PHYLETIC GRADUALISM; PUNCTUATED EQUILIBRIUM & STASIS; ADAPTIVE RADIATION; COEVOLUTION

15.1 SEQUENTIAL AND DIVERGENT EVOLUTION

Evolution has been described as the process of gradual modification in the living organisms (plants or animals) so as to establish diversity in the world of living beings. Two fundamental patterns could be envisaged in the process of evolution:

1. Minor changes in the gene pool of a population are passed on from one generation to the next, with the result that no new populations are formed, but the descendent population is not genetically identical with its predecessor. This is known as **sequential evolution.**
2. The changes which result in sudden evolution of new populations, species, families, groups or classes represent **divergent evolution.**

(The **sequential evolution** is therefore, an example of random fluctuations over a long period of time without producing new populations. Therefore, the changes occurring on account of evolutionary forces like mutations, variations, natural selection and genetic drifts produce only temporary changes which fluctuate at random. For example, in human population, we find that not even two real sisters or brothers are identical or resemble their parents, yet the changes do not divide the individuals of a population or race into subcategories. Secondly, these changes are not directional.)

(The **divergent evolution,** on the contrary, is an example of directional evolution. The changes occur in a cumulative direction and result in the origin of new populations from the old ones. Therefore, the varied groups of plants and animals either related or unrelated provide an example of divergent evolution. It is the divergent evolution which is more evident.)

As a matter of fact, sequential evolution and divergent evolution are rather inseparable. Not even a single population exclusively exhibits sequential evolution, because all populations diverge in due course of time and split up into new populations. Moreover, the forces responsible for bringing about changes are rather the same in both the cases except that they operate for a very long period and are assisted by additional factors.

Sequential evolution, though helps in understanding the operation of various evolutionary forces, does not play any role in the evolution of new species or groups. It is, therefore, the divergent evolution as is seen in fossil records, illustrates the results of evolution.

The sequential evolution is actually microevolution and the divergent evolution, in its simplest form causing diversification or splitting of population, is nothing but macroevolution only. The fragmentation and development of new populations from the existing population is called **speciation** and usually leads to the evolution of new species.

Evolutionary changes which are responsible for establishing the taxonomic categories above species level represent **macroevolution.** It includes adaptive radiation of a population to different new habitats. The **megaevolution** includes those changes in the organisation which enable the organisms to enter into a new major adaptive zone.

15.2 PHYLETIC GRADUALISM AND PUNCTUATED EQUILIBRIUM

Speciation can happen at a rapid rate or gradually. On a global level, the life on earth has passed through periods of bursts of speciation followed by long periods of relatively little changes. It means evolution may be **gradual** or **punctuated.**

15.2.1 Phyletic Gradualism

The persistent accumulation of small changes within a lineage is described as **phyletic gradualism.** It involves accumulation of small changes over millions of years within one lineage so that the parent population passes through a series of intermediate stages, and the descendant population or populations appear as distinct species differing from antecedent populations. The transformation of a lineage over time is termed as **anagenesis.** For example, in Fig. 15.2, a new species-B arises by slow and steady transformation of a large antecedent population-A.

According to Gould and Eldredge the phyletic gradualism is very slow and is unable to produce major events of evolution.

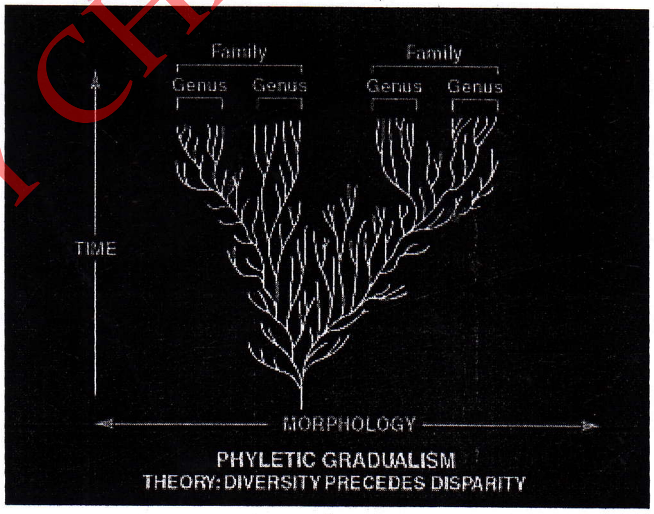
Cyanobacteria can be taken as an example of gradualism since they have changed a little to adapt to environmental changes.

15.2.2 Punctuated Equilibrium

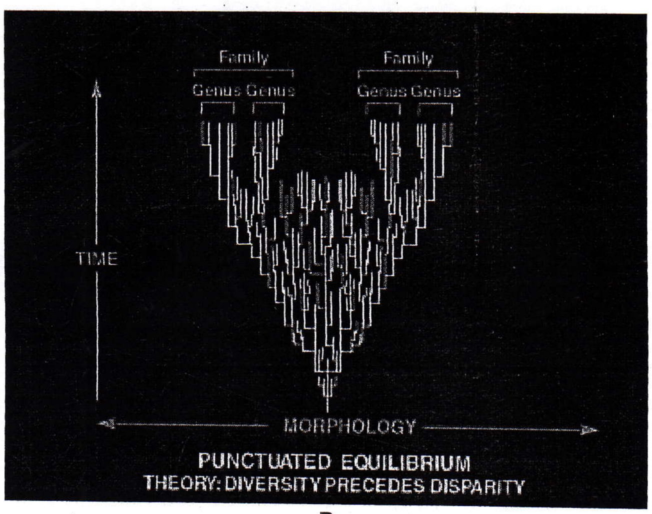
George Gaylord Simpson (1944) suggested that the gaps in the fossil records represent the sudden appearance of a new species from an ancestral form followed by periods of little change. In 1972, Stephen Jay Gould and Niles Eldredge advocated that most evolutionary changes are rapid bursts of speciation. They alternate with long periods in which individual species remain virtually unchanged. The long intervals of geologic time in which very limited or no significant morphological changes occur represent **'period of stasis'** or **'period of equilibria'.** The intervals interrupting the period of equilibria and marked by conspicuous active evolutionary changes are called **'punctuations.'** During these brief periods the lineages actually branch into new lineages. These patterns of fast evolutionary changes were called **punctuated equilibria.**

The fossil records reveal that both gradual and punctuated equilibrium contribute to evolution of lineages. Gradualism is seen during anagenesis, while punctuated equilibrium occurs during cladogenesis.

