See Blackboard for section 4 readings.

Overview:

I. Introduction to Chondrichthyes: Origin, systematics and taxonomy.
II. Sharks
III. Skates & Rays
IV. Conservation

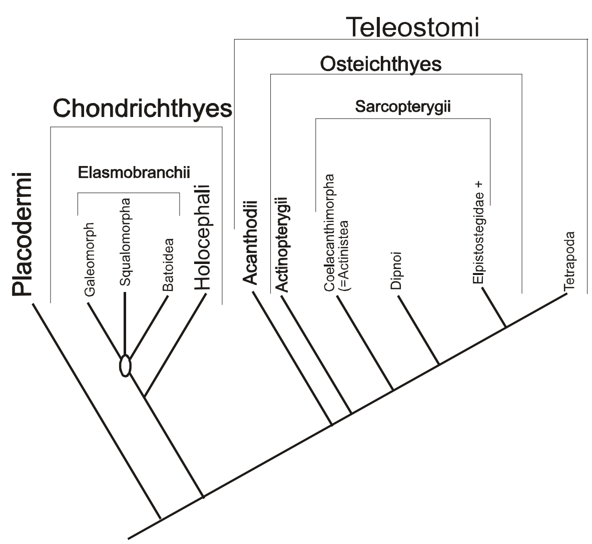
I. Introduction to the Chondrichthyes: Origin, systematics and taxonomy

A. Some dates

1. The fossil record of this group extends to the late Silurian
2. First radiation was well underway in the Devonian; by the Late Devonian, they were found primarily in fresh-water habitats
3. The group underwent several major radiations throughout the Carboniferous (~363 mybp).
4. Extant species are members of a radiation that was well underway by the early Triassic (~245 mypb); some modern genera had appeared by the Jurassic (208 mypb)
5. Members of the most recent radiation differed from earlier lineages in 3 major ways, all related to increasing efficiency in feeding and locomotion:
   a. The position of the mouth relative to the rostrum:
      1) Early forms had a terminal mouth more strongly attached to the cranium
      2) Later forms have a ventral mouth that can be extended past the tip of the rostrum (more on this later).
   b. A solid calcified vertebral column completely replaced the notochord; this was probably associated with greater efficiency of swimming via lateral undulation.
   c. Thicker, more complex enamel on the teeth was probably associated with predatory life style.
6. This is an old lineage of very well-adapted organisms.

B. Systematics and taxonomy

1. Chondrichthyes is a good monophyletic group (single common ancestor + all descendants)
2. The relationships among modern Chondrichthyes are poorly understood, in part because
   a. Major changes in teeth, jaws, and fins evolved at different rates in different lineages, resulting in
      1) extensive morphological variation among groups
      2) extant groups with confusing combinations of primitive and derived traits
   b. Extensive convergence and parallelism as different lineages responded similarly to similar selection pressures.
3. Relationships to each other, other fish illustrated using 3 traditional elasmobranch lineages:
   a. **Placodermi** = extinct lineage of armored, jawed fish
   b. Because relationships among modern **Elasmobranchii** not well understood, left unresolved
   c. Fairly well established that the group includes two major lineages that diverged in the Devonian:
      1) **Holocephali** ("complete head")= ratfish, chimaeras
      2) **Elasmobranchii** ("plate-gills")= sharks, skates, rays



4. Traditionally, taxonomists recognized 9-11 orders grouped into three superorders within Elasmobranchii:
   a. **Squaloidea**: deep, cold-water sharks with more primitive characters

   b. **Galeoidea**: more derived, shallow, warm-water sharks
   c. **Batoidea**: skates and rays
5. Now, though, we recognize that those groups don't necessarily portray relationships within or among orders accurately – so use alternative approach: group orders based on a variety of biological similarities and differences (grades), and leave question of relationships open
6. Result = taxonomy used, e.g., by Dr. Carpenter in ichthyology:
   a. Class Chondrichthyes
      1) Subclass Holocephali (chimaeras) - ~ 56 species of deep-water fish; very poorly known
      2) Subclass Elasmobranchii (sharks, skates, rays) = 800+ species
         a) Superclass Euselachii
            i) Galeomorph orders ("classic" sharks)
            ii) Squalomorph orders (deep water sharks)
            iii) Squatinomorph order (angel sharks)
            iv) Batoid fishes (order Rajiformes - skates and rays)

C. Major characteristics
1. Important shared, derived characters uniting all Chondrichthyes :
   a. **Cartilagenous skeleton**, rather than bony skeleton:
      1) Older thought was that, since bone typically forms from cartilage, the cartilagenous skeleton represented a primitive condition from which a true bony skeleton evolved – fossil evidence refutes that, and we now recognize that this is a derived trait.
      2) Note that skeleton does include calcium deposits, but isn't true bone
   b. Dermal armor reduced to **placoid scales** = denticles
      1) These give shark skin its "sandpapery" texture
      2) Function is to reduce tubulence & increase swimming efficiency
      3) Works well enough that swimsuits are now being made with similar properties; they may actually shave time off races.

