

ECOLOGICAL SPECIATION

Species Concepts:

1. **Typological species concept** (*morphospecies* (species defined by their form, or phenotypes), and *taxonomic species* (whatever a taxonomist calls a species)).
2. **Biological species concept**
Ernst Mayr defined a species as follows:
"species are groups of interbreeding natural populations that are reproductively isolated from other such groups."
3. **Evolutionary species concept** – single lineage of organisms which maintain identity from other such lineages and has its own evolutionary tendencies

Incorporates time
4. **Phylogenetic species concept** - incorporates unique, evolved traits, organisms developed from the same ancestor
5. **Ecological species concept** -species is lineage that occupies adaptive zone

Incorporates niche

biological species concept:

1. It is hard to apply especially to fossil data.
2. Species exist in time and space: the biological species concept has no time component.
3. What do we do with asexual organisms?



- Bdelloid Rotifers haven't reproduced sexually for > 80 million years- each individual is reproductively isolated !
- An estimated 2000 species are completely asexual.

"species are groups of interbreeding natural populations that are reproductively isolated from other such groups."

Mechanisms of reproductive isolation

I) Premating – prezygotic

1. **Behavioural** (preventing courtship or copulation)
2. **Ecological** – barriers as direct consequence to adaptation habitat or temporal isolation (breeding at different times-phenology), different pollinators or pollinators body parts
3. **Mechanical** – incompatibility of genitalia
4. **Gametic isolation**



compatibility of spider genitalia⁵

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12



13



6



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15



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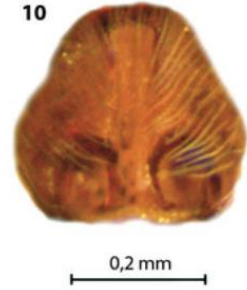
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Mechanisms of reproductive isolation

II) Postzygotic

1. **ecological unviability** – hybrids cant find appropriate niche
2. **behavioural sterility**- unattractive
3. **postzygotic** – intrinsic - hybrid inviability or sterility



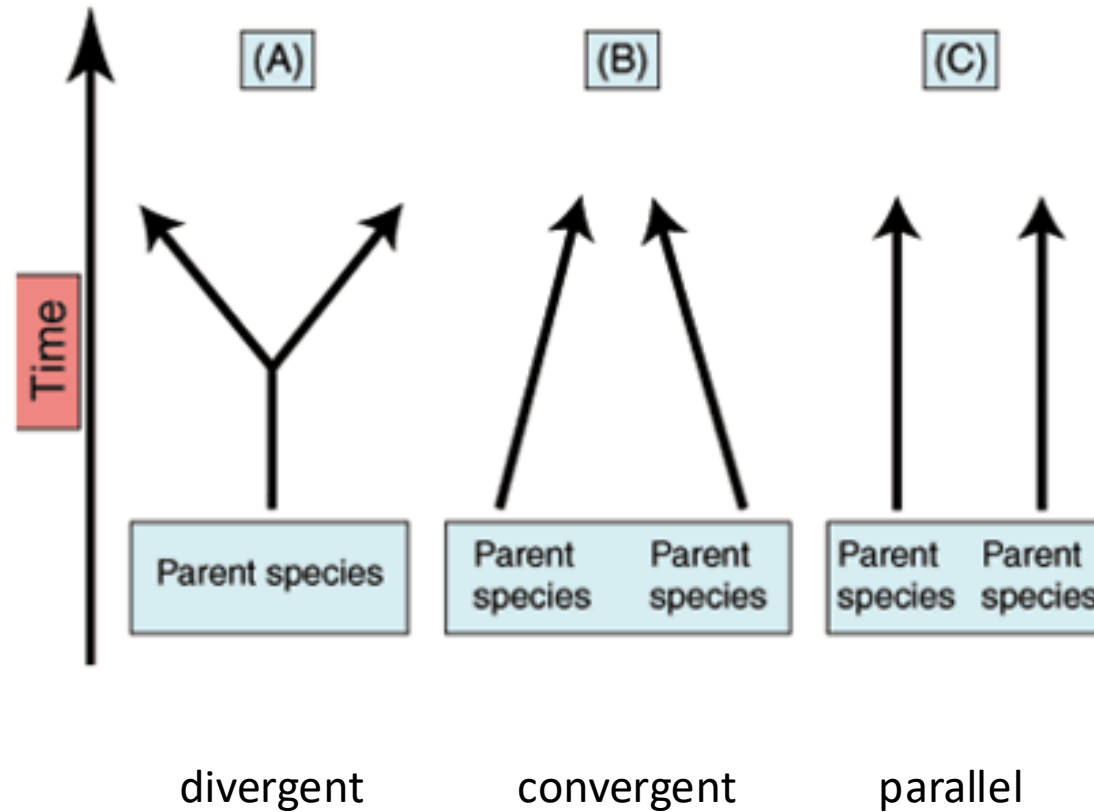
convergent vs. divergent evolution

Convergent evolution

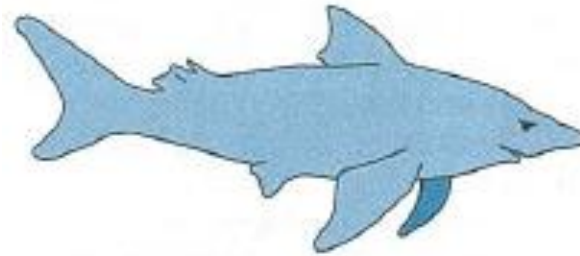
Parallel evolution

Divergent evolution

defined by similarity in function and ancestral stage



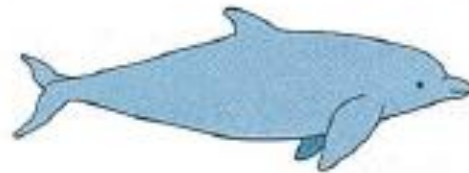
- Convergent evolution refers to ancestrally independent evolution with enhanced similarity in function – resemblance in focal feature is higher in descendants than in ancestors



Fish: Shark



Reptile: Ichthyosaur (extinct)

