



Konik, Tarpan, European wild horse: An origin story with conservation implications

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ABSTRACT

Horses are gaining importance in European nature conservation management, for which usually so-called primitive breeds are favored due to their claimed robustness. An increasingly popular breed, the Konik horse, is often said to be the direct descendent of the alleged European wild horse, the Tarpan. However, both the direct descent of the Konik from European wild horses and the existence of the Tarpan as a wild species are highly debated. In this review, we scrutinized both contemporary research and historical sources and suggest that the Tarpan and the Konik as its direct descendent are manmade myths that hinder effective conservation management. We did not find evidence that the Tarpan was a wild horse rather than a feral horse. We did not find any evidence either for a closer connection between the Konik and any extinct wild horse than between other domestic breeds and wild horses. We discuss three perspectives on why the myth has become widely accepted and survived to this day: a historical-political, a biological-ecological, and an emotional perspective. It seems that the origin story of the Konik and its connection to the Tarpan was shaped by personal and political interests, including nationalistic ideas. These as well as general human emotions towards horses have influenced researchers and laypeople to keep the myth alive, which has been possibly negatively impacting contemporary nature conservation. Indeed, today's Koniks originated from a small founder population of only six male lines that were selected according to their phenotypic traits, with the aim to rebreed the 'wild Tarpan'. Strict breeding practices have led to high inbreeding levels in recent Konik populations, which may undermine nature conservation purposes. Therefore, we suggest that mythologized origin stories should not be an argument for selecting breeds of grazers for nature conservation.

1. Introduction

Natural meadow ecosystems in Europe are increasingly managed using large herbivores as ecosystem engineers. Such management schemes often involve so-called primitive horse breeds (Chodkiewicz, 2020; Fraser et al., 2019). Indeed, domestic horses can counteract woody plant encroachment and the spread of invasive plant species (Cosyns et al., 2001; Henning et al., 2017; Svenning et al., 2016). Domestic horses are thus thought to be capable of taking the ecological role that extinct wild horses once played (Sandom et al., 2014; Vermeulen, 2015) by contributing to a dynamic vegetation equilibrium in European temperate ecosystems (Vera, 2000). Nature conservation initiatives in Europe, such as Rewilding Europe (<https://rewilding-europe.com>), are successfully popularizing grazing by

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horses, emphasizing the importance of robust and local horse breeds (Linnartz and Meissner, 2014). One of these breeds, the Konik, stands out from the others as it is generally associated with the Tarpan, the alleged “original European wild horse” (Sutherland, 2002). Although the Tarpan officially went extinct a century ago (Groves, 1986), it is not only claimed that Koniks are direct descendants of this alleged wild horse but in some cases that Koniks *are* Tarpans. This practice of calling the Koniks Tarpans seems to be attractive for some contemporary conservationists in Europe (see, e.g., Michelot, 2015; Widstrand, 2016).

However, the history of the European wild horse has been controversially debated during the past centuries, and discussions continue until today, both in science and applied nature conservation (Linnell et al., 2016). A wide range of opinions have been proposed about the Tarpan, without a clear consensus (see Table 1). For example, there are claims that the Tarpan is a present-day equine species (Bernáldez-Sánchez and García-Viñas, 2019), while others doubt that it had ever been a wild species and not simply a domestic breed (Ewart, 1906; Linnell et al., 2016; Smith and Gesner, 1841; Librado et al., 2021).

The origin of the Konik has also been debated (Forrest, 2019; van Vuure, 2014, 2015), with strong ties to the question of the Tarpan. Some believe that today's Koniks are direct descendants of the Tarpan (i.e., of the European wild horse; e.g., Gurgul et al., 2019; Michelot, 2015; Stefaniuk-Szmukier et al., 2017), claiming that there is a “genetic line that has never really been broken” (ARTHEN, 2012) between Tarpans and present-day Koniks. However, others argue that both the Konik and the Tarpan are results of a certain “bricolage” (Lizet and Daszkiewicz, 1995), products of manmade myths (Forrest, 2019) rather than direct descendants of truly wild horses.

In this review, we aimed to summarize different perspectives on the theory of the Tarpan as a wild horse and how this theory affects contemporary nature conservation, in view of the growing number of Koniks grazing in European nature reserves. We traced back original literature until the 1760s and screened contemporary articles, both from the scientific and the grey literature, to describe the origins of the story behind the common beliefs that the Konik is the closest descendant of the Tarpan and that the Tarpan is the extinct ‘European wild horse’.

In the following, we thus start with a description of the historical and anecdotal events leading to the alleged discovery of the Tarpan and outline the story of how the Tarpan transitioned into Konik (Section 2). In Section 3, we then provide a summary of the different perspectives on how and why this story persisted to this day, and on the evolutionary and phylogenetic origin of wild and domestic horses in general. In Section 4, we discuss practical implications of the origin stories for modern nature conservation.

2. The origin story of the Konik-Tarpan confusion

2.1. The beginnings: inventing the wild horse

The story about the Tarpan probably started in 1768. A young and ambitious German naturalist, Samuel Georg Gmelin, had been travelling around the Russian steppes, commissioned by the empress Catherine II. The task was to discover and describe the Russian empire.

Soon after launching on his expedition, as we can read in his memoir, Gmelin (1770) was in search of wild horses. Rumors from locals reached him that some of these animals were roaming just around the region he was travelling through: a group of six passed near a town called Bobrowsk just a few days before Gmelin's arrival. To ensure the success, he equipped himself with a group of skilled local hunters. It did not take long for the locals to find the group of horses and thus fulfil the wish of the – likely well-paying – Western traveler. According to the locals, the group consisted of both “wild” and “Russian” horses and their “bastard” offspring (Gmelin, 1770). The hunters managed to kill the leading stallion and two mares and captured the hybrid foal alive (Fig. 1). Gmelin briefly summarized the characteristics of these horses in his memoir: They were mouse-colored [“Mausfarben”] with very long hair that looked more like a fur than a horse hair [“Ihre Haare sind sehr lang, und so dicht, daß man mehr einen Pelz, als ein Pferdefell, anzufühlen glaubt”]. The feet below the knee were black [“die Füße sind unterhalb ihrer Mitte bis an die Klauen schwarz”]. Their eyes were fiery [“ihre Augen sind feurig”]. Their ears were either short or long like that of a donkey [“entweder in der Grösse der zahmen Pferde ... oder lang, bey nahe wie Esels-Ohren”]. Their mane was very short and frizzy [“Ihre Mähne ist sehr kurz und kraus”]. Their tail was more or less hairy but shorter than that of tame horses [“Ihr Schweif ist mehr oder weniger haarig, doch immer etwas kürzer, als bey den zahmen Pferden”] (Gmelin, 1770).

A few years after Gmelin, Pieter Boddaert created a scientific name based on Gmelin's memoir: *Equus ferus*, Wild horse, Cheval

Table 1
Variations about explanations of what a Tarpan is in the scientific literature.

| What is a Tarpan? | |
|---|--|
| Synonym for wild horses | Kovalevskaya (2020) |
| A subspecies of a wild horse that lived into historic times | Groves (1994); Kefena et al. (2012) |
| European wild horse | Heck (1952); Kolbas (2002); Spassov and Iliev (1998) |
| Russian wild horse | ICZN (2003) |
| Ancestor of the domestic horse | Bökönyi (1987); Rudik (2003) |
| Feral horse (domestic breed living in a wild state) | Ewart (1906); Nobis (1971); Pallas (1773); Ståhlberg and Svanberg (2011) |
| Ecomorphotype of the Eurasian wild horse | Bennett and Hoffmann (1999) |
| Plateau horse | Jordana et al. (1995) |
| Steppe wild horse | Pasicka (2013); Pruski (1959) |
| Primordial horse | Martellozzo (2020) |
| A present-day horse species | Bernáldez-Sánchez and García-Viñas (2019) |



Fig. 1. The depiction of the wild horse (not yet called Tarpan) by Gmelin in his travel memoir dated to 1770 (Gmelin, 1770). The animal is a foal without obvious external characteristics that were later attributed to the Tarpan. Image source: Gmelin (1770).

sauvage (Boddaert, 1785). With his work, the *Elenchus Animalium*, published in 1785, the *wild horse* was born for the scientific world.

