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# Notes on the reproductive biology of three Taiwanese species of the genus *Kurixalus* (Anura: Rhacophoridae)

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**Abstract:** The reproductive biology of Taiwanese arboreal frogs of the genus *Kurixalus* shows a distinct tendency towards arboreality or terrestriality. Four species breed in phytotelmata and feed the tadpoles with unfertilized eggs; one species has terrestrial eggs and its tadpoles develop in lentic water. Here we provide additional information on habitats, breeding biology and oviposition sites of *K. beryllíniris*, *K.* cf. *eiffingeri* and *K. idiootocus* obtained in northern and southeastern Taiwan. *Kurixalus beryllíniris* prefers tree trunk holes and considers the size of the cavity opening, rather than the height of the opening above the ground. *Kurixalus* cf. *eiffingeri* appears to be an adaptable species that reproduces in a wide spectrum of natural and artificial waterfilled cavities. Epiphytic plants do not play a significant role in the reproduction of these species.

**Keywords:** *Kurixalus beryllíniris*, *K.* cf. *eiffingeri*, *K. idiootocus*, phytotelmata

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## Introduction

Members of the genus *Kurixalus* Ye, Fei et Dubois, 1999 (Rhacophoridae) are small arboreal frogs inhabiting primary and secondary forests of southeastern Asia. Currently, 23–25 species are recognized in the area extending from northeastern India and southern China to the Malayan peninsula, Sumatra, Borneo, the Philippines, and Taiwan and Ryukyu islands (Nguyen et al. 2020, Dufresnes et Litvinchuk 2022, Frost 2023). The reproductive modes of most *Kurixalus* species are still unknown. However, the available information on oviposition sites, development of eggs and larvae and type of parental care demonstrates that the reproductive biology of some species shows a distinct tendency towards arboreality or terrestriality. While eggs and tadpoles of *K. yangi* Yu, Hui, Rao et Yang, 2018 from northeastern India, Myanmar and China (Yunnan Province) develop in lentic water (reproductive mode 1 sensu Haddad et Prado 2005), arboreal eggs and oophagous tadpoles of Taiwanese

*K. beryllliniris* Wu, Huang, Tsai, Lin, Jhang et Wu, 2016, *K.* cf. *eiffingeri* (an unnamed species), *K. pollicaris* (Werner, 1914), *K. wangi* Wu, Huang, Tsai, Lin, Jhang et Wu, 2016 and Japanese (southern Ryukyu Islands) *K. eiffingeri* (Boettger, 1895) develop in waterfilled tree and bamboo holes (reproductive mode 26 sensu Haddad et Prado 2005; see Kuramoto et Wang 1987, Wu et al. 2016, Yang et Lee 2019, Humptsoe et al. 2020). Another two species, Taiwanese *K. idiootocus* (Kuramoto et Wang, 1987) and closely related *K. silvaenais* Hou, Peng, Miao, Liu, Li et Orlov, 2021 from China (Sichuan Province), have terrestrial eggs and lentic tadpoles (reproductive mode 17 sensu Haddad et Prado 2005; see Kuramoto et Wang 1987, Yang et Lee 2019, Hou et al. 2021).

Although the reproductive biology of Taiwanese *Kurixalus* species is better studied than that of most other congeners, little attention has been paid to the question of whether there are any differences in reproductive places and behavior between the phytotelmata-using species. Due to the small ranges of *K. beryllliniris* and *K. wangi* (the first is distributed in the difficult-to-access mountains of southeastern Taiwan, the second is limited to the southernmost tip of Taiwan), only basic information on the reproduction of these species is currently available (Wu et al. 2016, Yang et Lee 2019). The situation also became rather confusing after the recent elevation of *K.* cf. *eiffingeri* and *K. pollicaris* to the specific level by Dufresnes et Litvinchuk (2022). Originally, both these species together with Japanese (southern Ryukyu Islands) *K. eiffingeri* sensu stricto were considered conspecific under the name *K. eiffingeri* sensu lato (e.g. Xiang et al. 2009, Wu et al. 2016). As a result of taxonomic changes, the detailed reproduction data of *K. eiffingeri* sensu lato from central Taiwan (e.g. Kam 1996, Kam et al. 1998a,b, Hsu et al. 2006, Lin et Kam 2008, Tung et al. 2015) apply to *K. pollicaris*, and the data obtained for *K. eiffingeri* sensu lato from the southern Ryukyu Islands (e.g. Ueda 1986, Sato et Iwai 2021) refer to *K. eiffingeri* sensu stricto. Interestingly, a reproductive biology of an unnamed species from northern Taiwan referred to by Dufresnes et Litvinchuk (2022) as *K.* cf. *eiffingeri* has not been the subject of such detailed studies as the populations from central Taiwan and the southern Ryukyu Islands.

