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 23.3ºC (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.

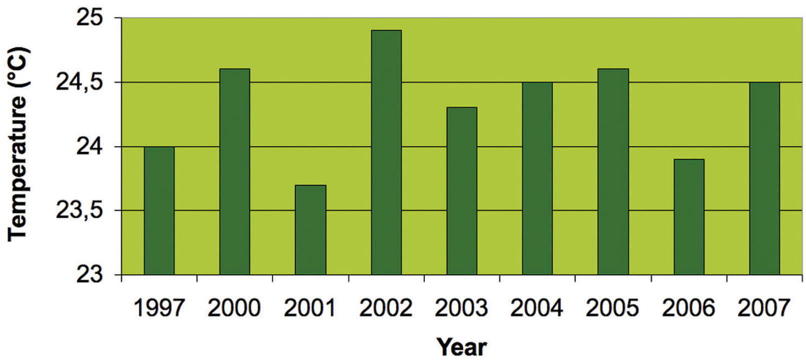

Fig. 12. Yearly mean temperature for Kaieteur National Park (data supplied by the Guyana Hydrometeorological Service, 2008).

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).

Year	Dry Bulb (°C)	Wet Bulb (°C)	Relative Humidity (%)	Dew Point Temperature (°C)
1997	24.4	22.3	84	21.4
2000	24.1	22.4	87	21.7
2001	23.3	21.0	81	19.9
2003	25.5	23.2	83	22.3
2004	25.1	22.9	83	22.0
2005	25.9	23.3	80	22.1
2006	25.2	22.9	83	22.0
2007	24.2	22.5	86	21.7

Table 1: Yearly average relative humidity of Kaieteur National Park (data supplied by the Guyana Hydrometeorological Service, 2008).

Year/ Months	1997	2000	2001	2002	2003	2004	2005	2006	2007	Mean
1	326.9	523.8	168.1	DD	187.4	249.9	403.8	892.2	346.1	387.4
2	589.1	227.3	106.1	DD	138.8	107.5	311.0	211.9	136.2	228.5
3	DD	219.3	84.4	DD	139.9	201.1	146.8	265	296.1	193.2
4	DD	DD	258.0	DD	334.7	493.9	730.9	95.4	547.1	410.0
5	551.6	DD	633.4	DD	837.7	1089.7	849.7	407.6	DD	728.3
6	DD	DD	467.2	DD	596.2	721.6	318.4	778.9	626.5	584.8
7	483.9	DD	DD	DD	448.2	464.4	331.5	964.4	401.6	515.7
8	88.0	DD	DD	DD	318.6	276.2	460.5	197.7	304.2	274.2
9	DD	162.7	DD	105.6	88.7	252.9	36.2	101.9	194.1	134.6
10	213.6	111.5	DD	41.6	99.8	DD	60.3	141.1	202.3	124.3
11	DD	367.4	DD	395.7	294.4	163.8	138.1	292.4	DD	275.3
12	DD	585.9	DD	331.4	240.7	206.0	814.6	467.4	DD	441.0

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).

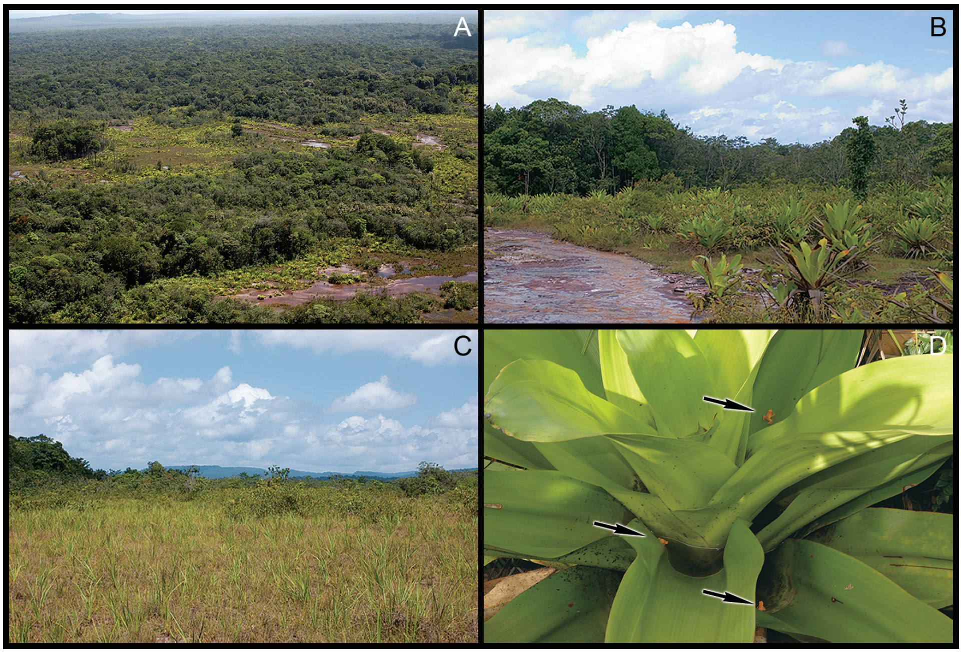

Fig. 15. Shrub and herbaceous formations found in Kaieteur National Park. A-B. Shrubland and forest at the top of Kaieteur Falls; C. Mostly anthropogenic herbaceous formation at the top of Kaieteur Falls; D. The terrestrial bromeliad *Brocchinia micrantha* is a major element of the savannah surrounding 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).

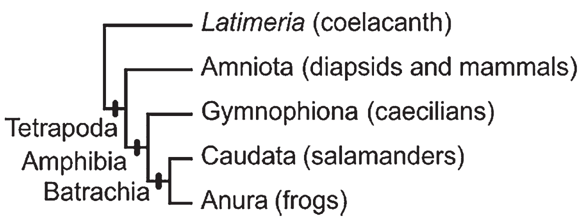

Fig. 16. Basal structure of Frost *et al.*’s (2006) consensus tree with respect to outgroups and major amphibian taxa. Copied from Frost *et al.* (2006: 113), with permission of D. R. Frost.

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 germinal 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 caecilians 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 (phallodeum) of the cloaca (Duellman & Trueb, 1986) and is a uniquely derived structure among vertebrates (Wake, 2006).

Fig. 17. Intromittent organ of the caecilian *Rhinatrema* 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 segmetation 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 Palearctic 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 (Señaris & 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. Amplectic 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 in 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, Bombinatoridae, **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**, Ptychadenidae, 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 aposematic 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 firmisternal, 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 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 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 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; 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 jaw, and the intermandibular muscle has variable development of accessory lips; 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 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 Hylinae, 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 (vertically elliptical in Phyllomedusinae). 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, opisthocoelous 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 Kaieteur 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.