A REVIEW OF JAPANESE-NATIVE CARNIVOROUS PLANTS

TAKAAKI KAGAWA • Tokyo • Japan • takaakikagawa036@gmail.com

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Abstract: We list Japanese-native carnivorous plant species and hybrids from four genera in two families, based on Komiya (2002) with some revisions and modifications. We also discuss facts and recent findings on selected species and hybrids from the list. Additionally, we review those of uncertain taxonomy or distribution as well as a potential carnivorous species.

Introduction

Japan is home to approx. 20 carnivorous plant species. The nation’s current territories consist of four main islands, namely Hokkaido, Honshu, Shikoku, and Kyushu, and smaller islands surrounding them. Each one of the main islands can represent a region or area. According to the Japan Meteorological Agency website, Japan covers a climate range from subarctic to subtropical.

A list of Japanese-native carnivorous plant species and hybrids

Following is a list of Japanese carnivorous plant species and hybrids after Komiya (2002) with revisions and modifications:

**Droseraceae**

*Aldrovanda vesiculosa* L.
Distr.: Honshu

*Drosera anglica* Huds.
Distr.: Hokkaido and North-central Honshu (Oze)

*Drosera indica* L. complex
Distr.: Honshu and Kyushu

*Drosera lunata* Buch.-Ham. ex DC.
Distr.: Kyushu, Shikoku, and Central and Southern Honshu

*Drosera rotundifolia* L.
Distr.: Hokkaido, Honshu, Shikoku, and Kyushu

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1 The southern limit is Yakushima (or Yaku Island) near Kyushu Island.
**Drosera spatulata** Labill.  
Distr.: Kyushu, Shikoku, Central and Southern Honshu, and Ryukyu Islands

**Drosera tokaiensis** (Komiya & C.Shibata) T.Nakamura & Ueda  
Distr.: Central Honshu and Northeast Shikoku (endemic)

**Drosera anglica × rotundifolia**  
= *D. × obovata* Mert. & Koch

**Drosera rotundifolia × spatulata** (Seno 2003; Hayakawa et al. 2012)

= *D. × hyugaensis* (Seno) Ichihashi, Hattori & Minami ex Kagawa comb. et stat. nov.  
= *D. hyugaensis* n. n. in Ichihashi et al. (2006)  

**Drosera rotundifolia × tokaiensis**

**Drosera spatulata × tokaiensis** (Nakamura 1993)

**Lentibulariaceae**

**Pinguicula macroceras** Pall. ex Link  
= *P. vulgaris* L. (unresolved)  
Distr.: Hokkaido, Honshu, and Shikoku

**Pinguicula ramosa** Miyoshi  
Distr.: North-central Honshu (Nikko; endemic)

**Utricularia aurea** Loir.  
Distr.: Central and Southern Honshu, Shikoku, Kyushu, and Ryukyu Islands

**Utricularia bifida** L.  
Distr.: Honshu, Shikoku, Kyushu, and Ryukyu Islands

**Utricularia caerulea** L.  
Distr.: Hokkaido, Honshu, Shikoku, Kyushu, and Ryukyu Islands

**Utricularia dimorphantha** Makino  
Distr.: Honshu (endemic)

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1 Seno (2003) described this F1 interspecific hybrid as *D. tokaiensis* (Komiya & C.Shibata) T.Nakamura & Ueda subsp. *hyugaensis* Seno. The original combination erroneously suggests that this hybrid branched from *D. tokaiensis*, which I think has a logical issue (Discussed in Kagawa 2017).

2 The author name ‘C.Sibata’ in Seno (2003) is corrected to the original spelling ‘C.Shibata’.

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**Utricularia gibba** L.\(^4\)

= *U. exoleta* R.Br. (unresolved)

Distr.: Central Honshu, West Shikoku (Fukuoka & Hayakawa 2019), Kyushu, and Ryukyu Islands

**Utricularia intermedia** Hayne

Distr.: Hokkaido, Honshu, and Northern Kyushu

**Utricularia macrorhiza** LeConte

Distr.: Hokkaido and extreme north of Honshu

**Utricularia minor** L.

Distr.: Hokkaido, Honshu, Shikoku, and Kyushu

**Utricularia minutissima** Vahl

Distr.: Central Honshu (Tokai Region)

