Remains of *Tapirus* Brisson, 1762 (Mammalia, Perissodactyla) from the Pleistocene of the southern North Sea

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Tapirs are odd-toed ungulates with an extensive fossil record since the early Eocene. Here, we present their first records from the North Sea. An Early Pleistocene m1/m2 dex. of *Tapirus arvernensis* Croizet & Jobert, 1828 from the beach of Maasvlakte 2 and an m3 dex. of *Tapirus* sp. from the beach of Hoek van Holland (both near Rotterdam, The Netherlands) were recovered by citizen scientist fossil collectors from dredged sediments deposited on these beaches. The original provenance of the Maasvlakte 2 specimen is a sand dredging pit in the North Sea reaching into Pleistocene deposits, just offshore Rotterdam (coordinates *c*. 52.01, 3.92), while the original provenance of the Hoek van Holland specimen remains somewhat unclear, but must have been situated in the southern part of the North Sea. These tapir records and a specimen from the Westerschelde reported earlier suggest a previously reported and contested occurrence of *Mammut borsoni* (Hays, 1834) from "the Scheldt" in fact may originate from the Westerschelde. These records are among the most northern records of *Tapirus* and demonstrate the scientific value of these nourished beaches and the cooperation with the citizen scientist fossil collectors that collect (*i.e.* save them from destruction through exposure) fossils there.

KEY WORDS: beach nourishments, citizen scientists, Early Pleistocene, Hoek van Holland, Maasvlakte 2, *Mammut borsoni*, Tapiridae, *Tapirus arvernensis*

Introduction

Tapirs (Perissodactyla, Tapiridae) are odd-toed ungulates with an extensive fossil record since the early Eocene (Prothero, 2009). With four well established extant species (Medici, 2011) and a fifth controversial one (Cozzuol *et al*., 2013; Ruiz-García *et al*., 2016), modern tapirs are large (up to 400 kg) solitary animals that live in dense tropical (lowland and mountainous) forests, typically in riparian forests near marshes, lakes and streams. They are well suited to move through thick undergrowth. Tapirs are browsers of leaves of a wide variety of plant species, and also consume buds, twigs, bark, flowers and fruits of low-growing terrestrial plants and occasionally aquatic plants. Although currently restricted to the tropical regions of South America, Central America and Southeast Asia (Medici, 2011), the fossil record shows tapirs of the genus *Tapirus* Brisson, 1762 were widely distributed in North America and the Old World in the Neogene and Pleistocene (Kurtén, 1968).

Several genera and species of Tapiridae are known from the late Miocene of Europe (Guérin & Eisenmann, 1994): *Tapirus balkanicus* Spassov & Ginsburg, 1999, *T. priscus* Kaup, 1833 and *T. antiquus* Kaup, 1833 and *Tapiriscus pannonicus* Kretzoi, 1951. *Tapirus jeanpiveteaui* Boeuf, 1991 is known from the Pliocene (Boeuf, 1991). *Tapirus arvernensis* Croizet & Jobert, 1828 is the most common species in the Pleistocene of Europe. It was described from Perrier-Les Étouaires (Puy-de-Dôme, France) based on an adult mandible, a fragment of a juvenile mandible, an incisor, an atlas and an upper molar (Croizet & Jobert, 1828). The species was not dissimilar from extant *Tapirus* (Kurtén, 1968) with an estimated total length of 1.8 to 2 m, a shoulder height of 80 cm and a weight of over 200 kg (Guérin & Tsoukala, 2013). Its fossils are known from MN 13 (Miocene, probably latest Turolian) until MNQ 18 (Early Pleistocene, Late Villafranchian) and sites are widely distributed in south-central Europe, but much less common in the north-western part of the continent (Gómez de Soler *et al*., 2012; Guérin & Tsoukala, 2013). Fossils are quite common in various sites in France and Italy, including (partial) skeletons (*e.g.* Rustioni & Mazza, 2001; Lacombat *et al*., 2008; Gómez de Soler *et al*., 2012). Quite abundant material is also known from Wölfersheim (Germany) from a fauna with *Anancus arvernensis* (Croizet & Jobert, 1828) and *Mammut borsoni* (Hays, 1834) (Tobien, 1952), while fewer, much more rare remains are known from the Pliocene to earliest Pleistocene of the Red Crag Formation in Suffolk, United Kingdom (Newton, 1891) and also from The Netherlands.

