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Höwenegg *Hippotherium primigenium*: geological context, cranial and postcranial morphology, palaeoecological and biogeographic importance

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ABSTRACT
Höwenegg is an early Vallesian (MN9, 10.3 Ma) vertebrate locality in Hegau, Southwest Germany renowned for its preservation of complete mammalian skeletons, diverse invertebrate and plant fossils. We provide the first to be published photographic images of the Höwenegg *Hippotherium primigenium* skulls, mandibles and dentitions for describing critical character states used to define hipparion species. We compare these states to those for North American *Cormohipparion occidentale*, Turkish *Cormohipparion sinapensis* Algerian '*Cormohipparion*' *africanum*, Austrian Pannonian C *Hippotherium* sp., Austrian locality Inzersdorf *Hippotherium primigenium*, the China type specimens of *Hippotherium weihoense* and '*Hipparion*' *chiai*, and Moldovan *Cremohipparion moldavicum*. Also provided are univariate statistical comparisons of cranial-dental characters and Log10 ratio analyses of third metapodials dimensions to better evaluate taxonomic comparisons and define the genetic pool from which Old World hipparions are derived. We concur with previous authors that North American *Cormohipparion* is the likely source of first occurring Old World hipparions offering alternatives of *Cormohipparion occidentale* or *Cormohipparion quinni* as the most closely related species for the Old World *Cormohipparion* Datum. We find that the best evidence for the chronology of the *Cormohipparion* Datum suggests and age of 11.4–11.0 Ma, or 11.2–11.1 Ma rather than the 11.5 Ma datum recently alleged for China.

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Höwenegg; *Hippotherium primigenium*; equids; Late Miocene; Evolution

Introduction

Höwenegg (Hegau), southwest Germany, is a vertebrate locality 35 km North of the Western limit of Lake Constance. Fossil vertebrates were first discovered there at the beginning of the 20th century, and the main site itself was discovered in 1936. Tobien and Jörg undertook extensive excavations from 1950 to 1963 excavating an area of over 150 sq. metres (Figure 1). Since these excavations, Höwenegg has become renowned for its preservation of complete mammalian skeletons, including the tridactyl horse *Hippotherium primigenium*, the archaic boselaphine antelope *Miotragocerus pannoniae*, and the rhinoceros, *Aceratherium incisivum* which are all known from multiple skeletons. Lesser abundant taxa include a dicrocerotine deer and a tragulid also represented by partial skeletons. Tobien (1986) provided an extensive review of this first phase of excavation and fossil retrieval of the Höwenegg excavations. Small mammals include complete skeletons (*Prolagus oeningensis*; Tobien 1986). Several groups of mammals have been studied since 1965: carnivores (Beaumont de 1986), rhinoceroses (Hünermann 1982), chalicotheres (Zapfe 1989), and hipparionine horses (Bernor et al. 1997). Höwenegg is a genuine Lagerstätte both from the standpoints of abundance and completeness of its vertebrate and invertebrate faunas and occurrence of associated plant material.

In 1985, Tobien and Bernor undertook an on-site review of the original excavations and the environs of Höwenegg including a large, abandoned basalt quarry near the site. A test trench was excavated on the eastern edge of the quarry to expose the geological section. In 1992, a more extensive trench was excavated, extending the 1985 test trench 15 metres westward over the north-central portion of the original Tobien and Jörg excavations (Figure 2). This trench was excavated in preparation for the Immendingen-Schloss Reisensburg (Ulm) Workshop hosted by the SMNK and the Town of Immendingen (near the Höwenegg locality) by Bernor, Fahlbusch, Mittmann and Rietschel. This workshop led to the 1996 Columbia University Press volume *Evolution of Western Eurasian Neogene Mammal Faunas* (Bernor, Fahlbusch and Mittmann, eds). The 1992 trench yielded a cranium of an adult male *Miotragocerus* skull and provided the opportunity for Carl Swisher to sample the deposits for single crystal argon and magnetostratigraphic dating yielding a date of 10.29 ± 0.07 Ma (Swisher 1996) and an MN9 correlation (Woodburne et al. 1996).

The SMNS and SMNK museums commenced new quarrying excavations in 2003 and expanded the western limit of the 1992 trench in 2003 including broadening of the trench at its western limit to 5 metres (Heizmann et al. 2003; Figure 2). The 2004 field season completed excavation of the 3 *Miotragocerus* skeletons and 1 *Trionyx* skeleton found in the westernmost extension of the trench, including a female *Miotragocerus* with 2 foetuses in situs utero (Supplementary Figure 1). In 2005, the excavation team led by Herr Wolfgang Munk established a new 130 sq. metre excavation adjacent to the westernmost extension of the Tobien and Jörg excavations. After removing a thick stand of trees and soil, 8 cubic metres of sediment were excavated during which 130 isolated specimens of diverse vertebrates were excavated. Following the 2005 season, a 23.5 metre deep core was drilled on the northern

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Figure 1. Locator map of the Höwenegg locality, Hegau, Germany.

