Identification of Rubus Seeds in Chinese Archaeological Sites: Based on the Morphological Atlas of 126 Modern Rubus Seeds

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Abstract

Rubus seeds constitute the predominant plant remains in archaeobotanical assemblages from Chinese archaeological sites. Nevertheless, no studies have yet reported the precise species-level identification of archaeological *Rubus* remains, as a result of the lack of systematic research on *Rubus* seed morphology. The first seed morphology atlas was established by systematically collecting and analyzing the morphological characteristics of 126 *Rubus* plants' mature seeds, which represent *Rubus* taxa in China (including 22 varieties). Utilizing this atlas, we identified *Rubus* seeds from seven archaeological sites, which ranged from the Shang-Zhou dynasties to the present day. Of these seeds, one was carbonized and six were uncarbonized. These specimens were identified as *Rubus lambertianus*, *R. parvifolius*, *R. flosculosus*, *R. coreanus* var. *tomentosus*, *R. trianthus*, and *R. adenophorus*. Furthermore, the atlas was employed to precisely identify *Rubus* seeds from nine archaeological sites that had been previously reported, primarily assigning them to *R. parvifolius*, *R. hirsutus*, and *R. rosifolius*. The results indicate that the *Rubus* seed morphology atlas developed in this investigation can serve as a critical reference for the identification of *Rubus* seeds that have been excavated from archaeological sites in China.

1. Introduction

Fruit and seed remains (whole or fragmentary) constitute a substantial proportion of plant remains excavated from archaeological sites [1–4]. other plant remains that have been excavated include rhizomes[5], tubers[6], bulbs[7], fibers[8,9], and leaves or stems[10]. While fruit and seed remains recovered from archaeological sites are most commonly associated with food crops, they also include less frequent remains from wild plants. Notably, the majority of such fruit and seed remains can only be identified to the family or genus taxonomic level[11]. The main reason for the difficulty in identification is that the fruit and seed of closely related sibling species usually exhibit similar morphological characteristics, so identifying the accurate provenance of fruit and seed remains in archaeological sites is a challenge.

According to relevant research reports, abundant *Rubus* seeds have been excavated from archaeological sites across China[12–22]. Among these *Rubus* seed remains, some are carbonized and others uncarbonized, yet both exhibit relatively well-preserved morphological features. In the aforementioned literature, only two sites yielded species-level identifications, while the remainder were identified only to the genus *Rubus*. Notably, China is home to a highly diverse Rubus flora, comprising over 200 species[23,24]. To date, there is no established morphological atlas of *Rubus* seeds in China, which affects the accurate identification of *Rubus* seeds excavated at Chinese archaeological sites. Identifying the seed remains of *Rubus* plants in archaeological sites can provide a reference for reconstructing the history of ancient ancestors' utilization of plants in the genus *Rubus*.

This article aims to systematically organize the seed morphological characteristics of 126 species of *Rubus* plants in China and provide a scientific basis for the identification of *Rubus* seeds excavated from archaeological sites. The objectives include (1) establishing a seed morphology atlas for identifying

Rubus seed in archaeological sites and (2) understanding the history of ancient Chinese ancestors using plants of the genus *Rubus*.

2. Research Ideas and Methods

2.1. Research Ideas

Rubus L. is a large genus in the Rosaceae family. There are 208 species of *Rubus* plants in China, among which 139 species are endemic[23,24], mainly deciduous shrubs, rarely evergreen shrubs, semi-shrubs, or perennial creeping herbs[25–29]. According to the sequence of phylogenetic evolution, Yu classified the *Rubus* plants in China into 8 sections and 24 subsections, including Sect. Idaeobatus, Sect. Lampobatus, Sect. Rubus, Sect. Malachobatus, Sect. Dalibardastrum, Sect. Chamaebatus, Sect. Cylactis, and Sect. Chamaemorus[30], revising and establishing a taxonomic system for *Rubus* in China.

The difficulties in identifying plants of the genus *Rubus* lie in their numerous species, similar morphological characteristics, small natural distribution range, rich morphological variation, and extensive convergent evolution, as well as polyploid hybridization and obvious frequent facultative apomixis[31–34]. From a morphological perspective, the genus *Rubus* exhibits enormous diversity, ranging from woody, semi-woody, shrubs to creeping dwarf herbaceous plants[28]. Seeds are vital organs for plant regeneration. Typically, the shape and structure of seeds serve as the basis for identifying many plant species. The sculptural patterns on the seed coat of many plants are highly diverse. Additionally, the structure and surface carving on the seed coat are maternal characteristics, so they vary among different species, and the seed coat ornamentation is the most prominent and variable feature for distinguishing genera and species[35]. There have been few descriptions of the seed morphology in the genus *Rubus* [36–38], and comprehensive research is lacking. Therefore, this study characterized the genus *Rubus* based on seed morphology (e.g., shape, seed coat ornamentation) and evaluated the feasibility of using these traits to determine the taxonomic provenance of *Rubus* seeds from excavated archaeological sites.

The core objective of this study is to accurately determine the taxonomic provenance of *Rubus* seed remains from archaeological sites, leveraging the known morphological characteristics of seeds within this genus.

2.2. Research methods

To further investigate the seed morphology of *Rubus*, we randomly selected several representative seeds during sample collection. Priority was given to highly mature seeds to ensure that subsequent observations and measurements accurately reflect the typical characteristics of seeds in this taxonomic unit (the genus *Rubus*).

For observation and measurement, a stereomicroscope (model: Keyence Digital Microscopy System-VHX-7000N) was used. Seeds were positioned on the microscope stage, and comprehensive observations were conducted from multiple angles by adjusting the focus and angle of the microscope. Using the microscope's integrated measurement software, precise measurements were taken along the long and short axes of seeds on high-resolution images. By switching the microscope to high magnification, the seed epidermis was focused on to meticulously examine its textural structure. Seed morphology terminology in this study follows the descriptions provided by Chernoff et al.[39] and Lersten et al.[40].

3. Research on the seeds of the genus in species

3. Research on the seeds of the genus *Rubus* in species

3.1. Collection of samples

Seed specimens are the material basis for conducting seed morphology identification and classification research, as well as an important reference for identifying seeds excavated from archaeological sites. This study collected mature seeds of *Rubus* from local populations in different regions of China. A total of 126 seeds (including 22 varieties) of *Rubus* were collected. According to the section and subsection classification system of *Rubus* in Flora of China, the collected seeds were classified at the species level, after which the micromorphological variation of seeds across 8 sections and 23 subsections was evaluated. The information on the investigated species is listed in Table 1.

Table 1
Seed source species and morphological determination of the genus *Rubus* L.