In order to provide additional information on the reproductive biology of *K. beryllliniris*, *K.* cf. *eiffingeri* and *K. idiootocus*, we summarize our data on breeding sites of these species obtained during short-term field research in northern and southeastern Taiwan.

## Material and Methods

Data on reproductive biology of *Kurixalus beryllliniris*, *K.* cf. *eiffingeri* and *K. idiootocus* were obtained during short-term surveys of amphibian and reptile fauna carried out in three localities in southeastern and northern Taiwan:

*K. beryllliniris*: (1) Mountain broadleaved forest along the Lijia Industry Road (Ligia timber trail), Taitung County (22.82206 N, 121.01368 E to 22.80587 N, 121.03087 E, ca. 1000–1200 m a.s.l., 14–16 April 2023).

*K.* cf. *eiffingeri*: (2) Left bank of Jingualiao River, covered by a mosaic of broadleaved forest, bamboo growths and anthropogenic habitats, New Taipei City (ca. 24.88444 N, 121.66500 E to 24.89606 N, 121.67399 E, ca. 330–340 m a.s.l., 18 April and 25–26 April 2023), (3) peripheral area of the Fushan Botanical Garden overgrown by mountain broadleaved forest, Yilan County (ca. 24.76293 N, 121.58049 E, ca. 670 m a.s.l., 19–21 April 2023).

*K. idiootocus*: data on the biology of this species were obtained on localities number 2 and 3.

The study localities were repeatedly visited during day and night hours. Rosettes of epiphytic ferns, leaf axils of plants of the Araceae family, and holes in tree trunks were examined for anuran eggs and larvae. The following data on the breeding sites, eggs and tadpoles of *K. beryllliniris* and *K.* cf. *eiffingeri* were recorded (terminology adopted from Lin et Kam 2008): (i) type of the observed breeding place (tree hole, bamboo cup, artificial tube), (ii) height of the hole above the ground (height of the lower margin of the tree hole opening above the ground or bamboo stump height; in mm), (iii) maximum dimensions of the hole opening (maximum height and maximum width of tree hole, inner diameter of bamboo cup/artificial

tube; in mm), (iv) tree hole or bamboo cup depth (in mm), (v) distance of water level from the lower margin of tree hole opening or from the bamboo cup opening; in mm), (vi) water depth (in mm), (vii) number of eggs, (viii) number of tadpoles, (ix) presence of adults.