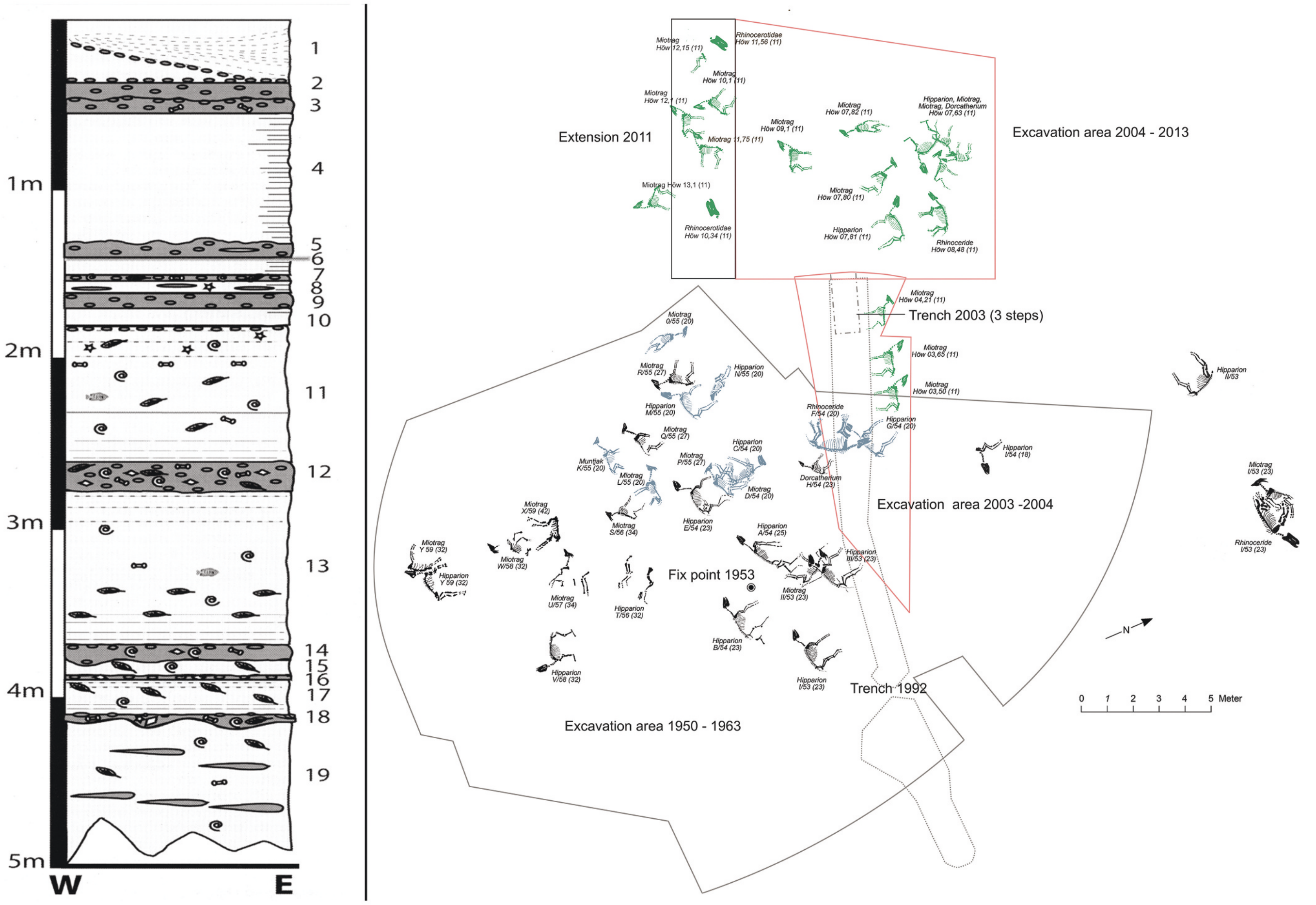

Figure 2. Original map (Lageplan) of the Höwenegg excavations with the statigraphic section. The Lageplan shows the different excavation areas of 1950–1963, 2003–2004 and 2011.

edge of the new excavation establishing that there exists 4 metres more of Höwenegg sediments below the 2005 excavation level. The 2006 season was spent extending the original quarry 100 sq. metres to the west. During the first year of this new excavated area, the team reported diverse plants, invertebrates and vertebrate material. Between 2007 and 2013 the SMNK excavated 19 stratigraphic units and added several skeletons of *Miotragocerus* and *Hippotherium* along with new mammalian species of cervid and rodent (Munk et al. 2007).

Figure 2 provides a stratigraphic section with a map of the site (Lageplan) of the 2003–2013 excavation season rendering 19 stratigraphic units wherein Unit 11 has the most abundant and diverse biotic assemblage. The Lageplan distinguishes the skeletons excavated by Tobien and Jörg (in grey/black) versus those excavated by the SMNK and SMNS in the 2003–2013 interval (in green). By the end of 2013, the new excavations had expanded the original Höwenegg Quarry by greater than 140 sq. metres and had excavated further than the deepest levels reached by Tobien and Jörg down to the underlying volcanic layers. Figure 3 provides a pie-diagram of the fossil content of the new excavations, 62% of which are fossil mammals. The excavations between 2003 and 2013 resulted in adding 24 new skeletons and to date the Höwenegg excavations, 1950–2013, have yielded a total of 49 skeletons.

A major contribution to the Höwenegg research programme was the publication of a single crystal argon age of the Höwenegg by Swisher (1996) of 10.29 ± 0.07 Ma reinforcing an MN9 correlation for the site (Woodburne et al. 1996) and correlation with other Central European MN9 localities (Bernor et al. 1996; Steininger et al. 1996, 1997; Scott et al. 2004, 2005). However, contrary to Berggren and Van Couvering (1974), the Höwenegg research programme has demonstrated that the site does not represent the '*Hipparion*' Datum (*Cormohipparion* Datum of Bernor et al. 2017, 2021a) but it is nearly 1 Ma younger than the Datum established in the Vienna Basin Pannonian C, 11.4–11.0 Ma (Bernor et al. 2017).

The Höwenegg *Hippotherium primigenium* sample of 14 skeletons (with 2 more yet to be prepared collected by the second phase of excavations) has been a key assemblage for analysing statistical hipparions and *Equus* samples in cranial and postcranial elements (e.g., Bernor et al. 2018; 2019, 2021b; Cirilli et al. 2021a, 2021b), because it is a genuine quarry sample of a single species accumulated over a short duration (Tobien 1986; Woodburne et al. 1996). The metrics of the entire Höwenegg *Hippotherium* sample has been published with a full range of parametric statistics demonstrating its single species homogeneity (Bernor et al. 1997). However, until now, only the line drawings of Otto Garaux have been published (Bernor et al. 1997), and herein we are illustrating images of the skulls, mandibles and dentitions critical for discriminating *Hippotherium primigenium* from other primitive Old World hipparions.

Materials and methods

The cranial-mandible sample from Höwenegg includes SMNK Hö A, HLMD Hö485, SMNK HöC and SMNK HöI (Figure 4(a,d), consecutively), and less well-preserved skulls HLMD Hö G, HLMD Hö491, HLMD III, HLMD Y and HLMD Hö488 (Supplementary Figures 2 a-e, consecutively). Maxillary cheek tooth dentitions are illustrated for SMNK Hö A, HLMD Hö485, SMNK Hö C and SMNK Hö I. (Figure 5 (,), consecutively). Mandibles SMNK Hö A, SMNK Hö C, HLMD Hö486 and SMNK Hö B are illustrated in lateral view (Figure 6 (,), consecutively) and mandibular dentitions (Figure 7 (,), consecutively). An image of the complete Höwenegg B skull and mandible in their original plaster jacket is illustrated in Supplementary Figure 3.

The Höwenegg *H. primigenium* monograph (Bernor et al. 1997) utilised the standards for measuring species of extant and fossil Equidae established by Eisenmann et al. (1988). These measurements were reillustrated in the monograph with revision of measurements for the dentition which we utilise herein (Bernor et al. 1997). Population statistics including mean, standard deviation, confidence limits, coefficient of variation, minimum, maximum and median were published for the entire skeletal sample. Measurements taken on all skeletal elements were clearly depicted as figures. The cranium was illustrated in 5 anatomical views, the mandible in 2 views and most bones in 4–6 anatomical views.

Because of a long-term interest in the Höwenegg *H. primigenium* sample and the importance of the skull, mandible and dentition anatomy we are taking the opportunity to provide photographic images of these particular elements for the first time. We do not repeat herein citation of all 49 discrete characters of the skull, mandible and dentition, but rather target those discrete characters