No	Species	Section	Subsection	location
1	*R. calycinus*	Sect. Chamaebatus		Hunan province
2	*R. calycinoides*	Sect. Chamaebatus		Taiwan province
3	*R. pectinellus*	Sect. Chamaebatus		Hunan province
4	*R. chamaemorus*	Sect. Chamaemorus		Inner Mongolia
5	*R. rubrisetulosus*	Sect. Cylactis		Sichuan province
6	*R. saxatilis*	Sect. Cylactis		Heilongjiang province
7	*R. nyalamensis*	Sect. Cylactis		Xizang autonomous region
8	*R. fockeanus*	Sect. Cylactis		Sichuan province
9	*R. tricolor*	Sect. Dalibardastrum		Sichuan province
10	*R. jinfoshanensis*	Sect. Dalibardastrum		Chongqing city
11	*R. multisetosus*	Sect. Dalibardastrum		Yunnan province
12	*R. tsangorum*	Sect. Dalibardastrum		Jiangxi province
13	*R. lucens*	Sect. Lampobatus		Yunnan province
14	*R. caesius*	Sect. Rubus		Xinjiang autonomous region
15	*R. pentagonus* var. *modestus*	Sect. Idaeobatus	Subsect. Alpestres	Sichuan province
16	*R. quinquefoliolatus*	Sect. Idaeobatus	Subsect. Alpestres	Yunnan province
17	*R. pentagonus*	Sect. Idaeobatus	Subsect. Alpestres	Sichuan province
18	*R. corchorifolius*	Sect. Idaeobatus	Subsect. Corchorifolii	Anhui province
19	*R. chingii*	Sect. Idaeobatus	Subsect. Corchorifolii	Anhui province

No	Species	Section	Subsection	location
20	*R. grayanus*	Sect. Idaeobatus	Subsect. Corchorifolii	Anhui province
21	*R. glabricarpus*	Sect. Idaeobatus	Subsect. Corchorifolii	Fujian province
22	*R. trianthus*	Sect. Idaeobatus	Subsect. Corchorifolii	Henan province
23	*R. idaeus* var. *glabratus*	Sect. Idaeobatus	Subsect. Idaeanthi	Heilongjiang province
24	*R. sachalinensis*	Sect. Idaeobatus	Subsect. Idaeanthi	Heilongjiang province
25	*R. austrotibetanus*	Sect. Idaeobatus	Subsect. Idaeanthi	Xizang autonomous region
26	*R. eucalyptus* var. *trullisatus*	Sect. Idaeobatus	Subsect. Idaeanthi	Sichuan province
27	*R. niveus*	Sect. Idaeobatus	Subsect. Idaeanthi	Xizang autonomous region
28	*R. trijugus*	Sect. Idaeobatus	Subsect. Idaeanthi	Xizang autonomous region
29	*R. eucalyptus* var. *yunnanensis*	Sect. Idaeobatus	Subsect. Idaeanthi	Yunnan province
30	*R. idaeus*	Sect. Idaeobatus	Subsect. Idaeanthi	Hebei province
31	*R. idaeus* var. *borealisinensis*	Sect. Idaeobatus	Subsect. Idaeanthi	Hebei province
32	*R. piluliferus*	Sect. Idaeobatus	Subsect. Idaeanthi	Gansu province
33	*R. irritans*	Sect. Idaeobatus	Subsect. Idaeanthi	Gansu province
34	*R. leucanthus*	Sect. Idaeobatus	Subsect. Leucanthi	Anhui province
35	*R. delavayi*	Sect. Idaeobatus	Subsect. Leucanthi	Yunnan province
36	*R. zhaogoshanensis*	Sect. Idaeobatus	Subsect. Leucanthi	Yunnan province
37	*R. columellaris*	Sect. Idaeobatus	Subsect. Leucanthi	Jiangxi province
38	*R. impressinervius*	Sect. Idaeobatus	Subsect. Leucanthi	Hunan province
39	*R. peltatus*	Sect. Idaeobatus	Subsect. Peltati	Zhejiang province
40	*R. komarovi*	Sect. Idaeobatus	Subsect. Pileati	Jilin province
41	*R. pseudopileatus*	Sect. Idaeobatus	Subsect. Pileati	Sichuan province
42	*R. pileatus*	Sect. Idaeobatus	Subsect. Pileati	Shaanxi province

No	Species	Section	Subsection	location
43	*R. macilentus*	Sect. Idaeobatus	Subsect. Pungentes	Yunnan province
44	*R. pinfaensis*	Sect. Idaeobatus	Subsect. Pungentes	Gansu province
45	*R. pungens*	Sect. Idaeobatus	Subsect. Pungentes	Shaanxi province
46	*R. stans*	Sect. Idaeobatus	Subsect. Pungentes	Sichuan province
47	*R. amabilis* var. *aculeatissimus*	Sect. Idaeobatus	Subsect. Pungentes	Sichuan province
48	*R. coreanus* var. *tomentosus*	Sect. Idaeobatus	Subsect. Pungentes	Anhui province
49	*R. coreanus*	Sect. Idaeobatus	Subsect. Pungentes	Anhui province
50	*R. amabilis*	Sect. Idaeobatus	Subsect. Pungentes	Shaanxi province
51	*R. inopertus*	Sect. Idaeobatus	Subsect. Pungentes	Hunan province
52	*R. tsangii*	Sect. Idaeobatus	Subsect. Rosaefolii	Hunan province
53	*R. eustephanus* var. *glanduliger*	Sect. Idaeobatus	Subsect. Rosaefolii	Sichuan province
54	*R. glandulosocalycinus*	Sect. Idaeobatus	Subsect. Rosaefolii	Taiwan province
55	*R. piptopetalus*	Sect. Idaeobatus	Subsect. Rosaefolii	Taiwan province
56	*R. rosaefolius*	Sect. Idaeobatus	Subsect. Rosaefolii	Anhui province
57	*R. hirsutus*	Sect. Idaeobatus	Subsect. Rosaefolii	Anhui province
58	*R. sumatranus*	Sect. Idaeobatus	Subsect. Rosaefolii	Anhui province
59	*R. glandulosocarpus*	Sect. Idaeobatus	Subsect. Rosaefolii	Guizhou province
60	*R. eustephanus*	Sect. Idaeobatus	Subsect. Rosaefolii	Anhui province
61	*R. erythrocarpus*	Sect. Idaeobatus	Subsect. Stimulantes	Yunnan province
62	*R. kulinganus*	Sect. Idaeobatus	Subsect. Stimulantes	Jiangxi province
63	*R. mesogaeus* var. *oxycomus*	Sect. Idaeobatus	Subsect. Stimulantes	Gansu province
64	*R. ellipticus* var. *obcordatus*	Sect. Idaeobatus	Subsect. Stimulantes	Sichuan province
65	*R. alexeterius* var. *acaenocalyx*	Sect. Idaeobatus	Subsect. Stimulantes	Yunnan province
66	*R. biflorus*	Sect. Idaeobatus	Subsect. Stimulantes	Gansu province

