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I: It's been said that we are living in golden age of palaeontology as the discovery of new species continues to rise and we are meeting all kinds of new prehistoric characters thanks to science. We are learning a lot about how they lived, but one question that doesn't seem to come up very often is where dinosaurs come from and by that, we don't mean what branch of evolution they stem from, we are asking how dinosaurs had sex. Fortunately, it's a topic science writer and palaeontologist Riley Black has come across often in her work, so we caught up with Riley to find out more about what science has discovered so far about the sex lives of dinosaurs. I'm Rachel Funnel and today I will be your host. Welcome to *The Big Questions*.

So, hello Riley Black, how are you doing today?

R: I'm doing well, and yourself?

I: Yeah very good thank you. I have to say, I have been looking forward to this chat for a while because at IFL Science I cover quite a lot of the palaeontology stories and yet, in my experience, I find that the idea of how did dinosaurs make other dinosaurs doesn't really come up that much.

R: No, it really doesn't and we figured that it would be a relatively popular area of interest because this is where the rubber meets the road, so to speak, for natural selection. You know, this is how we make new dinosaurs, this is the raw stuff that evolution works with and admittedly, there is somewhat period interest of how did other animals do this? How did these gigantic, sometimes 100 foot long, 70 tonne animals make other dinosaurs. You would think it would be in every single dinosaur textbook and it's usually not.

I: Yeah, exactly. I guess I've always figured it kind of makes sense in the respect that we've got quite little in the way of soft tissue evidence, so how do we begin to try and suss out the sex life of an animal when that's the case?

R: So we have to look at what actually gets preserved in the fossil record. What are we likely to find? As much as I would love to find non-avian dinosaurs preserved in a mating position while they're copulating, that would be [unclear 0:02:18] but we have found such fossils before for things like turtles and some prehistoric sharks but never for non-avian dinosaurs so, we have to look at what areas of information can we draw from. There are actually a few. Some of them are trace fossils, so trace fossils are evidence of prehistoric behavior. Things like footprints and as I'm sure we will get into, there are some places where we have what we think are dinosaur courtship displays preserved in the fossil record because of trace fossils and we look at the anatomy of the animals themselves. The skeletal anatomy and what they're capable of, but also

sometimes soft tissue anatomy. There's at least one case of some of the relevant anatomy of dinosaurs being preserved and we can also look at the modern relatives. We have not only birds, which are living dinosaurs, but things like alligators and crocodiles and gharials, which are the nearest living cousins. So, if birds and crocodiles and their relatives have anatomy in common, it's likely that non-avian dinosaurs did as well. So we can at least narrow down the search image of what we're looking for, even if we haven't found it just yet.

I: Yeah I remember when I spoke to the team behind the *Prehistoric Planet* series and they mentioned a lot, this thing, phylogenetic bracketing is it? So, looking to the living guys to see what they're doing. You mentioned there in terms of that we may have found some of the soft tissue of genitalia, is that right? So, do we have a couple of dinosaur genitalia specimens?

R: So far as I know, there's just the one described so far. So it's a specimen of a little horned dinosaur called *Psittacosaurus*. If you imagined a reptilian parrot, which is a little bit redundant, but still if you imagine a more reptilian parrot, that's more or less what they were like and this particular specimen has extensive soft tissue preservation including the cloaca and this is something that has been hypothesized for a long time because crocodiles and alligators have a cloaca, birds do as well. It's a single outside opening where various tracts of the body, reproductive tracts, respiratory tract, urinary tract, they all empty out into. Basically, it's Latin for sewer which gives you an idea of what early man thought of this anatomy but it's almost certain that non-avian dinosaurs had the same kind of anatomy that any genitals would be held behind that cloaca and this particular specimen is a confirmation. In terms of that part of our inference we were correct. Unfortunately, there is not much preserved beyond it, we're just getting the outside view but at least there is something that gives us sort of some expectations about if we are to find additional soft tissue anatomy in non-avian dinosaurs, what that's going to look like, and we can look to alligators and crocs and some birds like ostriches and waterfowl and things like that to get an idea of what dinosaur genital anatomy was like.

I: Weirdly enough, actually it was only a couple of days ago I was writing about the alligator penis and it brought to my attention that for a lot of these animals, they can look very similar on the outside, as in the cloaca kind of looks the same between males and females, is that right?

