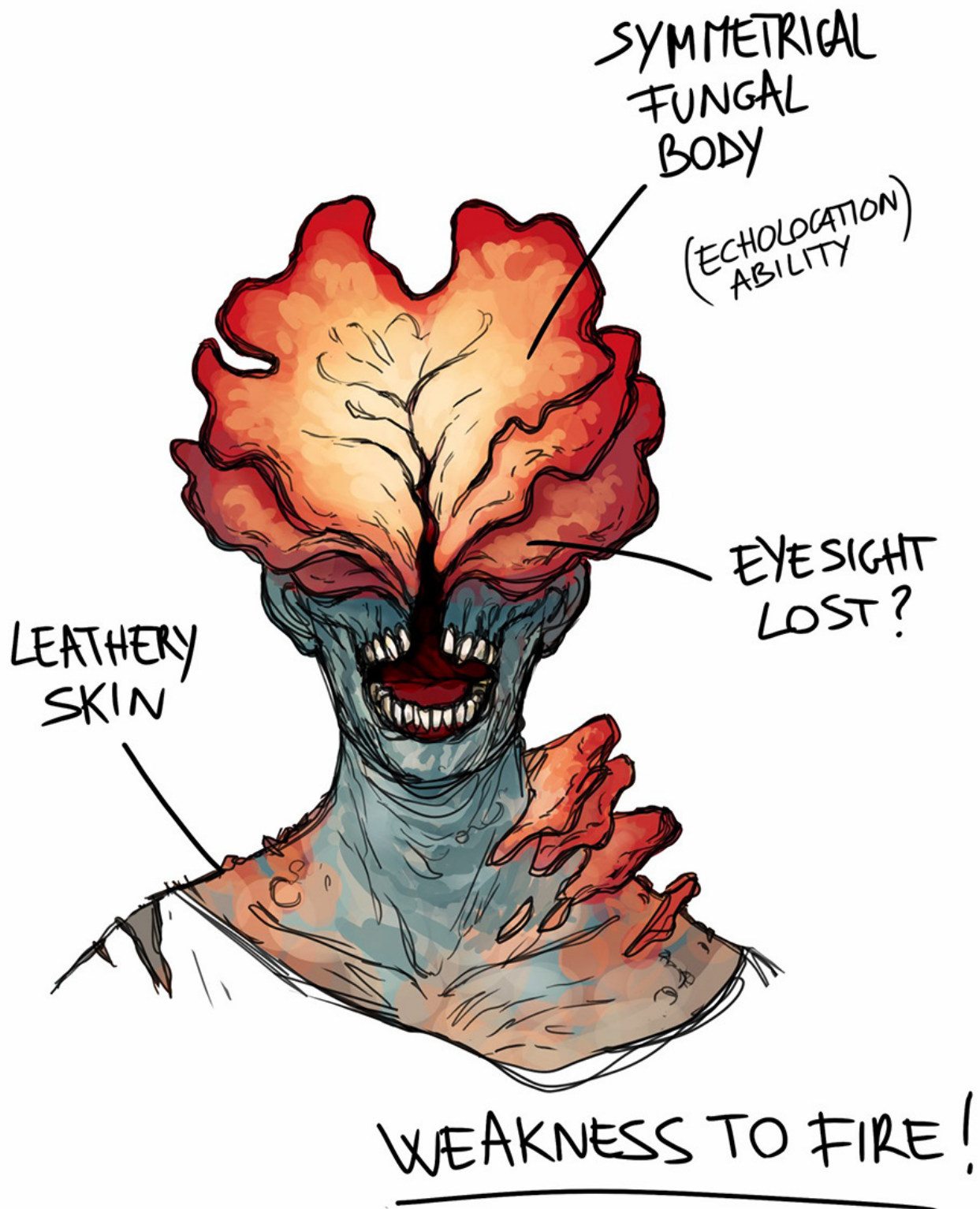


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Cover art: Sketch of a clicker, showing important features of this kind of infected (artwork by: Flavia Strani).



Morphological and behavioural aspects of the infected in *The Last of Us*: a natural science look at a videogame fungus-human parasitoid interaction

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Starting in 2013 and recently back to hit the headlines with the sequel, *The Last of Us* (TLoU, herein referring to either the franchise as a whole or the first game in the series) is one of the leading franchises created by the software house Naughty Dog. This award-winning series of horror-themed action-adventure games takes place in a dystopic future where civilization collapsed due to an emergent disease caused by a parasitoid fungus that transforms humans into violent zombie- or better ghoulish-like creatures (Fig. 1).

The disease was called *Cordyceps* Brain Infection (CBI), and is reported as originating from a new species of the genus *Cordyceps* that evolved to infect humans instead of arthropods, as usual for these parasitoid fungi (see medical pamphlet published by the Center of Disease Control found in the outskirts of Boston in TLoU). While some information on the CBI were already given within the games, that was mainly resulting from studying the disease and its effects under a medical point of view. Less attention was given to the fungal infection under its biological and evolutionary aspects (somehow understandably given that most of the knowledge was gathered under emergency conditions and trying to oppose a pandemic of unprecedented violence).

We explore here the CBI-infected using a natural science approach, with special focus

on their morphological and especially ethological or behavioural features. Our main aim is to shed some light on the possible functional and evolutionary significance of those features.

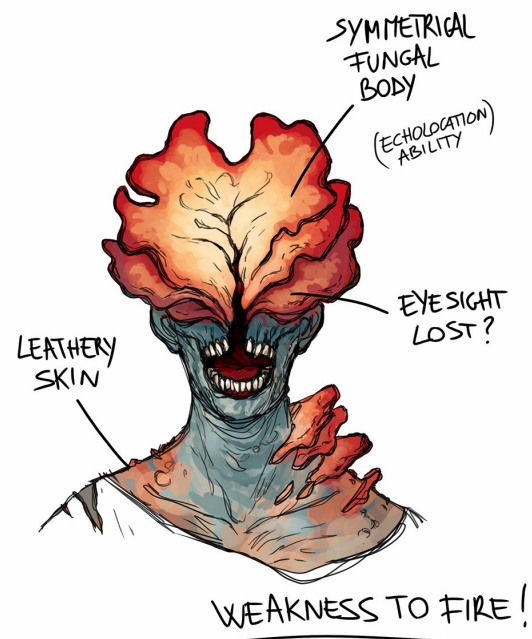


Figure 1. Sketch of a clicker, showing important features of this kind of infected. Artwork by Flavia Strani, used with permission.

METHODOLOGY

The main source of the morphological data presented herein are the 3D models of the CBI infected available as additional con-

tent in *The Last of Us Part II* (TLoU2). Information of the ethology of the infected was observational data retrieved from encounters in both TLoU and TLoU2. The Last of Us Wiki on Fandom (https://thelastofus.fandom.com/it/wiki/The_Last_of_Us_Wiki) was used as a supplementary source of information.

In this article, we take the stance of researchers analysing the infected as if we were in the reality of TLoU, taking the game's world at face value. We draw parallels with real-world species and phenomena to enrich our explanations and explore the possibilities of that fictional world.

RESULTS

Six different types of infected are currently known. They represent successive stages of the infection, except for shamblers that might be an alternative stage to bloaters (possibly related to a more humid environment; see the Shambler Note in TLoU2, but also Turi, 2019) and the Rat King, whose real nature is still not clear. The fungus growth seems to give increased strength and physical resistance to the host with the progression of the infection.

Runners

Runners (Fig. 2A) are the simplest kind of infected, representing the first stage of the CBI. They still have a generally human aspect, with few appreciable changes. Lesions are usually present on the body, but it is not always clear whether these may be due to the fungus or just the accidental results of a lower self-care of the host. Hyphae are visible through the skin. Very dark blood (or another kind of fluid) pours out from head orifices. The eyes are strongly reddened and the dermis has a more or less vaguely ashy colour. They are still capable of both hearing and seeing. Behavioural features include relatively fluid movements, vocalizations (mainly screams and moans), and capacity of walking large distances. They form hordes and are found in both indoor

and outdoor environments.

Stalkers

The looks of these infected is still vaguely human (Fig. 2B), but with a more decomposed appearance: e.g., more lacerated skin, unhealthier colour. This is likely due to the longer time elapsed since the infection. Hyphae are starting to come out from the host body. The exposed hyphae are mainly located in the upper part of the body: the head, where the most mature fungi are, and also the shoulders. Leathery areas of the skin start to appear in sparse parts of the body. The behaviour includes relatively fluid movements and hiding/ambush habits. They still react to both auditory and visual stimuli, and are also capable of rudimentary echolocation. They are usually encountered in small groups, but it is not known if they may also form hordes. They are mostly found indoors, but sometimes out in the open as well, in particular at night or in darker areas.

Clickers

Clickers (Figs. 1, 2C) are still human-like in body shape, but their skin is now completely leathery. Real hyphae are not visible anymore on the body, but the body is overall bulging. Like the hyphae in other infected, these bulges are also more concentrated in the upper part of the trunk. The skull is broken by a large fungal body coming out to cover the entire upper part of the face. This fungal body has an almost symmetrical shape, with two lobes flanking a sort of median vertical opening through which the clicker takes advantage of its echolocation abilities. The broken head and the fungal body covering the face prevent clickers from seeing, even though functional eyes may still be present in at least some of them (as it seems to be testified by their reaction to visual stimuli when the fungal body is damaged or artificially removed). In any case, they react to auditory stimuli and are able to echolocate. Their movements are less fluid than that of runners and stalkers,



Figure 2. Infected from TLoU at different stages (not to scale): A) runner; B) stalker; C) clicker; D) shambler; E) bloater. Images taken from the additional content section of TLoU2.

with twitchy movements particularly while walking. They can be found in small groups, both indoors and outdoors, but they also aggregate in hordes.

Shamblers

Shamblers (Fig. 2D) have a human-like aspect, but a leathery skin and a swollen physique. They are larger than other infected, but not as large as bloaters. Subcutaneous hyphae are vaguely visible here and there, especially on the head. Fungal bodies similar to arboreal fungi are present on the arms, legs, and part of the trunk, distributed principally on the posterolateral sides.

Rounded pomegranate-like structures filled with corrosive ichor and gas accumulate between the shoulders and the head, without covering the face. Shamblers can detach and throw these rounded structures, which explode upon contact, releasing their content. The facial area is usually broken or damaged, but not in the same way as the clickers (i.e., there is no emerging fungal body). Eyes are still present and functional. Shamblers are slow, but they do not show the same twitchy moves as clickers do. They can chase efficiently with rather rapid runs. These infected are apparently restricted to small delimited areas, and it seems that they do not gather in hordes. They are usually encountered in very small groups of



Figure 3. The Rat King from TLoU2 in anterior (A) and posterior (B) views. Images taken from the additional content section of TLoU2.

one or two individuals, together with other kinds of infected.

Bloaters

These infected (Fig. 2E) are larger than shamblers. They have a swollen humanoid appearance, with their skin completely covered by different kinds of fungal structures: filiform hyphae, rounded structures (similar to those of the shamblers, but located instead on their limbs and trunk), bulges, and more elongated structures. The skull is broken and almost completely obscured by an emerging fungal body, as in clickers. There are no visible eyes anymore, thus suggesting hearing/echolocation-mediated sensorial activity. Echolocation in bloaters is indeed well developed. Like shamblers, they can throw the rounded structures present on their body. They are generally found alone or with few infected of other kinds, in closed places. They do not form hordes.

Rat King

This is a very peculiar infected (Fig. 3), currently only known from a single individual in the depths of the hospital in Seattle

(the quarantine area). Because of this, it is possible that this is not a real stage of the infection, but rather the outcome of a random event that was made possible by the conditions present in that location (i.e., numerous infected stored together in the same closed space for a long amount of time). The Rat King is very large, with an overall deformed humanoid aspect. It apparently results from the merging of numerous infected from which it takes, without a real regular pattern, the main features. Its components include a bloater, at least one stalker (Fig. 4), and various clickers. The bloater and the stalker, at least, are still able to act independently.



Figure 4. Stalker separated from the Rat King, showing features usually not present in the other stalkers. Image taken from the additional content section of TLoU2.

DISCUSSION

The modified behaviour of the host is part of the extended phenotype of a parasite (Andersen et al., 2009), thus having evolutionary significance for the latter. In the so-called “zombie ants”, the fungus induces a set of actions that differs from the normal habits of those insects (including erratic wandering, convulsions preventing the host to climb high on trees, and death grips on specific points on leaves), which are function to bring the host to a suitable location that maximises the spread of fungal spores (Hughes et al., 2011).

This kind of interaction is also present in other fungi-arthropods symbiotic relationships, sometimes even attesting for convergent evolution in very distantly related fungi parasitizing different hosts (Hughes et al., 2016). Following Tinbergen’s (1963) view on understanding animal behaviour, there are four different approaches to the study of the manipulations carried out by the parasites. Those approaches focus on: 1) the functionality of the modified behaviour, 2) its phylogenetic history, 3) its proximate causes, and 4) its ontogenetic development.

We can discuss the CBI infected under the point of view of at least the first and the last approaches, intertwining behavioural aspects with morphological changes caused by *Cordyceps*. It is known that researchers in the TLoU universe were investigating the proximate causes behind the *Cordyceps*-human interactions (i.e., the molecular and physical mechanisms that acted on the host, generating the manifestations of the infection) to better understand the infection and develop either a cure or a vaccine. This is not our focus here (also because we, fortunately, do not have specimens of infected available), but we can briefly report that the CBI fungus operates starting from the victim’s brain, manipulating its nervous system and its perceptions. More precise information on the molecular path behind this are not available to us. We cannot say much about the phylogenetic approach either, due to the unknown specific identity of the CBI fungus and the obvious impossibility of obtaining molecular sequences use-

ful to reconstruct its phylogeny.

From another point of view, the progression of the CBI has a clear ontogenetic aspect, related to the development of the parasitoid fungus inside (and outside) its host. This is manifested in the very different appearances of the infected at subsequent stages and also in the behaviours displayed. Early stages of the infection seem to be more mobile, forming large hordes that move for long distances in a sort of dispersal event (maybe even a migration if the movement from and towards the areas involved is persistent; Dingle & Drake, 2007). Participation of stalkers in hordes, even though not clearly observed by us, is expected given their mobility; possibly, their presence in such gatherings is simply overlooked because of their more secretive habits. Later CBI stages, such as the shamblers and the bloaters, seem to lose their mobility, becoming more restricted to limited areas that are often those where fructification of other infected takes place.

Development of fungal structures over the body of the infected is another ontogenetical manifestation of the CBI, being logically more expressed in later stages. In this context, a peculiar feature is the development of echolocation abilities and the related breakage of the host’s skull. Echolocation starts to appear in stage 2 infected (stalkers), but it is still imperfect. It develops further in clickers, when the fungus opens a way through the skull of the host, likely creating a structure that improves the echolocation ability. Bloaters are good echolocators as well. It is impossible to say whether the structure emerging in clickers evolved to favour echolocation or if the development of echolocation is a by-product of this morphological trait originated to counterbalance the loss of other senses. It is interesting to note that shamblers do not present the same degree of breakage in their skull as clickers and bloaters do, in spite of being considered a possible alternative stage 4 of the infection. If this hypothesis were true, then one would expect the development of the fungus through the cranial bones to remain quite evident, given that the sham-

bler would derive from a clicker displaying this damage. A possible explanation for the different morphology seen in these infected could be that they indeed represent a parallel line of development for the *Cordyceps*, but coming from an earlier stage (i.e., either runners or stalkers) and accelerating the realization of a bloater-like morphology for some reason. Unfortunately, there is no way to verify this hypothesis based on our current knowledge of TLoU infected, and we can only speculate for the moment. In all those ontogenetic aspects of the infection, the Rat King is of course an extreme due to its peculiar nature and the uniquely extended time of fungal development.

Adding to the previously-mentioned traits, another important ontogeny-related feature in the CBI is the timing of fructification. Considering what we can see in TLoU and TLoU2, it seems that fructification takes place when the infected is either at stage 2 (stalkers) or stage 3 (clickers) of the infection. Given that passage from the stalker to the clicker phase happens roughly around one year from contamination, this means that it is apparently possible for the *Cordyceps* to reach maturity in less than one year, and that either maturation or fructification time may be variable or delayable. Factors related to this postponed maturation/fructification are unknown, but they may include availability of a place suitable for spore release. We are not aware of any fructification event in either shamblers or bloaters, even though this is not definitive evidence of a lack of fructification abilities in *Cordyceps* at those stages of the infection (absence of evidence is not evidence of absence, in particular when we have so little data to work with).

All the morphological and behavioural changes *Cordyceps* induces in the hosts can be observed under a functional lens as well. Within its life cycle, the main “objective” of the *Cordyceps* fungus that causes the CBI is to reproduce, that is, to produce spores and spread the infection to other hosts. There are numerous factors that play a role in this, including: 1) availability of possible new hosts (i.e., uninfected humans); 2) capacity

of the infected to actually infect potential new hosts; 3) possibility of the infected and spores to survive long enough to reach maturation; and 4) presence of suitable environments for fructification and spore survival. All modifications induced in the host by the fungus likely take part in trying to secure success for its main “objective”.

