CONTENTS

- 6 Introduction
- 58 Archaeobatrachia
- 68 Mesobatrachia
- 86 Neobatrachia
- 234 Glossary
- 236 Further Reading and Useful Resources
- 237 Index
- 240 Picture Credits and Acknowledgments





CAMOUFLAGE AND CRYPSIS

Some of the camouflage capabilities of frogs are truly astounding, with some species blending in perfectly with their background. Perhaps one of the best examples of this can be found in the Vietnamese Mossy Frog (*Theloderma corticale*), which looks remarkably like moss. Not only is their color speckled in a dark to light green and brown, but they have tuberculate skin (having small, rounded projections) and their eye pattern and color even matches their skin. Other species have evolved to match even unexpected features in their environment, such as the South American hylid *Dendropsophus marmoratus*, which resembles bird poo!

Aquatic frogs have also had to adapt to blend into their environment. The Suriname Toad (*Pipa pipa*) has evolved to look very much like a dead leaf sitting at the bottom of slow-flowing rivers. They have triangular-shaped heads, a flattened body, are brown/olive, and have tubercles along their skin. They will rest with their arms to the sides of their body and remain motionless for extended periods of time.

Some species opt to confuse predators and use a disruptive coloration tactic to do this. They achieve this by using colors and patterns to break up their body outline. The most common ways are by incorporation of blotches or a dorsal line. **ABOVE LEFT** Suriname Toads (*Pipa pipa*) will rest motionless in slow moving water waiting for prey to swim close enough for them to capture. Their body form makes it difficult for predators to spot them.

ABOVE RIGHT Vietnamese Mossy Frogs (*Theloderma corticale*) display incredible camouflage when resting on mossy substrates.

COLOR AS A WARNING

Many species of frog are vibrant in color. This may seem counterintuitive from a predation perspective because they will be highly visible. However, these bright colors act as warning signals to would-be predators about the toxic nature of the frogs; this toxic advertisement is known as aposematism. No frogs exemplify this more than the Central and South American poison dart frogs (Dendrobatidae), cryptic dart frogs (Aromobatidae), and harlequin toads (*Atelopus* spp.); the Atlantic Forest of South America's saddleback toads (*Brachycephalus* spp.); and Madagascar's tomato frogs (*Dyscophus* spp.) and mantellas (Mantellidae).

Other species do not continuously display their aposematic coloration and instead conceal it when resting. Fire-bellied toads (*Bombina* spp.) only have aposematic coloration on their ventral surface and when threatened they will lift their body off the ground, displaying their bright-red underside, a tactic known as unkenreflex.

Other species have eye spots, such as the Brazilian leptodactylid frog *Physalaemus deimaticus*, which when threatened raises up its rear end and puffs up its body, displaying dramatic black spots that are thought to mimic the eyes of snakes. This behavior is known as a "deimatic" display.





TOP The Yellow-banded Poison Frog (*Dendrobates leucomelas*) has bright coloration to warn predators of its toxicity.

MIDDLE The red coloration of Tomato Frogs (*Dyscophus antongilii*) is a warning that when harassed they will secrete a sticky toxic substance from their skin.

RIGHT The exceptionally brightly colored Purple Harlequin Toad (*Atelopus barbotini*) uses its colors as a signal about its toxicity.



OTHER ADAPTATIONS

There are lots of other mechanisms that frogs use to avoid predation. When attacked, the Hairy Frog and night frogs (*Astylosternus* spp.) from Central Africa will break their bones in their hind feet and then push these through their own skin. They then use these protruding bones to stab into the attacking animal. This adaptation has given *Astylosternus robustus* the alternate name of the Wolverine Frog, in reference to the claws that emerge from the hands of the Marvel superhero Wolverine.

Many frogs will urinate when harassed. This urine can be smelly and foul-tasting, meaning that if a predator has the frog in its mouth, it might be tempted to release it. Other species may bury themselves in mud or feign death by remaining motionless to avoid confrontations with predators in the first place. The Pebble Toad (*Oreophrynella nigra*) from northern South America will curl up into a ball and roll away from danger.

USING OTHER ANIMALS FOR PROTECTION

Some frogs use other animals as protection. For example, members of the species-rich narrow-mouthed frogs (Microhylidae) from South America and Asia live with spiders. These small frogs gain protection from these often large spiders, and in return it is believed that the frogs eat the small arthropods that would otherwise cause problems





ABOVE A Dotted Humming Frog (*Chiasmocleis ventrimaculata*) coexisting in a mutualistic relationship with a large Peruvian Tarauntula (*Pamphobeteus* sp.).

LEFT | The bones on the hindfoot of the Wolverine Frog (*Astylosternus robustus*) have been pushed through the skin as a defense mechanism.

Introduction



for the spiders. This is a mutualistic behavior because both the frog and spider benefit from the relationship. It is possible that the relationships between the spiders and frogs are species-specific. The Dotted Humming Frog (*Chiasmocleis ventrimaculata*) from the western Amazon region of South America is known to co-occur with several species of tarantula and other spiders. The spiders use chemical signals to recognize these frogs instead of eating them, as they have been recorded to do for other species of frog.



LOCOMOTION

Frogs move in a number of different ways but the most well known is hopping or jumping. Almost everywhere that frogs occur there will be at least one species that hops or jumps. Frogs are particularly adept at jumping due to their enlarged hind limbs and strong thigh muscles. These large limbs are capable of propelling the frogs forward, often over incredibly large distances for their size. The American Bullfrog (Aquarana catesbeiana) is a large frog at about 7 in (180 mm) in length, but despite this the species has a truly impressive jumping capability, recorded at up to 7 ft 2 in (2.2 m), which is a staggering 12 times its total length. However, the American Bullfrog's leap looks miniscule considering its body size when comparing it to the Sharp-nosed Grass Frog (Ptychadena oxyrhynchus) from southern Africa, where one

individual jumped 17 ft 6 in (5.35 m), which was more than 90 times its total length! Although not all species are capable of such large leaps, other species are capable of extreme speed. The Coastal Ecuador Smoky Jungle Frog (*Leptodactylus peritoaktites*) when disturbed is incredibly fast, combining powerful leaps one after the other. The speed is so great that even on flat ground it is often difficult for a human to keep up when running from a standing start.

WALKING AND RUNNING

Not all frogs jump when navigating through their environment, with some opting to walk or run instead. All frogs are capable of walking, but it is often cumbersome for many species due to their large hindlimbs. However, some species are better adapted to walking and running than others, with



these species often having shorter hindlimbs than those of other frogs, meaning that their hindlimbs are more similar in length to their forelimbs. One species that almost exclusively moves in this way is the European Natterjack Toad (*Epidalea calamita*), which is capable of running at fairly quick speeds. This, coupled with the "go-faster stripe" that tracks down the center of its dorsum, gives the species its other common name of Running Toad.

SWIMMING

As discussed earlier, tadpoles are well adapted to an aquatic lifestyle, but many adult frog species are also adapted to life in an aquatic environment. Species that have some association with water courses generally have webbed feet to enable them to swim more efficiently. The level of webbing usually depends upon the extent to which the species is linked with water for example, species that are fully aquatic have extensively webbed feet. The African Clawed Frog (*Xenopus laevis*,) has large webbing on its hindfeet that it fans out and uses to make big paddle-like strokes while moving. Perhaps the most interesting aquatic adaptation of any frog can be seen in the Hairy Frog (*Astylosternus robustus*) from West Africa, where there is extreme sexual dimorphism and the males spend most of their lives in the water. The males have papillae on the sides and thighs, increasing their surface area for highly efficient gas exchange while in the water.