2.2. The story continues: the alleged wild horses of the Białowieża forest

In the early nineteenth century, the general forester of Poland, Julius Brincken, was commissioned by the Russian tsar Nicholas I to describe the Białowieża Forest. In his memoir (Brincken, 1826) about the flora and fauna of the Great Wilderness – situated in today's Poland – he wrote about half a page on wild horses. He named these horses as “*Equus sylvestris*, Cheval sauvage” (meaning wild horse), apparently creating a new horse species although regretting that a description of the horses is not possible, given they were last seen 40 years before Brincken's memoir. As Brincken explained, the number of these “Chevaux sauvage” continuously decreased by the end of the eighteenth century, until the last individuals were captured and taken to the animal park of an influential Polish aristocrat, count Zamoyski, who collected exotic animals. Then, because these horses had “no use at all” (a notion that was not explained by Brincken, 1826), they were supposedly handed over to local farmers in 1806. The farmers then, as asserted by Brincken, crossed their domestic horses – called Koniks – with these *Equus sylvestris*. Therefore, as the author argues, this *Equus* legacy can still be recognized among these little farm horses (Brincken, 1826). The name Tarpan was again not yet mentioned.

2.3. Reinventing the wild horse: the back-breeding experiment of a Polish professor

A century after Brincken's book appeared, in the 1930s, Brincken's idea of wild horses in Poland was revisited by a Polish professor, Tadeusz Vetulani. Vetulani presented a project proposition of back-breeding the “Forest Tarpans” to the Polish government, calling it *Equus caballus gmelini Antonius forma silvatica Vetulani* (Vetulani, 1939). The idea of the Polish wild horse was born. Vetulani's experiment meant selecting for the ‘ancient traits’ by crossing little farm horses around the Bilgoraj region of Poland (an area not far from the Białowieża forest, where count Zamoyski's estates were located), by means of selection of individuals with specific phenotypic traits at each generation (van Vuure, 2015). The traits Vetulani aimed for were those he believed to be of the original Tarpans (Vetulani, 1928). The notion of the Tarpan was by this time apparently known among scientific circles, even though Brincken did not give any phenotypical description nor the name Tarpan to his *Equus sylvestris*. Vetulani selected in total 19 mares and four stallions (Vetulani, 1938) as a founder population and started the breeding experiment that involved a high degree of inbreeding (van Vuure, 2015). The project soon became popular in Poland: a large breeding center was established in the Białowieża forest, and politicians and the public supported the initiative. The project soon gained international fame, for example in Germany, where the Heck brothers – who had already been working on breeding back the aurochs – also started a back-breeding experiment using Koniks to reconstitute a wild horse (van Vuure, 2015).¹

2.4. The outcome of story-telling: a contemporary myth

The above three intermingling stories raise a number of concerns and doubts, and call for further investigation.

¹ For details about the back-breeding initiation of the Heck-brothers see van Vuure (2015) or Forrest (2019).

First of all, were those horses that were allegedly seen in the 18th century really wild in the biological sense and not just escaped individuals of domestic stocks and hence only feral (where feral refers to free-roaming domesticated animals living in a wild state (King et al., 2021))? Second, how could a back-breeding experiment of the 1930s result in *genetic* successors of an extinct horse, while until today the only evidence for the existence of this extinct horse can solely be found in some anecdotal sources? Third, why are all of these alleged wild horses referred to as Tarpan today, together with the clearly domestic Konik, and what does the term Tarpan actually refer to?

The debate is ongoing since the turn of the nineteenth and twentieth century (Ewart, 1906; Smith and Gesner, 1841). Today, several authors consider the story of the Tarpan and the Konik as a contemporary myth rather than reality (Castelli, 2016; Lizet and Daszkiewicz, 1995; van Vuure, 2015).

In spite of the uncertainty, according to the current official taxonomical status (Gentry et al., 2004; ICZN, 2003), the Tarpan is still recognized as a wild horse: in 2003, the International Commission on Zoological Nomenclature (ICZN) conserved as valid the usage of the name “Tarpan, Russian wild horse, *Equus ferus* BODDAERT (1785)”. However, this status lacks scientific evidence (see below). Often, the Tarpan is regarded as the direct ancestor of the Konik horse breed, and along this idea, the ‘wild’ characteristics of the Koniks are emphasized in nature conservation.

The current general belief that the Tarpan is an extinct wild horse species and the Konik is its closest descendant seems to have been created along romantic ideas and political agendas and reinforced by superficial science (Forrest, 2019; Kolbas, 2002; van Vuure, 2015). There does not seem to be sufficient evidence that the Tarpan had ever been a wild and not only a feral horse (Linnell et al., 2016; Olsen and Zeder, 2006). There seems to be no consensus over which horse (if any) should be regarded as Tarpan (Pruski, 1959). Additionally, there is no genetic evidence that the Konik horse would show genetic proximity to any wild horse (see Section 3.2.3.). Yet the old phrases about direct descentance of the Koniks from a nineteenth century mythical wild horse population keep circulating among scientists and conservationists and seem to influence nature conservation initiatives around Europe, raising this horse breed to a status of being a perfect candidate for introduction into protected areas (Linnell et al., 2016; Vermeulen, 2015). It is more and more common among conservationists and laypeople to mix the terms Tarpan and Konik (e.g., Michelot, 2015; Unknown, 2020; Widstrand, 2016), which amplifies the confusion. How could this happen?

3. How and why the myth became common knowledge

So far, we described the origin of the alleged story that the Tarpan is a wild horse that survived until historic times and that the Konik is a direct descendant of this wild horse. In the following, we discuss four perspectives on why the story could become widely accepted and survive to this day: the historical-political, the biological-ecological, and the emotional perspective.

3.1. Historical-political perspective

3.1.1. Naming the Tarpan

Many researchers agree that the name “Tarpan” is controversial both considering its history and what it refers to (Forrest, 2019; Linnell et al., 2016; Lizet and Daszkiewicz, 1995). It is already not easy to trace back the first written evidence of the name; therefore it is no surprise that sources often do not give a reference for the first mention, but refer to it as having “popped up” on the Russian steppes during the 18th century (Lizet and Daszkiewicz, 1995; van Vuure, 2014).

When we scrutinized the original literature of the 18th century, we found that the name Tarpan seems to first appear in the memoir of Peter Simon Pallas (Pallas, 1773). Pallas was another Western scholar, contemporary of Gmelin, who also travelled around Russia to describe the vast empire (see below). In his book, Pallas reported about horses seen in the wild. He believed, however, that these steppe horses descended from feral domestic horses that escaped human care during the turmoil of various wars (Jeziński and Jaworski, 2008; Pallas, 1773). Pallas did not give a detailed description of these horses, but interestingly, after mentioning the name Tarpan, he continued with describing the Khulan (Pallas, 1773)² – an equid that is today recognized as the Mongolian wild ass (*Equus hemionus hemionus*). It seems like the two names, Tarpan and Khulan, referred to the same animal at the time of Pallas.

Jeziński and Jaworski (2008) mentioned a different ‘first mention’: according to the authors, Peter Rytschkow was pioneer in using the term Tarpan in 1762. The original Russian text of Rytschkow (or Rychkov), however, reads as Tarlan (Тарланы = tarlans) instead of Tarpan. The author also mentioned another horse type, the Kumans (Куманы = kumani), yet it is not clear whether he meant wild or feral horses under either name.

Nevertheless, by about the middle of the 19th century, the term Tarpan had become established as the name for the wild horses of Eastern Europe. As James Cossar Ewart, a Scottish zoologist, wrote: “for more than a century all the horses living in a wild state in Europe, which happened to be of a mouse-dun colour, seem to have been regarded as Tarpans” (Ewart, 1906). It is therefore not clear whether the term originally meant to be ‘wild’ or ‘in a wild state’.

As Ståhlberg and Svanberg (2011) summarized, the Kazakhs called the Tarpans as Taga and they were considered to be not originally wild, but feral horses. Pruski (1959) reported that in Russia, horses that were commonly called Tarpans could have been a number of things: feral domestic horses, hybrids between domestic and wild horses, or even different wild asses: kulans, kiangs, khurs

² “On m’a dit que l’on rencontrait souvent des tarpanes, ou chevaux sauvages, près de la source de l’Irtek, qui est dans les montagnes des landes, à plus de quarante verstes. Le cheval des landes, nommé Koulans par les Kirguis, est souvent le conducteur des tabanes; il ressemble beaucoup à un petit mulet. J’y vis un jeune étalon sauvage qui différerait d’un cheval Russe ordinaire”. Pallas (1773).

and onagers (Jezierski and Jaworski, 2008).

According to Forrest (2019) and Heptner et al. (1988), the names Takhi and Tarpan were used interchangeably during the course of the 18th and 19th century, likely referring to the same – yet unclear – animal, or even potentially referring to a number of different horses, regardless of them being ordinary domestic or feral or wild.