The best preserved Dutch remains are those from Maalbeek near Tegelen, province of Limburg (Kortenbout van

der Sluijs, 1960; Mol *et al.*, 2008). Furthermore, one specimen, tentatively identified as a dp4 of *Tapirus arvernensis*, was recovered *ex situ* at Baarland (province of Zeeland) from sediments dredged from the Westerschelde estuary and tentatively dated as late Pliocene (Goetheer, 2013). Unpublished teeth and post-crania mentioned as *Tapirus arvernensis* by Mol *et al.* (2011), not identified to genus by Peters & De Vos (2013) and mentioned as *Tapirus* sp. by Peters (2013) are also known from the former sand dredging pit 'De Kuilen' (Mill-Langenboom, province of Noord-Brabant), yielding *ex situ* Miocene to Pliocene material. Recently, the beaches of Maasvlakte 2 and Hoek van Holland (both near Rotterdam) yielded two new fossil teeth of tapir, originating from the southern North Sea. Here, we describe these specimens, adding to the poor Dutch record of *Tapirus*.

Geological setting

The publicly accessible beaches of Maasvlakte 2 and Hoek van Holland were artificially created from/extensively nourished with dredged sediments, respectively. The original provenance of the sediment used for Maasvlakte 2, and hence the original provenance of the Maasvlakte 2 *Tapirus* specimen, can be traced with certainty to the large underwater sand dredging pit (coordinates *c.* 52.01, 3.92) just offshore the Rotterdam harbour (Reumer *et al.*, 2010; Kuitems *et al.*, 2015), just south of the Eurogeul, a fossiliferous dredged navigational channel that traditionally yields Late Pleistocene and Early Holocene material (Mol *et al.*, 2006). This fauna is also recovered from Maasvlakte 2, but the site additionally yields abundant terrestrial mammal material from the Early and/or Middle Pleistocene, due to deeper sand dredging (up to 20 meters below seafloor) into older deposits (Busschers *et al.*, 2013; Mol & Langeveld, 2014, 2016; Kuitems *et al.*, 2015). The dredged sediments consist of some sediment from the Holocene Naaldwijk Formation, and predominantly fluvial deposits from the Late and Middle Pleistocene of the Kreftenheye Formation and late Early or Middle Pleistocene deposits of the Urk Formation or Waalre Formation (Busschers *et al.*, 2013).

The beach of Hoek van Holland has a more complex history. It was first nourished in 1971 with sediments that originated from the (original, or first) Maasvlakte (not to be confused with the recent extension, known as Maasvlakte 2), from the port of Rotterdam, just to the south of Hoek van Holland. These sediments were dredged from the Maasvlakte to create shipping lanes and docks. The sediments consist of a mix of local Late Pleistocene and Holocene terrestrial to marine sediments as well as sediments that were first dredged offshore of Great Yarmouth (Norfolk, United Kingdom). These foreign sediments were deposited at Maasvlakte to facilitate construction but were later partially removed and thus deposited on the beach of Hoek van Holland. They consist of Early to Middle Pleistocene marine and estuarine deposits of course sand and gravel. After this early nourishment, the beach was repeatedly nourished with sediments from just offshore of Hoek van Holland, generally from the Eurogeul area and of Late Pleistocene to Holocene age. Fossil finds at Hoek van Holland are dominated by that Late Pleistocene and early Holocene material (Langeveld, 2013a) and are comparable to the fauna from the Eurogeul area (Mol *et al.*, 2006); material from the Early/Middle Pleistocene occurs much more rarely and could be of local reworked origin (Dieleman, 2013; Langeveld, 2013b), but given the long and diverse history of sand nourishments on this site, the original provenance of the Hoek van Holland *Tapirus* specimen remains unclear.

