Introduction to the taxonomy of the amphibians of Kaieteur National Park, Guyana

One of the impediments to understanding amphibian diversity in the Neotropics is the lack of complete, taxonomically accurate treatments of the amphibian species from geographically restricted areas. Botanists have long appreciated the importance of such studies and have reported the studies as florulas. The present work can be paraphrased as the amphibian fauna of Kaieteur National Park. A successful florula or fauna must be based on intensive sampling. It needs to be presented in such a way that users of the work can incorporate new taxonomic changes because sufficient information provided in the faunula/florula allows the worker to assess whether new taxonomic results apply to the faunula/florula involved. This is particularly critical for amphibian species, which are undergoing massive taxonomic revisions, especially in tropical regions. The authors of the Kaieteur National Park fauna present the data needed to determine the proper name(s) for Kaieteur National Park taxa.

Another feature of this work is the only detailed resource of which I am aware that documents how to successfully undertake amphibian fieldwork, including permit application procedures, equipment needed for work in remote areas, sampling methodology, collecting equipment, data collection, voucher specimen preservation, molecular study samples, advertisement call recordings, etc.

The amphibian faunula of Kaieteur National Park is a welcome addition to the altogether too few intensive amphibian publications of northern South America such as those for Santa Cecilia, Ecuador and Reserve Ducke, Brasil.

December 2008

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Introduction to the taxonomy of the amphibians of Kaieteur National Park, Guyana

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Cover illustrations: background photo, Kaieteur Falls; clockwise from top left, Hypsiboas sibleszi (Rivero), Anomaloglossus beebei (Noble), Hypsiboas liliae Kok, Anomaloglossus kaiei (Kok et al.). This page, Stefania evansi (Boulenger), a female carrying 30 juveniles. (Photos by P. J. R. Kok).
"To be a Naturalist is better than to be a King"

Preface by His Excellency Patrick Gomes, Ambassador of Guyana in Brussels

The people of Guyana, our ancestors as well as the present generation, have always cherished the spectacular beauty of the Kaieteur Falls, known to most, however, mainly by the remarkable photography of that world-famous sight of a crystal clear sheet of 226 metres of water that sprays a mist of several million litres.

Accompanied by a thunderous roar, that is said to be enchanting and mysterious to the would-be visitor, Kaieteur Falls is truly the jewel and wondrous gift that our country shares with the world through its Kaieteur National Park, an area of more than 60,000 hectares, richly endowed by a biological diversity, little documented by scientists.

Now, this remarkable achievement of two young scientists, one Guyanese and the other Belgian, provides a seminal scientific account to serve as a manual with both theoretical and practical guidelines for other scientists, students and the reading public. All readers interested in learning more of the amphibians that make their habitat in the locale of the Kaieteur National Park within the wider region of the Guiana Shield, will benefit from the discussion and detailed descriptions provided by this Manual.

Beyond the readership and practitioners, whose knowledge and skills will be enriched by the study and use of this Manual, the publication will serve also as a significant step towards the designation by the United Nations Education and Scientific Organisation (UNESCO) of the Kaieteur National Park as a World Heritage Site.

Guyana is truly proud of the work of Philippe Kok and Michelle Kalamandeen.

Brussels, November 2008
Foreword by the authors

Original idea of writing this manual occurred in 2004 while working with amphibians in Kaieteur National Park in the context of a “training through research” program generously funded by the Directorate-General for Development Cooperation (DGDC) through the Belgian Focal Point to the Global Taxonomy Initiative.

We strongly believe that the science of taxonomy should be communicated to researchers, ecologists, and environmentalists - both beginners and experts - as it often shapes the survival of species in key ecosystems. Species are key in biodiversity conservation and estimation of biodiversity. Therefore it is important to properly identify the species in a given area. This is where taxonomy comes in.

There are numerous texts on amphibian taxonomy, but relatively few are dedicated to teaching the methods and techniques used in performing taxonomy. Concurrently, field guides dealing with amphibians of the Guiana Shield are surprisingly scarce. This manual will hopefully give extensive insight into the world of taxonomy of amphibians, using our knowledge from Kaieteur National Park.

We wrote the manual as a “frogs for dummies”, bearing in mind the kind of information that would have been most useful to us at the beginning of our own herpetological activities. Keeping it under the maximum number of pages allowed by the editors was quite challenging and sometimes frustrating. We expect this volume will stimulate the interest of Guyanese teachers, students and researchers that would like to specialize in amphibians, specifically given the increasing rate of disappearance of these vital bellwethers of the environment.

The manual is written to captivate undergraduate and graduate students with an interest in amphibian taxonomy, but can also be used to stimulate the interest of tourists and nature lovers. Professional herpetologists will enjoy the informative sections, which are easy to access and in a convenient format.

Studying and working with amphibians is not always glamorous, but it can be fulfilling and interesting working with these wonderful and complex animals. We trust we succeeded in synthesizing the most important information in this handy book.

So many questions are left unanswered and many things remain to be done!

Brussels, Belgium
Georgetown, Guyana
October 2008
Abstract

Kaieteur National Park is a protected area covering ca. 63,000 ha located at the eastern edge of the Pakaraima Mountains, in a largely unexplored region of west-central Guyana. Next to providing description of the area, its vegetation and climate, an overview of the equipment and appropriate techniques needed to study amphibian taxonomy, this manual also provides a brief summary of our current knowledge of the amphibian systematics in the region, key features useful to identify amphibians, and the very first field guide dealing with the amphibian fauna of Guyana, notably with the amphibians of Kaieteur National Park. A total of 48 species (46 anurans and 2 caecilians) are treated and illustrated in colour. Field keys, field identifications, brief information on natural history, calls, tadpoles and distribution within and outside the Park are also included. This work also reports the microhylid *Synapturanus salseri* Pyburn, 1975 for the first time from Guyana.

Keywords – advertisement calls; Allophrynidae, amphibian taxonomy; Aromobatidae; Bufonidae; Caeciliidae; Centrolenidae; collecting methods; descriptions; Eleutherodactylidae; field keys; Guiana Shield; Guyana; Hemiphractidae; Hylidae; Kaieteur National Park; Leptodactylidae; local communities; Microhyliidae; Pipidae; preservation techniques; Rhinatrematidae; South America; Strabomantidae; tadpoles.
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ix
1. Introduction to Kaieteur National Park, jewel of Guyana

Kaieteur National Park is located in west-central Guyana, South America, at the eastern edge of the Pakaraima Mountains (also known as Sierra Pacaraima).

The Cooperative Republic of Guyana (Guyana) is one of the six countries covering the geologically and biologically distinct unit called the Guiana Shield (Fig. 1), which contains one of the largest remaining tracts of untouched rainforest in the world and is well known for its high species richness and endemism.

Guyana is bordered on the northwest by Venezuela, on the east by Suriname, on the south and southwest by Brazil, and on the north by the Atlantic Ocean, and is dissected by several major drainages (Fig. 2). More than 70% of the country is still covered with pristine tropical forest, making Guyana a biologically rich country, and an invaluable and attractive experience for scientists and any visitor captivated by nature.

Kaieteur National Park is probably one of the most neglected national parks in South America and its herpetofauna was hitherto never properly studied, although specimens were sporadically collected in the area since the beginning of the 20th century. The first and only published list of the reptile and amphibian species occurring in Kaieteur National Park is Kelloff’s (2003) short compilation of 29 species, which unfortunately includes several obvious errors and dubious records.

Fig. 1. Map of northern South America showing the boundaries of the Guiana Shield (red line). (Map elaborated by P. J. R. Kok after a radar image of South America by NASA/JPL/NIMA available at http://photojournal.jpl.nasa.gov/catalog/PIA03388 and the Guiana Shield map provided by Señaris & MacCulloch, 2005).
Fig. 2. Map of Guyana showing major drainages and the location of Kaieteur National Park (in grey, pointed by a red arrow); black star = Georgetown, capital city. (Map elaborated by P. J. R. Kok after a radar image of South America by NASA/JPL/NIMA available at http://photojournal.jpl.nasa.gov/catalog/PIA03388).
The British explorer and geologist Charles Barrington Brown was probably the first non-native to see the spectacular Kaieteur Falls in 1870.

Several decades later, in 1929, Kaieteur National Park (Fig. 3, located between ca. 5°08’ to 5°19’N and ca. 59°22’ to 59°38’W) was established by the British Commonwealth as one of the very first national parks in South America. Historically the boundaries of the original Park were drastically reduced from 11,400 ha to 1,940 ha in 1961, before being expanded in 1999 by President Cheddi Jagan (Kelloff, 2003).

At present the Park encompasses an area of 62,680 ha and lies in the Potaro-Siparuni District (formerly called Mazaruni-Potaro District).

1.1. Physiography and hydrography

Although Kaieteur National Park lacks the extensive mountainous topography and spectacular landscapes made from impressive plateaus (table-top mountains, locally called tepuis) that dominate the rest of the Pakaraima Mountains, its geological and biological diversity is significant.

Kaieteur National Park lies on Precambrian sandstone - one of the oldest exposed rock formations on earth - at the eastern edge of the Pakaraima Mountains, approximately 200 km airline SW of Georgetown, the capital city of Guyana. Formed about 300 millions years ago, the Pakaraima Mountains are located in the highlands of the Guiana Shield along the border between Venezuela, Brazil and Guyana, extending west to east for over 800 km. That region is also referred to as the phytogeographic province of Pantepui, which includes all upper slopes and summits of the Guiana Shield highlands. Mount Roraima (2,810 m above sea level) lies at the conjunction of the three countries and is the highest peak in the area.

This largely unexplored area is known for its relatively unspoiled habitat and highly endemic flora and fauna, however, as mentioned above, the herpetofauna of the region remains essentially undocumented. Elevation in the Park extends approximately 100–900 m (from the gorge to highest point on the plateau, see Fig. 3). The highest areas of the Park are located in the southwestern and southeastern parts, which remain largely unexplored. The centrepiece of the Park is the well-known 226 m high Kaieteur Falls situated where the Pakaraima Mountains give way to the interior lowlands (Figs 4, 5, 6A-B). This superlative phenomenon expels millions of litres of water as mist. The surrounding mist and prevailing winds partially influence the densities of some species in the vicinity of the fall. Many rivers and streams, including fast moving cascading streams with smaller waterfalls (Fig. 6C), are found throughout the Park. The largest river running through the Park is the Potaro River, which is 225 km long, travelling approximately 32 km through the deep Kaieteur gorge (Figs 6D, 7) and eventually into the Essequibo River, Guyana’s largest waterway. The origin of the Potaro River is located in Mount Ayanganna (5°23’N, 59°59’W). Other major drainages running in the Park are Kurubia River, Aki River, Muri Muri River, Elinkwa River, Amamuri River, Amakwa River, and Chetu River (see Fig. 3).
Fig. 3. Map of Kaieteur National Park with major drainages and main sampling localities (= localities where sampling efforts were concentrated): (1) Kaieteur Falls; (2) Menzies Landing trail; (3) Kaieteur airstrip; (4) Muri Muri trail; (5) Right bank Potaro River, opposite Menzies Landing; (6) Tukeit trail; (7) Tukeit Landing; (8) Elinkwa River mouth; (9) Elinkwa River; (10) Elinkwa camp #1; (11) Elinkwa camp #2; (12) Amakwa River mouth; (13) Amamuri River mouth. Insert map indicates the location of Kaieteur National Park in Guyana. (Maps elaborated by P. J. R. Kok after the Natural Resources Management Project, Topographic Map of Kaieteur National Park, Guyana and a radar image of South America by NASA/JPL/NIMA available at http://photojournal.jpl.nasa.gov/catalog/PIA03388).
Fig. 4. Scenic view of Kaieteur Falls from its base. (Photo by P. J. R. Kok).

Fig. 5. Kaieteur Falls splashing into the Kaieteur gorge. (Photo by P. J. R. Kok).
Fig. 6. Rivers and waterfalls. A. Kaieteur Falls flows at a rate of 660,000 litres per second during the wettest months; B. The physiognomy of Kaieteur Falls drastically changes during the driest months; C. Many smaller waterfalls like this one are found throughout the Park; D. The Potaro River running in the Kaieteur gorge. (Photos by P. J. R. Kok).
1.2. Local communities

A small permanent settlement, called Menzies Landing (Fig. 8), is located inside the Park, less than 2 km SW by foot from the fall (Fig. 9). Menzies Landing is considered the gateway to the gold and diamond mining fields - some of them located within the Park - for “porkknockers” (local, low tech, freelance miners). These miners have built small wooden houses (Fig. 10) in which they live and rest when coming back from the “backdam” (mining field). In 2007, two small stores sold food and other basic supplies to miners and nearby Amerindian communities, but also bought diamonds and gold, which continue to be sent to Georgetown by plane from the Kaieteur airstrip. These human activities caused habitat destruction and pollution and are a serious threat to the biota of certain parts of the Park (Fig. 11).

The nearest community outside Kaieteur National Park is the Amerindian village of Chenapou (also spelled Chenapau or Chenapowu), located along the Potaro River, about 54 km SW of Kaieteur Falls by boat.

The Park encompasses ancestral lands and is an important traditional site for hunting and fishing for local indigenous communities. These local communities opposed the extension of the Park as it was made without their knowledge and without meaningful consultations. In the late nineties there were no regulations defining the rights of indigenous peoples to hunt, fish and conduct other traditional activities in the area, but by gazetting the 2006 Amerindian Act, traditional Amerindian practices are now officially allowed in the Park.
Consistent with the National Development Strategy (Anonymous, 2000), the community at Menzies Landing and all mining operations within the Park needed to be closed down in order to rehabilitate and restore the area. Additionally, mining operations outside the Park were to be monitored so as to prevent damage to the Park’s environment or, where this is not possible, terminated.

According to the National Parks Commission (NPC), the agency responsible for the management of Kaieteur National Park, effective monitoring and enforcement is currently unachievable due to the lack of financial and human resources. At present, four wardens control the Park, with two persons from the village of Chenapou currently involved in park ranger training by the joint Iwokrama-EPA-GFA programme. The NPC is considering hiring these trainees as full-time wardens to assist in the monitoring of the Park (N. Roopnarine, pers. comm. 2008).

Fig. 8. Menzies Landing along the Potaro River. (Photo by P. J. R. Kok).
Fig. 9. Area map of Menzies Landing (orange dot) and surroundings. Brown dashed lines = Menzies trail; light green dashed lines = Muri Muri trail; dark green dashed lines = Tukeit trail; blue dashed lines = Water gauge trail; green house = Kaieteur guesthouse. (Map elaborated by P. J. R. Kok after “Kaieteur Sheet 43 SW” published by the Survey Department of Guyana, 1972).
Fig. 10. A. Small store at Menzies Landing, centre of diamond and gold business; B. Typical wooden house at Menzies Landing. (Photos by P. J. R. Kok).
Fig. 11. Human activities and associated habitat destruction and pollution are a major threat to the fauna of certain parts of Kaieteur National Park. A. Illegal diamond-mining camp in the southeastern part of the Park; B. Illegal deforestation for farming around Menzies Landing; C. Burning of the savannah at the top of Kaieteur Falls in November 2004 - this kind of event could have extirpated several endemic species; D & E. Illegal mining (dredging) in the southeastern part of the Park. (Photos by P. J. R. Kok).
1.3. Climate

Guyana has a tropical climate, lying between 1-9°N and 56-62°W, with uniformly high temperatures, humidity and rainfall. Average annual rainfall ranges between 1778 mm and 2800 mm with a relative humidity of approximately 70%. Along the coast, temperature ranges from 20 to 38°C, while in the interior regions it ranges from 16 to 39°C (although temperatures on the summit of the highest tepuis may drop below 10°C).

There is a slight seasonal variation in temperature with two distinct wet seasons and two dry seasons. According to the Ministry of Agriculture, Hydrometeorological Service, Guyana (2008), seasonal rainfall variability is generally the dominant characteristic of climate in Guyana. The long wet season usually commences from mid-April to July, with major peak rainfall in June. The short wet season is from November to January with peak rainfall in December. The long dry season starts from August to November while the short dry season is from February-mid April.

At Kaieteur National Park, the yearly average relative humidity ranges between 80 and 87% with a dew point temperature averaging 21.6°C and an average mean temperature of 23.3°C (Guyana Hydrometeorological Service, pers. comm. 2008). Figure 12 illustrates yearly mean temperature in the Park for the years 1997 and 2000-2007. The highest recorded month for rainfall is May (on average 728.3 mm) while the lowest is October (averaging 124.3 mm). The physiognomy of Kaieteur Falls is highly dependent on the seasons (see Fig. 6A-B). The data provided in Tables 1 & 2 are from the Meteorological Station located in the savannah at the top of Kaieteur Falls (Fig. 13). Due to the many different local environments (soils, elevations, exposures) occurring in the Park, average temperature and humidity may considerably vary in other locations. Some parts of the Park may experience intense downpours while a few kilometers away there is clear sky and strong sunlight.

![Figure 12. Yearly mean temperature for Kaieteur National Park (data supplied by the Guyana Hydrometeorological Service, 2008).](image-url)
Fig. 13. Kaieteur Hydrometeorological Station (indicated by black arrow in the upper left corner), along the Kaieteur airstrip at the top of Kaieteur Falls. (Photo by P. J. R. Kok).

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Table 1: Yearly average relative humidity of Kaieteur National Park (data supplied by the Guyana Hydrometeorological Service, 2008).
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Table 2: Monthly average rainfall (mm) for Kaieteur National Park for 1997, 2000 to 2007 (data supplied by the Guyana Hydrometeorological Service, 2008); DD = Data Deficient.
1.4. Vegetation

The vegetation at Kaieteur National Park is spectacular and supports a variety of different habitats. The Park harbours a mixture of the upland and lowland flora found on the Guiana Shield and supports a mosaic of forest, shrub and herbaceous formations.

According to Kelloff (2003), there are currently 22 endemic species of plants recorded for the early sixties’ delineation of Kaieteur National Park (1,940ha), although some of these plants might prove to be more widespread both within and outside the Park. Aechmea brassicoides for instance, one of the 22 endemic species reported by Kelloff (2003) from the early sixties’ delineation, was seen in other locations in the Park (P. Kok, pers. obs.). See Kelloff (2003) and Kelloff & Funk (2004) for more details on plants of Kaieteur.

Forest formations

Tall, mixed, evergreen, basimontane and submontane forests on white sand occur throughout the Park (Fig. 14A-B) and are mainly composed of tree species in the genera Dicymbe, Dimorphandra, Eperua, Micrandra and Peltogyne. Typical lower story trees belong to the families Annonaceae, Guttiferae, Lecythidaceae, Leguminosae, and Palmae, while members of the Araceae, Bromeliaceae, Marantaceae, Melastomataceae, and Rapateaceae noticeably dominate the vegetation of the forest floor.

Riparian forest consists of tree species such as wallaba (Eperua), brazilnut (Lecythidaceae), aromata (Clathrotropis macrocarpa), kakaralli (Eschweilera spp.), and coffee (Rubiaceae) families (Kelloff, 2003). The understory of this type of forest supports Heliconia, Marantaceae, and many species of Melastomataceae (Fig. 14C).

Patches of cloud forest are found in several parts of the Park, usually at elevations over 500-600m. One cloud forest habitat created by the cool mist rising from the gorge is found at the top of Kaieteur Falls (Fig. 14D). This habitat sustains numerous epiphytes, mosses, orchids, ferns and aroids.

Shrub and herbaceous formations

Patches of “savannah” (Fig. 15A-C) surround the top of Kaieteur Falls, but are also found elsewhere in the Park. These savannahs support a shrub-herb plant community with only few small trees. The pink sands mixed with bare rocks support scattered shrubs and a dense mat of small herbaceous plants (Kelloff, 2003). It must be noted that part of the savannah surrounding the top of Kaieteur Falls is anthropogenic (Fig. 15C).

During the rainy season, numerous species of lichens such as Cladonia spp. and Cladina spp., the small blue flowered herb Burmannia bicolor, two types of carnivorous plants, Utricularia spp. (bladderworts) and Drosera kaieteurensis (red sundew), appear from tiny cracks and on the surface of the bare, flat sandstone (Kelloff, 2003).

Usually the first plant to catch the eye in the vicinity of Kaieteur Falls is the tank bromeliad (Brocchinia micrantha), which can reach a height of 3.5 m as it takes...
advantage of the humus caught in larger cracks and crevices. The water that collects in the phytotelm of this plant is an important habitat for the golden rocket frog, *Anomaloglossus beebei* (Fig. 15D), and the tiny bladderworts, *Utricularia humboldtii*, which uses its aquatic roots to capture insects that live in the stagnant waters.

Other notable bromeliads are the cabbage head, *Aechmea brassicoides*, and the carnivorous *Brocchinia reducta*, with tall, narrow, yellowish leaves, which often serves as a daytime refuge to the endemic frog *Tepuihyla talbergae*.

Kelloff (2003) highlighted that small trees such as *Andira grandistipula* and shrubs such as *Clusia* and *Erythroxylum* can develop into “bush islands” which support an entire community of plants and often differ from island to island.

**Fig. 14.** Forest formations found in Kaieteur National Park. A. Basimontane forest on white sand; B. Submontane forest; C. Riparian forest along the Potaro River; D. Cool mist rising from Kaieteur Falls creates a patch of cloud forest at the top of the fall. (Photos by P. J. R. Kok).
Fig. 15. Shrub and herbaceous formations found in Kaieteur National Park. A-B. Shrubland and forest at the top of Kaieteur Falls; C. Mostly anthropogenic herbaceous formation at the top of Kaieteur Falls; D. The terrestrial bromeliad *Brocchinia micrantha* is a major element of the savannah surrounding the top of Kaieteur Falls and is the exclusive habitat of *Anomaloglossus beebei* (three specimens are indicated by arrows). (Photos by P. J. R. Kok).

2. Class Amphibia Gray, 1825

Amphibian classification is undergoing major rearrangements. According to Frost *et al.* (2006), Amphibia is a monophyletic taxon composed of Gymnophiona (“caecilians”) and Batrachia (“salamanders” + “frogs”) (see Fig. 16).

![Consensus Tree](image)

*Fig. 16. Basal structure of Frost et al.’s (2006) consensus tree with respect to outgroups and major amphibian taxa. Copied from Frost et al. (2006: 113), with permission of D. R. Frost.*

The term Amphibia derives from the Greek *amphi* meaning both or double and *bios* meaning life; this is an allusion to the ability of amphibians to live both in
aquatic and terrestrial environments. Note that the term “Lissamphibia” is
sometimes applied to the extant amphibian species. Amphibians are tetrapods
(although limbs are reduced or secondarily lost in some groups) with a glandular
skin that lacks epidermal scales, feathers, or hair. They are ectotherms, which
means that they are dependent on external heat sources. Many internal and
external morphological characters define the Class Amphibia. The purpose of
this work is not to detail all of these features and we suggest the reader to refer
to the numerous works extensively defining Amphibia (e.g. Duellman & Trueb,
1986; Trueb & Cloutier, 1991; Pough et al., 2004) for more exhaustive
information. According to Trueb & Cloutier (1991) synapomorphies of Amphibia
include the loss of the postparietal bones, the loss of the supratemporal bone,
the loss of the tabular bone, the loss of the postorbital bone, the loss of the jugal
bone, the loss of the interclavicle, the loss of the cleithrum, the presence of a
specialized sensory area, the papilla amphibiorum, in the inner ear, the opercular
element associated with the columella, the presence of fat bodies that originate
from the germain ridge associated with the gonads, and the presence of
pedicellate and bicuspid teeth that are replaced mediolaterally (reversed in some
taxa).

2.1. Order Gymnophiona Müller, 1832

Members of the order Gymnophiona, also called caecilians, are limbless
amphibians that resemble earthworms or even snakes; the taxonomic name
Gymnophiona derives from the Greek gymnos meaning naked and ophis
meaning snake. Caecilians are found in most of the tropical regions, except
Madagascar and Oceania.

The caecilian body is elongated and partly or completely segmented by annuli,
which are separated by grooves. Limbs, rudiments of pectoral and pelvic girdles
are lacking; frontal and parietal bones are distinct; palatoquadrate articulates with
skull; atlas articulates with skull by atlantal cotyles. Only one currently known
species is lungless [Atretochoana eiselti (Taylor, 1968)], all other known
aeacilians have lungs with the left one being usually rudimentary (similar
adaptation is found in snakes). The tail is short or absent (it may sometimes be
difficult to state if a tail is present or not). The cloaca is located at the end of the
body. Variation in size is considerable ranging from ca. 100 mm to ca. 1500 mm.
Eyes are small, often barely visible, covered by skin or by the bones of the skull.
There is no tympanum, nor developed vocal structure (although sound
production has been reported in a few species, see Duellman & Trueb, 1986),
and all species have two small protrusible sensory tentacles on the head, each
one usually located between the eye and the naris, sometimes below the naris.
The skin is smooth; many species have numerous fish-like scales in pockets in
the skin. Most species are drab in colour, although some are brightly coloured.
Some caecilians produce skin toxins. All species have a dual-jaw closing
mechanism and are equipped with several rows of sharp teeth used to capture
small animals, mostly invertebrates. Larvae are very similar to adults, but are
smaller and have gill slits, lateral line sensory organs and labial folds.

Unlike all other amphibians (with the exception of the leiopelmatid frog genus
Ascaphus, and possibly the bufonid genus Mertensophryne), male caecilians
have a copulatory organ (phallus) and have internal fertilisation. The caecilian phallus (Fig. 17) is an eversible chamber (phalodeum) of the cloaca (Duellman & Trueb, 1986) and is a uniquely derived structure among vertebrates (Wake, 2006).

Fig. 17. Intromittent organ of the caecilian *Rhinatremia* cf. *bivittatum*. (Photo by Philippe J. R. Kok).

A number of species are viviparous, with epitheliophagous foetuses that, once the yolk mass is resorbed, feed on particular cells of the oviduct with specialized scraping teeth. These teeth are shed after birth. Foetal teeth are mainly specific to viviparous species, but at least two egg-laying species [*Boulengerula taitanus* Loveridge, 1935 and *Siphonops annulatus* (Mikan, 1820)] are known to feed their young - which are equipped with the same kind of teeth - by developing a special outer layer of skin that is peeled off by the young (Kupfer *et al.*, 2006b; Wilkinson *et al.*, 2008). Oviparous species lay gelatinous eggs that are guarded by the female (larvae may be terrestrial or aquatic).

Most caecilian species are soil-dwelling predators, but some are semiaquatic or aquatic (*i.e.* Typhlonectidae).

The caecilians are taxonomically challenging and several classifications have been suggested (see Wake & Campbell, 1983; Duellman & Trueb, 1986; Laurent, 1986; Lescure *et al*., 1986; Nussbaum & Wilkinson, 1989; Frost *et al*., 2006). The most recent classification was proposed by Wilkinson & Nussbaum (2006), who recognized the following six families: Rhinatrematidae, Ichthyophiidae, Uraeotyphlidae, Scolecomorphidae, Typhlonectidae and Caeciliidae. Only Rhinatrematidae, Typhlonectidae and Caeciliidae have representatives in South America.

Two families of caecilians are currently known to occur in Kaieteur National Park: Rhinatrematidae and Caeciliidae.

**Rhinatrematidae Nussbaum, 1977**

The main features characterizing this family are (Frost *et al*., 2006; Wilkinson & Nussbaum, 2006): tail present; skin divided into annuli that are not congruent with segmentation of trunk musculature and with no distinction between primary and secondary annular grooves; scales numerous; nasals and premaxillae
present as separate bones; tentacle immediately anterior to or on the anterior edge of eye; eyes visible externally.

The family Rhinatrematidae contains two genera, one of which is present in Kaieteur National Park (*Rhinatrema*).

**Caeciliidae Rafinesque, 1814**

The main features characterizing this large family are (Frost *et al.*, 2006; Wilkinson & Nussbaum, 2006): tail absent (although a pseudotail is present in Typhlonectidae); skin divided into primary annuli congruent with segmentation of trunk musculature, some of which may be divided posteriorly by secondary annular grooves; scales absent or present; nasal and premaxilla fused; septomaxilla reduced or absent; pterygoid absent; fused third and fourth ceratobranchials greatly expanded; vent circular or transverse; tentacle variously positioned; eyes visible or not.

The family Caeciliidae contains 21 genera, one of which is present in Kaieteur National Park (*Microcaecilia*).

### 2.2. Order Caudata Fischer von Waldheim, 1813

Members of the order Caudata, also called urodeles or simply “salamanders”, are characterized by the presence of a tail (*caudata* meaning tail in Latin) and two pairs of limbs (but see below). Most urodeles show a transition of aquatic life to a terrestrial mode of life. Urodeles are principally Holarctic and are found in Palaearctic Eurasia, northwestern Africa and the Americas (Frost, 2008). Only one living family (Plethodontidae) extends into South America.

The salamander body is moderate or somewhat elongate, not annulated (although costal grooves may be present), with a long tail. Four limbs are present (except in the family Sirenidae, whose members lack pelvic limbs and girdle). Frontal and parietal bones are distinct; palatoquadrate fused by processes to cranium; atlas articulates with skull by atlantal cotyles and medio-ventral forward-directed process that meets the walls of foramen magnum on either side.

Since no urodeles are known to occur in the Guiana Shield (Señarís & MacCulloch, 2005) and *a fortiori* in Kaieteur National Park, we will not further discuss this order.

### 2.3. Order Anura Fischer von Waldheim, 1813

Members of the large and diverse order Anura, commonly called “frogs”, are easily distinguished from other amphibians by the absence of a tail (*anura* derives from the Greek *an* meaning without and *oura* meaning tail). Anurans are cosmopolitan, their diversity is greatest in tropical, subtropical and warm temperate regions and they are absent from high latitudes in the Arctic, Antarctica, most oceanic islands, and some xeric deserts (although they may be present in oases) (Duellman & Trueb, 1986; Frost, 2008).

The body of an anuran is short, relatively robust, not annulated, with elongated hindlimbs and feet. The mouth is usually large. Four limbs are present and adults lack a tail. Frontal and parietal bones are fused on each side (into a
frontoparietal); palatoquadrate fused by processes to cranium; atlas articulates with skull by atlantal cotyles. Eyes are functional and exposed. Most species have a functional tympanum, and well-developed vocal structures. Size varies from ca. 10 mm to more than 300 mm. Texture of the skin is highly variable, from smooth to warty.

While numerous anuran species are cryptic (which means that they cannot be easily detected), many species have bright colours that often serve as warning colourations (aposematism) associated with unpalatability and/or the presence of poisonous secretions. Many anurans exhibit defence behaviours when faced by a potential predator, some species feign death, other produce loud distress calls and some even bite (e.g. the hemiphractid Stefania woodleyi from Guyana, see Kok et al., 2007a).

Most anurans are carnivorous and sit-and-wait predators. They feed on a great variety of invertebrates and sometimes on small vertebrates for the largest species. Preys are usually visually detected (olfactory and auditory detections are also reported) and captured with the tongue, on which they adhere due to the presence of a sticky secretion. The diet of the hylid Xenohyla truncata (from Brazil) includes fruits that are especially consumed during the dry season, when invertebrates are less abundant (da Silva & de Britto-Pereira, 2006).

Males almost invariably attract females with an advertisement call, although some species do not always produce sound and attract females using other strategies like “semaphoring” (arm waving, foot flagging). The latter behaviour is mainly observed in species living in noisy environments [e.g. the bufonid Atelopus varius from Costa Rica and Panama, see Hödl & Amézquita (2001) for more information]. Some species (e.g. the ranids Huia cavitympanum and Odorrana tormota) even produce ultrasonic calls, shifting the frequencies beyond the spectrum of the background noise (Feng et al., 2006).

Mating typically takes place by the male grasping the female in a position that will allow him to externally fertilize eggs. Amplexic positions are variable and of phylogenetic significance. The male can grasp the female around the waist (inguinal amplexus, mostly in “primitive” frogs), behind the forelimbs (axillary amplexus, mostly in “advanced” frogs), or around the head (cephalic amplexus, mostly in “advanced” frogs). The male can also simply straddle the female, or be glued to the posterior part of the female by dermal secretions. Males of Ascaphus (see above) have an extension of the cloaca that is inserted into the cloaca of the female allowing internal insemination (internal insemination is also suspected in the bufonid Mertensophryne). In some cases amplexus is completely absent, like in species of the genus Oophaga (Dendrobatidae), which accomplish internal fertilization by cloacal apposition.

Reproductive strategies are amazingly diverse in anurans: 29 reproductive modes were recognized by Duellman & Trueb (1986), 16 years later Savage (2002) reported 35 reproductive patterns, and more recently Haddad & Prado (2005) recognized 39 reproductive modes in anurans. Since then, additional reproductive modes and strategies were identified (see for instance Gibson & Buley, 2004; Kok & Ernst, 2007). Eggs may be aquatic (e.g. simply deposited in water, laid in foam nests constructed in or over water, or even imbedded in
dorsum of the aquatic female), terrestrial (e.g. laid in burrows, on the ground, in excavated nests, in terrestrial foam nests), or arboreal (e.g. laid between leaves, above leaves, below leaves overhanging water, in leaf nests, in tree holes, etc.). Eggs can also be carried by one of the parents (on legs, on the dorsum, in a dorsal pouch, or even in the stomach), or be retained in the oviducts (ovoviviparous and viviparous species). Kok & Ernst (2007) recently described *Allobates spumaponens* (Aromobatidae) from Guyana that deposits tadpoles in foam nests of leptodactylid species, which is the first case of interspecific brood parasitism in amphibians. Some species provide extensive parental care (egg clutch attendance, larvae feeding, etc.).

Anuran larvae are nonreproductive and morphologically very distinct from adults. They have a short, usually globular, body and a long tail, which is resorbed during metamorphosis. Tadpole diversity is remarkable and McDiarmid & Altig (1999) provided no less than 15 ecomorphological guilds. Tadpoles may be endotroph (non-feeding tadpole) or exotroph (feeding tadpole) and present many adaptations to their environment (see McDiarmid & Altig, 1999 for further details). Tadpoles are vegetarian and/or carnivorous, some are cannibalistic.

The following 47 anuran families (ca. 5500 species) are currently recognized, even if some of them are still in debate among the herpetological community (families occurring in South America are in bold): *Allophrynidae*, *Alytidae*, *Aromobatidae*, *Arthroleptidae*, *Bominaidae*, *Brachycephalidae*, *Brevicipitidae*, *Bufonidae*, *Calyptocephalellidae*, *Centrolenidae*, *Ceratobatrachidae*, *Ceratophryidae*, *Craugastoridae*, *Cycloramphidae*, *Dendrobatidae*, *Dicroglossidae*, *Eleutherodactylidae*, *Heleophrynidae*, *Hemiphractidae*, *Hemisotidae*, *Hylidae*, *Hylodidae*, *Hyperoliidae*, *Leiopelmatidae*, *Leiuperidae*, *Leptodactylidae*, *Limnodynastidae*, *Mantellidae*, *Megophryidae*, *Micrixalidae*, *Microhylidae*, *Myobatrachidae*, *Nyctibatrachidae*, *Pelobatidae*, *Pelodytidae*, *Petropedetidae*, *Phrynobatrachidae*, *Pipidae*, *Pyxicephalidae*, *Ranidae*, *Ranixalidae*, *Rhacophoridae*, *Rhinophrynidae*, *Scaphiopodidae*, *Sooglossidae*, and *Strabomantidae*.

Note that it may be difficult to confidently assign an anuran species to a family because many species closely resemble other species in unrelated families (due to convergent evolution); the most significant morphological diagnostic characters are often features of the internal anatomy (especially the skeleton). For some families none or very few external features allow identification, and in most cases only a combination of characteristics technically defines the family. In some cases, families are primarily defined by genetics.
Fig. 18. A few examples of the diversity of anurans in South America. A. *Lithobates palmipes* (Ranidae), a typical frog (note: this species is not recorded from KNP); B. *Rhinella marina* (Bufonidae), a typical toad; C. *Dendrobates tinctorius* (Dendrobatidae), a poisonous species that displays aposmotic colouration (note: this species does not occur in KNP); D. The terrestrial and semi-fossorial *Otophryne steyermarki* (Microhylidae) (note: this species does not occur in KNP); E. The arboreal *Phyllomedusa bicolor* (Hylidae); F. The mainly aquatic *Pipa arrabali* (Pipidae). (Photos by Philippe J. R. Kok).

Eleven families of anurans are currently known to occur in Kaieteur National Park: Allophrynidae, Aromobatidae, Bufonidae, Centrolenidae, Eleutherodactylidae, Hemiphractidae, Hylidae, Leptodactylidae, Microhylidae, Pipidae, and Strabomantidae.

**Allophrynidae**

Although Frost et al. (2006) ranked the genus *Allophryne* in the subfamily Allophryninae of the family Centrolenidae, we maintain the use of Allophrynidae [see Guayasamin & Trueb (2007), and Guayasamin et al. (2008) for arguments].
The following main features are characteristic of the family (based on Zug et al., 2001): skull strongly ossified dorsally, with paired palatines and frontoparietals; vertebral column with eight holochordal, procoelous presacral vertebrae; ribs absent; maxillae toothless; sacrum with moderately dilated diapophyses and bicondylar articulation with urostyle; facial nerve exits through anterior acoustic foramen in auditory capsule; trigeminal and facial nerve ganglia fuse to form a prootic ganglion; pectoral girdle arciferal with distinct sternum; fibulare and tibiale fused at their proximal and distal ends; no intercalary cartilage between terminal and penultimate phalanges of digits; tips of terminal phalanges T-shaped; pupil horizontally elliptical. Amplexus axillary.

The family Allophrynidae currently contains only one genus, Allophryne, which is present in Kaieteur National Park.

**Aromobatidae**

Previously included in the Dendrobatidae, but removed after genetic analysis (Grant et al., 2006).

Similar to Dendrobatidae, but do not appear to have the ability to sequester alkaloids in their skin, and are usually not as brightly coloured. Members of this family are characterized by the following main features: skull with paired palatines (absent in Allobates and most Aromobates) and frontoparietals; vertebral column with eight holochordal, procoelous presacral vertebrae; ribs absent; upper jaw dentate; sacrum with cylindrical diapophyses (dilated in Aromobates) and bicondylar articulation with urostyle; facial nerve exits through anterior acoustic foramen in auditory capsule; trigeminal and facial nerve ganglia fuse to form a prootic ganglion; pectoral girdle arciferal, rarely pseudofirmisternal, with distinct bony sternum; fibulare and tibiale fused at their proximal and distal ends; no intercalary cartilage between terminal and penultimate phalanges of digits; supradigital scutes present; tips of terminal phalanges T-shaped; pupil horizontally elliptical. Amplexus cephalic or independent (absent).

The family Aromobatidae currently contains five genera, one of which is present in Kaieteur National Park (Anomaloglossus).

**Bufonidae**

The following main features are characteristic of the family (based on Zug et al. (2001), and Savage (2002)): skull with paired palatines and frontoparietals; vertebral column with 5-8 holochordal, procoelous presacral vertebrae; ribs absent; upper jaw toothless; sacrum with moderately dilated diapophyses and bicondylar articulation with urostyle (except in some species); monocondylar or sacrum fused to vertebral column in taxa with reduced vertebral numbers; facial nerve exits through anterior acoustic foramen in auditory capsule; trigeminal and facial nerve ganglia fuse to form a prootic ganglion; pectoral girdle arciferal, rarely pseudofirmisternal, with distinct bony sternum; rudimentary ovary (Bidder’s organ) retained in adult males (except in a few species); fibulare and tibiale fused at their proximal and distal ends; no intercalary cartilage between terminal and penultimate phalanges of digits; tips of terminal phalanges blunt to pointed; pupil horizontally elliptical. Amplexus axillary.
The family Bufonidae currently contains 45 genera, three of which are present in Kaieteur National Park (Atelopus, Rhaebo, Rhinella).

**Centrolenidae**

Members of this family are characterized by the following main features [based on Zug *et al.* (2001), and Savage (2002)]: ventral skin transparent, internal organs visible; skull with paired palatines and frontoparietals; vertebral column with eight holochordal, procoelous presacral vertebrae; ribs absent; teeth on upper jaw; sacrum with moderately dilated diaphyses and bicondylar articulation with urostyle; facial nerve exits through anterior acoustic foramen in auditory capsule; trigeminal and facial nerve ganglia fuse to form a prootic ganglion; pectoral girdle arciferal, with distinct cartilaginous sternum; fibulare and tibiale fused along entire lengths; short intercalary cartilage between terminal and penultimate phalanges of digits; tips of terminal phalanges T-shaped; pupil horizontally elliptical. Amplexus axillary.

The family Centrolenidae currently contains four genera, three of which are present in Kaieteur National Park (Centrolene, Cochranella, Hyalinobatrachium).

