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DUNKLEOSTEUS TERRELLI: FIRST KING OF THE OCEANS

The Devonian Era was the Age of Fishes. From 419.2 million years ago (MYA) to 358.9 MYA, fishes dominated the Earth. In the vast, warm seas of the glacier-free planet swam the ancestors of today's fishes, most of which would look quite familiar. We'd certainly have no trouble recognizing the sharks and coelacanths of the age. But this was also the age of placoderms, members of a spectacularly successful branch that ruled the waves until their disappearance in the Hangenberg event that ended the Devonian.

The skull of the scariest creature ever (all photos Matt Bille)

Placoderms developed over 300 species. Founding species *Entelognathus primordalis,* from the watery days of the Silurian period, predates the Devonian itself. This fish was hardly a giant

predator (the holotype is 11 cm long) but it may have been the ancestor of everything from Germany's scarily-named "Rapacious Strong-Bone" fish (*Hadrosteus rapax*) to the flat "armored flounder" *Jagorina pandora*. One species from China, *Mizia longhuaensis*, looks like it has a Chinese word for rice, "mi," engraved on its armor, while *Romundia stellina* from Canada was covered in discs of armor. Australia's meter-long *Wuttagoonaspis fletcheri* perfected armor in an aesthetic sense, adorning its head with fins of bone that make it look like a spaceship from science fiction.

The ruling class has rulers, too, and there is no doubt who was in charge: *Dunkleosteus terrelli*. Six to eight meters long as an adult, *D. terrelli* was the culmination of several evolutionary trends. The placoderms had long since "invented" jaws, shown at their earliest in *Entelognathus*, which lived in what's now China 419 MYA. They'd had millions of years – since, approximately, the placoderms began in the Silurian – to perfect armor, from the little box-headed or shovel-headed fish of shallow waters to bearers of much heavier, better jointed protection. Pelvic fins, a huge step forward in allowing larger body size and eventually four legs, may have first appeared with the placoderms. Finally, placoderms came up with a more secure and certain method of reproduction: modern intromittent sex, paired with the first appearance of viviparity (bearing live young).

These developments reached a peak in *D. terrelli*. Early estimates of the fish as nine or even 10 meters long are out of favor today, but the animal was still bigger than today's largest predatory shark, *Carcharodon carcharias*, and undoubtedly heavier (the largest great whites may approach seven meters and 2,000 kg, with reliably measured records being a bit smaller). There is an exceptional Dunk specimen in the Cleveland Museum of Natural History estimated to have been 8.9m long in life, making it the size of a large male orca.

Discussing the Dunk with eminent paleontologist Dr. Robert Bakker

We know exactly what the skull and armor of this apex predator looked like. Richard Ellis (*Sea Dragons*, 2003) won the all-time Dunkleosteus description title by calling it "a giant staple remover." The Dunk in action wielded the biggest toothlike structures ever seen on Earth. Anything it could catch was simply chopped up in a living guillotine that sheared through flesh, cartilage, shell, or bone with ease. Once the Dunk reached adulthood, it had no enemies. Only its cousin *Titanichthys* (which most paleontologists consider a filter-feeder, although there is some dispute) rivaled it in size. There are ten or more species of *Dunkleosteus*, but *D. terrelli* was the apex predator of apex predators, a hypercarnivore: it ate anything, but nothing ate it.

This fish seems almost over-armored for its role, and maybe it was. The bone armor of its head and forebody was up to 50mm thick. Rings of bone gave extra protection to the eyes. There was

just nothing like the Dunk, before or since. While it was eventually shouldered aside for the predator size record by some of the great marine reptiles and the shark *C. megalodon*, plus a couple of toothed whales, it remains a unique and no doubt terrifying animal. Paleontologists have joked that the reason vertebrates first came ashore in the Devonian was because they got a good look at *D. terrelli* and announced, "We're leaving."

The Dunk's diet included other Dunks. Pieces of armor have been found with unmistakable Dunk bite marks, and others appear in the boluses these fish vomited up after the edible parts of their prey were digested. It's not clear whether Dunks hunted smaller specimens as a significant part of their diet or if this was opportunistic cannibalism, only carried out when two specimens happened to meet.

As the apex predator, the Dunk established itself wherever it liked. While countless remains are buried or long since destroyed under seabeds that are still seabed, famous Dunk sites include the Cleveland Shale of Ohio and other locations in North America and Morocco.

