Assembling the Tree of Life

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Amphibians

Leading a Life of Slime

Amphibians have generally not been regarded with much favor. An often-cited paraphrasing of Linnaeus's *Systema Naturae* suggests that they are such loathsome, slimy creatures that the Creator saw fit not to make many of them. In fact, the number of living amphibians, about 5300, exceeds that of our own inclusive lineage, Mammalia (Glaw and Köhler 1998). The rate of discovery of new species exceeds that of any other vertebrate group. Since the publication of *Amphibian Species of the World* (Frost 1985), the number of recognized amphibians has increased by 36%. More than 100 undescribed frog species have been reported in Sri Lanka (Meegaskumbura et al. 2002). Yet, the decline and extinction of amphibian populations are visible signals of environmental degradation (Hanken 1999).

Amphibians are named for their two-phased life history: larva and adult. Typically, the larva is aquatic and metamorphoses into a terrestrial adult. In a loose, descriptive sense, amphibians bridge the gap between fishes, which are fully aquatic, and amniotes, which have completely escaped a watery environment and have abandoned metamorphosis. However, amphibians are not in any sense trapped in an evolutionary cul-de-sac, because they exhibit a far greater diversity of life history modes than do amniotes.

Each type of living amphibian—frog, salamander, and caecilian—is highly distinctive. Frogs are squat, four-legged creatures with generally large mouths and eyes and elongate hind limbs used for jumping. There is no tail (the meaning of Anura), because the caudal vertebrae have coalesced into a bony strut. About 90% of the living amphibian species are frogs; they rely mostly on visual and auditory cues. Salamanders are more typical-looking tetrapods, all with a tail (hence, Caudata) and most with four legs. Some are elongate and have reduced the limbs and girdles; these are usually completely aquatic or fossorial species. In general, they rely more on olfactory cues. Living caecilians are all limbless and elongate. Grooved rings encircle the body, evoking the image of an earthworm; most caecilians are fossorial, but some are aquatic. All have reduced eyes, although the root *caecus*—Latin for "blind"—is a misnomer. Near the eye or the nostril is a unique protrusible tentacle used for olfaction. The tail is essentially absent.

Modern Amphibians

By modern amphibians, we mean the lineage minimally circumscribed by living taxa; this is known as the crown clade Amphibia. In the language of phylogenetic taxonomy (discussed below), Amphibia are a node-based name defined as the most recent common ancestor of frogs, salamanders, caecilians, and all the descendants of that ancestor (Cannatella and Hillis 1993). Frost (1985) and Duellman (1993) summarized the species of amphibians. Up-to-date Internet resources include Frost (2002) and D. B. Wake (2003). The

distribution of modern amphibians is treated in Duellman (1999). Aspects of modern amphibian biology can be found in two recent textbooks (Pough et al. 2001, Zug et al. 2001) and in a treatise (Laurent 1986). The most comprehensive treatment is that of Duellman and Trueb (1986).

Modern amphibians are at times called lissamphibians to distinguish them from the Paleozoic forms referred to as "amphibians." Modern amphibians include frogs, salamanders, and caecilians, and their Mesozoic [245–65 million years ago (Mya)] and Cenozoic (65 Mya to present) extinct relatives (including albanerpetontids), all of which are readily identifiable as belonging to this group. In contrast, their Paleozoic relatives include the traditional groups termed the Labyrinthodontia and Lepospondyli. Labyrinthodonts, including the earliest four-legged vertebrates, ranged from the Upper Devonian (375 Mya) through the Permian (290 Mya), with numbers declining into the Triassic and one small lineage persisting into the Cretaceous. Lepospondyls range from the Lower Carboniferous (240 Mya) to the base of the Upper Permian (250 Mya). Labyrinthodonts are a paraphyletic group and also gave rise to amniotes. Lepospondyls are a heterogeneous group but have a characteristic vertebral morphology (Carroll et al. 1999); their monophyly is unclear.

Several features set modern amphibians apart from other vertebrates. Some of these characters support monophyly of the group compared with both fossil and living taxa. The significance of other characters, such as soft tissue features (Trueb and Cloutier 1991a), is less certain because they cannot be assessed in extinct forms. But these characters do support amphibian monophyly relative to amniotes and fishes.

Most adult amphibians have teeth that are pedicellate and bicuspid, or modified from this condition. Pedicellate teeth have a zone of reduced mineralization between the crown and the base (pedicel). In fossils the crowns are often broken off, leaving a cylindrical base with an open top. Pedicellate teeth are also found in a few temnospondyl labyrinthodonts believed to be closely related to modern amphibians (Bolt 1969).

Living amphibians also share the absence or reduction of several skull bones. On the dorsal skull, the jugals, postorbitals, postparietals, supratemporals, intertemporals, and tabulars are absent. On the palate, the pterygoid, ectopterygoid, and palatines are reduced or absent so as to produce a large space, the interpterygoid vacuity, below the eye sockets (Reiss 1996). The reduction/loss of many skull bones in modern amphibians is a result of pedomorphosis (Alberch et al. 1979). Pedomorphosis is a pattern derived from a change the timing of development; specifically, a species becomes sexually mature (adult) at an earlier stage of development than its immediate ancestor. As a result, the adult of amphibians resembles the juvenile (or larval) stage of Paleozoic relatives. A secondary result of pedomorphosis is miniaturization (Hanken 1985); because living amphibians mature at an earlier age, they are typically much smaller than the Paleozoic forms (Bolt 1977, Schoch 1995).

Amphibians employ a buccal force-pump mechanism for breathing (Brainerd et al. 1993, Gans et al. 1969). Air is forced back into the lungs by positive pressure from the mouth cavity. In contrast, amniotes use aspiration to fill the lungs, in which the rib cage and/or diaphragm creates negative pressure in the thorax. Amphibians have distinctive short ribs that do not form a complete rib cage as in amniotes, so aspiration is not possible.

In addition to the stapes-basilar papilla sensory system of tetrapods, living amphibians have a second acoustic pathway, the opercular-amphibian papilla system. This system is more sensitive to lower frequency vibrations than is the stapes-basilar papilla pathway. In frogs and salamanders, the operculum (a bone of the posterior aspect of the braincase, not in any way similar to the homonymous bone of fishes) is also connected to the shoulder girdle by way of a modified levator scapulae muscle, the opercularis. This muscle transmits vibrations from the ground through the forelimb and shoulder girdle to the inner ear.

The skin is a significant respiratory organ: it is supplied by cutaneous branches of the ductus arteriosus (the presence of these is not clear in caecilians). The skin has a stratum corneum (outer layer) like that of other tetrapods, although it is thinner than that of amniotes. However, living amphibians retain the primitive feature of mucous glands and granular glands. Granular glands secrete poisons of varying toxicity, some lethal. Mucous glands keep the skin moist, which allows the dissipation of heat, as well as the loss of water through the skin. Many caecilians have dermal scales, similar to those of teleost fishes, embedded in the skin.

The Name "Amphibia"

In the *Systema Naturae* of Carolus Linnaeus, the Amphibia were one of six major groups of animals, the others being mammals, birds, fish, insects, and mollusks. The group included not only frogs, salamanders, and caecilians but also reptiles and some fish that lacked dermal scales. Later, as early fossil tetrapods were uncovered, these were also relegated to "Amphibia" because of their presumed ancestral position to other tetrapods. In 1866 the great German biologist Ernst Haeckel divided Amphibia into Lissamphibia (salamanders and frogs) and Phractamphibia (caecilians and fossil labyrinthodonts; Haeckel 1866). "Liss-" refers to the naked skin of frogs and salamanders, and "phract-" means helmet, in reference to the armor of dermal skull bones and scales found in early tetrapods and, in a reduced form, in caecilians. Gadow (1901) transferred the caecilians from Phractamphibia to Lissamphibia.

For most of the 20th century, the name Amphibia was used for tetrapods that were not reptiles, birds, or mammals. Thus, the earliest tetrapods (labyrinthodonts from the Devonian) were included in Amphibia, as were the Lepospondyli. This

rendition of Amphibia appeared in most comparative anatomy and paleontology texts, largely because of the influence of the paleontologist Alfred Romer. Modern amphibians were believed to be polyphyletic and derived from different "amphibian" lineages; frogs from Labyrinthodontia, and salamanders and caecilians from Lepospondyli. Parsons and Williams adduced evidence for the monophyly of modern amphibians and resurrected Gadow's Lissamphibia for living amphibians (Parsons and Williams 1962, 1963). However, the term Lissamphibia is used mainly among specialists to distinguish the modern groups from extinct Paleozoic forms. Most biologists and most textbooks refer to frogs, salamanders, and caecilians simply as amphibians.

Use of Amphibia in the Romerian sense of a paraphyletic taxon has been largely abandoned and the name has been redefined as a monophyletic group in two contrasting ways (fig. 25.1). First, the name Amphibia is applied to the node that is the last (most recent) ancestor of living frogs, salamanders, and caecilians (de Queiroz and Gauthier 1992). Amphibia includes this ancestor and all its descendants, which are the modern forms, including albanerpetontids. Second, Amphibia is defined as the stem or branch that contains living frogs, caecilians, salamanders, and all other taxa more closely related to these than to amniotes (e.g., Gauthier et al. 1989, Laurin 1998a). In other words, the stem-based name Amphibia includes all taxa along the stem leading to modern amphibians; this includes either the temnospondyls, the lepospondyls, or both, depending on which phylogeny one accepts. Under a stem-based definition, the content of Amphibia, in terms of fossil taxa, may change dramatically. Laurin (1998a) proposed such changes based on his application of principles of priority and synonymy to phylogenetic taxonomy. He argued that the definition of Amphibia as a stem-based name by Gauthier et al. (1989) must be accorded priority over the node-based definition of Amphibia of de Queiroz and Gauthier (1992). One result of accepting the stem-based definition is that the content of Amphibia under Laurin's phylogeny (Laurin and

Reisz 1997) is very different compared with the content under other definitions of Amphibia.

