Basic Course in Ornithology
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Lecture -4
Evolution and Speciation Part 1

Hello viewers! welcome back to the NPTEL's basic course in ornithology. In this video, we will learn about the evolutionary origin of birds and how and when modern birds evolved. We will also look at the phenomenon of adaptive radiation, a process of rapid speciation in a small geographic area. As we know, birds are perhaps the best studied groups of animals in the world but ironically origin of birds also remains one of the most contentious topics that has led to some of the most bitter rivalries that we know in biology.

Paleontologists and evolutionists continue to spar over the origin of birds, it is an interesting story! So, we will now see what are the major theories of origin of birds. And also the origin of flight, because both the origin of birds and origin of flight are actually very closely intertwined and different viewpoints been put forward in support of their hypotheses and also evidences against their competing hypotheses.

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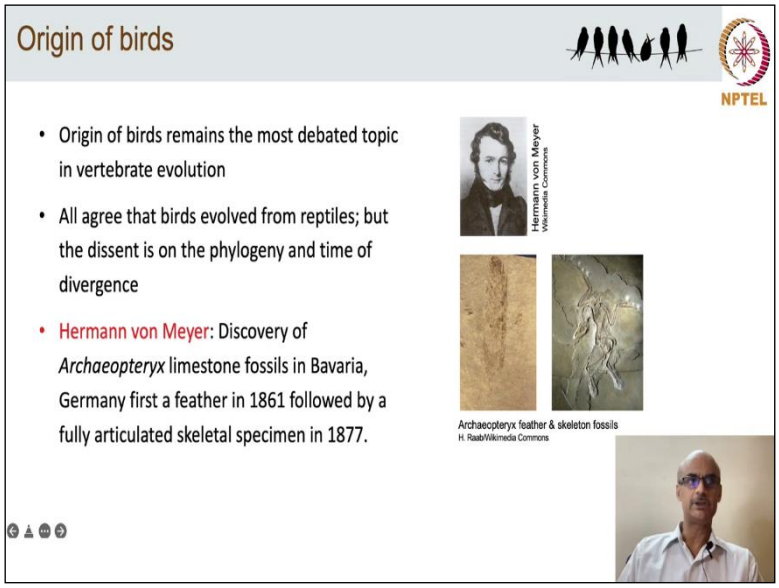

Origin of birds remains the most debated topic. We all agree in fact everyone agrees there are no two opinions about where birds evolved from. Birds evolved from reptiles. In fact, you

know, birds are often mentioned as glorified reptiles but the actual difference of opinion lies in the phylogeny and the time of divergence. So, whether the birds originated from the Theropod dinosaurs in a much later period or did they originate from the Archosaurian reptiles which are the common ancestors to both dinosaurs and birds.

That is the bone of contention between these two groups. Well, the discovery of the Archaeopteryx limestone fossils in Bavaria, Germany in late 19th century is the turning point in the history of studies on origin of birds. So, it was Hermann von Mayer who actually discovered the limestone fossils of Archaeopteryx. First, we had feather which you can see there and followed by a series of 7 to 8 series of fully articulated specific skeletal specimens in 1877.

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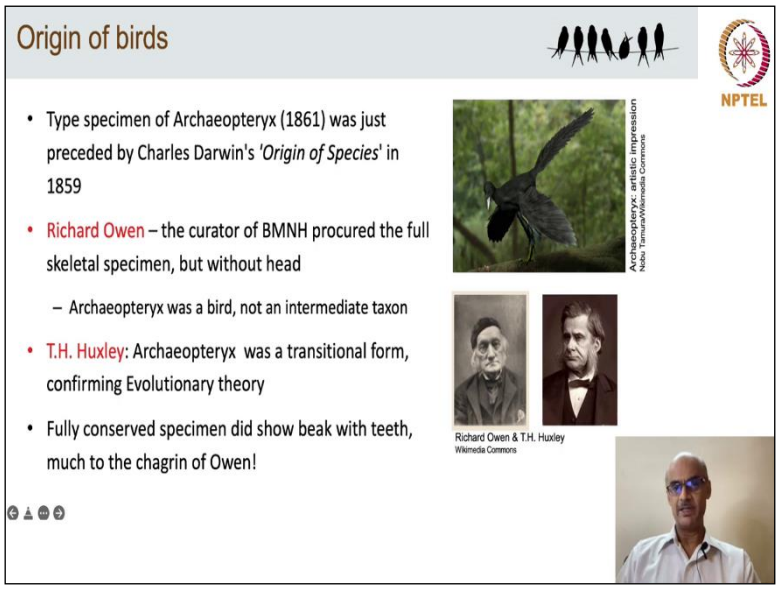

So, the type specimen of Archaeopteryx was just the time when Charles Darwin actually published the 'the origin of species' the iconic theory which put forward natural selection as the basis for the evolution of organisms in 1859. So, what you see is the artist's impression about how an Archaeopteryx would have actually looked like if it would have been alive today based on the skeletal structure and feather bearing sediments.

