



Basic Course in Ornithology
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Lecture -5
Evolution and Speciation Part 2


Now it is very important to look at the origin of bird feathers and bird flight; the reason is that often the origin of bird flight and the origin of birds themselves are so complex and so intertwined that often the arguments get buried under the ambiguity between these two propositions.


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Origin of bird feathers



- Theories of origin of birds and origin of their flight are often intertwined.
- **Origin of feathers**
- Long held view till early 20th century: Scales → Feathers
 - Scales, feathers, and hairs are homologous, but with different structural origins
- Richard Prum & Alan Brush's re-analysis of feather development pathway
 - Scales did NOT give rise to feathers
- Functional hypotheses: flight, thermoregulation, tactile communication, body protection, etc





We will first see the origin of feathers. So, for a very long time, feathers were considered as actually the modified forms of scales. You know they always consider scales, feathers, and hairs are homologous but with different structural origins right. But, Richard Prum and Alan Brush's re-analysis of further developmental pathway found that scales did not give rise to feathers; in fact, they found that feathers and scales have completely different ontogeny. So, they probably they think that they are not probably as homologous as we think.

And instead, Richard Prum proposes saying that maybe feathers had different functions other than the flight like thermoregulation or tactile communication or body protection etc; even for

thermoregulation, there are recent studies that tend to demonstrate that smaller birds -smaller bodied birds have much higher density of feather compared to the large bodied birds.


See in birds have actually what we call as feather tracts you know the pteryla or pterylosis what we call. So the feather tracts are actually if you see the smaller bodied birds which actually suffer from cold or heat because of their volume to surface area.. much higher volume to surface area ratio they have to develop a much higher degree of adaptations than large bodied birds.

So, the fact that the density of feathers are much higher in smaller bodied birds indicate that feathers perhaps evolved as a response to the thermoregulation than for the flight per se.


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Origin of bird flight




- Arboreal hypothesis / 'Trees-down' view
 - Proposed by O.C. Marsh & William Pycraft (1880-1900)
 - Seemingly '*more plausible*' and hence treated as proof of thecodont origin of birds
 - Thecodonts were much smaller in size unlike theropod dinosaurs
 - G. Heilmann - the original proponent of Thecodont origin of birds favoured this.
 - Claws on forelimbs of *Archaeopteryx* as a postulate to their tree-climbing behaviour
 - Observed in chicks of Hoatzin today



ILLUSTRATIONS: S. Chatterjee & R.J. Templin, 2012, Earth and Life, Pp. 385-412.



ILLUSTRATIONS: Wikimedia Commons



So, when you look at the origin of the bird flight again there are two theories or hypotheses. One is that the arboreal hypothesis and the other one is the cursorial hypothesis. Basically arboreal hypothesis is that trees-down view. So, what it proposes is that perhaps this illustration taken from Chatterjee and Templin's book. You know, the early theropod dinosaurs or any other ancestors of birds they climbed the trees and from the height of the branches they probably would glide down the ground.

In that process they probably they developed the flight. It was originally proposed by O.C. Marsh and William Pycraft in late 19th century and early 20th century. So, now this was taken up by the Thecodont origin proponents saying that “wow! this is why we were saying that birds did not evolve from Theropod dinosaurs but from Thecodont reptiles”. Because, Thecodonts were much smaller in size and Theropod dinosaurs at least the early period were much huge...they are really gigantic which have been unlikely then to climb the trees and fly per the arboreal hypothesis.

So, the origin of bird flight the arboreal hypothesis was favored by the Thecodont origin the proponents of the Thecodont origin of birds. We said that, remember Gerard Heilmann the original proponent of the thecodont origin, he strongly favoured this saying that “well, look, this is what exactly what we were telling why the birds evolved actually more from the Thecodonts.



And one of the things Heilmann also said is that Archaeopteryx had very strong claws you know you could see from this illustration very strong claws on its fore limbs. So, they say that well see look archaeopteryx had claws on its four limbs. So, that would have enabled them to climb the trees or branches even today you know Hoatzin, Hoatzin is a very ancient looking bird of South America. So, they actually you know Hoatzin is a very mysterious bird in fact their phylogenetic affinity is still to be resolved fully.