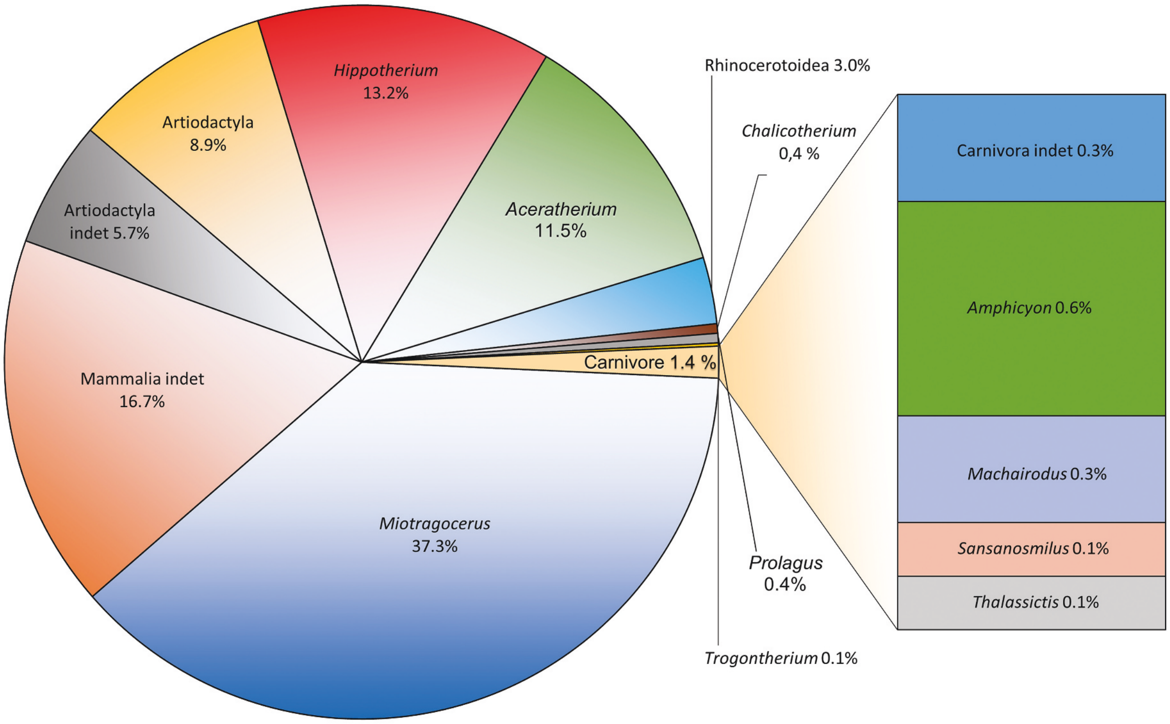

Figure 3. Pie diagram showing the Höwenegg faunal composition.

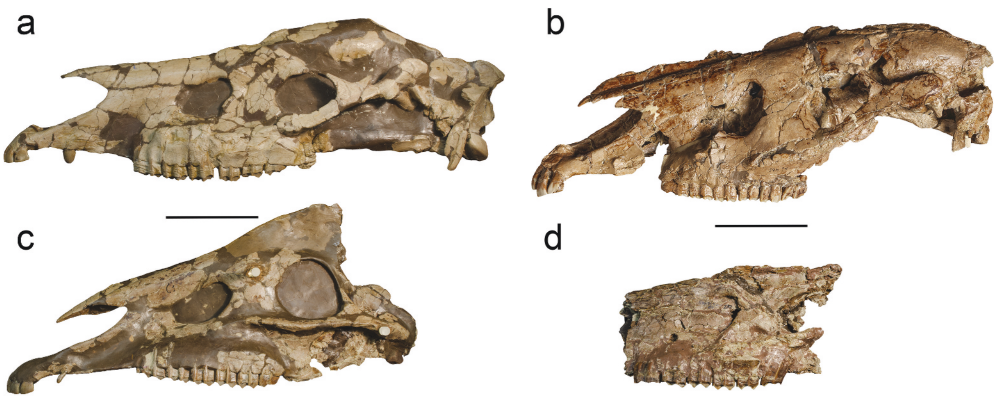

Figure 4. Höwenegg *Hippotherium primigenium* crania in lateral view. A) SMNK HoA; b) HLMD Ho485; c) SMNK HoC; d) SMNK HoI. Scale bar 10 cm.

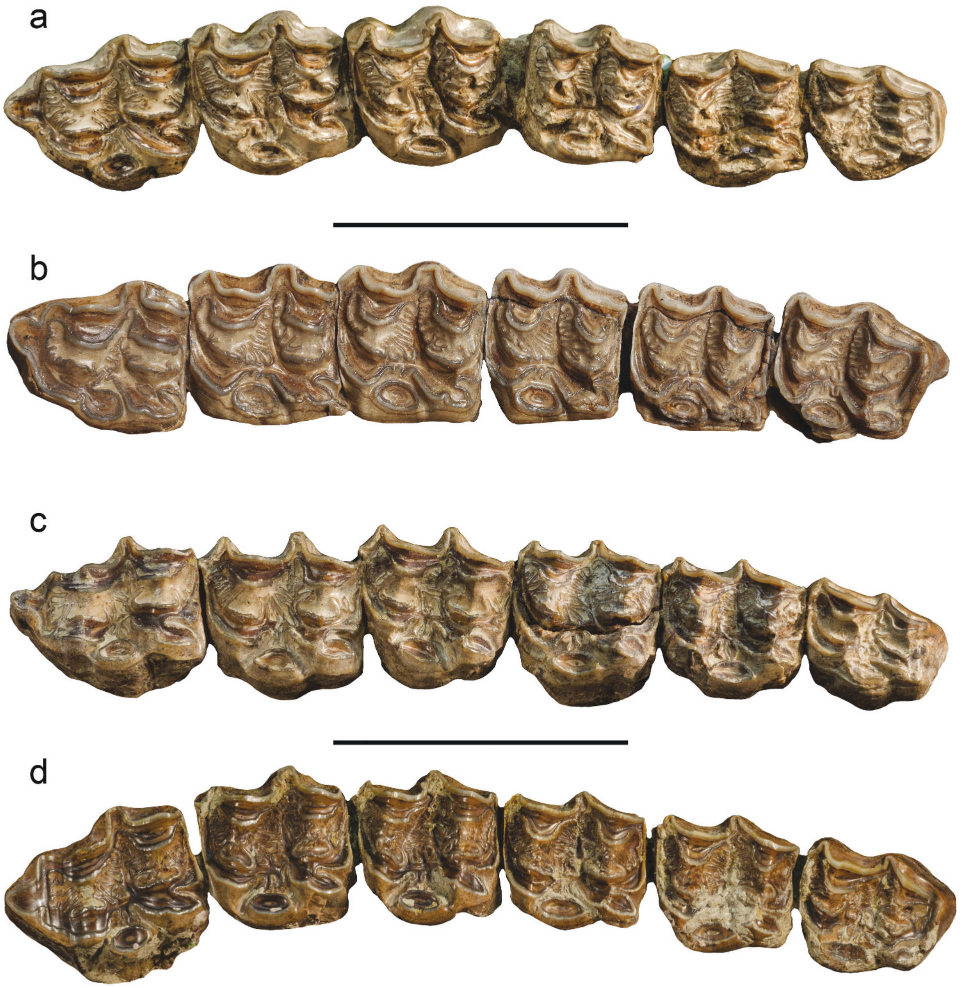

Figure 5. Höwenegg *Hippotherium primigenium* maxillary cheek tooth morphology in occlusal view. A) SMNK HoA; b) HLMD Ho485; c) SMNK HoC; d) SMNK HoI. Scale bar 5 cm.

of these elements relevant to the origin of Old World hipparions and their specific relationship to North American *Cormohipparion* and primitive Eurasian and African hipparionin taxa (Supplementary Table 1; Bernor et al. 2003; Woodburne 2007, 2009, 2017). The Vienna Basin Pannonian C hipparions from Gaiselberg, Atzelsdorf and Mariathal are represented largely by maxillary and mandibular cheek teeth and have been demonstrated to be amongst the most primitive Old World hipparions and derived from North American *Cormohipparion*. They were also determined to be browser dominant, mixed 'opportunistic' feeders (Bernor et al. 2017).

