New discovery of the oldest maize weevils in the world from Jomon potteries, Japan

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The maize weevil *(Sitophilus zeamais)* and rice weevil *(Sitophilus oryzae)* are two of the most damaging insects for stored grains, and are characteristic species of ancient Japan. Both species and the granary weevil (*Sitophilus granarius*) are common elsewhere in the world, but the natural distribution of maize and rice weevils is restricted to the Old World[1]. Japanese archaeological records contain a few maize weevil fossils after the Middle Yayoi period (ca. 2000 aBP)[2]. However, since evidence of weevils was discovered as impressions in Jomon potsherds in 2004[3], many weevil impressions have been found. The oldest is from the Late Jomon (ca. 4000 to 3200 aBP). These findings and other archaeological evidence suggest that the maize weevil invaded Japan from Korea, accompanying the spread of rice cultivation[4]. However, in 2010 we discovered older weevil impressions dating to ca. 9000 aBP. These specimens are the oldest harmful insects discovered from archaeological sites around the world. The new discovery is valuable for future entomological research because such specimens are absent from the fossil record. It is also archaeologically and culturally interesting because this provides evidence of harmful insects living in Jomon villages. However, the new discovery raises the question of what these weevils infested: did cereal cultivation exist 9000 years ago? We have no persuasive answer, but hope one will be provided by future interdisciplinary collaborations among geneticists, entomologists, and archaeologists.

Maize weevil life cycle

Granary, rice, and maize weevils, known as "snout weevils", feed inside rice or barley grains during their larval stage and pupate inside the grains[1]. Rice and maize weevils are widespread in warm regions. In Europe and North America, they are replaced by temperate species such as the granary weevil[5]. Granary and Japanese rice weevils cannot fly, unlike the maize weevil. Rice weevils spend their life in storage facilities, whereas maize weevils leave in winter to shelter under fallen leaves or in the soil[5]. After awakening in spring, they feed on nectar from flowers. Their home range is within 400 m from human villages with grain storage facilities; thus, dispersal over longer distances requires human assistance (e.g., via grain transport). The pattern of spending most of their life outdoors is thought to result from ancient adaptation to surviving on wild seed plants[6].

Discovery of weevil impressions on potsherds

Greek and Roman records describe weevils infesting wheat. In China, the oldest record appears in the "Ěryǎ", which was published between the 5th and the 2nd centuries BC. Maize weevils infest stored rice. The first Japanese description of maize weevils appears in the record in 10th centuries. However, archaeological records reveal granary weevils in barley offered to a dead king of the Egyptian Sixth Dynasty (ca. 4300 BP), and rice weevils infesting barley were discovered in a grave from the Han Dynasty (ca. 168 BC)[7,8]. These examples suggest that weevils have coexisted with humans for thousands of years.

Before maize weevil impressions were discovered on Jomon potteries (in 2004), the oldest specimens in Japanese archeological records (fossils) came from a ditch deposit at the Ikegamisone site (ca. 2000 aBP). The fossils of maize weevils were recovered from the Fujiwara Palace (ca. 8th century AD) and Kiyosu Castle (ca. 16th century AD)[2]. In 2004, maize weevil impressions were discovered (ca. 3500 aBP) in Late Jomon pottery on Kyushu[3]. Weevil models were recovered from impressions in the clay using "the replication method" developed by European paleoethnobotanists and adopted by Japanese archaeological researchers in the late 1970s. This method injects silicone into a cavity, resulting in a model of the original form that created the cavity. Another recent discovery using this method revealed soybean and adzuki bean cultivation during the Jomon Period[9,10].

Subsequently, many maize weevil impressions were discovered at Late Jomon sites, especially on Kyushu. In 2007, two maize weevil specimens were discovered at a Final Jomon site in Yamanashi Prefecture[11]. By 2008, 32 weevil impressions had been obtained from 13 sites (Fig.1, Table 1; 1-32) . Most impressions appear to be of maize weevils based on their size and anatomical characteristics. These new discoveries suggest that maize weevils might have coexisted with humans as early as the Late Jomon period. The earliest specimen was found inside a Kanegasaki 3–type deep bowl dating to ca. 4000 aBP. Later impressions of maize weevils have been reported from the Late to Final Jomon periods. The number of specimens increases rapidly by the Nishibira pottery phase (ca. 3800 aBP), with a peak during the last quarter of the Late Jomon[4]. Subsequently, specimen rates remain stable. We discovered three new specimens at early Late Jomon sites in Kagoshima Prefecture in 2009. This finding dates the appearance of weevils 200 or 300 years earlier than in previous research (Fig. 1, Table 1; 35-37).