The famous naturalist Charles Hamilton Smith reported about his discussion with Tahtar and Cossack informants (with the aid of an interpreter whose language skills were “not super abundant”) and with the Mongolic troopers who were “stupid or unwilling” (Smith and Gesner, 1841)³ and came to the general conclusion that his informants were talking about both real wild horses and a feral breed, and called the former as Tarpan or Tarpani and the latter as Takja, Taga or Muzin.⁴ In addition to this uncertainty, Hamilton-Smith was apparently not sure to have read his own notes correctly.⁵ Interestingly, he assigned three different colors to the “Tarpani”: tan, isabella and mouse, although tan and isabella describe those horses that we know today as the Przewalski's horse or Takhi (Fig. 2).

Additionally, as it turns out from Forrest (2019), the hide and skull of a horse that was captured between 1876 and 1878 and given to Colonel Przewalski was first referred to as Tarpan – before the classification by Poliakov as *Equus przewalski*. It seems like there had not always been a distinction between Przewalski's and Tarpan.

The chromosome number of the Przewalski's horse (66) justifies its difference to any other domestic horse (64). In the Tarpan, however, no specimen seems to have yet been found that could serve as a proof for its existence as a wild species.

Today two alleged Tarpan skeletons exist in museums: the so-called Cherson Tarpan (which is also called Shatilov Tarpan by Spasskaya and Pavlinov, 2008) that was likely captured in the Zagradoyskaya steppe near the Cherson region in the Ukraine in 1866 and considered to be lectotype (Fig. 3); and the Shatilov Tarpan (which is sometimes called Taurian or Crimean Tarpan (Pasicka, 2013)) that was probably captured in the Rakhmanovskaya steppe and is considered to be paralectotype (Spasskaya and Pavlinov, 2008). However, already an earlier craniometric analysis (Spasskaya and Pavlinov, 2008) unambiguously classified one of these specimens as a domestic horse, and grouped the other with most recent Przewalski's horses or their hybrids. (A recent genomic characterization of the Crimean Tarpan is discussed in Section 3.2.3.).

Several important questions arise from these independent lines of evidence: what should one regard as Tarpan? Has the Tarpan ever referred to the same animal as the present-day Przewalski's horse? Is the Takja the same as the Przewalski's horse? Are the Takja and the Tarpan feral breeds or truly wild species? So far, there is no strong scientific evidence supporting one hypothesis or the other. Nevertheless, strong but apparently unfounded scientific claims have shaped the public opinion over the years (Table 1).

Groves (1994) reported that there should be two subspecies of wild horses that survived into historic times: the Tarpan and the Przewalski's horse. Ten years later, the scientific decision was made: the International Commission on Zoological Nomenclature (ICZN) conserved as valid the usage of the name “Tarpan, Russian wild horse, *Equus ferus* Boddaert (1785)”.

On the one hand, this was a step forward compared to the “plethora” of scientific and common names (as put by Gentry et al., 2004) and combinations of them (Table 2) given for wild or non-wild horses (reviewed, e.g., in Groves, 1994; Spasskaya and Pavlinov, 2008; Spassov and Iliev, 1998).

On the other hand, giving such credit to what appears to be a rather uncertain taxonomic identification seems dangerous as it allows researchers to refer to the Tarpan as a wild horse as a plain fact instead of handling the issue as a highly questionable hypothesis.

Naming new species has always been a pride for scientists – so much so that today there are even auctions on giving scientific names to newly discovered species (Jacobs, 2018). As a result, often several synonyms may refer to one single organism (Alroy, 2002). Today, giving a name to a new species has rigorous rules, including having a designated holotype (a single specimen that acts as the identifier for the entire species) and first and foremost a reliable source of information and documentation of the identity of the species (Hone, 2013). However, this has not been the case with regard to the Tarpan: No specimen of a real Tarpan has been preserved, and no holotype of the Tarpan exists.

3.1.2. Romanticism in the 19th century – Should we believe Gmelin?

The eighteenth century brought growing romantic interest in wilderness in the Western countries (Forrest, 2019). Russia did not wait long to follow the movement, especially after Catherine II the Great, the pragmatic “enlightened empress” (Kahn, 2020), took over the throne and – as a continuation of the work of Peter I – started Westernizing the Russian cultural and scientific life (Thaden, 1954). The aim was to raise the empire's reputation to the level of Western Europe (Griffiths, 1973; Ståhlberg and Svanberg, 2011) and to refute the widespread contemporary perception of Russia as a “barbaric other” (Kahn, 2020).

As one of the means, she established the Imperial Academy of Arts and Sciences in St Petersburg as a scientific and educational

³ Hamilton Smith described his source of information as “...an independent trooper of the desert; who had spent ten or twelve years on the frontier of China, and, I understand, was often seen at Paris attending his Tahtar chief at the theatres, in 1814. My interpreter was an officer in the Don Cossack regiment of Colonel Bigaloff, whose French was not super abundant. From the Mongolic troopers I obtained little information; they were stupid or unwilling.” Smith and Gesner (1841).

⁴ “From the answers of Russian officers of this irregular cavalry, who spoke French or German, we drew the general conclusion of their general belief in a true wild and untameable species of horse, and in herds that were of mixed origin. Those most acquainted with a nomadic life, and in particular an orderly Cossack attached to a Tahtar chief as Russian interpreter, furnished us with the substance of the following notice. “The tarpani form herds of several hundreds, subdivided into smaller troops, each headed by a stallion; they are not found unmixed excepting towards the borders of China.” Smith and Gesner (1841).

⁵ “If I mis-read not my note, Takja, and this name, I find also, in Nemnich, written Taga; but I am not sure if it is there meant to bear the same definition as above. I took the word, on one or two occasions, to be applied to all unowned horses of the steppes.” Smith and Gesner (1841).



Fig. 2. A depiction of the Tarpan as imagined by Charles Hamilton Smith (Smith and Gesner, 1841) after consulting alleged eye-witnesses of these horses. In comparison with the Tarpan of Gmelin (Fig. 1), the depicted animal seems to be more similar to today's Przewalski's horses. Image source: Smith and Gesner (1841).

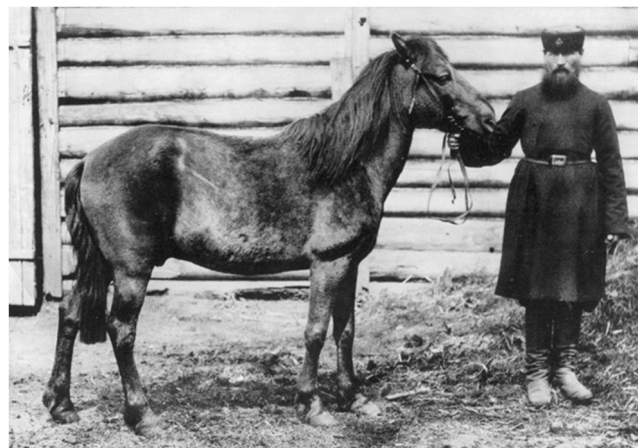


Fig. 3. The famous “last photo” of a “living Tarpan”, from – supposedly – 1884. The origin of the photo is unknown just like that of the horse. It is generally referred to as a “non-pure Tarpan”, believed to be captured around the Cherson region in the Ukraine and transported to the Moscow zoo (Groves, 1994). Image source: Wikimedia (2021).

center and set out expeditions by Western scholars around her empire to describe the *terra incognita* (Chantreau, 1794). Pallas, Gmelin or Humboldt are only a few examples. The *terra incognita* also attracted naturalists in their own interest, for example from Britain: a variety of British geologists, geographers, ornithologists and botanists started visiting the remote parts of Russia in search of new material (Pethybridge, 1972).

It is no surprise that finding rare or even extinct horses as mysteries of the *terra incognita* meant success and pride for the visiting scholars, especially as there was also a growing romanticization of the untamed horse itself in the Western culture (Forrest, 2017).

Despite the romantic era of the 19th century, there was already much doubt about the existence of wild horses among the Western scientific community, and researchers parted to the two extremes of the issue. Charles Hamilton Smith's bitterness about the skeptics who questioned the existence of real wild horses well demonstrates these fierce oppositions: “Whatever may be the lucubrations of naturalists in their cabinets, it does not appear that the Tahtar or even the Cossack nations have any doubt upon the subject, for they assert that they can distinguish a feral breed from the wild by many tokens” (Smith and Gesner, 1841).