Maxillary cheek tooth characters documented in this sample included, with specific reference to Bernor et al. (1997 character state scores): maximum measured crown height (C18), complexity of the pre- and postfossettes (C19), incidence of protocone flattening (C23), incidence of protocone connected to protoloph (C24), presence of pli

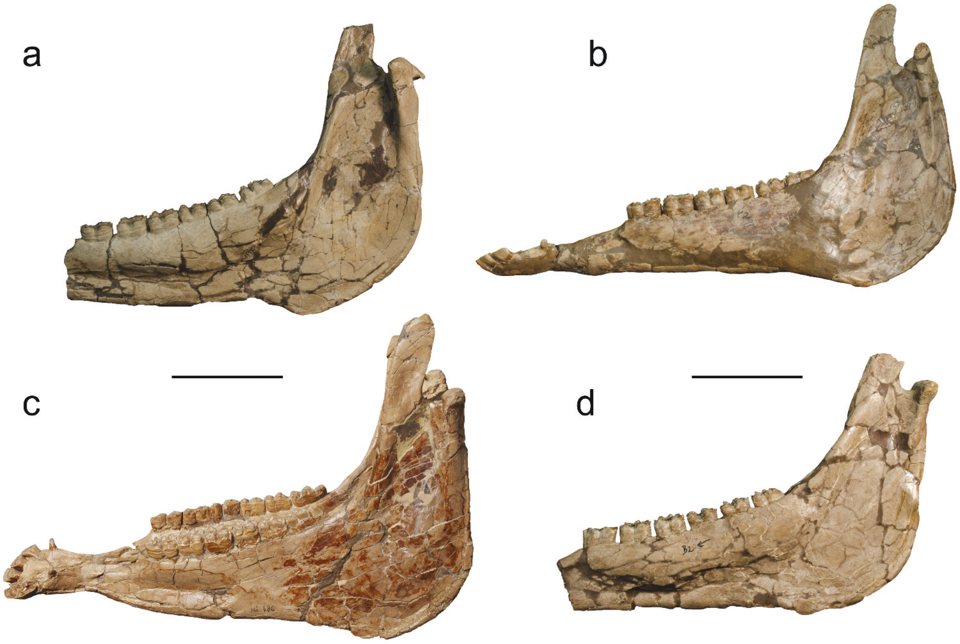

Figure 6. Höwenegg *Hippotherium primigenium* mandibles in lateral view. (a) SMNK HoA; (b) SMNK HoC; (c) HLMD Ho486; (d) SMNK HöB. Scale bar 10 cm.

Figure 7. Höwenegg *Hippotherium primigenium* mandibular dentitions in occlusal view. (a) SMNK HoA; (b) SMNK HoC; (c) HLMD Ho486; (d) SMNK HöB. Scale bar 5 cm.

protocone (C25), P2 anterostyle morphology (C28). Mandibular cheek tooth characters documented by Bernor et al. (2017) included anterostylid morphology (C28), premolar metaconid morphology (C32), molar metaconid morphology (C33), premolar metastylid morphology (C34), premolar metastylid spur (C35), molar metastylid morphology (C36), molar metastylid spur (C37), presence of pli caballinids (C40) and ectostylid occurrence (C43). Following Woodburne (2007, 2009) we added incidence of linkage of opposing borders of pre- and post-fossettes (FLink = Yes/No) (Supplementary Text and Supplementary Table 1). We provide comparative character state and measurement data for the following taxa: the *Cormohipparion occidentale* complex (Woodburne 2007) including *Cormohipparion goorisi* (Fleming Formation, Gulf Coastal Plain, Texas, USA; Early Barstovian; MacFadden and Skinner 1981), *Cormohipparion quinni* (Devil's Gulch Horse Quarry, Valentine Formation, Nebraska, USA; 14–12.5 Ma, Middle-Late Barstovian; Woodburne 1996, 2007), *Cormohipparion johnsoni* (Burge Member of the Valentine Formation, Nebraska, USA; 12.5–12 Ma, Late Barstovian – Early Claredonian; Woodburne 2007), *Cormohipparion matthewi* (X-Mas Quarry, Nebraska, USA; ca. 11.5–9.95 Ma, Claredonian; Woodburne 2007), *Cormohipparion fricki* (MacAdams Quarry, Texas, USA, 12–11.5 Ma, Late Barstovian – Early Claredonian; Woodburne 2007), *Cormohipparion merriami* (June Quarry, Burge Member of the Valentine Formation, Nebraska, USA; Late Barstovian – Early Claredonian; Woodburne 2007), *Cormohipparion skinneri* (Gidley Horse Quarry, Texas, ca. 10 Ma, Middle Claredonian; Woodburne

2007) and *Cormohipparion occidentale* (Burge Member of the Valentine Formation, X-Mas Quarry, Hans-Johnson Quarry, Machairodus Quarry Nebraska, USA; 12.7–9.95 Ma, Late Barstovian – Early Claredonian; Woodburne et al. 1981; Woodburne 1996, 2007), *Cormohipparion sinapensis* (Sinap, Turkey; ca. 10.8 Ma, MN9; Bernor et al. 2003), Pannonian C hipparions (Austria; 11.4–11.2 Ma, MN9; Bernor et al. 2017), Inzersdorf *Hippotherium primigenium* (Pannonian D-E, Austria; 10.4–9.8 Ma, MN9; Bernor et al. 2017), '*Cormohipparion*' *africanum* (Bou Hanifia, Algeria; 10.5 Ma, MN9; Bernor and White 2009), *Hippotherium weihoense* (China; 11.1–8.7 Ma; Qiu et al. 1997; Qiu et al. 2013; Bernor et al. 2021a; Sun et al. 2022), *Cremohipparion moldavicum* Type (Taraklia, Moldova; MN10, 9.7–8.9 Ma; Gromova 1952; Eisenmann, 2019 (V. Eisenmann website)).

Morphometric analyses are undertaken here for the most important measurements of the cranial morphology and for third metapodials. Boxplots analyse the length of the upper cheek tooth row (M9), length of the preorbital bar (POB; M32), length of the preorbital fossa (POF; M33), height of the POF (M35), distance between the POF and the facial-maxillary crest (M36) and height of the POF from the posterior rim of the POF (M38). The measurements included in the Log10 ratio diagrams of third metapodials include maximum length (M1), midshaft width (M3), depth of the diaphysis at level of the midshaft width (M4), proximal articular width (M5), proximal articular depth (M6), maximum diameter of the articular facet for the third carpal/tarsal (M7), diameter for the anterior facet for the fourth carpal/tarsal (M8), distal maximum supra-articular width (M10), distal maximum articular width (M11), distal maximum keel depth (M12), distal maximum depth of the lateral condyle (M13), distal maximum depth of the medial condyle (M14).

Boxplots were calculated in R v. 1.4.1103 (R Core Team 2013) using the package *ggplot2()* v. 3.3.3 (Wickham 2016). The Log10 ratio diagrams on third metapodials use the log-transformed mean values of the Höwenegg *Hippotherium primigenium* sample (Bernor et al. 1997). Measurements were taken to the nearest 0.1 mm using digital calipers, following the international equid measurement guidelines (Eisenmann et al. 1988; Bernor et al. 1997). Anatomical nomenclature and osteological landmarks follow Bernor et al. (1997).

Taxonomic note

In the present work, we recognise the different genera of Hipparionini reported by Bernor et al. (2021a), in particular *Cormohipparion, Hippotherium* and *Cremohipparion*. We use '*Hipparion*' for those species which cannot be confidentially included in one of the 10 genera recognised by Bernor et al. (2021a).