**Eleutherodactylidae**

The following main features are characteristic of the Eleutherodactylidae (Hedges *et al.*, 2008; refer to that paper for extensive definition of the family): vertebral column with eight holochordal, procoelous presacral vertebrae; ribs absent; maxillary usually dentate; sacrum with rounded or barely dilated diaphyses and bicondylar articulation with urostyle; facial nerve exits through anterior acoustic foramen in auditory capsule; trigeminal and facial nerve ganglia fuse to form a prootic ganglion; pectoral girdle arciferal, rarely pseudofirmisternal, with distinct cartilaginous sternum; fibulare and tibiale fused at their proximal and distal ends; no intercalary cartilage between terminal and penultimate phalanges of digits; tips of terminal phalanges T-shaped; pupil usually horizontally elliptical. Amplexus axillary.

The family Eleutherodactylidae currently contains four genera, one of which is present in Kaieteur National Park (Adelophryne).

**Hemiphractidae**

Hemiphractidae is considered polyphyletic by Frost *et al.* (2006), who recognized Amphignathodontidae and Cryptobatrachidae as distinct from Hemiphractidae. Guayasamin *et al.* (2008) formally placed Amphignathodontidae and Cryptobatrachidae in synonymy with Hemiphractidae. Hemiphractidae (as Hemiphractinae) was formerly regarded as a subfamily of Hylidae, with which it is morphologically close.

Members of this family carry eggs and endotrophic embryos on the back or in a specialized dorsal pouch until hatching. The following main features are characteristic of the family [based on Hemiphractinae of Zug *et al.* (2001), and Savage (2002)]: skull with paired palatines and frontoparietals, strongly ossified, with or without dermis co-ossified to roofing bones; vertebral column with eight holochordal, procoelous presacral vertebrae; ribs absent; teeth on upper jaw; of the superficial mandibular musculature, the interhyoideus lies within the lower
The family Hemiphractidae currently contains five genera, one of which is present in Kaieteur National Park (Stefania).

**Hylidae**

The following main features are characteristic of the family [based on Hylineae, Pelodryadinae, and Phyllomedusinae of Zug et al. (2001), and Savage (2002)]: skull with paired palatines and frontoparietals, ossification variable, dermis usually not fused to roofing bones; vertebral column with eight holochordal, procoelous presacral vertebrae; ribs absent; teeth on upper jaw; of the superficial mandibular musculature, the interhyoideus extends posteriorly beyond the lower jaw, and the intermandibular muscle is undifferentiated, has lateral accessory slips or a separate apical element; sacrum with rounded (cylindrical in some genera) slightly to moderately dilated diapophyses and bicondylar articulation with urostyle; facial nerve exits through anterior acoustic foramen in auditory capsule; trigeminal and facial nerve ganglia fuse to form a prootic ganglion; pectoral girdle arciferal, with distinct cartilaginous sternum; fibulare and tibiale fused at their proximal and distal ends; short intercalary cartilage between terminal and penultimate phalanges of digits; tips of terminal phalanges pointed or claw-shaped; pupil horizontally elliptical. Amplexus axillary.

The family Hylidae currently contains 45 genera, seven of which are present in Kaieteur National Park (Dendropsophus, Hypsiboas, Osteocephalus, Phyllomedusa, Scinax, Tepuihyla, Trachycephalus), but see taxonomic comments about Hypsiboas liliae on page 172.

**Leptodactylidae**

The following main features are characteristic of the family [mostly based on Leptodactylinae of Zug et al. (2001), and Savage (2002)]: no webbing on hand; skull with paired palatines and frontoparietals; vertebral column with eight holochordal, procoelous presacral vertebrae; ribs absent; maxillary dentate; sacrum with rounded diapophyses and bicondylar articulation with urostyle; facial nerve exits through anterior acoustic foramen in auditory capsule; trigeminal and facial nerve ganglia fuse to form a prootic ganglion; pectoral girdle arciferal, with distinct cartilaginous sternum; fibulare and tibiale fused at their proximal and distal ends; no intercalary cartilage between terminal and penultimate phalanges of digits; tips of terminal phalanges variable; pupil horizontally elliptical. Amplexus axillary.
The family Leptodactylidae currently contains four genera, one of which is present in Kaieteur National Park (*Leptodactylus*).

**Microhylidae**

This family is characterized by the following main features [mostly based on Zug *et al.* (2001), and Savage (2002)]: 1-3 transverse dermal folds running across palate anterior to pharynx (except in two taxa); skull with paired palatines and frontoparietals; vertebral column with eight holochordal, procoelous presacral vertebrae, or eighth presacral vertebra biconcave and sacrum biconvex; ribs absent; maxillary toothless (except in Dyscophinae and some Cophylinae); sacrum with cylindrical to broadly dilated diapophyses and bicondylar articulation with urostyle; facial nerve exits through anterior acoustic foramen in auditory capsule; trigeminal and facial nerve ganglia fuse to form a prootic ganglion; pectoral girdle firmisternal, with distinct cartilaginous sternum; fibulare and tibiale fused at their proximal and distal ends; no intercalary cartilage between terminal and penultimate phalanges of digits (except in one genus); tips of terminal phalanges variable; pupil horizontal or round. Amplexus usually axillary, but in some robust taxa males adherent to posterior part of female.

The family Microhylidae currently contains 52 genera, one of which is present in Kaieteur National Park (*Synapturanus*).

**Pipidae**

This family is characterized by the following main features [based on Duellman & Trueb (1986), and Zug *et al.* (2001)]: body dorsoventrally depressed; hindlimbs large and muscular; feet extensively webbed; tongue absent; presence of a lateral-line organ; skull lacking palatines, with a single frontoparietal; vertebral column with 6-8 epichordal, episthocoelous presacral vertebrae; ribs present; maxillary usually toothless, but dentate in some species; sacrum with broadly expanded diapophyses, fused with urostyle; facial nerve exits through anterior acoustic foramen in auditory capsule; trigeminal and facial nerve ganglia fuse to form a prootic ganglion; pectoral girdle pseudofirmisternal, with distinct sternum; fibulare and tibiale fused at their proximal and distal ends; no intercalary cartilage between terminal and penultimate phalanges of digits; tips of terminal phalanges pointed; pupil round. Amplexus inguinal.

The family Pipidae currently contains five genera, one of which is present in Kaieteur National Park (*Pipa*).

**Strabomantidae**

Characteristics of this family are mostly similar to those of the family Eleutherodactylidae, from which it is mainly distinguished on the basis of molecular data (Hedges *et al.*, 2008). The following main features are characteristic of Strabomantidae (refer to Hedges *et al.*, 2008 for extensive definition of the family): vertebral column with eight holochordal, procoelous presacral vertebrae; ribs absent; maxillary usually dentate; sacrum with rounded or barely dilated diapophyses and bicondylar articulation with urostyle; facial nerve exits through anterior acoustic foramen in auditory capsule; trigeminal and facial nerve ganglia fuse to form a prootic ganglion; pectoral girdle arciferal,
rarely pseudofirmisternal, with distinct cartilaginous sternum; fibulare and tibiale fused at their proximal and distal ends; no intercalary cartilage between terminal and penultimate phalanges of digits; tips of terminal phalanges T-shaped, knobbed, or bearing hook-like lateral process; pupil usually horizontally elliptical. Amplexus axillary or inguinal.

The family Strabomantidae currently contains 16 genera, one of which is present in Kaiteteur National Park (Pristimantis).

3. **Taxonomic study of amphibians**

Unless you plan to work on already collected material (*i.e.* museum collections), taxonomic study of any group of animals implies the development of various techniques and protocols to build a reference collection. This also means that you must spend significant time in the field to gather specimens and detailed, accurate and associated data.

The collected or “voucher” specimens are specimens that are sacrificed to serve as a basis of study and reference. These specimens must be deposited in a recognized natural history collection, which will ensure long-term care and maintenance, accessibility to other researchers, and independent verification of results.

Voucher specimens are an extremely important part of scientific research. Their main purposes are: (1) to allow correct identification of the species under study, (2) to allow resolution of species limits [*e.g.* in a complex of closely related species] and understand intraspecific variation, (3) to allow confirmation and a verification of the occurrence of a species at a certain place at a certain time.

It must be emphasized that the collection of voucher specimens is essential in almost any biological research project, including systematics, ecological or behavioural research, environmental assessment, etc. Correct identification of the animals under study is always crucial to the outcome of the research, and the quality of your sample will play a major role. Identifying specimens that were poorly prepared or lack accurate data is very frustrating and these specimens are of little or no scientific use. Additionally it poses ethical problems to collect specimens that will prove to be useless. High quality of preparation will also ensure proper future studies of important morphological traits that could disappear in ill-prepared specimens, and is also a token of respect for the killed animal.

In case new species are discovered among the collected material, some individuals will be selected as “type specimens” (= permanent and objective standards of reference to the scientific name given to the new species). Other kind of samples (*e.g.* photographs, drawings, call recordings, etc.) can complement the type series.

It is thus essential to master collection techniques, fixation protocols, and collection management. The protocols to succeed in these tasks are explained below.
3.1. Permits

The first step of any biological fieldwork is to obtain appropriate permits to conduct research, including permits to capture, handle and euthanize a number of specimens. Permits to export those specimens from their country of origin will also be required if you plan to take them away or send the material to foreign specialists. This can be a time-consuming and frustrating task, since it is not unusual that the official authorities in charge to grant permits have poor or inadequate knowledge of the biota and/or the ways fieldwork must be completed. Each country has developed its own set of requirements for granting collection and exportation permits. It is essential to comply with local laws and regulations, even when the required documentation seems unreasonable. If the latter is the case good reasoning and communication will usually resolve many problems and might even help to simplify the bureaucracy for future researchers.

Do note that if you are collecting species protected by the Convention on International Trade in Endangered Species (CITES), additional export permits will be required (and usually supplementary fees will must be paid).

In case you plan to work in indigenous land, additional permits might be required to allow you to conduct field research among indigenous communities.

In Guyana the following agencies must be consulted before any biological research is conducted:

The Environmental Protection Agency (EPA), Lot 7 Broad and Charles Street, Charlestown, Georgetown, Guyana.

The Ministry of Amerindian Affairs (MoAA), 251-252 Quamina & Thomas Sts. South Cummingsburgh, Georgetown, Guyana.

3.2. Living in the field

As mentioned above, building a reference collection usually implies spending a long period in the field. This is certainly a very enjoyable part of the research, if you are well prepared. Ill-prepared fieldtrips will usually not yield good results and may sometimes become a true nightmare. Over the many months spent in the field, we have tested a large number of different equipment and we would like to share parts of our experience and preference here.

Here are a few basic tips and tricks that, we hope, will facilitate your fieldwork:

**Carrying food and equipment**

The amount of material needed during biological field research may be pretty large: a total weight of 250 kg (including food) is not uncommon for a 3-week field trip in remote areas (based on three main investigators total). Most of the time you will rely on the assistance of local inhabitants to help you carry food and equipment. Sometimes you will have to hire boats to reach your final destination.

Solid, waterproof bags that can be easily carried on the back should be used to carry food and most of the material. We have a preference for the Ortlieb® X-Tremer dry bags, which are valuable alternative to rigid boxes. They are waterproof, and have shoulder straps that support up to 500 kg (!). When empty,
they are easy to fold flat into a small package. They can be filled with air to ensure protection of fragile equipment. Some of our indigenous counterparts even used them as sleeping bags during very cold nights.

Try to put each specific equipment in a specific bag/container.

For cameras, laptop and other delicate precision devices we use watertight, crushproof and dust proof Peli™ cases. These cases even float if your boat flips over. When carrying cameras and DAT recorder out of the base camp we use the waterproof Dryzone 200 backpack from LowePro®.

**Comfortable base camps for sweet jungle nights**

An important consideration in establishing a base camp is the amount of time you plan to spend in it. You may intend only to spend one or two nights, but you also may plan to stay more than two weeks at the same location. Hammocks are by far the most comfortable way to sleep in the jungle; in addition they avoid contact with the ground and its numerous small inhabitants (see “Hygiene” below). In case of overnight camps or short-time stays, a simple hammock tied between two trees is generally sufficient (Fig. 19A); during rain specimens will be processed on the ground, just below the hammock’s tarp. We recommend Hennessy Hammock™, which are light, solid, all-in-one hammocks that include a mosquito net and a tarp. In cases of long-term stays, a larger “solid” camp should be built. We usually build two separate “rooms”; one will house hammocks and people, the other will serve as a “field lab” where specimens will be photographed and processed (Fig. 19B-C).

The location of the base camp is important and the following points should always be considered: (1) proximity of water (for drinking water, washing, etc.), but keep in mind that the area you chose could be flooded in case of heavy downpours; (2) proximity of large dead trees or very high trees with many bromeliads that could fall on your camp in case of a storm or heavy rain. Falling branches and trees are a real hazard in tropical rainforests. If you travel with local companions, always rely on their judgment; they know the place better than you.

In case of camping in savannah or on the summit of tepuis (table-top mountains) where trees and other supports are absent or too small to attach a hammock, light tents are an excellent alternative (Fig. 19D). Note that expeditions on tepuis require robust equipment due to cold temperatures, heavy rains and harsh winds. Products made for extreme conditions are expensive but are the only ones that will ensure more or less comfortable nights.
**Basic equipment needed to set up your base camp:**

- Hammock with mosquito nest (or robust lightweight tent if necessary).
- Large heavy-duty tarps (size will depend on the number of researchers staying in the camp).
- Plenty of solid rope to attach your hammock and fix the tarps.
- Heavy-duty tape to repair potential tears in the tarp.
- Light sleeping bag (nights may be surprisingly cold in the forest).
- Light pillow.
- Machete + file.
- Light foldable seat (an optional luxury).

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**Fig. 19.** Base camps. A. Basic base camp for short-time stays; B-C. Solid base camps for longer stays, note the separated "field lab" on photograph C (front); D. Tents on the summit of a tepui, note solar panels and 12 volts battery to provide electric power. (Photos by P. J. R. Kok).

**Energy solutions**

We use rechargeable batteries, which are charged through a 12 volts solar battery alimented by two solar panels (Fig. 20). All of our electronic and electric equipment (laptop, satellite phone, recorder, headlamps, etc.) runs thanks to solar power. Rechargeable LR6 (AA) NiMH batteries (used in headlamps, DAT recorder, etc.) are charged with a 15 minutes charger. If you plan to run a laptop, solar panel(s) with a minimum power output of 52 watts is recommended. We chose this solution mainly for ecological reasons and for minimizing our impact.
on the environment (no dead batteries, no fuel to run a polluting generating unit). Note that this technology evolves very quickly and many new excellent products can be found on the market. Modern solar panels are very light, foldable, and charge even in cloudy conditions. Some new batteries include an inverter, are very small and lightweight. We have a preference for Brunton® products and use two Solaris® 26 foldable solar panels.

### Basic equipment needed to provide electric power:

- Foldable solar panel(s), minimum power output of 52 watts recommended.
- Inverter: necessary to operate your electronic/electric devices.
- Solar controller: prevents overcharging the 12 volts battery and safely permits the battery to remain in constant charging.
- 12 volts solar battery, preferably dry cell.

![Electric power provided by solar panels, here charging the emergency satellite phone. See text for details. (Photo by P. J. R. Kok).](image)

**Fig. 20.**

**Food and cooking**

Adequate food is essential during field research. Do not forget that you will probably walk long distances, sleep little and work hard. We believe that food should always be bought in the country where the research is done, avoiding expensive excess baggage costs, contribute to the local economy instead!
You will need to find a clever compromise between weight and calorific value. We usually take cereal bars, oatmeal instant packs (there are different flavours), cereals, raisins, coffee/tea, sugar cane and dehydrated milk for breakfast; Chinese noodles instant packs, rice, cassava farine, dehydrated soya (called “chunk” in Guyana), onions, garlic, and hot sauce for other meals. When in the field, we usually only eat twice a day, once in early morning and once in late afternoon.

Lighting a wood fire can be somewhat tricky in some wet places and it may be risky to rely on it to cook. Furthermore, cooking on wood fire is often time-consuming and maintaining the fire requires time and attention. We prefer to use a liquid-fuel stove and we have a fondness for the Dragonfly from MSR®, which is lightweight and burns many different fuels (white gas, kerosene, unleaded auto fuel, diesel, and jet fuel). Only a few minutes are needed to boil water and the stove is very fuel-efficient.

![Basic equipment needed for cooking and eating:](#)

- Multifuel stove and accessories.
- Set of lightweight cookware.
- Robust cups, knifes, and spoons.
- Weatherproof lighter(s).
- Small fuel container.

**Water**

In tropical rainforests water is everywhere and is usually not a problem. It is recommended that all water be sterilized, especially near local communities, as there might not be a distinction between washing and drinking water. We usually do not disinfect water when travelling in remote areas, but it is always better to do it (gastric problems can ruin your expedition). You can obtain safe water by adding water purification tablets (e.g. Micropur). However, we prefer to use Ultraviolet disinfection (SteriPEN®) because it is much faster (about 50 seconds for 0.5 litres) and does not give a bad taste to water. You also can collect rainwater using a tarp and adequate containers. We always take an inflatable water container to stock water at the base camp.

**Hygiene and clothing**

Good hygiene is important in the field, especially to avoid skin problems. Avoid walking barefoot near some local communities, especially those in sandy areas as you have a high chance of collecting sand fleas (*Tunga penetrans*, also called “chiggers”). These parasites may be very painful and must be carefully extracted. Regularly check your body and remove ticks and other parasites as soon as possible as some carry diseases.

Use lightweight clothes that dry quickly, wear long rubber boots in the field (do not forget good socks), and slippers in the camp. Always try to keep a set of dry clothes and use small waterproof bags to pack them. Do not forget a robust rain cap.
Pharmacy and safety equipment

During field research you will probably be out of reach of immediate medical aid, as such some basic safety equipment and drugs from a good pharmacy, and some common sense precautions are thus necessary.

Covering all health hazards is beyond the scope of this manual; you should always carefully check with your doctor for the recommended vaccination and the appropriate medication to carry with you in the field. When possible, use orodispersible tablets as you can take them while walking or if clean water is not immediately available.

Malaria is rampant in many tropical countries and, if contracted, oftentimes kills both residents from local communities and researchers. An adequate malaria prophylaxis is mandatory. Note that antimalarial tablets are often much less expensive in tropical countries.

Leaving your pharmacy to local communities once the field trip is completed is an excellent idea, but this is only valuable if you explain drugs indication and dosage!

**Basic field first-aid kit:**

- Plenty insect repellents.
- Malaria prophylaxis.
- Thermometer.
- Skin suture set.
- Syringes and needles.
- Topical anaesthetics.
- Disposable scalpels.
- Sterile skin closure strips, several sizes (*Steri-Strip™*).
- Tourniquet.
- Sterile compresses.
- Sterile plasters, including blister plasters (*Compeed®*).
- Bactericide aqueous disinfectant.
- Pain tablets (avoid aspirin if there is a malaria risk).
- Allergy relief/allergy symptoms medicine.
- Epinephrine.
- Broad-spectrum antibiotics.
- Antibiotic cream for skin/eyes.
- Antifungal cream.
- Flu medicine.
- Anti-inflammatory cream.
- Elastic bandages.
- Anti-diarrhoea medication/adsorbing preparations.
- Intestinal amoebiasis treatment.
- Non-steroidal anti-inflammatory (also exist in very useful patches).
- Sun blocker.
- Sleeping tablets.
- Tweezers.
Basic safety equipment:
- Venom suction pump.
- Survival blanket.
- Satellite phone (optional).

3.3. Specimens and data collection
For further detailed information, we strongly suggest the reader to refer to Heyer et al. (1994), which is the most important reference available for researchers interested in measuring and monitoring biological diversity in amphibians. Also see Simmons (2002).

3.3.1. Basic collecting equipment
In order to collect specimens and data you will need some basic equipment (additional specific equipment is provided below, under specific sections).

As most amphibians are nocturnal, a good headlamp is probably one of the most important devices you will need in the field: at night frogs and toads may be spotted by their bright red eyeshine, which is the reflective effect of the tapetum lucidum, a reflecting layer found behind the retina that improves vision in low light conditions. We use the Duo Led 5 from Petzl® (with rechargeable batteries, see “Energy solutions” above), which is waterproof down to -5 meters and allows two kinds of lighting: halogen for focused lighting (up to 100m) and LED’s for wide, proximity lighting. The Petzl® Myo XP is lighter and is an excellent alternative.

Most of the time, amphibians are captured by hand or with a small aquarium net, quickly slamming the net over them.

It sometimes happens that a member of the collecting team detects a frog at a certain distance (by eyeshine detection for instance) that other field investigators cannot locate. While walking through dense vegetation it may be difficult to stay focused on the animal and the specimen may be lost. To circumvent that problem, a member of the team can use a small laser pointer to indicate the frog’s position while another investigator goes to collect it.

To avoid getting lost take some colour flagging tape to mark the trails, which will help you find your way back.

For note taking at nights in the camp, we use a small dynamo headlamp (rarely candles) in order to save batteries. If you have a well-charged 12 volts battery, an economic bulb in the camp is helpful.

After capture, medium to large specimens are placed in plastic bags (ziplock bags are quite effective), and small or tiny specimens are transferred in screw-top small containers (urine sample containers are ideal). If possible the field tag should be immediately placed with the associated specimen (see “Field notes and labels” below).
A global positioning system (GPS) is a must that will allow you to record the exact geographic coordinates of your base camps and collecting localities. We use the 60CSx model from Garmin®, which also records altitude.

You will also need some measuring devices to record environmental and specimen data. A thermometer and a hygrometer are the basics, a pHmeter will be useful to record acidity of water in which tadpoles are found. We use callipers for measuring small specimens and measuring tape for larger individuals. Measuring tape is also used to record, for example, distances between animals and water, or distance between the animal and the ground. Spring scales are used to weigh specimens.

Basic equipment needed for collecting specimens and data:

- Headlamp, batteries and spare bulbs.
- Dynamo headlamp, candles, or economic bulb to take notes at night.
- Small aquarium net.
- Airtight plastic bags and small containers.
- Shoulder bag to carry the collected specimens.
- Global Positioning System (GPS).
- Colour flagging tape for trail marking.
- Thermometer/Hygrometer, pHmeter (optional).
- Callipers.
- Measuring tape.
- Spring scales (10, 100, and 500 grams are sufficient for amphibians).
- Hand lens.
- Binoculars.
- Machete and knife + file.

3.3.2. Number of voucher specimens required

The number of specimens required to establish identification is variable from one species to another and it is impossible to generalize. Whenever possible, we recommend the minimum of 10 adult voucher specimens from each site; ideally 25 adult specimens should be collected. It is recommended to collect both sexes, juveniles, and larvae. The minimum number of collected larvae should be 20, preferably including different stages of development (see “Sampling of amphibian larvae” for further details).

The number of specimens collected will, of course, depend on the rarity of the species and/or the difficulty to collect species representatives (e.g. in case of highly arboreal species or fossorial species). It is usual that even during an extensive survey you will not encounter more than one specimen of a peculiar taxon.

Preparing specimens is time-consuming and you should never collect more specimens than you will be able to handle properly. Fewer well-prepared specimens associated with accurate data are always better than many specimens in poor state of preservation and lacking pertinent information.
Note that collection of rare species may endanger the population: in case of known endangered species or very rare taxa, fewer vouchers should be collected, but at least a single representative should be retained. It should be mentioned that some species considered as common are curiously poorly represented in museum collections, which for example precludes exhaustive study of intraspecific variation. Thus do not refrain to collect good samples of so-called “common species”.

3.3.3. Field notes and labels

It is crucial that each collected specimen be associated with detailed relevant data. In order to do so, a numbered label (tag) is securely attached to each specimen. Tags should be made of solid paper instead of any hard material (like metal or plastic) that could damage the specimen during transport. Indelible ink or tags with perforated numbers (Fig. 21A) should be used. The use of coloured tags or coloured inks must be avoided as they might discolour the specimens.

In frogs the tag should be attached around the knee (Fig. 21C), or around the waist in very small specimens (Fig. 21D). In caecilians, the tag is attached around the neck or around midbody. The best knot to attach the tag, avoiding that it unties during transport, is probably the surgical double knot (Fig. 21B); make two to be sure. Our numbered tags always include initials of the main investigator (Fig. 21A).

Series of tadpoles, or other very small samples collected together, are preserved separately in screw-top vials (see below) and are kept in a small leakproof plastic bag (we use Whirlpak® from Nasco), in which the tag is inserted (Fig. 22).

The tag number will be retranscribed in the field book and associated with temporary field identification and detailed data about the collected specimen.

Minimum data associated with the collected specimens are: precise locality (if possible geographic coordinates, which are referenced to map datum WGS84), elevation, date and time of collection, collector’s name, sampling/detection method, general habitat, microhabitat, type of activity before capture and basic weather data (see Fig. 23). It might be difficult to take extensive notes while collecting in the field, especially at night or during heavy rains. An interesting alternative is to use a mini voice recorder to record the data on a tape (digital ones are very small and record on a hard drive) and subsequently report the data in your field book. These recordings are also great back-up solutions.

Field books should be made of solid, all-weather, waterproof material, and waterproof inks must be used (we recommend Rite in the Rain® products, Fig. 23). We always use paper with metric grid, which is useful when taking photographs (see below). Pencils are suitable and cheaper alternative to all-weather pens. All data should be saved as soon as possible in electronic format (e.g. on a CD or external hard drive) in case you lose or damage your field book. Keep in mind that your field book itself is as valuable as your voucher specimens.
Fig. 21. Tagging voucher specimens. A. Two different types of tags that can be used in the field: printed tag with indelible black ink (upper), and tag with perforated number (lower); B. How to tie a surgical double knot; C. In frogs, tag should be attached around the knee; D. In very small specimens tag should be attached around the waist. (Photos by P. J. R. Kok).

Fig. 22. Series of tadpoles (like illustrated here) and other small samples are packed in small leakproof plastic bags in which the field tag is inserted. (Photo by P. J. R. Kok).
Fig. 23. *Rite in the Rain®* field book and basic notes about a voucher specimen. (Photo by P. J. R. Kok).

**Basic equipment needed for labelling your specimens and recording your data:**

- Field tags (to be sure, take ca. 1000 tags for a three weeks long fieldtrip).
- String to attach field tags to specimens.
- Small scissors to cut strings and tags.
- Small forceps.
- All-weather notebook(s).
- All-weather pen(s) and/or pencil(s).
- Digital mini voice recorder (optional).
- Laptop and external hard drive to back-up your data (optional).

### 3.3.4. Photography of voucher specimens and habitats

Most amphibians quickly lose their colour in preservative. Sometimes colours may drastically change (e.g. the bright green *Phyllomedusa bicolor* becomes purple in preservative, the green *Hypsiboas cinerascens* fades to white). Good photographs of preserved specimens in life are invaluable. They will facilitate the description of colours and patterns, and zooming in the digital picture will help you to distinguish some features that often disappear in preservative (folds, texture of skin, etc.). You will sometimes be surprised to see some details that were completely overlooked in the field.
Photographs should show features used for identification. We suggest taking at least a dorsolateral and a ventral view of each specimen (ventral view on paper with metric grid if possible). We usually take much more photographs of each individual, from different angles, including details of peculiar patterns and/or morphological characters.

Photographs of tadpoles are also very valuable. We usually take photographs of larvae in a Petri dish deposited on a paper with metric grid (the same paper used in our field book, Fig. 24).

![Tadpole](image)

**Fig. 24.** Taking photographs of tadpoles is invaluable, notably to record their colour in life. (Photo by P. J. R. Kok).

When possible, photographs should be taken *in situ*, but this is rarely achievable. We recommend the use of a small tent with a large front opening (Fig. 25A) in which you will reconstitute the microhabitat of the animal. In case the animal tries to escape (which will happen many times!), it cannot disappear in the surrounding vegetation and can easily be secured with a net or a small container.

A good tip to photographing “nervous” specimens is to place an opaque container over them and wait a few minutes. Usually the specimen will stay quiet for some time when you remove the container.

To avoid any confusion between specimens and photographs, we always photograph the tag associated with the specimens before taking photographs of the next specimen. Many digital cameras allow you to assign a peculiar number to each photograph, but we found that method slower and more restricting.

Most recent digital cameras are robust and can be used in the field on condition that it avoids contact with water. Be sure to keep them in waterproof bags or suitcases when you are not using them (see “Carrying food and equipment” above). Always place desiccant in your bags/cases; we use reusable silicagel.
placed in small transparent containers that have small holes in the lid. This type of silicagel is blue when dry and becomes pink while wet, so you can easily detect changing conditions and when necessary, the time to replace it. The silicagel will become blue again once exposed to high temperature (on the stove for example), allowing for water evaporation.

A digital reflex body camera with a macro lens is a must to photograph amphibians. A wide-angle lens should be used for habitats and microhabitats. The senior author uses a remote macro flash system that gives excellent results (Fig. 25C). We also carry a small shockproof and waterproof compact digital camera that record short video sequences, which may be useful when observing a peculiar behaviour.

Taking good photographs requires some skills and is time-consuming, but efforts are worthwhile!

Basic equipment needed for taking photographs of your specimens:

- Camera body (preferably digital).
- Macro lens.
- Wide-angle lens (a 18-70 mm zoom is ideal).
- Flashes, remote macro flash system is ideal.
- Several memory cards (or film rolls if you run a non-digital camera).
- Memory card reader.
- Batteries.
- Battery charger.
- Compact digital camera allowing recording video sequences (optional).
- Small tent with large front opening.
- Net to secure the animal if it tries to escape.
- Laptop and external hard drive or other media storage device to backup your photos and empty your memory cards (optional if you have plenty memory cards).
Fig. 25. Taking photographs of specimens. A. Small tent with large opening used as a “field studio”; B. Digital images are downloaded on a laptop right in the field and saved on an external hard drive; C. Digital reflex with macro lens and remote macro flash system as used in the field by the senior author, note the protective Pelitm™ case. (Photos by P. J. R. Kok).
3.3.5. Recording of advertisement calls

Male anuran advertisement calls are species-specific, and bioacoustics analyses of frog vocalizations are invaluable in the discovery of new taxa, assessment of taxonomic rank, and species identification (see “Call analysis” below). Frog recordings can even detect species otherwise thought to have been absent in a specific area. In some studies tape recordings may be used as voucher material.

It can be surprisingly challenging to locate a calling frog or toad. Some species call from beneath leaves or under the ground, and in many cases their calls are so ventriloquial that the position of the calling male is very difficult to estimate.

You should always collect the specimen recorded as a voucher and take associated data as recommended in “Field notes and labels” above; do not forget to include tape identification (name of the person making the recording + tape number) and temperature during recording (see below). One voucher specimen per species per calling site is a minimum.

To acquire quality recordings that will allow you to perform reliable analyses you will need a good recording system that offers very ultra-low distortion levels and is immune to speed errors, tape noise, and non-linear frequency anomalies. Dominant frequency of the advertisement call must be accurately captured and a recorder with a flat frequency response from ca. 20-15000 Hz is appropriate. A recording level-meter is mandatory to avoid distorted signals due to too high-level recording. Avoid devices that utilize an audio compression algorithm (like Digital MiniDisc recorders). We recommend DAT recorder, Hi-MD recorder, digital hard drive or solid-state recorders. Using an expensive recorder with a low quality microphone is not recommended. Choose a directional, omnidirectional or a shotgun microphone with no noticeable distortion in the 20-10000 Hz range. Preferably use 30 minutes tapes. Headphones will allow you to evaluate the quality of your recordings in the field and should offer some degree of isolation from ambient noises. We use a Sony DAT TCD-D100 recorder with a Sony ECM-MS907 microphone with very good results.

Note that temperature variation affects call parameters and a critical step in recording frogs is obtaining temperatures during recordings. If a frog is calling in water, water temperature should be recorded. Do not forget to always carry a waterproof thermometer along with your recording equipment.

Single calling individuals or choruses may be recorded. For the purpose of taxonomic research, recording of calling individuals is required. Frogs should be recorded at distances from 0.5 to 1.5 meters using an appropriate gain level (test gain level before recording). Record at least 5-10 calls from each individual and do not forget to keep recording between calls, this will allow you to know the intercall interval (see “Call analysis” below). Before each recording you should add a voice label giving basic information like the name of the person recording, locality, time, temperature and field identification. Some species are very shy and stop calling if they are only slightly disturbed (by your voice for example), you might thus prefer to report these data in your notebook referring only to the number of the recording. Saying “stop” at the end of each recording will help you to locate different recordings from different individuals. DAT recorders allow to
automatically stamp the current date and time on the tape and allow quick access to the starting points of your recordings thanks to an indexing system. The caveat of digital audio recorders is that they are sensitive to high humidity level and might stop working in very humid environments. We always protect the device in a ziplock bag during recordings and place the recorder in a protective case with desiccant (see above) when not in use.

Some species call only during heavy rain, which creates a lot of background noise. Rain falling on your microphone or on the ground next to the frog may be a problem. We use a small umbrella to avoid that trouble.

### Basic equipment needed for recording frog advertisement calls:

- Recorder.
- Microphone.
- Headphones.
- Batteries.
- Tapes.
- Ziplock bag to protect the recorder from rain.
- Waterproof thermometer.
- Small light umbrella.

### 3.3.6. Euthanasia of voucher specimens

Once voucher specimens have been photographed, they must quickly be killed using a humane method of euthanasia. This for evident ethical reasons and practical motivations: specimens humanely killed will be relaxed and much easier to fix in the proper position. Do not expose your specimens to inappropriate handling, temperature extremes or any other undue suffering. Never place living specimens in formalin without prior euthanasia, their agony will be long and painful and specimens could be contracted making further examination problematical.

Many investigators use a chlorobutanol solution in which the animal is immersed. We prefer to use local anaesthetics like lidocaine or similar drugs that have the advantage of not being controlled substances. Also they usually are easily available in pharmacies in most countries, and are available in a wide range of presentations (injection, spray, gel).

Specimens are immersed for a few minutes in the solution, which must be regularly replaced. Note that amphibians are species-specific in their response to anaesthetic chemicals and that some large specimens (e.g. large *Rhinella* or *Leptodactylus* species) may require intracardiac or intraperitoneal injection of the solution.
Basic equipment needed for voucher specimens euthanasia:

- Syringes and needles.
- Containers for euthanasia.
- Lidocaine or similar drug.

3.3.7. Preservation of voucher specimens

As stated above, good preservation of the voucher specimens will simplify their identification and the description of possible new species; it will also guarantee long-term preservation. Preserving specimens is basically a two-step process: (1) the specimen is fixed in preservative; (2) the specimen is transferred to 70% ethanol for permanent storage. For step 1 we typically use 10% formalin. Pure formalin can be bought in pharmacies or drugstores in many countries and you just will need to dilute it: one part of 100% formalin in nine parts of water will give you a 10% formalin solution. Be careful with formalin because it is irritating, carcinogenic, and very harmful to the environment. Always wear gloves and be careful not to receive projection of the solution in the eyes. This can happen when you inject specimens or simply if a bottle falls on the ground. Formalin in the eyes is a very unpleasant experience and eyes must be immediately washed with water for several minutes. Never abandon formalin in the field.

Ideally the 10% formalin solution should be buffered with magnesium carbonate to avoid acidification or alkalinisation of your fixation solution (use 1/2 teaspoon of magnesium carbonate per litre of 10% formalin). Acidification or alkalinisation will cause excessive discolouration, clearing and/or decalcification of your specimens.

70% ethanol is an alternative fixing solution if formalin is not available.

Step 2 will usually only happen once you are back from the field (see “Collection management” below).

Once the formalin solution is ready you can prepare your fixative trays. We typically use lidded plastic containers of ca. 40x25x9 cm (Really Useful Boxes®). The bottom of the tray is covered with white tissue saturated with 10% formalin (we use strong cellulose paper or cheesecloth; avoid coloured tissues that could discolour your specimens, see Fig. 26).

Once you are sure that the specimens are killed and completely relaxed – for frog specimens a stimulus on the frog’s eye is a good indicator: if the eye retracts, the frog is still living – you must dispose them in a way that will facilitate measurements and further examination of important morphological characters (webbing for instance, see Figs 26, 27A-B). In case of large specimens, you will need to gently inject them with 10% formalin to be sure that they will not partly rotten. Figure 28 shows multiple injection points, and figure 27C positioning of amphibians for final fixation. We usually attach a tag before fixing the specimen to avoid tags and specimens mixing. However, this is not always feasible, especially in small specimens that will not fix in the right position with the tag. In this case, the tag is deposited on the back of the specimen and will be attached
immediately after fixation. Once your specimens are correctly positioned, cover them with another piece of saturated tissue, gently add a little more of fixing solution and cover the tray.

Fig. 26. Fixative tray. (Photo by P. J. R. Kok).
Fig. 27. Fixation of specimens. A. Hand of a properly fixed frog, note that webbing is easily examined and that measurements will be taken without difficulty (length of Finger III for example); B. Hand of an incorrectly fixed frog, note that measurements could be approximate and examination of webbing difficult; C. Ideal position of a frog in the fixative solution, which will facilitate measurements and further examination. (Photos by P. J. R. Kok).
After a few hours or a full day, depending on the size of the animal, specimens are hard enough to be transferred to a container filled with 10% formalin (Fig. 29). Check specimens often to judge when the transfer may occur, but do not be afraid to leave them too long in the trays. Specimens will remain in 10% formalin-filled containers until the end of the field trip. We use different sizes of wide-mouth jars and try to keep together specimens having approximately the same size. Avoid mixing tiny specimens with large ones and be sure to not overcrowd your jars, but do not leave too much space because if you transport the specimens – which will be the case if you move from one location to another with all your equipment – they might be damaged by friction with others. To avoid that, we usually fill the container with soaked tissue, or wrap most fragile specimens with cotton tulle. Fragile specimens can also be kept in separate small vials. Jars and containers must absolutely be kept out of direct sunlight because this will accelerate discolouration, could interfere on the fixation process of the specimens, and could modify the pH of your solution (which will affect your specimens, see above).
When they are hard enough, specimens are transferred to a container filled with 10% formalin in which they will remain until the end of the field trip. (Photo by P. J. R. Kok).

If you are not a local resident, at the very end of the field trip you will probably need to have your specimens checked by local colleagues before exporting them. This is the perfect occasion to pack them for transport. Good packing of specimens is almost as important as fixation because if you are careless you might have disagreeable surprises (specimens desiccated, distorted, etc.).

The best procedure to pack specimens is the following: use large pieces of formalin-saturated cotton tulle to wrap 1-10 specimens together (again do not mix small specimens with large ones). Once the specimens are wrapped, be sure that the packet is wet enough and transfer it in a leakproof plastic bag (Fig. 30). Close the plastic bag tightly. We usually pack specimens by species and by size to facilitate our work in the laboratory. Avoid overcrowding your plastic bags and be careful that toes and fingers of specimens will not be stressed. We usually slightly inflate the plastic bags for shock protection. Insert the bag in a second plastic bag for security, put all the plastic bags in solid waterproof jars – the same you used in the field for your fixative solution – and add a notice for customs with the following text: "This package contains dead, preserved animals for scientific studies that have no commercial value. If this shipment is inspected, it is absolutely imperative that animals wrapped in wet tissue be returned to and sealed inside the plastic bag. If not, the material will dry rapidly and become useless. We thank you very much for taking good care of this invaluable resource".

Specimens are now ready to be shipped to the laboratory.
Fig. 30. Packing of specimens for transport. A-C. Specimens are wrapped in formalin-saturated cotton tulle; D. The packet is well soaked and transferred in a leakproof plastic bag. (Photos by P. J. R. Kok).

Basic equipment needed for preserving and packing voucher specimens:

- Full-strength formalin (ideal), 70% ethanol (alternative).
- Buffer for formalin (magnesium carbonate).
- Plastic teaspoon.
- Forceps (long and small).
- Dissecting scissors.
- Syringes and needles (various sizes).
- Preserving trays with lids.
- Tissue (strong cellulose paper or cheesecloth).
- Cotton tulle.
- Leakproof plastic bags.
- Nitril gloves.
- Wide-mouth air/watertight bottles for fixation solution.
- Wide-mouth air/watertight jars for fixation solution, storage of large specimens and shipping.
3.3.8. Collecting tissues for molecular study

Molecular analyses can help to elucidate taxonomic problems and as such are complementary to morphological taxonomy.

Tissue must be removed immediately after euthanasia, never after fixation because formalin breaks DNA (although researchers already succeeded in DNA extraction from formalin-preserved samples). A small incision is made in the upper part of the abdomen and a small piece of liver is cut (Fig. 31A-B). In case you need several samples from the same individual, the whole liver can be extracted and divided into small pieces. A piece of thigh muscle is a suitable alternative. The slice of tissue is placed into a small screw-top plastic vial filled with 95% ethanol and a piece of waterproof paper on which you will write the number of the voucher specimen from which the tissue has been removed (Fig. 31C). Be very careful to write the number associated with the specimen during this process! Make sure that the ethanol completely covers the tissue sample. Do not screw the lid on too tightly. Vials are kept on plastic stands during the process, and packed in leakproof plastic bags for transport (Fig. 32). Keep the samples away from direct sunlight and try to store them in a cold place.