Institutional abbreviation

NMR Natural History Museum Rotterdam, Rotterdam, The Netherlands.

Material and methods

Our material consists of two molars that were recovered *ex situ* from the beaches of Maasvlakte 2 on 21 February 2020 and Hoek van Holland on 14 March 2010 (both near Rotterdam) by citizen scientist fossil collectors A.L.M. Kolder and D. Chrispijn, respectively. The Maasvlakte 2 specimen is kept in NMR with catalogue number NMR999100161339 (Moeliker & Langeveld, 2021). The Hoek van Holland specimen is kept in the private collection of Harold van der Steen (Oss, The Netherlands), catalogued as GL57B; a cast is kept as NMR999100007475. Measurements were taken at the base of the crown with Vernier callipers at 0.1 mm accuracy.

Results

Maasvlakte 2 specimen

The tooth (Fig. 1) is of a simple bilophodont morphology with two distinct lophs, consisting of a protoloph connecting the protocone and paracone and a metaloph connecting the hypocone and metacone. There is no ectoloph. Cingula are present on both the anterior and posterior sides of the tooth. The cingula show contact facets from other teeth on both the anterior and posterior sides of the specimen. The tooth preserves the bases of four roots that have broken off. It shows very light wear from use by the animal, with the largest dentin basin (width 3.7 mm) developed on the hypocone, followed by the protocone (width 2.4 mm). On the metacone the dentin basin is *c.* 1 mm and on the paracone the enamel is intact. The length of the tooth is 22.0 mm; the width of the anterior loph is 17.8 mm; posterior loph width is 16.4 mm. The enamel is black in colour with some subtle hints of very dark red; the roots are very dark brown in colour with some reddish specks of iron oxide.

The simple bilophodont morphology allows identification as tapir (Hillson, 2005), while the elongated shape shows it is from the lower jaw (Hohl *et al.*, 2020). Ob-