The fossil records of bryozoa show punctuated equilibrium because this group remained unchanged for millions of years and then suddenly branched to yield new species.



A



B

Fig. 15.1 A. Phyletic gradualism; **B.** Punctuated equilibrium.

Difference

Table 15.1 Punctuated Equilibrium

Gradualism	Punctuated Equilibrium
1. Gradualism occurs during anagenesis.	1. It occurs during cladogenesis.
2. Morphological change is gradual and occurs continuously.	2. Morphological change is sudden and rapid and occurs only rarely.
3. New species originate gradually.	3. New species originate abruptly.
4. An ancestral species can be transformed into a new species.	4. The subpopulations of the ancestral species transform into new species.
5. Phyletic replacement does not involve splitting of the lineage.	5. Phyletic replacement involves splitting off of a new lineage/species, which then replaces its ancestor abruptly.

George Goylord Simpson described gradualism and punctuated equilibrium as **bradyletic evolution** (*G. brady*, means slow) and **tachytelic evolution** (*G tachy*, means first).

15.3 ANAGENESIS AND CLADOGENESIS

Rensch (1954) had used the above terms to differentiate various types of evolutions.

Anagenesis: It represents progressive change in characters of a lineage through time. It results in linear succession of lineage through time, *i.e.*, succession of one species by other in due course of time. It is characterised by the replacement of one lineage by another without any branching. Anagenesis represents any kind of unidirectional evolutionary change whether it leads to a marked advance or not but not the branching pattern of lineage origin.

Anagenesis creates organisms with novel characters and abilities, beyond those of their ancestors (Fig. 15.2)

Cladogenesis: It represents divergent evolution or phylogenetic evolution in which parental population or parental lineage branches into several lineages. Lineage branches resulting due to cladogenesis are called **clades.** A **clade** is a group that includes common ancestor and all its descendants. It represents **monophyletic evolution,** *i.e.*, a group of organisms arising from one ancestor. This ensures rapid origin of new species.

In cladistic approach, the characters of a clad or taxa are classified as follows:

1. Apomorphic Characters: These are the characters that are derived by evolution so they are also called **derived characters.**

2. Plesimorphic Characters: These are those characters that are shared with the ancestral species.

3. Synapomorphy: It is the possession by two or more related lineages of the same phenotypic character derived from a different but homologous character in ancestral lineage.

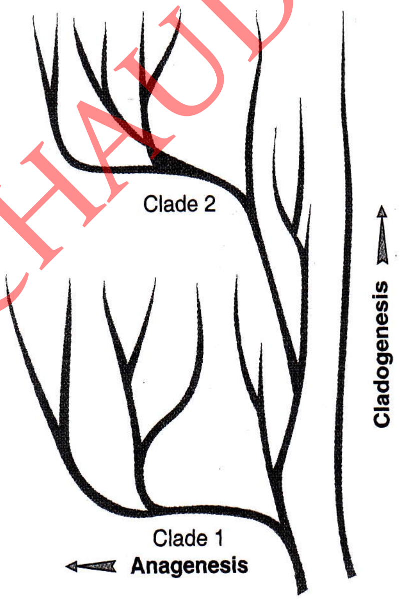


Fig. 15.2 Diagram showing anagenesis (evolutionary advance) and cladogenesis (branching lineage).

15.4 MONOPHYLETIC, POLYPHYLETIC AND PARAPHYLETIC EVOLUTION

15.4.1 Monophyletic Evolution

Taxa whose members have descended from a common ancestor are called **monophyletic.** All members or species of monophyletic taxon descend either from the same parents or same population or same species *i.e.*, the new species is the temporal extension of the parent species. For example, a class is monophylectic if all its lineages ancestral to the class originated from the same family. The phenomenon of origin of monophyletic taxa is called **monophyletic evolution** or **monophyly.** (Fig. 15.3: Taxa D, E, F)

All vertebrates have a common ancestor. All the mammals also represent monophyletic group.

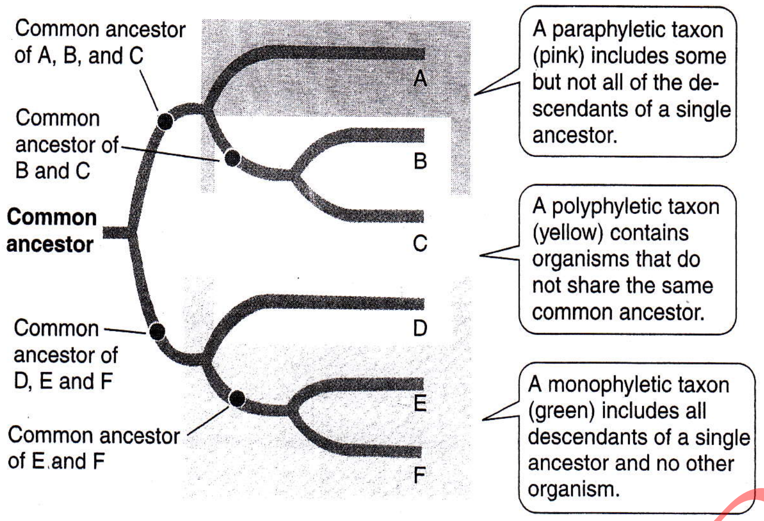


Fig. 15.3 Monophyletic, polyphyletic and paraphyletic taxa.

15.4.2 Polyphyletic Evolution

The members of a single taxon if descended from two or more ancestral lineages through convergent or parallel evolution represent a **polyphyletic taxon.** The origin of such a taxa is called polyphyletic origin and their evolution as **polyphyletic evolution** or **polyphyly** (Fig. 15.3: Taxa B, C and D).

15.4.3 Paraphyletic Evolution

A group of organisms that has a common ancestor but does not include all the descendants of that ancestor is called **paraphyletic taxon.** The origin of such a taxon is called **paraphyletic origin** and their evolution as **paraphyletic evolution.** (Fig. 15.3 Taxon A)

For example, class Reptilia is a paraphyletic group because it does not include all the descendants of its common ancestor. The birds which are very close to crocodiles and can be placed with crocodiles in the same taxon are placed in a separate class. Similarly, Gymnosperms also form a paraphyletic group.

