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REPRODUCTION AND TERRRESTRIAL DIRECT DEVELOPMENT IN SRI LANKAN SHRUB FROGS (RANIDAE: RHACOPHORINAE: *PHILAUTUS*)

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ABSTRACT. – Two distinct nesting behaviours are reported from 98 clutches (80 in situ and 18 ex situ) of 17 species of direct-developing *Philautus* from Sri Lanka. The species examined, belong to three communities spanning 400–2,200 m elevation. Sixteen species are 'ground nesters', depositing 6–155 cream or white eggs in 5–35 mm deep nests excavated by the female in the rainforest floor. This is the first record of terrestrial egg burying in soil by the direct-developing anurans, a behaviour commonly employed by tetrapod reptiles. A single species (*Philautus femoralis*) however, is an arboreal nester, depositing 7–22 green, adhesive eggs in a disc-like mass on the underside of leaves. Parental care is not provided by any of the species.

Larval development in *Philautus* differs from the Neotropical direct-developing leptodactylid, *Eleutherodactylus coqui:* the former lack external gills and have a rudimentary cement gland, a coiled gut and a larger, spatulate, heavily vascularized tail. They also lack an egg tooth. The first two of these apparently primitive characters have so far been observed only in aquatic anuran tadpoles and not in direct-developing larvae. Furthermore, the *Philautus* larvae studied possess atrophied internal gills, respiration apparently being facilitated primarily via the tail.

KEY WORDS. – direct development, *Philautus*, Rhacophorinae, staging table, ground nesting, conservation

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INTRODUCTION

Sri Lanka is considered a global amphibian hotspot (Meegaskumbura et al., 2002; Manamendra-Arachchi & Pethiyagoda, 2005). A survey of anurans in about 350 locations in Sri Lanka during the period 1993–2003 served to uncover a large number of new species of frogs, the vast majority of them tree frogs of the genus *Philautus* (Meegaskumbura et al., 2002). Recently, a similar diversity of anurans has been announced also in the Western Ghats of India (Biju, 2001).

Based essentially on indirect evidence—the chance discovery clutches of large terrestrial eggs containing embryos—rather than observations of reproductive ethology, it has long been known that some Sri Lankan rhacophorines now assigned to *Philautus* have terrestrial direct-developing eggs (Günther, 1876; Ferguson, 1876; Kirtisinghe, 1946, 1957; Dutta & Manamendra-Arachchi, 1996). Dring (1979) showed that the type species of *Philautus*, *P. aurifasciatus* too, is a direct developer (see also Alcala & Brown, 1982), while Yong & Ramly (1987) described direct development of *Philautus* from Malaysia.

Eleven genera of Ranidae (including Rhacophorinae and Mantellinae) are known to exhibit direct development of which however, only *Philautus* and *Taylorana* are distributed in Asia (Thibaudeau & Altig, 1999). Marmayou et al. (2000) showed that endotrophy had arisen independently in these two genera, while Bossuyt & Milinkovitch (2000) showed that direct development, among other remarkable similarities, between *Mantidactylus* (Mantellinae, until then considered a subfamily within Rhacophoridae) and *Philautus* are in fact the result of remarkable convergence.

Although about 110 nominal species of *Philautus* are recognized as valid (Bossuyt & Dubois, 2001; Manamendra-Arachchi & Pethiyagoda, 2005), terrestrial direct development in this genus has been observed in relatively few species. Dring (1987) observed reproduction in Sunda Shelf species, while Kanamadi et al. (1996) and Patil & Kanamadi (1997) observed direct development in an Indian species of *Philautus*. Arboreal direct development has also been observed in the Indian species *P. bombayensis* (see Bossuyt et al., 2001), *P. tinniens* (see Bossuyt & Dubois, 2001) and *P. glandulosus* (see Biju, 2003). None of these authors however, provided data beyond the breeding event itself.

The discoveries of significant hitherto unsuspected species richness within this genus in Sri Lanka and the Western Ghats, both of which are generally considered herpetologically ‘well studied’, suggests that the radiation of *Philautus* in tropical Asia could parallel that of the direct-developing *Eleutherodactylus* (Leptodactylidae), a remarkably speciose genus which includes over 600 Neotropical species. While development in a handful of *Eleutherodactylus* species, especially *E. coqui,* has been well studied (Townsend & Stewart, 1985, 1994; Ovaska & Rand, 2001; Rogowitz et al., 2001; see also Callery et al., 2001 and references therein), hardly any data are available on reproductive ethology and development in *Philautus*.

It now seems likely that Thibaudeau & Altig’s (1999) reckoning that direct developers comprise about 1,000 of the world’s approximately 5,000 amphibian species (Hanken, 1999; Stuart et al., 2004) was in fact an underestimate. Despite the frequency of this developmental mode however, the terrestrial and arboreal eggs of endotrophic anurans are usually well-concealed and difficult to find, making direct observation problematical. Indeed, Thibaudeau & Altig (1999) noted with some justification that “developmental data on endotrophic anurans generally are sparse or absent.” Here we attempt to address this deficiency by presenting data on reproduction and development in 17 species of Sri Lankan *Philautus*, which includes a cloud-forest community of nine species in the central highlands of the island.

Our study has also been motivated by the need to develop captive breeding techniques as a tool of last resort for the ex situ conservation of Critically Endangered species. Given that a large number of Sri Lankan *Philautus* species have already become extinct (Stuart et al., 2004; Manamendra-Arachchi & Pethiyagoda, 2005), and given population declines or extreme rarity in others, it is imperative that methods for large scale ex situ conservation programmes be developed and made available.

MATERIALS AND METHODS

Breeding behaviour (both in captivity and in the wild: see Table 1) was observed in 17 species of *Philautus* at the four sites listed below, principally at Site 1, incidentally at other sites. Three of the 17 species are as yet undescribed, and are referred to here by comparison with species they resemble: *Philautus* cf. *alto, P.* cf. *silus* and *P.* cf. *sordidus*.

***Site 1.* – WHT Field Station** (06º50’N, 80º40’E, 1,650 m above sea level) adjacent to the 61.9 km^2 Agra-Bopath Forest Reserve in the central highlands of Sri Lanka. We selected twelve species for captive breeding (*Philautus alto*, *P. asankai*, *P. caeruleus, P. femoralis*, *P. frankenbergi, P. microtympanum*, *P. schmarda*, *P. sarasinorum*, *P. silus*, *P.* cf. *silus, P.* cf. *sordidus* and *P. viridis*). Nine of these inhabit secondary forest and scrub in the 25 ha Wildlife Heritage Trust field station site (06º50’36” N, 80º40’37” E; alt. 1,650 m) and adjacent forest. The other three species were from Horton Plains (2,135 m alt., 06º46’ N, 80º47’ E, *Philautus frankenbergi*), Peak Wilderness (on the Bogawantalawa-Balangoda road, 1,300 m alt., 06º45’ N, 80º42’ E, *P. caeruleus*), and Check Polleat Gap (900 m alt., 06º56’ N, 80º30’ E, *Philautus* cf. *silus*).

Temperatures at Site 1 vary from daily minima in the range 12.3–22.1ºC, to maxima in the range 18.9–28.1ºC. Annual rainfall at the site is approximately 2,000 mm yr^{-1} (the nearest meteorological station, at Nuwara Eliya, 06º57’N, 80º47’E, at an altitude of 1,710 m records an annual average rainfall of approximately 1,900 mm). Relative humidity is high (>70%) throughout much of the year, reaching 100% during periods of mist cover. Wind speeds during the southwest monsoon (May–September) are typically high (12–20 km hr^{-1}), reaching a maximum of 86 km hr^{-1} during the study period.