The progressive enhancement in strength and damage resistance that is observed throughout different infection stages clearly gives an advantage in the struggles with possible new hosts, but also with other types of prey. It is demonstrated that the infected attack other animals as well, which are likely not susceptible to the CBI and so, that is done maybe for food and sustenance. Alternatively, these attacks may be simple by-products of the increased aggression of the infected, even though observations of infected actively consuming the meat of the hunted preys may suggest otherwise. In any case, the strengthening of the host implemented by the fungus works in parallel to a decrease in its response to pain and in tandem with increased ferocity and lack of self-preservation and fleeing; all of which enhances the chances of CBI spreading. Suppression of host responses to external stimuli has already been observed in other parasitoid fungi (de Bekker et al., 2015), being thus not surprising in this case. Parasitoid fungi infecting ants are also known to remodel the cuticle of the insect to increase resistance of their weaker parts (Anderson et al., 2009).

The search for new hosts may be invoked to explain the formation of hordes that travel across great distances in early CBI stages. Infected that form hordes are the ones in which CBI transmission is documented through active aggression towards a potential new host and also those in which development of the fungus to fructification is still undisputedly possible. Later, less mobile stages are not documented to bite when they attack, thus not spreading the CBI by fluid contact. As mentioned above, they are also not known to fructificate, even though this may be biased by lack of observations.

These behavioural differences may be

due to different roles in the *Cordyceps* life cycle of the two groups of infected. Early stages, up to the clickers, may be devoted to spreading the infection by chasing and attacking suitable hosts as well as moving towards new areas. On the other hand, later stages may have a protective role: being tied to the places where fructification of other infected takes place, they may act as defenders, confronting and killing whoever threatens the defenceless fully-developed *Cordyceps*.

Indeed, humans actively destroy fructification clusters in TLoU to clean the areas where they are located. Adaptations devoted to host protection seems to be present in real *Ophiocordyceps*, but are generally focused on protecting the infected ants by moving it away from sources of harm or producing antimicrobial compounds (Anderson et al., 2009), but not protecting other parasitized ants. Under this point of view, the behaviour displayed by CBI infected looks more like nest protection, similar to social insects. Of course, we cannot confirm the real nature of the behaviours observed in shamblers and bloaters, and they may alternatively result simply from an extreme development of the prolonged infection causing very high aggressiveness but making it impossible for them to bite. This, however, would not explain why these infected progressed so much without fructification; so, a different (and possibly functional) reason may be involved. The protection role hypothesis is further supported by the development of offensive weapons: i.e., the ichor-filled rounded structures.

CONCLUSIONS

Looking at characters from videogames and other fictional contexts with a natural science approach is not easy and inherently subject to a high degree of speculative thinking, due to the general limitation of the observations that can be made together with the impossibility of actively confirming hypotheses derived from the data collected. Still, highlighting and discussing

such data remains an interesting exercise for those who are interested in diving deeper into the lore of works of fiction that fascinated them.

Despite being of course not canonical, the hypotheses proposed here to explain the observed phenomena contribute to pointing out emergent narrative elements that may or may not be in the original concept created by the authors. In this context, CBI infected from the TLoU game series are an excellent example. Features that can be observed in the different kinds of infected were of course included by the developers because they are functionally tuned to the need of an action-adventure game or to their integration within the setting of the series. As an example, progressive stages displaying increasing strength and resistance, as well as the development of new abilities, clearly respond to the requirement of presenting the players with new challenges while they advance in the game, whereas fungal structures appearing on the infected bodies help in depicting them as victims of the *Cordyceps* parasitism. However, all these observed features can still be coherently interpreted using a “scientific” eye, being thus both the umpteenth evidence of the impressive level of attention to details in Naughty Dog’s work and an opportunity for people like us to further explore the universe they created.

As such, a careful description of the morphology and behaviour of the infected brought us to the reconstruction of an ontogenetical pattern in most of the observed features, which parallels the idea of an increased difficulty in dealing with them in some cases, while in other cases it revealed interesting departures from a simple continuous development. The most outstanding examples of the latter are probably the apparent ability of some infected to avoid fructification and progress to a successive infection stage and maybe even more the possibly unclear position of shamblers within the standard CBI progression. Both in the case of shamblers being an alternative form to bloaters (appearing because of more humid conditions) and the case of them

being an earlier-diverging form, their existence opens up tantalizing scenarios about the adaptive potential of the *Cordyceps* causing the CBI and the evolutionary outcomes that it can have. Similar implications may be retrieved from the functional analysis of the reported data, with particular emphasis on the recognition of two possible groups within the CBI stages. These groups may play very different roles in the *Cordyceps* life cycle: one group is composed by runners, stalkers, and clickers, having the “task” of spreading the infection; the other is composed by shamblers and bloaters, having a “nest”-protection role. Presence of anomalies such as the Rat King further stresses the adaptability of the CBI *Cordyceps* as well as the complex nature of the interactions within this, its hosts, and the surrounding environment. Further insights in all these issues may be fuelled by the prospective publication of further TLoU material in the future, such as (but hopefully not only) the forthcoming TV series.

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Facing extinction in *Endling*

Interview with Javier Ramello

Endling – Extinction is Forever is an upcoming multi-platform game developed by Herobeat Studios and published by Handy-Games. As its name implies¹, the game tells the story of the last known survivors of a species. This is a very timely game, as it touches upon a topic that is the forefront of current environmental concerns: the human-caused Holocene extinction.² We interviewed Javier Ramello, co-founder of Herobeat Studios, to learn more about *Endling*. So, let us tell you what we discovered.

In *Endling*, players take control of the very last adult red fox on Earth. Red foxes are one of the animal species who can successfully live in urban areas. So, if even foxes are going extinct in the world of *Endling*, we can only imagine how grim things might be. What is the cause of this situation in the game and what is the extent of the damage on the planet?

During the conception phase of *Endling*, we researched quite a bit and gathered a lot of predictions based on scientific facts about



¹ The word 'endling' was first coined in 1996 to designate the last person in a lineage or family, but it was never adopted in that sense. Instead, it was transformed to mean the last known individual of a species (Jørgensen, 2017). Therefore, when the endling dies the species becomes extinct.

² Also known as the "sixth mass extinction" or "Anthropocene extinction". Due to the impact humankind has on the environment, the current rate of extinction is 100 times larger than it should be (Ceballos & Ehrlich, 2018).



how human society and our own planet may be if we keep doing what we do right now. With all that data, we created a word cloud and some of the biggest words were: Climate change, droughts, floods, garbage, polluted groundwater, electronic wastes, mass extinction, unemployment, crime, violence, environmental degradation, collapsing capitalism, poverty, mass protests, global warming, climate refugees, migrants.

You are right; indeed, things look very grim. We tried hard to represent all this in the game, although most of these topics are not part of the game plot, at least they are in the background for any player to discover them.

Being the last of your species is a great responsibility, but one that doesn't come with a great power. What is the players' ultimate goal in *Endling* and what abilities do they have to achieve it?

For the sake of authenticity and immersion, we didn't even internally give a name to the vixen. She is "the mother fox" for us.

Players will play as a mother fox, and she can do only things that a real fox would do. She won't learn human skills like pulling levers or solving complex puzzles. OK, perhaps she is a very smart fox, but a fox still. The only motivation for her, and hence for the player, is to find food and save her litter.

The three cubs are all distinct from one another, with different fur colors. We suppose the reason for that choice is to facilitate recognition by the players, but the different fur colors imply different genetics. So how would you prefer to explain it: is any the cubs adopted or are they from different fathers?³

This was quite a discussion between the art team and the game vision department. We wanted the player to create a bond with the cubs and love them. It was very important because we are delivering a message and we need players to get emotional. They are your lives, and because of that, their survival is vital from a gameplay perspective, but at the same time they have to be important for you as well, and to reinforce that players

³ Studies with wild foxes have shown that multiple paternity occurred in over one third of litters (e.g., Baker et al., 2004).

need to physically and behaviorally recognize them. Whether they belong to different fathers or not is up to the player's imagination. It's okay for us as long as it's feasible and doesn't break the immersion.



Going back to our first question, if even foxes are threatened with extinction, that means a large chunk of biodiversity has already gone extinct in *Endling*. What are some of the other animal species that the players can expect to find? Are all of them urban species like the fox? And are they friends, foes or prey?⁴

Since the player will incarnate a fox, and foxes can't read, we are not telling explicitly the reason why there are a few, just a few non-urban living animals other than the vixen and her cubs. After all, she wouldn't understand the world's situation. However, some observing players may connect the dots that we placed using environmental storytelling. What I can anticipate is that if you explore a bit and are willing to take the risk and visit the garden of horrors, you may find industrial livestock in large numbers.

Would you mind sharing a bit of the story behind *Endling*? What inspired you to create this game? Are why foxes?

We have been developing video games for years, but felt that we were missing the opportunity to deliver a meaningful message and use this medium to reach young audiences that, just like us, are worried about the climate crisis and how next generations will have to deal with the consequences of the present. As you mentioned before, foxes are very adaptable, and that was one of the reasons to use an animal which can be present everywhere, so *Endling's* story is global. On the other hand, foxes are both predators and prey, so this decision was enriching for the gameplay. And last but not least, foxes are beautiful animals! If we don't feel sorry about climate refugees starving to death, maybe we will feel emotional about the chance of losing a fox cub.



The gameplay videos show natural movement and behaviors of the foxes. How was the process to achieve that? What kind of reference material did you use?

Let's say that for the last three years, our social network feed was all about foxes. We have read a lot and watched any wildlife documentary that we found in order to get the pieces we needed to develop an interesting and authentic experience.

⁴ For instance, red foxes are known to attack domestic cats and, of course, chicken, but in turn they can be killed by dogs (Gil-Fernández et al., 2020).



The same question goes for the environments in *Endling*. Are they based on real-world locations and the expected outcomes climate change and other human impacts will have on them?

At no time we imply that the action occurs in a specific place. It is a concern on a global scale. However, we tried hard to show how humans may be in this near and absolutely not sci-fi future if we don't change our habits.

Does the studio currently have any kind of partnership with nature (or fox) conservation NGOs and similar institutions? Or do you plan to do so in the future?

That's something that we tried to achieve several times. We got in touch with many NGOs and talked about possible ways to cross-promote our actions in order to reach wider audiences, but we are a very small studio, a grain of sand in the sea and not many NGOs are used to working with video game developers. Perhaps in our next title.

Many games are now being used in classrooms and other centers for education, such as zoos and museums. Do you think *Endling* could become one of those?

I recall the movie *Matrix* being used as a philosophy example back in school. It was a good way to keep us engaged and interested in the lesson. Way more enjoyable than a standard philosophy documentary. We are presenting a feasible situation based on scientific predictions and then we let the players reflect upon it, so I don't see why it couldn't.

Do you hope *Endling* can inspire people to take better care of our planet and the fauna? And do you have any takeaway message you would like the players to get from *Endling*?

We are aware that many players will play *Endling* just for fun, and that's absolutely okay. At the end of the day, it's an entertainment product. I would feel successful if at least some of them have an introspection moment after finishing the game and think if there is something we can do to avoid that dystopian future becoming real.

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ABOUT THE TEAM

Herobeat Studios is an independent video game studio based in Barcelona, Spain. The team was originally composed of former colleagues with a wide range of experience in video game development gathered in companies such as Atari, King, Ubisoft, and Electronic Arts. Despite the fact that we grew up in different countries, we shared a deep concern about environmental issues and animal welfare. This inspired us to create something meaningful that explores these issues. From the very beginning we attracted the attention of very talented people. Developers who believed in our project and joined us in this adventure, including our publishing partner HandyGames. This is how Herobeat Studios and the idea of *Endling* started taking shape. Nowadays we are over twenty colleagues, excited about the release of our first title, and excited as well about the future to come.





The sea slugs of *Shiroi Suna no Aquatope*

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Shiroi Suna no Aquatope (白い砂のアクアトープ) is a new anime by P.A. Works that started airing in the summer season of 2021 (Fig. 1). In a broad sense (to avoid spoilers), the anime focuses on the daily life of the staff working in a small aquarium in Okinawa. Its official title in English is *The Aquatope on White Sand* and, from this point on, we'll refer to it as *Aquatope* for simplicity.



Figure 1. Poster of *Shiroi Suna no Aquatope*. The protagonist Kukuru is the one holding the penguin. Source: MAL (www.myanimelist.net).

As expected of an anime about an aquarium, sea life features prominently in it. It is

always great when a new series or game allows us to talk a bit about biology, so we'll just go ahead and take this opportunity. While you'll see plenty of penguins and fish in *Aquatope*, the typical fare of aquariums everywhere, we'll focus instead on the sea slugs. Yes, we know what you're thinking, "Eew, why slugs of all things?". But hey, they're quite cool and we hope you'll also think that way after you read a bit about them. Now let's get to it, shall we?



Figure 2. Screen captures of *Shiroi Suna no Aquatope* episode 15 (19:03 and 19:07). Kukuru goes on to say: "Sea slugs are full of mysteries. You wouldn't believe it, but they are a kind of sea snails. There's a ton of species and they are all different; some of them have camouflage, some of them have toxins. And they're just so colorful and pretty. I want more people to know how interesting sea slugs are."

WHAT'S A SEA SLUG?

Sea slugs are gastropod mollusks, which means that they belong to the Class Gastropoda inside the Phylum Mollusca. Class Gastropoda contains animals living in the sea, in freshwater, and on land; they are commonly known by names such as snails, slugs, limpets, and abalones.

Gastropods are a very diverse group of animals, with an estimate of 70,000 known species, with many still undiscovered (Rosenberg, 2014). Just to give you a point for comparison, that is more than all vertebrates (mammals, birds, “reptiles”, amphibians, and fish) put together. The most diverse branch within Class Gastropoda is known as Infraclass Euthyneura, which counts for circa half of all gastropod diversity (Rosenberg, 2014).

It is thought that the more complex nervous system and sensory structures of euthyneuran gastropods allowed them to diversify in such a large group, with a wide variety of body shapes, and living in many types of habitats (Brenzinger et al., 2021). The Euthyneura contains many marine and freshwater families of gastropods and, notably, the vast majority of terrestrial species. It also contains all the lineages that we commonly refer to as ‘sea slugs’.

‘Sea slugs’ is not a term that applies to a particular scientific grouping of animals. That is, it does not represent a single branch of the gastropod tree of life. Rather, it’s a grab-all term for all marine gastropods that have a reduced shell or no shell at all. Shell reduction and shell loss evolved multiple times independently within gastropods, so the term ‘sea slug’ can be applied to all of the following groups: sea hares, sacoglossans (a.k.a. solar-powered sea slugs), head-shield slugs, sea angels, and nudibranchs. The Japanese term for sea slugs is ウミウシ, *umiushi*. Taken literally, this word means ‘sea oxen’ or ‘sea cattle’, though the origins of this name are unclear.

In this article, we will focus mostly on

nudibranchs for a few reasons. First, they are the most diverse group of sea slugs, and thus, they are what comes to mind with the term ‘sea slug’. They also have the most colorful and amazing forms,¹ rendering them favorites among nature-loving people, wildlife photographers, and diving enthusiasts (Jensen, 2013; Hewitt et al., 2021; Fig. 3). And, finally, because the species from *Aquatope* that we will discuss are all nudibranchs.



Figure 3. The sea slug *Hypselodoris festiva*, photographed in Hong Kong by Ryan Yue Wah Chan, 2020. Source: iNaturalist (<https://www.inaturalist.org/observations/42689203>).

Formally, nudibranchs are animals belonging to Order Nudibranchia within the Euthyneura. The term ‘nudibranch’ comes from the Latin word for ‘naked’ and the Greek word for ‘gills’. That name highlights the fact that the gills of these animals are “free-floating” so to speak (Fig. 4). The specific term for nudibranchs in Japanese is 鰓類, *rasairui*.

SEA SLUG BIOLOGY

Sea slugs evolved from populations of sea snails. Sea snails, as expected from snails, have hard calcareous shells. Throughout the evolutionary history of euthyneuran gastropods, natural selection has favored forms with smaller shells in some lineages. Those lineages eventually gave rise to the

¹ Though species of the genus *Melibe* are nightmare fuel. Check out this 2019 video by the Monterey Bay Aquarium: <https://www.youtube.com/watch?v=VAle2HPkXcw>

sea slugs we know today.

Having a reduced shell decreases the animals' immediate defensive capabilities against predators, but increases their mobility (Ponder et al., 2020). Just like deciding whether your character should have heavy armor, light armor, or no armor at all. Sometimes, evolutionary trade-offs work in a similar way to RPGs.

