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1 A fossil aphid gall from the middle Pleistocene sediment in Hyogo Prefecture, western
2 Japan

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4 Running title: Fossil aphid gall

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1 **Abstract**

2 We described the external morphology of a fossil insect gall collected from the middle
3 Pleistocene sediment in the Osaka Group of Nishinomiya City, Hyogo Prefecture,
4 western Japan. The fossil was well preserved without major compression and was
5 identified as a gall induced by an aphid species of the genus *Nipponaphis*
6 (Nipponaphidini: Hormaphidinae: Aphididae), based on its external morphology. This
7 is the first reliable fossil record of an Aphididae gall. This fossil provides evidence that
8 the intimate aphid-plant association can be traced back to the middle Pleistocene,
9 approximately 0.4 million years ago.

10

11 **Key words:** coevolution, *Distylium*, Hamamelidaceae, Hormaphidinae, host plant,
12 *Nipponaphis*.

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1 **INTRODUCTION**

2

3 Plant galls are distinct structures formed by abnormal cell proliferation and can be
4 induced by various organisms, such as bacteria, insects, and mites. Insect galls are
5 induced by herbivores such as gall wasps, gall midges, thrips, and aphids, and they
6 exhibit diverse morphologies (e.g. Price *et al.* 1987; Yukawa & Masuda 1996; Stone &
7 Schönrogge 2003). A number of insect species (approximately 13,000) can induce
8 species-specific galls on their host plants (Crespi & Worobey 1998; Nyman *et al.*
9 2000; Wool 2004). Fossil records of plant galls are limited, and a few examples of
10 fossil galls were found in North America, Europe, and Antarctica, including those
11 induced by dipterans, hymenopterans, and acari (Larew 1992; Diéguez *et al.* 1996;
12 Lopes-Vaamonde *et al.* 2006; Sawada *et al.* 2008). So far, no reliable fossil records of
13 aphid galls have been documented apart from galls produced by phylloxerids (Wittlake
14 1969).

15 Sawada *et al.* (2008) compiled fossil insect galls and host plants that had been
16 reported from Cenozoic samples, showing that almost all compiled fossil galls were
17 impression fossils on leaves. Taylor *et al.* (2009) produced information on morphology
18 and taxonomy of plant fossils, including interactions between plants and animals.
19 Impressions or traces of organisms may remain after the tissue of the organisms is
20 decomposed by diagenetic processes and long-term effects of underground or
21 geothermal water. In impression fossils, the shape of an organism is typically
22 preserved within a plane. Impression fossils are thus suitable for investigating shapes
23 of organisms and plant venations. In contrast, compression fossils maintain the tissues
24 of past organisms which may, however, be distorted. Compression fossils may be
25 flattened due to physical compaction in the sediments, which complicates examination
26 of the internal structure.

1 The fossil described here can be classified as a compression fossil. However, as
2 this specimen was not completely compressed, the shape was examined
3 three-dimensionally. Furthermore, this fossil gall was exceptionally well preserved,
4 and it was thus possible to examine the external morphology of the gall in detail. In the
5 list of Miki's collection at the Osaka Museum of Natural History, Kokawa *et al.* (2006)
6 recorded this fossil gall describing it as a gall on *Distylium* sp. (Hamamelidaceae).
7 However, their report lacks descriptions and photographs and did not indicate why this
8 fossil material was determined as a gall on *Distylium* sp. Therefore, in the present
9 study, we describe the morphology of this fossil gall to reconfirm their identity.

11 **MATERIALS AND METHODS**

13 **Locality**

14 Hirotayama, Nishinomiya City, Hyogo Prefecture, western Japan (B bed in Miki *et al.*
15 1957) (Fig.1). This bed appeared during the construction of the schoolyard of Hirota
16 Elementary School. Although plant fossils were collected from the bed during the
17 construction, it is not currently possible to access to the bed.

19 **Formation**

20 Uegahara Formation, upper part of the Osaka Group (Miki *et al.* 1957) (Fig. 1). The
21 Osaka Group is widely distributed around the Osaka Bay (Itihara 1993).

23 **Age**

24 Middle Pleistocene. The horizon of the locality is associated with the Ma9 Marine Clay
25 Bed (Momohara 2015), which is associated with the marine oxygen isotope stage

1 (MIS) 11 (0.424 – 0.374 million years ago [Ma]) of the middle Pleistocene
2 (Yoshikawa & Mitamura 1999).