Node- and stem-based names have their respective advantages in communicating taxonomy. However, a stem-based definition of Amphibia, a name in general parlance, has an undesirable effect, because generalizations about the biology of modern amphibians can be wrongly extended to extinct temnospondyls and/or lepospondyls (de Queiroz and Gauthier 1992). These groups bear little resemblance to the living forms, and their biology was presumably very different. Under a stem-based definition of Amphibia, the common statement "all amphibians have mucous glands" would be interpreted to mean that lepospondyls had mucous glands, an inference for which there is no evidence. In contrast, under the node-based definition of Amphibia, one can reasonably infer that extinct frogs, salamanders, and caecilians have mucous glands, but the inference does not extend inappropriately to extinct temnospondyls and lepospondyls. Although some neontologists and most paleontologists appreciate the semantic distinction between Amphibia and Lissamphibia, most biologists use Amphibia to mean frogs, salamanders, and caecilians.

Amphibians and the Origin of Tetrapods

The exact relationships of modern amphibians to extinct Paleozoic forms is not clear. Heatwole and Carroll (2000) provided a summary of the phylogeny of various fossil groups. The favored family of hypotheses (fig. 25.2A,B) posits that the group of frogs, salamanders, and caecilians is monophyletic and that this clade is nested within dissorophoid temnospondyls (Bolt 1977, 1991, Milner 1988, 1993, Trueb and Cloutier 1991a). (Temnospondyls are labyrinthodonts that include Edopoidea, Trimerorhachoidea, Eryopoidea, Stereospondyli, and Dissorophoidea.) The most thorough and data-rich analysis, in terms of characters and taxa (Ruta et al. 2003; fig. 25.2B), also reached this conclusion.

A recent variant of the monophyly hypothesis (fig. 25.2C) is that modern amphibians are nested within the lepospondyls (e.g., Anderson 2001), particularly within the Microsauria (Laurin 1998a, 1998b, Laurin et al. 2000a, 2000b, Laurin and Reisz 1997; but see Coates et al. 2000, Ruta et al. 2003). Because temnospondyls are distantly related to amphibians under this second hypothesis, the derived similarities between them and dissorophoid temnospondyls are interpreted as convergent.

A very different hypothesis claims polyphyly of the modern groups (fig. 25.2D), with caecilians derived from goniorhynchid microsaurs (Carroll 2000b, Carroll and Currie 1975), and salamanders and frogs from temnospondyls. The polyphyly hypothesis gained some strength with the discovery of the fossil *Eocaecilia* (see below), which possessed characters seemingly intermediate between goniorhynchid
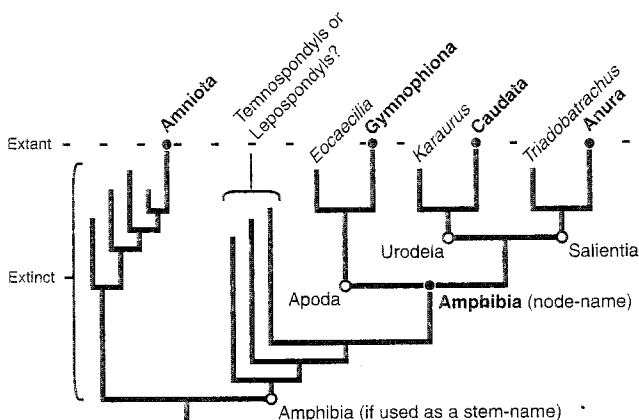

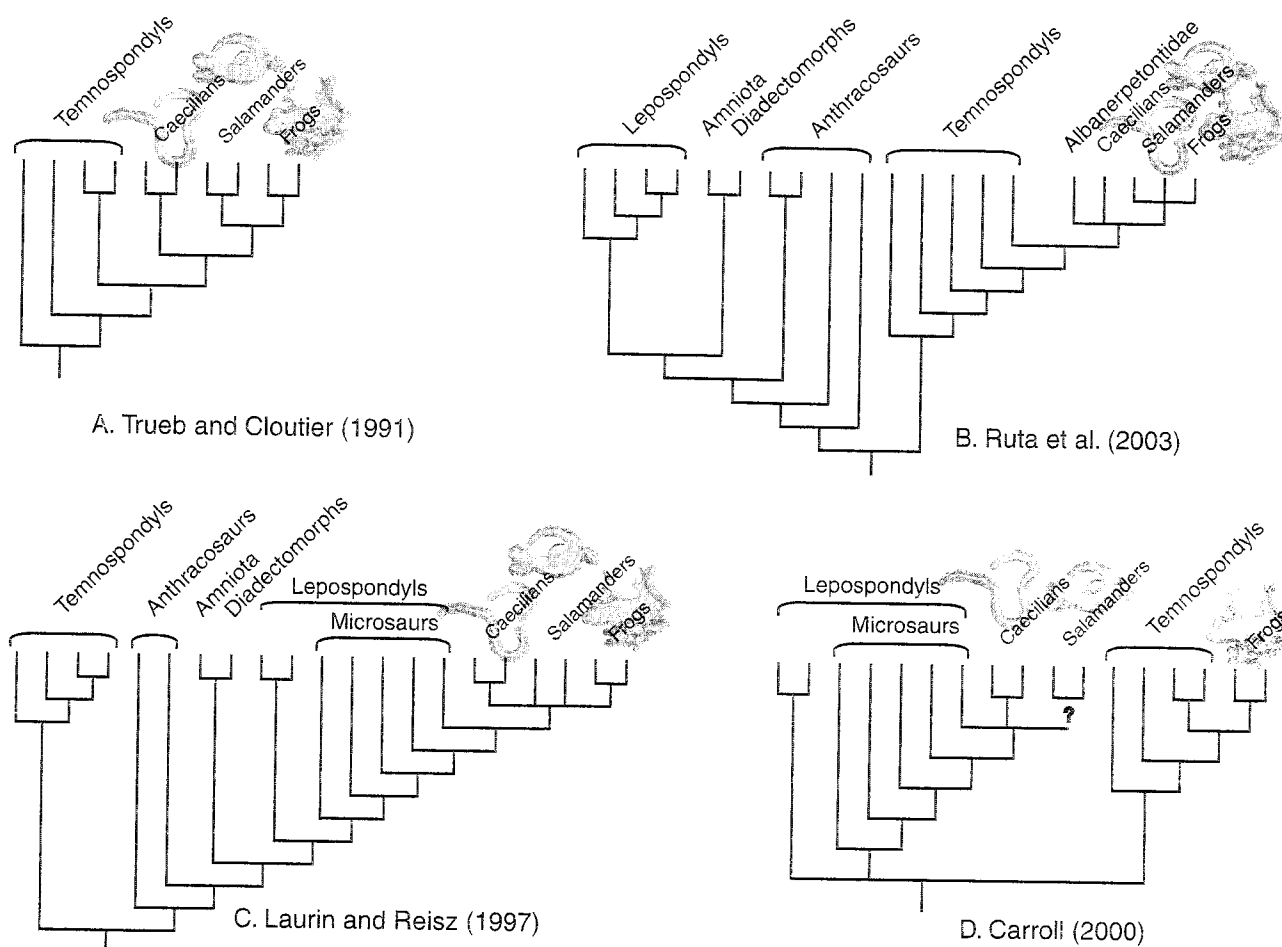**Figure 25.1.** Node-based (boldface) and stem-based definitions of Amphibia.

Figure 25.2. (A–D) Alternative relationships among modern amphibians (caecilians, frogs, and salamanders) and Paleozoic groups (temnospondyls, microsaurs, and lepospondyls).

microsaurs and living caecilians (Carroll 2000a)—this interpretation remains controversial.

Interrelationships of Modern Amphibians

Two general alternative hypotheses have been considered for relationships among the groups of modern amphibians. One tree, based primarily, but not exclusively, on non-molecular data, allies frogs and salamanders, with caecilians as the odd group out (fig. 25.2A,B). The name Batrachia, formerly synonymous with Amphibia, has been applied to this clade. In the second hypothesis, the earliest analyses of DNA sequence data slightly favored salamanders and caecilians, a group named Procera, as closest relatives (Feller and Hedges 1998, Hedges and Maxson 1993, Hedges et al. 1990), as in figure 25.2D. However, Zardoya and Meyer (2001) analyzed complete mitochondrial sequences of one species each of a frog, salamander, and caecilian and found the frog and salamander to be sister groups. Although their level of taxon sampling was shallow, the results suggest sig-

nificant uses for character-rich data sets such as mitochondrial genomes.

A fourth group of amphibians is Albanerpetontidae, known only from fossils from the Jurassic to the Miocene (Milner 2000); the name Allocaudata has been used infrequently for these, because it is redundant with Albanerpetontidae. This group closely resembles salamanders in skull shape and in the primitive tetrapod features of a generalized body shape, four limbs and a tail. Albanerpetontids lack most of the same dorsal skull bones as do living amphibians but do not have pedicellate teeth. They have been considered to be nested within salamanders, or the sister group of Batrachia (McGowan and Evans 1995); the most recent and extensive analysis (Gardner 2001) placed them in the latter position. Ruta et al. (2003; fig. 25.2B) placed them in a basal polytomy with the modern forms.

Both nucleotide sequence data and "soft" anatomy ally frogs, salamanders, and caecilians as a clade relative to living amniotes and fishes. Because fossils do not so easily yield information about nucleotides or soft tissue characters, these data sets provide no direct evidence for the monophyly of

Amphibia with respect to Paleozoic tetrapods (Trueb and Cloutier 1991a, 1991b).

Caecilians

The node-based name for modern caecilians is Gymnophiona, meaning "naked snake." Caecilians include 165 extant species, restricted to tropical America, Africa, and Asia. They are grouped into five or six families (fig. 25.3, table 25.1).

