Zootaxa 1238: 35–61 (2006)
www.mapress.com/zootaxa/

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

1238

A new species of *Colostethus* (Anura: Dendrobatidae) with maternal care from Kaieteur National Park, Guyana

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Abstract

A new species of *Colostethus* is described from Kaieteur National Park, Guyana, South America. The new species can be distinguished from close relatives by the presence of a median lingual process, first finger equal to second, Finger III not distinctly swollen but all fingers slightly swollen in males, presence of fringes on fingers, presence of a dorsolateral stripe from posterior corner of eye, absence of an oblique lateral stripe, and differences in tadpole morphology, colouration and pattern, vocalizations and ecology. This is only the second species of *Colostethus* known to provide maternal care for tadpoles.

Key Words: Amphibia, Dendrobatidae, *Colostethus kaiei* **sp. nov.**, maternal care, Kaieteur National Park, Guyana, Guiana Shield

Introduction

Thus far no herpetological surveys have been focused on the Kaieteur National Park biota of central western Guyana, in spite of several efforts to obtain appropriate permits (C. J. Cole, pers. comm.). Its status of protected area was apparently a formidable obstacle to obtain both research and export permits for scientific specimens. While researchers were generally prevented from investigating and inventorying the biological diversity of Kaieteur National Park, itinerant gold and diamond miners were “permitted” to work in

Accepted by S. Carranza: 25 May 2006; published: 21 Jun. 2006

several locations within park boundaries. These exploitative activities are threatening the forest ecosystem by uncontrolled anthropogenic alterations of habitat and associated pollution. Fortunately the situation changed recently, and during 2004 we initiated studies of amphibians and reptiles in Kaieteur National Park, with the strong and enthusiast support of the Prime Minister of Guyana, the Honorable Samuel Hinds. These inventories were undertaken in close collaboration with a team of local counterparts and trainees, primarily with the aim of contributing to increasing local research capacity, and laying ground work for effective conservation planning and management.

Collecting efforts were well rewarded and currently *ca.* 100 species of amphibians and reptiles are recorded from the park (Kok *et al.* in prep.). Our investigations also led to the discovery of several new amphibian and reptile taxa (*e.g.* Kok 2005), most are either still under study or results have recently been submitted for publication. During the course of fieldwork, we secured a series of specimens and tadpoles of a *Colostethus* species that is not represented in any of the literature relevant to Guyana or the Guiana Shield region [region *sensu* Huber & Foster (2003); see also Hollowell & Reynolds (2005)]. Here, we provide a description of this new species, its tadpole, and advertisement vocalizations, and observations of biparental care with a crucial contribution of maternal care. This is only the second report of maternal care within the genus. This new discovery confirms that the diversity of the genus *Colostethus* Cope (*sensu lato*) has been largely underestimated (Caldwell & Lima 2003) and suggests that most of the *Colostethus* species have low vagility and limited range of distribution. It also indicates underestimation of the behavioural diversity of the genus.

Material and methods

Phylogenetic relationships of the genus *Colostethus* are notably complex and not fully resolved (Coloma 1995; Kaplan 1997; Vences *et al.* 2000, 2003; Grant & Rodríguez 2001; Santos *et al.* 2003; Grant 2004). Yet, until there is a better elucidation of the relationships and affinities within the genus *Colostethus*, it is logical to assign the new species to this genus based on its resemblance to the sympatric *Colostethus beebei* (Noble, 1923).

We collected 13 males, 11 females, 3 juveniles and 24 tadpoles of the new species in Kaieteur National Park, Guyana (05°10’ N, 59°29’ W at elevations between 150–450 m). Specimens were collected by hand or using fences and pitfall traps in June, November and December 2004, and November and December 2005. All specimens are deposited in the herpetological collections of the Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (IRSNB). Contractual agreements with the Guyana Environmental Protection Agency (EPA) provided that some of the specimens will be returned to the Centre for Study of the Biological Diversity (CSBD) at the University of Guyana (UG) after study. Museum catalogue numbers of additional specimens examined are provided in the Appendix. Specimens were collected according to approved animal use and care

protocols (Heyer *et al.* 1994), by euthanization in Xylocaïne solution prior to fixation. Adult specimens were fixed in 10% formalin for 24 hours and transferred to 70% ethanol for permanent storage, whereas larvae were preserved in 10% formalin. Some tadpoles were reared in small glass containers to obtain later stages samples. Tissue (small piece of liver) was removed from most of the specimens and preserved in 95% ethanol. Colour in life was taken from field notes and numerous digital photographs. Sex was confirmed by dissection and presence of vocal slits.

We measured preserved specimens to the nearest 0.01 mm with electronic digital calipers or ocular micrometers on a Wild stereomicroscope; all measurements were rounded to one decimal point (Hayek *et al.* 2001). We follow the terminology, diagnostic characters and measurements given in Caldwell *et al.* (2002), with modifications from Grant & Rodríguez (2001) to facilitate congeneric comparison. Fifteen standard measurements were recorded: (1) snout-vent length (SVL); (2) head length from corner of mouth to tip of snout (HL); (3) head width at level of angle of jaws (HW); (4) snout length from anterior corner of eye to tip of snout (SL); (5) eye to naris distance from anterior corner of eye to centre of naris (EN); (6) internarial distance (IN); (7) eye length (EL); (8) interorbital distance (IO); (9) diameter of tympanum (TYM); (10) forearm length from proximal edge of palmar tubercle to outer edge of flexed elbow (FAL); (11) hand length from proximal edge of palmar tubercle to tip of Finger III (HAND); (12) width of disc on Finger III (WFD); (13) tibia length from outer edge of flexed knee to heel (TL); (14) foot length from proximal edge of outer metatarsal tubercle to tip of Toe IV (FL); and (15) width of disc on Toe IV (WTD). Webbing formulae follow Savage & Heyer (1967) and Lescure (1975) with modifications suggested by Myers & Duellman (1982) and Savage & Heyer (1997).

Developmental stages of tadpoles were determined using Gosner's (1960) protocol; oral disc characters follow Altig & McDiarmid (1999a). We recorded the 15 following measurements: (1) total length (TL); (2) body length (BL); (3) tail length (TAL); (4) body width (BW); (5) body height (BH); (6) head width at level of eyes (HW); (7) tail muscle height at base of tail (TMH); (8) tail muscle width at base of tail (TMW); (9) maximum height of tail (MTH); (10) eye-naris distance (END); (11) naris-snout distance (NSD); (12) internarial distance (IND); (13) interorbital distance (IOD); (14) eye diameter (ED); and (15) vent tube length (VTL).

The oral disc of a stage-27 tadpole (IRSNB 13766) and the tongue of an adult male specimen (IRSNB 1957) were dissected, critical-point dried and coated with gold following the usual protocol (Echeverría 1997) for scanning electron microscopy (SEM). Observations and photomicrographs were made with a Philips XL-30 ESEM scanning electron microscope.