15.5 DIVERGENT EVOLUTION (Adaptive Radiation or Adaptive Divergence)

The living organisms exhibit plasticity in their organisation *i.e.*, organisms with same genotype can change their phenotype in response to changes in the habitats. Because of this characteristic, organisms of the same group or closely related groups appear very different when found in different habitats (divergence). This is called adaptive divergence or adaptive radiation.

15.5.1 Definition of Divergent Evolution

Adaptive divergence or adaptive radiation is the rapid speciation and ecological diversification within a single species or a single lineage of species in several specialised directions.

Adaptive divergence occurs when organisms of a parental stock or of a lineage enter new adaptive zones and each group gets adapted to survive in the new zone. The concept of adaptive radiation was introduced by Osborn. The concept states:

"Each isolated region if large and sufficiently varied in its topography, soil, climate and vegetation, will give rise to a diverse fauna. The larger the region and more diverse the conditions, the greater will be the varieties of animals found."

Therefore, adaptive radiation is evolution in several specialised directions starting from a common and generalised ancestral type, or the entry of the organisms of the original stock to new adaptive zones.

Examples of Divergent Evolution

1. Adaptive Radiation in Limb Structure of Mammals: The limbs in different groups of placental mammals are modified for climbing, flying, swimming, tearing food, burrowing and running. But their ancestry can be traced back to a primitive insect eating, five-toed creature that lived on land and walked with pentadactyle, plentigrade flat feet. The radiation of modern mammals into five different types of feet occurred when they occupied different habitats.

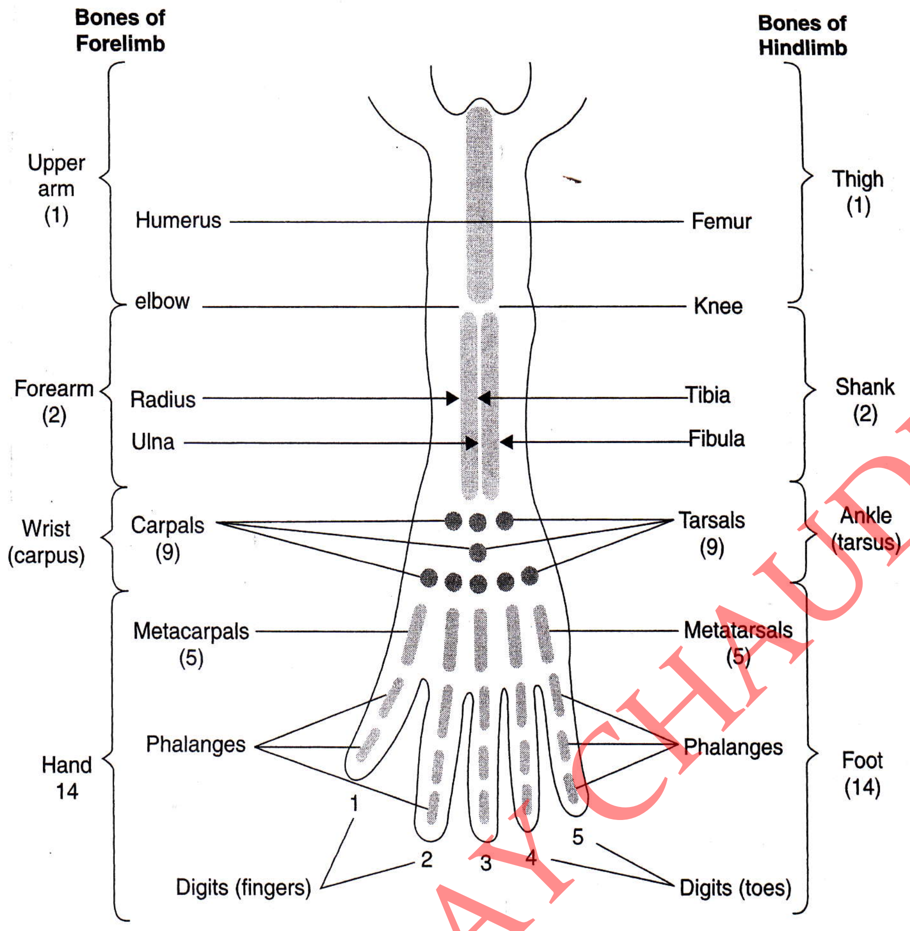


Fig. 15.4 Structure of prototype or generalised pentadactyle limb.

Just read.

- **Arboreal or tree dwelling mammals developed grasping limbs.** In sloths, monkeys and apes the limbs are modified to have powerful grip of the branches. Their fingers are elongated for grasping and limbs are adapted for swinging from one branch to another.
- **Aerial mammals,** *i.e.,* bats have their forelimbs modified into **wings** for flight.
- In **aquatic mammals,** *e.g.,* whales, porpoises and walruses, the limbs are modified into **flippers** that help in swimming.
- In **carnivorous and anteater mammals** the digits of forelimbs are modified for tearing the prey.
- The forelimbs of **fossorial mammals** (*e.g.,* mole) are spade-like. They are specialised for digging and are poorly adapted for locomotion on ground.
- In **cursorial mammals** (like horses and deers) the limbs are modified for fast running over hard ground.

All the aforesaid limb structures are constructed on the same fundamental pattern as shown in **Fig. 15.5** and can be derived from the prototype, pentadactyle limb structure. In other words it could be said that all of them represent evolutionary lines radiating out in various directions from the prototype limb structure. This is known as **adaptive radiation** which represents evolution of new forms in several directions from the common ancestral type (divergence).

2. Adaptive Radiation in Marsupials in Australia: In Australia, a number of marsupials evolved from the ancestral stock, all adapted to new habitats. Because of this, they developed appearance, structure of limbs and tails very different from ancestral stock. (Fig. 15.6).

3. Adaptive Radiation in Darwin's Finches: Different species of Finches on Galapagos Islands have evolved from one mainland species present on West Coast of South America. On these islands, finches got adapted to exploit different niches and habitats and evolved into different species. Their beaks became modified to eat different types of foods available in different niches.