Anatomical elements

POB: preorbital bar; POF: preorbital fossa; UTR: upper cheek tooth row; LTR: lower cheek tooth row; P: protocone; I1: maxillary first incisor; I2: maxillary second incisor; I3: maxillary third incisor; P2: maxillary second premolar; P3: maxillary third premolar; P4: maxillary fourth premolar; M1: maxillary first molar; M2: maxillary second molar; M3: maxillary third molar; i1: mandibular first incisor; i2: mandibular second incisor; i3: mandibular third incisor; p2: mandibular second premolar; p3: mandibular third premolar; p4: mandibular fourth premolar; m1: mandibular first molar; m2: mandibular second molar; m3: mandibular third molar; mc3: third metacarpal; mt3: third metatarsal; rt: right; lt: left.

Repositories and institutional acronyms

AMNH: American Museum of Natural History, New York (USA); HLMD: Hessisches Landesmuseum, Darmstadt (Germany); IVPP: Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing (China); LACM, Los Angeles County Natural History Museum, Los Angeles, California (USA), MNHN, Museum National d'Histoire Naturelle, Paris (France); PIN: Palaeontological Institute, Moscow (Russia); SMNK: Staatliches Museum für Naturkunde, Karlsruhe (Germany).

Systematic palaeontology

Class Mammalia Linnaeus 1758

Order Perissodactyla Owen 1848

Family Equidae Gray 1821

Tribe Hipparionini Quinn 1955

Genus Hippotherium *von Meyer, 1829*

Hippotherium primigenium von Meyer, 1829

Description

SMNK Hö A. The Hö A skeleton (SMNK Hö A) is a male individual and the basis for description of *H. primigenium* in the Höwenegg monograph (Figure 4a, lateral view; Bernor et al. 1997). The skull is large, mediolaterally crushed but preserves a long POB with the anterior limit of the lacrimal placed more than half the distance from the anterior orbital rim to the posterior rim of the POF (C1C); the POF is subtriangular shaped and anteroventrally oriented (C4D); the POF is deeply posteriorly pocketed (C5A); the POF medial depth is greater than 15 mm (C6A); the POF peripheral outline is strongly delineated around its entire periphery (C8A); the POF anterior rim is present (C9A); the nasal notch is placed approximately half the distance between the canine and P2 (C15B); maximum crown height is estimated to have been slightly greater than 50 mm (C18C). Maxillary cheek teeth (Figure 5a) have the following characteristics: cheek teeth have complex plications of the pre- and postfossettes (C19A); there is no incidence of opposing borders of the fossettes being linked (FLink = No); protocone shape elongate oval with some lingual flattening (C23D/E); protocone is isolated from the protoloph in all cheek teeth (C24B); protocone spur absent (C25C); P2 anterostyle elongate (C28A).

HLMD Hö V (Hö485). The Hö V skeleton is a female and the least distorted medio-laterally of the Höwenegg *Hippotherium* assemblage (Figure 4b). Its character state distribution is very similar to the HöA skeleton with some minor differences: the POF is fundamentally antero-ventrally oriented but more vertical on the left side. This individual is a later stage adult (Figure 5b) with more worn cheek teeth than the HöA skeleton and as a result expresses the following ontogeny-related differences in the dentition: all protocones are oval to rounded (C23C/G); protocone is linked to the protoloph on P2 only (C24A); anterostyle has become shortened with wear (C28B) and M3 has become quadrangular shaped.

SMNK Hö C. The Hö C skull is mediolaterally very flattened (Figure 4c). The canine is small, indicative of a female, and mesially placed so that the nasal notch is placed closer to the mesial border of P2 (C15C). The POB and POF are very similar to the HöA skeleton with POF being anteroventrally oriented. While an adult, the maxillary cheek teeth are in an earlier stage-of-wear with fossettes not well worn yet on P2-P3 and M3 but very well developed and complex on M1 and M2 (C19A); protocones on all teeth are elongate-oval with some flattening (C23D/E; Figure 5c) and P2-P3 show linkage of the superiormost opposing borders of pre- and postfossettes (Flink = Yes).

SMNK Hö I. The Hö I skull is of an unknown sex lacking the snout and cranium but preserving the POF and maxillary cheek teeth. This individual is similar to the HöA skull in facial morphology (Figure 4d). The maxillary cheek teeth are of an adult exhibiting very complex plications of the fossettes (C19A), oval-elongate protocones that are not lingually flattened (23C; Figure 5d).

HLMD Hö G. The Hö G specimen is complete, but severely crushed adult skull and mandible of a female with a small mandibular canine. The facial area has been badly damaged not preserving details of the POF. Occlusal morphology of the cheek teeth cannot be studied because of the close occlusion of the maxilla and mandible. The nasal retraction appears the same as in Hö A. We have scored nasal notch position (15B), maximum crown height (18C) as in the Hö A skull (Supplementary Figure 2a).

HLMD Hö491 is a poorly preserved and crushed skull and mandible with P2-M3 and p2-m3 lacking the cranium and superior portion of the maxilla. Facial morphology has been lost, and occlusal features of the maxillary and mandibular cheek teeth cannot be studied on this specimen (Supplementary Figure 2b).

HLMD III is a badly crushed and poorly preserved adult skull and mandible. Facial morphology is not preserved. Maxillary cheek teeth are preserved, but occlusal surfaces are not observable. The mandible is badly crushed, and cheek teeth are not observable (Supplementary Figure 2c).

HLMD Y is a foetal skeleton preserving a partial skull and the two mandibles. Morphology is not well enough preserved to be reported (Supplementary Figure 2d).

HLMD Hö488. The Hö488 specimen is an adult maxilla with right and left P2-M3 lacking the facial region, snout and cranium (Supplementary Figure 2e). Remarkable herein is that in advanced wear P2 exhibits linkage of the opposing borders of the fossettes (FLink = Yes); all protocones have become shortened and oval (C23D); protocone is linked to the protoloph in P2 (C24A); protoconal spur is absent (C25C); P2 has a shortened, rounded anterostyle (C28B).

SMNK Hö A. The Hö A mandible lacks the symphysis and the incisor arcade, but it preserves the mandibular horizontal corpus and ascending ramus with a large posterior angle (Figure 6a). The mandibular dentition is characterised by the following salient features (Figure 7a): p2 anterostylid is elongate, albeit bent lingually (C28A); premolar metaconids are consistently rounded (C32A); molar metaconids are as in the premolars (C33A); premolar metastylids are round (C34A); premolar metastylid spur is slightly developed on p2-p4 (C35A); molar metastylid is squared on the distal border of m1 and m2 (C36E); molar metastylid spur is absent (C37B); premolar ectoflexid does not separate metaconid and metastylid (C38A); pli caballinid is present on p2-p4, absent on m1-m3 (C40B/C); ectostylid is absent on all cheek teeth (C43B).

SMNK Hö C is an almost complete even deformed mandible, preserving the incisor arcade, the symphysis, the horizontal corpus and the mandibular ramus with a large posterior angle (Figure 6b). The mandibular dentition also has similar morphological features as the SMNK Hö A, except: premolar ectoflexid does separate metaconid and metastylid making a deep incursion on right and left p2 (C38B) (Figure 7b). Premolar and molar metaconids are rounded (C32A, C33A); premolar metastylids are square (C34E) and molar metastylids are squared (C36E); metastylid spurs occur on p3 and p4 with no molar metastylid spurs (C35A and C37B, respectively); premolar ectoflexid separates metaconid and metastylid on p2 (C38B); pli caballinids occur on the premolars only (C40B), and there are no ectostylids on any of the cheek teeth (C43B).