So, it was Richard Owen the curator of British Museum of Natural History, who procured the full skeletal specimen but without head. Richard Owen was a very legendary paleontologist and biologist and was very strongly skeptical about Charles Darwin's natural selection theory.

Owen said that archaeopteryx actually was a bird and it was not an intermediate taxon as predicted by Charles Darwin.

In fact, Darwin was actually looking for an intermediate form because he proposed that birds evolved from reptiles but the fossil evidence were not to be seen. Now, what would be the intermediate form that that would actually prove that birds did evolve from reptiles as predicted by the theory of natural selection. Thomas Huxley, often called in the history of biology as the bulldog of Charles Darwin, was a very strong supporter of Darwin.

So, he argued that Archaeopteryx was in fact a transitional form and it confirmed evolutionary theory. So, there was a kind of war of words erupted between Richard Owen and Thomas Huxley. And later specimens… because when Richard collected his fully articulated specimen, his specimen did not have the head. So, when a fully conserved specimen did emerge, it turned out that Archaeopteryx actually did have a beak with teeth. So, you know it's ancestral characteristic of the reptiles.

So, its kind of intermediate having characters which are common to both reptiles and birds. Richard Owen was apparently disappointed with the discovery that they could actually be the intermediate form confirming the Darwin's theory of natural selection.

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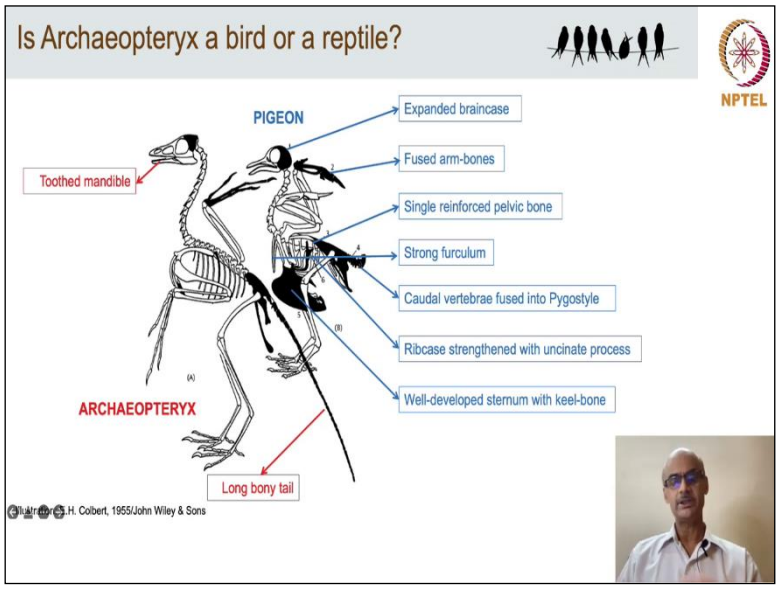

Well, is archaeopteryx a bird or a reptile? It was an intermediate form as it turns out to be; now let us see some of the key characters which are actually for Archaeopteryx. So, the reptilian

characters that you would see; what you see here on the left side is the skeleton of Archaeopteryx and on the right side is the (that of) modern pigeon. So, the reptilian characters include the toothed mandible also the long bony tail with a series of caudal vertebrae… basically elongated caudal vertebrates. but on the other hand, the modern pigeon has the expanded brain case.

That is also found in the Archaeopteryx and the fused arm-bones, single reinforced pelvic bone, and a strong furcula, caudal vertebrate fused into pygostyle that what you do not find in the Archaeopteryx but that you find in the modern birds. And rip case strengthened with the uncinate process, basically to enable the modern birds to fly. So, that you know the fly not at the cost of the body weight; it is a trade-off between the body weight and the aerodynamic lift.

And also the well developed sternum because the flight is a very energetically costly mechanism. So, these are the characteristics that the modern birds had. So, in the sense the Archaeopteryx was you know the intermediate between reptiles and birds.