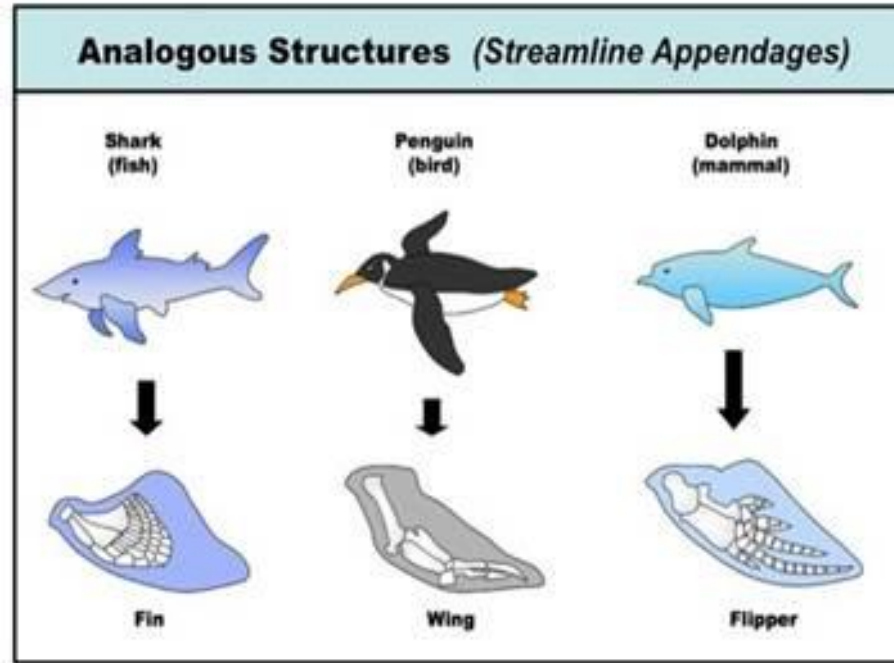


Mammal: Dolphin



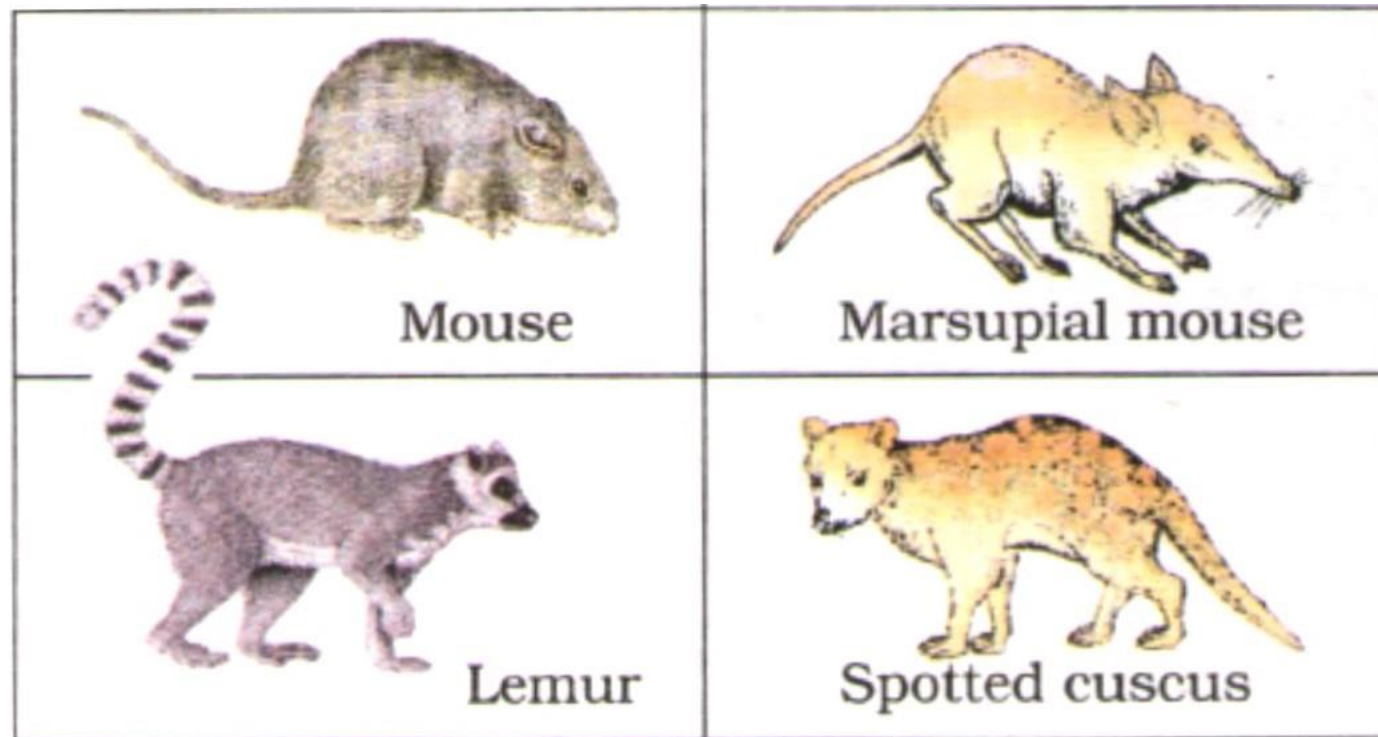
Bird: Penguin

- Within **convergent evolution** we often see **analogous organs** – similar in function, but not present in the last common ancestor of those groups

