Zootaxa 1397: 1–15 (2007)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

New species amongst Sri Lanka's extinct shrub frogs (Amphibia: Rhacophoridae: *Philautus*)

MADHAVA MEEGASKUMBURA[1,2*], KELUM MANAMENDRA-ARACHCHI[2],
CHRISTOPHER J. SCHNEIDER[1] AND ROHAN PETHIYAGODA[2]

[1] *Department of Biology, Boston University, 5 Cummington Street, Boston, MA 02215, USA*
[2] *Wildlife Heritage Trust of Sri Lanka, 95 Cotta Road, Colombo 8, Sri Lanka*
[*] *Corresponding author (e-mail: madhava@bu.edu)*

Abstract

An extensive survey of amphibians in Sri Lanka, a 65,000 km^2 continental island, has recently served to uncover ~100 new species of amphibians, mostly Oriental shrub-frogs of the endotrophic genus *Philautus*. Comparison of specimens acquired in the course of this survey with type and other historical collections have previously shown that 19 species have disappeared from the island. The final two extinct species, *Philautus pardus* and *P. maia,* known only from collections made in the island prior to 1876, are described herein as new. A contemporaneous account of the latter species reported that the female carried its clutch of eggs adhered to its belly, a behaviour which, if true, is unique in Anura. The remarkable extinction of anurans in Sri Lanka appears to be largely a result of the loss of *c.* 95 % of the island's perhumid forests. Sri Lanka's amphibian extinctions have been detectable only because of the baseline offered by specimens collected in the period 1850–1940 and preserved in overseas natural-history museums. Historical biodiversity collections in the world's natural history museums thus offer outstanding value as baselines for contemporary biodiversity conservation assessments.

Key words: Amphibia, endotrophy, extinct species, habitat loss, museum collections, *Philautus,* new species, Red List, Sri Lanka

Introduction

The ubiquitous tinkling calls of the shrub frogs of the genus *Philautus* help to characterize the forests of tropical Asia. About 140 species are presently recognised in the genus (AmphibiaWeb 2006), and several others await description (Biju 2001; Manamendra-Arachchi and Pethiyagoda 2005). All known *Philautus* are endotrophic (i.e., they undergo their 'tadpole' stage within the egg, emerging as metamorphosed imagos), with nesting taking place on the forest floor or on trees (Bossuyt and Dubois 2001; Meegaskumbura *et al.* 2002; Bahir *et al.* 2005). The genus shows a remarkable endemic radiation in Sri Lanka—a 65,000 km^2 continental island narrowly separated from southern India by the 20 km wide Palk Strait—from which 62 species of *Philautus* are recognized (Meegaskumbura *et al.* 2002; Bossuyt *et al.* 2004; Dubois 2005; Manamendra-Arachchi and Pethiyagoda 2005; Meegaskumbura and Manamendra-Arachchi 2005).

From 1993-2003, the Wildlife Heritage Trust of Sri Lanka (WHT) conducted an extensive survey of the island's amphibian fauna (Pethiyagoda and Manamendra-Arachchi 1998; Manamendra-Arachchi and Pethiyagoda 2005). While serving to uncover a large number of new species, this work also necessarily involved the examination of type and other specimens preserved in museums worldwide, principally the approximately 140 specimens in the collection of The Natural History Museum, London. Much of this material had been col-

Accepted by M. Vences: 19 Dec. 2006; published: 25 Jan. 2007

lected in Sri Lanka between 1850 and 1940, a period during which rainforests of the island's central mountains and south-western 'wet zone' were being cleared to make way for cinchona and coffee plantations, since replaced by tea and rubber (Meyer 1998). Although locality information beyond 'Ceylon' is usually lacking, these specimens provide the only available baseline of the amphibian fauna before the island's rain- and montane forests were reduced from their former *c.* 16,000 km^2 to their present-day extent of approximately 750 km^2.

In addition to one species each of the endemic ranid genera *Adenomus* and *Nannophrys* (Manamendra-Arachchi and Pethiyagoda 1998) our surveys failed to detect 19 species of *Philautus* represented in these historical museum collections. While 15 of these species had previously been described and named, Manamendra-Arachchi and Pethiyagoda (2005) described two as new, and the final two are described herein. The 17 hitherto described *Philautus* were determined to be Extinct in terms of the IUCN's Red List criteria in the Global Amphibian Assessment (GAA; Stuart *et al.* 2004).

Both the new (but extinct) *Philautus* we describe herein are known only from museum specimens collected around 1860, if not for which these extinctions would have gone unnoticed. One of these species may have possessed a unique reproductive mode, with fertilized eggs remaining adhered to the female's belly in a disc-shaped mass, presumably until they hatched.

We also seek to explain the apparent paradox of so many new species and extinctions being recorded simultaneously from Sri Lanka; and draw attention to the importance of the world's natural-history museum collections, which represent invaluable and often unique historical biodiversity baselines of great value to contemporary conservation studies.

Material and methods

The material referred to in this paper is deposited in The Natural History Museum, London, UK (BMNH); the Museum of Comparative Zoology, Cambridge, Massachusetts, USA (MCZ); Naturhistorisches Museum, Basel, Switzerland (NHMB); Wildlife Heritage Trust, Colombo, Sri Lanka (WHT); Zoologisches Museum der Humboldt-Universität zu Berlin, Germany (ZMB); and Zoological Survey of India, Kolkatta, India (ZSI).

Morphological measurements, made using dial Vernier callipers and taken to the nearest ±0.05 mm, are abbreviated as follows (for a more detailed, illustrated version see Manamendra-Arachchi and Pethiyagoda 2005): DBE, distance between back of eyes; DFE, distance between front of eyes; DL, length of disk of third finger; DW, width of disk of third finger; ED, horizontal diameter of eye; EN, eye to nostril distance; ES, distance between anterior-most point of eye and tip of snout; FEL, thigh (femur) length; FL, finger length; FOL, foot length; HL, head length; HW, Head width; IML, length of inner metatarsal tubercle; IN, internarial distance; IO, interorbital width; LAL, lower-arm length; LPH, height of lingual papilla; LPW, width of lingual papilla; MBE, distance between angle of jaws and posterior-most point of eye; MFE, distance between angle of jaws and anterior-most point of eye; MN, distance between angle of jaws and middle of nostril; NS, distance between middle of nostril and tip of snout; PAL, palm length, taken from posterior-most margin of inner palmar tubercle to tip of disk of third finger; SVL, snout–vent length; TAD, distance between anterior-most point of inner margin of inner rim of tympanum and posterior-most point of eye; TBL, shank (tibia) length; TL, toe length, taken as distance between posterior margin of most proximal subarticular tubercle or crease of articulation and tip of disk; TND, tympanum–nostril distance; TPD, distance between anterior-most point of inner margin of inner rim of tympanum and anterior-most point of eye; TYE, tympanum outer diameter; UAW, upper arm length; UEW, upper eyelid width.

Webbing diagrams are schematic, the nodes indicating the position of subarticular tubercles.

The Red List criteria are those of IUCN (2001).

Morphological measurements with high coefficients of variation or low repeatability were omitted. Prior to analysis, all mensural data were log transformed to stabilize variances. The following measurements were log transformed and used in the final analyses: DBE, DFE, ED, ES, FEL, FOL, HL, HW, IN, IO, LAL, PAL, SVL, TBL, and lengths of third and fourth fingers. SYSTAT (Version 11.00.01 for WindowsXP) was used for statistical analysis.

Principal components analysis (PCA) of the character correlation matrix was used to reduce dimensionality of continuous morphological variables and to identify those variables that best discriminate between species. Various axis rotations were tested and the one that depicted optimal interpretability of variation among the characters was selected.