ABOVE A European Tree Frog (*Hyla arborea*) displaying a typical jumping motion of a frog.





ABOVE Like other treefrogs, *Phyllomedusa bahiana* climbs and sticks to surfaces using its adhesive toe pads and subarticular tubercles.

CLIMBING

Frogs have adapted equally well to life in trees as they have to living in water and on the ground. Arboreality has evolved numerous times, to occupy the countless niches that life in the trees offers. Throughout the tropics, tree-dwelling frogs are as abundant as frogs that live on the ground. Arboreal frogs have had to adapt to ensure that they are capable of supporting their body weight in the trees, regularly achieving this by having adhesive toe pads that are often wider than their ground-dwelling counterparts, a lengthening of their foreand hindlimbs, and increased flexibility in their ankle joints.

GLIDING

There are several species of frog that can sail through the air to escape predators or to move through their environment with more energy efficiency, in a process termed parachuting or gliding. This behavior is especially prevalent in members of the Flying Frogs (*Rhacophorus*). These frogs have extensive webbing between their digits that act like



parachutes when the frogs jump from a high point. The skin flaps, patagia, are extended during flight, increasing the surface area and enabling the frog to slow its descent and glide through the air.

BURROWING

Burrowing is a common feature among frogs, scattered across several families. Almost all burrowing species will use the metatarsal tubercles on their hind feet, which act like shovels, to excavate the soil. Other species will burrow forward. For example, the Shovelnose Frogs (*Hemisus* spp.) of Africa burrow headfirst by using their shovel-shaped nose to push their way through the substrate.

Different species use burrowing behavior in different ways. Some will use the behavior to escape or hide from predators, some will burrow to retain moisture, some dig burrows in order to breed or rear young, and others will forage for soil-dwelling invertebrates. **ABOVE** | The Wallace's Flying Frog (*Rhacophorus nigropalmatus*) extends the patagia between its toes to allow it to slow its descent from high in the canopy.

LIFE IN EXTREME CONDITIONS

Frogs have a global distribution, occurring on every continent except Antarctica. They can be found in almost every terrestrial habitat on earth, and in many temperate regions they are considered ubiquitous within wetland habitats. However, frogs have an incredible ability to adapt when we consider that their anatomy and physiology mean they are tied to water and are ectothermic. As discussed on page 18, some species can form cocoons to estivate during extreme conditions.

Frogs do not cope well with salt water due to their need to use their skin for gas exchange,

and salt prohibits this. This is one reason why amphibians are rare on geologically recent islands. Some families seem to tolerate transoceanic dispersal, such as the Hyperoliidae of Africa, which have colonized islands to the west and east of the main landmass, including as far as the Seychelles archipelago. The Cane Toad (*Rhinella marina*) can tolerate saline conditions and has even been observed swimming in the sea on occasion. The Crab-eating Frog (*Fejervarya cancrivora*) of Southeast Asia lives in brackish environments and eats a range of crustaceans (for example, crabs) and insects that inhabit these environments.

ABOVE Crab-eating Frogs (*Fejervarya cancrivora*) are unusual among frogs because they are one of just a handful of species capable of surviving and hunting in saline conditions.

OPPOSITE | Wood Frogs (*Boreorana* sylvatica) have the amazing ability of being able to be frozen during extremely cold weather conditions without any ill effects.

Many frogs hibernate to escape the cold temperatures of winter. Perhaps the most amazing frog species to have adapted to extreme cold conditions is the Wood Frog (*Boreorana sylvatica*) of North America, which occurs as far north as northern Alaska. These frogs essentially freeze, with up to 60 percent of their body becoming frozen solid for up to eight months of the year! During this time ice crystals form between the muscles and the skin, and large amounts of glucose enter each cell. The outside of each cell freezes but the glucose in each cell prevents the internal parts of the cell from freezing. During this time, metabolism effectively shuts down and the heart completely stops. Once temperatures increase the frog thaws and prepares for breeding. No other known tetrapod is capable of such feats!

At the other end of the spectrum, some frogs tolerate extremely hot environments. The Ryukyu Kajika Frog (*Buergeria japonica*) inhabits hot springs in Taiwan and the Ryukyu Archipelago in Japan. Tadpoles have been reported to occur in pools of 115°F (46.1°C); average human bath temperatures are 95–104°F (35–40°C).

CONSERVATION

Frogs are vital for proper ecological equilibrium in both aquatic and terrestrial environments. Tadpoles eat algae, keeping aquatic environments from being inundated with detrimental algal blooms. Adults eat pest invertebrate species that could otherwise cause devastation to natural environments and result in enormous economic impact upon agriculture. Frogs are food for countless other animals, including terrestrial mammals, bats, birds, reptiles, and invertebrates. Additionally, they help humans beyond being ecologically important by acting as bioindicators and keeping mosquito-borne diseases at bay (some tadpoles eat mosquito larvae and adult frogs eat the adults).

THREAT STATUS

Amphibians are the most threatened terrestrial vertebrate group on the planet, with tens of species likely going extinct each year. The

International Union for Conservation of Nature (IUCN) is the primary international organization for the conservation of animals, plants, and fungi. The IUCN maintains the Red List of Threatened Species, which is the main resource for categorizing the threat status of organisms. To date, 6,580 of the 7,600+ known frog species have been evaluated, and only 46 percent of these are considered to be free from any imminent danger of becoming extinct. We know of at least 33 frog species that have become completely extinct in recent years and two that are Extinct in the Wild; however, this number could be much higher, as many species have not been seen for decades. Some estimates suggest that upward of 200 species have gone extinct in recent years. Over 1,500 species are in immediate danger of becoming extinct and are classified as either Endangered or Critically Endangered. Most of the approximately 2,000 species that have been classified as Data Deficient

> **OPPOSITE** | The Kihansi Spray Toad (*Netophrynoides asperginis*) has been the focus of a successful captive breeding program and reintroductions have started to take place in the wild.

LEFT The Southern Gastric Brooding Frog (*Rheobatrachus silus*) of Australia is now extinct, possibly caused by chytrid fungus.

Introduction

or have not been evaluated are almost certainly at risk of extinction because they have not been evaluated due to a general lack of observations, probably because they are rare.

There are numerous threats to amphibian populations, including loss of habitat, disease, climate change, agricultural practices, pollution, and invasive species. Unfortunately, it is usually a combination of these factors that are causing amphibian populations to suffer.

HABITAT LOSS

Habitat loss and the conversion of amphibian habitat into agricultural land is the greatest factor causing declines. Many of the areas with the highest diversity, such as Brazil and Madagascar, have been the most affected by habitat destruction.

Habitat destruction comes in various forms, and the most notable contributions to amphibian

declines are total loss of habitat, removal of aquatic breeding grounds, and habitat fragmentation. While fragmentation may not necessarily cause noticeable declines at first, it can lead to a loss of genetic diversity—meaning that the animals become less fit within their environment or are unable to adapt to changing conditions.

The Kihansi Spray Toad (*Nectophrynoides asperginis*) from the Udzungwa Mountains in Tanzania is now considered Extinct in the Wild, according to the IUCN Red List. The species was only known within the spray zone of the Kihansi Falls. A dam constructed farther up the Kihansi River decreased the flow of water passing over the falls by 90 percent, removing the only known habitat of the species. This is just one of hundreds, possibly thousands, of examples of habitat loss that have led to catastrophic declines in frog populations.

