History of fishes - Structural Patterns and Trends in Diversification

AGNATHANS = Jawless

- Class – Pteraspidomorphi
- Class – Myxini?? (living)
- Class – Cephalaspidomorphi
  - Osteostraci
  - Anaspidiformes
  - Petromyzontiformes (living)

Major Groups of Agnathans

- 1. Osteostracida 2. Anaspida 3. Pteraspidomorphida
- Hagfish and Lamprey = traditionally together in cyclostomata

Jaws = GNATHOSTOMES

- Gnathostomes: the jawed fishes -good evidence for gnathostome monophyly.
- 4 major groups of jawed vertebrates:
  Extinct Acanthodii and Placodermi (know)
  Living Chondrichthyes and Osteichthyes

- Living Chondrichthyans - usually divided into Selachii or Elasmobranchi (sharks and rays) and Holocephali (chimeroids).
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- Living Osteichthyans commonly regarded as forming two major groups -
  - Actinopterygii – Ray finned fish
  - Sarcopterygii (coelacanths, lungfish, Tetrapods).

- SARCOPTERYGII = Coelacanths + (Dipnoi = Lung-fish) + Rhipidistian (Osteolepimorphi) = Tetrapod Ancestors (Eusthenopteron) Close to tetrapods

Lungfish - Dipnoi

- Three genera, Africa+Australian+South American

ACTINOPTERYGII

Bichirs – Cladistia = POLYPTERIFORMES
Notable exception = Cladistia – Polypterus (bichirs) - Represented by 10 FW species - tropical Africa and one species - *Erpetoichthys calabaricus* – reedfish.

Highly aberrant Cladistia - numerous uniquely derived features – long, independent evolution:

- Strange dorsal finlets, Series spiracular ossicles, Peculiar urohyal bone and parasphenoid

- But retain # primitive Actinopterygian features = heavy ganoid scales (external layer of ganoine), gular plates, spiral valve in the intestine and lung-like swim bladder

Historical Context

Agassiz (1833-44) compendium fossil fish & Muller's (1845) classification living actinopterygians - 3 major assemblages: Chondrostei (sturgeon/paddlefish), Holostei (Gars/Amia), and Teleostei - "Interrelationships of fishes" (1973) - by Greenwood, P. H., Miles, S., Patterson, C. eds, J. Linn. Soc. (London) 53 Supplement 1. Academic Press, New York,

Basal actinopterygians – (1) FYI – not required (fossil Paleonisciformes), (2) Polypteriformes (Cladistia), (3) Acipenseriformes=Chondrosteans=sturgeon/paddlefish, (4) Neopterygians.
1+2 = Most taxa represented are fossil - Polypterids living.

(3) Acipenseriformes=Chondrosteans – 2 living = Acipenseridae - sturgeons (25 recent species) and Polyodontidae - paddlefishes

4) Neopteryii - Three major groups: Lepisosteiformes (Ginglymodi) - gars (Lepisosteidae – 2 genera and 7 spp.; ganoin scales) and Amiiformes=Halecostomi - halecomorphi - several fossils, and amia (bowfin=cycloid scales) – traditionally Holostei plus Teleosteii

Teleostei - subject of much of rest diversity survey – 20,000 + species.

Evolution of particular function in Actinopterygian fishes in context of historical sequence of structural changes within clade

- Function = feeding; specifically the elaboration of inertial suction feeding mechanisms.
- Remember - aquatic medium (800 times more dense and 80 times more viscous than air). Also oxygen less, temperature stable, hydrate, buoyancy, viscosity (more drag).
- Food acquisition on land is a very different matter than that underwater.
- Understand fundamental differences in aquatic versus terrestrial feeding modes

- Functionally Actinopterygian feeding can be grouped into three major categories:
- 1) Ram feeding, 2) Inertial suction and 3) Manipulation

- Actinopterygian feeding mechanism - mouth opening in primitive Actinopterygians mediated by two musculoskeletal couplings:
- 1. Dorsal epaxial - neurocranial coupling; Elevates the head.
- 2. Ventral coupling - hypaxial musculature, cleithrum, sternohyoideus and hyoid apparatus = causes mandibular depression

Where did jaws come from?
How to study feeding? - High speed cinematography, Electromyographic analyses, Measurement of buccal cavity pressure differentials, Strain gauge analyses

Chondrichthyes – Sharks, Skates, Rays
MOUTH OPENING - Lift head with epaxial muscles, Mandible pulled down by ventral muscles between hyoid/mandible and pectoral girdle, Enlargement of mouth/pharynx (suction) = BIG GAPE
MOUTH CLOSING – ADDUCTION; Formidable bite – Large adductor mandibulae (AM) and preorbitalis muscles = optimized out-force at teeth

Evolution of Feeding

- Actinopterygian feeding mechanism = increase structural complexity. Cladistically derived lineages structural complex - number of connections in the structural network - increases.