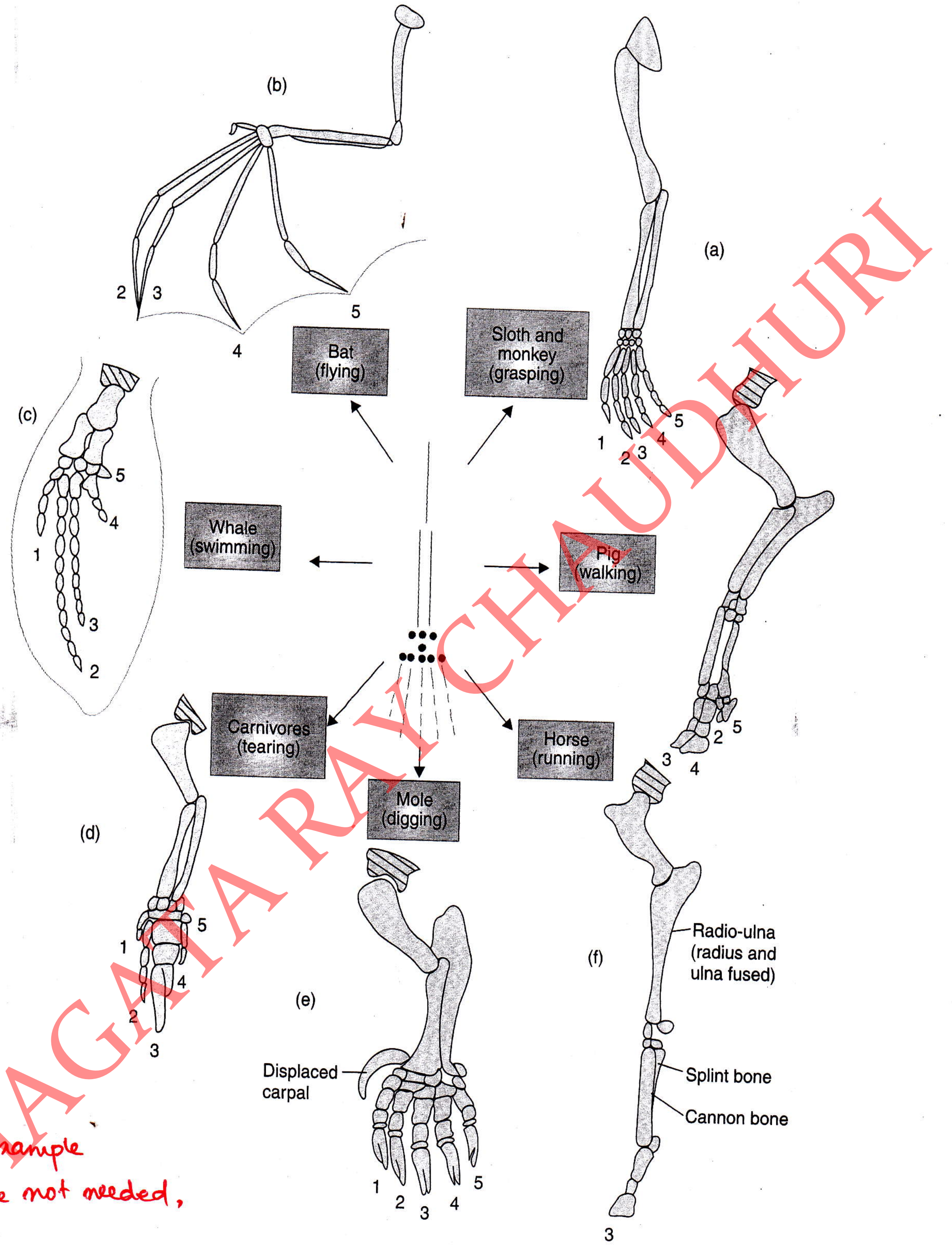


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Fig. 15.5 Adaptive radiation of forelimbs in mammals.

Finches, in general, possess stout, conical beaks adapted for crushing seeds. But they have undergone great diversification in their feeding habits and accordingly in the shape and size of their beak. (Fig. 15.6)

- **The ground finches** of the subgenus *Geospiza* exhibit great variations in their beak structure. Although, chiefly seed crushers, the size of beak is correlated with the size of seeds they eat.
- **Warbler finch** has a slender warbler-like beak and is insectivorous in habit.