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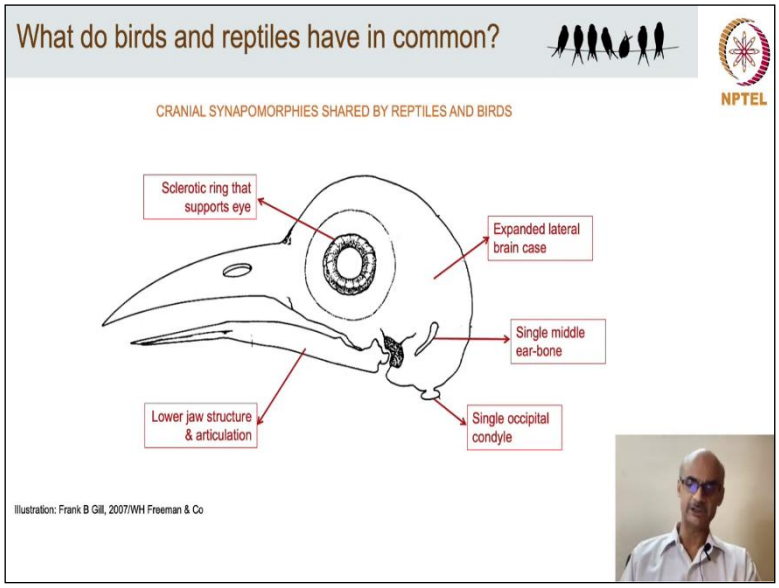

There are certain cranial synapomorphies. Synapomorphy actually means derived shared characters; basically, in phylogenetic studies its the synapomorphy versus symplesiomorphy. So, synapomorphy are the characters that actually taxonomists and biologists look for. So, what are these cranial synapomorphic characters in the cranial that along the brain case that we see in reptiles and birds.

Let us see this sketch of skull. So, you can see the sclerotic ring that supports the eye. This is a character that is both common to reptile and bird, expanded lateral brain case to accommodate a larger brain, single middle ear bone that is again common to reptiles and birds and single occipital condyle in contrast to two or three in lesser vertebrates and also the lower jaw structure and articulation; composed of multiple bones in the lower jaw. So, these are the characters which are actually not found in their ancestor of the both reptiles and birds as they share the same common ancestor but they are found in both reptiles and birds. They are derived taxa that is why we call the term as a synapomorphy.

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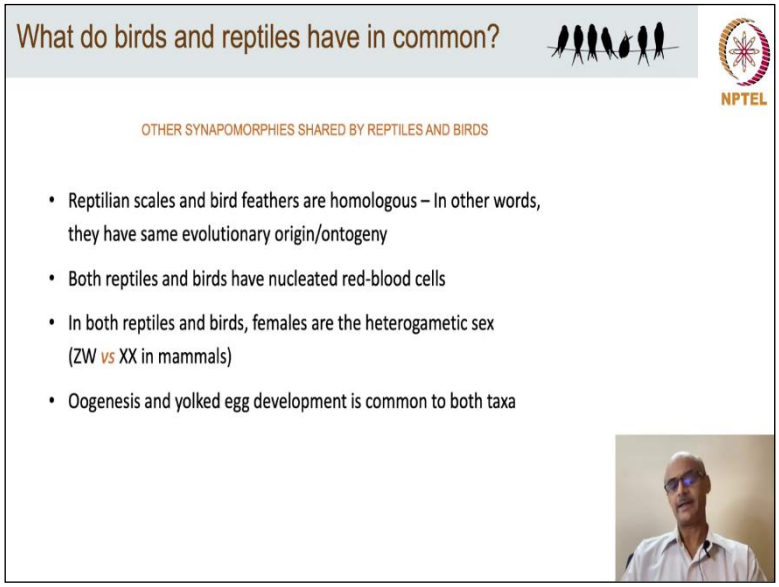

There are also other characteristics that have been common between reptiles and birds. One is that reptilian scales and bird feathers are homologous. So, in other words they have the same evolutionary pathway or ontogeny; but this is the point that is still being debated but nonetheless it is more or less it is accepted. So, both reptiles and birds have nucleated red blood cells.

So, that again differentiates them from the other vertebrates rather than the mammals. In both reptiles and birds females are the heterogametic sex. So, you know ZW. So, the females will be like ZW chromosomes; like in mammals the sex chromosomes are XX in females and XY in males but in reptiles and birds the females are ZW and the males will be WW.

It is an extremely important distinction and it has very large ramifications in population genetics. And of course, the oogenesis - the developmental ontogeny of the egg and yolked egg

development is common to both taxa. So, these are the characteristics -the key characters that are found common between birds and reptiles. Yes, these characters both cranial characters and these anatomical and hematological characters do prove that and reptiles and birds had common ancestors.