Because of their habits, caecilians are rarely seen in the wild. A dedicated herpetologist might find them by digging, and occasionally individuals are found on the surface of the ground after a heavy tropical rains Most caecilians are 0.3–0.5 m long, although one species is as large as 1.5 m and one as small as 0.1 m. All caecilians are elongate, but some are more elongate than others; the number of vertebrae ranges from 86 to 285. Caecilians are almost unique among amphibians (two species of frogs are the exception) in having a male intromittent organ, the phallodeum, and internal fertilization occurs during copulation.

Living caecilians have reduced eyes with small orbits, and scolecomorphids and some caeciliids have eyes covered by the skull bones. Compared with other amphibians, the skulls of caecilians are highly ossified and many bones are fused. The resulting wedge-shaped cranium is used for digging and compacting the soil. Most caecilians are oviparous with free-living larvae. Viviparous species occur in a few families; in some of these the embryos derive nutrition from the lining of the oviduct, so far as is known. They have a species-specific "fetal dentition" that apparently is used to help ingest the nutritive secretions. Most caecilians are fossorial, but the
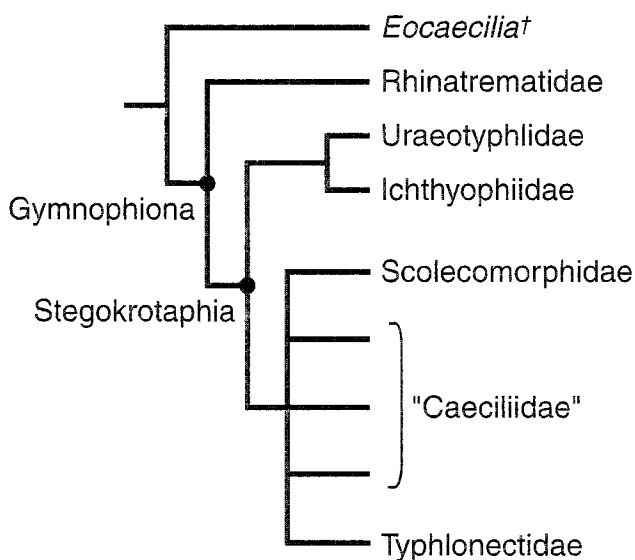

Figure 25.3. A generally accepted phylogenetic hypothesis of relationships among caecilians. "Caeciliidae" indicates a group that is paraphyletic with respect to Scolecomorphidae and Typhlonectidae. The dagger indicates extinction.

Typhlonectidae are aquatic and most have laterally compressed bodies, especially posteriorly, and a slight dorsal "fin," presumably for swimming.

Fossil caecilian vertebrae are known from the Upper Cretaceous, Tertiary, and Quaternary of Africa north of the Sahara and Mexico to Bolivia and Brazil (summarized in Wake et al. 1999). Although living caecilians are limbless, and nearly or completely tailless, the earliest putative caecilian had legs and a tail! *Eocaecilia micropodia* from the Jurassic has a somewhat elongate body and small but well-developed limbs (Carroll 2000a, Jenkins and Walsh 1993, Wake 1998). *Eocaecilia* has pedicellate teeth and a groove in the edge of the eye socket is interpreted to be for passage of the tentacle; thus *Eocaecilia* is inferred to have a feature otherwise unique to living caecilians. The evidence suggests it is the sister group of all other caecilians. The stem-based name for the clade containing *Eocaecilia* + Gymnophiona is Apoda (Cannatella and Hillis 1993).

Gymnophiona are the least understood of all vertebrate lineages, given its size. Caecilians are restricted to tropical regions of America, Africa (excluding Madagascar), the Seychelles Islands, and much of Southeast Asia. In general, phylogenetic relationships among caecilian families have not generated as much controversy as have those among salamanders or frogs, but little work has been done and sampling of species is poor. Taylor (1968) presented a monographic revision of the systematics of caecilians that stimulated work for the next 30 years, including considerable molecular and morphological research. Lescure et al. (1986) presented a radically different classification of caecilians based on sparse new data. Nussbaum and Wilkinson (1989) reviewed this unorthodox classification in a larger context; they argued for maintaining the current generic and familial relationships pending further research.

Hedges et al. (1993) analyzed sequence data for the 12S and 16S ribosomal RNA (rRNA) genes for 13 species in 10 genera; and M. Wilkinson et al. (2002) examined relationships among Indian species. Although molecular data have added substantially to caecilian phylogenetics, new morphological characters have contributed as well. Wake (1993, 1994) found that neuroanatomical characters in isolation are not a robust character base, but are useful within a larger morphological set; Wilkinson (1997) confirmed the "eccentricity" of the neuroanatomical set. The description of a bizarre new typhlonectid used 141 morphological characters and resulted in a new analysis of Typhlonectidae (Wilkinson and Nussbaum 1999). Similarly, phylogenetic analysis of Uraeotyphlidae has made use of new anatomical features (Wilkinson and Nussbaum 1996). Only recently has the osteology of the entire group been surveyed (M. H. Wake 2003).

Rhinatrematidae are almost universally considered to be the sister taxon of other living gymnophiones (fig. 25.3) based on both morphological and molecular data (Hedges et al. 1993, Nussbaum 1977). These caecilians retain a very short tail behind the cloaca, as do the Ichthyophiidae, in contrast to other

Table 25.1

Geographical Distribution of the Major Extant Groups of Amphibia.

Taxon	Distribution
Gymnophiona	
Rhinatrematidae	Northern South America
Ichthyophiidae	India, Sri Lanka, Southeast Asia
Uraeotyphlidae	South India
Scolecomorphidae	Africa
"Caeciliidae"	Mexico, Central and South America, Africa, Seychelles, India, Southeast Asia
Typhlonectidae	South America
Caudata	
Hynobiidae	Continental Asia to Japan
Sirenidae	Eastern United States and adjacent Mexico
Cryptobranchidae	China, Japan, eastern United States
Ambystomatidae	North America
Rhyacotritonidae	Northwest United States
Dicamptodontidae	Western United States and adjacent Canada
Salamandridae	Eastern and western North America, Europe and adjacent western Asia, northwest Africa, eastern Asia
Proteidae	Eastern United States and Canada, Adriatic coast of Europe
Amphiumidae	Southeast United States
Plethodontidae	North and Central America, northern South America, Italy and adjacent France, Sardinia
Anura	
Ascaphus	Northwest United States and adjacent Canada
Leiopelma	New Zealand
Bombinatoridae	Europe and eastern Asia, Borneo and nearby Philippine Islands
Discoglossidae	Europe, northern Africa
Pipidae	South America and adjacent Panama, sub-Saharan Africa
Rhinophrynidae	Central America, Mexico, and south Texas
Pelobatidae	North America, Europe, western Asia
Pelodytidae	Western Europe, western Asia
Megophryidae	Southern Asia to Southeast Asia
Heleophryne	Southern Africa
Myobatrachinae	Australia, New Guinea
Limnodynastinae	Australia, New Guinea
"Leptodactylidae"	South America, Central America, Mexico, southern United States
Bufonidae	All continents (including Southeast Asia) except Australia and Antarctica
Centrolenidae	Mexico, Central and South America
Dendrobatidae	Northern South America, Southeast Brazil, Central America
Sooglossidae	Seychelles
Hylidae	The Americas, Europe and adjacent Asia, northern Africa, eastern Asia, Japan, New Guinea, Australia
Pseudidae	South America
Rhinoderma	Southern South America
Allophryne	Northern South America
Brachycephalidae	Atlantic forests of southeastern Brazil
Microhylidae	Southern United States, Mexico, Central America, South America, sub-Saharan Africa, Madagascar, southern Asia, Southeast Asia, New Guinea, northeastern Australia
"Ranidae" (including Mantellinae)	All continents (northern South America only northeastern Australia only)
Arthroleptidae	Sub-Saharan Africa
Hyperoliidae	Sub-Saharan Africa, Madagascar, Seychelles
Hemisus	Sub-Saharan Africa
Rhacophoridae	Sub-Saharan Africa, Madagascar, southern Asia, Southeast Asia, Japan

family groups. Ichthyophiidae are a group of semi-fossorial forms from southern and Southeast Asia. Uraeotyphlidae, generally considered the sister taxon of Ichthyophiidae, are also from southern Asia; these are tailless.

Most taxonomic uncertainty resides in the geographically and biologically diverse taxon "Caeciliidae," which is prob-ably paraphyletic with respect to Scolecomorphidae and Typhlonectidae. Caeciliids occur pantropically, and include a great diversity of taxa—including the smallest and largest species—and many reproductive modes, such as egg-layers with free-living larvae, direct developers, and viviparous forms, and several kinds of maternal care.

Scolecomorphidae are an African group with some bizarre features; in some taxa the eye is completely covered by a layer of bone, and in at least one species the eye can be protruded beyond the skull because of its attachment to the base of the tentacle (O'Reilly et al. 1996). The last group of caecilians, Typhlonectidae, is semi-aquatic to aquatic with attendant modifications, such as slight lateral compression of the posterior part of the body. Hedges et al. (1993) found the one species of Typhlonectidae analyzed to be nested among neotropical caeciliids. Accordingly, they synonymized the Typhlonectidae within Caeciliidae. Wilkinson and Nussbaum (1996, 1999) rejected that conclusion because of poor taxon sampling, preferring to wait until the relationships of the Caeciliidae, *sensu lato*, were fully explored.

Salamanders

The node-based name for living salamanders is Caudata. The 502 species of living salamanders are arranged into 10 families (fig. 25.4, table 25.1). Historically, salamanders are a primarily Holarctic group of the north temperate regions; one clade, the Bolitoglossini, has diversified in the Neotropics. The largest salamanders are the Cryptobranchidae; adult *Andrias* can reach 1.5m in total length. The smallest are *Thorius* (Plethodontidae), which may have an adult length as small as 30 mm.

Several salamanders are elongate and have reduced limbs. Some are larger, aquatic, neotenic forms, such as Sirenidae, Proteidae, and Amphiumidae. Fully aquatic salamanders typically retain gill slits, and some have external gills resembling crimson tufts of feathers. Elongate terrestrial salamanders typically have reduced limbs and digits, and occupy a semifossorial niche in leaf litter or burrows. At another extreme are arboreal forms with palmate hands and feet and reduced digits resulting from heterochrony.

