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Scanning electron microscopy for differentiating charred endocarps of *Rhus/Toxicodendron* species and tracking the use of the lacquer tree and Asian poison ivy in Japanese prehistory

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ABSTRACT

The use of natural lacquer for preservation and decoration of various commodities is a remarkable invention. In Japan lacquer production dates back to the Neolithic Jomon period and has been mainly based on the sap extracted from the lacquer tree (*Toxicodendron vernicifluum* (Stokes) F.A. Barkley). However, it is still unclear, if lacquer production evolved in Japan independently or was introduced from Neolithic China, another centre of early lacquer production. A debate also revolves around the origin of the lacquer tree itself and whether it occurs in Japan naturally or was introduced from the continent along with the skills required for lacquer production. Records of *Rhus/Toxicodendron* fruit remains, recovered from cultural layers of archaeological sites and natural palaeoenvironmental archives across Japan, provide an opportunity to answer the existing questions. This paper presents a method for differentiating charred endocarps of the six *Rhus/Toxicodendron* species growing in Japan, which is not feasible based on size or morphological properties of whole fruits or endocarps. To develop this method, we used a set of modern reference fruits. Identification is based on the species-specific tissue structure of the charred endocarp in longitudinal sectional view observed by scanning electron microscopy (SEM). We suggest a simple identification key that is based on two prominent traits of the endocarp's tissue structure, i.e., tissue alignment and density. The method was successfully applied to an abundant record of charred *Rhus/Toxicodendron* endocarps recovered by flotation from Okhotsk culture layers dating to ca. 490–880 CE at the multi-component Hamanaka 2 archaeological site, Rebun Island, Hokkaido region, northern Japan. The recovered endocarps belong to Asian poison ivy (*Toxicodendron orientale* Greene, 1905) and the chronology of the archaeobotanical assemblages suggests that fruits and/or other parts of this plant were used by different local populations over a period of up to 3000 years (Final Jomon to Classic Ainu period). This indicates that not only lacquer tree was an important economic plant in Japanese prehistory, but also other *Rhus/Toxicodendron* species were used for unknown purpose. While use of *T. orientale* for medical effects or as an alternative source for lacquer production seems possible, we hypothesise that at Hamanaka 2 it was utilised for its high tannin content to tan hides and furs of sea mammals. This interpretation emphasises the discussed function of Hamanaka 2, famous for its rich zooarchaeological record of sea mammal remains, as an important site of marine hunting and raw material processing.

1. Introduction

The production and use of lacquer, which is labour-intensive and requires a high level of knowledge and skills (Shelach-Lavi, 2015; Matsumoto, 2018), have been identified as an outstanding prehistoric cultural and technological achievement. A centre of early lacquer production is East Asia, where this natural polymer has been applied for its superb preservation (anti-oxidation, water and corrosion resistance) and aesthetic properties on various materials, such as wood, bamboo and pottery, for millennia. Regions from which the earliest evidence of the

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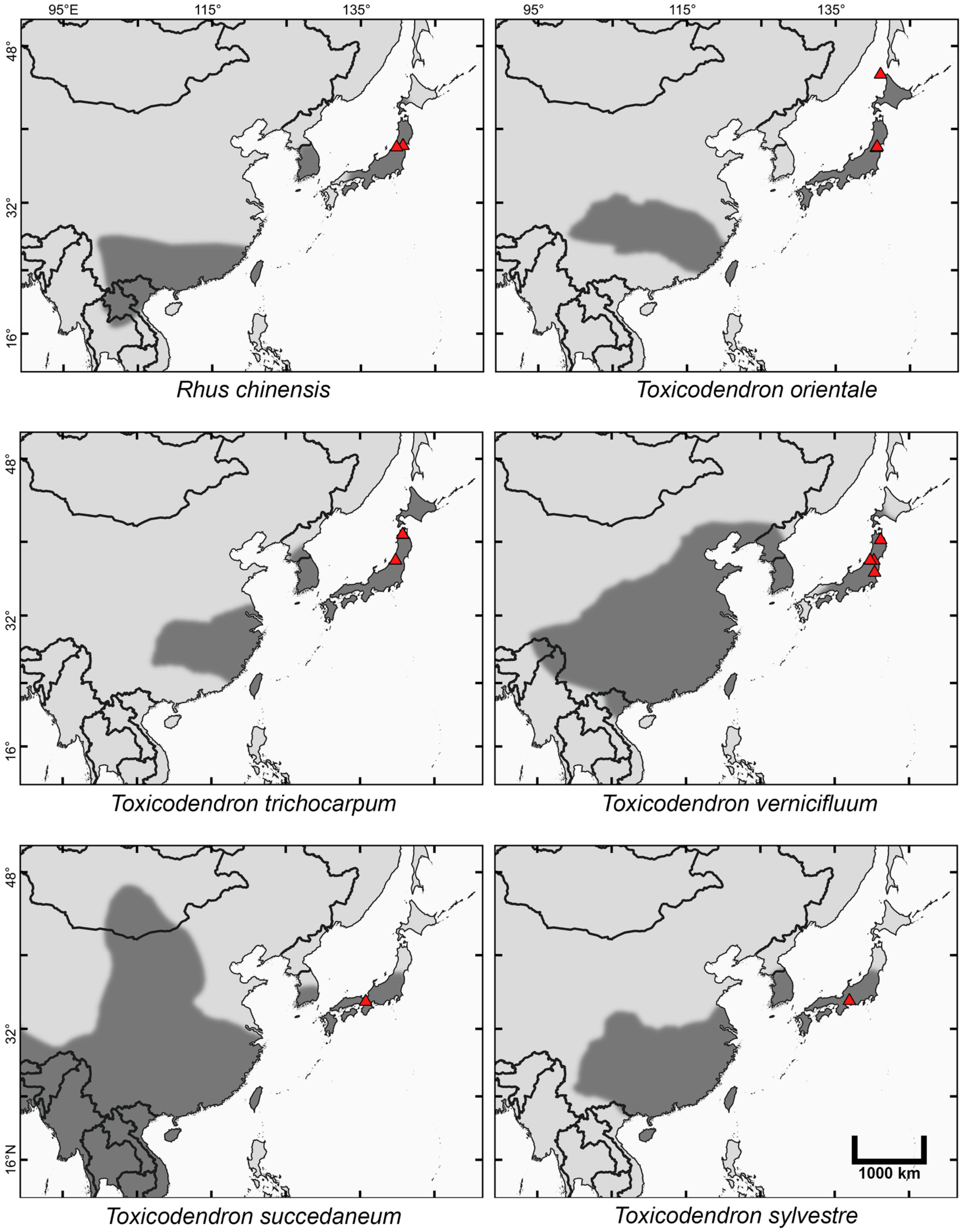
use of lacquer has been reported are the Yangtze River delta and Japan (Matsumoto, 2018). In the former region lacquered objects have been documented from Middle Neolithic archaeological sites, which also yield some of the earliest evidence of the domestication of rice (Ma et al., 2018 and references therein). This includes lacquered artefacts from cultural layers at Hemudu, dated to ca. 5000–4000 BCE (Liu, 2006), at Tianluoshan, dated to ca. 5000–4600 BCE (Nakamura, 2010) and Kuahuqiao, dated to ca. 6000–5000 BCE (Wu et al., 2018). In China, lacquered items became important trade goods and symbols of authority by the Early Bronze Age (2000–1000 BCE), as reflected by burial goods in elite tombs (Flad and Chen, 2013). A first peak of lacquer production was reached during the Warring States Period (475–221 BCE) (Sung et al., 2016). Particularly influential was apparently the lacquer craft practiced in the late Chu state (8th–3th century BCE) from which a high level of lacquering technology and a large amount of lacquerware have been reported (Wang et al., 2017; Fu et al., 2020).