3

4 **Fossil flora**

5 Forty-one species belonging to 36 genera of 29 families were reported by Miki *et al.*
6 (1957). Evergreen broad-leaved trees were dominant in this fossil flora, including
7 species of the families Myricaceae (*Myrica rubra* Lour.), Fagaceae (*Quercus glauca*
8 Thunb., *Q. phillyraeoides* A. Gray), Lauraceae (*Cinnamomum doederleinii* Engl., *C.*
9 *daphnoides* Siebold et Zucc.), Hamamelidaceae (*Distylium rasemosum* Siebold et
10 Zucc.), and Myrtaceae (*Syzygium buxifodium* Hook. et Arn.), among others.
11 *Cinnamomum doederleinii*, *C. daphnoides* and *S. buxifolium* are currently growing
12 wild on Kyushu and Ryukyu Islands, at a latitude of approximately 5° southward from
13 Nishinomiya (Yonekura 2016; Ohashi 2016). This fossil flora indicates a warm climate
14 during the interglacial age, suggesting a milder climate than at present.

15

16 **Collector**

17 Shigeru Miki

18

19 **Depository and register number**

20 Osaka Museum of Natural History, Miki's collection OSA F23300.

21

22 **RESULTS AND DISCUSSION**

23

24 **Morphology of the fossil material**

25 Black plant remains (Fig. 2) were flattened and distorted to an elliptical shape of 32
26 mm length, 20 mm width, and 6 mm thickness in a flattened state. This deformation

1 most probably resulted from compaction of the strata after deposition. The basal part
2 was missing.

3 There were no septa in the cavity, no traces of styles, and no projection at the
4 apex. The wall of the relic was 0.5–1.0 mm thick and lignified. The basal part showed
5 some abrasion and, on the surface, showed some pressure marks from plants that were
6 buried with this relic. Vascular bundles in the wall were exposed in the broken basal
7 part. Protuberant veins of vascular bundles on the surface extended from the base to
8 apex. No setae were present on the surface in the fossilized state. One hole, 6 mm in
9 the major axis and 5 mm in the minor axis, was present on the lateral side.

10

11 **IDENTITY OF THE FOSSIL MATERIAL**

12 Aphids of the Eriosomatinae and Hormaphidinae induce several types of galls on
13 broad-leaved trees as the primary host plant. Aphids reproduce parthenogenetically
14 inside galls, thus they can use this cavity to establish an aphid colony. Furthermore,
15 aphid galls produce a winged generation to migrate to the secondary hosts which is
16 why aphid galls have an exit hole or a crack through which winged individuals can exit.
17 The present fossil from Nishinomiya (Fig. 2) shares such characteristics with aphid
18 galls and was thus unambiguously identified as a gall induced by an eriosomatine or
19 hormaphidine aphid.

20 Large galls formed by *Nipponaphis* (Hormaphidinae: Nipponaphidini) species on
21 *Distylium* spp. are typically completely closed and lignified and have a circular exit
22 hole in the lateral surface (Yukawa & Masuda 1996; Aoki *et al.* 2015; Blackman &
23 Eastop 2018). Regarding the gall's shape, size, wall, and exit hole, the characteristics
24 of the present fossil gall can be identified as induced by a *Nipponaphis* species, which
25 typically produce fig-shaped galls on *Distylium* sp. Galls formed by closely related
26 genera (i.e. *Monzenia*, *Metanipponaphis*, *Quadratus*, and *Neothoracaphis*) (Aoki *et al.*

1 2015) can be distinguished from *Nipponaphis* galls based on the smaller gall size and
2 the presence of irregular dehiscence instead of a circular hole (Yukawa & Masuda
3 1996). Although the present fossil material lacked leaves or twigs that would facilitate
4 identification of the host species, the fossil aphid can be assumed to have been
5 associated with a species of *Distylium* as its primary hosts plant. The fossil leaves and
6 fruits of *D. racemosum* were excavated from the same sediment, further supporting the
7 identification of the gall.