***Site 2.* – Peradeniya**, near Hantana (07º16’36” N, 80º37’E, 600–1,000 m) and Gannoruwa (07º17’ N, 80º35’ E, altitude 600 m) Forest Reserves, for *Philautus hallidayi, P. rus*, *P. sarasinorum*, *P.* cf. *sordidus* and *P. zorro*.

***Site 3.* – Eastern Sinharaja** (06º24’ N, 80º38’ E, altitude 1,060 m) for *P. decoris*.

***Site 4.* – Knuckles** mountains (07º24’ N, 80º47’ E, altitude 1,100 m) for *Philautus* cf. *alto* and *P. femoralis.*

***Captive breeding.* –** Mature imagos of the 17 species of *Philautus* studied here were maintained in terraria for up to 30 months, fed on wild-collected grasshoppers, crickets and cultured fruit flies, coated with Sera® Reptimineral C vitamin powder. The frogs were reared in all-glass terraria, 60×30×30–75×75×45 cm (l×w×h) in dim light comparable with that of the forest understorey. No artificial lighting was used. The terraria were provided with a substratum of humus-rich forest topsoil about 5–10 cm deep, about 50% of the floor area being covered with an approximately 3 cm deep layer of leaf litter from the forest floor. Branches from native local shrubs and potted plants were provided as perches. In-terraria relative humidity was maintained at > 90% using a hand-operated horticultural sprayer at least three times daily at approximately 8 h intervals. A few frogs developed eye infections, which we suspect was contracted from bacteria in the stream water used for spraying: given their wholly terrestrial life cycle, these frogs would not normally come into extended contact with surface water, which may contain pathogens not found in rain/mist water. Bacterial cultures showed these infections to be the result of coliform and beta haemolytic streptococci (Group C) bacteria; these were treated successfully with ophthalmic chloramphenicol application.

Climate data (accuracy: rainfall to ±0.2 mm; temperature to ±0.5ºC; wind speed to ±1 km hr^{-1}; and relative humidity to ±5%) at Site 1 were measured and logged on a Davis Weather Monitor II system using Weatherlink® software. Additionally, in-terraria temperature and humidity were measured on an Oregon Scientific® EMR963HG cable-free thermo-hygrometer (accuracy ±0.1º C). Metric measurements were made using dial vernier callipers (accuracy ±0.05 mm). Specimens and ova were weighed on a Acculab® PP-2060D electronic balance (accuracy ±1 mg).

Abbreviations of larval measurements are as follows: BD (body depth), maximum depth of head and body; BW (body width), maximum width of body; HBL (head-body length), distance from tip of snout to posterior extremity of body; TD (tail depth), maximum depth of the tail including fin; TL (total length), distance from tip of snout to tip of tail.

Eggs and embryos were preserved in a solution of equal parts (by volume) of 10% buffered formalin and 70% ethanol. All the specimens preserved in this study, mostly embryos, are in the collection of the Wildlife Heritage Trust of Sri Lanka, registration numbers WHT 5473–5784. After study, adult frogs and most froglets were released at the same locations from which they had originally been collected.

A simple regression analysis was performed for data on the 8 species of ground nesting *Philautus*, *P. alto*, *P. asankai*, *P. microtympanum*, *P. sarasinorum*, *P. schmarda*, *P. silus*, *P.* cf. *sordidus* and *P. viridis*, from the Agra-Bopath community to investigate the relationships between mean female snout–vent length and the means of the following variables: male snout–vent length; number of eggs per clutch; mass of eggs; egg diameter; egg-mixing duration; nest-covering duration; and incubation time.

RESULTS

Breeding behaviour. – All 17 species of *Philautus* bred in captivity. Observations of breeding in 10 species were also made in the wild (see Table 1). Despite in-terrarium relative humidity being maintained > 90% through frequent spraying, mating always coincided with episodes of heavy rainfall and/or mist cover, usually accompanied by high (80–100%) ambient relative humidity (Fig. 1).

Table 1. The number of successful matings observed in captivity and in the wild for 17 species of Sri Lankan *Philautus,* including three undescribed species.

species	number of matings	
	in captivity	in the wild
Philautus alto	20	2
Philautus cf. *alto*	3	1
Philautus asankai	3	1
Philautus caeruleus	1	–
Philautus decoris	1	–
Philautus femoralis	11	2
Philautus frankenbergi	1	1
Philautus hallidayi	2	1
Philautus microtympanum	4	2
Philautus rus	2	–
Philautus sarasinorum	3	1
Philautus schmarda	1	–
Philautus silus	5	–
Philautus cf. *silus*	1	–
Philautus cf. *sordidus*	2	–
Philautus viridis	19	6
Philautus zorro	1	1
total	80	18

The 17 species studied exhibited two distinct reproductive behaviours: (a) depositing eggs in soil on the forest floor (16 species); and (b) depositing adhesive eggs on the leaves of understorey shrubs (one species, *Philautus femoralis*).

Ground nesting. – (see Figs. 2 and 3). Excluding *P. femoralis,* Sri Lankan *Philautus* males perch and vocalize from the branches of trees and shrubs 0.3–5 m above ground, or in terrarium, from the leaves of plants (15–40 cm above floor level). In the forest, males are entirely arboreal, descending to the forest floor only to nest. Males advertise throughout the year and during daytime, but more intensively at night, especially during periods of rainfall and episodes of high (>80%) relative humidity (Fig. 1). Females usually occupy the lower branches of understorey shrubs.

In terrarium, courtship commences with the male calling from his perch (Fig. 2a) and a female advancing towards him (Fig. 2b). Ripe ova are externally visible in females in mating condition (Fig. 2b) except in *P. schmarda*, the only species with heavily tuberculated skin among the species studied; large eggs are visible in all ripe females however, in ventral view. Males were never observed to move from their perches until visual contact was made with the female prior to amplexus (Fig. 2b). The male then moves towards the female and engages in axillary amplexus (sensu Duellman & Trueb, 1986) while still perched on a branch or, in some species, on the ground (Fig. 2c). The male ceases to call once amplexus commences, whereupon the pair descends to the forest floor (Figs. 2d; 3a). By this time their dorsal and lateral coloration changes to match that of leaf litter or soil (Figs. 2j, k; 3a).