In Japan the application of lacquer to wooden items and pottery became common from the Early Jomon period (5000–3400 BCE) (Noshiro et al., 2007). Palaeobotanical evidence suggests that since this period lacquer tree stands had been managed (Noshiro and Sasaki, 2014). Lacquered threads found at the Kakinoshima B archaeological site in southern Hokkaido, Japan (Minamikayabe Town Archaeological Research Group, 2002) are believed to be the oldest evidence of lacquer use (Noshiro et al., 2007). The threads originate from a tomb associated



Rhus chinensis

Toxicodendron orientale

Toxicodendron trichocarpum

Toxicodendron vernicifluum

Toxicodendron succedaneum

Toxicodendron sylvestre

Fig. 1. Maps showing the modern geographical distribution of the six *Rhus/Toxicodendron* species growing in Japan (dark grey area) and the locations of the living plants from which fruits were used as reference samples in the current study (red triangles). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

with the late Initial Jomon period (6000–5000 BCE) from which bottom soil has been dated to around 7000 BCE (Kudo, 2017). However, like those of the earliest lacquered objects from the Chinese Neolithic sites, this age determination is not based on direct dating. These dating uncertainties further fuel the debate about the origin of lacquer production (Kudo, 2017; Matsumoto, 2018) and whether it developed independently in both regions (Okamura, 2010) or was introduced from one region to the other. The so far oldest direct radiocarbon (^{14}C) date calibrated to 5200 BCE was obtained from a lacquered comb from the Mibiki archaeological site in Ishikawa Prefecture, central Honshu (Kudo and Yotsuyanagi, 2015).

Another debated aspect is the natural distribution of the lacquer tree (*Toxicodendron vernicifluum*, formerly *Rhus verniciflua*), which has been mainly used to extract sap for lacquer production in East Asia. Today *T. vernicifluum* is distributed across the north-eastern parts of Southeast Asia, south-eastern and eastern China, the Korean Peninsula and Japan between Shikoku and southern Hokkaido (Fig. 1). However, some botanists have argued that the tree is not part of the natural vegetation on the Korean Peninsula and the Japanese Islands (e.g., Rein, 1886; Ohwi, 1965; Iwatsuki et al., 1999), since it is only found in the vicinity of settlements but not in natural forests (Noshiro et al., 2007; Suzuki et al., 2014). This would corroborate the hypothesis that *T. vernicifluum* and the technology of lacquer production was introduced from eastern China, where the tree is believed to occur naturally, to Japan sometime during the Jomon period. Based on the analysis of chloroplast DNA of modern *T. vernicifluum* from China, the Korean Peninsula and Japan, Suzuki et al. (2014) argued that, if the tree was introduced to these two regions, it originates from the region around the Bohai Bay. Ming (1980b) sees the roots of the *Toxicodendron* genus in the mountain regions of central and south-western China. On the other hand, a wood sample of *T. vernicifluum* recovered from Incipient Jomon culture (13,000–9000 BCE) layers at the Torihama shell mound archaeological site (Fukui Prefecture, central Honshu) directly ^{14}C-dated to ca. 9000–8000 BCE proves the existence of the tree in Japan already in the early Holocene. This argues for its natural distribution in the archipelago (Suzuki et al., 2012), although a very early introduction by humans still remains possible.

Besides *T. vernicifluum*, other species belonging to the '*Rhus/Toxicodendron* complex' have also been used for different purposes. *Toxicodendron succedaneum* (L.) Kuntze is another tree that is widely distributed across East and Southeast Asia (Fig. 1) and whose sap has been used for lacquer production. In western Japan, the tree was cultivated at least since the 16th century CE for its wax, which was extracted from the fruit mesocarp for the production of candles (Hiraoka et al., 2018). *Rhus/Toxicodendron* taxa are also known to have been used as food, seasoning or for hunting and warfare in different regions of the world. Jones (2009) described that North American indigenous tribes have used *Rhus toxicodendron* L., which contains the toxin urushiol, a combination of chemical compounds that is also contained in *T. vernicifluum*, to poison arrows. Early archaeobotanical evidence of the use of *Rhus coriaria* L. fruits as a seasoning, as such it is still widely used across West Asia today, has been reported from Early Neolithic sites in Anatolia (Asouti and Fairbairn, 2002). The fruits have been valued for their sour-astringent taste. For the same property the fruits of *Rhus glabra* L. have been used by North American indigenous tribes as seasoning and to prepare beverages or tea (Kindscher, 1987). Other functions are known from ethnobotanical studies in Yunnan Province, south-western China (Long et al., 2003; Han and Cui, 2012). Ethnic groups, such as the Lemo and Nu, use every part of the lacquer tree. While the wood is used to make insect resistant timber and tools, pesticides are made from the roots and bark and the leaves are used to extract tannin. Leafy shoots are consumed as vegetables. From the pericarp wax is extracted for making crayons, wax paper and candles. The oil extracted from the seeds is used as nutritious cooking oil but also as medicine. The Nu consider the seed oil as galactagogue, styptic, anti-inflammatory and a remedy for cough and asthma, pain, anaemia, stimulating blood flow, dysmenorrhea and postnatal treatment (Han and Cui, 2012). While the use of *Rhus/Toxicodendron* in folk medicine has been documented, evidence from prehistoric contexts is extremely rare, and science has only recently started to understand and prove the specific medical properties of different *Rhus/Toxicodendron* taxa (e.g., Rayne and Mazza, 2007; Djakpo and Yao, 2010).

Charred and non-charred *Rhus/Toxicodendron* fruit remains have been reported from different archaeological sites in northern Japan. Charred remains assigned to the *Rhus* genus were recovered from the Middle Jomon (3400–2400 BCE) settlement site Tominosawa located in northern Honshu (D'Andrea, 1995b) and from Epi Jomon (300–100 BCE) culture layers at the Mochiyazawa site in south-western Hokkaido (D'Andrea, 1995a). In the latter region, *Rhus* sp. fruit remains were also reported from Satsumon culture (700–1300 CE) layers at the Sakushu-Kotoni River site in Sapporo (Crawford, 1986). At the Hamanaka 2 site on Rebun Island, northern Hokkaido (Fig. 2) *Rhus/Toxicodendron* endocarps were recovered from Final Jomon (1300–300 BCE), Epi Jomon (300–100 BCE), Okhotsk (500–1000 CE) and Classic Ainu (1600–1868 CE) culture layers, suggesting that this plant was an inherent part of the local people's subsistence. In addition, Crawford (2011) reports 'a significant number' of *Rhus/Toxicodendron* remains from different Jomon culture sites located in Minamikayabe (south-western Hokkaido), which appear to represent at least two different species. Based on Yoshikawa and Ito (2004), who attempted to identify *Rhus/Toxicodendron* fruit remains from water-logged Early Jomon culture layers at the Iwatarikotani 4 site (Aomori Prefecture, northern Honshu) to species level, Crawford (2011) concluded that one of the contained species in the Minamikayabe records is likely *T. vernicifluum*. The other type of *Rhus/Toxicodendron* endocarps was not determined to species level. *Rhus/Toxicodendron* endocarps assigned to the Middle and Late (2400–1300 BCE) Jomon periods were also found further south in central Honshu (Kanto region) in water-logged deposits at the Shimoyakebe site (Sasaki et al., 2007). Attempts have been made to identify these deformed non-charred fruits to species level (Yoshikawa et al., 2014). Like for the fruits from Iwatarikotani 4 (Yoshikawa and Ito, 2004), this was only partly successful. Yoshikawa and Ito (2004) analysed four fruits from Iwatarikotani 4; three were identified as *T. vernicifluum* and one could not be identified. Regarding identification of the fruits from Shimoyakebe, Yoshikawa et al. (2014) used different traits, such as fruit size, structure of the endocarp surface and structure of the endocarp in cross section view, and identified seven of the 28 analysed specimens as *T. vernicifluum* and four as *Rhus chinensis* Mill. The authors mention that in different cases identification was ambiguous.

