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REPORT ON THE DISCOVERY OF FOSSIL MARES WITH PRESERVED UTEROPLACENTA FROM THE EOCENE OF GERMANY

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Abstract: I report on the discoveries of three pregnant mares from the middle Eocene of Germany that contain remains of fetuses still wrapped in the fossilized uteroplacenta. These are the first and up to now only discoveries of this kind. One specimen comes from the Eckfeld Maar (Eifel Mountains). It is 44 million years of age. The other two were discovered at Grube Messel and are 48 million years old. These are the oldest fossil uteroplacentae known so far. Their morphology corresponds to recent homologues. Presumably, the uteroplacenta developed as part of the propagation system of mammals during the Palaeocene, perhaps already during the late Mesozoic.

Key words: Equoidea, pregnant mares, uteroplacenta, Eocene, Eckfeld, Messel

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Introduction

Vertebrates are normally fossilized as isolated teeth and bones, sometimes also as jaws with teeth. Partial skeletons are rare, and complete ones even rarer. Extraordinary is fossilized soft tissue. In Germany, we are lucky to have three Eocene sites that are famous for the preservation of soft tissue. These are the classic locality of the Geiseltal near Halle/Saale, Grube Messel near Darmstadt, and the Eckfeld Maar NW of Trier in the Eifel Mountains (Text-fig. 1). At Grube Messel feathers, hair and even the soft body silhouettes of fossil vertebrates are preserved as black shadows. Unique in the world is "Ida", *Darwinius masillae*, the most complete fossil primate ever discovered (Franzen et al. 2009). In some cases, even internal organs, such as lung, liver and veins of frogs, or the intestine of mammals, are preserved due to bacterial metabolism (Wuttke 1983, 1992). Amazing is the preservation of three-dimensional ovaries of a turtle (Gassner et al. 2001).

Here, I present a summary of the discovery of fossil mares with preserved uteroplacentae. These are the first discoveries of this kind ever made. One comes from Eckfeld, the other two from Messel. The report refers to investigations published in detail elsewhere (Franzen et al. 2006, 2015, 2016), but a third pregnant mare with preserved uteroplacenta was recognized only recently. It is presented and analyzed here for the first time.

Text-fig. 1. Map of Germany showing the topographic situation of the Eocene localities of Eckfeld (Eifel Mountains), Messel near Darmstadt and Geiseltal near Halle/Saale. Drawing by Mascha Siemund (at that time Senckenberg Research Institute Frankfurt).