c. **Lack of lung, swim bladder** – (use regulation of oil in liver to regulate buoyancy)
   1) Again, early thought was that lack of lungs, swim bladder (specialized features) was primitive
   2) More recent evidence suggests that these features were present in placoderms, lost in Chondrichthyes

2. Other important features of Chondrichthyes (doesn't matter whether derived or not):
   a. The internal skeleton is well developed and includes
      1) a robust skull, jaws;
      2) "u-shaped" pectoral girdle supporting robust fins
      3) laterally flexible vertebral column permitting swimming via lateral undulation
   b. Teeth not fused to jaws; serially replaced as lost (under ideal conditions, a young modern shark can replace each lower jaw tooth every 8.2 days; each upper jaw tooth every 7.8 days!!)
   c. Gills not covered by operculum
   d. Internal fertilization; in most, male pelvic fins are modified as claspers to transfer sperm
   e. Embryos encapsulated in leathery case

3. Characteristics of Holocephali:
   a. Single gill slit on each side
   b. Teeth in the form of grinding plates; lack enamel and have slow replacement
   c. Feed on shrimp, gastropods, sea urchins – but our knowledge of their feeding biology is very limited, so this isn't an exclusive list.
   d. Males with claspers on the head in some species
   e. No scales, except for small denticles on back and on claspers
   f. Palatoquadrate fused to cranium = **holostylic jaw suspension**

g. Live in deep water (> 80m) and move to shallow water to deposit eggs.
h. Name comes from odd appearance: look like they're made from parts of several different animals

4. Characteristics of Elasmobranchii (sharks, skates, rays)
   a. 5-7 gill slits on each side of head
   b. Palatoquadrate not fused to cranium = **hyostylic jaw suspension**; **protrusible jaw**
      1) Jaw can swing forward past rostrum
      2) This permits
         a) very wide, unobstructed gape during biting, but
         b) streamlined rostrum maintained when not feeding
      3) It also permits strong suction feeding by permitting large, rapid change in volume of the oral cavity
   c. Numerous teeth with serial replacement ("conveyer belt" of replacement teeth from within jaw)
   d. Specialized sensory organs = **ampullae of Lorenzini** for electroreception, thermoreception (more on this later)

II. Sharks and shark-like orders
   A. Characteristics:
      1. Generally elongate, streamlined body ranging in size from 25 cm (green dogfish shark) to 18 m (whale shark – biggest fish); average ~ 2 m
      2. **Heterocercal tail** (upper lobe bigger than lower lobe) powers swimming
      3. Usually 7 fins: 2 pectoral, 2 pelvic, 2 dorsal, 1 anal
      4. Teeth sharp, numerous, continuously replaced
      5. Mostly carnivorous
      6. Largest forms are filter feeders (whale sharks, basking sharks), using **gill rakers** as filters
   B. Distribution and diversity
      1. Total of ~ 360 species

2. Galeomorph orders
   a. 4 orders, one of which (Carchariformes = order including tiger, hammerhead sharks) has ~ 208 species
   b. Also includes great whites, nurse sharks, whale sharks (largest fish, avg ~12 m), basking sharks (second largest)
   c. Generally found in relatively shallow tropical waters, either coastal or oceanic
3. Squalomorph orders
   a. Generally found in deep water, often colder than inhabited by Galeamorph orders
   b. Includes frilled sharks, dogfish sharks, cookie-cutter shark, saw sharks
   c. ~ 75 species
4. Squatinomorph order
   a. One order, 12 species
   b. Angel sharks
   c. Mostly from shallow, temperate and tropical oceans

C. Reproduction is sophisticated and variable
1. Fertilization internal; males have specialized regions of pelvic fins = claspers
   a. inserted into female's cloaca
   b. groove on upper surface carries sperm from male's cloaca to female
2. Birth varies
   a. **Oviparous** – eggs develop, hatch outside female's body
      1) Nourishment comes from yolk – often as big as or bigger than the yolk of a chicken egg – called **lecithotropy**
      2) Eggs encased in proteinaceous sheath, often with hooks or other structures that snag the substrate and hold the egg in place
      3) Embryos move within egg case, creating currents that ventilate the embryo as it develops (water moves through openings in the case).
      4) Development takes 6-10 months (a long time)

b. In some, eggs retained within female's body (**ovoviviparity**) but still nourished by yolk (still **lecithotrophy** egg-nourished);
   1) In some cases, hatched young may be retained after hatching
   2) Ovoviviparous species typically have ~ 12 young at a time

c. **Viviparity** (live birth) with **matrotrophy** (mother-nourished) = embryos nourished continuously by mother throughout development; several forms possible
   1) Extensions of oviduct walls secrete nutritive fluid into mouth, gills of developing young
   2) Continued ovulation provides food in the form of eggs
   3) **Placentotrophic viviparity** = development of yolk sac placenta which transfers nutrients via mother's uterine bloodstream
   4) In several species of shark, intrauterine cannibalism occurs (most developed eats least developed)
   5) Viviparous species have the fewest young – sometimes only 2

d. Regardless of mode of birth:
   1) No parental care is known.
   2) Life history is "K-selected": low reproductive potential
      a) Individuals may take up to 16 years to reach sexual maturity
      b) Gestation periods are long – 9 months to 2 years
      c) Relatively few young are born (average is ~ 12) per litter

D. Sharks are primarily solitary, but observations of schooling in some species suggests that they may aggregate for reproduction

III. Skates and rays

A. Characteristics of skates, rays: generally related to benthic (bottom-dwelling), **durophagous** ("hard-eating") habits

1. Teeth are generally hard, flattened plates for crushing shells of invertebrates)
   a. In some rays, teeth are sexually dimorphic: females retain hard, flattened

plates, but male teeth may change to sharper biting teeth during breeding season.