Vocalizations of the holotype and one paratype (IRSNB 1959) were recorded by PJRK at a distance of *ca.* 50 cm from frogs using a Sony ECM-MS907 microphone attached to a DAT Sony TCD-D100 recorder on a Maxell DM60 digital audio tape. Jamie L. Talley and

GRB recorded vocalizations of paratype IRSNB 1964 and five uncollected specimens on an analogue Sony TCM-500DV cassette recorder through a Sennheiser ME-66 microphone at a distance of *ca.* 1 m from frogs. A Macintosh iBook computer with Canary version 1.2.4 software was used to analyze quantitative spectral and temporal characteristics of advertisement vocalizations at a sampling rate of 22 kHz (Charif *et al.* 1996). Temperature during recordings was taken with an Oregon Scientific thermo-hygrometer and varied from 24–25°C. Descriptive statistics were obtained from multiple measurements from each of the aforementioned males *Colostethus kaiei* on the mid-point of the fundamental and the three harmonic frequencies (kHz), note duration (ms), intranote interval (time in ms between paired notes), and internote interval (time in sec among paired or single notes), using SYSTAT 7.0 statistical package for Windows (Wilkinson 1997).

Species description

***Colostethus kaiei* sp. nov.**
Figs 1–8

Material

Holotype. IRSNB 1938 (field no. PK1159), an adult male, collected by Philippe J. R. Kok, Hemchandranauth Sambhu and Indranee Roopsind, 5 December 2005, Kaieteur National Park, along Tukeit trail, Guyana, 5°11'06" N, 59°28'51" W, elevation *ca.* 400 m.

Paratypes (26 specimens). IRSNB 1939 (female), collected by P. J. R. Kok and D. Arjoon, 22 June 2004, on Muri Muri trail, Kaieteur National Park; IRSNB 1940 (female), IRSNB 1941 (male), collected by P. J. R. Kok and D. Arjoon, 22 June 2004, along Tukeit trail, Kaieteur National Park; IRSNB 1942 (juvenile) collected by P. J. R. Kok and D. Arjoon, 24 June 2004, along Tukeit trail, Kaieteur National Park; IRSNB 1943 (juvenile) collected by P. J. R. Kok and D. Arjoon, in mist forest along the Kaieteur gorge, Kaieteur National Park; IRSNB 1944 (juvenile), collected by D. Arjoon, 28 June 2004, in Archer Simon backdam, Kaieteur National Park; IRSNB 1945 (female), collected by D. Arjoon, 9 July 2004, on Muri Muri trail, Kaieteur National Park; IRSNB 1946–47 (males), collected by P. Benjamin, 15 July 2004, on Muri Muri trail, Kaieteur National Park; IRSNB 1948 (male), collected by D. Arjoon, 19 July 2004, next to the rangers house, Kaieteur National Park; IRSNB 1949 (female), collected by D. Arjoon, 25 July 2004, at the savannah edge, Kaieteur plateau, Kaieteur National Park; IRSNB 1950 (female), collected by P. J. R. Kok, H. Sambhu, F. Marco and R. Williams, 20 November 2004, along Tukeit trail, Kaieteur National Park; IRSNB 1951 (male), collected by P. J. R. Kok, H. Sambhu, F. Marco and R. Williams, 21 November 2004, on the trail across from Menzies Landing, on the right bank of the Potaro River, Kaieteur National Park; IRSNB 1952-54 (females), collected by P. J. R. Kok, H. Sambhu and F. Marco, 4 December 2005, on the left edge of the Kaieteur

gorge, Kaieteur National Park; IRSNB 1955 (male), collected by P. J. R. Kok, H. Sambhu, I. Roopsind and F. Marco, 12 December 2005, along Tukeit trail, Kaieteur National Park; IRSNB 1956-57 (males), IRSNB 1958 (female), IRSNB 1959-60 (males), collected by P. J. R. Kok, H. Sambhu, I. Roopsind and F. Marco, 5 December 2005, along Tukeit trail, Kaieteur National Park; IRSNB 1961-62 (females), collected by H. Sambhu and I. Roopsind, 7 December 2005, along Tukeit trail, Kaieteur National Park; IRSNB 1963 (male), collected by H. Sambhu and I. Roopsind, 10 December 2005, along Tukeit trail, Kaieteur National Park; IRSNB 1964 (male) collected by F. Marco and J. L. Talley, 6 December 2005, in disturbed forest adjacent to Menzies Landing, Kaieteur National Park.

Etymology

The new species is named in honour of Kaie, a great Chieftain of the Patamona tribe, from whom Kaieteur Falls was named. According to the legend, Kaie, in order to save his people from being destroyed by a warrior tribe, the Caribs, sacrificed himself to the Great Spirit Makonaima by canoeing over the Falls.

Adult definition and diagnosis

A small species of *Colostethus* (males to 18.9 mm SVL, females to 19.8 mm SVL); body robust; Finger I and II equal in length when fingers appressed; Finger IV length reaching distal subarticular tubercle on Finger III when fingers appressed; distal tubercle on Finger IV; all fingers slightly swollen in adult males; moderate webbing between Toes I–IV; lateral fringes on fingers present; throat in adult males light greyish pink with discrete dark spotting to extensive stippling extending to chest and venter (however, the throat is never totally grey nor solid black), throat in females immaculate yellow; belly in males whitish with minute dark stippling, belly in females orangish yellow, free of melanophores; dorsolateral stripe present, sometimes barely visible; oblique lateral stripe absent; ventrolateral stripe absent; median lingual process present; cloacal tubercles absent; black arm-band absent in males; testis white (unpigmented) in adult males.

When compared to congeners from the Guiana Shield region, *Colostethus kaiei* is easily distinguished from *C. brunneus* (*fide* Cope 1887), *C. fuliginosus* Jiménez de la Espada, 1871, *C. sumtuosus* Morales, "2000" [2002], and *C. undulatus* Myers & Donnelly, 2001 by the presence of a median lingual process (absent in *C. brunneus*, *C. fuliginosus*, *C. sumtuosus*, and *C. undulatus*). *Colostethus kaiei* differs from *C. ayarzaguenai* La Marca, "1996" [1997], *C. guanayensis* La Marca, "1996" [1997], *C. parimae* La Marca, "1996" [1997], *C. parkerae* Meinhardt & Parmelee, 1996, *C. shrevei* Rivero, 1961, *C. tamacuarensis* Myers & Donnelly 1997, and *C. tepuyensis* La Marca, "1996" [1997] by adult size (adult SVL < 20 mm in *C. kaiei* versus > 20 mm in *C. ayarzaguenai*, *C. guanayensis*, *C. parimae*, C. *parkerae C. shrevei*, *C. tamacuarensis*, and *C. tepuyensis*); from *C. murisipanensis* La Marca, "1996" [1997], *C. praderoi* La Marca, "1996" [1997], *C. roraima* La Marca, "1996" [1997], and *C. wothuja* Barrio-Amorós, Fuentes & Rivas, 2004 in having dorsolateral stripes (absent in *C. murisipanensis*, *C. praderoi*, *C. roraima*

and *C. wothuja*); from *C. sanmartini* Rivero, Langone & Prigioni, 1986 in having a smooth dorsum (granular in *C. sanmartini*), Fingers I and II equal in length when appressed (Finger I shorter than II in *C. sanmartini*), and in having fringes on fingers (absent in *C . sanmartini*); from *C. breweri* Barrio-Amorós, 2006 and *C. triunfo* Barrio-Amorós, Fuentes & Rivas, 2004 in having fringes on fingers (absent in *C. breweri* and *C. triunfo*); from *C. degranvillei* Lescure, 1975 in having a light venter (venter dark stippled with white in *C. degranvillei*), from *C. beebei* (Noble, 1923) in having Fingers I and II equal in length when appressed (Finger I shorter than II in *C. beebei*), light pink throat stippled with melanophores in males (immaculate yellow in *C. beebei*), and in having a smooth dorsum (granular in *C. beebei*); and from *C. baeobatrachus* Boistel & de Massary, 1999 and *C. stepheni* Martins, 1989 in having Finger III not distinctly swollen in males (distinctly swollen in *C. baeobatrachus* and *C. stepheni*), and Fingers I and II equal in length when appressed (Finger I longer than II in *C. baeobatrachus* and *C. stepheni*).