Because the PCA results suggest that for all the groups analyzed, the first principal component is a size axis, we adjusted for size so as to determine the characters that best discriminate between the species. All variables were regressed against SVL and the residuals of these regressions were used in a discriminant function analysis (DFA). Classical discriminant analysis as implemented in Systat with all variables included in the model (equal priors, tolerance = 0.001) was used and canonical-function plots were made to depict the distinctiveness of the species.

Results

Philautus pardus new species
Figs 1, 2

Holotype

Adult female, 32.1 mm SVL, BMNH 1947.2.7.96, Ceylon [Sri Lanka], a paralectotype of *Ixalus variabilis* Günther, 1859; provenance, H.H. Cuming.

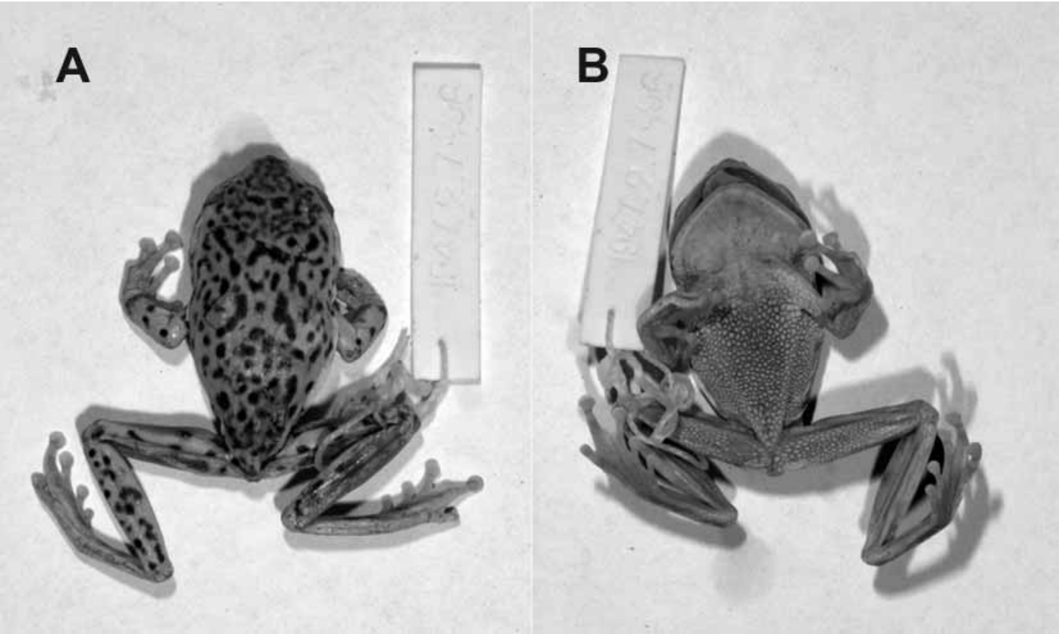

FIGURE 1. Holotype female of *Philautus pardus*, 32.1 mm SVL, BMNH 1947.2.7.96. A. Dorsal view. B. Ventral view.

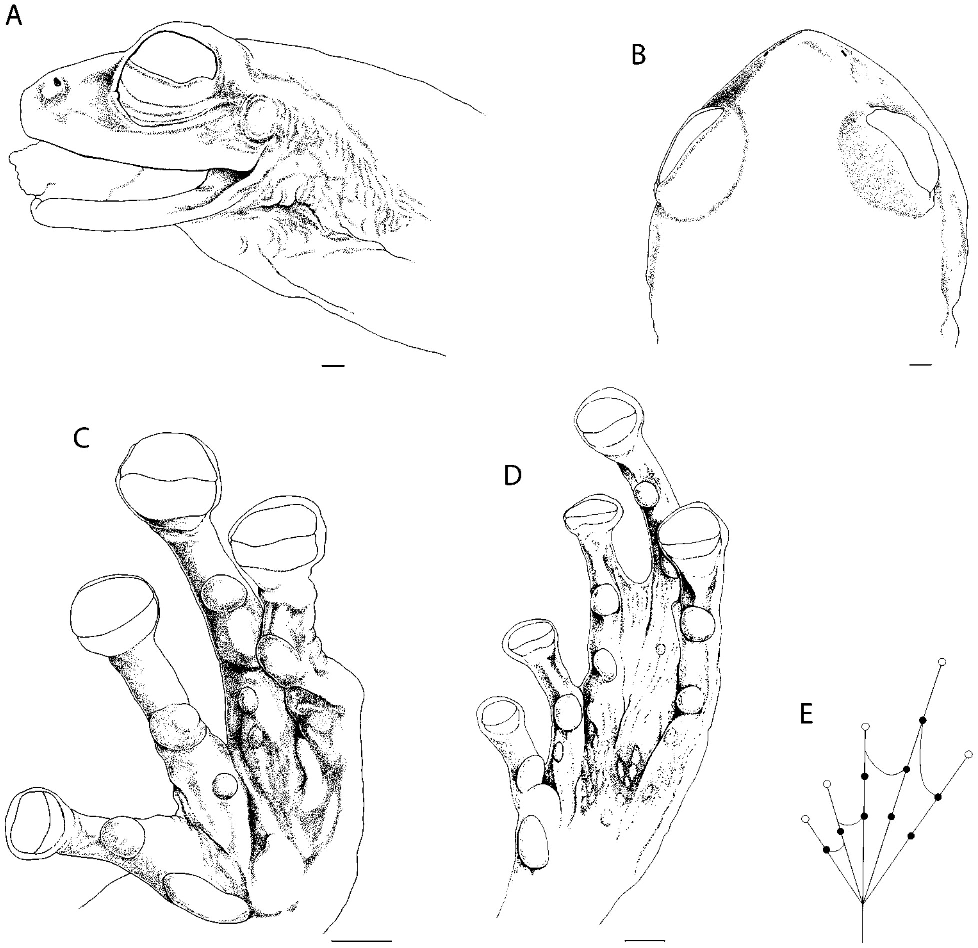

FIGURE 2. Holotype female of *Philautus pardus*, 32.1 mm SVL, BMNH 1947.2.7.96. A. Lateral view of head. B. Dorsal view of head. C. Left hand. D. Left foot. E. Diagrammatic representation of left-foot webbing. Scale bars = 1 mm.

Etymology

The species epithet is the Latinised form of ‘pardos’, Greek for leopard, applied here as a noun in apposition; it alludes to the leopard-like coloration of this frog.

Diagnosis

Philautus pardus is distinguished from all other Sri Lankan species of *Philautus* by the following combination of characters: (1) distinctive colour pattern, comprising of dark spots on the head and dorsum; (2) angle of snout ~110° in dorsal aspect; (3) absence of a vomerine ridge, calcar, lingual papilla and lateral dermal fringe on fingers.

Description of the holotype

(See Figs. 1, 2.) Mature female, 32.1 mm SVL. Body stout. Head dorsally convex; snout rounded in lateral aspect, its angle about 110° in dorsal aspect; canthal edges indistinct; loreal region flat; interorbital space flat; internasal space concave; tympanum oval, vertical; pineal ocellus, vomerine ridge, cephalic ridges, calcar, lingual papilla and co-ossified skin on skull absent. Supratympanic fold indistinct. Lateral dermal fringe on fingers absent. Webbing present on toes (see Fig. 2E). Tarsal folds absent. Snout, interorbital space, side of head and dorsum smooth; both upper and lower flanks granular; dorsal part of forelimb, thigh, shank and foot smooth; granules on throat smooth, those on chest, belly and underside of thigh rough. Inner vocal slits and nuptial pads absent.

Colour in preservative: Dorsum yellowish brown, scattered with distinct, dark-brown spots of diameter about ¼–¾ that of eye, some of them coalesced to form larger blotches (see Fig. 1). Spots extend on to the head, femur, inguinal zone, tibia, tarsus (absent on hands and feet) and sides to the mid-lateral fold. Upper lip yellow. Posterior part of thigh yellow to ashy brown with dark-brown spots. Venter a uniform dull yellow, slightly lighter than background colour of dorsum.