2. Ventrally situated, protrusible jaws provide suction to pick up shells from sediments
3. Body dorsoventrally flattened
4. Pectoral fins enlarged, support elements actually fused to skull
5. Swimming via undulation of pectoral fins
6. Placoid scales largely absent, modified in some forms into venomous spines at base of tail
7. Eyes large, dorsally placed
8. **Spiracles** for intake of water for gas exchange also dorsally placed; gill slits ventral
9. Largest forms (e.g., manta ray, 6 m across), like sharks, are filter feeders
10. Torpedo and electric rays have specialized gill muscle tissues capable of generating weak to strong electric fields (more on this later)
11. Differences between skates and rays:
    a. Skates generally have elongate, thick tail stalk with 2 dorsal fins & 1 terminal caudal fin; are oviparous ("mermaid's purses" are skate egg cases)
    b. Rays have long, whip-like tail stalks with fins replaced by one or more venomous barbs; are viviparous

B. Distribution and diversity
1. ~ 456 species,
2. Almost entirely marine
3. Found at a variety of depths in temperate, tropical waters

IV. Elasmobranch conservation (mostly sharks)

A. Elasmobranchs (especially sharks) are commercially valuable for many reasons
1. As a protein source for developed countries & subsistence fishing
2. As a source of cartilage and other products for traditional medicine

3. For sport/recreational fishing

B. Fisheries – especially shark fisheries – are in decline world-wide for 3 major reasons:

1. **Directed fishing**: “catching on purpose”
   a. Over the past few decades, as other commercially valuable species have been overharvested, sharks, skates & rays are replacing other fish species
      1) E.g., in England, replace cod in fish & chips
      2) In U.S., government started major marketing campaign in 1980's, increasing the consumption of, e.g., shark steaks
   b. At the same time, rising Asian markets have increased the demand for shark fins for soup served at traditional celebrations (e.g., weddings)
      1) Before finning was banned in the U.S., fresh “wet” fins could be sold for $100/pound
      2) Soup can cost $90/bowl
      3) In 1997, long-line fishing in Hawaii took 100,000 sharks; 98.6% of that mass was discarded.
   c. So demand (and catch) has steadily increased
      1) In 2000, the official FAO estimate was that 800,000 tonnes were harvested worldwide (70 million individual fish, mostly sharks)
      2) U.S. catch is estimated at ~ 20,000 tonnes/year
      3) Because of problems with official documentation, this is undoubtedly an understimate
   d. Sport/recreational fishing is also a problem
      1) In the U.S., East Coast anglers took 280,000 sharks in 1996.
      2) Many of these are caught in nursery areas, so may represent young individuals
2. **By-catch** of sharks, especially from long-line fishing and deep-water trawling, is also huge (although hard to estimate accurately)

a. According to one FAO document, by-catch in the late 1980's was 11.6-12.7 million fish (mostly sharks)
b. By some estimates, by-catch kills as many as directed fishing.

3. **Habitat loss and degradation**
   a. Many species use coastal waters (e.g., mangrove swamps, estuaries) as nurseries
   b. These types of habitats are being lost and degraded at a higher rate globally than any other

C. The result: some U.S. fisheries have declined 50-85% over the last 20 years; similar trends are seen elsewhere.

D. These losses, combined with life-history patterns, creates significant conservation challenges

1. For all species, but for ovoviviparous and viviparous species especially, relatively low reproductive rates mean populations are particularly vulnerable to overexploitation – may take decades to recover even with total bans on harvest
2. Low population growth rates also make it hard to document the effects of regulations (i.e., reducing allowable take now may not have a measurable effect for 30 years) – which can create political problems.
3. An important ongoing challenge is gathering data – on fishing, and on the biology of the species involved – so we can make sound management recommendations.
4. What's being done? National and international conservation organizations (public and private) are beginning to work on conservation issues – gathering baseline data, establishing management policies, regulating trade, etc.
   a. In US
      1) We started regulating shark fisheries in 1993 and have expanded those efforts since then

- a) Even with those efforts, though, by 2000, emergency seasonal bans on dogfish catches were being implemented well before the end of planned "seasons"

2) The U.S. banned finning in 2000 (but at least some long-liners just moved their operations from Hawaii to waters outside U.S. jurisdiction)

b. The UN General Assembly passed a resolution requesting an end to finning, but no enforcement provided.

c. CITES is proposing international regulations, but those are problematic

1) Migratory species cross "boundaries" among countries, so need international cooperation

2) Many spend time in international waters where no country has jurisdiction

3) Not all countries are members or, if members, are willing to comply