Old hypothesis: Maize weevils document the origins of rice cultivation in Japan

Maize weevils feed on stored grains and on fruits such as peach or apple in North America, and also inhabit forests or grasslands in southern Japan, where they feed on flowers in the spring. The adult weevils feed on 37 families and 96 species of plants, but the larvae feed on only 11 families and 31 species[5]. To understand their biology, we fed maize weevils many different foods. The adults preferred large grains such as rice, barley, and wheat. They did not feed on adzuki bean, hemp, or unhusked rice. The weevils also infested acorns without seed coats and successfully reproduced[4]. However, during the Jomon period, acorns were generally stored with seed coats to protect them from decay, so few or no maize weevils would have infested acorns. Although adult maize weevils feed on rice flour, they never oviposit there. Therefore, even if sufficient suitable food is available to stimulate oviposition, weevils must still be able to penetrate the seed coat to oviposit successfully[12].

The maize weevil should appear at roughly the same time as agriculture expanded in Japanese archeobotanical records, and indeed, archaeological artifacts suggest strong cultural relationships between the southern Korea and northwestern Kyushu increased at this time. Furthermore, rice phytoliths have been recovered from Late Jomon pottery in northwestern Kyushu. The presence of maize weevils therefore suggests the existence of rice or barley cultivation during the Late to Final Jomon periods, and that they invaded Japan from Korea, accompanying rice cultivation[4].

New evidence: older maize weevil impressions

The new evidence contradicts the original hypothesis. In February 2010, we discovered the oldest impressions of maize weevils from early Jomon potsherds dated to ca. 9000 aBP from the Sanbonmatsu Site in Kagoshima Prefecture. The site, which is on a terrace (50 m asl) on the eastern coast of Tanagashima Island, 40 km southeast of the Oshumi Peninsula, was excavated in 2007 by the Nishinoomote City Board of Education. Researchers discovered cultural layers containing many artifacts, mainly from the Early Jomon period.

Potsherds were examined to find seed and other impressions in February 2010. We found two fragments that contained maize weevil impressions (SBM0011 and SBM0024; Fig. 2). Both came from a Yoshida-type deep bowl (one from the body, the other from the base). Both fragments are ornamented with shells, a popular ornamentation during the first half of the Early Jomon period in southern Kyushu[13]. This cluster has ^{14}C dates from ca. 9400 to ca. 8700 aBP, suggesting that the Yoshida type dates to ca. 9000 aBP. In April 2010, we recovered five additional potsherds with maize weevil impressions (SBM0060, SBM0061, SBM0062, SBM0067, and SBM0073; Fig. 2). These were also Yoshida types based on their ornamentation and morphological characteristics. One is a rim fragment, two are bottom fragments, and two are parts of the body.

Identification

Adult granary weevils have elongated punctations on their thorax and other body parts, whereas adult rice and maize weevils have round or irregular punctations[14]. The maize weevil resembles the rice weevil, but adult rice weevils are 2.1 to 2.9 mm long (mean, 2.3 mm), versus 2.3 to 3.5 mm (mean,2.8 mm) for adult maize weevils[15]. Most replicas lack legs and the rostrum, but have round or irregularly shaped punctations, similar to those of maize weevils (Fig. 2).