Measurements of holotype (BMNH 1947.2.7.96, in mm): DBE, 12.1; DFE, 6.5; DL, 1.4; DW, 1.7, ED, 4.7; EN, 3.0; ES, 5.1; FEL, 16.1; FL I, 2.5; FL II, 3.2; FL III, 5.3; FL IV, 4.0; FOL, 21.1; HL, 12.9; HW, 14.1; IML, 1.4; IN, 3.2; IO, 3.8; LAL, 6.6; MBE, 4.7; MFE, 8.7; MN, 11.3; NS, 2.2; PAL, 9.0; SVL, 32.1; TBL, 15.8; TL I, 2.3; TL II, 2.8; TL III, 4.6; TL IV, 6.5, TL V, 4.6; TYD, 1.2; TYE, 1.8; UAW, 5.6; UEW, 2.4.

Remarks

The key of Manamendra-Arachchi and Pethiyagoda (2005) refers *P. pardus* to *P. viridis*, while the diagnoses of Meegaskumbura and Manamendra-Arachchi (2005) affine it to *P. stuarti*. It can be distinguished morphologically from these two species, however, by the dorsal colour pattern in preserved specimens of distinct dark spots (*vs* uniform brown); having the loreal region flat (*vs* concave); possessing an indistinct supratympanic fold (*vs* distinct); and the absence of a lateral dermal fringe on fingers (*vs* present). The holotype of *P. pardus* is a paralectotype of *P. variabilis* (type locality: Sri Lanka). It is distinguished from *P. variabilis*, however, by having the snout rounded in lateral view (*vs* truncate in *P. variabilis*), head dorsally convex (*vs* flat), loreal region flat (*vs* concave), supratympanic fold indistinct (*vs* distinct), and a lateral dermal fringe present on fingers (*vs* absent).

Philautus pardus also separates well from *P. variabilis*, *P. viridis* and *P. stuarti* in morphological space. Principal components analysis (Fig. 3A) shows that the four species are distinguished by a combination of body size, internarial distance, fourth-toe length, interorbital width, palm length and third-finger length. The PC(1) axis, which explains 87 % of the variance, is a size axis (snout–vent length loads most heavily and fourth-toe length least heavily, but all variables have high, positive loadings on this axis; component loadings range from 0.858–0.980, suggesting that the variation relates mostly to size). The PC(2) axis represents 4 % of the variance, with internarial distance, fourth-toe length, interorbital distance, palm length, and third-finger length contributing most heavily. While interorbital width and internarial distance load positively, the other variables load negatively (component loadings 0.302–0.363). All four species separate well on the PC(1) axis, *P. variabilis* being the largest and *P. stuarti* the smallest. While the new species also separates from the other three on the PC(2) axis, *P. variabilis, P. stuarti* and *P. viridis* almost completely overlap. *Philautus pardus* has a relatively greater internarial distance and interorbital diameter, but relatively shorter palm, fingers and toes compared to *P. variabilis*, *P. viridis* and *P. stuarti*.

The size-adjusted DFA (Fig. 3B) shows *P. pardus* to be clearly distinct from *P. viridis*, *P. stuarti* and *P. variabilis*. The analysis correctly classified 100 % of each of the four species (Wilks' lambda 0.001, p = 0.5). The first canonical variable best discriminates between the groups and accounts for 69 % of the total dispersion (eigenvalue 51.64), while the second variable accounts for 29 % (eigenvalue 22.32). In the canonical variables plot, the centroids are (2.307, -3.655) for *P. viridis*, (-3.039, 2.944) for *P. stuarti*, (15.183, 1.728) for *P. variabilis*, and (14.230, 9.134) for *P. pardus*. The first canonical variable represents mostly distance between back of eyes (standardized canonical discriminant function, SCDF, 8.070), distance between front of eyes (SCDF -7.352), head length (SCDF 3.376), head width (SCDF 2. 517), internarial distance (SCDF -2.333) and eye-to-snout distance (SCDF -2.231). The second represents mostly distance between front of eyes (SCDF -4.528), head width (SCDF 4.230), eye-to-snout distance (SCDF 2.901), eye diameter (SCDF -2.878), and foot length (SCDF 2. 530).

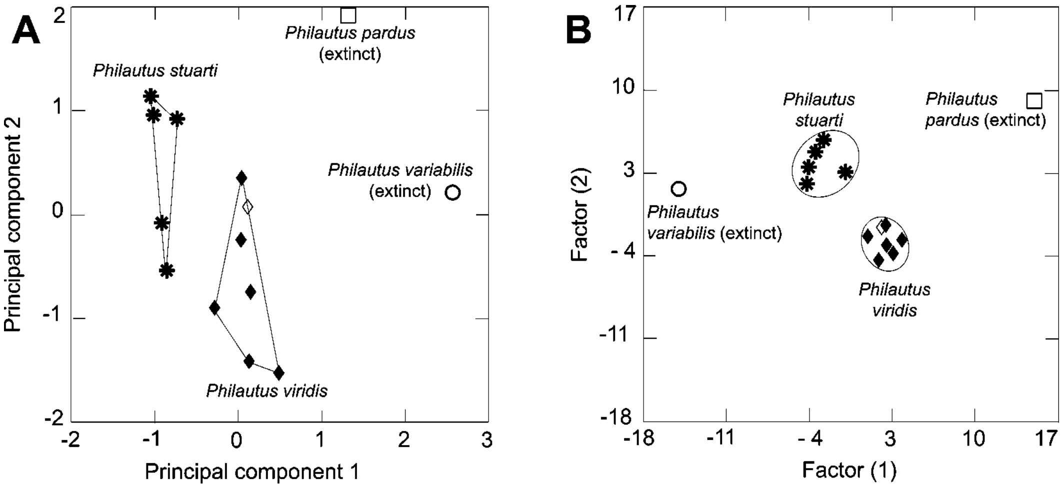

FIGURE 3. A. Factor scores (no rotation) of principal components analysis of mensural data of *Philautus pardus* (square), *P. viridis* (rhombus), *P. stuarti* (star), and *P. variabilis* (circle) (females represented by open symbols, males by solid symbols). B. Canonical variables plot of discriminant function analysis of size-adjusted residuals (the 95% confidence ellipses are centered on the centroid of each species).

Philautus variabilis has long been a catchall taxon for difficult-to-identify *Philautus* in Sri Lanka and India, and a number of distinct species have erroneously been referred to it (e.g., Kirtisinghe 1957; Dutta and Manamendra-Arachchi 1996; Kanamadi *et al.* 1996; Kadadevaru and Kanamadi 2001; Vasudevan *et al.* 2001; Daniels 2003). Designation of a lectotype by Bossuyt and Dubois (2001) helped to define this species, which we failed, however, to record in our decade-long (1993–) amphibian survey of Sri Lanka. Accordingly, the GAA (Stuart *et al.* 2004; see also Manamendra-Arachchi and Pethiyagoda 2005) concluded that *P. variabilis sensu stricto* is Extinct: it is now known only from its lectotype.

Conservation status

Not having been recollected since the holotype was collected prior to 1859, and not recorded in the WHT survey (see Manamendra-Arachchi and Pethiyagoda 2005), *P. pardus* is considered Extinct in terms of the IUCN's *Red List* criteria.

Philautus maia **new species**

Figs 4, 5

Holotype

Adult female, 44.6 mm SVL, BMNH 76.3.21.18. Paratype: female, 46.1 mm SVL, BMNH 76.3.21.19. Both collected at "Poojagodde" [Poojagoda] Estate, Ramboda, Sri Lanka, by a Mr Perera (Ferguson 1876).