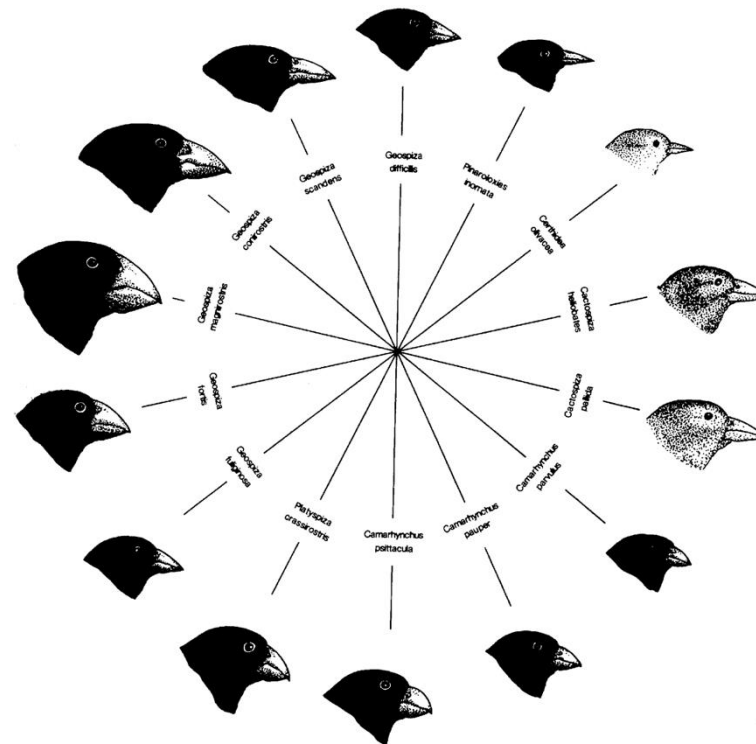


- another example- wings of birds, insects and bats

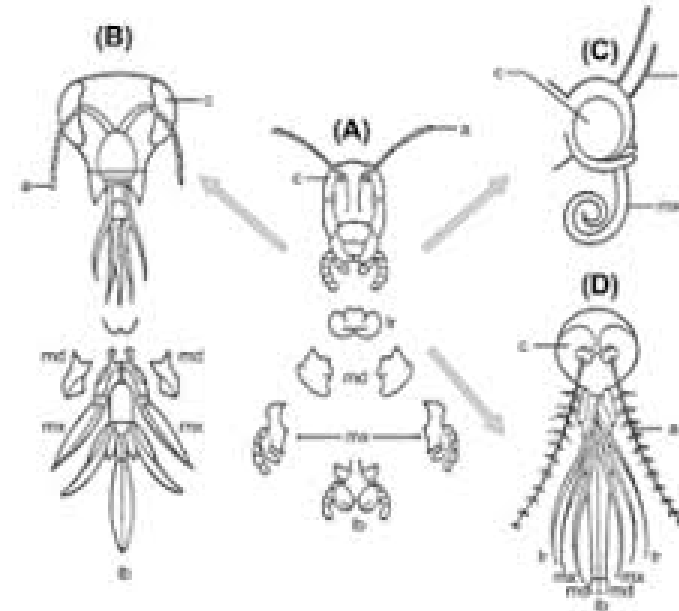
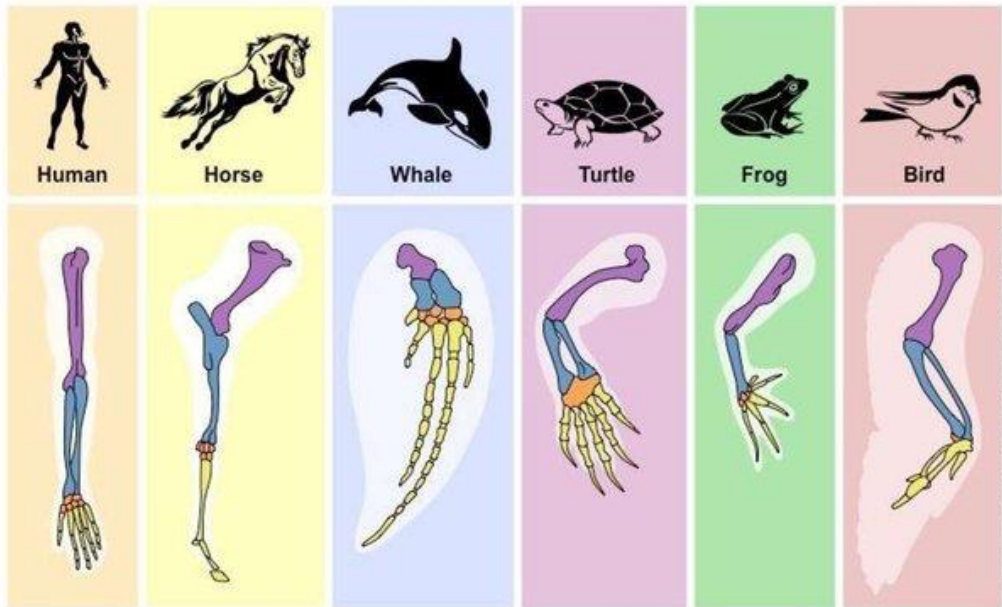
- Parallel evolution – similar to convergent evolution, but descendants don't resemble each other much more their ancestor did
- example : parallel evolution between marsupials and placentals



- **Divergent evolution** – same ancestor, loss of similarity in function, evolutionary accumulation of phenotypic differences
- leads to speciation, example of Darwin finches



- **Divergent evolution** – same ancestor, loss of similarity in function, evolutionary accumulation of phenotypic differences
- in the long term it can result in the **homologues organs – common ancestor, difference in function**



feeding
apparatus of
insects

Ecological speciation is defined as the build-up of reproductive isolation as a direct consequence of divergent **natural selection** stemming from the environment

Adaptive radiation occurs when a single or small group of ancestral species rapidly diversifies into a large number of descendant species.

Adaptive radiations are often characterized by:

Ecological opportunity – new ecological space

Competitive interactions among closely related taxa

Acquisition of **novel adaptive traits** (phenotypic)