R: That's right. Even the genitals themselves, we are a more dimorphic species when it comes to genital anatomy for the most part, but for alligators and crocodiles, female alligators and crocs, they have a large clitoris which is actually very hard to distinguish from a phallus amongst the males. You have to be an expert to do this. There was actually a guide, I think I found online, that's how the experts do so which I can only imagine what that's like as part of your job description and that this is [unclear 0:05:58] that you really do need an up-close look at that anatomy to be able to tell. So, it's likely that non-avian dinosaurs had reproductive anatomy that was much more like alligators and crocs. We know that many modern birds, especially songbirds, are able to pass sperm through a cloacal kiss and that's something that does not involved any kind of what we would call intermittent organ in the jargon. But that's what we called derived feature. That's something that evolved over the evolution of birds and it was something that happened, likely sometime in the Cenozoic, likely after the mass extinction that

ended the Cretaceous. So if we're looking at models for non-avian dinosaur anatomy, the way that alligators and crocs are set out as well as some of what we may think of as the more archaic birds, the birds that are at the base of the family tree, that's our best guide for what an animal like a *Stegosaurus* or an *Allosaurus* might have had.

I: So, in that respect then, in terms of the most likely mode of fertilisation, does that mean that we reckon for dinosaurs it probably was an internal situation?

R: Yeah it probably was some form of penetrative sex. If you think about… if you were to go back to the late Triassic and you're about to see two *Apatosaurus* mate you wouldn't really see anything external in the lead up to this, you would just see their cloaca on the outside and then likely as mating was to happen, you would see the phallus on the male animal. It's unlikely that you would see the clitoris on the female one, but that's likely some form of penetrative sex that, like, was the way the dinosaurs reproduced.

I: Okay. I know you mentioned we are looking to crocodiles and birds but with that, are there any specific analogs that we might look more closely at to try and work out how the mechanics of dinosaur sex could have gone down?

R: I think our best models are probably amongst the alligators and crocodiles for two reasons. One is the tail, in that birds do not have long, bony tails and alligators and crocs do and the tails actually are a major impediment that you need to get around in being able to mate. Fortunately for alligators and crocs, they live in these aquatic environments, the mating usually takes place in the water, they're able to use almost zero gravity nature of being buoyant in the water to get around some of this. The other is that birds are dinosaurs but they are relatively derived dinosaurs, they've become specialized in a number of ways whereas alligators and crocs, even though they're specialized in the semi-aquatic habitats, their anatomy seems much more conserved. There's a lot more ancient parts. So, it's more likely that non-avian dinosaurs are going to be alligator- and croc-like but I do want to stress this is, imagine that we were surviving non-avian dinosaurs and having this discussion and mammals have gone entirely extinct and we're saying, what was mammal sex like? You know, what kind of sex do mammals have and we know it would be quite different with all sorts of specializations. So, we're talking about an entire group of animals, so there is no single modern animal that's going to explain it for the width and breadth of Dinosauria, but the base model was probably a lot more like what you would see on a saltwater crocodile than on something like a [unclear 0:09:26].

I: Okay great. I remember I was reading one of your articles about the anatomy of dinosaur sex the other day and I loved a bit you had in it about invariably, when you start having these discussions, its not long before people are wondering about the penis. The possibility of the dinosaur penis. So, based on what you were saying there in terms of the analogs, because I know famously within birds there are some pretty crazy designs out there. Do we have any idea of what possibly this appendage might have looked like?

R: We don't really know for sure and it likely varied quite a bit, especially when you think about dinosaurs like our armoured dinosaurs, the thyreophorans, things like *Stegosaurus* and *Hylaeosaurus*. They are absolutely covered in plates and spikes and body armor, over their hips and the length of their tail. How they were able to copulate is something of a mystery. I joke