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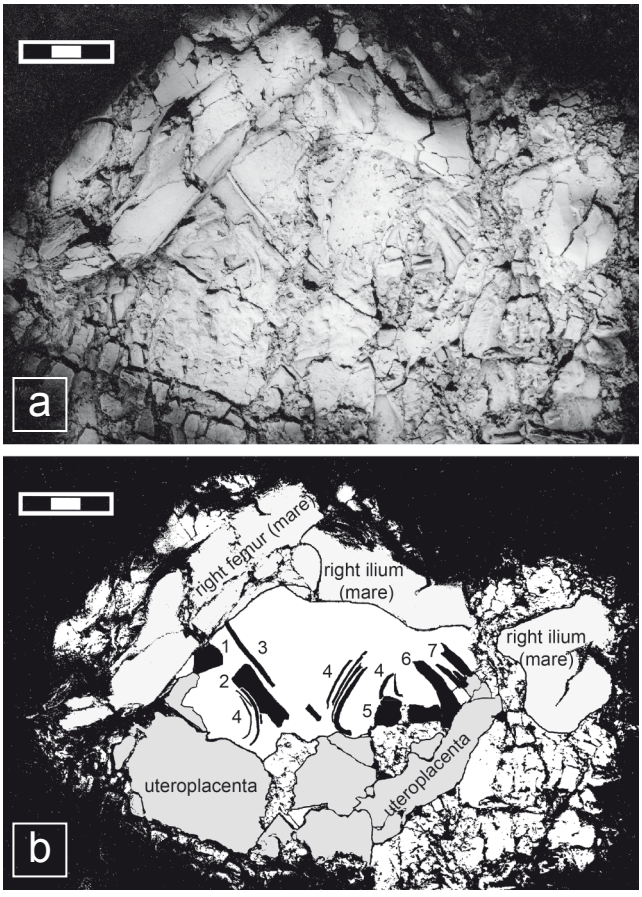
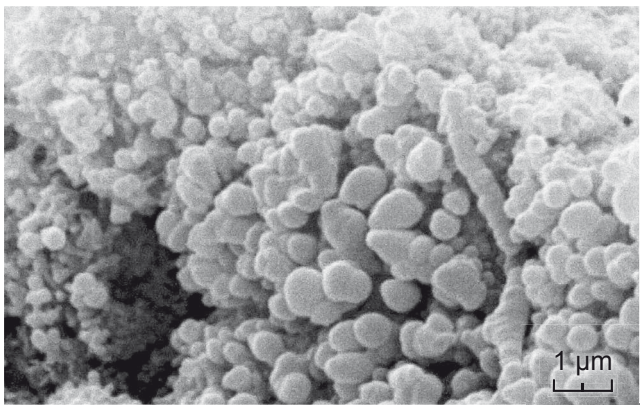
Text-fig. 2. Skeleton of a pregnant mare of *Propalaeotherium voigti* (Matthes, 1977) from the middle Eocene maar of Eckfeld (Germany); Maarmuseum at Manderscheid (PW 1992/52-LS). A white ellipse indicates the position of the uteroplacenta. Scale = 10 cm. Photo by Ulrike Nies (Natural History Museum Mainz).

The pregnant mare from the Eckfeld maar

The first remains of the uteroplacenta of a fossil mare and of a fossil mammal in general were not discovered at Messel but at Eckfeld, another Eocene maar in Germany (Franzen 2006). A virtually complete and articulated equid skeleton turned up in August 1991 during excavations carried out by the "Museum für Naturkunde Mainz/ Landessammlung für Naturkunde Rheinland-Pfalz" at the middle Eocene maar of Eckfeld (Eifel Mountains, Germany; Text-fig. 2). The specimen is exhibited in the Maarmuseum at Manderscheid (Eifel; inventory no. PW 1992/52-LS). Biochronologically, the site is situated within the upper Geiseltalian (MP 13; Franzen 1993, 1994). The radiometric age of the maar explosion that led to a crater lake, in which the fossil lagerstaette developed, is dated at 44.3 ± 0.4 my (Mertz et al. 2000). Correspondingly, the age of the fossil-bearing strata is estimated at 44 million years. Lutz (1993) described the discovery and taphonomy of the specimen, whereas Franzen (1993) determined it as a pregnant mare of *Propalaeotherium voigti* (Matthes, 1977). In 2006, when describing the skeletons of the mare and the fetus in detail, he discovered remains of the placenta still enwrapping the fetus (Franzen 2006). This was the first time that a fossilized uteroplacenta of a mammal became known.



Text-fig. 3. The abdomen of *Propalaeotherium voigti* from Eckfeld contains the remains of a fetus, a) coated with ammonium chloride (NH_4Cl), b) anatomical interpretation. The bones of the mare are colored light grey and those of the fetus black. The fetal bones represent tibia (1), femur (2), fibula (3), costae (4), scapula (5), humerus (6), ulna and radius (7). Remains of the uteroplacenta are colored dark grey. Scale (a and b) = 3 cm. Photo by Elke Pantak-Wein; anatomical interpretation by author (both Senckenberg Research Institute Frankfurt).



Text-fig. 4. Coccal bacteria within the grey crust covering the fetus of *Propalaeotherium voigti* from Eckfeld. SEM photo by Marie-Louise Tritz and author (both Senckenberg Research Institute Frankfurt).