HLMD Hö486 is a complete mandible of a mature adult female in relatively advanced wear (Figure 6c). Salient features of this individual are similar to the Hö A mandible except: p2 anterostylid is truncated by wear (C28B); premolar and molar metaconids are as in the HöA mandible; premolar metastylids are rounded rather than square (C34A); molar metastylids show some squaring (C36E); premolar metastylid spurs are absent (C35A); p2 ectoflexid separates metaconid-metastylid while deeply penetrating p3 and p4 (C38B); pli caballinids are absent on all cheek teeth (C40C); p3 has a small, but distinct ectostylid that has been exposed by wear (C43A) (Figure 7c).

SMNK Hö B. The Hö B mandible has a similar shape to SMNK Hö A, preserving the horizontal corpus and ramus while lacking the symphysis with the incisor arcade (Figure 6d). The mandibular dentition is of a young adult. There are no salient differences from the Hö A skeleton except that this individual is in an earlier stage of wear with prominent metastylid spurs (C37A) on p2-p4 (Figure 7d).

SMNK Hö E is a female with a foetus in situs utero with a very crushed skull and mandible. Its cranial and dental features compare closely to the HöA skeleton (Bernor et al. 1997).

Morphological and morphometric comparisons

We describe herein the results of the morphological and morphometric comparisons with the North American *Cormohipparion* species (hereafter *Co.*), *Co. goorisi, Co. quinni, Co. johnsoni, Co. matthewi, Co. fricki, Co. merriami, Co. skinneri* and *Co. occidentale* with the Old World *Co. sinapensis*, '*Co*'. *africanum*, the Inzerdorf *Hippotherium* (hereafter, *Hi.*) *primigenium*, Höwenegg *Hi. primigenium*, the Chinese *Hi. weihoense* holotype, the recently reported Chinese *Hi. weihoense* sample (Sun et al. 2022) and the *Cremohipparion* (hereafter, *Cr.*), *Cr. moldavicum* type specimen in cranial values (Figure 8). Log10 ratio diagrams include the X-Mas Quarry sample and the Old World species (Figure 9). No specific metapodials have been assigned to *Co. occidentale* however, the X-Mas quarry sample includes two species, *Co. occidentale* (larger) and *Co. matthewi* (smaller) (Bernor et al. 2003; Woodburne 2007). Herein, we consider the whole sample of the X-Mas Quarry in the Log10 ratio analyses as a reference for the North American *Cormohipparion* spp.

Supplementary Table 1 provides the character state distribution of skull, maxillary and mandibular cheek tooth characters scored herein. The top line, Höwenegg *Hi. primigenium* summarises the scoring across six skulls and dentitions figured in the text and six less well preserved skulls and dentitions. We compare the *Cormohipparion, Hippotherium, 'Hipparion'* and *Cremohipparion* character state distributions and further compare the results of the box plots and Log10 ratio diagrams below. Supplementary Table 2 lists statistical ranges for measurements of the total maxillary cheek tooth row length (M9), and facial measurements (M32, M33, M35, M36 and M38) of the Höwenegg *Hi. primigenium* sample for comparison with the North American and Eurasian *Cormohipparion* species, Eurasian *Hippotherium* species and the type *Cr. moldavicum* samples given below.

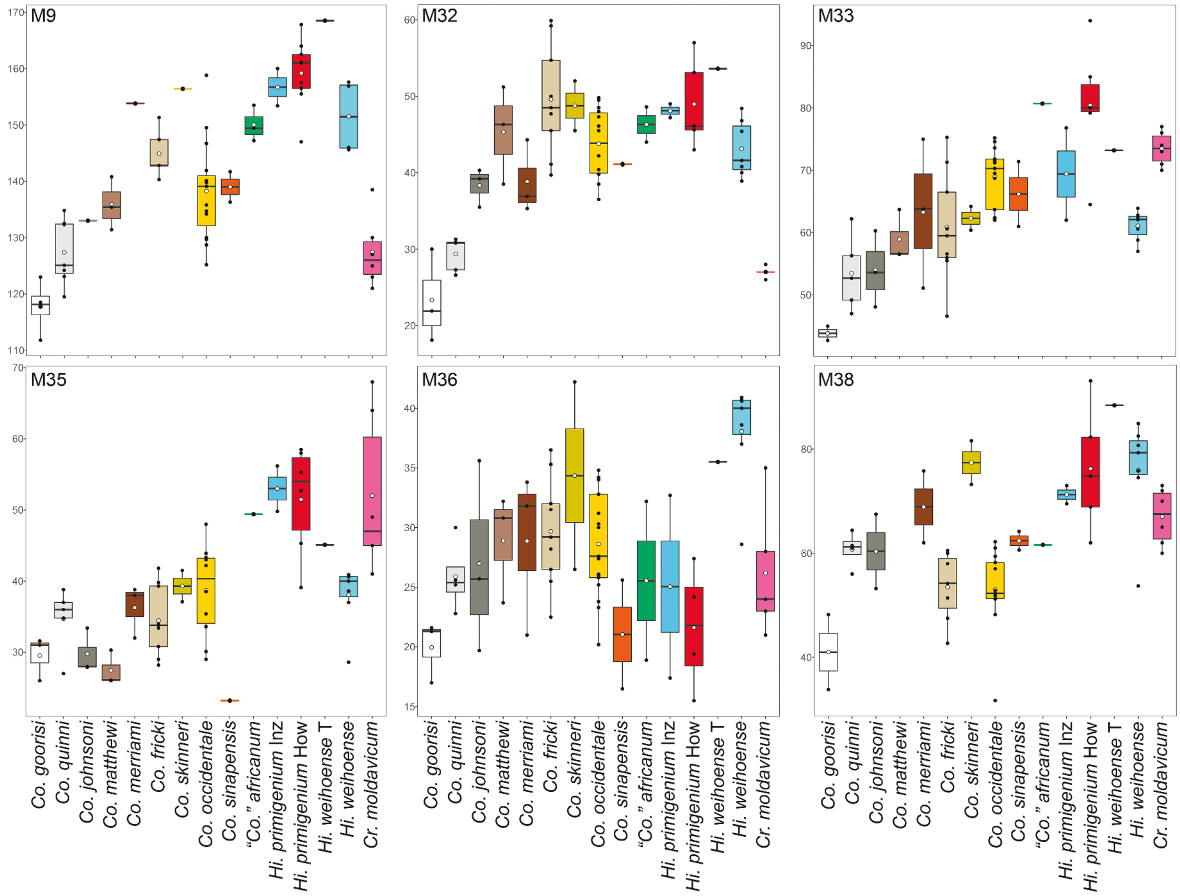

Figure 8. Univariate cranial comparison of the species discussed in the text. Boxplots include minimum, median, mean, and maximum values with 25th and 75th percentile of each sample. Measurements refer to the international guidelines for studying fossil and extant horses (Eisenmann et al. 1988; Bernor et al. 1997).