Most of the major groups of salamanders have internal fertilization accomplished by way of a spermatophore, typically a mushroom-shaped mass of spermatozoa and mucous secretions. The male deposits a spermatophore either in water or on land, depending on the group. The female retrieves it with her cloaca during courtship. The sperm may be retained live in a cloacal pocket, the spermatheca, for months or even years. Fertilized eggs are deposited and develop either directly, in which case a small salamander hatches, or indirectly, in which a larval salamander emerges, and later metamorphoses.

Relationships among Salamanders

Karaurus sharovi, the oldest salamander, is a fully articulated Middle Jurassic fossil from Kazakhstan. The stem-based name for the clade of *Karaurus* + Caudata is Urodela ("with a tail"), so *Karaurus* is a urodele but not part of Caudata. Although the fossil *Karaurus* firmly established salamanders in the Jurassic, the fossil record of salamanders has not contributed to resolution of relationships among extant taxa until recently. However, crown-group salamanders belonging to the Cryptobranchidae are now known from the Middle Jurassic (Gao and Shubin 2003). Also, Gao and Shubin's (2001) analysis of Jurassic urodeles (fig. 25.4) placed these at the base of the extant salamander tree with Hynobiidae and Cryptobranchidae (Cryptobranchoidea). The Sirenidae formed a clade with two other neotenic taxa (Proteidae and Amphiumidae). In contrast, Duellman and Trueb (1986) placed Sirenidae as the sister of all other salamanders, followed by Cryptobranchoidea as sister to remaining salamanders. A possible explanation for this discordance is that salamanders are notorious for the amount of homoplasy in pedomorphic features (Wake 1991). Of course, this alone does not explain incongruence in nuclear and mitochondrial rRNA data (mt-rRNA; see below).

Larson and Wilson (1989) and Larson (1991) presented a tree (fig. 25.4) based on nuclear-encoded rRNA, which differed dramatically in placing Plethodontidae and Amphiumidae at the base of the tree. Larson and Dimmick (1993) combined these molecular data with morphological data from Duellman and Trueb (1986). The resulting tree effectively rerooted the Larson (1991) tree to place Sirenidae and Cryptobranchoidea at its base. Analyses of 12S and 16S mitochondrial DNA (mtDNA; Hay et al. 1995, Hedges and Maxson 1993) also placed Sirenidae at the base (fig. 25.4), but with different relationships among other taxa.
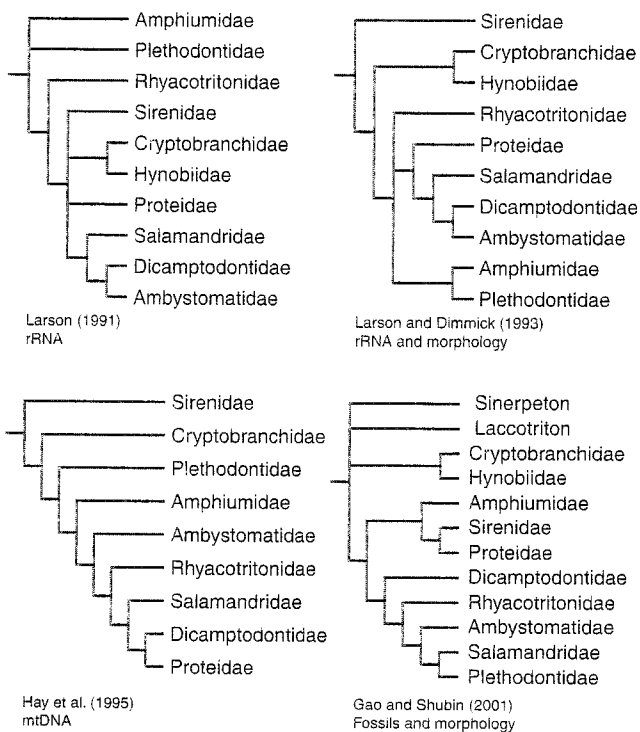

Figure 25.4. Alternative relationships among the families of salamanders.

Compared with caecilians and frogs, the placement of family-level groups of salamanders remains in an extreme state of flux, with very different topologies resulting from different data sets (sequences, morphology, and fossils) and combinations of those data sets. In contrast, there is almost no disagreement about the content of the Linnaean families. Ten families of living salamanders are generally recognized; all clearly are monophyletic. Four are species-rich and extensively sampled using molecular techniques. Substantial progress has been made in generating phylogenetic hypotheses at the species level, in contrast to frogs and caecilians. In several families nearly all species have been examined.

Sirenidae include two genera of non-metamorphosing, elongate neotenic forms that retain external gills as adults. In contrast to most elongate salamanders, the front limbs are present and robustly developed, whereas the hind limbs and pelvic girdle is absent. Cryptobranchoidea are a clade generally acknowledged to be among the most plesiomorphic of living salamanders. The included families are Cryptobranchidae and Hynobiidae. Cryptobranchidae include the largest salamanders; adult *Andrias* may reach 1.5 m in length. Recently described Jurassic cryptobranchid fossils (Gao and Shubin 2003) represent the oldest crown-group salamanders, i.e., members of Caudata. All Hynobiidae but 2 of the 42 species have been studied using mtDNA (A. Larson and R. Macey, unpubl. obs.).

The Dicamptodontidae and Rhyacotritonidae each include one living genus. *Dicamptodon* and *Rhyacotriton* have been considered closely related and were united in the Dicamptodontidae, but recent analyses (Good and Wake 1992, Larson and Dimmick 1993) place them as separate but adjacent lineages.

Amphiumidae include only *Amphiuma*. This elongate neotenic form lacks external gills and has limbs reduced to spindly projections with remnants of the digits. Proteidae include species both in North America and Europe. *Necturus*, the beloved mudpuppy of comparative anatomy labs, is a large pedomorphic salamander with large fluffy external gills. *Proteus*, a very elongate and aquatic cave-dweller in SE Europe, also retains external gills.

Ambystomatidae include 30 extant species of *Ambystoma*. Nearly all have using mtDNA sequences and allozymes (Shaffer 1984a, 1984b, Shaffer et al. 1991). Some species are facultatively neotenic and retain the ability to metamorphose; others are obligately trapped in the larval morphology, spending their entire lives in lakes. Most have a larval period that is always followed by metamorphosis to the adult condition.

Many species of Salamandridae are aposematic (having a bright warning coloration) and have highly effective cutaneous poison glands to deter predators. At least two species are viviparous, a rare occurrence among salamanders. Salamandridae are also diverse in morphology and life history, although not as speciose as Plethodontidae (see below). Relationships among salamandrids have been examined using morphological data (Özeti and Wake 1969, Wake and

Özeti 1969), although not with current phylogenetic algorithms. All 62 species of this widely distributed family have been studied using molecular markers (Titus and Larson 1995, D. Weisrock and A. Larson, unpubl. obs.).

Plethodontidae are by far the largest family taxon, with 27 genera and 348 species (from a total of 502 species of salamanders). Plethodontids are lungless and use primarily cutaneous respiration. The release of the hyoid musculoskeleton from the constraints of buccal force-pump breathing has apparently permitted the diversification of mechanisms prey capture by tongue protrusion. In addition to being the most diverse in morphology and life history—there are highly arboreal, aquatic, terrestrial, saxicolous, and fossorial forms—this is the only clade with a neotropical radiation. Four major groups of Plethodontidae are recognized: Desmognathinae, Plethodontini, Bolitoglossini, and Hemidactyliini; work has concentrated on relationships within each clade, and relationships among the four are not clear.

All species of Desmognathinae have been studied with mtDNA (Titus and Larson 1995, 1996). Detailed studies of many species of Plethodontini have been published by Mahoney (2001), and studies of all species are in progress (M. Mahoney, D. Weisrock, and D. Wake et al., unpubl. obs.). The Bolitoglossini have been sampled broadly. About 40% of all salamanders are in the mainly Middle American clade *Bolitoglossa*, and all genera and about 80% of its species have some sequence data (García-París et al. 2000a, 2000b, García-París and Wake 2000, Parra-Olea et al. 1999, 2001, Parra-Olea and Wake 2001). Data from three mtDNA genes have been collected for almost all tropical species in the lab of D. Wake (pers. comm.). Jackman et al. (1997) examined relationships of bolitoglossines based on a combination of morphological and molecular data sets. Work is also underway on the mostly aquatic plethodontids, the Hemidactyliini, using ribosomal mtDNA and recombination activating protein 1 (RAG-1) (P. Chippindale and J. Wiens, unpubl. obs.).

Frogs

Living frogs include about 4837 species arranged in 25–30 families (fig. 25.4, table 25.1). The earliest forms considered as proper frogs are *Notobatrachus* and *Vieraella* from the Middle Jurassic of Argentina. *Prosalirus vitis* from Lower Jurassic of Arizona (Jenkins and Shubin 1998, Shubin and Jenkins 1995) is fragmentary, but clearly a frog. All of these have skeletal features that indicate that the distinctive saltatory locomotion of frogs had evolved by this time.

The sister group of frogs proper is *Triadobatrachus massinoti*, known from a single fossil from the Lower Triassic of Madagascar. It has been called a proanuran and retains many plesiomorphic features, such as 14 presacral vertebrae (living frogs have nine or fewer) and lack of fusion of the radius and ulna and also of the tibia and fibula (living frogs have fused elements, the radioulna and tibiofibula; Rage and Rocek

1989, Rocek and Rage 2000). The clade containing *Triadobatrachus* and all frogs is named Salientia.

Frogs have a dazzling array of evolutionary novelties associated with reproduction. Their diverse vocal signals of the males are used for mate advertisement and territorial displays. Parental care is highly developed in many lineages, including brooding of developing larvae on a bare back, in pouches on the back of females, in the vocal sacs of males, and in the stomach of females. Some females in some unrelated lineages of Hylidae and Dendrobatidae raise their tadpoles in the watery confines of a bromeliad axil and supply their own unfertilized eggs as food. Whereas amniotes escaped from the watery environment once with their evolution of the amniote egg, frogs have done so many times; direct development, with terrestrial eggs in which the tadpole stage is bypassed in favor of development to a froglet, has evolved at least 20 times.