## Results

***Kurixalus berylliniris.*** In the area along the Lijia Industry Road, *K. berylliniris* inhabits steep mountain slopes covered by broadleaved cloud forest. The forest is characterized by the frequent occurrence of tree and epiphytic ferns (e.g. *Asplenium* sp. *Cyathea* sp., *Drynaria* sp.; Fig. 1A). A rare occurrence of conifers was recorded in the upper parts of the forest. At the time of the research, the forest was shrouded in clouds, and it rained heavily every day. The frogs were active after dusk; calling males were observed sitting on shrubs and trees 40–230 cm above the ground (Fig. 1B). During the day, adult individuals of *K. berylliniris* were hidden in aboveground vegetation (e.g. in a large rosette of epiphytic fern *Aplenium* sp. growing on tree ca. 350 cm above the ground). Other rhacophorid species found in sympatry with *K. berylliniris* included *Zhangixalus aurantiventris* (Lue, Lai et Chen, 1994) and *Z. moltrechti* (Boulenger, 1908). Reproduction of *K. berylliniris* was only observed in tree holes at the investigated locality (no eggs or tadpoles were found in fern rosettes or leaf axils). Of the 16 cavities found filled with rainwater (14 holes in trees, 2 holes in tree ferns), breeding was recorded in only five (for data on holes, eggs, and tadpoles see Table 1). *Kurixalus berylliniris* does not appear to be selective in the aboveground height of the tree hole, as the occupied hole height ranged between 22–450 cm (the upper limit is probably higher, as the treetops were inaccessible). The maximum opening width and height of the occupied holes were 120 and 240 mm (Table 1; no eggs or tadpoles were found in large open holes in stumps or lying logs). During rainy weather, the occupied holes were filled by rainwater up to the lower margins of their openings. The eggs were attached both in small compact clumps and individually on the wall of the hole above the water (Figs. 1D,E) or just at the level of the water surface (Fig. 1C). In one case, two clutches of different stage of development were present in one hole (Fig. 1D). The observed tadpoles were concentrated in the layer of leaf litter and detritus at the bottom of the hole, and ingested eggs were visible in the stomachs of some individuals (Fig. 1E). Despite repeated inspections of the tree holes during two subsequent nights, adult individuals were not observed within or in the vicinity of the holes. Numerous insect larvae lived in the water in all occupied cavities – mostly members of the families Culicidae (Diptera) and Scirtidae (Coleoptera).

***Kurixalus* cf. *eiffingeri.*** An adaptable species, able to occupy various types of natural and anthropogenic habitats. In the middle elevations (area of the Fushan Botanical Garden), it was encountered in the relatively well-preserved broadleaved forest, whereas in the lower elevations (along the Jingualiao River), it was common also in disturbed habitat along the riverbanks and roads. In the area of the Fushan Botanical Garden, the calling males occupied shrubs and trees up to ca. 5 m above the ground. At the Jingualiao River, they also called from bamboo growths and low vegetation along road ditches. In the latter area, the cavities in the bamboo stumps served as frequented diurnal shelters (Figs. 2A,D). Other rhacophorid species encountered syntopically with *K.* cf. *eiffingeri* included *Buergeria robusta* (Boulenger, 1909), *Kurixalus idiootocus* and *Zhangixalus taipeanus* (Liang et Wang, 1978) in the Fushan Botanical Garden, and *Buergeria* cf. *choui* Matsui et Tominaga, 2020, *B. robusta*, and *K. idiootocus* at the Jingualiao River. Depending on the type of habitat, the species uses a wider range of breeding sites. In the broadleaved forest of the Fushan area, only breeding in a tree hole (Fig. 3A) was observed. In disturbed habitats along the Jingualiao River, the frogs used both tree holes and bamboo stumps (Figs. 3B,C), and even metal tubes installed along the road ditch (Figs. 2C,E). The aboveground height of eight occupied holes did not exceed 90 cm, and the inner diameter of bamboo/metal tube cups ranged 35–50 mm (Table 1). Numerous larvae of Culicidae developed in all inspected bamboo stumps. Eggs of *K.* cf. *eiffingeri* were attached in small clumps (mostly in a single layer) just at the level of the water surface (Figs. 3A,B). However, the water depth fluctuated, depending on the current rainfall, so the