Etymology

The species-epithet is derived from the Greek term for a 'good mother'—a reference to the care the female of this species appears to have taken of its clutch of eggs. It is applied here as a substantive in apposition.

Diagnosis

Philautus maia is distinguished from all other Sri Lankan species of *Philautus* by the following combination of characters: (1) tympanum discernible; (2) angle of snout in dorsal aspect ~100º; (3) supratympanic fold distinct; (4) canthal edges sharp; (5) lingual papilla absent; (6) supernumerary tubercles present on fingers but absent on toes; (7) tarsal tubercle absent; (8) webbing up to or beyond second and third toes (Fig. 6D); (9) posterior surface of thigh with a dark-brown reticulated pattern.

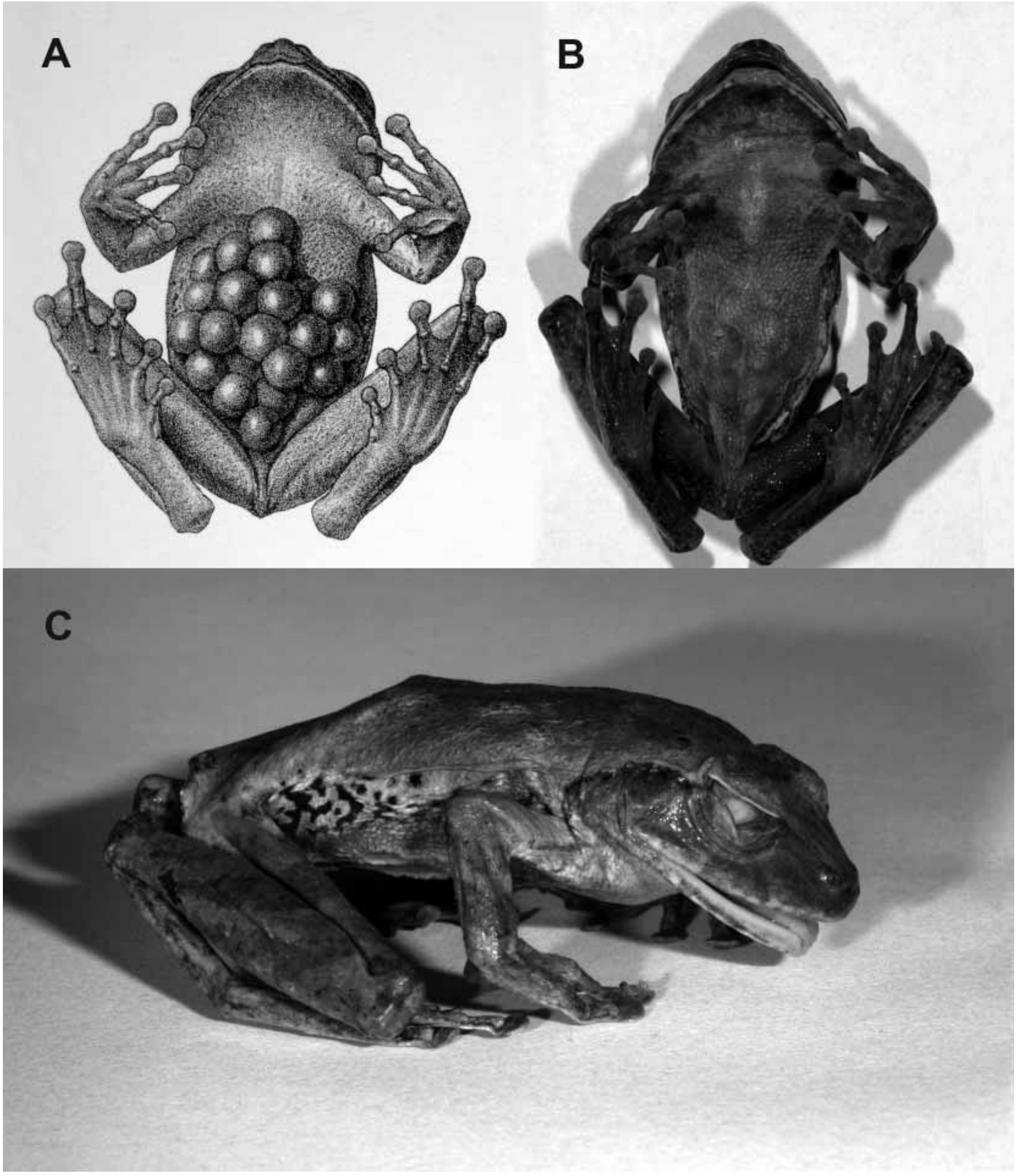

FIGURE 4. Holotype female of *Philautus maia*, 44.6 mm SVL, BMNH 76.3.21.18. A. Illustration of eggs carried on venter in Günther (1876). B. Ventral view, showing depressions made by eggs. C. Lateral view, showing speckled pattern.

Description of the holotype

(See Figs. 4, 5.) Mature female 44.6 mm SVL. Body elongate. Head dorsally concave; snout truncate in lateral aspect, angle of snout 102º in dorsal aspect; canthal edges sharp. Loreal region concave; interorbital space concave; internarial space flat; tympanum oval, oblique; pineal ocellus absent. Vomerine ridge present, bearing about 6 small teeth angled at about 45º relative to body axis, the ridges shorter than distance between them. Cephalic ridges, calcar, lingual papilla and co-ossified skin on skull absent. Supratympanic fold distinct. A lateral dermal fringe present on fingers; webbing on fingers rudimentary. Toes webbed (see Fig. 6D); tarsal folds absent. Snout, interorbital space and side of head smooth; dorsum and both upper and lower flanks with glandular warts. Dorsal part of forelimb, thigh, shank and foot smooth. Throat, chest, belly and underside of thigh granular. Inner vocal slits and nuptial pad absent. Egg depressions present on belly; 15 oval eggs measuring ~4.0 x 4.8 mm, lacking jelly capsules, preserved in jar containing holotype.