about this in one of my books, try and take models and okay, how would this actually work? It's likely that they might have had longer intermittent organs and being able to mate, they would have certainly circumvented some of those problems but, you know, nature as we know is ever inventive so we could be entirely wrong about this as well. It's easy to look at some of these larger dinosaurs, some of these dinosaurs that might have less flexibility in their tails and their hips and suggest that they might have had, you know, more length to bridge the gap, but we can't entirely be sure. I do want to stress, this is kind of funny, this is sexism and science right? So, everybody is obsessed with the dinosaur penis and it's easy to make boner jokes and things like that but if dinosaurs are anything like, you know, alligators and crocs as we expect them to be, females also had a prominent clitoris and we know this from studies of modern reptiles that the role of the clitoris in reproduction and mating has been historically overlooked. It was really only in the last year that we can confirmed anatomically that snakes have hemiclitoris, so female snakes have a pair of them and that it is important to their mating rituals and how they copulate. So, as much as we often think about the function of dinosaur sex it's important to remember that sex, even amongst these animals, was not solely for reproduction and it was not simply a matter of bridging the anatomical gap. There are other aspects of this in all sexes of the species that's going to be relevant to how they court each other and how they mate.

I: **Yeah, that's such an interesting idea. I certainly remember when I was growing up, you learn about the reproductive anatomy, that's all it's there for and you're right, to find out all the different ways in which the sexual organs have evolved, not just for the purpose of creating another animal but to get some sensation out of it and things like that. In terms of the possibilities of dinosaur genitalia, how do we think that dinosaur sex might have unfolded when it comes to things like distance and whether it was a brief or a drawn-out encounter?**

R: [unclear 0:12:38] dinosaurs were anything like their modern relatives, there will probably be some sort of prolonged courtship, not necessarily over days or months but some sort of ritual involved and I'm sure we will get to that in a moment. In terms of the act of mating itself, the dinosaurs would have to get pretty close to each other. They would have to make relatively close contact and this is something that we see amongst alligators and crocs and certainly amongst birds. So, no matter how long the intermittent organ is, the male dinosaur would have to get basically right up on top of the female dinosaur in order to fertilize. This is something that was probably relatively awkward, it might have been uncomfortable, it probably would have involved a lot of bracing. Just imagine the weight of these animals. You know, for some of them they are tens of tonnes and I sometimes wonder about them skeletally, it doesn't seem to be the case but I almost wonder if some females dinosaurs would see sort of more bone strength, their sort of anatomical [unclear 0:13:41] to bear that weight and the fact that we're not seeing that might be a clue that dinosaurs were doing something unique. So, as best we can imagine, there is actually a paper that came out about this more than a decade ago but they had an artist draw their best conceptions of how different dinosaurs species would pair with each other. I imagine it would almost be easier amongst the quadrupedal species because at least they have those front legs to brace and kind of work it out a little bit. If you're a bipedal species and especially if you're the one clambering on top, you know, being able to balance on one leg with that tail and not fall over and break anything potentially would have been a little

bit tricky. So, certainly it would have been fascinating and probably hilarious if someone was to watch these dinosaurs fumble their way through this. There is probably no non awkward way for non-avian dinosaurs to mate.

I: In terms of that, do you have one in particular that you look at it's size and the shape of it and just think, how on earth could that ever have worked?

R: There is a particular dinosaur, it's a particular Stegosaur that I don't understand how these animals managed to reproduce. Its name is *Kentrosaurus*, it comes from Tanzania and it is a relative of the more famous *Stegosaurus* from the Western US and rather than plates all the way down its back, the plates go from the base of the neck to the shoulders and then they turn into spikes and this had spikes on its shoulders, it had spikes, these paired long spikes running down its back all the way to the tip of its tail and where the tail moving out of the way is so crucial, unless both of these dinosaurs are laying on the ground and going belly to belly, or the male is sideways or the female perhaps, or something like that, like it would have had quite a bit of creativity in terms of the positioning. So, in terms of what dinosaur sex positions were, I feel like specifically the more spiky Stegosaurs would have had to have been the most creative out of all of them.

I: I totally agree. When you're describing it the other thing I was thinking is that I suppose this would be a pretty vulnerable moment as well, right? Like, you don't want to be halfway through getting there and then someone else comes along that you've got to worry about.

