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A literature review of horn and horn-like structures in vertebrates to correlate placement to function, behavior, and niche.

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By J.T. Cottingham (advised by Nancy Holcroft Benson)

Abstract

In this paper, the true horns of bovids are compared to the many horn-like structures found throughout the animal kingdom. Literary sources were reviewed for a variety of horn-like structures. The review was limited to extinct and extant terrestrial vertebrates. 3D models of these organisms' skulls and “horns” were created or acquired and 3D printed at the same scale to illustrate their differences and similarities and to analysis of their comparative size easier between large and small genera.

Bovids (e.g., *Bison*): true horns. *

To truly understand horn-like structures the term “horn” must be defined. “Horn” is a complex term used in many different fields and contexts within biology and beyond. Hickman *et al.* (2016) define horns as belonging to members of Family Bovidae and existing as “hollow sheaths of keratinized epidermis that embrace a core of bone arising from the skull.” Furthermore, they state, “true horns are not branched (although they may be greatly curved), grow continuously, and occur in both sexes.”

Bovids are one of the most diverse groups on Earth today with regards to horn shape and placement, representing a variety of defensive and sparring techniques (Gentry, 1990). The term “horn” only refers to that structure found in bovids, and they can be highly adaptable and highly specialized. They can be used for sparring, guarding, the more conventional ramming and interlocking, display, and even more advanced maneuvers such as parrying (Janis, 1982).

Bovids have been referred to as the hollow-horned ruminants, which refers to their hollow keratinized sheath overlying a bony core typically consisting of spongy bone (Gentry, 1990). No living bovids have branched sheaths or cores or shed seasonally. Both sexes may possess horns, e.g., domestic cattle (*Bos taurus*) depending on breed, bison (*Bison*), and goats (*Capra aegagrus*), or there can be sexual dimorphism in horn possession, such as in the Alpine Ibex (*Capra ibex*) or Afican Impala (Aepyceros melampus) depending on the species (Gentry, 1990).

Bison Fighting Video:https://www.youtube.com/watch?v=OLWQ59w1b58
Ibex Fighting Video:https://www.youtube.com/watch?v=SI307EWVtNc
Gemsbok Fighting Video:https://www.youtube.com/watch?v=-xqmBYJUlAY


A


B

A,B anterior view of Bison skull. A includes reconstructed sheaths. B only Bone materials. Sheaths sculpted based on image reference, oversized to allow for functionality.
IMBH R-163 skull specimen. Link to models of skull: https://sketchfab.com/3d-models/imnh-r-163-bison-cranium-5dc3c61b3aa04b04a1a97982fe1339d2

Giraffes (*Giraffa*): ossicones. *

Giraffes (*Giraffa*) are the largest ruminants of all (Geist, 2003). Brown *et al* (2007) looked at morphological data as well as some genetic data to formulate taxa with six distinct species that are all reproductively isolated though not by natural means. These six species range from the deserts of North Africa in Niger and Chad to the savannahs of Southern Africa in Namibia and Botswana and Eastern Africa in Tanzania (Muller, Z. et al, 2018). Giraffes are herbivorous, mostly feeding on leaves from trees (Geist, 2003). Giraffes have very fluid group dynamics with group sizes ranging from 1 to 44 individuals. Males tend to be less sociable and more likely to

break off on their own, while females have more rigid social groups and hierarchies (VanderWall, et al, 2014).

Giraffes and other giraffoids (e.g., pronghorn antelope, see below) have a variety of skull appendages, none of which are “true” horns as they are not bovids. Giraffes do however have “ossicones.” The ossicones are covered in skin similar to the velvet on a deer's antlers. However, this skin and the ossicones themselves are permanent structures shared by both males and females (Churcher, 1990). They are used in the giraffes’ unique style of neck sparring. The ossicones add extra weight to the head, which can in turn add to the force of the neck strikes and jab their opponent if the head hits them.The giraffe’s fighting style can be best described as mace like, relying on blunt force to damage their opponents (Churcher, 1990).