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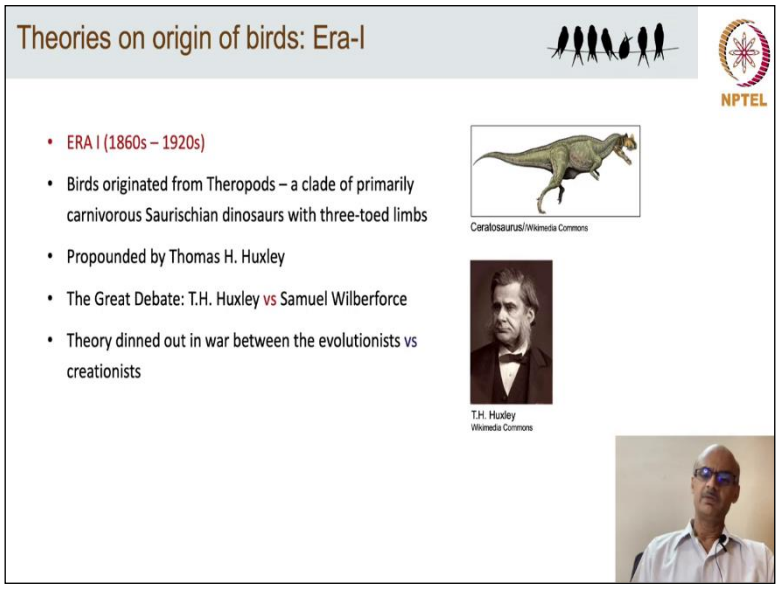

Now let us see the history of different theories on origin of birds. So, theories of origin of birds can be actually divided into three eras in the history right from the middle of the 19th century to the current era. So, the first era would actually range from late 19th century to early 20th century. So, this is the era which is dominated by Thomas Huxley the very strong supporter of Darwin's theory of natural selection.

Huxley proposed that birds originated from Theropods. So, Theropods are actually dinosaurs. So, it is a group of dinosaurs clade, of primarily carnivorous Saurischia dinosaurs; these dinosaurs have multiple lineages. So, these belong to Theropods, actually a group of Saurischia dinosaurs with three-toed limbs, all the three toes pointed forward. So, what you see here is the Ceratosaurus which is the probably the closest to the modern birds in terms of phylogeny among the dinosaurs.

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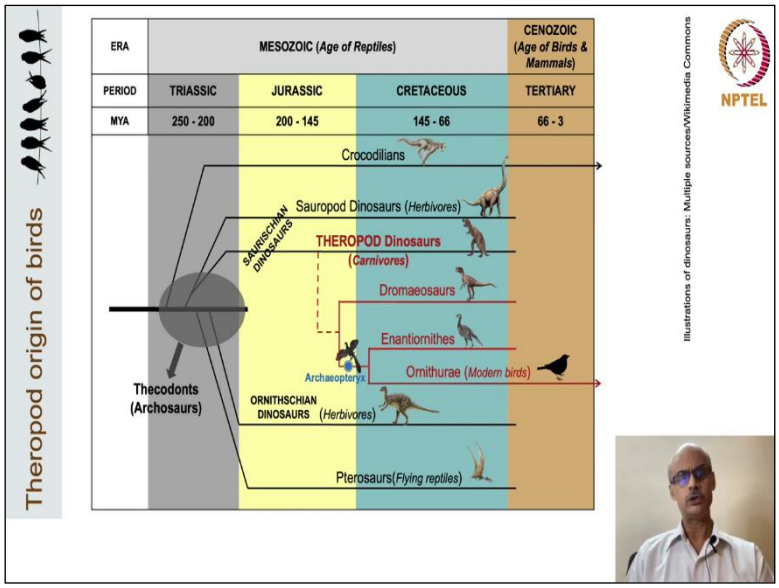

So, this is an explanatory diagram which would show the actual origin of birds along the geological time scale. The geological time scales have been divided into Eras and Periods. Mesozoic Era that is the age of reptiles and the Mesozoic era is again divided into three Periods Triassic, Jurassic and Cretaceous. So, this is millions of years ago.

For example, from 250 to 200 million years ago it is Triassic Period and from 200 to 145 million years ago is Jurassic and 145 to 65 million years ago is the Cretaceous and these three periods constitute the Mesozoic era which is generally known as the age of reptiles and also birds since they are glorified reptiles. And the Tertiary is the next one in the Cenozoic Era that is the age of modern birds and mammals that is 3 million years ago to 66 million years ago that is the Tertiary Period.