| Species | Hole characteristics, number of eggs and tadpoles, presence of adult individuals | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Type of the hole | Height above the ground (cm) | Maximum width and maximum height of the tree hole / inner diameter of bamboo cup (mm) | Tree hole or bamboo cup depth (mm) | Distance of water surface from the hole opening (mm) | Depth of water (mm) | Number of eggs | Number of tadpoles | Presence of adults |
| ***K. berylliniris*** | | | | | | | | | |
| Hole 1 | tree | 90 | 70 × 120 | 90 | 0 | 90 | 39 | 30+ | 0 |
| Hole 2 | tree | 85 | 80 × 100 | 100 | 0 | 100 | 34 | 15+ | 0 |
| Hole 3 | tree | 22 | 120 × 100 | 20 | 0 | 20 | 20+ | 0 | 0 |
| Hole 4 | tree | 104 | 50 × 60 | 60 | 0 | 60 | 20+ | 0 | 0 |
| Hole 5 | tree | 450 | 80 × 240 | 65 | 0 | 65 | 6+ | 0 | 0 |
| ***K.* cf. *eiffingeri*** | | | | | | | | | |
| Hole 1 | bamboo | 43 | 35 | 165 | 80 | 85 | 39 | 15+ | 0 |
| Hole 2 | bamboo | 36 | 40 | 150 | 70 | 80 | 20+ | 0 | 0 |
| Hole 3 | bamboo | 39 | 35 | 240 | 10 | 230 | 30+ | 0 | 0 |
| Hole 4 | tree | 90 | 90 × 190 | 120 | 70 | 50 | 0 | 0 | calling male |
| Hole 5 | bamboo | 75 | 50 | 190 | 90 | 100 | 0 | 20+ | 0 |
| Hole 6 | bamboo | 68 | 40 | 85 | 35 | 50 | 10+ | 10+ | 0 |
| Hole 7 | metal tube | 29 | 50 | 260 | 220 | 40 | 41 | 0 | a male guarding eggs |
| Hole 8 | tree | 60 | 20 × 55 | 40 | 0 | 40 | 10+ | 0 | a pair laying eggs |

**Table 1. Characteristics of the breeding sites of *Kurixalus berylliniris* along the Lijia forest road (Taitung County) and *K.* cf. *eiffingeri* in the area of Jingualiao river (New Taipei City; holes 1–7) and in the area of the Fushan Botanical Garden (Yilan County; hole 8).**

eggs were partially flooded in some cases. In holes containing both eggs and tadpoles, only eggs above water were observed. One of eight inspected holes contained tadpoles with ingested eggs, another contained metamorphosing tadpoles (Fig. 3C). The tadpoles left the water gradually on subsequent nights. The snout-vent length and the length of the tail of one freshly metamorphosed individual (Fig. 3D) were 12 and 9 mm, respectively. Adult individuals of *K.* cf. *eiffingeri* were present in three phytotelmata during the time of their inspections. One observed calling male sat on the edge of a tree hole opening and hid in the water in the cavity when disturbed. Another male probably guarded the eggs when sitting in their immediate vicinity inside the metal tube. Oviposition was observed in the Fushan area during a night after heavy rains. The female, with the male in amplexus, took up her position in the opening of the hole in the tree with the back of her body in the hollow. During fertilizations the male held his hind legs against the sides of the cavity and pressed the released eggs against the wall of the cavity with the back of his body (Fig. 3A).

***Kurixalus idiootocus*.** Along the Jingualiao River and in the Fushan area, *K. idiootocus* occupied the same habitats as *K.* cf. *eiffingeri* (Fig. 4A). At night, both adults and subadults were usually found in above-ground vegetation up to 10 m high (Fig. 4C,F). Bamboo stumps were among the daytime shelters around the Jingualiao River (Fig. 4B). In the Fushan area, adults descended to the ground during heavy rains, and males called from low vegetation and from rock shelters on the ground (Fig. 4D). A fresh clutch of eggs was found under a flat stone on a stony place near a small stream, where numerous choruses of calling males took place during the previous night (Fig. 4E).