Giraffe Fighting Video:https://www.youtube.com/watch?v=KQLPL1qRhn8

Lateral view of IMNH R-2283
Link to model of skull: https://sketchfab.com/3d-models/imnh-r-2283-modern-giraffe-cranium-3a3f979fe5864c438cd44d2c058ff7b9

Pronghorn antelope (*Antilocapra americana*): horn-like structures. *

The pronghorn antelope (*Antilocapra americana*) is the only extant member of Family Antilocapridae, which—along with Family Giraffidae—is one of two families in Superfamily Giraffoidea. Pronghorn antelope are herbivores endemic to the west and the midwestern United States and a small portion of southern Canada (Geist, 2003).

The pronghorn antelope is an oddity among animals with horns and horn-like appendages. The unique keratinized epidermal sheath (keratovelvet) of pronghorns is more reminiscent of the

keratinized sheath in bovids than the skin covering the ossicones in other giraffoids (Bubenik, 1990). Notably, they exhibit a pronounced branch in the horn, and—most importantly—they shed the keratinized epidermis of the horn structure every season, leading to the creation of the term “keratovelvet” because of its distinction from true horns and from the velvet of cervid antlers (O’Gara, 1990).

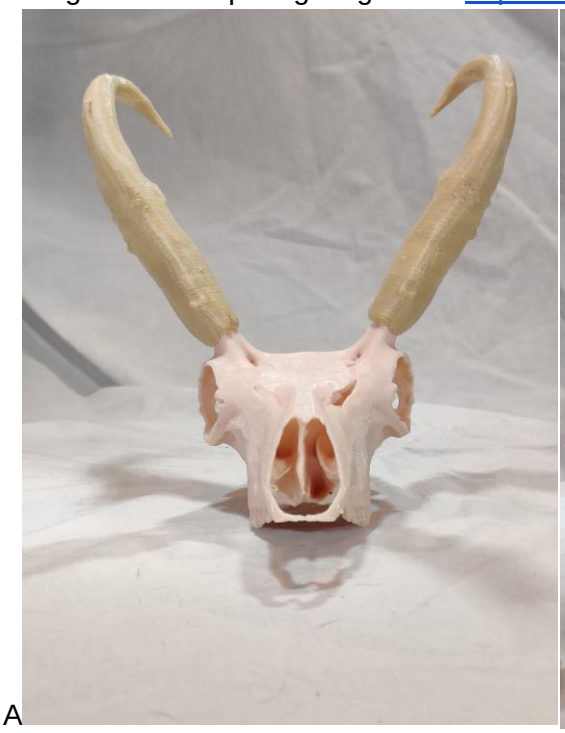
These horn structures are found in both sexes but female horns will never exceed ear length or will be absent (Animal Diversity Web). Males’ sheaths are perennial, shed after every mating season. They can be used defensively against predators such as wolves, bears, coyotes, and pumas, but this is not their primary purpose and the antelope will generally flee as a first line of defense (O’Gara, 1990).

Running is by far the best defense for pronghorns because they are the fastest land animal in regards to sustained running, with speeds approaching 100kph (Einarsen, 1948). This begs the question if they are so fast, faster than any predator in their environment, why have they evolved this?

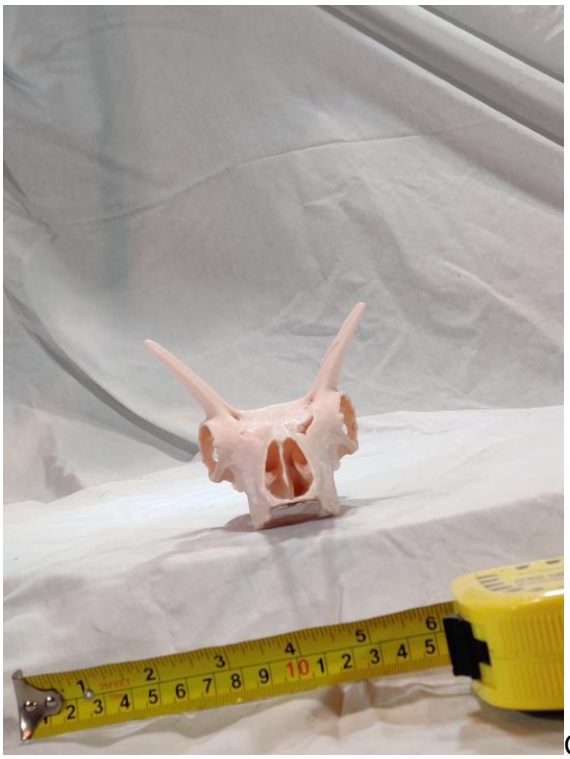
In his 1997 book *American Pronghorn: Social Adaptations and the Ghosts of Predators Past* John Byers uses his own research as well as compiling the works of others to support an amazing claim, that the pronghorns speed and social adaptations, among others, are remnants of a world long forgotten, when the plains of North America more closely resembled the savannas of Africa today. Byers combed through fossil data of the ecosystem at the time showing extraordinary evolutionary pressure from predators such as their modern day predators wolves, cougars, coyotes and bears as well as Pleistocene predators such as dire wolves, dholes, *Protocyon*, the giant short-faced bear, saber toothed cats, lions, jaguars, cheetahs, and hyenas. All of thes predators preyed upon the large quantity of megafauna at the time including various bison, camels, horses, zebras, tapirs, muskoxen, and even a few varieties of proboscideans (elephant relatives). Byers then talks about the adaptations that make pronghorns so fast and how these predators placed evolutionary pressure to spur these changes. Byers makes a very compelling case for these adaptations, Indeed other papers, such as *Ghosts Chasing Ghosts: Pronghorn and the Long Shadow of Evolution* by Michael Branch (2008), have been written on the subject bolstering the hypothesis.