In this study, we present a method to distinguish endocarps of the six *Rhus/Toxicodendron* species distributed in Japan, which is not possible based on the size and morphology of fruits/endocarps alone. We created an identification key based on scanning electron microscopic (SEM) analysis of a set of reference endocarps collected from 14 living specimens of the six species growing in Japan. The method allows to identify charred and non-charred endocarps from archaeological contexts based on the structural properties of the endocarp longitudinal section. To test the method, we employed archaeological *Rhus/Toxicodendron* endocarps recovered by flotation from Okhotsk culture layers of Hamanaka 2 (Müller et al., 2016; Leipe et al., 2017).

2. Study material

2.1. Modern reference samples

In this study, we used fruits of the six *Rhus/Toxicodendron* species growing in Japan. There is no general agreement about the taxonomic standing within the *Rhus/Toxicodendron* complex (Miller et al., 2001; Nie et al., 2009). Here we treat *Toxicodendron* not as a subgenus of *Rhus* but as a separate genus. Thus, our dataset includes five species of the genus *Toxicodendron*, comprising *T. vernicifluum*, *T. trichocarpum* (Miq.) Kuntze (syn. *Rhus trichocarpa*), *T. orientale* (syn. *Rhus orientale*,

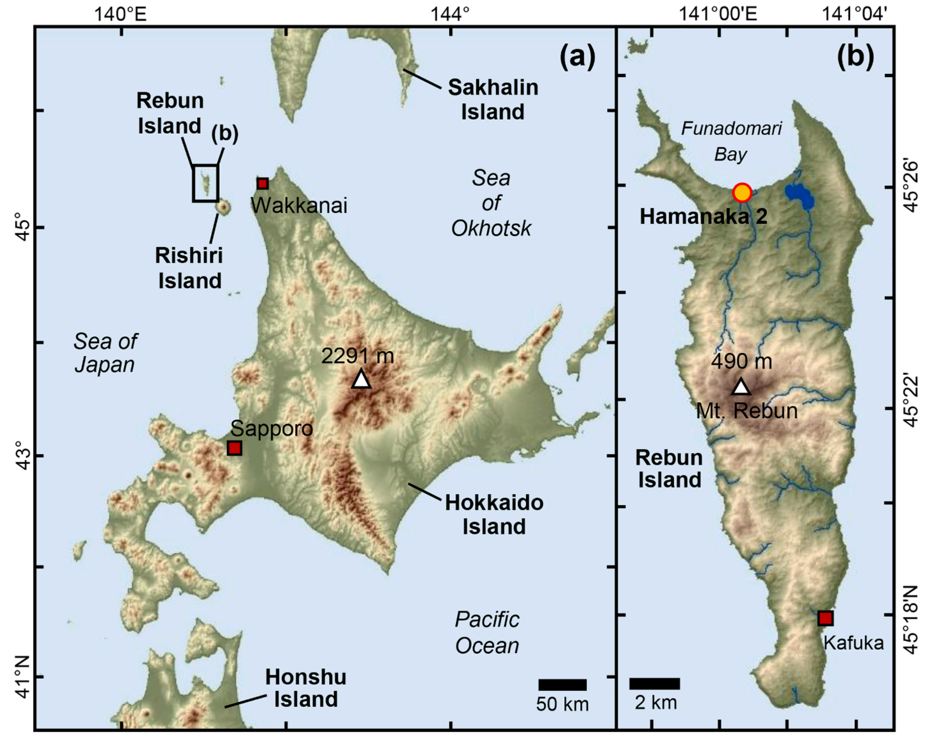


Fig. 2. Maps showing the locations of (a) Rebun Island in the Sea of Japan and (b) the archaeological site Hamanaka 2 from which records of charred *Rhus/Toxicodendron* endocarps from Final Jomon, Epi Jomon, Okhotsk and Ainu cultural layers were analysed in the current study.

R. ambigua), *T. succedaneum* (syn. *Rhus succedanea*, *Rhus erosus*) and *T. sylvestre* (Siebold & Zucc.) Kuntze (syn. *Rhus sylvestris*,) and one *Rhus* species, *R. chinensis* (syn. *Rhus javanica*). The set of reference fruits is composed of 14 samples, each containing several fruits from a single plant. The fruits were collected between 2003 and 2020 and comprise four samples of *T. vernicifluum* from Yamagata ($n = 2$), Iwate ($n = 1$) and Ibaraki ($n = 1$) prefectures, three samples of *T. trichocarpum* from Aomori ($n = 2$) and Yamagata ($n = 1$) prefectures, three samples of *T. orientale* from Miyagi ($n = 2$) and Hokkaido ($n = 1$) prefectures, two samples of *R. chinensis* from Miyagi ($n = 1$) and Yamagata ($n = 1$) prefectures, one sample of *T. succedaneum* from Kyoto Prefecture and one sample of *T. sylvestre* from Aichi Prefecture (Fig. 1). Regarding growth form, *T. orientale* is categorised as a liana (woody vine) and the remaining taxa as trees. All six species produce dry indehiscent fruits with thin exocarps and mesocarps. According to Ohwi (1965), the fruits of the species have the following average size ranges: *T. vernicifluum* = 6–8 mm, *T. trichocarpum* = 5–6 mm, *T. orientale* = 5–6 mm, *T. succedaneum* = 8–10 mm, *T. sylvestre* = 6–8 mm and *R. chinensis* = ca. 4 mm. In our reference collection fruits of the four sampled *T. vernicifluum* trees had the largest size compared to that of the remaining five species. The apparently large fruit size variations in *T. vernicifluum* might be related to the existence of at least 100 varieties of this plant (Wei et al., 2010), which also show differences in bark structure, lacquer yield and urushiol content (Zhao et al., 2013). Length measurements on ten fresh endocarps per plant and taxon contained in our reference set revealed the following average values: *T. vernicifluum* = 8.0 mm, *T. trichocarpum* = 4.7 mm, *T. orientale* = 4.8 mm, *T. succedaneum* = 7.6 mm, *T. sylvestre* = 7.2 mm and *R. chinensis* = 4.5 mm.

2.2. Distribution of *Rhus/Toxicodendron* species in Japan

There is no agreement about the natural distribution of the six *Rhus/Toxicodendron* species, which grow in Japan at present. For the distribution across East and Southeast Asia, we refer to information provided by the Global Biodiversity Information Facility (https://www.gbif.org/) (Fig. 1). For the taxa distribution across Japan, we combine this data with information in Ohwi (1965). Accordingly, *T. orientale* and *T. trichocarpum* naturally occur across all Japanese regions (Hokkaido, Honshu, Shikoku, Kyushu and the Ryukyu islands). *R. chinensis*, the only *Rhus* species occurring in Japan (Suzuki et al., 2007), is distributed between southern Hokkaido, i.e., the northern limit of the temperate deciduous forest zone, and the warm mixed forest zone on Honshu (except the westernmost Chugoku region) and Shikoku (Fig. 1). By contrast, Ohwi (1965) claims that it is naturally distributed all over Japan, including hills and lowlands in Hokkaido. *T. vernicifluum* grows in the eastern, south-eastern and south-western (including eastern Tibet) regions of China between ca. 800 and 2800/3800 m above sea level (Ming, 1980a) as well as in the northern parts of Vietnam and Myanmar, Northeast India and most of the Korean Peninsula. The distribution in Japan is similar to that of *R. chinensis*. It has been cultivated in the temperate deciduous forest and warm mixed forest zones in an area stretching from southern Hokkaido to Shikoku. Compared to the other four species, *T. sylvestre* and *T. succedaneum* prefer a warmer climate and do not appear in the Hokkaido and northern Tohoku regions. *T. sylvestre* has been reported to grow between southern Tohoku (ca. 38°N) in the north and the Ryukyu islands in the south. According to Ohwi (1965), its northern distribution is even limited to the south-facing Pacific coast of Honshu. *T. succedaneum* has been also reported to grow between southern Tohoku and the Ryukyu islands, although Ohwi (1965) states that it grows all across Honshu.