So, earlier they were thought to be very closely related to cuckoos sometimes to the bustards and rails and you know all or also Galliformes on its own different order as well. But I think now the tendency is to put them into its own order. Hoatzin's chicks even today you could see you know see they actually nest along the water bodies. So, Hoatzin chicks have they have developed these claws on its fore wings to climb the trees because they fall down into the water, running waters.

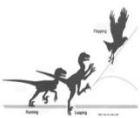
So, that is the argument that they put forward saying that you know this arboreal hypothesis is strongly favoured.

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Origin of bird flight


- **Cursorial hypothesis / 'Ground-up' view**
 - Proposed by Baron Nopcsa (1907)
 - Favoured by theropod-origin proponents
 - Theropods were much larger in size and therefore fitted this hypothesis
 - *"If the protobirds had legs adapted for running, why did they have to develop wings?"*
 - J.H. Ostrom: Non-flight functions of feathers/wings
 - Ken Dial (2003): *'Wing Assisted Incline Running'* in Chukar Partridges
 - Supports Theropod origin of birds



ILLUSTRATIONS: S. Chatterjee & R.J. Templin, 2012, Earth and Life, Pp. 585-612.



Chukar Partridge
Kavunakar Rayker/Wikimedia Commons



So, the second alternate view was the cursorial hypothesis or what we call ground-up view. It was proposed by Baron Nopcsa and again around at around the same time of the early 20th century. So, according to this hypothesis probably the dinosaurs, the ancestors were actually cursorial, in the sense that they could run, they had the adaptation for running legs.

So, when they were running probably you know at one point of time they started you know that velocity gave them the enough thrust to launch into the air and probably what was just a short flap turned into a full full-fledged flight much later. So, this was the view of the cursorial hypothesis. And you remember the early Theropod dinosaurs which were supposed to be the origin for ancestors for the birds they were much larger in size.

And Theropod dinosaurs were also known for their cursorial adaptation in their legs they were very extremely fast running dinosaurs. So, probably the proponents of the Theropod origin of birds they strongly favoured cursorial hypothesis. Well again the criticism came up: if the protobirds, the ancestors of birds had legs adapted for running why did they have to develop wings?

So, because the both the wings and the legs meet the purpose of locomotive movement. So, when the movements are already achieved by running what was the need for the flight to evolve. Then

J.H Ostrom, John Ostrom again he said the non-flight functions of the feathers or wings as we saw in the previous slide.

Now in 2003, Ken Dial, and his team... they came from America. So, they came out with a very interesting model for bird flight. It is called wing assisted inclined running. Actually they use the experimental studies and they used the Chukar Partridges in captivity. So, Chukar Partridges is actually found along the Himalayas and also the Middle East and they live in a very steep mountain slopes. When they have to fly out of a danger or out of predation what they do is they have to really climb the very steep mountains.

So, when they run uphill they use their wings to balance. So, this actually prompted Ken Dial to look more closely at how these wings are helping the thermodynamic [aerodynamics] and the balance of the birds while you know running and climbing in Chukar Partridges in captivity. Then the very interesting thing is that they found that actually the wings do not help the birds to actually lift but instead they help the birds to balance.

So, Ken Dial came out with this theory saying that wings are actually the primary function of the wing is actually not flying but probably give a balance to that aerodynamic lift. This supported the Theropod origin of birds. Now this is this the theory which has been proved in experimental aerodynamic studies as well which again moves the clocks in strongly in support of the Theropod dinosaurs origin of birds.

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Origin of bird flight

Is the arboreal hypothesis truly inconsistent with theropod relationship?
L.M. Witmer, 2002

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Decoupling of the origin of flight from the origin of birds




In the past decades there has been a general dichotomy in the discussion of the origin of avian flight, i.e., the arboreal hypothesis or 'trees-down' theory of flight which dont origin of birds

The wings before the bird: an evaluation of flapping-based locomotory hypotheses in bird antecedents