**Utricularia tenuicaulis** Miki

= *U. australis* R.Br. sensu Kadono (2014)

Distr.: Honshu, Shikoku, Kyushu, and Ryukyu Islands

**Utricularia uliginosa** Vahl

Distr.: Hokkaido, Honshu, Shikoku, and Kyushu\(^5\)

**Utricularia tenuicaulis**\(^6\) × **macrorhiza** (Kameyama et al. 2005)

= *U. ×japonica* Makino (according to Kadono 2014)

**Utricularia intermedia** × **minor**

= *U. ×ochroleuca* R.W.Hartm.\(^7\)

Notes on selected Japanese-native carnivorous plant taxa from the list

**Droseraceae**

**Aldrovanda vesiculosa** (Fig. 1)

Flowers of this species were unknown until Makino (1893). Komiya (1989) lists 10 Japanese populations, including two introduced ones, from parts of Honshu. The plants of Japanese forms stay green. This species is nearly or completely extinct in the major habitats in the country, although a previously unknown population was discovered in 2022 (Nishihara et al. 2023).

\(^4\) I adopted Taylor’s (1989) classification, but Japanese researchers often mention it as *U. exoleta* R.Br. (e.g., Fukuoka & Hayakawa 2019; Kadono 2014; Komiya 2002). Further taxonomic research would be required.

\(^5\) The southern limit is Yakushima (or Yaku Island) near Kyushu Island.

\(^6\) As *U. australis* f. **tenuicaulis** in Kameyama et al. (2005).

\(^7\) Komiya (2002) lists *U. ochroleuca* as a species, but I adopted the hypothesis that it is a group of natural hybrids between *U. intermedia* and *U. minor* (Böcher et al. 1968 among many others), and therefore I treated *U. ×bentensis* Komiya as one of its synonyms. Rice (2018) considers *U. ×bentensis* as synonymous to *U. bremii* Heer ex Köllicher.
White-flowered and pink-flowered groups are known from Japan. The white-flowered group is reported from Honshu and Kyushu while pink-flowered group is confined to a part of Central Honshu. In Japan, this species complex has an annual life cycle, and seeds of both the groups germinate after exposure to low temperature.

Watanabe et al. (2013) argue that the white-flowered and pink-flowered groups belong to separate species after their allozyme/morphology/cross-pollination analysis, supporting *D. makinoi* Ma-sam. for the white-flowered group. Watanabe (2014) refers to the pink-flowered group as *D. toyoakensis* M.Watanabe, but no published description seems to exist.8 Robinson et al. (2017) tentatively treat both the pink-flowered and white-flowered groups as *D. indica*.

Kagawa (2017) compares with limitations the epidermal hairs in the two groups, pointing out the morphological similarities between the pink-flowered and white-flowered groups in this regard as well as between these groups and *D. serpens* Planch.9 Having said that, the relationship between *D. serpens* and Japanese *D. indica* complex is still poorly understood. Also, most Japanese studies of this section have only focused on the local *D. indica* complex, but these *Arachnopus* members would require to be a part of comprehensive research for further insight.

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8 There is a confusion on the status of *D. toyoakensis* M.Watanabe in Kagawa (2017). Watanabe et al. (2013) revise the white-flowered group as *D. makinoi*, but they include no description of the pink-flowered group.

9 Schlauer et al. (2019) consider the pink-flowered group as a form of *D. serpens* and the white-flowered group as a separate taxon after observing the epidermal hairs.
Drosera lunata

*D. lunata* is the only tuberous species that is reported from Japan. Mature plants of Japanese forms mostly start ascending without producing basal leaves. Young plants, however, form a basal rosette. Some populations are found in limestone areas.

Drosera rotundifolia (Fig. 3)

*D. rotundifolia* is the most common *Drosera* species in Japan. It has adapted to a wide range of environments such as marshlands, mountain forests, limestone areas, or even coasts in some cases. There is high diversity in the morphology/ecology of this species.