However, two beetles are morphologically similar to maize weevils: *Diocalandra* spp. and *Paracythopeus melancholicus*. *Diocalandra* spp. is slenderer and longer than maize weevils[16]. The ratio of thorax to elytron length also differs among the three species: 0.898 for *Diocalandra* spp., 0.500 for *P. melancholicus*, and 0.757 for weevil impression SBM0024, which equals the ratio of 0.776 for *S. zeamais* (Fig. 3). The side view of weevil impression SBM0024 is most similar to that of *S. zeamais* (Fig. 3). The diagnostic criterion that distinguishes *S. zeamais* from *P. melancholicus* is the elytron end, which is shorter than the tail in *S. zeamais* but covers the tail in *P. melancholicus* (Fig. 3). These criteria can be seen clearly on the elytron end of other impression weevils SBM0060, SMB0061 and SBM0062 (Fig. 2) and suggest that the weevils from the Sanbonmatsu site were maize weevils. These are the oldest maize weevil relics in the world.

To confirm this identification, we obtained CT scans at the X-Earth Center, Kumamoto University. These revealed previously unseen details of the insect's legs and rostrum end. An unexpected benefit of this approach is that it also recorded antenna projections, which have never previously been seen in weevil impressions (Fig. 4). These findings demonstrate the method's superiority to the replication method for correctly identifying insects.

Significance of maize weevils during the Early Jomon

We discovered seven maize weevil impressions. The high discovery ratio is similar to that from the Late Jomon sites on Kyushu, indicating that these weevils were already pests in the Early Jomon. If the Late Jomon maize weevils were associated with the spread of rice or barley cultivation into Japan, what is the significance of the Early Jomon records? Were other cereals cultivated in Japan at that time?

Two hypotheses explain the diffusion of rice cultivation into Japan. First, it may have diffused from the Shantong Peninsula through Korea ca. 4000 aBP[4,17]; alternatively, it may have diffused from southern China through the Ryukyu Islands ca. 6700 aBP[18]. The former is accepted by most archaeologists. Evidence from archaeological sites at those times (charred seeds and seed impressions) suggests the cultivation of cereals in the Poaceae (e.g., rice, barley), introduced to Kyushu from Korea. The second hypothesis is not supported by archeological or archeobotanical evidence[19,20]. The earliest rice cultivation on Kyushu occurred in the 10th century AD, and was it not introduced from southern China; instead, it was introduced at the time of human immigration into the region. The Early Jomon is nearly synchronous with the beginning of rice cultivation in the Lower Yangtze River Valley in China, the origin of Asian rice cultivation. The oldest evidence of barley and wheat cultivation in East Asia is younger than ca. 4000 aBP. Thus, the archaeological evidence strongly suggests there were no cultivated cereals that maize weevils could infest in Japan at ca. 9000 aBP.

This suggests that the existence of maize weevils in the Early Jomon was not associated with rice cultivation. Nevertheless, the high weevil density at that time suggests the weevils were related to the Jomon people and lived in Jomon houses, where they fed on stored foods. We do not know what kind of wild plant food they fed on or infested. One candidate is the seeds of bamboo *Bamb* spp.). These seeds can be stored for long enough periods to permit weevil development, and have sometimes been used as an emergency food source during famines. Indeed, we found some charred bamboo seeds at archaeological sites from the Late Jomon to the Ainu Culture period on Hokkaido[21]. However, phytolith analysis suggests rapid decreases in bamboo in this region from 11 300 to 7300 aBP because of the expansion of evergreen forest[22,23]. Thus, we cannot state with certainty what food maize weevils infested at that time.

The new discovery should encourage additional research on the ecology of maize weevils, and particularly, when they began infesting stored food. This will require additional maize weevil specimens from other time periods and regions. No fossils of maize weevils or their ancestors have been discovered, so the origin and history of this taxon are unclear. DNA analysis would provide important insights.

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Author Contributions Hiroki OBATA directs the research and wrote the paper. Aya MANABE did the laboratory work at Kumamoto University and took SEM photos for identification of the impression weevils. All co-authors contributed to this research.

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Figure legends

Figure 1 SEM images of replicas of the impression maize weevils from Jomon sites discovered by 2009.

The 37 impression weevils were discovered on Jomon potteries mainly in Kyushu dating ca. 4300 aBP to ca. 3000 aBP by 2009. Judging from the diagnostic criteria and the size, these impression weevils are identified as maize weevils *(Sitophilus zeamais)*.