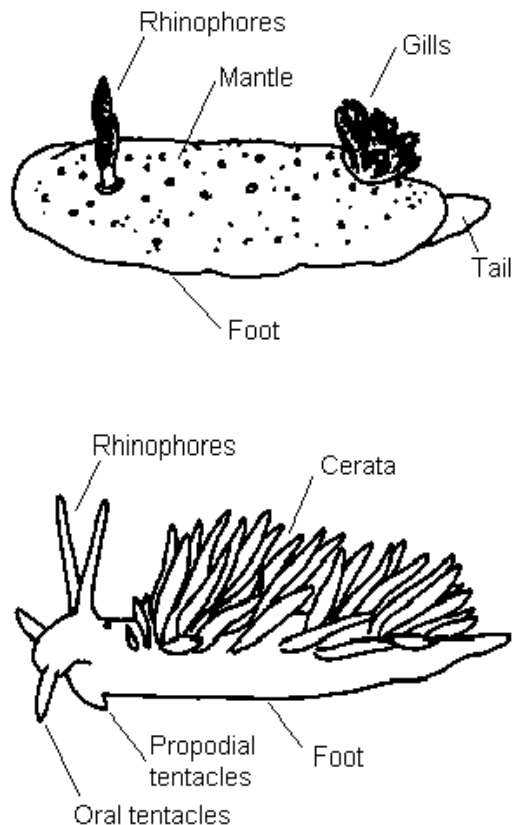


Figure 4. Simple diagrams of the two main nudibranch body plans: dorid nudibranchs (top) and aeolid nudibranchs (bottom). You can see the “naked gills” that give the group its name. In aeolids, the structure known as cerata function like gills. The rhinophores look like a pair of horns or ears, but are chemosensory organs (for taste and smell). Source: SeaSlug.org (<https://www.seaslug.org.uk/>).

Throughout millions of years, this trend in favoring smaller shells eventually resulted in the rise of forms with just a vestigial (and internalized) shell or even no shell at all. That gave sea slugs some ability to swim and also, the possibility of hiding in small crevices (Ponder et al., 2020). But then again, their defenses were impaired by the lack of a shell. Or were they?

Sea slugs rely on other sorts of defense mechanisms. They have colorful patterns that may help them camouflage themselves in their habitats (which includes colorful corals and sponges) or serve as a warning sign (Debelius & Kuitert, 2007). In nature, stark body colors and patterns (like a wasp's black and yellow stripes) often indicate that the animal is poisonous – or at least has an awful taste if eaten. That strategy is called aposematism and it is used to ward off potential predators.

The toxins of some nudibranchs, for instance, can kill predators like fishes and crustaceans (Debelius & Kuitert, 2007). Those toxins are obtained or derived from the slugs' main food items, which include animals such as sponges and ascidians (Fig. 5; Cheney et al., 2016).



Figure 5. The variable neon slug *Nembrotha kubaryana* obtains toxins from their ascidian prey (Paul et al., 1990). Source: Wikimedia Commons, photo by Alexander R. Jenner, 2009.

Some sea slugs can co-opt more defenses from their food source than any other animal. For instance, aeolid nudibranchs steal entire cells from corals and anemones (Fig. 6; Wägele & Klussmann-Kolb, 2005). These cells are called cnidocytes and are present in all cnidarians (this notably includes stinging jellyfish). Aeolid nudibranchs feed on those cnidarians, ingest their tissues, and somehow can retain the fully functional cnidocytes. They use the cnidocytes as an anemone would: to sting harassers. Naturally, the cnidocytes are functional only for a limited time in the nudibranch's body.



Figure 6. The Spanish shawl *Flabellinopsis iodinea* gathers stolen cnidocytes on the cerata on its back (the same structures that it uses for breathing). Source: Wikimedia Commons (cropped), photo by Yury Velikanau, 2016.

Some sea slugs can steal other types of cells that, although not as awesome as defensive stingers, represent an even greater feat. They steal chloroplasts from algae (Cartaxana et al., 2021; Maeda et al., 2021). That's right, those are the cells responsible for photosynthesis. The sea slugs known as sacoglossans can retain functional chloroplasts in their body, which essentially enable them, an animal, to photosynthesize like a plant. The chloroplasts act like an extra energy source for the sacoglossans, which gives them their common name 'solar-powered sea slugs'. Like the cnidocytes above, the chloroplasts are only functional for a limited time. One species of sacoglossans, known as sea sheep, went a bit viral on social media some years ago because it looks so damn cute (Fig. 7).

There are other ways in which sea slugs are awesome too. Some sea hares have giant neurons and this has allowed groundbreaking neurobiology research on learning and memory (Gillette, 1991). That research, in turn, has led to a deeper understanding of

human neurobiology. The 2000 Nobel Prize in Physiology or Medicine was granted to researchers studying *Aplysia* sea hares.



Figure 7. The sea sheep *Costasiella* sp. Source: ND Awards (<https://ndawards.net/winners-gallery/nd-awards-2014/macro/hm/802/>), photo by Lynn Wu.

The next big thing for the crossover between sea slugs and medicine could be regeneration. The sacoglossan *Elysia marginata* can auto-decapitate, which means it can fully separate its head from its body. This is thought to be an extreme but controlled system to eliminate parasites (which remain in the body), while the head crawls away and then fully grows a new body (Mitoh & Yusa, 2021). The head can survive and obtain energy from all those stolen chloroplasts mentioned above.

SHIROI SUNA NO AQUATOPE

Sea slugs live in a variety of marine habitats worldwide, though the greatest diversity can be found in warmer waters, such as the Indo-Pacific and the Caribbean. There are circa 3,000 known species of nudibranchs globally and a bit over 1,000 of them are known to inhabit Japanese waters (Ono & Kato, 2020). Expectedly, there is a wealth of species from the warmer waters in Okinawa, where *Aquatope* takes place.

In episode 15 of *Aquatope*, protagonist Kuku is tasked by her boss to come up with ideas for a special temporary exhibition. One of her ideas – and the one that her

boss greenlights – is an exhibit of umiushi (Fig. 8).



Figure 8. Kuku's manager Tetsuji, as he greenlights her sea slug proposal. Screen capture of *Shiroi Suna no Aquatope* episode 15 (6:15).

Naturally, Kuku chose an ensemble of nudibranch species that she could easily find (and capture) on the shores of Okinawa (Fig. 9). So let us talk a bit about the species she listed.² It's a great opportunity to go over some cool biology facts and an even better chance to show some amazing photographs. The information in the next section comes from Debelius & Kuitert (2007) and Ono & Kato (2020) unless otherwise noted.



Figure 9. Screen capture of episode 15 (6:20) of *Shiroi Suna no Aquatope* showing the nudibranch species Kuku proposed for the aquarium's special umiushi exhibition. See the Appendix in the end of this article for the translation of Kuku's notes.

Ardeadoris cruenta (Family Chromodor-

ididae): The species' Latin name *cruenta* means 'bloody' or 'stained with blood' (Brown, 1954), a reference to the red spots around the slug's mantle that look like drops of blood (Fig. 10). In older scientific literature, it was classified in a different genus, under the name *Glossodoris cruenta*. Though the species doesn't have a vernacular name in English, *Ardeadoris cruenta* is known as アカテンイロウミウシ in Japanese (akaten iroumiushi). 'Akaten' means 'red dot(s)' and the term 'iroumiushi' is used to refer to members of the family Chromodorididae in general.

This species can be found throughout the tropical Western Pacific, from Okinawa to Australia. The animal typically measures between 3 and 4 cm (Rudman, 1986), but can reach up to 5 cm. It feeds on sponges.



Figure 10. *Ardeadoris cruenta*. Source: Wikimedia Commons, photo by Chad Ordeltide.

Tambja sagamiana (Family Polyceridae): This species was named after the place where it was first discovered, Sagami Bay, just to the south of Tokyo. Its name in Japanese is サガミリュウグウウミウシ (Sagami ryūgūumiushi). The term 'ryūgūumiushi' applies to members of the family Polyceridae.³

² There are a few more species that appear in the episode, but we won't talk about all of them. Otherwise, this article would become way too long.

³ While we could not find enough evidence explaining the vernacular Japanese name for polycerids, the term 'ryūgū' is the name of the legendary undersea dragon palace particularly famous as Ryūgū-jō from the tale of Urashima Tarō. 'Ryūgū' is used in other marine species names to indicate animals that look particularly superb or mystical, or that live deep in the sea. It has been used, for instance, for giant oarfish (*Regalecus glesne*), sea stars (phylum Echinodermata; Kogure et al., 2009) and mud dragons (phylum Kinorhyncha; Yamasaki, 2016).

This species lives in waters around Japan, Korea and Taiwan. The animals can grow to 13 cm and feed on bryozoans (Pola et al., 2006).



Figure 11. *Tambja sagamiana*. Source: 世界のウミウシ [Seaslug World] (https://seaslug.world/species/tambja_sagamiana), photo by Manabu Kakegawa, 2016.

Goniobranchus coi (Family Chromodorididae): This species was named in honor of the person who collected the first specimen in Vietnam, whose name was M. Nguyen-van-Co (Risbec, 1956). The masculine genitive (possessive) case in Latin renders 'Co' into 'coi'. Its Japanese name is シラナミイロウミウシ (shiranami iroumiushi); 'shiranami' means 'white-capped waves'.

The species can be found throughout the tropical Western Pacific, from Japan to Australia. It measures circa 6 cm and feeds on sponges.



Figure 12. *Goniobranchus coi*. Source: 世界のウミウシ [Seaslug World] (https://seaslug.world/species/goniobranchus_coi), photo by Akihito Iwakiri (oasis), 2018.

Phyllidia coelestis (Family Phyllidiidae): The name *coelestis* means 'of the sky' and is a reference to this slug's blue color (Fig. 13). Its name in Japanese is ソライロイボウミウシ (sora iroiboumiushi). The term 'iroiboumiushi' refers to members of family Phyllidiidae (イロ and イボ mean 'colorful' and 'wart(s)'), while 'sora' refers to its sky color.

This species is very widespread and can be found from Japan, throughout the Indo-Pacific, to South Africa. It measures about 6 cm in length and feeds on sponges.



Figure 13. *Phyllidia coelestis*. Source: 世界のウミウシ [Seaslug World] (https://seaslug.world/species/phyllidia_coelestis), photo by Manabu Kakegawa, 2016.

Dermatobranchus ornatus (Family Arminidae): The name *ornatus* means simply 'ornate'. It doesn't mean much, as countless species in all animal groups bear some form of the name "ornate"; besides, *D. ornatus* is not particularly more ornate than other nudibranchs. Its Japanese name is ハナオトメウミウシ (hana otome umiushi). The name 'otome umiushi' refers to members of the genus *Dermatobranchus* ('otome' means 'girl'), while 'hana' means 'flower' or 'flowery'.

This species is distributed throughout the Indo-Pacific, from Japan to Oman. It can reach 8 cm in length and feeds on gorgonian corals (Zhang et al., 2006).



Figure 14. *Dermatobranchus ornatus*. Source: 世界のウミウシ [Seaslug World] (https://seaslug.world/species/dermatobranchus_ornatus), photo by Manabu Kakegawa, 2016.

THE UNKNOWNNS

One important point that Kukuuru makes is that despite the best efforts of researchers, actually very little is known about sea slugs (Fig. 15). We can identify them to some extent, though many species undoubtedly still await to be discovered. We have even learned a few things about their toxins and their ability to steal cnidocytes and chloroplasts, as we mentioned above. But for the vast majority of species out there, we still don't know much: what they eat or what eats them, their reproduction, seasonality, behavior – the list goes on. More urgently, we don't have much of an idea about how they will respond to increasing global temperatures and ocean acidification. There is still plenty to be studied about these fantastic creatures.

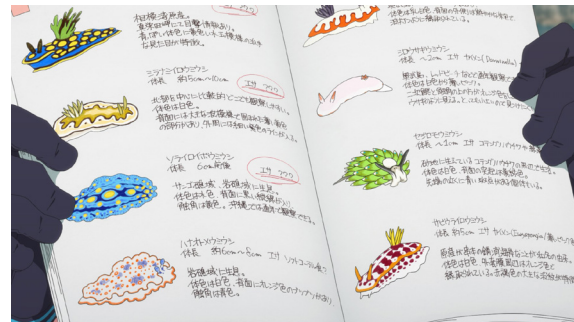


Figure 15. Kukuuru shows her notebook, telling her friends how much we don't know about sea slugs: the entries marked in red represent missing data regarding the slugs' diet. Screen capture of *Shiroi Suna no Aquatope* episode 15 (10:18).

UMIUSHI IN JAPAN

Although invertebrate animals such as slugs rarely are in the spotlight (Black et al., 2001; Salvador et al., 2021), umiushi seem to hold a special niche with the public in Japan. We will briefly go over some examples below.

Video games

There are some nice examples of umiushi in Japanese video games, the most prominent of which is of, course, *Pokémon*.⁴ Both forms of Shellos and Gastrodon are based on real-life species of nudibranchs belonging to the genera *Chromodoris* and *Hypselodoris*.⁵ Goomy was based on species of the genus *Goniobranchus* (Fig. 12), and both Phione and Manaphy were based on the sea angel *Clione limacina*. You can find more information about all mollusk Pokémon in the article of Salvador & Cavallari (2019).

Sea slugs can also be found in *Animal Crossing* games (Nintendo), together with sea angels.⁶ The sea slug is *Hypselodoris fes-*

⁴ This relationship goes the other way too. The species *Thecacera pacifica* was discovered in the Indo-Pacific and described in the late 19th century, but has recently been dubbed the “Pikachu slug” because its body is completely yellow with the exception of the tips of its rhinophores and gills, which are black.

⁵ Though East Sea Gastrodon, in particular, might bring in some design choices from sea hares (Salvador & Cavallari, 2019).

⁶ Sea angels are called “sea butterflies” in the English translation of the games. Sea slug: https://animalcrossing.fandom.com/wiki/Sea_slug / Sea butterfly: https://animalcrossing.fandom.com/wiki/Sea_butterfly

tiva (Fig. 3) and the sea angel is *Clione limacina*, like in *Pokémon. Puzzles & Dragons* (GungHo Online Entertainment, 2012) also has its nudibranch: the Great Witch's Disciple, Ponno (大魔女の弟子・ボンノ).⁷ Its design was inspired by *Hypselodoris apolegma*,⁸ the same species that was likely the inspiration for West Sea Shellos in *Pokémon*.

Sea angels were the likely inspiration for the Moon Slug (ツキミアゲ)⁹ from *Monster Hunter: World* (Capcom, 2018). In *Monster Hunter Rise* (Capcom, 2021), there is the Monksnail (ウミウシボウズ, 'umiushi bōzu'),¹⁰ which is a play on the words umiushi and the name of a yōkai, umibōzu (海坊主, sea monk). The design of the Monksnail is based partly on a generic nudibranch (its body) and part on depictions of the head of a umibōzu (its "shell").

A further example is the monster Oilboyle (オイルシッパ)¹¹ from *Final Fantasy VIII* (Squaresoft, 1999), which has a design somewhat reminiscent of nudibranchs like the blue sea dragon *Glaucus atlanticus*.

If we go way back in time to the 16-bit era, we can also find some umiushi-inspired creatures. *Demon's Crest* (デモンズブレイゾン) (Capcom, 1994) has a boss called Holothurion¹² that looks like a gigantic demonic snail, but its blue soft body might have some design choices inspired by nudibranchs such as *Chromodoris willani* and *Glaucus atlanticus* (Cavallari, 2015).

Another one is the Sea Slug (うみうし, umiushi) from *Dragon Quest II* (Enix, 1987), now known as Merlusc.¹³ It is supposedly a purple sea slug, but it has only a generic cartoon-like slug design. It is just a different

color from the yellow Maulusc, which is a terrestrial slug. Anyway, we cannot be too strict with the art of a 1987 game.

Last but not least, we need to acknowledge a umiushi from the *Kirby* franchise, though this one comes from the anime, not the game. The so-called Great Sea Slug Monster (ウミウシ大魔獣)¹⁴ from *Kirby: Right Back at Ya!* (星のカービィ; Studio Sign & Studio Comet, 2001–2006) was based on the species *Hypselodoris festiva* (Fig. 3).

The list above is by no means exhaustive – it just reflects the games we played. We must have missed quite a few examples, so please feel free to write to us if you come across more umiushi in other Japanese games.

Toys and collectibles

If you look at Japan's thriving commerce of game and anime goodies, you'd be excused to think that this "toys" boom is a current phenomenon. However, toys were a vibrant part of Japanese culture ever since the Edo Period (Ryōsuke, 1990; Alt, 2020). And more than that, after Japan opened up to the rest of the world in the mid-19th century, its toys rose to prominence in the global market, going up against the then leader Germany in the first half of the 20th century (Sadao, 1967; Phoenix, 2006).

After a sad pause in their production during World War II, toys helped kickstart Japanese economy and bounced back to the forefront of Japanese exports, to the extent that by the end of the 1950s Japan had

⁷ <https://www.appbank.net/2020/04/09/iphone-application/1880493.php>

⁸ The similar *Hypselodoris variobranchia* was described too recently.