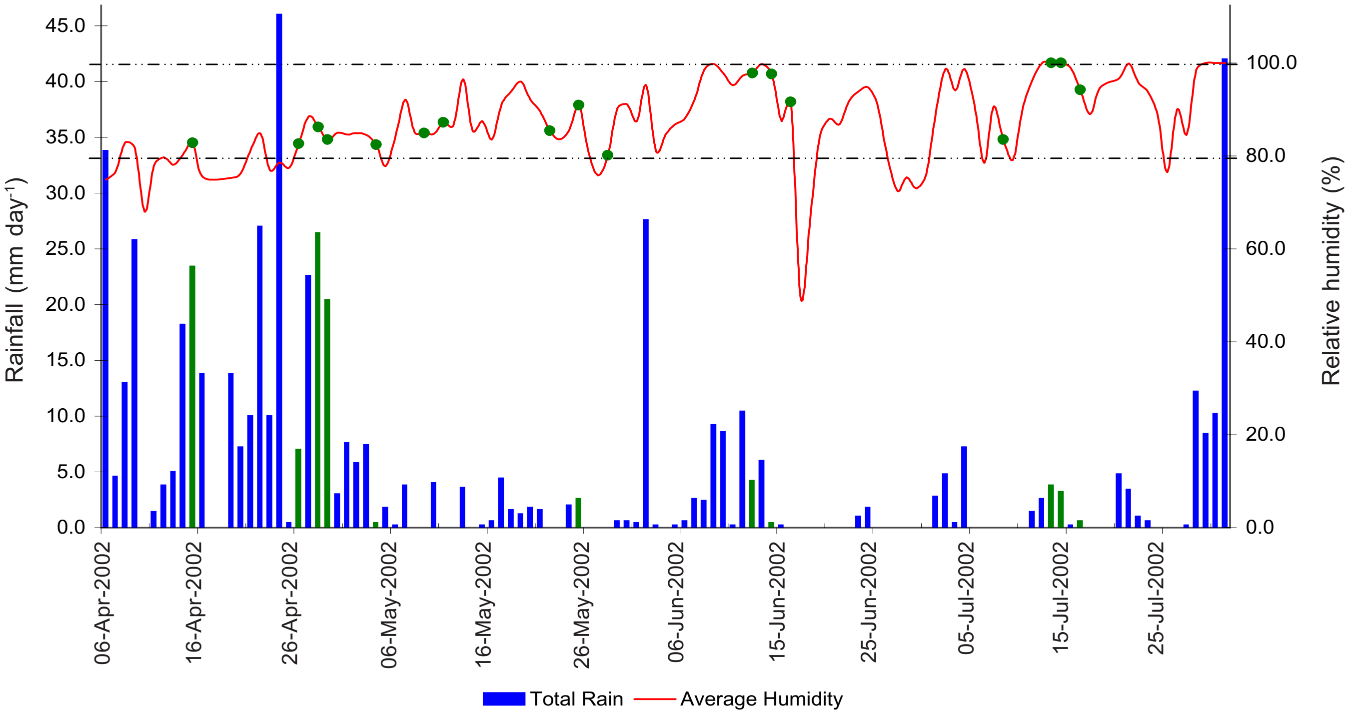

Fig. 1. Relative humidity (percent) and rainfall (mm day^{-1}) from April to July 2002 at the WHT field station, indicating in green the dates on which *Philautus* mating occurred (weather data for few days are unavailable), usually at the onset of periods of sustained rainfall and when relative humidity was 80–100 %.

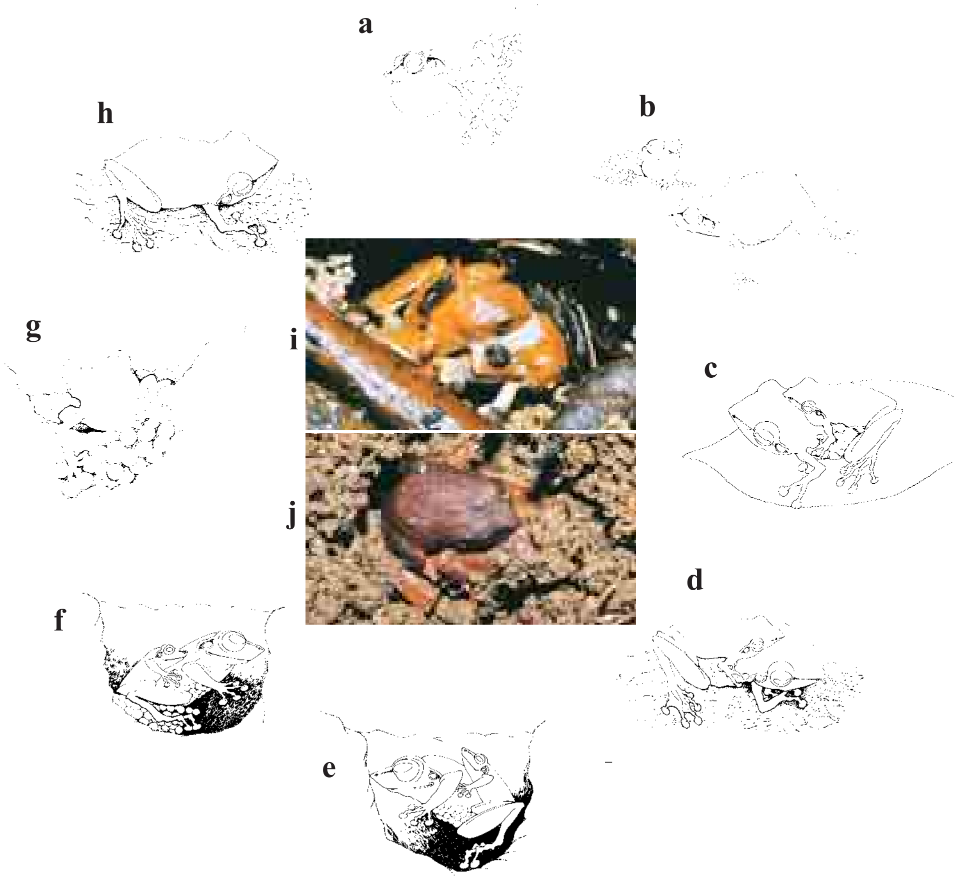

Fig. 2. Mating behaviour of ground-nesting *Philautus*. a, a male calls from his perch; b, ripe female approaches male; c, amplexus occurs on a branch; d, the pair descends to the forest floor, the female locates a suitable nest-site and commences excavation; e, female uses snout and rear limbs to widen the cavity; f, oviposition occurs within the nest cavity; g, after oviposition, the male departs and the female uses her hands to mix the eggs with soil; h, after mixing, she uses her hands to cover the nest with soil and then abandons it; i, a pair of *Philautus viridis* excavate a nest in soil (a few leaves have been removed to facilitate the photograph); j, a pair of *P. viridis* excavate a nest in bare soil.

The female then locates a suitable patch of ground on which to nest, usually under leaf litter in moist soil (Fig. 3b). There, with the male still in axillary amplexus, she excavates a cavity 1.5–50 cm^3 (Figs. 2, 3c) using primarily her forelimbs and to a lesser extent her hind limbs and snout (Fig. 2f). Moist soil is scooped to the sides using both hands sequentially, completing 3–9 strokes with one hand before changing to the other. As excavation proceeds, the female slowly revolves her body clockwise and anti-clockwise, using her hind limbs and snout to shape and enlarge the excavation. Body rotation occurs in steps of about 60–180º at a time. From the inception of nest excavation to oviposition the female keeps her head depressed against the nest wall. A single pair each of *P. alto* and *P.* cf. *sordidus* used only their hind limbs and snouts to excavate the cavity, rotating their bodies as in other species; but this may have been because the soil was saturated with water—these species may use burrowing methods similar to the other species when in unsaturated soil.

Amplexus lasts 1.5–29.5 hr, during which 6–155 eggs, 3.7–5.7 mm in diameter, are laid (Figs. 2f, 3d). After oviposition, the female begins mixing the eggs with soil and the male dismounts and returns to a perch. Egg mixing is performed by the female alone (Figs. 2g, 3e) using her hands and rotating her body as in nest excavation. Mixing results in the eggs being mixed with sperm and covered with grains of sand and decaying leaf matter, while absorbing water from the moist soil. This action serves also to separate the eggs from one another, possibly facilitating increased respiration. After mixing the eggs, the female depresses the clutch into the cavity by swivelling her body 1–4 rotations in either sense, and then loosely covers the nest with soil and debris using her hands (Fig. 2i) and sometimes her snout, employing the same actions as in nest cavity excavation, following which she abandons the clutch. We noted also that the eggs absorb water during the mixing process, resulting in a volume and weight increment of 165–185% and 90–95% respectively in the case of *P. viridis* eggs, the only species for which this was quantified.

Regression analysis shows that for mating pairs, female SVL is strongly correlated to average number of eggs ($R^2 = 0.929$) and male snout–vent length ($R^2 = 0.822$) (Fig. 7) but not egg size or other variables ($R^2 = <0.29$). Incubation takes from 24–68 days, with imagos emerging between stages 12–14 (see staging table, Fig. 5, Table 2), with or without the tail fully absorbed but with the yolk sac still visible. All ground-nesting *Philautus* froglets show adult colouration.