8 A total of six extant species of the genus *Nipponaphis* are known to induce galls
9 on *Distylium* spp. Five Japanese species are associated with *D. racemosum* (i.e. *N.*
10 *distyliicola* Monzen, *N. monzeni* Takahashi, *N. distychii* Pergande, *N. machilicola*
11 (Shinji), and *N. loochooensis* Sorin) (Aoki *et al.* 2015) and one unidentified species
12 from *D. chinensis* in China (Chen & Qiao 2012). *Nipponaphis distyliicola* galls usually
13 have several small spine-like projections on the surface, which were not observed in
14 the present fossil gall. *Nipponaphis monzeni* galls are similar in shape to the present
15 fossil but are typically larger and have thicker walls (Sorin 1958; Yukawa & Masuda
16 1996; Kurosu & Aoki 2009). *Nipponaphis* sp. sensu Chen & Qiao (2012) induces
17 elongate bottle-shaped galls with a flattened apex and longitudinal thick vascular veins
18 on the surface. These characteristics differ from those of the present fossil gall. In
19 contrast, some galls of the extant *N. distychii* show longitudinal stripes due to vascular
20 veins on the surface, which was also observed in the present fossil (Aoki *et al.* 2015;
21 Fig. 1 (b)). Thus, morphological comparisons suggest that the fossil gall can be
22 attributed to *N. distychii*. However, the gall may have been produced by *N. machilicola*
23 or *N. loochooensis*, both of which are distributed in the Ryukyu Islands, southernmost
24 Japan, in the present day (Aoki *et al.* 2015), because the fossil gall was found in
25 sediments deposited during a particularly warm period, MIS 11. The galls of these
26 species are also fig-shaped; however, detailed information about the gall morphology

1 is lacking (Aoki *et al.* 2015). Furthermore, we cannot exclude that the present gall was
2 produced by an extinct species closely related to *N. distychii*.

3 The genus *Nipponaphis* includes several morphologically similar species (Aoki
4 *et al.* 2015) which are difficult to identify based on the gall shape only. Although the
5 available information at present does not allow reliable identification of the species
6 that produced the present gall, the distinct characteristics of the fossil strongly suggest
7 that it can be attributed to a *Nipponaphis* species, probably *N. distychii* or a closely
8 related species. The wall of *Nipponaphis* galls is typically lignified and durable, and
9 thus likely to be fossilized.

10 This is the first reliable fossil record of an Aphididae gall and suggests a close
11 association between *Nipponaphis* aphids and *Distylium* plants in the middle
12 Pleistocene, about 0.4 Ma. More systematic investigations for such fossils in future
13 will provide better understanding of insect-plant associations.

