Lissamphibia: modern amphibians

I. Who's who: dates, systematics, taxonomy
II. General characteristics
III. Special traits
   A. Skin
   B. Feeding adaptations
   C. Life history variation
IV. Conservation

I. Who's who: dates, systematics, taxonomy

   A. Some dates:

      1. earliest fossil fragments of modern amphibians date to Permian
      2. earliest complete fossil = early Triassic *Triadobatrachus* (see fig 9-5a . 232)
      3. modern families date to Jurassic
         a. fossils very like modern forms of all three groups
         b. indicates long period of independent evolution from each other

   B. Systematics, taxonomy, diversity:

      1. The relationships among the three major lineages (frogs, salamanders, caecilians) are still unresolved
         a. problem is that frogs and caecilians are very highly specialized
         b. so traits are either shared among all three groups or unique to one – few, if any, shared, derived characters can be identified
      2. Three groups (usually considered orders within the class **Lissamphibia**) (read pages indicated for basics of each group)
         a. **Urodela** = **Caudata** ("tailed ones"): salamanders (p. 223)
            i. ~ 10 families, 415 species
            ii. found primarily in North America, with peak diversity in Central America
            iii. some legless forms, but most are terrestrial tetrapods as adults
         b. **Anura** ("no tail") = **Salienta** ("jumpers"): frogs (pp. 228-9)
            i. ~27 families, 4300 species
            ii. cosmopolitan distribution (except Antarctica)

iii. body modified for jumping

a) see figs. 9-5 for basic structure

b) on your own, study relationships between body form and locomotion, fig. 9-6 & related text

c. **Gymniophiona** = **Apoda** (“no feet”): caecilians (pp. 232-3)

i. tropical, burrowing forms; very poorly known (not even number of families, species)

II. General characteristics of Lissamphibia (see table 9.1 p. 222)

A. Note that this group is highly modified relative to earlier batrachomorphs, etc. – do not think of them as “primitive”!

B. General characteristics (not exhaustive list!) include:

1. Skin thin, permeable, highly modified for gas exchange (more later)

a. this is a key shared, derived character for group

b. this is also where group gets its name (liss = smooth skin”)

2. all forms are carnivorous, at least as adults

3. anamniote egg (like fish)

a. no extraembryonic membranes

b. eggs dependent on external moisture to avoid desiccation

4. hyomandibular modified to form columella (= stapes) to transmit sound to inner ear

5. lungs present in all terrestrial forms except Plethodontid salamanders (more later)

a. lungs relatively simple, with relatively small surface area

b. ventilated by buccal pumping (like lung fish)

6. remnants of lateral line persist in larval forms and in some secondarily aquatic adult forms

7. temperature regulation depends on habitat:

a. aquatic forms poikilothermic (but can be adapted to remain active under ice!)

b. terrestrial forms somewhat homeothermic via ectothermy:
   i. can decrease T_B by evaporative cooling
   ii. can increase T_B by basking

8. Circulatory system/heart different from fish:
   a. patterns of circulation can be highly variable depending on site of gas exchange (lung, skin, gills, etc.)
   b. heart consists of 3 chambers: two atria, one ventricle
   c. circulation = “dual circuit pump”
      i. **pulmonary circuit** = oxygen-depleted blood leaves heart, goes to site of gas exchange, returns to heart
      ii. **systemic circuit** = oxygenated blood from heart to tissues, then back to heart
      iii. complex internal structure of ventricle keeps blood streams well-separated (so little or no mixing of oxygenated and deoxygenated blood)
   d. complex arrangement of heart and major blood vessels permits extreme flexibility in circulatory patterns:
      i. can switch among gas exchange modes (e.g., lungs vs. skin)
      ii. can alter pattern depending on whether animal is in water or on land

9. Urinary bladder important for water regulation
   a. amphibians produce dilute urine, so good source of water for reabsorption
   b. terrestrial anurans can store 20-30% of body mass as water in urinary bladder!

10. Generally have two-phase life history (more later)
   a. aquatic tadpole
   b. terrestrial adult

III. Special traits of amphibians

A. Skin highly modified for gas exchange

1. ancestral forms had dermal scales; modern amphibians have very thin, permeable skin with extensive blood supply
    a. thin to decrease the distance gasses must diffuse
    b. poorly keratinized to increase permeability
2. Poor keratinization means skin more easily damaged; reduces protection from predators
    a. extensive mucus glands provide protection from damage, predation, desiccation
    b. poison glands produce a huge variety of toxins
        i. protein and alkaloid; many with pharmacological uses
        ii. range from ~ deadly to just making animals taste bad
        iii. poison often advertised with aposematic coloration (with consequent mimicry as well)
        iv. in 3 species, poison made more effective by unique delivery mode: ribs pierce poison gland, then body wall when animal grabbed by predator – so literally stab predators with poisoned ribs!
3. Even partial reliance on cutaneous gas exchange constrains amphibian behavior, ecology, etc:
    a. constrains size: must be ~ small to maintain favorable SA/V (only relatively small animals will have sufficient skin surface to supply volume)
    b. constrains habitats: permeable to oxygen = permeable to water, so always at some desiccation risk

B. Feeding specializations of plethodontid salamanders illustrate evolutionary tradeoffs (pp. 223-226 – read on your own)
1. Plethodontidae = largest family of salamanders; all species lack lungs
2. All species use modified, protrusible tongue to capture prey
    a. requires modification of hyoid apparatus that make hyoid apparatus less useful for “normal” functions:

i. buccal pumping to ventilate lungs in adults
ii. suction feeding in aquatic tadpoles

b. solution has been to
i. eliminate lungs completely
ii. in most highly derived group (Bolitoglossinae), eliminate aquatic larval stage as well (so “adult” specializations appear during embryonic development rather than after metamorphosis)