Leaf nesting.– (see Fig. 4). The breeding sequence of the arboreal, leaf-nesting *Philautus femoralis* commences as for the ground-nesting species, with the male advertising while perched on a leaf about 0.3–3 m above ground. A gravid female with ripe eggs (Fig. 4a) approaches the male, whereupon axillary amplexus occurs (Fig. 4b). The pair in amplexus do not descend to the ground as in ground-nesting species, but the female selects a leaf suitable for deposition of eggs, about 0.3–2 m above ground, on which she deposits 7–22 (n = 13) adhesive, green eggs while the male fertilizes them (Fig. 4c). Unlike the ground-nesting species, mating *P. femoralis* do not appear to alter colour at any stage of the reproductive process. During egg laying the male places his vent on the leaf, slightly below the female's vent, and thrusts each egg under the female's body as he fertilizes the clutch. The male departs soon after the last egg is laid, while the female sits on the adhesive eggs from 1–3 h, occasionally pressing an egg down more firmly using her feet (Fig. 4d). When compared with ground nesters, the females of *P. femoralis* do not revolve their bodies on the egg clutch or attempt to camouflage the

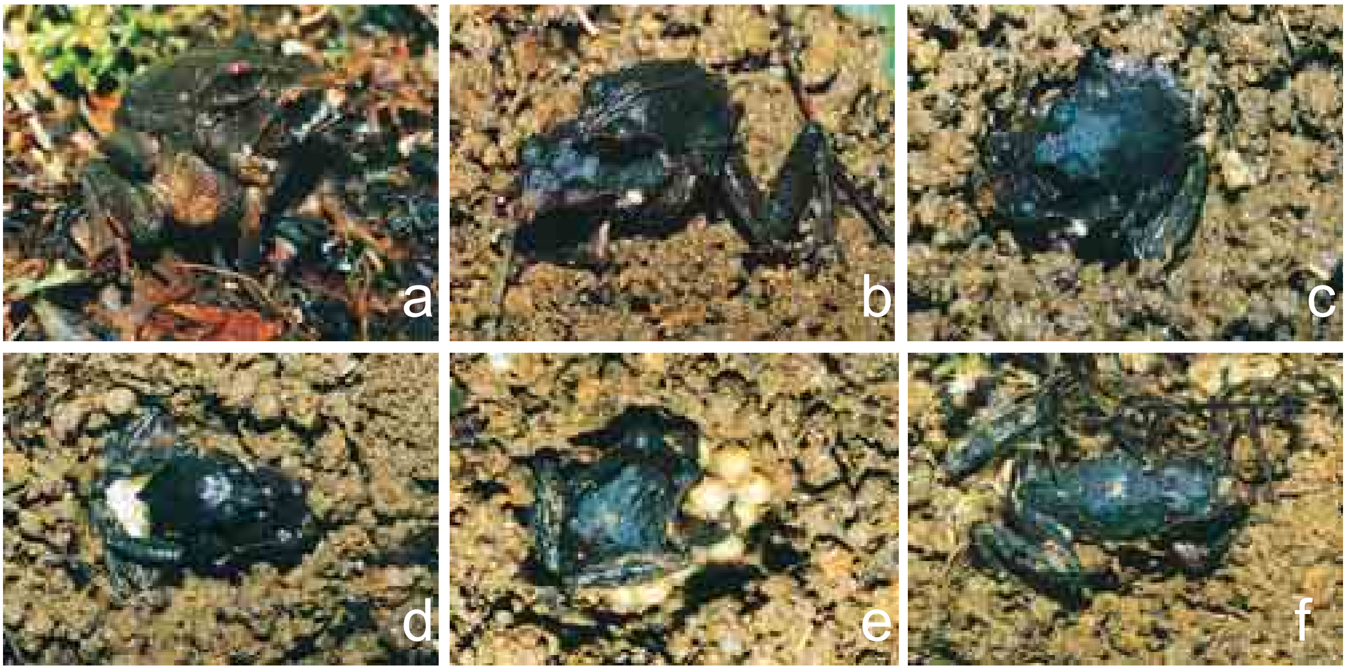

Fig. 3. Egg-laying sequence of *Philautus alto* from Agarapatana. a, the pair in amplexus descend to the ground; b, the female selects a nesting site and starts excavating a nest pit; c, a further stage of digging the nest pit; d, laying eggs inside the pit, while the male is still in amplexus; e, the female mixes the eggs and soil together after the male's departure; and f, the female covers and camouflages the nest pit, and abandons it.

nest. The female then abandons the clutch (Fig. 4e). Brown-black froglets emerge (Fig. 4f) 37–49 (n = 5) days later.

The eggs of both ground- and leaf-nesting species of *Philautus* are intolerant of desiccation. Three clutches of *P. femoralis* were rendered unviable following a three-day period during which relative humidity was reduced to < 75%. Similarly, egg clutches (n = 6) of ground nesting species became unviable following exposure to air or by failure to moisten the soil for 4–5 days during periods of low (< 75%) relative humidity.

Juveniles of all ground nesting species were observed on leaf litter throughout the year, but were more abundant during periods of havy rainfall. *Philautus femoralis* juveniles and clutches, however, were seen only during periods of sustained rainfall, especially during the May–September southwest monsoon.

Direct development in Sri Lankan Philautus. – Fourteen stages (Fig. 5, Table 2) are distinguishable in the development of the *Philautus* species reported on here. Post-larval growth in the first 12 months was recorded for a single species, *Philautus* cf. *sordidus*, at which point the juveniles had reached, on average, 63% and 68% of adult male and female SVL, respectively. Males among these began vocalizing at 15 months.

Description of embryos. – *Philautus silus*. Stages 6–13. General description: eyes laterally orientated; mouth subterminal, open, lower and upper lips prominent.

Stage 6 (WHT 5625). BH 3.0 mm, BW 3.4 mm, HBL, 4.5 mm, TD, 2.0 mm, TL, 6.6 mm. Snout rounded in all aspects; lower eyelid not visible; endolymphatic calcium deposits visible; mouth width 0.8 mm; forelimbs concealed under opercular