Rapid phenotypic diversification

Convergent/Parallel evolution

Adaptive radiation of Darwins finches

Geospiza

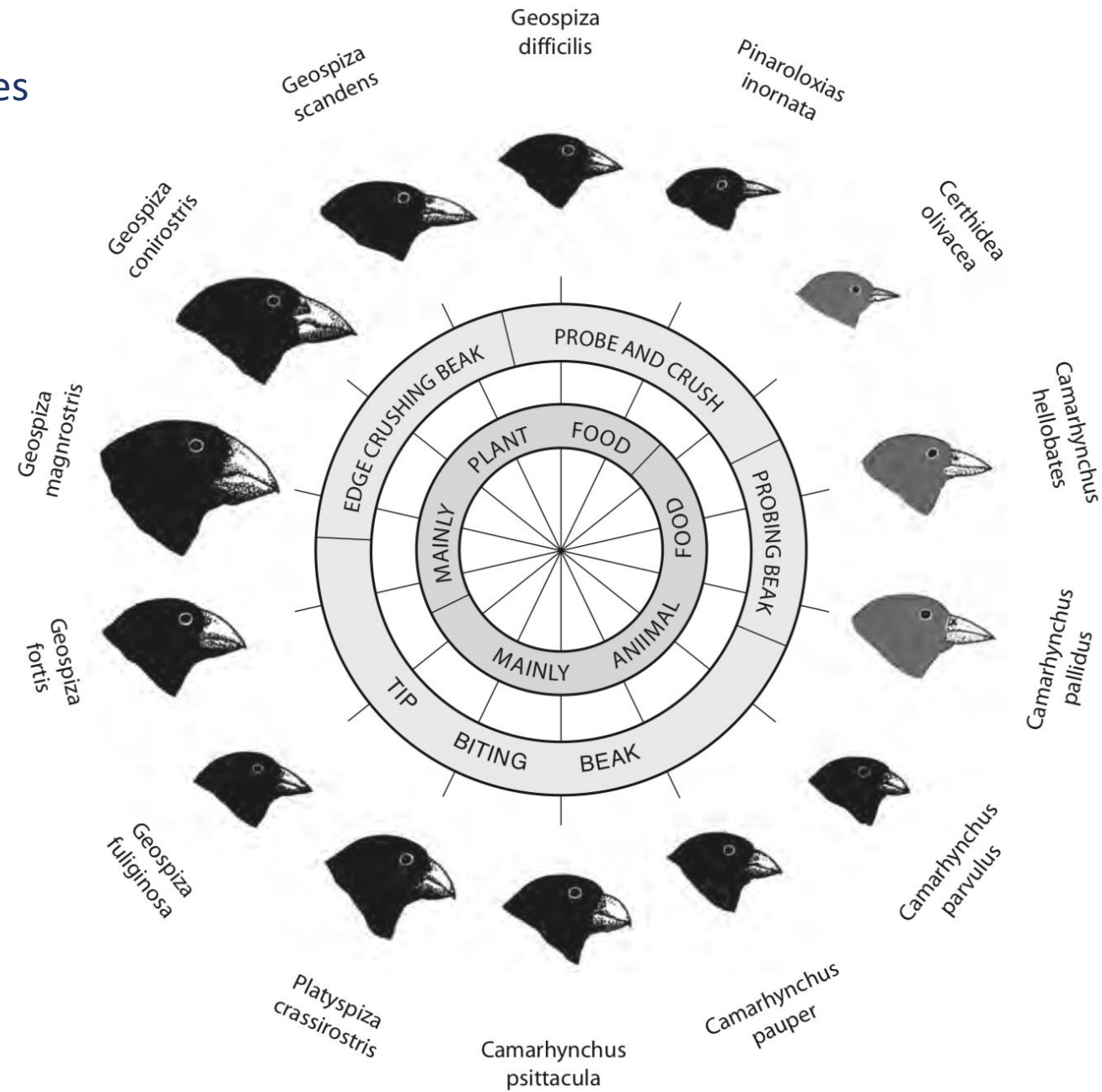
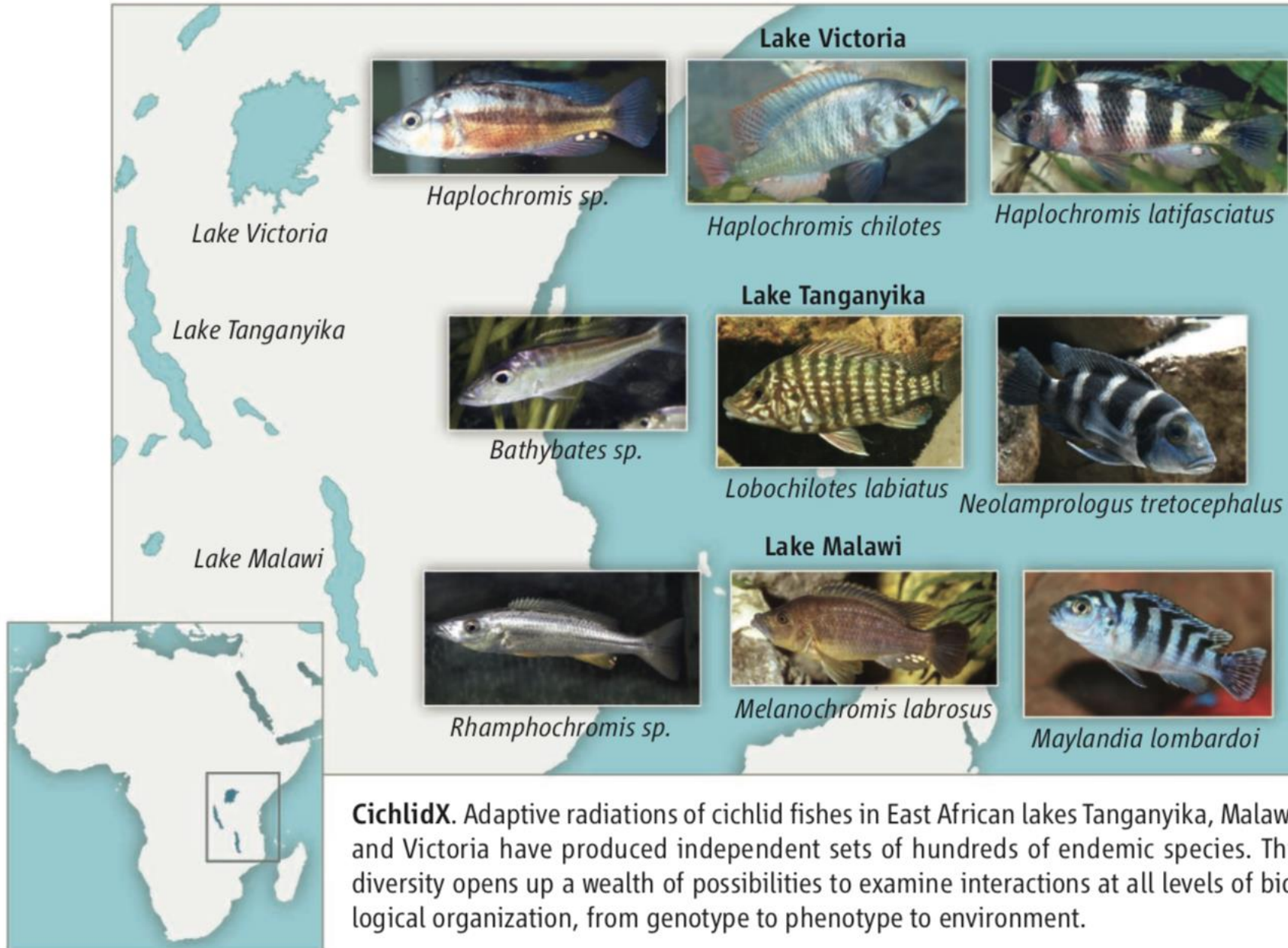


Figure 3. Adaptive radiation in Darwin's finches. Diagram illustrating the morphological and associated ecological diversity among the radiation of Darwin's finches in the genus *Geospiza* (Emberizidae). The 14 species evolved from a common ancestor

about 3 million years ago. (From Grant, P. R., and B. R. Grant. 2008. *How and Why Species Multiply: The Radiation of Darwin's Finches*. Princeton, NJ: Princeton University Press)

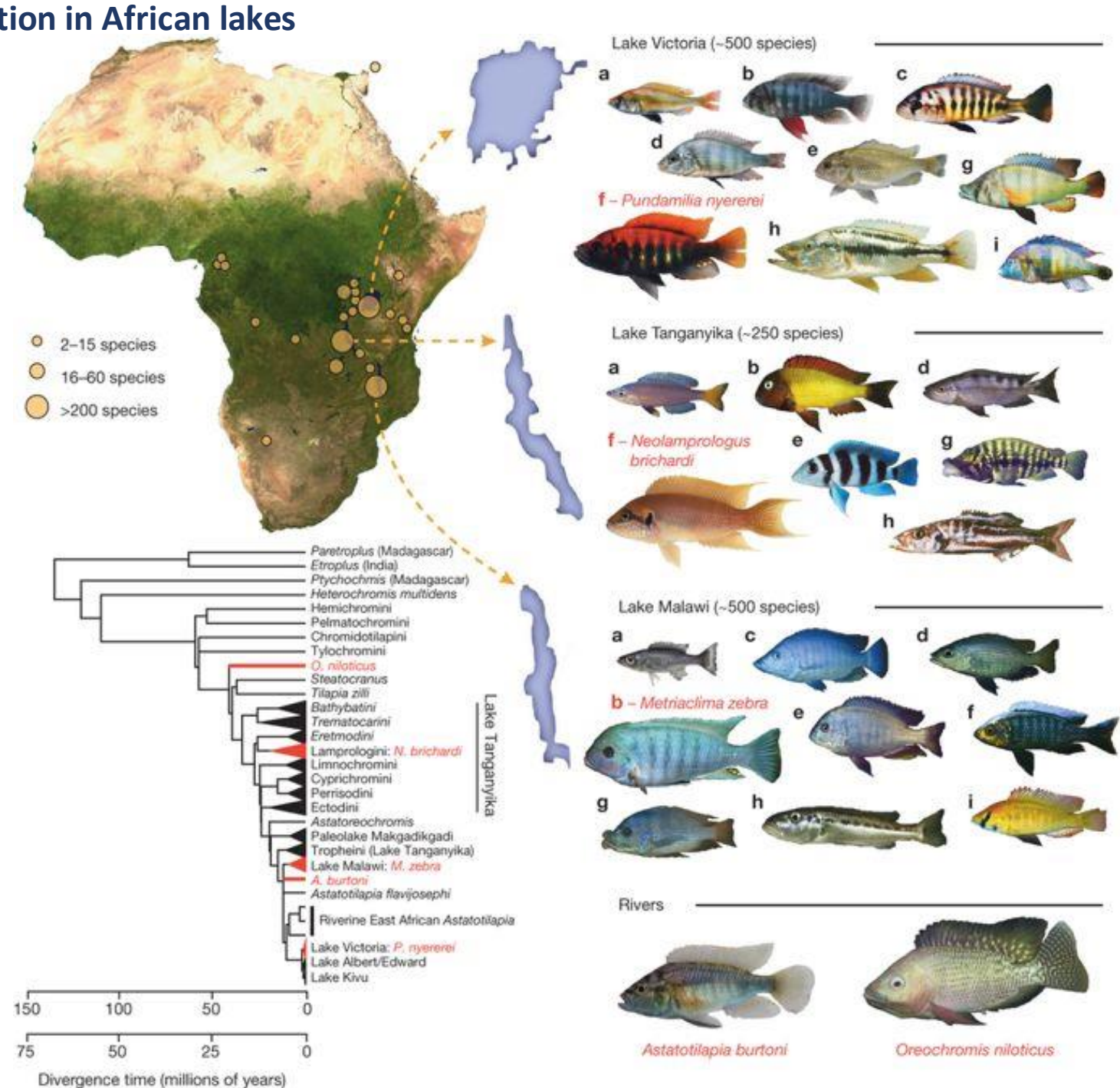
African cichlids – hybridisation as a source of novel variation