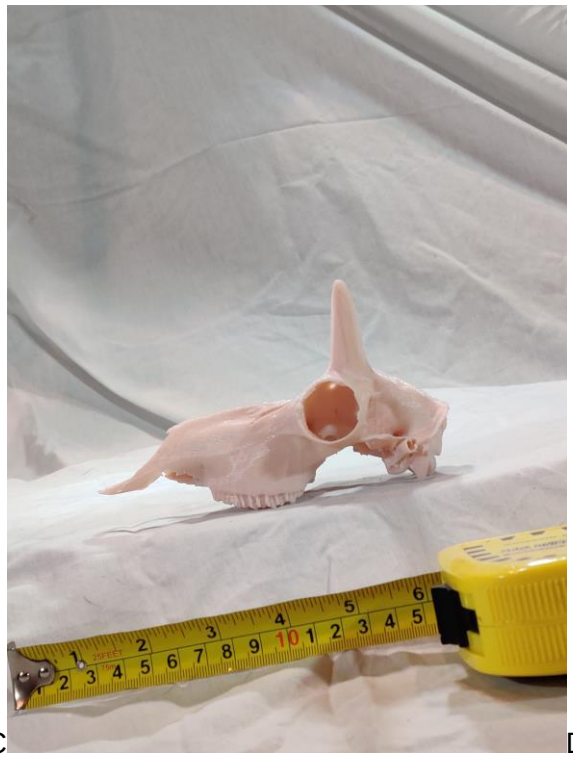
Is it possible that these ghost predators not only impacted the pronghorn's speed, but also their keratovelvet? Data made no mention of this, but it seems to be a viable possibility. Keratovelvet isn't nearly as useful as running against predators when there are so few that stand a chance of chasing them. When the pronghorns’ ancestors roamed the prairies contending with a wide variety of predators, and especially fast predators like the previously mentioned American cheetah and the variety of pack hunting animals such as wolves, dire wolves, and the American lion, it may have been a much more likely occurrence that a pronghorn would find itself cornered and having to defend itself. This may be another reason for both sexes containing some form of horn. It is clear there are many evolutionary factors involved in these “horns”. At least it seems to be an avenue of consideration and possible future research.

Pronghorn antelope Fighting Video:https://www.youtube.com/watch?v=HLTvnqDphls


A


B


C


D

A, anterior view including keratovelvet. B, lateral view including keratovelvet. C, anterior view only bone material. D, lateral view only bone material.

Pronghorn Skull from Idaho Visualization Laboratory IMNH R-143: https://sketchfab.com/3d-models/imnh-r-143-pronghorn-cranium-69f0d1b500cf40df80c14f7116af87fb

Keratovelvet Sculpted based on KU 42579 Pronghorn keratovelvet

Triceratops: ceratopsian dinosaur horns.*

Triceratops was a genus of large herbivorous ornithischian dinosaur from the Cretaceous period (~68 million years ago) living in what is now North America.