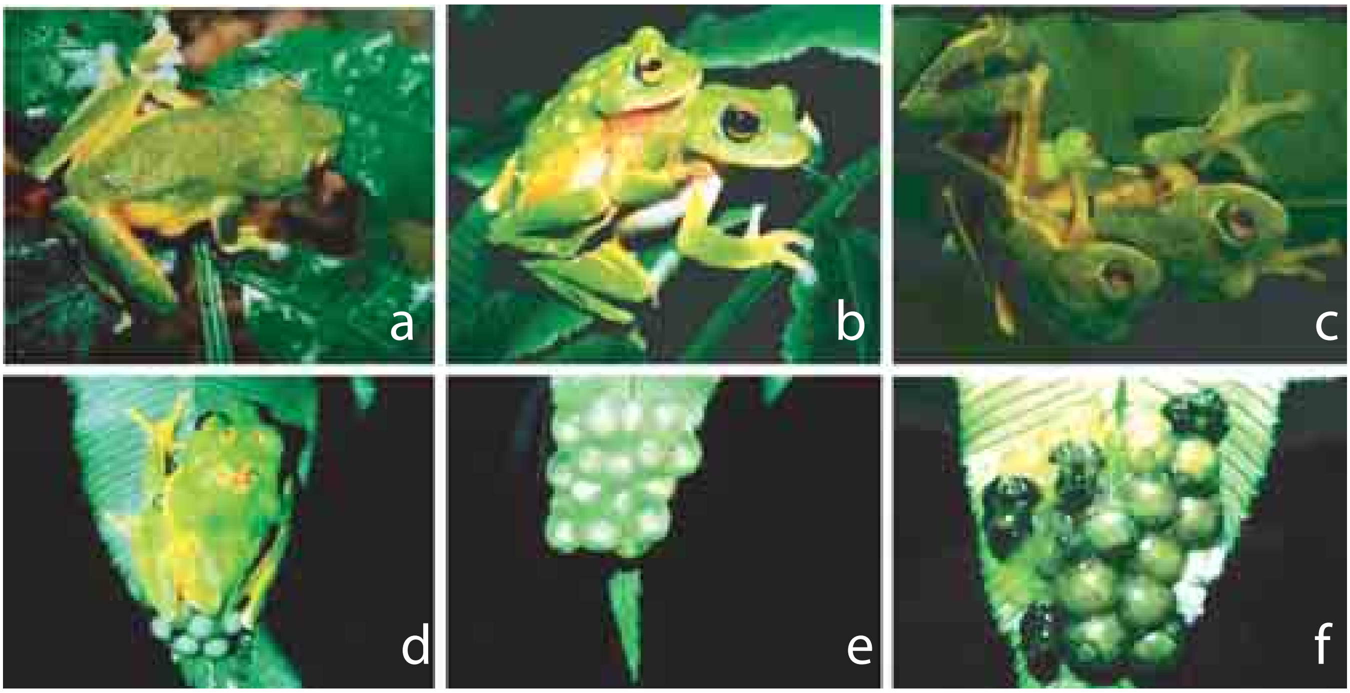

Fig. 4. Egg laying sequence of *Philatus femoralis* from Agarapatana. a, the female in breeding condition approaches a male; b, the pair engage in amplexus on a leaf; c, the female lays eggs on the underside of the leaf while the male fertilizes the eggs; d, the female sits on the clutch after the male departs; e, the developing clutch; f, froglets emerge from the nest.

Fig. 5 (opposite page). Developmental stages 1–14 of *P. viridis*. Stage 1 (dorsolateral aspect), egg unpigmented, creamy white, no limb-buds visible, neural groove closed, head and tail ends differentiable; Stage 2, a (lateral aspect), front limb-buds feebly defined; cement gland visible; b (dorsal aspect), hindlimb-buds distinct, tail bud visible; Stage 3, a, b (lateral aspect), unpigmented subdermal eyes visible; mouth opens; tail about twice its length at Stage 2, laterally curved left or right; endolymphatic calcium deposits visible; cement gland visible; Stage 4 (lateral aspect),dorsal and lateral surface of yolk sac pigmented; eyes pigmented, not subdermal; nostrils appear; tail about ¼ diameter of yolk-sac, almost its maximum length; hind-limb buds elongate; cement gland indistinct; Stage 5 a (posterior aspect); b, hind limb bud of tadpole; notch separating toes 4 and 5 distinct; Stage 6 a (posterior aspect), toe 3 demarcated; coiled gut forms; b, hind limb, toe 3 demarcated; Stage 7 a (posterior aspect), toes 1 and 2 demarcated; toes 3, 4 and 5 clearly separated; b, hind limb, toes 3, 4 and 5 clearly separate; c, hind limb, toes 1 and 2 demarcated; toes 3–5 clearly separate; Stage 8 a (lateral aspect), tips of toes enlarged, 'elbow slit' appears in forelimbs, still concealed under opercular fold; lower eyelid appears; b, hind limb, toes 1–5 distinctly separated; Stage 9 (lateral aspect), forelimb elbow emerges; hand subdermal; Stage 10 (lateral aspect), forelimbs fully emerged; nictitating membrane visible; metatarsal tubercle distinct; subarticular tubercles visible on toes; tail fin spatulate, fully developed; Stage 11 a (lateral aspect), digits enlarged, rounded; palmar tubercles visible; b (ventral aspect of hand), enlarged digits rounded; palmar tubercles visible; c (ventral aspect of foot), enlarged digits rounded; subarticular tubercles visible; Stage 12 (lateral aspect of head), upper eyelid visible; Stage 13 (lateral aspect), tail reduced; gape reaches mid-length of eye; palm and foot pigmented, more densely dorsally and laterally; Stage 14 a (dorsal aspect at emergence of imago), tail reduced to a small protuberance; terminal groove visible on discs; yolk sac still present; b (lateral aspect of head), gape reaches beyond mid-length of eye. Scale bar = 1 mm.

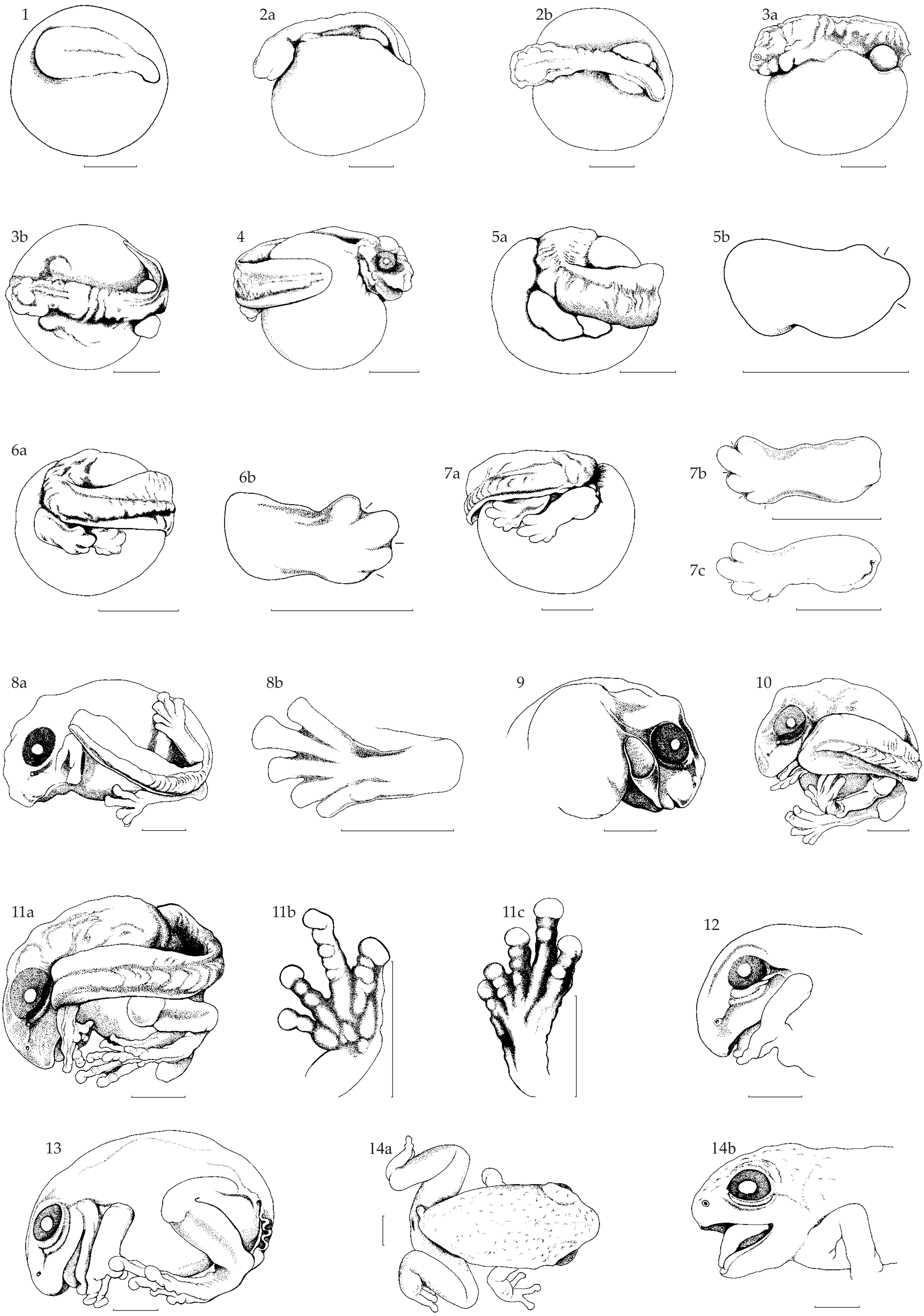

Fig. 5. (For caption, see opposite page.)