R: Absolutely. There likely was forms of mate competition amongst dinosaurs. A lot of elaborate dinosaur traits we know are social signals. They could be used for defense but more often were more important to communication within the species, whether that was fighting like we have in *Triceratops* where we know that *Triceratops* were locking horns with each other and pushing back and forth, or the elaborateness of a lot of these armored dinosaurs, like yeah we call them armored but the fact that their ornamentation is so different suggests that there wasn't one ideal way to defend themselves, but rather that there is some sort of social selection going on, whether to distinguish the species or being attractive to mates of that species or what have you. So, we can pick up some of the barest hint of some of these social systems and in the moment of mating, yeah, you won't only have to potentially another dinosaur interrupting but predation as well, we know that non-avian dinosaurs starting reproducing before they hit skeletal maturity, before they hit adult size. They're actually kind of like us, they start being sexually active in their puberty before they are fully grown. So, if you are a relatively young dinosaur and you're in this moment and predators are stalking the landscape and you are basically otherwise occupied for a little while, that could be a very vulnerable moment in terms of looking out for carnivores or other potential dangers. This was something that likely required a fair bit of attention from these animals and I'm sure there are all sorts of moments throughout their millions of years of history where the intent to mate didn't turn out quite as the dinosaurs expected.

I: Sounds like a nightmare. You mentioned the ornamentation there and social selection and I think you said earlier possibly about… because we see in a lot of crocodilians

mating signals and almost rituals, like behaviors that come before, so do we think that may have been the case for dinosaurs also?

R: So, most of this conversation is hypotheticals right, this is one case where we can say yes, that we are certain that at least some dinosaurs had some kind of courtship ritual. For alligators and crocs it's absolutely beautiful when you see it. The males in particular, when they are courting females they will lay in the water at almost this 45-degree angle and they will rumble and make these deep bellowing calls and the water will dance on their back, they will kind of shake. Even though we can't tell whether non-avian dinosaurs did exactly something like that, looking at birds and the way that they court, there are a number of bird species that scratch on the ground as part of their courtship, that they will form these [unclear 0:18:53] where they are showing off in different spaces. There are track sites, one of which is in Colorado, there are a few more scattered around the planet, where you find huge scratch marks in the ground that looks like, basically, Godzilla chickens must have lived here and were on their own spot scratching at the ground with these three-toed feet and these were made by theropod dinosaurs, these were made by dinosaurs that were probably something like *Allosaurus*, even though they are a bit later in time but it's a decent image of what this animal probably looked like. So, we have a sense that, at least for some of these dinosaur species, they were coming together in groups and they were showing off and advertising themselves as part of courtship. That's not only the behaviour but that's a whole mating system in terms of if we could determine what sex or sexes were displaying in this way then we can look at, okay who is doing the selecting of mates? How does that affect the way the evolution of the species unfolds? So, it's actually pretty wonderful that we have this [unclear 0:19:59] trace fossil record is really our best chance to find more of these behaviors. I know an Ichnologist, Tony Martin, has written about the subject as well, saying it wouldn't be impossible to find the awkward steps of two dinosaurs courting and then going into a mating embrace, you may see a foot come off the ground or something like that because this is fossilized behavior. So, these are relatively recent finds, within the last 10 years or so but at least it reminds us that they are out there and if we know what we are looking for, we might potentially find more of these courtship traces that dinosaurs were making, if they had these elaborate mating rituals.

I: I think that's such a lovely idea because so often, dinosaurs are painted as these aggressive, meat-eating killing machines, but they were just animals. They were out there doing all these behaviours that had nothing to do with fearsome hunting and things like that. The thought of a Theropod putting on a display hoping that it gets picked is a very sweet one.

R: It's very relatable. As an awkward teen myself, I find the idea that they were probably the nerd dinosaurs that were trying very hard, very empathic across time.

I: The one at the [unclear 0:21:14] that just didn't get chosen.

R: Yes.

I: This is a slight segway but, Ichnology, is that the right word for these trace evidence?

R: Yes.

I: I know that they exist. I've always wondered how is it that something like a scratch mark can be preserved for such a long time?