The remains of one (and only one!) fetus occur between the right ilium and femur of the mare (Text-fig. 3a). The fetus displays the left side. The fact that there is only one fetus is remarkable because at this early time in equid history it already corresponds to the normal situation with living horses and to the so-called k-strategy of propagation. This means to keep the number of offspring low, but the amount of parental care high. Cranium and dentition of the fetus are missing. Perhaps they were originally hidden below the right ilium of the mare. In any case, they are not visible within a window, which was kept open in the epoxy resin from the opposite side. Relative to the mare, the vertebral column of the fetus is obviously situated cranially, whereas the limb bones point in a caudal direction. This corresponds with a final stage of parturition of modern horses, when the fetus has turned around its long axis for about 180°, and moves with the head placed on the anterior limbs into the birth canal (Benesch 1957).

Identifiable elements of the fetus are several ribs (some of which are preserved as secondary casts of the embedding epoxy resin), parts of the scapula, humerus, radius and ulna, diaphysis of the femur, fibula, and a proximal fragment of the tibia, all of the left side (Text-fig. 3b). Surprisingly, larger fragments of a hard undulated bright-grey crust cover parts of the skeleton of the fetus, such as the fetal vertebral column, which is only indicated by traces of its outline. In some places the crust was removed during preparation to expose the fetus. The anatomical position as well as the form of the crust as a thin layer lead to the conclusion that it represents the fossilized uteroplacenta. Histological details, however, are no longer recognizable. But we discovered fossilized coccal bacteria, which appear within the grey crust (Text-fig. 4). Presumably, they participated in the fossilization process as it is the case with the preservation of soft tissue at Messel (Wuttke 1983, 1994).

Text-fig. 5. Skeleton of a pregnant mare of *Eurohippus messelensis* (Haupt, 1925) from the early middle Eocene maar of Messel (Germany); Senckenberg Collection (SMF ME 11034). A white ellipse indicates the position of the uteroplacenta. Scale = 10 cm. Photo by Sven Tränkner (Senckenberg Research Institute Frankfurt).