Figure 2 SEM images of replicas of the impression maize weevils and potsherds from Sanbonmatsu Site In 2010 we discovered

Maize impressions on pottery (a), pottery section illustrations with rubbing (b), photos of cavity (c) and SEM images of their replicas (d,e,f). The white circles point the position of cavity on the pottery. "A" and "B" show the positions of the potsherds with maize impressions on the same type potteries. "A "is from the Ohnakahara Site and "B" is from the Kakoinoharu Site in Kagoshima Prefecture.

Figure 3 Diagnostic characteristics for Identification of weevils.

Three species of weevils, *Sitophilus zeamais, Diocalandra elongata* and *Paracythopeus melancholicus* are distinguishable by the ratio of thorax to elytron length. The diagnostic criterion that distinguishes *S. zeamais* from *P. melancholicus* is the elytron end.

Figure 4 CT scan images of the impression maize weevils (SBM0024) from Sanbonmatsu Site

CT scan images show us the details of the insect's legs, rostrum end and antenna that are previously unseen on the replicas. These findings demonstrate the method's superiority to the replication method for correctly identifying insects.

Table legends

Table 1 The list of the maize weevil impressions from Jomon sites by 2009

Table 2 The list of the maize weevil impressions from Sanbonmatsu Site

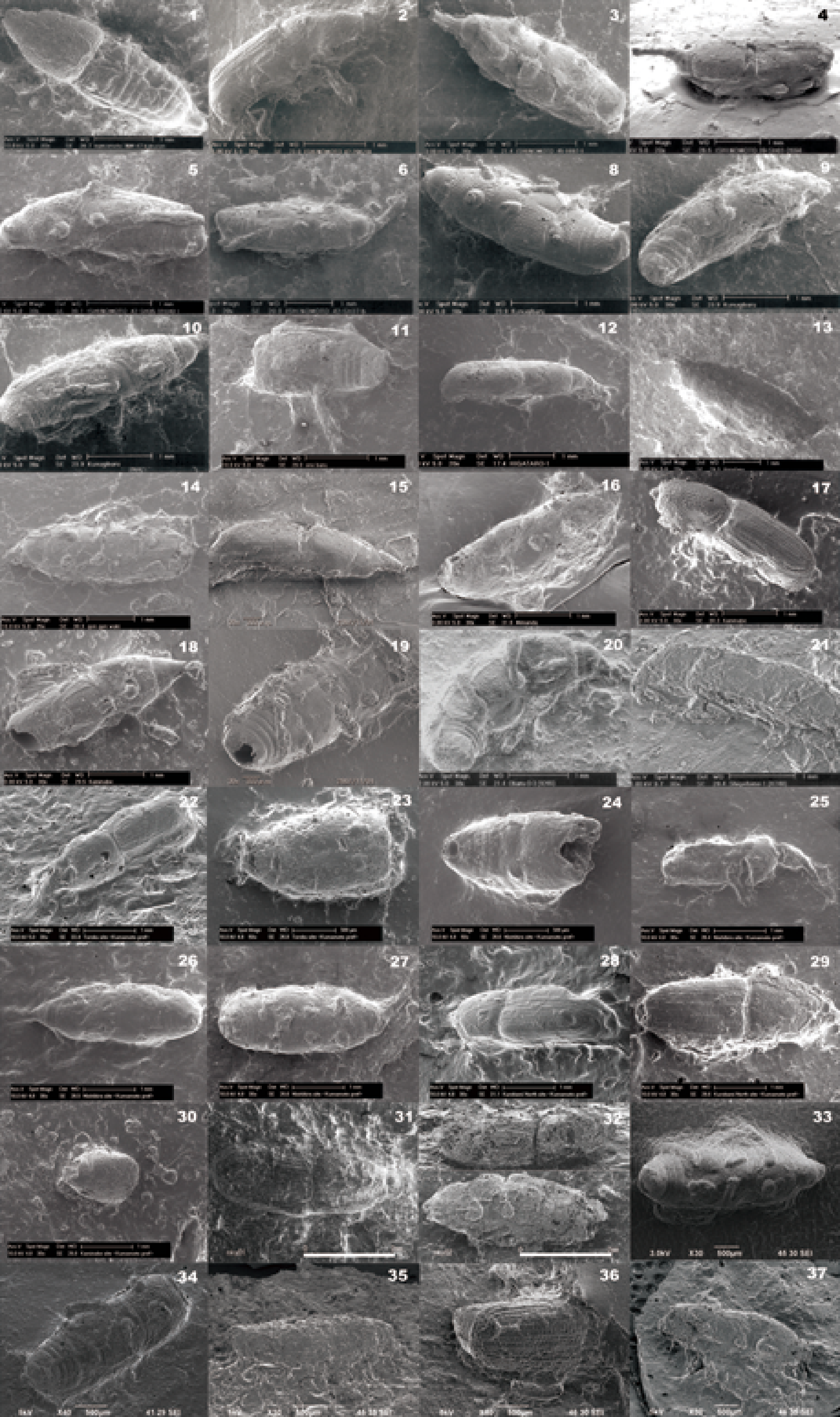
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Table 1 Maize weevil impressions on the Jomon Potteries