the story of cichlids – adaptive radiation in African lakes



the story of cichlids – adaptive radiation in African lakes

In Lake Victoria, several hundred endemic species emerged within the past 15,000–100,000 years



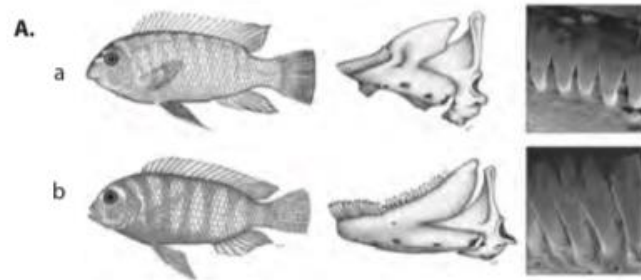
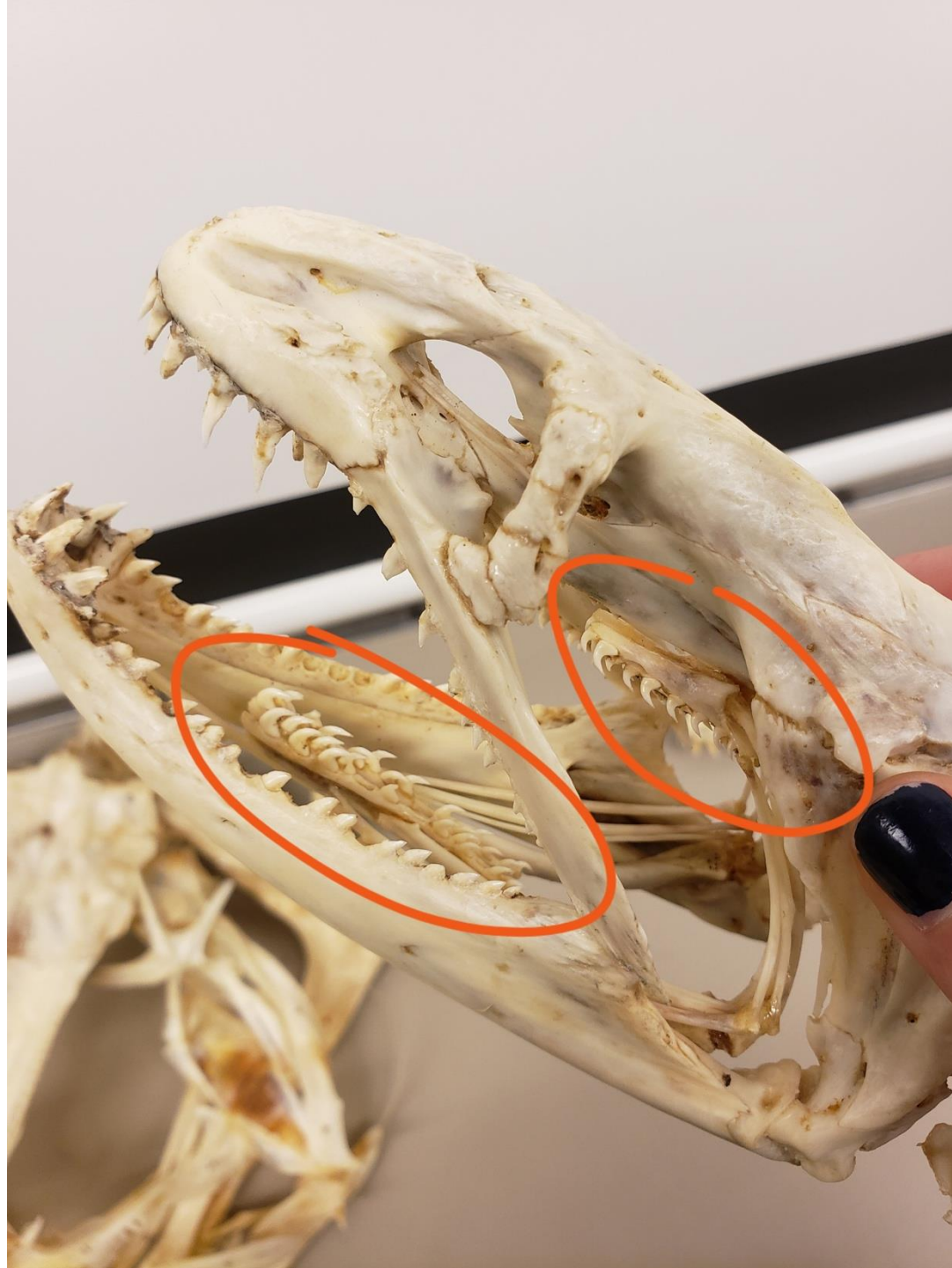












Figure 1. Adaptive radiation in cichlid fish. The pharyngeal jaw morphology, which allows dietary specialization, appears to have served as a key innovation in facilitating adaptive radiation in this group. (A) Biting and sucking species exhibit distinct morphologies. *Labeotropheus fuelleborni* (top) is a specialized biting species characterized by a short, robust lower jaw and an outer row of closely spaced tricuspid teeth. *Metriaclicma zebra* (bottom) forages with a sucking mode of feeding and has a more elongate jaw and an outer series of larger bicuspid teeth. (B) Cichlids exhibit remarkable evolutionary convergence. Similar ecomorphs have evolved repeatedly within different cichlid assemblages. All of the cichlids in the left-hand column are from Lake Tanganyika. All of the cichlids in the right-hand column are from Lake Malawi and are more closely related to one another than to any species within Lake Tanganyika. Note the similarities among color patterns and trophic morphologies. (From Albertson, R. C., and T. D. Kocher. 2006. Genetic and developmental basis of cichlid trophic diversity. *Heredity* 97: 211–221, <http://www.nature.com/hdy/journal/v97/n3/full/6800864a.html>)

pharyngeal jaw morphology allows dietary specialisation- key innovation convergent evolution

