Fossil Fruits of *Ceratophyllum* from the Upper Eocene and Miocene of South China

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Simple Summary: Two fruit fossil species of *Ceratophyllum* L. are discovered from South China, namely *C*. cf. *muricatum* Chamisso from the upper Eocene of the Maoming Basin, Guangdong, and *C. demersum* L. from the Miocene of the Guiping Basin, Guangxi. Our findings provide evidence for the distribution of *Ceratophyllum* in South China in the late Eocene, and its wide expansion in subtropical China during the Miocene.

Abstract: *Ceratophyllum* L. is a cosmopolitan genus of perennial aquatic herbs that occur in quiet freshwaters. Fossils of this genus have been widely reported from the Northern Hemisphere, most of them occurring in the temperate zone. Here, we describe two species of fossil fruits discovered from subtropical areas of China. The fossil fruit discovered from the upper Eocene Huangniuling Formation of the Maoming Basin is designated as *C*. cf. *muricatum* Chamisso, and fruits discovered from the Miocene Erzitang Formation of the Guiping Basin are assigned to the extant species *C. demersum* L. The discovery of these two fossil species indicates that *Ceratophyllum* had spread to South China by the late Eocene and their distribution expanded in subtropical China during the Miocene.

Keywords: *Ceratophyllum*; Eocene; Miocene; fruit fossil; palaeophytogeography; South China

1. Introduction

*Ceratophyllaceae* Gray is a family of submersed, hydrophilous, perennial, and herba-

ceous plants. It consists of only one cosmopolitan genus, *Ceratophyllum* L., and about six

extant species [1]. *Ceratophyllaceae* is a sister group of the eudicots [2]. The infrageneric
taxonomy of *Ceratophyllum* is largely based on fruit characters. It is generally divided into
three sections, with two species in each section. Sect. *Ceratophyllum* has fruits with three
to five long spines, sect. *Muricatum* has fruits with spiny and sometimes winged margins
with stylar and basal spines and sect. *Submersum* has fruits with a spiny margin without
stylar and basal spines [3,4].

*Ceratophyllaceae* is estimated to have diverged from the rest of the eudicots in the
Early Cretaceous based on a time-calibrated global angiosperm phylogeny [5]. The earliest
fruit fossil convincingly assigned to *Ceratophyllum* was reported from the Upper Creta-
ceous of Mexico, namely *C*. *lesii* Estrada-Ruiz, Calvillo-Canadell et Cevallos-Ferriz [6].
*Ceratophyllum* has only one fossil record from the Paleocene: *C*. *furcatispinum* Herendeen,
Les et Dilcher from Fort Union Formation, Montana, USA [7]. *Ceratophyllum* fossils have
been recorded from the Eocene of North America and China, which are assigned to
*C. muricatum* subsp. *incertum* (Berry) Herendeen, Les et Dilcher, and *C. aff. muricatum*
Cham. [7,8]. Oligocene to Pleistocene fossil fruits are relatively abundant and widely dis-
tributed in the Northern Hemisphere, including North America, Europe, and Asia [9–17].
In this paper, two species of *Ceratophyllum* fruit fossils are described from the late Eocene and Miocene strata of South China. The new fossil occurrences provide important insights into the palaeophytogeography of this genus.

2. Materials and Methods

The fossil specimens investigated here were collected from two localities within South China (Figure 1). One specimen was collected from the upper part of the Huangniuling Formation (21°42′33.2″ N, 110°53′19.4″ E) of the Maoming Basin, Guangdong. This formation is composed mainly of gray, yellow to white sandstones, siltstones, and conglomerates [18]. The age of Huangniuling Formation is late Eocene according to palaeomagnetic data [19] and pollen assemblages [20]. Other fruit specimens were collected from the Erzitang Formation (23°23′09.67″ N, 110°09′55.21″ E) of the Guiping Basin, Guangxi. The Erzitang Formation is mainly composed of greyish yellow and red mudstone. The geological age of this formation is Miocene based on the mammal fossil *Prolipotes yujiangensis* Zhou, Zhou et Zhao [21,22].