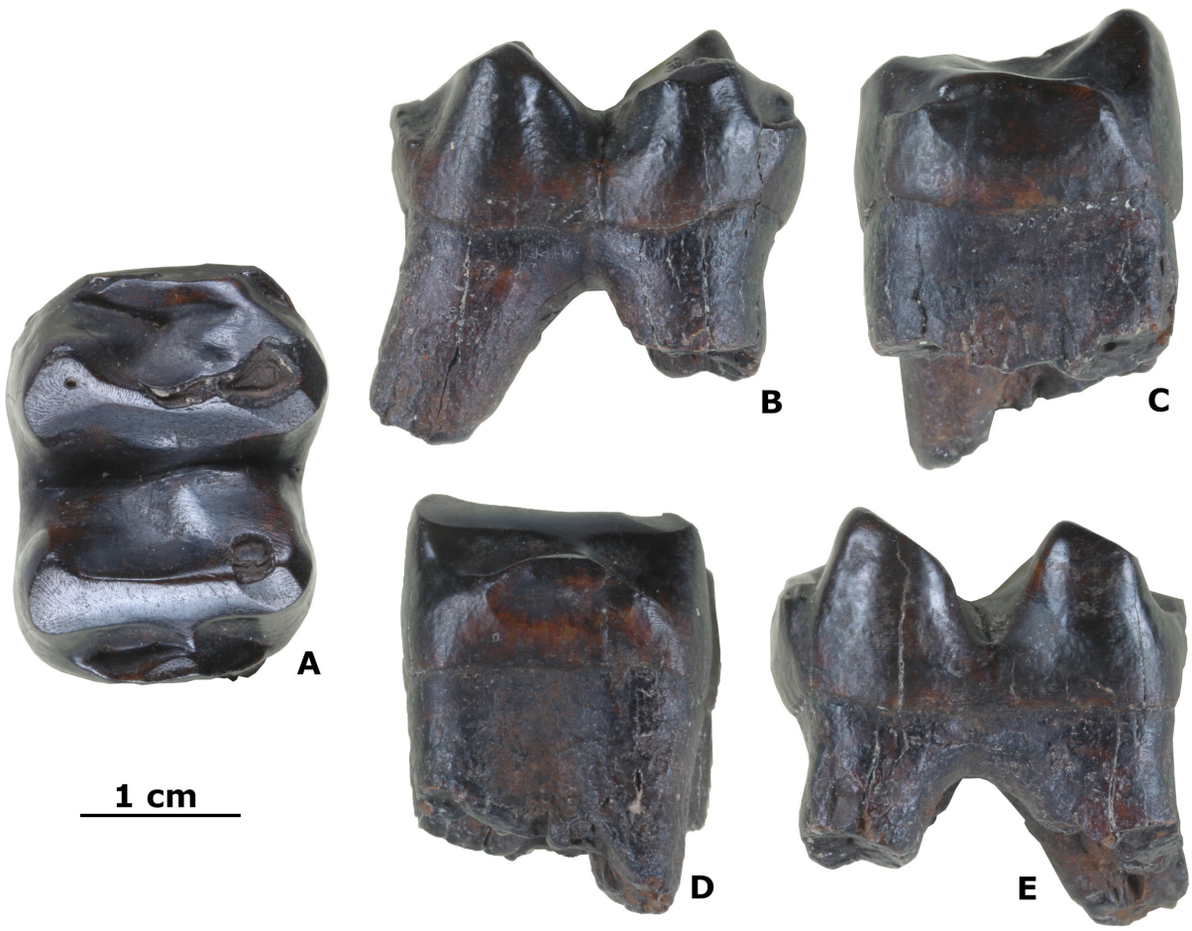

Figure 1. *Tapirus arvernensis* Croizet & Jobert, 1828, m1/m2 dex., beach of Maasvlakte 2, Rotterdam, The Netherlands, 21 February 2020, *leg.* A.L.M. Kolder, collection Natural History Museum Rotterdam NMR999100161339. A occlusal, B buccal, C anterior, D posterior, E lingual view.

servations on a skeleton of a recent juvenile *Tapirus terrestris* (Linnaeus, 1758) (NMR999000000961) and on material illustrated in Schap & Samuels (2020: fig. 3) show that the protoloph and metaloph connect the posterior parts of their respective cones and arch slightly towards the posterior and that the lingual side of the teeth in occlusal view is straight, while their buccal side is asymmetrical in occlusal view. This indicates our specimen is from the right mandible. As the anterior loph is wider than the posterior loph, our specimen is a molar (Hohl *et al*., 2020). Based on the contact facets on both sides of the tooth, the m3 can be ruled out, thus our specimen can be identified as an m1 or m2. Based on its size it can be assigned to *Tapirus arvernensis*, as Croizet & Jobert (1828) gave 21 and 22 mm for the m1 and m2 length, respectively and Eisenmann & Guérin (1992) reported a mean length of 19.4 mm (range 18.0-21.0), anterior width 14.6 mm (13.0-16.0) and posterior width 13.8 mm (12.5-15.0) for m1 and a mean length of 21.6 mm (19.0-24.0), anterior width 15.7 mm (14.0-17.5), posterior width 14.7 mm (13.5-17.0) for m2 of *Tapirus arvernensis*, suggesting the Maasvlakte 2 specimen is most likely an m2 dex.