A) Biting and sucking species exhibit distinct morphologies. *Labeotropheus fuelleborni* (top) is a specialized biting species characterized by a short, robust lower jaw and an outer row of closely spaced tricuspid teeth. *Metriaclicma zebra* (bottom) forages with a sucking mode of feeding and has a more elongate jaw and an outer series of larger bicuspid teeth. (B) Cichlids exhibit remarkable evolutionary convergence. Similar ecomorphs have evolved repeatedly within different cichlid assemblages. All of the cichlids in the left-hand column are from Lake Tanganyika. All of the cichlids in the right-hand column are from Lake Malawi and are more closely related to one another than to any species within Lake Tanganyika. Note the similarities among color patterns and trophic morphologies. (From Albertson, R. C., and T. D. Kocher. 2006. Genetic and developmental basis of cichlid trophic diversity. *Heredity* 97: 211–221, <http://www.nature.com/hdy/journal/v97/n3/full/6800864a.html>)

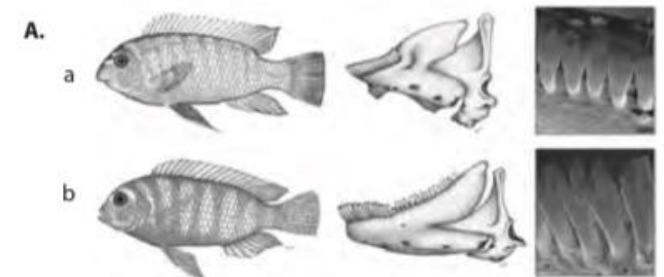
pharyngeal jaws of the eel



Lake Tanganyika species	Lake Malawi species
 <i>Julidochromis ornatus</i>	 <i>Melanochromis auratus</i>
 <i>Tropheus brichardi</i>	 <i>Pseudotropheus microstoma</i>
 <i>Bathybates ferox</i>	 <i>Ramphochromis longiceps</i>
 <i>Cyphotilapia frontosa</i>	 <i>Cyrtocara moorei</i>
 <i>Lobochilotes labiatus</i>	 <i>Placidochromis milomo</i>

Similar ecomorphs evolved independently in different lakes !

pharyngeal jaw morphology allows dietary specialisation- key innovation



Convergent evolution - similar phenotypes in separated ecosystems

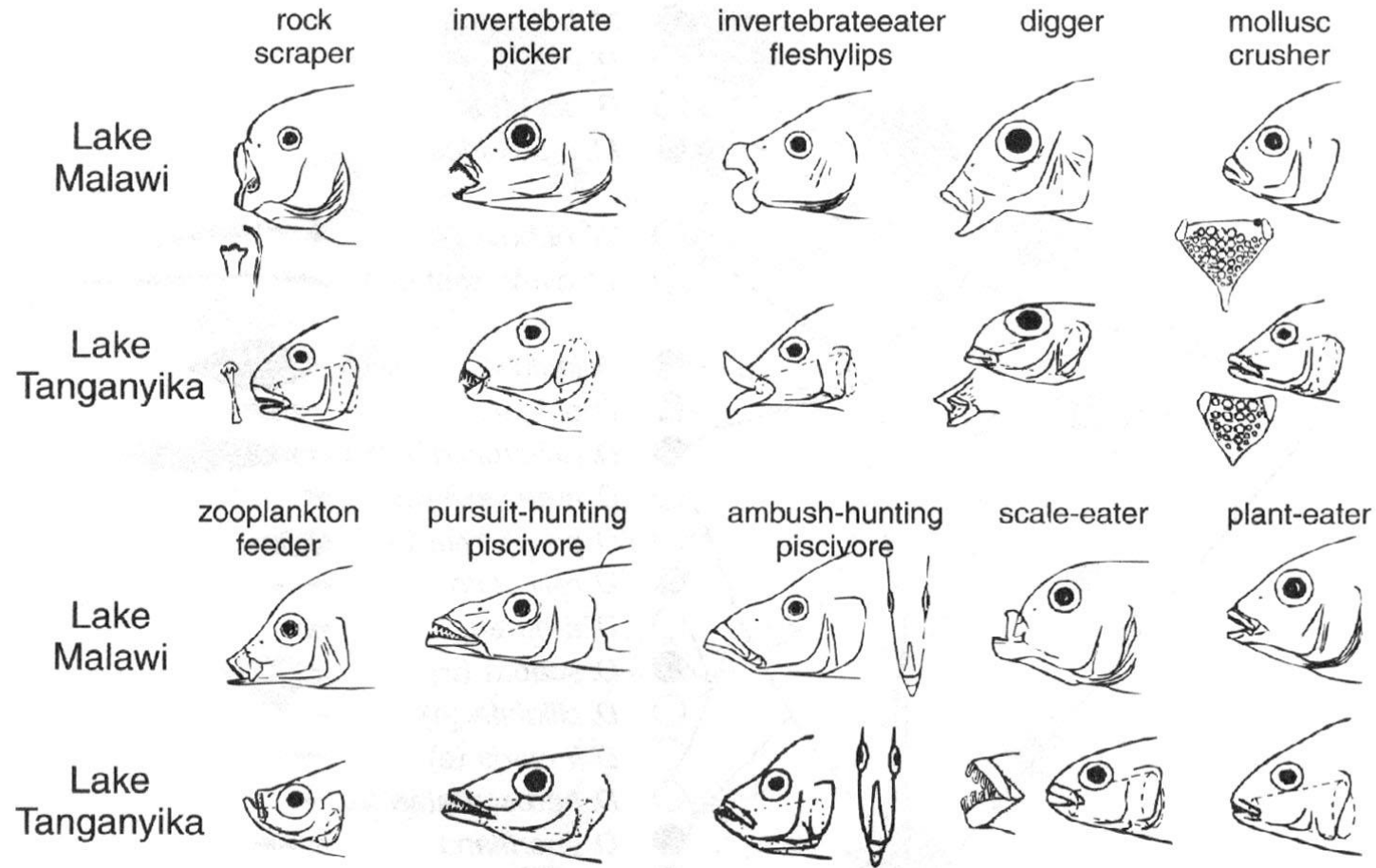


Fig. 1.3 Similar phenotypes in the cichlid fish radiations of Lake Malawi and Lake Tanganyika in East Africa. Images are from Fryer and Iles (1972; Malawi) and Liem (1991; Tanganyika) and are reprinted with kind permission of G. Fryer and Kluwer Academic Publishers, respectively.