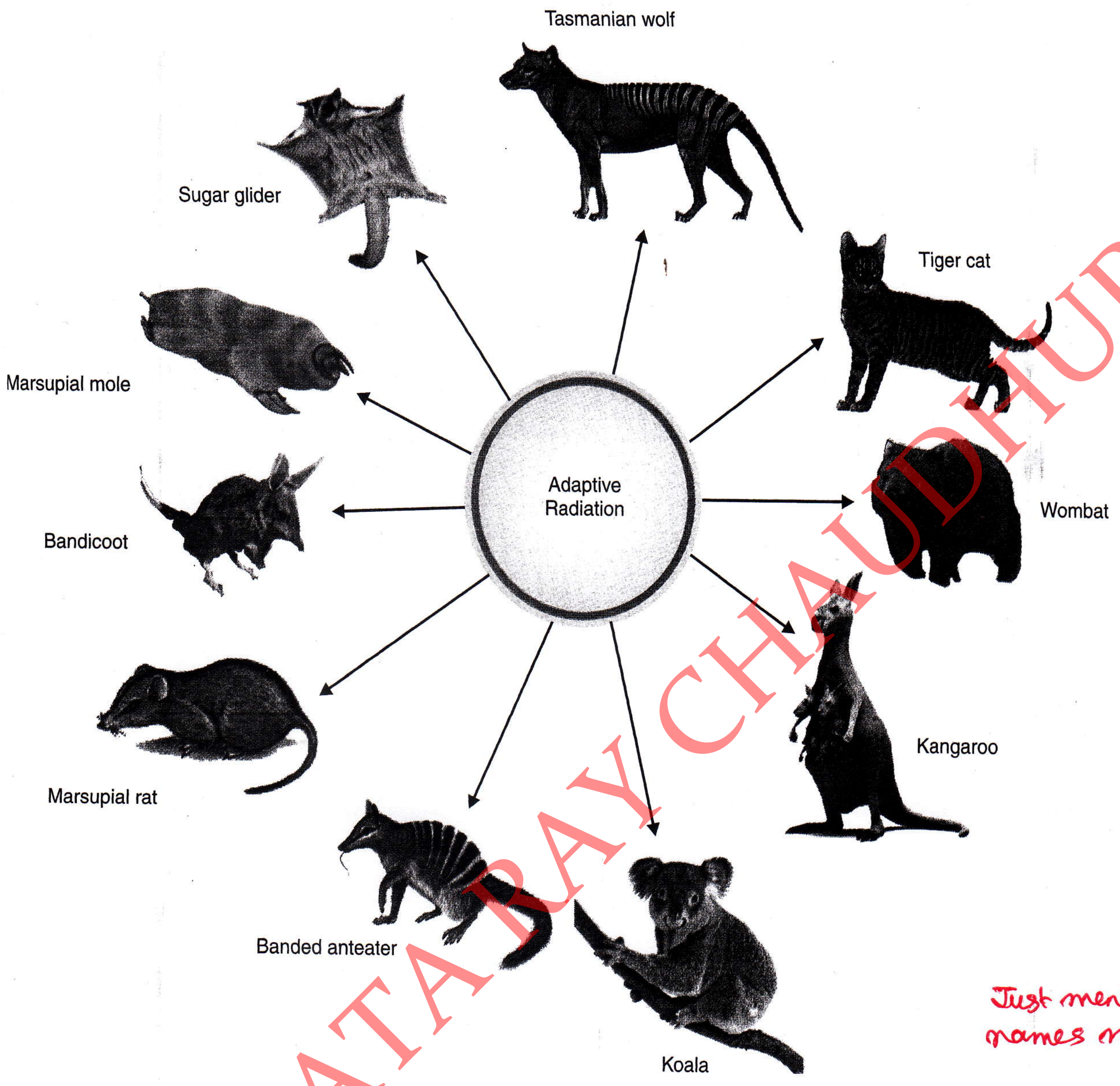

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Fig. 15.6 Adaptive radiation in marsupial mammals in Australia.

- **Vegetarian tree finches** have a short, thick and somewhat parrot-like beak and feed upon leaves, buds and fruits.
- **Woodpecker finches** have stout and straight but long beak and are completely insectivorous. These search bark and leaf clusters and bore into the wood like a woodpecker.
- **Insectivorous tree finches** have a beak very similar to vegetarian tree finch but they feed upon beetles and other insects.
- **Cactus ground finches** have a long, somewhat decurved beak and a split tongue. It probes the flowers of prickly pear cactus for nectar and feeds upon the soft pulp of this cactus.

4. Tooth Radiation in Mammals: Mammals possess **heterodont dentition,** *i.e.,* **incisors** for biting, **canines** for tearing and grasping and the **premolars** and **molars** adapted for grinding. The premolars and molars exhibit greatest structural modifications for different types of food:

- In **insectivorous type** (which feed on insects), the premolars and molars are low crowned with few simple cusps, generally suited for crushing feeble prey.
- In **carnivorous type** these become high crowned with complicated cusps and with shearing structures **(carnasial).**
- In **herbivorous forms,** the premolars and molars are either short crowned **(brachydont)** adapted for succulent vegetation or long crowned **(hypsodont)**

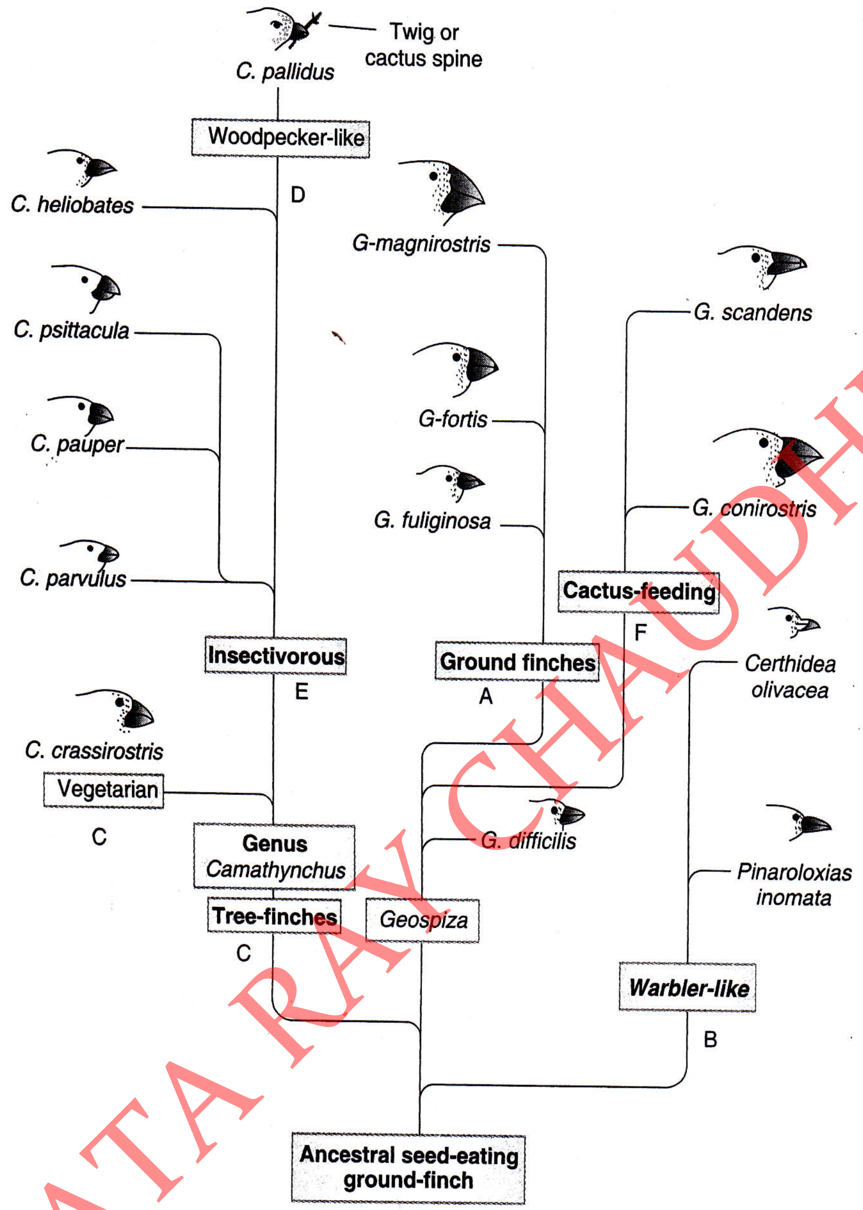


Fig. 15.7 Radiation in the beak structure of finches **A.** Beak of ground finch subgenus *Geospiza;* **B.** Beak of warbler finch; **C.** Beak of vegetarian tree finch; **D.** Beak of woodpecker finch; **E.** Beak of insectivorous tree finch; **F.** Beak of cactus ground finch.

adapted for harsh grasses. Their incisors are sharp and adapted for seizing and cutting the vegetation.