The fate of Gmelin's captured horse does not become clear from the naturalist's memoir. It does not seem to have reached a museum so that the specimen could have been examined by other researchers or preserved for later investigation (e.g., through extraction and analysis of the ancient DNA). Besides, Gmelin's description is incomplete regarding whether the observed horses were truly wild in the zoological sense, or were feral domestic horses (Jeziński and Jaworski, 2008). At that time, this was probably not even an issue, because of the lack of genetic knowledge: a horse found in the wild was simply a ‘wild’ horse. The name Tarpan does neither appear in Gmelin's notes nor in the book of Boddaert. Nevertheless, later researchers (e.g., Fages et al., 2019; Antonius, 1938;

Table 2

Variations of scientific and vernacular names for recent domestic and wild horses (Bennett and Hoffmann, 1999; Groves, 1994; ITIS, 2021; Spasskaya and Pavlinov, 2008) with special regard to those concerning the Tarpan. Species names in bold are considered currently valid by the International Commission for Zoological Nomenclature (ICZN, 2003). Tarpans are indicated with an *.

| Scientific name | Vernacular name |
|---|---|
| <i>Equus caballus</i> Linnaeus, 1758 | Feral horse, Horse (valid) |
| <i>Equus caballus caballus</i> Linnaeus, 1758 | Domestic Horse, Northwestern European Horse |
| * <i>Equus caballus ferus</i> Boddaert (1785) | *Russian wild horse, Tarpan |
| <i>Equus caballus przewalskii</i> Poliakov, 1881 | Mongolian Wild Horse, Przewalski's Horse |
| * <i>Equus caballus gmelini</i> Linnaeus, 1758 | *Wild tarpan |
| * <i>Equus ferus</i> Boddaert (1785) | *Russian wild horse, Tarpan (valid) |
| <i>Equus ferus caballus</i> Linnaeus, 1758 | Domestic Horse, Northwestern European Horse |
| * <i>Equus ferus ferus</i> Boddaert (1785) | *Tarpan |
| <i>Equus ferus przewalskii</i> Poliakov, 1881 | Mongolian wild horse, Przewalski's Horse |
| * <i>Equus gmelini</i> Antonius, 1912 | *Tarpan / the Tarpan of Europe |
| * <i>Equus przewalskii gmelini</i> Geptner, 1955 | *South Russian steppe tarpan |
| * <i>Equus przewalskii przewalskii</i> Geptner, 1955 | *Dzhungarian / eastern tarpan |
| * <i>Equus przewalskii silvaticus</i> Geptner, 1955 | *Forest tarpan |
| <i>Equus przewalskii</i> Poliakov, 1881 | Przewalski's horse, takh (valid) |
| * <i>Equus przewalskii silvaticus</i> , Vetulani 1936 | *Forest tarpan |
| * <i>Equus sylvestris</i> von den Brincken (1826) | *Forest tarpan |
| <i>Equus hagenbecki</i> Matschie, 1903 | Przewalski's horse, takhi |
| <i>Equus caballus pumpelli</i> Duerst, 1908 | Afro-turkic Horse, Oriental horse |
| <i>Equus gracilis</i> Ewart, 1909 | European wild horse |

Pasicka, 2013) made the connection themselves, attributing the Tarpan to Gmelin's name and considering it as a real wild horse.

3.1.3. A forester's fantasy – Should we believe Brincken?

Brincken based his description of the Białowieża forest on his impressions after having visited the forest merely twice (Brincken, 1826) on the occasions of so-called hunting parties (van Vuure, 2015). It has been questioned whether such visits should be considered reliable sources of information (Daszkiewicz et al., 2004; van Vuure, 2015). As discussed in van Vuure (2015), Brincken had a political reason for writing his essay. He was commissioned by the Russian tsar Nicholas I, who considered the forest as his hunting ground (the Białowieża forest had been under Russian control until 1917). Because Brincken had already gained some enemies across Poland, he had an interest to maintain good relations to other powerful circles in order to keep his position in forestry (van Vuure, 2015). Supposedly, an extended description about the forest with a long list of wild animals could have been a good means for pleasing the tsar.

Brincken's contemporaries heavily criticized his work for inaccuracies and fabrications regarding the flora and fauna of the Białowieża forest, and for even inventing species (van Vuure, 2015). For example, *three* different types of brown bear, two species of red squirrel, the wolverine, the Russian flying squirrel, or the steppe polecat are animals that – as scientists of Brincken's times reported (reviewed in Daszkiewicz et al., 2004 and van Vuure, 2015) – could either not have existed or have never lived in the forest, or at least not at the time of Brincken's essay.

Although Brincken's book is valuable as it aims to describe this natural area (van Vuure, 2015), it seems that it played a major role in forming the myth around the Tarpan. van Vuure (2015) gives a detailed critique about Brincken's book regarding wild horses. Indeed, Brincken's story relies on anecdotal information: by the time Brincken visited the Białowieża forest, the horses – if they ever had been there – had long disappeared (van Vuure, 2014; Brincken, 1826). Therefore, the 'evidence' on which the beliefs about wild horses that survived to modern times are based is no more than second-hand information about stories passed on between fellow hunters (van Vuure, 2015).

3.1.4. Victorian fashion of cross-breeding – a bridge to back-breeding

In the Victorian age, scientists often engaged in transcending species boundaries, crossing different plant and animal species (Moine, 2017) both to trace hereditary origins and to assess how nature can be artificially modified. Professor James Cossar Ewart successfully crossed, for example, zebras with horses (Button, 2018). He also carried out an experiment crossing ancient British horse breeds to see whether their offspring would result in a wild horse – a Tarpan. Ewart, "having ascertained that, by crossing carefully selected forms, remote types are sometimes restored in all their original purity" (Ewart, 1906), crossed a Shetland pony mare with a Welsh pony stallion. The result were two foals: one ordinary Celtic pony, and one "which, though bred in Scotland, will, I believe, be regarded by Continental naturalists as typical a Tarpan as ever roamed the Russian steppes" (Ewart, 1906).

Apparently, the phenotypic traits attributed to the Tarpan could be reproduced by some randomly crossed breeds. This hardly means that such an animal is a wild species. The explanation lies in more profound reasons, namely of the inheritance of dominant alleles (see Section 3.2.1). Ewart concludes that "there seems no escape from the conclusion that the Tarpan, once common in the east of Europe, cannot be considered as a true wild species."

Vetulani himself was aware of the work of Ewart who might actually have been a precursor for Vetulani's breeding-back experiments (van Vuure, 2015). Yet, contrary to Ewart, Vetulani did believe that the Tarpan is an original wild species and was also

convinced that this Tarpan played a major role in the constitution of the Polish Konik (van Vuure, 2015). Vetulani was successful in reproducing Ewart's experiment on the large scale by selecting horses to cross for achieving his desired Tarpan-traits.

3.1.5. Horses and nationalism – Should we believe Vetulani?

Horses, as explained below (Section 2.3), are an important part of human history and culture. Throughout centuries, the horse has been not only a functional animal but also a cultural icon (Edwards et al., 2011). Nations still have their own horse breed(s), and keeping the genetic line of these breeds in its 'purity' is of high interest to a huge industry (Forrest, 2019).

There seems to be also an interest to claim a country to have been the place where the last 'wild horse' was seen (Pasicka, 2013). Interestingly, the emergence of the lobby for a Polish wild horse, the forest Tarpan, coincides with the beginning of an independent era in Poland: after the first world war, following more than a century of foreign rule, an independent Polish state was restored (BBC, 2018; van Vuure, 2015). As a symbol of freedom, owning the last wild horse might have been particularly important for a country where freedom was deprived such as in Poland. The seeds of Vetulani's idea of having an own, independent, national wild horse potentially fell on fertile soil among contemporary politicians. As van Vuure puts it, "Breeding the konik contributed significantly to national pride" (van Vuure, 2014; Lizet and Daszkiewicz, 1995). Poland was 'back on the map' and had been able 'to breed back the European wild horse', a horse that was so strongly associated with Polish nature and Polish history" (van Vuure, 2014). In the interpretation of Vetulani in 1927, the Tarpan had "retained its superior features not only in the Koniks of Biłgoraj, but in more Polish horses" (van Vuure, 2014).