In order to avoid contamination between specimens, we use sterile disposable surgical blades (one blade per specimen) and sterilize the forceps in bleach. Before reusing the forceps, they are carefully rinsed with fresh water and dried with toilet tissue.
Fig. 31. Collecting tissues for molecular study. A. A small incision is made in the upper part of the abdomen; B. The liver or a piece of it is removed using small bleach-cleaned forceps (black arrow indicates liver); C. Tissue sample is placed in a vial together with a tag bearing the number of the voucher specimen (black arrow indicates liver, blue arrow indicates tag). (Photos A-B extracted from the documentary “Kaieteur” © Kanari Films, C by P. J. R. Kok).

Fig. 32. Tissue samples. A. Vials with tissue for molecular analyses are kept in plastic stands during the process; B. They are packed in leakproof plastic bags for transport. (Photos by P. J. R. Kok).
**Basic equipment needed for collecting tissues from voucher specimens:**

- Disposable surgical blades (expect 300 for a 3-weeks field trip).
- Scalpel(s).
- Small forceps.
- Syringes and needles to inject ethanol in vials.
- Bleach (ca. 250 ml).
- Small containers for bleach and rinsing water.
- Toilet paper to dry your forceps.
- Lidded vials for tissue samples (expect 300 for a 3-weeks field trip).
- 95% ethanol (expect ca. 1 litre for a 3-weeks field trip)
- Waterproof paper and pencil for labelling the tissue samples.
- Plastic stand for vials.
- Leakproof plastic bags to place your vials for transport.
- Latex gloves (optional).

### 3.4. Methods of collection

We mainly focus here on techniques used to collect voucher specimens within the framework of taxonomic studies.

The following descriptions of collecting techniques are mostly based on Heyer *et al.* (1994), a publication that should not be missed by investigators having an interest in collecting amphibians and measuring and monitoring amphibian diversity. Also see Simmons (2002) and Rödel & Ernst (2004).

#### 3.4.1. Opportunistic collecting

This is probably the most traditional collecting technique in herpetological inventories. The principle of this productive technique is to slowly walk through adequate habitats, by day and by night, systematically searching for amphibians (visually and acoustically) in all possible microhabitats, turning over and breaking up logs, searching through the vegetation, in the leaf litter, turning over rocks, checking crevices and tree holes, and searching along the watercourses, checking both upper and undersides of leaves. Calling males are detected and collected. This technique does not involve any prescribed time period.

#### 3.4.2. Visual encounter surveys

The visual encounter survey (VES) is a standard method for terrestrial herpetofauna inventories and monitoring. VES is conducted by walking through an area or habitat for a prescribed time period while systematically searching for animals that are visible to the researcher. Observers search surfaces, vegetation, turn over objects such as logs and rocks, and look in crevices in rocks and bark, replacing all surface objects after examining the ground.

The searching period is expressed as the number of person-hours searching in the sampled area. VES can be conducted day or night using flashlights. It is often
better to sample 10x100m transects than 1x1000m transect as it provides comparable data sets for analysis.

VES can be used to document the species richness of an area via a species checklist and to estimate the relative abundance of species within an assemblage. Often, VES is used in conjunction with other techniques such as transect sampling, mark-recapture, drift fences and pitfall traps, etc. VES is often best used to sample species that are unlikely to be caught using other techniques such as traps. The design for a VES will depend on the objectives of the research (e.g. is it a one-time inventory or long-term monitoring programme?), the information required e.g. species abundance, species composition or both, type and size of habitat, time frame e.g. diel or seasonal, species composition, and number of persons available to execute the VES. According to Heyer et al. (1994), there are three basic methodologies used for VES: randomized walks, quadrat and transect.

If only one methodology is used for sampling herpetofauna, VES is often the best to use due to its effectiveness across all habitat conditions and ease of implementation.

When sampling using VES, there are several assumptions to consider: every individual species has the same chance of being observed, each species will have the same probability of being detected regardless of seasonality, size, behaviour, activity, etc, an individual is recorded only once per survey, and results collected from the same area are not observer-related.

### 3.4.3. Quadrat sampling

Quadrat sampling (QS) entails exhaustively checking a series of small-defined (e.g. 10 m x 10 m) squares (quadrats), which are placed randomly in selected sites within the study area. The study area can be visualized as a series of numbered grids; a random number is then selected, indicating which square to sample. A preselected number of quadrats are chosen to be sampled e.g. Heyer et al. (1994) recommend 25 to 30 units be sampled in order to provide sufficient data for statistical analysis.

Quadrats can be sampled using either point sampling or broad sampling. Point sampling uses small squares to study single species with small, densely distributed individuals. Broad sampling uses large quadrats to sample species in which individuals are widely dispersed, large-bodied or both and to sample multispecies populations. In either case, all quadrats are of equal size in their respective study areas.

QS is often used to estimate the total number of species (whether species richness, abundance or densities) within the study area. Although QS is labour intensive, it is effective for sampling a variety of habitats and, for high-density species in forest litter, open-area habitats and aquatic environments. QS should only be used when animals do not leave the quadrat due to sampling disturbance before being counted, quadrats can be randomly but systematically placed, and quadrats yield independent data.
3.4.4. Transect sampling

Transects are predetermined length of straight lines that are established either permanently, or temporarily, depending on the objectives of the study, using a measuring tape. Data is collected by systematically walking the line and collecting/counting all herpetofauna seen on either side of the line. Randomized transects can be used to estimate species numbers, relative abundance and densities across habitat gradients. Transects are often effective for sampling along elevational gradients or lowland to upland habitat gradients.

The underlying theory behind the use of transects is that not all individuals will be detected as the probability of detecting species decreases as its distance from the line increases.

3.4.5. Patch sampling

Patch sampling (PS) entails randomly sampling microhabitats or patches where concentrations of herpetofaunal densities are the highest. As species composition and density changes dramatically from one type of microhabitat to another, PS is a very useful tool in sampling species confined to particular microhabitats within a larger study area.

PS is a sub-technique of quadrat sampling allowing to determine the number, relative abundance, and densities of species confined to particular microhabitats of an area of interest; QS indiscriminately samples all microhabitats while PS focuses on specific species that occupy specific microhabitats, ignoring all other species that occur between patches. As such, the patches that are sampled can be considered quadrats themselves. PS involves identifying all discrete patches in a particular area and systematically searching for amphibians in these specific microhabitats (e.g. leaf litter, bromeliads, etc.). As patches are discovered within the wider study area, a number is assigned to each patch in sequential order. The type and amount of patches will influence how they are sampled and how many are sampled respectively. Every individual of every species occurring in each patch must be detected and voucher specimens preserved.

The basic assumptions in PS are that each patch has a defined border, can be dimensionally defined e.g. 3m x 5m, can be observed and located within the wider study area, and individual species can be counted within the patches.

3.4.6. Drift fences and pitfall traps

Drift fences and pitfall traps are designed to collect animals that would not be found on opportunistic and other classical searches. This technique can be highly effective at surveying herpetofaunal communities and is particularly useful to collect fossorial and rare species. It can be used to encircle specialized habitats (breeding ponds for example).

Drift fences are barriers, usually 5-100 meters long, that redirect the travelling animal into traps placed at the ends, besides, or under the barriers. Drift fences can also be placed in arrays designed in Y or X. Traps can be pitfalls, funnel traps or a combination of the two, and made from either various sizes of plastic buckets or cans. Drift fences can be constructed from various materials, plastic
sheets being our preferred material because it is light and easy to transport.

We usually set 30 meters-long or 60 meters-long lines. Traps (plastic buckets of about 28 cm diameter at the top, 30 cm deep) are buried into the ground at ca. 3 m intervals under a drift fence of plastic sheet (approximately 50 cm in height) positioned to run across the open midline top of the buckets (Fig. 33A-B). Small holes are drilled into the bottom of the buckets for drainage. Traps are usually checked twice a day (in early morning and late afternoon).

Pitfall traps are more labour intensive and require significant personnel time and funding relative to vertebrate area searches and are often associated with high mortality rates for non-targeted taxa. However, they are effective in detecting a broad array of species, specifically the species richness of an area, the presence of rare species (if long-term monitoring is undertaken), relative abundance and habitat use of selected species. Drift fences with pitfall traps tend to capture terrestrial species more easily than other species (e.g. frogs that are strong jumpers or climbers).

A combination of three to four drift fences with pitfalls are better for sampling than a single drift fence with pitfalls. The length of the drift fences influences the number of animals captured, and this varies by habitat type. Shorter drift fences capture less amphibians than longer fences and larger traps tend to increase the number of specimens collected. Pitfall traps assembled in a matrix without fences can also be used to study the population ecology and habitat use of selected species. Population density can be estimated with this technique if used in conjunction with mark-recapture techniques.

Heyer et al. (1994) recommended that operating drift fences opportunistically, after rainfall to maximize capture of species. Other studies have indicated an operation of 30 days to 2 years, this depending on the available funds, personnel and time period for sampling.

Basic equipment needed for setting a simple drift fence and pitfall traps

- Plastic sheet (ca. 50-100 cm in height, at least 100 m).
- Plastic buckets (ca. 35 buckets for a 100 meters-long drift fence). 20 litres buckets are efficient, but size of traps will mostly depend on what is locally available.
- Staple gun and staples.
- Stove.
- Machete.
3.4.7. Canopy access

Accessing the canopy is very useful to collect arboreal species and/or record their advertisement call. We successfully used the single-rope technique (Fig. 34) both to climb in trees and to access bottom of caves in the forest. The technique was also used to reach the base of Kaieteur Falls in 2004.

Single-rope technique involves ascending a single length of rope through the use of a mechanical ascender. Climbing in the canopy using that technique is basically a two-step process: (1) the tree must be equipped with a climbing rope. To do so, a light line must be shot over a solid limb (we use very strong fish line, shot with a crossbow). The light line is used to haul a heavier line (usually 4 mm strong rope) that is then used to haul a climbing rope up and over the limb (usually 10.5 mm static rope). One end of the rope is tied off to a nearby tree trunk; (2) the investigator ascends into the canopy on the other end of the rope using specific equipment.

Please note that climbing techniques are life-threatening practices that require a lot of training. Never try to use single-rope technique or any other caving/climbing technique without having received proper professional instruction beforehand!

An alternative to the single-rope technique is the use of tree climbing spurs, but...
this technique causes damage to the tree and should be used with caution. For those interested in techniques to reach the canopy, do not miss Mitchell et al. (2002) and Merchant (2007).

Fig. 34. The senior author using single-rope technique to access bromeliads along the Kaieteur gorge. (Photo by H. Sambhu/P. J. R. Kok).

Basic equipment needed for single rope technique

- 10.5 mm static rope (ideally 2 x 100 m).
- Harness (basic caving harnesses work great).
- Descender (we use Petzl® Stop D09).
- Ascender (we use Petzl® Ascender B07).
- Chest ascender (we use Petzl® Croll B16).
- Foot loop (we use Petzl® Footape).
- Shoulder strap for positioning the chest ascender (we use Petzl Torse).
- Asymmetrical Y-shaped lanyard used during rope manoeuvres (we use Petzl® Spelegyca).
- Gloves.
- Helmet.
- Maillons semi-circular.
- Maillons 7 mm inox.
- Webbings (various sizes).
- Carabiners (various sizes).
3.4.8. Sampling of amphibian larvae

Depending on the habitat, different techniques are used for sampling amphibian larvae such as seining, dipnetting, trapping and enclosure sampling. These techniques are quick, relatively thorough, with minimum personnel, material and time.

Seining is effective in shallow bodies of water with little vegetation; with an ideal length of 3-4 m long seine but length varies with the size of water body to be sampled. The seine is dragged from shore to shore, touching the bottom of the substrate and moved slowly along the aquatic habitat. Quantifying seine sampling can be done using square meter of bottom sampled (distance travelled x length of seine).

Dipnetting is the simplest method for sampling bodies of water clogged with vegetation, limited access stream habitat or specialized habitats such as tree holes. A standard small aquarium net (10 cm wide) is used to sweep under vegetation and in specialized structures. Sampling procedure can either cover approximately 20 to 50 sweeps in an hour or survey each aquatic habitat for an equal period. The rate of sweeps will either increase or decrease depending on the size of the aquatic environment. To collect tadpoles in bromeliads or small aquatic depressions, an aquatic pipette (turkey baster) is very effective (Fig. 33C).

Enclosure sampling (ES) includes box sampling, quadrat sampling and stovepipe sampling, and involves trapping animals inside an enclosure. ES is effective in shallow water habitats with relatively uniform substrates. ES can be objects such as PVC sewer pipes; 0.5 m$^2$ x 0.5 m deep metal box sampler or bottom net. The enclosure is dropped onto the substrate and pressing the sharp edge downwards, trapping the animal. The number of animals trapped within the closure is estimated.

Trapping is conducted using a funnel-trap principle and may be used to sample deep-water habitats or those with complex bottoms of stones, wood or rocks. Animals are encouraged to enter the funnel but cannot escape due to the small diameter and central location of the exit. Trapping is used specifically for estimating species richness and relative abundance.

Once collected, a number of tadpoles should be immediately euthanized and placed in small vials containing 10% formalin. Some tadpoles should be kept alive and reared in the field to obtain different developmental stages. Tadpoles can be reared in small containers or plastic bags. We usually use fish food to feed them.

Some tadpoles should be preserved in 95% ethanol for further molecular analyses.
3.4.9. Sampling of caecilians

Due to their secretive habitat (most adult caecilians are terrestrial burrowers, some are aquatic), caecilians are difficult to collect and few sampling techniques have been established. In addition to drift fences and pitfall traps (with very variable success) and methods to sample amphibian larvae (see above), digging in suitable habitat (soft soil, under rotting plant materials, in fine gravel along streams for example) is required for terrestrial species. Aquatic species may be collected with a net, or by passive tracking by means of collapsible, nylon-meshed funnel traps using fresh fish bait (see Kupfer et al., 2006a for details).

3.5. Collection management

As mentioned above, museum collections are extremely important, both to understand the past and to perform future research. Specimens must be preserved in a way that retains their original composition and be made available to the scientific community. As we saw before, adequate fixation is mandatory for long-term maintenance of your specimens. After all the efforts you have done to correctly fix the material you have the right to request that specimens’ integrity will be preserved as long as possible. This means that loss of fluid preservative and protection from fluctuation in temperatures and humidity (two important threats to fluid preserved specimens) will be adequately supervised.

Adult specimens are best kept in 70% ethanol, while tadpoles are preserved in 10% formalin. Tissues should be preserved in a cold place, in 95% ethanol, or ideally cryopreserved (by freezing).

Describing herpetological collections management is beyond the scope of this manual and we encourage the reader to refer to Simmons (2002) for detailed guidelines and curatorial practices.

3.6. Deposition of specimens in Guyana

The Centre for the Study of Biological Diversity (CSBD) is the key institution in Guyana for the management of the national biodiversity collections and research information (Bernard et al., 2002). All floral and faunal specimens left in or returned to Guyana as a result of collecting expeditions are housed at the CSBD. These collections serve as a resource in the study of Guyanese flora and fauna and enable the identification of priority areas for conservation planning and resource management.
The CSBD, founded in 1992 and housed in the Department of Biology, University of Guyana (UG) on the Turkeyen Campus, has played an important role in the development of research as it relates to biodiversity conservation in Guyana.

The Museum houses approximately 668 specimens (58 species) of amphibians with approximately 119 species of amphibians known from Guyana (Señaris & MacCulloch, 2005).

The Collections are currently under the care of two Scientific Officers who are trying to reorganize, clean and database the specimens; some of which were damaged by a flooding in 2005. According to Bernard et al. (2002), and through the efforts of the staff of the Biology Department, UG, environmental NGOs in Guyana and foreign researchers, the collection and identification of plants and animals has progressed to the point that an estimated 70% of the plants, 90% of the mammals and birds, and 60-70% of the remaining vertebrate groups are known in Guyana.

Unfortunately specimens housed at the CSBD are currently of difficult (if not impossible) access to foreign researchers due to the lack of financial and human resources for sending material or for hosting investigators. Lack of resources could also affect the preservation of the specimens that demand storage in a cool place (which means functional air-conditioning) and regular checking of the amount and quality of the preservative.

If we agree that the deposition of voucher specimens at the CSBD is imperative to allow local students and researchers to examine museum material (it is also required by EPA), we also strongly suggest that part of the collections remains in larger institutions that have sufficient financial resources to ensure adequate conservation and accessibility to foreign researchers. This is especially true for type specimens.

4. Systematics

As we saw above (see Chapter 2), it may be very difficult to confidently assign an amphibian species to a family, notably because of convergence. Significant morphological diagnostic characters of families are often features of the internal anatomy and some families are even primarily defined by genetics. Readers should refer to Chapter 2 for basic descriptions of the amphibian families found in KNP.

Fortunately, several features of the external morphology are very informative to identify an amphibian to the generic or specific level, hence again the importance of well-preserved voucher specimens in which those morphological diagnostic characters are retained, and thus easily observed and studied. In the field, most of these characters can easily be observed without extensive handling of the animal, but some will require the usage of a magnifying glass. In the laboratory you will need a stereomicroscope to examine small characters.

Experienced taxonomists are usually able to easily assign a species to a genus, or identify the taxon without close examination; this could be much more difficult for the beginner. Below we list and illustrate the most important external
morphological characters that will help you to identify the amphibian genera and species occurring in Kaieteur National Park and in the Guiana Shield.

4.1. Caecilians (Order Gymnophiona)
Readers should refer to Chapter 2 for more information about the group.

4.1.1. Caecilians identification: key features
Identification of caecilians is mostly based on the following external morphological key features (many subtle characters are not discussed here):

Relative position and visibility of the eye
The eyes of caecilians may be plainly visible and functional or invisible and covered by a thin layer of skull bone or skin (Fig. 35). The distinctiveness and location of the eye are of taxonomic importance as well as its relative position to nostril, tentacle and mouth.

Location of the protrusible sensory tentacle in relation to the eye and external nostril
The tentacle is a protrusible, usually very small, sensory organ that is present in all caecilian species (Fig. 35). Its relative position to the nostril, eye, and mouth helps in species identification.

Presence or absence of tail and shape of terminal shield
The tail is absent in most caecilians, but is distinct in certain genera and species. The distinctiveness of the tail is very variable and it may be difficult to state if a tail is present or not. The tail may be considered as present if complete, discernible folds occur posterior to vent; but note that in some species these folds, although discernible, are incomplete. When the tail is not distinct, the terminal portion of the body is sometimes called the terminal shield, which may be conical, compressed or depressed.

Shape of cloacal opening
The cloacal opening (vent) may be longitudinal, circular, transverse, or V-shaped.

Number of primary, secondary and total folds
The number of folds (= annuli) is an important diagnostic character. The number of primary annuli reflects the number of vertebrae, but is never identical (usually there are slightly more vertebrae than primary folds). Secondary (= supernumerary) annuli develop on the primary annuli; they may be absent or very few in some species, while in others their number exceeds the number of primary annuli. Annuli may be complete or variously incomplete. Figure 35 shows how to distinguish primary annuli from secondary annuli.

Presence or absence of splenial teeth
Splenial teeth are located on the lower jaw, on the splenial bone (usually fused to the dentary bone) and their number is often lower than the number of dentary
teeth (= outer dental teeth located on the dentary bone) (see Fig. 36 for location of splenial teeth). Splenial teeth are absent in a number of genera.

Fig. 35. Caecilian morphology and key morphological characters used in the identification of species. Modified from Taylor, 1968. (Photo by P. J. R. Kok).
Fig. 36. Diagrammatic view of lower jaw and floor of mouth in caecilians. A. Splenial teeth absent; B. Splenial teeth present. Modified from Savage, 2002.

4.1.2. Field key to the caecilian genera of Kaieteur National Park

1. True tail present (complete folds discernible posterior to vent), yellow lateral band on body ................................. Rhinatrema (p. 246)

1’. True tail absent (complete folds absent posterior to vent), no yellow lateral band on body ................................. Microcaecilia (p. 244)
4.2. Frogs and toads (Order Anura)

Reader should refer to Chapter 2 for more information about the group.

4.2.1. Frogs and toads identification: key features

Identification of anurans is based on a very large number of external morphological characteristics.

Each genus generally has its own important diagnostic characters and it is impossible to list and detail all these characters of each anuran genus here. The following features are thus general and the reader should refer to specialized references to obtain more detailed information (some references are given in Chapter 5).

Figure 37 shows main general features (see “Morphometrics” below for additional terms and the manner in which various measurements are taken).

Fig. 37. An adult frog (*Hypsiboas calcaratus*, Hylidae) showing general morphology and features. (Photo by P. J. R. Kok).
The main and easiest observed key features are:

**Size**

Adult size is a useful distinguishing character in frogs and toads (Fig. 38). Size of anurans is measured from the tip of snout to the posterior margin of vent (see Fig. 55); it is usually abbreviated SVL (snout-vent length).

![Fig. 38. Relative sizes of anurans in Kaieteur National Park. A. Very small/tiny (< 20 mm), e.g. *Adelophryne gutturosa*, Eleutherodactylidae; B. Small (20-30 mm), e.g. *Cochranella helenae*, Centrolenidae. C. Medium (30-60 mm), e.g. *Tepuihyla talbergae*, Hylidae; D. Large (60-200 mm), e.g. *Phyllomedusa bicolor*, Hylidae; E. Very large/giant (> 200 mm), e.g. *Rhinella marina*, Bufonidae. Photos by P. J. R. Kok.](image)
Colour and pattern

Although colours and patterns have a large intraspecific variation and may change depending on light intensity, they are very important distinguishing features in anurans. Colours on flanks and anterior and posterior surfaces of thighs are highly diagnostic in some genera (Scinax, Leptodactylus for example).

In most anurans, the colouration depends on the arrangement of the following chromatophores (pigment-containing and light-reflecting cells found in the skin): xanthophores, erythrophores, iridophores, melanophores, and cyanophores.

Some species are uniform and cryptic, while others display vivid colours and complex patterns. Figure 39 shows principal colour patterns in frogs and toads, which are:

- **Spots**: small to medium, regular, roundish light or dark markings contrasting with the background colouration (Fig. 39A).
- **Blotches**: medium to large, irregular light or dark markings contrasting with the background colouration (Fig. 39B).
- **Ocelli**: medium to large light spots outlined by a darker border (Fig. 39C).
- **Flecks/speckles**: small or minute, more or less regular light or dark markings contrasting with the background colouration (Fig. 39D).
- **Anastomosis/reticulum**: dark or light network of lines contrasting with the background colouration (Fig. 39E).
- **Lines**: short to medium lineate dark or light markings (Fig. 39F).
- **Bands/stripes**: lines of various widths that may be transverse (bands) or longitudinal (stripes) (Fig. 39G).
- **Chevrons**: a dark or light V-shaped pattern contrasting with the background colouration (Fig. 39H).

Many species exhibit a combination of different patterns.

Do note that preserved specimens usually lose their bright colours, which commonly fade to white. Colour may also be drastically modified by the preservative [e.g. green may become lavender (in some glass frogs for example) or deep purple (in Phyllomedusa for example)]; patterns are usually retained but are lost in some species. Colour in preservative may thus be an additional useful distinguishing feature.
Fig. 39. Principal colour patterns in anurans. A. Spots; B. Blotches; C. Ocelli; D. Speckles; E. Anastomosis; F. Lines; G. Stripe; H. Chevron. (Photos by P. J. R. Kok).
**Shape of head**

Head shape is very variable in anurans and the dorsal outline of the snout and the snout profile are informative characters (Fig. 40). Note that there are subtle variations in dorsal outlines of snout, which are not illustrated here. We suggest the reader to refer to Heyer *et al.* (1990) for more information and original drawings.

![Diagram showing different snout profiles](image1)

**Absence or presence of cranial crests**

Cranial crests are bony ridges on the skull that are found in many toads and in some frogs. The following cranial crests may occur: labial crest, suborbital crest, preorbital crest, canthal crest, supraorbital crest, postorbital crest, supratympanic crest, pretympanic crest, and parietal crest (Fig. 41). In some species these crests may be greatly expanded.
Shape of pupil and condition of palpebral membrane

In bright light, pupils of anurans may be horizontally elliptical (sometimes more or less heart-shaped), vertically elliptical (sometimes more or less triangular) or circular (Fig. 42). Note that this character is sometimes difficult to appreciate in preserved specimens.

The palpebral membrane (or nictitating membrane, the transparent lower eyelid) may be unpigmented or have a pigmented reticulation (Fig. 42D).
**Fig. 42.** Shape of pupils and palpebral membrane in anurans. A. Pupil horizontally elliptical (*Hypsiboas cinerascens*, Hylidae); B. Pupil vertically elliptical (*Phyllomedusa bicolor*, Hylidae); C. Pupil circular (*Pipa arrabali*, Pipidae); D. Palpebral membrane with pigmented reticulation (*Hypsiboas geographicus*, Hylidae). (Photos by P. J. R. Kok).

**Condition of tympanum**

Tympanum may be externally distinct or not, and tympanum condition is sometimes described as: prominent (very distinct with tympanic annulus prominently ringing the well visible tympanum), distinct (tympanum well visible, but tympanic annulus less visible), indistinct (tympanic annulus not visible, upper tympanum barely visible), very indistinct (tympanic annulus not visible, most tympanum barely visible) or absent (no tympanic annulus and tympanum visible). Most of the time the tympanum is described as distinct (Fig. 43A), indistinct (Fig. 43B) or absent (Fig. 43C). Note that this character is prone to post-mortem and preservation artefact.
Fig. 43. Condition of tympanum in anurans (eye is in the right upper corner). A. Distinct (*Leptodactylus longirostris*, Leptodactylidae); B. Indistinct (*Anomaloglossus beebei*, Aromobatidae); C. Absent (*Atelopus hoogmoedi*, Bufonidae). (Photos by P. J. R. Kok).

Texture of skin

Texture of dorsal skin is of considerable taxonomic importance. Skin texture is very variable in anurans and can mostly be described as:

- **Smooth**: free from projections (Fig. 44A).
- **Shagreened**: rough to the touch, covered with numerous very small close-set tubercles (Fig. 44B).
- **Granular**: bearing small, rounded, relatively flat grains of approximate equal size (granules) (Fig. 44C).
- **Tuberculate**: bearing rounded bumps of various sizes (tubercles) with no keratinized tip (Fig. 44D).
- **Spiculate**: bearing small pointed tubercles, often with keratinized tip (Fig. 44E).
- **Warty**: bearing protuberances of various sizes, often with keratinized tip (Fig. 44F).
- **Areolate**: skin covered with circular, closely-set, barely elevated protuberances (Fig. 44G); a condition most often found on the flanks or the venter.

There is some variation among these textures, and adverbs like weakly, finely, coarsely, thickly, etc. are often used to refine the description of the skin.

Some species exhibit a combination of skin textures (the dorsum may be shagreened anteriorly and granular posteriorly like in some *Anomaloglossus* for example, Fig. 44H).

Note that skin texture is prone to post-mortem and preservation artefact and may be difficult to appreciate on preserved specimens.
Fig. 44. Principal skin textures in anurans. A. Smooth (*Phyllomedusa bicolor*, Hylidae); B. Shagreened (*Hypsiboas calcaratus*, Hylidae); C. Granular (*Hypsiboas liliae*, Hylidae); D. Tubercular (*Leptodactylus petersii*, Leptodactylidae); E. Spiculate (*Pipa arrabali*, Pipidae); F. Warty (*Rhinella marina*, Bufonidae); G. Areolate (flanks of *Osteocephalus leprieurii*, Hylidae); H. Combination of skin textures in *Anomaloglossus cf. roraima* (Aromobatidae), a species that does not occur in KNP (red arrow shows shagreened skin on anterior dorsum, blue arrow shows granular skin on posterior dorsum). (Photos by P. J. R. Kok).
Presence or absence of an axillary membrane

The axillary membrane is a skin membrane that may occur at the posterior insertion of the upper arm (= axilla or armpit) (Fig. 45). It is characteristic of some species and may be more or less developed.

**Fig. 45.** Axillary membrane in anurans. A. Absent (*Osteocephalus leprieurii*, Hylidae); B. Present (*Dendropsophus marmoratus*, Hylidae). (Photos by P. J. R. Kok).

Presence or absence of dermal folds and fringes

A number of variously visible folds in the skin may occur on the anuran body and limbs: dorsolateral fold, middorsal fold, lateral fold, supratympanic fold, ulnar fold, tarsal fringe, etc. (see Fig. 46 for location of the principal fringes and folds). Folds may be interrupted or not and more or less elevated. A relatively developed ventral discoidal disc (thickening of ventral integument) may be visible in some species.
Fig. 46. Principal fringes and folds in anurans. A. Dorsolateral fold (red arrow) and supratympanic fold (blue arrow) in *Leptodactylus knudseni*, Leptodactylidae; B. Supratympanic fold (blue arrow) and dorsolateral and lateral folds (red arrows) in *Leptodactylus longirostris*, Leptodactylidae; C. Pectoral (= thoracic) fold (green arrow) in *Leptodactylus lutzi*, Leptodactylidae; D. Ulnar fold (black arrow) in *Dendropsophus marmoratus*, Hylidae; E. Fringes and folds on arm and leg: (1) fringe on postaxial edge of Finger IV, (2) metacarpal fold, (3) ulnar fold, (4) tarsal fringe, (5) fringe on postaxial edge of Toe V, (6) metatarsal fold, (7) tarsal fold. (Photos A-D by P. J. R. Kok; E modified from Kok & Castroviejo-Fisher, 2008).
**Presence or absence of glands**

Parotoid glands and other small glands may be visible on the skin (Fig. 47); some of them produce toxins (e.g. parotoid glands), others are used in defensive postures (e.g. inguinal glands).

**Fig. 47.** Some glands found in anurans. A. Parotoid glands (black arrows) in *Rhaebo guttatus*, Bufonidae; B. Inguinal glands (blue arrows) in *Pleurodema brachyops*, Leiuperidae (note: this species does not occur in KNP); C. Mental gland (red arrow) in *Hypsiboas cinerascens*, Hylidae. (Photos by P. J. R. Kok).
Palmar structures

Figure 48 shows main palmar structures, which involve various tubercles, fringes, folds (see also Fig. 46), and the presence or absence of a visible prepollical spine. See Fabrezi (2001) for prepollex and prehallux variation in anuran limbs.

Fig. 48. Palmar structures in anurans. (Photo by P. J. R. Kok).
Degrees of webbing on hand and foot

Similar species may be distinguished by the amount of finger and/or toe webbing they possess. Although some authors (see Edwards, 1974; La Marca, 1997) proposed different terminologies, the most widely used system for webbing formula follows Savage & Heyer (1967), with modifications proposed by Myers & Duellman (1982) and Savage & Heyer (1997). Recently, Guayasamin et al. (2006) slightly refined the system for centrolenid frogs.

The degree of webbing is described in enumerating phalanges (including metacarpals and metatarsals) that are free of webbing. Each finger and toe is represented by a Roman numeral and the number of phalanges completely or partially free of webbing by an Arabic numeral (Fig. 49). A notation of “0” indicates that the web extends to the disc, while “1” indicates that the web extends to the intercalary tubercle (distal, just below the disc). A “+” indicates that the web reaches the proximal margin of the structure (tubercle or disc), a “-” indicates that the web reaches the distal margin of the structure, and no superscript means that the web reaches the middle of the structure. Fractions are used when the web does not reach a structure, but only a point between two structures: for example “1/2” when half of the phalanx is free of webbing, “1/3” when the distal one-third of the phalanx is free of webbing, “2/3” when the distal two-thirds of the phalanx are free of webbing, etc.

Note that webbing may be somewhat variable intraspecifically and that females may have slightly more webbing than males.

Fig. 49. Degrees of webbing in anurans. A. Unwebbed; B. Basally webbed; C. Half-webbed; D. Fully webbed. (Photos by P. J. R. Kok).
Plantar structures
Figure 50 shows main plantar structures, which involve various tubercles, fringes, and folds (see also Fig. 46).

Fig. 50. Plantar structures in anurans. (Photo by P. J. R. Kok).
Structure of digital discs and subarticular tubercles

Variation in external digital features is of taxonomic importance. Digital disc structure is very variable (and not related to the shape of the distal phalanx); figure 51 shows some common shapes (see Savage, 1987 for additional digital disc character states).

Fig. 51. Diagrammatic views of main structures of digital disc and tip of digit in anurans. A. Disc unexpanded (e.g. in Leptodactylus petersii, Leptodactylidae); B. Disc expanded, broadened (e.g. in Hypsiboas liliae, Hylidae); C. Disc expanded, truncate (e.g. in Allophryne and some glass frogs); D. Disc not, or slightly, expanded with pointed tip (e.g. in Adelophryne gutturosa, Eleutherodactylidae); E. No terminal disc, but four minutes lobes (e.g. in Pipa arrabali, Pipidae); F. Dorsal surface of finger disc with two scutelike flaps (e.g. in Anomaloglossus, Aromobatidae).

Presence/absence and structure of the distal subarticular tubercle on the fourth finger is also variable and helpful for identification (Fig. 52).

Fig. 52. Diagrammatic views of structures of distal subarticular tubercle on Finger IV. A. Absent; B. Single; C. Bifid; D. Divided. Modified from Duellman, 1970.
Buccal structures: condition of odontophores, and shape of tongue

Maxillary teeth (= teeth that are on the maxilla) may be absent (e.g. in Allophrynidae and Bufonidae) or present, in which case they may have various shapes that are characteristic and helpful for identification.

The absence or presence of odontophores (= the portion of the vomer bearing the vomerine teeth) and their shape and position is also of taxonomic importance (Fig. 53). The number of vomerine teeth is usually related to the age of the frog and juveniles may lack vomerine teeth or have only a few while adults of the same taxon may have very distinct odontophores bearing numerous teeth.

Shape of choanæ (singular choana) and interchoanal distance is also considered of taxonomic importance in some genera, but this character may be intraspecifically variable.

Shape of vocal slits is variable with taxa and may also help for identification (see below “Condition of vocal sacs”).

Fig. 53. Generalized diagrammatic view of anuran buccal cavity showing principal structures and some conditions of odontophores. A. Odontophores oblique and barely separated, between choanae. B. Odontophores oblique and widely separated, between choanae. C. Odontophores arched and widely separated, below choanae. Modified from Duellman & Trueb, 1986.
Shape of tongue is also variable with taxa and is of some taxonomic importance. Figure 54 shows the principal shapes of tongue in anurans. Note that this character is prone to post-mortem and preservation artefact.

![Diagram of tongue shapes](image)

**Fig. 54.** Diagrammatic views of principal shapes of tongue in anurans. A. Round; B. Cordiform; C. Ovoid; D. Lanceolate. Modified from Duellman, 1970.

**Morphometrics**

Morphometric comparisons, including comparison of relative length of fingers (e.g. relative length of Finger I versus Finger II, or relative length of Toe III versus Toe V), and relative position of various structures (e.g. the relative position between the tip of Finger II and the distal subarticular of Finger III when Finger II and III are adpressed together, or the relative position between the tibiotarsal articulation and the tip of snout when hindlimb is adpressed along the body) are helpful to distinguish similar species.

The use of statistics and comparison of measurement ratios are also invaluable in many cases.

It is thus mandatory to take a number of measurements in order to compare species’ morphometry. Principal landmarks are indicated in figure 55 and are defined below:

- **Snout-vent length** (SVL): from the tip of the snout to the posterior margin of the vent.
- **Head length**: from the posterior edge of the jaw (sometimes from the posterior edge of the tympanum) to the tip of the snout.
- **Head width**: the greatest width of the head, usually at the level of the anterior edges of the tympani, sometimes at the level of the angle of jaws.
- **Eye-naris distance**: from the posterior edge of the naris to the anterior edge of the eye.
- **Eye length** (= diameter): the greatest length of the orbit from the anterior margin to the posterior margin of the eye.
- **Tympanum length** (= diameter): the greatest length of the tympanum from the anterior margin to the posterior margin of the tympanum.
• **Eyelid width**: the greatest transverse width of the upper eyelid.

• **Interorbital distance** (IOD): the distance between the median margins of the orbits.

• **Internarial distance** (IND): the distance between the median margins of the nares.

• **Snout length**: from the anterior margin of the eye to the tip of the snout.

• **Hand length**: from the proximal edge of the palmar tubercle to the tip of Finger III.

• **Upper arm length**: from the margin of the body insertion to the tip of the elbow.

• **Forearm length**: from the tip of the elbow to the proximal edge of the palmar tubercle.

• **Thigh length**: from the vent to the outer edge of the flexed knee.

• **Shank length**: from the outer edge of the flexed knee to the tip of the heel.

• **Tarsus length**: from the heel to the proximal edge of the inner metatarsal tubercle.

• **Foot length**: from the proximal edge of the inner metatarsal tubercle to the tip of Toe IV.

• **Width of disc** (usually on Finger III and Toe IV): the greatest width of the disc.

Remark: taking precise, comparable, measurements in amphibians is almost impossible due to the soft and flexible nature of preserved amphibians (see Hayek *et al.*, 2001). The value of the measurements used in morphometric studies is also closely related to the quality of the preservation of the specimens and the training level of the observer. Hayek *et al.* (2001) pointed out that intra- and interobserver differences in measuring specimens are recurrent and can lead to statistically significant differences in the variables, which may result in different biological interpretations. They suggested several recommendations to use in frog morphometric studies (e.g. remeasure at least one individual 20 times for estimation of measurement error) and we encourage the reader to refer to that publication.
Fig. 55. Main terms and landmarks in anurans. Abbreviations are explained in the text. (Photos by P. J. R. Kok).
The following external morphological diagnostic features are secondary sexual characters found only in males:

**Condition of vocal sacs**

The vocal sac(s) communicates with the buccal cavity via two small apertures called the vocal slits, which may be round or slitlike and variously elongated (see Fig. 53). The skin covering the external vocal sac is usually modified and it is possible to discern some dermal lobes or folds. In some species males lack an external vocal sac, in this case the skin covering is totally unmodified. Some species completely lack vocal sac and vocal slits (e.g. *Stefania* spp., Hemiphyllactidae). Vocal sacs may be subgular (single, bilobate, or paired) or lateral (paired) (Fig. 56).

The pulsating sac may increase the attractiveness of advertisement calls in some species (see Rosenthal *et al.*, 2004).

![Diagram of vocal sacs](image-url)

**Fig. 56.** Diagrammatic views of main types of vocal sacs in anurans. A. Single, median, subgular; B. Bilobate subgular; C. Paired subgular; D. Paired, lateral. Modified from Duellman, 1970.
Presence or absence of humeral spine

The humeral spine is the ventrolateral extension of the *crista ventralis* (a prominent ridge in the humerus) and is present only in a few anuran species, most of them belonging to the family Centrolenidae. Its presence or absence is of taxonomic importance and helps, for example, to identify glass frog genera (Fig. 57).

![Fig. 57. Humeral spine in anurans. A. Absent (e.g. in *Hyalinobatrachium*, here *H. crurifasciatum*); B. Present (e.g. in *Centrolene*, here *C. gorzulae*). (Photos by P. J. R. Kok).](image)

Condition of nuptial pads

Nuptial pads are horny or thickened structures of various sizes and shapes usually located on the male’s thumb (Fig. 58). Testicular hormones influence their development and they are especially prominent during the breeding season. Condition of nuptial pads is of taxonomic importance and is useful to distinguish species.

Presence or absence of keratinized prepollical spines

Keratinized prepollical spines (= thumb spines, Fig. 58) are nuptial excrescences found in several anuran species. In some species the thumb bears a single developed spine, while in other taxa there may be two developed spines or no spine at all. The presence or absence of spines may help to distinguish similar taxa, although there is some intraspecific variation in this character.

Presence or absence of a fleshy proboscis

In some species males have a shovel-shaped projecting snout probably used to excavate underground nesting chambers (Fig. 58).
4.2.2. Field key to the anuran genera of Kaieteur National Park

The only purpose of the following dichotomous key is to help the reader to identify in the field the anurans of Kaieteur National Park to the genus level. It will guide the reader to a specific generic account by reference to a page number. A key to the species is provided in each of the generic accounts.

This key is not infallible and the reader should always verify any identification made by using the key through detailed comparison with the descriptions and illustrations in the species accounts. Do also note that only a few subjective characters are used in the key and that these characters are not sufficient for genus or species identification.