Feeding in Primitive Actinopterygians - Anatomy

1. Dorsal epaxial muscles-neurocranial coupling; Elevates head
2. Ventral coupling – (hypaxial musculature, cleithrum, sternohyoideus and hyoid apparatus) = causes mandibular depression via insertion of mandibulohyoid ligament
Found also in lungfish, coelacanths and Sharks

Primitive Actinopterygians - living Polypterids - jaw adapted to "gripping" and "biting" habit.

Amiiformes=Halecostomes Feeding Mechanism = Amiidae

2 independent biomechanical pathways for mandibular depression:
- 1) Primitive ventral coupling retained.
- 2) New coupling = opercular series.
- Why have two biomechanically independent pathways of mandibular depression?

Next Innovation - Halecostomes
1. Maxilla - is free, pivots on medially directed process posterior to vomer.

Food capture accomplished by highly effective suction mechanism. Theoretically any kind of prey in water can effectively be collected by this basic feeding mechanism.
'Corollary' - no marked specializations or adaptations in trophic apparatus necessary to collect wide variety of aquatic organisms
Fundamental dichotomy between this aquatic feeding model and basic terrestrial model

Teleosts

Teleost feeding mechanism - 3 major changes occurred in structural network of head.
- 1) Insertion of mandibulohyoid ligament to interoperculum - effectively shifts action of hyoid and opercular couplings onto interoperculum.
- 2) Elongate ascending process on premaxilla - associated with jaw protrusibility.
- 3) Adductor mandibulae muscle complex - associated with evolution of jaw protrusion.

Teleosts – Other Morphological Innovations
- Pharyngeal Jaws (Cyprinids, Cichlids, Labrids etc) - Functional Decoupling
- Modular Multiplicity - Hardware vs Software (Patterns Neuromuscular Firing)

Modular Multiplicity
- 1. Inertial suction (is); slow and horizontal - Universal mode of feeding strategy in teleosts.
- 2. Inertial suction; slow and upward; any food on water surface.
- 3. Inertial suction; slow down; food from bottom
- 4. Biting - Extreme mouth opening and jaw protrusion
- 5. Manipulation - Continuously modulated, non-cyclical pattern is most complex.

Summarize aquatic feeding model

Fish feeding apparatus = truncated cone or cylinder. Suction is generated when cone expands. Dense aquatic medium and expanding cone suction generating device = extremely versatile feeding model. Versatility of expanding cone model = restricted not only to prey capture. Acts as a hydrodynamic tongue.
Aquatic medium + suction + hydrodynamic tongue = unparalleled prey capture opportunities for teleosts

Basic Terrestrial Feeding Model
Feeding cycle = slow opening - tongue fitted to prey. Second phase = fast opening - skull and mandible move apart., Prey transported by tongue. Fast closure. Final phase is slow close or power stroke during which prey is crushed.
Pattern pervasive among terrestrial vertebrates. Very conserved muscle actions.
Two major implications are:
1) prey capture must proceed actively by special adaptations and pursuit.
2) prey processing requires a precise design in the "hardware" of feeding apparatus to match nature of prey, as neuromuscular output (software) is constant.

Fundamental differences in aquatic and terrestrial feeding models

Liem - ecological performance of aquatic and terrestrial vertebrates. Generalizations don't fit.
Aquatic paradigms

1. Increased opportunism, food overlap prevail. Extensive diet switching, opportunism and reduced resource partitioning during normal food abundance. Resource partitioning in fishes = flexible partitions depending upon species present and prevailing resources.

Terrestrial - precise match of design w/ biological role. Less opportunistic feeding, increased resource partitioning and limited diet switching. Match bill design with preferred food & limited food overlap = Darwin's finches and Hawaiian Honeycreepers
2) Aquatic vertebrate feeding systems - convergent evolution uncommon.
3) Aquatic vertebrate feeding systems - relaxed competition and absence of character displacement.

Teleost Radiation ~ 20,000 species.