Measurements (mm) of the holotype

SVL 16.5, HL 5.5, HW 5.4, SL 2.9, EN 1.7, IN 2.3, EL 2.4, IO 2.3, TYM 1.0, FAL 3.8, HAND 4.6, WFD 0.7, TL 8.8, FL 7.3, WTD 0.7.

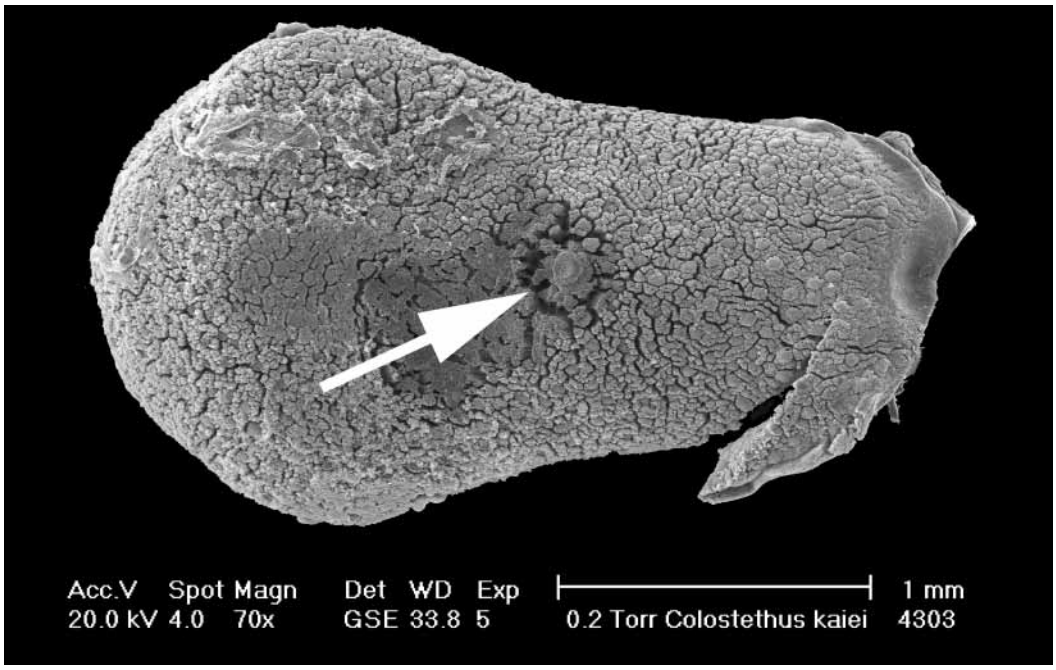

FIGURE 1. Scanning electron micrograph of the dorsal surface of the tongue of *Colostethus kaiei*, new species (male paratype, IRSNB 1957) showing the position and orientation of the median lingual process (white arrow). The short, blunt tipped MLP is directed toward the anterior part of the tongue (on the right on the picture).

Description of the holotype

An adult male 16.5 mm SVL; body robust; head slightly longer than wide, head width 98.2% length; head length 33.3% SVL; snout broadly rounded to nearly truncate in dorsal view, acutely rounded in lateral view, extending past lower jaw, snout 52.7% head length. Nares located laterally, opening posterolaterally; canthus rostralis rounded, loreal region feebly concave (nearly flat); internarial distance 42.6% head width; eye-naris distance 30.9% head length, 70.8% eye length. Tympanum nearly round, directed posterolaterally, 41.7% of eye length; separated from eye by a distance equal to 30% of tympanum diameter; supratympanic fold absent; tympanic annulus visible; posterodorsal aspect of tympanum barely visible; anteroventral margin of tympanum distinct.

Tongue attached anteriorly, longer than wide, broadly rounded posteriorly, median lingual process present (Figs 1–2). Choanae circular, lateral. Vocal slits long, lateral. Small teeth present on maxillary and premaxillary, prevomerine teeth absent. Cloacal tubercles absent; vent at level of upper thighs; a small anal flap above vent.

Skin on dorsum and belly smooth.

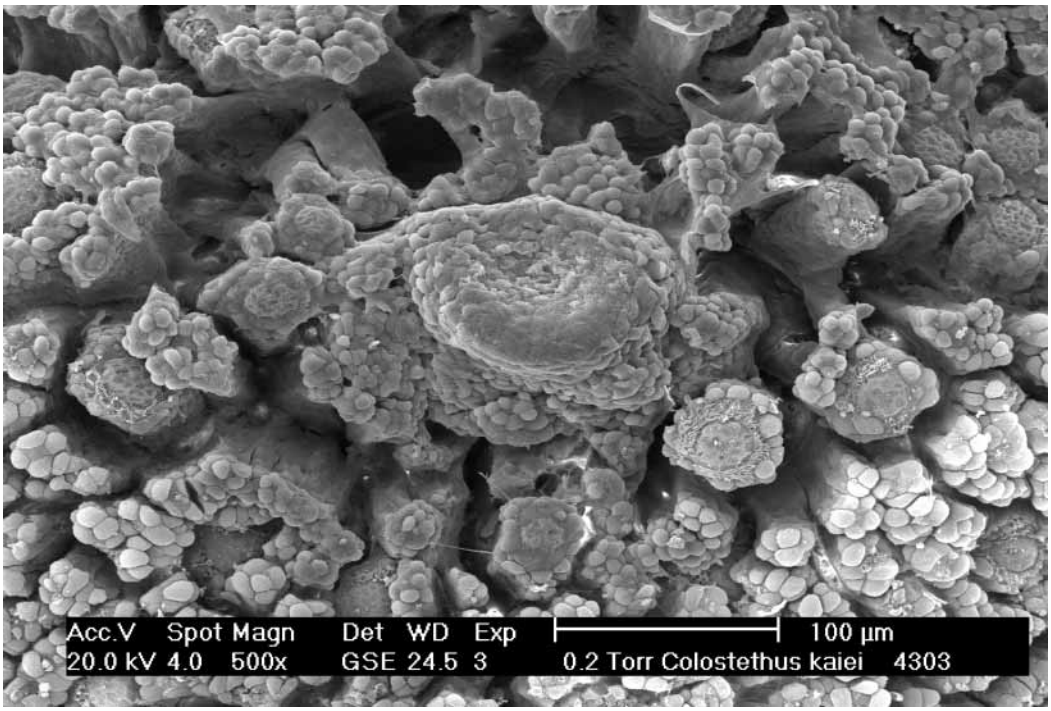

FIGURE 2. Scanning electron micrograph of the median lingual process of *Colostethus kaiei*, new species (male paratype, IRSNB 1957). Note the granular surface of the MDL, which is surrounded by fungiform and filiform papillae.