DISEASE

Disease is a major cause of frog declines. The most prominent and devastating to frog populations is the amphibian chytrid fungus *Batrachochytrium dendrobatidis*, which is a fungal disease that often leads to the death of its hosts. However, some species seem more resistant than others and the fungus has only limited effects. The fungus grows in the skin layers and can eventually lead to heart failure given that the frog's permeable skin cannot regulate water and gas intake.

Chytrid fungus has caused an estimated 90+ species to go extinct and hundreds of other species to decline significantly. The fungus has been confirmed in every amphibian-inhabited region in the world except for the Seychelles Archipelago. The worst-affected regions are Central and South America, and Australia.

You can help stop the spread of chytrid between populations by maintaining good biosecurity and ensuring footwear is clean and free of dirt when traveling to new areas.

ABOVE | Drought and chytrid fungus (*Batrachochytrium dendrobatidis*) has caused the Northern Corroboree Frog (*Pseudophryne pengilleyi*) to be isolated to just three small subpopulations in southeast Australia.

BELOW The Cusco Andes Frog (*Bryophryne cophites*) from Peru has been killed by the lethal amphibian chytrid fungus (*Batrachochytrium dendrobatidis*).

CLIMATE CHANGE

Frogs are ectothermic animals with osmotically sensitive physiology, so it is no surprise that their ecologies and distributions are intrinsically linked to climatic variables. It is widely believed that the rapid onset of climate change means that most frog species will be unable to adapt quickly enough to these changes. We are already seeing the results of climate change on frogs from around the world. The Lowland Leopard Frog (*Lithobates yavapaiensis*) from North America has undergone massive declines in many parts of its range due to severe droughts, and the Northern Corroboree Frog (*Pseudophryne pengilleyi*) from Australia has declined and lost at least 42 percent of its breeding sites due to drought.

LEFT A swab sample is being taken from a Majorcan Midwife Toad (*Alytes muletensis*) to test for the presence of the amphibian chytrid fungus (*Batrachochytrium dendrobatidis*).

CHEMICAL CONTAMINATION

Amphibian survival is closely linked to their environment. Frogs have highly sensitive skin important for transfer of gases and water into their body, their eggs are porous, and the larvae have gills. Environmental contaminants from an industrial or agricultural landscape can have cataclysmic effects on amphibians, leading to death, a loss of fitness, or infertility. Chemicals, including antimicrobials and microplastics as well as other common pesticides and heavy metals, usually accompany other factors such as habitat loss, causing increased pressure on populations.

CONSERVATION ACTIONS

It is not all doom and gloom, though, and there have been some fantastic conservation success stories. Conservation actions are driven by dedicated people throughout the world, including academic institutions, conservation organizations, governmental agencies, and members of the public. These inspirational people have at times brought species back from the brink of extinction, whether directly or indirectly, even by doing seemingly simple things like recording sightings of species. There are three major amphibian organizations dedicated to the conservation of amphibians, working very closely with one another but each having unique responsibilities:

1.

The Amphibian Survival Alliance promotes and coordinates conservation actions for amphibians, including outreach with local communities and establishing partnerships.

2.

The IUCN SSC Amphibian Specialist Group provides the scientific foundation to inform effective amphibian conservation action.

3.

The Amphibian Ark leads on the *ex situ* conservation of amphibians, building in-country expertise, and Conservation Needs Assessments (a framework for identifying immediate conservation requirements for individual species).

SUCCESS STORIES

We will finish the introductory section of this book by discussing some of the incredible stories of species recovery. The Mountain Chicken Frog (Leptodactylus fallax) is the largest amphibian in the eastern Caribbean, occurring on the small islands of Dominica and Montserrat. The Mountain Chicken has been an economically important species for the people living on the islands, acting as a major food source. In 2002 (Dominica) and 2009 (Montserrat), chytrid devastated the populations, resulting in one of the most rapid declines in a vertebrate species ever recorded. It is likely that no wild individuals now survive on Montserrat. Due to a fast response from the amphibian conservation community, however, Mountain Chickens were taken into captivity to form a successful conservation breeding program in Europe. Subsequently, a breeding facility and a genetics diagnostics lab that performs regular testing for chytrid has been established on Dominica. Most recently a seemingly successful semi-wild control area has been established to investigate reintroduction potential—and the results from this look promising, meaning that the future of the Mountain Chicken might be secured.

The Pool Frog (*Pelophylax lessonae*) is a ubiquitous species across many parts of Europe but native populations became extinct in the UK in 1995 due to a loss of habitat. By translocating animals from Sweden (part of the same clade as the native UK population), two sites in Norfolk in eastern England were selected for a series of reintroductions. These reintroductions have so far been successful, with yearly breeding over the past few years, showing very positive signs for the species in the UK.

> **OPPOSITE ABOVE** | Map showing global distribution of the Anura. Colors denote approximate species diversity with red representing highest diversity areas through to blue, indicating lowest diversity.

OPPOSITE BELOW It is hoped that with the successful reintroduction program the Pool Frog (*Pelophylax lessonae*) will become more widespread in Britain over the coming years.

LEFT A long-term recovery strategy has been put in place to help conserve the Mountain Chicken Frog (*Leptodactylus fallax*).

Introduction

THE FROG SUBORDERS AND SUPERFAMILIES

The Anura contains three suborders, the Archaeobatrachia, Mesobatrachia, and Neobatrachia, although authors have differed with regard to which families comprise the first two of these.

The Archaeobatrachia (archaeo- = ancient; batrachia = frogs) contains the oldest extant frog families, the Ascaphidae and Leiopelmatidae of NW North America and New Zealand respectively, which together comprise the superfamily Leiopelmatoidea, and the European Alytidae and Bombinatoridae, forming the superfamily Discoglossoidea. These extant frogs are linked to long extinct frogs by a number of primitive anatomical characters (see page 59).

The Mesobatrachia (meso- = middle; batrachian) contains those frog families that are more recent than the archaeobatrachians, but which still exhibit primitive anatomical characters (see page 69). This suborder comprises two superfamilies, the Afro-American Pipoidea, with two families, and Eurasian-American Pelobatoidea, with four families.

All other extant anurans belong to the complex Neobatrachia (neo- + new; batrachia). The most basal family is the South African Heleophrynidae, with the remaining families in the Sooglossoidea (2 families, Seychelles and India), Myobatrachoidea (3 families, Australasia and Chile), Hyloidea (21 families), and Ranoidea (19 families).

BELOW The Strawberry Poison Frog (*Oophaga pumilio*) comes in as many as thirty different color phases ranging from bright red, red with blue legs (blue jeans phase), to green with black spots.

> The Frog Suborders and Superfamilies For general queries, contact info@press.princeton.edu

For general queries, contact info@press.princeton.edu

OPPOSITE | The Yellow-bellied Toad (*Bombina variegata*) is a widely distributed species in Europe.

ARCHAEOBATRACHIA

The Archaeobatrachia contains 4 primitive anuran families, 7 genera, and 27 species, survivors from the dinosaur age. The Ascaphidae of northwestern North America, and the Leiopelmatidae from New Zealand, date back to the Late Jurassic, 163–145 MYA. The Alytidae and Bombinatoridae of Eurasia are traced back to the Mid-Jurassic, 180 MYA, with some of the earliest fossils from England.