No	Species	Section	Subsection	location
67	*R. parvifolius*	Sect. Idaeobatus	Subsect. Stimulantes	Anhui province/ Hunan province
68	*R. mesogaeus*	Sect. Idaeobatus	Subsect. Stimulantes	Shanxi province
69	*R. subornatus* var. *melanadenus*	Sect. Idaeobatus	Subsect. Stimulantes	Sichuan province
70	*R. ellipticus*	Sect. Idaeobatus	Subsect. Stimulantes	Sichuan province
71	*R. idaeopsis*	Sect. Idaeobatus	Subsect. Thyrsidaei	Guizhou province
72	*R. innominatus* var. *macrosepalus*	Sect. Idaeobatus	Subsect. Thyrsidaei	Zhejiang province
73	*R. innominatus* var. *aralioides*	Sect. Idaeobatus	Subsect. Thyrsidaei	Fujian province
74	*R. chiliadenus*	Sect. Idaeobatus	Subsect. Thyrsidaei	Hunan province
75	*R. flosculosus*	Sect. Idaeobatus	Subsect. Thyrsidaei	Shanxi province
76	*R. grandipaniculatus*	Sect. Idaeobatus	Subsect. Thyrsidaei	Sichuan province
77	*R. cockburnianus*	Sect. Idaeobatus	Subsect. Thyrsidaei	Henan province
78	*R. adenophorus*	Sect. Idaeobatus	Subsect. Thyrsidaei	Fujian province
79	*R. innominatus*	Sect. Idaeobatus	Subsect. Thyrsidaei	Anhui province
80	*R. lasiostylus* var. *hubeiensis*	Sect. Idaeobatus	Subsect. Wushanenses	Hubei province
81	*R. lasiostylus* var. *dizygos*	Sect. Idaeobatus	Subsect. Wushanenses	Sichuan province
82	*R. lasiostylus*	Sect. Idaeobatus	Subsect. Wushanenses	Gansu province
83	*R. poliophyllus*	Sect. Malachobatus	Subsect. Acuminati	Yunnan province
84	*R. lambertianus* var. *paykouangensis*	Sect. Malachobatus	Subsect. Acuminati	Chongqing city
85	*R. laxus*	Sect. Malachobatus	Subsect. Acuminati	Yunnan province
86	*R. lambertianus*	Sect. Malachobatus	Subsect. Acuminati	Anhui province
87	*R. cochinchinensis*	Sect. Malachobatus	Subsect. Cochinchinenses	Hainan province

No	Species	Section	Subsection	location
88	*R. angustibracteatus*	Sect. Malachobatus	Subsect. Dolichophylli	Sichuan province
89	*R. dolichophyllus* var. *pubescens*	Sect. Malachobatus	Subsect. Dolichophylli	Guizhou province
90	*R. parkeri*	Sect. Malachobatus	Subsect. Dolichophylli	Hunan province
91	*R. howii*	Sect. Malachobatus	Subsect. Dolichophylli	Sichuan province
92	*R. ichangensis*	Sect. Malachobatus	Subsect. Dolichophylli	Jiangxi province
93	*R. feddei*	Sect. Malachobatus	Subsect. Elongati	Guizhou province
94	*R. salwinensis*	Sect. Malachobatus	Subsect. Elongati	Yunnan province
95	*R. luchunensis* var. *coriaceus*	Sect. Malachobatus	Subsect. Elongati	Yunnan province
96	*R. fuscorubens*	Sect. Malachobatus	Subsect. Elongati	Chongqing city
97	*R. lobophyllus*	Sect. Malachobatus	Subsect. Elongati	Guangxi province
98	*R. tephrodes*	Sect. Malachobatus	Subsect. Elongati	Anhui province
99	*R. paniculatus*	Sect. Malachobatus	Subsect. Elongati	Yunnan province
100	*R. reflexus* var. *lanceolobus*	Sect. Malachobatus	Subsect. Fuscifolii	Anhui province
101	*R. malipoensis*	Sect. Malachobatus	Subsect. Fuscifolii	Yunnan province
102	*R. reflexus*	Sect. Malachobatus	Subsect. Fuscifolii	Anhui province
103	*R. jambosoides*	Sect. Malachobatus	Subsect. Jambosoides	Guangdong province
104	*R. lineatus* var. *glabrescens*	Sect. Malachobatus	Subsect. Lineati	Yunnan province
105	*R. lineatus* var. *angustifolius*	Sect. Malachobatus	Subsect. Lineati	Yunnan province
106	*R. lineatus*	Sect. Malachobatus	Subsect. Lineati	Yunnan province

No	Species	Section	Subsection	location
107	*R. wardii*	Sect. Malachobatus	Subsect. Metoenses	Yunnan province
108	*R. echinoides*	Sect. Malachobatus	Subsect. Moluccani	Guangxi province
109	*R. nagasawanus*	Sect. Malachobatus	Subsect. Moluccani	Taiwan province
110	*R. lasiotrichos*	Sect. Malachobatus	Subsect. Moluccani	Yunnan province
111	*R. hunanensis*	Sect. Malachobatus	Subsect. Moluccani	Hunan province
112	*R. buergeri*	Sect. Malachobatus	Subsect. Moluccani	Anhui province
113	*R. setchuenensis*	Sect. Malachobatus	Subsect. Moluccani	Hubei province
114	*R. faberi*	Sect. Malachobatus	Subsect. Moluccani	Sichuan province
115	*R. alceaefolius*	Sect. Malachobatus	Subsect. Moluccani	Jiangxi province
116	*R. multibracteatus*	Sect. Malachobatus	Subsect. Moluccani	Anhui province
117	*R. reticulatus*	Sect. Malachobatus	Subsect. Moluccani	Sichuan province
118	*R. pirifolius*	Sect. Malachobatus	Subsect. Pirifolii	Fujian province
119	*R. doyonensis*	Sect. Malachobatus	Subsect. Sozostyli	Yunnan province
120	*R. swinhoei*	Sect. Malachobatus	Subsect. Sozostyli	Anhui province
121	*R. preptanthus*	Sect. Malachobatus	Subsect. Sozostyli	Yunnan province
122	*R. henryi*	Sect. Malachobatus	Subsect. Sozostyli	Hunan province
123	*R. fujianensis*	Sect. Malachobatus	Subsect. Sozostyli	Fujian province
124	*R. irenaeus*	Sect. Malachobatus	Subsect. Stipulosi	Anhui province
125	*R. pacificus*	Sect. Malachobatus	Subsect. Stipulosi	Anhui province

No	Species	Section	Subsection	location
126	*R. fanjingshanensis*			Guizhou province

3.2 Identification of the seeds of the genus Rubus in China

In this study, the seed micromorphology of *Rubus* taxa native to China was first systematically documented. At the micromorphological level, certain morphological features of *Rubus* seeds (such as size, shape, color, etc.) may overlap across taxa, but the surface ornamentation of the seed coat exhibits significant variation among different species (Fig. 1–4).

3.2.1. Seed size

The seed length ranges from 1.23 mm to 6.11 mm, with *R. chamaemorus* having the longest seeds, while *R. howii* has the shortest. Based on length, the seeds can be divided into four categories: Class A: Above 3.5 mm (e.g., *R. pirifolius*, *R. quinquefoliolatus*, *R. chamaemorus*); Class B: 2.5 mm – 3.5 mm (e.g., *R. parkeri*, *R. henryi*, *R. flosculosus*); Class C: 1.5 mm – 2.5 mm (e.g., *R. pacificus*, *R. adenophorus*, *R. piluliferus*); Class D: Below 1.5 mm (e.g., *R. reticulatus*, *R. sumatranus*, *R. ellipticus*).