R: If you think about any time that you've walked along the shore, the edge of a lake or a stream somewhere muddy, on the beach and you're leaving footprints behind you. We often think of those things as very ephemeral and in a sense they are, but water isn't always covering over everything and washing everything away. Let's say you walk along a muddy area, alongside a stream and that area remains exposed and in the sun that mud dries and it holds it's shape. It maintains, not just the shape of your foot but also the pressure underneath housed to form the sediment below and then when the rain comes back it washes new sediment on top of that dried cast of your foot and it hardens. Millions and millions of years later, through being pressed into the earth and coming back up again and becoming exposed, you'd wind up with a part and a counterpart, so you basically would wind up with the mold and a cast, much like you might make with plaster of Paris and it's more or less the same concept, that we think of footprints as things that don't last very long but as someone even looking for dinosaurs, walking around the desert I can find footprints from people who passed the same way years before. They might not always be the highest resolution but in the right situation and the right circumstances where you have a wet sediment that's able to take the shape of the foot, that becomes dried out then covered over, you're basically recreating a mold and cast naturally and that's how so many of these traces become preserved. So it's really remarkable that they can be preserved at all, that all these moments where these things would otherwise be eroded away would just disappear. Most of the time that's what happens, but it's the same thing as fossil bones. We think of bones and things as sturdy but they still require relatively rapid burial, they still need to be protected within the sediment to be preserved and the same principles are at play with Ichnology as well.

I: That's amazing. It really ties into the way that I've always seen Palaeontology as like, feels like a form of detective work doesn't it. You're going around picking up the clues, trying to piece everything together, it's stunning to hear about. Hopefully one day we will stumble across these fumbling footsteps of two mating dinosaurs. I figure we're probably getting back into hypothetical territory here but do we have any knowledge of how, once they've had a successful reproductive event, the dinosaurs are likely to have long gestational periods or would it have been a short thing and would [voice tapers off]

R: So, you're absolutely right that this is getting back into hypothetical and gleaning from modern animals. We know that all non-avian dinosaurs laid eggs, partially because all birds lay eggs and we've only found eggs from non-avian dinosaurs. We have never found an embryo without an egg, inside the body of a mother dinosaur. It's potential that some species could have done that, you know, reptiles have certainly done this over and over again through their history, but so far as we presently know all non-avian dinosaurs laid eggs and it seems that from a few specimens that we have of the Oviraptors, so these parrot-like dinosaurs that we often find in the Northern Hemisphere in the Cretaceous, they're able to produce two eggs at a time and that's why we look at some of their nests, you see pairs of two eggs arrayed around each other in a ring and that was likely the default for dinosaurs. So, in terms of how long it went from fertilization to egg laying it was probably relatively brief. I am not aware of any way that we could possibly know whether dinosaurs were able to store sperm for later or hold on to

eggs for a more proper season, it was probably relatively direct and it was likely involved seasonal mating, like you don't want to keep copulating when you've already had fertilization for your eggs and now you go about the business of nest building and for some species, protecting those eggs for some species like the Sauropods, like the big long-necked dinosaurs we're pretty confident that they had a lay 'em and leave 'em kind of behavior, much like modern day sea turtles. They'd make a nest, dump all these eggs in them, walk away and the environment would just be flooded with baby Sauropods and it was really a statistics game at that point in terms of survival. So, if we look at modern egg-laying animals, you know, modern relatives it probably resembled a lot of those patterns where shortly after fertilization you have egg-laying and nest building and from there it's a matter of whether they took care of their offspring or not and that seemed to be relatively variable.

I: Fantastic. It's a wonderful idea to think of the statistics [unclear 0:26:18] when you have all these babies running around. Finally, just in terms of the mechanics of mating, you mentioned that we've got that one cloaca that we can look to but are there any other ways of sexing a dinosaur that don't require soft tissue?