Forelimb slender, skin smooth; metacarpal ridge absent; hand length 27.9% SVL; Finger I and Finger II equal in length when fingers appressed; rudimentary webbing between Fingers II and III, lateral fringes present on pre- and postaxial edges of all fingers;

Finger III not swollen but all fingers slightly swollen when compared with those of females; Finger IV reaching distal subarticular tubercle on Finger III when fingers appressed; terminal discs expanded, wider than long, about 1.5X width of digit; width of disc on Finger III 0.70; discs with distinct dorsal scutes. Relative lengths of appressed fingers III > IV > II = I; palmar tubercle large, ovoid, 0.85 in diameter, 15.5% HL; thenar tubercle small, elliptic, half the size of palmar tubercle, well separated from palmar tubercle. One subarticular tubercle present on Fingers I and II; two subarticular tubercles on Finger III and IV; basal subarticular tubercles on Fingers I, II, and III largest, subequal, basal and distal subarticular tubercle on Finger IV smaller, subequal; distal tubercle on Finger III very small, inconspicuous (Fig. 3).

FIGURE 3. *Colostethus kaiei*, new species (holotype), ventral view of hand (left) and foot (right). Not same scale: scale bars = 1 mm. Photographs by P. J. R. Kok.

Hindlimb robust, skin granular; tibia length 53.3% SVL; heels touching each other but not overlapping when hindlimbs are flexed at right angles to sagittal plane of body; foot length 44.2% SVL; relative length of appressed toes IV > III > V > II > I; Toe I very short, reaching the base of subarticular tubercle on Toe II when toes appressed; discs on toes larger than width of toes; disc on Toe I only slightly larger than width of digit. Size of disc on Toe IV 0.70. Feet moderately webbed, webbing present between toes I–IV, webbing with melanophores; lateral fringes present on all toes but very weak on the postaxial edge of Toe IV. Toe webbing formula **I** 1-2^{-} **II** 1½-3^{+} **III** 2¾ -3^{+} **IV**. One to three subarticular tubercles on toes as follows: one on toes I and II, two on toes III and V, and three on toe IV (distal tubercle poorly defined). Inner metatarsal tubercle elliptical, 0.84 in length, outer metatarsal tubercle round, very protuberant, 0.40 in diameter, entirely pigmented. Tarsal keel well defined, tubercle-like and strongly curved at proximal end, extending distally to the fringe on preaxial edge of Toe I. Metatarsal fold strong (Fig. 3).

Colour of holotype in life

Dorsal ground colour medium brown. A wide black band extending from tip of snout laterally around the body and above the vent, containing most of the tympanum and tapering posteriorly from axilla; a thin, white, partly broken dorsolateral stripe above this band, extending from posterior edge of orbit to vent. Upper lip bar dirty white with a few white and light blue dots. Flank same colour as upper lip. Chin same colour as upper lip; throat and chest medium pink, belly cream stippled with melanophores; underside of thigh and shank creamy yellow. Iris metallic reddish bronze.

FIGURE 4. *Colostethus kaiei*, new species, holotype in life. Photograph by P. J. R. Kok.

Upper arm and forearm orange, posterior edge of the latter with a black longitudinal stripe tapering from wrist to elbow. Dark spot on upper surface of wrist. Dorsal surfaces of thigh, shank and tarsus same colour as dorsum, with ill-defined black crossbars, more crossbars on tarsus. Pale paracloacal mark. Toes and digits with small light blue dots. Palms and soles black (Fig. 4).

Colour of holotype in preservative

After two months in preservative, the dorsal ground colour became greyish brown; flanks and upper lips became pale grey; the orange and yellow colouration disappeared and ventral surfaces are white; all black bands and spots remain visible.

Male secondary sexual characters

Males are slightly smaller than females (maximum SVL in males 18.9 mm; maximum SVL in females 19.8 mm), with a cream belly (orangish yellow in females) and a light pink throat stippled with melanophores (throat immaculate orangish yellow in females). Under surface of arms and legs and posterior venter are creamy yellow in males, orange in females. Upper surface of hand is yellow in females, grey in males. In males, throat spotting varies from a few scattered tiny dots to extensive stippling extending to chest and venter, but the throat is never deep grey nor solid black (Fig. 5).

Variation among type specimens

Measurements (range, mean, and standard deviation) of the type series are provided in Table 1. Intraspecific variation is high and adult dorsal colouration varies from medium to reddish brown. Some specimens have small darker blotches on dorsum. Flanks can be yellow or grey. Light blue or white dots on flanks may be absent or present. The dorsolateral stripe is sometimes broken and/or very narrow, but always originates from posterior corner of eye. The width of the lateral black band is also variable; in some individuals it is twice the width found in other specimens. Additionally, overall colouration may vary with light intensity and time of day. The black crossbars on thigh, shank and tarsus may be nearly absent or broken into blotches in some individuals. The iris can be completely red (Fig. 6). In preservative, the dorsal colouration varies from brown to grey, apparently depending on the time spent in preservative. Other changes are similar than those observed in the holotype.

TABLE 1. Measurements in millimetres of type specimens of *Colostethus kaiei*. Abbreviations are defined in the text. Mean ± SD are followed by the range in parentheses.

Character	Males (N=13)	Females (N=11)	Juveniles (N=3)
SVL	17.4 ± 1.14 (16.3-18.9)	18.9 ± 0.65 (17.8-19.8)	11.4 ± 0.47 (10.7-11.7)
HL	4.8 ± 0.65 (3.7-5.5)	5.4 ± 0.63 (3.9-6.3)	2.7 ± 0.26 (2.3-2.9)
HW	6 ± 0.48 (5.3-6.9)	6.6 ± 0.39 (5.9-7.3)	4.2 ± 0.15 (4.2-4.4)
SL	2.6 ± 0.57 (1.7-3.4)	2.8 ± 0.42 (2.1-3.5)	1.5 ± 0.14 (1.3-1.6)
EN	1.6 ± 0.14 (1.3-1.8)	1.8 ± 0.21 (1.4-2.1)	1 ± 0.12 (0.9-1.2)
IN	2.4 ± 0.15 (2.1-2.6)	2.6 ± 0.22 (2.1-2.9)	1.6 ± 0.25 (1.3-1.9)
EL	2 ± 0.18 (1.6-2.4)	2.2 ± 0.26 (1.7-2.5)	1.4 ± 0.17 (1.2-1.6)
IO	2.2 ± 0.23 (1.9-2.8)	2.5 ± 0.28 (1.9-3)	1.4 ± 0.19 (1.3-1.7)
TYM	1 ± 0.18 (0.7-1.3)	1.1 ± 0.11 (1.1-1.3)	0.6 ± 0.09 (0.5-0.7)
FAL	3.8 ± 0.32 (2.9-4.1)	4 ± 0.26 (3.3-4.4)	2.3 ± 0.24 (2-2.5)
HAND	4 ± 0.50 (2.6-4.6)	4.3 ± 0.30 (3.7-4.9)	2.4 ± 0.29 (2-2.7)
WFD	0.6 ± 0.10 (0.4-0.7)	0.7 ± 0.08 (0.5-0.7)	0.4 ± 0.05 (0.3-0.4)
TL	8.6 ± 0.51 (7.2-9.3)	8.8 ± 0.43 (8.4-9.4)	5.4 ± 0.20 (5.2-5.7)
FL	7.3 ± 0.68 (5.7-8.3)	7.7 ± 0.55 (6.7-8.5)	4.3 ± 0.46 (3.7-4.8)
WTD	0.6 ± 0.11 (0.4-0.7)	0.7 ± 0.10 (0.5-0.8)	0.4 ± 0.05 (0.3-0.4)

Tadpole definition and diagnosis

A Type 4 tadpole (Orton 1953), exotrophic, benthic type (Altig & Johnston 1989). Size small, up to 16.7 mm TL in stage 27. Tail length 59–64% TL, caudal musculature robust, terminating anterior to tail tip, oral disc emarginate, LTRF 2(2)/3, body dark with minute pale dots, venter transparent.