Figure 2: Specimens of Japanese *Drosera indica* complex. (A-B) Pink-flowered plants from Aichi Prefecture, Honshu. Photos by Masaaki Senda. (C-D) White-flowered plants (= *D. makinoi* in Watanabe et al. 2013) in Chiba Prefecture, Honshu.
Despite its circumboreal distribution, this species is sometimes found in habitats where the plants are exposed to hot summer\textsuperscript{10}. In Southern Kyushu, for example, some populations have adapted to a subtropical climate and acquired more heat tolerance and a shorter winter dormancy than others have. Some populations in such environments have developed an almost annual life cycle and produce more flowers in order to survive the summer heat and/or drought as seeds, rather than as plants (Yotsumoto, Susumu. 2005. Personal communication, published in Kagawa 2017).

In Honshu and Kyushu, pink-flowered clones are sometimes found, even though this species normally produces white flowers. These clones are also characterised by redder petioles and/or

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\textsuperscript{10} There are tropical populations reported from the Southern Hemisphere, but they occur in cool tropical highlands (Coritico & Fleischmann 2016; Fleischmann 2021).
laminae than those of white-flowered clones from the same populations. The petal pigmentation, however, is inconsistently exhibited. The pink flowers are likely to be genetic, but they require certain conditions to be expressed, without which the same plants can produce white flowers\textsuperscript{11}. What triggers the coloration is still a mystery.

\textit{Drosera tokaiensis} (Fig. 4)

\textit{D. tokaiensis} is a Japanese endemic of a hybrid origin. This species was previously known as \textit{D. spatulata} Labill. subsp. \textit{tokaiensis} Komiya \& C.Shibata (Komiya \& Shibata 1978), or the ‘Kansai

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure4}
\caption{(A) \textit{Drosera tokaiensis} in Shiga Prefecture, Honshu. Photo by Masaaki Senda. (B) \textit{D. tokaiensis} in Kagawa Prefecture, Shikoku. Photo by Takaaki Kagawa. (C) In cultivation. Photo by Takaaki Kagawa. (D) Flowers of white-flowered \textit{D. tokaiensis}. Photo by Takeru Okamoto.}
\end{figure}

\textsuperscript{11} kokebohusi (2013) has a similar note.
form of \textit{D. spatulata}'. However, Nakamura & Ueda (1991) concluded in their morphological and chromosomal study that it is an allopolyploid species which originated from a hybrid between \textit{D. rotundifolia} and \textit{D. spatulata}.

The plant morphology varies slightly among the regional forms. As far as the flowers are concerned, they are normally pink, but enthusiasts have noticed white-flowered clones on a small island under the administration of Hyogo Prefecture. White flowers are commonly observed in anthocyanin-deficient plants, but these white-flowered clones of \textit{D. tokaiensis} exhibit full anthocyanin pigmentation in their plants (cf. Ksepka 2022).

Nakanishi (2019) claims to have discovered a new population of \textit{D. tokaiensis} in a habitat of \textit{D. rotundifolia} and \textit{D. spatulata} in Kyushu, where the two species hybridise. Previously, no \textit{D. tokaiensis} habitat had been reported from Kyushu. The new population, according to the author, has the ability to sexually reproduce and the morphology of \textit{D. tokaiensis}. This may suggest that it is (1) an introduced population, (2) a geographically isolated yet natural population of \textit{D. tokaiensis}, or (3) one that independently emerged by allopolypoidisation.

If (3) is true, there arises a question about whether this new population can be treated as \textit{D. tokaiensis} per se or its subtaxon, because it would share no common F1 hybrid ancestor with \textit{D. tokaiensis} from Honshu and Shikoku. Their F1 hybrid ancestors would have separately originated from paraphyletic/polyphyletic strains of the parent species, namely \textit{D. rotundifolia} and \textit{D. spatulata}, in different regions in different time periods. Additionally, morphology is an important factor in identification of organisms, but whether a morphology-only approach is always sufficient is another question. In any case, further research would be required for this new population.