2.3. Archaeological sample

To test the proposed identification method, we used a set of charred *Rhus/Toxicodendron* endocarps from the multi-phase Hamanaka 2 archaeological site on Rebun Island, northern Japan (Fig. 2). Endocarps of *Rhus/Toxicodendron* fruits with comparable morphological features have been recovered from Final Jomon, Epi Jomon, Okhotsk and Ainu culture layers by flotation (Müller et al., 2016; Leipe et al., 2017; Leipe et al., 2018). Most of the archaeological and archaeobotanical records of this site are assigned to the occupation by Okhotsk culture groups, which has been estimated by Bayesian modelling based on ^{14}C dates of short-living (mainly seeds) terrestrial plant remains to 490–880 CE (95% confidence interval) (Junno et al., 2021). With a total of 265 charred endocarps, *Rhus/Toxicodendron* is the second most abundant taxon after naked barley (*Hordeum vulgare* var. *nudum*), which comprises 318 seeds (Leipe et al., 2017).

3. Methods

3.1. Treatment of reference samples

We carbonised reference fruits of all six taxa in order to experimentally reproduce structural changes of the endocarp that possibly occur during charring of archaeological specimens. The fresh fruits were carbonised in the lab of the Scientific Department of the Head Office of the German Archaeological Institute, Berlin using a tube furnace. To control anoxic conditions during carbonisation we placed the fruits on ceramic trays and covered them tightly with aluminium foil (Wagner, 1982). In a first step, carbonisation was done on whole fruits in order to test its effect. Since this did not produce remains most commonly recovered from archaeological contexts (i.e., endocarps), we removed exocarps and mesocarps before carbonisation. Prolonged exposure to heat at relatively low temperatures has been proven to be the best way to obtain undistorted or weakly distorted charred seeds suitable as reference material (Braadbaart, 2008; Fraser et al., 2013). To select proper charring conditions for each taxon we conducted carbonisation tests at different temperatures and heat exposure times.

3.2. Endocarp morphological analysis

Charred modern reference endocarps and the archaeological specimens from Hamanaka 2 were cut open in longitudinal direction, i.e., parallel to the fruit axis (scar to apex), (see Supplementary Fig. S1 for details) by a fine-bladed bistoury to allow inspection of their longitudinal sections. To obtain a representative reference for the longitudinal section structures, we tried to cause natural breaking of the endocarps, rather than obtaining an artificial, smooth cutting edge. Tests using a light microscope showed that magnifications of at least ×100 to ×200 are necessary to observe the longitudinal section structures (Fig. 3a). Better results (Fig. 3b) were obtained when using a SEM (Zeiss Supra 40VP). This enhances the examination and identification of the endocarp layers and their internal morphological structures.

4. Results and discussion

4.1. Carbonisation of reference material

Even after exposure to relatively high temperatures of around 300 °C for several hours, the mesocarp of fruits of all six *Rhus/Toxicodendron* species was well-preserved and tightly attached to the endocarp, which is not the case for the archaeological specimens from the different cultural layers at Hamanaka 2 (see image in Müller et al., 2016) or other archaeological sites (e.g., Crawford, 2011). This suggests that the mesocarp of the ancient fruits must have been removed manually before they became carbonised or the mesocarp was lost by taphonomic processes after charring. Thus, from all reference fruits used in this study mesocarps were removed before carbonisation. While it was easy to remove the very thin and brittle exocarp of all fresh fruits by hand, the mesocarp came off easily only from endocarps of *T. vernicifluum*, *T. trichocarpum*, *T. succedaneum* and *R. chinensis*. Mesocarps adhered firmly to the endocarps of *T. sylvestre* and *T. orientale* so that a bistoury was used to facilitate their removal. Carbonisation tests revealed that different temperature and exposure time settings (Fig. 4) are required to obtain suitable reference endocarps of the six *Rhus/Toxicodendron* taxa (Fig. 5). A temperature of 400 °C damaged and distorted the *Rhus/Toxicodendron* reference endocarps even at relatively short exposure times of 80 min. A temperature of 250 °C and an exposure time of 90 min proved suitable to produce non-distorted carbonised endocarps of *R. chinensis*. For *T. vernicifluum* best results were obtained at 260 °C and an exposure time of 180 min. Slightly higher temperature proved suitable for *T. trichocarpum* (300 °C) and *T. orientale* (330 °C) at exposure times of 120 min and 210 min, respectively.

4.2. Rhus/Toxicodendron species identification

Images obtained by SEM provide a high-resolution view of the morphological characteristics of the internal structures of the fruits' endocarp. The endocarp of each *Rhus/Toxicodendron* species comprises three layers (Figs. 6 and 7). Measurements on fresh and charred endocarps contained in our reference set revealed that the inner layer represents on average between 60% and 70%, the middle layer around 10% and the outer layer between 15% and 30% of the total thickness of the endocarp. The endocarp structures in longitudinal section view of the fresh endocarps also resemble those of the carbonised ones, demonstrating that the morphological characteristics of the structures of the inner layer are not changed by the carbonisation process and that both fresh and carbonised endocarps could be used as reference material. However, experiments conducted on the reference endocarps demonstrated that the outer and middle layers are less resistant to

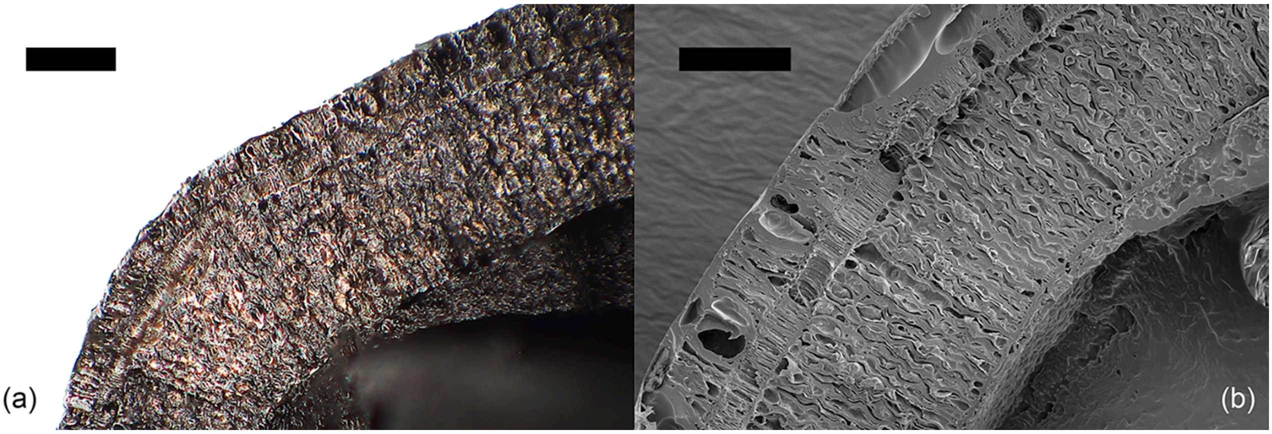


Fig. 3. Comparison of images showing the longitudinal section of a charred modern *Rhus chinensis* endocarp derived by (a) a digital microscope and (b) a scanning electron microscope (SEM). Scale bars = 100 μm.