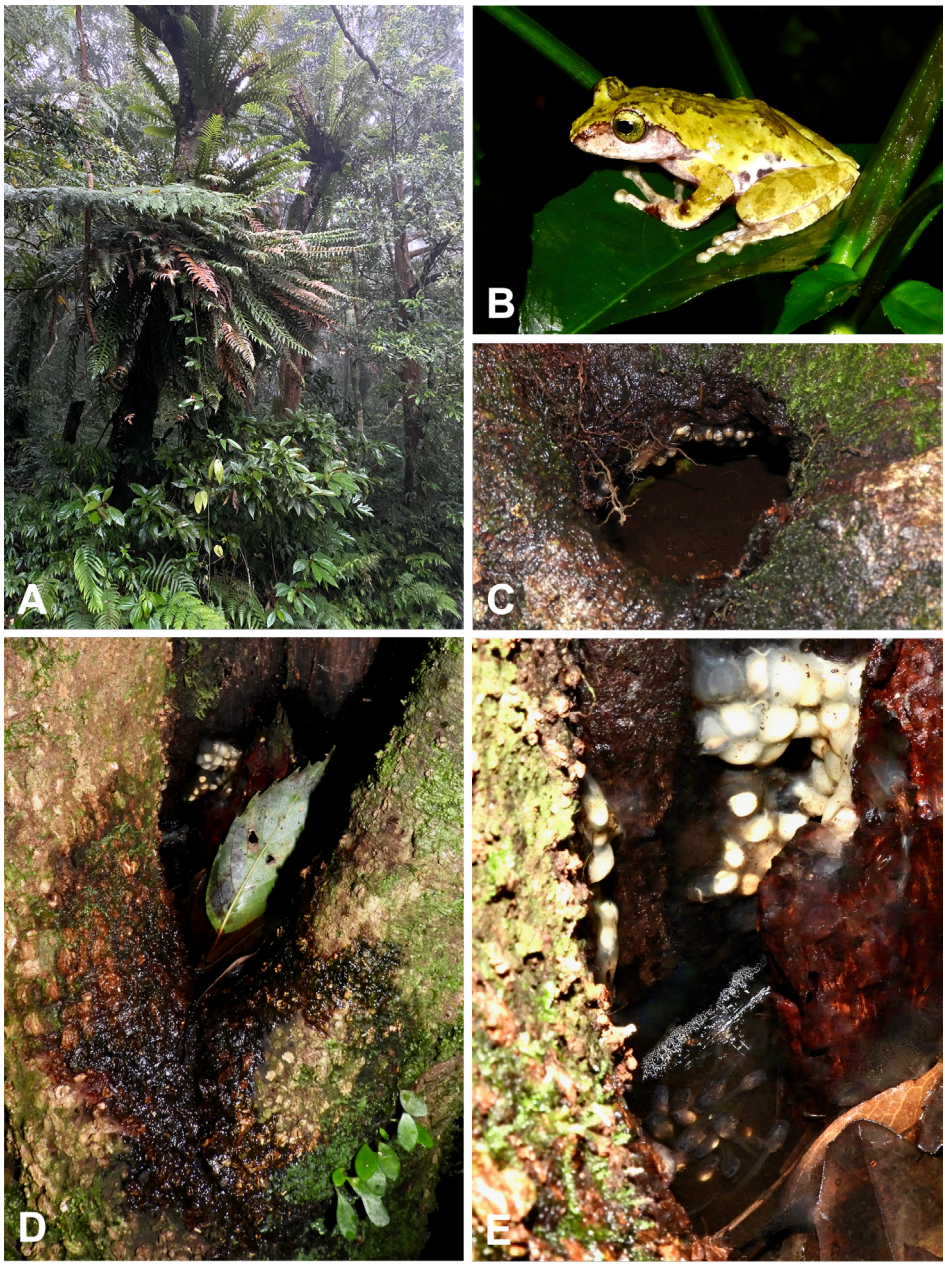


**Fig. 1. Habitat and breeding sites of *Kurixalus beryllíniris* at Lijia Forest Road (Taitung County). (A) Forest margin with *Drynaria* ferns dominating among epiphytic plants; (B) adult male of *K. beryllíniris* in calling position; (C) tree hole with eggs of *K. beryllíniris* attached at level of water surface; (D) eggs of *K. beryllíniris* in tree hole in *Quercus* cf. *longinus* – eggs of two different developmental stages attached above water; (E) tree hole with eggs and tadpoles of *K. beryllíniris* – ingested eggs visible in stomachs of some tadpoles. Photos: J. Moravec.**


**Fig. 2.** Habitat and breeding sites of *Kurixalus* cf. *eiffingeri* at Jingualiao River (New Taipei City). (A) Bamboo stumps serving as diurnal shelters and breeding places of *K.* cf. *eiffingeri*; (B) adult female of *K.* cf. *eiffingeri*; (C) adult male of *K.* cf. *eiffingeri* at opening of metal tube; (D) adult female of *K.* cf. *eiffingeri* in diurnal shelter inside bamboo stump; (E) metal tube serving as breeding site of *K.* cf. *eiffingeri*. Photos: J. Moravec.