Research article Evolutionary Studies Paleontology

T. Alexander Dececchi¹, Hans C.E. Larsson², Michael B. Habib^{3,4}

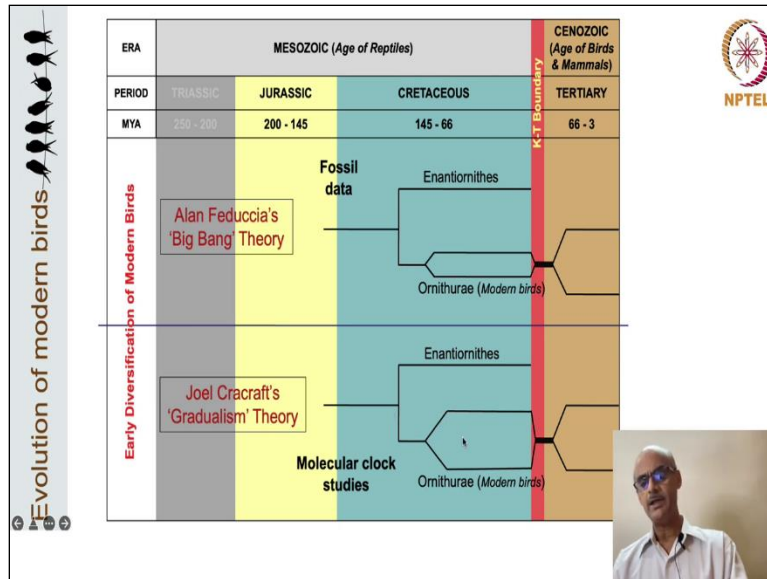
ARCHAEOPTERYX AND THE EVOLUTION OF BIRD FLIGHT
TAKING Wing
PAT SHIMMAN

So, now there are two issues, right? One is the origin of birds and other is the origin of the bird flight. So, obviously that is now the confusion but the origin of bird flight how is it you know how do they actually you know clash with each other is like arboreal hypothesis truly inconsistent with the Theropod relationship in the in other words can we say that you know the cursorial hypothesis will support Theropods.

On the other hand, like you know can it be or is it necessary to separate these two issues. So, there are several you know opinion pieces that have come up in the late 20th century and also 21st century. So, now biologists increasingly say that you know there is no necessary that we have to really you know keep them separate one is the origin of bird flight other is the origin of birds and the proponents often you know take sides in both cases and that kind of masks the truth in the whole argument.

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So, we looked at the early that that is the origin of birds. Now let us see the modern birds the evolution of the modern birds. So, if you look at the same you know time geological time scale one again there are two theories one is that Big bang theory as put forward by Alan Feduccia. So, Feduccia is looking at the fossil data, Feduccia says is that you know the modern birds yes they did originate from the late Jurassic and you know early Cretaceous the ancestors of the modern birds.

So, that is well accepted by both schools but you know this is the Ornithurae it gave back to a non you know an Enantiornithes actually became extinct at KT boundary this is the Ornithurae modern birds. So, this actually modern birds evolved and then this KT boundary this red band this is the band time around you know 65 to 66 million years ago it was that hit you know the dinosaurs became extinct the mass extinctions of the dinosaurs because of you know most likely to be the because of the impact of the asteroid hit on the earth.

And scientists have discovered based on the iridium you know Alvarez hypothesis based on the iridium deposits in the KT boundary rocks all over the world and they even found that crater to be the to be in Yucatan peninsula in Mexico. So, now the KT boundary around 65 million years ago a big asteroid of probably 150 to 200 kilometer diameter it hit the earth and created a dust storm

and the dust storm has killed almost 80% of all the biota are known to earth around this 65 million years ago.

So, in that dust storm created by the asteroid collision, dinosaurs became extinct completely extinct and even the modern birds which evolved much before the KT boundary. So, they survived but then 20% of these modern birds are Ornithurae survived this asteroid collision and then after the dust storm has settled around you know around 50 million years ago they started diversifying because the new niches what we call niches that habitat let us say habitat or any you know ecological any ecological resource.