3.2.2. Seed shape

Most seeds exhibit an elliptical shape (e.g., *R. mesogaeus*, *R. trijugus*), semi-elliptical shape (e.g., *R. tephrodes*, *R. idaeus*), semi-circular shape (e.g., *R. lambertianus*, *R. trianthus*), ovate shape (e.g., *R. feddei*, *R. parkeri*), long-oval shape (e.g., *R. cinclidodictyus*), or shield shape (e.g., *R. impressinervius*, *R. glabricarpus*). A few seeds show a square shape (e.g., *R. ichangensis*), crescent shape (e.g., *R. henryi*, *R. laxus*), long-strip shape (e.g., *R. idaeus* var. *borealisinensis*, *R. multisetosus*), or irregular shape (e.g., *R. retinulatus*).

3.2.3. Surface ornamentation of seeds

The seed coat ornamentation of *Rubus* exhibits specific changes, which seem to have taxonomic significance. The seed coat ornamentation of seeds is reticular or striped, but different species have their own characteristics in terms of the depth of the holes, the composition of the reticular pattern, and the thickness, arrangement, and direction of the stripes. It mainly includes two categories: The first group is seeds with prominent reticulate sculpture (e.g., *R. reflexus*, *R. parvifolius*, *R. flosculosus*). The second group is seeds with less prominent reticulate sculpture (e.g., *R. salwinensis*, *R. cinclidodictyus*, *R. fujianensis*). Among them, the first group can be further divided into two types based on the depth of the holes: deep-hole type (e.g., *R. lobophyllus*, *R. cochinchinensis*) and shallow-hole type (e.g., *R. faberi*, *R. lambertianus*).

4. Identification of Seeds from Archaeological Sites

4. Identification of *Rubus* Seeds from Archaeological Sites

The climate in China has undergone certain changes throughout history, which may have led to subtle differences in the distribution range of *Rubus* plants between ancient and modern times, thereby affecting the identification of seeds excavated from archaeological sites. Therefore, this study evaluated the seed characteristics of *Rubus* taxa distributed in different regions. The results indicated that the seeds selected for this study were representative, covering the morphological variation range of the genus across geographic populations.

Considering that seed size is closely related to the plant's growth environment and may be affected by environmental factors during burial, causing expansion or shrinkage, in this study's identification work, seed morphology and seed coat ornamentation were mainly used as identification criteria, while seed size was only used as a reference. This study collected *Rubus* seed samples from seven archaeological sites (Table 2).

Table 2
Plant Remains Information of *Rubus*

Serial number	Site name	Location	^{14}C Dating	Period	Origin(Grains)	Fruit period
1	Wutongtu Site *	Jiangjing Chongqing	1416 – 1235 cal BC (3190 – 3184 cal BP)	the Shang and Zhou dynasties	*R. coreanus* var. *tomentosus*(1 grains)	Jun. to Aug.
2	Nanshan Site	Shaoxing, Zhejiang	-	the Eastern Zhou Dynasty	*R. lambertianus*(25 grains)	Sep. to Nov.
3	Tianshengcheng Site	Wanzhou, Chongqing	-	the Song Dynasty	*R. flosculosus*(5 grains)/ *R. parvifolius*（17 grains）	Aug. to Sep. / Jul. to Aug.
4	Fanjiayan Site	Hechuan, Chongqing	1222–1286 cal AD(728 – 664 cal BP)	the Southern Song Dynasty	*R. trianthus*(15 grains)/ *R. parvifolius*（15 grains）	May to Jun. / Jul. to Aug.
5	Taipingmen Site	Yuzhong, Chongqing	1165–1265 cal AD (785 – 685 cal BP)	the Southern Song Dynasty	*R. adenophorus*(6 grains)	Jun. to Jul.
6	Drum Tower Yamen Site	Yuzhong, Chongqing	1221–1282 cal AD (729 – 668 cal BP)	the Southern Song Dynasty	*R. trianthus*(20 grains)	May to Jun.
7	Yuanmingyuan site	Haidian, Beijing	-	The Ming and Qing Dynasties / the Modern Times	*R. lambertianus*(1 grains /1 grains)	Sep. to Nov.

4.1. Wutongtu Site

The Wutongtu Site is located on a crescent-shaped platform on the left bank of the Yangtze River in Youxi Town, Jiangjin District, Chongqing City. In this study, one *Rubus* seed was selected from an ash pit dating to the Shang and Zhou dynasties.

Although the seed has been carbonized, the seed coat ornamentation remains clearly visible under microscopy. Observations show that it is elliptical in shape (Fig. 5j), with reticular intersecting ornamentation. Based on these characteristics and comparison with modern specimens, it is identified as *R. coreanus* var. *tomentosus* (Table 2).

4.2. Nanshan Site

The Nanshan Site is located in Yuecheng District, Shaoxing City, Zhejiang Province. In this study, 25 *Rubus* seeds were obtained from the site dating to the Eastern Zhou Dynasty.

The *Rubus* seeds are uncarbonized, with distinct seed coat ornamentation. They are half-moon shaped (Fig. 5g), with bluntly rounded ends, and the seed coat ornamentation branches from the hilum in a tree-branch pattern. Based on these characteristics and correspondence with morphological descriptions of *R. lambertianus* in taxonomic literature, the seeds excavated from the Nanshan Site are inferred to originate from *R. lambertianus* (Table 2).

4.3. Tianshengcheng Site

The Tianshengcheng Site is located in Zhoujiaba Street, Wanzhou District, Chongqing City, adjacent to the confluence of the Zhuxi River and the Yangtze River to the south. It is an important Song and Yuan dynasties mountain city site. In this study, 22 *Rubus* seeds were selected from Southern Song Dynasty water wells.

The seeds are uncarbonized. Based on morphological characteristics, they can be divided into two types: semicircular (Fig. 5c) and oval (Fig. 5d).

Semi-circular type: Seeds are semi-circular, with bluntly rounded ends and a small aspect ratio. The seed coat ornamentation consists of intersecting polygonal meshes with relatively dense reticulation. Identification confirms they belong to *R. flosculosus*.

Oval type: Seeds are oval, with one end sharp and the other bluntly rounded. The seed coat exhibits polygonal intersecting patterns with relatively loose overall reticulation. Identification confirms they belong to *R. parvifolius* (Table 2).

4.4. Fanjiayan Site

The Fanjiayan Site is located on Diaoyu Mountain in the northeastern part of Dongcheng Peninsula, Hechuan District, Chongqing City. As a significant component of the Fishing Town Site, it is a well-preserved relic of governmental establishments from the Song and Yuan Dynasties. In this study, 30 *Rubus* seeds were selected from a Southern Song Dynasty pool (archaeologically identified as a water storage facility).

Notably, the excavated *Rubus* seeds are uncarbonized and exhibit diverse shapes. Based on morphology, they can be categorized into two types: oval (Fig. 5a) and semi-oval (Fig. 5b).

Oval type: Seeds are oval, with one end pointed and the other bluntly rounded. The seed coat exhibits intersecting polygonal patterns with relatively sparse reticulation, consistent with the seed characteristics of *R. parvifolius*.

Semi-oval type: Seeds are semi-oval, with one end slightly protruding and the other bluntly rounded, showing a large aspect ratio. The seed coat ornamentation features branching patterns originating from the hilum, with overall sparse reticulation, matching the seed characteristics of *R. trianthus* (Table 2).