- The **carrion-feeding forms** have blunt teeth while in fish-eating mammals the teeth become simplified and prehensile.
- In **toothed whales,** the teeth have become secondarily homodont, *i.e.,* these are practically all alike, slightly decurved and adapted for grasping the prey.
- In **sperm-whales** or **baleen whales,** the teeth are absent.
- In **myrmecophagous forms,** the teeth have disappeared and jaws reduced. They have developed a tubular snout with a sticky tongue inside to feed on ants.

15.5.2 Conditions Responsible for Adaptive Radiation

Major triggers for adaptive radiation can be discussed under two major heads:

15.5.2.1 Entry into New Adaptive Zones and New Ecological Opportunity

Adaptive radiation is triggered with the entry of a lineage into new adaptive zones which provide new resources, competition, free environment and trigger tremendous burst of evolutionary activities. In the new zone, individuals multiply rapidly and become diversified at an explosive rate. During this explosive phase, the organisms acquire more and more specialisation to the new habitat. The products

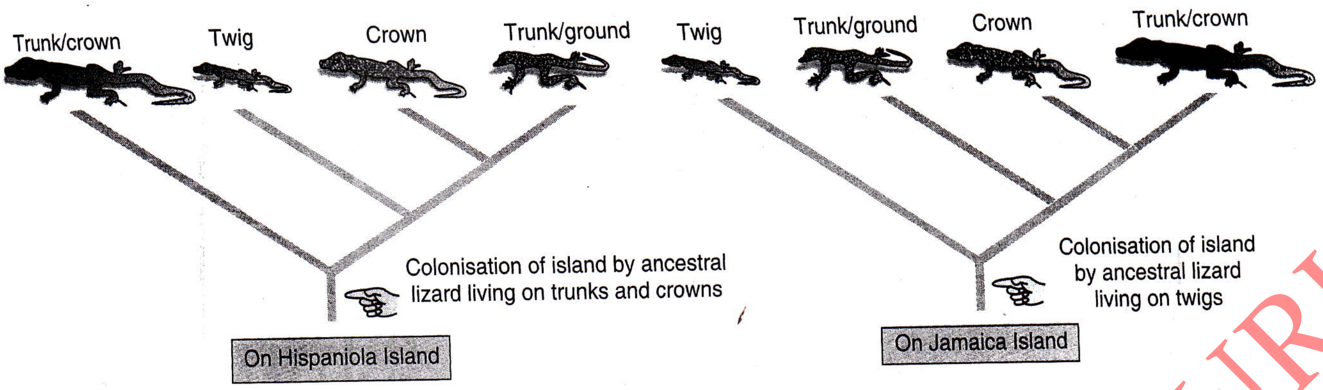


Fig. 15.8 Adaptive radiation in *Anolis* lizards.

of adaptive radiation may form a genus, a family, a subclass or a class. A few examples of those groups which have recently undergone adaptive radiation are spiny-rayed teleost fishes, characin fishes of South Africa, dorosophilid frogs, geckonid lizards, finches and mammals.

- **Radiation in mammals** occurred immediately after the extinction of dinosaurs, when habitats were unoccupied.
- **Radiation in Anolis lizards** on two different islands Hispaniola and Jamaica evolved from two different ancestral stocks but assumed the same adaptive features to same type of habitats.
- Lizards that started living on broad tree trunks and crown developed long legs and tails for clinging and balance.
- Lizards that continued to live on the ground also evolved long legs and tails for running.
- Twig-dweller and crown-dweller lizards developed relatively short body, short legs and short tails.

15.5.2.2 Development of Novel Characters or Morphological Innovations

Some adaptive radiations or breakthroughs in new adaptive zone were triggered due to the evolution of some intrinsic factor/factors or the acquisition of some key morphological innovations. For example, multicellularity, exoskeleton, shells, pentadactyle limbs and wings, etc., were driving force behind adaptive radiation which occurred from time to time.

- Evolution of protective exoskeleton, three pairs of legs and wings led to the evolution of first terrestrial and aerial invertebrates.
- The great success of Cichlid fishes is due to the evolution of jaws in their throat. These additional or second pair of jaws enabled them to crush snail shells and shredding tissues from other fishes.
- Feathers and wings in some dinosaurs gave them the ability to fly and they evolved into birds.
- Development of large, cleidoic eggs in reptiles provided them to lead a complete land life.
- Transition of terrestrial life from aquatic life in vertebrates in Devonian Period was made possible when rhipidistian crossopterygian fishes developed some innovative morphological modifications such as stiff fins which they could use to walk on the bottom of shallow water, lung and nostrils to breathe atmospheric air.

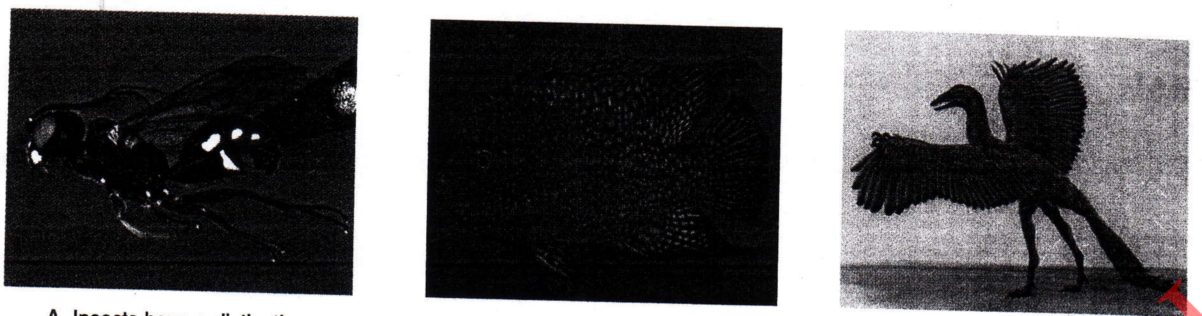
15.5.3 Causes of Adaptive Radiation

The impelling causes of adaptive radiation are the need for food, safety and for better breeding grounds. Naturally, the animals migrate to such new habitats which are still unoccupied and with no competition.