Speciation in rapidly diverging systems: lessons from Lake Malawi

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Three cladogenetic events with different selection pressures

- 1) Two groups – sand and rock dwellers
- 2) Competition for food resources within those groups
- 3) Male coloration differentiation – sexual selection

Abstract

Rapid evolutionary radiations provide insight into the fundamental processes involved in species formation. Here we examine the diversification of one such group, the cichlid fishes of Lake Malawi, which have radiated from a single ancestor into more than 400 species over the past 700 000 years. The phylogenetic history of this group suggests: (i) that their divergence has proceeded in three major bursts of cladogenesis; and (ii) that different selective forces have dominated each cladogenic event. The first episode resulted in the divergence of two major lineages, the sand- and rock-dwellers, each adapted to a major benthic macro-habitat. Among the rock-dwellers, competition for trophic resources then drove a second burst of cladogenesis, which resulted in the differentiation of trophic morphology. The third episode of cladogenesis is associated with differentiation of male nuptial colouration, most likely in response to divergent sexual selection. We discuss models of speciation in relation to this observed pattern. We advocate a model, divergence with gene flow, which reconciles the disparate selective forces responsible for the diversification of this group and suggest that the nonadaptive nature of the tertiary episode has significantly contributed to the extraordinary species richness of this group.

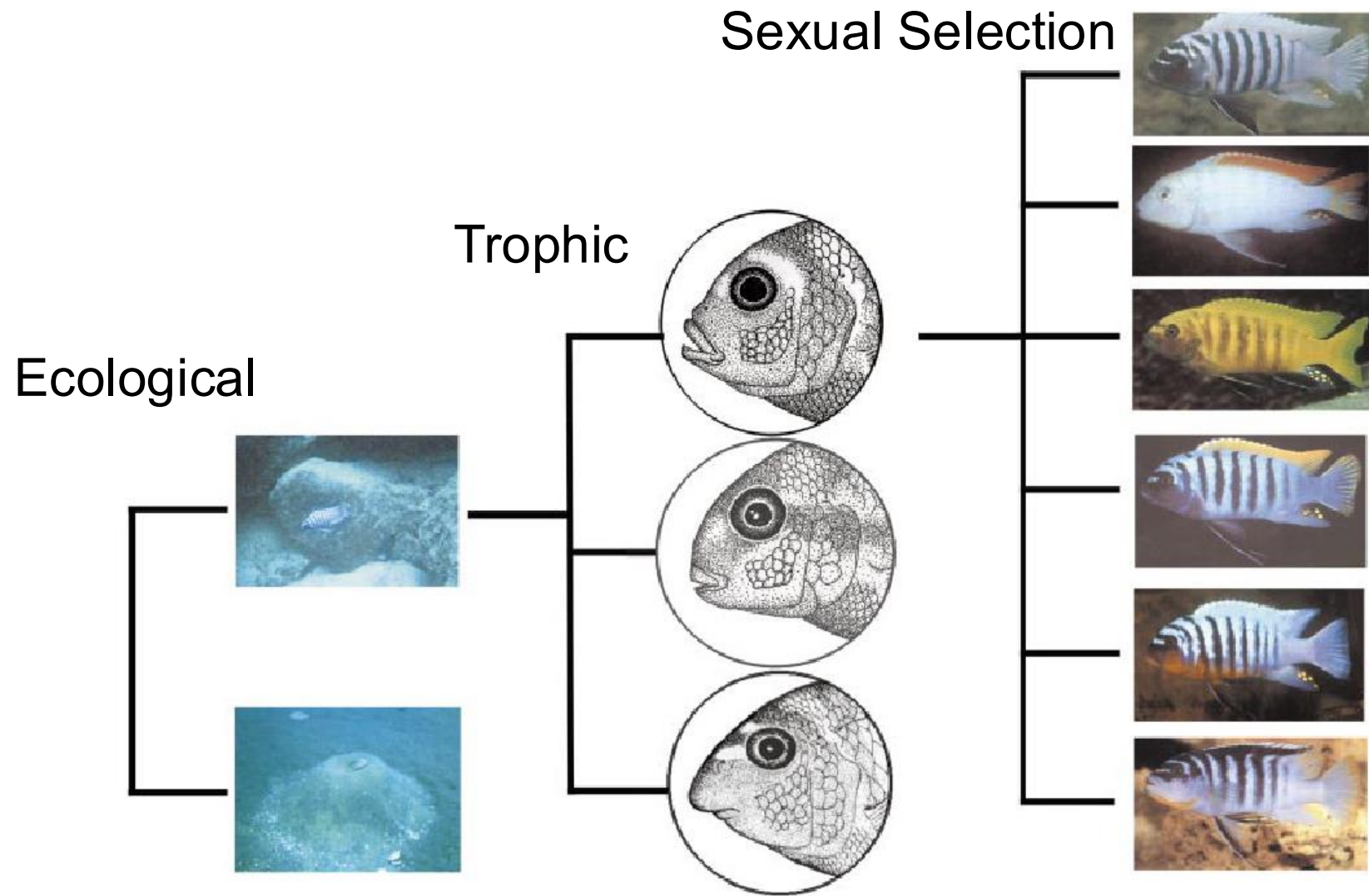


Fig. 1 A proposed phylogenetic history of Lake Malawi's rock-dwelling cichlids based on several molecular phylogenies of Lake Malawi cichlids (Meyer *et al.* 1990; Kocher *et al.* 1993; Meyer 1993; Moran *et al.* 1994; Moran & Kornfield 1995; Albertson *et al.* 1999). Lake Malawi is presumed to have been invaded by a riverine generalist closely allied with Lake Tanganyika's haplochromine tribe approximately 700 000 years ago. This common ancestor subsequently diverged during the primary radiation into the sand-dwelling and rock-dwelling lineages. The rock-dwelling lineage diverged during the secondary radiation into the 10–12 currently recognized mbuna genera. These genera are distinguished primarily on the basis of trophic morphology suggesting the importance of trophic competition during this period of the radiation. The spectacular species richness of the mbuna principally arose during the tertiary radiation. During this period, as many as 25 species per genus diverged presumably in response to sexual selection via female choice for male secondary sexual characteristics such as colour pattern. Line drawings courtesy of R. C. Albertson, colour images courtesy of Konings (1990).