About 1/2 living vertebrates = teleosts, First = Triassic 240 my;

Teleost Monophyly
1. Mobile premaxilla.
2. Unpaired basibranchial tooth plates (trend -consolidation dermal tooth patches in pharynx).
3. Internal carotid foramen enclosed in parasphenoid (all characters functional?)

Teleost Caudal Fin
Halecomorphs-ginglymodes = caudal fin rays articulate with posterior edge of haemal spines and hypurals (modified haemal spines). Fin is heterocercal (inside and out).
"Chondrostean hinge" at base of upper lobe - weakness btw body and tail lobe. Asymmetrical tail = asymmetrical thrust with respect to body axis.
Teleosts
(1) Ural neural arches elongated into uroneurals.

(2) Preural and ural centra is important. Pre-urals carry normal haemal arches and spines - ural centra carry hypurals. Boundary marked by caudal artery and vein.
(3) The hypurals expanded - into a broad plate
Internally asymmetrical but externally symmetrical tail fin.

Lauder - Found continuous locomotion hypurals appear to distort and twist resulting in anterioventrally inclined thrust (asymmetrical). Fast start accelerations strain patterns consistent with symmetrical anteriorly directed thrust.

Other Teleost Traits
Teleosts have Mauthner system - specialized nerve cells.

Teleost Taxonomy - Four major groups.
1) Osteoglossomorpha, 2) Elopomorpha, 3) Clupeomorpha, 4) Euteleostei

1-Osteoglossomorphs (bony tongues – parasphenoid bite)
- Divided into two main groups. A) Osteoglossoidei and B) Neotopteroidei (Tremendous mormyrid radiation and peculiar type of otophysic connection (btw ear and swimbladder), strangely modified ventral branchial muscles.

Why group within lineage is so "successful" or speciose.
Complex social communication via unique electrical modality. Electric communication used in aggression, courtship and appeasement, and in identifying sex, species and individual.

Lateral line - complex sensory system - detect pressure waves in water - in some teleosts - modified into electroreceptors

2-Elopomorpha
2 elopocephalan lineages: Elopomorpha & Clupeomorpha - long time included together - clearly two distinct teleostean lineages

Elopomorpha - comprising 5 major groups and (Eels, tarpons, bonefish etc.) about 650 species - most Elopomorphs primarily marine fishes
1. Leptocephalus larva
2. Fusion of angular and retroarticular bones of lower jaw.
3. Presence of rostral and prenasal ossicles.

3) Clupeomorpha - clearly defined aggregates of living teleosts - five families with about 300 species) – but unsurpassed in terms of biomass and importance for fisheries. Largest taxon of non-domesticated vertebrates harvested by man.

Neurocranium architecture- two prominent foramena - temporal (bordered by frontals & parietals) and auditory foramen (bordered by prootic, exoccipital & basioccipital)
Unique caudal skeleton.

Engraulidae - Anchovies, 16 genera 140 species worldwide - Characteristic snout overhanging mouth and Clupeidae - herrings, shads and menhadens 50 genera and 190 species.

REMEMBER:
Teleosts = Osteogloss+Elopomorpha+Clupeomorpha+Euteleostei
Euteleosts=OSTARIOPHYSI+PROTACANTHOPPTERYGII+NEOTELEOSTS

OSTARIOPHYSI = Gonorynchiformes+Otophysii – Many fish species in freshwater in ostariophysi.

- Weberian apparatus - a complex otophysic connection involving considerable specialization of the swimbladder, inner ear, ligaments and anterior vertebrae.

What are gonorynchiformes?

- Presence of "fright reaction" and production of "alarm substance" (shcreckstoff), pheromone produced by specially modified epidermal club cells.

Otophysi -
Cypriniformes 2422 (6 families 256 genera)
Characiformes 1335 (10 families 253 genera)
Gymnotoids 55 (6 families 23 genera)
Siluroids 2211 (30 plus families 400 genera)

Elaboration of pharyngeal jaw apparatus - is mirrored in the cyprinids
Characiformes – Ecologically diverse, adipose fin, replacement dentition, and ctenoid scales – Africa (Tiger fish) – tetras, pacus, silver dollars, piranhas.