Although some frogs have escaped an aquatic existence, many have embraced it, taking the biphasic life to an extreme. In contrast to caecilian and salamander larvae, frog tadpoles are highly morphological specialized to exploit their transitory and often unpredictable larval niche. The tadpole is mostly a feeding apparatus in the head and locomotor mechanism in the tail. The feeding apparatus is a highly efficient pump that filters miniscule organic particles from the water. Tadpoles do not reproduce; there are no neotenic forms. They live their lives eating until it is time to make a quick and awkward metamorphosis to a froglet.

Anura and Salientia

The names of higher frog taxa are used here following Ford and Cannatella (1993). Their general rationale was (1) to recognize only monophyletic groups except when it was not feasible to reduce the nonmonophyletic group to smaller clades (as in the case of "Leptodactylidae" and "Ranidae"), (2) to identify nonmonophyletic groups as such, and (3) to avoid the use of family names that are redundant with the single included genus.

Ford and Cannatella (1993) defined Anura as the ancestor of living frogs and all its descendants. The use of living taxa as reference points or anchors for the definition follows the rationale of de Queiroz and Gauthier (1990, 1992), who convincingly argued that this stabilizes a definition. In contrast, the incompleteness of fossil taxa and the discovery of new fossils renders definitions based on extinct reference taxa less stable.

The taxonomy of frogs illustrates this issue of taxonomic practice. The Jurassic fossil *Notobatrachus* was considered by Estes and Reig (1973) to be closely related to, and in the same family as, the living taxa *Ascaphus* and *Leiopelma*. Thus, *Notobatrachus* would be included in Anura according to Ford and Cannatella's definition. In contrast, the analyses by Cannatella (1985) and Báez and Basso (1996) placed *Notobatrachus* as

the sister group to the clade containing *Ascaphus*, *Leiopelma*, and other living frogs. The latter placement means that *Notobatrachus* is not part of Anura, because Anura is defined as the last common ancestor of living frogs and all its descendants. Some herpetologists or paleontologists may be rankled by the proposition that the very froglike *Notobatrachus* is not part of Anura. But this concern is based on a typological notion that the definition of a taxon name is tied to a combination of characters, rather than to a branch of the Tree of Life.

We can ask, Are there characters that make a frog a frog? The *eidos* of a frog requires a big head, long legs, no tail, and a short vertebral column. But how short? Most living frogs have eight presacral vertebrae. *Notobatrachus* and two of the most "primitive" frogs, *Ascaphus* and *Leiopelma*, have nine. Another Jurassic fossil, *Vieraella herbsti*, has 10 vertebrae (Báez and Basso 1996). All of the aforementioned look like proper "frogs." The Triassic fossil *Triadobatrachus* has 14 vertebrae (Rage and Rocek 1989). It has several unambiguous synapomorphies that place it as the sister group of frogs. It is considered froglike, but not quite a frog. In summary, it seems the consensus of published work is that 10 or fewer presacral vertebrae make a frog a frog.

When fossil X with 11 presacral vertebrae is discovered, will the boundary of "frogness" move one node lower in the tree, so as to include fossil X? This question highlights the problem: when a taxon name is defined by a diagnostic character, each new fossil with an intermediate condition will stretch the definition of the name (Rowe and Gauthier 1992). However, it is less likely that the discovery of a new living frog species will stretch our concept of frogness. Therefore, attaching the taxon name Anura to a node circumscribed by living taxa will yield a more stable definition. Because Anura is defined as the ancestor of living frogs and all its descendants, the discovery of a new fossil just below this node, no matter how froglike, will not require a change in the meaning of Anura. And, we can still argue about which characters make a frog a frog.

"Salientia" is the stem-based name for the taxon including Anura and taxa (all fossils) more closely related to Anura than to other living amphibians. Salientia include *Triadobatrachus*, *Vieraella*, *Notobatrachus* (Báez and Basso 1996), *Czatkobatrachus* (Evans and Borsuk-Bialynicka 1998), and *Prosalirus* (Shubin and Jenkins 1995). Because the name is tied to a stem, the discovery of new fossils on this stem will not destabilize the name. The use of Salientia for *Triadobatrachus* plus all other frogs is widespread and not controversial.

Our understanding of frog phylogeny rests primarily on morphological data (Griffiths 1963, Inger 1967, Kluge and Farris 1969, Lynch 1973, Noble 1922, Trueb 1973), summarized by Duellman and Trueb (1986) and Ford and Cannatella (1993; fig. 25.5). In general, morphological characters resolved the plesiomorphic basal branches known as archaeobatrachians (Cannatella 1985, Duellman and Trueb 1986, Haas 1997). The family-level relationships within Neo-
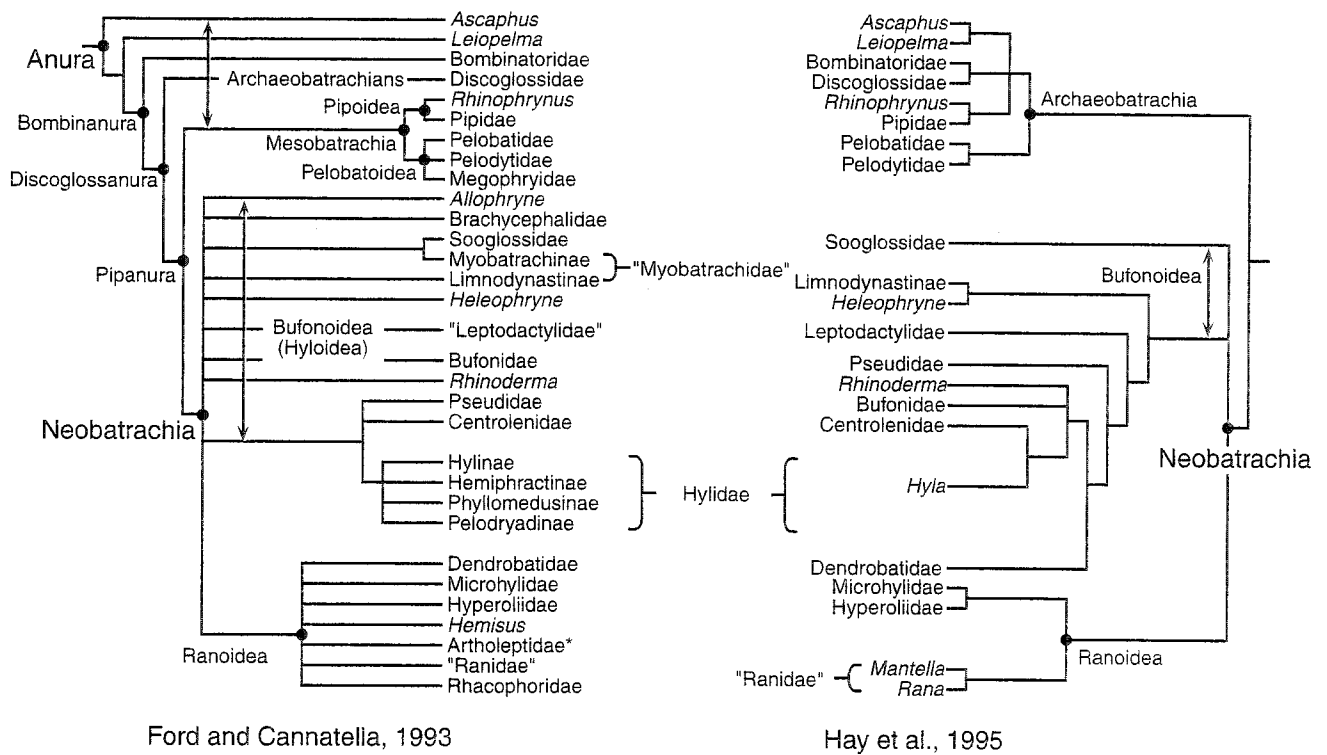
Figure 25.5. Alternative phylogenies of frogs. The tree on the left is labeled with taxon names (see text).

batrachia, a large clade with more than 95% of frog species, are mostly unresolved (Ford and Cannatella 1993) by morphological data, although Ranoidea is strongly supported. Most remaining neobatrachians are known as hyloids or bufonoids, but no morphological evidence for their monophyly has been proposed (with the possible exception of sperm morphology; Lee and Jamieson 1992). Ranoidea is primarily Old World; hyloids are mostly New World.

The distinctive and diverse morphology of tadpoles has been a source of characters to elucidate frog phylogeny. At one time it was thought that the larval morphology of the pipoid frogs argued for their position as the most primitive (early-branching in this context), but highly specialized, group (Starrett 1968, 1973). However, other interpretations (Cannatella 1999, Haas 1997, Sokol 1975, 1977) indicate that although pipoids are highly specialized, the discoglossoids are the earliest-branching frog lineages (see below). However, the most comprehensive analysis of larval morphology (Haas 2003) found *Ascaphus* to be the most basal frog and pipoids to be the next adjacent clade (fig. 25.6), rather than other discoglossoids. Maglia et al. (2001) reported Pipoidea to be the sister taxon of all other frogs, a hypothesis reminiscent of Starrett (1968, 1973).

The fossil record of frogs was thoroughly reviewed by Sanchiz (1998). Báez and Basso (1996) included Jurassic fossils in a phylogenetic analysis of early frogs. Gao and Wang (2001) analyzed data for a combined treatment of fossil and living archaeobatrachians and pre-archaeobatrachians, but

they reached very different conclusions than did Ford and Cannatella (1993); a full analysis of this is beyond the scope of this chapter.