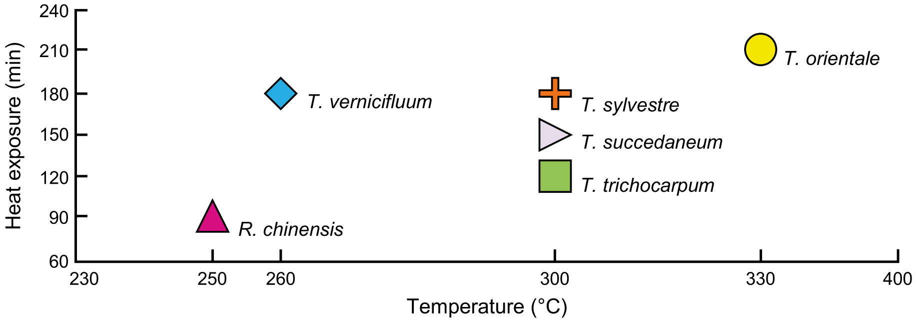


Fig. 4. Experimentally determined optimum charring conditions for the six analysed reference *Rhus/Toxicodendron* species.

carbonisation and become easily damaged or lost. Thus, it must be assumed that the outer or both the outer and middle layers of charred archaeological specimens are damaged or absent. This is confirmed by the *Rhus/Toxicodendron* endocarps from Hamanaka 2, where the outer layer is missing (Fig. 8), and the photograph of a charred endocarp from the Jomon period Usujiri Shogakko archaeological site (south-western Hokkaido) identified as *T. vernicifluum* that is missing the outer and middle endocarp layers (Crawford, 2011). The inner endocarp layer, on the other hand, appears to be more stable and better preserved in the archaeological samples. Accordingly, differentiation of the six *Rhus/Toxicodendron* species is exclusively based on the structural characteristics of the tissue of the inner layer of the endocarps in longitudinal section view.

The different *Rhus/Toxicodendron* species show unique tissue structures of the inner endocarp layer (Figs. 6 and 7). To allow identification of the different species, we developed an identification key (Fig. 9) based on two morphological traits of the longitudinally elongated tissue of this layer. This comprises the traits ‘alignment’ and ‘density’, each represented by three different expressions, two extremes and one intermediate one. Alignment covers ‘very wavy’, ‘wavy’ and ‘straight’ and density is represented by ‘loose’, ‘dense’ and ‘very dense’. To assign these criteria to the six *Rhus/Toxicodendron* species, we examined the inner endocarp layer of 22 carbonised specimens, two to six of each available plant. This revealed the following species-specific properties (Figs. 6 and 7) used in the identification key (Fig. 9). The endocarp structure of *R. chinensis* is very wavy and loose. *T. trichocarpum* is also characterised by extreme values but in opposite direction; the tissue structure appears straight and very dense. Like *R. chinensis*, the structure of *T. vernicifluum* is very wavy but the density is very high as in *T. trichocarpum*. The inner endocarp layer of *T. sylvestre* has a very wavy tissue structure and a density that is on an intermediate level and is therefore defined as dense. Similarly, *T. succedaneum* is marked by one extreme value for density (very dense) and one intermediate value (wavy) for tissue alignment. *T. orientale* is characterised by intermediate values for both indexes. Its tissue structure is wavy and dense.

The outlined categorisation of the endocarp longitudinal section does not show any overlap and thus allows differentiation of the six investigated species. Thus, species identification is possible when values for both traits can be assigned to a specimen. At least partly, the properties of the endocarp structure appear to be related to the phylogenetic relation of the species. The structure of *T. succedaneum* is relatively similar to *T. vernicifluum*. Genetic analyses have shown that this taxon is most closely related to the lacquer tree (Wang et al., 2020). A similar relation may be expected for *T. sylvestre*, which has also properties similar to *T. vernicifluum* and, like *T. succedaneum* (Fig. 1) and probably *T. vernicifluum* (Ohwi, 1965), appears to prefer warmer environments.

In contrast to the method suggested here, Yoshikawa and Ito (2004) and Yoshikawa et al. (2014) aimed to differentiate uncharred *Rhus/Toxicodendron* fruits/endocarps recovered from deposits under waterlogged conditions. Their methods are based on light microscopic analysis of thin (micrometre-scale) sections of the endocarp, which provides a slightly different impression of the cross-sectional structures compared to the SEM-based technique used in the current study. The current method has been designed and tested to identify charred *Rhus/Toxicodendron* endocarps, which are, compared to uncharred ones, more commonly found in cultural layers of archaeological sites, and thus it has a greater application potential in archaeological and palaeoecological research. Future applications to archaeological specimens of this taxa group will show whether the various depositional conditions may have a negative effect on the preservation of the endocarp layer structures and how this may hamper confident species identification. However, the current study shows that, like in *T. trichocarpum* and *R. chinensis*, density and alignment of the analysed tissue structures of lacquer tree endocarps are at extreme values, suggesting that endocarps of this taxon have a high potential to be differentiated from those of other species. This has special significance for identifying the origin of the lacquer tree in Japan and the history of its diverse uses, such as a source of sap for lacquer production, as a building material (Noshiro et al., 2007) or for nutritious, medical and hunting purposes (e.g., Kindscher, 1987; Long et al., 2003; Han and Cui, 2012).

4.3. Identification and use of Rhus/Toxicodendron endocarps from Hamanaka 2

Examination of the longitudinal section view of the charred *Rhus/Toxicodendron* endocarps from Hamanaka 2 (Fig. 8) shows that the internal structure is wavy but not as much as in *T. sylvestre*, *T. vernicifluum* or *R. chinensis* (Figs. 6 and 7), which are assigned a very wavy tissue alignment (Fig. 9). Regarding the density, the structure appears dense but not as much as in *T. vernicifluum* or *T. succedaneum*, which are assigned a very dense tissue structure. Therefore, the tissue structure can be described by an intermediate alignment (i.e., wavy) and intermediate density (i.e., dense), which identifies the endocarp as *T. orientale*. Although the density level of the archaeological specimens appears slightly lower than in the modern references of *T. orientale* (Fig. 6b and Fig. 7b), the tissue alignment is still not as wavy as in *R. chinensis* (Fig. 6a and Fig. 7a), which allows to confidently identify the endocarps from Hamanaka 2. Thus, we can securely exclude that the endocarps, which have been deposited at Hamanaka 2 by different cultural groups, indicate the use of the lacquer tree. Our identification also agrees with the presumed *Rhus/Toxicodendron* distribution (Fig. 1), which suggests that only *T. trichocarpum* and *T. orientale* occur in northern Hokkaido naturally. In addition, Haruki et al. (2004) report that exclusively *T. trichocarpum* and *T. orientale* were found growing on the island during a vegetation survey on Rebun Island and neighbouring Rishiri Island (Fig. 2a).

While the robust chronology (Junno et al., 2021) of the multi-layer Hamanaka 2 site proves the long-term use of *T. orientale* by Final Jomon, Epi Jomon, Okhotsk and Ainu culture groups, which spans a period of up to 3000 years, it remains unclear which purpose the fruits or other plant parts served. Although the fruits of *T. orientale* are reported to contain oil that can be used for making candles (Grieve, 1971),