In being exotrophic and in having keratinized and typical oral structures, the tadpole of *C. kaiei* is readily distinguished from those of *C. degranvillei* and *C. stepheni* (these tadpoles are endotrophic and lack keratinized and typical oral structures [Lescure 1984, Juncá *et al.* 1994]). When compared to other congeneric tadpoles from the Guiana Shield region, *C. kaiei* differs from *C. beebei* by its dark colouration, smaller size and terrestrial habitat (*C. beebei* tadpoles are yellow, larger and "arboreal"); from *C. parkerae* in position of nares (naris-snout distance 1.3X eye-naris distance in *C. kaiei*, 0.5X in *C. parkerae*); from *C. tamacuarensis* by the number and size of marginal papillae (papillae smaller and much more numerous in *C. tamacuarensis*); from *C. undulatus* by the height of tail (23% of total length in *C. undulatus*, 17% in *C. kaiei*), *C. undulatus* further differs in having smaller jaw sheaths and a less robust caudal musculature; and from *C. wothuja* by LTRF formula [2(2)/3 in *C. kaiei*, 2(2)/3(1) in *C. wothuja*].

FIGURE 5. *Colostethus kaiei*, new species, two paratypes showing the variation of colouration and sexual dichromatism. Top and bottom left, IRSNB 1959, adult male (16.5 mm SVL). Middle and bottom right, IRSNB 1958, adult female (19.6 mm SVL). Photographs by P. J. R. Kok.

FIGURE 6. *Colostethus kaiei*, new species, four paratypes from the type locality showing variation in colour and pattern. Top row: Adult males, left to right, IRSNB 1960 (18.9 mm SVL), IRSNB 1957 (18.4 mm SVL). Bottom row: Adult females, left to right, IRSNB 1954 (17.8 mm SVL), IRSNB 1953 (18.1 mm SVL). Photographs by P. J. R. Kok.

Tadpole description

Twenty-four larvae were collected: five individuals in Stage 25, eight individuals in Stage 26 and 11 individuals in stage 27. Two stage-25 larvae were reared to stage 26 and 27, and two stage-26 larvae were reared to stage 28 before preservation. The following is a description of IRSNB 13767, a specimen collected in stage 25 and raised to stage 27: total length 16.7, body length 6.2, tail length 10.5 (63% total length), body width 4.1, body height 2.8 (68% body width), head width at level of eyes 3.8 (93% body width), tail muscle height at base of tail 1.5, tail muscle width at base of tail 1.3, maximum height of tail 2.9, dorsal fin equal in height to ventral fin, greatest fin height 0.9, eye-naris distance 0.6, naris-snout 0.8, internarial distance 9.5, interorbital distance 1.1, eye diameter 0.6, vent tube length 0.95, limb bud length 0.5.

Snout round in dorsal and lateral profiles, nares directed anterolaterally, eyes dorsal, directed anterolaterally. Spiracle sinistral, a short tube, directed dorsolaterally, its base located 30% of body length from snout and 14% of body height from venter. Vent tube distinct, dextral.

Tail musculature highest at body/tail junction, tapering posteriorly, terminating anterior to tail tip. Tail tip rounded. Upper fin originates at junction of body and tail (Fig. 7).

FIGURE 7. Dorsolateral view of the tadpole of *Colostethus kaiei*, new species, in life (IRSNB 13767, stage 25, 10.5 mm TL). Photograph by P. J. R. Kok.

Mouth ventral, oral disc emarginate, width about 1 mm. Labial teeth short, strongly curved, each with at least 15 cusps. LTRF 2(2)/3. A-1 slightly longer than A-2, P-3 slightly subequal to P-2 and P-1. Papillae in a single row, a wide medial gap in upper labium. Papillae tapered, blunt-tipped. Jaw sheaths large, serrate; each side of upper sheath sigmoid, lower sheath V-shaped (Fig. 8).

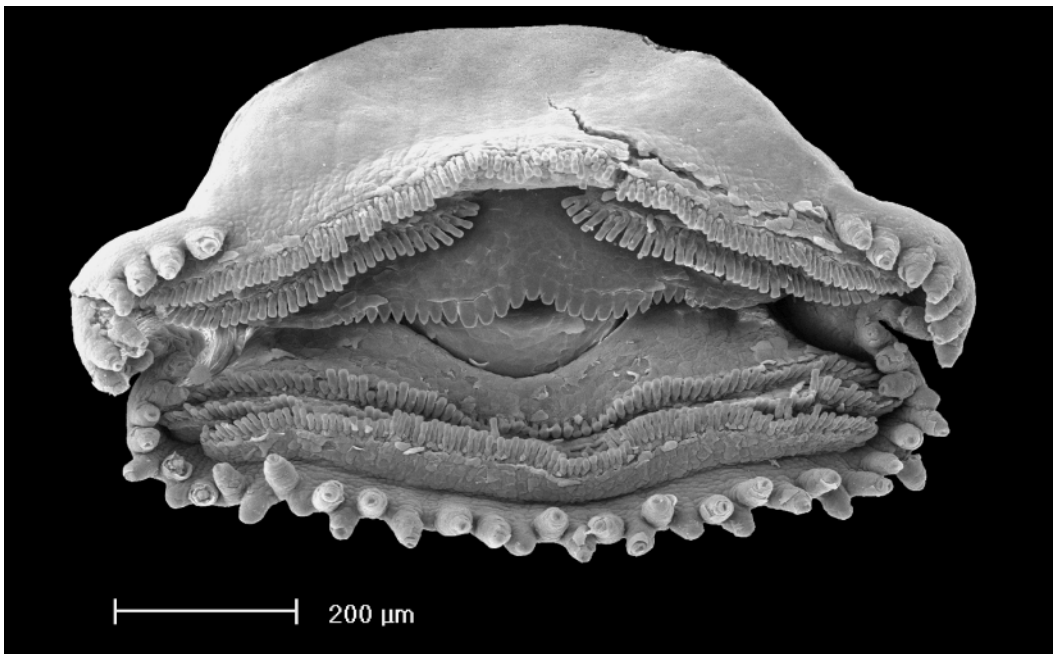

FIGURE 8. Scanning electron micrograph of the oral disc of the tadpole of *Colostethus kaiei*, new species (IRSNB 13766, stage 27, 16.8 mm TL).

Variation

Variation of 15 meristic characters from tadpoles in stage 25–28 is given in Table 2. No remarkable differences are noted among larvae from our sample except that tooth row P-3 is usually shorter in larger tadpoles.

TABLE 2. Measurements in millimetres of characters of tadpoles of *Colostethus kaiei*. Abbreviations are defined in the text. Mean ± SD are followed by the range in parentheses.