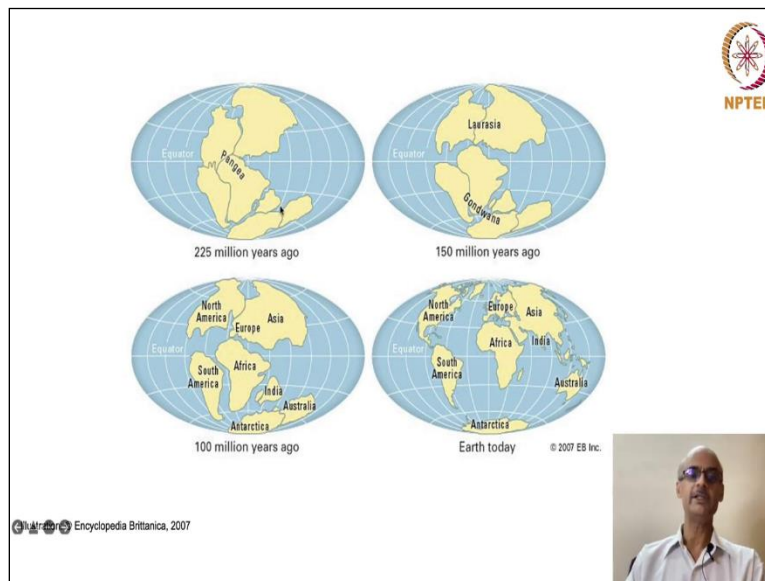
So, they were now completely available because 70% of the biota are already become extinct because of the KT boundary. So, the unoccupied niches were occupied by the modern birds and they rapidly diversified. So, it is called big bang theory you know there is a rapid multiplication or speciation of the modern birds around 50 million years ago after the KT boundary. So, this is this was put forward by the ornithologist Alan Feduccia.

On the contrary, Joel Cracraft a phylogeneticist and cladist so, he is a cladistic school. So, he propounded saying that it was not true. So, he put forward an alternate hypothesis called Gradualism theory. He looked at the molecular clock studies of the modern birds and the ancestors of the modern birds and he propounded saying that the modern birds actually evolved much earlier on 150 million years ago and so they expanded with along with the dinosaurs along with the Enantiornithes dinosaurs.

So, the modern birds coexisted with dinosaurs and the KT boundary that as you know as asteroid collision with the earth in the dust storm the dinosaurs died down but the modern birds the 20% of the modern birds they survived and again they diversified rapidly because of the available of niches. So, these are the two alternate views of the the early diversification whether the origin the modern birds originated by big bang speciation after the KT boundary or the modern birds actually they were there along with the dinosaurs much before the KT boundary that was the question.

Now you would ask the question saying that when Feduccia saying that the modern birds did not speciate much before the KT boundary but why did Joel Cracraft propose saying that modern birds actually diversified much faster more rapidly here before the KT boundary, the answer lies in one particular event that happened around 150 million years ago that is the continental movement.

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The plate tectonic moment. So, as you know 225 million years ago it was the Pangea was the one single composite landmass; around 150 million years ago, Pangea split into Laurasia and Gondwana and 100 million years ago Gondwana again to South America, Africa, India, Australia and Laurasia into Europe, Asia and North America now that is a modern India. So, you remember 150 million years ago this thing happened right the continental split. So, when the plate tectonics forced this continental movement.


So, the land mass became more and more isolated and it is a theory suggesting that any isolation under distance would lead to rapid diversification in species. Species would tend to speciate, you know, diversify into multiple species in even in remote and remote islands remote and distant and islands. So, that is a pattern even we see today. That is the reason why Joel Cracraft who studied the biogeography of the continental movement proposed saying that the modern birds must have speciated along with the dinosaurs during the time of time of the dinosaurs much even before the KT boundary. You see that is second you know proposal second theory by Joel Cracraft.

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Summary of views



Topic	School A	School B
Origin of birds	Thecodonts / Archosaurian reptiles	Theropod dinosaurs
Origin of bird flight	Arboreal hypothesis	Cursorial hypothesis
Early diversification of modern birds	Tertiary Period after K-T boundary (c. 65 mya)	Cretaceous Period before K-T boundary (c. 100 mya)



Now we will just see there are three things one is the origin of birds, origin of bird flight and the early diversification of the modern birds. Interestingly, when we look at the summary there are only two schools you know the paleontologists and biologists seem to have divided themselves only into two schools and very interestingly they stick to one particular point. Like if you look at the origin of birds, school A they say that the birds are originated from Thecodonts or archosaurian reptiles but other things they are not Theropod dinosaurs.