These frogs exhibit a suite of primitive characteristics absent in modern anurans. Modern frogs have five to eight presacral vertebrae but the Ascaphidae and Leiopelmatidae possess nine, while Jurassic *Prosaliurus bitis* and *Vieraella herbstii* had ten. These extinct Jurassic frogs also had ribs which are retained in Ascaphidae and Leiopelmatidae on the II–IV vertebrae. The Alytidae and Bombinatoridae have eight presacral vertebrae, also with ribs on numbers II–IV. All modern frogs lack ribs.

Ascaphid and leiopelmatid frogs have amphicoelous vertebrae (see Glossary), while alytid and bombinatorid frogs possess opisthocoelous vertebrae, and all modern frogs have procoelous vertebrae. The ascaphids and leiopelmatids also possess an epipubic cartilage anterior to the pubic bone, a feature otherwise only seen in some pipid frogs.

ASCAPHIDAE TAILED FROGS

The tailed frogs do not actually possess a tail; rather, males possess a highly vascularized intromittent organ, a cloacal extension that resembles a tail. Supported by cartilaginous strands known as Nobelian rods, this is a ridged structure that is folded forward and inserted into the female's cloaca when the pair are in amplexus. Tailed frogs are the only frogs that internally fertilize their ova.

The Acaphidae is an ancient family from the Late Jurassic (c.163–145 MYA). Today it is represented by one genus and two species, the

Coastal Tailed Frog (*Ascaphus truei*) and the Rocky Mountain Tailed Frog (*A. montanus*), which inhabit southern British Columbia, Canada, and parts of five US states (California, Washington, Oregon, Montana, and Idaho). They occur from near to sea level on the coast to 8,390 ft (2,557 m) elevation in the Rocky Mountains. These are delicate frogs that are dorsally brown or gray with translucent pink venters.

Ascaphus is an ancient genus, as evidenced by its nine amphicoelus presacral vertebrae, three pairs

LEFT Tailed frogs (*Ascaphus* spp.) lack a tympanum (external ear drum).

OPPOSITE | The "tail" of the male Coastal Tailed Frog (*Ascaphus truei*) on the right is clearly visible.

DISTRIBUTION

Pacific northwest United States and southwest Canada

GENUS Ascaphus

HABITATS

Cold torrential rocky streams through humid forest to 8,390 ft (2,557 m) ASL

SIZE

1¼ in (30 mm) ♂¹ to 2 in (50 mm) ♀ Coastal Tailed Frog (*A. truei*) and Rocky Mountain Tailed Frog (*A. montanus*)

ACTIVITY Nocturnal; highly aquatic, occasionally terrestrial

REPRODUCTION

Inguinal amplexus with internal fertilization using male's taillike copulatory organ, eggs laid in bead-like strings attached under stones

DIET

Terrestrial and aquatic insects

IUCN STATUS None designated

ARCHAEOBATRACHIA

of ribs, and an epipubic cartilage. Tailed frogs also lack a tympanum, the external eardrum visible in most frogs, and males do not call to attract a mate, possibly because the sound of the water might drown out their calls.

Tailed frogs are highly aquatic with extensively webbed toes, but they leave the water to venture into woodlands on wet nights. When they mate, the male grasps the female using inguinal amplexus. Mating occurs in the water and females lay strings of 28–96 eggs attached to the undersides of streambed stones. Tadpoles inhabit fast-flowing water and exhibit small tail fins and large oral suckers to anchor themselves and graze algae and they have been observed using these suckers to clamber up rocks in the splash zone. Tadpoles may take up to five years to fully develop.

Neither species is considered endangered by the International Union for Conservation of Nature (IUCN), although *A. truei* is protected in California and Oregon.

LEIOPELMATIDAE NEW ZEALAND FROGS

OPPOSITE Archey's Frog (*Leiopelma archeyi*) is the smallest New Zealand frog, confined to North Island, New Zealand.

BELOW Hochstetter's Frog (*Leiopelma hochstetteri*) is the most widely distributed species of New Zealand frog. The Leiopelmatidae contains a single endemic New Zealand genus with four species. Among the most primitive living frog families, it dates back to the Late Jurassic (c.163–145 MYA). Leiopelmatids exhibit nine amphicoelous presacral vertebrae, three pairs of ribs, and an epipubis.

The smallest species is Archey's Frog (*Leiopelma archeyi*). This species inhabits the Coromandel Peninsula and Whareorino Forest on North Island. The largest species is Hamilton's Frog (*L. hamiltoni*), confined to Stephens

Island in the Cook Strait. Hochstetter's Frog (*L. hochstetten*) is the most widely distributed species, distributed through most of the northern half of North Island and Great Barrier Island. The species with the smallest range is the recently described Maud Island Frog (*L. pakeka*) from a single island in the Marlborough Sounds.

New Zealand frogs are dorsally cryptically patterned with brown, gray, or green, and darker below. *Leiopelma hamiltoni* and *L. hochstetteri* have raised dorsal tuberculate ridges on their backs, while *L. archeyi* is smooth-skinned or exhibits only small ridges.

DISTRIBUTION New Zealand

GENUS Leiopelma

HABITATS

Lowland to upland, and under rocks, logs, or leaf-litter

size 1¼ in (31 mm) ♂¹ Archey's Frog (*L. archeyi*) to 2 in (52 mm) ♀ Hamilton's Frog (L. hamiltoni)

ACTIVITY

Nocturnal; terrestrial, semiaquatic, occasionally scansoriall

REPRODUCTION Inguinal amplexus; < 22 eggs laid in small pools (*L. hochstetteri*) hatching into larvae with part-developed limbs, or < 19 eggs laid on damp ground (*L. archeyi* and *L. hamiltoni*) hatching as froglets, without larval stage

DIET Insects, spiders, and mites

IUCN STATUS CR = 1, VU = 2; percentage species in trouble = 75%

ARCHAEOBATRACHIA

Inhabiting native forests close to running water, *L. archeyi*, *L. hamiltoni*, and *L. pakeka* adopt a terrestrial lifestyle while *L. hochstetteri* is more semiaquatic with strongly webbed hindfeet. *Leiopelma archeyi* may also climb into low vegetation. They feed on insects and small arachnids but being unable to extend their tongues must lunge forward open-mouthed to catch prey.

Males do not call. *Leiopelma hochstetteri* lays up to 22 eggs in a small wet depression, which hatch into tadpoles with partially developed legs and a tail. Females of terrestrial species lay up to 19 eggs in leaf-litter where they are guarded by the male. These hatch into tiny froglets with short tails, which ride on their father's back until fully developed.

Leiopelma archeyi is listed as Critically Endangered, while L. hamiltoni and L. pakeka are Vulnerable. New Zealand frogs are listed in the EDGE of Existence program's 100 Evolutionary Distinct and Globally Endangered amphibians, with L. archeyi at the top of the list.

ALYTIDAE MIDWIFE TOADS & PAINTED FROGS

The Alytidae (formerly Discoglossidae) dates back to the Mid-Jurassic (c. 180 MYA) and comprises three Mediterranean genera. They possess the modern number of eight sacral vertebrae, but they are opisthocoelous in arrangement and associated with three pairs of ribs, both primitive characters.

Midwife toads, *Alytes* (6 spp.), inhabit southwestern Europe, northwest Africa, and the Balearic Islands. They are small, stocky frogs with large eyes, and a dorsal pattern of greens, grays, and browns. The most widely distributed is the Common Midwife Toad (*A. obstetricans*) and its name hints at the curious reproductive strategy of these frogs. When the female has laid her strings of eggs, the male will wrap them around his hindlegs and carry them for six weeks before depositing them into water,

TOP LEFT A male Midwife Toad (*Alytes obstetricans*) may carry strings of eggs from several females for six weeks.