**Fig. 3. Breeding sites, eggs, tadpoles and metamorphs of *Kurixalus* cf. *eiffingeri*. (A) Pair of *K.* cf. *eiffingeri* in amplexus laying eggs in tree hole in Fushan area (Yilan County); (B) eggs of *K.* cf. *eiffingeri* at water level in bamboo stump; (C) metamorphosing tadpoles of *K.* cf. *eiffingeri*; (D) fresh metamorph of *K.* cf. *eiffingeri* leaving bamboo stump (Figs. B–D taken around Jingualiao River, New Taipei City). Photos: J. Moravec.**

## Discussion

*Kurixalus berylliniris* was distinguished from *K. eiffingeri* based on genetic, morphological and call differences (Wu et al. 2016). It is also stated in the original description that *K. berylliniris* differs from *K. eiffingeri* in its reproductive season (November to February vs. February to August in *K. eiffingeri*), and that its eggs and tadpoles were found in pooled water in decaying trunks of tree ferns *Cyathea spinulosa*. According to our observation made 1–3 km southeast of the species type locality, *K. berylliniris* can also reproduce in April. However, *K. berylliniris* probably has a greatly extended breeding season, as indicated by Hsu et al. (2006), who provided data on seasonal activity of the *Kurixalus* population from eastern Taiwan, representing today's *K. berylliniris.* Our observations also show that *K. berylliniris* is less selective in breeding sites, and commonly breeds in tree trunk holes. At the surveyed locality, tree holes