15.5.4 Significance

As already discussed, adaptive radiation had resulted in the formation of new genera, species, orders, subclasses and even classes. The phenomenon of adaptive radiation is, therefore, responsible for **macroevolution** and **megaevolution.**

The illustrations of adaptive radiation or divergent evolution throw light on how the forms would have modified and evolved into new forms or in other words how the evolution would have occurred. Such an evolution of a group is known as **macroevolution.**



A. Insects have a distinctive body plan

B. Cichlids have "throat jaws" that can bite and process food

C. Feathers evolved in dinosaurs

Fig. 15.9 Some morphological innovations leading to exploitation of new habitat and adaptive divergence.

15.6 CONVERGENT EVOLUTION OR ADAPTIVE CONVERGENCE OR PARALLEL EVOLUTION

15.6.1 Definition

When unrelated orgnisms with completely different organisation living in the same habitat or same adaptive zone are found to possess superficial resemblance, this is called **convergent** or **parallel evolution.** This striking similarity in appearance in distantly related organisms is due to natural selection that favours parallel evolutionary adaptations in similar environment. Similarity due to convergent evolution represents **analogy** or **homoplasty.**

15.6.2 Examples of Adaptive Convergence

1. Adaptive Convergence in the Body Shape and Limbs in Aquatic Vertebrates: Cartilaginous and bony fishes, aquatic reptiles (Ichthyosaurs), bird penguin and seals, whales and dolphins belong to different classes of vertebrates, but have similar fish-like appearance and have fins or flippers for swimming (Fig. 15.10). The similarity in their body shape is so well marked that whale and seal are understood as fish by laymen. Similarity in body shape between animals of distantly related groups represents **convergent evolution** and their fin or flippers form **analogous** or **homoplastic organs.**

2. Adaptive Convergence in the wings of Insects, Flying Reptiles, Birds and Flying Mammals: The most common example of convergent or parallel evolution is the occurrence of wings in insects, flying reptiles, birds and flying mammals. All of them belong to totally different groups, but have one common feature, the development of wings for flight.

3. Adaptive Convergence in the Eyes: The eyes of *Octopus* and vertebrates are remarkably similar in appearance as well as in structure. They seem to be homologous structures but they are analogous. Eyes in *Octopus* and *Sepia* do not have a 'blind spot' and they do not form inverted image as in the case of vertebrate eyes. This shows that the two types of eyes are the products of convergent or parallel evolution along two distinct lines.

4. Convergent Evolution in Marsupial and Placental Mammals: The two groups of mammals, marsupials and placentals, have evolved in a very similar way independently on separate continents: Marsupials in Australia and placental eutherian mammals in other continents. As seen in Fig. 16.11 the two groups present parallel evolution and each placental type is similar to corresponding marsupial variety. For example, eutherian moles correspond to marsupial moles or eutherian wolf to Tasmanian wolf and eutherian bobcat corresponds to Tasmanian tiger cat.

Australia, the home of marsupials separated from the mainland of Asia more than 50 million years ago. At that time the eutherian mammals were not evolved and land was inhabited by marsupials only. After the separation of Australian Continent eutherian mammals appeared on mainland, evolved into various forms and competed with marsupials. Therefore, marsupials disappeared from the main land. However, marsupials on Australian Continent faced no competition with eutherians and diversified for the next 50 million years.

The similarity between different members of marsupials and eutherians can be due to convergent or parallel evolution because of similar selective pressure in similar environments.