Specimens were photographed and measured using a Sony Alpha 6400 Camera and a Nikon SMZ25 stereo microscope. The pericarp of the fossil fruit was examined using a JSM–6330F scanning electron microscope. The terminology for *Ceratophyllum* fruit description follows that used in the monograph of Les [3]. All fossils described here are deposited in the Museum of Biology, Sun Yat-sen University, Guangzhou.

![Figure 1.](image-url) The geographic location, and stratigraphic sections of two fossil sites, one in the Maoming Basin and one in the Guiping Basin, South China. (A) Geographical location map of the Maoming and Guiping basins. (B) Field photo of lithological characteristics of the Huangniuling Formation, Maoming, the blue arrow indicates the fossil layer. (C) Stratigraphic column of the outcrop section in B, the upper part of Huangniuling Formation (modified from Herman et al. [23]). (D) Field photo of lithological characteristics of the Erzitang Formation from Guiping, the blue arrow indicates the fossil layer. (E) Stratigraphic column of the outcrop section in D (modified from Huang et al. [24]).

3. Results

3.1. *Ceratophyllum cf. muricatum* Chamisso

Family: Ceratophyllaceae Gray  
Genus: *Ceratophyllum* L.  
Section: *Muricatum* Les  
Species: *Ceratophyllum cf. muricatum* Chamisso
Parmotrema reniforme has only 2 lateral spines, while those reported fossils have at least five lateral spines [7,8,14]. Despite minor intraspecific variation, there is very small amount of evolutionary change in C. muricatum Chamisso from the Maoming Basin. C. muricatum has three subspecies, among which, fruits of C. muricatum subsp. australe (Grisebach) Les and subsp. muricatum Cham. have more lateral spines compared with those of subsp. kossinskyyi (Kuzen.) Les [4]. Our fossil fruit can be easily distinguished from previously reported fossil species assigned to sect. Muricatum based on the number of lateral spines: our fossil fruit has only two lateral spines, while those reported fossil species have at least five lateral spines [7,8,14]. Despite minor intraspecific variation, there is very small amount of evolutionary change in Ceratophyllum [28]. Therefore, we prefer to assign the fossil to Ceratophyllum cf. muricatum Chamisso.

Figure 2. Fossil and reconstruction image of Ceratophyllum cf. muricatum Chamisso from the Maoming Basin. (A) Fossil fruit of C. cf. muricatum with five prominent spines, red arrow shows marginal wing, the dotted line shows the position of seed, MMJ3–2907. (B) Enlargement of A, the middle part of the fruit exhibits a granular surface texture. (C) Fossil reconstruction, red arrow shows marginal wing. Scale Bars = 1 mm.
Table 1. Morphological comparison of two fruit fossils Ceratophyllum cf. muricatum Chamisso and C. demersum L. with other Ceratophyllum fruit fossils.