	Part of impression	Site	Sample name	Type of Pottery	Shape /Part	Phase	Estimated Age
1	Dorsal view (lose a rostrum, wings and legs)	Ishinomoto (Kumamoto Pre.)	INM-47	Amagi	Deep bowl/ rim	End of Late J.	ca. 3450 aBP
2	Side view (lose legs)	Ishinomoto (Kumamoto Pre.)	42-29629-1	Amagi	Deep bowl/ rim	End of Late J.	ca. 3450 aBP
3	Ventral view (lose a rostrum and legs)	Ishinomoto (Kumamoto Pre.)	45-1697-1	Goryo	Shallow bowl/ rim	L.H. of Late J.	ca. 3500 aBP
4	Dorsal view (lose a legs)	Ishinomoto (Kumamoto Pre.)	39-SH01-2694	Koga	Shallow bowl/ body	End of Late J.	ca. 3400 aBP
5	Ventral view (lose a rostrum and legs)	Ishinomoto (Kumamoto Pre.)	47-SH35-31040-1	Amagi	Deep bowl/ unknown	End of Late L.	ca. 3450 aBP
6	Ventral view (lose legs)	Ishinomoto (Kumamoto Pre.)	47-SX-07-b	Goryo	Shallow bowl/ unknown	L.H. of Late J.	ca. 3500 aBP
7	Unknown	Ishinomoto (Kumamoto Pre.)	Unknown	Unknown	Unknown	Latest J.	ca.3400-3000 aBP
8	Ventral view (lose a rostrum and legs)	Kunugibaru (Kagoshima Pre.)	Kunugibaru-1	Unkhown	Deep bowl/ rim	F.H. of Latest J.	ca.3200-3000 aBP
9	Side view (lose a rostrum and legs)	Kunugibaru (Kagoshima Pre.)	Kunugibaru-2	Unknown	Deep bowl/ rim	F.H. of Latest J.	ca.3200-3000 aBP
10	Side view (lose a rostrum and legs)	Kunugibaru (Kagoshima Pre.)	Kunugibaru-3	Unknown	Deep bowl/ rim	F.H. of Latest J.	ca.3200-3000 aBP
11	Ventral view (lost a thorax and legs)	Ohnobaru (Nagasaki Pre.)	ONB1010	Tarozako	Deep bowl/ base	The end of Late J.	ca. 3600 aBP
12	Side view (lose legs)	Higataro (Nagasaki Pre.)	HIG115	Kurokawa？	Deep bowl/ body	F.H. of Latest J.	ca. 3300 aBP
13	Side view (lose legs)	Higataro (Nagasaki Pre.)	10381-03	Kurokawa?	Deep bowl/ body	F.H. of Latest J.	ca. 3300 aBP
14	Ventral view (lose a rostrum and legs)	Gongenwaki (Nagasaki Pre.)	GGW-021	New Kurokasa	Bowl/ bod	Middle of Latest J.	ca. 3000 aBP
15	Side view (lose rostrum and legs)	Ohnobaru (Nagasaki Pre.)	ONB1018	Tarozako?	Deep bowl/ body	L.H. of Late J.	ca. 3600 aBP
16	Ventral view (lose rostrum and legs)	Mimanda (Kumamoto Pre.)	MD0019	Tarozako	Bowl/ base	Middle of Late J.	ca. 3600 aBP
17	Side view (lose a head and legs)	Kaminabe (Kumamoto Pre.)	KNB05	Amagi	Deep bowl/ rim	The end of Late J.	ca. 3450 aBP
18	Side view (lose a head and legs)	Kaminabe (Kumamoto Pre.)	KNB32	Koga?	Deep bowl/ body	The end of Late J.	ca. 3400 aBP