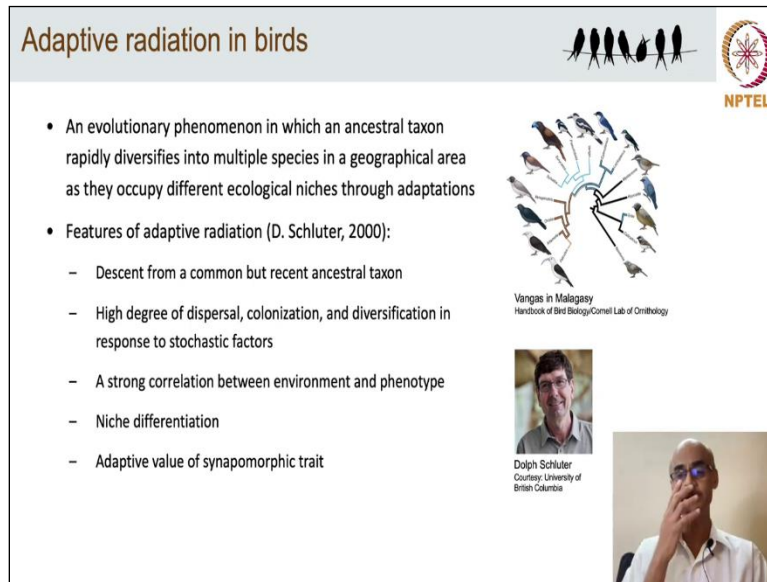
And the people who support the Thecodont origin they also supported the arboreal hypothesis of the bird flight. On the other hand, people who supported support Theropod dinosaurs origin also support the cursorial hypothesis of the bird flight and the same you know dichotomy also you know extends to the when we come to the early diversification of the modern birds. So, these people believe that the modern birds you know diverged 65 million years ago after the KT boundary.

But the Theropod dinosaurs people they believe that probably modern birds know they diverged much before the KT boundary around 100 million years ago. So, this is the overall summary of the views. And so this is very important to understand that because if you look into the bird literature we will be confusing and confounding arguments have been put forward but all boil down these two schools and these three hypotheses.

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Adaptive radiation in birds

- An evolutionary phenomenon in which an ancestral taxon rapidly diversifies into multiple species in a geographical area as they occupy different ecological niches through adaptations
- Features of adaptive radiation (D. Schluter, 2000):
 - Descent from a common but recent ancestral taxon
 - High degree of dispersal, colonization, and diversification in response to stochastic factors
 - A strong correlation between environment and phenotype
 - Niche differentiation
 - Adaptive value of synapomorphic trait



Vangas in Malagasy
Handbook of Bird Biology/Cornell Lab of Ornithology

Dolph Schluter
Courtesy: University of British Columbia

Now we will move on to next one; we have seen the early diversification of the modern birds. Now there is also one phenomenon that is related to what it is called adaptive radiation. Basically adaptive radiation is an evolutionary phenomenon in which an ancestral taxon rapidly diversifies into multiple species in a small geographic area, probably perhaps in response to availability of lots of niches which is unoccupied niche.

And they also, in that process, they also develop phenotypic adaptations like in bill or wing or in body structure or body size or in any phenotypic adaptation. So, one example is the Vangas in Malagasy which you can see here. So, the Vangas are actually suboscine you know early passerines and Malagasy you know Madagascar. So, in Malagasy you could see more than 15 species of Vangas.

So, they all had the common ancestor but look at it you know the differences in their body size and the bill size and other things and probably perhaps they also evolve different feeding diet and other things. So, it was Dolph Schluter who came out with what would you know who studied Dolph Schluter from University of British Columbia. Schluter developed what we call as a syndrome of adaptive radiation for adaptive radiation to happen in birds.

Because adaptive radiation is very common in islands like you know we will see next the classic study of the Galapagos finches.

So, these are the characteristics or what called as you know the preconditions for adaptive radiation to occur. One is that it should descend from the common but recent ancestor taxon, high degree of dispersal colonization and diversification because obviously the ancestral taxa have to disperse from the mainland to the island and they should also have the high degree of diversification.