A range of morphological phylogenetic studies treats relationships within particular family-level groups: Pelobatoidea (Maglia 1998); Hyperoliidae (Drewes 1984); Rhacophoridae and Hyperoliidae (Liem 1970); Myobatrachidae *sensu lato*, including Myobatrachinae and Limnodynastinae (Heyer and Liem 1976); Leptodactylidae (Heyer 1975); Hylinae (da Silva 1998); Microhylidae (Wu 1994); Hemiphractinae (Mendelson et al. 2000); and Pipidae (Cannatella and Trueb 1988a).

Sequences from both nuclear and mt-rRNA genes provided new data (Emerson et al. 2000, Graybeal 1997, Hay et al. 1995, Hedges and Maxson 1993, Hedges et al. 1990, Hillis et al. 1993, Ruvinsky and Maxson 1996, Vences et al. 2000). Several alternative hypotheses emerged from these works, including (1) monophyly of "Archaeobatrachia," (2) weak monophyly of the bufonoids (= Hyloidea), (3) dendrobatids excluded from Ranoidea, and (4) extensive paraphyly of the large families Hylidae and Leptodactylidae.

The "Basal" Frogs—Discoglossoids

A group of plesiomorphic lineages includes *Ascaphus, Leiopelma,* Bombinatoridae, and Discoglossidae (Ford and Cannatella 1993); this group has been called discoglossoids and is paraphyletic with respect to other frogs, the Pipanura.
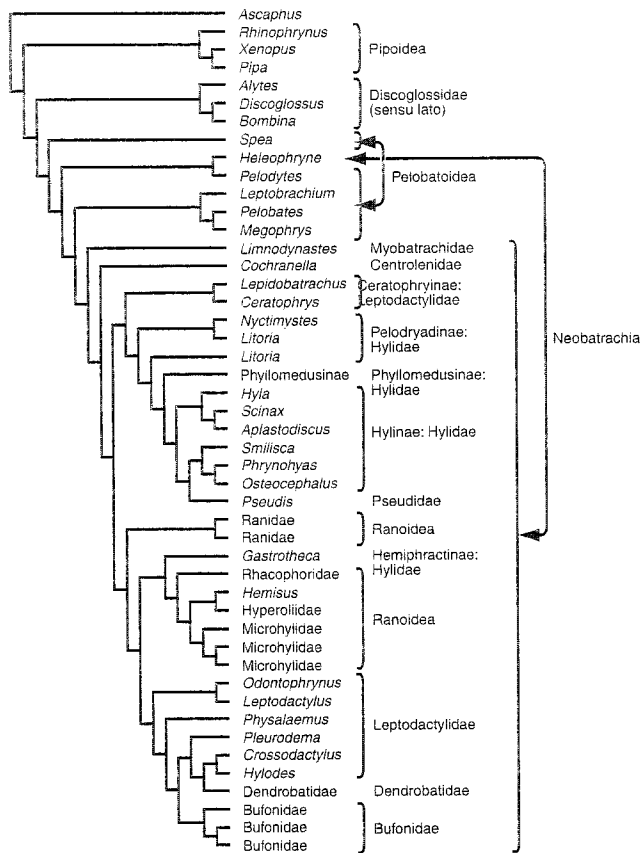
Figure 25.6. A phylogeny of frogs based mostly on larval morphology, simplified from Haas (2003: fig. 3).

Ascaphus and *Leiopelma* are plesiomorphic, now-narrowly distributed relicts of a once more widely distributed Mesozoic frog fauna (Green and Cannatella 1993). The family name Ascaphidae is redundant with *Ascaphus*. The family name Leiopelmatidae is redundant with the single genus *Leiopelma*. Formerly, The name Leiopelmatidae (*sensu lato*) has also been used to include *Ascaphus* and *Leiopelma*, a group that is probably paraphyletic.

"Bombinanura" is the node-based name for the last common ancestor of Bombinatoridae + Discoglossanura; Bombinatoridae is the node name for the ancestor of *Bombina* and *Barbourula* and all of its descendants (Ford and Cannatella 1993); this node is well supported (Cannatella 1985; but see Haas 2003).

The names Discoglossoidei (Sokol 1977) and Discoglossoidea (e.g., Duellman 1975, Lynch 1971) were used for the group containing *Ascaphus*, *Leiopelma*, *Bombina*, *Barbourula*, *Alytes*, and *Discoglossus*. The Discoglossoidei of Sokol (1977) and Duellman and Trueb (1986) were a clade; however, other morphological analyses strongly reject this conclusion. As an informal term, the name discoglossoids is a useful catchall for plesiomorphic anurans that are not part of Pipanura. One general primitive feature of this group is the rather rounded,

disklike tongue; hence the name. *Alytes* and *Discoglossus* are included in the Discoglossidae, although the two are fairly divergent and evidence of monophyly is not overwhelming. Some evidence indicates that Discoglossidae are more closely related to other frogs than to Bombinatoridae, *Ascaphus*, or *Leiopelma* (Ford and Cannatella 1993).

Pipanura

Pipanura consists of Pipoidea, Pelobatoidea, and Neobatrachia, that is, living frogs minus discoglossoids. Specifically, it is the node name for the last ancestor of Mesobatrachia + Neobatrachia, and all of its descendants (Ford and Cannatella 1993). Pipoidea and Pelobatoidea are regarded as intermediate lineages between discoglossoids and Neobatrachia. Mesobatrachia is the node name applied to the last ancestor of Pelobatoidea + Pipoidea. Support for this clade is not strong (Cannatella 1985). Pelobatoids and pipoids are represented by a large number of Cretaceous and Tertiary fossils (Rocek 2000, Sanchiz 1998).

The node name Pelobatoidea was defined by Ford and Cannatella (1993) as the (last) common ancestor of living Megophryidae, Pelobatidae, and *Pelodytes*, and all its descendants. The content of Pelobatoidea is not controversial. Historically, Pelobatidae has included Megophryidae as a subfamily (e.g., Duellman and Trueb 1986), although recent summaries recognize Megophryidae (e.g., Zug et al. 2001). This follows Ford and Cannatella (1993), who defined Pelobatidae as the node name for the last common ancestor of *Pelobates*, *Scaphiopus*, and *Spea*, and all its descendants. This definition was based on a sister-group relation between the European (*Pelobates*) and American spadefoots (*Scaphiopus* + *Spea*), which were united by synapomorphies related to their habitus as fossorial species (Cannatella 1985, Maglia 1998).

In contrast, Garcia-Paris et al. (2003) reexamined relationships among all pelobatoids using mtDNA and found *Scaphiopus* + *Spea* to be the sister group of other pelobatoids (*Pelobates*, Pelodytidae, and Megophryidae). Because *Scaphiopus* + *Spea*, which they termed Scaphiopodidae, were no longer related to *Pelobates*, they inferred the fossorial habitus of the two groups to be convergent. The taxonomic implication of this finding is that Pelobatidae as defined by Ford and Cannatella (1993) applies to the same node as Pelobatoidea. One solution would be to redefine Pelobatidae as a stem name so as to include the fossil taxa that are thought to be closely related, such as *Macropelobates*. But the issue remains unresolved.

The node name Megophryidae was used by Ford and Cannatella (1993) for the group of taxa referred to as megophryines, previously been considered to be a subfamily (Megophryinae) of Pelobatidae. Although preliminary work exists (Lathrop 1997), relationships among the Megophryidae have not been assessed in detail; however, the content is uncon-

troversial. In contrast to most of the family-level names, Pelodytidae was defined as a stem name by Ford and Cannatella (1993) because its use as a node name for the clade of living taxa would make it redundant with *Pelodytes*. Also, use of a stem name retains the several taxa of fossil pelodytids within Pelodytidae, a placement that is well supported (Henrici 1994).

Pipoidea was implicitly defined as the node name for the most recent common ancestor of Pipidae and Rhinophrynidae, and all its descendants. By this definition, the fossil family Palaeobatrachidae are included within Pipoidea, as has generally been the case (but see Spinar 1972). Relationships among pipoids have been examined by Cannatella and Trueb (Báez 1981, Báez and Trueb 1997, Cannatella and de Sá 1993, Cannatella and Trueb 1988a, 1988b, de Sá and Hillis 1990)

As pointed out by Ford and Cannatella (1993), the phylogenetic definition of the name Pipidae excluded several fossils previously and currently included in Pipidae (Báez 1996). The stem name Pipimorpha was proposed to accommodate these. Because the name applies to those taxa that are more closely related to (living) Pipidae than to Rhinophrynidae, it is a useful descriptor for the increasingly specialized taxa on the stem leading to the Pipidae. Báez and Trueb (1997) defined Pipidae slightly differently; their tree is unresolved at the crucial point. The single species of highly fossorial frog *Rhinophrynus dorsalis* is regarded to be the sister group of Pipidae, among living forms. Like Pelodytidae, the name Rhinophrynidae was defined as a stem name by Ford and Cannatella (1993).

Neobatrachia

Neobatrachia consist of the "advanced" frogs and includes 95% of living species. Except for the Late Tertiary, they are not well represented in the fossil record. Neobatrachia is well supported by both morphological and molecular data (Ford and Cannatella 1993, Ruvinsky and Maxson 1996, but see Haas 2003). Two groups of Neobatrachia have been generally recognized: Bufonoidea (Hyloidea has priority; see below) for arciferal neobatrachians, and Ranoidea for the firmisternal neobatrachians. These correspond roughly to the classic Procoela and Diplasiocoela of Nicholls (1916) and Noble (1922), respectively. Hyloidea are primarily a New World clade, and Ranoidea an Old World group, although the hyloids have significant radiations in the Australopapuan region as do Ranidae and Microhylidae in the New World.

Hyloidea (formerly Bufonoidea) include Bufonidae, Hylidae, "Leptodactylidae," Centrolenidae, Pseudidae, Brachycephalidae, *Rhinoderma*, and *Allophryne*. Ford and Cannatella (1993) noted that Hyloidea and Bufonoidea apply to a nonmonophyletic group, that is, neobatrachians that were not ranoids. Ranoidea (see below) consist of ranids (including arthroleptids and mantellines), hyperoliids, rhacophorids, *Hemisus*, and microhylids. Some authors have placed

microhylids in the superfamily Microhyloidea to reflect the distinctiveness of the microhylid larva (e.g., Starrett 1973). But agreement is universal that microhylids are more closely related to ranoids than to hyloids.