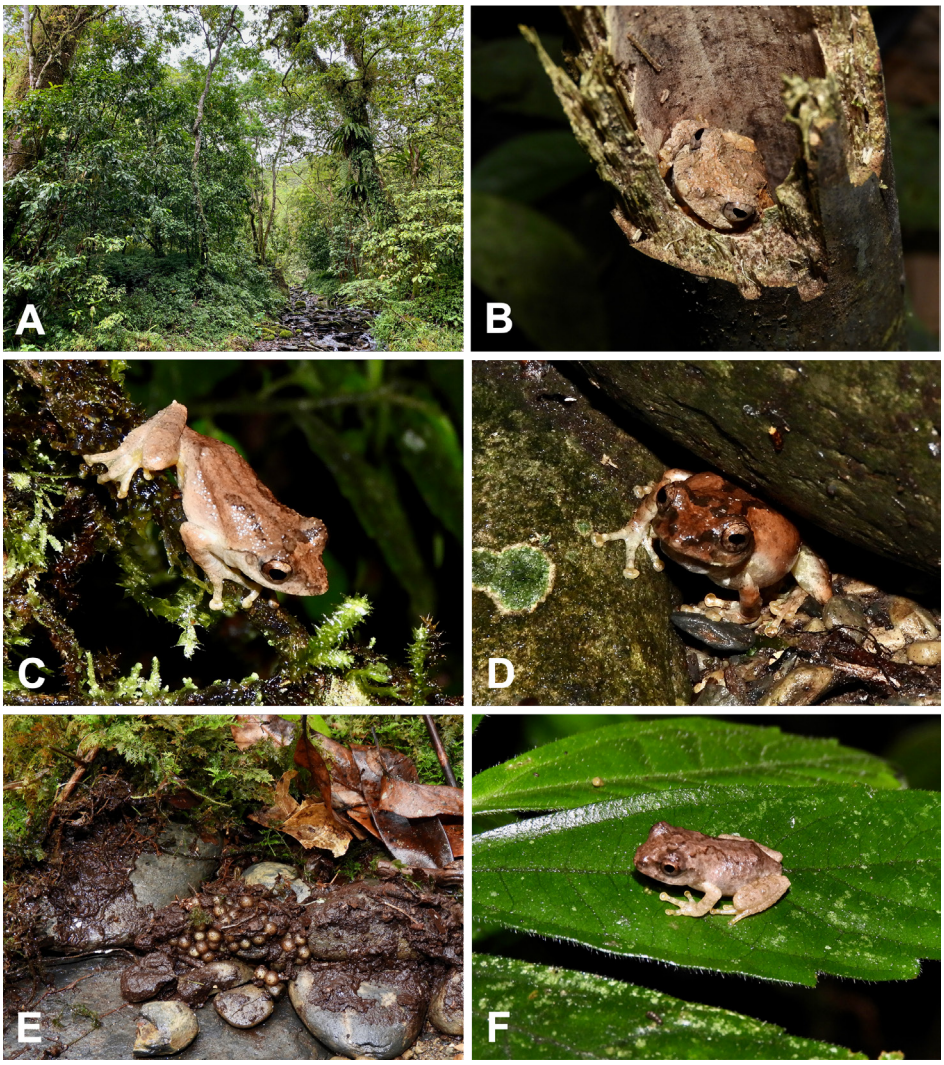


**Fig. 4. Habitat and breeding sites of *Kurixalus idiootocus*. (A) Habitat of *K. idiootocus* in Fushan area (Yilan County); (B) adult female of *K. idiootocus* in diurnal shelter in bamboo stump at Jingualiao River, New Taipei City); (C) adult male of *K. idiootocus* descending aboveground vegetation; (D) adult male of *K. idiootocus* calling from entrance to oviposition site beneath flat stone; (E) clutch of freshly laid eggs deposited beneath stone; (F) juvenile individual of *K. idiootocus* in aboveground vegetation (Figs. C–F taken in Fushan area). Photos J. Moravec.**

occurred much more frequently than holes in the trunks of tree ferns. It appears that the frogs did not consider the height of the cavity above the ground, but rather the size of the cavity opening. A more opportunistic choice of nest sites (e.g. bamboo stumps) is also shown in the photographs published by Yang et Lee (2019).

It appears generally that *Kurixalus* cf. *eiffingeri*, an unnamed species from northern Taiwan, is an adaptable species that can breed in a wide spectrum of natural and artificial waterfilled cavities. However, it is likely that, depending on the nature of the habitat, it may prefer cavities that better protect eggs and tadpoles from predation and desiccation. Such

selective behavior was documented in *K. pollicaris* (originally considered *K. eiffingeri*) in an experimental bamboo forest in the cloud forest zone in central Taiwan (Kam et al. 1996, Kam et al. 1998a, Lin et Kam 2008, Tung et al. 2015). Similarly, *K. eiffingeri* sensu stricto from the southern Ryukyu Islands, which breeds in waterfilled tree holes and leaf axils (Ueda 1986) selects higher tree holes and holes with a larger opening angle to avoid the greater predation risk present in lower tree holes with a steeper opening (Sato et Iwai 2021).

Breeding in phytotelmata (arboreal eggs and oophagous tadpoles developing in water-filled tree holes – reproductive mode 26 sensu Haddad et Prado 2005) represents a successful reproductive strategy of four Taiwanese *Kurixalus* species. It is associated with arboreality, and may be particularly advantageous for life in wet forests on steep mountain slopes, where stagnant water reservoirs are rare. An inspection of epiphytic plants (mainly ferns of the genera *Asplenium* and *Drynaria*) carried out at all investigated localities showed that *K. berylliniris* and *K.* cf. *eiffingeri* do not use epiphytes for reproduction, but rely mostly on phytotelmata. In comparison with Neotropics, where epiphytic plants (especially bromeliads with extensive water tanks) play an important role in reproduction of many anuran species (e.g. Ladino et al. 2019), native epiphytic plants with suitable water tanks are not found in Taiwan. On the other hand, Old World epiphytic ferns forming leaf rosettes, like Neotropical bromeliads, can also provide important services to frogs – for example cool and moist daytime shelters or breeding sites for frogs with direct egg development (Scheffers et al. 2014, Ortega-Solis et al. 2021). Our observations demonstrate that at least *Asplenium* rosettes can serve as diurnal shelters for *K. berylliniris.*

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