19	Side view (lose legs)	Kaminabe (Kumamoto Pre.)	KNB34	Amagi?	Deep bowl/ body	The end of Late J.	ca. 3450 aBP
20	Side view (lose a rostrum and legs)	Ohbaru D (Fukuoka Pre.)	Ohbaru-D-3(9265)	Unknown	Deep bowl/ unknown	F.H. of Latest J.	ca.3200-3000 aBP
21	Side view (lose a rostrum and legs)	Shigetome (Fukuoka Pre.)	Shigetome1(8748)	Amagi	Deep bowl/ body	The end of Late J.	ca. 3450 aBP
22	Dorsal view (lose legs)	Toroku S.M. (Kumamoto Pre.)	TR11	Kanegasaki 3	Deep bowl / body	F.H. of Late J.	ca. 4000 aBP
23	Dorsal view (lose a rostrum and a trunk)	Toroku S.M. (Kumamoto Pre.)	TR21	Mimanda	Deep bowl / body	L.H. of Late J.	ca. 3550 aBP
24	Ventral view (a trunk)	Nishibira S.M. (Kumamoto Pre.)	NB02	Nishibira	Bowl/ body	F.H. of Late J.	ca. 3700 aBP
25	Side view (lose legs)	Nishibira S.M. (Kumamoto Pre.)	NB07	NIshibira?	Bowl/ body	F.H. of Late J.	ca. 3700 aBP
26	Dorsal view (lose legs)	Nishibira S.M. (Kumamoto Pre.)	NB08	Nishibira?	Bowl/ body	F.H. of Late J.	ca. 3700 aBP
27	Ventral view (lose legs)	Nishibira S.M. (Kumamoto)	NB17	Goryou	Shallow bowl/ rim	L.H. of Late J.	ca. 3500 aBP
28	Dorsal view (lose a rostrum and legs)	Kurokamimachi (Kumamoto Pre.)	KKN07	Unknown	Deep bowl / body	L.H. of Late？ J.	ca.3600-3400 aBP
29	Dorsal view (lose a rostrum and legs)	Kurokamimachi (Kumamoto Pre.)	KKN08	Unknown	Deep bowl / body	L.H. of Late？ J.	ca.3600-3400 aBP
30	Dorsal view (a thorax)	Kaminabe (Kumamoto Pre.)	KNB22	Amagi?	Deep bowl / body	The end of Late J.	ca. 3450 aBP
31	Dorsal view (lose a rostrum and legs)	Nakaya (Yamanashi Pre.)	Nky01	Shimizutennouzan	Deep bowl / body	F.H. of Latest J.	ca. 3000 aBP
32	Side view (lose a rostrum and legs)	Nakaya (Yamanashi Pre.)	Nky02	Shimizutennouzan	Deep bowl / body	F.H. of Latest J.	ca. 3000 aBP
33	Ventral view (lose a rostrum and legs)	Mimanda (Kumamoto Pre.)	MMD2054	Unknown	Deep bowl / body	L.H. of Late？ J.	ca.3600-3400 aBP
34	Ventral view (lose a head and legs)	Ohnobaru (Nagasaki Pre.)	ONB1116	Unknown	Deep bowl / body	L.H. of Late？ J.	ca.3600-3400 aBP
35	Ventral view (lose a rostrum and legs)	Kakiuchi (Kagoshima Pre.)	KKU0019	Namiki-Nanpukuji	Deep bowl / body	The beginning of Late J.	ca.4500-4000 aBP
36	Dorsal view (abdomen)	Izumi Shell Midden (Kagoshima Pre.)	KZK0008	Izumi	Deep bowl / rim	The beginning of Late J.	ca. 4300 aBP
37	Side view (lose a rostrum and legs)	Nanbarauchibori (Kagoshima Pre.)	NBU0005	Ichiki	Deep bowl / rim	The beginning of Late J.	ca. 4200 aBP