LEFT | The Hula Painted Frog (*Latonia nigriventer*) is a "Lazarus species" from Israel.

OPPOSITE | The Iberian Painted Frog (*Discoglossus galganoi*) is widely distributed from Gibralter to Portugal and the Pyrenees.

DISTRIBUTION

Southern Europe, northern Africa, and Israel

GENERA Alytes, Discoglossus, Latonia

HABITATS

Most habitats near water, including anthropogenic habitats

SIZE

2 in (47 mm) Moroccan Midwife Toad (A. maurus) to 3 in (80 mm) North African Painted Frog (D. pictus), Moroccan Painted Frog (D. scovazzi), and Iberian Painted Frog (D. galganoi)

ACTIVITY

Nocturnal and fossorial (Alytes) or both day and night, and terrestrial/aquatic (Discoglossus and Latonia)

REPRODUCTION

Axillary amplexus; < 1,000 eggs laid in loose clumps in water (*Discoglossus*), or 20–100 eggs laid and

ARCHAEOBATRACHIA

often carrying eggs from several females. Midwife toads like dry, rocky, or wooded hillsides near water, with loose soil for burrowing.

Painted frogs, *Discoglossus* (5 spp.), inhabit Spain, Portugal, southern France, Morocco, Sicily, Sardinia, and Corsica, up to 6,230 ft (1,900 m) above sea level (ASL). A former species, the Hula Painted Frog (*Latonia nigriventer*), inhabits Israel. Last seen in the 1950s, following the draining of the Hula marshes, it was declared extinct in 1996, but it was

carried by the male (*Alytes*) until close to hatching

DIET

Insects and other invertebrates

IUCN STATUS CR = 1, EN = 2, VU = 1, NT = 1; percentage species in trouble = 42%

rediscovered in 2011, making it a "Lazarus species." Painted frogs are distinctively marked with contrasting stripes or large spots on their pale-brown, warty dorsums. They are more robust than midwife toads, with smaller eyes.

The widest distributed are the Iberian Painted Frog (*D. galganoi*) and the Moroccan Painted Frog (*D. scovazzi*), but the North African Painted Frog (*D. pictus*) is expanding into Europe. They inhabit natural and man-made aquatic habitats, including brackish or stagnant water. Females may lay up to 5,000 eggs, fertilized by several males.

Latonia nigriventer is listed as Critically Endangered, A. muletensis and A. maurus (Mallorcan Midwife Toad and Moroccan Midwife Toad) are Endangered, A. dickhilleni (Betic Midwife Toad) is Vulnerable, and D. montalentii (Corsican Painted Frog) is Near Threatened.

BOMBINATORIDAE FIRE-BELLIED TOADS, BELL TOADS & ASIAN FLAT-HEADED FROGS

The Bombinatoridae is an ancient frog family from the Mid-Jurassic (c.180 MYA), with eight opisthocoelous sacral vertebrae, and three pairs of ribs.

Genus *Bombina* (7 spp.) contains two European species, the Fire-bellied Toad (*B. bombina*) in eastern Europe, and the Yellow-bellied Toad (*B. variegata*) of central and southern Europe. The Oriental Fire-bellied Toad (*B. orientalis*) inhabits eastern China, Russia, and the Korean Peninsula. The other four *Bombina* are usually called bell toads. The widest-distributed is the Large-webbed Bell Toad (*B. maxima*).

These are stout-bodied frogs with short limbs, drab brown or green bodies with large warty tubercles, but they have brightly colored undersides,

LEFT | The European Fire-bellied Toad (Bombina bombina) has vivid red markings on its belly that it exposes defensively when it adopts the "unkenreflex" posture.

OPPOSITE Oriental Fire-bellied Toads (*Bombina orientalis*) occur in Russia, China, and the Korean Peninsula.

OPPOSITE RIGHT

Only found on the islands of Palawan and Busuanga, the Philippine Flat-headed Frog (*Barbourula busuangensis*) is Endangered.

DISTRIBUTION

Europe, Turkey, Russia, China, Korea, Vietnam, Philippines, and Borneo

GENERA Barbourula, Bombina

HABITATS

Small ponds and lakes, even stagnant water and temporary ponds, in woodland or open habitats (*Bombina*) or fast, shallow streams in rainforest habitats (*Barbourula*)

SIZE

1½ in (40 mm) Apennine Yellowbellied Toad (Bo. pachypus) to 3¼ in (85 mm) Philippine Flat-headed Frog (Ba. busuangensis)

ACTIVITY

Primarily diurnal but also active at night

ARCHAEOBATRACHIA

which are displayed when the toad feels threatened and adopts a posture known as "unkenreflex," rolling its hands and feet upside down above its head and displaying the aposematic ventral colors. This is not a bluff, *Bombina* sequester toxins from their invertebrate prey into their own skins.

Males make a soft call by passing air from their vocal sacs to the lungs, the reverse of the way most other frogs call. Females attach their eggs to submerged vegetation.

Genus *Barbourula* (2 spp.), the flat-headed frogs, were originally included with *Alytes* and *Dicroglossus*,

REPRODUCTION

Males grasp females in inguinal amplexus and fertilize the egg clumps that are attached to aquatic vegetation

DIET Small invertebrates

IUCN STATUS EN = 2, VU = 2, NT = 1; percentage species in trouble = 56% but are closer to *Bombina*. The Philippine Flatheaded Frog (*Ba. busuangensis*) inhabits Busuanga and Palawan, while the Bornean Flat-headed Frog (*Ba. kalimantanensis*) is endemic to Indonesian Borneo. Highly aquatic with flattened bodies and heads, they inhabit fast-flowing montane or rainforest streams respectively. Although poorly known, some tantalizing clues have been uncovered. Known from only two specimens, the Bornean Flat-headed Frog is the world's only known lungless frog, respiring by gas exchange through the skin. The reproductive strategy of the Philippine Flat-headed Frog is unknown, but as tadpoles have not been found and females contain very large eggs, it may be a direct breeder without a larval stage.

Barbourula busuangensis is Endangered, Bombina lichuanensis and Bo. fortinuptialis (Lichuan Bell Toad and Large-spined Bell Toad) are Vulnerable, while Ba. kalimantanensis is Near Threatened.

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OPPOSITE Hendrickson's Litter Frog (*Leptobrachium hendricksoni*) is a big-eyed species from the Malay Peninsula and Borneo.

MESOBATRACHIA

The Mesobatrachia contains frogs that are more advanced than those in the Archaeobatrachia, but most families still date back to the Late Jurassic or Early Cretaceous, 163–100 MYA, and they exhibit some primitive characteristics such as amphicoelous or opisthocoelous vertebrae, while the vertebrae of modern, neobatrachian frogs are procoelous. The Mesobatrachia contains six families split between two superfamilies (suffix = -oidea).

The Pipoidea contains the entirely aquatic Pipidae, which is divided into two subfamilies, the South American Pipinae and sub-Saharan African Dactylethrinae. Also included in the Pipoidea is the monotypic, fossorial Rhinophrynidae from Mexico.

The Pelobatoidea comprises the Pelobatidae from Europe, Asia, and North Africa, the Eurasian Pelodytidae, the North American Scaphiopodidae, and the large Asian Megophrynidae. Most members of the Pelobatoidea are terrestrial frogs, in contrast to the aquatic and fossorial Pipoidea. The Pelobatidae and Pelodytidae diverged around 150 MYA.