4.5. Taipingmen Site

The Taipingmen Site is located on Wanglongmen Street, Yuzhong District, Chongqing City. Situated on the first river terrace of the left bank of the Yangtze River in the Yuzhong Peninsula, it is one of the important city gates of Chongqing. In this study, six *Rubus* seeds were selected from Southern Song Dynasty drainage ditches of the city walls.

The seeds are uncarbonized, semi-oval with slightly blunt ends. The seed coat ornamentation is indistinct, faintly appearing as an irregular cross pattern (Fig. 5f). Based on these characteristics and comparison with R. adenophorus specimens in collections, the excavated *Rubus* seeds are inferred to derive from R. adenophorus (Table 2).

4.6. Drum Tower Yashu Site

The Drum Tower Yashu Site is located in Wanglongmen Street, Yuzhong District, Chongqing City. Situated on a terrace at the foot of Jinbi Mountain and the left bank of the Yangtze River, it served as the administrative center of Sichuan and Chongqing Prefecture during the Southern Song Dynasty. In this study, 20 *Rubus* seeds were selected from Southern Song Dynasty ponds.

The seeds are uncarbonized, semi-oval with one end slightly protruding and the other blunt and round, and have a large aspect ratio. The seed coat ornamentation features a network-like, cross-shaped pattern with relatively loose overall reticulation. Based on these characteristics and comparison with specimens of R. trianthus, they are identified as originating from R. trianthus (Table 2).

4.7. Yuanmingyuan Site

The Yuanmingyuan Site is located in Haidian District, Beijing City. One *Rubus* seed was excavated from each of the Ming and Qing Dynastic relics (Fig. 5h) and modern deposits (Fig. 5i).

The seeds are uncarbonized, all crescent-shaped with bluntly rounded ends. The seed coat ornamentation branches from the hilum in a tree-branch pattern, with ornamentation lines approximately parallel. Based on morphological consistency across historical and modern specimens, the *Rubus* seeds excavated from both periods at this site are identified as *R. lambertianus* (Table 2).

5. Discussion

5.1. Application of This Identification Methodology to Rubus Seed Remains from Other Archaeological Sites in China

This study preliminarily demonstrates that the established identification method is effective for identifying seeds of the genus *Rubus* excavated from archaeological contexts, based on the collection and analysis of a large dataset of modern Rubus seed samples. However, the archaeological *Rubus* seed assemblages discussed above are predominantly from Chongqing, Zhejiang, and Beijing. To further validate the universality of this methodology, we applied it to the re-identification of Rubus seed remains excavated from additional archaeological sites across China, spanning diverse geographical regions and chronological periods (Table 3).

Table 3
Re-identification of *Rubus* seed remains in reported archaeological sites.

No	Site	Location	Grains	re-identification Result	references
1	Bashidang Site	Changde, Hunan	-	*R. parvifolius*	1
2	Yuchisi Site	Bozhou, Anhui	2	*R. parvifolius*	11,13
3	Liangzhu Ancient City Site	Hangzhou, Zhejiang	24	*R. parvifolius*	21
4	Chengtoushan Site[&]	Changde, Hunan	-	*R. parvifolius*	1
5	Guangfulin Site	Shanghai	81	*R. hirsutus*	14
6	Daxinzhuang Site*	Jinan, Shandong	18	*R. parvifolius*	18
7	Changdun Han Tomb Cemetery	Nanchang, Jiangxi	11	*R. rosifolius*	16
8	Nanyue Palace Site: J264 Water Well	Guangzhou, Guangdong	15000	*R. rosifolius*	20,13
9	Nanyue Palace Garden: Nanhan Kingdom Palace Pool Site	Guangzhou, Guangdong	1	*R. rosifolius*	12,13

*Carbonized; [&]Identification error

Through identification, *Rubus* seeds excavated from the Bashidang Site, Yuchisi Site, Liangzhu Ancient City Site, Chengtoushan Site, and Daxinzhuang Site all exhibit a pointed-obtuse shape. The seed coat ornamentation consists of polygonal intersections with an overall loose pattern. These seeds are uniformly identified as *R. parvifolius*. Notably, the previously reported identification of *Rubus* seeds from the Chengtoushan Site as *R. lambertianus* is revised herein. This study clarifies that *R. lambertianus* seeds are distinctively characterized by bluntly rounded ends and forked, hilum-branching ornamentation, whereas the Chengtoushan seeds display reticulate interwoven ornamentation, consistent with *R. parvifolius* rather than *R. lambertianus*. Therefore, this study posits that the provenance of the *Rubus* seeds excavated from the Chengtoushan Site should be *R. parvifolius* rather than *R. lambertianus*.

The *Rubus* seeds excavated from the Guangfulin Site exhibit a semicircular shape with seed coat ornamentation featuring reticulate intersections in a hexagonal pattern, consistent with the seed morphology of *R. hirsutus*. Based on these diagnostic traits—specifically the semicircular outline and dense hexagonal reticulation distinct from other sympatric species (e.g., *R. parvifolius* with looser polygonal patterns)—these seeds are taxonomically identified as *R. hirsutus*.

The *Rubus* seeds excavated from the Changdun Han Tomb Cemetery, Nanyue Palace Site (Well J264), and Nanyue Palace Garden (Palace Pool Site of the Southern Han Kingdom) exhibit a relatively high length-to-width ratio with bluntly rounded ends. Their seed coat ornamentation features densely interwoven reticulate patterns, diagnostic of *R. rosifolius*. These morphological traits—specifically the elongated oval shape and anastomosing reticulation distinct from other congeners (e.g., *R. lambertianus* with bifurcating hilum patterns)—consistently align with the seed characteristics of *R. rosifolius*.

The above identification results fully demonstrate that the identification method established in this study can be effectively applied to the identification of *Rubus* seed remains in Chinese archaeological sites (Table 3).

5.2 Established an illustrated guide to the seeds of common Rubus plants in China

Stereoscopic microscopy and scanning electron microscopy (SEM) have revealed many important seed characteristics, which contribute to resolving taxonomic problems in botanical origin identification[41,42]. This article is the first to use a stereomicroscope to study the microscopic morphological characteristics of seeds in Chinese plants of the genus *Rubus* and systematically describes the microscopic morphological characteristics of many taxonomic groups. In recent years, the use of stereomicroscopes as a means of studying microstructural changes in plants has gained advantages in plant systems[43–45], with observed data achieving high precision and being irreplaceable by other techniques. At different classification levels, there are significant differences in the seed micromorphology of the genus *Rubus* in terms of different traits such as seed size, shape, and seed coat ornamentation. The micromorphological characteristics of seeds are key features for plant species identification and classification, reflecting the genetic, physiological, and ecological characteristics of plants.

This paper uses stereomicroscopy to study the micromorphological characteristics of the seeds of *Rubus* plants in China and systematically describes the micromorphological characteristics of many taxonomic groups for the first time. In recent years, the use of stereomicroscopy as a means to study plant micromorphological changes has gained an advantage in plant systems[43–45]. Stereomicroscopic observations yield highly precise data and cannot be replaced by other technologies. At different taxonomic levels, there are significant differences in the seed micromorphology of the genus *Rubus* in different traits (such as seed size, shape, and seed coat ornamentation). Seed micromorphological characteristics are key features for plant species identification and classification, reflecting the genetic, physiological, and ecological characteristics of plants.