Table 2. Principal characters used to stage embryonic development in *P. viridis* (see Fig. 5).

Incubation period (days)	Stage	Developmental characters
6	1	Egg unpigmented, creamy white; no limb-buds visible; neural groove closed; head and tail ends demarcated.
8	2	Hind-limb buds clearly visible; tail bud visible; forelimb buds feebly defined.
10	3	Unpigmented subdermal eyes visible; mouth opens; tail about twice its length at Stage 2, laterally curved left or right; endolymphatic calcium deposits visible.
13	4	Dorsal and lateral surface of yolk sac pigmented; eyes pigmented, not subdermal; nostrils appear; tail about ¼ diameter of yolk-sac, almost its maximum length; hind-limb buds elongate.
16	5	Notch separating toes 4 and 5 distinct.
19	6	Toe 3 demarcated.
20	7	Toes 1 and 2 demarcated; toes 3, 4 and 5 clearly separated.
23	8	Tips of toes enlarged; 'elbow slit' appears for forelimbs, concealed under opercular fold; lower eyelid appears; Toes 1–5 distinctly separated.
27	9	Forelimb elbow emerges; hand subdermal.
29	10	Forelimbs fully emerged; nictitating membrane visible; metatarsal tubercle distinct; subarticular tubercles visible on toes; tail fin fully developed.
31	11	Enlarged digits rounded; palmar tubercles visible.
35	12	Upper eyelid visible.
39	13	Tail reduced; gape reaches mid-length of eye; palm and foot pigmented, more densely dorsally and laterally.
46	14	Tail reduced to a small protuberance; gape reaches beyond mid-length of eye; terminal groove visible on discs; yolk sac still present.

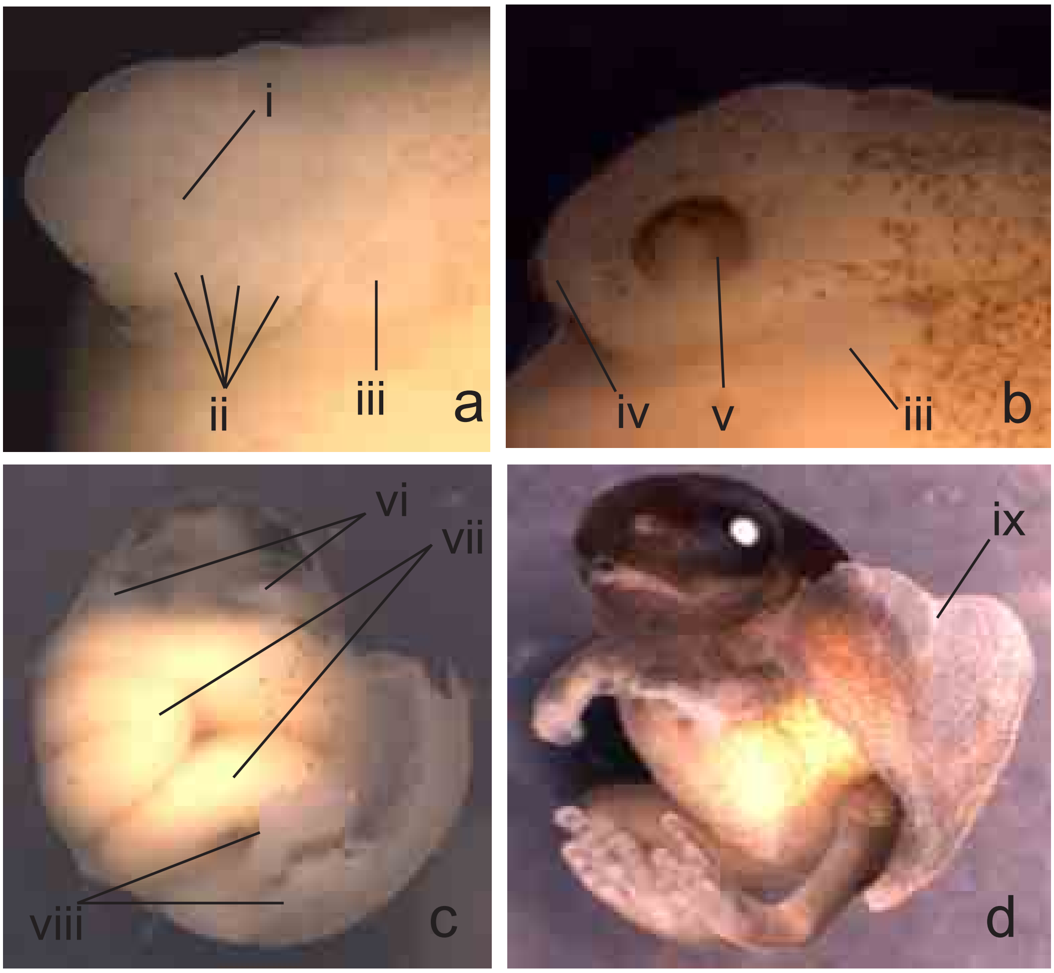

Fig. 6. Micrographs of developmental stages of *P. sarasinorum* and *P. hallidayi*. a, Stage 3 larvae of *P. hallidayi* (i, eye, before deposition of pigments; ii, four internal gill chambers; iii, forelimb bud); b, *P. sarasinorum,* anterior lateral view of Stage 4 larvae (iv, cement gland; v, eye, after deposition of pigments); c, *P. sarasinorum* stage 7 larvae (vi, forelimbs concealed under opercular fold; vii, coiled gut; viii, hind limbs before disks develop); d, *P. hallidayi* stage 11 larvae (ix, large, spatulate, heavily-vascularized tail).

fold, elbow slit not differentiable; tips of toes not enlarged, toes 3–5 distinct; tail large, spatulate, curved left, reaching forelimb, concealed under opercular fold; dorsal and anal fins deep, vascularized, their tips rounded; head, mid-dorsal and anterior side of body heavily pigmented; a pigmented mid-ventral band present; hind limbs unpigmented; coiled gut visible below forelimbs.

Stage 8 (WHT 5631). BH 3.1 mm, BW 3.5 mm, HBL, 4.6 mm, TD, 2.6 mm, TL, 9.7 mm. Snout rounded in all aspects; lower eyelid visible; endolymphatic calcium deposits visible; mouth width 1.0 mm; elbow slit (see Fig. 5, stage 8a) prominent on forelimb, concealed under opercular fold; tips of toes enlarged, toes 1–5 distinctly separated; tail large, spatulate, curved right, reaching posterior margin of eye; dorsal and anal fins deep, vascularized, their tips rounded; head, mid-dorsal and anterior side of body heavily pigmented; hind limbs slightly pigmented; tail and ventral foot lack pigmentation.

Stage 12 (WHT 5635). BH 3.2 mm, BW 3.9 mm, HBL, 6 mm, TD, 2.4 mm, TL, 11.7 mm. Snout rounded in all aspects; lower and upper eyelids prominent; endolymphatic calcium deposits indistinct; mouth width 1.5 mm; forelimbs well developed; vent slit prominent; tips of toes enlarged; toes 1–5 distinctly separated; subarticular tubercles visible; tail curved left, reaching up to forelimb; dorsal and anal fins deep, vascularized, their tips rounded; body heavily pigmented except for posterior side of abdomen, and ventral surfaces of hand and foot; tail lacks pigmentation.

Stage 13 (WHT 5641). BH 3.2 mm, BW 4.2 mm, HBL 5.1 mm, TD 1.9 mm, TL, 9.1 mm. Snout obtusely pointed in all aspects; lower and upper eyelids prominent; endolymphatic calcium deposits indistinct; mouth width 1.8 mm; gape reaches mid-length of eye; tail reduced, curved right, reaching forelimbs; dorsal and anal fins not deep, vascularized, their tips rounded; body heavily pigmented except posterior surface of abdomen, and ventral surfaces of hand and foot; tail lacks pigmentation.

