapollenites* group. Umetsu and Kurita (2007) showed that gymnosperm pollen dominates the palynoflora of the upper part of the Tamagawa Formation (54–68%) with frequent *Taxodiaceaepollenites* and coniferous winged pollen. Pollen of the *Aquilapollenites* group also occurs frequently from the upper part of the Tamagawa Formation (Umetsu and Kurita, 2007).

Takahashi *et al.* (2001b) described an assemblage of dispersed megaspores of Marsileales and Selaginellales from the Tamagawa Formation. The well-preserved mesofossil assemblage recovered in the present study demonstrates that the flora of the Tamagawa Formation is dominated by conifers, but also includes a diversity of pteridophytes and angiosperms. The mesofossil assemblage is complementary to the macrofossil and microfossil floras. Results from the present preliminary study suggest that further investigation of mesofossil floras may help to elucidate the early evolution of flowering plants in northeastern Asia. A possibility of special interest would be the recovery of flowers or fruits that could be attributed to the *Aquilapollenites* group, an important and enigmatic group of angiosperms of Late Cretaceous age that experienced significant extinction at the Cretaceous-Paleogene boundary. Finding fossil flowers bearing *Aquilapollenites* pollen would be particularly significant because no mesofossils have yet been documented with this type of pollen.

Comparison between the fossil floras of the Kuji Group and the Futaba Group

The Kuji and Futaba groups are regarded as the western marginal facies of Late Cretaceous forearc basin sediments that are now exposed along the Pacific coast of northeastern Japan (Ando, 2003; Ando and Takahashi, 2017). Their geological sedimentary environments are generally similar, consisting of fluvial, estuarine to shallow-marine sandstone-dominated sedimentary successions, associated with alluvial fan conglomerates and fluvial-marsh carbonaceous mudstone bearing mesofossils and amber (Uchida *et al*., 2018).

The mesofossil horizons from the lower part of the Ashizawa Formation of the Futaba Group (Kamikitaba locality: Takahashi *et al*., 1999a) and the upper part of the Tamagawa Formation of the Kuji Group are estimated to be of a similar late Turonian to middle Santonian age. This is also reflected in components of the mesoflora. The cornalean fruits, *Hironoia*, occur in both the Futaba Group and the Kuji Group. In both cases the fossils recovered from the upper part of the Tamagawa Formation (85.9 ± 0.7 Ma: Arimoto *et al*., 2018; 90.51 ± 0.54 Ma: Hirayama *et al.*, 2021) in the Kuji Group are very similar to those recovered from the Kamikitaba locality (about 89 Ma) in the Futaba Group (Takahashi *et al*., 2002, 2007; Ando and Takahashi, 2017). The nymphaealean seeds, *Symphaenale*, also occur both in the lower part of the Tamayama Formation of the Futaba Group (Santonian, Gokurakuzawa locality: Takahashi *et al.*, 2007), and the Tamagawa Formation of the Kuji Group.

Based on fossil pollen, Miki (1977) identified 57 species (48%) of pteridophytes, 26 species (22%) of gymnosperms and 37 species (30%) of angiosperms from the Futaba Group, and suggested that these microfloras are very similar to each other in their floristic composition, except for the *Aquilapollenites* group from the Kuji Group.

Some difference between the two is also shown in the gymnosperm components and their inferred vegetation. Fragments of leafy shoots showing acicular leaves with acute apices are very common in the Kamikitaba assemblage (conifer leaf type 1: Takahashi *et al*., 1999a), do not occur frequently from the Kuji Group. Additional studies of mesofossil assemblages from the Kuji Group have the potential to provide critical new data toward resolving the history of angiosperm and gymnosperm diversification in eastern Asia during the Late Cretaceous and clarifying biogeographic patterns.

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Author contributions

M. T. initiatied the study and carried out all process of the study, such as collecting samples, cleaning, bulk sieving process, sorting, and SEM work. P. H. and F. H. have contributed to the taxonomic aspects. R. H and H. A are responsible for the geological aspects. K. S. has contributed to the field work and collecting samples. All authors contributed to the writing of the paper.