Lynch (1973) considered Pelobatoidea an explicitly paraphyletic group transitional between "archaic frogs" and the "advanced frogs." He included here Pelobatidae, Pelodytidae, Heleophrynidae, the myobatrachids, and Sooglossidae. His dendrogram (Lynch 1973: fig. 3-6) showed Bufonoidea and Ranoidea as independently derived from the paraphyletic Pelobatoidea. Duellman (1975) used Reig's (1958) Neobatrachia to include Lynch's Bufonoidea and Ranoidea. Subsequent morphological and molecular analyses have supported monophyly of Neobatrachia (Cannatella 1985, Hay et al. 1995, Ruvinsky and Maxson 1996). However, supposed basal neobatrachians such as myobatrachids, sooglossids, and *Heleophryne* are of uncertain position.

Until recently, Limnodynastinae and Myobatrachinae were included as subfamilies of "Myobatrachidae" (e.g., Heyer and Liem 1976). Ford and Cannatella (1993) could find no synapomorphies for "Myobatrachidae." However, Lee and Jamieson (1992) provided some characters from spermatozoan ultrastructure that support myobatrachid monophyly. Some textbooks (Zug et al. 2001) have recognized each group as a distinct family [which was not Ford and Cannatella's (1993) intention]. Ruvinsky and Maxson (1996) placed Myobatrachinae, Limnodynastinae, and *Heleophryne* (Heleophrynidae) in a clade of at the base of Hyloidea. Some recent phylogenies have placed Sooglossidae as the sister group of all other Hyloidea (Ruvinsky and Maxson 1996), sister group to Ranoidea (Emerson et al. 2000), basal to both (Hay et al. 1995), or as the sister of Myobatrachidae (Duellman and Trueb 1986) or Myobatrachinae (Ford and Cannatella 1993).

Hyloidea

Hyloidea has been used to refer to neobatrachians with an arciferal pectoral girdle, in contrast to those with a firmisternal girdle, the ranoids. The name has Linnaean priority over Bufonoidea (Dubois 1986), although it has not been used often. Ford and Cannatella found no published data to support its monophyly. Hay et al. (1995) were the first to use character data to support the monophyly of Hyloidea (as Bufonoidea). This lineage included Myobatrachidae, Heleophrynidae, and Dendrobatidae, Centrolenidae, Hylidae, Bufonidae, Rhinodermatidae, Pseudidae, and Leptodactylidae. They also identified the Sooglossidae as a "distinct major lineage" of Neobatrachia apart from Hyloidea and Ranoidea. Ruvinsky and Maxson (1996), using mostly the same data as Hay et al. (1995), concluded that Sooglossidae was included within Hyloidea.

Darst and Cannatella (in press) identified a well-supported clade (fig. 25.7) for which they defined the name Hyloidea in a phylogenetic context. They excluded from the definition taxa such as Dendrobatidae whose phylogenetic

position might make the content of this taxon unstable. Also, they excluded certain neobatrachian groups whose placement is more relatively basal and also less well resolved, such as Myobatrachinae, Limnodynastinae, and Sooglossidae.

"Leptodactylidae" are a hodgepodge of hyloids that lack distinctive apomorphies. Historically, the derived features of the other hyloid families separated them from Leptodactylidae, suggesting it was paraphyletic. Hylidae have cartilaginous intercalary elements between the ultimate and penultimate phalanges of the hands and feet; Centrolenidae has the two elongate ankle bones (tibiale and fibulare) fused into a single element; Pseudidae have bony intercalary elements, in contrast to the generally cartilaginous ones found in hylids; has a Bidder's organ present in males; this is a portion of embryonic gonad that retains an ovarian character. Rhinodermatidae have rearing of larvae in the vocal sac of the male; Brachycephalidae lack a well-developed sternum.

Phylogenetic relationships among the genera of "Leptodactylidae" were analyzed using morphology by Heyer (1975). Basso and Cannatella (2001) analyzed relationships among leptodactyloid frogs from 12S and 16S mtDNA and found "Leptodactylidae" to be polyphyletic. Darst and Cannatella (2003) also found the same, based on a smaller sample of leptodactylid taxa (fig. 25.7).

Pseudidae, Centrolenidae, Brachycephalidae, and Dendrobatidae are node names whose content is not controversial. Recent work has clarified the relationships of some of these groups. Darst and Cannatella (in press) found Dendrobatidae to be nested clearly within Hyloidea and were able to reject the alternate hypothesis that dendrobatids are within Ranoidea (Ford 1989, Ford and Cannatella 1993). Duellman (2001) reduced Pseudidae to a subfamily. However, this action stopped short of what would be demanded by the Linnaean system. If Pseudidae is not acceptable as a family within Hylidae, then Pseudinae cannot be accepted as a subfamily within the subfamily Hylinae. Darst and Cannatella (in press) also found Pseudidae to be nested within hylines, specifically the sister group to *Scarthyla ostinodactyla*. Assuming an adherence to Linnaean taxonomy coupled with a desire to recognize only monophyletic groups, then there is no basis for recognition of the group at a subfamily or even tribe level.

Darst and Cannatella also found Brachycephalidae to be within eleutherodactylines ("Leptodactylidae"); the taxonomic changes necessitated by these new findings are in progress. *Allophryne ruthveni* is an enigmatic hyloid (Fabrezi and Langone 2000) that has been placed in a monotypic (and redundant) family Allophrynidae; it is probably the sister group of Centrolenidae (Austin et al. 2002). The two species of *Rhinoderma* have been placed in Rhinodermatidae. Were it not for the apomorphic life history of the two species, in which the males brood the developing larvae in their vocal sacs, *Rhinoderma* would be included in the "Leptodactylidae." Ford and Cannatella (1993) provided phylogenetic names for these taxa.

Hylidae is the node name for the most recent common ancestor of Hemiphractine, Phyllomedusinae, Pelodryadinae, and Hylinae, and all of its descendants. These latter four names have not been formally defined in a phylogenetic manner, but the composition of each is well established. Some workers elevated Pelodryadinae to family level (Dubois 1984, Savage 1973). Morphology-based phylogenies of Hylinae and Hemiphractinae exist (da Silva 1998, Mendelson et al. 2000). According to Darst and Cannatella (in press), Hylidae is polyphyletic; however, their sample of hemiphractines, which are the troublesome species, was small.

Bufonidae is also a node name. Recent work (Gluesenkamp 2001, Graybeal 1997, Graybeal and Cannatella 1995) found no basis for the subfamilies or tribes recognized by Dubois (1984). Relationships among the higher groups of Bufonidae are unresolved.

Ranoidea

Ford and Cannatella (1993) defined Ranoidea as the node-based name for the clade anchored by the last common ancestor of hyperoliids, rhacophorids, ranids, dendrobatids, *Hemisus*, arthroleptids, and microhylids. With the possible exception of the controversial dendrobatids, the content of this group includes the classic "firmisternal" frogs, Firmisternia. Wu (1994) treated the Ranoidea and Microhyloidea as the two components of Firmisternia. The resurrection of this arrangement has merit in recognizing the two major clades of firmisternal frogs, as in the past where the groups were Microhyloidea and Ranoidea. Duellman (1975), for example, recognized distinct superfamilies Microhyloidea and Ranoidea.

Growing evidence suggests that Microhylidae (or at least a large clade of those) is the sister group to Hyperoliidae or Hyperoliidae + arthroleptines within the Ranoidea (Darst and Cannatella in press, Emerson et al. 2000, Hay et al. 1995) rather than the sister group of all other ranoids. Thus, inclusion of Microhylidae within Ranoidea is appropriate in one sense. However, one could argue equally that Microhyloidea could include Microhylidae (minimally the type-genus) and whatever else is more closely related to these than to Ranidae. Microhyloidea and Ranoidea would be sister taxa in Firmisternia. For example, Darst and Cannatella (in press) and Emerson et al. (2000) each recovered two major clades of ranoids, one including hyperoliids, arthroleptids, microhylids (including brevicipitines), and *Hemisus*, and the other containing rhacophorids, mantellines, and the remaining "ranids." However, Blommers-Schlösser (1993) recognized Microhyloidea as consisting of Microhylidae, Sooglossidae, Dendrobatidae, and Hemisotidae. We have not followed this unusual rearrangement pending a broader synthesis of morphological and molecular data of ranoids. For the moment, we continue the use of Ranoidea for all these firmisternal frogs because of its recent common use.