Dunkleosteus takes its name from Dr. David Dunkle, of the Cleveland Museum of Natural History. This set up some confusion over pronunciation: the most common version is "Dunk-LEE-oss-tee-us," but "DUNN-kel-OSS-te-us" is more correct. *Dunkleosteus* is a genus name now widely accepted, after being untangled from the older and once-conflated *Dinichthys* (still a good genus of its own, though with only one species) and the latter's proposed synonym or replacement, *Ponerichthys*.

WHAT WE DON'T KNOW

That's what we know. What we don't know… well, we don't really know what the fish looked like. Was the main armament constantly on display, or were there lips for streamlining and

keeping debris out of mouth? Lips seem probable, but we be sure from the fossils we have. How much, if any, of the bone armor was visible and how much was streamlined by skin and tissue? Probably most of it was covered (the forepart was, after all, the skull, although the brain was encased in a cartilage capsule suspended in it), but we're not sure.

What did the rest of the body, aft of the armor, look like? We can assume a full set of fins, and that, while the distribution is unknown, the fins need to add up to a substantial surface area (they were stabilizing and directing a head-forebody that, in large specimens, might have weighed a ton). We can only extrapolate from full-body impressions left by some much smaller placoderms, such as *Coccosteus*. These generally show a tail with the upper lobe much better developed than the other. There are countless variations extrapolated by scientists and artists: a bilobate tail like most modern fishes, a heterocercal tail like modern sharks, or even an eel-like tail.

The eel-like tail was always problematical to some experts because the tail, like the fins, needed plenty of surface area to propel this massive animal. A recent paper (Ferrón, Martínez-Pérez, and Botella, 2017) has reinforced this thinking. The authors used a recent find of fragmentary Dunk tail support cartilage (ceratotrichia) fossil material and the "relationship between the locomotory patterns and the morphological variability of the caudal region in extant sharks" to conclude a wide tail with well-developed lobes was indicated.

A fossil dealer at a show in Colorado Springs once told me he'd seen a full-figure impression fossil of a young Dunkleosteus but could not afford it. Crowd-sourcing information on this via the Internet indicated this was probably another species or possibly a fake: no one else I can find has seen it.

We also don't know how many young were carried, how big they were when born, how fast they grew, or how long they lived. We don't know whether combat was inevitable when large Dunks met, or whether they sometimes opted to "live and let live" or even shared bites of a large prey item. The modern spectacle of sharks or orcas gathering *en masse* to feast on a whale did not occur with Dunks, though, as prey simply wasn't big enough.

TEETH, OR NO TEETH?

Let us turn our attention back to the business end. Those choppers look like enormous teeth – as in, a big Dunk might sport hardware the size of small traffic cones – but what are they? Dunkle and others believed them extensions of the jawbones, a rare if not unique arrangement for a fish. Constantly resharpened by sliding and grinding against each other, they made the Dunk a predator that could chomp large fish in half and bite through armor and shells. A paper in 2003 (Smith and Johanson) reported "the present of tooth rows in more derived placoderms, the arthodires [the group including *D. terrelli*]," but this was a distinctly minority view until the question resurfaced in a 2012 paper in *Nature* by Martin Rücklin, *et. al*. (10.1038/nature11555A) team of five researchers argued high-tech scans of an arthrodire called *Compagopiscis croucheri* showed the "gnathal ossification" (biting plates) were not specialized bone but "composed of distinct teeth that developed in succession." The effect is a little like making a wall of candy corn "teeth" and covering it with bone "frosting."

This paper only started the discussion. While some scientists accepted the concept and built on it, exploring other species, and Rücklin and company published a follow-up in 2015, others found the concept unconvincing: an example is a 2016 paper by Carole Burrow of the Queensland Museum, with Yuzhi Hu and Gavin Young, arguing the other side of "…whether these gnathal plates were modified from external dermal bones, or had 'denticles' representing

true teeth with pulp cavities…" Burrow *et. al.* felt pro-tooth authors were misidentifying tubercles and other features of dermal bone and there was no evidence of enamel or other tooth features in their scans. Rücklin and colleagues fired back, and the professional but passionate exchange of abstracts, papers, and images continues. Asked to summarize the state of the debate, Dr. Burrow felt the evidence right now indicates that while some placoderms had evolved teeth, later species, including Dunkleosteus, took an evolutionary step *past* teeth and produced new all-bone weaponry. That's a debate I'm not going to solve here.