So, this is how the geological time is divided. If you look carefully along this figure, at the origin are the Thecodonts. They are the Archosaurs. Thecodonts are actually ancestors of both dinosaurs also reptiles and also the birds. From Thecodonts, originated the Crocodilians in early Triassic period; then, of course, the middle Triassic period the Sauropod dinosaurs and Theropod dinosaurs together they are called the Saurischian dinosaurs, they diverged, they originated.

And then the by middle to the later Triassic Period is the Ornithschian dinosaurs which are herbivores and also the Pterosaurs the flying reptiles. So, this is the general accepted view of the diversification of the dinosaurs. Now Thomas Huxley, he proposed the theory that Archaeopteryx and then early bird ancestors - they probably diverged from the Theropod

dinosaurs sometime in the middle of the Jurassic maybe it is around 150 to 160 million years ago. So, the Theropod dinosaurs gave way to a group of ancestral taxa which again diversified into Dromaeosaurs, Enantiornithes, Ornithurae that is the modern birds. And Archaeopteryx sometime in late Jurassic period. So, what Thomas Huxley says is that the birds actually originated from Theropod dinosaurs around the Jurassic and also early Cretaceous -for the modern birds.

This is the hypothesis which Thomas Huxley proposed by studying various fossil dinosaurs that had been obtained. And thereafter there was a big debate the great debate - if you know the history of biology you would know the great debate between Thomas Huxley and Samuel Wilberforce. Samuel Wilberforce in fact was the spokesperson for Richard Owen and also the so-called theology in the 18th and early 19th century.

So, the next 50 almost 40 to 50 years, Thomas Huxley actually spent time on arguments, counter arguments and debates with the creationists led by Samuel Wilberforce. So, the whole theory of the Theropod dinosaurs got completely buried under because of the war of words between these two over the actual theory of natural selection.

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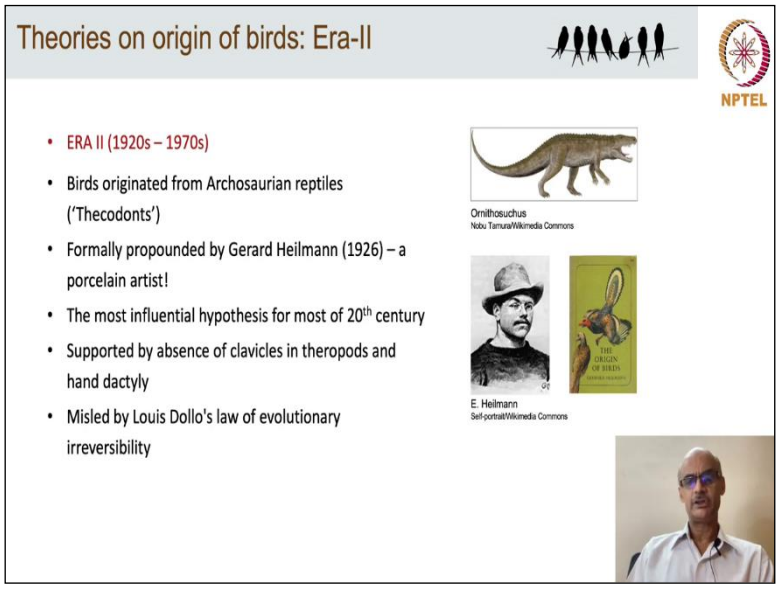

Now the second era started in 1920s after Thomas Huxley's period and in the second era the dominant hypothesis was that well the birds did not originate from the Theropod dinosaurs but they originated from Thecodonts that is much much earlier along with crocodiles and

dinosaurs; ancestors which were also ancestors for Crocodilians, dinosaurs and this. So, they are called Archosaurian reptiles.

Now this hypothesis was put forward by Gerard Heilmann; actually he was a porcelain artist but a polymath considered as one of the brilliant biologists not formally trained in biology. So, Gerard Heilmann an Austrian, he published the book on origin of birds in the early 20th century which propounded saying that the birds did not evolve from dinosaurs but from the Archosaurian reptiles along with crocodilians and the other reptiles.