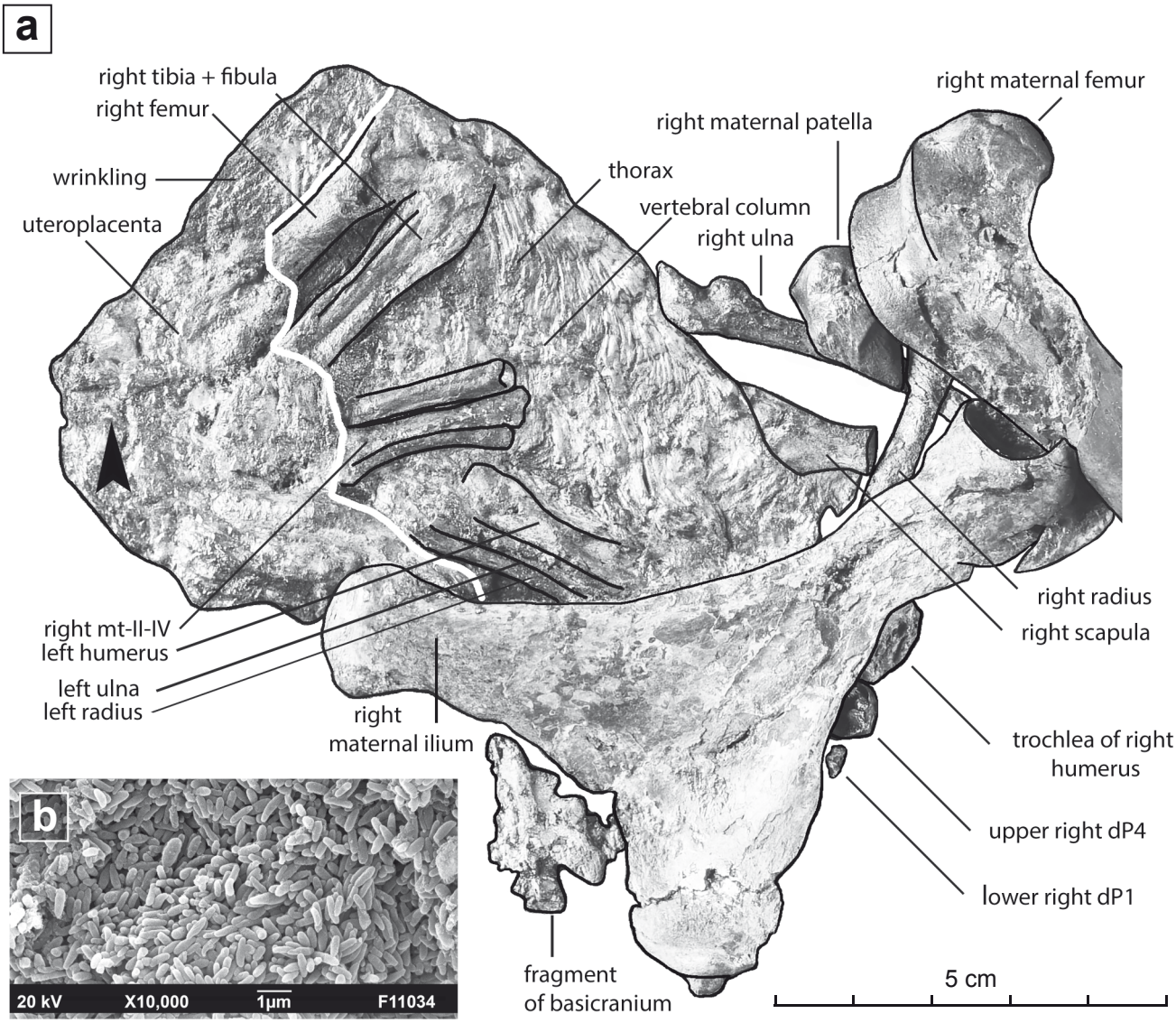
A pregnant mare with preserved uteroplacenta from Messel

A nearly complete and articulated skeleton of a pregnant mare of *Eurohippus messelensis* (Haupt, 1925) was discovered and excavated by a team of the Senckenberg Research Institute Frankfurt at Grube Messel in 2000 (Text-fig. 5). It is archived in the Institute's Department of Messel Research under the inventory no. SMF ME 11034. Within the abdomen occurs the nearly complete and articulated skeleton of a fetus. When we described this in detail (Franzen et al. 2015), we discovered that most of the fetus is still enwrapped in a bright-yellow crust containing petrified bacteria (Text-fig. 6a–b). Corresponding with the Eckfeld mare, the crust displays a fine wrinkling. Such a wrinkling is well known in the uteroplacenta of recent mares. After foaling it appears on the external wall of the uteroplacenta, when the muscles relax (Schlafer 2004, Taverne and Noakes 2009). Evidently, the feature corroborates our hypothesis that we are dealing with the uteroplacenta, which is outstandingly well preserved. Additionally, micro-x-ray shows a conspicuous grey shadow between the fetus and the lumbar vertebrae of the mare (Text-fig. 7a). This is partially dispersed into stripes, which run parallel to one another and frame longitudinally elongated holes. Their structure points dorsocaudally in the direction of maternal lumbar vertebrae 4–7. Morphology and position of the structure correspond to the broad ligament (ligamentum latum uteri) of recent mares of *Equus caballus*. There, it attaches the uterine horn to the lumbar vertebrae and the pelvis (Text-fig. 7b). An alternative interpretation as abdominal muscle can be excluded, because of differing position and direction. In recent horses, the musculus transversus abdominis extends in vertical direction from the lumbar vertebrae and the pelvis down to the ventral midline of the abdomen, whereas the musculus obliquus abdominis stretches from the tuber coxae to the last rib and rib cartilage.