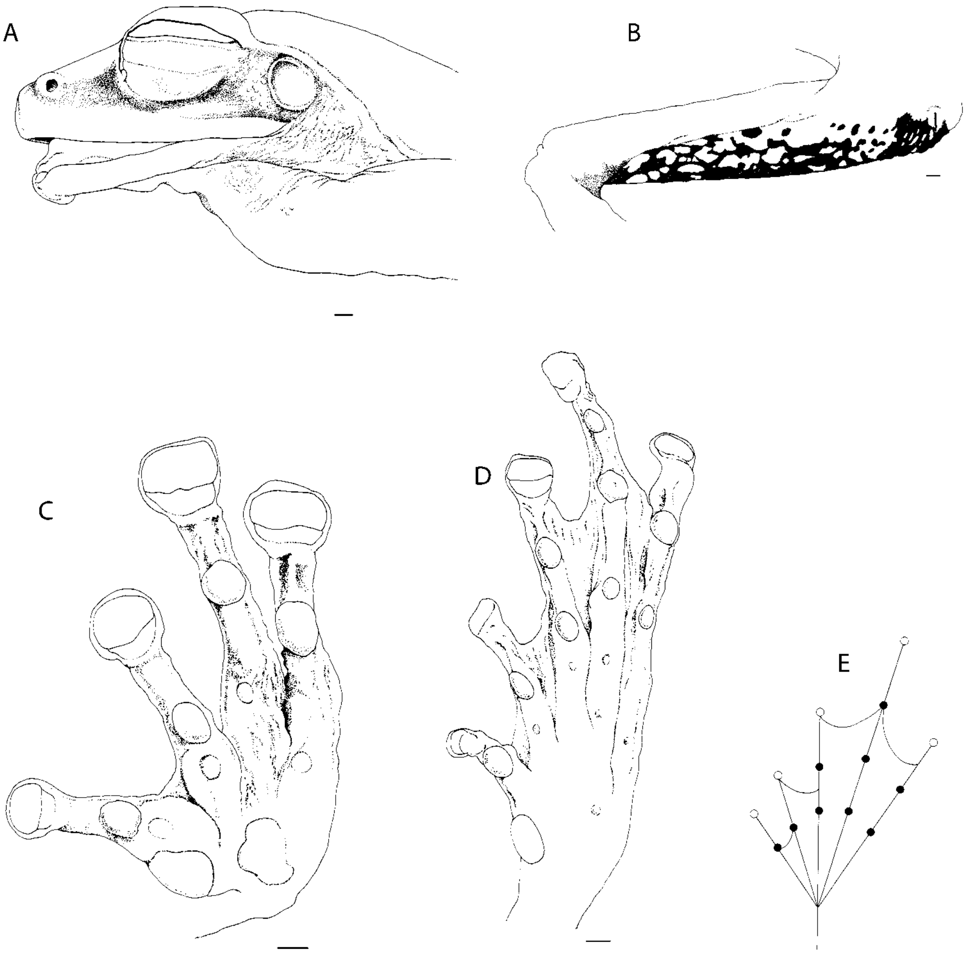

FIGURE 5. Holotype female of *Philautus maia*, 44.6 mm SVL, BMNH 76.3.21.18. A. Lateral aspect of head. B. Thigh, showing reticulated pattern. C. Left hand. D. Left foot. E. Diagrammatic representation of left-foot webbing. Scale bars = 1 mm.

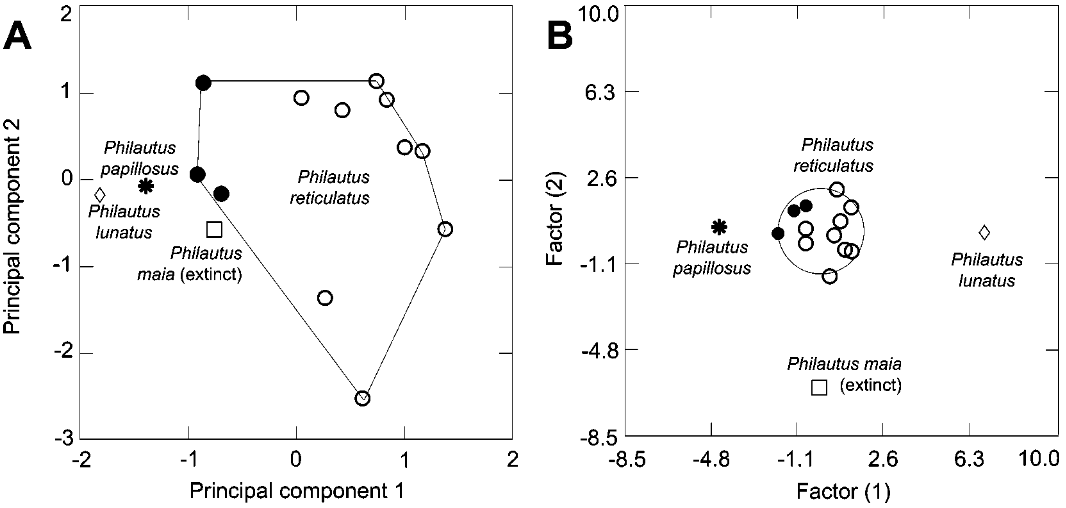

FIGURE 6. A. Factor scores (no rotation) of principal components analysis of mensural data of *P. maia* (square), *P. reticulatus* (circle), *P. lunatus* (rhombus) and *P. papillosus* (star) (females represented by open symbols, males by solid symbols). B. Canonical variables plot of discriminant function analysis of size-adjusted residuals (the 95% confidence ellipse is centered on the centroid).

Colour in preservative: Dorsum ashy brown. Interorbital area dark brown. Both upper and lower flanks pale yellow with black speckles (Fig. 4C). Loreal region, tympanic region and tympanum dark brown. Upper lip ashy brown. Dorsal parts of forelimb, thigh, shank and foot ashy brown with dark-brown spots; posterior surface of thigh with a dark-brown reticulation (Fig. 5B); underside of thigh and webbing on foot dark brown. Throat, margin of throat, chest and belly yellow with brown pigments.

Measurements of holotype (BMNH 76.3.21.18, in mm): DBE, 16.4; DFE, 9.6; DL, 2.1; DW, 2.2, ED, 6.6; EN, 4.5; ES, 7.7; FEL, 27.0; FL I, 4.1; FL II, 5.2; FL III, 7.8; FL IV, 6.7; FOL, 35.1; HL, 18.0; HW 19.0; IML, 1.7; IN, 4.6; IO, 4.7; LAL, 9.8; MBE, 7.0; MFE, 12.1; MN, 15.7; NS, 3.0; PAL, 13.2; SVL, 44.6; TBL, 27.3; TL I, 3.4; TL II, 4.7; TL III, 7.5; TL IV, 11.2, TL V, 8.0; TYD, 2.0; TYE, 2.7; UAW, 8.6; UEW, 4.6.

Remarks

Günther (1876) assigned this species to *P. reticulatus*, from which it differs, however, by the absence of a lingual papilla and tarsal tubercle. Both these characters are consistently present in *P. reticulatus*, an extant, Endangered species restricted to the rainforest canopy in the island's south-western lowlands up to 900 m elevation (Manamendra-Arachchi and Pethiyagoda 2005). The same two characters also serve to distinguish *P. maia* from *P. lunatus*, *P. papillosus* and *P. reticulatus*, to which the diagnoses and key of Manamendra-Arachchi and Pethiyagoda (2005) refer it.

Günther (1876) observed of the holtype of *P. maia*, "In a small collection of Ceylonese frogs submitted to my examination by Mr. W. Ferguson, F.L.S., there was a frog which I consider to be *Polypedates reticulatus*, and which had the ova attached to the abdomen when that gentleman obtained it. The ova are now detached, but still firmly adhere to one another, forming a flat disk." Remarkably, despite the passage of time, the depressions formed on the belly of this specimen are still clearly visible (Fig. 4B).

We have not observed such a brooding behaviour in any of the 17 Sri Lankan *Philautus* for which reproduction has thus far been investigated (Bahir *et al.* 2005). Of these 17, all but one deposit their eggs in nests excavated in the forest floor. A single species in Sri Lanka (*P. femoralis*) and two in India are known, however, to attach their clutch to leaves, in the form of a flat disc, where they are then abandoned to hatch (Bossuyt *et al.* 2001; Biju 2003). We feel it unlikely that the gait of a frog would permit a clutch of eggs to be carried adhered to its abdomen over the incubation period of several weeks typical of Sri Lankan *Philautus*. Further, the disc-shaped clutch and the absence of soil particles on the egg mass suggest that this frog was an arboreal, leaf-nesting species similar to *P. femoralis*. An examination of the eggs that were originally attached to the specimen also suggests that eggs had been freshly deposited, or perhaps were unfertilized, due the distinct absence of well formed embryos within, further reinforcing the notion that this species did not provide brood care. Although we do not entirely discount the possibility that *P. maia* carried its clutch on its belly (a behaviour unknown in Anura: Thibaudeau and Altig 1999) or remained positioned on it, we think it more likely that it was an arboreal nester captured while still positioning its clutch, or an individual that died while doing so. The collector may have assumed that the eggs, in addition to being adhered to one another to form a disc, were also attached to the female's abdomen. We observed this to be the case in *P. femoralis* in some instances, when the leaves on which eggs were deposited were not sufficiently damp. There is also no sign that the skin of the abdomen of *P. maia* was in any way adapted to carry adhesive eggs: as is also in the case with *P. femoralis*, the skin on its venter is granular.