1. Tongue absent, pupil circular (Fig. 42C), no disc on the tip of digits but four small lobes (Fig. 51E), body distinctly flattened .............................................................. \textit{Pipa} (p. 234)
1'. Not as above .................................................. 2
2. Pair of dermal scutelike flaps on dorsal surface of each disc (Fig. 51F) .................................................. Anomaloglossus (p. 114)
2'. Not as above .................................................. 3
3. Fingers lacking expanded terminal discs (Fig. 51A, D) .................................................. 4
3'. Fingers with expanded terminal discs (Fig. 51B-C) .................................................. 9
4. Parotoid glands present (Fig. 47A) .................................................. 5
4'. Parotoid glands absent .................................................. 6
5. Parotoid glands ovoid, small to large (Fig. 47A), cranial crests absent or weakly developed .................................................. Rhaebo (p. 124)
5'. Parotoid glands trianguloid, very large, cranial crests well developed (Fig. 41) .................................................. Rhinella (p. 130)
6. Terminal disc on digits with pointed tip (Fig. 51D), digits flattened, subdigital pads rather than subarticular tubercles, very small size .................................................. Adelophryne (p. 148)
6'. Not as above .................................................. 7
7. Tympanum distinct (Fig. 43A) .................................................. Leptodactylus (p. 212)
7'. Tympanum indistinct or absent (Fig. 43B, C) .................................................. 8
8. Dorsum black with yellow reticulation, toes webbed .................................................. Atelopus (p. 120)
8'. Dorsum brown without reticulation, body ovoid, toes unwebbed .................................................. Synapturanus (p. 230)
9. Pupil vertically elliptical (Fig. 42B), fingers and toes opposable .................................................. Phyllomedusa (p. 190)
9'. Pupil horizontally elliptical (Fig. 42A), fingers and toes not opposable .................................................. 10
10. First finger shorter than second .................................................. 11
10'. First finger equal or longer than second .................................................. 18
11. Toes no more than basally webbed (Fig. 49A) .................................................. Pristimantis (p. 238)
11'. Toes at least one-third webbed (Fig. 49B, C, D) .................................................. 12
12. Head very small, triangular, terminal disc on digits truncate (Fig. 51C), throat black with white spots ................................. Allophryne (p. 110)
12'. Not as above ........................................................................ 13

13. Web between Toes I-II absent or reduced (does not reach the subarticular tubercle of Toe II) and webbing on fingers absent or much reduced (Fig. 49), skin smooth to shagreened (Fig. 44A, B), dorsal ground colour not green ....................................................... 14
13'. Web between Toes I-II usually extends beyond the subarticular tubercle of Toe II and webbing on fingers usually present (Fig. 49) [except in Hypsiboas liliae, in which the dorsal skin is granular (Fig. 44C), and the dorsal ground colour green] ....................................................... 15

14. Dorsal outline of snout truncate (Fig. 40A), snout not protruding beyond lower jaw, inner metatarsal tubercle projecting .................. Tepuihyla (p. 202)
14'. Dorsal outline of snout rounded (Fig. 40A), snout protruding beyond lower jaw, inner metatarsal tubercle not projecting ............... Scinax (p. 196)

15. Axillary membrane extensive (more than 1/2 upper arm length), orange or yellow with black spots (Fig. 45B) ......................... Dendropsophus (p. 158)
15'. Axillary membrane usually absent or indistinct (Fig. 45A), when present (Fig. 45B) small (no more than 1/2 upper arm length), never orange ........ 16

16. Bones green and skin on dorsum thick and glandular .............................. Trachycephalus (p. 206)
16'. Not as above .......................................................................... 17

17. Skin of head fused to skull, males usually with paired vocal sacs (Fig. 56C-D) and dorsal skin distinctly tuberculate or spiculate (Fig. 44D-E) (smooth in females, Fig. 44A) [Except in O. exophthalmus and O. oophagus] ................................. Osteocephalus (p. 178)
17'. Skin of head not fused to skull, males with subgular vocal sac (Fig. 56A), dorsal skin not sexually dimorphic .......................... Hypsiboas (p. 162)

18. Venter not transparent, internal organs not visible .............................. Stefania (p. 152)
18'. Venter transparent, internal organs visible ..................................... 19
Fig. 59. Condition of the parietal peritoneum in glass frogs (Centrolenidae). A. White
(indicated by a red arrow), heart not visible (black arrow) (here in Cochranella helenae); B.
Transparent, heart visible (indicated by a black arrow) (here in Hyalinobatrachium
crurifasciatum). (Photos by P. J. R. Kok).

19.
Anterior third of parietal peritoneum white, heart not visible (Fig. 59A) . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . Cochranella (p. 138)
19’.
Parietal peritoneum transparent, heart at least partially visible (Fig. 59B) .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 20

Fig. 60. Ventral view of the area between the legs showing absence/presence of enlarged
tubercles below vent in glass frogs (Centrolenidae). A. Absent (here in Hyalinobatrachium
taylori); B. Present (here in Centrolene gorzulae). (Photos by P. J. R. Kok).

20.
Distinctly enlarged round tubercles below vent (Fig. 60B), prepollical
spine projecting, humeral spine present in adult males (Fig. 57B) . . . . . . . . . . . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .Centrolene (p. 134)
20’.
No distinctly enlarged round tubercles below vent (Fig. 60A), prepollical
spine not projecting, humeral spine absent in adult males (Fig. 57A) . . . . . . . . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . Hyalinobatrachium (p. 142)

90

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4.2.3. Tadpoles identification: key features

Characteristics of anuran larvae (= tadpoles) are often used in taxonomic descriptions. In some taxa adults may be problematic to identify even though their tadpoles are very distinctive. Reversely (and surprisingly) some fairly different species may have extremely similar larvae.

Tadpoles show a great diversity in morphological types and are perfectly adapted to the many different environments in which they are found (from ponds and streams to bromeliads and tree holes); their morphology also reflects phylogenetic relationships.

Gosner’s (1960) staging system subdivides tadpole development in 46 stages, those below 25 being of little use for identification. Ideally tadpoles should be in stages 26 to 38 to be accurately identified. Hence it is important to rear some larvae in the field and preserve tadpoles at different developmental stages.

The Gosner (1960) staging system is recommended for use with exotroph tadpoles. Figure 61 illustrates Gosner stages from 23 to 41, which are briefly explained below [see Gosner (1960) and McDiarmid & Altig (1999)]. Before stage 23 larvae are non-feeding and mostly immobile.

**Stage 23:** oral disc distinct, external gills very distinct on both sides.

**Stage 24:** oral disc distinct, external gills atrophied, operculum closes on right.

**Stage 25:** oral disc obvious, external gills absent, spiracle forms on left.

**Stage 26:** hind limb development begins, length of hind limb bud inferior to 50% of its height.

**Stage 27:** length of hind limb bud superior or equal to 50% of its height.

**Stage 28:** length of hind limb bud superior or equal to its height.

**Stage 29:** length of hind limb bud inferior or equal to 150% of its height.

**Stage 30:** length of hind limb bud equal to 200% of its height.

**Stage 31:** foot paddle visible.

**Stage 32:** indentation between the fourth and the fifth toes visible.

**Stage 33:** indentation between the third and the fourth toes visible.

**Stage 34:** indentation between the second and the third toes visible.

**Stage 35:** indentation between the first and the second toes visible.

**Stage 36:** Toes III-V separated.

**Stage 37:** all toes separated.

**Stage 38:** inner metatarsal tubercle appears.

**Stage 39:** subarticular patches visible.

**Stage 40:** outer metatarsal tubercle and foot subarticular tubercles visible, vent tube still present.
**Stage 41**: forelimbs bud visible, vent tube absent.

From stage 41 the larval mouthparts disappear and are replaced by adult jaws, tail is resorbed and limbs become functional. Stage 46 corresponds to complete metamorphosis.

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**Fig. 61.** Gosner (1960) developmental staging system, from stage 23 to stage 41. Modified from McDiarmid & Altig (1999).
The principal structural features of anuran larvae are illustrated below (Fig. 62).

![Diagram of anuran larva with labeled structures: nostril, eye, tail muscle axis, tail musculature, tail fin, oral disc, spiracle, vent tube, tip of tail, body, tail.]

**Fig. 62.** Principal structural features of anuran larvae (here the arboreal tadpole of *Anomaloglossus beebei*, Aromobatidae). (Photo by P. J. R. Kok).

Shape and position of several structural characters are of taxonomic importance in tadpoles. The spiracle, for example, may be single and sinistral with a short spiracular tube (as illustrated in Fig. 62); single and sinistral with a long spiracle tube; dual and lateral; dual and lateroventral; single and posterior ventral; single and midventral. As for the eyes, they may be lateral or dorsal; the tail tip may be pointed or ending by a filament; the body may be adpressed or not; the tail fin may be extensive or not (compare Figs 62 & 63); the vent tube may be dextral or medial; etc. The development of the lateral line system is also variable. See McDiarmid & Altig, 1999 and Altig, 2007 for extensive descriptions of these structural characters.

Colour and pattern are also helpful for identification and are usually not very variable intraspecifically (although they may change during development, hence the importance to compare larvae of the same developmental stage).

As in adults, comparisons of morphometrics and measurement ratios are helpful to distinguish similar species. Grosjean (2005) recommends tadpoles between stages 32-40 for best morphological intra- and interspecific comparisons.

Principal landmarks are indicated in figure 63 and are explained below:

- **Total length** (TL): from the tip of the snout to the tip of the tail.
- **Body length** (BL): from the tip of the snout to the junction of the posterior body and the tail musculature.
- **Tail length** (TAL): from the junction of the posterior body and the tail musculature to the tip of the tail.
- **Body width** (BW): the highest width of the body.
• **Body height** (BH): the highest height of the body.
• **Head width at level of eyes** (HW): self-explanatory.
• **Tail muscle height at base of tail** (TMH): self-explanatory.
• **Upper tail fin height** (UTF): the highest height of the upper fin, from the upper margin of the tail musculature to the upper margin of the upper fin.
• **Lower tail fin height** (LTF): the highest height of the lower fin, from the lower margin of the lower fin to the lower margin of the tail musculature.
• **Tail muscle width at base of tail** (TMW): self-explanatory.
• **Maximum height of tail** (MTH): the highest height of the tail.
• **Eye-naris distance** (END): from the anterior corner of the eye to the posterior margin of the naris (nostril).
• **Naris-snout distance** (NSD): from the anterior margin of the naris to the tip of the snout.
• **Snout-spiracle distance** (SSD): from the tip of the snout to the posterior margin of the spiracle.
• **Internarial distance** (IND): the distance between the median margins of the nares.
• **Interorbital distance** (IOD): the distance between the median margins of the orbits.
• **Eye diameter** (ED): the greatest length of the orbit from the anterior margin to the posterior margin of the eye.

Note that measurements are accurately compared only when they involve the same landmarks and tadpoles of the same developmental stages!

Some authors suggest that measurements between structures should be taken from the centre of these structures (*e.g.* internarial distance measured between the centre of the nares). As the centre of a structure is not a fixed point, we find this method too subjective and prefer taking measurements between anterior or posterior margins of structures.

See also aforementioned remark in “Morphometrics".
Fig. 63. Principal landmarks in anuran larvae (here a benthic tadpole of a still undetermined species). A. Lateral view; B. Dorsal view. Abbreviations are explained in the text. (Photos by P. J. R. Kok).

Shape and location of the oral disc are also very characteristic (see McDiarmid & Altig, 1999 for further details) and are usually related to the feeding habit of the larva (which may feed on detritus, dead invertebrates, other tadpoles, conspecific or heterospecific eggs, etc.). Figure 64 shows principal terminologies used in oral disc description, which are briefly explained below (see McDiarmid & Altig, 1999 and Altig, 2007 for extensive details):

- **A-1, A-2, etc.:** anterior tooth rows (= rows of labial teeth), which are numbered from the anterior margin of the upper labium toward the mouth.
- **Dorsal gap in marginal papillae and A-2 gap:** the term “gap” is used to indicate that there is a space (usually medially) that is free of papillae or labial teeth. There is often a medial gap in marginal papillae on the upper labium and sometimes a gap in the second anterior tooth row. Medial gaps may also occur elsewhere (in P-1 for example). They should not be confused with “artificial” gaps due to the loss of labial teeth or papillae. Number and location of gaps are of taxonomic importance; the size of the gap may vary with developmental stage.
• **P-1, P-2, P-3**, etc.: posterior tooth rows, which are numbered from the mouth toward the posterior margin of the lower labium.

• **Marginal papillae**: they are found on the edges of the oral disc. They may completely encircle the disc, or be interrupted by gaps. Marginal papillae may be laterally indented (= emarginated). The number of papillae rows and the length and shape of papillae vary among taxa and are helpful for identification.

• **Upper and lower jaw sheath**: they form what is sometimes called the tadpole "beak". Shape of jaw sheath is of some taxonomic importance.

• **Jaw sheath serration**: they are the keratinized projections of various sizes and shapes occurring on the cutting edge of the jaw sheaths.

The LTRF (abbreviation of Labial Tooth Rows Formula) is very useful for comparison. It is expressed as a fractional notation in which the numerator equals the number of anterior tooth rows and the denominator equals the number of posterior tooth rows. Natural gaps are noted between parentheses [e.g. LTRF of the tadpole illustrated in Fig. 64 (*Anomaloglossus kaiei*, Aromobatidae) is 2(2)/3]. Numbers in bracket indicate variation in the presence of a medial gap.

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**Fig. 64.** Oral disc of an anuran larvae (*Anomaloglossus kaiei*, Aromobatidae) showing principal terminologies. Abbreviations are explained in the text. (Scanning electron micrograph by J. Cillis & P. J. R. Kok).
4.2.4. Preparation of tadpole oral disc for electronic microscopy

Observation of the tadpole oral disc using scanning electron microscopy (SEM) is very effective to distinguish very small features that are of taxonomic importance (variation in labial teeth for example).

The oral disc must first be carefully dissected under a stereomicroscope and transferred to 100% ethanol. The sample will then be “critical-point dried”. Critical point drying is a technique of drying soft, naturally hydrated, tissues without deforming their structure. This technique is mostly used for examination under high vacuum conditions, as in the case of a scanning electron microscope. Allowing the oral disc to dry under high vacuum conditions would damage it due to the surface tension that occurs when changing from the liquid to the gaseous phase.

Within the critical-point drier apparatus, the ethanol (called the intermediate fluid) is exchanged for the transition fluid (CO₂) and the “critical point” at which the density of the liquid and the gas is the same is achieved by controlling pressure and temperature within the instrument. Once the CO₂ is fully converted to gas the specimen is dry.

Because freshly dried specimens are highly hygroscopic (which means they readily absorb water), they must be quickly coated with a thin layer of conductive metal (usually gold).

After gold coating the oral disc is carefully positioned on a small stand with a sticky surface and is ready to be examined.

4.2.5. Call analysis

Although sound emission is reported in some caecilians (see Duellman & Trueb, 1986), only anurans produce sounds to attract conspecific females, defend their territory and communicate stress. Call analysis is a valuable tool in species identification: the advertisement call is an important mate recognition character and anuran advertisement calls are species-specific.

Vocal communication in anurans and call analysis are rather complex matters and we only provide here a brief introduction to the very basics of frog call analysis, i.e. the principal terms used in call analysis, their meaning, and the way to obtain essential information from your recordings through the sound analysis software.

The sound analysis software

There are several software programs available on the market; some of them may be downloaded for free from the Internet. We use Raven Pro (version 1.3) from the Cornell Lab of Ornithology, thus the appearance of the oscillograms and spectrograms provided below (and the calculation methods) may change according to the software you will use.

Acquiring input

This depends on the software you use. Connect your recorder to the audio input device on your computer and follow the software user guide.
Types of calls and terminology

There are four types of calls in anurans:

- **The advertisement call**: is produced by males and has two principal functions: attracting conspecific females, and announcing to other males (both conspecific and heterospecific) that the territory is occupied.

- **The reciprocation (or response) call**: is emitted by receptive females in response to conspecific males advertisement call (currently known only in a very few species).

- **The release call**: is produced by males and unreceptive females in response to a tentative amplexus. Often accompanied by body vibrations.

- **The distress call**: is emitted by several species in response to severe disturbance. Usually explosive and very loud (Fig. 65).

![Fig. 65. Distress call of Rhaebo guttatus, Bufonidae. Compare with advertisement call in figure 86.](image)

We focus here on the advertisement call, the most commonly heard call that is widely used in species identification.

The advertisement call is the assemblage of one or more acoustic signals (called the notes) produced in a given time sequence. The notes are nothing else than sound waves transmitted through the air (most of the time) or through water (in some species, *e.g.* *Pipa aspera*, Pipidae).

The characteristics of a sound wave (Fig. 66) are:

- **The amplitude**: usually measured in decibels (dB), the amplitude is the loudness of the sound. Variation of amplitude is visible on an oscillogram (also called the waveform).
• **The frequency**: measured in Hertz (Hz) or kilohertz (kHz), the frequency is the pitch of the sound, which depends on the number of vibrations imposed on the air per second. Variation of frequency is visible on a spectrogram (= audiospectrogram).

Acoustic components of the call are well visible on a spectrogram (Fig. 66) and are:

• **The note**: the smallest unit of the call. The advertisement call may be a single note (Fig. 67), or a series of similar or different notes (Figs 68-70).

The notes may be unpulsed, meaning that there is no extreme change in the amplitude over time (Fig. 71A), or pulsed, meaning that there is severe change(s) in amplitude over time (Fig. 71B). This phenomenon is called the amplitude modulation. Notes may contain one or several pulses of various intensities.

The frequency (= pitch) of the note may be unmodulated, meaning that there is no variation in the pitch over time (Fig. 72A), or distinctly modulated, meaning that there are conspicuous changes in frequency over time (Fig. 72B). This phenomenon is called the frequency modulation. Frequency modulation may have different patterns (*e.g.* upwards, downwards, up-down, etc.).

• **The fundamental frequency**: the lowest (= first) frequency harmonic.

• **The dominant frequency**: the frequency harmonic within which the greatest amount of sound energy is concentrated; also called the main harmonic. In some cases, the dominant frequency is the fundamental frequency (see Fig. 68 for example).

• **The harmonics**: the separated, evenly spaced frequencies that are multiples of the fundamental frequency.

![Diagram showing oscillogram and spectrogram](image_url)

**Fig. 66.** Oscillogram and spectrogram of the call of *Scinax boesemani* (Hylidae) showing acoustic components.
Fig. 67. Oscillogram and spectrogram of the call of *Leptodactylus lutzi* (Leptodactylidae) illustrating a call composed of a single note.

Fig. 68. Oscillogram and spectrogram of the call of *Adelophryne gutturosa* (Eleutherodactylidae) illustrating a call composed of a series of notes (here 13 notes).
Fig. 69. Oscillogram and spectrogram of the call of *Scinax boesemani* (Hylidae) illustrating a call composed of a series of identical notes (here 18 notes) produced in a very short period of time. This kind of call is named a trill. In this case the entire call is given in less than half a second; compare with figure 68 in which the call is given in about 2s.
Fig. 70. Oscillogram and spectrogram of the call of *Osteocephalus leprieurii* (Hylidae) illustrating a complex call composed of a series of very different notes.
Fig. 71. Oscillograms and spectrograms illustrating amplitude modulation. A. An unpulsed note *Allobates spumaponens* (Aromobatidae); B. A pulsed note *Allobates granti* (Aromobatidae). None of these species occur in KNP.

Fig. 72. Spectrograms illustrating frequency modulation. A. Dominant frequency of the call of *Centrolene gorzulae* (Centrolenidae), mostly unmodulated; B. Dominant frequency of the call of *Leptodactylus longirostris* (Leptodactylidae), distinctly modulated (upwards). Red arrows highlight the change of frequency between the beginning of the note (on the left) and the end of the note (on the right).

The following principal temporal variables and parameters are usually considered in the call analysis and allow comparisons between calls:

- **The call duration**: measured in seconds (s), from the beginning of the first to the end of the last note.
- **The note duration**: measured in seconds (s), from the beginning of the note to the end of the note.
- **The inter-call interval**: measured in seconds (s), from the beginning of one call to the beginning of the next.
- **The number of notes**: the number of notes within the call.
• **The inter-note interval**: measured in seconds (s), from the end of one note to the beginning of the next.

• **The note period**: measured in seconds (s), from the beginning of one note to the beginning of the next.

• **The call rate**: the rate at which entire calls are produced, expressed in calls/min.

• **The note repetition rate**: the rate at which notes are produced, expressed in notes/s. The note repetition rate is obtained by measuring the time between the beginning of the first note and the beginning of the last note, and dividing the number of notes included within this period by the time in seconds. Equivalent to the call rate when the call is composed of a single note.

• **The dominant frequency**: generally measured from a spectral slice taken through the portion of the note with the highest amplitude, expressed in Hertz (Hz).

**Acquisition of the data**

Open your sound using the sound analysis software. Calls and notes are usually not well visible (Fig. 73A) and you will need to zoom in the recording to see the calls and the notes closer (Fig. 73B-C). Play with the contrast if needed and use the software tools to calculate the data you need.

Figure 74 illustrates how to calculate the call duration using the selection borders in *Raven Pro*. The same method is applied for other temporal variables.

Figure 75 shows calculation of the dominant frequency from a spectral slice in *Raven Pro*. Placing the cursor at the top of the first peak will provide the frequency at the bottom of the display.

**Remarks:**

• Descriptive data are always obtained from multiple measurements of different calls from an individual (ideally from as many individuals as possible).

• As we saw above (in “Recording of advertisement calls”), temperature notably influences some attributes of the acoustic signals (*e.g.* frequency, note repetition and note repetition rate) and comparisons between calls recorded at different temperatures may lead to misinterpretations.
Fig. 73. Zoom in the sound recording to identify calls and notes (here the call of Anomaloglossus beebei, Aromobatidae). A. Calls are difficult to detect and details are not discernible; we zoom in the area highlighted yellow; B. After zooming, five calls are well visible and the number of notes is discernible; we zoom again in the area highlighted in yellow; C. After zooming, one call composed of three notes is isolated.
Fig. 74. Example of calculation of a temporal variable: estimation of the call duration of *Anomaloglossus beebei*, Aromobatidae. The call is pinpointed between the selection borders. The black arrow indicates the beginning of the call (= time at the beginning - in seconds, which is encircled in black in the left column); the blue arrow indicates the end of the call (= time at the end - in seconds, which is encircled in blue in the left column). The difference (delta) between these two times (which is encircled in red in the left column and shown by a red curly bracket on the oscillogram) is the call duration (0.291 s in this case).

Fig. 75. Spectral slice of the first note of the first call illustrated in figure 74 (*Anomaloglossus beebei*, Aromobatidae). The first harmonic is the fundamental harmonic. In this case, the dominant frequency is the second harmonic. The black arrow indicates the peak at which the dominant frequency is measured.
5. Identification guide, and how to use it

The main goal of this identification guide is to allow for a quick and easy identification of the species of amphibians currently known from Kaieteur National Park.

Most of the time, collection and handling of the animal will be necessary for examining discrete structures and hidden colour patterns. Always handle amphibians with wet hands, as their skin may be fragile. Additionally, you should never handle an amphibian if you have insect repellent on your hands, as it would kill it. No “poison frogs” (family Dendrobatidae) are currently recorded from the Park, but some species secrete large amounts of toxins (e.g. large *Leptodactylus*, *Rhaebo* and *Rhinella*) that can irritate your skin and mucous membranes, or even kill other amphibian species if they are in contact with the secretions. Always rinse your hands thoroughly after handling an amphibian.

Genera and species are treated alphabetically within each family. Each species is illustrated by at least a dorsolateral view in life and a ventral view (in life or in preservative). Whenever possible the colour variation is illustrated. Illustration of hand and foot, peculiar morphological characters that may help the identification, and an oscillogram and spectrogram of the call (if known and when relevant) are provided as well. Whenever possible, oscillograms and spectrograms were generated from recordings made in Kaieteur National Park. When adequate recordings were not available we prepared audiospectrograms from recordings made outside the Park. This was the case for the following species: *Allophryne ruthveni*, *Rhinella marina*, *Hypsiboas calcaratus*, *H. boans*, *H. geographicus*, *Osteocephalus leprieurii*, *O. taurinus*, *Phyllomedusa bicolor*, *Trachycephalus coriaceus* (species recorded in French Guiana, calls courtesy of C. Marty and P. Gaucher), *Atelopus hoogmoedi*, *Rhaebo guttatus*, *Trachycephalus resinifictrix*, *Leptodactylus mystaceus*, *L. rhodomystax*, *Pristimantis cf. marmoratus* (species recorded at Mabura Hill Forest Reserve, Guyana, calls courtesy of R. Ernst), *Dendropsophus marmoratus* (species recorded in Ecuador, Napo, Jatun Sacha, call courtesy of K. H. Jungfer), *Phyllomedusa vaillantii* (species recorded in Peru, Panguana, call courtesy of A. Schlüter), and *Leptodactylus lineatus* (species recorded in Peru, Tambopata, call courtesy of A. Schlüter).

You can use the field keys provided on p. 64 (caecilians) and p. 87 (anurans) to identify the genus, and then use the field keys provided under each generic account to identify your specimen up to the species. You also may wish to first consult the colour figures that illustrate the species and check the diagnostic characters given in the accounts. Both methods should allow for fast identification. If you experience problems in identifying a specimen you can contact one of the authors (see the beginning of the manual for contact information), as it is possible that you have found a species not previously reported from the Park or even an undescribed taxon.

In addition to the field key for species, each generic account provides basic information on the genus, some external morphological characters that may be useful for identification, and, when necessary, briefly mentions species of possible occurrence in the Park that were not collected during our surveys. Do
note that morphological characters provided for each genus are not always
discriminant because no morphological synapomorphies have currently been
detected in some genera (e.g. Dendropsophus, Hypsiboas).

The taxonomy of a few specimens collected in the Park remains too unclear and
so these possible new taxa were voluntarily excluded from this guide. The
elucidation of the taxonomy of these specimens will be dealt with later, once
more material becomes available.

Cryptic species are distinct taxa that are not, or hardly distinguishable on a
morphological basis (see for example Hypsiboas cinerascens and Hypsiboas sp.
on p. 168 and 176, respectively). Some widespread species might in fact be
complexes of cryptic taxa (Fouquet et al., 2007) and many of those species
probably remain to be described. This suggests that current estimates of
amphibian species richness are too low, but also that the taxonomic status
and/or the distribution of some species treated in this manual could be re-
evaluated in the future.

Each species account is provided as follows:

- **Scientific name of the species** (Genus and species) followed by authorship
  and date of publication.
  Year and page of the original description + references to original illustrations
  (when relevant) are also given.

- **Pictograms** illustrate the size of the animal and its nychthemeral activity
  pattern (Fig. 76). This may be useful for quick identification and comparison
  without reading the text.

  Diurnal species are active during the day (whatever the meteorological
  conditions). Nocturnal species are primarily active by night, or near dawn or
dusk (or both), but some may be found during the day when cloudy and/or
heavily raining.

**Fig. 76.** Pictograms illustrating the nychthemeral activity patterns. A. Diurnal. B. Nocturnal.
C. Used for nocturnal species that may be found during cloudy days and/or heavy rains.

- **English name**: the most commonly used English name(s). We usually
  propose an English name if none is currently available.

- **Local name**: the name of the species in Patamona dialect, when known.
• **Type locality:** the geographical location where the holotype (= the original preserved specimen designated for naming and describing the species) or the lectotype (= a specimen serving the function of a holotype when no holotype was designated in the original description) was collected.

• **Selected references:** a maximum of three important references that should be consulted by the reader.

• **Field identification:** this section provides the maximum theoretical size (SVL) in males and females (*i.e.*, the maximum size reported in the literature, not the maximum size reported from KNP). If examination of specimens collected in Kaieteur National Park resulted in increases in the known maximum size for a species, this is indicated by an asterisk (*). Eight to nine characters that are easily observable in the field, even for people having little knowledge in amphibian taxonomy, are emphasized. The reader should refer to the previous chapters of this manual for more details about diagnostic characters. We tried to deal with the same characters for each species of a same genus in order to facilitate comparisons. Colour arrows refer to these characters in the identification section and pinpoint them in the corresponding figures.

• **Life history:** this section provides basic information on the biology of the species.

• **Call:** this section provides reference to the first description of the advertisement call (when relevant), and a brief description.

• **Tadpole:** this section provides reference to the first description of the tadpole (when relevant), a brief description as well as its ecomorphological guild (see McDiarmid & Altig, 1999 for details).

• **Abundance and distribution in KNP:** this section provides a subjective estimation of the abundance of the species in the Park, which is expressed as very common (occurs in considerable numbers and easily observed every day), common (commonly seen, easily observed every week), rare (not usually observed more than once every few month), or very rare (seen very occasionally, sometimes known from a single specimen). Note that a species may be rare in some parts of the Park, but locally abundant due to adequate habitat, environmental conditions, etc. (this is especially true for species like *Anomaloglossus beebei* and *Leptodactylus lineatus*). Some species may be locally abundant only during a very short period of time (*e.g.* explosive breeders) and otherwise be seen only very occasionally. Main sampling localities where the species was recorded in KNP are provided as well (refer to Fig. 3 to locate sampling localities on a map).

• **Geographic range:** the general distribution of the species.

• **Taxonomic comments:** when necessary, this section provides some important remarks on the taxonomy of the species.

• **Remark:** when necessary, this section mentions if some photos used to illustrate the species have been taken outside the Park.
**Allophryne Gaige, 1926**

“TUKEIT HILL FROGS”

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**Fig. 77. Allophryne ruthveni**, the only described species in the genus. (Photo by P. J. R. Kok).

- Small size
- Head small, triangular
- Snout short
- Maxillary teeth absent
- Pupil horizontally elliptical (Fig. 42A)
- Skin on dorsum smooth with unevenly distributed spicules (Fig. 44A, E)
- Vocal sac single, subgular (Fig. 56A)
- Fingers basally webbed
- Finger I < II when fingers adpressed
- Toes half-webbed
- Finger discs truncate, wider than digits (Fig. 51C)
The genus is monotypic, but more species probably await description (see below).

Generic and specific characteristics are illustrated together in the species account of the only currently described taxon, *Allophryne ruthveni* (p. 112).

Tukeit Hill frogs are nocturnal, mostly arboreal, and inhabit primary forest where they are mainly found in the close vicinity of streams. They are explosive breeders, having apparently short breeding periods during the rainy season.

The genus *Allophryne* is taxonomically challenging with a long history of controversy, sharing many characteristics with Centrolenidae. There is still some debate regarding the family ranking of the genus. Frost *et al.* (2006) formerly ranked *Allophryne* in the family Centrolenidae, but Guayasamin *et al.* (2008) argued to maintain the use of Allophrynidae, pointing out a sister-group relationship between *Allophryne* and glass frogs (Centrolenidae).

**Sexual dimorphism**

Females of the only described species have more white spots on the black throat and less spicules on the dorsum. Males have a whitish central area visible through the skin on the chest and the belly.

**Eggs**

Deposited on a leaf overhanging water.

**Tadpoles**

Not formally described yet. Exotroph (possibly benthic, or fossorial like those of centrolenids).

**Distribution**

The genus *Allophryne* is currently reported throughout the Guiana Shield and in the states of Pará, Maranhão, and Rondônia in Brazil (Frost, 2008).

*Allophryne ruthveni* is expected in Bolivia according to De la Riva *et al.* (2000).

A putative new species of *Allophryne* has been reported from Peru (Rodrigues & Knell, 2003), which would suggest that the genus is more widespread than previously thought. However no description appeared since the discovery of the putative new species.
**Allophryne ruthveni Gaige, 1926**

ENGLISH NAME: Tukeit Hill frog.

LOCAL NAME (PATAMONA): Unknown.

TYPE LOCALITY: “Tukeit Hill, below Kaiteur [sic] Falls, British Guiana”.

SELECTED REFERENCES: Lynch & Freeman, 1966 (expanded description, in English); Hoogmoed, 1969 (additional data on natural history and colouration, B&W photos, in English); Caldwell & Hoogmoed, 1998 (extended account, colour photo, in English).

**Field identification** - Males reach 24.7 mm SVL, females 31.0 mm.

- Dorsal ground colour and pattern variable, ranging from greyish-brown to creamish bronze with dark irregular spots and/or reticulum; often a conspicuous cream spot on posterior face of upper arm; skin on dorsum smooth, covered with horny spicules (larger and more extensive in males).
- Ventral surface thickly areolate, translucent dark grey, with a whitish central area visible through the skin in males.
- Throat black with white spots (more extensive in females).
- Head very small, triangular, broader than long.
- Iris dark reddish brown.
- Fingers basally webbed, with lateral fringes.
- Tip of fingers and toes truncate.
- Toes moderately webbed, with lateral fringes.

**Life history** - Nocturnal, arboreal. Found in primary forest, often in the vicinity of creeks. Males call from 1-3 m above the ground. Eggs are deposited on a leaf overhanging water, from which tadpoles will fall into the water as they hatch; tadpoles probably feed on detritus.

**Call** - First described by Caldwell & Hoogmoed (1998: 666.2), who provided a spectrogram. It consists of a short, low, raspy trill produced at a rate of ca. 30 calls/min.

**Tadpole** - Not formally described. Lescure & Marty (2001) reported it as brownish grey, mottled with black, dorsoventrally flattened with a gradually tapering tail.

**Abundance and distribution in KNP** - Rare, collected only around main sampling localities # 2 and 5 (see Fig. 3), but the species is probably more widespread in the Park.

**Geographic range** - Has been reported throughout the Guiana Shield and in the states of Pará, Maranhão, and Rondônia in Brazil. Expected in Bolivia according to De la Riva et al. (2000).

**Taxonomic comments** – See generic account (p. 110).
Fig. 78. *Allophryne ruthveni* Gaige, 1926. A. Dorsolateral view. B. Ventral surface of a male in life. C. Palm (preserved male specimen). D. Sole (preserved male specimen). E. Call, oscillogram. F. Call, spectrogram. (Photos by P. J. R. Kok).
Fig. 79. *Anomaloglossus kaiei*, one of the 20 currently described species in the genus. Here a male carrying tadpoles. (Photo by P. J. R. Kok).

- Small to medium size
- Maxillary teeth present
- Presence of a median lingual process (Fig. 80)
- Pupil horizontally elliptical (Fig. 42A)
- Skin on dorsum smooth to slightly granular (Fig. 44 A-C, H)
- Vocal sac single, subgular (Fig. 56A)
- Fingers unwebbed
- Finger I ≤ II when fingers adpressed
- Dorsal surface of finger disc with two scutelike flaps (Fig. 51F)

The genus currently contains 20 species, but many still await description. Rocket frogs are diurnal, mostly terrestrial (some, like *A. kaiei* are forest-dwellers, some, like *A. beebei*, are bromeliad-dwellers, others like *A. degranvillei* are stream-dwellers), and inhabit a wide range of habitats, from savannah to tepui summits.
Sexual dimorphism

Not present in all species. Males of some species have the third finger or all fingers swollen, and/or a darker throat than females.

Eggs

Terrestrial, deposited on the ground, or on leaves of bromeliads (= phytotelmata).

Tadpoles

Exotroph (benthic or arboreal), or endotroph.

Distribution

The genus *Anomaloglossus* is currently reported from the northern and eastern Amazon Basin, the Guiana Shield, and the Pacific slopes of the Andes in Colombia and Ecuador (Grant *et al*., 2006).

Field key to the *Anomaloglossus* species of Kaieteur National Park

1. Finger I distinctly shorter than Finger II; lateral fringes present on Fingers II & III; palm yellow; digits without small sky blue spots; hindlimbs without dark brown bars; dorsal colour usually yellow, and pattern usually absent or inconspicuous ........................................... *A. beebei* (p. 116)

1'. Finger I and II equal in length; lateral fringes present on all fingers; palm dark brown or black; digits with sky blue spots; hindlimbs usually with distinct dark brown bars; dorsal colour brown, and pattern usually conspicuous .................. ........................................... *A. kaiei* (p. 118)
Anura | Aromobatidae | Anomaloglossus Grant, Frost, Caldwell, Gagliardo, Haddad, Kok, Means, Noonan, Schargel & Wheeler, 2006

**Anomaloglossus beebei** (Noble, 1923)
1923: 289, figs 1-4.

**ENGLISH NAME:** Golden rocket frog, Beebe rocket frog.

**LOCAL NAME (PATAMONA):** Kayatik.

**TYPE LOCALITY:** “Near Kaieteur Falls, British Guiana”.

**SELECTED REFERENCES:** Bourne, 2001 (colour pattern, natural history, in English); Bourne et al., 2001 (vocal communication, reproductive behaviour, in English); Kok et al., 2006b (redescription, call description, tadpole description, colour photos, natural history, distribution, in English).

**Field identification** - Males reach 16.8 mm SVL, females 18.7 mm.

+ Dorsal ground colour very variable (at least five different colour patterns), ranging from bright yellow to pale brown, with dorsolateral stripes (sometimes inconspicuous), with or without dark brown markings, juveniles greenish/yellowish white; skin on dorsum slightly granular.

+ Ventral surface granular, immaculate yellow to yellowish orange in both sexes (fades to white in preservative).

+ Throat immaculate in both sexes.

+ When adpressed, Finger I shorter than II; Finger III not swollen in males.

+ Subarticular tubercles small, single.

+ Fingers unwebbed, lateral fringes present on Fingers II and III.

+ Toes moderately webbed.

+ Discs on digits larger than adjacent phalange, with distinct dorsal scutes.

**Life history** - Diurnal. Found exclusively in large terrestrial bromeliads (*Brocchinia micrantha*). Males call from bromeliads. Eggs are deposited on the leaves of the bromeliad and tadpoles live in the water-filled phytotelm where they feed on detritus, insect larvae, other tadpoles, and unfertilized eggs deposited by the female.

**Call** - First described by Kok et al. (2006b: 60), who provided a spectrogram. It consists of 3-4 notes (high-pitch chirps) repeated at a rate of 44-51 calls/min.

**Tadpole** - First described by Kok et al. (2006b: 59). Exotroph, arboreal; yellow with dark mottling; LTRF = 2(2)/3.

**Abundance and distribution in KNP** - Very common locally in suitable habitat. Collected only around main sampling localities # 1 and 11 (see Fig. 3), but possibly more widespread in the Park in suitable habitats.

**Geographic range** - Reported only from Guyana, in KNP and on Mt Ayanganna.

**Taxonomic comments** - Identification of specimens from Mt Ayanganna needs formal confirmation, notably by call and tadpole comparisons.
Anura | Aromobatidae | *Anomaloglossus* Grant, Frost, Caldwell, Gagliardo, Haddad, Kok, Means, Noonan, Schargel & Wheeler, 2006

**Anomaloglossus kaiei** (Kok, Sambhu, Roopsind, Lenglet & Bourne, 2006)
2006a: 38, figs 1-8.

**ENGLISH NAME:** None; we propose “Kaie rocket frog”.

**LOCAL NAME (PATAMONA):** Kokonbasli.

**TYPE LOCALITY:** “Kaieteur National Park, along TuKeit trail, Guyana, 5°11’06”N, 59°28’51”W, elevation ca. 400 m”.

**SELECTED REFERENCE:** Kok *et al.*, 2006a (original description, call description, tadpole description, colour photos, natural history, distribution, in English).

**Field identification** - Males reach 18.9 mm SVL, females 19.8 mm.

* Dorsal ground colour variable, ranging from medium to reddish brown, with thin to inconspicuous dorsolateral line from eye to vent, and a wide black band from tip of snout laterally around body and above vent; skin on dorsum smooth to shagreened, posteriorly granular.

* Ventral surface smooth, immaculate orangish yellow in females, cream in males.

* Throat light greyish pink with dark spotting in males, immaculate yellow in females.

* When adpressed, Fingers I and II equal in length; all fingers slightly swollen in males.

* Subarticular tubercles small, single.

* Rudimentary webbing between Fingers II and III, lateral fringes present on all fingers.

* Toes moderately webbed.

* Discs on digits larger than adjacent phalange, with distinct dorsal scutes.

**Life history** - Diurnal, terrestrial. Mostly found in primary forest, but also occurs in disturbed areas. Males call from over or under dead leaves on the ground. Eggs are probably laid in the leaf litter; tadpoles are usually carried by the male (rarely the female) and are deposited in very small pools where they feed on detritus, and sometimes on unfertilized eggs that are deposited by the female.

**Call** - First described by Kok *et al.* (2006a: 51), who provided a spectrogram. It consists of 1-2 notes (cricket-like chirps) repeated at a rate of 22-33 calls/min.

**Tadpole** - First described by Kok *et al.* (2006a: 47). Exotroph, benthic; dark brown with minute light dots; LTRF = 2(2)/3.

**Abundance and distribution in KNP** - Very common locally. Collected around all main sampling localities (see Fig. 3).

**Geographic range** - Reported only from Guyana, in KNP, but the species is widespread in the Pakaraima Mountains of Guyana (Kok, unpublished data).
Atelopus Duméril & Bibron, 1841

“HARLEQUIN TOADS”

Fig. 83. Atelopus hoogmoedi, one of the ca. 83 currently described species in the genus. (Photo by P. J. R. Kok).