| Species                          | Achene Shape          | Length (mm) | Width (mm) | L/W Ratio | Surfaces Ornament          | Length of Stylar Spine (mm) | Length of Basal Spine (mm) | Facial Spines | Marginal Wing | Lateral Spines | Occurrence | Age          | References |
|----------------------------------|-----------------------|-------------|------------|-----------|-----------------------------|-----------------------------|----------------------------|---------------|--------------|----------------|------------|--------------|------------|
| Ceratophyllum cf. muricatum      | elliptic to suborbicular | 3.6         | 3.2        | 1.1       | granular                   | 0.9                         | 2.7-3.8                   | -             | +            | 2              | Guangdong, China | late Eocene | This paper   |
| C. demersum                      | ovate                 | 3.42-4.68   | 2.09-2.80  | 1.48-1.79 | tuberculate, with striated grooves | 0.22-2.79                   | 0.15-1.35                 | -             | -            | -              | Guangxi, China | Miocene     | This paper   |
| C. lesii                         | elliptical            | 2.1         | 1          | 2.1       | smooth                     | incomplete                  | 4.2                       | -             | +            | -              | Northern Mexico | Late Cretaceous | [6]        |
| C. furcatispinum                 | /                     | 4.8         | 1.8        | 2.7       | /                          | 2.3                        | -                         | +            | 9-10         | -              | Montana, USA, Tennessee, USA | Paleocene | [7]        |
| C. maritimum subspecies incertum | elliptical            | 3.4         | 2.2        | 1.65      | smooth                     | 1.8                        | 3.3                       | -             | -            | 8-11          | Tibet, China | Eocene       | [7]        |
| C. aff. maritimum                | ellipsoidal           | 3           | 2.2        | 1.4       | smooth                     | 1.5                        | /                         | -             | -            | -              | Tibet, China | Middle Eocene | [8]        |
| C. zaianicum                     | elliptic              | 4.0         | 2.7        | 1.48      | finely rugose              | /                          | /                         | -             | -            | 9-19          | Kazakhstan | Oligocene | [11]        |
| C. tenuicarpum                   | oblong                | /           | /          | /         | /                          | /                          | /                         | narrow        | +            |                | Siberia, Russia | Oligocene | [11]        |
| C. submersum                     | elliptic              | 2.7-3.5     | 1.7-2.6    | 1.44      | smooth, rarely rugose       | /                          | /                         | -             | -            | -              | Russia; Odessa | Oligocene | -Paleocene |
| C. echinatum                     | elliptical            | 5.0         | 3.6        | 1.6       | not sure                   | 4.1                        | 3.1                       | +            | 10-11        |                | Nevada, USA | Miocene | [7]        |
| C. spinulosum                    | wide-elliptic         | /           | /          | /         | /                          | /                          | /                         | -             | wide         |                | Siberia, Russia | Miocene | [11]        |
| C. miocenicum                    | obovate               | 2.0-2.1     | 1.8-1.9    | 1.11      | smooth or slightly rugose   | -                          | -                         | narrow        | toothed      | -              | Russia; Odessa | Miocene | [11]        |
| C. tanaciticum                   | elliptic              | /           | /          | /         | /                          | /                          | /                         | -             | -            | -              | Ukraine; Odessa | Miocene | [11]        |
| C. pannonicum                    | elliptic              | 3.0-3.8     | 2.0-2.7    | 1.45      | finely rugose              | +                          | /                         | -             | 10-18        |                | Ukraine | Miocene | [11]        |
| C. pannonicum                    | /                     | 3 (without stylus) | 2.3       | 1.3       | tuberculate                | /                          | /                         | +             | 4-5          |                | Klettwitz, Germany | Middle | Miocene | [12]        |
| C. sinjanum                      | /                     | 6-8         | 2.5-3      | /         | /                          | /                          | /                         | /             | /            |                | Sinj, Croatia | Miocene | [29]        |
| C. demersum                      | ovate to elliptical   | 3.9 ± 0.3   | 2.9 ± 0.5  | 1.3       | papillae or are smooth      | 5.9                        | 5.2                       | -             | -            | -              | Yunnan, China | Late Miocene | [17]        |
| C. demersum                      | elliptic              | 3.6-4.1     | 2.1-2.8    | 1.6       | rugose                     | +                          | +                         | -             | -            | -              | Siberia, Russia, Voronezh, Rostov, Russia | Miocene, Plioocene | [11]        |
| C. tenuicarpum                   | oblong oval           | 3.1-4.9     | 1.6-2.5    | /         | /                          | /                          | /                         | -             | /            | wide, irregular margin + | Siberia, Russia, Voronezh Region | Plioocene | [11]        |
| C. protanaticum                  | oblong                | /           | /          | /         | /                          | /                          | /                         | -             | -            | -              | Russia Bashkortostan, Russia | Plioocene | [11]        |
| C. platyaanthum                  | oblong                | /           | /          | /         | /                          | /                          | /                         | +             | +            |                |                    |              |             |

/: No description; (+): present; (−): absent.
3.2. *Ceratophyllum demersum* L.