The Höwenegg sample has a maxillary cheek tooth row length mean of M9 = 159.2 mm and a range of 147.0–167.8 mm. Ranges of facial measurements are: M32 (POB length) = 43.0–57.0 mm; M33 (POF length) = 64.5–94.0 mm; M35 (POF height) = 39.1–58.5 mm; M36 (POF ventral rim – facial maxillary crest dimension) = 15.5–27.4 mm; M38 (height distal mid-POF rim to maxillary alveolus) = 62.0–93.1 mm. Most of the Höwenegg skull material was laterally crushed but without distorting these skull linear measurements. The Höwenegg *Hi. primigenium* skull and dental morphology yielded the following character states. C1C: POB long with the anterior edge of the lacrimal placed more than half the distance from the anterior orbital rim to the posterior rim of the fossa. C4D: POB subtriangular shaped and anteroventrally oriented. C5A: POF deeply pocketed, greater than 15 mm in its deepest place. C6A: POF medially deep, greater than 15 mm in the deepest place. C8A: POF peripheral outline strongly delineated around the entire periphery. C9A: POF anterior rim present. C15B: nasal notch placed approximately half the distance between canine and P2. C18C: maximum cheek tooth crown height 40–60 mm. C19A: maxillary cheek tooth fossette ornamentation complex, with several deeply amplified plications. FLink: P2 fossette linkage only apparent in SMNK Hö C and HLMD Hö488. C23D/E: protocone shape is mostly oval with some lingual flattening. C24B: protocone is isolated except occasionally in the worn P2 of HLMD Hö488. C25C: protocone spur is absent. C28A: anterostyle is mostly elongated (except HLMD V and Hö488). C32A: premolar metaconid rounded. C33A: molar metaconid rounded. C34A: premolar metastylid rounded. C35A: premolar metastylid spur present. C36E: molar metastylid mostly square shaped (Hö B and Hö I are rounded). C37B: molar metastylid spur is absent. C38A/B: premolar ectoflexid varies in its separation of metaconid and metastylid wherein two p2s show this separation (SMNK Hö C and HLMD Hö486). C40ABC: pli caballinid varies from being complex to absent. C43B: ectostylids are absent except for a small one on HLMD Ho486 (15/85).

The morphometric comparisons between the Höwenegg *Hi. primigenium* with the species of the *Cormohipparion* complex (Woodburne 2007) and the primitive *Cormohipparion*, *Hippotherium* and *Cremohipparion* species of the Old World reveal some new insights. There is a general trend of size increase and increase in cheek tooth crown height in the North American *Cormohipparion* species, with the primitive *Co. goorisi* and *Co. quinni* being the smallest and chronologically younger *Co. fricki*, *Co. skinneri* and *Co. occidentale* being the largest (Figure 8).

Cormohipparion occidentale overlaps the range of variability of *Co. sinapensis* in most cranial values, although the latter shows a smaller POF height (M35). Nevertheless, the larger *Co. occidentale* individuals (second quartile) overlap the smallest of *Hi. primigenium* (first quartile), in M9, M32, M33, M35 and M38. *Cormohipparion occidentale* exhibits a mostly greater distance between the POF and the maxillary crest (M36) than Höwenegg *Hi. primigenium* (Figure 8) reflecting the dorsal-ventral expansion of the Höwenegg POF (M35). *Cormohipparion occidentale* has less complex enamel plications of the cheek teeth (C19B) than the Höwenegg sample and has very elongate-oval protocones with

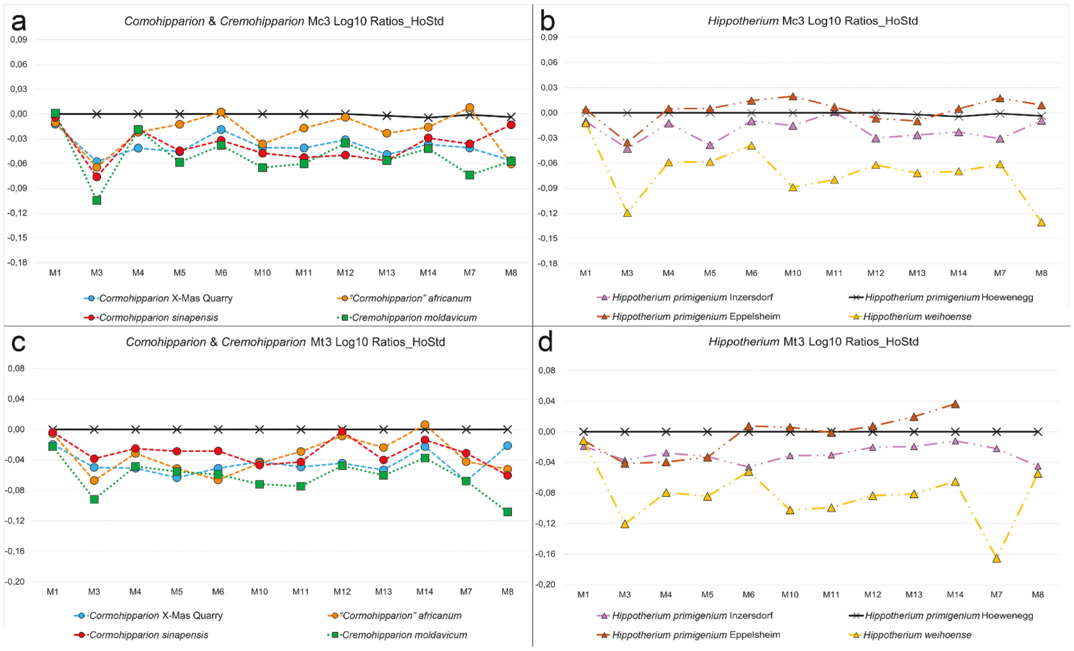

Figure 9. Log10 ratio diagrams in third metacarpal (a, b) and third metatarsal (c, d) based on the Log10 transformed mean of the *Hippotherium primigenium* sample from Höwenegg (Germany, Late Miocene). a) Höwenegg *Hippotherium primigenium* third metacarpal mean compared with the North American *Cormohipparion* X-Mas Quarry sample, *Cormohipparion sinapensis*, '*Cormohipparion*' *africanum* and *Cremohipparion moldavicum*. b) Höwenegg *Hippotherium primigenium* third metacarpal mean compared with *Hippotherium primigenium* from Inzersdorf and Eppelsheim and with *Hippotherium weihoense* (Sun et al. 2022). c) Höwenegg *Hippotherium primigenium* third metatarsal mean compared with the North American *Cormohipparion* X-Mas Quarry sample, *Cormohipparion sinapensis*, '*Cormohipparion*' *africanum* and *Cremohipparion moldavicum*. d) Höwenegg *Hippotherium primigenium* third metatarsal mean compared with *Hippotherium primigenium* from Inzersdorf and Eppelsheim and with *Hippotherium weihosense* (Sun et al. 2022).

flattened lingual surfaces (23DE). The X-Mas Quarry third metapodials have a more slender morphology than *Hi. primigenium*, and is close to *Co. sinapensis* and '*Co*'. *africanum* in their dimensions (Figure 9a,c).

Cormohipparion sinapensis is smaller than the Höwenegg hipparion with shorter P2-M3 dimension (M9); shorter POB length (M32); shorter POF height dimension (M35). It has a shorter POF length than the Höwenegg sample (M33); the height from the posterior POF rim to facial maxillary crest overlaps with the Höwenegg sample (M36) and lies at the lowest portion of the Höwenegg sample range for height from posterior rim of POF to maxillary alveolus (M38). Of the facial characters, *Co. sinapensis* differs from the Höwenegg *Hi. primigenium* in having a moderately delineated POF periphery (C8B). *Cormohipparion sinapensis* exhibits moderately complex fossette plications (C19B), linkage of the opposing borders of the pre- and postfossettes on P2 (Flink = Yes), protocone shape that is oval with flattened lingual surfaces (C23CE), and with a short, rounded anterostyle (C28B). Third metapodials (mc3 and mt3) are more slender (particularly midshaft) than Höwenegg *Hi. primigenium* and have a similar pattern to the X-Mas Quarry sample (Figure 9a,c).