DISCUSSION

***Reproductive behaviour.* –** Kanamadi et al. (1996) and Patil & Kanamadi (1997) reported on ethology and development respectively in an Indian species of *Philautus* they identified as *P. variabilis*. This species, originally described from Sri Lanka by Günther (1859), was reported extinct by Manamendra-Arachchi & Pethiyagoda (2005). It is also likely that it was, like all other *Philautus* species occurring on the island, endemic to Sri Lanka. We suspect therefore that Patil & Kanamadi (1997) misidentified this species, but cannot verify this inference as they do not list the preserved material on which their study was based. Biju (2001) reported the discovery of more than 100 species of putatively new anuran species, most of them *Philautus*, in south-western India—we presume the species studied by Kanamadi et al. (1996) and Patil & Kanamadi (1997) was an undescribed one or one described recently by Kuramoto & Joshy (2004).

Patil & Kanamadi's (1997) observations are nevertheless of value in comparing Sri Lankan and south Indian *Philautus*, which form a monophyletic group (Meegaskumbura et al., 2002). Although Patil & Kanamadi report no detailed ethological observations, larval development in the Indian species studied by them appears to differ in several respects from Sri Lankan *Philautus* reported here—a development period of 12 days, vs. 24–68 days for Sri Lankan *Philautus*; the appearance of external gills (Patil & Kanamadi, 1997: fig. 2i) vs. absence of external gills; and the early, simultaneous appearance of hind and forelimbs (Patil & Kanamadi, 1997: Fig. 2d, comparable to Stage 3 in Sri Lankan *Philautus*) vs. forelimbs concealed under opercular fold until Stage 10 (Fig. 5.10). We speculate that the much shorter incubation period recorded by Patil & Kanamadi (1997) is a consequence of the higher ambient temperature at their study site (Dharwat) than at the Sri Lankan sites.

Kanamadi et al.'s (1996) behavioural observations too, differ from ours in several respects: their females attacked the males after copulation, vs. voluntary departure of the male in our study; and the female guarded the eggs for 3 h after oviposition, vs. female abandoned the nest immediately after she concealed it. We observed neither aggression between the sexes nor nest guarding by either parent in the 85 clutches of ground-nesting species we studied. We suspect that Kanamadi et al.'s (1996) results may have been influenced by their apparent failure to provide their terrarium with an adequately deep soil and leaf-litter substrate.

Dring (1987) described the deposition of 6–8 eggs by *Philautus kerangae* in the pitcher of *Nepenthes bicalcarata* in Sarawak, and deduced the occurrence of male parental care from the presence of a calling male beside the clutch. He noted also that embryos of *P. kerangae* had subdermal forelimbs (as in the Sri Lankan species studied by us, but not the Indian one described by Patil & Kanamadi, 1997). In common with the Sri Lankan embryos reported on here, Dring's specimens lacked beaks, labial teeth, expanded lips and oral suckers. Dring (1987) also noted a snout-tip tubercle in females of *P. petersi,* a high-altitude (1,300–1,500 m) Bornean and Malaysian species, and speculated that this may facilitate nest excavation. No such character has been observed in any Sri Lankan *Philautus*.

Alcala & Brown (1982) recorded arboreal clutches of *Philautus lissobrachius* (from leaf axils of *Pandanus* trees and *Asplenium* ferns) and *P. schmackeri* (from leaf axils of *Asplenium* ferns in the Philippines). Brown & Alcala (1994) also recorded clutches of *P. surdus* (5–19 eggs) from the leaf axils of *Pandanus* and from the "base" of arboreal *Asplenium* ferns, together with clutches of a species thought to be *P. acutirostris* from leaf axils of wild banana plants and aerial ferns. We have hitherto failed to find evidence that Sri Lankan *Philautus* use leaf axils as nest sites. Further, in their Fig. 5, Alcala & Brown (1982: 224) note and depict the presence of a prominent operculum in their embryos, a structure we have not observed in the embryos of Sri Lankan *Philautus*.

With more than 600 species, the Neotropical leptodactylid genus *Eleutherodactylus* comprises the largest and arguably the hitherto best studied group of endotrophic anurans

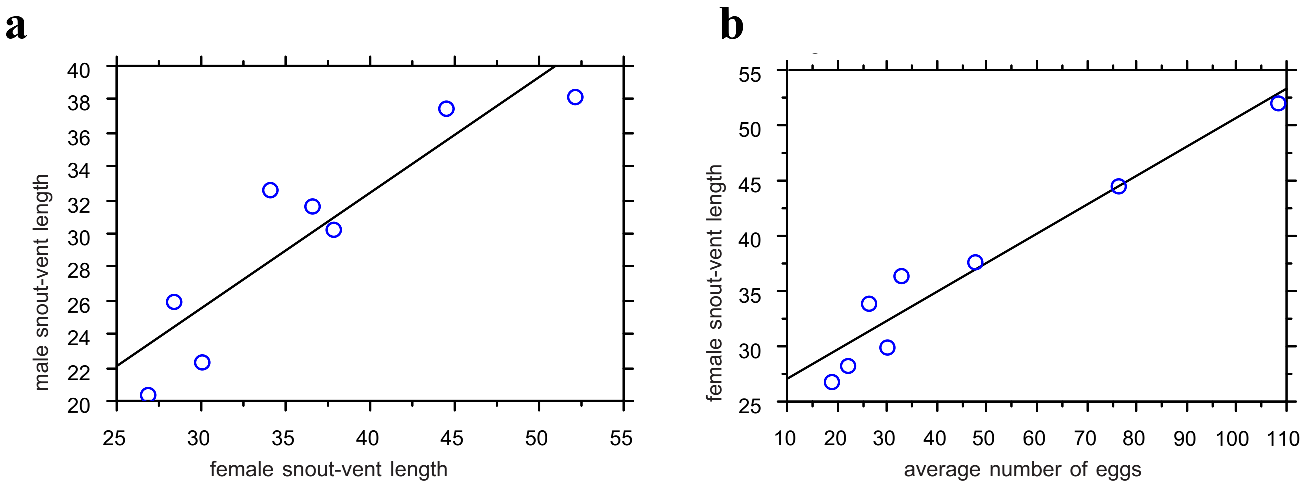

Fig. 7. a, female snout–vent length (FMSVL) shows a strong positive correlation ($R^2 = 0.822$, n = 8) with male snout–vent length (MSVL) for mating pairs; b, FMSVL shows a strong positive correlation with number of eggs ($R^2 = 0.920$). Other reproductive variables (egg mass; egg diameter; egg-mixing duration; nest covering duration; and incubation time) show only weak correlations ($R^2 = <0.296$, n = 8).

(Hanken, 1999). Breeding and nesting behaviour of four species are well studied (Townsend & Stewart, 1994; Bourne, 1997; Rogowitz et. al., 2001; Ovaska & Rand, 2001); parental care occurs in all but one of these. Oviposition sites are known for 16 species of *Eleutherodactylus* (Schwartz & Henderson, 1991; Thibaudeau & Altig, 1999). Fourteen of these deposit eggs under various objects while *E. coqui* deposits eggs on elevated sites (Thibaudeau & Altig, 1999) and *E. diastema* deposits its clutch between leaves, plant stems or inside bromeliads (Ovaska & Rand, 2001). No *Eleutherodactylus* is known to excavate a nest in soil as Sri Lankan *Philautus* do.