The key of Manamendra-Arachchi and Pethiyagoda (2005) and the diagnoses of Meegaskumbura and Manamendra-Arachchi (2005) show *P. maia* to be closest morphologically to *P. lunatus* and *P. papillosus*. Principal components analysis (unadjusted for body size, see Fig. 6A) shows that *P. maia* separates from these species on both PC axes. However, both sexes of *P. maia* separate from *P. reticulatus* (to which Günther 1876, referred its type specimens) only on a single PC axis. The PC(1) axis explains 88 % of the variance with all variables showing high, positive loadings (component loadings range from 0.799 to 0.980), suggesting that the variation relates mostly to size. The PC(2) axis explains only 4 % of the total variance and represents mostly the variation in eye diameter, eye-to-snout distance, and femur length. Eye diameter loads positively, while femur length and eye-to-snout distance load negatively. *Philautus maia* also separates from females of *P. lunatus, P. papillosus* and *P. reticulatus* on the PC(1) axis, with *P. lunatus* being the smallest species and *P. reticulatus* being the largest. The new species completely overlaps females of *P. reticulatus* on PC(2) axis.

The size-adjusted discriminant function analysis serves to distinguish *P. maia* from *P. lunatus*, *P. papillosus* and *P. reticulatus* (Fig. 6B). The analysis correctly classified 100 % of each of the four species (Wilks' lambda 0.016, p = 0.7). The first canonical variable best discriminates between the species and accounts for 57 % of total dispersion (eigenvalue 6.24). The second variable accounts for 35 % of dispersion (eigenvalue 4.05). In the canonical variables plot, the centroids are (-0.238, -6.447) for *P. maia*, (6.874, 0.243) for *P. lunatus*, (-4.577, 0.485) for *P. papillosus* and (-0.172, 0.477) for *P. reticulatus*. The first variable represents mostly distance between front of eyes (standardized canonical discriminant function, SCDF -6.410), distance between back of eyes (SCDF 5.224), foot length (SCDF -3.870), eye-to-snout distance (SCDF 2. 990), eye diameter (SCDF -2.520), and third finger length (SCDF 2.112).The second canonical variable represents mostly foot length (SCDF -2.751), eye to snout distance (SCDF 2.257), distance between front of eyes (SCDF -1.691), third finger length (SCDF 1.593), and internarial distance (SCDF -1.335).

Conservation status

Ferguson (1876) stated that the type specimen was sent to him by "Mr Perera, then conductor on the Poojagodde estate in the Ramboda District, and from a high elevation." Poojagoda is in fact a division of Frotoft Estate, Ramboda (7°04'30"N, 80°42'15"E), a tea plantation ~1400 m above sea level. The Pedro Forest Reserve, which extends along a forested ridge bordering Frotoft Estate about 1 km north of Poojagoda, is now the only remaining undisturbed habitat in this area. However, surveys of this forest failed to detect this species. Clearance of the cloud forest adjacent to Frotoft Estate in 1978 also resulted in the extinction of *Albizia lankaensis* (Mimosaceae), a tree species formerly endemic to this site (Kostermans 1980). Given that *Philautus maia* has not been recorded since 1876 despite surveys that have included forests in the vicinity of the type locality in the period 1993–2003 (see Manamendra-Arachchi and Pethiyagoda 2005), and given the disappearance of its habitat, we consider this species Extinct in terms of the IUCN's *Red List* criteria.

Discussion

The Sri Lankan Amphibia have benefited from a decade of intensive exploration, resulting in the formal description of 42 new species thus far. These descriptions necessarily depended on a review of the surviving type and other material deposited in museums worldwide (see Materials and Methods; interestingly, decades of neglect have resulted in the disappearance of almost all amphibian specimens deposited in the Sri Lanka's own natural-history museum, established in 1877). This process enabled us, in addition to confirming the identities of extant species and describing newly discovered ones, to verify that 21 species had indeed disappeared from the island. In addition to finding four previously overlooked species in these collections, Manamendra-Arachchi and Pethiyagoda (2005) also found that several valid species had been uncritically relegated to synonymy or reduced to subspecies rank by previous authors (e.g., Kirtisinghe 1957; Kotagama *et al.* 1981).

It is interesting to note that of the 34 amphibian species confirmed as extinct worldwide in the GAA, 19 were from Sri Lanka (the GAA also considered a further 122 species 'possibly extinct'). Of Sri Lanka's 84 surviving anuran species, 11 (seven *Philautus*) were determined to be Critically Endangered, 28 (20) Endangered and 5 (0) Vulnerable (GAA, Stuart *et al.* 2004). Eight further species of *Philautus* were described and provisionally assessed for the GAA by Meegaskumbura and Manamendra-Arachchi (2005). Of the 62 valid species of Sri Lankan *Philautus*, 19 (including the two described herein) are extinct. Only two other Sri Lankan anurans are known to be extinct (Stuart *et al.* 2004): *Adenomus kandianus* and *Nannophrys guentheri,* both of which belong to endemic genera of Ranidae, and each of which is represented by two extant species.

Although climate change may also be implicated, the extinctions among Sri Lankan Amphibia appear to have been driven mainly by habitat loss. Between 1850 and 1880, much of the perhumid forest in the island's central mountains and south-western quarter was lost to coffee and cinchona plantations, later to be replaced by tea and rubber. By 1880 the island's governor, Sir James Longdon, noted: "It may without an exaggeration be said that there are no forests left of such value as to require or justify the creation of an expensive Forest Department," (Meyer 1998, p. 799). At present, less than 800 km^2 (5 %) of the island's original rainforest cover persists, in the form of more than 100 fragments. Even as 19 species of shrub frogs became extinct, then, it is remarkable that 43 species persisted, 35 of them to be discovered and described only in the past decade.

Shrub frogs are restricted largely to the rain-forested south-western 'wet zone' quadrant of the island, where annual precipitation usually exceeds 2000 mm (only a single species is restricted to the dry zone). Of the 43 extant species, it is of concern that as many as 15 are known only from a single site each, and 11 from only two—usually nearby—sites each (Manamendra-Arachchi and Pethiyagoda 2005; Meegaskumbura and Manamendra-Arachchi 2005). While future exploration may show that some of these species enjoy wider ranges, it is clear that loss or degradation of some of these sites, many of which are less than 5 km^2 in extent, could easily result in further extinctions. It is important to note, however, that many species of *Philautus* have extremely small ranges regardless of the availability of continuous habitat. Indeed, this could be one of the factors that led to their extraordinary diversification in Sri Lanka (Dubois 2005), and, given the loss of ~95 % of the island's rainforest habitat, could be the primary driver of their demise.

Although we have no evidence of Sri Lankan amphibians falling victim to climate-driven epidemic disease (see Pounds *et al.* 2006), we suspect that recent climatic change may have served to stress shrub-frog populations in the island. Bahir *et al.* (2005) showed that *Philautus* breed only during periods of sustained rainfall and continuously high relative humidity (80-100 %). While historical relative-humidity data are lacking in Sri Lanka, trends calculated by Schaefer (1998) show that at Nuwara Eliya (1,800 m elevation) in the central mountains, average annual temperature had increased by 1.3° C and average annual precipitation had decreased by ~20 % in the period 1869-1995; similar desiccation and warming trends were noted also in other parts of the country.

Is it useful to describe new but recently extinct species? We believe that it is, if only so that better estimates of lost biodiversity could be made, in turn serving to inform the conservation planning process. We hold out the albeit slim hope that some of these species may in the future be discovered in small, localized populations. It is not without misgivings, however, that we categorize these species as Extinct, bearing in mind the "Romeo error" (Collar 1998), whereby species declared Extinct risk being struck off from the conservation planning process. We hope the present descriptions will facilitate recognition of these distinctive species should they ever be encountered in future surveys.