And a very strong correlation between the environment and phenotype the adaptations in the phenotypes should be very evident and niche differentiation they should also occupy different niches different niches should be available and the adaptive value of the synapomorphic traits. So, synapomorphic traits as you remember it is the shared derived character from the ancestor it is a character absent in ancestor but present in all, its descendant species.

So, that adaptive phenotypic adaptive characters should have been present in all the you know derived taxa but not in the ancestral taxa. So, these are the preconditions for adaptive radiation as listed by Dolph Schluter.

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Adaptive radiation in Darwin's finches

Adaptive radiation in Galapagos finches

Charles Darwin
Julius Jäskeläinen/
Wikimedia Commons

NPTEL

BEAK OF THE FINCH
JULIUS JÄSKELÄINEN

Peter & Rosemary Grant
Courtesy: PNAS

Illustration: © Encyclopedia Britannica, 2010

The diagram illustrates the adaptive radiation of Darwin's finches. At the center is the 'ancestral tree-eating ground finch'. Seven numbered circles (1-7) represent different adaptive niches: 1. large cactus finch (Geospiza conirostris), 2. cactus finch (Geospiza scandens), 3. sharp-beaked ground finch (Geospiza officinosa), 4. large ground finch (Geospiza magnirostris), 5. medium ground finch (Geospiza fortis), 6. small ground finch (Geospiza fuliginosa), and 7. woodpecker finch (Campephilus palmarum). Other species shown include small tree finch (Campephilus parvulus), medium tree finch (Campephilus palmeri), large tree finch (Campephilus porteri), mangrove finch (Campephilus heliodytes), and veery finch (Certhidea olivacea). A map of the Galapagos Islands is shown in the bottom left, and a photo of Peter and Rosemary Grant is in the bottom right.

Now we will see the adaptive radiation in Darwin's finches which are a textbook example which you would often come across. So, when Charles Darwin visited the Galapagos islands it's a history, we all very well know that when he began the voyage on The Beagle to Galapagos islands he was struck by the island forms in Galapagos whether it is land tortoises or the Galapagos finches

and he came out and published this origin of species and developed the theory of natural selection as a means for speciation.

Galapagos finches...like almost some 13 to 14 species are involved in the groups of islands in Galapagos in Pacific ocean. So, now if you currently the Galapagos finches have like you know insectivorous. So, if you look at this in you know one ancestral ground finch probably it from the mainland from Ecuador or from mainland South America to Galapagos it arrived, colonized and rapidly multiplied into different species with different food habits.

Like for example these seven species you know right from small tree finches to mangrove finch and woodpecker finch and warbler finches. So, they all have insect eaters so all these seven. Now the ground finches ground feeding ground finches they are all seed eaters and there is two species which are specialized which have developed a specialized bills and beaks adapted to feed on insects from the cactus from the larger they called cactus, cactus finches you know they use the even the cactus spines to extract insects from the tree cavities.

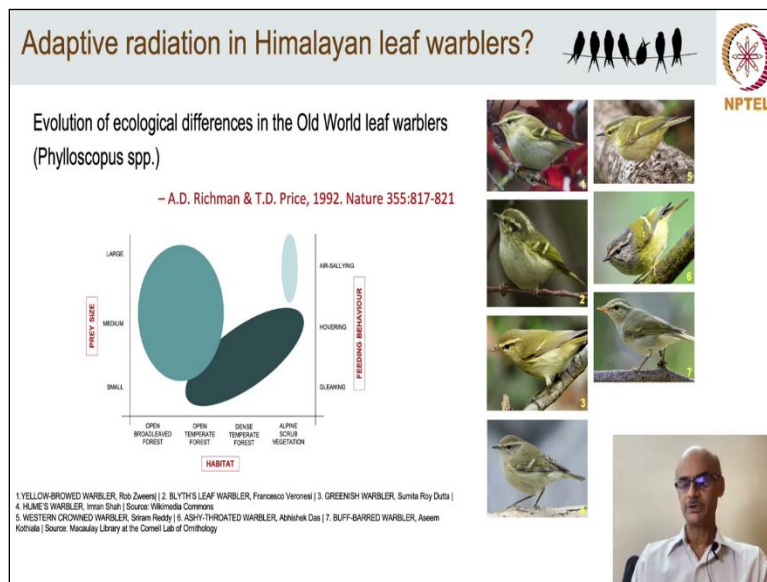
And then the buds and fruits as one species which is specialized adaptation to feed on buds and fruits. So, one ancestral ground finch arrived in Galapagos island some point of time in the history and rapidly speciated into more than 15 species which have completely different bill morphology and different diet types. So, this is exact this is a very classical case of adaptive radiation. So, this is adaptive radiation, it is also been seen in Hawaiian honeycreepers, you know, honey eaters and also in Vangas as we saw earlier in Malagasy.