The idea also seemed and still seems to be popular among scientists. There are only a few Polish authors who acknowledged that there is not really a convincing background for claiming the Konik to be a descendant of the Tarpan; for instance, Jezierski and Jaworski (2008) wrote that "What is known in the literature about the descent of the Koniks from the Tarpan is based on historical sources, craniometric analyses and speculations resulting from it". On the other side, there is a long list of local research on Koniks, popularizing the idea that Poland was home to the last wild horses that lived in Europe before going to extinction (e.g., Janikowski, 1942; Komosa and Purzyc, 2009; Pasicka, 2013; Vetulani, 1928, 1939).

Poland, however, is not the only country where alleged descendants of the Tarpan are claimed to still exist.

3.1.6. Other candidates for being 'direct descendants of Tarpans'

Although the marketing of the Koniks seems to be the most successful of all, they are not the only horse breed competing for the prestigious title of being direct descendants of the Tarpan.

For example, the Portuguese Sorraia breed has similar phenotypic characteristics as the Konik, with mouse-dun coloration and dorsal stripes; and although it comes from the other side of Europe, is also considered to have a direct connection to Tarpans (Von Lettow-Vorbeck, 2005). The Sorraia faces similar problems with inbreeding effects as does the Konik (Section 4.1.2.): according to the official studbook (Oom et al., 2004), all of today's individuals descended from only 12 founders. Besides, the Sorraia also is believed to be the ancestor of the Lusitano and Andalusian breeds, and it is claimed to be an ancestor of the "entire World's light saddle horses" (Luís et al., 2006; Oom and Cothran, 1994).

Another candidate is the Exmoor pony of England that is argued to be "not a 'man-made' breed, but a wild horse type with a separate history that has been uninfluenced by domestic horses" (Hovens and Rijkers, 2013), explaining this with their "primeval form", which is mainly their bay-dun coat color (Oelke, 2012).

The eastern part of Europe also has some alleged wild-horse descendants: the Hucul and the Bosnian Mountain horse. The Hucul's origin is debated between Slovakia, Romania (Georgescu et al., 2011) and Poland (Purzyc, 2007) and, just like the origin of the Konik, it also fades into anecdotes. There are suppositions that the Hucul derives from a number of different breeds; others claim that they are "the direct descendants of the Tarpan horses (...) representing a subpopulation of Tarpan horses that adapted to the conditions in mountainous areas" (Georgescu et al., 2011). The Bosnian Mountain horse is mentioned alongside Koniks as the "only close descendants of the extinct *Equus ferus ferus* (Tarpan)" (May-Davis et al., 2019), but it is also said to be a product of a cross between the Tarpan and the Przewalski's horse (Maletić et al., 2018).

Based on this alleged origin of the Hucul and the Konik, the Estonian Native Horse recently entered the scientific literature as another descendant of the Tarpan: a recent study (Castaneda et al., 2019) claims to describe "genetic evidence for the alleged Tarpan ancestry of the Estonian Native Horse", although the authors have not sampled any Tarpan. The basis of the 'evidence' is that the Estonian horse is clustered together with the Hucul and Konik in a phylogenetic analysis. As the Konik is said to be a "direct descendent of the Tarpan", a similar origin for the Estonian horse was inferred by the authors. Of course this result is based on the assumption that the alleged Tarpan horse would be the direct ancestor of the Konik horse, which remains highly hypothetical in the absence of genetic-based evidence.

Closing the list of examples, the Gotland pony, a Swedish so-called ancient horse breed is sometimes also regarded to be directly originating from the Tarpan (Fortini et al., 2015). A study investigating genetic relationships within horse breeds revealed low genetic diversity within the breed, which may indicate isolation of the population (Castaneda et al., 2019), but not necessarily a connection to a 'wild horse'.

3.2. Biological-ecological perspective

3.2.1. Phenotypic resemblance – to the unknown?

The main argument for regarding Koniks as descendants of wild horses is that Konik horses have been bred to phenotypically resemble an alleged Tarpan (Linnell et al., 2016). However, we do not know what the Tarpan looked like. Indeed, also Gmelin's

description does not correspond to what later scholars described as attributes of a Tarpan, as discussed in the following.

3.2.1.1. Coloration, dorsal stripe. The major alleged indicator that the Konik could be a direct descendant of the Tarpan is the coat coloration. Koniks generally exhibit a mouse-dun coloration, that is, they are mouse-grey with dark mane and tail and have a black dorsal stripe, occasionally horizontal bars on the legs and dark patches on the shoulder (Imsland et al., 2016; Stefaniuk-Szmukier et al., 2017).

According to Gmelin, the ‘wild’ horses in the Voronezh area were mouse grey. This might mean a mouse-dun color, yet the most visible characteristics of the dun coloration, namely the dorsal stripe and the zebra-stripes on the legs, are not mentioned by Gmelin. These stripes, very often associated with ‘wildness’, would therefore have been absent from the alleged Tarpan horses described by Gmelin. Nevertheless, later scholars still referred to Gmelin’s mouse color as dun, attributed it to everything that is called a Tarpan, and used it as an argument for claiming that Koniks must have Tarpan genes because they show this phenotype (Martin, 1845; Stachurska, 1999; Stefaniuk-Szmukier et al., 2017).

Additionally, even if Gmelin would have forgotten to mention the strikingly conspicuous dorsal stripe, this dun coat would not necessarily represent any guarantee for wildness. Indeed, the dun gene is fully dominant over non-dun (let the owner of the color be wild or non-wild; Imsland et al., 2016), and therefore this coloration easily appears in domestic horses as well, e.g., in the Arabians, Thoroughbreds, Spanish breeds, Quarter horses, Paints and Appaloosas (Animal Genetics Inc, 2021; Thiruvankadan et al., 2008).

3.2.1.2. Fur length. The fur length of Gmelin’s horses was described to be long, at least longer than those of “Russian horses” (Gmelin, 1770). However, the season of Gmelin’s horse adventure was winter, and horses that live under non-stabled (non-boxed, non-shaved) conditions are known to grow longer hair during winter. A study that measured hair coat properties of different equids in different seasons reported an average 12.15 mm (SD 4.12) hair length in summer and 47 mm (SD 10.72) in winter, in ordinary domestic horses with outdoor housing (Osthaus et al., 2018). Hair length similarly varies between seasons in donkeys and mules, but differs between equid species (Osthaus et al., 2018). It is likely that the general view of local people on their Russian horses developed from seeing horses that received, at least partially, indoor housing and therefore had a characteristic of shorter hair than their free-roaming conspecifics. Also, as different equids show different hair lengths, different horse breeds likely also show a difference. The individuals in the group of Gmelin’s horses may have well shown differences in hair length if the group consisted of different breeds. Therefore, fur length can hardly be taken as evidence for wildness.

3.2.1.3. Mane. The erect mane without a forelock is considered a feature of wildness (Janikowski, 1942): every current wild equid species from zebras through donkeys to wild asses possesses such a mane. About the adult horses in Gmelin’s adventure, we only know that their mane was “short and frizzy”, but there is no mention about a missing forelock or about an upright-standing mane. The frizziness even seems to refer to a longer mane, as a very short mane rarely can curl. Besides, the drawing presented in Gmelin’s book represents a foal and not an adult specimen (Fig. 1; Gmelin, 1770). Since every horse foal has an upright-standing mane until it matures and the mane grows longer, this depiction does not seem relevant in this context.

3.2.1.4. Fiery eyes. Eye and facial expressions of domestic horses have been suggested to show emotional states (Dalla Costa et al., 2017; Hintze et al., 2016; Wathan et al., 2016). Fiery eyes are therefore not a distinguishing feature for wild horses but can appear in domestic horses as well.

3.2.1.5. Short or long ears, short tail. The length of the ears and tail seem to be explained by individual variation rather than being species-specific traits of horse breeds or populations (e.g., Brooks et al., 2010). Therefore, these phenotypic traits cannot be taken as proxies to identify the origin of modern horses.

In conclusion, many of these traits appear to be rather controversial. As Olsen and Zeder (2006) reports, horses with dun coats, zebra striping on the legs, and prominent stripes down their backs are very common today in domestic herds in Mongolia. Yet, those Mongolian horses are not thought to be of wild origin; at maximum they may be hybrids between domestic and Przewalski’s horses (Olsen and Zeder, 2006).

3.2.2. The transition from wild to domestic – The domestication process and its impact on wild horses

The equid family originated some 55 million years ago, and equids are extremely well represented in the fossil record until the end of the Pleistocene (Librado and Orlando, 2021; Orlando, 2015). The group from which today’s domestic horses are derived originated in North America and colonized the Old World by spreading to Eurasia through Beringia. While horses became extinct in the Americas at the time of the massive extinctions around 10,000 years ago, they continued to persist in the Old World (MacFadden, 2005; Orlando, 2015).