The Mesobatrachia contains 360 species in 20 genera, a small proportion of the total number of 7,600+ frogs described.

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher. PIPIDAE – DACTYLETHRINAE AFRICAN CLAWED FROGS & PLATANNAS

actylethrinae contains three genera of sub-Saharan African aquatic clawed frogs. The largest is Xenopus (29 spp.), although some authors place the Tropical Clawed Frog (X. tropicalis) and three rainforest Xenopus in Silurana. They are called "platannas" in South Africa, in Afrikaans meaning "flat-handed." Hymenochirus (4 spp.) are dwarf clawed frogs from the West and Central African rainforests, the largest being the Gaboon Dwarf Clawed Frog (H. feae), while Merlin's Dwarf Clawed Frog (Pseudohymenochirus merlini) is a monotypic species from Guinea-Bissau and Sierra Leone. Because of its importance to science (see page 71), the Smooth Clawed Frog (Xenopus laevis) was the first amphibian to have its entire genome mapped.

Clawed frogs are dorsoventrally flattened and pear-drop-shaped, with smooth skin, large dorsally positioned eyes, wide splayed legs, webbed toes, and long clawed fingers. *Xenopus* have nictitating membranes over their eyes and an epipubis on the pelvis, features absent in the other two genera. Although fully aquatic, they can crawl over land.

Xenopus tadpoles filter-feed but those of the other genera are carnivorous. Adults feed on aquatic invertebrates, fish, tadpoles, and smaller frogs, but large species can take birds or small mammals.

DISTRIBUTION

Sub-Saharan Africa, including Bioko Island, and introduced worldwide

GENERA Hymenochirus, Pseudohymenochirus, Xenopus

HABITATS

Still or slow-moving waters, from lakes to stagnant pools and man-made fish ponds, in close canopy rainforest to open grassland, and perianthropic habitats

SIZE

1 in (27 mm) Boulenger's Dwarf Clawed Frog (*H. boulengeri*) to 5 in (130 mm) ♀ Smooth Clawed Frog (*X. laevis*)

ACTIVITY Nocturnal, diurnal; fully aquatic

REPRODUCTION

Males grasp females in inguinal amplexus and fertilize the eggs, which are attached to aquatic vegetation, usually at night

MESOBATRACHIA

INDEX

A

Acanthixalinae 216-17 Acanthixalus 217 Acris 136 Adelastes 225 Adelastinae 224-5 Adelophryne 167 Adelotus 95 Adenomera 106 Afrixalus 214-15 Agalychnis 20, 148-9 Aglyptodactylus 171 Alcalinae 196-7 Alcalus 196-7 Allobates 114 Allobatinae 114 Allophryne 100-1 Allophrynidae 100-1 alpine toads 83 Alsodes 121 Alsodidae 121 Alytes 32, 35, 64-5 Alytidae 35, 59, 64-5 Ameerega 117 Amietia 178 Amolops 192, 194 amplexus 28-9, 30 Anaxyrus 128 Anhydrophryne 179 Anomaloglossinae 115 Anomaloglossus 115 Ansonia 130, 131 Aquarana 44, 190 Archaeobatrachia 58-67 Archev's Frog 62-3 Arenophryne 96 Argus Reed Frog 27 Aromobates 116 Aromobatidae 41, 114-16 Arthroleptella 179 Arthroleptidae 218-23 Arthroleptides 184-5 Arthroleptinae 218-19 Arthroleptis 218-19 Ascaphidae 29, 35, 59, 60-1 Ascaphus 13, 60-1 Assa darlingtoni 32 Asterophrvninae 230-3 Asterophrys 230 Astrobatrachinae 204 Astylosterninae 220-1 Astylosternus 17, 42, 45, 220-1 Atelognathus 153 Atelopus 23, 25, 30, 41, 129 Atlantihyla 141 Atympanophrys 84-5 Aubria 181

В

Bahia Forest Frog 125 Bale Mountain Frog 184-5 banjo frogs 95 Barbourula 67 Barrio's Frog 127 Barycholos 163 Batrachia 8 Batrachyla 152–3 Batrachvlidae 152-3 bell toads 66-7 Blommersia 172 Boana 138 Bokermannohvla 142 Bombina 25, 41, 66 Bombinatoridae 59, 66-7 Boophinae 170 Boophis 170 Boraceia Tree Toad 21 Boreorana 49, 190-1 Boulenophrys 84-5 Brachycephalidae 158-9 Brachycephalus 41, 158-9 Brachytarsophrys 85 Breviceps 29, 37, 212-13 Brevicipitidae 212-13 bromeliad frogs 108-9 brown frogs 190-1, 192-5 Bryophryne 162 Budgett's Frog 15, 150-1 Buergeria 49, 174 Buergeriinae 174 Bufo 30, 130, 131, 132 Bufonidae 8, 15, 38, 87, 128-33 Bufotes 130, 132 bullfrogs 44, 150, 171, 180-1, 190, 206, 226 Burrowing Toad 74-5 bush frogs 230 button frogs 122-3

C

Cacosterninae 178-9 Cacosternum 178 Callimedusa 149 Callulina 213 Calyptocephalella 98 Calyptocephalellidae 87, 98-9 camouflage 19, 40 Cane Toad 31, 38, 48, 128 Cardioglossa 218-19 cascade frogs 192-5 Celsiella 104-5 Centrolene 103 Centrolenidae 19, 102-5 Centroleninae 102-3 Ceratobatrachidae 196-9 Ceratobatrachinae 198-9

Ceratophryidae 150-1 Ceratophrys 36, 37, 150-1 Ceuthomantidae 160 Centhomantis 160 Chacophrys 150 Chaltenobatrachus 153 Charadrahvla 140 Chiasmochelis 224 Chiasmocleis 43 Chiromantis 175 chirping frogs 168-9 chorus frogs 136 chromatophores 18 chytrid fungus 52, 54 circulatory system 16 clawed frogs 34, 45, 70-1 climate change 51, 52 climbing 46 Clinotarsus 38 cloud frogs 116 Coastal Tailed Frog 13, 60-1 cocoons 18, 48 collared frogs 116 color 18 aposematism 41, 67, 117, 129, 159 camouflage 40 dichromatism 26-7 mate attraction 30 Colostethinae 117 Colostethus 117 Common Frog 31 Common Toad 30 Conraua 30, 182-3 Conrauidae 182-3 conservation 50-5 Cophixalus 231 Cophyla 228 Cophylinae 228-9 coquis 168-9 Cornufer 198-9 corrugated frogs 204-5 Crab-eating Frog 48, 206 Craugastor 161 Craugastoridae 161 Crinia 96 cross frogs 231 Crossodactylodes 109 Crossodactylus 112 Cryptobatrachus 157 Cycloramphidae 122-3 Cycloramphus 122-3

D

Dactylethrinae 69, 70–1 dainty frogs 178–9 dancing frogs 30, 200–1 Darwin's Frog 126–7 defense 37–43 Dendrobates 119 Dendrobatidae 30, 38-9, 41, 117 - 20Dendrobatinae 118-19 Dendrophryniscus 129 Dendropsophus 40, 138 Diasporus 168 Dicroglossidae 206-7 Dicroglossinae 206-7 diet 34-6 dink frogs 168-9 dirt frogs 161 Discoglossus 65 Dotted Humming Frog 43 Drvobhytes 135 Duellmanohyla 140 Duttaphrynus 130 dwarf swamp frogs 110-11 dwarf treefrogs 138 Dyscophinae 228-9 Dyscophus 41, 229