⁹ <https://monsterhunterworld.wiki.fextralife.com/Moon+Slug>

¹⁰ <https://monsterhuntermise.wiki.fextralife.com/Endemic+Life>

¹¹ <https://finalfantasy.fandom.com/wiki/Oilboyle>

¹² <https://www.sprisers-resource.com/snes/demonscrest/sheet/13689/>

¹³ <https://dragonquest.fandom.com/wiki/Merlusc>

¹⁴ https://wikirby.com/wiki/Great_Sea_Slug_Monster

around three quarters of the global market (Sadao, 1967; Alt, 2020). Japanese toys were not only cheap overseas back then, but were also of excellent quality and artisanship.¹⁵ That rich background fed into the “cult of kawaii”, spearheaded by Sanrio, and the overall otaku culture that extends to this day (Wallin & Sandlin, 2020). Today, of course, most plastic toys are made in China or elsewhere, but to the specifications of Japanese companies such as Sanrio.

True to this long-standing tradition, there are plenty of umiushi toys around Japan. They go from gacha capsule toys to meter-long plush toys. And all of them are as kawaii as you could expect.

Charles Eames, one of the most influential industrial designers of the last century, once said: “Toys and games are the preludes to serious ideas.” Eames was thinking about the industry and “just” talking about creativity and innovation. But we can take this sentence one step further: playfulness, including toys, is something that facilitates education. This is not only widely recognized by educators everywhere (for instance, Raw, 1982; Stein & Miller, 1997; Swiniarski, 2012), but also by the characters in *Aquatope*. In episode 18, they use a cosplay event and a “hunt” for stickers to raise awareness about some species of fish and other marine life that are not particularly popular.

It could be argued that toys of unusual animals (that is, non-mammal) such as umiushi can increase awareness and thus open venues for education. The knowledge obtained about said animals will hopefully lead to a greater appreciation and more positive attitudes. Such public awareness and appreciation are certainly lacking in regards to invertebrate animals and is considered a major cause of the lack of protection and conservation efforts directed at them (New, 1993; Knight, 2008).



Figure 16. Example of umiushi toys: the gacha series ウミウシドラゴン マスコットフィギュア (“dragon-nudibranch mascot figures”) by Qualia Co., 2021. Source: Qualia (https://qualia-45.jp/distinations/umiushidragon_mf/).

Aquariums

While toys and presence in pop culture certainly help to increase awareness of animals and conservation among the public (Salvador, 2017), few things – if any – can substitute the real deal. As such, having “contact” with live animals in aquariums is what will make the message stick, as recognized by *Aquatope*’s protagonist, Kukuru. And Japanese aquariums seem to be doing an excellent job in this regard, with many thematic umiushi exhibitions.

In 2021, Oga Aquarium GAO (男鹿水族館ガオGAO, in Akita Prefecture), the Shellfish Museum Palais la Mer (貝の博物館 ぱれ・らめーる, in Ōshima, Tokyo), and Teradomari Aquarium (寺泊水族博物館, in Niigata Prefecture) had umiushi-themed exhibitions.¹⁶ Another recent exhibition took place at Shinagawa Aquarium (しながわ水

¹⁵ A miniature of the Cadillac produced in the 1950s in Japan was so expensive as to be considered a luxury item according to local laws (Alt, 2020). That’s something like the ancestor of the many fancy collectibles that dry our wallets to this day.

¹⁶ Oga Aquarium GAO: <https://www.gao-aqua.jp/event/32535.html> / Shellfish Museum Palais la Mer: <https://bit.ly/3Di6eCL> / Teradomari Aquarium: <https://www.ohbsn.com/radio/programs/snp/2021/01/029392.php>.

族館, in Tokyo; Fig. 17) in 2018.¹⁷ The year of 2021 was timely to feature umiushi because that was the year of the ox in the Chinese zodiac; as we explained above, umiushi means “sea oxen” in Japanese. But you can see lovely umiushi any time in places like the Kaiyukan (海遊館, in Osaka).¹⁸



Figure 17. Poster for the exhibition at Shinagawa Aquarium, 2018. Source: Fashion Press (<https://www.fashion-press.net/news/41030>).

The mascots of Awashima Marine Park (あわしまマリンパーク, in Numazu; Fig. 18) are a pair of umiushi siblings named Umine Awashima (淡島 うみね) and Otome Awashima (淡島 おとめ).¹⁹ Their designs were inspired, respectively, by the fan-favorite *Hypselodoris festiva* (Fig. 3) and *Dermatobranchius albopunctulatus*. The latter is a species of otome umiushi, of course. A third mascot, and friend to the siblings, is Mashi-

ro Uchiura (内浦 ましろ), whose design was based on *Hypselodoris placida*.



Figure 18. The mascots of Awashima Marine Park. From left to right: Umine, Otome, and Mashiro. Source: Awashima Marine Park (<http://www.marinepark.jp/umine/>).

Aquariums (and zoos) are institutions devoted to education (and edutainment), research, and animal conservation. It is an obvious fact, as related by Kuku's manager Tetsuji in *Aquatope*, but it needs to be repeated here. The importance of these institutions in those three fields, but particularly in education, is undeniable (Packer & Ballantyne, 2010). However, there is growing concern about animal welfare in zoos and aquariums.

While part of those concerns is just the loud and typically nonsensical Twitter/Facebook outrage, this is an issue of utmost importance – especially concerning the entertainment factor (Carr & Cohen, 2015). Animals should be treated humanely and zoos and aquaria are striving to reach higher standards of welfare (Norton et al., 1995; Maple & Perdue, 2013). So, it was really good to see Kuku fighting so hard in *Aquatope* to ensure her umiushi had the best conditions possible.

Sea slugs are notably difficult to keep in captivity due to their strict feeding habits,

¹⁷ Shinagawa Aquarium: <https://www.museum.or.jp/event/91377>.

¹⁸ Kaiyukan Satellite Gallery: <https://www.kaiyukan.com/thv/marketplace/event/detail.php?id=6061>. See also their Facebook profile for more info: <https://www.facebook.com/umiushi.kaiyukansatellitegallery>.

¹⁹ <http://www.marinepark.jp/umine/>

dependent on specific corals and sponges (Calado & Dinis, 2005).²⁰ This fact is something that Kukuuru repeatedly reminds everyone about and is at the forefront of her concerns about the animals' wellbeing (Fig. 19). This is of particular importance because Japan has a track record of poor performance in all global measures of animal welfare (World Animal Protection, 2020).

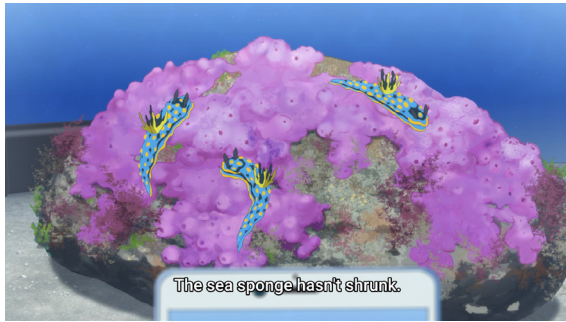


Figure 19. Kukuuru worries that she has the wrong type of sponge to feed her *Tambja sagamiana*. Screen capture of *Shiroi Suna no Aquatope* episode 15 (12:18).

CONCLUSION

We certainly hope we've given you, dear reader, the chance to appreciate sea slugs. But we are just secondary players here. The actual work was done by the people behind *Aquatope*, who managed to bring actual knowledge of marine life into an entertaining anime.



Figure 20. Screen capture of *Shiroi Suna no Aquatope* episode 15 (19:28).

Invertebrate animals typically come across as ugly or even repulsive creatures to

the public. But given the chance, most people will be able to recognize their amazing diversity and complex evolutionary history, and maybe even to appreciate some of those animals (Cardoso et al., 2011).

Ultimately, awareness and knowledge of how important invertebrate animals are for the ecosystem should feed into efforts to preserve them (Czekanski-Moir & Rundell, 2020). After all, if current trends go on unchecked and ecosystems collapse, it's our survival that's at stake.

Case in point, the franchise *Kemono Friends* (けものフレンズ) was able to draw more people to zoos in Japan and increase the amount of Google searches and Wikipedia views about the animals it featured (Fukano et al., 2020). Furthermore, it also drove people to donate more money to zoos and conservation funds related to those animals (Fukano et al., 2020). While *Aquatope* does not have a kemonomimi army like *Kemono Friends* to attract people's attention and yen, let us hope it has enough heart and biology to renew interest in aquariums and generate some funding to study and protect our oceans and their inhabitants.

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²⁰ One reason why some nudibranch species can eat only a few types of sponges could be because each species can only deal with a limited variety of sponge toxins (Cheney, 2016).

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ABOUT THE AUTHORS

Dr. Rodrigo Salvador is a malacologist – that's a weird word that means he researches mollusks. He specializes in the study of land snails but has always been interested in nudibranchs (West Sea Gastrodon is one of his favorite Pokémon). Notably, it is dangerous to leave him alone in Japanese aquarium shops: he will buy lots of nudibranch merch.

Ken Kuroki is a PhD student of bioinformatics, a field of study where, according to him, “computer geek meets biology.” Sounds fun, right? He also runs a YouTube channel named Yurufuwa Biology with his friends to play various video games and enjoy super nitpicky details from the viewpoint of geeks and biologists.

APPENDIX

Here you can find the translation of Kukurū's notes (screen capture showed in Fig. 9).

アカテンイロウミウシ

黄色い体色と赤い水玉模様が目を引くウミウシダイバーの人気者。学名の *Ardeadoris cruenta* の *Cruenta* は「血だらけの」という意味。かわいい見た目とは裏腹に恐ろしい名前を秘めているウミウシです。

[Its yellow body color and red polka dots make it a popular choice for nudibranch divers. In its scientific name, *Ardeadoris cruenta*, *Cruenta* means “bloody”. Despite the cute appearance, this nudibranch has a frightening name.]

サガミリュウグウウミウシ

何だか毒々しい見た目をしているこちらの海牛は名前に「サガミ」とあるように最初に確認されたのが相模湾だったことから由来しています。ウミウシの中では10 cm ほどと大型の部類に入ります。

[In the name of this nudibranch is “Sagami”, which comes from the fact that it was first found in Sagami Bay. It is one of the larger nudibranchs, measuring about 10 cm in length.]

シラナミイロウミウシ

触覚からエラにかけて波のような模様が

背中全体を囲んでいるのが特徴的。波の穏やかな岩礁域に生息しており、外套膜をヒラヒラとさせて動く活発な性格のウミウシです。

[It is characterized by the wave-like pattern that surrounds its entire back from the antennae to the gills. It lives in reefs where the waves are calm, and is an active nudibranch with a fluttering mantle.]

ソライロイボウミウシ

沖縄でよく見られるウミウシの一種で、背中にオレンジ色のイボがあるのが特徴。他の海牛より体の表面が少し堅く、ザラザラしています。

[A type of nudibranch commonly found in Okinawa, characterized by the orange warts on its back. The surface of its body is a little harder and rougher than other sea slugs.]

ハナオトメウミウシ

多種多様な色、見た目をしているウミウシたちですが、オトメと名前がつくウミウシの間は基本的に白い色がベースで、「清楚」、「華蓮」なイメージがぴったりだと思っています。こちらのウミウシも名前の通りかわいらしい見た目をしています。

[Nudibranchs come in a wide variety of colors and appearances, but the nudibranchs with the name “Otome” are basically white in color, which I think gives them the perfect image of “neatness” and “floweriness”. This nudibranch also has a cute appearance as its name suggests.]



A critical reappraisal of dinosaur reconstructions in *Zoo Tycoon 2: Extinct Animals*

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Zoo Tycoon 2 is a zoo-building simulation game developed by Blue Fang Games and originally released in 2004 as a sequel to the classic *Zoo Tycoon* game. In *Zoo Tycoon 2* (henceforth referred to as ZT2), the player's goal is to build a successful zoo, which involves not only creating an aesthetically pleasing design but also making sure it is able to fulfill the needs of both your guests and, most importantly, your animals. With animals as its central element, ZT2 offers the player dozens of different species, each with its own conservation status, enrichment needs and habitat preferences. The game puts great emphasis on environmental education, depicting the importance of zoos as tools in conservation and rewarding the player for fulfilling specific conservation goals, such as reintroducing individuals from endangered species to the wild. Additionally, the game even has its own in-game encyclopedia (dubbed *Zoopedia*) with additional information on each species' taxonomy, ecology and conservation.

Over its development, ZT2 spawned four expansion packs adding new species and other content focused around a specific theme: *Endangered Species*, *African Adventure*, *Marine Mania* and *Extinct Animals*. In total, the game with all expansions has 130 animal species available to the player. It is also interesting to note that, since its release, ZT2 has nurtured a very prolific modding community that is still active over ten

years since the game's official development ceased. Over the years, several thousands of user-made mods were added to the game, ranging from simple additions to total remakes of the original game (ZT2 Download Library, 2021). As such, it is clear that ZT2 is still a much beloved game and also a powerful tool in representing biodiversity, as a fully modded game can have thousands¹ of real animal species from many different taxa.

This paper will focus on the game's last official expansion pack, *Extinct Animals*. As hinted by its title, this expansion focuses on adding extinct species to the game. It contains a roster of 31 animals, ranging from long-lost creatures from millions of years ago to species that have only become extinct in the past decades. As a way to justify their inclusion in a zoo game, the expansion includes a minigame in which the player has to hunt for fossils from each species, which can then be assembled and used as a source of DNA for cloning them into your zoo. This is, of course, nonsense from a scientific point of view. DNA degrades quickly over time and the very few genetic samples we have from fossils are largely incomplete and only present in specimens from up to 1.5 million years ago (Willerslev et al., 2004; Kirkpatrick et al., 2016). Still, it is an interesting way to engage the player in paleontology and deserves praise for not outright copying the "fossil mosquitoes" idea from

¹ The game engine actually has a limit in how many assets can be added to the game before it crashes, so technically it can only hold a few hundred mods at the same time. Still, the player can pick and mix the mods they wish to have in a specific game session from the large pool of user-made content.



Figure 1. Comparison between vanilla *Zoo Tycoon 2* (left) and a game with the *Radical Remake* mod (right). Most mods move away from the cartoon-like vanilla style in favor of a more realistic style. Left image extracted from the official *Zoo Tycoon 2* website²; right image by Aurora Designs (<https://sites.google.com/site/auroradesignshome/gallery-game>).

Jurassic Park.

As mentioned above, environmental education is one of the core aspects of the game. *ZT2* attempts to present the animal species in a relatively accurate (albeit still very stylized) way. This is a no-brainer for extant species, as we all know how they live and what they look like. However, creating an accurate reconstruction is a challenge when it comes to extinct species. Even someone unfamiliar with paleontology will notice that every time you see a dinosaur depicted in a movie, videogame or toy, it will look different from other depictions of the same animal. This is not only due to artistic liberties taken by each media, but also because of the gaps in our knowledge of these animals. The fossil record, our main source of information on prehistoric organisms, only offers limited data and fossils are often fragmentary and incomplete. As such, the process of reconstructing prehistoric animals is always a work in progress, with new discoveries adding to our knowledge and prompting updated reconstructions. In this context, paleoart³ plays an important role in translating paleontological knowledge to the greater public and inspiring people to learn more about these animals (Witton et al., 2014).

With this in mind, this paper reviews the paleontological reconstructions presented in *Zoo Tycoon 2: Extinct Animals*. Since the game contains too many species to discuss at once, this article focuses specifically on the dinosaurs (including birds), which are arguably the most popular group of extinct animals. An interesting detail about this is that the *ZT2* not only depicts the animals' appearances, but also aspects of their ecology. As such, alongside with their anatomy, it is possible to evaluate whether the ecological aspects presented in the game are accurate considering what we currently know about these animals.

A QUICK OVERVIEW OF DINOSAUR BIODIVERSITY

Dinosaurs are a very diverse and well-known group of animals. The first dinosaurs are thought to have evolved in the Late Triassic period, approximately 245 million years ago. They would then come to dominate most terrestrial ecosystems for the next two geological periods, the Jurassic and the Cretaceous, before facing a devastating mass extinction event at the end of the Cretaceous period. The Mesozoic era,

² As all other *ZT2* images used herein. Archived at: https://web.archive.org/web/20121012035800/http://zootycoon.com/About/about_zoo_tycoon_2.htm

³ The general term for artistic depictions of extinct animals.