While the small ranges of many Sri Lankan *Philautus* necessarily increase their conservation risk (Köhler *et al.* 2005), it is necessary to consider whether direct-developing anurans are in greater peril than 'conventional' ectotrophic ones. Though it contains significantly fewer species, *Philautus* in Asia appears to mirror the large Neotropical radiation of the direct-developing leptodactylid genus *Eleutherodactylus,* in which 611 species were assessed in the GAA (*cf.* 149 *Philautus*). Together, these two genera account for 74% of all direct-developing anurans. The GAA data (Table 1) show that while no species of *Eleutherodactylus* have become Extinct, the proportions of species in the various threat categories are remarkably similar to those of *Philautus*. Table 1 also shows that while the percentages of Critically Endangered, Endangered and Vulnerable ectotrophic anurans are 7, 10 and 9, respectively, those of direct-developing species, at 10, 22 and 15 percent respectively, are significantly higher. The proportion of Data Deficient species in each group, however, is the same (24 %). It is important therefore that conservation plans for amphibians pay particular attention to direct-developing species and seek to ascertain the causes of the differential threat status awarded to direct developers. It is noteworthy, however, that *Philautus* is the only direct-developing anuran genus in which extinctions have been recorded.

TABLE 1. Genera of endotrophic (direct-developing) anurans, showing also the number and percentage (in parentheses) of species in the various Threatened categories of the IUCN Red List as assessed in the Global Amphibian Assessment (www.globalamphibians.org), and also the total ectotrophic species in each conservation category: Extinct (EX), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), Data Deficient (DD).

Family	**Genus**	**EX**	**CR**	**EN**	**VU**	**NT+LC**	**DD**	**Total**
Arthroleptidae	*Arthroleptis*	-	1 (3 %)	3 (9 %)	2 (6 %)	14	14 (41 %)	34
Bufonidae	*Didynamipus*	-	-	1 (100 %)	-	-	-	1
	Laurentophryne	-	-	-	-	-	1 (100 %)	1
	Oreophrynella	-	-	-	6 (86 %)	-	1 (14 %)	7
Leptodactylidae	*Eleutherodactylus*	-	76 (12 %)	150 (25 %)	86 (14 %)	175	124 (20 %)	611
Microhylidae	*Breviceps*	-	-	-	3 (20 %)	10	2 (13 %)	15
	Cophixalus	-	1 (3 %)	3 (9 %)	4 (11 %)	13	14 (40 %)	35
	Oreophryne	-	-	1 (2 %)	3 (7 %)	8	30 (71 %)	42
	Myersiella	-	-	-	-	1	-	1
Myobatrachidae	*Arenophryne*	-	-	-	-	1	-	1
	Myobatrachus	-	-	-	-	1	-	1
Ranidae	*Anhydrophryne*	-	-	1 (100 %)	-	-	-	1
	Arthroleptella	-	1 (13 %)	-	-	5	2 (25 %)	8
	Ceratobatrachus	-	-	-	-	1	-	1
	Philautus	18	16 (11 %)	40 (27 %)	24 (16 %)	23	28 (19 %)	149
	Platymantis	-	1 (2 %)	11 (20 %)	13 (24 %)	18	12 (22 %)	55
Sooglossidae	*Sooglossus*	-	-	-	3 (100 %)	-	-	3
Total endotrophic		18	117 (10 %)	221 (22 %)	159 (15 %)	295	220 (24 %)	1,033
Total ectotrophic		14*	270 (7 %)	407 (10 %)	393 (9 %)	2,085	1,021 (24 %)	4,178

* An additional species is Extinct in the Wild.

The anomaly of 21 of the 33 anuran species that have been confirmed extinct worldwide having been endemic to Sri Lanka needs to be viewed in the context in which this datum was derived. Our survey uncovered no evidence of the large-scale amphibian population declines observed in other parts of the world (Stuart *et al.* 2004). The Sri Lankan case is unusual, however, in that it combines intensive recent exploration with a re-examination of all historical material, which in turn has been possible only because so many species had been collected before their habitats disappeared altogether, and preserved in natural history museums worldwide.

All 21 extinct species are known only from their original collections: 15 date from the period 1851–1890, the remaining six from 1901–1940. The known material relating to all 21 is preserved in BMNH (13), MCZ (2), NHMB (1) and ZMB (4); material relating to a single species was evidently not preserved. The names of collectors and locations mentioned on the labels associated with these collections, and the fact that almost all of them were contemporaneously studied and identified (even if erroneously), leads us to believe that they were indeed collected in Sri Lanka. We hope in the future to demonstrate this by including these species in a molecular phylogenetic analysis.

The extraordinary value these collections offer by way of biodiversity baselines against which present-day surveys may be assessed, remains to be widely appreciated. This is especially relevant at a time in which natural history museums worldwide are facing declines and financial crises (Dalton 2003). We urge that enhanced curatorial investment in the unique biodiversity collections of developed countries—and the handful of developing countries in which such collections survive—be recognized as a legitimate form of international development assistance. In the case of Sri Lanka, for example, information from these collections has been invaluable in demonstrating that widespread extinctions have indeed occurred: if not for this, the 21 amphibian extinctions now catalogued would have gone unnoticed.

We predict that examination of historical museum collections, where they exist, from elsewhere in the range of *Philautus* (e.g., India) will show in the future that the extinction of so many Sri Lankan amphibian species, though remarkable, is not unique.

Acknowledgements

We thank Mark Wilkinson, Barry Clarke and David Gower (BMNH) for access to collections in their care, for hospitality and many kindnesses extended to us in the course of several visits. We are also grateful to Mohamed M. Bahir (WHT) for assistance with fieldwork in Sri Lanka.

Literature cited

AmphibiaWeb (2006) *AmphibiaWeb: information on amphibian biology and conservation,* University of California, Berkeley, California: Available from http://amphibiaweb.org/ (accessed 23 October 2006).

Bahir, M.M., Meegaskumbura, M., Manamendra-Arachchi, K., Schneider, C.J. & Pethiyagoda, R. (2005) Reproduction and terrestrial direct development in Sri Lankan shrub frogs (Ranidae: Rhacophorinae: *Philautus*). *The Raffles Bulletin of Zoology,* Supplement No. 12, 339–350.

Biju, S.D. (2001) A synopsis to the frog fauna of the Western Ghats, India. *Occasional Papers of the Indian Society for Conservation Biology,* 1, 1–24.

Biju, S.D. (2003) Reproductive mode in the shrub frog *Philautus glandulosus* (Jerdon, 1853) (Anura: Rhacophoridae). *Current Science*, 84, 283–284.

Bossuyt, F. & Milinkovitch, M.C. (2000) Convergent adaptive radiations in Madagascan and Asian ranid frogs reveal covariation between larval and adult traits. *Proceedings of the National Academy of Sciences,* 97, 6585–6590.

Bossuyt, F. & Dubois, A. (2001) A review of the frog genus *Philautus* Gistel, 1848 (Amphibia, Anura, Ranidae, Rhacophorinae). *Zeylanica,* 6, 1–112.

Bossuyt, F., Roelants, K., Spithoven, L. & Daro, M.H. (2003) *Philautus bombayensis* (Bombay Oriental Shrub-frog). Reproduction. *Herpetological Review,* 32, 34–35.

Bossuyt, F., Meegaskumbura, M., Beenaerts, N., Gower, D.J., Pethiyagoda, R., Roelants, K., Mannaert, A., Wilkinson, M., Bahir, M.M., Manamendra-Arachchi, K., Ng, P.K.L., Schneider, C.J., Oommen, O.V. & Milinkovitch, M.C. (2004) Local endemism within the Western Ghats–Sri Lanka Biodiversity Hotspot. *Science,* 306, 479–481.

Collar, N.J. (1998) Extinction by assumption; or, the Romeo Error on Cebu. *Oryx,* 32, 239–244.

Dalton, R. (2003) Natural history collections in crisis as funding is slashed. *Nature*, 423, 575.