Hoek van Holland specimen

The tooth (Fig. 2) is of a similar bilophodont morphology as the Maasvlakte 2 specimen, but significantly larger with a length of 28.0 mm, anterior loph width 20.1 mm and posterior loph width 18.0 mm. Its roots are better preserved and show that both anterior roots and both posterior roots are fused together, the posterior roots arching conspicuously posteriorly. Only on the anterior side a facet where the tooth was in contact with another tooth is present. The specimen shows light wear from use by the animal, with the largest dentin basin (width 5.5 mm) developed on the hypocone, followed by the protocone (width 2.9 mm). The metacone is damaged and on the paracone the enamel is intact. The enamel is black in colour, while the roots are a slightly lighter shade of greyish black.

The morphology of the tooth, the posteriorly arched root, and the wear facet on the anterior side only, show this specimen is an m3 from the right mandible. Croizet & Jobert (1828) gave 21 mm for the m3 length of *Tapirus arvernensis* and Eisenmann & Guérin (1992) gave a length of 22.1 mm (21.0-25.0), anterior width 15.7 mm (14.5-17.0) and posterior width 14.5 mm (12.5-17.5). The Hoek van Hol-

Figure 2. *Tapirus* sp., m3 dex., beach of Hoek van Holland, Rotterdam, The Netherlands, 14 March 2010, *leg.* D. Chrispijn, private collection Harold van der Steen (Oss, The Netherlands) GL57B. A occlusal, B buccal, C anterior, D posterior, E lingual view. Photos: Hans Wildschut.

land specimen clearly falls outside these values; its dimensions are over 10% larger than the largest known *T. arvernensis*. *Tapirus jeanpiveteaui*, *T. balkanicus* and *Tapiriscus pannonicus* are (significantly) smaller than *T. arvernensis* (Spassov & Ginsburg, 1999; Franzen, 2013; Guérin & Tsoukala, 2013), while *Tapirus priscus* and *T. antiquus* are larger than *T. arvernensis*, the poorly known *T. antiquus* being larger still than *T. priscus* (Kaup, 1833; Guérin & Eisenmann, 1994). For *Tapirus priscus*, Kaup (1833) gave an m3 length of 26 mm and Eisenmann & Guérin (1992) reported m3 length 24.7 mm (22.5-27.0), anterior width 18.5 mm (17.0-20.0) and posterior width 16.6 mm (15.5-18.0). Given the unclear original provenance and stratigraphic age of the Hoek van Holland specimen and the conservative and highly similar morphology of the dentition of *Tapirus* spp. (*e.g.* Eshelman *et al*., 2018), we take a careful approach and identify the Hoek van Holland specimen as *Tapirus* sp., most likely *T. priscus* or *T. antiquus*.

Discussion

For decades the North Sea has yielded Pleistocene mammalian fossils as well as archaeological remains as bycatch in the nets of fishing vessels (Staring, 1861; Maarleveld, 2020). Especially the southern part (below 53° N) is a rich source. Although recovered *ex situ*, fossils from the North Sea do hold significant potential to increase our knowledge on Pleistocene mammals (Van Kolfschoten & Vervoort-Kerkhoff, 1999), a.o. due to the sheer volume having been recovered by fishing vessels over the past decades including some very rare or unique specimens such as the youngest European record of *Homotherium latidens* (Owen, 1846) (Reumer *et al*., 2003) and more recently the easy accessibility of millions of cubic metres of fossiliferous sediments as these are used to nourish Dutch beaches to prevent damage from sea-level rise. The fossils wash free from these sediments and are saved from destruction through erosion and weathering by citizen scientist fossil collectors that are often willing to work together with palaeontologists to study their specimens (Mol, 2016; Curry, 2020). A recent example is the *Macaca sylvanus* (Linnaeus, 1758) material that was published by Reumer *et al.* (2018) and represents one of the most north-western records of this taxon. Late Pleistocene (Weichselian) material dominates the North Sea terrestrial mammal record (Mol *et al*., 2008). Material from the Early or Middle Pleistocene is much rarer and

generally confined to small localities within the North Sea (Mol *et al*., 2003; Mol & Mulder, 2019).