All but one of the 44 described extant species of Sri Lankan *Philautus* occur in the island's south-western wet zone, annual rainfall > 2,000 mm (Manamendra-Arachchi & Pethiyagoda, 2005; Meegaskumbura & Manamendra-Arachchi, 2005), a distribution probably determined by the dependence of these species on loose, moist, shaded soil in which to deposit their eggs. We note that egg separation has not been observed in other direct-developing species (Thibaudeau & Altig, 1999) and conclude that this behaviour serves to space eggs and increase the effective area available for aeration, while also facilitating better distribution of sperm. This is especially relevant given the much larger clutch sizes observed in Sri Lankan *Philautus* (6–155 ova) compared to other South and Southeast Asian *Philautus* (5–62 ova: Alcala & Brown, 1994; Patil & Kanamadi, 1997).

Terrestrial nest excavation has evidently not hitherto been recorded in other direct-developing anurans (Thibaudeau & Altig, 1999), though it is a behaviour commonplace among reptiles. While terrestrial nest excavation in *Philautus* shows marked similarities to tetrapod reptiles, this behaviour is different in these frogs in that the pair remain in amplexus while the female excavates the nest and mixes the eggs, sperm and soil after oviposition.

Although two Indian *Philautus* species are arboreal leaf nesters (Bossuyt et al., 2001; Biju, 2003), the only known Sri Lankan leaf nester, *Philautus femoralis,* differs from them by laying green eggs only on the underside of leaves, whereas the Indian species lay white or cream-coloured eggs on the upper surface of leaves (Bossuyt et al., 2001; Biju, 2003). For *P. femoralis*, nesting on the underside of leaves, rather than on upper surfaces, may offer several advantages, such as preventing predators from locating the clutch; reducing risk of the eggs being dislodged by rain or other mechanical damage; and reducing exposure to solar radiation.

The colour change that ground-nesting *Philautus* undergo (Fig. 2 and 3) may have an adaptive function through reducing the risk of predation, especially given that these frogs often nest in daytime. On the other hand, the bright-green *Philautus femoralis,* which deposits its eggs on the underside of leaves, does not change colour.

The critical humidity dependence of *Philautus* eggs makes them vulnerable to even short periods of desiccation. For example, *P. femoralis* eggs at Agrapatana incubate for 37–49 days, subjecting the clutch to risk from stochastic climate events. This danger is underlined by the fact that juveniles of ground nesters were observed throughout the year and those of *Philautus femoralis*, only during periods of sustained rainfall. Climate warming could therefore place this fauna at risk, though arboreal nesters would appear to be more immediately threatened than ground nesters.

The strong correlation between female body size and number of eggs (though not egg diameter) has been noted also in other species of frogs (Duellman & Trueb, 1986). The lack of correlation between female size and egg diameter and mass however, could be the result of inconsistencies in our measurements: eggs almost double in volume immediately after release (through absorption of water from the soil), rendering repeatable measurement difficult.

Comparative development. – Embryos of Sri Lankan *Philautus* show a degree of external morphological convergence with *Eleutherodactylus coqui.* Embryos of *Philautus* differ from those of *E. coqui* however, in having a larger, spatulate, vascularized tail; absence of external gills; presence of internal gill chambers; presence of a cement gland; presence of a coiled gut; forelimbs concealed under opercular fold up to an advanced stage of development (Fig. 5.10); and the absence of an egg tooth (Fig. 5.13, 5.14) (see Townsend & Stewart, 1985 for development in *Eleutherodactylus coqui*). *Philautus* species also differ in the tempo and sequence of development of some characters, such as early enlargement of the tail (vs. relatively late enlargement in *Eleutherodactylus*).

The relatively large (compared to SVL) vascularized tail in *Philautus* is evidently important for respiration since the embryo lacks external gills or well-developed internal gills. Kirtisinghe (1946) noted the presence of four pairs of atrophied internal gills and concluded that it was the heavily vascularized tail and not the gills that facilitated respiration in *Philautus* embryos (see Fig. 6d). In *Eleutherodactylus*, the tail expands only after the external gills are absorbed (see Fig. 1 in Townsend & Stewart, 1985), reinforcing the importance of the respiratory role of the tail in terrestrial direct developers. The consistent orientation of the tail to the left in *Eleutherodactylus coqui* has been remarked on by Thibaudeau & Altig (1999: 178–179) and Wassersug (2000). Although the tail in the larval specimens of *P. silus* described above happen to be orientated to the left, we note that in general the larvae of Sri Lankan *Philautus* have the tail orientated both left and right, and occasionally even folded under the body. Mature larvae were also seen to re-orientate themselves within the egg, moving the tail from left to right and vice versa. We note also Thibaudeau & Altig's (1999: 179) questioning of the respiratory function of the vascularized tail in *E. coqui:* "Whether or not there is sufficient increase in vascularity to suggest a specific respiratory function for the tail is debatable." We suspect however, that in *Philautus* the tail does indeed play an important role in respiration given that the gills are internal and atrophied in all the Sri Lankan larvae hitherto studied.

We suspect that the poorly developed cement gland in *Philautus* is a primitive character. This 'gland', which is a feature common in the early stages of the exotrophic larvae of aquatic tadpoles, facilitates attachment to aquatic objects (Duellman & Trueb,1986; Callery et al., 2001); such a function is, of course, irrelevant to endotrophic larvae.

A coiled gut has not been observed in other lineages with direct-developing embryos. In Sri Lankan *Philautus,* this persists without degeneration up to stage 14. A coiled gut is usually associated with aquatic tadpoles that rely on a herbivorous diet, the elongated gut facilitating digestion and absorption (Callery et al., 2001). The function of such a gut in early stages of *Philautus* is difficult to explain: we suspect it has a role in the absorption of the yolk associated with rapid development, although it could simply be a primitive character. *Philautus* have, however, lost many other larval characters associated with aquatic tadpoles, such as keratinized denticles around the mouth and a lateral-line sensory organ.

Conservation. – Little attention has been paid up to now to the conservation of Sri Lanka's Amphibia, despite the island's 'hotspot' status (Myers et al., 2000; Meegaskumbura et al., 2002) and the listing of some 44 species, including 27 *Philautus,* in the various 'threatened' categories of the IUCN Red List (see www.globalamphibians.org). More than 95% Sri Lanka's original rainforest extent of about 15,000 km^2 has disappeared during the past two centuries: only about 750 km^2 now survives, mostly in the form of < 10 km^2 fragments surrounded by tea and rubber plantations, and human settlements. The attrition caused by island effects (Ferraz et al., 2003), taken together with edge effects, invasive alien species, poor land management, industrial emissions, irresponsible pesticide use, rainwater acidification and global and local climatic change are likely to result in continued species loss. This is particularly relevant because several species are restricted to individual forest fragments. While Sri Lanka's human population density (300 km^{-2}) is the highest among the world's 25 biodiversity hotspots (Cincotta et al., 2000), human population density in the biodiversity-rich south-western wet zone (to which all but one species of *Philautus* are restricted) is more than twice the national average. The pressures on forest fragments, in terms of deforestation and habitat alteration, are therefore immense.

Given Sri Lanka's extraordinary amphibian species richness, it is imperative that every effort be made to conserve this remarkable fauna, especially in view of its still being so poorly known: of the 17 species treated here, eight have been described only recently (Manamendra-Arachchi & Pethiyagoda, 2005), while a further five remain to be described. *Philautus* shows a high degree of localized endemism within the Western Ghats-Sri Lanka biodiversity hotspot. This fauna is gravely at risk, and its security will depend on the conservation of habitats, a fuller understanding of the ecology of the species involved and intensive measures, both in and ex situ, to restore populations of threatened species. Considering the difficulties associated with addressing many of these threats, ex situ conservation may, in the short term, provide the only realistic prospect for many Critically Endangered species. We hope that the data in this paper will contribute to the body of knowledge necessary for such conservation efforts, which are now a matter of overwhelming priority.

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