A second pregnant mare of *Eurohippus messelensis* from Messel with a fossilized uteroplacenta

Only recently, we recognized that another pregnant mare of *Eurohippus messelensis* from Messel contains also a fossilized uteroplacenta (Text-fig. 8). The skeleton was found and prepared by a private collector and belongs to the private collection of Dr. Burkhard Pohl, who offers open access for scientific research.

Franzen (2007) supposed already that the uteroplacenta of this specimen still surrounds the fetus, because four thoracic and three lumbar vertebrae of the mare avoided that area when they shifted ventrally into the abdominal cavity. Obviously, something prevented them from entering that region, presumably the uteroplacenta. When I recently investigated and analyzed the complete and mostly articulated skeleton of the mare, I recognized that most of the fetal area is still lined with the uteroplacenta, although the skeleton



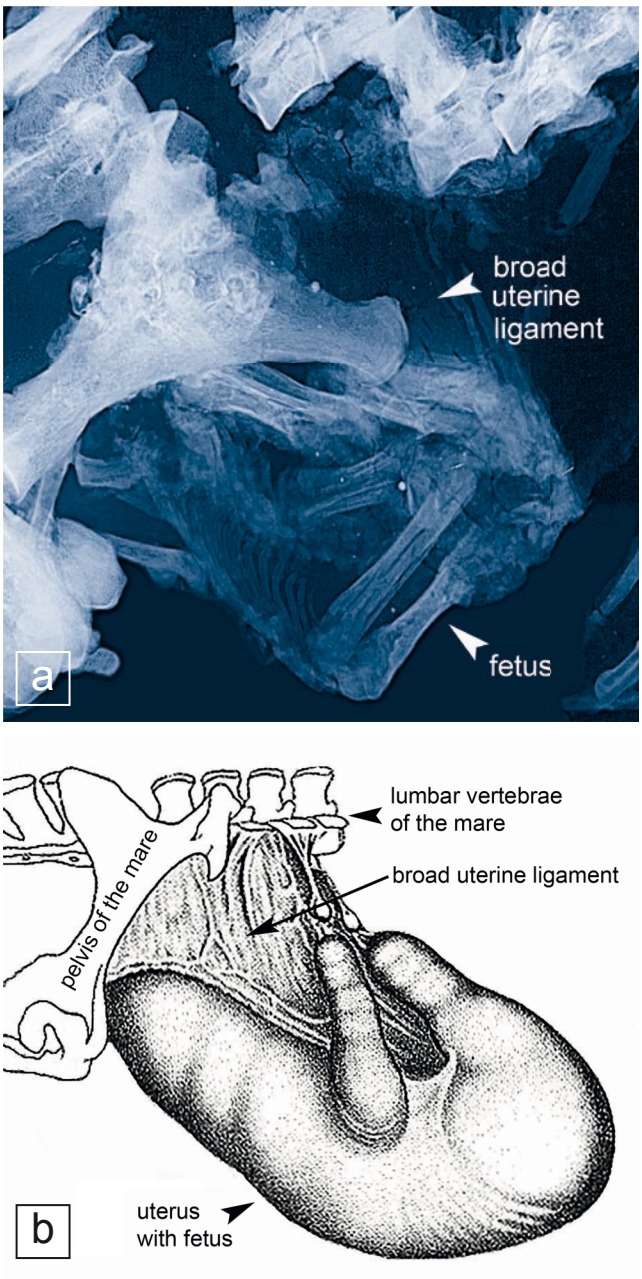
Text-fig. 6. a) Line drawing of the exposed side of the fetus of *Eurohippus messelensis* from Messel. Bones of the mare are shown for orientation. Notice the fine wrinkling lateral to the right femur of the fetus. The white line distinguishes the uteroplacenta on the left from the exposed bones of the fetus on the right. Scale = 5 cm; b) the SEM photo reveals that the wall of the uterus is replaced by petrified bacteria, preserved as siderite ($FeCO_3$). Drawing and anatomical interpretation by author; SEM photo by Renate Rabenstein (both Senckenberg Research Institute Frankfurt).