\textbf{Lentibulariaceae}

\textit{Pinguicula macroceras/vulgaris}

One of the native \textit{Pinguicula} species from Japan has been identified as \textit{P. macroceras/vulgaris}. Researchers have long disputed over the validity of \textit{P. macroceras} against \textit{P. vulgaris} (Casper 1962; Komiya 1999; Kondo & Shimai 2006; Rice \textit{et al.} 2008; Shimai \textit{et al.} 2021 among many others), and there has been no agreement. In Japan, Komiya (1972) supported \textit{P. vulgaris} L. for the populations from Japan, which Komiya & Shibata (1980) synonymised to \textit{P. vulgaris} L. var. \textit{macroceras} (Link) Herder. Later, Komiya (1999) revised it as \textit{P. macroceras} Link. Recent phylogenetic studies, such as Kondo & Shimai (2006) or Shimai \textit{et al.} (2021), are in favour of those who support \textit{P. macroceras} despite the morphological similarities and diversity. So far, authors in Japan imply that all the local populations pertain to a single species, whether it is \textit{P. macroceras} or \textit{P. vulgaris}.

\textit{Pinguicula ramosa} (Fig. 5$^{12}$)

\textit{P. ramosa} is a rare species that is endemic to a confined area of Honshu Island. Habitats of this species are wet cliffs/slopes on the Nikko mountains. Flower scapes of \textit{P. ramosa} can branch 2-3 times, or sometimes more, even though it does produce solitary flowers like other species of the genus.


\footnotesize{\textsuperscript{12} Image use permission statement (in Japanese):
http://www.nikko-kankou.org/image/index.cfm?action=detail&id=8361}
numbers that \( P. \) ramosa and \( P. \) variegata are separate species. Later Shimai (2016) systematically compared \( P. \) ramosa, \( P. \) variegata, and \( P. \) villosa to clarify the differences in the morphology, cytology, and ecology. Both Komiya & Shibata (1998) and Shimai (2016) indicate that the branched flower scapes are one of the distinctive features of \( P. \) ramosa.

**Utricularia dimorphantha** (Fig. 6) 

*U. dimorphantha* is a suspended aquatic species that is endemic to Honshu Island. It is found in still or slow-flowing waterbodies such as ponds, lakes, or irrigation ditches where the water is slightly eutrophicated. After habitat loss, this species is only left in limited parts of the island. This
species produces few or no traps, which may suggest that it has evolved while choosing eutrophi-
cated environments to directly intake abundant nutrients from water, instead of having to digest
microorganisms (cf. Fleischmann 2011). *U. dimorphantha* produces underwater cleistogamous
flowers as well as yellow/cream-coloured opening flowers on areal inflorescences.

**Utricularia minor** (Fig. 7)

A few infraspecific taxa have been reported from Japan. One of such taxa is *U. minor* Hayne
f. *natans* Komiya, which is a free-floating form that lacks undersubstrate stolons (Ishidaka & Ku-
hara 2007; originally in Komiya 1972). However, further research would be required to elucidate
whether all the populations belong to this taxon.

A small terrestrial form is also reported. Komiya (1980) identified it as *U. minor* Hayne f.
*terrestris* Glück\(^\text{13}\). The undersubstrate stolons can be absent depending on the population (Ishidaka &

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\(^\text{13}\) Previously as *U. minor* f. *natans* in Katagiri (1977).
Kuhara 2007). In the Hayade Valley area in Niigata Prefecture, Honshu, it is found on the surface of a wet cliff (Ishidaka & Kuhara 2007; Tsuboya 2008). It is unclear whether all the populations reported as *U. minor f. terrestris* pertain to this taxon, not to mention that little has been revealed on the taxon itself in the first place.

**Utricularia minutissima**

The Japanese range of *U. minutissima* only covers a part of Central Honshu. This is probably a margin of the range of this tropical species reported from Asia and Oceania. In Japan, it was first published by Makino (1906) as *U. nipponica* Makino. The current designation is based on Komiya’s (1980) revision.