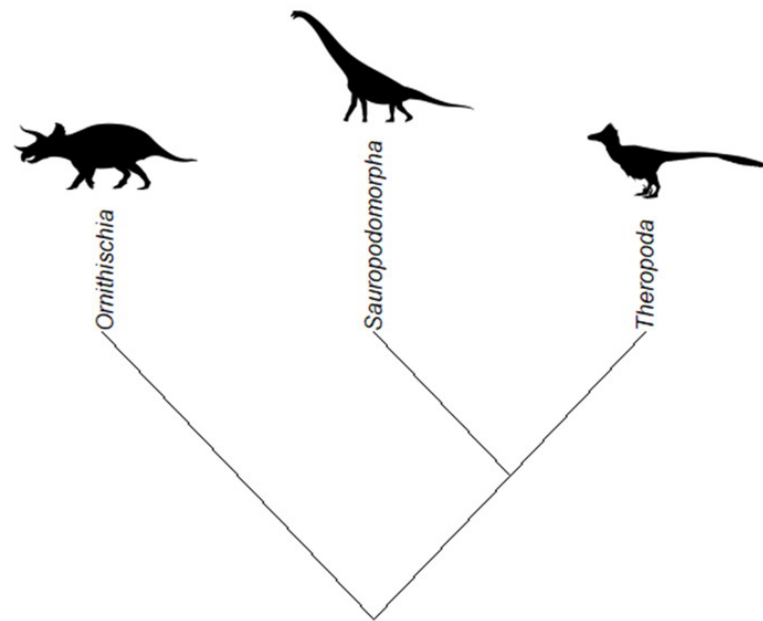


Figure 2. Evolutionary tree showcasing the relationships between the main groups of dinosaurs. Silhouettes by Matt Dempsey, Scott Hartman and Emily Willoughby, extracted from PhyloPic (<http://phylopic.org/>).

comprising the Triassic, Jurassic and Cretaceous periods, has thus been dubbed “the age of reptiles” due to the predominance of dinosaurs and other large reptiles. Despite suffering many losses during the Cretaceous-Paleogene mass extinction event, the remaining dinosaurs (birds) quickly diversified and are still the most diverse group of terrestrial vertebrates in modern times (Benton, 2014; Sues, 2019).

There are approximately 1208 well-established genera of non-avian dinosaurs and several genera of extinct birds (Olshevsky, 2021). As the fossil record is largely incomplete, this number represents only a fraction of the total diversity of dinosaurs in the past. In addition, there are nearly 11,000 described species of birds alive today (Clements et al., 2019; Gill et al., 2021) and new dinosaur species (both extinct and living) are still discovered every year.

There are three major clades (or groups) of dinosaurs: Ornithischia, Sauropodomorpha and Theropoda. In recent years, there have been some controversies concerning the relationships between these clades (Baron et al., 2017; Langer et al., 2017). In spite of that, the classic and most widely adopted hypothesis proposes that theropods and sauropodomorphs are more closely related

to each other than to ornithischians, with both Theropoda and Sauropodomorpha constituting a clade named Saurischia (Fig. 2).

Understanding those relationships gives us some context as to where each species fits in the tree of life. It’s not this article’s intent to give a detailed account of dinosaur phylogeny and evolution, but this basic framework will be useful to discuss how this diversity is translated to ZT2.

DINOSAURS IN ZOO TYCOON 2: EXTINCT ANIMALS

Out of the three major clades of dinosaurs, only Ornithischia and Theropoda are represented in ZT2. This is unfortunate, since Sauropodomorpha is a very interesting lineage that includes some of the earliest dinosaurs and also some of the largest terrestrial animals of all time (Benton, 2014), so there are many iconic sauropodomorphs that could have been represented in the game. The ornithischians and theropods represented in ZT2 are discussed separately below.

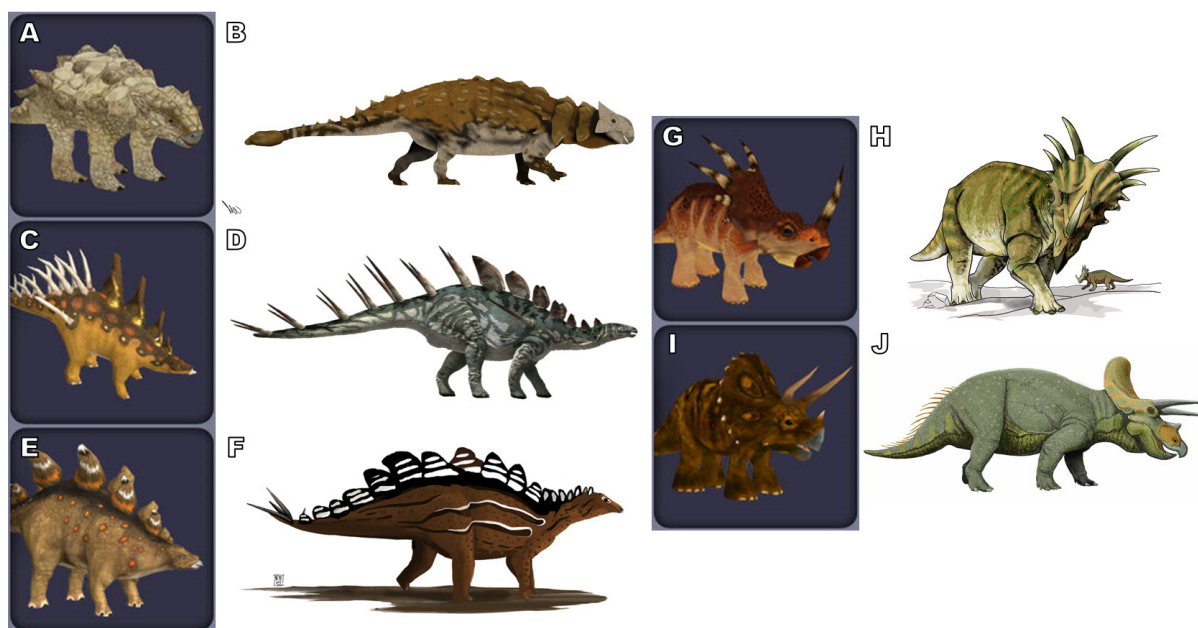


Figure 3. Ornithischians depicted in ZT2 and more accurate depictions of their real-life counterparts (reconstructions extracted from Wikimedia Commons). **A.** *Ankylosaurus magniventris* as depicted in ZT2. **B.** *A. magniventris* by Sphenaphinae (2019). **C.** *Kentrosaurus aethiopicus* as depicted in ZT2. **D.** *K. aethiopicus* by Dinosaur Zoo (2011; cropped). **E.** *Stegosaurus stenops* as depicted in ZT2. **F.** *Se. stenops* by Matthew Martyniuk (2015). **G.** *Styracosaurus albertensis* as depicted in ZT2. **H.** *Sy. albertensis* by LadyofHats (2007). **I.** *Triceratops horridus* as depicted in ZT2. **J.** *T. horridus* by Dmitry Bogdanov (2008).

Ornithischia

In total, five species of ornithischians are represented in ZT2: *Ankylosaurus magniventris*, *Kentrosaurus aethiopicus*, *Stegosaurus stenops*, *Styracosaurus albertensis* and *Triceratops horridus*. Out of these, *A. magniventris*, *K. aethiopicus* and *Se. stenops* belong to the clade Thyreophora, while *Sy. albertensis* and *T. horridus* belong to the clade Ceratopsia.

Ornithischians were one of the two major clades of herbivorous dinosaurs during the Mesozoic, the other being the sauropodomorphs. Among ornithischians, thyreophorans were distinctive for many of them possessed rows of plates, spikes or large scutes covering their backs, which led to them being often described as “armored” dinosaurs. Ceratopsians, in turn, are known for the large frills and horns that some of its later members bore on their heads (Benton, 2014; Sues, 2019). Those two clades include some of the most famous dinosaurs, but Ornithischia also includes other very iconic lineages, such as the pachycephalosaurs and the duck-billed dinosaurs, which sadly are not represented in ZT2.

A common trend seen among ZT2’s ornithischians (and other animals as well) is that their proportions are a bit off. Their heads are usually too large, the legs are too stubby and the body is overall too short. This is likely due to the cartoon-like aesthetic adopted by the game and more of a case of stylization than of anatomical mistake. *Ankylosaurus* in particular seems to suffer from this (Fig. 3A), since the real animal was actually quite long and comparatively not very tall (Carpenter, 2004; Arbour & Mallon, 2017), while the ZT2 representation is much taller and not long enough. Moreover, the feet on all the ornithischians in ZT2 are too stocky and cylindrical, looking more like the feet of elephants than what would be expected of real ornithischians.

Odd proportions aside, there are relatively few anatomical inaccuracies in ZT2’s ornithischians. One of those is that the *Kentrosaurus* in ZT2 has its pair of lateral spikes placed on its hips (Fig. 3C). This was common in past reconstructions, but more modern reconstructions place these spikes on the animal’s shoulders, since close relatives

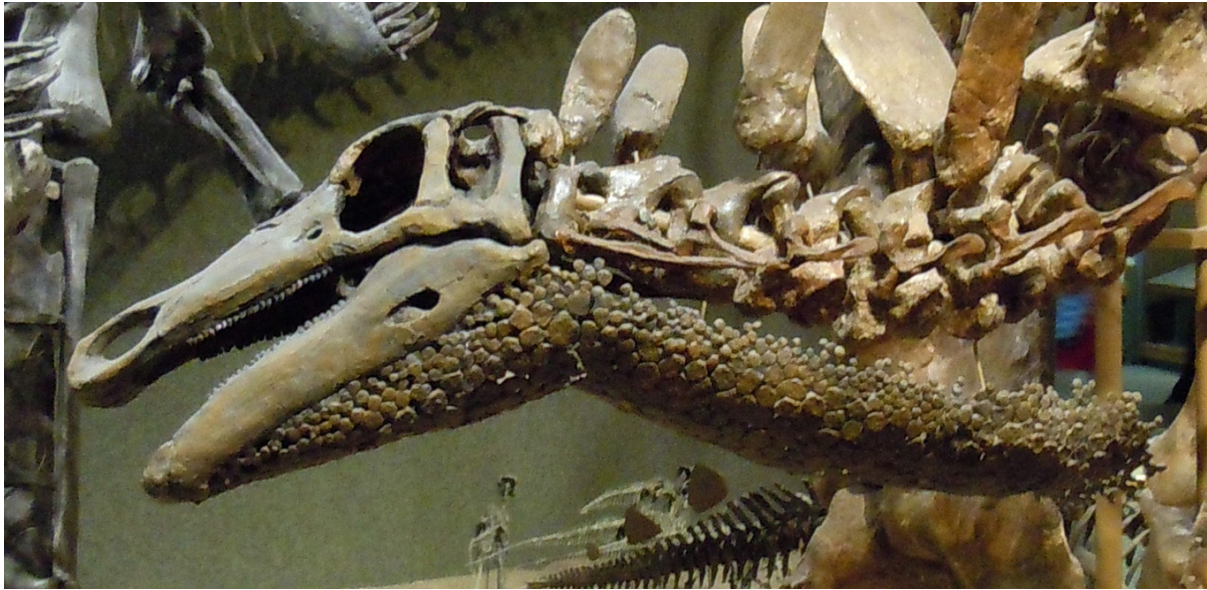


Figure 4. Reconstruction of a *Stegosaurus* skeleton at the Denver Museum of Science and Nature (photo by mrwynd, 2013, extracted and cropped from Wikimedia Commons). Note the large number of ossicles covering its throat.

of *Kentrosaurus* were known to have similar shoulder spikes (Galton & Upchurch, 2004). Another inaccurate detail is related to the fact that real-life *Stegosaurus* had its throat covered by an armor of ossicles (Fig. 4), which likely granted them protection from predators (Main et al., 2005). This is not represented in ZT2's *Stegosaurus* (Fig. 3E), although it is a relatively minor detail that would likely be barely visible in the game.

It should be mentioned that the ornithischians in ZT2 are featherless and presumably covered in scales. Feather-like integument has been recovered in some early ornithischian fossils, including ceratopsians (Mayr et al., 2002; Zheng et al., 2009; Ksepka, 2020). As such, it is possible that such structures were present to some extent in other ornithischians. As a matter of fact, it has even been suggested that feathers or feather-like structures could be an ancestral feature of all dinosaurs and other related lineages (Yang et al., 2019; Ksepka, 2020). However, current evidence suggests that the bodies of large ceratopsians and thyrophorans, such as the ones represented in ZT2, were covered mostly or entirely in scales (Ksepka, 2020). Thus, since we have no direct evidence of feathers in the species represented in ZT2, depicting them with a

featherless skin is a valid choice.

The biome preferences of the ornithischians in ZT2 are a mixed bag. Both *Ankylosaurus* and *Kentrosaurus* are depicted as living in the wetlands biome. Data from the geological formations in which *Ankylosaurus* fossils were recovered indicate that it inhabited an environment similar to a subtropical or temperate forest (Johnson, 1997; Ósi et al., 2016). *Kentrosaurus*, in turn, is found in a formation that is associated with coastal lagoons, plains and vegetated inlands with a warm and dry climate (Abberhan et al., 2002). Thus, it is possible that wetlands were frequented by both *Ankylosaurus* and *Kentrosaurus*, but it seems that they are not a good representative of their primary habitats.

Stegosaurus and *Triceratops*, in turn, are depicted in ZT2 as having a preference for the boreal forest biome. This is likely a reference to the fact that gymnosperms, like conifers, were the most abundant plants during the Mesozoic, while today they are only dominant in a few ecosystems, such as boreal forests (Leslie et al., 2018; Condamine et al., 2020). However, the climate during the Jurassic and Cretaceous periods (when *Stegosaurus* and *Triceratops* lived, re-

spectively) was far warmer than it is today, making cold environments like today's boreal forests very rare or even absent (Nordt et al., 2003; Sellwood & Valdes, 2008; Huber et al., 2018). *Stegosaurus* fossils have been found in a formation associated with a semi-arid environment composed of forests and fern savannas (Chure et al., 2006). Triceratops fossils have been recovered from several distinct geological formations, most associated with a variety of subtropical environments (Estes & Berberian, 1970; Derstler, 1994). As such, the choice of attributing one of today's coldest biomes to *Stegosaurus* and *Triceratops* is quite questionable.

Styracosaurus, on the other hand, is represented with a preference for tropical rainforests in ZT2. The formations in which *Styracosaurus* fossils have been found indicate a floodplain or swamp-like environment with a warm climate (Eberth, 2005). Tropical rainforest is overall not a bad choice to represent such environments, but perhaps wetlands would be a better choice. Nonetheless, it is important to note that biomes in the distant past were likely very different from any of today's biomes, making it difficult to find accurate analogs for them.

Theropoda

In total, nine extinct species of theropods are represented in ZT2: *Carnotaurus sastrei*, *Stokesosaurus clevelandi*, *Tyrannosaurus rex*, *Protarchaeopteryx robusta*, *Deinonychus antirrhopus*, *Utahraptor ostrommaysi*, *Velociraptor mongoliensis*, *Aepyornis maximus* (the elephant bird) and *Raphus cucullatus* (the dodo). Out of these, *C. sastrei* belongs to the clade Abelisauridae; *S. clevelandi* and *T. rex* belong to the clade Tyrannosauroidae; *P. robusta* belongs to the clade Oviraptorosauria; *D. antirrhopus*, *U. ostrommaysi* and *V. mongoliensis* belong to the clade Dromaeosauridae; and *A. maximus* and *R. cucullatus* belong to the clade Aves.

Theropoda is the most diverse out of the three major clades of Dinosauria and includes most carnivorous dinosaurs, some of which were the largest land predators of all time, although many omnivorous and her-

bivorous theropods are also known (Benton, 2014; Sues, 2019). Only a few lineages of theropods are represented in ZT2. *Carnotaurus* is only distantly related to the other theropods mentioned here, being a representative of a strange lineage of theropods that were the main predators in the southern continents during the Cretaceous. The remaining theropods in ZT2 are part of a large clade known as Coelurosauria, which includes a wide variety of dinosaurs ranging from the *T. rex* to birds (Benton, 2014; Hendrickx, Hartman & Mateus, 2015; Sues, 2019). In fact, both *A. maximus* and *R. cucullatus* are coelurosaurs and the only extinct dinosaurs in ZT2 that did not live during the Mesozoic.

Overall, the theropods in ZT2 have similar problems to the ornithischians. Namely, their proportions are quite odd and cartoonish, with heads and feet being too large in comparison to the bodies. In large theropods, such as *Carnotaurus* and *Tyrannosaurus*, the back is often arched upwards (Fig. 5A, E), while it should be essentially straight and horizontal. Furthermore, the heads of both *Carnotaurus* and *Deinonychus* look a bit too blocky and only vaguely resemble their real shapes (Fig. 5A, I). Another mistake, shared by most non-avian theropods in ZT2, is that their hands are pronated, which means their palms are facing down. Generally speaking, theropods did not possess the ability to pronate their hands and instead had their palms facing each other constantly, with very limited movement (Carpenter, 2002).