So, these Darwin's finches...which I would strongly recommend to you to pick up this book 'Beak of the Finch'. So, it is a very one of the loveliest books it is immensely readable book. 'The Beak of the Finch' is written by Peter and Rosemary Grant. So, Peter and Rosemary Grants are the biologists evolutionary biologists from Princeton University.

So, the Grants they spent almost five to six decades in the Galapagos island they had probably the world's longest running experimental study on a single group of birds. Almost four to five decades of their research they captured each and every individual finch, they id tagged them they measured

the morphology and then they actually saw birth of a couple of species you know they actually they are the one they demonstrated to the world how species... you know, the general perception is that species takes thousands and even millions of years thousands and thousands of years to evolve. But apparently it is not, and Peter and Rosemary Grant's long term study on Galapagos clearly proves that species can evolve even within 100 years time in response to any environmental stochasticity like a drought or high rainfall and things. So, please read this book pick up this book *Beak of The Finch* and you know it tells the they tell the story of how these finches evolve and they also narrate the story of how the drought led to food scarcity and food scarcity led to specialization of the niche specialization among these finches.

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Do we have any example from South Asia or Oriental region or India? Perhaps not as extreme as you know Hawaiian honeycreepers or Galapagos finches but one example that could be close to what we call as adaptive radiation is the Himalayan leaf *Phylloscopus* leaf-warblers. So, it is Adam Richman and Trevor Price biologists evolutionary biologist and from University of Chicago.

And Trevor Price is one authority on the *Phylloscopus* leaf-warblers in the Himalayas. So, he and his colleague Adam Richmond they published one article in *Nature* way back in 1992 is the evolution of ecological differences in Old World leaf warblers. So, *Phylloscopus* leaf-warblers in

the Himalayas, they are the hot bed of the *Phylloscopus* leaf-warblers, very tiny greenish to grey looking birds and they can be identified mostly by call or their song and they breed along the Himalayas most of them also winter in the peninsular India and other Southern Asia.

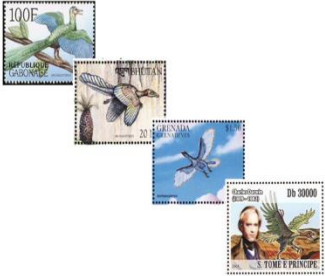


And they have a very distinct niches -ecological niches and Richman and Price also found that these diversification of these *Phylloscopus* leaf-warblers in the Himalayas...Indian Himalayas actually are in response to three axis one is the prey: large, medium, and small; other is the habitat is the open broadleaved forest or open temperate forest, dense temperate forest, or alpine scrub, you know, Krumholz vegetation about 3000 to 4000 meter altitude along the Himalayas.

And the third axis is by the feeding behaviour; see all these leaf warblers some of them are mostly, they take their insects, they are insectivores. So, mostly techniques by air sallying and some one group the hovering and other thing are the gleaning. So, these leaf warblers seem to have diversified in response to these three ecological characteristics in precise habitat choice and also the feeding behaviour. So, this is a phenomenon which I would personally believe it comes very close to adaptive radiation.

Though phenotypically they may not show as extreme in variations as Galapagos finches but ecologically and behaviorally they do show these things.


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Thank you...



Stamp illustrations: <http://www.birdtheme.org>

rajah.jp@gmail.com



Well, that shows that the origin of birds and the bird flight and you know hypothesis and for you but so these are the you know some of the countries. In fact, quite a few countries have published postage stamps honoring the role of Archaeopteryx in understanding the evolutionary biology and Archaeopteryx still plays a major role in that. So, thank you very much.