Radiation of the Chondrichthyes

Focus especially on 5.5: The Extant Radiation pp. 119-130

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   A. Characteristics
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I. Origin, systematics and taxonomy

   A. Some dates

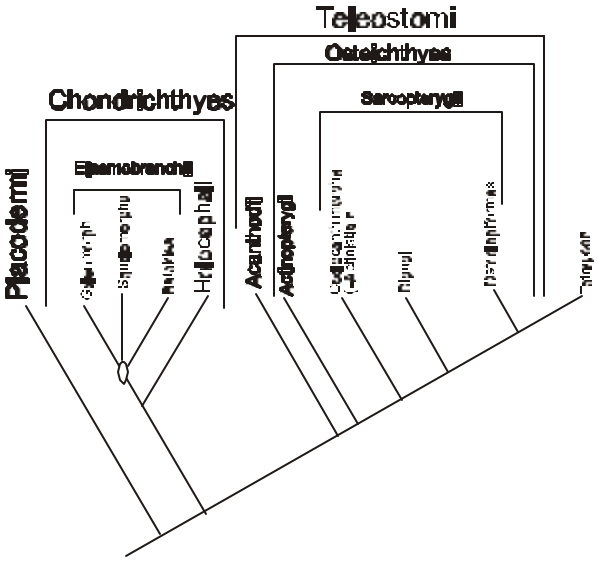
      1. The fossil record of this group extends to at least the late Silurian; they had probably originated by early Devonian.
      2. The group underwent several major radiations throughout the Carboniferous (~363 mybp).
      3. Extant species are members of a radiation that was well underway by the early Triassic (~245 mypb);
      4. Some modern genera had appeared by the Jurassic (208 mypb)
      5. So this is an old lineage of obviously really well-adapted organisms!

   B. Systematics and taxonomy (note differences from text!)

      1. Chondrichthyes is a good monophyletic group (single common ancestor + all descendants)
      2. The relationships among modern Chondrichthyes are poorly understood, in part due to
         a. extensive morphological variation
         b. extensive convergence and parallelism
         c. lots of variation in evolutionary rates (so groups often characterized by mixes

of primitive and unique, derived characters)

3. Relationships to each other, other fish illustrated:
   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, recognized 9-11 orders grouped into three superorders within Elasmobranchii:
   a. **Squaloidea**: sharks
   b. **Galeoidea**: more sharks
   c. **Batoidea**: skates and rays
5. Now, though, recognize that those groups don't necessarily portray relationships 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)
   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: note that skeleton often includes calcium deposits, but not true bone
   b. dermal armor reduced to **placoid scales** = denticles
   c. lack of lung, swim bladder – (use regulation of oil in liver to regulate buoyancy) note: we used to think that lack of lungs, swim bladder (specialized features) was primitive
      1) more recent evidence suggests that these features were present in placoderms, lost in Chondrichthyes
      2) so, in this case, lack of a specialized feature is actually derived
2. Other important features of Chondrichthyes (doesn't matter whether derived or not):
   a. internal skeleton is well developed and includes
      1) 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. in most, males have claspers on pelvic fins for internal fertilization
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. males with claspers on the head in some species
   d. no scales, except for small denticles on back and on claspers
   e. palatoquadrate fused to cranium = **holostylic jaw suspension**
   f. 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) permits
         a) very wide, unobstructed gape during biting, but
         b) streamlined rostrum maintained when not feeding
      3) also permits strong suction feeding
   c. numerous teeth with serial replacement ("conveyer belt" of replacement teeth from within jaw)

II. Sharks and shark-like orders (read about sensory systems, social behavior on your own)

A. Characteristics:
1. generally elongate, streamlined body ranging in size from 25 cm (green dogfish shark) to 20 m (whale shark – biggest fish); average ~ 2.5 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. all marine, 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 (read details p. 123-124):
      a. **oviparous** – eggs with leathery sheaths develop, hatch outside female's body

b. eggs retained within female's body (**ovoviviparity**) but still nourished by yolk = **lecithotrophy** (egg-nourished)
c. **viviparity** = **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)

D. Life history and conservation (see FMNH website for good coverage; some of the following data are from that site)
1. Many shark fisheries seem to be in decline world-wide,
    a. data are not easily available (seems that only recently has much attention been paid to these organisms)
    b. in US, some coastal species have experienced declines of 50-85% over last 20 years
2. For all species, but for ovoviviparous and viviparous species especially, relatively low reproductive rates mean populations are particularly vulnerable to overexploitation (see fig 5-7 p. 126).
    a. may take anywhere from 3-16 years to reach sexual maturity (depending on species)
    b. gestation periods range from 6 months - 2 years!
    c. average = ~12 young/litter, but may be as few as one or two (especially in species with intrauterine cannibalism)
    d. means that overexploited population may take decades to recover, even if total ban on harvest is imposed

3. Threats take several important forms:
    a. Over-harvest for human consumption is very important:
        1) shark, skate, and ray catches worldwide over 800,000 metric tons annually (70 million sharks annually make up bulk of catch)
        2) meat is used for food, especially with decline of other fisheries
        3) lots of sharks are killed annually just for fins (for soup) –
            a) fresh fins in US sell for $100/lb, making them hugely valuable compared to other fish products
            b) often, individuals are "finned" and thrown back into the ocean to die – read figures p. 125
        4) cartilage is used for medicine (e.g., in arthritis treatment); oil and skin also used
    b. habitat loss/degradation is another big problem
        1) many species use coastal waters (e.g., mangrove swamps, estuaries) as nurseries
        2) these types of habitats are being lost and degraded at a very high rate
    c. other problems (hard to determine how severe) include
        1) by-catch: caught while fishing for other species and killed
        2) sport fishing
4. 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, e.g., started regulating shark fisheries in 1993
    b. by 2000, emergency seasonal bans on dogfish catches were being implemented
    c. but regulating international trade is very difficult (see text for e.g.'s).

III. Skates and rays

A. Characteristics of skates, rays: generally related to benthic (bottom-dwelling),

durophagous ("hard-eating") habits

1. teeth generally hard, flattened plates for crushing shells of invertebrates)
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. some families have specialized 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 dorsal fins; 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