⇒ Small to medium size
⇒ Maxillary teeth absent
⇒ Usually brightly coloured with contrasting pattern
⇒ Pupil horizontally elliptical (Fig. 42A)
⇒ Skin on dorsum usually smooth (Fig. 44A), but shagreened to warty in some species (Fig. 44B-F)
⇒ Vocal sac single, subgular (Fig. 56A)
⇒ Finger I < II; first finger and toe very short; finger webbing at least between Fingers I-II, toes webbed
⇒ Finger discs unexpanded (Fig. 51A)
⇒ Tympanum absent (Fig. 43C)
The genus currently contains 83 species, although the taxonomic status of some of its members needs verification. Harlequin toads are diurnal and mostly terrestrial. Many species are stream-dwellers (meaning that they inhabit stream banks), but individuals may be found far from water. Several different toxins have been reported in a number of *Atelopus* species (*e.g.* tetradotoxin).

Many populations of *Atelopus* recently drastically declined, and the genus appears to be very sensitive to the chytrid fungus *Batrachochytrium dendrobatidis*, which is one of the putative causes of the global amphibian decline.

**Sexual dimorphism**

Females are larger than males. Forearm in males is thicker proximally than distally, and Finger I has nuptial excrescences.

**Eggs**

Aquatic, deposited in gelatinous strings in streams or small adjacent pools, sometimes attached to submerged rocks.

**Tadpoles**

Exotroph (gastromyzophorous).

**Distribution**

The genus *Atelopus* is widespread and reported in Central and South America, from Costa Rica to Bolivia (Frost, 2008).

Only *Atelopus hoogmoedi* (p. 122) is currently recorded from Kaieteur National Park, where several healthy populations occur.
Anura | Bufonidae | Atelopus Duméril & Bibron, 1841

**Atelopus hoogmoedi** Lescure, 1974

**ENGLISH NAME:** None; we propose “Hoogmoed harlequin toad”.

**LOCAL NAME (PATAMONA):** Patakàlàlàk.

**TYPE LOCALITY:** “monts Atachi-Bacca (Guyane française)”

**SELECTED REFERENCES:** Lescure, 1974 (original description - under *A. pulcher hoogmoedi* – B&W photo, in French); Lescure & Marty, 2001 (brief description - under *A. spumarius hoogmoedi* - distribution, colour photo, in French); Lötters *et al.*, 2005 (brief description, colour photo, in French, English and Dutch).

**Field identification** - Males reach 31.8 mm SVL, females 42.8* mm.
- Dorsal ground colour dark brown to black, with variable pattern consisting of broad irregular yellow dorsolateral bands and markings, in which black spots are usually present; skin on dorsum smooth.
- Ventral surface smooth, yellow, orange or pinkish, usually with irregular black markings.
- Throat yellow, orange or pinkish, usually with irregular black markings.
- Tympanum absent.
- Arms and legs slender.
- First finger reduced, when adpressed Finger I much shorter than II, fingers unwebbed.
- Toes I-II much reduced included in a pad-like web, toes moderately webbed.
- Disc on fingers and toes unexpanded.

**Life history** - Diurnal, terrestrial. Found on the leaf litter in primary forest, often near streams. Individuals may be found sleeping on low vegetation at night. Males call from the ground, close to small streams. Eggs are deposited in gelatinous strings in streams or in small adjacent pools.

**Call** - First described by Lescure (1981a: 900), who provided a spectrogram. It consists of a series of pulses increasing in pulse rate from the beginning to the end of the call and produced in about one second.

**Tadpole** - Unknown. Very likely exotroph, gastromyzophorous, like in other species of the genus.

**Abundance and distribution in KNP** - Rare, but may be locally common. Collected only around main sampling localities # 4 and 11 (see Fig. 3).

**Geographic range** - Reported only from the Guianas (French Guiana, Suriname and Guyana) and adjacent northern Brazil (states of Roraima, Pará and Amapá).

**Taxonomic comments** - Often reported as *Atelopus spumarius hoogmoedi* in the literature. Probably a complex of species that deserves a thorough revision.
Rhaebo Cope, 1862

“COPE TOADS”

Fig. 85. Rhaebo guttatus, one of the eight currently described species in the genus. (Photo by P. J. R. Kok).

- Medium to very large size
- Maxillary teeth absent
- Pupil horizontally elliptical (Fig. 42A)
- Skin on dorsum smooth, tuberculate or spiculate (Fig. 44A, D-E)
- Vocal sac single, subgular (Fig. 56A)
- Fingers unwebbed to basally webbed
- Finger I \( \leq \) II when fingers adpressed
- Finger discs unexpanded (Fig. 51A)
- Tympanum present, distinct or indistinct (Fig. 43A-B)
- Parotoid glands present, ovoid to elongate (Fig. 47A)
- Cranial crests absent or weakly developed
The genus currently contains eight species and includes the species formerly assigned to the *Bufo guttatus* species group.

Cope toads are diurnal or nocturnal, strictly terrestrial. They mainly inhabit tropical rainforest where they are often found along rivers and streams; some species are also found in open areas.

**Sexual dimorphism**

Males are usually smaller than females, in some species throat colour may vary between sexes (*e.g.* black in male vs. dark brown with white spots in female).

**Eggs**

Aquatic, deposited in long strings in temporary or permanent pools, sometimes close to streams, and possibly in slow-moving water.

**Tadpoles**

Unknown for several species. Exotroph (benthic); Lescure & Marty (2001) suggested a possible rheophilous tadpole in *Rhaebo guttatus*.

**Distribution**

The genus *Rhaebo* is widespread and currently reported from eastern Honduras to Ecuador west of the Andes, and from the Guiana Shield to the upper Amazon Basin (Frost, 2008).

**Field key to the *Rhaebo* species of Kaieteur National Park**

1. Skin on dorsum tuberculate (Fig. 44D); parotoid glands large, well visible (Fig. 47A); snout truncate in profile (Fig. 40B), not distinctly projecting beyond mouth; upper eyelid not laterally projecting beyond the eye; tympanum well distinct (Fig. 43A). .................. *R. guttatus* (p. 126)

1’. Skin on dorsum spiculate (Fig. 44E); parotoid glands small to moderately large; snout acute in profile (Fig. 40B), distinctly projecting beyond the mouth; upper eyelid laterally projecting beyond the eye; tympanum barely distinct (Fig. 43B). .................. *R. nasicus* (p. 128)
**Rhaebo guttatus (Schneider, 1799)**

1799: 218.

**ENGLISH NAME:** Spotted toad.

**LOCAL NAME (PATAMONA):** Walà.

**TYPE LOCALITY:** “India Orientali” [restricted to Suriname by Rivero, 1961]

**SELECTED REFERENCES:** Duellman, 1997 (brief description, colour photo, in English); Lescure & Marty, 2001 (brief description, distribution, colour photo, in French); Duellman, 2005 (brief description, tadpole description, call description and colour photo, in English).

**Field identification** - Males reach 137.8 mm SVL, females 177.0 mm.

- Dorsal ground colour orange tan to greyish brown, with no distinct pattern, but some large tubercles may be orange, reddish brown or dark brown; skin on dorsum tuberculate, sometimes spiculate, but always smooth on head.

- Ventral surface smooth to finely granular, orangish brown, pale grey or greyish brown with cream spots.

- Flanks dark reddish brown to dark brown, highly contrasting with the dorsal colour.

- Lower lip with creamy spots.

- Cranial crests absent, but presence of a canthal and a short preorbital ridge.

- Parotoid glands large, ovoid.

- When adpressed Finger I much longer than II, fingers unwebbed.

- Disc on fingers and toes unexpanded.

**Life history** - Nocturnal, terrestrial. Found in primary forest, near streams and rivers. Individuals may be found in very rocky areas (i.e. along the Potaro River at the base of Kaieteur Falls) and in caves. Males call from the ground, usually at the edge of streams or rivers. Eggs are deposited in gelatinous strings in streams or in small adjacent pools.

**Call** - The first comprehensive description seems to be that of Duellman (2005: 183), who provided a spectrogram. It consists of a series of loud notes (a plaintive mewing diminishing in frequency and loudness) repeated at a rate of about 75 notes/min.

**Tadpole** - The first detailed description is apparently that of Duellman (2005: 183), who provided a description of a stage-37 tadpole resulting from captive breeding. Exotroph, benthic, possibly rheophilous according to Lescure & Marty (2001); dark brown; LTRF = 2(1)/3.

**Abundance and distribution in KNP** - Common. Collected around main sampling localities # 1, 2, 6, 7, 10 and 12 (see Fig. 3). Probably widespread in the Park.

**Geographic range** - Widespread in the Amazon Basin, found from eastern Ecuador and Peru to the Guiana Shield and from Venezuela and Colombia to northern Bolivia.
**Rhaebo nasicus** (Werner, 1903)
1903: 252.

**ENGLISH NAME:** Werner’s toad.

**LOCAL NAME (PATAMONA):** Unknown.

**TYPE LOCALITY:** Unknown, restricted to “South America, probably along the Atlantic drainage” by Smith & Laurent (1950).

**SELECTED REFERENCE:** Hoogmoed, 1977 (description, habitat, distribution, B&W photos, in English).

**Field identification** - Males reach 47.2* mm SVL, females 68.5* mm.

- Dorsal ground colour very variable: medium brown, or greyish brown to reddish brown, sometimes with small greyish blue to sky blue spots (often present on flanks), and usually with a distinct pattern consisting of a black inverted triangle between the eyes connected further down on the back to a black “hour-glass” marking; in some specimens (especially juveniles) the dorsum only has one or more small dark spot; skin on dorsum spiculate.

- Ventral surface granular, dirty white with more or less extensive brown mottling.

- Upper eyelid laterally projecting beyond the eye.

- Snout acute in profile, distinctly projecting beyond the mouth.

- Cranial crests present, but low and not very distinct.

- Parotoid glands small to moderately large, elongate.

- When adpressed Finger I much longer than II, fingers unwebbed.

- Disc on fingers and toes unexpanded.

**Life history** - Diurnal, terrestrial. Found in primary forest only. Individuals are usually observed on the forest floor among leaf litter, sometimes far from water. Nothing is known about the reproductive behaviour of the species, but males probably call from the ground at the edge of small pools or slow-moving streams. Eggs are probably deposited in gelatinous strings in small water bodies or in slow-moving streams.

**Call** - Unknown.

**Tadpole** - Unknown. High probably exotroph, benthic, like in other species of the genus.

**Abundance and distribution in KNP** - Rare. Observed around main sampling localities # 6, 10 and 11 (see Fig. 3). Probably widespread in the Park.

**Geographic range** - Restricted to eastern Venezuela and Guyana.
Rhinella Fitzinger, 1826

“SOUTH AMERICAN TOADS”

Fig. 88. Amplectant pair of Rhinella marina photographed in French Guiana. (Photo by P. J. R. Kok).

- Medium to very large size
- Maxillary teeth absent
- Pupil horizontally elliptical (Fig. 42A)
- Skin on dorsum rarely smooth, usually tuberculate to warty (Fig. 44A, D-F)
- Vocal sac single, subgular (Fig. 56A)
- Finger I ≤ II when fingers adpressed
- Finger discs unexpanded (Fig. 51A)
- Tympanum present, distinct or indistinct (Fig. 43A-B)
- Parotoid glands present, round, ovoid, trianguloid, or elongate (Fig. 47A)
- Cranial crests absent or present (from weakly developed to hypertrophied)
This large genus currently contains 77 species and includes all the former South American *Bufo* species, excluding those of the *Bufo guttatus* species group (now *Rhaebo*), the *B. valliceps* species group (now *Incilius*), and the *B. variegatus* species group (now *Nannophryne*).

South American toads are diurnal or nocturnal; some species are terrestrial, while others are arboreal. They inhabit a wide range of habitats, from savannah to cloud forest.

**Sexual dimorphism**

Males are usually smaller than females; males of many species have keratinous nuptial excrescences on first finger(s). In some species females develop hypertrophied supratympanic crests (*i.e.* *Rhinella margaritifera*).

**Eggs**

Aquatic, deposited in long strings in temporary or permanent pools, also in slow-moving and fast-moving water. Clutch deposition site is unknown in several species.

**Tadpoles**

Unknown in several species. Exotroph (benthic or gastromyzophorous).

**Distribution**

The genus *Rhinella* is widespread and currently reported from southern Texas (USA) to southern South America, including Trinidad and Tobago (Frost, 2008). *Rhinella marina* has been introduced widely and is now considered as a major threat for local fauna in many parts of the world (*e.g.* Australia).

Only *Rhinella marina* (p. 132) is currently reported from Kaieteur National Park.
**Rhinella marina** (Linnaeus, 1758)

1758: 211.

**ENGLISH NAME**: Giant toad.

**LOCAL NAME (PATAMONA)**: Wāla or Pālātuku.

**TYPE LOCALITY**: “America”.

**SELECTED REFERENCES**: Duellman, 1978 (brief description, tadpole description, B&W photo, in English); Easteal, 1986 (definition, distribution, pertinent literature, call spectrogram); Duellman, 2005 (brief description, tadpole description, call description and colour photo, in English).

**Field identification** - Males reach at least 140.0 mm SVL, females may exceptionally reach about 300.0 mm; most specimens range in size from 150 to 200 mm.

- Dorsal ground colour brown to greyish or reddish brown, with or without dark brown or black mottling and/or cream spots; skin on dorsum warty.
- Ventral surface granular, creamy white, with or without a distinct pattern consisting in greyish brown, dark brown or black spots and/or mottling.
- Flanks similar to dorsum, not contrasting with the dorsal colour.
- Lower lip without creamy spots.
- Cranial crests present and distinct.
- Parotoid glands very large, trianguloid.
- When adressed Finger I longer than II, fingers unwebbed.
- Disc on fingers and toes unexpanded.

**Life history** - Nocturnal (although juveniles may sometimes be found by day), terrestrial. Occurs in a wide range of habitats, from savannah to primary forest, and is highly anthropophilic. Individuals prefer open areas and are usually found in disturbed habitats, in large clearings in secondary forest, more rarely in primary forest (where the largest specimens seem to occur). Males call from the ground, usually at the edge of slow-moving streams, rivers, or in swampy areas. Eggs are deposited in gelatinous strings in slow-moving water, rocky pools, ponds, lakes, swamps, etc.; always in open areas that receive high amount of sunlight during the day.

**Call** - First described by Blair (1956: 96), who provided a spectrogram. Easteal (1986: 2) provided a spectrogram, but no description; see also Duellman (2005: 185), who provided a short description and a spectrogram and oscillogram. It consists of a long low-pitched rattling trill repeated at a rate of about 4 calls/min.

**Tadpole** - The first description is apparently that of Ruthven (1919: 7), but see also that of Breder (1946: 395) and Savage (1960: 233). Exotroph, benthic, black; LTRF = 2(2)/3.

**Abundance and distribution in KNP** - Very common locally. Observed around all main sampling localities (see Fig. 3).

**Geographic range** - Widespread from southern Texas to central Brazil. Introduced worldwide.
Anura | Centrolenidae | Centrolene Jiménez de la Espada, 1872

Centrolene Jiménez de la Espada, 1872

“GIANT GLASS FROGS”

![Centrolene gorzulae](image)

Fig. 90. *Centrolene gorzulae*, the only *Centrolene* reported from Kaieteur National Park. (Photo by P. J. R. Kok).

- Small to medium size
- Maxillary teeth present
- Pupil horizontally elliptical (Fig. 42A)
- Humeral spine in adult males (Fig. 57B)
- Skin on dorsum smooth or shagreened to finely granular (Fig. 44A-C)
- Ventral skin transparent, internal organs visible (Fig. 59)
- Vocal sac single, subgular (Fig. 56A)
- Finger I < = > II when fingers adpressed
- Finger discs expanded (Fig. 51B-C)
- Tympanum present, distinct or indistinct (Fig. 43A-B)

The genus *Centrolene* currently contains 42 species.
Frogs of the genus *Centrolene* are nocturnal and mostly arboreal. They inhabit tropical rainforest and are usually found along streams or rivers.

*Centrolene* was found to be paraphyletic with regards to *Cochranella* by Frost et al. (2006) [see also taxonomic comments by Cisneros-Heredia & McDiarmid (2007) and Guayasamin et al. (2008)].

**Sexual dimorphism**

Males have a humeral spine and nuptial excrescences on fingers or along flanks. In most species males are smaller than females, except in *Centrolene geckoidum*.

**Eggs**

Egg masses are deposited outside of water, usually on leaves overhanging lotic water, but some species occasionally place them over lentic water. *Centrolene gorzulae* was found to deposit egg masses in moss on branches overhanging the water (Fig. 91), or between two leaves (P. Kok, pers. obs.), and *C. buckleyi* might deposit eggs in bromeliads (Lynch & Duellman, 1973).

![Fig. 91. Egg mass of *Centrolene gorzulae* (Photo by P. J. R. Kok)](image)

**Tadpoles**

Exotroph (fossorial).

**Distribution**

Species belonging to the genus *Centrolene* are found from Honduras to Panama, along the Andes from Venezuela to Peru, on the Cordillera de la Costa of Venezuela and in the western part of the Guiana Shield (Cisneros-Heredia & McDiarmid, 2007).

Only *Centrolene gorzulae* (p. 136) is currently reported from Kaieteur National Park.
**Centrolene gorzulae (Ayarzagüena, 1992)**
1992: 19, figs 3e, 4.

**English Names:** Bolivar giant glassfrog.

**Local Name (Patamona):** Unknown.

**Type Locality:** “Cerro Auyantepuy-Cento, Edo. Bolívar, Venezuela (5°56′N, 62°34′W), 1.850 msnm”.

**Selected References:** Noonan & Harvey, 2000 (description of the synonym *C. papillahallicum*, B&W photo and drawings, in English); Señaris & Ayarzagüena, 2005 (description, natural history, call description, tadpole description, B&W drawings, distribution, in Spanish); Kok & Castroviejo-Fisher, 2008 (description, synonymy, natural history, colour photos, distribution, in English).

**Field Identification** - Males reach 22.5 mm SVL, females 22.0 mm.

- Dorsal ground colour dark green with scattered minute paler flecks, upper lip yellowish white; iris metallic copper with black reticulations; skin on dorsum finely shagreened.
- Ventral surface strongly granular, translucent green, internal organs visible through the skin: parietal peritoneum mostly transparent, pericardial peritoneum white, hepatic and visceral peritonea white.
- Bones green, visible through the skin.
- Humeral spine in adult males.
- Prepollical spine projecting.
- When addpressed, Fingers I and II equal in length.
- Enamelled fringes present on postaxial edges of Finger IV and Toe V.
- Enlarged round tubercles below vent.

**Life History** - Nocturnal, arboreal. Exclusively found in primary forest. Males call from the upper surface of leaves above or along small streams, usually 1.0-1.5 m above the ground, but the species can be found as high as 4 m above the forest floor. Gelatinous masses of eggs are deposited on mosses overhanging water, from which tadpoles will fall into the water as they hatch; tadpoles probably feed on detritus.

**Call** - First described by Señaris & Ayarzagüena (2005: 83), who provided a spectrogram. It consists of a single short pulsed note repeated at a rate of about 10 notes/min.

**Tadpole** - Still undescribed, description by Kok in progress. Exotroph, fossorial; greenish brown; LTRF = 0/0 (Kok, unpublished data).

**Abundance and Distribution in KNP** - Locally common. Collected only around main sampling localities # 4 and 11 (see Fig. 3), but the species is certainly more widespread in the Park.

**Geographic Range** - Known from Auyantepui and neighbouring localities in Bolivar State, Venezuela, and from the Pakaraima Mountains in Guyana.
Cochranella Taylor, 1951

“COCHRAN FROGS”

Fig. 93. Portrait of Cochranella helenae, the only Cochranella species currently reported from Kaieteur National Park. (Photo by P. J. R. Kok).

- Small size
- Maxillary teeth present
- Pupil horizontally elliptical (Fig. 42A)
- Humeral spine absent in adult males (Fig. 57A)
- Skin on dorsum smooth or shagreened to granular (Fig. 44A-C)
- Ventral skin transparent, internal organs visible (Fig. 59)
- Vocal sac single, subgular (Fig. 56A)
- Finger I \(\leq\) II when fingers adpressed
- Finger discs expanded (Fig. 51B-C)
- Tympanum present, distinct or indistinct (Fig. 43A-B)

The genus Cochranella currently contains 42 species.
Frogs of the genus *Cochranella* are nocturnal and mostly arboreal. They inhabit tropical rainforest and are usually found along streams or rivers.

The genus is diagnosed only on the basis of a plesiomorphic character (the absence of a humeral spine in males) and the taxonomy of *Cochranella* needs revision (see comments in Cisneros-Heredia & McDiarmid, 2007, and Guayasamin *et al.*, 2008).

**Sexual dimorphism**

Males have nuptial excrescences on fingers. In most species males are smaller than females.

**Eggs**

Egg masses are deposited outside of water, usually on leaves overhanging lotic water, but some species occasionally place them over lentic water. Some taxa (*e.g.* *Cochranella euhystrix* from Peru, *C. nola* from Bolivia) attach egg masses to rocks in the spray zone of waterfalls or in streams (Cadle & McDiarmid, 1990; Lötters & Köhler, 2000).

**Tadpoles**

Exotroph (fossorial).

**Distribution**

Species belonging to the genus *Cochranella* are found from Nicaragua to Amazonian Brazil, in the Guiana Shield, Ecuador, Peru and Bolivia (Frost, 2008). Only *Cochranella helenae* (p. 140) is currently reported from Kaieteur National Park.
Cochranella helenae (Ayarzagüena, 1992)

ENGLISH NAME: Venezuela Cochran frog.
LOCAL NAME (PATAMONA): Unknown.
TYPE LOCALITY: “Quebrada Jaspe, San Ignacio de Yuruani, Edo Bolívar, Venezuela”.

Field identification - Males reach 20.4 mm SVL, female not known.
- Dorsal ground colour pale lime green to greenish yellow with scattered dark brown flecks, iris yellow speckled with minute dark brown punctuations; skin on dorsum shagreened.
- Ventral surface granular, transparent, internal organs visible through the skin: parietal peritoneum white, pericardial peritoneum white, hepatic and visceral peritonea white.
- Bones pale green, visible through the skin.
- Humeral spine absent in adult males.
- Prepollical spine not projecting.
- When adpressed, Fingers I and II almost equal in length.
- Fringes on postaxial edges of Finger IV and Toe V (first phalange only) not enamelled.
- Paired enlarged round tubercles below vent.

Life history - Nocturnal, arboreal. Exclusively found in primary forest. Males call from the upper surface of leaves above or along streams (typically large streams or rivers, but sometimes small streams), usually 3.0-4.0 m above the ground, but the species can be found as high as 10 m above the forest floor. Gelatinous masses of eggs are deposited on leaves overhanging water, from which tadpoles will fall into the water as they hatch; tadpoles probably feed on detritus.

Call - First described by Señaris & Ayarzagüena (2005: 119), who provided a spectrogram. It consists of two or three short-pulsed notes repeated at a rate of about 4-6 calls/min.

Tadpole - First described by Señaris & Ayarzagüena (2005: 120). Exotroph, fossorial; light green; LTRF = 1/3.

Abundance and distribution in KNP - Rare. Observed and heard calling only around main sampling localities # 2, 5 and 12 (see Fig. 3), but the species is probably more widespread in the park.

Geographic range - Known from the type locality and Salto Karuay, Bolívar State, Venezuela, and from KNP in Guyana.
Anura | Centrolenidae | Hyalinobatrachium Ruiz-Carranza & Lynch, 1991

Hyalinobatrachium Ruiz-Carranza & Lynch, 1991

“GLASS FROGS”

Fig. 95. Hyalinobatrachium taylori, one of the ca. 31 described species in the genus. (Photo by P. J. R. Kok).

⇒ Small size
⇒ Maxillary teeth present
⇒ Pupil horizontally elliptical (Fig. 42A)
⇒ Humeral spine absent in adult males (Fig. 57A)
⇒ Skin on dorsum smooth or shagreened to granular (Fig. 44A-C)
⇒ Ventral skin transparent, internal organs visible (Fig. 59)
⇒ Vocal sac single, subgular (Fig. 56A)
⇒ Finger I < = > II when fingers adpressed
⇒ Finger discs expanded (Fig. 51B-C)
⇒ Tympanum present, distinct or indistinct (Fig. 43A-B)

The genus *Hyalinobatrachium* currently contains 31 species, although the taxonomic status of several of its members needs clarification.
*Hyalinobatrachium* species are nocturnal and mostly arboreal. They inhabit tropical rainforest and are usually found along streams or rivers.

The genus is diagnosed on the basis of a character shared by *Centrolene* and *Cochranella* [a bulbous liver (i.e. not tri- or tetralobate) with white hepatic peritoneum] and requires a taxonomic revision (see comments in Cisneros-Heredia & McDiarmid, 2007, and Guayasamin *et al.*, 2008).

**Sexual dimorphism**

Males have nuptial excrescences on fingers. In most species males are smaller than females.

**Eggs**

Egg masses are deposited outside of water, on the upper side or on the underside of leaves (Fig. 96), overhanging lotic water, but some species occasionally place them over lentic water.

![Fig. 96. Egg mass of *Hyalinobatrachium crurifasciatum*. (Photo by P. J. R. Kok).](image)

**Tadpoles**

Exotroph (fossorial).

**Distribution**

Species belonging to the genus *Hyalinobatrachium* are found from Nicaragua to Amazonian Brazil, in Tobago, in the Guiana Shield, Ecuador, Peru and Bolivia (Frost, 2008).

**Field key to the *Hyalinobatrachium* species of Kaieteur National Park**

1. Snout truncate in profile (Fig. 40B); dorsum light green with pale yellowish spots; iris yellowish with small brown flecks and usually a reddish ring around pupil; bones translucent green (visible through skin) ................................................................. *H. crurifasciatum* (p. 144)

1'. Snout slightly sloping in profile (Fig. 40B); dorsum dark green with pale green spots, usually bearing a white fleck in their centre; iris metallic lavender with dark brown reticulations; bones white (visible through skin) ................................................................. *H. taylori* (p. 146)

**Hyalinobatrachium crurifasciatum** Myers & Donnelly, 1997

1997: 9, figs 7-10.

**ENGLISH NAME:** None; we propose “Banded limb glassfrog”.

**LOCAL NAME (PATAMONA):** Pakak.

**TYPE LOCALITY:** “north base of Pico Tamacuari, 1160-1200 m elevation, Sierra Tapirapeco, Amazonas, Venezuela (1°13'N, 64°42'W).”

**SELECTED REFERENCES:** Myers & Donnelly, 1997 (original description, call description, tadpole description, in English); Noonan & Bonett, 2003 (description and tadpole description as *H. ignioculus*, in English); Sefarish & Ayarzagüena, 2005 (description, osteology, natural history, call description, tadpole description, distribution, in Spanish).

**Field identification** - Males reach 24.0 mm SVL, females 22.8 mm.

- Dorsal ground colour light green with scattered dark green to dark brown flecks and pale yellowish spots; iris variable, yellowish with small brown flecks and usually a reddish ring around pupil (complete or incomplete); skin on dorsum shagreened to slightly granular.

- Ventral surface strongly granular, transparent, internal organs visible through the skin: parietal peritoneum transparent, pericardial peritoneum partly white, hepatic and visceral peritoneum white.

- Bones white, visible through the skin.

- Humeral spine absent in adult males.

- Prepollical spine not projecting.

- When adpressed, Finger I longer than II.

- Enameled fringes present on postaxial edges of Finger IV and Toe V, and on metacarpal, ulnar, metatarsal and tarsal folds.

- No distinctly enlarged round tubercles below vent.

**Life history** - Nocturnal, arboreal. Exclusively found in primary forest. Males call from the lower surface of leaves above or along streams, usually 2.0-4.0 m above the ground (up to 15 m). Gelatinous masses of eggs are deposited on the lower surface of leaves overhanging water, from which tadpoles will fall into the water as they hatch; tadpoles probably feed on detritus.

**Call** - First described by Myers & Donnelly (1997: 13), who provided a spectrogram. It consists of a single pulsed note repeated at a rate of about 20 notes/min.

**Tadpole** - First described by Myers & Donnelly (1997: 13); see also Noonan & Bonett (2003: 95, as *H. ignioculus*). Exotroph, fossorial; tan peppered with melanophores; LTRF = 2(2)/2(1).

**Abundance and distribution in KNP** - Rare. Heard calling only around main sampling locality # 5 (see Fig. 3), but the species is certainly more widespread in the park.

**Geographic range** - Known from Amazonas and Bolívar states in Venezuela, Guyana, Suriname and French Guiana.

**Taxonomic comments** - The taxonomic status of this species is under review by S. Castroviejo-Fisher and colleagues.
Anura | Centrolenidae | Hyalinobatrachium Ruiz-Carranza & Lynch, 1991

Hyalinobatrachium taylori (Goin, 1968)
1968: 115, fig. 1.

ENGLISH NAME: Taylor’s glassfrog.
LOCAL NAME (PATAMONA): Unknown.
TYPE LOCALITY: “at an elevation of 750 ft. along the New River, Guyana”.
SELECTED REFERENCES: Goin, 1968 (original description, in English); Señaris & Ayarzagüena, 2005 (description, osteology, natural history, call description, tadpole description, distribution, colour photo, in Spanish); Kok & Castroviejo-Fisher, 2008 (description, synonymy, natural history, colour photos, distribution, in English).

Field identification - Males reach 20.5 mm SVL, females 21.5 mm.
- Dorsal ground colour dark green with pale green spots, usually bearing a white fleck in their centre, bronze flecks/lines sometimes present on dorsal surfaces; iris metallic lavender with dark brown reticulations; skin on dorsum smooth to finely shagreened.
- Ventral surface granular, transparent, internal organs visible through the skin: parietal peritoneum transparent, pericardial peritoneum partly white, hepatic and visceral peritonea white.
- Bones translucent green, visible through the skin.
- Humeral spine absent in adult males.
- Prepollical spine not projecting.
- When adpressed, Finger I longer than II.
- Enameled fringes present on postaxial edges of Finger IV and Toe V, and on metacarpal, ulnar, metatarsal and tarsal folds.
- No distinctily enlarged round tubercles below vent.

Life history - Nocturnal, arboreal. Exclusively found in primary forest. Males call from the upper surface of leaves above or along large streams and rivers, usually 1.0-10.0 m above the ground. Gelatinous masses of eggs are deposited on the lower surface of leaves overhanging water, from which tadpoles will fall into the water as they hatch; tadpoles probably feed on detritus.

Call - First described by Señaris & Ayarzagüena (2005: 228), who provided a spectrogram. Typically, the call consists of five to eight short notes given in very quick succession and repeated at a rate of about 1-3 calls/min.


Abundance and distribution in KNP - Locally common. Heard calling around main sampling localities # 5, 12 and 13 (see Fig. 3), but the species is certainly more widespread in the park.

Geographic range - Known from French Guiana, through Suriname and Guyana, to Bolívar and Amazonas states in Venezuela.

Taxonomic comments - Hyalinobatrachium taylori has been confused with H. crurifasciatum by several authors.
Anura | Eleutherodactylidae | Adelophryne Hoogmoed & Lescure, 1984

Adelophryne Hoogmoed & Lescure, 1984

“SHIELD FROGS”

Fig. 99. The recently described Adelophryne patamona, a species that does not occur in Kaieteur National Park; here from Mt. Maringma. (Photo by P. J. R. Kok).

- Very small to small size
- Maxillary teeth present
- Pupil horizontally elliptical (Fig. 42A)
- Skin on dorsum smooth or shagreened to granular (Fig. 44A-C)
- Digits flattened with subdigital pads rather than subarticular tubercles
- Finger IV reduced in size with single subdigital pad
- Vocal sac single, subgular (Fig. 56A)
- Finger I < II when fingers adpressed
- Discs with pointed tips (Fig. 51D) and lateral fringes (Fig. 46E)
- Tympanum present, distinct (Fig. 43A)

The genus Adelophryne currently contains six species.
Frogs of the genus *Adelophryne* are strictly terrestrial, mainly nocturnal, but some species are also active by day (especially during heavy rains). They are cryptic inhabitants of the leaf litter in tropical rainforest and are not dependent on water bodies for reproduction (see below).

**Sexual dimorphism**

There is no evident sexual dimorphism or dichromatism. Males have a large subgular vocal sac and are usually slightly larger than females.

**Eggs**

Very little is known about the reproductive biology of *Adelophryne* species. Our observations in Kaieteur National Park indicate that in *A. gutturosa*, one large egg is laid among plant roots or in the leaf litter. The large vitellin reserve strongly suggests direct development in this species (see MacCulloch *et al.*, 2008), and probably in other *Adelophryne* as well.

![Terrestrial egg that was laid among leaf litter by a female *Adelophryne gutturosa*. (Photo by P. J. R. Kok).](image)

**Tadpoles**

Endotroph (direct developer).

**Distribution**

*Adelophryne* species are found in northern South America, east of the Andes (Frost, 2008).

Only *Adelophryne gutturosa* (p. 150) is currently reported from Kaieteur National Park.
**Adelophryne gutturosa Hoogmoed & Lescure, 1984**

1984: 101, figs 4, 8-11.

**ENGLISH NAME:** Guiana Shield frog.

**PATAMONA NAME:** Unknown.

**TYPE LOCALITY:** “Between camp IV and V, northern slopes of Mount Roraima, Guyana (60°46'W 5°17'N), 3000 feet (914 m).”

**SELECTED REFERENCES:** Hoogmoed & Lescure, 1984 (original description, B&W drawings, in English); Hoogmoed et al., 1994 (B&W photos, description refined, in English); MacCulloch et al., 2008 (description, colour variation, colour photos, natural history, call description, in English).

**Field identification** - Males reach 14.7 mm SVL, females 16.0 mm.

- Dorsal ground colour variable, medium brown to grey with numerous small sky blue dots and scattered dark markings, a middorsal black “)” usually present; skin on dorsum smooth to slightly shagreened.
- Ventral surface smooth, brown to grey with small irregular sky blue dots.
- Upper arm orange.
- Iris copper with a red ring around pupil.
- When adpressed, Finger I slightly shorter than II, fingers unwebbed.
- Tips of fingers pointed, discs absent.
- Tips of toes dilated into small narrow discs.
- Inner and outer metacarpal tubercle large, flat.

**Life history** - Diurnal and nocturnal, terrestrial. Found exclusively in primary forest, usually hidden in the leaf litter or among the rootlets at the base of plants. Males call from the base of plants, among rootlets or dead leaves. In KNP the species is often closely associated with the plant *Monotagma spicatum* (Marantaceae). Probably no more than one large egg is laid on the ground, among rootlets at the base of plants, froglets directly hatched from egg capsule.

**Call** - First described by MacCulloch et al. (2008: 46). It consists of a group of 2-15 short notes produced in quick succession with the interval between notes increasing progressively from the beginning to the end of the call.

**Tadpole** - Eggs of *Adelophryne* species undergo direct development and hatch as tiny frogs. Endotroph, direct developer.

**Abundance and distribution in KNP** - Very common, but difficult to spot. Collected or heard around all main sampling localities (see Fig. 3).

**Geographic range** - Widespread in the Guiana Shield from Bolivar State in Venezuela to Amapá, Brazil.
Stefania Rivero, 1968

“STEFANIAS”

Fig. 102. *Stefania roraimae*, a species that does not occur in Kaieteur National Park; here from Mt Maringma. (Photo by P. J. R. Kok).

- Medium to large size
- Maxillary teeth present
- Pupil horizontally elliptical (Fig. 42A)
- Skin on dorsum smooth, shagreened, granular or tuberculate (Fig. 44A-D)
- Vocal sac absent (no vocal slits, Fig. 53)
- Fingers unwebbed
- Finger discs expanded (Fig. 51B)
- Finger I > II when fingers addpressed
- Toe V > III when toes addpressed
- Tympanum present, distinct (Fig. 43A)
- Frontoparietal and supratympanic crests absent or present (Fig. 41)
The genus currently contains 18 species assigned to two different species groups: the *Stefania evansi* group ("narrow-headed") and the *S. goini* group ("broad-headed").

Stefanias are nocturnal, terrestrial or arboreal. They inhabit tropical rainforest, high-tepui forest and tepui bog.

**Sexual dimorphism**

Males are distinctly smaller than females; there is no other evident sexual dimorphism or dichromatism.

**Eggs**

Eggs and neonates are carried on the back of the female, adhering to a mucus layer. A female of *Stefania evansi* with 30 near-term juveniles on the back has been reported (Kok & Benjamin, 2007) (see the frontispiece of the manual).

**Tadpoles**

Endotroph (paraviviparous).

**Distribution**

The genus *Stefania* is endemic to the Guiana Shield (Frost, 2008).

**Field key to the *Stefania* species of Kaieteur National Park**

1. Snout elongated, head noticeably longer than wide; tympanum separated from eye by a distance equal or slightly greater than tympanum diameter; toes extensively webbed; outer metatarsal tubercle indistinct (Fig. 50). ................................. *S. evansi* (p. 154)

1’. Snout not elongated, head as long as, or slightly longer than wide; tympanum separated from eye by a distance lower than tympanum diameter; toes basally webbed; outer metatarsal tubercle distinct (Fig. 50) ................................. *S. woodleyi* (p. 156)
**Stefania evansi** (Boulenger, 1904)

1904: 106, pl. 5.

**ENGLISH NAME:** Evan's Stefania.

**LOCAL NAME (PATAMONA):** Unknown.

**TYPE LOCALITY:** “Groete Creek, Essequibo, British Guiana”.

**SELECTED REFERENCES:** Duellman & Hoogmoed, 1984 (description, habitat, distribution, B&W drawings, in English); MacCulloch & Lathrop, 2006a (description, distribution, colour photos); MacCulloch et al. 2006 (description, colour photo, in English).

**Field identification** - Males reach 53.0 mm SVL, females 97.5 mm.

- Dorsal ground colour very variable, ranging from pale greenish brown, medium brown or dark brown to greyish or reddish brown, with or without dark brown mottling, chevrons, and/or interorbital stripe and dorsolateral stripes; skin on dorsum shagreened.

- Ventral surface granular, dirty white to cream, usually with more or less extensive dark brown mottling, sometimes in an anastomotic pattern, throat dirty white, cream or pale reddish brown, with more or less extensive dark brown mottling, often with pale median ill-defined longitudinal stripe.

- Snout elongated, head noticeably longer than wide.

- Tympanum separated from eye by a distance equal or slightly greater than tympanum diameter.

- Prominent tubercles in temporal and post-tympanic region.

- When adpressed, Finger I longer than II, fingers unwebbed with large discs.

- Toes extensively webbed.

- Outer metatarsal tubercle indistinct.

**Life history** - Nocturnal, mainly arboreal, but sometimes observed on the ground (especially large females carrying eggs or juveniles). Found exclusively in primary forest, usually on rocks or low vegetation along streams and rivers. Reproductive biology poorly known, call and calling site undescribed (but see below), females carry eggs and neonates (up to 30) exposed on their back, adhering to a mucus layer; juveniles leave the mother’s back at about 17–19 mm SVL.

**Call** - Unknown, but note that Sinsch & Juraske (2006: 159) described the call of a specimen from La Escalera, Venezuela. Since *Stefania evansi* does not occur in that area, the call described is probably that of *Stefania scalaris*.

**Tadpole** - No tadpole stage, completely developed froglets hatched from egg capsule. Endotroph, paraviviparous.

**Abundance and distribution in KNP** - Very common. Collected around all main sampling localities (see Fig. 3).

**Geographic range** - Known only from west-central Guyana.
Stefania woodleyi Rivero, 1968
1968: 146, pl. 2, fig. 2.

ENGLISH NAME: Woodley’s Stefania
LOCAL NAME (PATAMONA): Unknown.

SELECTED REFERENCES: Duellman & Hoogmoed, 1984 (description, habitat, distribution, B&W drawings and photo, in English); MacCulloch & Lathrop, 2006b (description, distribution, colour photos); MacCulloch et al. 2006 (description, colour photo, in English).

Field identification - Males reach 46.0 mm SVL, females 60.0 mm.
- Dorsal ground colour variable, ochre to dark brown with dark brown to black spots and irregular markings, yellowish interorbital bar often present, a pair of distinct or ill-defined dorsolateral yellowish stripes present in some specimens; skin on dorsum shagreened to granular.
- Ventral surface shagreened to granular, medium brown to cream with irregular dark brown or ochre mottling, throat medium brown with cream to ochre mottling, no trace of pale median longitudinal stripe on throat.
- Snout not elongated, head as long as, or slightly longer than wide.
- Tympanum separated from eye by a distance less than tympanum diameter.
- Rounded warts in temporal and post-tympanic region.
- When adpressed, Finger I longer than II, fingers unwebbed with large discs.
- Toes basally webbed.
- Outer metatarsal tubercle distinct.