E

ears 24-5 Ecnomiohyla 138-9 ecomorphs 13 Ectopoglossus 120 Edalorhina 110 egg frogs 220-1 eggs 12, 26, 31-2 Elachistocleis 224 Eleutherodactvlidae 167-9 Eleutherodactylinae 168-9 Eleutherodactylus 22, 29, 39, 168-9 emerald-barred frogs 160 Engystomops 110, 111 Epidalea 45, 130 Epipedobates 117 Ericabatrachus 184-5 escuerzos 124-5 estivation 18, 48, 49, 77, 151 Euparkerella 163 Euphlyctis 206-7 Eupsophus 121 evolution 8-11 extinctions 50-1, 52 eyes 6-7, 15, 20-1 eye spots 41

F

 $\begin{array}{l} Fejervarya \ 48, 206 \\ fertilization \ 26, 28-9 \\ fire-bellied toads \ 25, 41, 66-7 \\ fishing frogs \ 180-1 \\ flat-headed frogs \ 66-7 \\ flea frogs \ 158-9, 167 \\ Flectonotus \ 156 \\ Flying Frogs \ 46-7, 177 \\ foam frogs \ 110-11 \\ foam-nest treefrogs \ 175-7 \end{array}$

forest frogs 38 fork-tongued frogs 206–7 fringe-limbed treefrogs 138–9 fringe-toed treefrogs 138 *Fritziana* 156

G

Galaxy Frog 227 Gardiner's Frog 92-3 gas exchange 16-17, 18, 34 Gastrophryne 225 Gastrophrvninae 224-5 Gastrophrynoides 232 Gastrotheca 15, 156, 157 Geocrinia 96 Gephyromantis 172 Gerobatrachus 8 ghost frogs 88-9 giant frogs 182-3 gills 12, 34 gladiator frogs 138 glass frogs 19, 30, 102-5 gliding 46-7 Glyphoglossus 226 Golden Coqui 29 Golden Dart-poison Frog 37-8.118 golden frogs 38-9 Goliath Frog 30, 182 grass frogs 188-9 ground frogs 94-5, 121 Guenther's Marsupial Frog 15, 157

Н

habitat loss 51, 53, 54 Haddadus 161 Hairy Frog 17, 42, 45, 220-1 Hamilton's Frog 62-3 heart 16 Heleioporus 94 Heleophryne 88-9 Heleophrynidae 87, 88-9 Hemiphractidae 156-7 Hemiphractus 15, 157 Hemisotidae 210-11 Hemisus 47, 210-11 Heterixalus 215 hibernation 49, 191 Hildebrandtia 189 Hochstetter's Frog 62-3 Holarctic treefrogs 134-5 Hole-in-the-head Frog 23, 195 Holoaden 163 Holoadeninae 162-3 Hoplobatrachus 206-7 Hoplophryninae 228-9 horned frogs 15, 34, 36, 150-1 horned toads 84-5 horned treefrogs 156-7 Huia 23, 195 Hyalinobatrachium 104-5 Hyalobatrachinae 104-5

Hydrolaetare 106 Hyla 134-5 Hylambates 216 Hylidae 38, 87, 134-49 Hylinae 134-43 Hylodes 21, 112 Hylodidae 112-13 Hylorina 153 Hyloscirtus 138 Hyloxalinae 120 Hyloxalus 120 Hymenochirus 70-1 Hyperoliidae 48, 214-17 Hyperoliinae 214-15 Hyperolius 27, 214 Hypodactylinae 162-3 Hypopachus 225

I

Ikakogi 102 incertae sedis 217 Incilius 27, 128 Indirana 202–3 Insuetophrynus 127 intromittent organ 29 Ischnocnema 159 Isthmohyla 141

J

jumping 8, 15, 44 jumping frogs 171

Κ

Kajika frogs 49, 174 Kalophryninae 226–7 Kalophrynus 227 Kaloula 226 Kassina 216 Kassininae 216–17 Kihansi Spray Toad 51 Kurixalus 176

L

Lake Titicaca Water Frog 17, 154 Laliostoma 171 Laliostominae 171 Lankanectes 204-5 Lankanectinae 204-5 Latonia 65 Lazarus species 65, 142, 155, 227 leaf-frogs 148-9 leaping frogs 202-3 Leiopelma 62–3 Leiopelmatidae 59, 62-3 Leiuperinae 110-11 leopard frogs 190-1 Lepidobatrachus 15, 18, 150-1 Leptobrachella 82,83 Leptobrachiinae 82-3 Leptobrachium 82-3

Leptodactylidae 41, 106-11 Leptodactylinae 106-7 Leptodactylodon 221 Leptodactylus 44, 54, 106-7 Leptopelinae 222-3 Leptopelis 222-3 Leucostethus 117 Limnodynastes 94-5 Limnodynastidae 87, 94-5 Limnomedusa 121 Limnonectes 29, 206-7 lingual frogs 115, 120 Lithobates 52, 190-1 Lithodytes 106-7 Litoria 19, 144, 146 litter frogs 164, 172-3 litter toads 82 Liurana 197 Liuraninae 196-7 Llanos Frog 18 long-fingered frogs 218-19 Lowland Burrowing Treefrog 18 Lowland Leopard Frog 52 lungs 16-17, 25 Lysapsus 143

Μ

Macrogenioglottus 125 Malabar Frog 38 Mannophryne 116 Mantella 41, 172-3 Mantellidae 38-9, 41, 170-3 Mantellinae 172-3 Mantidactylus 172 marsupial treefrogs 156-7 mating balls 30-1 Maud Island Frog 62-3 Megaelosia 112 Megastomatohyla 140 Megophryidae 82-3, 84-5 Megophryinae 84-5 Megophrynidae 69 Megophrys 34, 85 Melanobatrachinae 226-7 Melanobatrachus 227 Melanophryniscus 39, 129 Mesobatrachia 68-85 metamorphosis 13 Metaphrynella 226, 232 Micrixalus 30, 200-1 Microhyla 226 Microhylidae 42, 87, 224-31 Microhylinae 226-7 Microkayla 162 Microxalidae 200-1 midwife toads 32, 35, 64-5 Mini 228, 232 Mixophyes 96, 97 monkey frogs 149 monophyletic groups 8, 10 Mountain Cascade Frog 34 Mountain Chicken Frog 54, 106, 107 mountain frogs 95, 196-7

mountains false toads 98–9 moustache toads 82–3 mouth-brooding frogs 126–7 mucoproteins 18 Myobatrachidae 39, 87, 96–7 *Myobatrachus* 96

Ν

narrow-mouthed frogs 42, 224 - 33Nasikabatrachidae 87, 90-1 Nasikabatrachus 90-1 Natterjack Toad 45, 130 Nectophryne 133 Nectophrynoides 29, 51, 133 Neobatrachia 86-233 Neobatrachus 18,94 New Zealand frogs 62-3 Niceforonia 163 nictitating membrane 20-1 night frogs 42, 220-1 Nimbaphrynoides 29 Noblella 162 Northern Burrowing Frog 18 Northern Corroboree Frog 52 Notaden 94 Nothophryne 179 nurse frogs 114 nurserv frogs 231 Nyctibates 221 Nyctibatrachidae 204-5 Nyctibatrachinae 205 Nyctibatrachus 205 Nyctimantis 32 Nyctimystes 146 Nymphargus 102, 103