The Maasvlakte 2 specimen fits with other Early Pleistocene mammalian remains recovered from this site (Mol & Langeveld, 2014, 2016). The Hoek van Holland *Tapirus* specimen remains somewhat problematical, as it cannot be assigned to *Tapirus arvernensis* and thus must predate the Pleistocene. Fossils from the Miocene and Pliocene are very uncommon on the beach of Hoek van Holland and if present, they have been fluvially reworked from (mostly marine) strata more to the south (Belgium) or east (Germany) (Langeveld, 2011; Slupik *et al.*, 2013), but the complex sand nourishment history of this beach precludes any definitive statements on the original provenance.

The *Tapirus* records, especially the *Tapirus* record from the Westerschelde published by Goetheer (2013) have implications for a unique fossil first published over 70 years ago. Von Koenigswald (1950) mentioned a molar fragment that he identified as part of an M3 of *Mammut borsoni*. He noted it was collected from "the Scheldt", although a more exact provenance (*i.e.* Westerschelde or Oosterschelde, and what part thereof) was unknown. It represented the first record of this taxon from the Netherlands. The specimen is kept in NMR, catalogued under NMR999100000698. In their description of two *M. borsoni* molars from the Hoogdonk brickyard at Hoogdonk near Liessel (province of Noord-Brabant), Mol & Van Essen (1990) reidentified the specimen as an m3 dex. of *M. borsoni* and questioned its origin. Braber *et al.* (1999) and Mol *et al.* (2008) cited the specimen and again noted its unclear provenance. As *M. borsoni* commonly co-occurs with *Tapirus*, *e.g.* at Vialette in France (Lacombat *et al*., 2008), Milia in Greece (Guérin & Tsoukala, 2013) and Wölfersheim (Tobien, 1952) and Wörth am Rhein (Ziegler, 2003) in Germany, the occurrence of *Tapirus* in the Westerschelde as published by Goetheer (2013) grants new validity to the contested claim of Von Koenigswald (1950) of *M. borsoni* occurring in "the Scheldt" and suggests it in fact originates from the Westerschelde. Its occurrence in the Early Pleistocene (MN17, Villafranchian; Scager *et al*., 2017) Oosterschelde fauna is highly unlikely, as this fauna postdates the extinction of *M. borsoni* at the end of the Pliocene (Tsoukala & Mol, 2016). Hence, we conclude that the fragment NMR999100000698 of an m3 dex. of *Mammut borsoni*, first reported by Von Koenigswald (1950), most likely originates from the Westerschelde.

Conclusions

The two *Tapirus* specimens reported here from the beaches of Hoek van Holland and Maasvlakte 2 are the first records of this genus recovered from the bottom of the North Sea and add to the scarce Dutch records; furthermore, they are among the most northern records of this genus. The Hoek van Holland specimen (m3 dex.) is larger than *T. arvernensis* and due to the complex sand nourishment history of the site its original provenance is somewhat unclear (although it must have originated from the southern part of the North Sea); it is not identified beyond genus level. The Maasvlakte 2 specimen (m1/m2 dex.) fits well with *T. arvernensis* and originates from Pleistocene deposits from the Maasvlakte 2 sand dredging pit, just offshore the coast of Rotterdam (coordinates *c*. 52.01, 3.92). Based on the known stratigraphical range, it fits well with other Early Pleistocene mammalian taxa recovered from this site. These unique specimens demonstrate the scientific value of these nourished beaches and the cooperation with the citizen scientist fossil collectors that collect (*i.e.* save them from destruction through exposure) fossils there.

Acknowledgements

The Hoek van Holland specimen was collected by D. Chrispijn; H. van der Steen allowed us to study it and to have casts produced by R. Bakker (Manimal Works, Rotterdam); H. Wildschut photographed it. H. Loeff alerted us to the Maasvlakte 2 specimen that was collected and donated by A.L.M. Kolder. J. de Vos (Naturalis Biodiversity Center) and J.W.F. Reumer (Utrecht University) reviewed the manuscript.

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