of the fetus is very incomplete, mostly disarticulated and dislocated (Text-fig. 9a). Following the idea that bones and many fragments of the rib cartilage of the mare should lie on the external wall of the uterus, whereas remains of the fetus should lie on the internal wall, it became possible to differentiate the uteroplacenta into the external wall, i.e., the uterus, and the internal wall, i.e., the placenta (Text-fig. 9b). Both display the typical wrinkling known in living mares, but also in the other two fossil mares with preserved uteroplacenta. At some places, a thin white layer is directly attached to the bones of the fetus. Two interpretations seem possible. It may be the innermost layer of the uteroplacenta, hence the amnion, or the skin of the fetus. This is still an open question.

At other places, the preparator, when applying the transfer technique of preparation and not knowing at that time to deal with a uteroplacenta, penetrated through the uteroplacenta and uncovered the underlying dark grey polyester, in which the fossil was transferred. Enigmatic are parallel structures that appear left of the tibia of the fetus (Text-fig. 9b). Presumably, as in the first pregnant mare from Messel they represent remnants of the broad uterine ligament. The third specimen and its uterine system are still being investigated.

What is the significance of the preserved uteroplacenta?

The three pregnant mares represent the only known uteroplacentae of fossil mammals. In contrast to the locomotory system, and despite at least 48 million years of subsequent evolution, these middle Eocene uteroplacentae reveal no major morphologic difference when compared with those of recent horses. Therefore, I conclude that the



Text-fig. 7. Comparison of the broad uterine ligament; a) x-ray of the abdomen of a pregnant mare of *Eurohippus messelensis* from Messel (Senckenberg Collection SMF ME 11034); b) drawing of the abdomen of a recent mare (after Benesch 1957). X-ray by Jörg Habersetzer; anatomical interpretation by author (both Senckenberg Research Institute Frankfurt).

uteroplacenta of mammals evolved early, at latest during the Palaeocene or even earlier, during the late Mesozoic, when dinosaurs were still thriving on our planet. Considering the protection, a uteroplacenta offers to growing fetuses compared to those developing in eggs, this could have been one of the reasons why viviparous mammals survived the catastrophic event at the K/Pg boundary, whereas oviparous dinosaurs did not (Franzen et al. 2016).

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Text-fig. 8. Skeleton of a mare of *Eurohippus messelensis* with fetus from the early middle Eocene maar of Messel (Germany); collection Dr. Burkhard Pohl. A white ellipse indicates the position of the uteroplacenta. Scale = 10 cm. Photo by author.