While a number of wild horse species and populations have been described from the Eurasian steppe between about 35,000–10,000 years ago (Azzaroli, 1990; Groves and Ryder, 2000), they have most likely become extremely rare by the beginning of the Holocene (Barron-Ortiz et al., 2019; Leonardi et al., 2018; Vilà et al., 2001). Wild horses became locally extinct in most geographical regions after the end of the Ice Age, with only a few populations persisting in small numbers in relic, scattered groups (Bendrey, 2012; Levine, 1999). It is unclear whether all the different relic populations belonged to different species or subspecies or whether differences may also reflect individual variation (Olsen and Zeder, 2006).

The reasons for the decline of wild horses are debated, but it is commonly thought that the decrease of suitable habitat due to

climate change and increasing human expansion were its main drivers (Clutton-Brock, 1992). Beside monopolizing habitats important for horses, human impact manifested in overhunting and the spread of domestication, which likely involved capturing wild individuals (probably mostly mares due to their calmer temperament) and integrating them into the stock of domestic horses (Orlando, 2015). The first evidence for horse domestication comes from Botai, an archaeological settlement located in Northern Kazakhstan, and dates back to approximately 5500 years ago (Outram et al., 2009). By the Bronze age (about 4000 ago), domestic horses had spread throughout Eurasia. In the millennium following the assumed first instance of horse domestication, a rapid increase in the number of horse remains was recorded in the osteological records, especially in the Eurasian steppes (Bibikova, 1986; Vilà et al., 2001). This, together with the archeological (Outram et al., 2009) and genomic (Allentoft et al., 2015; Orlando, 2020) evidence, suggests that the number of horses rose due to focused breeding and spread associated with human continental expansions (Olsen and Zeder, 2006) and not because of natural expansion (de Barros Damgaard et al., 2018).

Until recently, it was believed that modern domestic mares were originating from numerous different regions while very few, closely related stallions with the same Y-chromosome haplotype contributed to the genetic makeup of extant horses (Jansen et al., 2002; Kavar and Dovč, 2008; Lindgren et al., 2004). However, recent genetic analyses of ancient male horses suggest a very different story, with a high Y-chromosome diversity observed in ancient domestic horses, at least until about 2000 years ago, followed by a drastic decline to reach present-day levels some 850–1350 years ago (Fages et al., 2019; Librado et al., 2017; Wutke et al., 2018). This pattern of broad maternal contribution may reflect the intense spread of domestic animals, or pastoralism itself, where people were moving from one locality to the other, capturing wild mares from local relic populations to add to the domestic stock.

Moreover, Bendrey (2012) adds a behavioral aspect for the widespread collapse of wild horse distribution in the early Holocene. Horses are known to be impeded in their reproduction when social groups are disrupted. As explained above, humans essentially disrupted social groups by capturing individuals to add to their domestic herds or simply to eat them. Such reduction in reproductive rate likely contributed to the exponential decrease in wild horse numbers.

Not only did the number of wild populations decrease in the pre-domestication times of the early Holocene up until the Bronze Age, but wild horse populations gradually mixed with domestic individuals, resulting in various levels of gene flow across Eurasia. Ståhlberg and Svanberg (2011) suggested that domestic animals (horses, sheep, goats, cattle) of the Asian steppe nomads roamed freely with little attention from humans. Even today, domestic horses in Kazakhstan, Mongolia, and Russia are released from the corrals in the evening to graze through the night on natural pasture (Olsen and Zeder, 2006). Many of these free-roaming animals essentially became feral. How much these individuals have been affected by human-driven selection remains unknown.

The social organization of horses also explains how wild and domestic populations could intermingle. Horses display female defense polygyny, forming harems that consist of a leading stallion and several mares; colts are expelled from the group and fillies also disperse. The young males then form bachelor groups, and as they achieve maturity, they emerge to capture mares from other groups and form their own harem (Boyd et al., 2016). It is likely that such a reproductive behavior added to the extent of gene flow between domestic and wild horses.

Further, since horses are very mobile animals, considerable displacements must have been characteristic of wild populations (Kavar and Dovč, 2008). Such mobility results in gene flow, which may partly explain the lack of phylogeographic structure found in the mitochondrial DNA of current domestic horses (Kavar and Dovč, 2008). It thus may be logical to assume that such mobile behavior facilitated gene flow between the relic wild horse populations and domesticated stocks. This, and the high ancestral mitochondrial variability inferred from pre-domestication horses, resulted in the relatively high mitochondrial diversity that is now observed in modern domestic horses (Cieslak et al., 2010).

In view of both horse behavior and of the numerous human migrations across Eurasia in the last five millennia, it seems unlikely that wild horses could have avoided contact with their domestic counterparts. There is also a very low probability that they have preserved their pristine wildness until the end of the eighteenth century without substantial gene flow from the domestic stock or from feral individuals.

3.2.3. Ancient genomics and the origins of horse domestication

The exact geographic and temporal origins of modern domestic horses have been highly debated. Importantly, the horses first herded at Botai have been shown to be the direct ancestors of the modern Przewalski's horses rather than of modern domestic horses, with Botai horses contributing only about 3% of their ancestry to the genomic makeup of ancient and modern domestic horses of the last 4000 years (Gaunitz et al., 2018). At the far western end of the Eurasian continent, the Iberian Peninsula has been suggested to be another independent center of horse domestication, based on archaeological evidence and genetic data from modern horses (Warmuth et al., 2011). However, recent paleogenomic evidence has again suggested a very limited genetic contribution of these horses to modern domesticates, thus strongly arguing against a major domestication process initiated in Iberia (Fages et al., 2019). These Iberian ancient horses dating back to about 4800 to 3900 years ago may have been either wild or domesticated and could correspond to the horses depicted in Paleolithic rock paintings. They have also been suggested to be putative ancestors of a hypothetical wild European horse population (Fages et al., 2019).

The two main remaining geographic sources of domestication origins are the Pontic-Caspian, encompassing South-West Russia north of the Caucasus mountains and present-day eastern Ukraine (Anthony, 2010), and Anatolia (Arbuckle, 2012). A recent study based on ancient mitochondrial genomes from ancient Turkey, Georgia and Armenia dismissed Anatolia as a likely center for horse domestication on the basis of substantial replacement of females about 4000 years ago in that region – although whether this also applies to males remains to be tested (Guimaraes et al., 2020). Further, a recent paleogenomic study analyzing the genomes of 273 ancient horses from all over Eurasia pinpointed the origin of modern domestic horses in the steppes of Western Eurasia (Librado et al., 2021). The authors revealed that all of the ancient horse domestic genomes dating back to the last 3000 years and spreading

throughout Eurasia show very close genetic affinities with each other and thus form a relatively homogeneous group whose origin lies in the lower Volga-Don region, north of the Caucasus (Librado et al., 2021). These horses are also very distinct from other extinct and extant lineages, including that of the Przewalski's horses and the now-extinct lineage of Bronze-Age Iberian horses, which also extended in the rest of Europe, further in the North to Scandinavia and in the East to Poland, Czech Republic and Hungary. The possibility that another European wild horse lineage existed until recent times – namely, the so-called Tarpan – cannot yet be ruled out by this apparent homogeneity in the domestic stock of the last three millennia. However, it suggests that if such a distinct European horse ever existed, it left little to no genomic signature in the makeup of modern domestic horses.

Interestingly, Librado et al. (2021) also performed genomic characterization of the alleged Tarpan specimen from North Crimea (see Section 3.1.1.), dating back to the nineteenth century. They showed that this individual shared genetic affinities with both the modern domestic lineage and an Eneolithic European lineage, suggesting that at least some of the horses identified as Tarpan in the past centuries may be the result of past admixture between these two lineages. The authors also showed that the alleged Tarpan lineage this specimen belonged to was not related to the Przewalski's horses, and that it did not contribute genetically to the domestic stock until its extinction. Therefore, the horse population this Crimean specimen belonged to cannot be the ancestor of domestic horses – including Koniks. Ideally, genomic characterisation of more alleged Tarpan and/or European wild horse specimens would be needed to get additional insight into the status and genetic contribution of the hypothetical European wild horse.