The micromorphological characteristics of seeds can provide useful information for the species classification of this genus. For example, although *R. ichangensis* and *R. angustibraceteatus* are very similar in plant morphological characteristics, their seed morphological features are completely different. However, many species assigned to different sections or subsections with distantly related macromorphological relationships exhibit similar seed morphological characteristics, such as *R. multibraceteatus* and *R. mesogeaus*, *R. fuscorubens* and *R. parkeri*. In other words, apart from the seed coat ornamentation, no section (except Sect. Ghamaemorus) or subsection (except Subsect. Pirifolii) exhibits unique seed morphology, and species of different subgenera or families have similar seed morphology (such as size, shape, color, etc.). Whether seed coat ornamentation can be used for intrageneric classification depends on the degree of variation between species[46]. Although this study observed the seed morphology of common plants in the Chinese *Rubus* genus, which covers almost all sections and subsections of the genus, it remains difficult to identify the evolutionary patterns of seed size, shape, and seed coat ornamentation, as well as their correlations with macromorphological characteristics.

The accurate identification of plant seed remains requires the support of a large number of modern seed specimens. Based on this, this study constructed the first seed morphology atlas of the genus *Rubus* in China according to key characteristics such as seed shape and seed coat ornamentation and applied it to the identification of seed remains in archaeological sites. Through the method of comparing ancient and modern specimens, this study provides an important reference for the identification of *Rubus* seeds unearthed from sites.

5.3 The Uses of Ancient Rubus Plants

In this study, some *Rubus* seed remains were unearthed from water pool remains at archaeological sites[12,13]. Meanwhile, in some sites, *Rubus* seeds were unearthed with abundant crop and fruit remains. Based on these comprehensive archaeological findings, it is inferred that the fruits or seeds of *Rubus* at the sites were intentionally collected and preserved[16,18]. Additionally, identification shows that the fruits of the original plants corresponding to *Rubus* seeds from archaeological sites are all red (Table 2), with a sweet and sour taste. Based on this, it can be inferred that the fruit of the original seed plant of the genus *Rubus* is highly likely to have been an important component of the ancient ancestors' plant-based diet.

The *Rubus* genus is a widely distributed plant and grows in mountainous areas, hills, and wasteland hillsides in most parts of southern and central China. The fruiting period of *Rubus* plants varies from May to November, making them common wild fruits. Its fruits are plump and juicy and taste delicious. It is highly probable that ancient people would pick and eat ripe *Rubus* fruits during their outdoor activities. Additionally, from the perspective of traditional medicine, some fruits of the *Rubus* genus have medicinal values and are rich in nutrients[47,48].

Numerous studies have shown that *Rubus* seed remains are prevalent in Chinese archaeological sites[12–22]. In some sites, a large number of seeds were unearthed; this is possibly because each *Rubus* fruit contains numerous seeds. This quantitative advantage naturally increases the probability of *Rubus* seeds being discarded in archaeological deposits, resulting in their general dominance in absolute numbers among unearthed seeds[13,20].

In addition, the seeds of plants in the genus *Rubus* are relatively small in size. When consuming the fruits, ancient people generally did not deliberately spit out the seeds, which were excreted through bodily waste. In natural environments, these seeds might be wrapped in other excrement; this process reduces erosion from the external environment and thus enables relatively complete preservation in archaeological sites. It is worth noting that plants of the genus *Rubus* also have the possibility of being cultivated as ornamental plants[20]. The abundant and well-preserved *Rubus* seed remains in some sites may be linked to special burial contexts or specific functions. Nevertheless, clarifying their specific roles demands more archaeological evidence and targeted research.

6. Conclusions

In this study, 126 mature seeds from wild *Rubus* populations across various regions of China were collected for systematic seed morphology analysis, leading to the construction of the first morphological atlas of seeds for common Chinese *Rubus* species. Through the analysis of *Rubus* seed remains from 7 unreported sites and 9 reported sites, the taxonomic identity of seeds was accurately identified.

This study employed modern plant seed morphology research methods to link modern samples to archaeological samples, thereby providing new ideas and methods for plant archaeology research. As seed identification of *Rubus* from more sites progresses and research deepens, this study is expected to further reveal the edible history and species of *Rubus* fruits, provide important historical background information for exploring the distribution shifts and utilization patterns of *Rubus* plants, and offer strong archaeological evidence for studying the biodiversity evolution of *Rubus*.

Declarations

Conflicts of Interest:

The authors declare no conflicts of interest.

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Author Contribution

A. R.: Writing-original draft, Writing-review and editing, Investigation; X. M.: Writing-original draft, Writing-review and editing, Investigation;; X. X.: Resources, Data curation; M. Y.: Writing-original draft, Writing-review and editing, Methodology, Investigation, Funding acquisition; H. J.: Writing-review and editing, Conceptualization, Project administration, Funding acquisition. All authors have read and agreed to the published version of the manuscript.

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Data Availability

Data are contained within the article. Further information can be obtained by contacting the corresponding author.