Life history - Nocturnal, mostly terrestrial. Found exclusively in primary forest, often on the ground, on rocks or very low vegetation along streams and rivers, but several specimens were found far from water. Some individuals emit a distress call and attempt to bite when captured. Reproductive biology unknown, call and calling site undescribed, females expected to carry eggs and neonates exposed on their back, adhering to a mucus layer, like in other species of the genus.

Call - Unknown, see above.

Tadpole - Likely no tadpole stage, with completely developed froglets hatching from egg capsule on the back of the female like in other species of the genus. Expected to be endotroph, paraviviparous.

Abundance and distribution in KNP - Uncommon. Collected around main sampling localities # 5, 10, and 11 (see Fig. 3).

Geographic range - Known only from western Guyana, in the eastern portion of the Pakaraima Mountains.
Dendropsophus Fitzinger, 1843

“FITZINGER NEOTROPICAL TREEFROGS”

Fig. 105. *Dendropsophus minutus*, a species that could be present in Kaieteur National Park; here from the vicinity of Philipi village. (Photo by P. J. R. Kok).

- Very small to medium size
- Maxillary teeth present
- Pupil horizontally elliptical (Fig. 42A)
- Axillary membrane absent or extensive (Fig. 45)
- No pigmented reticulation on palpebral membrane (Fig. 42D)
- Vocal sac single, subgular (Fig. 56A)
- Skin on dorsum smooth, shagreened, tuberculate, or finely spiculate (Fig. 44A-B, D-E)
- Fingers webbed
- Finger I < II when fingers adpressed
- Finger discs expanded (Fig. 51B)
- Tympanum present, distinct or indistinct (Fig. 43A-B)
The genus *Dendropsophus* currently contains 90 species.

Frogs of the genus *Dendropsophus* are nocturnal and mostly arboreal. They mainly inhabit tropical rainforest, but are also found in forest-edge situations, clearings, and other open areas like savannah; *Dendropsophus* species are often associated with water bodies and flooded areas.

The genus was resurrected by Faivovich *et al.* (2005) on the basis of unique DNA sequences, and contains all species formerly assigned to the genus *Hyla* believed to have 30 chromosomes. However, no strict morphological synapomorphies have currently been detected. Most *Dendropsophus* species are allocated to several different species groups, a few remain unassigned to any group.

**Sexual dimorphism**

Males often have different throat pigmentation than females, and are usually smaller. A few species exhibit sexually dichromatic dorsal colouration, with females having dorsolateral bands that are lacking in males (*e.g.* *Dendropsophus subocularis*). In some species males become yellow during the breeding season.

**Eggs**

Egg masses are usually deposited outside of water, on leaves, grasses, and other vegetation material overhanging or emerging from lentic water, although some species are reported to deposit eggs as a film on the water surface (*e.g.* *Dendropsophus koechlini*) or in clumps in the water (*e.g.* *D. melanargyreus*).

**Tadpoles**

Exotroph (benthic, nektonic, carnivorous, macrophagous).

**Distribution**

Species belonging to the genus *Dendropsophus* are found from southern Mexico, through tropical Central and South America to northern Argentina and Uruguay, including Trinidad and Tobago (Frost, 2008).

Only *Dendropsophus marmoratus* (p. 160) is currently reported from Kaieteur National Park, but we suspect the presence of other species like *D. minutus*. Several tadpoles collected in small forested water bodies could belong to an undetermined *Dendropsophus* species.
Anura | Hylidae | *Dendropsophus* Fitzinger, 1843

*Dendropsophus marmoratus* (Laurenti, 1768)
1768: 29.

**ENGLISH NAME:** Marbled treefrog.

**LOCAL NAME (PATAMONA):** Ambak.

**TYPE LOCALITY:** “Surinami”.

**SELECTED REFERENCES:** Bokermann, 1964 (description, B&W photos, in English); Duellman, 1978 (description, call description, tadpole description, natural history, in English); Lescure & Marty 2001 (description, distribution, colour photo, in French).

**Identification** - Males reach 44.0 mm SVL, females 56.0 mm.

- Dorsal ground colour variable, ranging from brown or brownish grey to grey, with a network of dark lines and markings that resemble lichens or bird droppings; colour varies significantly with light intensity; skin on dorsum weakly tuberculate.

- Ventral surface granular, usually white centrally, orange on the periphery, with black spots or mottling (may be completely white or pale yellow with black spots or mottling).

- Snout short and blunt.

- Axillary membrane extensive, orange or yellow with black spots.

- Scalloped white dermal folds on limbs.

- Small tubercles on lower lip.

- Fingers and toes extensively webbed.

- Discs on digits large and round, larger than adjacent phalange.

**Life history** - Nocturnal, highly arboreal. Mostly found in primary forest, but also occurs in disturbed forest. Males call during heavy rains, from the ground, grasses or bushes around temporary ponds, usually in clearings. Eggs are deposited as a surface film on the water; tadpoles probably feed on detritus.

**Call** - First described by Duellman (1978: 155). It consists of 1-3 low-pitched notes repeated at a rate of ca. 20 notes/min.

**Tadpole** - First described by Duellman (1978: 154). Exotroph, carnivorous; olive green with brown markings; LTRF = 0/0.

**Abundance and distribution in KNP** - Very rare. Collected only around main sampling locality # 1 (see Fig. 3), but the species is certainly more widespread in the park.

**Geographic range** - Widespread: occurs in the Guiana Shield and the Amazon Basin in Brazil, Colombia, Ecuador, Peru and Bolivia.
**Hypsiboas Wagler, 1830**

“WAGLER NEOTROPICAL TREEFROGS”

![Hypsiboas ornatissimus](image)

**Fig. 107.** *Hypsiboas ornatissimus*, a species currently not reported from Kaieteur National Park; here from the vicinity of Wayalayeng village. (Photo by P. J. R. Kok).

- Medium to large size
- Maxillary teeth present
- Pupil horizontally elliptical (Fig. 42A)
- Pigmented reticulation on palpebral membrane absent or present (Fig. 42D)
- Vocal sac single, subgular (Fig. 56A)
- Skin on dorsum smooth or shagreened to granular (Fig. 44A-C)
- Fingers unwebbed to extensively webbed
- Finger I < II when fingers adpressed
- Finger discs expanded (Fig. 51B)
- Tympanum present, distinct or indistinct (Fig. 43A-B)
The genus *Hypsiboas* currently contains 79 species, which are nocturnal and mostly arboreal. They mainly inhabit tropical rainforest.

The genus was resurrected by Faivovich *et al.* (2005) on the basis of unique DNA sequences, and contains species formerly assigned to the genus *Hyla*. However, no strict morphological synapomorphies have currently been detected.

**Sexual dimorphism**

Males often have an enlarged prepollex and/or nuptial excrescences on the first finger. In most species males are smaller than females and in some species they have different throat pigmentation.

**Eggs**

Eggs are deposited in lentic or lotic water, in natural or constructed basins in some species. Some *Hypsiboas* species lay eggs as gelatinous masses, while others deposit eggs as a gelatinous film on the water surface.

**Tadpoles**

Exotroph (benthic).

**Distribution**

Species belonging to the genus *Hypsiboas* are found in tropical Central and South America, from Nicaragua to Argentina, including Trinidad and Tobago (Frost, 2008).

**Field key to the *Hypsiboas* species of Kaieteur National Park**

1. Dorsal colouration mostly brown ............................................. 2
1'. Dorsal colouration mostly green ............................................. 3

2. Palpebral membrane not reticulated. ................. *H. calcaratus* (p. 166)
2'. Palpebral membrane reticulated (Fig. 42D) ......................... 4

3. Dorsal skin smooth (Fig. 44A) ....................... *H. sibleszi* (p. 174)
3'. Dorsal skin granular (Fig. 44C) ................................. 5

4. Fingers fully webbed ........................................... *H. boans* (p. 164)
4'. Fingers not fully webbed ................................. *H. geographicus* (p. 170)

5. Snout truncate in profile (Fig. 40B); webbing not reaching subarticular tubercle on Finger IV; no prepollical spine in males .......... *H. liliae* (p. 172)
5'. Snout rounded in profile (Fig. 40B); webbing reaching subarticular tubercle on Finger IV; prepollical spine in males (Fig. 48) ............... 6

6. Iris reddish orange, all fingers green ............ *H. cinerascens* (p. 168)
6'. Iris silver, Fingers I-II whitish ............... *H. sp.* (p. 176)
Anura | Hylidae | Hypsiboas Wagler, 1830

**Hypsiboas boans** (Linnaeus, 1758)
1758: 213.

**ENGLISH NAME:** Giant gladiator treefrog.

**LOCAL NAME (PATAMONA):** Wàl-oma.

**TYPE LOCALITY:** “America”.

**SELECTED REFERENCES:** Duellman, 1970 (description, tadpole description, call description, natural history, B&W drawings, colour drawings, in English); Duellman, 1978 (description, call description, natural history, B&W photo, in English); Hoogmoed, 1990 (comparison with Hypsiboas wavrini, B&W photos and drawings, in English).

**Field identification** - Males reach 132.0 mm SVL, females 118.0 mm.
- Dorsal ground colour variable, ranging from tan to greyish or dark brown, often with darker markings (spots or blotches), occasionally with scattered white spots and/or a middorsal line; skin on dorsum smooth.
- Ventral surface granular, white to greenish white, throat white to greenish white in females, greyish in males.
- Flanks whitish or greyish tan with diffuse dark brown vertical marks.
- Small triangular calcar on heel.
- Iris bronze, lower eyelid reticulated with silvery gold.
- Fingers with extensive brown webbing.
- Curved projecting prepollical spine in males.
- Toes with extensive brown webbing.

**Life history** - Nocturnal, arboreal. Found in primary and secondary forest, also occurs in open areas. Males call mainly on low vegetation along slow-moving rivers or streams, sometimes from the margin of small shallow natural basins or basin-like nests that they construct in sand or mud near water. Males usually defend egg-laying sites. Eggs are deposited as a film on the water surface of the nest basin from where the tadpoles will be washed into the stream; tadpoles feed on detritus.

**Call** - First described by Duellman (1970: 260), who provided a spectrogram. It consists of a series of 3-10 loud notes produced at a rate of 21-82 notes/min.

**Tadpole** - First described by Kenny (1969: 4, under Hyla maxima); see also Hero (1990: 228). Exotroph, benthic; transparent olive brown; LTRF = 2(1-2)/3-4(1).

**Abundance and distribution in KNP** - Common, observed around main sampling localities # 1, 2 and 5 (see Fig. 3), probably widespread in the Park

**Geographic range** - Widespread in lowland and upland tropical forests of South America, found also in eastern Panama, northern Colombia, and Trinidad.

**Taxonomic comment** - Duellman (1997) stated that the "Hyla boans" from Gran Sabana, Venezuela, could be specifically distinct from the widespread H. boans in the lowlands. Apparently specimens from Gran Sabana do not construct basin-like nests, but breed in small permanent streams. Interestingly, we never found constructed basin-like nests in KNP, but found eggs and tadpoles of *H. boans* in rocky streams.
**Anura | Hylidae | Hypsiboas Wagler, 1830**

**Hypsiboas calcaratus** (Troschel, 1848)
1848: 660.

**ENGLISH NAME:** Troschel's treefrog, Blue flanked treefrog.

**LOCAL NAME (PATAMONA):** Kon kon yun.

**TYPE LOCALITY:** "Britisch-Guiana".


**Field identification** - Males reach 41.0 mm SVL, females 61.0 mm.

- Dorsal ground colour variable, ranging from pale yellowish tan to brown, greyish brown or reddish brown, sometimes with darker markings (e.g. broad transverse marks, narrow transverse lines), often with a dark brown middorsal line.
- Ventral surface granular, white.
- Flanks and hidden surfaces of thighs bluish white to blue, with bold black markings (usually in the form of vertical bars).
- Large, elongate triangular calcar on heel.
- Eyelid without reticulations.
- Fingers with basal webbing.
- No prepollical spine in males.
- Supernumerary palmar and plantar tubercles present.

**Life history** - Nocturnal, arboreal. Found in primary and secondary forests. Males call from low vegetation along, or over, slow-moving streams and ponds. Eggs are deposited as a film on the water surface of slow-moving streams, swamps, or small ponds; tadpoles feed on detritus.

**Call** - First described by Duellman (1973: 518), it consists of one to three low-pitched rattling notes produced at a rate of ca. 8 notes/min.

**Tadpole** - First described by Duellman (1978: 138). Exotroph, benthic; dark brown with tan mottling and a tan interorbital bar; LTRF = 2(2)/3.

**Abundance and distribution in KNP** - Locally common, observed only around main sampling localities # 4 and 5 (see Fig. 3), but probably widespread in the Park.

**Geographic range** - Widespread in tropical South America, east of the Andes.
**Hypsiboas cinerascens** (Spix, 1824)
1824: 35, pl. 8, fig. 4.

**ENGLISH NAME:** Demerara Falls treefrog.

**LOCAL NAME (PATAMONA):** Unknown, but green treefrogs are generally called "Pakoko" (pron. Pa-go-go).

**TYPE LOCALITY:** "Ecgá prope flumen Tefé" [= Ega, Rio Tefé, Brazil].


**Field identification** - Males reach 54.0 mm SVL, females 44.0 mm.

+ Dorsal colour yellowish green to grass green with yellow dots, sometimes with reddish flecks/dots, and/or reddish interorbital bar; skin on dorsum finely granular.
+ Ventral surface coarsely granular, pale green to bluish green, translucent in the central portion of abdomen (internal organs visible).
+ Outer edge of upper eyelid yellow.
+ All fingers yellowish green to green.
+ Iris light orange to reddish orange.
+ Outer fingers about 1/3 webbed, other fingers basally webbed.
+ Prepollex enlarged, with small prepollical spine in breeding males.
+ Toes about 2/3 webbed.

**Life history** - Nocturnal, arboreal. Found in primary forest along slow-moving streams and rivers. Males call from low vegetation, usually not far from the water surface. Eggs are deposited in slow flowing rivers and streams, as a film on the water surface; tadpoles feed on detritus.

**Call** - Apparently first described by Duellman (1978: 150), but see also Schlüter (1979: 216), who provided a spectrogram. It consists of a series of two to three loud, unpulsed, notes ("hoot-hoot-hoot"), which are produced at a rate of about 30-60 notes/min.

**Tadpole** - First described by Duellman (1978: 149); see also Hero (1990: 230). Exotroph, benthic; pale green to olive brown; LTRF = 2(1, 2)/3-4(1)[2].

**Abundance and distribution in KNP** - Rare, observed only around main sampling locality # 5, but probably more widespread in the Park.

**Geographic range** - Exact distribution is unclear due to the confusion between at least two species (see *Hypsiboas* sp., p. 176). Probably widespread in the Amazon Basin from eastern Ecuador, Peru, northern Bolivia to northeastern Brazil and the Guiana Shield.

**Taxonomic comments** - A complex of at least two sympatric species (see Kok, 2006). Descriptions of tadpoles and calls in the literature did not discriminate between the similar but distinct taxa, and might thus involve more than one species. Re-evaluation of the taxonomic status of these very similar species is in progress by Kok and colleagues.
**Hypsiboas geographicus** (Spix, 1824)  
1824: 39, pl. 11, figs 1-2.

**ENGLISH NAME:** Map treefrog.  
**LOCAL NAME (PATAMONA):** Unknown.  
**TYPE LOCALITY:** “flumen Teffé” [Rio Tefé, Brazil].

**SELECTED REFERENCES:** Duellman, 1973 (description, call description, ontogenetic change in colour pattern, variation, natural history, B&W photos and drawings, in English); Lutz, 1973 (description, variation, in English); Duellman, 1978 (description, call description, tadpole description, natural history, B&W photo, in English).

**Field identification** - Males reach 62.0 mm SVL, females 83.0 mm.  
+ Dorsal ground colour very variable and depending on light intensity, ranging from brown or greyish brown to yellowish tan or orangish brown, often with darker markings (e.g. X-shaped mark on scapular region, irregular transverse bars, black flecks) and/or middorsal line extending to varying lengths on body, but usually more conspicuous on head, occasionally with few irregular white spots; in juveniles dorsum cream with many small black dots, flanks black (not illustrated); skin on dorsum smooth.  
+ Ventral surface granular, orangish yellow to orange, excepted on throat and chest, which are white to creamy yellow (females), or whitish, with some creamy yellow laterally and posteriorly (males).  
+ Flanks bluish with white flecks.  
+ Small triangular calcar on heel.  
+ Iris orangish bronze, lower eyelid reticulated with gold.  
+ Fingers with moderate, orange webbing (finely pigmented in preservative).  
+ No prepollical spine in males.  
+ Toes with moderate, orange webbing (finely pigmented in preservative).

**Life history** - Nocturnal, arboreal. Found mainly in secondary forest and disturbed vegetation, also occurs in primary forest and in open areas. Males call from low vegetation along, or over, slow-moving streams and ponds. Eggs are deposited as a film on the water surface of slow-moving streams or ponds; tadpoles feed on detritus.

**Call** - First described by Duellman (1973: 518), who provided a spectrogram; see also Duellman (1978: 148). Complex and highly variable, consisting of a series of short chuckles and/or a long groan, notes are produced at a rate of 2-60 notes/min.

**Tadpole** - First described by Kenny (1969: 36); see also Hero (1990: 229). Exotroph, benthic; black; LTRF = 2-3[1] (3)/3-5[1].

**Abundance and distribution in KNP** - Locally common, observed around main sampling localities # 5, 9, 10 and 11 (see Fig. 3).

**Geographic range** - Widespread in tropical South America, east of the Andes.
**Hypsiboas liliae** Kok, 2006

**ENGLISH NAME:** None; we propose “Lili treefrog”.

**LOCAL NAME (PATAMONA):** Unknown, but green treefrogs are generally called “Pakoko” (pron. Pa-go-go).

**TYPE LOCALITY:** “Between Boy Scout View and Johnson View on the Kaieteur Plateau (5°10'51"N, 59°28'57"W), ca. 400 m elevation, Kaieteur National Park, Potaro-Siparuni district, Guyana”.

**SELECTED REFERENCE:** Kok, 2006 (original description, call description, colour photos, B&W drawings and photos, in English).

**Field identification** - Males reach 37.1 mm SVL, female not known.
- Dorsal colour and pattern strongly dependent on light intensity, from bright green to bright yellowish green during the day, to greenish brown at night; skin on dorsum thickly granular.
- Ventral surface thickly granular, blue, translucent in the central portion of abdomen (internal organs visible).
- Snout truncate in dorsal view, with strongly protuberant nostrils.
- Ulnar fold distinct.
- Iris silver with black periphery during the day, bronze at night.
- All fingers unwebbed.
- Prepollex enlarged, without prepollical spine.
- Toes extensively webbed.

**Life history** - Nocturnal, arboreal. Primary forest and forest-edged situations. Males call from the water-filled phytotelm of large terrestrial bromeliads (*e.g.* *Brocchinia micrantha*) or at high elevation in trees (> 10 m above the ground). Reproductive biology is totally unknown.

**Call** - First described by Kok (2006: 196), who provided a spectrogram. It consists of a long series of loud percussive notes (“tuk-tuk-tuk-tuk-tuk…” gradual increasing in speed and loudness; the duration of the entire call is about 50 s.

**Tadpole** - Unknown.

**Abundance and distribution in KNP** - Rare, observed only around main sampling localities # 1 and 11.

**Geographic range** - Reported only from Guyana, in KNP. We heard the species calling on the slopes of Mt Maringma at the Guyana-Brazil border (Kok, unpublished data); the species is probably widespread in the Pakaraima Mountains of Guyana.

**Taxonomic comments** - Lack of known morphological synapomorphies for the genus *Hypsiboas* (Faivovich *et al.*, 2005) precludes definite generic allocation for this species; generic allocation of *H. liliae* remains thus uncertain (J. Faivovich, pers. comm.).
Hypsiboas sibleszi (Rivero, 1972)

ENGLISH NAME: La Escalera treefrog.
LOCAL NAME (PATAMONA): Unknown, but green treefrogs are generally called “Pakoko” (pron. Pa-go-go).
TYPE LOCALITY: “Paso del Danto, La Escalera, entre El Dorado y Sta. Elena de Uiarén, 1300-1400 m; Serranía de Lema, Edo. Bolívar, Venezuela”
SELECTED REFERENCES: Rivero, 1972 (original description, B&W photos, call spectrogram, in Spanish); Hoogmoed, 1979 (extensive description, distribution, B&W photos, call spectrogram, in English); Señaris & Ayarzagüena, 2006 (description, call description, osteology, distribution, in English).

Field identification - Males reach 39.0 mm SVL, females 38.0 mm.
- Dorsal colour variable: yellowish green to pale lime-green, with or without reddish brown and/or white or yellow flecks/spots, yellow dorsolateral and interorbital stripes may be present; skin on dorsum smooth.
- Ventral surface coarsely granular, pale green to bluish green, translucent in the central portion of abdomen (internal organs visible).
- Discs of fingers and toes orange.
- Outer edge of upper eyelid not yellow, unless presence of yellow dorsolateral stripes.
- Iris yellowish bronze with black flecks.
- Outer fingers about 1/3 webbed, other fingers basally webbed.
- Prepollex enlarged, with large protruding prepollical spine in breeding males.
- Toes about 2/3 webbed.

Life history - Nocturnal, mostly arboreal. Found in primary forest along slow-moving streams or ponds. Males call from low vegetation, usually not far from the ground or the water surface, sometimes partly submerged in the water. Eggs are deposited in slow-flowing streams or ponds, as a film on the water surface; tadpoles feed on detritus.

Call - Rivero (1972: 188) and Hoogmoed (1979: plate 5) provided spectrograms, but no formal description. Señaris & Ayarzagüena (2006: 315) provided a brief description and a spectrogram. The call consists of one or two “chucks”, which are produced at a rate of about 10-15 notes/min.

Tadpole - First described by Hoogmoed (1979: 27). Exotroph, benthic; grey with dark grey spots; LTRF = 2(2)/4(1).

Abundance and distribution in KNP - Rare, observed only around main sampling locality # 4, but could be more widespread in the Park.

Geographic range - Restricted to the uplands and highlands of eastern Venezuela and western Guyana.
**Hypsiboas sp.**

**English Name:** “Demerara Falls treefrog” (confused with *Hypsiboas cinerascens*).

**Local Name (Patamona):** Unknown, but green treefrogs are generally called “Pakoko” (pron. Pa-go-go).

**Type Locality:** -


**Field Identification** - Males reach 54.0 mm SVL, females 44.0 mm (but see taxonomic comments).

- Dorsal colour yellowish green to grass green with yellow dots, often with reddish flecks/dots, and/or reddish interorbital bar; skin on dorsum finely granular.
- Ventral surface coarsely granular, pale green to bluish green, translucent in the central portion of abdomen (internal organs visible).
- Outer edge of upper eyelid yellow.
- Fingers I-II unpigmented, whitish, other fingers yellowish green to green.
- Iris silver, may become light brown or brown in certain light condition.
- Outer fingers about 1/3 webbed, other fingers basally webbed.
- Prepollex enlarged, with small prepollical spine in breeding males.
- Toes about 2/3 webbed.

**Life History** - Nocturnal, arboreal. Found exclusively in open areas (e.g. forest-edge situations, savannah), along streams or small ponds. Males call from small bushes and trees, up to 4 m above the ground, sometimes from rocks along streams. Eggs are deposited in streams and small ponds, as a film on the water surface; tadpoles feed on detritus.

**Call** - See *Hypsiboas cinerascens* (p. 168), with which it is confused in the literature, see also taxonomic comments. It consists of a loud, metallic, pulsed “cluck”, which is produced at a rate of about 10-60 notes/min.

**Abundance and Distribution in KNP** - Locally very common, observed around main sampling localities # 2, 3, 4 and 12, probably widespread in the Park in adequate habitats.

**Geographic Range** - Exact distribution is unclear due to the confusion with *Hypsiboas cinerascens* (see p. 168). Might be widespread in the Amazon Basin from eastern Ecuador, Peru, and northern Bolivia to northeastern Brazil and the Guiana Shield.

**Taxonomic Comments** - Confused with *Hypsiboas cinerascens*, which is a complex of at least two sympatric species (see Kok, 2006). Re-evaluation of the taxonomy of these morphologically very similar species is in progress by Kok and colleagues.
**Osteocephalus Steindachner, 1862**

“SLENDER-LEGGED TREEFROGS”

![Image of Osteocephalus mutabor]

**Fig. 115. Osteocephalus mutabor**, a species that does not occur in the Park (compare with *O. leprieurii*); here from Volcan Sumaco, Ecuador. (Photo by K. H. Jungfer).

- Medium to large size
- Maxillary teeth present
- Pupil horizontally elliptical (Fig. 42A)
- Usually exostosed skulls (skin attached to the skull bone)
- Vocal sacs paired, lateral/subgular or both in most species (Fig. 56C-D) or vocal sac single, subgular (e.g. *O. oophagus*) (Fig. 56A)
- Skin on dorsum often, but not always, sexually dimorphic: smooth or shagreened in females (Fig. 44A-B), smooth, but usually tuberculate or spiculate in males (Fig. 44A, D-E)
- Fingers unwebbed to basally webbed
- Finger I < II when fingers adpressed
- Finger discs expanded (Fig. 51B)
- Tympanum present, distinct (Fig. 43A)
The genus *Osteocephalus* currently contains 20 species, which are nocturnal and arboreal. They mainly inhabit tropical rainforest.

Some species (*e.g.* *Osteocephalus buckleyi*) might be complexes of distinct taxa and a taxonomic revision of the genus is needed. Two additional undetermined *Osteocephalus* species have been collected in KNP and are not treated here.

**Sexual dimorphism**

Males are smaller than females and often have the skin on dorsum tuberculate or spiculate (variable among species, dorsal skin not sexually dimorphic in some taxa), while females have smooth or shagreened dorsal skin. Breeding males yellow and/or with nuptial excrescences on prepollex reported in several species.

**Eggs**

Eggs are laid in lentic or lotic water, as a film on the water surface, or as a gelatinous mass. Some species lay eggs in the canopy (up to 30 m high), in water-filled bromeliads or treeholes (*e.g.* *Osteocephalus oophagus*).

**Tadpoles**

Exotroph (benthic, arboreal).

**Distribution**

The Guiana Shield and the Amazon Basin (Frost, 2008).

### Field key to the *Osteocephalus* species of Kaieteur National Park

| 1. Iris with conspicuous radiating black lines | 2 |
| 1'. Iris lacking conspicuous radiating lines | 3 |
| 2. Vocal sac single, subgular (Fig. 56A); frontoparietal ridges indistinct; toes not fully webbed; when leg extended, tibio-tarsal articulation does not reach snout-tip | 4 |
| 2'. Vocal sacs paired, lateral (Fig. 56D); frontoparietal ridges prominent; toes almost fully webbed; when leg extended, tibio-tarsal articulation reaches snout-tip or beyond | 4' |
| 3. Dorsal colour primarily greenish; tarsal tubercles very prominent | 5 |
| 3'. Dorsal colour primarily brownish or greyish; tarsal tubercles absent or few and not very prominent | 5' |
| 4. Vocal sac single, subgular (Fig. 56A); ventral surface greyish with dark flecks; foot webbing blackish brown; distal tubercle on Finger IV single (Fig. 52B) | 6 |
| 4'. Vocal sacs paired, subgular (Fig. 56C); ventral surface whitish or yellow, immaculate; foot webbing tan, orange or red; distal tubercle on Finger IV bifid (Fig. 52C) | 6' |

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**Osteocephalus buckleyi** (Boulenger, 1882)

1882: 362, pl. 25, fig. 1.

**ENGLISH NAME:** Buckley's slender-legged treefrog.

**LOCAL NAME (PATAMONA):** Unknown.

**TYPE LOCALITY:** restricted to “Canelos, Provincia Pastaza, Ecuador” by Cochran & Goin (1970).

**SELECTED REFERENCES:** Trueb & Duellman, 1971 (description, B&W drawings, distribution, in English); Duellman, 1978 (description, tadpole description, natural history, B&W photo, in English); Lima et al., 2006 (brief description, colour photos, in English).

**Field identification** - Males reach 50.0 mm SVL, females 75.1 mm.

- Dorsal ground colour variable, from greenish brown to green, with dark brown markings often in the shape of a black inverted triangle between the eyes followed on the back by a V or a X and two large dark lumbar spots; skin on dorsum tuberculate/spiculate, especially in males.
- Ventral surface granular, greyish white, with brown blotches located mainly on throat, chest, and sides of belly; ventral surface sometimes entirely covered by brown flecks.
- Broad, irregular, green subocular spot.
- Frontoparietal ridges absent.
- Iris greenish bronze to gold without radiating black lines, but with irregular black vermiculations.
- Flanks areolate, inguinal region and inner thigh blue.
- Tarsal tubercles very prominent.
- Toes about 2/3 webbed.

**Life history** - Nocturnal, arboreal. Found in primary forest, usually near streams and ponds. Males call from low vegetation along streams or ponds. Eggs are deposited as a film on the water surface of streams and ponds; tadpoles feed on detritus.

**Call** - Probably still undescribed due to confusion with other species (see *Osteocephalus oophagus*, p. 186).

**Tadpole** - First described by Hero (1990: 236). Exotroph, benthic; dark blue; LTRF = 2(2)/3-8 [1].

**Abundance and distribution in KNP** - Rare, observed only around main sampling locality # 11 (see Fig. 3), but probably more widespread in the Park.

**Geographic range** - Occurs in the Amazon Basin, from eastern Ecuador and Peru, and northern and central Bolivia to northeastern Brazil and the Guiana Shield.

**Taxonomic comments** - Some data suggest that this taxon holds several cryptic species (K.-H. Jungfer, pers. comm.; P. Kok, unpubl. data).
Anura | Hylidae | Osteocephalus Steindachner, 1862

Osteocephalus exophthalmus Smith & Noonan, 2001
2001: 349, figs 1-3.

ENGLISH NAME: None; we propose “Big-eye slender-legged treefrog”.
LOCAL NAME (PATAMONA): Unknown.
TYPE LOCALITY: “ca 30 km SE Imbaimadai, Mazaruni-Potaro District, Guyana... 5°37’30” N, 60°14’42” W”.
SELECTED REFERENCE: Smith & Noonan, 2001 (original description, osteology, B&W photo and drawings, in English).

Field identification - Males reach 33.1* mm SVL, females 42.5* mm.
➤ Dorsal ground colour medium brown, with dark brown blotches, interorbital bar usually present; skin on dorsum smooth with very few tiny tubercles.
➤ Ventral surface granular, greyish white, with brown spotting located mainly on throat and belly, almost absent on chest.
➤ Eyes large and bulgy.
➤ Frontoparietal ridges absent, snout short.
➤ Iris greenish bronze to gold without conspicuous radiating black lines, but with irregular black vermiculations.
➤ Hidden surface of thighs black.
➤ Tarsal tubercles low, not very prominent.
➤ Toes about half-webbed.

Life history - Nocturnal, arboreal. Found in primary forest, usually not very far from water. Reproductive biology is totally unknown. Interestingly, non-spinous dorsa are present in males of bromeliad-breeding Osteocephalus species (vs. spinous dorsa in pond-breeding species, see comment by Jungfer & Hödl, 2002) and Osteocephalus exophthalmus might be a phytotelm-breeding species.

Call - Unknown

Tadpole - Unknown

Abundance and distribution in KNP - Very rare, observed only around main sampling localities # 1 and 4 (see Fig. 3), but probably more widespread in the Park.

Geographic range - Currently only reported from the type locality (Imbaimadai area, Guyana) and from Kaieteur National Park, Guyana.
Osteocephalus leprieurii (Duméril & Bibron, 1841)
1841: 553.

ENGLISH NAME: Cayenne slender-legged treefrog.
LOCAL NAME (PATAMONA): Unknown.
TYPE LOCALITY: “Cayenne” [French Guiana].
SELECTED REFERENCES: Lescure & Marty, 2001 (brief description, colour photo, in French); Jungfer & Hödl, 2002 (redescription, B&W drawings, colour photos, natural history, call description, distribution, in English).

Field identification - Males reach 45.7 mm SVL, females 61.0 mm.
- Dorsal ground colour variable, ranging from ochre, tan or reddish tan to dark tan, usually with up to four narrow, usually fragmented, dark brown transverse lines, and a narrow dark brown interorbital bar; skin on dorsum spiculate in males (more or less pronounced depending on breeding condition), smooth in females.
- Ventral surface granular, immaculate, creamy white to bright yellow.
- Broad, irregular, light subocular spot.
- Frontoparietal ridges absent, snout moderately long.
- Iris golden in its superior half, darker in its inferior half, lacking conspicuous radiating black lines, but with irregular black vermiculations.
- Hidden surface of thighs and foot webbing orange to reddish.
- Tarsal tubercles absent.
- Toes almost fully webbed.

Life history - Nocturnal, arboreal. Found in primary forest. The species is an explosive breeder, males congregate for a very short period (usually one or two nights) at the beginning of the rainy season and call from low vegetation, from the ground along flooded pools, sometimes floating in water. Eggs are deposited as a film on the water surface in seasonally flooded pools; tadpoles probably feed on detritus.

Call - The call of Osteocephalus leprieurii sensu stricto (see taxonomic comments) was described by Jungfer & Hödl (2002: 32), who provided a spectrogram. It is a complex call involving at least two different types of notes, which according to Lescure & Marty (2001) are produced at a rate of about 18 calls/min.

Tadpole - Probably still undescribed due to confusion with other species.

Abundance and distribution in KNP - Common, observed around main sampling localities # 1, 2, 4, 5 and 12 (see Fig. 3), probably widespread in the Park.

Geographic range - The species is found in the Guiana Shield and in northern Brazil, exact range unknown due to misidentification with other species.

Taxonomic comments - A composite of several cryptic species, Osteocephalus leprieurii Duméril & Bibron sensu stricto was recently redescribed by Jungfer & Hödl (2002). Many descriptions available in the literature involve other taxa.
**Anura | Hylidae | Osteocephalus Steindachner, 1862**

**Osteocephalus oophagus Jungfer & Schiesari, 1995**
1995: 1, figs 1-4.

**ENGLISH NAME:** None; we propose “Oophagous slender-legged treefrog”.

**LOCAL NAME (PATAMONA):** Unknown.

**TYPE LOCALITY:** “Reserva Florestal Adolfo Ducke (2°55’S, 59°59’W), situated at km 26 of the Rodovia AM-010 (Manaus-Itacoatiara), Estado do Amazonas, Brazil”.

**SELECTED REFERENCES:** Jungfer & Schiesari, 1995 (original description, call description, tadpole description, reproductive biology, B&W photos and drawings, distribution, in English); Lescure & Marty, 2001 (brief description, colour photo, in English); Lima *et al*., 2006 (brief description, natural history, colour photos, in English).

**Field identification** - Males reach 53.0 mm SVL, females 62.7 mm.
- Dorsal ground colour ranging from tan to brown, marbled with dark brown, individuals with white spots are reported; skin on dorsum smooth to weakly tuberculate.
- Ventral surface granular, creamy white to yellowish white, with brown spots and flecks on chin and throat.
- Distinct dark transverse bars on limbs.
- Frontoparietal ridges indistinct, never prominent.
- Iris gold with conspicuous radiating black lines.
- No calcar on heel, but some small tubercles.
- Tarsal tubercles present, low.
- Toes about 2/3 webbed.

**Life history** - Nocturnal (although the species occasionally call during the day), arboreal. Found in primary forest, often in disturbed areas (*e.g.* clearings). Males call from near or inside bromeliads, usually between 0.5-10 m above the ground, but up to 30 m high. Eggs are deposited in the phytotelm of bromeliads (both epiphytic or terrestrial) or in holes in trees; tadpoles feed on fertilized eggs laid by the female.

**Call** - First described by Zimmerman (1983: 241 [*Osteocephalus* sp.]); see also Zimmerman & Bogart (1984: 479 [*Osteocephalus* sp.] and 1988: 98 [*O. buckleyi*]), who provided spectrograms. The advertisement call is intraspecifically variable and mainly consists of one to six croaking notes; the call is produced very irregularly, usually not more than 2 calls/m.

**Tadpole** - First described by Hero (1990: 237 [*Osteocephalus* sp.]); see also Jungfer & Schiesari (1995: 8) and Schiesari *et al.* (1996: 115). Exotroph, arboreal; chestnut brown; LTRF = 2(2)/3[1].

**Abundance and distribution in KNP** - Rare, observed and heard only around main sampling locality # 11 (see Fig. 3), but probably more widespread in the Park.

**Geographic range** - Exact range unknown. The species is found in the Guiana Shield and in the Amazon Basin, from east and north of State of Pará to eastern Colombia.
**Osteocephalus taurinus** Steindachner, 1862

1862: 77, pl. 6, figs 1-3.

**ENGLISH NAME:** Manaus slender-legged treefrog.

**LOCAL NAME (PATAMONA):** Unknown.

**TYPE LOCALITY:** “Barra do Rio Negro in Brasilien”.

**SELECTED REFERENCES:** Trueb & Duellman, 1971 (description, B&W drawings, distribution, in English); Duellman & Lescure, 1973 (call description, in English); Duellman, 2005 (description, tadpole description, call description, natural history, colour photo, in English).

**Field identification** - Males reach 92.0 mm SVL, females 104.0 mm.

- Dorsal ground colour very variable, ranging from tan to dark brown, with or without dark irregular markings, sometimes with a yellow middorsal stripe, rarely with small cream spots; skin on dorsum smooth to shagreened in females, spiculate in males.
- Ventral surface smooth, creamy white, usually with brown blotches on throat, chest, and sides of belly.
- Distinct dark transverse bars on limbs.
- Frontoparietal ridges prominent.
- Iris greenish bronze to gold with conspicuous radiating black lines.
- No calcar on heel, but some small tubercles.
- Tarsal tubercles absent or not prominent.
- Toes almost fully webbed.

**Life history** - Nocturnal, arboreal. Found in primary and secondary forest. Males call from low vegetation or from the ground along small pools. The species is an explosive breeder, and many males and females may be found in and around a same pool. Eggs are deposited as a film on the water surface of pools and small ponds; tadpoles feed on detritus.

**Call** - First described by Duellman & Lescure (1973: 9), who provided a spectrogram; see also Schlüter (1979: 224). It mainly consists of a series of low, strongly pulsed, growls produced at a rate of about 8-36 calls/min.

**Tadpole** - Confused with the tadpole of *Hypsiboas geographicus* by Duellman & Lescure (1973) and Duellman (1978). A complete description is provided in Duellman (2005: 228); see also Hero (1990: 238). Exotroph, benthic; brown; LTRF = 2(2)/3-7(1).

**Abundance and distribution in KNP** - Locally common, observed around main sampling localities # 5 and 11 (see Fig. 3), probably widespread in the Park.

**Geographic range** - Widespread in the Amazon Basin, from eastern Ecuador, Peru and northern Bolivia to northeastern Brazil and the Guiana Shield.

**Taxonomic comments** - Very probably a complex of several cryptic species (see comments by De la Riva *et al.*, 1995).
Phyllomedusa Wagler, 1830

“MONKEY FROGS”

Fig. 121. Calling male of Phyllomedusa vaillantii, one of the 32 described species in the genus. Here a specimen photographed in French Guiana. (Photo by P. J. R. Kok).

- Medium to large size
- Maxillary teeth present
- Pupil vertically elliptical (Fig. 42B)
- Skin on dorsum smooth, shagreened or finely granular (Fig. 44A-C)
- Vocal sac not distinct (but vocal slits present, Fig. 53), single, subgular (Fig. 56A)
- Digits opposable
- Fingers and toes unwebbed
- Finger discs expanded (Fig. 51B)
- Tympanum present, distinct or indistinct (Fig. 43A-B)

The genus Phyllomedusa currently contains 32 species.
Phyllomedusa species are nocturnal and mostly arboreal, although some taxa are terrestrial (e.g. *P. atelopoides*). They mainly inhabit tropical rainforests, but are also found in savannah and seasonally arid areas. Some species (e.g. *Phyllomedusa bicolor*) produce waxy skin secretions containing opioid peptides with analgesic properties (e.g. dermorphin, deltorphin) that are used by certain Amerindian tribes as a hunting aid and for disease prevention. Frog secretions are scraped off, dried and later mixed with saliva and applied to self-inflicted skin burns. The chemicals produced by the frog proved to be effective against various diseases, from heart and liver diseases to malaria.

**Sexual dimorphism**

Males have nuptial excrescences on the first finger. In most species males are slightly smaller than females.

**Eggs**

Egg masses are deposited above lentic water in most species (above lotic water in some taxa), on the tip of the upper surface of leaves, or in “leaf nests” made by folding one or two leaves into a funnel (into which eggs are laid).

**Tadpoles**

Exotroph (nektonic, suspension-rasper).

![Image of a tadpole](image)

*Fig. 122. The tadpole of *Phyllomedusa vaillantii*. (Photo by R. Ernst).*

**Distribution**

Species belonging to the genus *Phyllomedusa* are found from Panama, through South America east of the Andes, to northern Argentina and Uruguay, including Trinidad (Frost, 2008).