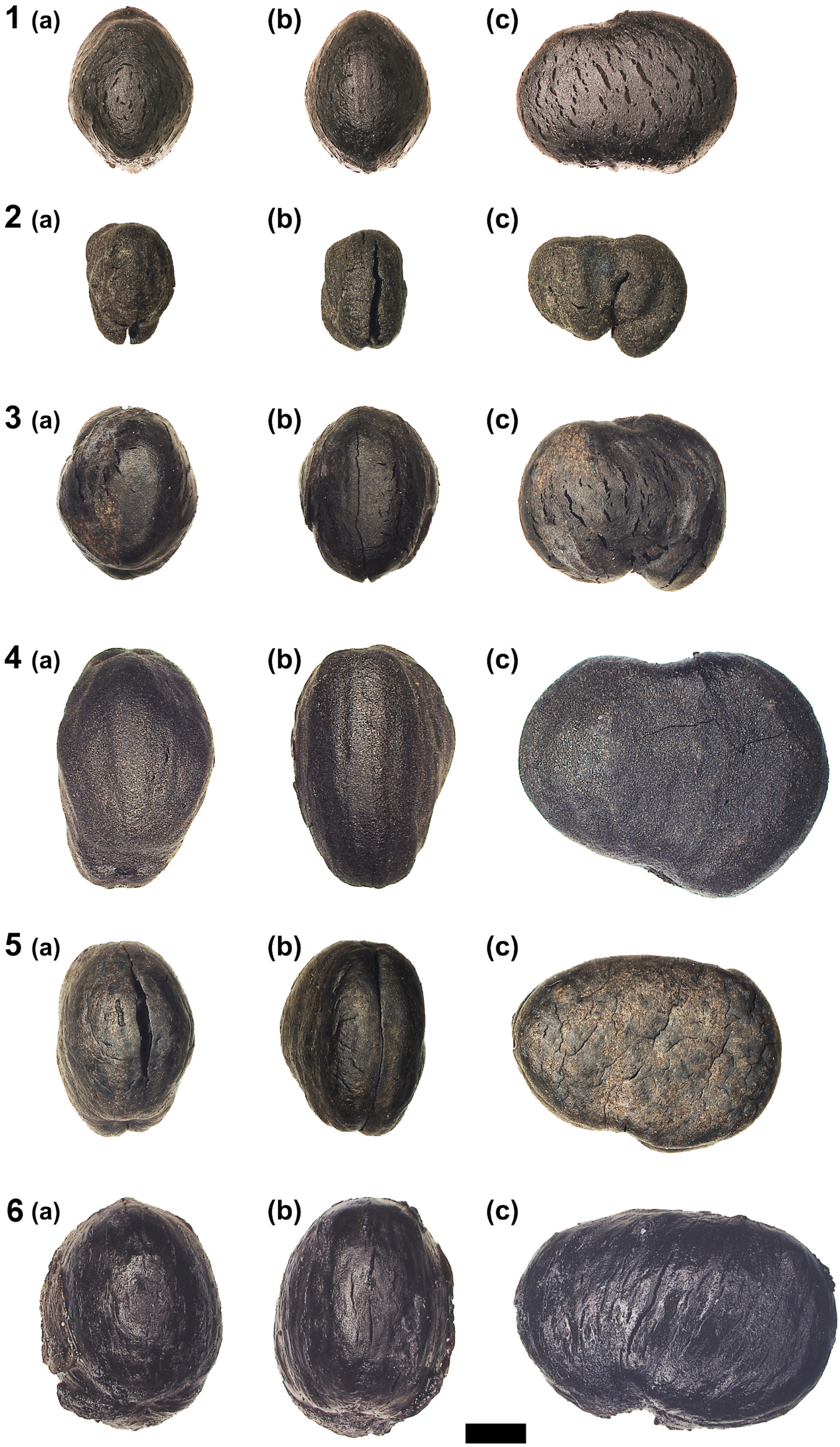


Fig. 5. Examples of charred modern endocarps of 1 – *Rhus chinensis*, 2 – *Toxicodendron orientale*, 3 – *Toxicodendron trichocarpum*, 4 – *Toxicodendron vernicifluum*, 5 – *Toxicodendron succedaneum* and 6 – *Toxicodendron sylvestre* in (a) ventral, (b) dorsal and (c) lateral views. Scale bar = 1 mm.

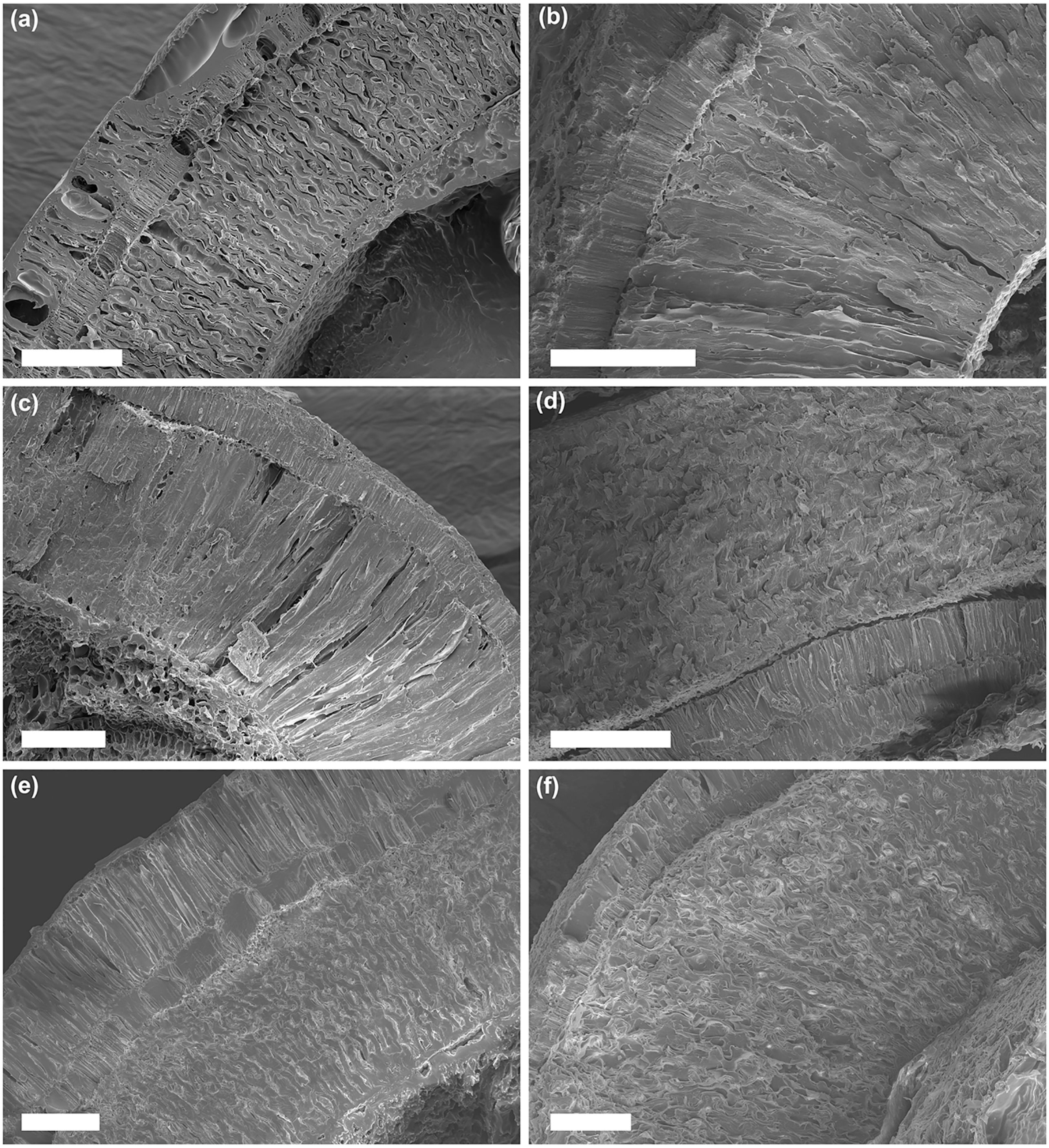


Fig. 6. SEM images of longitudinal sections of the inner layer of charred reference endocarps of (a) *Rhus chinensis*, (b) *Toxicodendron orientale*, (c) *Toxicodendron trichocarpum*, (d) *Toxicodendron vernicifluum*, (e) *Toxicodendron succedaneum* and (f) *Toxicodendron sylvestre*. Scale bars = 100 μm.

this seems an unlikely function, since the smoke would spread the contained urushiol (comprised of resinous phenolic compounds), which can cause severe allergic reactions when coming into contact with skin (dermatitis) or being inhaled (airway irritation) (Pennacchio et al., 2010). According to Shery (1972), lacquer can be also produced from the sap of *T. orientale*. From Rebun Island there have been no reports on artefacts to which lacquer was applied. However, a recent lipid residue study at Hamanaka 2 detected dehydroabietic acid (DHA) associated with tree resin on Final Jomon, Epi Jomon and Okhotsk culture ceramic sherds from the site (Junno et al., 2020). Junno et al. (2020) interpreted this as evidence of the use of wood resin-based pottery sealants or traces of burning coniferous wood during firing of the pottery or during cooking in them. However, the DHA may also point to the processing of sap for lacquer production.