Character	Stage 25 (n = 3)	Stage 26 (n = 4)	Stage 27 (n = 11)	Stage 26 field-reared (n = 1)	Stage 27 field-reared (n = 2)	Stage 28 field-reared (n = 2)
TL	10.24 ± 0.66 (9.31-10.77)	12.67 ± 1.16 (11.04-13.83)	14.51 ± 0.62 (12.64-15.03)	13.97	16.00 ± 0.70 (15.30-16.70)	15.90 ± 0.47 (15.43-16.36)
BL	9.82 ± 0.60 (3.33-4.66)	4.76 ± 0.50 (3.99-5.32)	5.48 ± 0.20 (5.32-5.99)	5.72	6.23 ± 0.03 (6.20-6.25)	6.06 ± 0.07 (5.99-6.12)
TAL	6.42 ± 1.26 (4.65-7.44)	7.91 ± 0.70 (7.05-8.78)	9.03 ± 0.60 (7.19-9.50)	8.25	9.78 ± 0.73 (9.05-10.50)	9.77 ± 0.34 (9.44-10.11)
BW	2.54 ± 0.56 (2.08-3.32)	3.29 ± 0.35 (2.80-3.64)	3.93 ± 0.13 (3.71-4.10)	4.29	4.26 ± 0.16 (4.10-4.42)	3.95 ± 0.04 (3.90-3.99)
BH	1.71 ± 0.26 (1.50-2.08)	2.08 ± 0.62 (1.17-2.93)	2.77 ± 0.24 (2.34-3.12)	3.06	2.87 ± 0.06 (2.80-2.93)	3.49 ± 0.23 (3.25-3.72)
HW	2.36 ± 0.54 (1.95-3.12)	2.81 ± 0.39 (2.41-3.45)	3.37 ± 0.16 (3.19-3.58)	3.64	3.66 ± 0.14 (3.51-3.80)	3.75 ± 0.02 (3.72-3.77)
TMH	1.11 ± 0.09 (0.98-1.17)	1.16 ± 0.18 (0.98-1.37)	1.44 ± 0.15 (1.24-1.69)	1.50	1.53 ± 0.03 (1.50-1.56)	1.74 ± 0.11 (1.63-1.86)
TMW	0.87 ± 0.17 (0.72-1.11)	1.13 ± 0.16 (0.98-1.37)	1.41 ± 0.13 (1.30-1.63)	1.24	1.30 ± 0 (1.30)	1.52 ± 0.15 (1.37-1.67)
MTH	1.60 ± 0.03 (1.56-1.63)	1.72 ± 0.27 (1.3-1.95)	2.16 ± 0.12 (1.95-2.34)	2.15	2.69 ± 0.22 (2.47-2.90)	2.77 ± 0.69 (2.08-3.46)
END	0.41 ± 0.06 (0.33-0.46)	0.54 ± 0.08 (0.46-0.65)	0.58 ± 0.06 (0.52-0.72)	0.65	0.66 ± 0.06 (0.60-0.72)	0.76 ± 0.09 (0.67-0.85)
NSD	0.59 ± 0.05 (0.52-0.65)	0.51 ± 0.12 (0.33-0.65)	0.73 ± 0.08 (0.59-0.85)	0.78	0.86 ± 0.06 (0.80-0.91)	0.50 ± 0.17 (0.33-0.67)
IND	0.74 ± 0.08 (0.65-0.82)	0.85 ± 0.11 (0.78-1.04)	0.96 ± 0.13 (0.78-1.17)	0.85	0.61 ± 0.11 (0.50-0.72)	0.96 ± 0.02 (0.93-0.98)
IOD	0.85 ± 0.05 (0.78-0.91)	0.90 ± 0.10 (0.78-1.06)	1.00 ± 0.04 (0.98-1.10)	1.04	1.00 ± 0.09 (0.91-1.1)	1.09 ± 0.03 (1.06-1.11)
ED	0.39 ± 0.05 (0.33-0.46)	0.41 ± 0.05 (0.33-0.46)	0.54 ± 0.03 (0.52-0.59)	0.52	0.56 ± 0.04 (0.52-0.60)	0.56 ± 0.03 (0.53-0.59)
VTL	0.66 ± 0.16 (0.43-0.78)	0.56 ± 0.10 (0.46-0.65)	0.68 ± 0.09 (0.52-0.85)	0.78	0.84 ± 0.12 (0.72-0.95)	0.99 ± 0.05 (0.93-1.04)

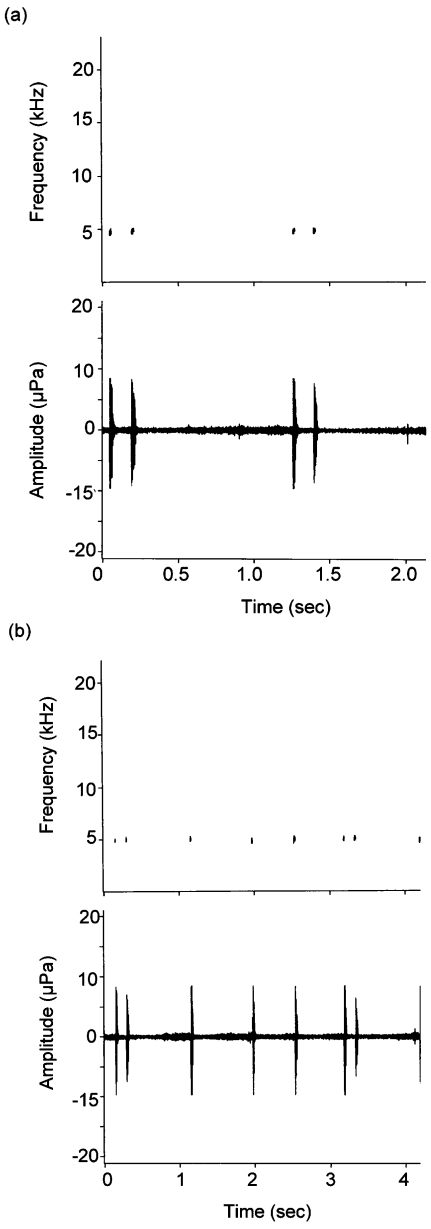

FIGURE 9. Sonogram (top) and amplitude waveform (bottom) of advertisement calls of males *Colostethus kaiei* from Kaieteur National Park Guyana. *Colostethus kaiei* advertisement calls are repetitive, unmodulated whistled short duration notes or syllables usually broadcast as paired notes (a; holotype IRSNB 1938) about 32 ms in duration, but sometimes as a mixture of paired and single notes (b; paratype IRSNB 1964). The waveform illustrates relative amplitude (sound volume) that is reflected in the height of the spikes above and below the 0 µPa axis.

Colour in life

Body and top of head dark brown (almost black) with minute light dots. Lateral head light purple (transparent but appearing purple due to blood vessels visible through the skin), with minute darker dots. Caudal musculature grey, heavily mottled with dark brown. Fins transparent, upper fin mottled with dark brown, lower fin free of melanophores. After two months in preservative the light purple disappears and the body colouration remains dark brown, or light brown in specimens left a few days exposed to the light. No other noticeable change occurs.

Vocalizations

Quantitative measures of the somewhat cricket-like chirps of eight males including the holotype [IRSNB 1938; Fig. 9 (a)], paratype IRSNB 1959 and paratype IRSNB 1964 [Fig. 9 (b)] indicated low variation among individuals (mean ± 1SE) for fundamental frequency (4.85 ± 0.40 kHz), harmonic frequency I (9.77 ± 0.30 kHz), harmonic frequency II (14.68 ± 0.07 kHz), and harmonic frequency III (19.59 ± 0.05 kHz) - unfortunately the harmonic frequencies while obvious in the original Canary generated sonograms, are not evident in Fig. 9 a, b — note duration (31.69 ± 1.17 ms), intranote duration (106.92 ± 2.41 ms), and internote duration (923.15 ± 34.07 ms; Fig. 9 a, b). The mean number of calls produced per 1-minute section was 74 and ranged from 49 to 101.