To our knowledge, no whole-genome characterization of the Konik breed has been performed yet. It is therefore difficult to place it in the diversity of modern horse breeds. Here again, genomic analyses are needed to shed light on the origin of this population, and whether it substantially differs from the rest of the modern domestic stock. However, based on mitochondrial genomes, Lippold et al. (2011) have shown close genetic affinities between one Konik horse and a German sport horse, falling within the diversity of matrilineal lineages observed in modern breeds and indicating that this Konik horse may not descend from a specific divergent maternal lineage. Additionally, analyzing the hypervariable D-loop of the mitochondrial genome of 173 Konik horses, Cieslak et al. (2017) have revealed high mitochondrial diversity in this breed, with no less than 19 distinct haplotypes represented. When compared to 79 D-loop sequences of 15 horse breeds, these once again fell within the overall maternal genetic diversity of modern breeds, suggesting a common maternal ancestry for the Konik horse and other domestic breeds. These findings support the hypothesis that the Konik horse may descend from the same ancestral wild mares as the rest of the modern domestic stock.

3.3. Emotional perspective

Horses seem to trigger very strong emotional response in humans (Bökönyi, 1987; Scasta, 2019). This emotionality may lie in the impact of horses on human history. During the almost six millennia of human-equine relationship, horses have revolutionized warfare and transportation, and by doing so played a key role in spreading language, religion, ideas, political units, inventions and information across cultures and continents, thus strongly contributing to shaping Eurasian civilizations (Anthony, 2010).

Among others, Clutton-Brock (1992), Lawrence (1988) and Kelekna (2009) argued that human history would have developed rather differently without horses: The nomadic empires of the Eurasian steppes, the Scythians, the Huns, the Mongols and the Turks could not have conquered much of the urban centers of the sedentary Western world without mastering horse-riding and mounted archery. Alexander the Great's conquer from Greece to India, Hannibal's invasion of Spain and Italy, Caesar's Gallic Wars would likely not have happened without horse power. Similarly, there would have been most probably no Crusades where armies of mounted knights crossed the old continent to Jerusalem, and Genghis Khan could not have broken through the Great Wall of China without the help of sixty thousand horses. More recently, horses played a crucial role in the conquest of the New World by European settlers, as well as in much of the Old World's wars until the nineteenth century. Besides warfare, the development of human cultures and the dispersion of human genes has been facilitated by horses for thousands of years (Kelekna, 2009): horses helped globalizing the world for the first time in history (Forrest, 2017).

It is probably due to this globalized and intermingled connection that the relationship between man and horse, according to some authors, became symbiotic (Scasta, 2019), and sometimes even regarded to be a coevolution (Robinson, 1999), although likely only in a cultural sense. Riding and/or owning a horse has been a status symbol throughout history (Edwards et al., 2011; Robinson, 1999).

Further, people have become emotionally attached to the animals they lived and worked with (Edwards et al., 2011). Horses have become interconnected with humans over many generations (Haraway, 2008), and even in people who have no direct personal experience with horses, a certain sentimental approach towards these animals may still persist due to the description given in books and media: Horses are usually associated with terms such as loyalty, speed, endurance, power, grace, and intelligence (Beever and Brussard, 2000).

Although the importance of horses has dramatically decreased in the economy of most countries since the industrial revolution and the progressive replacement of horses by machines, the horse still represents a cultural icon (Edwards et al., 2011), a national heritage (Notzke, 2016), and an ecological agent (Notzke, 2013). Horses are still admired and highly valued companions (Walsh, 2009) and are used in recreation and tourism (Notzke, 2016). Importantly, horses are also highly valued in the sport and breeding industry, and are thus associated with huge financial stakes (Derry, 2016). Further, they have a growing importance in nature conservation and in particular in maintaining valued landscapes and nature protection areas (Beer et al., 2020; Chodkiewicz, 2020; Mills and McDonnell, 2005; Naundrup and Svenning, 2015).

This modern role of horses in nature conservation may, however, be often hindered by the strong emotions of people towards these animals. The sentimental approach often results in subjective interpretation of facts, which affects efficient horse-management (Ransom and Kaczynsky, 2016) and apparently also scientific research. Not only laypeople, but often also scientists tend to interpret certain claims about horses as truths, and especially about wild horses, without clear scientific evidence.

As a historical example, several ancient texts can be found referring to ‘wild’ horses that roamed across Europe and Asia. Herodotus narrated about magnificent white wild horses, roaming about 2500 years ago in Scythia (Groves, 1994). Mentions of ‘wild horses’, either by hunting or eating them, tend to pop up in archaic literature from Pope Gregory III (in 732) through the Nibelungenlied (13th century) until 18th century articles (for details, see van Vuure, 2015). None of these stories can be evidenced, as there is no osteological evidence pointing towards their validity. Yet such anecdotes seem to have been attractive enough to shape the way we think about horses.

Such emotionality towards horses may have contributed to formulate a myth around the Tarpan and the Konik, both among the public and among scientists, rather than handling the issue with caution, acknowledging uncertainty.

Indeed, part of the scientific literature still contains unfounded yet strong claims, such as: “*there cannot be any doubt that the tarpan was the wild form from which the first domestic horses of Europe were derived*” (Bökönyi, 1987). Unless strong evidence is provided, such overconfident claims are often simply opinions, based on emotions rather than facts. Scientific opinions and scientific evidence are then often confounded, leading to misconceptions both among scientists and the public (Haddaway et al., 2015). Thus the hypothesis that the Tarpan is the extinct European wild horse and the Konik is its closest descendant became reported as a fact in research articles, often without providing any reference for the claim, because it seemed to have entered common knowledge (for example, see the claims in Gurgul et al., 2019; Mackowski et al., 2015; Pasicka, 2013). As often, the problem with common knowledge is that there seems to be no need to provide references, let alone to check the available references (Roig, 2003).

Today, researchers who investigate horse domestication are showing that the picture is far from being clear and that several – if not many – horse populations may have coexisted in the early stages of horse domestication (Orlando, 2020; Librado et al., 2021); hence, there was probably never one unique ‘European wild horse’. Nevertheless, the accepted yet probably wrong common knowledge about the Tarpan and the Konik stays very strong. Beside heavily diminishing the chance of any counterclaim to be heard, this common knowledge might be detrimental for applications in nature conservation, as discussed in the following section.

4. Outlook

4.1. How the myth influences nature conservation

4.1.1. Practical issues – the Konik-Tarpan lobby: easier fundraising?

There seems to be still a strong lobby for considering certain horse breeds as the closest descendants of the Tarpan, regardless of the presence or absence of evidence for what a Tarpan was. The Konik breed has been particularly subject to this fashion (e.g., Michélot, 2015; Vera et al., 2007; Vetulani, 1928; Widstrand, 2016). In Poland, and more generally in Europe, the Konik has been successfully popularized as the direct descendant of the Tarpan (aka the European wild horse; Linnell et al., 2016).

In Europe, the idea of rewilding (Soule and Noss, 1998) with horses became known probably most prominently in the Netherlands, in the vast rewilding project of the Oostvaardersplassen. With this rewilding project, it seems, the concept of introducing Koniks in nature reserves on the basis of being direct wild-horse descendants has also started to spread across Western Europe (van Vuure, 2015). It did not take long for the Konik to start becoming more and more widespread in other European countries as well, with France currently being one of the Konik-Tarpan hotspots in nature conservation (Lizet and Daszkiewicz, 1995).

Although all lines of evidence indicate that the Konik is simply a domestic breed, popularizing them as the direct descendants of Tarpans, and thus of wild horses, seems to make it hard to grasp for both scientists and laypeople that Konik horses do not represent a wild species. The Konik-Tarpan parallelism seems to be a successful marketing tool in terms of promoting important nature conservation projects both among laypeople and politicians, by evoking romantic feelings towards wild horses and wilderness (Scasta, 2019), and therefore helping fundraising (Lizet and Daszkiewicz, 1995).

This raises the question of whether mis-claiming a breed as being wild type would be justified for conservation purposes.

Interestingly, some examples can be found where the alleged wildness of the Koniks may facilitate conservation management. In Bulgaria, for example, the Tarpan is apparently on the national red list as a wild species, and horses registered as Tarpan (namely, Koniks) are exempt from veterinarian law, thus they do not need to be microchipped (as the European animal welfare law requires) and can be managed as wild animals (Vermeulen, 2015). This practice would largely facilitate nature conservation management, since in such schemes, horses are untamed and are kept in wild circumstances. Therefore, any veterinary intervention in rewilding projects may mean unnecessary stress and potentially more harm than benefit. In such wild conditions, it is usually best practice to only intervene when an animal suffers and has no chance for self-healing. The only reasonable solution is then often euthanasia – other initiatives may only cause unnecessary further suffer for the animal. However, even if declaring the Konik a wild species may facilitate conservation management, initiating such measures across Europe would lack a scientific basis, would lead to further confusion about the origins of wild horses, and, most importantly, would increase the chance of inbreeding (see below).