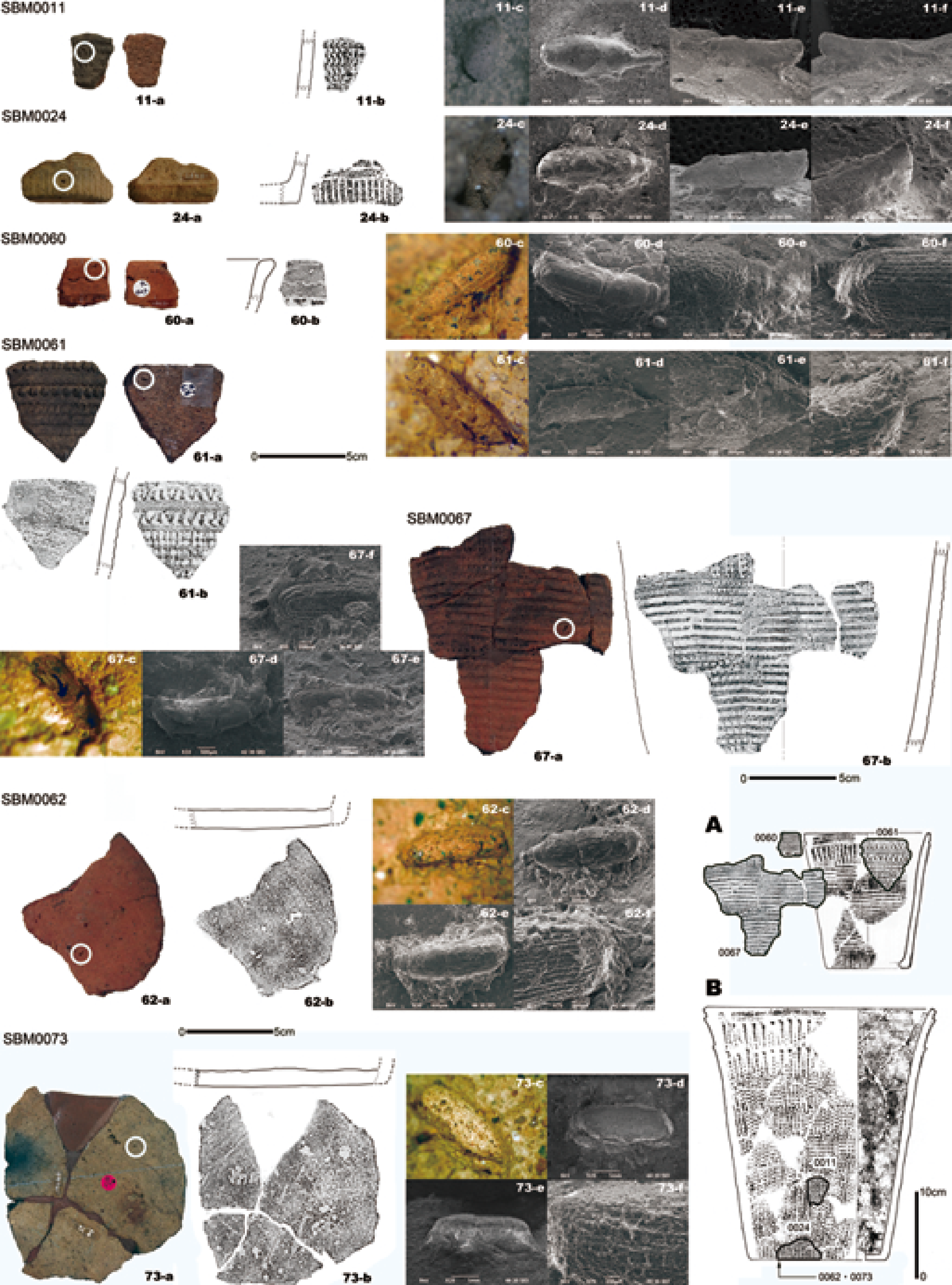
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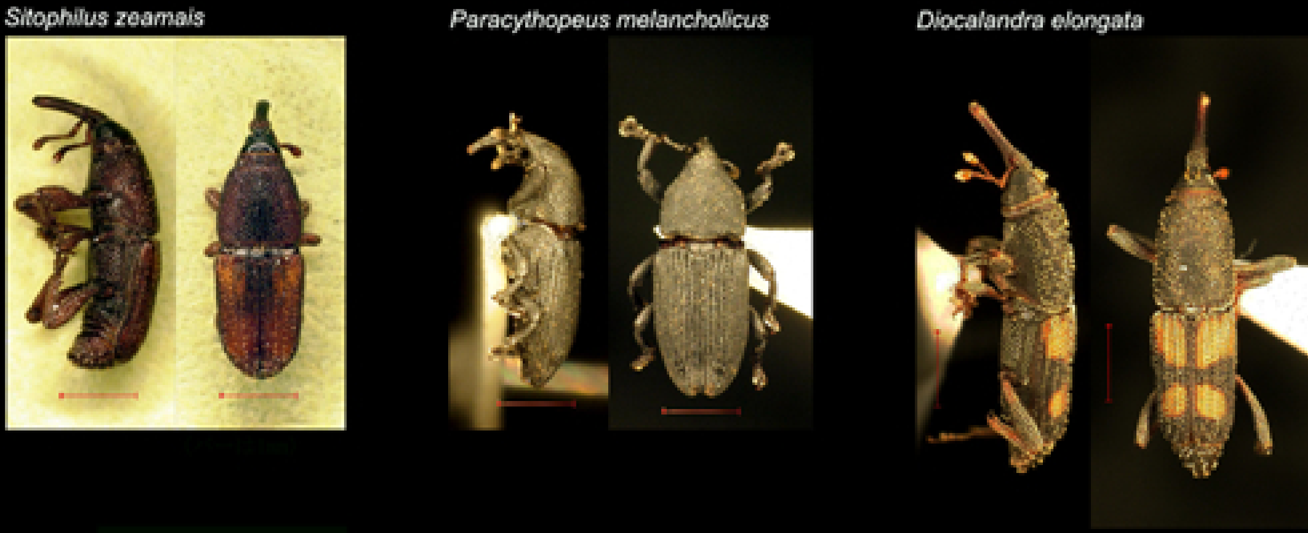
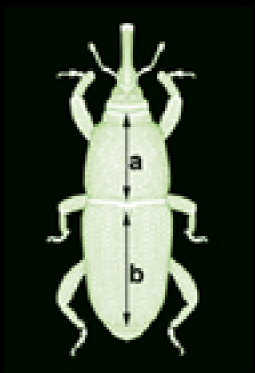
Table 2