**Utricularia tenuicaulis**


Carnivorous plant taxa of uncertain distribution in Japan

**Droseraceae**

**Drosera burmanni (= burmannii) Vahl**

Japan is often included as a part of the range of *D. burmanni* (e.g., Lowrie 2013). However, there has been no record of this species from the nation. In fact, *D. burmanni* is excluded from Komiya & Shibata’s (1978) or Komiya’s (2002) lists of Japanese carnivorous plants. The most probable hypothesis is that incorrect usage of the name *D. burmanni* L. accounts for this mystery. Makino (1905a) pointed out in his short article that *D. spatulata* (as *D. loureirii*) was commonly referred to as *D. burmanni* L. in Japan. He states in Japanese:

こまうせんごけノ学名ガ能ク間違ヘラレ即チ往々Drosera Burmanni Vahl.ノ名ガ用ヰラレテアルガコレハ Drosera Loureirii Hook. et Arn. トセネバナラヌ又 Burmanni Vahl. ハ之レニ似テハ居レドモ全ク別ノ一種デアル

Translation: The botanical name for the Spatulate Sundew is often mistaken: The name Drosera Burmanni Vahl. is frequently used, but it should be Drosera Loureirii Hook. et Arn. *D. burmanni* Vahl. resembles it, but it is altogether a different species.

14 Komiya & Shibata (1980) also recognise the non-floating populations as *U. australis* R.Br. f. *fixa* Komiya, which are likely to be forms of *U. tenuicaulis* from the turion morphology.
Also, Makino (1905b) comments in English as follows:

So far as I know, this species has been found nowhere in Japan, except in Formosa; while *D. spathulate* Labill = *D. Loureirii* Hook. et Arn. (Jap. Ko-mōsengoke) are frequently met with. According to Forbes and Hemsley, Carpenter collected it in Amami Ōshima, but we have no specimen of it from there.\(^{15}\)

Other hypotheses include the loss of the population(s) in Japan and the nation’s withdrawal from territories in the range of *D. burmanni* (Also see Kagawa 2017).

**Lentibulariaceae**

**Pinguicula villosa L.**

According to Hultén (1968), *P. villosa* is found on Shikotan Island, one of Japan’s disputed territories with Russia. It is one of the islands that consist the Kuril Islands in the Northeast of Hokkaido Island.

Additional carnivorous plant species from Japan which are unidentified or disputed

**Lentibulariaceae**

**Pinguicula sp.**

Komiya & Shibata (1999) comment on an unknown Hokkaido *Pinguicula* species in Ito (1979) as completely unimaginable. It is mentioned in Japanese as Manshū-mushitorisumire, which translates into Manchurian Butterwort. However, no *Pinguicula* species is known to have such a Japanese name. The Flora of China website lists two species, namely *P. alpina* L. and *P. villosa* L., neither of which is reported from Hokkaido Island.

**Utricularia siakujiiensis S.Nakaj.** (Fig 8.)

Sadao Nakajima (as his affiliation Tōkyōfu Dobokubu 1937) described a suspended aquatic species of *Utricularia* from Sanpoji Pond in Tokyo, which is currently a part of Toritsu Shakujii Kōen, a municipal park. The population was lost due to pollution during the urbanisation of the local area, and there has been no sign of revival. Authors propose different hypotheses on the identity of this mystery *Utricularia*.

Komiya & Shibata (1980) treated this *Utricularia* population as *U. australis*, which later turns out in Kameyama et al. (2005) to be hybrids between *U. tenuicaulis*\(^{16}\) and *U. macrorhiza*. Komiya (2014) then synonymised *U. siakujiiensis* to *U. australis* sensu Kadono (2014), namely *U. tenuicaulis* sensu Miki. Kadono & Tanaka (2015) examined the herbarium specimens and argue that it is *U. macrorhiza*, a circumboreal species\(^{17}\). It would be no surprise if a circumboreal *Utricularia* species were found in Tokyo, because this region has waterbodies sourced by cool spring water. Sanpoji Pond is one of such waterbodies, which has retained Ice Age relicts such as *Menyanthes trifoliata* L. (Menyanthaceae).

\(^{15}\) All the spellings are as in the original.

\(^{16}\) As *U. australis f. tenuicaulis* in the original study.