Siluriformes – teeth on roof of mouth, reduction in skull bones, adipose fin, locking spines; Naked = lack true scales but some have overlapping bony plates; some huge 3 m – 330 kg = Siluris glanis.NA = flathead and blues = 1.5 m; Candiru = trichomycterids swim into urethra??=rheophilic, Air breathing and terrestrial locomotion

Gymnotids – Most advanced, produce and receive weak electric impulses – South American Knifefish (not osteoglossiform)

PROTACANTHOPTERYGII - Adipose fin, no spiny fin rays, Pelvic axillary process-flap base of pelvic fin, Maxilla included in gape, Vertical barring in young = parr marks

3 forms of diadromy: Anadromy, Catadromy and Amphidromy

- Esociformes – Pikes and mudminnows; maxilla bone in gape but toothless
  Osmeriformes – Smelts, icefish, argentines etc.; Marine, Freshwater and diadromous.
- Salmoniformes – Three major groups: Coregonid whitefishes, thymallid graylings and salmonid salmons. = One major group Salmonidae??

NEOTELEOSTS
Neoteleosts: Emergence of a Pharyngeal Retractor Muscle - seven super orders recognized.

Anterior end = Dorsal gill arch elements (pharyngobranchials) and posterior end (first to sixteenth elements). Connects pharyngeal jaws w/ vertebral column.
Also changed way vertebral column connects to skull – three bones (basi and two exoccipitals) versus basioccipital only (primitive).
Other characters include (a) medial rostral cartilage between premaxillae and neurocrania & some muscles I will not bore you with.

Seven “Super Orders”
Super order groups
1) Stenopterygii = stomiiforms and ateleopodiformes (jellynose fish = weird deep water – swim just above bottom).

- Stomiiformes = deep-sea, mesopelagic and bathypelagic w/ luminescent organs (photophores) present; include the lightfishes or bristlemouths including - Cyclothone = greatest abundance individuals); Hatchetfish; Viper fishes; dragon fishes; snaggletooths; Dragon fishes; etc. 9 families, 53 genera and about 248 species

2) Cyclosquamata = Aulopiformes = pelagic & bathypelagic; many synchronous hermaphrodites; 40 genera w/ 188 species; greeneyes; pearleyes; waryfishes; Lizard fishes; Tripod fishes – elongate pectoral, pelvic and caudal rays to sit on bottom

All fishes above Cyclosquamata - lost fifth pharyngeal tooth plate

3) Scopelomorpha - Myctophiformes with 2 families; 35 genera & about 241 species; laternfishes – lost tooth plate but still have cycloid scales (versus ctenoid)

Now ACANTHOMORPHA = True fin spines (rather than hardened rays) = in dorsal, anal and pelvic fins; = Spiny rayed teleosts - changes include the maxilla, pharyngeal teeth diversified, etc

4) Lampridiomorpha = include opahs and oarfish = one can enlarge its mouth volume 40 fold during feeding; have no true spines but maxilla helps premax and has no teeth

5) Polymixiomorpha = beardfishes – unsure of exact phylogenetic position- mixed combination of characteristics

6) Paracanthopterygii – major side branch; Marine, benthic and nocturnal fishes; Defined - caudal skeleton and holes in skull. About 1200 species – only 20 primitive are freshwater

- Percopsiformes – Troutperch and blind scaleless cave fish (amblyopsid),
- Ophidiiformes - Pearlfish and cusk eels – some live inside body cavities and are parasitic;
- Gadiformes - Cods, hake etc – some of most important commercial fishes in the world – largest food fishery in world is for Pacific walleye Pollock > 6 million tons in 1989
- Batrachoidiformes - Toadfish – some venomous , acoustics and midshipmen (lateral photophores and very vocal during breeding
- Lophiiformes = anglerfishes; Goosefish & frogfish (esca or lure used to mimic small fish) and batfish –strange morphologically, 150 + species, males small - parasitic on females.

7) Superorder Acanthopterygii – 13,500 species in 251 families.

- a) Ascending process of premaxilla
- b) Pharyngeal dentition and action great – retractor dorsalis now inserts on 3rd pharyngobranchial arch and upper pharyngeal jaws supported by 2nd and 3rd epibranchials

Typically - ctenoid scales, physoclistous gas bladder, no maxilla in gape; two distinct dorsal fins (spiny and soft); pelvic and anal fins with spines; externally symmetric tail

Three ‘Series’
1) Mugilomorpha – mullets – 66 species, economically important; leap from water

2) Atherinomorpha – Successful at surface of water.