No.	Pottery Type	Shape/ part	Part of impression weevil	Length (mm)	Estimated lengh(mm)
SBM0011	Yoshida Type	Deep bowl/ body	Ventral view（lose legs）	3.69	3.69
SBM0024	Yoshida Type	Deep bowl/ rim	Ventral view (lose a rostrum and legs)	3.62	3.93
SBM0060	Yoshida Type	Deep bowl/ rim	Dorsal view (lose a rostrum and legs)	3.11	4.02
SBM0061	Yoshida Type	Deep bowl/ rim	Ventral view (lose legs)	4.12	4.40
SBM0062	Yoshida Type	Deep bowl/ bottom	Dorsal view (lose a rostrum)	3.45	4.15
SBM0067	Yoshida Type	Deep bowl/ body	Side view	3.17	3.71
SBM0073	Yoshida Type	Deep bowl/bottom	Dorsal view (lose a rostrum)	3.58	4.38





S. zeamais	a : b=1.11 : 1.40	(mm)	a/b=0.776
P. melancholicus	a : b=0.96 : 1.92	(mm)	a/b=0.500
D. elongata	a : b=1.58 : 1.76	(mm)	a/b=0.898
SBM0024	a : b=1.40 : 1.85	(mm)	a/b=0.757

a = thorax
b = elytron