The genus *Triceratops* has two brow “horns” (“superorbital horns”) which curve slightly forward toward the animal's nose, plus a single nasal horn. The horns in *Triceratops* are called epi-ossifications. Epi-ossifications, also referred to as accessory ossifications, are separate ossifications that lie on actual cranial material rather than being extensions of already existing cranial bones (Horner and Goodwin, 2008). *Triceratops* has five epi-ossifications; the epi-parietal, epi-squamosal, epi-jugular, epi-nasal, and rostral all attach to, or lie above, cranial elements early in life (Horner and Goodwin, 2008). In addition, the parietal and squamosal bones are extended to form a frill behind the horns (Marsh, 1891). While a survey of the published literature failed to indicate whether these skull appendages were covered in a layer of keratinized epidermis (as in the true horns of bovids), it may still be considered as a possibility.

There is quite a bit of evidence as to the use of these horns. Farke (2004) tested whether *Triceratops* could have used its horns to spar with one another in a way similar to modern-day cattle and Jackson's chameleons, in which males spar over females, and possibly territory (Farlow and Dodson, 1974). The idea that ceratopsian dinosaurs sparred is supported by fossil evidence; this fossil evidence also supports the hypothesis that they used their horns for defense from the numerous large and fearsome predators in their environment (Farke *et al.*, 2009; Farlow and Dodson, 1974). Numerous skull lesions match the likely positions of the horns during sparring, and gashes that were most likely made by another animal, possibly a claw or tooth of a predator, have also been observed (Farke *et al.*, 2009; Farlow and Dodson, 1974).

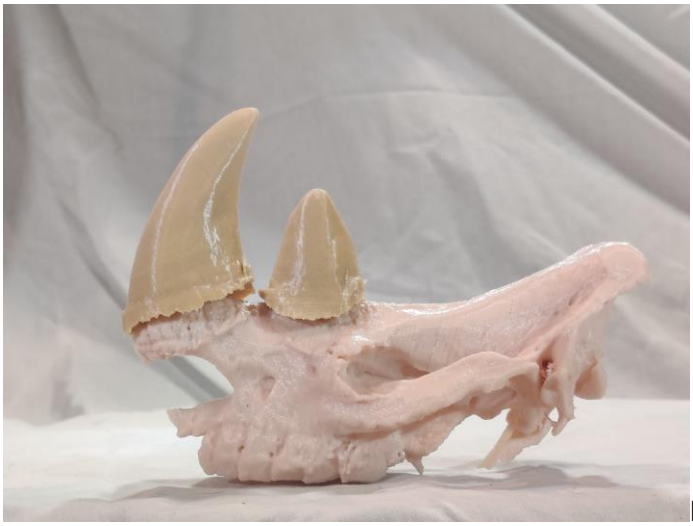
Lateral view of Triceratops horridus

Triceratops horridus Skull based on scan:https://sketchfab.com/3d-models/triceratops-horridus-178e061463754af3b521933e59c498bb printing file https://www.thingiverse.com/thing:1058961

Rhinoceros (Rhinocerotidae): keratin structure “horn” *

The white rhinoceros (*Ceratotherium simum*) is the second largest land mammal and is native to Africa (World Wildlife Fund). Despite what the name suggests the black and white rhinos do not differ much in color but rather in lip shape. Black rhinos’ pointed triangular lip is for browsing while the white rhino has a broad squarish lip for grazing on grass.(National Geographic) The white rhinos grazing behavior means that it resides in the African grasslands and savannas. It shares its habitat with many bovids possessing “true” horns in a dazzling array of shapes and sizes as well as other animals presenting other defensive features such as the African elephants’ ivory tusks. However when a layman is asked to imagine a horn, they often think of that on a rhino. Rhinos, however, do not possess true horns and their horn structure is actually very far from the true horns of Bovidae, the keratovelvet of Antilocapridae, or the ossicones of Giraffidae. Rhinoceros horns have no ossification whatsoever, rather their horn(s) comprise keratin with no bone core.(Sims. M, Yates. B, 2010)


A


B

A, lateral view of white rhinoceros skull. B, lateral view of white rhinoceros skull with horns.