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Figures

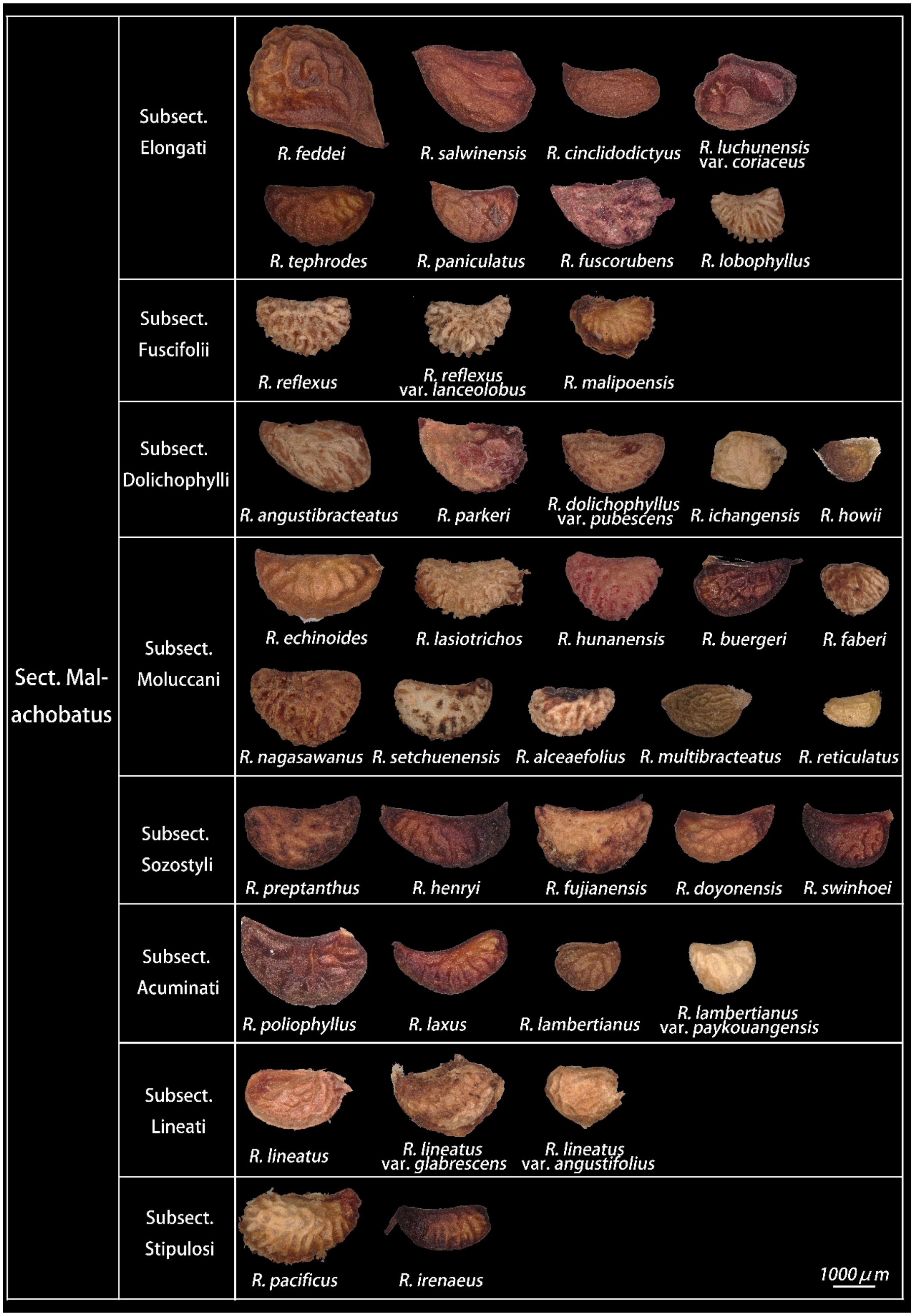

Figure 1

Comparison of Seed Morphology in the *Rubus* L. (I)

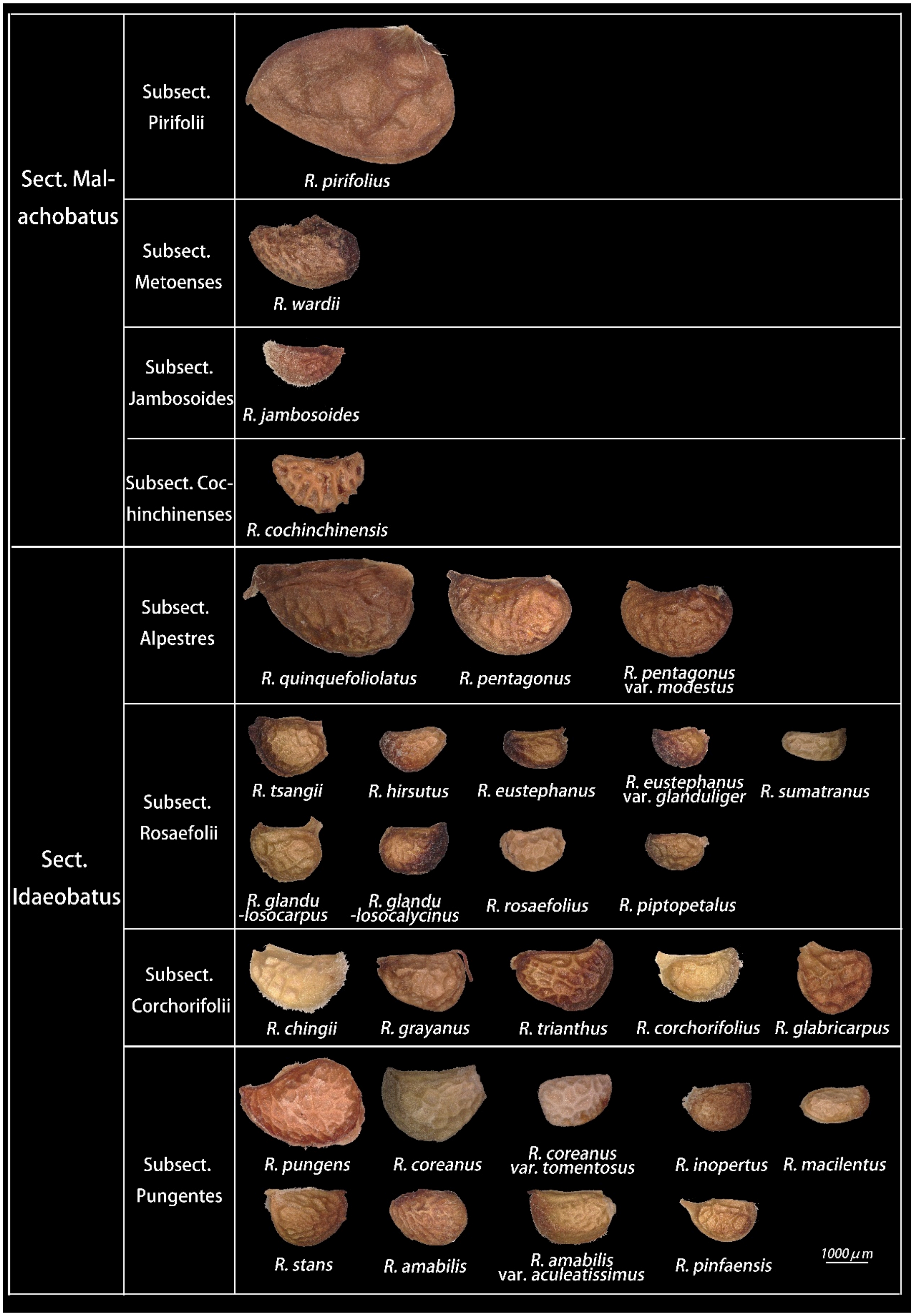

Figure 2

Comparison of Seed Morphology in the *Rubus* L. (II)