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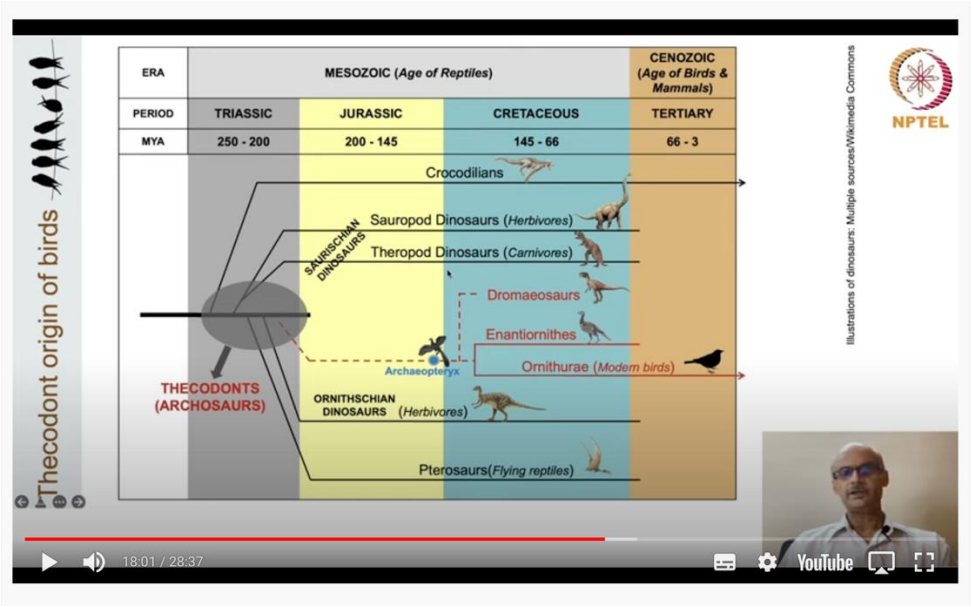

So, the same time graph, but instead of the what earlier Thomas actually said the birds originated here from late Jurassic from the Theropod dinosaurs but now Heilmann what he says is that no actually they originated not 150 million years ago but around 200 million years ago. The Archaeopteryx and other ancestral taxa for birds originated from Thecodonts what is called Archosaurs. So, the Archosaurian reptiles are called as Thecodonts.

So, the birds actually diverged from the Archosaurian reptiles in late Triassic Period almost 180 to 200 million years ago instead of 160 million years ago; he pushed the date of divergence to almost 60 to 80 million years before and also he propounded by saying that they had the common ancestors as shared with the crocodilians and dinosaurs and also the Pterosaurs and other dinosaurs.

So, this is the argument put forward by Heilmann and this turned out to be the most influential hypothesis for most part of 20th century. So, in the second era… okay, birds are not dinosaurs but they actually share their ancestor with dinosaurs and crocodilians in the Archosaurian reptiles. It was also supported… this hypothesis was supported by absence of clavicles in Theropods.

Remember Huxley said that birds diverged from theropod dinosaurs but the theropod dinosaurs did not have the clavicles. Clavicles are the shoulder bones. So, he (Heilmann) said how could the birds would have diverged from them and the clavicles were present in the Thecodonts; And also the hand dactyly basically the toe structure, which we see a little later.

One of the things which Heilman was very confident was that he was actually misled by what we call Louis Dollo's law of evolutionary irreversibility. See sometime in the middle of 20th century, Louis Dollo propounded that in an evolutionary lineage any characteristic or any trait if it disappears, once disappears cannot reappear in a line. So, once it is lost it is lost permanently. It is called law of evolutionary irreversibility.

This is the law that was strongly believed by many biologists in most part of the 20th century. And so, Gerard Heilmann went by this law and say that in the theropods, clavicles were absent in theropod. So, they cannot reappear in birds. But Thecodonts had clavicles or equivalent of clavicles. So, as per the Dollo's law it is very much likely that the Thecodonts gave birth to birds than the Theropod dinosaurs. So, that was his argument.

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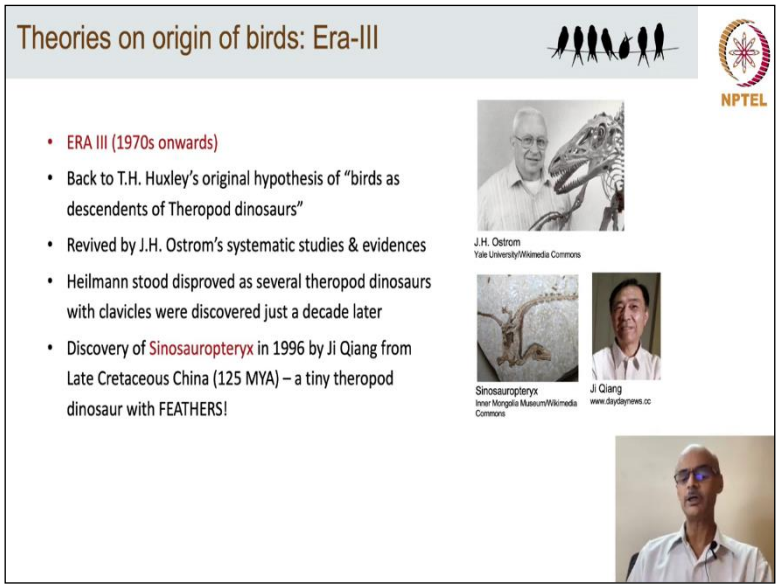

So, now the era 3 - the third era 1970s onwards. This is the very interesting thing you know; now the entire hypothesis hovered back to Huxley's original hypothesis of birds as descendants of Theropod dinosaurs. It was actually revived by John Ostrom. So, Ostrom was also not a trained biologist but he was a very well-respected paleontologist and he probably did the most extensively he did you know very systematically studied the fossils and other evidences.