Skull model was modified from WitmerLab at Ohio University which provided access to this data originally through the Visible Interactive Rhino website,, the collection of which was funded by NSF. The files were downloaded from www.MorphoSource.org, Duke University. https://www.morphosource.org/Detail/MediaDetail/Show/media_id/37129

White Rhino Fighting Video:https://www.youtube.com/watch?v=tslqq_8ELIw

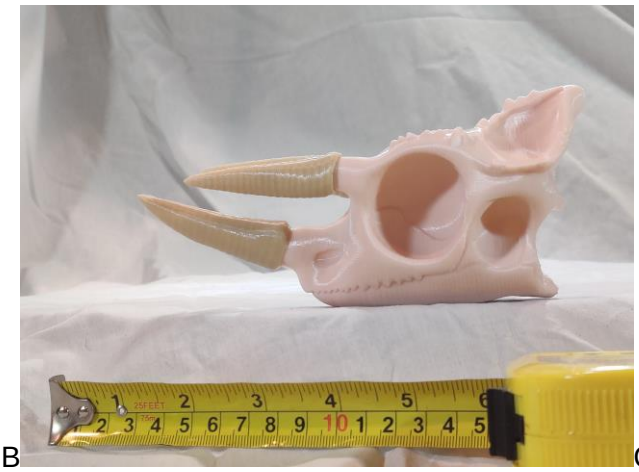
Jackson's Chameleon (*Trioceros jacksonii*): modern reptile horns *

Jackson's Chameleon (*Trioceros jacksonii*) are native to East Africa, mostly the Tanzanian and Kenyan rainforests (Spawls et al, 2002), but are invasive in the US in states such as Hawaii (Holland, Montgomery, Costello, 2010). In addition to some other chameleons' color-oriented battles, the Jackson's Chameleon primarily engages in horn locking in an attempt to flip the opponent onto its side. These chameleons have sexualy dimorphic horns, males have three front-facing horns, two brow horns connected to the orbitals directly and one nasal horn, the longest of the three (Animal DIversity Web). One interesting feature of Jackson's Chameleon horns is that images can be found of very misshapen horns that have grown in odd or even detrimental patterns. This often happens in the few females that end up growing horns (Animal Diversity Web).

Jackson's Chameleon Fighting Video (warning loud music):
https://www.youtube.com/watch?v=spYJvPCI1Vw

Male Jackson's Chameleon caught (abnormally long horns). https://www.kauaiisc.org/jacksons-chameleon/


A


B C

D

A, anterior view of skull without sheaths. B, lateral view of skull without sheaths. C, lateral view of skull with sheaths. D anterior view of skull with sheaths.
Jackson's Chameleon skull sculpt based on reference images.

Ceratogaulus: Fossorial horns *

Ceratogaulus is a genus of extinct fossorial rodents nicknamed "horned gophers" from the Miocene epoch of North America. Unlike all other rodents, they possessed structures highly

reminiscent of horns in structure but located on the snout. This is an oddity as they are one of only two fossorial mammals known to have structures like these. The other is a xenarthran "horned armadillo" from the Miocene of South America (*Peltaphylus*) (Hopkins, 2005).

It is unknown what these structures could have been used for or how similar in structure they would have been to the true horns of bovids. Several hypotheses regarding their uses have been put forward (Hopkins, 2005). One such hypothesis is the possibility that these structures could have been used to help aid in the digging of their burrows using a rare form of burrow digging known as "head-lift digging" in which the animal primarily uses its nose and the top of its snout and sometimes lower incisors instead of its claws or chewing with their incisors to break up dirt. Head-lift digging is not seen in any modern day North American mammals but is seen in two fossil groups from the Miocene and Oligocene (Hopkins, 2005). However, Hopkins (2005) notes that this hypothesis is contentious due to lack of impressions of horn impacts on the sides of their burrows. *Ceratogaulus* has many features associated with scratch digging and head-lift digging such as an anteriorly tilted occipital plate, slightly thickened nasal bone, most likely very strong neck muscles. However, despite possessing these adaptations, Hopkins (2005) concludes that *Ceratogaulus* was not a head-lift digger, citing inconsistencies with evidence at hand and our knowledge of modern head-lift diggers. She argues that the horns would most likely be ineffective in digging due to their position on the posterior of the nasal bone. The horns would have a very short sweep making them not very useful for digging. Hopkins (2005) also cites the orientation of the nasal bone as evidence against head-lift digging; the anteriorly oriented nasal bone would make it very difficult for the animal to orient their digging in the anterior direction which would be necessary.

