

First record of fossorial foam nesting in the Forest Green Treefrog, *Zhangixalus arboreus* (Okada and Kawano, 1924) in Japan

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The treefrog genus *Zhangixalus* comprises 46 species and is widely distributed across South, East, and Southeast Asia (Frost, 2025). All species in the genus construct foam nests for oviposition, and the reproductive types can be classified into three categories according to the location of oviposition sites (Dufresnes et al., 2022): (1) arboreal foam nests on a tree branch or leaves above water; (2) scansorial foam nests attached on biotic substrates (e.g., on the ground or grasses) or abiotic surfaces adjacent to water; and (3) fossorial foam nests buried in the ground, concealed in moss, leaves or mud. Type 1 is considered the ancestral characteristic, and during subsequent epochs of climate cooling the other types emerged (Dufresnes et al., 2022).

Zhangixalus arboreus (Okada and Kawano, 1924) occurs on Honshu and Sado Islands, Japan (Kato et al., 2010; Matsui et al., 2019). Its reproductive behaviour has been well reported (e.g., Kasuya et al., 1996; Ichioka and Hijii, 2021; Ichioka and Kajimura, 2024). Applying the classification by Dufresnes et al. (2022), the spawning locations reported for *Z. arboreus* satisfy two of the three categories: the foam nest developed by *Z. arboreus* is located often on a tree overhanging water, and sometimes above grasses or on the ground beside stagnant water (Matsui and Maeda, 2018; Ichioka and Hijii, 2021), corresponding to (1) and (2) above, respectively. *Zhangixalus arboreus* is sympatric with *Z. schlegelii* (Günther, 1858) on Honshu Island but the latter is absent from Sado Island (Matsui and Maeda,

2018). On Honshu, the two species can be partially distinguished by their breeding strategies: *Z. arboreus* sometimes breeds on the ground, but to the best of our knowledge, fossorial foam nests of *Z. arboreus* have not previously been reported, whereas *Z. schlegelii* spawns mainly beneath the ground (Matsui and Maeda, 2018), corresponding to category (3) above. Here, we summarize seven cases of fossorial oviposition by *Z. arboreus* on Sado Island (Table 1). In addition, we describe in detail two representative observations below.

Observation 1. On 30 April 2025 at 18:40 h, we found a fossorial foam nest in holes in the ground adjacent to a paddy field (No. 6 in Table 1; Fig. 1C) in Sado City, Sado Island, Niigata Prefecture, Japan (38.0400°N, 138.4416°E, elevation 2 m). Although the frogs were not directly observed in this case, this nest is presumed to belong to *Z. arboreus* since among anurans on Sado Island only this species is known to construct foam nests. The dimensions of the elliptical egg mass were approximately 50 × 90 mm and the nest was in a burrow with a depth of 40 mm.

Observation 2. On 4 May 2025 at 23:30 h, we observed a female (snout–vent length, SVL = 65 mm; weight 16.0 g) and a male (SVL = 52 mm; weight 8.9 g) in amplexus during oviposition in the ground (No. 7 in Table 1; Fig. 1A). The foam nest was in a shallow depression adjacent to a paddy field in Sado City, Sado Island, Niigata Prefecture, Japan (38.0405°N, 138.4417°E, elevation 2 m; Fig. 1B). The air and soil temperature were 10.3°C and 13.4°C, respectively. The dimensions of the elliptical egg mass were 89 × 120 mm and it was buried in a shallow mud burrow with a depth of 165 mm.

It is suggested that each *Zhangixalus* species has secondarily and independently acquired its reproductive behaviour multiple times by microevolutionary processes (e.g., drift or local adaptation), and it could also reflect phenotypic plasticity in some species related to microhabitat availability, predation risks, and competition for spawning sites (Dufresnes et al., 2022).

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Table 1. An overview of confirmed localities of fossorial foam nests by *Zhangixalus arboreus* on Sado Island, Japan.

No.	Date	Coordinates	Nest size (mm)	Note	Observer
1	May 2013–2020	38.0263°N, 138.4506°E	-	Almost every year	Harue Abe
2	May 2020	38.0193°N, 138.5008°E	-		Harue Abe
3	27 May 2023	38.1344°N, 138.4412°E	89 × 92		Takeshi Fujita
4	1 Jun 2023	37.9621°N, 138.3619°E	74 × 103		Takeshi Fujita
5	1 Jun 2023	37.9621°N, 138.3619°E	49 × 68		Takeshi Fujita
6	30 Apr 2025	38.0400°N, 138.4416°E	50 × 90	Fig. 1C	Masaya Miyata
7	4 May 2025	38.0405°N, 138.4417°E	89 × 120	Fig. 1A, B	Koruri Fukai