0

Occidozyga 207 Occidozyginae 206-7 Odontobatrachidae 208-9 Odontobatrachus 208-9 Odontophrynidae 38, 124-5 Odontophrynus 124-5 Odorrana 23, 194-5 Oophaga 119 Ophryophryne 85 Orejuela's Glassfrog 30 Oreobates 165 Oreolalax 83 Oreophrvne 231 Oreophrynella 42, 129 Oriental Fire-bellied Toad 25, 66 Osteopilus 137 Otophryne 225 Otophryninae 224-5 owl frogs 94

Ρ

pacman frogs 37, 150 Paedophryne 232

Index

Painted Ant-nest Frog 106-7 painted frogs 65 pandanus 172-3 papilla-tongued frogs 196-7 Papurana 195 Paracassina 216 Paradox Frog 13, 143 Paradoxophyla 229 Paratelmatobiinae 108-9 Paratelmatobius 108-9 parental care 32-3 parsley frogs 80-1 Paruwrobates 120 Pebble Toad 42 Pelobates 78-9 Pelobatidae 38, 69, 78-9 Pelobatrachus 85 Pelodrvadinae 144-7 Pelodytes 80-1 Pelodytidae 69, 80-1 Pelophylax 54, 192, 195 Peltophryne 128 pest control 7, 50 Petropedetes 184-5 Petropedetidae 184-5 Phantasmarana 112-13 Philoria 95 photoreceptors 21 phragmosis 32 Phrynobatrachidae 186-7 Phrynobatrachus 186-7 Phrynoidis 131 Phrynomantis 229 Phrynomedusa 148, 149 Phrynomerinae 228-9 Phrynopus 165 Phyllobates 37-8, 118-19 Phyllomedusa 149 Phyllomedusinae 148-9 Physalaemus 41, 110 Phyzelaphryne 167 Phyzelaphryninae 167 piglet frogs 210-11 Pipa 32-3, 40, 72-3 Pipidae 35, 69, 70-3 pipid frogs 22 Pipinae 69, 72-3 Pithecopus 149 platannas 70-1 plate tectonics 8-10 Platymantis 198-9 Platyplectrum 95 Plethodontohyla 228 Pleurodema 111 poison 7, 37-9 poison dart frogs 30, 38-9, 41, 118-19 poison frogs 117-20 pollution 53 Polypedates 176 Pool Frog 54, 192 Pouched Frog 32 Pristimantinae 164-5 Pristimantis 164-5

Probreviceps 213 Proceratophrys 124-5 Pseudacris 136 Pseudis 13, 143 Pseudohymenochirus 70, 71 Pseudopaludicola 111 Pseudophryne pengilleyi 52 Psychrophrynella 162, 163 Ptychadena 44, 188-9 Ptychadenidae 188-9 puddle frogs 186-7 Puerto Rican Coqui 22 pumpkin toadlets 158-9 purple pig-nosed frogs 90-1 Pyxicephalidae 178-81 Pyxicephalinae 180-1 Pyxicephalus 180-1

Q

Qosqophryne 162

R

rain frogs 29, 37, 161, 164-5, 168-9, 212-13 Rana 31, 192 Ranidae 87, 190-5 Ranixalidae 202-3 Ranoidea 144-5, 146 Rapids Frog 121 red-bellied toads 39, 129 Red-eyed Tree Frog 20, 148 reed frogs 27, 214-15 Rentapia 131 reproduction 26-33 Rhacophoridae 174-7 Rhacophorinae 175, 176-7 Rhacophorus 46-7, 177 Rheobates 115 Rheobatrachus 33, 97 Rhinella 31, 38, 48, 128, 129 Rhinoderma 126-7 Rhinodermatidae 126-7 Rhinophrynidae 69, 74-5 Rhinophrynus dorsalis 74-5 Rhombophryne 228 river frogs 122-3, 178-9, 186, 195. 206 robber frogs 39, 158-9, 161, 164-5, 166 robust frogs 204-5 rocket frogs 115, 117, 120, 144 Rockhole Frog 19 Rocky Mountain Tailed Frog 60 rubber frogs 229 running frogs 216-17 Rupirana 109

S

Sachatamia orejuela 30 saddleback toadlets 41, 158–9 Sahona 170 sand frogs 178–9 Santa Marta Harlequin Toad 30 Sarcohyla 140 Scaphiophryne 229 Scaphiophryninae 228-9 Scaphiopodidae 69, 76-7 Scaphiopus 76 Scarthyla 143 Scinax 138, 139 Sclerophrys 132 Scotobleps 220-1 Scutiger 83 Scythrophrys 109 Sechellophryne 92-3 sexual dichromatism 26-7 sexual dimorphism 26-7, 29 Sevchelles frogs 92-3 Sevchelles Palm Frog 92-3 Sevchelles Treefrog 31 sharp-nosed grass frogs 44, 188 - 9shield frogs 167 shovel-headed tree frogs 15 shovel-nosed frogs 47, 210-11 Siamophryne 232 Sigalegalephrynus 131 Silverstoneia 117 skeleton 14-15 skin 16-17, 18-19 skulls 14-15 skunk frogs 116 slippery frogs 182-3 Smilisca 18, 139 Smoky Jungle Frog 44 smooth horned toads 124-5 Sooglossidae 87, 91, 92-3 Sooglossus 92-3 spadefoot toads 12-13, 76-9, 82 - 3Spea 12-13, 76-7 Spicospina 97 spider mutualism 42-3 spiny-chest frogs 121 spiny frogs 216-17 spiracles 12 splash frogs 194 squeakers 218-19 Staurois 194 Stefania 157 Strabomantidae 162-6 Strabomantinae 166 Strabomantis 166 stream frogs 161, 174, 178 Strongylopus 178 stubfoot toads 23 Sulawesi Fanged Frog 29 Sumaterana montana 34 Suriname toads 32-3, 40, 72-3 swimming 45 Synapturanus 225

T

Tachycnemis 31 tadpoles 12–13, 32, 34, 49 tailed frogs 29, 35, 60–1

Taudactvlus 97 teeth 15 Telmatobiidae 154-5 Telmatobius 17, 154-5 Telmatobufo 99 thanatosis 217 Theloderma 40, 176 Thomasset's Frog 92-3 Thoropa 123 Tlalocohyla 140 tomato frogs 41, 229 Tomopterna 179 toothed frogs 208-9 toothed toads 83 torrent frogs 23, 112-13, 184-5, 192-5 treefrogs 31-2, 38, 134-47, 156-7, 172-3, 175-7, 222-3 Triadobatrachus 8 trilling frogs 94 Triprion 15, 140 true toads 128-33 Túngara Frog 110 Turkeit Hill frogs 100-1 tympanum 23, 24

U

unkenreflex 41, 67, 216 Uperodon 226 Uperoleia 96 urostyle 15

V

venomous frogs 39 Vieraella 8, 59 Vietnamese Mossy Frog 40 Vietnamophryne 232 Vitreorana 103 viviparous species 29 vocalization 22–3, 26, 37

W

Walkerana 202–3 water frogs 154–5, 190–1, 192–5 water loss 18–19 water toads 98–9 Waynad Dancing Frog 200 West Indian treefrogs 136–7 Wolverine Frog 42, 221 woodfrogs 49, 152–3, 190–1 wot-wots 216–17 wrinkled ground frogs 198

Х

Xenophrys 85 Xenopus 34, 45, 70–1 Xenorhina 232

Y

Yellow Toad 27