14

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24

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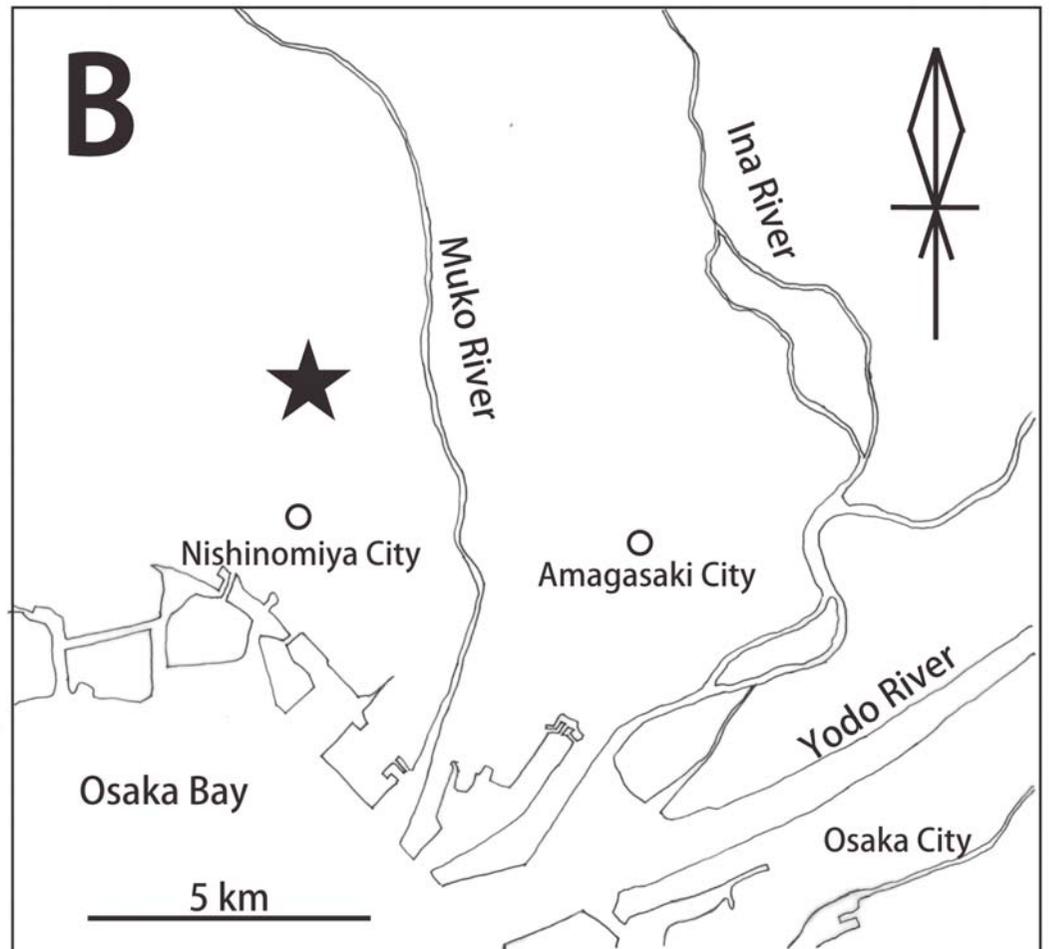
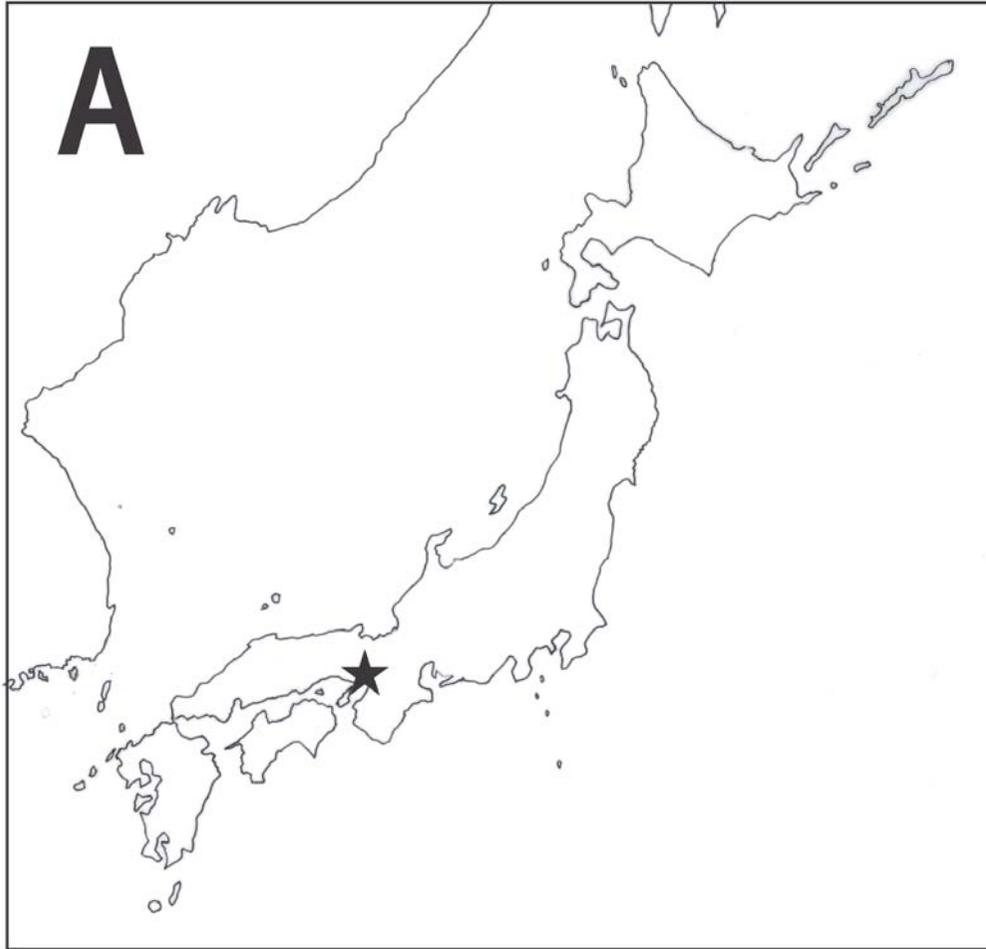
1 **Figure captions**

2

3 **Fig. 1.** Maps showing the location of the fossil gall. (A) generalized map of the
4 location. (B) close-up map of the locality. Asterisks indicate the location
5 (Hirotoyama, Nishinomiya City, Hyogo Prefecture, western Japan).

6

7 **Fig. 2.** A fossil gall induced by an aphid species of the genus *Nipponaphis*. (A, B)
8 frontal view. (C) Side view. (D) Enlargement of an exit hole. Scale bars indicate
9 10 mm (A–C) and 5 mm (D).



(B)



(C)



(D)