An alternative to the Bulgarian example would be to give semi-natural grazers the status of wild animals (Blom, 2019), without the need of declaring them biological wild types. Such a status of ‘ecological wildness’ would help conservation initiatives not only focused on horses but on other domestic animals as well, such as cattle, goat or sheep breeds.

A paradigm-shift to a marketing by emphasizing the ecological importance of Koniks (see, e.g., Kohler et al., 2016; Lovász et al., 2021) and other horses (e.g., Duncan, 2012; Loucougaray et al., 2004), rather than the importance of biological origin, could be just as efficient as the marketing of biological origin, while it would be an example of evidence-based science communication.

4.1.2. Practical issues – inbreeding

Beside the misleading myth about the origins, there are practical consequences of a lobbying focus on the Konik-Tarpan story.

Koniks are valued in nature conservation for their robust constitution that makes them self-sustainable in natural conditions (Gurgul et al., 2019). One explanation for their robustness is usually that they have undergone little selective breeding and thus possess many characteristics of their wild or feral ancestors (Vera, 2009). However, due to the ideas of wild-horse descent, nature conservationists seem to have been trying to conserve the assumed wild haplotype in Koniks, with the aim of preserving the lines that Vetulani once established (Cieslak et al., 2017). And those lines were already a quite narrow selection from the gene pool.

Vetulani started breeding with a very small population of 22 horses (van Vuure, 2015) by explicitly selecting for certain phenotypic traits among local farm horses (Vetulani, 1938). The practice continues, and from 1985 the Konik studbook has been closed, meaning that the addition of “outside blood” to the official breeding program is forbidden (Cieslak et al., 2017; Fornal et al., 2020; Kaminski et al., 2017). Additionally, in 1999, the program of conservation breeding of Koniks introduced a regulation that only those horses are allowed to enter the breeding registry that descended from the parents entered in the main registry and possess mouse grey coat color with a stripe (Pasicka, 2013).

Such practice does not differ from ordinary horse-breeding practices where breeders aim for certain characteristics: a process that is associated with domestication. Domestication, on the other hand, is associated with inbreeding and an excess of deleterious mutations (Schubert et al., 2014).

Wolc and Balińska (2010) showed that a high proportion of genes from only a few founders suggests a small gene pool in today's Koniks. This may be due to the population bottleneck created by the selection by Vetulani and the early breeders to achieve horses that exhibit the “Tarpan-like” features. In the first studbook issued in 1962, 34 maternal and six paternal lines were included (Cieslak et al., 2017). Of these, 19 of the maternal lineages were lost during the following 40 years, so contemporary Koniks descend from six paternal and 15 maternal lineages (Cieslak et al., 2017; Fornal et al., 2020). A recent study investigating genomic inbreeding in Koniks in Poland showed an inbreeding coefficient (i.e., the probability that two alleles at a locus are identical by descent (Wright, 1922)) ranging from 5.25% to 22.41% (Kaminski et al., 2017), and Pluta et al. (2016) reported inbreeding coefficients from > 5% to > 15%. Further, Wolc and Balińska (2010) pointed out that inbreeding levels have been gradually increasing in Koniks in Polish breeding stocks, from 0.11% in 1956 to 9% already in the 2000s.

These rates seem to be rather high, given that the general rule of thumb suggested in animal breeding is to restrict the rate of inbreeding to below 1%, preferably below 0.5% (Oldenbroek and van der Waaij, 2015); a rate of inbreeding of 1% means that at least 25 males and 25 females need to be used for breeding (Oldenbroek and van der Waaij, 2015).

Because the European Koniks originate from Polish stocks, the high inbreeding rates reported in studies carried out in Poland likely also apply to stocks in other European countries; however, to our knowledge, so far there are no studies on inbreeding in Konik populations outside Poland. Reportedly, some countries where Koniks are used for conservation projects prefer breeding their own ‘national’ Koniks. This may lead to more serious decrease in genetic variability if it hinders genetic exchange with Konik populations from other countries. As reported by Kaminski et al. (2017), breeders may even aim to mate horses of relatively high inbreeding levels.

Such inbreeding may affect the health of today's Koniks and could influence their suitability in rewilding and other conservation initiatives. Inbreeding likely results in homozygosity on the genome, which may then increase the chances of offspring being affected by deleterious or recessive traits (Stearns and Hoekstra, 2000). As Pluta et al. (2016) summarize, the negative consequence of increased homozygosity can manifest in inbreeding depression, resulting in a decrease of fertility, vitality, and resistance to disease, in phenotype delicacy (i.e., a weaker skeleton), increased susceptibility to adverse environmental conditions, and a weakening of psychological resistance.

Apparently, the expectation that Konik horse populations were mainly shaped by natural selection (Gurgul et al., 2019) seems not to be fulfilled. Selective breeding and mating in closed populations makes their genetic characteristics highly uniform within the breed – a problem that is also found in other horse breeds (Gurgul et al., 2019).

Therefore, for nature conservation projects, it would be wise to regard the Konik as an ordinary breed, where it is preferable to have the largest possible genetic distance between individuals rather than to try preserving a specific genetic line that is claimed to be that of the alleged Tarpan.

5. Conclusion

In our extensive literature search, we did not find scientific evidence, neither in historical sources nor in the reported phenotypic or genetic traits, for wild horses to have survived until recent historic times (i.e., until the 16th to 18th century; Olsen, 2017; van Vuure, 2015). We also found no scientific evidence that the Tarpan had ever been wild and not simply a feral horse. Additionally, there seems to be no consensus on which of the ancient horse populations roaming in different parts of Eurasia should be regarded as Tarpan, leading to the simple conclusion that we apparently do not know what sort of horse the various alleged Tarpan populations were. Finally, the Konik has never been shown to have genetic proximity to this alleged Tarpan.

5.1. What is the European wild horse, if not a Tarpan?

Recent research in ancient genomics and archaeology has shown that the Przewalski's horse cannot be considered as the ancestor of modern domestic horses, and that the earliest domesticated horses do not represent the ancestors of modern horses either (Gaunitz et al., 2018). Instead, modern domestic horses are now thought to descend from a distinct population roaming in the southern Pontic Caspian steppes that became progressively managed by humans throughout the third millennium Before Common Era, thus starting from about 5000 years ago (Anthony, 2010; Librado et al., 2021). Interestingly, recent genomic evidence has also shown that several now-extinct horse lineages may have marginally contributed some genes to present-day domestic horses (Fages et al., 2019). Horses

that have survived the glaciation period but predated the domestication period have been referred to as post-glacial (Sandoval-Castellanos et al., 2017), pre-domestic (Pruvost et al., 2011), or simply wild (Orlando, 2020), regardless of any assumption about their contribution to the modern domestic stock of horses. Only two of these horse lineages still exist today: the one leading to modern domesticated horses and the one leading to present-day Przewalski's horses.

It would thus be advisable to revise the current official taxonomic vernacular name of the entry of the *Equus ferus* and refer to *Equus ferus* as a species complex (e.g., Guthrie, 2003) rather than a single species.

5.2. What is the Konik, if not a Tarpan?

Although regarding the Konik as a simple breed would likely mean that its reputation as a wild horse or as a direct descendant of a wild horse would disappear, this would not mean that the breed would be any less valuable and unique (Lizet and Daszkiewicz, 1995). As we reviewed, its wildness has not been evidenced genetically. Accurate determination of the status of this breed will therefore leverage further investigation of its genomic makeup and its genetic relationships with other Eurasian modern and ancient horse populations.

5.3. The role of horses in nature conservation

Comparative studies on dietary differences between horse breeds are lacking (Fraser et al., 2019), but judging from studies on single breeds, the ecological effects of horses do not seem to strongly depend on the breed. Irrespective of the investigated type of horse, several studies have shown a general positive correlation between grazing by horses and biodiversity and the abundance of target species, while controlling undesired vegetation (Catorci et al., 2012; Freedman et al., 2011; Henning et al., 2017; Kohler et al., 2016; Lamoot et al., 2005; Lovász et al., 2021). Also, horses have been assumed to be highly adaptive (Goodwin, 2007), which contributes to their suitability in nature conservation management. Nonetheless, to investigate whether certain horse breeds may be more suitable than others, further research would be necessary, for example by experimentally comparing the performance of different breeds in natural environments. From our review, we conclude that the mythologized wild origin of the Konik horses is not the factor that may make them more or less suitable than other breeds.

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