Relationships

Colostethus kaiei shares some phenotypic characters with most Guiana Shield *Colostethus*, like the median lingual process (MLP) (which is quite variable in size and shape among the species), toe webbing (extensive in some species) and robust body (*Colostethus* species without MLP have slender bodies). As pointed out by Barrio-Amorós (2006) we can assume that all the species having a MLP form a monophyletic group, but contrary to his assertions our recent discoveries show that not all of the species having a MLP share the oblique lateral stripe (absent in *C. kaiei*, but also in *C. parkerae* after original description) and the absence of dorsolateral stripes (present at least in *C. kaiei*, *C. beebei* and *C.* sp1 from Paramakatoi, the latter having a broad dorsolateral stripe).

Natural history

Colostethus kaiei is a diurnal, terrestrial, cryptically coloured species mostly found in primary forest where it can be locally abundant. A few specimens were collected in disturbed forest and one specimen was collected at the savannah edge. The species is not closely associated with bodies of water and all specimens were observed far from any stream or pond. Males are territorial and were observed calling from brown dead leaves accumulated at the base of spiny terrestrial bromeliads *Aechmea rubiginosa* Mez (Fig. 10) but also from over and under dead leaves on the ground. Some males were observed calling from elevated sites such as boulders (up to 120 cm high). Calling activity is mainly

restricted to the morning and after rains. We have so far been unable to observe courtship, and still do not know anything about the characteristics of ovipostion sites, but we observed complex maternal care.

FIGURE 10. *Aechmea rubiginosa* Mez (Bromeliaceae), one of the favourite calling sites of *Colostethus kaiei*, new species, along Tukeit trail. White arrow indicates typical location of a calling male. Photograph by I. Roopsind.

Maternal behaviour was a serendipitous discovery - in order to detect the presence of amphibians and reptiles along Tukeit trail, a series of 10 pitfalls (plastic buckets of about

28 cm diameter at the top, 30 cm deep) were installed beneath a thirty meters sheet-plastic drift fence along the trail (Fig. 11). Specimens of *Colostethus kaiei* were commonly observed along the fence, apparently visiting the pitfalls on regular basis. Several specimens (both males and females) were collected along the fence during our daily inspections. Some others were collected into pitfalls from where they were able to escape easily by jumping. On 12 July 2005 at about 10:40 h, two of us (HS and IR) went to inspect the pitfalls. It had rained heavily the previous night and intermittently during that morning. The forest soil (white sand) was saturated, and as a result some pitfalls were half filled, the water entering the traps through the small holes made in the bottom of the buckets. At pitfall 2 (half filled with water) we observed a female *Colostethus kaiei* that was not driven off by our presence (Fig. 12). The usual behaviour of these frogs in human presence is to quickly escape when disturbed. This behaviour led us to sit down and further observe the frog. During a 30 minutes observation period, the frog was observed jumping into and out of the bucket, and moving along the fence - but not travelling more than 20 cm from the bucket before returning and entering the bucket. After about 45 minutes the female suddenly moved to the rim of the bucket (*ca.* 15 cm from the water), her cloaca facing the bottom of the bucket, and laid a single egg into the bucket. The female had her mouth slightly open during the laying process. The frog was immediately collected and six tadpoles in stage 25 were discovered and collected in the pitfall. Two of them were immediately preserved while the four others were kept in a small glass container to obtain later stages. The next day, we observed another female in pitfall 4, which still contained about 2 cm water. This female was video taped for about 20 minutes hopping around the bottom of the bucket, exiting the bucket and returning, but she finally escaped without showing any particular behaviour. No tadpole was found in the bucket.

Considerable time was devoted to finding natural tadpole deposition sites. We carefully checked small terrestrial bromeliads without any success, but we quickly found four additional tadpoles in stage 27 in a very small pool measuring 39 cm x 43 cm x 6 cm (maximum) deep, between roots at the base of a tree (Fig. 13). Two of these tadpoles were immediately preserved. Two other tadpoles in stage 27 were collected in another small pool adjacent to the first one, and these were immediately preserved. Two small egg masses from a still unidentified, presumably hylid frog, were also observed in the same pool. These two pools were full of dead leaves and detritus. Still investigating the surrounding forest, we found a large egg (about 4 mm diameter), apparently unfertilized, in a third small pool between rocks. This egg that we attribute to *C. kaiei* was collected and brought back to the base camp to be deposited with the tadpoles in one of the small glass containers. On 9 December 2005, PJRK observed a tadpole vigorously pushing its head inside the egg, apparently feeding on it. Some other tadpoles were kept separately in another container without any egg provisioning but with a dead insect and some detritus found in the pitfall in which the tadpoles were collected. Cannibalism was not observed and all specimens kept in captivity survived. At the end of the field trip, after 8 days of captivity, we did not notice any significant difference in the size of these tadpoles

compared to the tadpoles provisioned with egg. This suggests non-obligatory oophagy. The amount of available food found with tadpoles in the small pools also advocates this hypothesis. Direct examination of gut contents of two tadpoles indicate that larvae mainly feed on detritus. We speculate that the supplementary amount of protein brought by trophic eggs could speed up the development of tadpoles that must survive in small, hostile environment commonly visited by predators, and probably prone to desiccation. This egg provisioning could also help to avoid intraspecific cannibalism among tadpoles. It should be noted that unidentified crabs (family Pseudothelphusidae?) were commonly encountered in the buckets filled with water, but also in small natural pools, and are probably preying on tadpoles as they do to the sympatric *Colostethus beebei* (Bourne *et al.* 2001, Kok *et al.* 2005). These crabs seem to be conspecific with the species feeding on adults and tadpoles of *C. beebei*.

FIGURE 11. One of the ten pitfalls (plastic buckets of about 28 cm diameter at the top, 30 cm deep) installed beneath a thirty meters sheet-plastic drift fence along the Tukeit trail in which *Colostethus kaiei* larvae were found. Photograph by P. J. R. Kok.

On 11 December 2005 around 13:00 h, on Tukeit trail approximately midway between the airstrip and Tukeit, we collected a male *Colostethus kaiei* carrying a single tadpole on his back. Unfortunately, the tadpole was lost in one of the several small rocky pools in which the male jumped, but the frog was collected and sex was confirmed by dissection.

Up to 8 tadpoles were collected in a single pitfall but it is not known if all of them come from the same parents or if different males deposit tadpoles in the same pool.

Further investigations are planned to better understand the reproductive ecology of this interesting little frog and will be the subject of future work (Kok *et al.* in progress).

FIGURE 12. Paratype female of *Colostethus kaiei*, new species (IRSNB 1961, indicated by white arrow) along the fence. The pitfall in which she deposited one unfertilized egg is visible on the right. Photograph by I. Roopsind.

FIGURE 13. Small pool (about 39 cm by 43 cm and 6 cm of maximum depth), between roots at the base of a tree in which tadpoles of *Colostethus kaiei* were found. Photograph by P. J. R. Kok.

Distribution

Colostethus kaiei is known only from Kaieteur National Park, Guyana, where it is known to occur in primary and disturbed forest at elevations between 150 and 450 m (Fig. 14). The species is locally abundant, especially along the Tukeit trail. Kok (2005) described the habitat types at this locality in detail.

FIGURE 14. Map showing the type locality of *Colostethus kaiei*, new species in northern South America (circle).