R: Palaeontologists have been thinking about sexual dimorphism in dinosaurs and how you would distinguish between different dinosaur sexes for decades at this point. In the past, sometimes it's been done with looking at skulls and saying these skulls seem to be of different shapes, are they different sexes? Are they different species? Usually it turns out to be different species. I know some researchers have looked to ornamentation or even the thickness of certain bones and it's often difficult because unlike modern animals, we can't get a good population sample for most dinosaur species and that's really what we would need. We would need a variety of animals from the same place and the same time in order to have a look, like, do we have the bimodal distribution that we would expect or multiple peaks on this graph for different dinosaur sexes and most of the time, even when we get a large accumulation of dinosaurs in one place, like, in Central Utah we have a place called Cleveland Lloyd Dinosaur Quarry where hundreds of *Allosaurus* have been preserved. It's likely that they were gathering for [unclear 0:27:45] or something related to mating, so we're already on the right track but how do we distinguish the sexes. The bones are jumbled and are laid down over multiple seasons, over multiple years, so we're not looking at a single population of animals, we're looking at different generations potentially in the same place. Dinosaurs are continuing to evolve so you always have to ask yourself is what I'm seeing evolution or species diversity or is it dinosaur sexes? There is one way that we can identify egg-laying female dinosaurs and that's something called a medullary bone. So we know modern birds formed this peculiar bone tissue when they're laying eggs, it's basically like a calcium store, so it's a way of mobilizing the calcium that's in the skeleton into a form that then can be used for egg-laying. That can at least identify a few female dinosaurs that were in the process of laying their eggs or just about to and we found this for *T. rex* and *Allosaurus* and a dinosaur called *Tenontosaurus* but there haven't really been other examples that have come up just yet. Then again just because a dinosaur doesn't have this tissue, does not automatically mean that it's a male dinosaur or a different sex. It just means that they weren't laying eggs at that time. As far as the skeletal anatomy goes, so far nobody has been able to conclusively identify a difference between dinosaur sexes, that they seem, oddly, very skeletally monotypic. Males, females, any other dinosaur sexes seem like that

they are pretty much the same so far as we have been able to detect so far, so it might have been that most of their dimorphism, most of their variety in terms of sexual signaling to each other might have been the soft tissues. It might have been in colour or feather patterns or things like that. We see this amongst some prehistoric birds. There is a Cretaceous bird called *Confuciusornis* that some specimens have these long streamer-like feathers coming off their tails and some do not and because we have a few examples of the unornamented birds with medullary tissue, we're pretty sure that the unornamented ones are females and the ornamented ones are males and that fits in with a lot of modern bird species. So, that difference between birds where sometimes the male birds are flashier than the females goes back into the Cretaceous. So a lot of what we see in birds might be [unclear 0:30:06] what we could be looking for, for dinosaurs but it's not necessarily one to one. I'm sure some day we're going to figure something out in terms of understanding why we're not seeing the anatomical variety between the sexes or what might explain the fact that they are so similar. We're finding new things all the time and I think the fact that we can tell the colors, even in some dinosaurs now, is a good reminder to never say never when it comes to the fossil record. The things that I was told that we would never know, when I was a young dinosaur fan, we are now starting to understand. So, I'm really hoping if we keep looking and keep searching all those rocks out there, many of which we haven't even looked at yet, that there are some clues in there that's going to better inform the sex lives of the dinosaurs.

I: You're right, there's a lot that we don't know but it's incredible the things that we do. In terms of going out and looking at those rocks, do you have any exciting projects in the pipeline you could tell us about?

R: Every summer I go out with different field and university crews to look for new fossils and one of the places that I return to, just about every summer is Cleveland Lloyd Dinosaur Quarry in Central Utah, and this is a spot where we have a minimum of 48 *Allosaurus* in one place. It's likely hundreds more that minimum number just comes off left thigh bones, so we know we have that many left thigh bones, but many more parts of *Allosaurus* of all different ages and eggs have been found there before and we know that they're *Allosaurus* eggs. I keep going out there every year hoping to find a nesting site or something that's relevant that puts that quarry in context, because there are bones all throughout that area. We have found other fossil sites and track sites there. So, of any place that I can think of where we're likely to find some kind of clue to the courtship and mating of these dinosaurs, it's probably there. So, I'm excited to get back out there and look at the rocks and, you know, I wish I could zoom right to it. I wish I could tell just looking at a map and say, it's got to be there. Really, you just get out there and you walk and you hike in the heat and you hope that you strike it lucky. You hope that you find something that no one has ever seen before. So, the fingers are crossed for this summer that this will be the year that I find that nest site that gives us a little bit more context for what was happening there.

I: You know that all of our fingers will be crossed too. I can't wait to see what you find. Is there a place where people can follow along if they want to see what you're up to?

R: Yes. So, I'm active on both Instagram, the handle restingdinoface and it's the same on Bluesky as well, restingdinoface.bluesky.social and those are the two main places where I do most of my updates from the field.

I: Excellent handle, by the way.

R: Thank you.

I: Riley Black, thank you so much for that deep dive into what we know so far about the sex lives of dinosaurs, it's been absolutely fascinating and I'm really excited to see what you discover next.

R: Absolutely, my pleasure. Thank you so much.

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