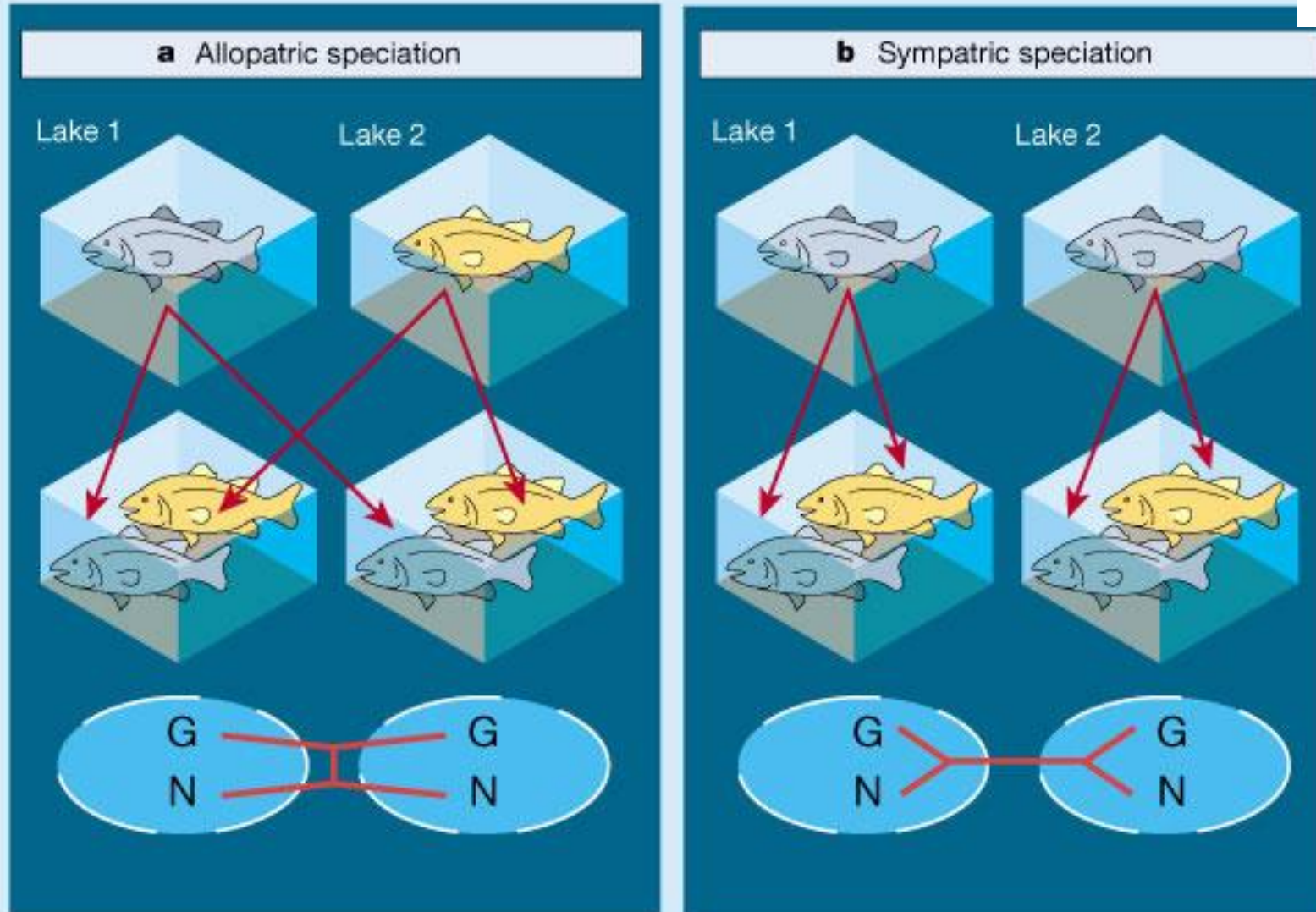
Alopatric and sympatric speciation

Speciation

Fish found in *flagrante delicto*

Mark Kirkpatrick 

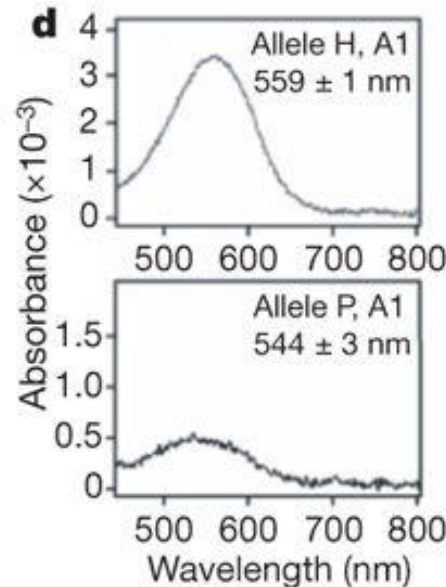
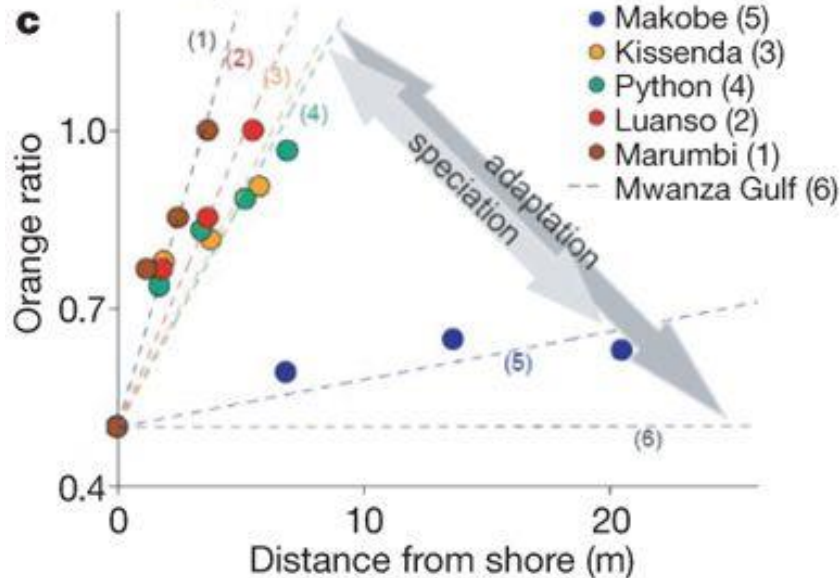
Nature **408**, 298–299(2000) | [Cite this article](#)



G and N – genes for golden and white color, more similar within the lakes SYMPATRIC SPECIATION



„For example, Seehausen et al. and Miyagi et al. have examined **the role of visual pigments in the recent divergence of Lake Victoria cichlids**. The heterogeneous light conditions in this lake led to **diversifying selection on opsin genes as a function of water depth**. The divergence in opsins, in turn, **affects sexual selection**, because differences in color perception influence the female preference for male coloration. Here, the interplay between natural and sexual selection resulted in speciation in the absence of geographic barriers **through selection on a sensory system** (“sensory drive”). „



Interaction of natural and sexual selection on sensory system drive the sympatric speciation

<https://youtu.be/Kh5Clc2Sr9w>

„Cloudy lake waters are causing two cichlid species—one mostly red and the other mostly blue—to breed with each other because the fish can no longer see clearly enough to choose mating partners of their own kind. According to biologist Ole Seehausen, of the University of Bern in Switzerland, the offspring, a blandly colored hybrid, represents a new species.

The new hybrid is taking over the habitat of both parent species, but is fulfilling the ecological role of neither, as it retains only some of the unique qualities of each parent species. For example, the new hybrid species is a generalist feeder and specializes on neither plankton nor bottom dwelling insects like its parent species. ”

<https://www.newscientist.com/article/dn14855-love-is-blind-for-fish-in-murky-waters/>

[Nature, DOI: 10.1038/nature07285](https://doi.org/10.1038/nature07285)



„In other cases, **natural and sexual selection act in opposite directions**. An orange-blotch coloration is common among females of Lake Malawi cichlids and provides camouflage over boulders. Blotched males, on the other hand, **seem to have a selective disadvantage because they do not possess the nuptial coloration that attracts females**. Roberts et al. have recently shown how this conflict between natural selection (the orange blotch pattern provides camouflage) and sexual selection (orange blotch males are less likely to reproduce) is resolved. A new female sex-determining gene has evolved in linkage with the *pax7* gene that makes the orange blotch coloration. **This linkage leads to low recombination; therefore, mostly females have this coloration.**”



Fig. 1 Representative BB (male) and OB (female) individuals of *Metriaclima zebra*.