The placoderms never had the predator niches all to themselves. Countering the size and power of *D. terrelli* and its relatives with agility and speed, the two-meter sharks of the genus *Cladoselache* were widespread and successful animals, many of which have been found with *D. terrelli* in the Cleveland Shale. Many smaller sharks, like the bizarre "living ironing board" *Stethacanthus*, took the prey too little for an adult Dunk and provided many meals for the bigger fish. The "comb-spine" sharks (*Ctenacanthus*) arose during the Dunk's reign and long outlasted it, while the weirdest shark of all, the living pincushion *Iniopteryx*, crept along the bottom. Sharks survived the placoderms essentially because species don't fight one-on-one: *D. terrelli* could destroy anything in the ocean, but wasn't as adaptable as the sharks, chimeras, and others. We may never know exactly why none of the smaller placoderms survived the extinction events. Some authorities think increased competition was already wearing the placoderms down before the Kellwasser and Hangenberg events wrecked the ecosystem they were adapted to. The details of their disappearance are obscured by the sheer complexity of ecosystem changes and may have been due to plain bad luck. (Two old claims of post-Hangenberg placoderm fossils are today almost universally rejected.) The sharks grew larger after the Dunk's demise, but didn't exceed it in size until almost 340 million years later, when *Megalodon* showed up.

DUNKS IN POPULAR CULTURE

Western popular culture loves prehistoric beasts, especially dinosaurs. Indeed, dinosaurs crowd out almost everything else. Exceptions are the mighty shark *Megalodon*, which has its own subculture of books, movies, and other stuff, the mammoth, and marine reptiles, which share space with the dinosaurs (and are often incorrectly called dinosaurs) as well as having some properties of their own and cross-fertilizing with the interest in the folklore of sea monsters and lake monsters. Despite its size and fearsome appearance, the Dunk hasn't cracked the top group of species of popular interest.

In film, the Dunk is rare despite its visual appeal. The awful 2002 film *Megalodon* includes a baby Dunk: a character says the species grew to 12 feet long, a rare understatement. (I found the "baby Dunk" prop on line for $50, but I passed for reasons I can't remember.) In the 1984 French-Italian horror film *Monster Shark*, the Dunk is (really) one of the "parent" species used to breed a monster by crossing it with an octopus. If the film is notable at all, it's for presaging the idiotic hybrid creatures on the SyFy Channel. The 2008 Studio Ghibli animated film *Ponyo* includes a beautiful if not technically perfect Dunk among its varied cast of fishy creatures.

TELEVISION

The Dunk has made almost no impact on American television, popping up only in a few places, like the second episode of *Animal Armageddon* on *Animal Planet*. The British have done more programs, such as *Sea Monsters* (a.k.a. *Chased by Sea Monsters*), where the seven most dangerous seas in history included, in fifth place, the Devonian world of the Dunk. This program includes terrific CGI of the Dunk scaring hell out of a time-traveling explorer in a shark

cage. There have been fundraisers for both documentaries and dramatic films featuring our species, but none have made it to market.

NOVELS

The *Dinotopia* series of books included “The Fish,” a Dunk that guarded the underwater entrance to a cavern. In the Bas-Lag fantasy novels of China Miéville, Dunks are called "bonefish." There are several self-published or small-press novels, like *The Twelve Seas: Deep Lagoon*, by Lenore Langland, that feature the Dunk, and the animal makes an appearance in Steve Alten’s popular Megalodon series in the 2009 novel *Meg: Hell’s Aquarium*. It pops up again in *Meg: Nightstalkers*. Finally, there’s a 1969 novel for young readers, *Corey’s Sea Monster,* by Rutherford George Montgomery, that centers on a *Dunkleosteus* (here called *Dinichthys*).