And he disproved Heilmann and saying that Theropod dinosaurs actually with clavicles were discovered much later. So, probably Heilmann did not have access to them… those dinosaurs- Theropod dinosaurs. So, it is wrong to say that characters cannot re-emerge along the lineage as what believed by Louis. But Louis Dollo but also you know it is true that the Theropod dinosaurs with clavicles were found. And now the most damning evidence in support of Theropod dinosaurs theory came from China in the late Cretaceous China 1996 one most one of the most interesting fossil of Sinosauropteryx it was named was discovered by Ji Qiang and his team from China. And it was a very tiny Theropod dinosaur with feathers. So, this kind of sealed the debate in favour of the Theropod dinosaurs.

So, it clearly showed that Theropod dinosaurs - later Theropod dinosaurs with much smaller in size they had developed feathers. So, the Sinosauropteryx actually turned out to be the turning point in the study of history of origin of birds of the bird flight.

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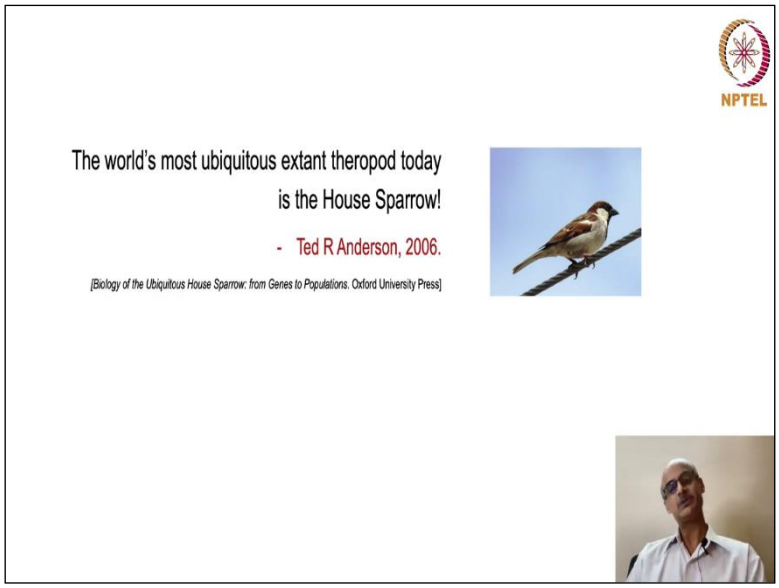

In fact, in a recent book Ted R Anderson even went on to say in his book on House Sparrow saying that the world's most ubiquitous extant Theropod today is the House Sparrow.

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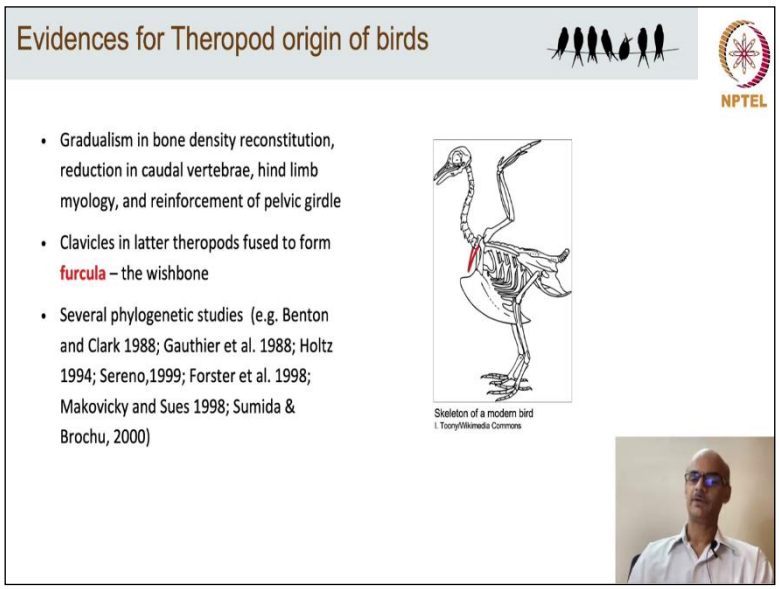

So, now what are the evidences for Theropod origin of birds put forward by theories. So, gradualism in bone density reconstitution because the bone density in birds have to be much less; but stronger and lighter bones would enable them for flight in the modern birds. Reduction in caudal vertebrae as you remember the archaeopteryx had a long tail with the caudal vertebrae, hind limb myology and also the reinforcement of the pelvic girdle.