\(^{17}\) There had been no report of *U. macrorhiza* from Japan until Komiya (1994).
A local school’s old biotope has recently drawn attention for having a species of *Utricularia* from Sanpoji Pond. According to the PR of Toritsu Shakujii Chūgakkō (2018a, 2018b, 2018c, 2018d), a local junior high school, their biotope was set up in 1959 by some of the teachers and students by laying local rice field soil as the substrate and then introducing plants collected from Sanpoji Pond. The school notes that the students from the period observed the carnivory action of the *Utricularia* species with a microscope and consulted a guidebook for identification. Recently, Toritsu Shakujii Kōen’s (2022) staff posted online a turion photograph of the *Utricularia* species from the school biotope. The brown-coloured turion that is slightly elongated lengthwise suggests that it is *U. tenuicaulis*, which the park staff also claims in the post, even though there is no concrete evidence that this is exactly what Nakajima published.

**Utricularia sp.** (Fig. 9)

Miyamoto (2021a, 2021b, 2021c) noticed a population of an unidentified *Utricularia* species in Hyogo Prefecture, Honshu and described the characteristics in his notes. This may be a form of *U. gibba*/*exoleta* or a closely related species, as far as I understand his notes and personal communication (Miyamoto, Makoto. July 2023) on the morphology. It resembles *U. minor* and partially grows within the substrate. The main stems produce thread-like shoots during summer. These thread-like shoots reach the water surface, are easily detached, and can have a trap near the apex. The detached thread-like shoots continue growth as independent plants. No turions are formed for winter. The flowers are yellow, and the lower lip is horizontal with the middle area raised, and the upper lip is curled.
Miyamoto remarks that the plants in cultivation appear as typical *U. gibba*/*exoleta* despite the behaviour *in situ*. He theorises that the thread-like shoots are for dispersal and asexual multiplication, and that the plants produce them in order to remain near the water surface without the entire plants being buried into the sediment and substrate. The thread-like shoots detach while he attempts to prepare a herbarium specimen with them connected to the main plants (Miyamoto, Makoto. July 2023. Personal communication.).

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A potential carnivorous plant taxon from Japan

**Tofieldiaceae**

*Triantha japonica* (Miq.) Baker (Fig. 10)

*T. japonica* is a Honshu-endemic monocot that is found in mountain wetlands. It often co-occurs with carnivorous plant species such as *Drosera rotundifolia*. The leaf blades are basal, linear, erect, and up to 40 cm in length. In summer it produces erect inflorescences, which are up to 40 cm long, with a scape covered with mucilaginous hairs. The flowers are white and approx. 1 cm across, which can be partially red. The mucilage secretion is weaker than in other carnivorous plant genera such as *Drosera*, and therefore it is only functional as a trap when the contact area is large enough for the size and/or physical strength of the prey.

Figure 10: *Triantha japonica* in cultivation. (A) A plant in bloom. (B) A closeup of a flower scape. Photos by Takaaki Kagawa.
Lin et al. (2021) reported carnivory in *T. occidentalis* (S.Watson) R.R.Gates. Flower scapes of *T. occidentalis* have mucilaginous hairs to capture and digest small insects, according to the authors. *T. japonica*, like its North American carnivorous sister, has also been known to trap insects on the flower scapes, even though it is yet to be investigated for carnivory.\(^{18}\) Japanese names for this species include *Mushitorizekishō*, which translates into *Bug-catching Acorus*.

**Conclusion**

We listed Japanese-native carnivorous plant species and hybrids after Komiya (2002) and discussed selected species and hybrids within the list. We also reviewed unidentified species which are out of the list as well as taxa of unconfirmed distribution in the country. Finally, we reviewed a potentially carnivorous monocot based on recent research (Lin et al. 2021).

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References


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\(^{18}\) Lin (2020) notes that *T. japonica* should be treated as synonymous to *T. occidentalis*, based on his plastid gene analysis.


Miyamoto, M. 2021a. Shinshu no tanukimo hakken ka?
Miyamoto, M. 2021c. Shinshu happyō Harimatanukimo to meimei.
都立石神井公園 [Toritsu Shakujii Kōen]. @ParksSyakujii. 28 October 2022. 【見ごろの生き物】サービスセンターロビーでイヌタヌキモの展示を始めました。
捕虫嚢でミジンコ等を捕える食虫植物で、昔三宝寺池から石神井中学校へ株分けされたものを展示用に頂きました。
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