Family: Ceratophyllaceae Gray
Genus: *Ceratophyllum* L.
Section: *Ceratophyllum* L.
Species: *Ceratophyllum demersum* L.
Specimens: GP427–GP456
Locality: Guiping Basin, Guangxi, South China
Geological horizon and age: Erzitang Formation, Miocene

Description: The fruit bodies (excluding spines) are ovate, slightly broad at the apex, 3.42–4.68 mm long and 2.09–2.80 mm wide (Figure 3A,B), with a length/width ratio of 1.48–1.79. The surfaces of the fruit bodies are tuberculate, with striated grooves near the edge (Figure 3A,E,G,I,J). The achenes have an apical stylar spine and a pair of basal spines (Figure 3A). The largest stylar spine is 2.79 mm in length and 0.33 mm in width (Figure 3K). The length of stylar spines ranges from 0.22 to 2.79 mm, with a mean of 0.76 mm. The length of basal spines ranges from 0.15–1.35 mm, with a mean of 0.59 mm. Cotyledons are observed when the fruits are longitudinally split into two halves (Figure 3D,F,H). Two symmetrical holes are present on the base, which represent the pedicel connection (Figure 3C). There is a small projecting part at the base (Figure 3G,L).

The outer surface of the fruit exocarp consists of irregular polygonal cells with lengths of 10–25 µm (Figure 4A,B,E), with some of the cells having parallel partitions (Figure 4C,D). The inner surface of the endocarp is composed mainly of rectangular cells, about 20 µm × 40 µm in size (Figure 4F).

Remarks: Our fossils have three spines, two basal spines, and one stylar spine. The fruits have a rough surface and no marginal wings. These characteristics are consistent with the fruit features of sect. *Ceratophyllum* (fruits with three to five spines but no winged margins). Sect. *Ceratophyllum* includes two species: *C. platyacanthum* Chamisso and *C. demersum* L. The fruit of *C. platyacanthum* has five spines, which include two distinctive facial spines. Our three-spined fruit fossils can be distinguished from this species. In comparison, the fruit of *C. demersum* is 3.5–6 × 2–4 mm in size, with two basal spines and one stylar spine, lacks a marginal wing, and its facial spines are absent.

By carefully comparing the shape, size, and spines of our specimens and the fruit characters of the extant species *C. demersum*, we cannot discern any significant morphological differences between them. Additionally, the morphological data of our fossil materials is close to other fossils designated as *C. demersum* [11,17] (Table 1). So, these fossil fruits are assigned to *C. demersum* L.
Figure 3. Fruit fossils of *Ceratophyllum demersum* L. from the Guiping Basin. (A–C) GP427. The blue arrow shows striated grooves near the edge, yellow arrows show holes at the base. (D) GP428a. Inner view of fruit, the red arrow shows the trace of a cotyledon. (E,F) GP428b. The blue arrow indicates the grooves on the surface, the red arrow shows the trace of a cotyledon. (G) GP429a Fruit outer surface, showing the location of spines. (H) GP429b. Inner view of fruit, red arrows indicate cotyledon traces. (I) GP430. Fruit with a stylar spine. (J) GP432. Fruit with an irregular tuberculate surface. (K) GP436. Lateral view of the fruit, showing a long stylar spine. (L) GP439. Lateral view of the dehiscent fruit. Scale Bars = 0.5 mm.
The discovery of this fossil indicates that C. demersum was widely distributed in the subtropical region at that time. This work was supported by the National Natural Science Foundation of China (Nos. 41820104002, 41820104003, 41421001). The production of the article was funded by the Key Laboratory of Palaeobiology and Paleoceanography of the Ministry of Education of China, the State Key Laboratory of Palaeobiology and Paleoceanography, and the Natural Science Foundation of China (41972144).