When it comes to feathers, theropods in ZT2 are a mixed bag. *Carnotaurus*, *Stokesosaurus*, *Tyrannosaurus* and *Deinonychus* are depicted as featherless, while the remaining theropods are at least partially feathered. For *Carnotaurus*, this is actually fine, since its fossil contains extensive skin impressions that suggest it was covered by scales (Czerkas & Czerkas, 1997). In regards to the two tyrannosauroids, the situation is trickier. Feathers have been found on several early tyrannosauroids and close relatives, indicating that they were an ancestral trait of this lineage. However, skin impressions

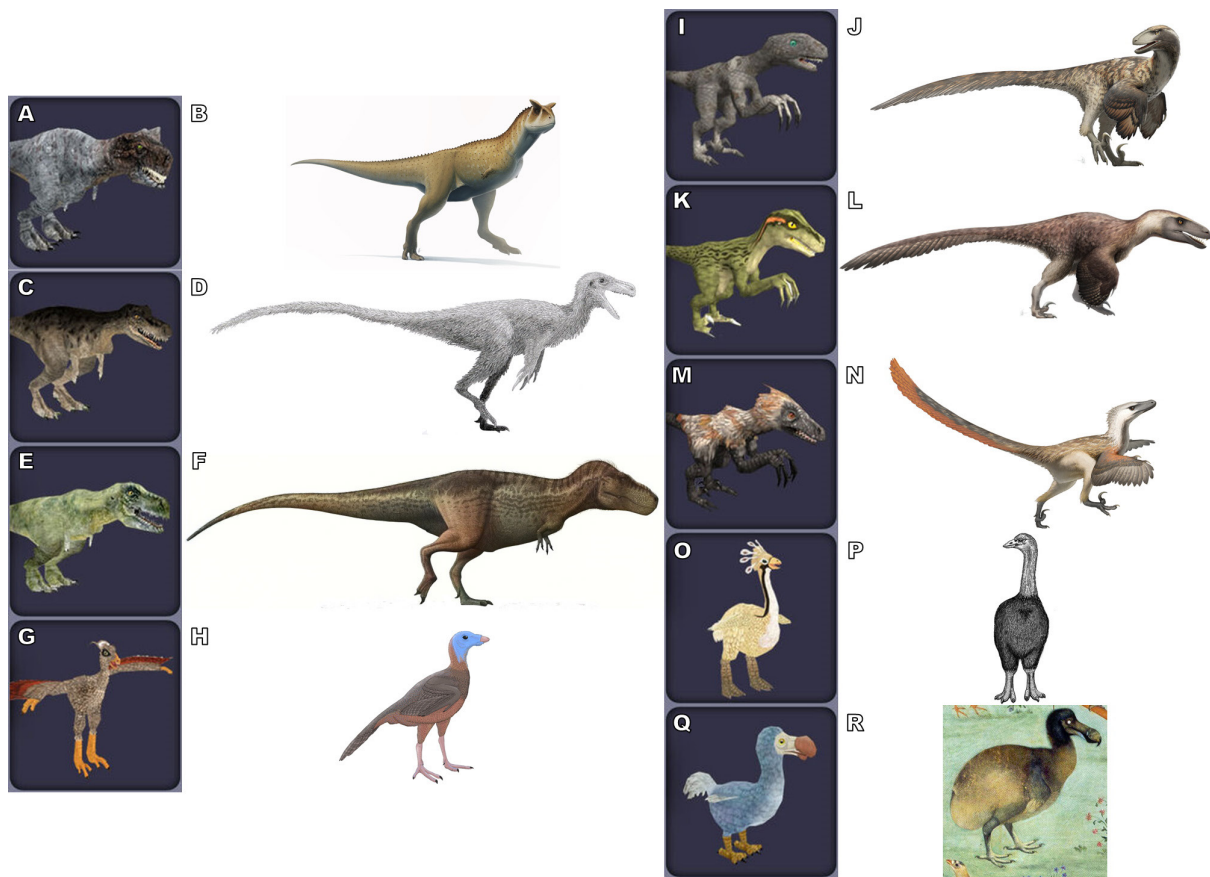


Figure 5. Theropods depicted in ZT2 and more accurate depictions of their real-life counterparts (reconstructions extracted from Wikimedia Commons). **A.** *Carnotaurus sastrei* as depicted in ZT2. **B.** *C. sastrei* by Fred Wierum (2017). **C.** *Stokesosaurus clevelandi* as depicted in ZT2. **D.** *S. clevelandi* by Tom Parker (2015). **E.** *Tyrannosaurus rex* as depicted in ZT2. **F.** *T. rex* by Steveoc 86 (2018). **G.** *Protarchaeopteryx robusta* as depicted in ZT2. **H.** *P. robusta* by Clara Takahashi (2020). **I.** *Deinonychus antirrhopus* as depicted in ZT2. **J.** *D. antirrhopus* by Fred Wierum (2017). **K.** *Utahraptor ostrommaysi* as depicted in ZT2. **L.** *U. ostrommaysi* by Fred Wierum (2017). **M.** *Velociraptor mongoliensis* as depicted in ZT2. **N.** *V. mongoliensis* by Fred Wierum (2017). **O.** *Aepyornis maximus* as depicted in ZT2. **P.** *A. maximus* by Acrocynus (2008). **Q.** *Raphus cucullatus* as depicted in ZT2. **R.** *Raphus cucullatus* by Ustad Mansur (c. 1625).

of *Tyrannosaurus* suggest that at least large portions of its body were featherless, which could be attributed to the evolution of gigantism in these animals (Bell et al., 2017). Although this matter is still debated, it seems that depicting *Tyrannosaurus* as featherless is fine. *Stokesosaurus*, on the other hand, is known only from a few bones (that is, no skin impressions are known). Considering it was a small-sized animal and closely related to other Jurassic tyrannosauroids, which are known to be feathered (Loewen et al., 2013), it's quite likely that *Stokesosaurus* would also be covered in feathers.

As for the remaining theropods in ZT2, however, the presence of extensive feather coverings is almost certain. Dromaeosaurids, such as *Velociraptor*, are among the

closest relatives of birds and some of the most unambiguously feathered dinosaurs we know of (Xu et al., 2003; Turner et al., 2007). While we still haven't found direct evidence of feathers in *Deinonychus* and *Utahraptor* fossils, it is only safe to assume that they were as feathered as their close relatives. The featherless *Deinonychus* depicted in ZT2 (Fig. 5I) is likely inspired by popular depictions of dromaeosaurids, such as those of Jurassic Park, but this is particularly puzzling considering that *Velociraptor* itself is depicted as feathered. *Utahraptor* is also depicted as almost featherless (Fig. 5K), with only the male possessing a crest of feathers on its head, which is also not nearly enough to represent what the real animal would have looked like. In regards to *Velocirap-*



Figure 6. *Protarchaeopteryx* fossil from the fossil-building minigame in ZT2 (left) compared to the Berlin specimen of *Archaeopteryx* (right; by H. Raab, 2009, extracted from Wikimedia Commons).

tor, while it is certainly the most accurately feathered dromaeosaurid in the game (Fig. 5M), its arms are mostly featherless, which conflicts with the evidence of large feathers constituting bird-like wings on this animal (Turner et al., 2007).

Protarchaeopteryx is case of its own (Fig. 5G). In real life, it was a small and feathered oviraptorosaur known only from a single skeleton (Qiang et al., 1998). As an oviraptorosaur, it was more closely related to dinosaurs like *Oviraptor* and *Incisivosaurus* than to birds. In ZT2, however, *Protarchaeopteryx* is depicted in a much more bird-like fashion, looking essentially like a bird with long tail, hands and teeth. In fact, it seems that the ZT2 *Protarchaeopteryx* was heavily based on the game's secretary bird, as it has a similar model and uses almost the same animations. While oviraptorosaurs certainly were bird-like, it seems like the game is trying to depict *Protarchaeopteryx* as an extinct bird like the much more famous and similar-named *Archaeopteryx*. This is further corroborated by the fact that the *Protarchaeopteryx* fossil used in the fossil-building minigame of ZT2 is clearly copied from the famous Berlin *Archaeopteryx* specimen (Fig. 6). Despite the similar names, *Protarchaeopteryx* and *Archeopteryx* are not closely related and not really similar at all. Perhaps the game developers intended to add *Archaeopteryx* to the game at first, but later decided

to change it to a larger and more terrestrial animal to make its implementation easier, or maybe to draw attention to a more obscure and often overlooked species.

The two extinct birds depicted in ZT2 are overall more accurate than their non-avian relatives. Interestingly, the elephant bird depicted in ZT2 is said to be *Aepyornis maximus*, which was considered the largest species of elephant bird by the time of the game's release. However, a recent study reclassified the largest *A. maximus* specimens in a new genus and species, *Vorombe titan*, which is now the largest species of elephant bird (Hansford & Turvey, 2018). It is uncertain whether the elephant bird in ZT2 should also be considered a representation of *V. titan*, since the game developers were likely trying to represent the largest elephant birds, or if it should remain *A. maximus* as was originally assigned. Regardless, its anatomy (Fig. 5O) is quite suitable and not so inaccurate for both *Aepyornis* and *Vorombe*, even though some details, such as the feather crest on its head, are merely speculative.

The dodo in ZT2 is also relatively accurate (Fig. 5P), but some things should be noted in regards to its color. Namely, it is depicted with a light blue and gray coloration. This is likely inspired by famous gray or blueish-gray depictions of the dodo, such as the *Edwards' Dodo* painting by Dutch



Figure 7. Roelant Savery's *Edwards' Dodo* (left) compared to Ustad Mansur's painting of a dodo (right). Images are public domain, extracted from Wikimedia Commons.

painter Roelant Savery (late 1620s; Fig. 7). However, the accuracy of such depictions has been questioned (Dissanayake, 2004). The most accurate depiction of a dodo is considered to be that of Mughal painter Ustad Mansur (c. 1625; Fig. 7), which shows the bird with a mostly brown plumage. The brown color of Mansur's dodo is consistent with other contemporary descriptions of this bird, indicating that dodos likely had a brown hue (Hume, 2006). As such, the light blue hue depicted in ZT2 seems to be inaccurate. It should be noted that most times we have no evidence on the color of extinct species and this discussion is relevant to the dodo only because it became extinct in historical times and so, many contemporary paintings and descriptions are available.

As a side note, there is another bird species present in ZT2's *Extinct Animals* expansion: the killer penguin. This is a fictional animal that can only be obtained by failing the cloning minigame. The killer penguin is depicted as a very large penguin with a toothed beak and eyes that glow. Overall, its design is similar to the rockhopper penguins of genus *Eudyptes* and the game even gives it the fictional scientific name *Eudyptes omnicidus*. It is depicted as very violent, being able and willing to kill literally every other animal in the game. The killer penguin in ZT2 is an easter egg and likely a reference to a bug in the original *Zoo Tycoon* game that made the emperor penguin able to kill most other animals. It is also described as being

native to Madagascar, which is probably a reference to the penguins in the *Madagascar* movie franchise. Nonetheless, despite the killer penguin being a fictional species, it is interesting to note that giant penguin species are known to have lived in the early Cenozoic era (Fig. 8) and some, such as *Anthropornis nordenskjoldi*, even reached sizes comparable to adult humans (Jadwiszczak, 2001).

Just like with the ornithischians, the biome preferences of the theropods in ZT2 contain a few odd choices. *Carnotaurus*, *Stokesosaurus* and *Utahraptor* are represented as boreal forest animals in-game, which is very unlikely for the reasons discussed earlier. The geological formation in which *Carnotaurus* was found is associated with an environment composed of estuaries and coastal plains (Pascual et al., 2000), although it is possible that it lived in other environments as well. *Stokesosaurus* was found in the same formation as *Stegosaurus* and thus probably shared the same semi-arid environment (Chure et al., 2006). *Utahraptor* was also found in a formation associated with a semi-arid environment composed of prairies and open woodlands (Joeckel et al., 2019).

Tyrannosaurus, *Deinonychus*, the elephant bird and the dodo are represented as tropical rainforest animals in ZT2. *Tyrannosaurus* fossils have been found in many different geological formations with

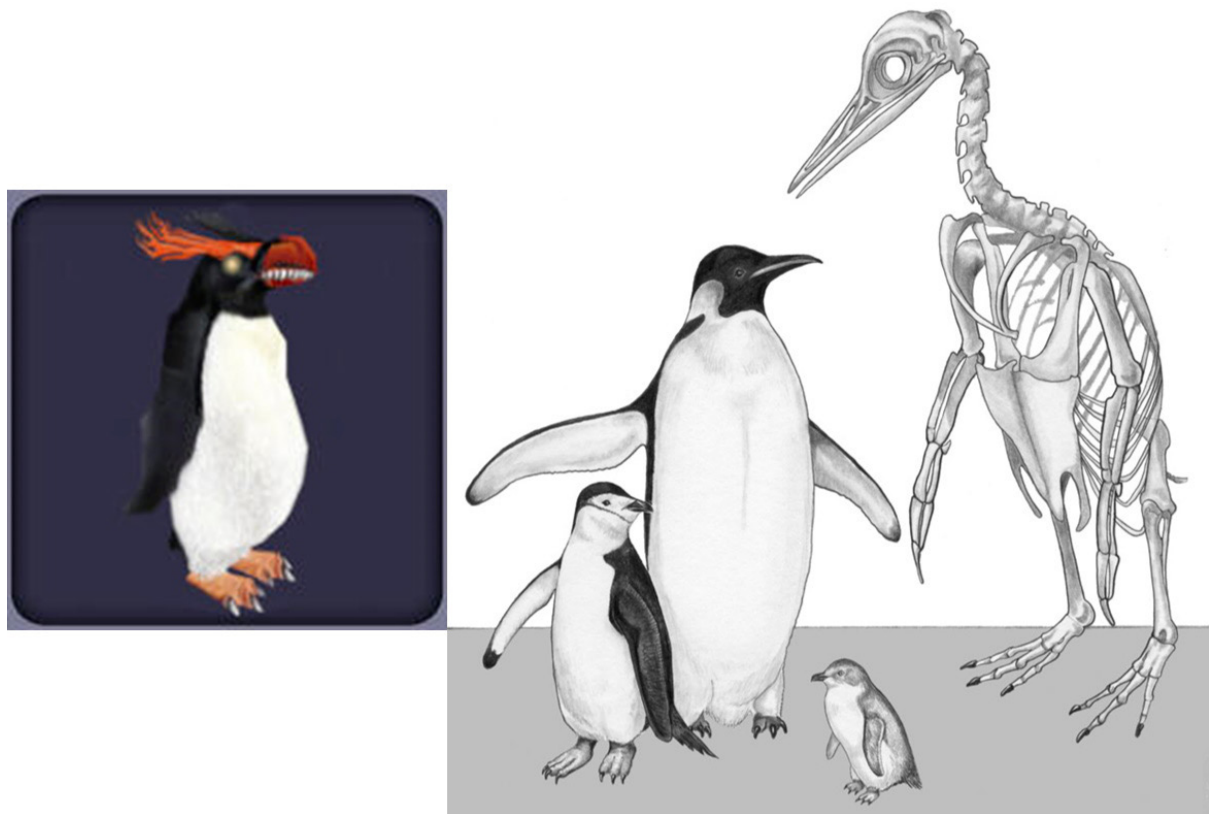


Figure 8. The fictional killer penguin as depicted in ZT2 (left) compared to artistic representations of three extant species of penguins (from left to right: *Pygoscelis antarctica*, *Aptenodytes forsteri*, *Eudyptula minor*) and a reconstructed skeleton of *Anthropornis nordenskjoldi* (right; by Kristin Lamm, reproduced from Ksepka et al., 2006: fig. 1).

paleoenvironments including subtropical plains and forests, both humid and semi-arid (Estes & Berberian, 1970; Derstler, 1994; Jasinski et al., 2011), indicating it could tolerate a wide range of habitats. *Deinonychus* has been found in formations indicating an environment composed of tropical or subtropical forests and swamps (Forster, 1984; Norell & Makovicky, 2004; Wedel & Cifelli, 2005), thus tropical rainforest is a suitable choice, although the wetlands biome would arguably be more accurate. The elephant bird, more specifically *Aepyornis maximus*, appears to have lived in forested environments in Madagascar (Torres & Clarke, 2018), making a tropical rainforest a reasonable choice as well. It is thought that the dodo lived in coastal woodlands in Mauritius (Fuller, 2002), which also makes tropical rainforest a relatively accurate choice.

Protarchaeopteryx is associated with the wetlands biome in-game, but the formation in which its fossils were found indicates an environment more akin to a temperate for-

est (Zhou, 2006). *Velociraptor* is associated with the desert biome, which is accurate, since the geological formation in which its fossils were found indicates a hot arid environment covered by sand dunes (Dashzeveg et al., 2005).

NOT A DINOSAUR, BUT A CLOSE RELATIVE

Also included in ZT2, *Deinosuchus hatcheri* (Fig. 9) is an extinct species of crocodilian that lived in North America during the Late Cretaceous period (Cossette & Brochu, 2020). Despite being often compared to them, crocodilians are not dinosaurs. However, both crocodilians and dinosaurs are grouped in a large clade named Archosauria, which also includes pterosaurs and other lesser-known extinct reptiles.