So, the pelvic girdle got really strengthened in modern birds. These are the some of the characters that could easily we see gradualism from Theropod dinosaurs to the ancestors of the

modern birds. And even you know the later Theropods. See can you see the the red colored bone highlighted here in the skeleton of a modern bird. So, that is called a wishbone that is the furcula what we call wishbone; in chicken.

So, the furcula you know is the clavicle they are actually the ones which actually clavicles in the later Theropods fused to form the furcula. So, that is again a very strong evidence for the origin of birds from the Theropod dinosaurs. And of course, there is a series of phylogenic studies which looked at the synapomorphic characters across the range of dinosaurs fossils of dinosaurs of also the fossils of the early the modern birds in the early era.

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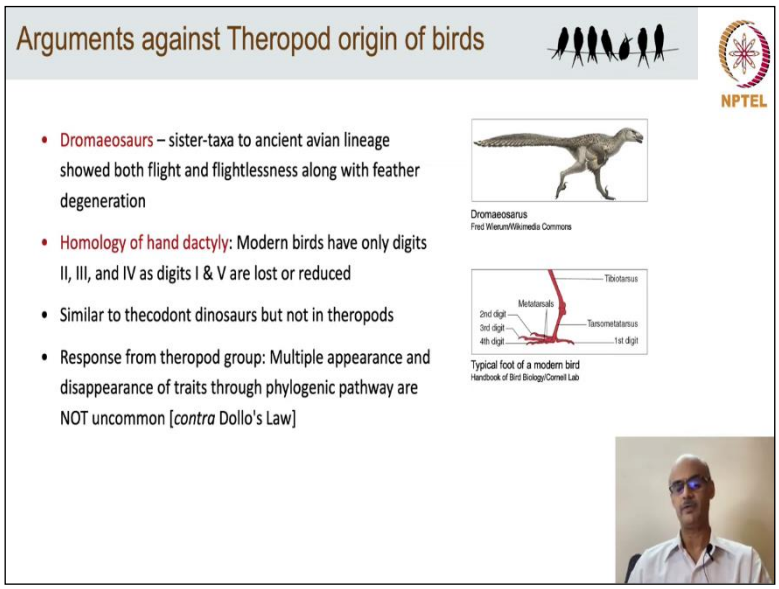

So, what are the arguments against Theropod origins? Of course, you know Heilmann and his team they first proposed saying that the birds did not originate from dinosaurs but originate from the Thecodonts that is much earlier 200 - 180 million years ago. Now, what are those evidences against the Theropod? Why birds cannot have originated from dinosaurs? One is that the Dromaeosaurs. See, Dromaeosaurs are sister taxa to the ancient avian lineage.

So, the Dromaeosaurs characteristics of Dromaeosaurs were very closely studied because they would actually tell us which are the synapomorphic characters or or symplesiomorphic characters that would be shared with the modern birds. Now the Dromaeosaurs fossils showed both flight and flightlessness along with feather degeneration. So, you know…means that the Dromaeosaurs are since they show both flight and flightlessness they may not have been the origin of the birds.

And homology of hand dactyly. So, in modern birds if you see these things in modern birds, the hind-toe is called the hallux the first digit in the passerines it is well developed, although this is one of non-passerine birds which are very short either short or sometimes even absent. But what we see very prominently is that second the inner digit that is the second digit the third digit and the fourth digit. Now modern birds have only the digits what you know conventionally speaking -two three and four and one and five- the fifth digit is lost or reduced and the first is actually reduced or lost and fifth is almost lost.

So, this is actually is very similar to the Thecodont you know but not in Theropod dinosaurs. But the response from Theropod groups - the birds are dinosaurs group, they say that the multiple appearance and disappearance of the traits through the phylogenetic pathway are not uncommon contra Dollo's law. In fact, Dollo's law now it is been increasingly disproven with findings actually contrary to what Dollo's proposed.

So, it is like BAD versus BAND. So, Birds Are Dinosaurs versus Birds Are Not Dinosaurs war. So, that war still goes on.