Hopkins (2005) also states that it is unlikely that these horns were used for sexual combat due to the apparent lack of sexual dimorphism in horns. Another hypothesis is that these horns developed as extra defense due to environmental changes at the time forcing them to spend more time outside of their burrows. It is also completely possible that both hypotheses are correct or at least semi-correct (Hopkins, 2005)


A


B C

A, lateral view of *Ceratogaulus* skull. B,anterior view of *Ceratogaulus* skull. C, dorsal view of *Ceratogulus* skull.

Ceratogulus skull was sculpted based on reference images then modified with photos and measurements of specimen KU-6886.

White-Tailed Deer (*Odocoileus virginianus*): Antlers *

The White-Tailed Deer (*Odocoileus virginianus*) is a cervid native to North, Central, and South America, however closely related Cervids reside all over the world, particularly in the Americas and in Eurasia (Bubenik, 1990). Cervids are known for head ornamentation referred to as antlers. Antlers comprise bony ossifications covered in a layer of skin known as velvet; the velvet is torn off by the individual after growth. Generally, antlers are usually grown seasonally by males. Antlers are then shed after the mating season. However, this is not always the case, e.g., reindeer/caribou (*Rangifer tarandus*), in which both males and females grow antlers with males generally shedding their antlers in winter or spring while females generally shed their antlers in summer. While they can and most certainly do serve a defensive purpose, their main purpose is as a sexual display to attract females (Bubenik, 1990).

White-Tailed Deer Fighting Video:https://www.youtube.com/watch?v=rD4tPPSBuiQ

Comparison of cranial anatomy in horn and appendage location among target specimens.

Comparison between the Pronghorn Antelope and Giraffe.—Both giraffes and pronghorn antelope have bony growths slightly behind the orbits and above the temporal fenestra. However, when viewed laterally, the pronghorn antelope bony cores appear to rise straight up from the skull, while the giraffe ossicones are angled posteriorly. (Figure 1.)

(Fig.1) Giraffe and Pronghorn side by side lateral view

Comparison between The Jackson's chameleon and *Triceratops*. Both Jackson's Chameleons and *Triceratops* have three "horns," one nasal and two from around the brow or orbit. The position of these three horns indicates that they could have very similar if not near identical fighting styles (locking and trying to flip each other over). In comparing the Jackson's Chameleon to *Triceratops* we can see a very similar placement of the nasal horn with a slight change in orientation. Jackson's Chameleon's nasal horn is very much perpendicular to the body with a slight curve upward and is much longer then the orbital horns, while *Triceratops* has a very similar horn though much smaller.

The orbital horns are very different however. While the chameleon's orbital horns jut straight out from the orbit anteriorly facing in line with the body, *Triceratops* horns begin posterior to the orbit

rising rapidly in an upward direction, curving anteriorly; the base of the horn almost seems to make up part of the orbit itself. One possible reason for *Triceratops'* different horn orientation may be the disparity in sizes between the two, or another possible reason could be that *Triceratops* horns are more adapted for offense. *Triceratops* was a large herbivore in an area with a variety of large predators. It is hypothesized that many large predators would usually stay away from adult healthy *Triceratops* due to their deadly abilities (Farke, 2009), whereas the Jackson's Chameleon has much to deal with being considerably smaller in size and thus more vulnerable, with many predators that won't think twice about attacking them. Jackson's Chameleon is also arboreal and, combined with its much smaller body size than *Triceratops*, is open to more predation from birds of prey, snakes and some monkeys not to mention the predators in areas they are invasive to such as dogs, cats and raccoons (Animal Spot, 2020). It is unknown if *Triceratops* horns would have keratin sheaths like in bovids or in the Jackson's Chameleon. Farlow and Dodson (1975) directly compare the Jackson's Chameleon and certain bovids to *Triceratops* in fighting style.


A


B


C

A,C: Lateral view, B: anterior view.

Material Examined

Ceratotherium simum: KU157349 (skull); 157350 (horns)
Giraffa camelopardalis: KU83572 (skull)
Ceratogaulus: KU 6886 (skull)
Antilocapra: KU 42579 (skull+sheath)

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