- a) Atheriniformes = silversides, rainbow fishes, 285 spp.;

- b) Beloniformes = needlefishes, flying fishes, Medakas
- c) Cyprinodontiformes = Poeciliids – mollies, guppies, swordtails; Killifish, pupfish etc. – highly salt tolerant and extreme environments; Annual aplocheilid rivulines. Rivulus marmoratus only self fertilizing fish;) Anablepid – four eye fish. Species flock of Orestias in Lake Titicaca (4570 m above sea level).

3) Percomorpha - 12,000 species
Defined - Anteriorly placed pelvic girdle connected to pectoral directly or by ligament; not well defined group

Basal Orders – these 3 sister to Percomorpha
- Stephanoberyciforms (gibberfishes & whalefish)
- Zeiforms – John dories
- Bericiformes - orange roughy & squirrelfishes

Basal Within Percomorpha
- Gasterosteiforms – dermal armour plates, small mouths; sticklebacks, Syngnathoidei = sea horses. Sea moths, pipefish, sea dragons, - only verts where males become pregnant, also trumpetfish & cornet fish and shrimpfish – head down in urchins.
- Synbranchiforms – Swamp Eels - palatoquadrate attaches at two points on skull = amphystilic suspension.
- Scorpaniformes – scorpionfish and rockfish; only freshwater = sculpins

Order Perciformes – 148 families and 9300 species
- Suborder Percoidei (many families) – 71 families with 2860 species

DO NOT NEED TO MEMORIZE ALL FAMILIES!!! BUT KNOW ORDERS AT END
- Centropomids – snooks, barramundi, Nile Perch etc
- Serranidae – sea basses, 450+ species – 3 spines opercle; 3 subfamilies inc.
- Centrarchidae – 29 spp. Sunfishes, crappies, rockbasses and basses
- Grammatidae – basslets
- Percidae – yellow perch and walleye and darters (162+ species)
- Cardinal fish (Apogonids) – 320+ spp. Nocturnal reef fish w/ big eyes
- Tilefishes (Malacanthids) – marine burroughs, move shells, rocks w/ mouth
- Nematistiidae – remoras – first dorsal fin modified as sucking organ;
- Cobia – monotypic – looks like ramora but no disk often w/ manta rays
- Dolphin fishes (dorado) - - 2pp. – sexual dimorphism in skulls
- Jacks – Carangids – 140 + species of predators – good swimmers – carangiform locomotion.
- Lutjanids – snappers 125+ spp.
- Lobotid tripletails – dorsal anal and caudal fins
- Gerreidae – mojarras – common inshore
- Haemulidae (grunts) – coral reef – pork fish
- Sparidae (Porgies)
- Polynemid threadfins
- Sciaenid Croakers – 270+ species Inc. Totoaba
- Mullid (goatfishes)
- Monodactylilid fingerfishes
- Toxotid Archerfishes – shoot water eyes submerged
- Chaetodontidae – butterfly fishes – 114 species
- Pomacanthidae – Anglefishes
- Kyphosids – sea chubs 42 sp.
- Nanid Leaf fish