BOOKS (NONFICTION)

Countless books on fossils, fishes, etc. have at least brief mentions of the Dunk. A 2005 example - this one for young readers - is *Dragons of the Deep: Ocean Monsters Past and Present* by Carl Wieland and Darrell Wiskur. *Deep Alberta: Fossil Facts and Dinosaur Digs* by John Acorn (2007) is of special interest because Alberta has produced some of the best Dunk fossils. The Dunk also appears in companion books to the above-mentioned TV documentaries, like the 2004 volume *Chased by Sea Monsters* by Nigel Marven and Jasper James. It appears only momentarily in Richard Ellis’ book *Sea Dragons*, just long enough for Ellis to create the “staple remover” line. A unique angle on the Dunk and its relations appears in the 2012 book *The Dawn of the Deed: The Prehistoric Origins of Sex*, by John A. Long. The placoderms were the first animals we know of to have “modern” sex (internal fertilization), and paleontologists are still

discussing just how the act was possible with all that armor. The male may have had to shove the female face-first into the seabed, which kind of takes the romance out of it.

GAMES

The Dunk appears briefly in *ParaWorld* and plays a bigger role in E.V.O. *Search for Eden* and *Ecco the Dolphin*. On Android phones, you can choose the Dunk as your player in the game *Dinosaur Assassin Pro*. There's also an old PlayStation game called *Aquanaut's Holiday* that includes the Dunk. There are some games in the *Jurassic Park-Jurassic World* line which allow you to raise your own Dunkleosteus. Dunk-based creatures, some with legs, appear in universes like *World of Warcraft*, and even the original *Dungeons and Dragons* from the 1970s included a Dinichthys.

Dunk art is popular: not only is the fish spectacular, but our lack of knowledge allows more speculative work than you can do with, say, *T. rex*. *DeviantArt* lists 1,585 Dunkleosteus and 82 Dinichthys works, from exacting scientific illustrations to speculative and fantasy art. Among classic paleontological illustrators, the great Charles R. Knight gave it a bit of a troutlike appearance ("pass the giant flies, please") while Zdeněk Burian opted for an extremely streamlined look, lively but with improbably tiny fins. John Sibbick did a couple of terrific Dunks that look both accurate and terrifying.

TOYS AND COLLECTIBLES

Some of the author's collectables

There aren't as many Dunks in the collectible works as there are velociraptors, but there are some very interesting ones. Safari has the most popular, with a streamlined body and a handsome golden tint (we know nothing about *D. terrelli*'s coloration). Favorite offers a soft-vinyl Dunk about 20cm long that fits the science well, although there's a splash of gold atop the dorsal fin that makes one think the artist was having fun. Schleich offers one that's very detailed and nasty-looking, but adds some details like a line of heavy scutes along the body that don't have any justification. This model also has a bigger soft-foam knockoff version from Haishunda (legal or not, I don't know). There are a few model-makers like Jeff Johnson who do very

detailed but more costly resin pieces, a hundred dollars and up. TST Advance of Japan sells the Shyaruru Palette plush toys, which include cuddly Dunks in several color patterns. CollectA just brought out a large (28cm) and beautiful new Dunk model. It's very detailed and carefully designed: the artist opted to bury most of the armor beneath flesh and sunk the sclerotic rings, correctly, into the eye sockets, making this the most streamlined Dunk except for the Safari toy. The surface detail is interesting: CollectA's Peter Leung explained, "The skin ornamentations are not scutes but I based them on the skin of the Devonian fossil fish *Gemuendina* and other skin decoration on those of large modern fishes such as the Wolf Fish." Those details and the asymmetrical tail with a large upper lobe may or may not be exactly right, but this model is a must-have.

More collectibles: the Dunk in models, stamps, cards and even a U.S. Navy Reserve unit patch.

There is, of course, nothing like seeing the Dunk for yourself. In the U.S, the Cleveland Natural History Museum, from which much research on the species continues to flow, has a large collection of fossils and a full-sized reproduction on display. Many other museums, including New York, the Smithsonian, Denver, etc. have skulls visitors can examine. The Rocky Mountain Dinosaur Resource Center near me in Woodland, Park, Colorado, Two Medicine Dinosaur Center in Bynum, Montana, the Lakeshore Museum Center in Muskegon, Michigan, and many others also offer Dunk exhibits. Others exist outside the U.S.: The Naturmuseum Senckenberg (Frankfurt) has an excellent display, and other Dunk exhibits pop up from Austria to Australia.

We will never see *Dunkleosteus terrelli* alive in our oceans, but its awesome presence and the effects of its passing are preserved for us in the rocks of the Earth. We can only marvel at what evolution once wrought.

See my page at:

https://www.facebook.com/DunkleosteusTerrelli/

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