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4. Discussion

Species of the genus Ceratophyllum are known to be highly tolerant of a wide range of temperature and salinity values, leading to their broad distribution (Figure 5). The aquatic environment in which representatives of this genus live provides relatively buffered conditions minimizing pressure on its evolution and distribution [30].

Figure 4. Scanning electron microscopic image of the pericarp of Ceratophyllum demersum L., GP440. (A–D) The outer surface of the exocarp with polygonal cells, red arrows show the parallel partitions. (E) Lateral view, showing the fiber structure of the pericarp. (F) The inner surface of the endocarp with rectangular cells. Scale Bars = 20 μm (A, B), 10 μm (C, D), 100 μm (E, F).

Figure 5. Geological distribution map of Ceratophyllum modern species, and fossil records.

Fossils of Ceratophyllum have been widely reported from the Northern Hemisphere (Figure 5). The earliest fossil C. lesii was found from the Upper Cretaceous of Mexico [6] and is similar to the modern species C. demersum. An extinct genus Donlesia Dilcher et Wang with affinities to Ceratophyllaceae was reported from the Lower Cretaceous of Kansas, USA [7].
USA [31,32]. Based on these findings, it is considered that Ceratophyllaceae may have originated in North and Central America during the Cretaceous, in accordance with the divergence time of Ceratophyllaceae from the rest of the eudicots based on a time-calibrated global angiosperm phylogeny [5].

The earliest Ceratophyllum fossil of sect. Muricatum was discovered from the Paleocene in the Fort Union Formation in the United States, designated as C. furcatispinum [7]. Later, C. muricatum subsp. incertum was discovered from the lower and middle Eocene in North America [7], and C. aff. muricatum from the middle Eocene of China [8]. The two species share a great number of morphological similarities. The discovery of fossils of Ceratophyllum in China suggests a floristic exchange between Asia and North America during the Eocene [8]. Our discovery of C. cf. muricatum from the upper Eocene of Maoming Basin provides further evidence supporting this supposition, which also suggests that Ceratophyllum was distributed in the subtropical region at that time.

Ceratophyllum fossils have also been reported from Asia in the Oligocene, such as C. zaisanicum Avakov from the Zaysan Basin of Kazakhstan [33], C. submersum L., and C. tenuicarpum Dorof. from Siberia, Russia [10,11]. The distribution area of this genus expanded during the Miocene, and Ceratophyllum fossils have been widely reported in Asia and Europe [11,12,16,17], such as the fruit fossils C. miocenicum Dorof. and C. pannonicum Dorof. from the Orlova and Lgov, Russia, respectively [11], and C. lusaticum Mai from Leipzig, Germany [12]. From the middle Miocene Shanwang Formation of eastern China, stems and fruits referred to Ceratophyllum have been reported [9,14]. The discovery of Miocene fruit fossils of C. demersum from the Erzitang Formation of the Guiping Basin, Guangxi, together with the discovery of the same species from the upper Miocene of Huangning County, Yunnan, Southwest China [17], suggest that C. demersum was widely distributed in subtropical China in the Miocene.

5. Conclusions

Two fruit fossil species of Ceratophyllum are reported from low latitude of Asia in this paper. By morphological comparison with modern and fossil species, fruit fossil found from the upper Eocene Huangniuling Formation of the Maoming Basin, Guangdong, is assigned to C. cf. muricatum Chamisso. The discovery of this fossil indicates that Ceratophyllum has been distributed in South China by the late Eocene. Fossils discovered from the Miocene Erzitang Formation of the Guiping Basin, Guangxi, are designated to the extant species C. demersum L. The emergence of these fossils, together with the discovery of the same species from the upper Miocene of Yunnan, confirms the wide distribution of this genus in the subtropical China during the Miocene.

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