**Field key to the *Phyllomedusa* species of Kaieteur National Park**

1. Parotoid region rounded, without longitudinal row of small whitish tubercles; Toes I-II equal or subequal in length when adpressed; finger discs large, covering the tympanum .......................... *P. bicolor* (p. 192)

1’. Parotoid region angulate, with longitudinal row of small whitish tubercles; Toe I longer than II when adpressed; finger discs not covering the tympanum .................................................. *P. vaillantii* (p. 194)
**Phyllomedusa bicolor** (Boddaert, 1772)

ENGLISH NAME: Giant monkey frog.
TYPE LOCALITY: “Guinea” [restricted to Suriname by Funkhouser, 1957].
SELECTED REFERENCES: Duellman, 1974 (description, B&W photo in English); Lescure et al., 1995 (description, breeding behaviour, colour photos, in French); Lescure & Marty, 2001 (brief description, natural history, colour photo, in French).

**Field identification** - Males reach 115.3 mm SVL, females 120.5 mm.
- Dorsal colour green, dark green by night; skin on dorsum smooth (sometimes reported as “rough”).
- Ventral surface granular, light grey, sometimes with a few white ocelli.
- White ocelli on lower lip, flank, and hidden surfaces of thigh.
- Parotoid region rounded, without longitudinal row of small whitish tubercles.
- Iris silvery grey.
- Fingers and toes unwebbed.
- Finger discs large, covering the tympanum.
- Toes I-II opposable, equal or subequal in length when adpressed.

**Life history** - Nocturnal, arboreal. Found in primary and secondary forest. Males call from trees (usually between 2-10 m), typically above or at the edge of pools or ponds. Eggs are laid over ponds and pools, in leaf nests made by folding one or more leaves into a funnel, from which tadpoles will fall into the water as they hatch; tadpoles feed on detritus.

**Call** - First description might be that of Zimmerman & Bogart (1984: 480), who provided spectrograms. It consists of a loud, explosive “bok” usually followed by several additional short, lower-pitched notes; the call is produced at a rate of about 3 calls/min.

**Tadpole** - First described by Hero (1990: 240) and Rada de Martínez (1990: 398). Exotroph, suspension-rasper; translucent orange with silver belly; LTRF = 2(2)/2-3(1).

**Abundance and distribution in KNP** - Common, observed only around main sampling localities # 5 and 11, but the species is probably widespread in the Park.

**Geographic range** - Widespread in the Amazon Basin from Ecuador, Peru and northern Bolivia east of the Andes to northern Brazil and the Guiana Shield.
ENGLISH NAME: White-lined monkey frog.
LOCAL NAME (PATAMONA): Might be “Pakalais”.
TYPE LOCALITY: “Santarém, Brazil”.
SELECTED REFERENCES: Duellman, 1974 (description, B&W photo in English); Lescure et al., 1995 (description, breeding behaviour, colour photos, in French); Lescure & Marty, 2001 (brief description, natural history, colour photo, in French).

**Field identification** - Males reach 65.0 mm SVL, females 87.3 mm.
- Dorsal colour pale or dark green to greyish green; skin on dorsum smooth (sometimes reported as “rough”).
- Ventral surface granular, orange to reddish brown or greyish brown, usually with a few white ocelli on throat and chest.
- Cream, orange or reddish ocelli on flank and hidden surfaces of thigh, lower lip white.
- Parotoid region angulate, with longitudinal row of small whitish tubercles.
- Iris silvery grey.
- Fingers and toes unwebbed.
- Finger discs medium, not covering the tympanum.
- Toes I-II opposable, Toe I longer than II when adpressed.

**Life history** - Nocturnal, arboreal, but often observed sitting or walking on the ground. Found in primary and secondary forest. Males call from bushes (usually between 0.5-2 m above the ground), typically above or at the edge of pools or ponds. Eggs are laid over ponds and pools, in leaf nests made by folding one or more leaves into a funnel, from which tadpoles will fall into the water as they hatch; tadpoles feed on detritus.

**Call** - First description might be that of Duellman (1978: 181); see also Schlüter (1979: 227), who provided a spectrogram. It consists of a harsh “cluck”; the call is produced very irregularly, at a rate of about 12-14 calls/min.

**Tadpole** - First described by Duellman (1978: 181); see also Caramaschi & Jim (193: 262) and Hero (1990: 243). Exotroph, suspension-rasper; translucent orange with silver belly; LTRF = 2[2]/2-3[1].

**Abundance and distribution in KNP** - Common, observed around main sampling localities # 5, 10 and 11, but the species is probably widespread in the Park.

**Geographic range** - Widespread in the Amazon Basin from Ecuador, Peru and northern Bolivia east of the Andes to northern Brazil and the Guianas.
Anura | Hylidae | Phyllomedusa Wagler, 1830

Scinax Wagler, 1830

“SNOUTED TREEFROGS”

Fig. 125. Scinax ruber, one of the 94 described species in the genus. (Photo by P. J. R. Kok).

- Small to medium size
- Snout relatively long, protruding beyond lower jaw
- Maxillary teeth present
- Pupil horizontally elliptical (Fig. 42A)
- Skin on dorsum smooth, shagreened, granular or tuberculate (Fig. 44A-D)
- Vocal sac single, subgular (Fig. 56A), bilobate subgular (Fig. 56B), or paired, lateral (Fig. 56D) in a few species
- Toes extensively webbed, but webbing reduced between Toes I-II
- Webbing between fingers absent or much reduced
- Finger discs expanded (Fig. 51B)
- Tympanum present, distinct (Fig. 43A)
The genus currently contains 94 species assigned to four different species groups (Faivovich et al. 2005): the *Scinax catharinae* group, the *S. perpusillus* group, the *S. rostratus* group, and the *S. uruguayus* group. Several species remain unassigned to any group.

Snouted treefrogs are nocturnal, terrestrial or arboreal. They inhabit a wide range of habitats, from savannah to tropical rainforest.

**Sexual dimorphism**

Males are smaller than females; there is no other evident sexual dimorphism or dichromatism, although males of some species are yellow when calling (*e.g.* *Scinax ruber*).

**Eggs**

Egg deposition sites are diverse in the genus: eggs may be laid in a foam nest constructed in temporary pools (*e.g.* *Scinax rizibilis*), in lotic water (*e.g.* *S. albicans*), or in lentic water (in most species). Lescure & Marty (2001) suggested deposition of eggs on a floating leaf or above water in *S. proboscideus*.

**Tadpoles**

Exotroph (benthic, nektonic).

**Distribution**

Species belonging to the genus *Scinax* are found from Mexico (eastern and southern parts) to Argentina and Uruguay, including Trinidad and Tobago and St Lucia (Frost, 2008).

**Field key to the *Scinax* species of Kaieteur National Park**

1. Posterior surface of thighs immaculate; no longitudinal stripes on dorsum .............................. *S. boesemani* (p. 198)

1’. Posterior surface of thighs with conspicuous yellowish blotches (Fig. 39B); usually distinct longitudinal stripes (Fig. 39G) on dorsum .............................. *S. ruber* (p. 200)
Anura | Hylidae | Scinax Wagler, 1830

Scinax boesemani (Goin, 1966)
1966: 229, fig. 1.

ENGLISH NAME: Boeseman’s snouted treefrog.
LOCAL NAME (PATAMONA): Unknown.
TYPE LOCALITY: “near Zanderij, Suriname District, Suriname”.

SELECTED REFERENCES: Goin, 1966 (original description, B&W drawings, in English); Lescure & Marty, 2001 (brief description, natural history, colour photo, in French); Lima et al., 2006 (brief description, natural history, colour photos, in English).

Field identification - Males reach 32.1 mm SVL, females 33.0 mm.
- Dorsal ground colour variable, ranging from tan to dark brown, depending on light intensity, with cream or yellow spotting (spots may be more or less visible depending on light intensity); skin on dorsum smooth to weakly granular.
- Ventral surface granular, white.
- Flanks with well-defined dark brown spots (spots may be more or less visible depending on light intensity).
- Dark line from nostril to arm insertion.
- Iris greyish brown to dark brown with inconspicuous irregular black vermiculations.
- Hidden surfaces of thighs greyish brown, immaculate.
- Webbing between Toes I-II reduced.
- Fingers unwebbed.

Life history - Nocturnal, arboreal. Found in savannah and open areas, very rarely observed in primary and secondary forest. Males call from low elevation in shrubs and bushes, sometimes from the ground, along seasonally flooded pools and small ponds, often in large choruses. Eggs are deposited as a film on the water surface of slow-moving streams, pools and small ponds; tadpoles feed on detritus.

Call - First described by Hödl (1977: 358), who provided a spectrogram. It consists of a buzzing trill produced at a rate of ca. 30 notes/min.

Tadpole - First described by de Sá et al. (1997: 15). Exotroph, nektonic; colour in life unknown; LTRF = 2(2)/3(1-2).

Abundance and distribution in KNP - Very common locally, observed around main sampling localities # 2, 3 and 4 (see Fig. 3), but probably widespread in the Park in suitable habitats.

Geographic range - The Guiana Shield and the Amazon Basin in Brazil.
**Scinax ruber** (Laurenti, 1768)

**ENGLISH NAME:** Red snouted treefrogs.

**LOCAL NAME (PATAMONA):** Waroma.

**TYPE LOCALITY:** "America".

**SELECTED REFERENCES:** Duellman, 1978 (description, natural history, tadpole description, call description, B&W photo, in English); Duellman & Wiens, 1993 (description, natural history, colour photo, in English); Lescure & Marty, 2001 (brief description, natural history, colour photo, in French).

**Field identification** - Males reach 41.0 mm SVL, females 44.0 mm.

- Dorsal ground colour variable, ranging from cream, tan or grey to dark brown, depending on light intensity, usually with broad dark brown dorsolateral and lateral stripes and distinct lumbar spots (stripes inconspicuous in some specimens, sometimes broken into longitudinal spots); skin on dorsum smooth to weakly granular.
- Ventral surface granular, greyish white, cream or yellow.
- Flanks usually lack well-defined dark brown spots.
- Broken interorbital bar often present.
- Iris bronze with conspicuous irregular black vermiculations.
- Groin and hidden surfaces of thighs with yellowish or orange blotches on a dark background.
- Webbing between Toes I-II reduced.
- Fingers unwebbed.

**Life history** - Nocturnal, arboreal. Found in disturbed and open areas, rarely observed in secondary forest, very anthropophilic. Males call from low elevation in shrubs, bushes, or grasses along seasonally flooded pools and small ponds. Eggs are deposited as a film on the water surface of pools and small ponds; tadpoles feed on detritus.

**Call** - First description might be that of Duellman (1978: 164); see also Schlüter (1979: 220), who provided a spectrogram. It consists of a series of short loud trills ("aaah") produced at a rate of ca. 45 notes/min.

**Tadpole** - First described by Kenny (1969: 33); see also Duellman (1970: 185) and Hero (1990: 235 [under *Ololygon cf. rubra*]). Exotroph, nektontic; silvery gold with black dots and a brown stripe from snout to eye; LTRF = 2(2)/3(1).

**Abundance and distribution in KNP** - Very common locally, observed around main sampling localities # 2, 3 and 10 (see Fig. 3), probably widespread in the Park.

**Geographic range** - Widespread (but see taxonomic comments), found from Panama through the Guiana Shield and northern Brazil, also on Trinidad & Tobago.

**Taxonomic comments** - A composite of as many as six cryptic species according to Fouquet *et al.* (2007). Call of specimens from the Rupununi savannah in southern Guyana is significantly different from specimens from KNP (Kok, unpubl. data).
Tepuihyla Ayarzagüena, Señaris & Gorzula, 1993

“TEPUI TREEFROGS”

Fig. 128. *Tepuihyla talbergae*, endemic to Kaieteur National Park, one of the eight described species in the genus. (Photo by P. J. R. Kok).

- Small to medium size
- Maxillary teeth present
- Pupil horizontally elliptical (Fig. 42A)
- Skin on dorsum smooth, shagreened, tuberculate or spiculate (Fig. 44A-B, D-E)
- Vocal sac poorly distinct (vocal slits small; absent in some species), single, subgular (Fig. 56A) or bilobate, subgular (Fig. 56B)
- Toes no more than half-webbed, webbing absent or vestigial between Toes I-II
- Webbing between fingers absent or vestigial
- Finger discs expanded (Fig. 51B)
- Tympanum present, distinct (Fig. 43A)
The genus currently contains eight species.
Tepui treefrogs are nocturnal, terrestrial or arboreal. They inhabit tropical primary forest and tepui summits and are often associated with bromeliads (Bromeliaceae). Very little is known about their natural history.

**Sexual dimorphism**
Males are distinctly smaller than females and have the dorsal skin spiculate, males in breeding condition have nuptial excrescences on the prepollex.

**Eggs**
Aquatic, lentic (e.g. in shallow swampy areas) or lotic (small streams), probably deposited as a film on the water surface. Breeding habits of most of *Tepuihyla* species are virtually unknown.

**Tadpoles**
Unknown, presumably exotroph (benthic, nektonic?).

**Distribution**
Species belonging to the genus *Tepuihyla* are restricted to the mountains of eastern and southeastern Venezuela (Amazonas and Bolívar states) and the Pakaraima Mountains in Guyana (Frost, 2008). It must be noted that one species, *Tepuihyla celsae*, is reported from Cerro Galicia in Falcón State, northwestern Venezuela (Mijares-Urrutia *et al.*, 1999); that species was never seen alive and the type locality is considered as doubtful by Barrio-Amorós (2004).

Only *Tepuihyla talbergae* (p. 204) is currently reported from Kaieteur National Park, which is the lowest and easternmost known locality for the genus.
**Tepuihyla talbergae** Duellman & Yoshpa, 1996

1996: 276, figs 1-3.

**ENGLISH NAME:** Kaieteur tepui treefrog.

**Local name (Patamona):** Unknown.

**Type locality:** “Kaieteur Falls, 366 m (05°10’S, 59°28’W), Mazaruni-Potaro District, Guyana”.

**Selected references:** Duellman & Yoshpa, 1996 (original description, B&W drawings and photo).

**Field identification** - Males reach 36.6⁰ mm SVL, females 50.3⁰ mm.

- Dorsal ground colour variable, ranging from pinkish grey, greyish tan to reddish brown, usually with minute dark brown flecks, sometimes with minute red flecks, rarely with a dark brown “hour-glass” pattern (exclusively observed in a few males); skin on dorsum smooth to shagreened in females, spiculate in males (breeding males have black keratinized nuptial excrescences on thumb).

- Ventral surface granular, greyish white; throat usually with brown spots and flecks (often more conspicuous in males).

- Dark brown canthal stripe from nostril to eye followed by a narrow dark brown stripe from eye to posterior edge of tympanum or to arm insertion.

- Upper lip white.

- Iris silver grey to bronze with inconspicuous irregular black vermiculations.

- Inner metatarsal tubercle projecting.

- Webbing between Toes I-II reduced.

- Fingers unwebbed.

**Life history** - Nocturnal, arboreal. Found in savannah and neighbouring forest-edge situations, usually perched on shrubs between 0.5-1.5 m above ground level. During the day the species typically takes refuge in terrestrial bromeliads (*e.g.* Brocchinia micrantha, *B. reducta*), but a few individuals were found in low-perched epiphytic bromeliads (max 1.5 m above the ground). Reproductive behaviour remains unknown, but males with keratinized nuptial excrescences and gravid females were exclusively collected at the end of November and at the beginning of December (which corresponds to the beginning of the short rainy season), which suggests that breeding might be restricted to a very short period of the year. One male in breeding condition was collected on 2 December 2005, in the water, sitting on an immersed rock at the edge of a small pool in savannah. Males (which lack vocal slits) probably call floating in the water or from the ground or low elevation in shrubs and bushes along seasonally flooded pools and small ponds. Eggs are probably deposited in seasonally flooded pools and small ponds in the savannah.

**Call** - Unknown.

**Tadpole** - Unknown.

**Abundance and distribution in KNP** - Common locally, observed only around main sampling localities # 2, 3 and 4 (see Fig. 3).

**Geographic range** - Endemic to Kaieteur National Park, Guyana.
Trachycephalus Tschudi, 1838

“CASQUE-HEADED TREEFROGS”

Fig. 130. Calling male of *Trachycephalus coriaceus*, one of the 10 currently described species in the genus. Here a specimen from French Guiana. (Photo by C. Marty).

- Medium to large size
- Maxillary teeth present
- Pupil horizontally elliptical (Fig. 42A)
- Vocal sacs usually paired, lateral (Fig. 56A), but vocal sac single, subgular in *T. hadroceps* (Fig. 56D)
- Skin glandular, very thick, smooth, shagreened or tuberculate (Fig. 44A-B, D)
- Toes extensively webbed
- Finger discs expanded (Fig. 51B)
- Tympanum present, distinct (Fig. 43A)
The genus *Trachycephalus* currently contains 10 species, which are nocturnal and highly arboreal. They mainly inhabit primary tropical rainforest.

The genus *Phrynohyas* was recently synonymized with *Trachycephalus* by Faivovich *et al.* (2005); the two species from Kaieteur National Park were formerly known as *Phrynohyas coriacea* and *P. resinifictrix*.

**Sexual dimorphism**

There is no evident sexual dimorphism; in most species males are slightly smaller than females.

**Eggs**

Eggs are deposited in lentic water, as a film on the water surface, or as a gelatinous mass. Some species lay eggs in the canopy (up to 32 m high), in water-filled tree holes (*e.g.* *Trachycephalus resinifictrix*).

**Tadpoles**

Exotroph (benthic, nektonic, arboreal).

**Distribution**

Species belonging to the genus *Trachycephalus* are found from Mexico, through Central and South America east of the Andes to northern Argentina and eastern Brazil, including Trinidad and Tobago (Frost, 2008).

**Field key to the *Trachycephalus* species of Kaieteur National Park**

1. Skin on dorsum smooth (Fig. 44A); iris dark bronze, lacking radiating lines (without a black cross); skin of flanks areolate (Fig. 44G); large bluish black spot above arm insertion. ......................... *T. coriaceus* (p. 208)

1’. Skin on dorsum tuberculate (Fig. 44D); iris golden with four radiating black lines (a black “Maltese cross”); skin on flanks not areolate; no bluish black spot above arm insertion ......................... *T. resinifictrix* (p. 210)
Trachycephalus coriaceus (Peters, 1867)

ENGLISH NAME: Surinam casque-headed treefrog.
LOCAL NAME (PATAMONA): Etáule.
TYPE LOCALITY: “Surinam”.
SELECTED REFERENCES: Duellman, 1978 (description, B&W photo, in English); Lescure et al., 1996 (description, tadpole description, natural history, colour photos, in French); Duellman, 2005 (description, tadpole description, natural history, colour photo, in English).

Field identification - Males reach 63.0 mm SVL, females 67.6 mm.
- Dorsal ground colour ranging from tan (by day) to reddish brown (by night), with a large dark brown rectangular blotch narrowly outlined with a creamy border extending from upper eyelids to middle of the back (blotch sometimes broken in two, rarely absent), followed by a similar saddle-shaped dark brown blotch over the sacrum; skin on dorsum smooth, thick, glandular.
- Ventral surface areolate, creamy white to yellow.
- Thick supratympanic glandular fold covering the upper part of the tympanum.
- Skin on flanks areolate.
- Large bluish black spot below supratympanic fold, at arm insertion.
- Iris dark bronze, lacking radiating lines.
- Fingers half-webbed, finger webbing red.
- Toes 3/4 webbed, toe webbing red.

Life history - Nocturnal, arboreal. Exclusively found in primary forest. The species is an explosive breeder, which congregates for a short period, at the time of the first heavy rains. Males call on shrubs (up to 2 m above the ground) or while floating on the surface of the water. Eggs are deposited as a film on the water surface of temporary pools and small ponds; tadpoles feed on detritus.

Call - First described by Schlüter (1979: 225), who provided a spectrogram. It consists of a loud grinding growl, produced at a rate of about 28 calls/min according to Lescure & Marty (2001).

Tadpole - First briefly described by Rodriguez & Duellman (1994: 42); see also Lescure et al. (1996: 70) and Schiesari & Moreira (1996: 404). Exotroph, nektonic; greyish brown with or without black spots; LTRF variable = 2-3(3)/5-6(1), 4(1,2,4)/6(1).

Abundance and distribution in KNP - Very rare, only one specimen collected in the western part of the Park without precise locality, but probably widespread in KNP.

Geographic range - Apparently a disjunct distribution, but it is expected that new records will fill the gap. One population in the Guianas, another found from eastern Ecuador, Peru and northern Bolivia through the Amazon Basin to near Manaus, Brazil.

Remark - Photos A & C in figure 131 are of a specimen from French Guiana, D & E are of a specimen from Peru.
Anura | Hylidae | Trachycephalus Tschudi, 1838

**Trachycephalus resinifictrix** (Goeldi, 1907)

1907: 135, figs 56-57.

**ENGLISH NAME:** Kunawalu casque-headed treefrog.

**LOCAL NAME (PATAMONA):** Kunawa.

**TYPE LOCALITY:** “Mission of San Antonio do Prata, at the River Macaraná” [Brazil].

**SELECTED REFERENCES:** Zimmerman & Hödl, 1983 (call description, natural history, colour patterns, B&W drawing, distinction from *Trachycephalus venulosus*, in English); Lescure *et al.*, 1996 (description, natural history, colour photos, in French); Lescure & Marty, 2001 (brief description, natural history, colour photo, in French).

**Field identification** - Males reach 83.8 mm SVL, females 93.7 mm.

- Dorsal ground colour dark brown, with one large whitish, tan or greenish brown blotch narrowly outlined with a creamy border on the flank and another on the top of the head, the latter often having the shape of a triangle; skin on dorsum tuberculate (tubercles usually with white tip), thick, glandular.
- Ventral surface granular, greenish white to light brown.
- Supratympanic glandular fold not covering the upper part of the tympanum.
- Skin on flanks tuberculate, never areolate.
- No black spot at arm insertion.
- Iris golden with four radiating black lines (a black "Maltese cross").
- Fingers half-webbed, finger webbing greenish blue.
- Toes 3/4 webbed, toe webbing greenish blue.

**Life history** - Nocturnal, arboreal. Observed only in primary forest. Males call exclusively from water-filled cavities in hollow trunks or branches, at heights between 2.2-32 m (usually between 10-20 m). Eggs are deposited as a gelatinous mass in water-filled treeholes; tadpoles feed on conspecific eggs and detritus.

**Call** - First described by Zimmerman & Hödl (1983: 343), who provided spectrograms. It consists of 3-4 loud barklike notes, produced at a rate of about 4 calls/min according to Lescure & Marty (2001).

**Tadpole** - First described by Hero (1990: 239); see also Grillitsch (1992: 53) and Schiesari *et al.* (1996: 115). Exotroph, arboreal; dark olive; LTRF = 2(2)/3-5.

**Abundance and distribution in KNP** - Common, heard around main sampling localities # 5, 8, 9, 10, 11, 12 and 13 (see Fig. 3).

**Geographic range** - Widespread from eastern Ecuador, Peru and northern Bolivia through the Amazon Basin to the Guiana Shield.

**Remark** - Photos in figure 132 are of a specimen from Manaus, Brazil.
Leptodactylus Fitzinger, 1826

“THIN-TOED FROGS”

Fig. 133. Leptodactylus lutzi, endemic to Guyana, one of the ca. 85 described species in the genus. (Photo by P. J. R. Kok).

- Small to large size
- Maxillary teeth present
- Pupil horizontally elliptical (Fig. 42A)
- Vocal sac single, subgular (Fig. 56A), bilobate, subgular (Fig. 56B), or paired, subgular (Fig. 56E); vocal sac internal and indistinct in some species (e.g. L. discodactylus)
- Skin on dorsum smooth to warty (Fig. 44A-F)
- Ventral skin smooth (Fig. 44A)
- Fingers unwebbed, toes no more than basally webbed
- Finger I >= II when fingers adpressed
- Finger discs unexpanded (Fig. 51A), or slightly expanded
- Tympanum present, distinct (Fig. 43A)
This large and diverse genus currently contains about 86 species. Thin-toed frogs are mostly nocturnal and terrestrial (some semiaquatic), they inhabit a wide range of habitats, from savannah to tropical primary forest. Several species produce toxic skin secretions.

The genera *Adenomera* and *Lithodytes* were synonymized with *Leptodactylus* by Frost *et al.* (2006). It has been suggested to use the term “*Leptodactylus marmoratus* group” (Heyer, 1973) for those species formerly included in *Adenomera* (Almeida & Angulo, 2006).

**Sexual dimorphism**

Very variable between species. Males of many species have enlarged forearms and/or keratinized spine(s) on the thumb (sometimes also on the chest); in some species males have a shovel-shaped snout used to excavate nesting chambers.

**Eggs**

Deposited in foam nests on land (sometimes in nesting chambers), or in water.

**Tadpoles**

Exotroph (benthic, carnivorous) or endotroph (nidicolous).

**Distribution**

The genus is widespread and known from southern North America, the West Indies, and South America (Frost, 2008).

**Field key to the *Leptodactylus* species of Kaieteur National Park**

1. Skin smooth to finely granular (Fig. 44A-C); at least one pair of well-defined, usually continuous, dorsolateral folds (Fig. 46A)  
   2. Skin warty, tuberculate or spiculate (Fig. 44D-F); no well-defined, continuous dorsolateral folds  
   3. Rear of thighs black with light spots (Fig. 39A) and immaculate pinkish stripe on the upper lip  
      2. Not as above  
      3. Body black with dorsolateral yellow stripes  
         4. Ventral surface yellow, centre of belly immaculate  
            5. Ventral surface whitish or greyish with dark mottling  
            6. Dorsolateral folds extend to sacrum only  
               7. Ventral pattern anastomosed (Fig. 39E), extending on the lower surface of legs  
                  8. Supernumerary plantar tubercles absent; stripe on the upper lip entering eye anteriorly  
                     9. Supernumerary plantar tubercles present (Fig. 50); stripe on the upper lip never entering eye anteriorly  
                     10. L. *rhodomystax* (p. 226)  
                     11. L. *lineatus* (p. 216)  
                     12. L. *lutzii* (p. 220)  
                     13. L. *knudseni* (p. 214)  
                     14. L. *petersii* (p. 224)  
                     15. L. *rugosus* (p. 228)  
                     16. L. *longirostris* (p. 218)  
                     17. L. *mystaceus* (p. 222)
**Anura | Leptodactylidae | Leptodactylus Fitzinger, 1826**

**Leptodactylus knudseni** Heyer, 1972
1972: 3, fig. 2.

**ENGLISH NAME:** Knudsen’s thin-toed frog.
**LOCAL NAMES (PATAMONA):** Chinau, Pùdùka.
**TYPE LOCALITY:** “Limoncocha, 0°24’S, 76°37’W, Provincia de Napo, Ecuador”.
**SELECTED REFERENCES:** Heyer, 1979 (description, call description, in English), Heyer, 2005 (description, variation, call description, tadpole description, distribution, in English), Heyer & Heyer, 2006 (extended account, colour photo, in English).

**Field identification** - Males reach 170.0 mm SVL, females 154.0 mm.

- Dorsal ground colour variable, ranging from pinkish or greyish tan to orangish or reddish brown, with two or more broad dorsal transverse brown bands, sometimes ill-defined; flanks reddish in males; juveniles greyish with reddish dorsal transverse broad bands and reddish dorsolateral fold (fold more conspicuous than in adult); skin on dorsum smooth, slightly granular posteriorly.
- Ventral surface smooth, variable in colour and pattern, often creamish white with diffuse brown mottling; throat dark brown with pale flecks.
- Pair of low, often interrupted, dorsolateral folds extending from eye to sacral region, never entering groin. Supratympanic fold bifurcating on shoulder.
- Upper lip with dark triangular marks.
- Posterior thigh pattern variable, often black with reddish orange vermiculations.
- When adpressed, Finger I much longer than Finger II.
- Lateral fringes on fingers and webbing absent.
- Male thumb with one large spine; large breeding males with chest spines.

**Life history** - Nocturnal, terrestrial. Found in primary and secondary forest, and in open areas, including savannah. Males call from various terrestrial sites, including edge of burrows or hollow trunks and flooded areas. Eggs are laid in foam nests, from which tadpoles escape into nearby water (temporary or semi-permanent) after heavy rains; tadpoles feed on frog eggs (hetero- and conspecific) and detritus.

**Call** - First described by Heyer (1979: 21), who provided a spectrogram. It consists of a single pulsed note (a loud rising “whoop”) repeated at a rate of about 16-66 calls/min.

**Tadpole** - Probably first described by Duellman (1978: 109, as *Leptodactylus pentadactylus*), see also Hero (1990: 247). Exotroph, benthic/carnivorous; grey or dark olive; LTRF = 2(2)/2-3[1-2].

**Abundance and distribution in KNP** - Common. Observed around main sampling localities # 2, 4, and 11 (see Fig. 3), probably widespread in the park.

**Geographic range** - Widespread in the Amazon Basin, from Bolivia, Ecuador, Colombia and Peru, through Brazil and the Guiana Shield to Trinidad.

**Taxonomic comments** - The broad distribution and notably the geographic variation of the juvenile pattern suggest a possible complex of cryptic species.
**Leptodactylus lineatus** (Schneider, 1799)
1799: 138.

**English name**: Gold-striped frog, painted antnest frog.

**Local names (Patamona)**: Kubi gobi.

**Type locality**: Not stated.

**Selected references**: Lamar & Wild, 1995 (natural history, tadpole description, B&W photos and drawings, in English); Schlüter & Regös, 1996 (tadpole description, in English); Duellman, 2005 (description, call description, tadpole description, colour photo, in English).

**Field identification** - Males reach 45.0 mm SVL, females 56.0 mm.
- Dorsal ground colour dark brown to black with yellowish to gold dorsolateral stripe from tip of snout to groin, sometimes shortly interrupted; skin on dorsum finely spiculate.
- Ventral surface smooth, light to dark grey with white flecks.
- Cream spots at angle of jaw and arm insertion.
- Bright red flashmarks (spots) on axilla, groin, and posterior surfaces of thighs and shanks (red spots totally absent in a 21.2 mm juvenile).
- More or less distinct transverse brown bars on limbs (bluish and more conspicuous in juveniles).
- Flanks immaculate light or dark grey to black.
- When adpressed, Finger I slightly longer than Finger II.
- Lateral fringes on fingers and webbing absent.

**Life history** - Mainly nocturnal (although sometimes found by day), terrestrial. Found exclusively in primary forest, often associated with large nests of leaf cutting ant (*Atta* spp.). Males call from the entrance of or from subterranean tunnels in *Atta*-nests. Eggs are laid in foam nests constructed at the edge of temporary pools or at the mouth of partially submerged burrows, possibly also in water reservoirs in *Atta*-nests, from which tadpoles escape to water; larvae probably feed on detritus. *Leptodactylus lineatus* is part of a mimetic complex involving several species of the genera *Allobates* (Aromobatidae) and *Ameerega* (Dendrobatidae).

**Call** - First described by Schlüter (1980: 240), who provided a spectrogram; see also Duellman (2005: 21). It consists of a short low whistle repeated at a rate of about 80-90 calls/min.

**Tadpole** - First described by Lamar & Wild (1995: 138); see also Schlüter & Regös (1996: 2). Exotroph, benthic; bright pink with a short metallic white middorsal stripe; LTRF varies from 0/0 to 2(2)/3(1) (apparently correlated with growth stages).

**Abundance and distribution in KNP** - Locally common (especially in the vicinity of large *Atta*-nests), but usually difficult to find. Observed around main sampling localities # 4 and 11 (see Fig. 3), probably widespread in the park.

**Geographic range** - Widespread in the Amazon Basin, reported from eastern Peru, Ecuador and Bolivia to the Guiana Shield.
**Anura | Leptodactylidae | Leptodactylus Fitzinger, 1826**

**Leptodactylus longirostris** Boulenger, 1882
1882: 240, pl. 16, fig. 3.

**English Name:** Long snouted thin-toed frog.

**Local Names (Patamona):** Kuma-pik.

**Type Locality:** “Santarém” [Brazil].

**Selected References:** Heyer, 1978 (description, call description, colour pattern variation, B&W drawing of colour pattern, distribution, in English), Crombie & Heyer, 1983 (call description, tadpole description, morphological variation, natural history, distribution, in English), Duellman, 1997 (description, tadpole description, natural history, in English).

**Field Identification** - Males reach 43.0 mm SVL, females 51.6 mm.

- Dorsal ground colour and pattern very variable, light brown to reddish brown, sometimes greyish or dark brown, uniform or with irregular dark brown markings, middorsal and paravertebral stripes absent or present; skin on dorsum smooth to finely granular.
- Ventral surface smooth, throat and chest cream or white, turning yellow on belly.
- Two to six dorsolateral folds (2-4 in most Kaieteur specimens). Distinct supratympanic fold forming an angle posteriorly to tympanum.
- Upper lip with a white, cream, light brown or pinkish stripe below eye, always entering eye anteriorly.
- Black stripe from tip of snout to eye.
- No distinct triangular dark brown interorbital bar, dorsal markings not bordered by cream lines.
- When adpressed, Finger I much longer than Finger II.
- Supernumerary plantar tubercles absent.

**Life History** - Mainly nocturnal (active by day during heavy rains), terrestrial. Found in open areas like savannah. Males call from the base of grass, hidden by the vegetation. Eggs are laid in foam nests, usually constructed in hidden small cavities excavated by the male, from which tadpoles escape after a heavy rain into shallow pools or small temporary streams flowing on rocks and sand; tadpoles feed on detritus.

**Call** - First described by Rivero (1971: 6) who provided a spectrogram, see also Crombie & Heyer (1983: 294). It consists of a short unpulsed note repeated at a rate of about 60-120 notes/min (weet, weet, weet).

**Tadpole** - First described by Crombie & Heyer (1983: 296), see also Duellman (1997: 24). Exotroph, benthic; pale brown with dark brown mottling; LTRF = 2(1)/3[1].

**Abundance and Distribution in KNP** - Very common in suitable habitat. Observed only around main sampling locality # 3 (see Fig. 3), but probably more widespread in other savannahs in the park.

**Geographic Range** - East of the Amazon Basin in northern Brazil and the Guiana Shield.
LEPTODACTYLUS LUTZI (HEYER, 1975)
1975: 315, fig. 1.

ENGLISH NAME: Lutz’s thin-toed frog.
LOCAL NAMES (PATAMONA): Quima.
TYPE LOCALITY: “Guyana, Chinapoon R., upper Potaro (probably Chenapowu River)”. SELECTED REFERENCES: Heyer, 1975 (original description, B&W photo, in English), Kok et al., 2007 (extended account, description, colour variation, call description, natural history, colour photos, in English).

FIELD IDENTIFICATION - Males reach 33.5 mm SVL, females 34.0 mm.
- Dorsal ground colour extremely variable, ranging from light or medium grey, dark brown or reddish brown to black, dorsal pattern usually present, very variable, consisting of more or less evident dark interorbital bar, postorbital ridges, and chevron between shoulders, sometimes with dark mottling and orangish brown oblique lateral stripe; skin on dorsum with numerous small warty tubercles.
- Ventral surface smooth, yellow to orangish yellow suffused with dark grey stippling on throat, chest, and perimeter of belly (centre of belly immaculate).
- Round black lumbar spots always present (inconspicuous in very dark specimens).
- Dark triangular seat patch always present.
- Posterior thigh pattern variable, but always black with distinct yellow, orange or red spotting or mottinging.
- When adpressed, Finger I slightly longer than Finger II.
- Lateral fringes on fingers and webbing absent.
- Fleshy proboscis on snout in males.

LIFE HISTORY - Mainly nocturnal, terrestrial. Found exclusively in primary forest. Males call on or under the leaf litter. Eggs are laid in foam nests constructed in excavated nesting chambers that have no entrance tunnel; high probably non-feeding tadpoles that complete development within the chamber.

CALL - First described by Kok et al. (2007: 54), who provided a spectrogram. It consists of single note (a high-pitch “peep”) repeated at a rate of about 17-23 calls/min.

TADPOLE - Unknown. Probably endotroph, nidicolous.

ABUNDANCE AND DISTRIBUTION IN KNP - Locally common. Observed around main sampling localities # 1, 5, 6, and 11 (see Fig. 3), the species is probably widespread in the park.

GEOGRAPHIC RANGE - Known only from the Pakaraima Mountains of Guyana.
Anura | Leptodactylidae | *Leptodactylus* Fitzinger, 1826

**Leptodactylus mystaceus** (Spix, 1824)

1824: 27, pl. 3, figs 1, 3.

**ENGLISH NAME:** Amazonian white-lipped frog.
**LOCAL NAMES (PATAMONA):** Kuma.
**TYPE LOCALITY:** “ad Bahiam in aqua fluvatilis; differ tab illa prope flumen Solimoens ” [Bahia and Solimoes, Brazil].

**Field identification** - Males reach 56.0 mm SVL, females 60.0 mm.
- Dorsal ground colour grey to light brown, sometimes reddish brown, with irregular dark brown, transverse, chevron-shaped bars bordered by cream lines; skin on dorsum smooth.
- Ventral surface smooth, creamy white (female and juvenile) to yellow (active male), some inconspicuous brown flecks on throat.
- Pair of dorsolateral folds extending from eye to groin, usually bordered by black ventrally, reddish in juveniles. Distinct supratympanic fold not forming an angle posteriorly to tympanum.
- Upper lip with a broad white or creamy white stripe below eye, not entering eye anteriorly.
- Broad black band from tip of snout to arm insertion.
- More or less triangular dark brown interorbital bar.
- When adpressed, Finger I much longer than Finger II.
- Supernumerary plantar tubercles present.

**Life history** - Mainly nocturnal (although individuals may be found by day), terrestrial. Usually found in primary forest, but occurs also in secondary vegetation and clearings. Males call from various secluded terrestrial sites, *i.e.* under logs, among leaves, or in small holes in the ground. Eggs are laid in foam nests, usually constructed in hidden small cavities excavated by the male, from which tadpoles escape into nearby water (temporary ponds) after heavy rains; tadpoles able to generate foam, feed on detritus.

**Call** - First described by Duellman (1978: 108) and Heyer (1978: 41, as *Leptodactylus amazonicus*) who provided a spectrogram, see also Heyer *et al.* (1996: 10). It consists of a series of pulsed notes (oit, oit, oit, oit, oit) repeated at a rate of about 40-120 notes/min.

**Tadpole** - First described by Duellman (1978: 108) and Heyer (1978: 41, as *Leptodactylus amazonicus*), see also Hero (1990: 248). Exotroph, benthic; olive tan; LTRF = 2(2)/3(1).

**Abundance and distribution in KNP** - Rare. Observed only around main sampling locality # 5 (see Fig. 3), but probably more widespread in the park.

**Geographic range** - Widespread in the Amazon Basin, from Paraguay to the Guiana Shield.
**Leptodactylus petersii** (Steindachner, 1864)

1864: 254, pl. 16, figs 2, 2a-c.

**ENGLISH NAME:** Peter’s thin-toed frog.

**LOCAL NAMES (PATAMONA):** Unknown.

**TYPE LOCALITY:** “Marabitanas” [Amazonas, Brazil].

**SELECTED REFERENCES:** Heyer, 1994 (description, call description, tadpole description, geographic variation, distribution, in English), Lescure & Marty, 2001 (short description, natural history, spectrogram, colour photo, in French).

**Field identification** - Males reach 41.1 mm SVL, females 51.3 mm.

- Dorsal ground colour variable, ranging from greenish or greyish brown to reddish brown, with irregular dark brown to black markings; skin on dorsum with many spicules and short elongated glandular ridges laterally.
- Ventral surface smooth, variable in pattern, white with extensive grey to black mottling always in an anastomotic pattern; throat dark grey with white spots.
- No prominent dorsolateral folds, but short glandular ridges and/or large to elongate glandular warts instead. Distinct supratympanic fold reaching arm insertion.
- Dark triangular interorbital mark.
- Iris bronze to reddish brown with two distinct light stripes from pupil to upper lip where they prolong into cream lip stripes.
- When adpressed, Finger I much longer than Finger II.
- Lateral fringes on fingers absent or very weak, but extensive on toes, which are basally webbed.
- Male thumb with two large spines, no chest spines.

**Life history** - Nocturnal, terrestrial. Found exclusively in primary forest, sometimes in clearings. Males call hidden in the mud or under vegetation along ponds, marshes and flooded areas; calling activity is intense during heavy rains. Eggs are laid in foam nests constructed next to water, under vegetation or in the mud, from which tadpoles escape into nearby water; tadpoles feed on detritus.

**Call** - First described by Heyer (1994: 97) who provided several spectrograms from different geographic populations. It consists of a single pulsed note repeated at a rate of about 48 calls/min (weet, weet, weet, weet).