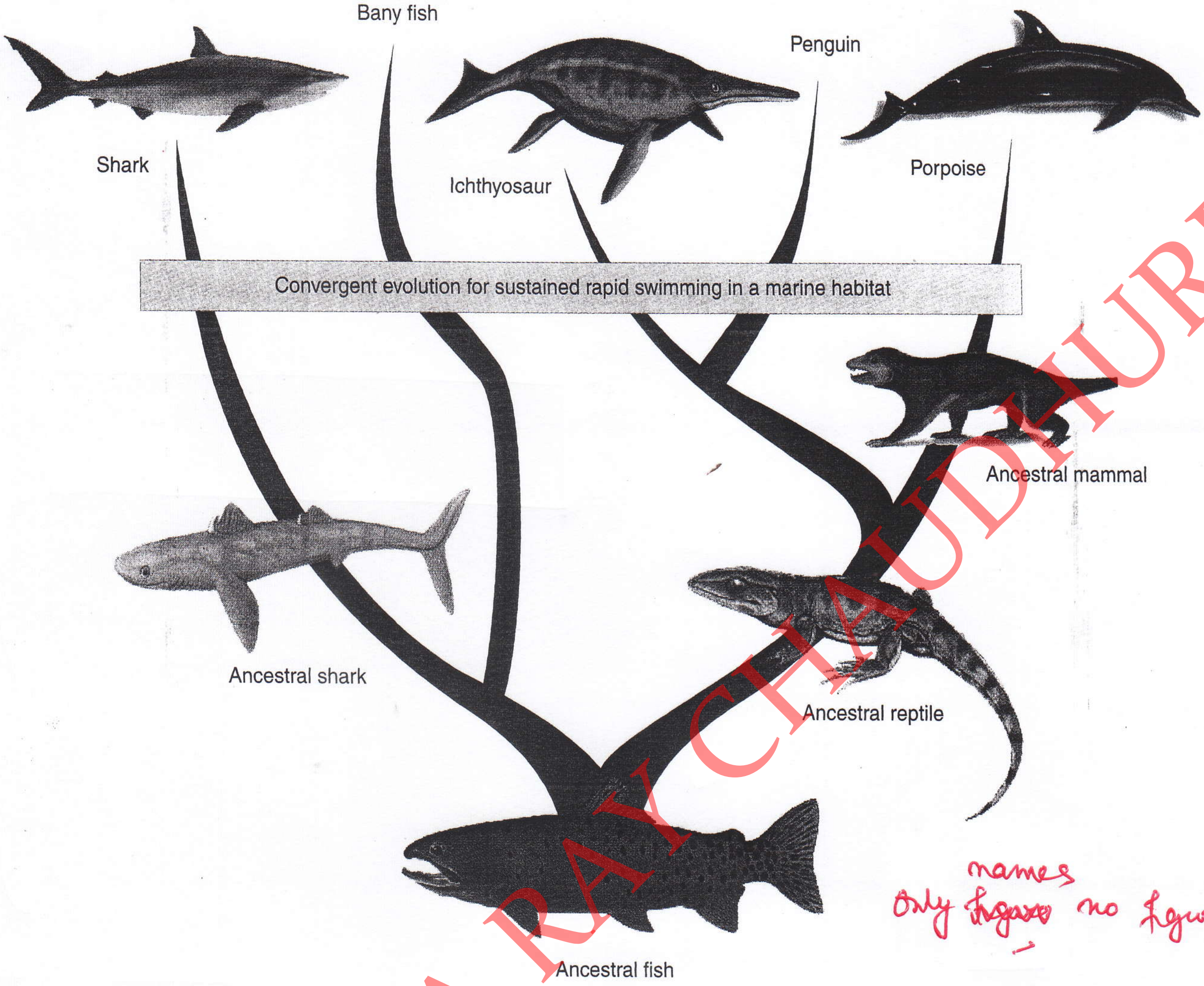


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Fig. 15.10 Convergent evolution in three marine vertebrates—Shark (cartilaginous fish), Bonyfish, ichthyosaur (an extinct reptile), Penguin (a bird) and Porpoise (a placental mammal), because similar adaptations for rapid movement through water were independently selected in each of the lineages.

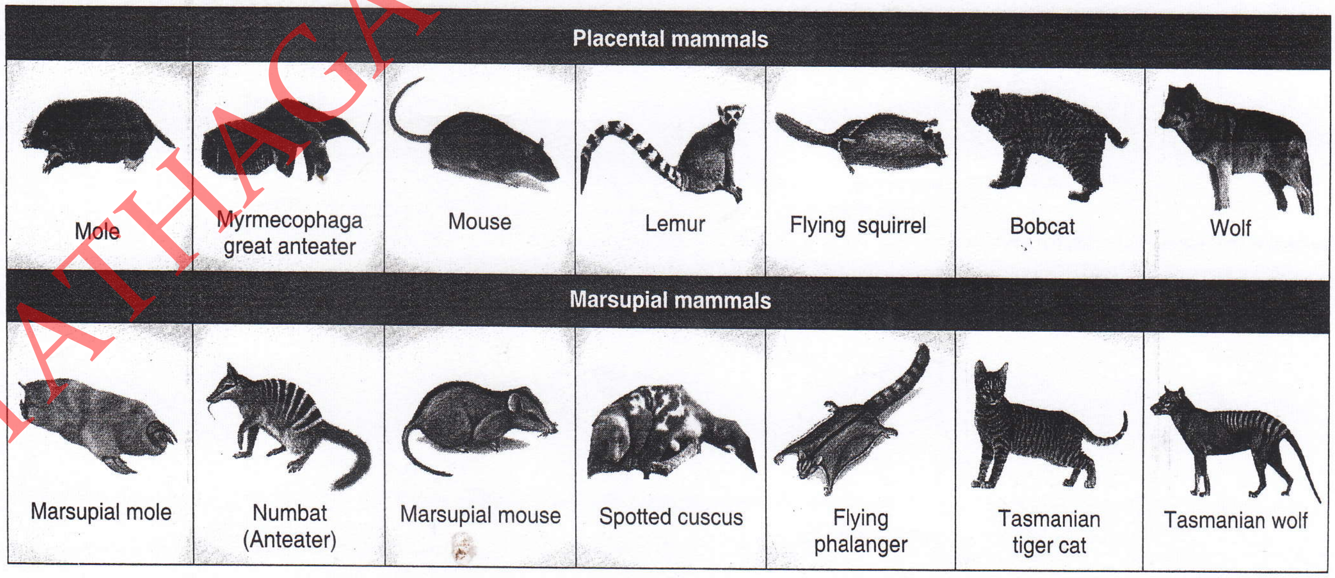

Fig. 15.11 Convergent evolution in placental mammals and marsupial mammals in Australia.

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15.6.3 Significance

The convergent evolution leads to the formation of analogous similarities among different groups of organisms which indicates that evolution may lead to superficial resemblances. N.W. Pirie has pointed out that a kind of convergence might have played a major role during prebiotic evolution, before the chemical system accumulated characteristics of living organisms and became dominant or led to organic evolution.

In the end it could be concluded that in the evolution of life from simple to more complex forms both divergence and convergence have played an important role, but divergence is more frequent at present than the convergence.

Table 15.2 Difference between Divergent and Convergent Evolution

Divergent Evolution	Convergent Evolution
1. Divergent evolution results in origin of new forms by diversification. So, the new forms are apparent from the existing forms.	1. Convergent evolution results in origin of new forms which resemble in appearance to the already existing form.
2. Organisms get adapted to different environments or different habitats.	2. Organisms get adapted to one environment for one habitat.
3. Divergent group splits into a number of groups, each having different appearance.	3. Organisms of different groups assume similar habitat.

15.7 COEVOLUTION

15.7.1 Definition

Coevolution is a pattern of evolution in which two interacting species influence each other's adaptive changes over the time. It means in co-evolution the interacting species evolve together in response to each other. For example, a change in species A induces a change in species B, which then selects another change in species A, which in turn introduces another change in species B and so on. The co-evolution results in **reciprocal adaptations** and leads to long-term changes in the interacting populations.

15.7.2 Examples of Coevolution

1. Cheetah-antelope or wolf-deer interactions are examples of coevolution. Deer are fast and agile in response to predators, wolves and cougars. The speed and agility of deer promotes agility in wolves to prey on deer. In turn speed and agility in deer increases further to escape from the predator. This is an example of coevolution in animals having antagonistic interaction.

2. Plants with long curved flowers are pollinated by humming birds that have long and curved beaks. Their beaks are curved to match the curved flowers. This is an example of **mutualistic coevolution.**

15.7.3 Outcome of Coevolution

In coevolution one organism evolves to its own benefit in response to other organism. As one changes, other dependent one also changes. In antagonistic interactions the end point could be complete elimination (*i.e.,* extinction). In mutualism the end point reaches when there is no further change (*i.e.,* stability).

KEY TERMS

- Adaptive convergence
- Anagenesis
- Clade
- Divergence
- Monophyletic
- Plesimorphic
- Synapomorphic
- Adaptive divergence
- Apomorphic
- Co-evolution
- Fussorial
- Paraphylectic
- Polyphyletic
- Adaptive radiation
- Cladogenesis
- Cursolial
- Limb
- Phyletic gradualism
- Punctuated equilibrium