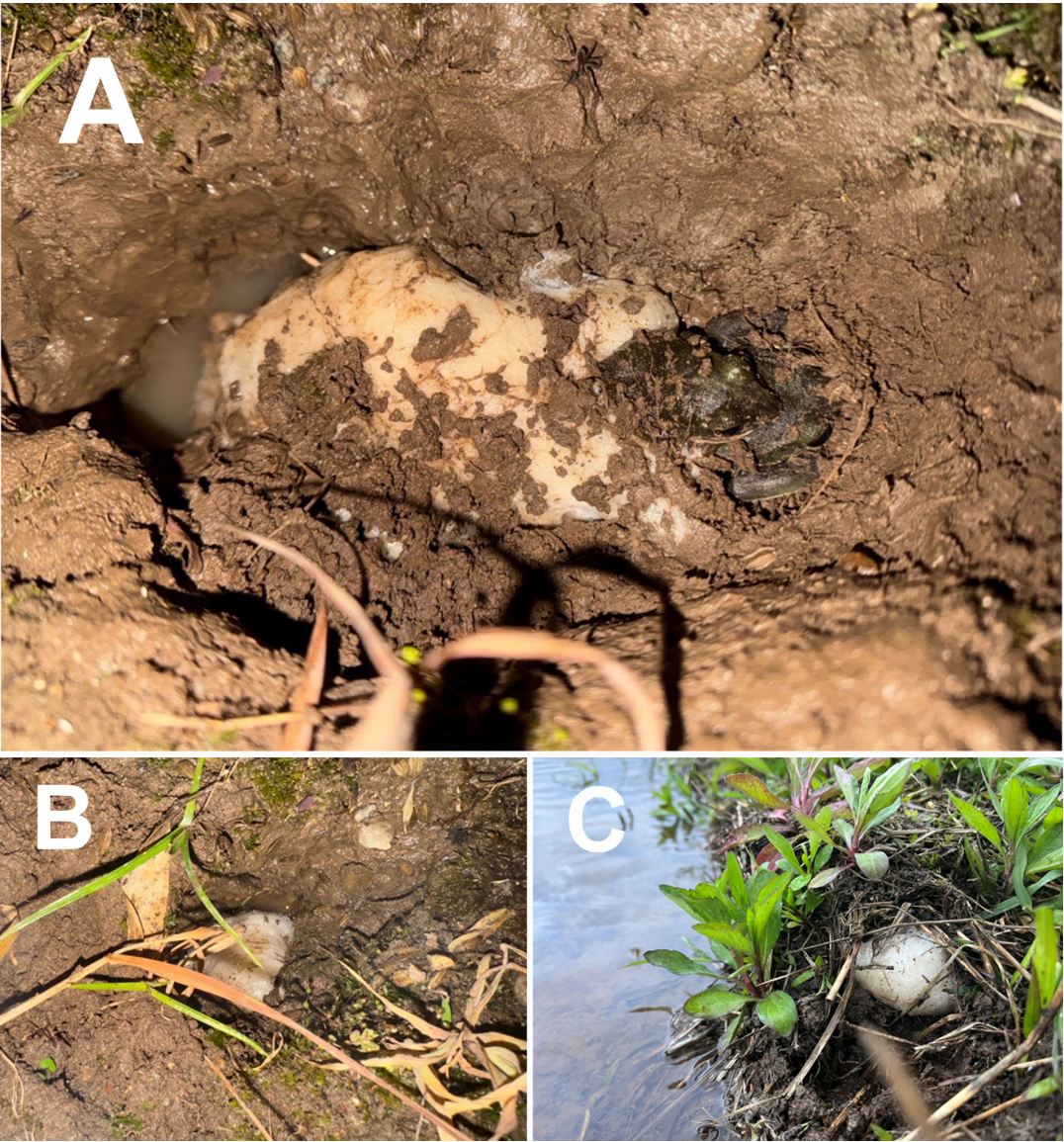


Figure 1. Fossorial foam nests by *Zhangixalus arboreus* on Sado Island, Japan. (A) Mating pair during oviposition. (B) Partially exposed fossorial foam nest at the time of discovery. (C) Foam nest in the soil. Photos by Fukai Koruri (A, B) and Masaya Miyata (C).

As pointed out by Matsui et al. (2019), in regions where *Z. arboreus* and *Z. schlegelii* co-exist they interfere with each other, probably resulting in the enhancement of arboreal breeding habits and the development of body markings in western populations of *Z. arboreus* on Honshu. On Honshu, the fossorial niche is occupied by *Z. schlegelii*, which might prevent *Z. arboreus* from using this niche, but on Sado Island *Z. arboreus* utilises fossorial sites for reproduction. Considering this, the release from interspecific competition with *Z. schlegelii* has presumably promoted the fossorial reproductive behaviour in *Z. arboreus* on Sado Island. A similar phenomenon was reported on Shikoku Island, Japan, where *Z. schlegelii* is the only *Zhangixalus* species (Matsui et al., 2019). There, *Z. schlegelii* was observed to build foam nests on trees overhanging a lake at a height of 1–2 m above the water surface (Fukutani et al., 2020). Collectively, these findings suggest that microevolutionary processes and/or reproductive plasticity enable *Zhangixalus* species to utilize both arboreal and terrestrial oviposition sites in response to varying ecological conditions.

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