The leaves of *T. orientale*, and thus also its fruits, are rich in tannin, a botanical tanning agent that has been used for millennia to convert hides into decay-resistant leather. Some of the earliest evidence of vegetable tanning based on oak apple (oak gall), oak bark, pomegranate (*Punica granatum*) bark or cereal and malt flour comes from ancient Mesopotamia (Levey, 1955, 1957). In ancient Greek, people used pine (*Pinus*) and alder (*Alnus*) bark, acorns, roots and grapes for tanning, as well as the leaves and the bark of *R. coriaria* (Forbes, 1966), which is often

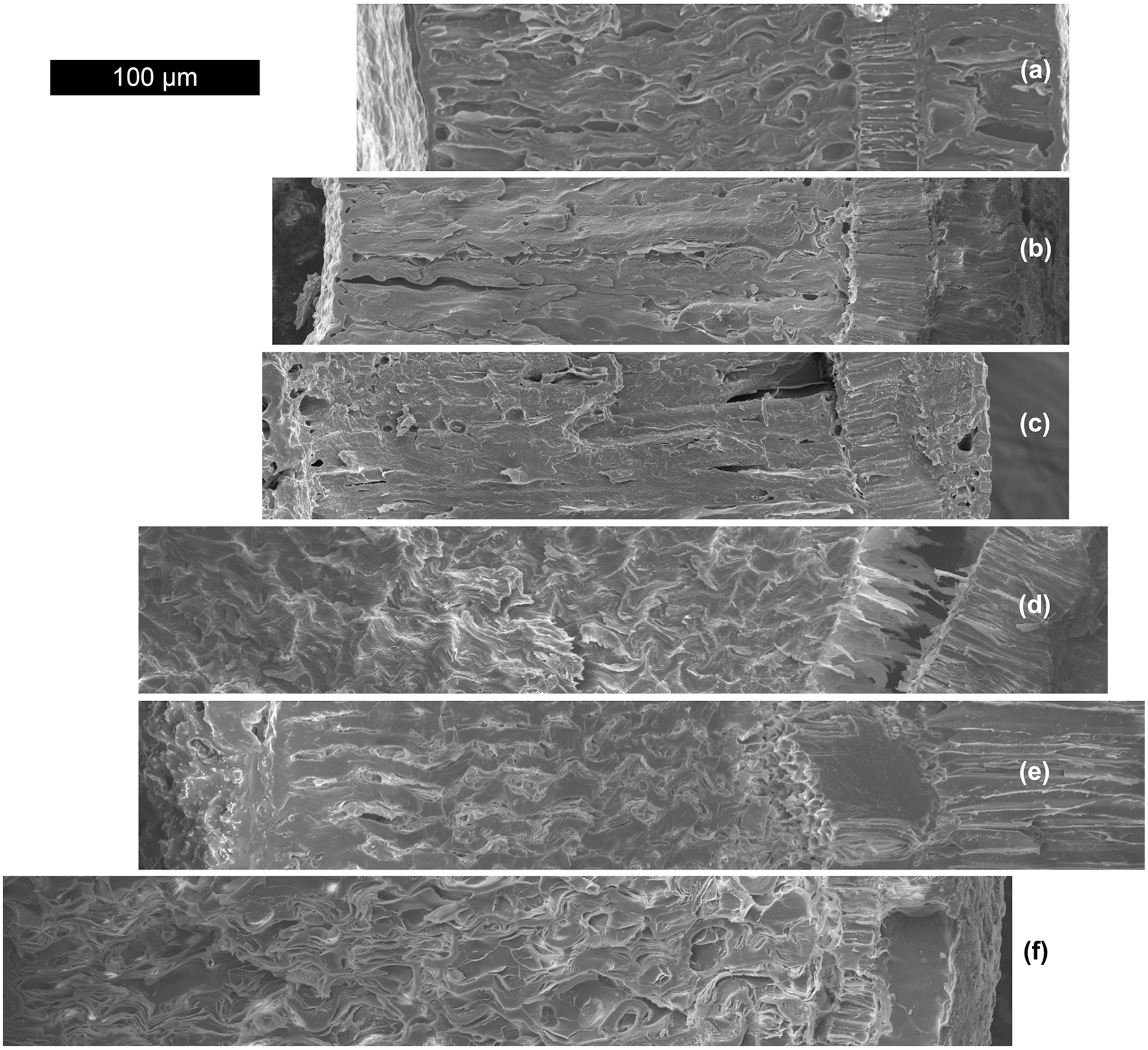


Fig. 7. SEM-based close-up view of the longitudinal sections of charred reference endocarps of (a) *Rhus chinensis*, (b) *Toxicodendron orientale*, (c) *Toxicodendron trichocarpum*, (d) *Toxicodendron vernicifluum*, (e) *Toxicodendron succedaneum* and (f) *Toxicodendron sylvestre*.

called tanner's sumac. Possibly, the charred *T. orientale* endocarps are remnants of tanning, for which parts of the plant (e.g., leaves and fruits) would have been boiled to extract the contained tannin. The use of the leaves of the lacquer tree as a source of tannin is also practiced by ethnic groups in Yunnan Province, south-western China (Long et al., 2003). This usage would provide an alternative explanation for the origin of the DHA detected on the inner surface of many pot sherds from Hamanaka 2 (Junno et al., 2020). The DHA may represent urushiol, which is comprised of different resinous phenolic compounds and represents the oil-soluble fraction of the sap of different *Rhus/Toxicodendron* species (Vogl, 2000), such as *T. vernicifluum*, *T. orientale* and *Toxicodendron radicans* (L.) Kuntze. However, urushiol is also contained in the leaves and bark and likely other parts of *T. orientale*. This interpretation agrees with the assumed function of Hamanaka 2. Based on its extensive record of zoological remains (Hirasawa and Kato, 2019), the site has been identified as a place of intensive hunting and processing of the rich local marine resources, especially sea mammals, which culminated during the Okhotsk culture occupation (Sakaguchi, 2007a, 2007b). The earliest evidence relating Hamanaka 2 with intensive sea mammal hunting comes from Late Jomon (ca. 2000–1300 BCE) culture layers from which no archaeobotanical data is available. Miyata et al. (2009) conducted a lipid residue study on Late Jomon pot sherds and concluded that mainly sea mammals were boiled in them, which supports an earlier study arguing that Late Jomon people used the site as a seasonal campsite for processing meat, fat and oil of sea mammals, mainly Japanese sea lion (*Zalophus japonicus*, extinct) (Nishimoto, 2000). Lipid residue analyses indicate predominant processing of sea mammals and fish also in ceramic containers associated with the Final Jomon occupation (Junno et al., 2020). It seems plausible that Late and Final Jomon groups and particularly the highly specialised marine hunters of the Okhotsk culture used the site also to tan hides and furs of hunted sea mammals, such as harbour seal (*Phoca vitulina*), fur seal (*Callorhinus ursinus*), Steller's sea lion (*Eumetopias jubatus*) and Japanese sea lion. The pot sherd lipid residue records from Hamanaka 2 (Junno et al., 2020) and the Kafukai sites located on the same island (Junno et al., in press) show an increased functional differentiation of vessels during the Okhotsk period, which indicates systematic resource processing and a broader spectrum of exploited resources compared to previous periods. The presence of sea mammal bones in the Late Jomon layers and in layers of Final Jomon, Epi Jomon, Okhotsk and Classic Ainu cultural occupation where they are accompanied by *T. orientale* endocarps may show a long history of tanning at Hamanaka 2 stretching at least from ca. 2000 BCE to the 19th century CE. This also puts the large number of barley seeds recovered from the Okhotsk culture layers in a different light. Besides the most