C. Life history variation (around general “two-stage” theme)

1. First, consider why a “two-stage” life cycle might have arisen and been maintained by selection:
a. in the earliest tetrapods, terrestrial adults were probably favored because land represented a favorable environment (many resources, little competition
b. but, anamniotic egg requires wet environment for development
c. for whatever reason, pattern seems to be maintained because it works:
i. meets the constraints imposed by anamniotic egg
ii. also allows flexibility in resource use: aquatic habitats for some activities and terrestrial for others

2. If general life history pattern is maintained, at least in part, by selection favoring use of different habitats when those habitats are favorable, then we should expect to see variation in that pattern when different habitats become “risky” (the benefits of using them are less than the costs)

3. Variations in life history I: tropical frogs minimize the use of water when risks are high
a. in many tropical areas, aquatic habitats have large numbers of potential predators, competitors – so may be adaptive to avoid them
b. tropical frogs exhibit a range of adaptations to minimize reliance on water: (see pp. 245-249)
i. Lay eggs in bromeliads in trees, on land near shore

ii. Lay eggs on floating "foam" nests; tadpoles drop into water when they hatch (presumably at less risk than eggs because they're bigger, more mobile)

iii. Lay eggs on leaves overhanging water; tadopoles drop when they hatch (as above, only more so!)

iv. Eliminate aquatic stage entirely: have direct development from egg to "froglet" with no larval stage

a) occurs in ~20% of frog species

b) often accompanied by parental care of eggs (to prevent desiccation), froglets

c) examples include:

i) male Darwin frog carries eggs in vocal sacs, "burps" them out when developed

ii) female *Hemiphractus* , Surinam toad carries eggs in specialized depressions/pouches on her back

iii) female gastric brooding frog (Australia) carries eggs in stomach – with concomitant modification of stomach lining, etc.

4. Variation in life history II: paedomorphic salamanders reduce reliance on terrestrial habitats (the opposite of the frogs) by remaining aquatic as adults

a. some definitions

i. **heterochrony** = change in the timing of development

ii. **neoteny** = appearance/retention of juvenile traits in adults

iii. **paedomorphosis** = process that produces neoteny –

a) in the case of salamanders = retention of gills and other traits associated with remaining aquatic as adults

b. phenomenon in salamanders is best studied in members of genus *Ambystoma* – within this genus, get whole range of variation:

i. some species have "normal" life history

ii. some have **facultative** paedomorphosis:
   a) normal metamorphosis in some populations under some conditions
   b) paedomorphosis in others under other conditions

iii. some are **obligate** paedomorphs: virtually never metamorphose (except possibly under extreme laboratory conditions)

c. general pattern: as aquatic habitats become more predictable and terrestrial habitats more hostile and unpredictable, paedomorphosis becomes more common

d. examples:

i. *Ambystoma gracile*:
   a) increased frequency of paedomorphosis in cold Rocky Mountain ponds (few fish, permanent water)
   b) increased frequency of "normal" metamorphosis in lowland habitats (ponds more likely to dry up; more predators present)

ii. *A. tigrinum*:
   a) "normal" metamorphosis in temporary ponds in eastern part of range (NJ)
   b) increased frequency of paedomorphosis in permanent ponds in western U.S.

iii. *A. mexicanum* (axolotl)
   a) populations from shallow, warm, turbid ponds are rarely paedomorphic; metamorphose easily
   b) populations from Xochimilco (deep, permanent, clear water) virtually obligate paedomorphs (even in the lab it's hard to induce metamorphosis)

e. Garstang addressed this phenomenon in one of his poems:

THE AXOLOTL AND THE AMMOCOETE

Ambystoma's a giant newt who rears in swampy waters,
As other newts are wont to do, a lot of fishy daughters:
These Axolotls, having gills, pursue a life aquatic,
But, when they should transform to newts, are naughty and erratic.

They change upon compulsion, if the water grows too foul,
For then they have to use their lungs, and go ashore to prowl:
But when a lake's attractive, nicely aired and full of food,
They cling to youth perpetual, and rear a tadpole brood.

And newts Perennibranchiate have gone from bad to worse:
They think aquatic life is bliss, terrestrial a curse.
They do not even contemplate a change to suit the weather,
But live as tadpoles, breed as tadpoles, tadpoles altogether!

Now look at Ammocoetes there, reclining in the mud,
Preparing thyroid-extract to secure his tiny food:
If just a touch of sunshine more should make his gonads grow,
The Lancelet's claims to ancestry would get a nasty blow!
(From Walter Garstang's Larval Forms and Other Zoological Verses. University of Chicago Press, 1985. written 1922 or earlier)

IV. Conservation status:

A. read "Why are amphibians vanishing", pp. 263-267)

B. Check out the summary of the problem at

http://www.mp1-pwrc.usgs.gov/amphib/frogsum.html#DOC

C. Notes about amphibian conservation

1. two (separate?) phenomena underway:

   a. population declines, even in relatively pristine areas

   b. frog malformations becoming more common, at least in U.S.

2. Causes may be different, may not – no one really knows yet

3. Almost certainly multiple causes for both phenomena – very unlikely that a single process or phenomenon could be affecting populations in the same way all over the world

4. Because of skin, life history, amphibians are susceptible to many types of environmental degradation
   a. so declines, malformations may be result of many “small insults”
   b. the same things that make amphibians susceptible make them good “miner’s canaries” – declines may be “early warning” of subtle environmental problems that, if left unchecked, could have more widespread effects.