In modern times, crocodilians are the closest living relatives to birds, which also makes them the closest living relatives to



Figure 9. *Deinosuchus hatcheri* as depicted in ZT2 (left) compared to a more accurate depiction of a closely related species, *Deinosuchus riograndensis* (right; by Sphenaphinae, 2020, extracted from Wikimedia Commons).

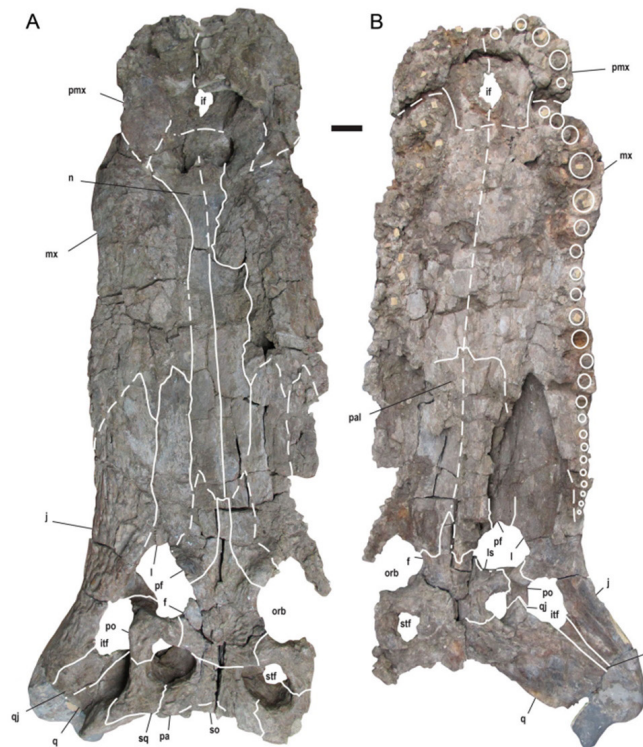


Figure 10. Dorsal (A) and ventral (B) views of a skull of *Deinosuchus riograndensis*. Images reproduced from Cossete & Brochu (2020: fig. 12).

dinosaurs as a whole (Benton, 2014; Grigg, 2015; Sues, 2019). As such, while *Deinosuchus* is not a dinosaur, it is part of a closely related lineage that shared its environment with many dinosaur species, making it appropriate to have a few comments about it here.

In regards to its anatomy, the ZT2 *Deinosuchus* is a bit strange (Fig. 9). *Deinosuchus* is a close relative of species in the genus *Alligator* and so, it probably looked somewhat similar to today's alligators. The overall shape of ZT2's *Deinosuchus* is certainly alli-

gator-like, although its proportions are also exaggerated and it could be argued that its snout is too short and narrow. The skull of *Deinosuchus* was proportionally larger, broader and longer than that of *Alligator*, with its dorsal profile being almost rectangular (Fig. 10). A strange detail about the *Deinosuchus* in ZT2 is that its skin is covered in what look like spike-like osteoderms⁴ (Fig. 9). The osteoderms on the real *Deinosuchus* were of similar shape to those of modern crocodilians and certainly not spiky like the ones in ZT2 (Cossete & Brochu, 2020).

⁴ Osteoderms are bony deposits that form scales, plates or other structures on the skin of non-mammalian land vertebrates.

Deinosuchus is represented with a preference for the wetlands biome in ZT2. This is relatively accurate, as the real *Deinosuchus* likely spent most of its time inside or near-by water and wetlands is the only primarily freshwater biome in ZT2. However, fossils of *Deinosuchus* are often found in formations associated with estuaries and brackish water bays, indicating that these animals might have inhabited coastal environments as well (Anglen & Lehman, 2000; Schwimmer, 2002).

CONCLUSION

Out of fourteen dinosaur species presented in *Zoo Tycoon 2: Extinct Animals*, five are ornithischians and nine are theropods. Since theropods are the most diverse lineage of dinosaurs, it is understandable that they have the largest number of species in-game as well. The species roster in ZT2 is interesting, as it includes not only famous dinosaurs, such as *Tyrannosaurus* and *Triceratops*, but also some rather obscure and lesser-known animals, like *Stokesosaurus* and *Protarchaeopteryx*. As such, the game serves its purpose as an educational tool by representing species that probably would not have reached the public's attention otherwise. However, the absence of sauropodomorphs in ZT2 is a wasted potential, as it leaves out one of the major clades of dinosaurs; its inclusion could have been an opportunity to represent some of the largest animals that ever walked the Earth.

Overall, it seems that the ornithischians are relatively more accurate than the theropods in ZT2. However, although there are many inaccuracies in the game's portrayals of the dinosaurs, it can be said that most of the time it does a good job at representing the most distinctive features of each species. The representation of ecological aspects for each species, such as their biome preferences, offers an interesting opportunity to discuss paleoecology as well, while most discussions regarding the accuracy of dinosaur reconstructions are purely restricted to anatomy.

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“Believe in Getter!” or “Believe in Humanity!”? *Getter Robo Saga* as a parable of technology

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Humanity’s technological progress is nothing short of incredible. If we consider that civilization is 12,000 years old, the vast majority of technological advances was produced in the last 200 years. 90% of all scientists that ever lived are alive today (Gastfriend, 2015). The stylized facts of growth, made possible by technology, are omnipresent in introductory economics courses (Fig. 1).

There is no doubt that technology changed our lives. Therefore, culture also reflected these new relationships between humanity and its creations, including in the area of philosophy and religion. The genre of science fiction is defined as an exploration of the relationships between humanity

and technology. This is clear in the “mecha” genre (メカ), which was inspired by the relationship between Japanese culture and technological advances, becoming a symbol of the anime industry.

The origins of the genre are in *Astroboy* (鉄腕アトム), by Ozamu Tesuka, first published in 1952, with its animated adaptation airing in 1963 (Hikawa, 2013: p. 1, 6; Giguk, 2018). Built by professor Tenma to replace his dead son, Astro’s inner conflict on being a symbol of progress and discovering if he can ever aspire to be truly human resonated with the post-war Japanese public, as “a gatekeeper of peace and democracy” (Nakao, 2014: p. 118). While, it did not focus on giant robots, Astro, being powered by

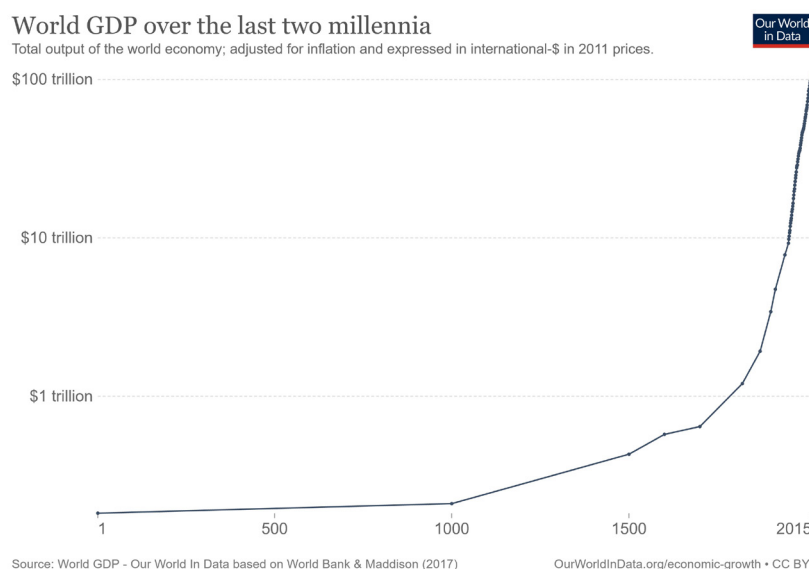


Figure 1. World gross domestic product (GDP) over the last two millennia. A logarithmic scale was used in order to properly show the changes caused by the first and second Industrial Revolutions. Source: Roser (2013).

nuclear energy, represented the hopes that the technology that once devastated Japan could lead it to a brighter future.

Although the first true giant robot series was *Tetsujin 28-go* (鉄人28号), published in 1956 and airing in 1960, robot anime would only become popular icons in the 1970s, with the airing of *Mazinger Z* (マジンガーZ) in 1972, written by the legendary Go Nagai. Mazinger was not controlled remotely, but its pilot, Koji Kabuto, joined together with it in the battlefield, after attaching in the Hover Pilder into Mazinger's head, as if he were its brain.

Soon, mecha anime was defined by three main tropes: 1) the gigantic size of the robots; 2) the fact they were piloted; and 3) their ability to transform or combine (Hikawa, 2013: p. 13). The last trait would be popularized by *Getter Robo* (ゲッターロボ), which stands out as a unique series. Created by Ken Ishikawa (1948–2006), with input from Nagai, *Getter Robo* started out as a manga in 1974 and quickly gained an animated adaptation (Fig. 2). It was the first series to use combining mecha (Hikawa, 2013: p. 18). Getter stands as an icon of Japanese culture, having influenced many creators such as Kazuki Nakashima and Hideaki Anno (Mrcheese, 2021: 4:00). Ever since its first issue, the Getter universe gained many spin-offs, but the manga continuity – the *Getter Robo Saga* – is Ishikawa's *magnum opus*.

The Getter series has a distinctive format: because the Getter machines are too powerful, they need a strong and insane enough trio of pilots, each representing the body, brains and heart of the machine. Ishikawa always had influences from Japanese history – as shown in some of his works such as *Yagyu Jubei Dies* (柳生十兵衛死す) and *The Samurai of the Meiji Restoration* (サムライたちの明治維新). As Mrcheese (2021: 2:47) said, "Ishikawa writes most of his characters as if they were modern-day ronin", doing what they want, but living through their unique moral code, while showing heroism when the situation gets tougher. This trait might be inherited from Nagai, who had a similar approach (Di Fratta, 2013: p. 4).



Figure 2. Cover of *Getter Robo*, the first volume the Saga. Source: Wikimedia Commons; © Go Nagai, Ken Ishikawa, and Dynamic Production.

Ishikawa was one of the most talented manga artists of his time. Mentored by Nagai, they worked together in the *Getter Robo* animated adaptation. Nagai had the general idea of a new mecha show and they had the idea of combining mecha after an accident during a test-drive, wondering how cool it would be if the cars combined into each other from different angles (Mrcheese, 2021: 10:10). At this point, *Getter* became Ishikawa's main work. When talking about his student and friend, Nagai always emphasized Ishikawa's talent and how well both his and Ishikawa's style complemented each other (Anonymous, 2021). The manga also took in more elaborate discussions on philosophy, religion and the nature of technology.

A synopsis of the *Saga* continuity is warranted. Be warned that from this point on there will be **spoilers**. If you want to experience the Saga unspoiled, please stop here and return when you finish. If you do not

mind, however, there are studies that argue spoilers might enhance the reader's experience (Leavitt & Christenfeld, 2013), especially if you are inclined to the analysis of themes in fiction.

THE GETTER SAGA

- *Getter Robo* (1974): the beginning of the series, it follows the pilots Ryoma Nagare, a genius martial artist, Hayato Jin, high schooler and terrorist¹, and Musashi Tomoe, judo practitioner and survivalist. Together, they form a dynamic trio and they are able to pilot Getter Robo against the Dinosaur Empire.

- *Getter Robo G* (ゲッターロボG, 1975): the first sequel to the series, after Musashi's death, he is replaced by Benkei Kuruma. The new antagonist is the Hyakki Empire, based on the folkloric *oni*, led by Emperor Burai. While the first series art style still was almost indistinguishable from Nagai's art, starting with *G* Ishikawa develops more his unique style.

- *Getter Robo Go* (ゲッターロボ号, 1991): set 16 years after the events of *G*, Hayato becomes the boss after everyone in the Saotome Institute vanished when a Getter ray experiment went wrong, according to official sources. Plasma technology has progressed to the point even small nations such as North Korea have their mecha corps. *Go* resembles more a political thriller in the beginning, with Japan not acting alone in the grand scheme of things anymore. The new enemy, professor Rando, launches attacks using his mechanical beasts from his base in the Arctic. The new Getter machine is not presented as a Super Robot² anymore, but as a Real Robot and it even has to be bailed out by the international team. The new pilots are Go Ichimonji, talented high

school athlete, Sho Tachibana, daughter of the main scientist, and Gai Dado, the mechanic of the base, enamored with the Getter machines. However, the plot changes significantly in latter chapters. It is here that Ishikawa's philosophical tropes start to appear and the implication of a "cosmic" scale in the *Saga*.

- *Shin Getter Robo* (真ゲッターロボ, 1996): an interquel between *G* and *Go*, it deals with an invasion of insectoid aliens after the defeat of the Hyakki Empire, which are revealed to be part of a confederation of aliens called the Andromeda Country. It also details the events that led to the Institute's desolation in *Go*. While it has the same cast as *G*, it is also where the nature of the Getter rays is explored in more detail.

- *Getter Robo Arc* (ゲッターロボアーク, 2001): the last work of the *Saga*, it follows the new Getter team: Takuma Nagare, son of Ryoma, Kamui, a half-reptiloid, and Baku Yamagishi, younger brother of Messiah Tayel from *Go*, and himself a religious figure. In *Arc*, the main antagonist is still the Andromeda Country; their attacks became so relentless that it called for a truce between humans and reptiloids. Unfortunately, *Arc* was left without a proper conclusion because of the cancellation of its magazine and Ishikawa's death.

Due to matters of space, only the original and parts of *Shin* and *Arc* are relevant for this text. The reader can be redirected to Mrcheese's (2021) retrospective on the entirety of *Getter* and Ishikawa's legacy.

The plot of the original *Getter Robo* manga is wild and very different from the anime. While the anime was aimed at young kids and resembled more a Saturday morning cartoon in the style of *Mazinger Z*, the manga was aimed at an older audience, with an edgier plot and gorier elements. The protagonists' manga incarnations are

¹ There was a small-scale communist insurgency in Japan. From 1969 to 2001, the Japanese Red Army promoted sparse terrorist attacks (Box & McCormack, 2004). Hayato was probably based on them, in terms of design because he turned his schoolmates into militiamen, promising revolution and would have tried to assassinate the prime-minister (out of boredom rather than a message) if he was not recruited by Saotome.

² For an evolution of Super and Real Robots in Japanese mecha culture, see Rusca (2017) and Gigguk (2018).

also more insane compared to the anime, bordering on unlikeable sometimes, but this makes their character development even more compelling.

The first chapter opens in the dead of the night, when the Saotome Institute, led by professor Saotome, successfully experiments with a new type of energy called "Getter Rays". The shadows of what seem to be dragons are sighted eclipsing the moon. Led by Emperor Gore, the Dinosaur Empire declares war on humanity. They are remnants of an civilization that once was and that were annihilated by the arrival of Getter rays to Earth, 65 million years ago. They only survived because they used their technology to build ships that could withstand the magma of Earth's mantle. Now, they seek to take over the surface and extinguish humanity from it.

The manga portrays the Empire as totalitarian invaders, in the same way many enemies in mecha anime were, like the Vegans from *UFO Robo Grendizer* (Pelliteri, 2009). Emperor Gore has no intention of dialoguing with the human race. For this reason, the reptiloid forces execute attacks with extreme prejudice and engaging in hostilely terraforming the Japanese islands. Besides attempts at xenocide³, torture and unethical experimentation are amongst the crimes committed by Gore. The organic quality of reptiloid technology is like the Vegan one: "melting, fleshy, and cybernetic forms versus the clean, rational, Japanese technology that is separate from, but implicates, humanity" (Pelliteri, 2009: p. 278). This organic technology gave rise to Ishikawa's most detailed panels and would be a staple of all antagonists in his works.

Many of their experiments made on humans remind us of the experiments made by Unit 731; the terraforming of Japan is similar to the imposition of Japanese culture over Korea and Manchuria. These are still topics of contention on manga and Japanese culture in general (Morris-Suzuki & Rimmer, 2002). By making these crimes similar to the ones committed by Imperial

Japan, Ishikawa is not just showing how urgent the reptiloids need to be defeated, but he is also trying to warn his readers of the dangers of imperialism that once infected his country, in an indirect way to not attract the ire of the revisionists.

Many times, the Getter team was cornered by the Dinosaur Empire. With a 65-million-year head start, the Empire's technology was superior and, if it was not for their weakness against Getter rays, the series would be short. They had a massive arsenal of mechasaurus that could be deployed with incredible speed. Not only that, they could send highly-trained infiltration soldiers or just overwhelm the humans with mutant newts or even a jellyfish that could just eat Japan whole. Only through sheer determination and cunning can humanity stand a chance; they put their faith in the unlimited potential of Getter Robo – "Believe in Getter!" It is really the fight of an underdog against an apparently invincible enemy and this costs dearly to the human protagonists. In a desperate attempt to stop a full invasion, Musashi overloads his Getter core and executes one of the greatest heroic sacrifices: "This is Getter's final power! [...] Even I couldn't believe the Getter was this powerful at maximum potential!" (Ishikawa, 2002: v. 2, p. 369–373).