**Tadpole** - First described by Hero (1990: 252, as *Leptodactylus wagneri/podicipinus*), see also Heyer (1994: 96). Exotroph, benthic; dark brown to black; LTRF = 2(2)/3.

**Abundance and distribution in KNP** - Common. Observed around main sampling locality # 5 (see Fig. 3).

**Geographic range** - Widespread in the Amazon Basin, from Colombia, eastern Ecuador and Peru, and northern Bolivia to the Guiana Shield and central Brazil.

**Taxonomic comments** - Possibly a complex of cryptic species, the species found in KNP might prove to be a different taxon.
Anura | Leptodactylidae | *Leptodactylus* Fitzinger, 1826

**Leptodactylus rhodomystax** Boulenger, 1884

1884 “1883”: 637, pl. 58, fig. 2.

ENGLISH NAME: Rose-lipped thin-toed frog.

LOCAL NAMES (PATAMONA): Pai-talo.

TYPE LOCALITY: “Yurimaguas, Huallaga River, Peru”.


**Field identification** - Males reach 90.0 mm SVL, females 83.0 mm.

- Dorsal ground colour greyish brown to reddish brown (more reddish in juveniles), sometimes with narrow transverse bands and an interorbital bar, flanks orange tan; skin on dorsum smooth.
- Ventral surface smooth, creamy white suffused with brown, throat dark brown to black with white small spots and flecks.
- Pair of dorsolateral folds extending from eye to groin, usually dark brown and bordered by black ventrally. Distinct supratympanic fold extending to arm insertion.
- Upper lip with a broad pinkish tan stripe, entering eye anteriorly.
- Groin and posterior surfaces of thighs dark brown to black with greenish yellow or creamy spots.
- Fingers lack lateral fringes, toes basally webbed.
- When adpressed, Finger I much longer than Finger II, male thumb with black spine (not illustrated).
- Supernumerary plantar tubercles absent.

**Life history** - Nocturnal, terrestrial. Found exclusively in primary forest. Males call from the ground, usually near puddles, sometimes partially submerged in water. Eggs are laid in foam nests constructed between the vegetation, near puddles or small ponds, sometimes floating on water, from which tadpoles escape into nearby water (small temporary ponds) after a heavy rain; tadpoles feed on conspecific and heterospecific eggs and tadpoles, probably also on detritus.

**Call** - First described by Zimmerman & Bogart (1988: 104) who provided a spectrogram. It consists of a powerful short, high-pitch, note repeated at a rate of about 12 notes/min.


**Abundance and distribution in KNP** - Common. Observed around main sampling localities # 1, 2, 4, 5, 6, 8,10, and 11 (see Fig. 3), can be considered as widespread in the park.

**Geographic range** - Widespread in the Amazon Basin, from eastern Ecuador and Peru to the Guiana Shield.
**Leptodactylus rugosus** Noble, 1923

1923: 297.

**ENGLISH NAME:** Rugose thin-toed frog.

**LOCAL NAMES (PATAMONA):** Quoi.

**TYPE LOCALITY:** “near Kaieteur Falls, British Guiana”.

**SELECTED REFERENCES:** Donnelly & Myers, 1991 (description, B&W photos, in English), Duellman, 1997 (description, tadpole description, call description, colour photo, in English), Heyer & Thompson, 2000 (extended account, call description, tadpole description, distribution, colour photo, in English).

**Field identification** - Males reach 72.0 mm SVL, females 74.0 mm.
- Dorsal ground colour variable, ranging from greyish or greyish brown to olive brown or reddish brown (dorsum bright red in some subadolescents), with irregular pale cream to greyish tan blotches and black markings; juveniles similar to adults, but dorsal markings more conspicuous; skin on dorsum rugose, warty.
- Ventral surface smooth, variable in pattern, white to light greyish brown with diffuse brown mottling (pattern more conspicuous in juveniles and subadolescents, which have ventral surface of thighs orangish); throat white, heavily marked with grey mottling in juvenile and female, grey in adult male.
- No dorsolateral fold, but short glandular ridges and/or large to elongate glandular warts on dorsum and flanks. Strong supratympanic fold.
- Dirty white, cream or brownish lines from eye to lip (ill-defined in some specimens).
- Dirty white, cream or brownish interorbital stripe.
- When adpressed, Finger I much longer than Finger II.
- Lateral fringes on fingers and toes absent, webbing absent.
- Male thumb with 1-2 large spines; breeding males with paired chest spines.

**Life history** - Nocturnal, terrestrial; juveniles often active by day. Found in rocky and sandy habitats in open areas, but juveniles and subadolescents may be found in adjacent primary forest. Males call sitting on or under rocks. Eggs are laid in foam nests constructed under boulders, from which tadpoles escape into shallow small temporary streams flowing on rocks and sand; tadpoles feed on detritus.

**Call** - First described by Heyer (1979: 35) who provided a spectrogram, see also Duellman (1997: 26). It consists of a single powerful high-pitch trill repeated at a rate of about 1-7 calls/min.

**Tadpole** - First described by Heatwole et al. (1965: 361), see also Duellman (1997: 25). Exotroph, semiterrestrial; reddish brown with dark brown transverse marks; LTRF = 2(1)/3(1).

**Abundance and distribution in KNP** - Very common in suitable habitat. Observed around main sampling localities # 1, 2, 3, 4, 6, 10, and 11 (see Fig. 3), the species is mostly restricted to rocky habitats in the park.

**Geographic range** - Known only from the Guiana Shield, in the Pakaraima Mountains from eastern part of Bolivar State in Venezuela to western Guyana.
Fig. 142. *Synapturanus mirandaribeiroi*, a species currently not reported from the Park (compare with *S. salseri*); here from Manaus, Brazil. (Photo by K. H Jungfer).

- Very small to medium size
- Body globular, ovoid, eyes small
- Maxillary teeth absent
- Pupil circular (Fig. 42C)
- Snout very long, acuminate (Fig. 40), protruding well beyond the lower jaw
- Skin on dorsum and venter smooth (Fig. 44A)
- Digits unwebbed
- Finger I < II when fingers adpressed
- First toe reduced
- Finger discs unexpanded (Fig. 51A)
- Tympanum present, distinct or indistinct (Fig. 43A-B)
The genus *Synapturanus* currently contains three species. Disc frogs are fossorial, mostly nocturnal, and are found in the leaf litter and soft soils in tropical rainforest. They usually call during rain (which seems to induce calling). Due to their fossorial habit, little is known about their natural history and they might be much more common than expected.

**Sexual dimorphism**

Males are smaller than females and breeding males have a glandular swelling on the upper side of the wrist. There is no other evident sexual dimorphism or dichromatism.

**Eggs**

Eggs are terrestrial, they are deposited in a small burrow below the soil surface.

**Tadpoles**

Endotroph (nidicolous).

**Distribution**

*Synapturanus* species are reported from Colombia and adjacent Ecuador through the Guianas Shield to northern Brazil (Frost, 2008).

Only *Synapturanus salseri* (p. 232) is currently reported from Kaieteur National Park.
**Synapturanus salseri** Pyburn, 1975
1975: 440, fig. 1.

**ENGLISH NAME:** Timbo disc frog.

**LOCAL NAMES (PATAMONA):** Unknown.

**TYPE LOCALITY:** "Timbó, Vaupés, Colombia".

**SELECTED REFERENCE:** Pyburn, 1975 (original description, call description, tadpole description, B&W photo, in English).

**Field identification** - Males reach 27.6 mm SVL, females 29.4* mm.
- Dorsal ground colour medium brown to greyish brown, with irregular small cream to orange spots; skin on dorsum smooth.
- Ventral surface smooth, pearl white, immaculate.
- Snout very long, acuminate, protruding well beyond lower jaw.
- Light cream line running from snout to upper eyelid, followed by small irregular spots from eye to shoulder.
- Tympanum indistinct.
- When adpressed, Finger I shorter than Finger II.
- First toe much reduced.
- Digits unwebbed.

**Life history** - Mainly nocturnal (although the species may be heard calling during rainy days), terrestrial, fossorial. Found in primary forest, the species seems to prefer clearings. Males call exclusively during rain, from small burrows in the ground, below the leaf litter. Eggs are laid in burrows below the soil surface; tadpoles do not feed and complete their development within the burrow.

**Call** - First described by Pyburn (1975: 441), who provided a spectrogram. It consists of a short single plaintive whistle repeated at a rate of about 12 notes/min.

**Tadpole** - First described by Pyburn (1975: 442). Endotroph, nidicolous; cream white with a longitudinal light brown stripe.

**Abundance and distribution in KNP** - Rare. Observed or heard around main sampling localities # 2, 6, and 11 (see Fig. 3), the species is probably widespread in the Park.

**Geographic range** - Known only from the type locality and two localities in southern and southwestern Venezuela. Our record from Kaieteur National Park extends the known range about 850 km to the west. The species is also reported from near Manaus (see Zimmerman & Rodrigues, 1990, and Lima et al., 2006), but we have some doubts about the identity of those specimens.

**Taxonomic comments** - Although our specimens fit very well the original description, we notice slight differences in the call between a recorded male from Kaieteur and the paratype recorded by Pyburn (1975). The specimens from central Amazonia illustrated in Lima et al. (2006) look quite different from our specimens and comparison between these populations and specimens from the type locality is required.
**Pipa Laurenti, 1768**

“PIPAS”

Fig. 144. Pipa pipa, a species not recorded from Kaieteur National Park; here from Mabura Hill Forest Reserve, central Guyana. (Photo by R. Ernst).

- Medium to large size
- Body and head dorsoventrally depressed
- Snout protruding beyond lower jaw
- Maxillary teeth absent or present
- Pupil circular (Fig. 42C)
- Presence of a lateral line organ
- Skin on dorsum spiculate (Fig. 44E)
- Feet large, toes extensively webbed
- Toes I-III usually capped with keratinous tips (except in Pipa pipa and P. snethlageae)
- Fingertips modified into various arrangements of lobes (*e.g.* Fig. 51E)
- Presence of dermal modifications around the mouth
The genus *Pipa* currently contains seven species.

Pipas are nocturnal and aquatic frogs. They live in permanent or temporary water bodies and in slow-moving streams in tropical rainforest. Individuals have been collected at considerable distance from water and they apparently cross land from a pond to another (when a pond dries out for example). Specimens disturbed in very small pools may quickly escape in the surrounding forest.

Courtship behaviour is complex, involving vertical circular turnovers.

**Sexual dimorphism**

Males are usually slightly smaller than females; no other evident sexual dimorphism or dichromatism is evident.

**Eggs**

Eggs are embedded in the dorsal skin of the female.

![Fig. 145. A juvenile *Pipa pipa* emerging from its mother’s back. (Photo by R. Ernst).](image)

**Tadpoles**

Endotroph (paraviviparous) or exotroph (suspension-feeder).

**Distribution**

*Pipa* species are found in northern South America, including Trinidad, and in Panama (Murphy 1997; Frost, 2008).

Only *Pipa arrabali* (p. 236) is currently reported from Kaieteur National Park.
**Pipa arrabali** Izecksohn, 1976

1976: 508, figs 1-3.

**ENGLISH NAME:** Arrabal's pipa.

**LOCAL NAMES (PATAMONA):** Unknown.

**TYPE LOCALITY:** “Vila Amazônia, Município de Parintins, Estado do Amazonas, Brasil”.

**SELECTED REFERENCES:** Izecksohn, 1976 (original description, B&W photos and drawing, in Portuguese); Trueb & Cannatella, 1986 (description, osteology, B&W drawings, distribution, in English); Buchacher, 1993 (natural history, breeding habits, in English).

**Field identification** - Males reach 40.0 mm SVL, females 57.0 mm.
- Dorsal colour greenish brown to greyish brown, with irregular dark brown spots; skin on dorsum spiculate.
- Ventral surface shagreened, slightly spiculate, whitish, pinkish to orangish brown with irregular dark spots; throat often darker.
- Body and head dorsolaterally depressed.
- Eyes small, pupil circular, iris greenish brown.
- Upper lip forming small pocket at angle of jaw.
- Keratinous tips on Toes I-III.
- Fingertips modified into four small equal-sized lobes.
- Feet large, toes extensively webbed.

**Life history** - Mainly nocturnal, highly aquatic, but can occasionally be found on land. Observed in primary forest, in slow-moving streams and in small pools and puddles along streams. Males probably call from the water as in other species of the genus. Eggs and larvae are kept in dermal pockets on the back of the female, and toadlets emerged when completely metamorphosed; juveniles and adults feed on insect larvae, earthworms and tadpoles.

**Call** - Unknown.

**Tadpole** - No free-swimming larval stage occurs in this species. Endotroph, paraviviparous.

**Abundance and distribution in KNP** - Rare. Observed only around main sampling localities # 2 and 11 (see Fig. 3), but the species is probably widespread in the Park.

**Geographic range** - Reported from eastern Venezuela, through Guyana and western Suriname to northern and central Brazil.
**Pristimantis Jiménez de la Espada, 1871**

“SOUTH AMERICAN RAIN FROGS”

![Image of a frog](image.jpg)

**Fig. 147. Pristimantis jester**, a beautiful species that does not occur in Kaieteur National Park; here from Mt Maringma (Photo by P. J. R. Kok)

- Very small to large size
- Maxillary teeth present
- Pupil horizontally elliptical (Fig. 42A)
- Head about as wide as body
- Parotoid glands absent
- Skin on dorsum smooth, shagreened, granular, tuberculate, spiculate or warty (Fig. 44A-F)
- Vocal sac single, subgular (Fig. 56A)
- Finger I ≤ II when fingers adpressed
- Fingers unwebbed
- Finger discs expanded (Fig. 51B-C)
- Tympanum present, distinct or indistinct, or absent (Fig. 43A-C)
Pristimantis is a very large genus currently containing ca. 430 species; additional species are described each year.

Heinicke et al. (2007) removed Pristimantis from the synonymy of Eleutherodactylus on the basis of molecular data. The genus is now subdivided in three subgenera and several species series and species groups (Hedges et al., 2008).

South American rain frogs are nocturnal and mostly arboreal. They inhabit tropical rainforest and are not dependent on water bodies for reproduction (see below).

The genus is highly polymorphic (especially in skin texture), and most species of Pristimantis are exceedingly polychromatic, often rendering their identification problematic. A revision of the genus in the Guiana Shield is necessary to delimit exact species distribution and identify possible cryptic species.

**Sexual dimorphism**

Variable among species. Males are usually smaller than females and may have spinous nuptial pads or not.

**Eggs**

No eggs are laid (froglet births from oviduct) in at least one species (Pristimantis jasperi); eggs are terrestrial with no tadpole stage in other species.

**Tadpoles**

Endotroph (ovoviviparous or direct developer).

**Distribution**

Species belonging to the genus Pristimantis are found from Honduras to Bolivia, in the Guianas and in Trinidad and Tobago (Frost, 2008).

Only two species are currently recorded from Kaieteur National Park, but we suspect many additional species to be discovered.

**Field key to the Pristimantis species of Kaieteur National Park**

1. Yellowish spot on groin ................................................................. P. cf. inguinalis (p. 240)
1’. No yellowish spot on groin ......................................................... P. cf. marmoratus (p. 242)
**Pristimantis cf. inguinalis** (Parker, 1940)

**1940: 263.**

**English name:** New River South American rain frog.

**Local names (Patamona):** Unknown.

**Type locality:** “New River, British Guiana”.

**Selected references:** Parker, 1940 (original description, in English); Lescure, 1981b (description, B&W photo, in French); Lescure & Marty, 2001 (brief description, colour photo, in French).

**Field identification** - Males reach 20.0 mm SVL, females 27.0 mm.

- Dorsal colour highly variable, greenish brown, brown or dark brown, with darker markings, with or without a broad dorsolateral stripe extending from upper eyelid to midbody; skin on dorsum tuberculate.

- Ventral surface smooth to weakly granular; throat and chest whitish with dark brown flecks, venter dark grey with whitish flecks.

- Iris grey to gold in its upper part, reddish grey in its lower part.

- W-shaped darker marking on neck.

- Yellowish spot on groin.

- Digital discs expanded, very large.

- When adpressed, Finger I shorter than II; fingers unwebbed.

- Webbing on feet absent or very basal.

**Life history** - Nocturnal, arboreal. Exclusively observed in primary forest, the species seems to be more common in clearings. Males call at dusk and during the first part of the night, at heights between 0.5-2.5 m, from small trees that usually have trunks of small diameter.

**Call** - Apparently not formally described. Lescure & Marty (2001: 347, 368) provided some data and an oscillogram and spectrogram. The call consists of a single metallic note (“tik”), repeated at a rate of about 10-20 notes/min.

**Tadpole** - No larval stage occurs in the genus. Endotroph, direct developer.

**Abundance and distribution in KNP** - Rare. Observed only around main sampling locality # 11 (see Fig. 3), but the species might be more widespread in the Park.

**Geographic range** - Restricted to the Guianas (Guyana, Suriname, French Guiana).

**Taxonomic comments** - Due to the high polymorphism and polychromatism of the genus, additional morphological, and ideally molecular comparisons are needed to clarify the identity of the Kaieteur specimens, which might prove to belong to a different species.
**Pristimantis cf. marmoratus** (Boulenger, 1900)

1900: 56, pl. 5, fig. 6.

**ENGLISH NAME:** Marbled South American rain frog.

**LOCAL NAMES (PATAMONA):** Unknown.

**TYPE LOCALITY:** “foot of Mt. Roraima” [Guyana].

**SELECTED REFERENCES:** Boulenger, 1900 (original description, B&W drawing, in English); Lescure, 1981b (description, in French); Lescure & Marty, 2001 (brief description, colour photo, in French).

**Field identification** - Males reach 19.0 mm SVL, females 22.5 mm.

- Dorsal colour highly variable, brown, greenish brown, greyish brown, reddish brown or dark brown, with darker markings; skin on dorsum tuberculate.
- Ventral surface weakly granular, greyish white.
- Iris greyish in its upper part, copper in its lower part.
- W-shaped darker marking on neck.
- No yellowish spot on groin.
- Digital discs expanded, large.
- When adpressed, Finger I shorter than II; fingers unwebbed.
- Webbing on feet basal.

**Life history** - Nocturnal, arboreal. Exclusively observed in primary forest. Males call at dusk and during the night, at heights between 0.5-1.5 m, from small bushes and trees.

**Call** - Apparently not formally described. Lescure & Marty (2001: 347, 368) provided some data and an oscillogram and spectrogram. The call consists of a series of 4-10 metallic notes, repeated at a rate of about 18 calls/min according to Lescure & Marty (2001).

**Tadpole** - No larval stage occurs in the genus. Endotroph, direct developer.

**Abundance and distribution in KNP** - Very rare. Only observed around main sampling locality # 10 (see Fig. 3), but the species might be more widespread in the Park.

**Geographic range** - Found in southern and eastern Venezuela, Guyana, Suriname, French Guiana, and Amapá State in Brazil.

**Taxonomic comments** - Due to the high polymorphism and polychromatism of the genus, additional morphological, and ideally molecular comparisons are needed to confirm the presence of this species in Kaieteur.

**Remark** - Photos in figure 151 are of a specimen from French Guiana.
Microcaecilia Taylor, 1968

“TINY CAECILIANS”

- Tail absent (no discernible folds posterior to vent)
- Primary annuli congruent with segmentation of trunk musculature, some may be divided posteriorly by secondary annular grooves
- Scales present
- Eyes covered by skull bone, not visible
- Tentacle closer to eye position than to naris

The genus currently contains five species (a sixth species, from Suriname, is in press by M. Wilkinson and colleagues).

Distribution
Occurs from Ecuador through southern Venezuela to the Guiana Shield, also reported from São Paulo in Brazil (Frost, 2008).

Microcaecilia sp

**English Name**: None.
**Local Name (Patamona)**: Unknown.
**Type Locality**: -
**Selected Reference**: -

**Field identification** - Reaches 145.0 mm in total length.
- Body pinkish to bluish grey, darker in its two posterior thirds.
- Eyes not visible, covered by skull bone.
- Tentacle located below level of eye, very close to mouth.
- Only 9-18 secondary annuli, maximum 130 folds in total.

**Life history** - Virtually unknown. The only specimen collected was crawling on the ground in primary forest by day, after a heavy rain.

**Abundance and distribution in KNP** - Very rare. A single specimen collected around main sampling locality # 11 (see Fig. 3), but the species is probably more widespread in the Park.

**Geographic range** - Unknown, only three specimens currently known (one specimen from Kaieteur National Park, two additional specimens collected by R. Ernst at Mabura Hill Forest Reserve, central Guyana).

**Taxonomic comments** - Microcaecilia is a taxonomically challenging group. This species seems close to Microcaecilia rabei but differs in some discrete characters.

**Remark** - Photos in figure 152 are of a specimen from Mabura Hill Forest Reserve, central Guyana.
Fig. 150. *Microcaecilia* sp. A. Dorsolateral view of a living specimen. B. Close-up of neck and head of a living specimen. (Photos by R. Ernst).
Gymnophonia | Rhinatrematidae | Rhinatremus Duméril & Bibron, 1841

**Rhinatremus** Duméril & Bibron, 1841

“TWO-LINED CAECILIANS”

- Tail present (discernible folds posterior to vent)
- Annuli not congruent with segmentation of trunk musculature, no distinction between primary and secondary annular grooves
- Scales numerous
- Eyes visible externally
- Tentacle immediately anterior to or on the anterior edge of eye

The genus is currently monotypic, but see below.

**Distribution**

Occurs in the Guianas (Guyana, Suriname, French Guiana) and adjacent Amapá State in Brazil (Frost, 2008), but see below.

**Rhinatremus cf. bivittatum** (Guérin-Méneville, 1838)

1838: 16, pl. 25, fig. 2.

**English name:** Two-lined caecilian.

**Local name (Patamona):** Unknown.

**Type locality:** “L’Amérique méridionale” [South America].

**Selected references:** Taylor, 1968 (description, B&W drawings and photos, in English), Nussbaum & Hoogmoed, 1979 (description, distribution, in English), Lescure & Marty, 2001 (brief description, colour photo, in French).

**Field identification** - Reaches 235.0 mm in total length.
- Body medium to dark brown, with yellow lateral band and usually many irregular yellow flecks.
- Eyes well visible externally.
- Tentacle located just anterior to eye.
- Total number of body annuli 315-384.

**Life history** - Fossorial, subterranean; diurnal and nocturnal. Found in primary forest only. Breeding habits unknown, but probably breeds in streams with aquatic larva like other members of the family.

**Abundance and distribution in KNP** - Very rare, collected only around main sampling locality # 11 (see Fig. 3), but probably widespread in the Park.

**Geographic range** - Same as for the genus.

**Taxonomic comments** - The Kaieteur specimens substantially differ from specimens from the type locality (Cayenne, French Guiana) and most likely belong to an undescribed species (M. Wilkinson, D. Gower, P. Kok, pers. obs.).

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Fig. 151. *Rhinatrema* cf. *bivittatum* (Guérin-Méneville, 1838). A. A living male. B. Close-up of neck and head of a living male. (Photos by P. J. R. Kok).
6. Conservation issues

It is hoped that the data presented here, most likely not complete, will serve as a basis for future research in the area. Rare or highly secretive species that could occur in the Park, including possible new taxa, might have been missed because not all the park area has been sampled with the same intensity. Higher elevation areas between 600-900 m above sea level in the western and southeastern parts of Kaieteur National Park were notably undersampled; special attention should be paid to arboreal habitats such as bromeliads and high canopy, which also remain understudied.

The exceptional beauty and superlative natural phenomenon of Kaieteur Falls coupled with our data on biodiversity (including published and unpublished information on the reptiles of Kaieteur) indicate that Kaieteur National Park meets several of the criteria used by UNESCO (2008) to establish a site’s eligibility for World Heritage Status (e.g. criteria vii-x). In fact, the high biodiversity and high level of endemism observed in the Pakaraima Mountains of Guyana advocates for the designation of the entire region as a protected area. Protection of the region would also be protection of an important watershed.

Although a national park and a protected area, Kaieteur is inhabited by diamond miners. Some of these miners are working within the boundaries of the Park, but fortunately it appears that many of them are now working outside the protected area. Mechanized mining activities such as dredging and their associated habitat destruction and pollution are a threat to the fauna in certain parts of Kaieteur National Park, which have been extensively deforested (either for mining activities, for camp constructions, or for farming). It should be noted that early and less invasive techniques used to find gold and diamonds such as panning may have some benefits for the herpetofauna: small diamond/gold pits provide pools used as breeding sites by several species (e.g. Osteocephalus taurinus, Phyllomedusa bicolor, Phyllomedusa vaillantii, Pipa arrabali).

There are considerable anthropogenic alterations and pollution around Menzies Landing, notably due to diamond miners who use Menzies trail to bring food and gasoline from the Kaieteur airstrip to Menzies Landing. Gasoline is transported in large barrels that are rolled along the trail from the airstrip to Menzies Landing. It is common to see a layer of gasoline in the small streams running on and parallel to the trail.

Policy makers should be aware of the presence of unique endemic species that could be easily made extinct by development projects. Therefore we strongly suggest policy makers to be advised by scientists before making decisions that could be environmentally irreversible.

Tourists should be better informed and educated to preserve ecological quality of the site by minimizing their ecological impact (e.g. by proper disposal of waste, not disturbing the flora and the fauna).
7. Glossary

We are aware that some terms might be newly introduced or uncommon to the beginner. Explanations of many technical terms are already within the text, main others are defined in this section.

**Acoustic foramen**: the natural opening of the acoustic meatus.

**Acuminate**: narrowing to a slender point.

**Acute**: ending in a sharp point, pointed.

**Alkalisation**: the process by which a substance becomes an alkali, which is a compound having very basic properties (the opposite of an acid).

**Amplexus**: the copulatory embrace of frogs and toads.

**Annulus (pl. annuli)**: a ring-shaped structure or marking.

**Anthropophilic**: human-seeking or human-preferring; a species attracted by human beings.

**Aposematic**: relating to, characteristic of, or exhibiting aposematism (see aposematism).

**Aposematism**: an antipredator defence involving warning signals (e.g. warning colouration).

**Aquatic**: adapted to live in water; consisting of, relating to, or being in water.

**Arboreal**: adapted to live in the trees. Also an ecomorphological guild that includes lentic tadpoles adapted to live in water-filled phytotelmata or similar arboreal sites.

**Arciferal pectoral girdle**: an anuran pectoral girdle in which the epicoracoid cartilages are free and overlapping.

**Atlantal**: relating to the atlas.

**Atlas**: the first vertebra of the neck, articulating immediately with the skull.

**Benthic**: an ecomorphological guild that includes lentic or lotic tadpoles that rasp food from submerged surfaces mostly at or near the bottom.

**Bicondylar**: having two condyles.

**Bicuspid**: having two points (cusps) or prominences.

**Bulbous**: resembling a bulb in shape.

**Carnivorous**: an ecomorphological guild that includes lentic tadpoles that feed on macroinvertebrates and conspecific and heterospecific tadpoles.

**Ceratobranchial**: pertaining to the bone, or cartilage, below the epibranchial in a branchial arch.

**Chorus (pl. choruses)**: several frogs calling together.
Clade: a group of biological taxa that share features inherited from a common ancestor.

Class: a taxonomic category of related organisms ranking below a superclass or phylum and above an order.

Cleithrum: a bone external and adjacent to the clavicle.

Cloaca: the common cavity into which the intestinal, genital, and urinary tracts open.

Columella: the ear bone of amphibians and reptiles.

Condyle: a rounded articulating prominence at the end of a bone.

Conspecific: a member of the same species.

Convergence: the adaptive evolution of superficially similar structures in distantly related organisms subjected to similar environment.

Cosmopolitan: occurring in many parts of the world.

Cotyle: a cuplike cavity or organ.

Crest: a narrow prominent ridge.

Cryptic: (1) difficult to detect, especially visually, because of the resemblance of an animal with its environment; (2) cryptic species are distinct taxa that are not or hardly distinguishable on the basis of morphology.

Dentary teeth: the teeth on the dentary bone in the lower jaw.

Dextral: of, or pertaining to the right side.

Diapophysis: the part of the transverse process of a thoracic vertebra that articulates with its corresponding rib.

Direct developer: an ecomorphological guild that includes species that have direct development (no tadpole stage).

Distal: remote from the point of attachment or origin.

Dorsal ground colour: the basic colour of the dorsal skin.

Ectotherm (or poikilotherm): an organism that depends on heat external sources to regulate its body temperature.

Endemic: restricted to a certain region or part of a region.

Endotroph (or endotrophic): an embryo or larva that entirely depends on vitellogenic yolk or other parentally produced material for its development; sometimes non-feeding.

Epiphytic: a plant that grows on another plant upon which it depends for mechanical support only (not for nutrients).

Euthanize: killing without pain.

Excrescence: a protruding outgrowth from a part of the body.
**Exotroph (or exotrophic):** a larva that feeds on various materials not parentally derived, or trophic eggs provided by the mother.

**Explosive breeder:** a species that breeds in a very short period (see explosive breeding).

**Explosive breeding:** when all animals of a population congregate and breed in a very short period.

**Family:** a taxonomic category of related organisms ranking below an order and above a genus.

**Fibulare:** the bone or cartilage of the tarsus that articulates with the fibula, which is the outer of the two bones of the hindlimb.

**Filament:** a slender tip of the tail in some tadpoles.

**Firmisternal pectoral girdle:** an anuran pectoral girdle in which the epicoracoid cartilages are fused along the midline.

**Fossorial:** adapted to live underground. Also an ecomorphological guild that includes lotic, fusiform tadpoles that inhabit leaf mats in slow water areas.

**Frontal bones:** cranial bones lying between the orbits and the parietal bones. Usually paired, but may fuse to form a single frontal bone, or fuse with the parietal bones to form a single frontoparietal bone.

**Frontoparietal bones:** cranial bones consisting of the fused frontal and parietal bones. May be paired or fused in a single frontoparietal bone.

**Ganglion (pl. ganglia):** an encapsulated neural structure consisting of a collection of cell bodies or neurons.

**Gastromyzophorous:** an ecomorphological guild that includes lotic tadpoles that have the belly modified in a ventral sucker.

**Genus (pl. genera):** a taxonomic category of related organisms ranking below a family and above a species.

**Gill:** respiratory organ of aquatic organisms that breathe oxygen dissolved in water.

**Gill slit:** one of a series of slitlike openings by which the water from the gill is discharged.

**Girdle:** an encircling arrangement of bones.

**Gonad:** a gland in which sex cells (= gametes) are produced.

**Groin:** the posterior part of the flank near hindlimb insertion.

**Groove:** a long narrow furrow or channel.

**Hepatic peritoneum:** the layers of tissue that cover the liver.

**Herpetofauna:** the amphibian and reptile fauna

**Heterospecific:** belonging to a different species.
**Holarctic**: a biogeographic region; of, or pertaining to the temperate and Arctic regions of the Northern Hemisphere (divided into the Nearctic and Palearctic regions).

**Holochordal vertebrae**: vertebrae in which the notochord (= the axial support of all embryonic vertebrates) is entirely replaced by bone.

**Hydrography**: the scientific description and analysis of the physical characteristics of earth's surface waters.

**Insemination**: the introduction of semen (the fluid containing spermatozoa) into the reproductive tract of the female.

**Interclavicle**: a median bone connected with the sternum.

**Interhyoideus**: a buccal elevator muscle.

**Intraspecific**: involving the members of one species; occurring within a species.

**Jugal bone**: the arch of bone beneath the eye.

**Kingdom**: the largest of the divisions of living organisms.

**Keratinized**: hardened with keratin, which is an insoluble protein substance that constitutes the bulk of various horny structures.

**Lentic**: of, or relating to, or living in any nonflowing water system.

**Lotic**: of, or relating to, or living in any flowing water system.

**Macrophagous**: an ecomorphological guild that includes lentic tadpoles that presumably feed by taking larger bites of attached materials on submerged substrates.

**Medial**: of, or pertaining to the midline.

**Mimetic**: relating to, characteristic of, or exhibiting mimetism (see mimetism).

**Mimetism (or mimicry)**: the advantageous superficial resemblance of a palatable organism to an unpalatable, toxic organism (Batesian mimetism), or of an unpalatable, toxic organism to another unpalatable, toxic one (Müllerian mimetism).

**Monophyletic**: a group containing a hypothetical common ancestor and all its descendants; characterized by the possession of synapomorphies (see synapomorphy; paraphyletic; polyphyletic).

**Monotypic**: consisting of a single species.

**Morphometrics**: the study of variation and change in the form of organisms.

**Nasal bones**: cranial bones lying above the nasal capsule. Usually paired, but may be fused in a single element.

**Nearctic**: a biogeographic region; of, or pertaining to the temperate and Arctic regions of North America and Greenland.

**Nektonic**: an ecomorphological guild that includes lentic or lotic tadpoles that rasp food from submerged surfaces somewhere within the water column.
**Nidicolous**: an ecomorphological guild that includes species that have non-feeding tadpoles.

**Nychthemeral**: of, or relating to a 24h period.

**Obtuse**: blunt or rounded at the apex (tip).

**Odontophores**: the tooth-bearing processes of the vomer and palatine bones.

**Opercular element**: an ear cartilage or bone.

**Order**: a taxonomic category of related organisms ranking above a family and below a class.

**Oviduct**: the tube through which eggs (ova) pass from the ovary to the uterus or to the outside.

**Oviparous**: eggs that hatch outside the body of the mother.

**Ovoviviparous**: eggs that hatch within the female’s oviduct without obtaining nourishment from it (birth of live offspring).

**Palatines**: paired bones in the anterior portion of the roof of the mouth.

**Palatoquadrate**: a series of bones or a cartilaginous rod constituting part of the roof of the mouth or upper jaw.

**Palearctic**: a biogeographic region; of, or pertaining to the temperate and Arctic regions of Europe and Asia.

**Papilla amphibiorum**: a sensory area in the wall of the sacculus (one of the maculae of the vestibular apparatus) of the inner ear of amphibians.

**Paraviviparous**: an ecomorphological guild that includes species in which froglets hatch at various sites in or on the mother’s body.

**Parietal bones**: cranial bones usually bordered by frontal bones anteriorly and occipital bone(s) posteriorly. Usually paired, but may fuse to form a single bone, or fuse with the frontal bones to form a single frontoparietal bone.

**Paraphyletic**: a group of taxa containing a hypothetical ancestor, but not all of its descendants; often characterized by the possession of plesiomorphic characters (see monophyletic; plesiomorphic; polyphyletic).

**Parietal peritoneum**: the layers of tissue that line the abdominal and pelvic cavities.

**Parotoid gland**: an enlarged external skin gland behind the eye in amphibians that secretes neurotoxic milky substance to deter predators.

**Pedicellate**: having or supported by a pedicel.

**Penultimate**: next to terminal.

**Pericardial peritoneum**: the layers of tissue that cover the heart.

**Phalanx (pl. phalanges)**: a bone of a finger or toe.

**Phylum**: a primary division of a kingdom of living organisms.
Physiognomy: the external aspect.

Physiography: the scientific description and analysis of the natural features of the earth's surface.

Phytotelm (pl. phytotelma): water-holding cavity in some part of a plant or plant product.

Plesiomorphic: primitive, as opposed to advanced; the quality of being group-defining only at a higher level.

Polychromatic: relating to, characteristic of, or exhibiting polychromatism (see polychromatism).

Polychromatism: the occurrence of several different colours and colour patterns in organisms of a same species (or in a population), independent of sexual variation.

Polymorphic: relating to, characteristic of, or exhibiting polymorphism (see polymorphism).

Polymorphism: the occurrence of several different morphological types in organisms of a same species (or in a population), independent of sexual variation.

Polyphyletic: a group of taxa containing some of the descendants of a hypothetical common ancestor, but not the hypothetical common ancestor itself; characterized by the possession of convergent characters (see monophyletic; paraphyletic).

Postorbital bone: cranial bone bordering the orbit posteriorly.

Postparietal bones: the series of paired bones on the posterodorsal surface of the skull.

Premaxilla (pl. premaxillae): one of a pair of bones located in front of and between the maxillary bones in the upper jaw of vertebrates; the anteriormost portion of the maxillary arch.

Presacral vertebrae: the vertebrae other than the sacral (pelvic) and caudal (tail) vertebrae.

Procoelous: a pattern of vertebral articulation in which the individual vertebrae have a concave anterior face and convex posterior face.

Prootic bone: a bone forming part of the auditory capsule.

Proximal: situated near the point of attachment or origin.

Pseudotail: the presence of a few postcloacal vertebrae in the terminal shield in some caecilians.

Pterygoid: a bone of the posterior palatal region (roof of the mouth).

Rank: to classify; a relative position in a classification.

Rheophilous: a generic term describing tadpoles adapted to live in microhabitats in the flowing parts of lotic systems.
Sacrum: a vertebra or vertebrae articulating with the pelvic girdle.

Sensu stricto: in the stricter sense; using a taxon restrictively in the sense of the original author.

Septomaxilla: a small bone between the nasal septum (which is the partition separating the two nasal cavities) and the maxilla (which is one of two identical bones that form the upper jaw).

Sexual dichromatism: an intraspecific difference in colour or colour pattern between the sexes.

Sexual dimorphism: an intraspecific morphological difference between the sexes.

Sinistral: of, or pertaining to the left side.

Species: a basic taxonomic category ranking below the genus (or subgenus) and consisting of related organisms capable of interbreeding and producing fertile offspring.

Splenial teeth: the teeth on the splenial bone in the lower jaw.

Superclass: a taxonomic category of related organisms ranking below a phylum and above a class.

Supratemporal bones: cranial bones situated in the temporal region.

Suspension-feeder: an ecomorphological guild that includes lentic tadpoles specialized in feeding on naturally suspended particles by pumping water in through the mouth, over the buccopharyngeal filtering system and out the spiracle.

Suspension-rasper: an ecomorphological guild that includes lentic tadpoles that apparently feed by filtering suspended particles from within the water column and rasping submerged surfaces.

Synapomorphy: a character shared by all basal members of a clade and derived from their hypothetical common ancestor (see monophyletic).

Tabular bones: cranial bones situated behind the supratemporal bones.

Taxon (pl. taxa): a particular taxonomic grouping, e.g. a particular species, genus, family, order, class, phylum or kingdom.

Tepui: a table-top mountain, typical of the Guiana Shield highlands.

Terminal: anatomical position pertaining to the end of a structure.

Terrestrial: adapted to live on land; consisting of, relating to, or being on land.

Tertiary: of third rank.

Tetralobate: having four lobes.

Tetrapod: literally an animal with four feet. Used here for members of the superclass Tetrapoda regardless the presence or absence of four limbs/feet.

Tibiale: the bone or cartilage of the tarsus that articulates with the tibia, which is
the inner of the two bones of the hindlimb.

**Trilobate:** having three lobes.

**Truncate:** terminating abruptly.

**Ulna:** the forearm.

**Ultrasonic:** of, or producing acoustic frequencies that are above the range audible by the human ear (*i.e.* frequencies above ca. 20,000 Hertz).

**Urostyle:** a styliform process forming the posterior extremity of the vertebral column.

**Vacuum:** a space that contains no air or other gas.

**Vent:** the cloacal opening.

**Visceral peritoneum:** the layers of tissue that cover the viscera (intestines).

**Viviparous:** live offspring develop within the oviduct or uterus by receiving nutrition from the mother.

**Xeric:** of, characterized by, or adapted to an arid habitat.
8. References


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11. Appendix – Taxonomic index

Species treated and page numbers that hold taxa descriptions are in bold, page numbers that hold species illustrations are in italics.

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Introduction to the taxonomy of the amphibians of Kaieteur National Park, Guyana

One of the impediments to understanding amphibian diversity in the Neotropics is the lack of complete, taxonomically accurate treatments of the amphibian species from geographically restricted areas. Botanists have long appreciated the importance of such studies and have reported the studies as florulas. The present work can be paraphrased as the amphibian faunula of Kaieteur National Park. A successful florula or fauna must be based on intensive sampling. It needs to be presented in such a way that users of the work can incorporate new taxonomic changes because sufficient information provided in the faunula/florula allows the worker to assess whether new taxonomic results apply to the faunula/florula involved. This is particularly critical for amphibian species, which are undergoing massive taxonomic revisions, especially in tropical regions. The authors of the Kaieteur National Park faunula present the data needed to determine the proper name(s) for Kaieteur National Park taxa.

Another feature of this work is the only detailed resource of which I am aware that documents how to successfully undertake amphibian fieldwork, including permit application procedures, equipment needed for work in remote areas, sampling methodology, collecting equipment, data collection, voucher specimen preservation, molecular study samples, advertisement call recordings, etc.

The amphibian faunula of Kaieteur National Park is a welcome addition to the altogether too few intensive amphibian publications of northern South America such as those for Santa Cecilia, Ecuador and Reserve Duske, Brasil.

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