Discussion

Colostethus tadpoles are known to be endotrophic or exotrophic (Altig & McDiarmid 1999b). Exotrophic tadpoles of the genus *Colostethus* are usually omnivorous and, to date, the only tadpole of the genus known to feed on conspecific eggs is that of *C. beebei* (Bourne *et al.* 2001). Maternal provisioning, *i.e.* females laying trophic eggs for their tadpoles, is reported in several species of the families Dendrobatidae, Hylidae, Leptodactylidae, Mantellidae, Microhylidae, Ranidae, Rhacophoridae and Rhinodermatidae (Lehtinen & Nussbaum 2003, Gibson & Buley 2004). All of them lay eggs or deposit larvae in phytotelmata (Lehtinen & Nussbaum 2003, Lehtinen *et al.* 2004) [arboreal type *sensu* Altig & Johnston (1989)] except one, *Leptodactylus fallax*, which lays eggs in subterranean foam nest (Gibson & Buley 2004). Within the genus *Colostethus*, only females of *C. beebei* are known to lay trophic eggs (Bourne *et al.* 2001). The function of this provisioning is clearly to provide resources to offspring living in small, food-limited habitat (Lehtinen & Nussbaum 2003). The case of *Colostethus kaiei* is particularly interesting because (1) tadpoles are not deposited in phytotelmata, (2) larvae do not live in a habitat with very low food availability and (3) egg provisioning is not preceded by courtship, which occurs in *C. beebei*. Interestingly, tadpole feeding does not

appear to be facultative in *Colostethus kaiei* as it is the case in *C. beebei* (Bourne *et al.* 2001) since trophic eggs are deposited even in presence of available food (*e.g.* detritus, dead insects etc.). As stated above, tadpoles of *C. kaiei* seem to survive in absence of trophic eggs (non-obligatory oophagy) and examination of gut contents indicates other food sources. We speculate that this reproductive mode will be discovered in other *Colostethus* with a median lingual process.

We examined a series of specimens from three other localities in Guyana (Paramakatoi, Waratuk Falls and Mount Wokomung) in the herpetological collections of the Royal Ontario Museum, Canada (ROM). To our eyes, these specimens although very similar are not conspecific with *C. kaiei* and probably belong to three still undescribed species.

Since the extent of the distributional range of *Colostethus kaiei* is unknown, it is premature to assign the species to any of the IUCN categories (IUCN *et al.* 2004), but if its distribution proves to be restricted to Kaieteur National Park, we would suggest classifying it as vulnerable (VU) due to impending development in the park.

Acknowledgements

We are indebted to Indarjit Ramdass and Ramesh Lilwah of the Environmental Protection Agency, Guyana (EPA), Kristine Erskine, Michelle Kalamandeen, Kaskyn Holder and Calvin Bernard (UG) for their help in obtaining export permits for the specimens; to CE IBA Biological Center and to Margaret and Malcolm Chan-A-Sue for their help in coordinating our travels to Kaieteur National Park; to the Nyron Rahaman family for housing us and for their logistic help at Menzies Landing; to the Menzies Landing porkknockers (diamond/gold miners) for their hospitality and, for some of them, deep interest in our research; to Deokie Arjoon, Paul Benjamin, Festus Marco and Reuben Williams for field assistance and companionship; to Joyce Wade for expert meal preparation and field assistance; to Jamie Talley for additional recordings of *Colostethus kaiei* vocalizations; to Jackie Van Goethem, Anne Franklin and Yves Samyn (Belgian Focal Point to the Global Taxonomy Initiative, IRSNB) for support of our research activities; to Julien Cillis (IRSNB) for technical assistance in SEM; to Sébastien Bruaux and Christophe De Mey (IRSNB) for technical help in Brussels and to Ross MacCulloch (ROM) for constructive discussions. We also thank Diane Okamuro for technical assistance and Carol Kelloff (Smithsonian Institution, Washington) and Bruce Holst (Marie Selby Botanical Gardens, Sarasota) for their identification of the bromeliad. For the loan or exchange of specimens under their care we thank E. La Marca (Universidad de los Andes, Mérida), R. MacCulloch and R. Murphy (ROM). We also gratefully acknowledge the financial support of the Belgian Directorate-General of Development Cooperation, and the National Science Foundation, and the enthusiast help and support of the Prime Minister of Guyana, the Honorable Samuel Hinds. Permission to conduct this

study was granted by Shyam Nokta and Inge Nathoo of the Guyana National Parks Commission, with research and collection permits issued by the Guyana EPA (research permits 180604BR011 and 030605BR006; export permits 100804SP010, 031204SP017 and 191205SP011).

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Appendix: additional specimens examined

Colostethus baeobatrachus

FRENCH GUIANA: **Régina**: Pic Matécho (03°45’ N, 53°29’ W, elevation 400 m), IRSNB 13001 (2 specimens), IRSNB 13011, IRSNB 13015 (4 specimens), IRSNB 13018 (3 specimens). **Roura**: Cacao (04°34’ N, 52°28’ W), not far from the village, IRSNB 12662; Crique Bagot, IRSNB 12663; Crique Bagot, Dégrad Kwata, IRSNB 12767–68, IRSNB 12975. **Saül**: Saül, Montagne Belvédère (03°37’ N, 53°10’ W, elevation *ca.* 250 m), *ca.* 7 km SE from the village, IRSNB 12753–55, IRSNB 12970, IRSNB 12976–79.

Colostethus beebei

GUYANA: **Potaro Siparuni**: Kaieteur National Park, Kaieteur plateau (05°10’ N, 59°29’ W, elevation 450 m), IRSNB 13721–26, 13728–53, ULABG 6817 (ex IRSNB 13727), IRSNB 13754 (3 tadpoles), IRSNB 13779–81 (tadpoles).

Colostethus degranvillei

FRENCH GUIANA: **Roura**: Cacao (04°34’ N, 52°28’ W), not far from the village, IRSNB 12683; Crique Ste Anne IRSNB 12684, IRSNB 12769 (4 specimens). **Saül**: Saül, Montagne Belvédère (03°37’ N, 53°10’ W, elevation *ca.* 250 m), *ca.* 7 km SE from the village, IRSNB 12950–12953. **Régina**: Pic Matécho (03°45’ N, 53°29’ W, elevation 400 m), IRSNB 13000 (13 specimens).

Colostethus kaiei

GUYANA: **Potaro Siparuni**: Kaieteur National Park, Kaieteur plateau (05°10’ N, 59°29’ W), ROM 42999.

Colostethus sp1

GUYANA: **Potaro Siparuni**: Paramakatoi (04°10’50” N, 59°47’12” W, elevation 800m), ROM 38224.

Colostethus sp2

GUYANA: **Potaro Siparuni**: Kaieteur National Park, Potaro River, Waratuk Falls, portage trail, ROM 20569.

Colostethus sp3

GUYANA: **Potaro Siparuni**: Mount Wokomung (05°06’35” N, 59°48’37”W, elevation 700 m), ROM 43221, ROM 43327, ROM 43333. Mount Wokomung (05°07’46” N, 59°49’16”W, elevation 1234 m), ROM 43320, ROM 43322, ROM 43325. Mount Wokomung (05°05’33” N, 59°50’35”W, elevation 1400 m), ROM 43323.

Colostethus pittieri

VENEZUELA: **Estado Aragua**: La Trilla (elevation 170 m), IRSNB 1931 (ex-ULABG 3959), ULABG 3960.