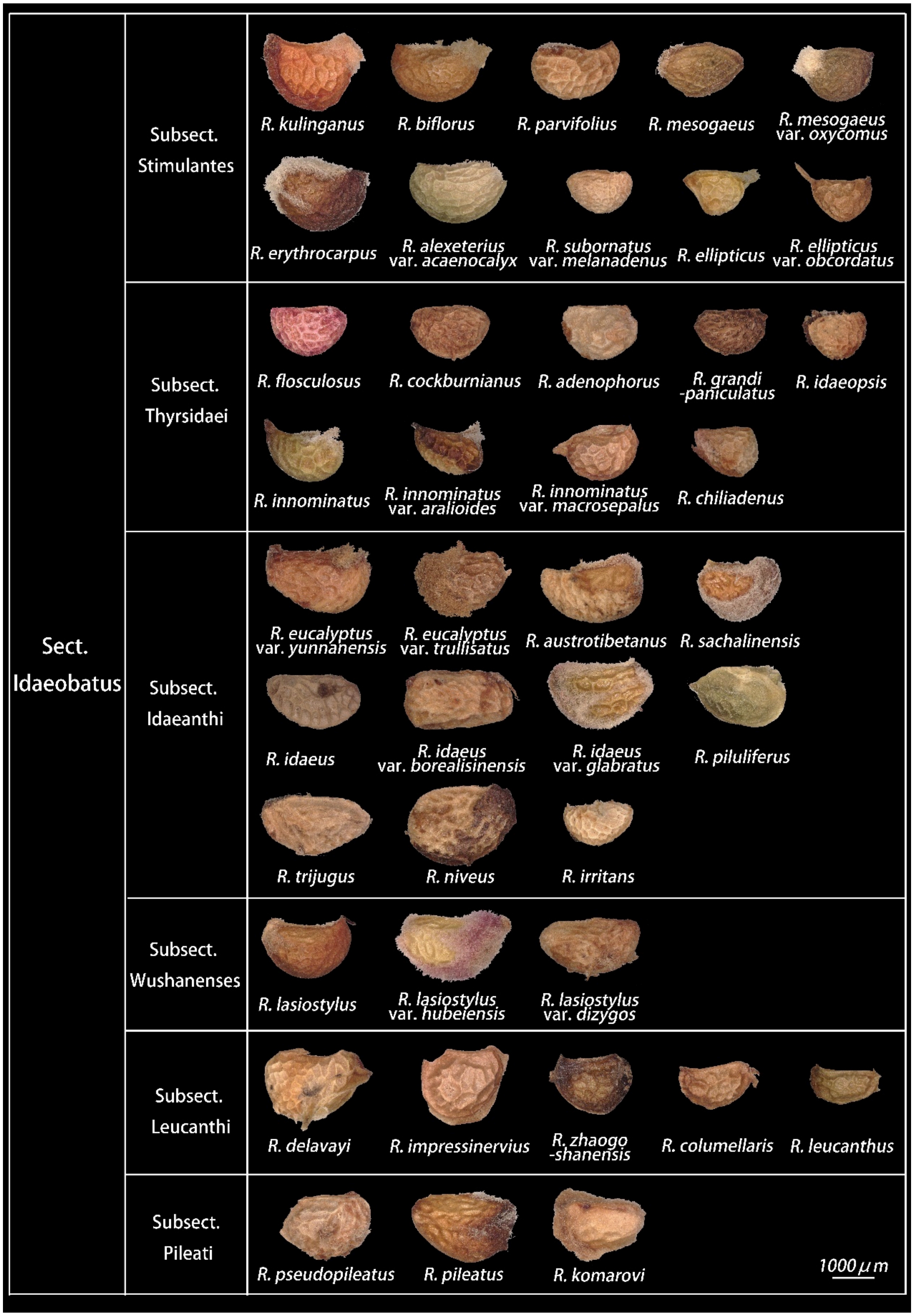

Figure 3

Comparison of Seed Morphology in the *Rubus* L. (III)

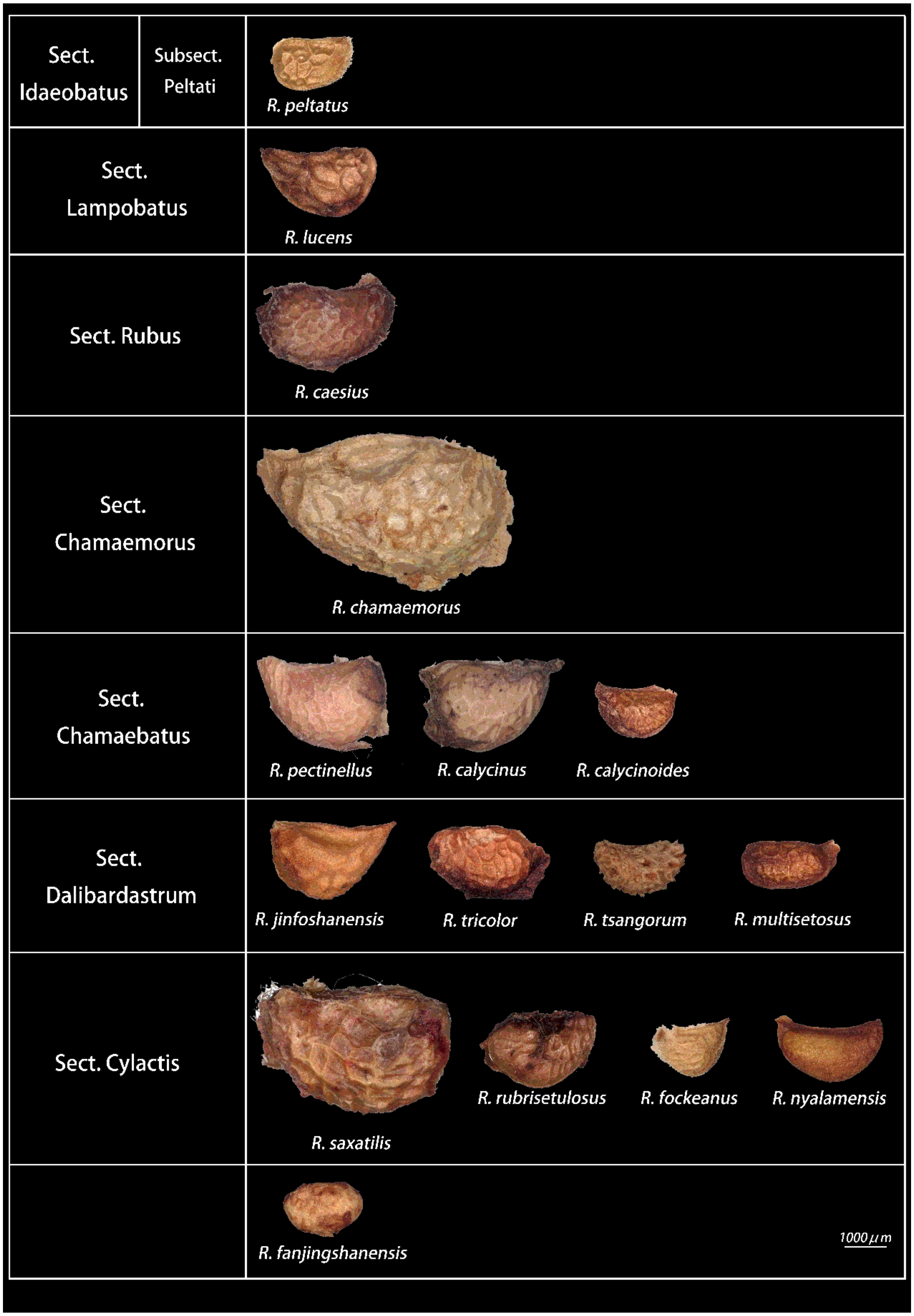

Figure 4

Comparison of Seed Morphology in the *Rubus* L. (IV)

Figure 5

Seeds of the genus *Rubus* excavated from archaeological sites (a, b: Fanjiayan site; c: Drum Tower Yashu Site; d. E: Tianshengcheng Site; f: Taipingmen Site; g: Nanshan Site; h, I: Yuanmingyuan Ruins; j: Wutongtu Site)

Note: a, d, g; b, c, e, f; h, I, j: each has a consistent scale.