Perhaps the most controversial group within Neobatrachia has been Dendrobatidae. Hay et al. (1995) and Ruvinsky
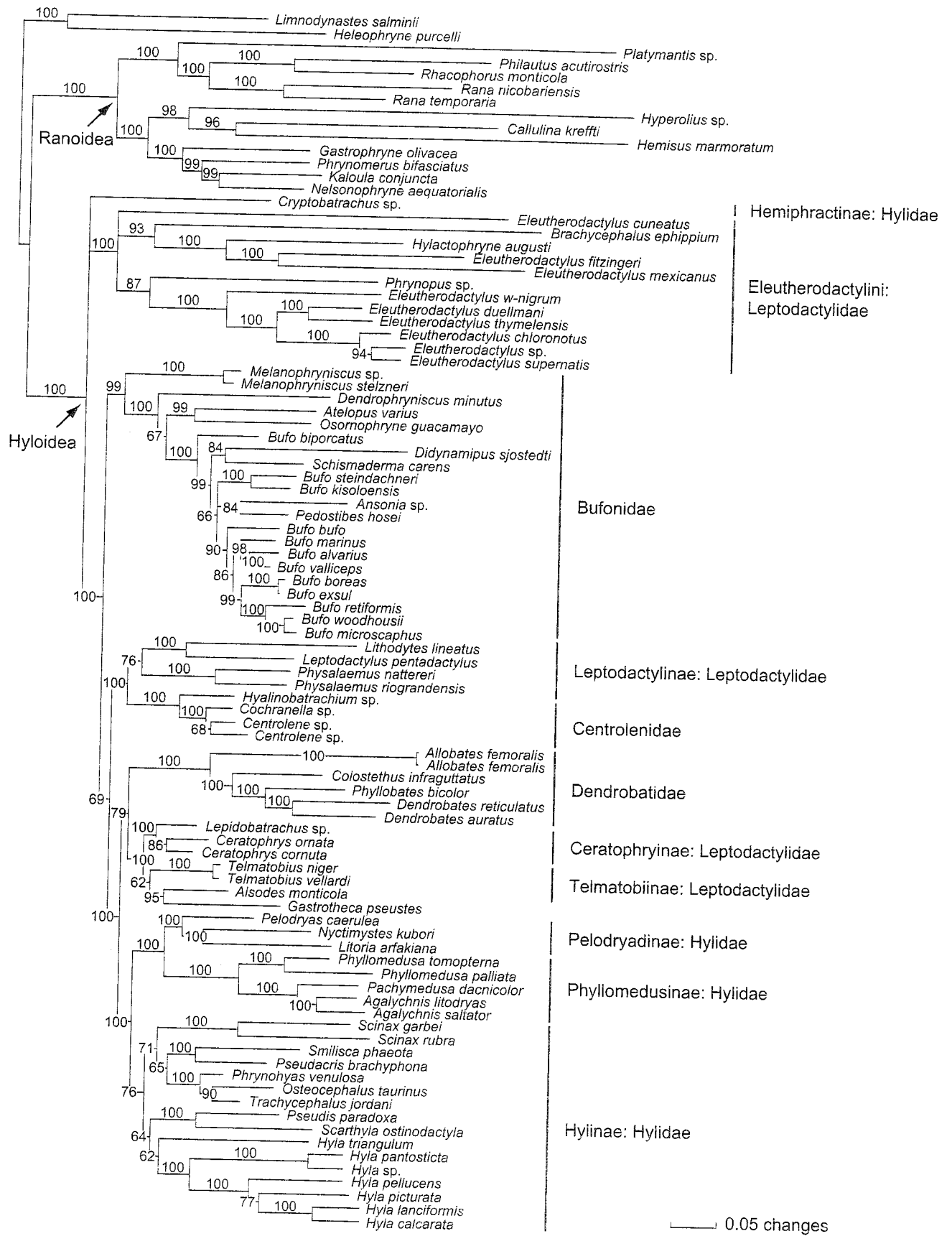
Figure 25.7. Phylogeny of Hyloidea based on a Bayesian analysis, after Darst and Cannatella (in press). The numbers on the branches are posterior probabilities.

and Maxson (1996) found dendrobatids to be nested within hyloids (bufonoids), and this was corroborated with a broader taxon sample by Darst and Cannatella (in press) and with mostly larval data by Haas (2003). In retrospect, Ford and Cannatella's (1993) inclusion of a potentially unstable taxon (Dendrobatidae) as a specifier taxon for Ranoidea was not wise. Accepting the new evidence for the position of Dendrobatidae, Ranoidea as they defined it has now the same content as Hyloidea + Ranoidea; this is a drastic departure from its usual content. Rather than redefine Ranoidea here (because of work in progress), for the moment we consider statements about Ranoidea to exclude Dendrobatidae.

Microhylidae were found to be nested within Ranoidea by Ford and Cannatella (1993), Hay et al. (1995), Ruvinsky and Maxson (1996), and (at least close to some) Haas (2003). Ford and Cannatella (1993) used larval evidence from Wassersug (1984, 1989) to formally recognize Scoptanura as a large clade within Microhylidae. This was corroborated by Haas (2003).

Wu (1994) produced the most comprehensive survey of microhylid osteology, examining 188 characters in 105 species in 56 of the 64 named genera. He adopted a rankless taxonomy, placing Microhyloidea and Ranoidea as sister groups in the Firmisternia. His Ranoidea included Hyperoliidae, Mantellidae, Ranidae, and Rhacophoridae, and his Microhyloidea consisted of two families, Brevicipitidae and Microhylidae. Wu's Brevicipitidae was unusual in that it included a clade Hemisotinae composed of Hemisus and Rhinophrynus. The latter has never been placed within Neobatrachia and shares many molecular and morphological synapomorphies with Pipidae (Cannatella 1985, Hay et al. 1995).

Relationships of ranoid frogs (microhylids aside) are in a kinetic state, and the taxonomy we follow is certainly arbitrary. For years an accepted arrangement was Ranidae, Hyperoliidae, and Rhacophoridae, the latter two families being treefrog morphs independently derived from within Ranidae. It was generally appreciated that the mantelline ranids (Mantellinae or Matellidae) shared some derived features with Rhacophoridae (e.g., Duellman and Trueb 1986). Ford and Cannatella (1993) embellished "Ranidae" with quotes to indicate its status as a nonmonophyletic group.

Most recent attempts to establish a classification of Ranidae have been based on a hypothesis of phylogeny (but see Dubois 1992, Inger 1996). Phylogenetic analyses of both sequence data and morphological characters exist for Hyperoliidae and Rhacophoridae (Channing 1989, Drewes 1984, Liem 1970, Richards and Moore 1996, 1998, J. Wilkinson et al. 2002). Although Rhacophoridae have generally been thought to be monophyletic, accumulating evidence suggests that the Malagasy rhacophorids are not the closest relatives of the Asian rhacophorids (J. Wilkinson et al. 2002) and may be more closely related to other Malagasy lineages, such as mantellines.

The most comprehensive analysis of ranoids (Emerson et al. 2000), which used mostly published molecular data and 10 morphological characters, found familiar results: the close relationship of Microhylidae and Hyperoliidae (Hay et al. 1995); the placement of Sooglossidae outside of Ranoidea (Hay et al. 1995); and mantelline ranids most closely related to, or nested within, rhacophorids (Channing 1989, Ford 1989). Relationships among a small sample of Indian ranoids were examined by Bossuyt and Milinkovitch (2001).

As had historically happened with hyloids, the recent taxonomic tendency for ranoids has been to elevate some loosely defined subfamily groups to family status; for example, the recognition of Arthroleptidae by Dubois (1984). These have usually been considered to be a subfamily of Ranidae, and its elevation to family level was more because of taxonomic tinkering than any new knowledge of relationships. Ford and Cannatella (1993) considered it a metataxon.

Blommers-Schlösser (1993) recognized a clade Ranoidea comprising Arthroleptidae, Hyperoliidae, and Ranidae, the last including Mantellinae and Rhacophorinae. Emerson et al. (2000: table 1) listed subfamilies of Ranidae as Raninae, Mantellinae, and Rhacophorinae, reportedly from Blommers-Schlösser (1993). Actually, Blommers-Schlösser (1993) included these three, plus Cacosterninae, Nyctibatrachinae, Petropedetinae, and Indiraninae, for a total of seven subfamilies of Ranidae. Of these, the petropedetines have been arbitrarily elevated to familial rank by some. Hemisus, one of the few frogs known to burrow headfirst, has usually been placed in the redundant family Hemisotidae. It was considered to be derived from some group of African ranids, but recent molecular analysis suggests closer relationships to brevicipitine microhylids (Darst and Cannatella in press; fig. 25.7), as did a morphological analysis (Blommers-Schlösser 1993).

Prospects for the Future

Rather than address the future of the systematics of Amphibia, we offer some general comments are possibly applicable to all groups. Information age technology has changed the nature of systematics. The flood of data from molecular systematics continue to rise as new technologies facilitate its collection. The program solicitation for the National Science Foundation's Assembling the Tree of Life competition (National Science Foundation 2003) indicated the need for "scaling up" the level of activity of data collection. But scaling up in nature is rarely isometric; a change in size demands a change in shape. Put another away, we will not reach the goal of the Tree of Life (or the Tree of Amphibia) without doing systematics differently. We suggest that some of the core practices of systematics pose a severe impediment to completing the Tree of Life. Methods and theory of tree construction have "gone to warp speed" relative to the practices of taxonomy, nomenclature, and biodiversity studies.

Our facility at reconstructing phylogeny now exceeds our ability to describe new species in a reasonable amount of time.

Classically trained systematists, even those with active programs in molecular systematics, must still linger over species descriptions. Descriptions of new species are not much different than those published more than a century ago. Some systematists have bemoaned the dearth of jobs for classically trained taxonomists. But even if positions were available, would there be systematists interested in filling them? Proposals for automation of species descriptions have not received rave reviews. Is the practice of taxonomy really a different enterprise than phylogenetic analysis (Donoghue 2001)? Perhaps it is time to redefine the mode and meaning of "describing a new species."

We are not advocating a reductionist, barcode approach (Blaxter 2003) in which a sequence of one gene is sole diagnosis of a species. However, DNA sequences are a powerful source of data for species discovery and description, and we welcome a fusion between traditional activities of species description and the opportunities offered by information technology. The nature of this compromise is not clear, but it is evident that our mandate will not succeed without consideration of this issue.

Related to the description of new species is nomenclature, the rules for bestowing and keeping track of names. Although the term "Phyloinformatics" has entered the language of systematics, it lacks a meaningful definition. We do not attempt one here, but certainly any concept of phyloinformatics must include storage and retrieval systems for taxonomy and nomenclature. Like others, we suggest that the Linnaean system needs informatics-based reengineering; it is a square peg in the world of information technology.

Last, the increasing difficulty of on-site biodiversity studies must be addressed. Legitimate concerns over the loss of natural resources and opportunities through bioprospecting and biopiracy have grown in the same regions that harbor the greatest proportion of biodiversity. If natural history collections and related information are as precious as we claim, then we must invest in the countries of origin to enable the development of those resources on-site. The alternative, the removal of collections to another country largely for reasons of convenience, meets with increasing and justifiable resistance. This investment must be genuine and durable, so that local researchers are enabled to do long-term research. Only this type of investment will ensure the survival of the biodiversity that we all value.

Acknowledgments

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