Daniels, R.J.R. (2003) Impact of tea cultivation on anurans in the Western Ghats. *Current Science*, 85, 1415–1422.

Dubois, A. (2005) Developmental pathway, speciation and supraspecific taxonomy in amphibians, 1: Why are there so many frog species in Sri Lanka? *Alytes*, 22, 19–37.

Dutta, S.K. & Manamendra-Arachchi, K. (1996) *The amphibian fauna of Sri Lanka*. Wildlife Heritage Trust of Sri Lanka, Colombo, 232.

Ferguson, W. (1876) Singular Ceylonese frogs. *Annals Magazine of Natural History,* (4) 18, 356–357.

Günther, A. (1859). *Catalogue of the Batrachia Salientia in the collection of the British Museum*. Taylor & Francis, London, xvi+160 pp.

Günther, A. (1876) Note on the mode of propagation of some Ceylonese tree-frogs, with description of two new species. *Annals Magazine of Natural History,* (4) 17, 377–380, pl. 20.

IUCN (2001) *IUCN Red List Categories and Criteria: Version 3.1,* IUCN: Gland, Switzerland and Cambridge, UK. Available from http://www.iucn.org/themes/ ssc/redlists/RLcategories2000.html (accessed 23 October, 2006).

Kadadevaru, G.G. & Kanamadi, R.D. (2001) Vocal interactions, territoriality and fighting behaviour of the rhacophorid frog *Philautus variabilis* (Gunther, 1858). *Current Science,* 80, 1486–1488.

Kanamadi, R.D., Nandihal, H.N., Saidapur, S.K. & Patil, N.S. (1996) Parental care in the frog, *Philautus variabilis* (Günther). *Journal of Advanced Zoology,* 17, 68–70.

Kirtisinghe, P. (1957) *The Amphibia of Ceylon.* Published by the author, Colombo, xiii+112 pp, 1 pl.

Köhler, J., Vieites, D.R., Bonett, R.M., GarcÌa, F.H., Glaw, F. Skeinke, D. & Vences, M. 2005. New amphibians and global conservation: a boost in species discoveries in a highly endangered vertebrate group. *BioScience,* 55, 693–696.

Kotagama, S.W., Arudpragasam, K.D. & Kotalawala, I. (1981) *A check list of Amphibia of Sri Lanka.* National Science Council, Colombo, 8 pp.

Kostermans, A.J.G.H. (1980) Mimosaceae. *In*: Dassanayake, M. D. & Fosberg, F. R. (Eds.), *A revised handbook to the flora of Ceylon.* Oxford & IBH Publishing Co., New Delhi, pp. 459–508.

Manamendra-Arachchi, K. & Pethiyagoda, R. (1998) A synopsis of the Sri Lankan Bufonidae (Amphibia: Anura) with description of new species. *Journal of South Asian Natural History,* 3, 213–248.

Manamendra-Arachchi, K. & Pethiyagoda, R. (2005) The Sri Lankan shrub-frogs of the genus *Philautus* Gistel, 1848 (Ranidae: Rhacophorinae), with description of 27 new species. *The Raffles Bulletin of Zoology,* Supplement No. 12, 163–303.

Meegaskumbura, M., Bossuyt, F., Pethiyagoda, R., Manamendra-Arachchi, K., Bahir, M.M., Schneider, C.J., & Milinkovitch, M.C. (2004) Sri Lanka: an amphibian hotspot. *Science*, 298, 379.

Meegaskumbura, M. & Manamendra-Arachchi, K. (2005) Description of eight new species of shrub frogs (Ranidae: Rhacophorinae: *Philautus*) from Sri Lanka. *The Raffles Bulletin of Zoology,* Supplement No. 12, 305–338.

Meyer, E. (1998) Forests, chena cultivation, plantations and the colonial state in Ceylon 1840–1940. *In*: Grove, R.H., Damodaran, V. & Sangwan, S. (Ed.), *Nature and the Orient: the environmental history of South and Southeast Asia*. Oxford University Press, Delhi, pp. 793–827.

Pethiyagoda, R. & Manamendra-Arachchi, K. (1998) Evaluating Sri Lanka's amphibian diversity. *Occasional Papers of the Wildlife Heritage Trust,* 2, 1–12.

Pounds, J. A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sánches-Azofeifa, G.A., Still, C.J. & Young, B.E. (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature*, 439, 161–167.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L. & Waller, R.W. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science*, 306, 1783–1786.

Schaefer, D. (1998) Climate change in Sri Lanka? Statistical analyses of long-term temperature and rainfall records. *In*: Domroes, M. & Roth, H. (Ed.), *Sri Lanka: past and present—archaeology, geography, economics—selected papers on German research.* Margraf Verlag, Weikersheim, pp. 103–117.

Thibaudeau, G. & Altig, G. (1999) Endotrophic anurans: development and evolution. *In*: McDiarmid, R.W. & Altig, G. (Ed.), *Tadpoles: the biology of anuran larvae*. University of Chicago Press, Chicago, pp. 170–188.

Vasudevan, K., Kumar, A. & Chellam, R. (2001) Structure and composition of rainforest floor amphibian communities in Kalakad-Mundanthurai Tiger Reserve. *Current Science,* 80, 406–412.

Appendix

Comparative material examined

Philautus lunatus, WHT 3283, holotype, female, 40.9 mm SVL, Handapan Ella Plains, alt. 1270 m (06º26’42”N, 080º36’35”E).

Philautus papillosus, WHT 3284, holotype, male, 40.0 mm SVL, Handapan Ella Plains, alt. 1270 m (06º26’42”N, 80º36’,35”E).

Philautus reticulatus, BMNH 1947.2.8.60, holotype, female, 58.3 mm SVL; WHT 2344, male, 44.1 mm SVL, Yagirala, alt. 30 m (06º22’N, 80º10’E); WHT 3366, male, 42.8 mm SVL, Haycock, alt. 660 m (06º20’N, 80º18’E); WHT 3230, female, 61.1 mm SVL, Induruwa, alt. 150 m (06º45’N, 80º26’E); WHT 2286-2287, females, 57.9 mm and 54.7 mm SVL, Kosmulla, alt. 320 m (06º24’N, 80º23’E); WHT 2288-2289, females, 57.2 mm and 52.2 mm SVL, Dediyagala Forest Reserve, alt. 150 m (06º10’N, 80º26’E); WHT 2290-2291, females, 57.2 mm and 51.0 mm SVL, Kosmulla, alt. 320 m (06º24’N, 80º23’E); WHT 2520-2521, females, 42.5 mm and 51.8 mm SVL, Check Poleat Gap (near Norton Bridge), alt. 800 m (06º56’N, 80º30’E).

Philautus stuarti, holotype, WHT 3208, male, 25.3 mm SVL; paratypes, WHT 3207, male, 24.2 mm SVL; WHT 3206, male, 25.2 mm SVL; WHT 3527, male, 25.0 mm SVL; WHT 3574, male, 25.1 mm SVL, Corbett’s Gap (Dumbara Hills), elevation 1,245 m (07º22’ N, 80º51’ E).

Philautus variabilis, lectotype, BMNH1947.2.7.87, female, 35.7 mm SVL, ‘Ceylon’ [Sri Lanka].

Philautus viridis, holotype, WHT 5127, male, 28.6 mm SVL; paratypes, WHT 2767, male, 27.6 mm SVL, Ambewela, alt. 1830 m (06º53’N, 80º48’E); WHT 5104-5106, males, 28.8 mm, 29.5 mm and 29.4 mm SVL, Agra arboretum, 1555 m (06º51’N, 80º41’E); WHT 3489, WHT 5099, males, 27.4 and 28.6 mm SVL, Agra arboretum, 1555 m (06º51’N, 80º41’E); WHT 3489, female, 27.4 mm SVL, Agra arboretum, 1555 m (06º51’N, 80º41’E).