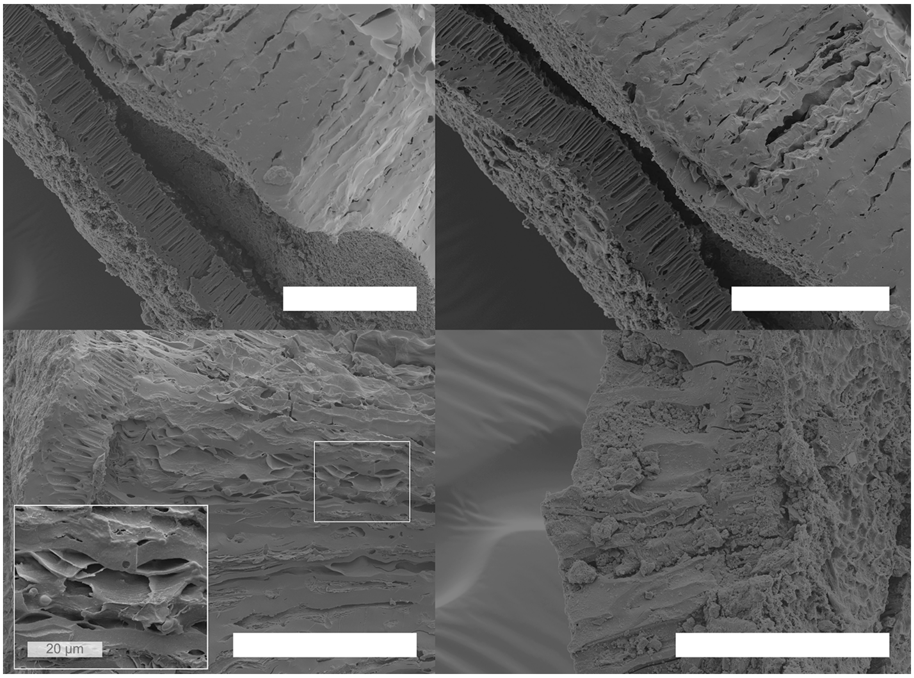


Fig. 8. SEM images of the longitudinal sections of charred fossil *Rhus/Toxicodendron* endocarps from Okhotsk culture layers of the Hamanaka 2 site, Rebun Island, northern Japan (Fig. 1). Inset marks the location of the close-up view. Scale bars = 100 μm, if not stated otherwise.

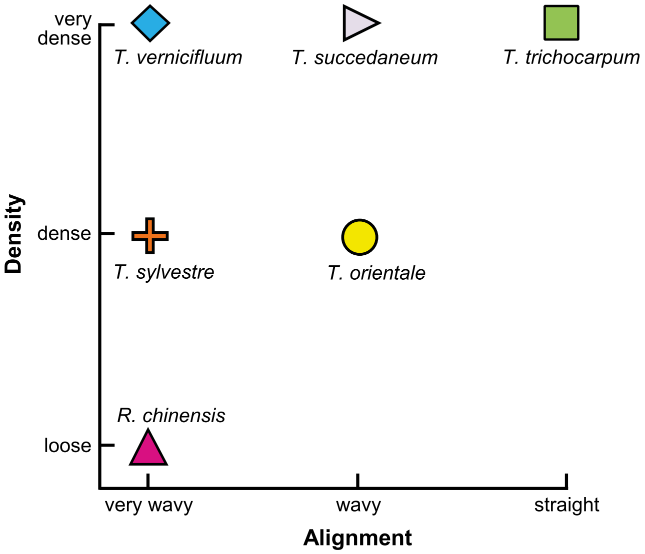


Fig. 9. Graphical presentation of the identification key for the six *Rhus/Toxicodendron* species growing in Japan. Identification is based on the characteristics of the alignment and density of the tissue of the inner layer of endocarps in longitudinal section view by means of SEM.

obvious use as supplementary food (Leipe et al., 2017) and/or for the production of alcoholic beverages, barley may also have been used for the production of leather. Evidence of this use is available from different regions and periods. In 1st-millennium BCE Mesopotamia wheat/barley flour was used in the manufacture of leather (Levey, 1955, 1957). The Encyclopædia Iranica also cites barley as an ingredient in traditional tanning of fleeces and pelts in southern and eastern Iran (Sa’idi Sirjane, 1993). From southern England there is evidence that during the Middle Ages barley or rye were used in the softening and de-liming of hides prior to tawing (Allan et al., 2021). The use of fermented barley or rye is also mentioned in the description about the nature and practices of tanning by the English preacher and scholar George Gregory (1807) in his ‘New and Complete Dictionary of Arts and Sciences’ from the beginning of the 19th century.

An alternative or additional function could have been medical effects and/or nutritional properties. Different studies have reported specific medical properties of different *Rhus/Toxicodendron* taxa, such as anti-inflammatory, anti-microbial, anti-bacterial, anti-viral, anti-diarrheal, anti-oxidant, anti-cancer and hepatoprotective effects (Rayne and Mazza, 2007; Djakpo and Yao, 2010). Zazharskyi et al. (2020) found bactericidal and fungicidal activity in leaves of *T. orientale*. While skin contact with the leaves of the plant may cause severe allergic reactions (Motegi et al., 2000), it is possible that ingestion of processed mesocarps or other plant parts may have been used for medical effects or served any other purpose. That indigenous peoples have been aware of various medical and nutritional properties and other functions of *Rhus/Toxicodendron* has been demonstrated by ethnobotanical research (e.g., Kindscher, 1987; Long et al., 2003; Han and Cui, 2012). More ethnobotanical and archaeobotanical studies are needed to clarify the different uses of *Rhus/Toxicodendron* taxa by prehistoric populations, including the use of *T. orientale* at Hamanaka 2.

5. Conclusions

The results of the current study show that differentiation of charred endocarps of the six *Rhus/Toxicodendron* species distributed in Japan can be done by SEM-based examination of their tissue structure in longitudinal section view. As charred endocarps are the most commonly found botanical remains in layers of archaeological sites, the presented method provides a valuable approach to study the ancient use of these plants in addition to the analysis of wood remains. This addresses the existing question of the identification of *Rhus/Toxicodendron* fruit remain records and their use from different archaeological sites and cultural periods. The investigation of reference samples showed that the endocarp structure of lacquer tree fruits is distinct from that of the other species and thus is readily identifiable. The presented identification key will help to track the use of this important economic plant in Japanese prehistory and to clarify whether it is distributed naturally across Japan or was introduced by early human migration or exchange, by allowing identification of fossil *Rhus/Toxicodendron* endocarps from archaeological context and palaeoenvironmental archives, such as bogs and mires. The current findings suggest that SEM-based analyses of morphological traits of endocarp longitudinal sections may be also used to differentiate between members of other genera that include important economic plants, such as *Prunus* and *Olea*.

The identification of *T. orientale* endocarps recovered from Hamanaka 2 based on the presented method raises questions about the long-term use of this plant at this site. While it is possible that the endocarps point to a medical and/or nutritional functionality or the use of the plant as a resource for sap to produce lacquer, it seems most plausible that the plant was exploited for its high tannin content and that the site was an important location for marine hunting and for tanning hides of sea mammals. In sum, these findings show that additional multidisciplinary research is needed to verify this conclusion and to improve the knowledge about the functionality of plant resources and their use by hunter-gatherer populations in Japan and elsewhere.

Data availability

All data needed to evaluate the conclusions in the paper are present in the paper.

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CRediT authorship contribution statement

Christian Leipe: Conceptualisation, Methodology, Writing – original draft, Writing – review & editing, Supervision. **Antonella Aquaro:** Conceptualisation, Methodology, Writing – review & editing, Visualisation. **Pavel E. Tarasov:** Conceptualisation, Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could influence the work reported in this paper.

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Appendix A. Supplementary data

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