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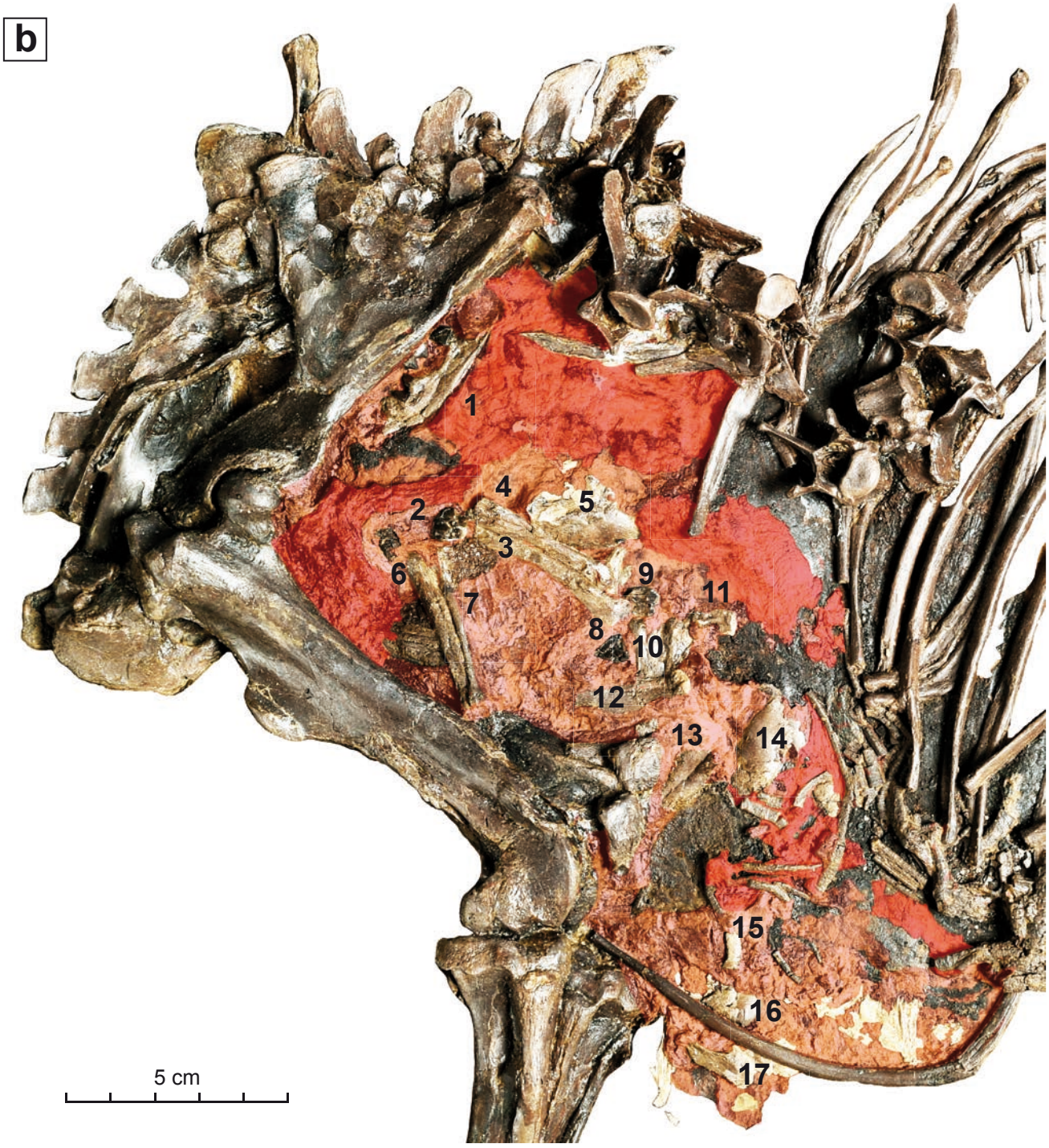
Text-fig. 9. The abdominal cavity of the mare of *Eurohippus messelensis* from the collection of Dr. Burkhard Pohl. a) after preparation; b) the anatomical interpretation differentiates the uteroplacenta, which is artificially colored. Dark red = external wall of the uterus; pink = internal wall of the placenta; white (original) = amnion or skin of the fetus; dark grey = where the preparator penetrated through the uteroplacenta and uncovered the underlying polyester. Fetal elements: 1 = left dP^4 followed by erupting M^1, below: fragment of left mandible with dP_3 or dP_4; 2 = left dP^3; 3 = left ulna; 4 = left radius; 5 = right frontal bone; 6 = right tibia; 7 = right fibula; 8 = right dP^2; 9 = right dP^3; 10 = right (?) humerus; 11 = left postglenoid process; 12 = left humerus; 13 = nasals; 14 = left frontal bone; 15–17 = skull fragments. Scale (a and b) = 10 cm. Photos by Sven Tränkner; drawing and anatomical interpretation by author (both Senckenberg Research Institute Frankfurt).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