At the moment the heroes defeat Emperor Gore, the threat of the Hyakki Empire emerges. The series enter its first sequel, *Getter Robo G*. But, as mentioned above, I will skip *G* and *Go*, and focus on *Shin* and *Arc*.

While the nature of the *Getter* rays is foreshadowed throughout the series and revealed in *Go*, it is in *Shin* that it is further developed – in fact, it might be argued *Shin* was written to wrap-up the events from *Go*'s last part. Getter *G* opens its "eyes" and Saotome realizes that it has somehow acquired a will of its own. Meanwhile, Ryoma sees visions of the future, of a massive Getter beast. A giant space cicada appears and tells humans to cease all research on Getter rays or else they will continue sending forc-

³ While genocide refers to destruction of a nation, xenocide is the destruction of an entire civilizational species.

es to destroy the Institute. The ghost of Burai calls Getter “the cancer of the universe” (Ishikawa, 2002: v. 7, p. 227) and Ryoma has another vision of a massive Getter machine annihilating an entire planet.

These enemies, a detachment of Andromedans led by sergeant Gimbug, came from the future, with the objective of destroying the Institute. The Getter team repels each attack, but, unlike the previous enemies, the Andromedans are not fighting for conquest. On the contrary, their dialogue implies they are fighting a losing war and have to take desperate measures. They are filled with as much determination as the heroes. Gimbug even proclaims: “we will save all of the inhabitants of the universe!” (v. 7, p. 338). All of that happens while professor Saitome becomes more and more unhinged in his desire to make the Getters stronger.

The reader is invited to question what is happening: why are the Andromedans so determined? What is the point of getting stronger? The Andromedans are defeated because an entity that could defy space appeared to lend its hand to the Getter team: Getter Emperor (Fig. 3). All of Ryoma’s visions led to Getter Emperor obliterating all “enemies” of humanity, with himself piloting the Emperor.

After the battle, Ryoma says something ominous: “You can’t control Getter rays... What’s going to happen to humanity if we continue to use Getter rays?! It may become a threat even greater than nuclear weaponry” (v. 7, p. 393–394). It is worth noting that the series has showed weapons that long surpassed nuclear ones in terms of destruction. Given the effects of the atomic bomb on Japanese culture, Ryoma is addressing the reader. He learned the same harsh truth Go learned in *Go*: Getter rays are evolution themselves and, somehow, sentient. They “chose” humanity. All the moments when an apparent *deus ex machina* saved the day, it was because the Getter rays responded to the prayers of determination of the protagonists. Hayato, on the other hand, takes Ryoma to a graveyard of prototype Getters and lists all the sacrifices made, saying “No matter what future lies ahead of us, we have no

choice but to advance” (v. 7, p. 398). He does not believe humanity is “being used” by the Getter rays, but if you read *Go* you know he will change his mind. Is “obeying” the Getter rays humanity’s destiny? Or should humanity defy them? But if destiny can be defied, was it because it was its destiny to be defied?



Figure 3. Getter Emperor after destroying a planet with ease (Ishikawa, 2002: v. 9, p. 274). Some fans consider it a Lovecraftian abomination, but we have to admit it is really an awesome abomination. Image extracted from the manga; © Ken Ishikawa, Go Nagai, and Dynamic Production.

The plot continues in *Arc*. Hayato becomes the new executive officer of the Getter team. Due to the constant Andromedan attacks, humans and reptiloids join forces. Kamui is a young pilot, highly popular among the reptiloids. His mother was brought as a test subject, in a situation that disturbingly resembles the “comfort women” from World War II (Morris-Suzuki & Rimmer, 2002). There are even sympathetic reptiloids, such as Professor Han, who regrets the crimes committed by the Empire and wants to make amends for a future where both races can coexist. However, the new emperor, Gore III, does not believe in

that and wants Kamui to betray the humans after the Andromedan threat is over, using his mother as a hostage.

The Human-Reptiloid Getter taskforce arrives in the future where the Andromedan attacks come from. They are overwhelmed by the enemy after landfall, but they are rescued by a military force, with helicopters, tanks and human soldiers, using apparently late 1990s military hardware. From one chopper, comes out no one else than Musashi Tomoe to greet the protagonists.

Arc's chapter 12 is aptly titled "The Alien 'Holy War'", with Musashi calling the protagonists' Getter machine, a "warrior of god" (v. 9, p. 254) before coldly executing the Andromedan prisoners. When confronted, Musashi casually explains this is a "holy war". In chapter 13, Musashi explains the backstory of how Getter Emperor saved humanity from hostile aliens and "ordered" them to conquer the universe. As humanity defeated more and more enemies, Getter Emperor grew stronger and larger. The conquest of the stars became humanity's "meaning of life": "We have been chosen by the god called Getter to become the greatest lifeform in the universe! The pinnacle of evolution is... universal domination!" (v. 9, p. 281).

Gone was the fun-loving heart of the original team's Musashi, who gave his life for his friends. This Musashi is a clone, created from the memories of Getter. He is humanity's representative, so all humans are just like him: having no purpose other than evolve, even at the cost of what makes them human. In many sci-fi works, humanity is portrayed as fighting a Locust-like enemy: the Zerg in *Starcraft*, the Tyranids in *Warhammer 40K*, the aliens in *Independence Day*. This time, humanity is the Locust.

Neither Takuma nor Kamui like what they see. Kamui gets separated from the

team and is brought to a Andromedan location, where he meets an oni. The oni gives Kamui a device that would allow him to construct "Bug" and to have a chance of defeating Getter Emperor in the past and crush humanity's sleeper imperialist ambitions⁴.

The protagonists manage to return to Earth and Kamui enacts a coup to take over the Dinosaur Empire. There are panels of Kamui fighting Takuma and Baku: while Kamui does this for the universe, Takuma agrees with him and announces he will not let the future they saw happen. Unfortunately, we will never know the conclusion due to Ishikawa's tragic passing.

TECHNOLOGY IN THE INTERSECTION BETWEEN THE PROFANE AND THE SACRED

One of biggest consensus among students of the economy is the importance of technology in the economic growth and development. Evolutionary models found a strong correlation between income and technological development in a nation, indicating that building a national system of innovation is a fundamental part of sustainable long-term economic development (Ribeiro et al., 2010). Most economists have been aware of the deep impact technology had in the human mind ever since the so-called Industrial Revolution. But what caused this?

Joel Mokyr has made a case that the Industrial Revolution was not a single event in Britain, but rather a cascade of many events that had their starting point in some English regions and extended through decades. They were translated into an open-access availability of scientific knowledge, political changes that gave protection to innova-

⁴ Comparisons with *Gurren Lagann* are inevitable at this point. Both Andromedans and Anti-Spirals have similar objectives, but, while it is never clear what the Spiral Nemesis actually is, we clearly know how Getter Emperor operates. See also the dark forest theory (Hendricks, 2018), in which civilizations will inevitably see each other as existential threats and, therefore, will try to exterminate each other.

tors – who, in many cases, had modest objectives when introducing an innovation, to either save labor or to make the production process more comfortable – in addition to the inventions themselves. They expanded the possibilities of production and society adjusted to this expansion, which caused the growth. In other words, what caused development was a “sharp decline in access costs” (Mokyr, 2010: p. 39). Greater availability of knowledge was translated into better access to tools that could create development. Soon, the innovation process could be rationalized, without depending of single entrepreneurs. Firms started to build entire departments to turn the innovation process into routine (Schumpeter, 1942 [2003 ed.]: p. 132).

This process is clearly seen in the evolution of the mecha anime genre and *Saga* in particular: a miraculous resource – the Getter rays – is employed in a “entrepreneurial” prototype in the original and, by the time of *Go*, the traits that made the Saotome Institute the forefront of innovation become diluted. The Getter designs become almost public domain, allowing different nations to catch up. The upward spiral is only stopped in *Arc* because the Andromedan attacks devastate civil society.

And, just like in *Saga*, there are costs to be reckoned. Joseph Inikori has argued that popular economic history tends to ignore that the British Industrial Revolution only happened because of the Atlantic slave trade (Inikori, 2020). The capture of Africans to serve as slaves developed a price mechanism to organize the production and trade of products and low-cost labor, allowing the regions of England that had direct contact with the Atlantic networks – Lancashire and Yorkshire – to be the focus of industri-

alization. In the end, this helped to develop technologies that allowed more developed nations to “crush resisting governments” in later imperialisms (Inikori, 2020: p. S168).

The Industrial Revolution itself evoked the image of “dark satanic mills”, from William Blake’s (1810) famous poem, a lament for a lost, more innocent time. The doubts about the project of technology have been studied by dozens of scholars⁵ and artists⁶. Both Blake and Ishikawa’s fears are similar because they touch upon the intersection between religion and the nature of technology. In a provocative essay, Rivers (2006: p. 519) argued that “technology has become a most powerful force because it challenges religion wherever it appears, but at the same time, it lays the foundation for itself as a religion”. Because we have expectations on technology, because we believe in it, it will take on religious traits. Szerszynski (2005: p. 817), reminding that “profane” comes from the Latin term *pro-faune*, the area in front of a temple, is puzzled that “modern secular thought and action understands itself as secular or profane in absolute, not relative, sense”. The appeal of many forms of popular science, such as cosmology – which has the most visible and awe-inspiring technology and is a large source of inspiration for the mecha genre⁷ – “seems to be its power to provide an overarching narrative for reality without making apparent normative prescriptions” (Szerszynski, 2005: p. 821).

Man creates Tool. What if Tool creates Man?

But there is an elephant in the room. *Saga* and the entire mecha genre is embedded in the Japanese culture and, as Kim (2015) argued, most discussions of religion and science and technology end up focusing on worldviews related to Western Christiani-

⁵ See for example the field of science and technology studies, which analyzes the relationship between people, technology and their production, attributing even agency to study how humans affect and are affected by technology (Latour, 2005). Due to matters of scope, I will not delve further into this topic, but it deserves at least a footnote due to its importance.

⁶ See van den Belt (2017) on *Frankenstein*. Gigguk (2018) notes that one of the main inspirations for Tetsujin was the classic 1931 *Frankenstein* movie, with Boris Karloff.

⁷ The launch of the James Webb telescope, in December 2021, was treated as a high-profile event.

ty, Western secularism included. Although Kim makes sure to note that the word for science “*kagaku*” (科学) was introduced after translating Western texts, proper non-Western ideas must also be considered.

DEUS EST MACHINA: MECHA AS A MEDIUM FOR SCIENTIFIC-RELIGIOUS DIALOGUE

Some would argue that mecha can be *kami* as well, for the sense of awe they can inspire. Unlike Western robots, Japanese ones are “exceedingly human” (Holland-Minkley, 2010: p. 38). They do not tend to work with Asimov’s Three Laws of Robotics, because they understand that their choice to do either good or evil is not very different than that of a human. Remembering the titular *Big O* is called a “megadeus” (megagod), Holland-Minkley (2010: p. 42) noted how the show’s characters pronounce the term with the same reverence for gods. In fact, a megadeus can judge whether the pilot is worthy, with either a “CAST IN NAME OF GOD, YE NOT GUILTY”, allowing the pilot to use its massive power, or a “YE GUILTY”

that may even kill the pretender. Angelic imagery is prominent in many designs, even in the *Gundam* universe, which is famous for having introduced the Real Robot genre (Fig. 4). In *Mazinger Z*, it is explicit that, while Koji is Mazinger’s brains, he cannot be Mazinger’s heart: it already has one of its own (Fig. 5).

Reviewing the work of the Japanese Buddhist philosopher Keiji Nishitani, Kim (2015: p. 163) argued that a possible Japanese relationship between its religious concepts and science would be the concept of *sunyata*, or “emptiness”. From the standpoint of *sunyata*, “life and death, and spirit and matter are taken as a mutually dependent relation”. Purely secular science is considered a (religious) problem because it is a science that makes its growth an end in itself, to satisfy ultimately selfish objectives. *Sunyata* allows one to understand the impersonality of the universe, that nothing can be its center, not even scientific progress. Thus, a bridge between science and religion can be built.

Would *sunyata* be a good source of applicability in *Getter*? References to Buddhism are abundant in the *Saga* (Fig. 6) and



Figure 4. Gundam model XXXG-00W0 Wing Gundam Zero, featured in the OVA *Mobile Suite Gundam Wing Endless Waltz* (Aoki, 1998). The details make it resemble an angel and were by no means unintentional. Image extracted from The Gundam Wiki (<https://gundam.fandom.com/>); © SUNRISE.



Figure 5. Koji Kabuto always treated Mazinger as if it was its own person and, for a rebellious teenager, that means a lot. In this episode, Spartan K-5 refuses to obey Dr. Hell's orders to fight and would rather chill. Koji understands its non-hostile intentions and comments: "Mazinger Z was built to be a war machine, but it doesn't like to fight very much. Ain't I speaking the truth, Mazinger Z?" Source: Onuki (1973), screen capture from Netflix; © Go Nagai and Toei.



Figure 6. The Getter Mandala, which shows how all Getter machines are linked. Mandalas are sacred spaces in Eastern religion, thus giving Getter a religious aura. Image extracted from Getter Robo Wiki (<https://getterrobo.fandom.com/>); © Go Nagai, Ken Ishikawa, Dynamic Planning, and Masao Otome Institute.

in Ishikawa's series *Void War Chronicles* (虚無戦記) (Mrcheese, 2021: 46:26). As said by Nagai himself, "Ishikawa Ken always sought a universal theme, an essence that pervades everything that he interpreted more as a form of energy instead of a spiritual entity like God" (Di Fratta, 2013: p. 21, translated). Go's climax illustrates this, of how Go can see how everything in the universe is united by a single thread. If "true" science unveils the truth about the universe, then "false" science is nihilistic, like a cancerous cell that forfeits its functions for chaotic growth, whose only objective is "universal domination". Getter Emperor will continue growing. At this point, it is only bigger than planets but it is estimated it will keep growing to the point of becoming a great attractor, like Tengen Toppa Gurren Lagann could be (Tomotani, 2016). Therefore, when Burai called Getter the "cancer of the universe", the metaphor is more than adequate. Unenlightened technology is the downfall of humanity.

Man creates Getter. What if Getter creates Man?

CONCLUSION: BELIEVE IN GETTER, BUT BELIEVE IN HUMANITY TOO

This article has analyzed Ken Ishikawa's *Getter Robo Saga* and hopes to have made some justice to his legacy. While we might never see a proper ending, Ishikawa wanted to create an effective cautionary tale yet full of the mad stuff that makes us fall in love with the mecha genre. Only someone with a great artistic talent and a curious mind to explore distinctive fields such as science and religion could have written *Saga*.

In spite of *Saga*'s inconclusive ending, Ishikawa had hopes for the future, to bring light to a dark forest. Throughout the entire *Saga*, it is constantly shown that what makes

humanity unique is not the fact the Getter rays chose them⁸, but rather its determination and capacity to build bonds. Getter may have been what united all teams, but what kept them united was the friendship and camaraderie they built with each other. While there is no in-story point of view from the Getter rays, in their inscrutable reasons to have chosen humanity, it is unlikely they understand this; maybe only on the instrumental level – like a soulless economist who claims friendship only serves to move the economy.

The *Arc* anime aired in 2021 and has been met with controversy whether it lives up to Ishikawa's legacy, but the ending still reflects his hope: the last scene is the Arc team about to fight against a "larval" Getter Emperor (Kawagoe, 2021). They all have smiles in their faces. The Getter rays gave humanity the privilege of being chosen to lead a crusade of evolution and power, and yet those humans defied them. It does not matter if the Arc team win or loses, they made their choice. Technology has also evolved humanity in practically literal terms, in contrast with the metaphorical ones of Getter rays. Therefore, it is up to humanity to decide if it will be lorded over by its own creations or take control of its destiny. And that is the parable of technology of *Getter Robo Saga*.

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⁸ It is worth noting that scientists have strong evidence to believe that cosmic rays have an important influence in life and evolution. The hypothesis is being discussed ever since the 1960s (see Shklovskii & Sagan, 1966: p. 66) and recent research has argued that cosmic rays were important in giving the helix structure to the DNA (Globus et al., 2021) in a way that might remind the reader of *Gurren Lagann*'s spiral power. It is, hopefully, unlikely that they are sentient like Getter rays.

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- **Villa, A. & del Negro, A.** _____ Pp. 1–8.
Morphological and behavioural aspects of the infected in *The Last of Us*: a natural science look at a videogame fungus-human parasitoid interaction
- **Interview** _____ Pp. 9–13.
Facing extinction in *Endling*
- **Salvador, R.B. & Kuroki, K.** _____ Pp. 15–28.
The sea slugs of *Shiroi Suna no Aquatope*
- **Rosa, R.M.** _____ Pp. 29–42.
A critical reappraisal of dinosaur reconstructions in *Zoo Tycoon 2: Extinct Animals*
- **Almeida, R.G.** _____ Pp. 43–54.
“Believe in Getter!” or “Believe in Humanity!”? *Getter Robo Saga* as a parable of technology