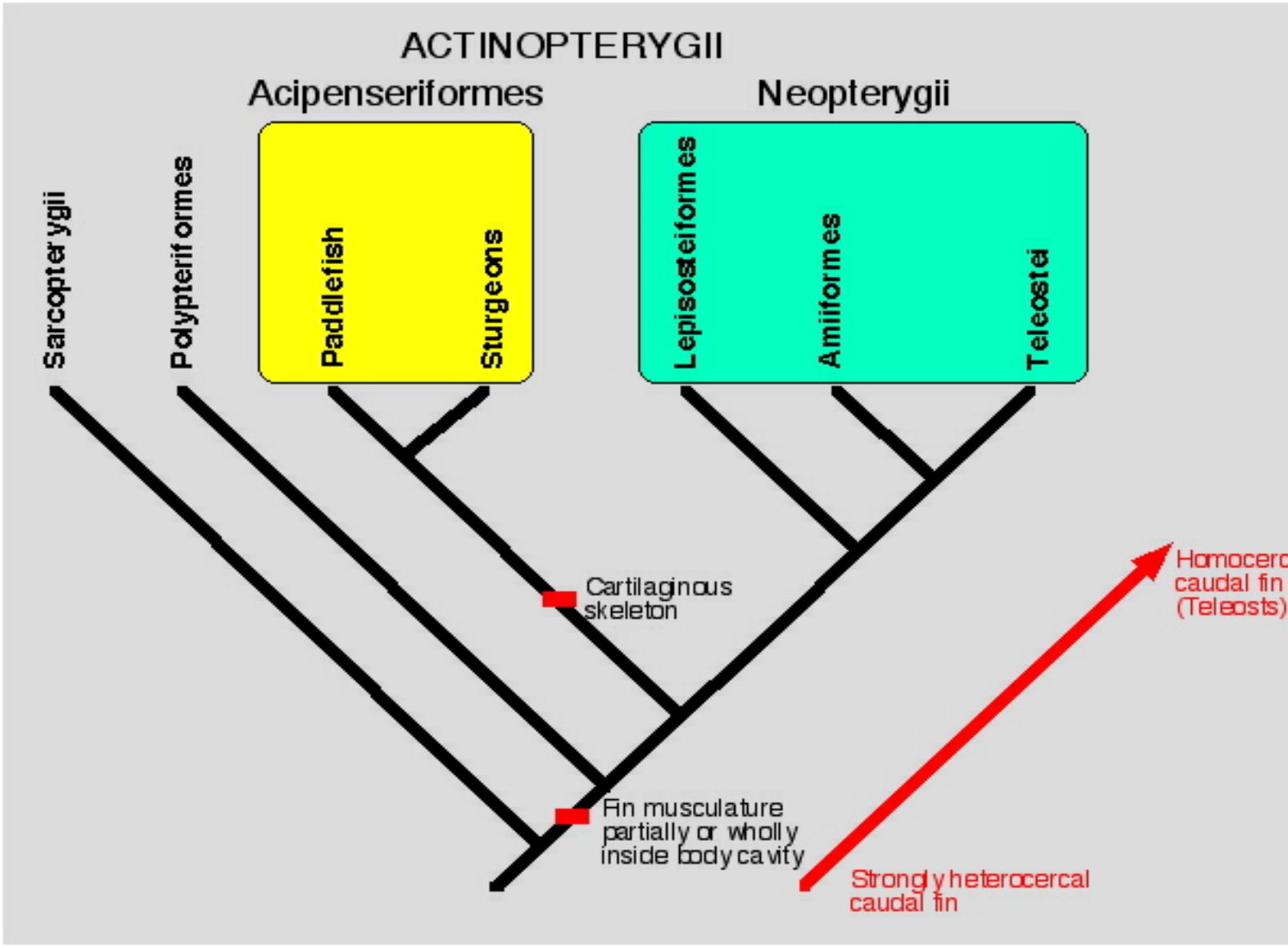
- Cirrhitid hawkfishes

Suborder - Elassomatids – pygmy sunfish – convergence w/ true sunfishes
KNOW THIS Suborder - LABROIDEI – species flocks and explosive speciation
•Cichlidae, Pomacentridae, Labridae, Scaridae, Embiotocidae & Odacids

- Suborder Zoarcoidei – eelpouts, wolffishes, wolf eels, gunnels
- Suborder Nototheniodei – icefishes, glycoprotein antifreeze
- Suborder Trachinoidei – stargazers, sand divers, sand lances, weeverfishes
- Suborder Icosteoidei, Gobiesocoidei, Callionymoidei – ragfish, clingfish, Dragonet
- Suborder Blennioidei – Blennies
- Suborder Gobioidei - Gobies
- Suborder Kurtoidei – Kurtids, males care eggs w/ attachment to supraoccipital crest
- Suborder Acanthuroidei – Acanthurids (72 spp), surgeon fish.
- Suborder Scombrolabracoidei
- Suborder Scombroidei – Mackerels, tunas, Barracudas, cutlass fishes, Xiphiid swordfish and istiophorid sailfish, spearfish and marlins
- Suborder Stromateoidei – medusafishes, squaretails, driftfishes, butterfishes
- Suborder Anabantoidei – labyrinth fishes – auxiliary breathing structure
- Suborder Channoidei –snakeheads

Order – Pleuronectiformes –symmetric larvae, metamorphose, Soles (usually right eyed), flounders, halibut (righteye flounder), tonguefishes.

Order - Tetradontiformes – triggerfish, filefishes, boxfishes, puffers, Mola Ocean Sunfishes


ACTINOPTERYGII
Acipenseriformes
Neopterygii
Sarcopterygii
Polypteriformes
Paddlefish
Sturgeons
Lepisosteiformes
Amiiformes
Teleostei
Cartilaginous skeleton
Homocerc
caudal fin
(Teleosts)
Fin musculature partially or wholly inside body cavity
Strongly heterocercal caudal fin