'*Cormohipparion*' *africanum* has a shorter P2-M3 dimension (M9) and height of posterior rim of POF to alveolar border (M38) than the Höwenegg sample but overlaps the Höwenegg *Hi. primigenium* individuals in POB (M32) dimensions and POF dimensions of M33 and M35 while having larger dimensions for M36 (distance of the POF from the maxillary crest). '*Cormohipparion*' *africanum* is intermediate in size between *Co. sinapensis* and the Höwenegg *Hi. primigenium*. '*Cormohipparion*' *africanum* is similar in facial features to the Höwenegg *Hi. primigenium* except for its nasal notch position which is incised closer to P2 (C15C). Cheek teeth have elongate-oval protocones (C23D); P2 anterostyle is elongate (C28A); premolar metastylid is rounded (C34A); premolar metastylid spur is present on p2 (C35A); molar metastylid is rounded (C36A); premolar ectoflexid sometimes separates metaconid-metastylid (C38AB); pli caballinid is absent (C40C); there are no ectostylids on the mandibular cheek teeth (C43B). Third metacarpal Log10 ratio diagrams (Figure 9A) have more slender proportions, especially at midshaft (M3) in *Cormohipparion* and *Cremohipparion* than Höwenegg *Hi. primigenium* and are at the same time very similar to *Co. occidentale* and *Co. sinapensis*. Third metatarsals remain slenderer in *Cormohipparion* and *Cremohipparion* than Höwenegg *Hi. primigenium* while distal epiphyses (M12 and M14) plot the same as the Höwenegg *Hippotherium* (Figure 9 (,)).

Pannonian C *Hippotherium* sp. is only represented by maxillary and mandibular cheek teeth. Bernor et al. (2017) demonstrated that the Gaiselberg and Atzelsdorf samples have the most primitive features, including slightly lower crown heights than the Mariathal sample. The maximum maxillary cheek teeth of the Gaiselberg and Atzelsdorf hipparions is slightly greater than 50 mm (C18C); maxillary cheek tooth fossettes are complex (C19A); linkage of opposing borders of pre- and postfossettes occurs with greater frequency than the rest of this sample under consideration (FLink = Yes); protocone shape is oval with a significant incidence of lingual flattening (C23DE); protocone is separated from protoloph until late wear (C24B); protocone spur was found to occur (C25B); P2 anterostyle is consistently short and rounded (C28B); premolar and molar metaconid and metastylid morphology is as in the Höwenegg population (C32A, C33A, C34A and C36E) premolar metastylid spur varies from being present to absent (C35AB); premolar ectoflexid variously separates metaconid-metastylid in the premolars (C38AB); pli caballin is present being single or rudimentary particularly in the premolars (C40B); there is a relatively high incidence of ectostylid presence on the permanent cheek teeth (C43A) being low crowned and welded to the labial enamel wall.

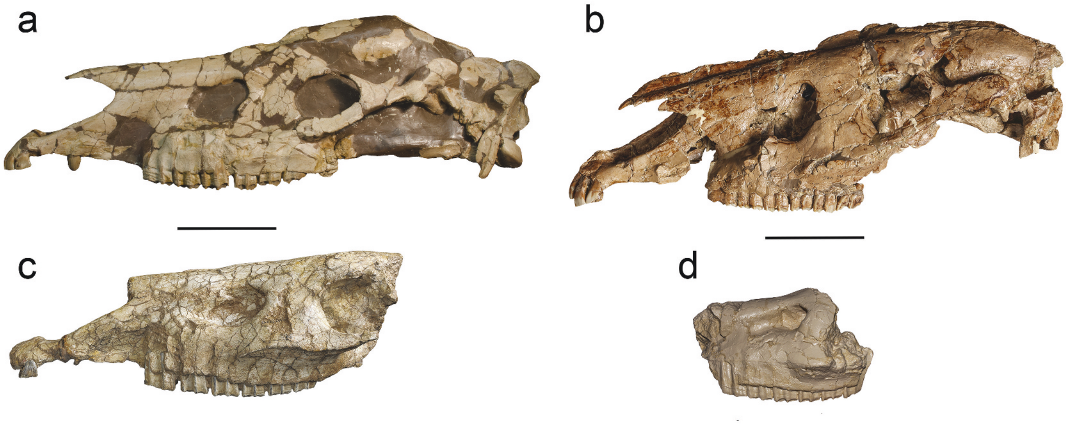

Figure 10. Morphological comparison of the Höwenegg *Hippotherium primigenium* SMNK HöA (a) and HLMD Hö485 (b), with the Chinese *Hippotherium weihoense* IVPP V3113-1 (c) and '*Hipparion*' *chiai* IVPPV31170 (d) Type skulls in lateral view. Scale bar 10 cm.

Observed occurrence was high because cementum was lacking on these teeth which would normally have obscured the ectostylids until very late wear. Pli caballinids and ectostylids often covaried and were shown to be independent structures (Figure 8 in Bernor et al. 2017). Bernor et al. (2017) followed Woodburne (2009) in recognising the Pannonian C hipparions as being a primitive species of *Hippotherium* sp. clearly more primitive than Höwenegg *Hi. primigenium.*

Inzersdorf (Pannonian D and E) *Hi. primigenium* is similar in age to the Höwenegg sample and shares multiple characters of the face and dentition (Supplementary Table 1). The morphometric range of the cranial measurements shown in Figure 8 overlaps variability of the Höwenegg *Hi. primigenium*. Compared to Höwenegg, the Inzersdorf *Hi. primigenium* overlaps but includes higher dimensions of the distance from the ventral rim of the POF to the facial-maxillary crest (M36), an indication that the Höwenegg sample had a more extensive POF height dimension. The Inzersdorf metapodials have a slenderer morphology (particularly midshaft – M3) than Höwenegg *Hi. primigenium*, while distal epiphyses approach the Höwenegg sample (M12 and M14) in their dimensions (Figure 9(b,d)). The Inzersdorf sample approaches Sinap *Co. sinapensis* in its size and proportions, and similar results for the postcranial elements were reported by Scott et al. (2004). To summarise, while the Inzersdorf skull and dentition are very similar to the Höwenegg *Hi. primigenium*, the metapodials retain the more primitive proportions of Sinap *Co. sinapensis.*

The type specimen of *Hippotherium weihoense*, IVPP V3113-1 is scored in this manuscript. The cheek tooth row length (M9) is just above the range of the Höwenegg hipparion and, in fact, is the longest of our sample (Supplementary Table 2). Likewise, POB length (M32) is near the top of the Höwenegg hipparion range. Length of the POF (M33), POF height (M35) and height from posterior POF to alveoli (M38) overlap the Höwenegg hipparion range, whereas the distance between the POF and the maxillary (M36) crest is greater than the Inzersdorf and Höwenegg *Hi. primigenium* (Figure 8).

The new *Hi. weihoense* sample reported by Sun et al. (2022) shows a different morphometric range, which does not compare well with the *Hi. weihoense* holotype being shorter than the type *H. weihoense* for M9, M32, M33, M35 and M38 and shorter than the Höwenegg sample for M33. As in the holotype, the Sun et al. (2022) *Hi. weihoense* sample exhibits greater values for M36, exceeding the Höwenegg range of variability. All facial characters of the type specimen *Hi. weihoense* score the same as the Höwenegg hipparion. There is no reported incidence of pre-postfossette opposing border linkage, and protocones are elongate-oval with some lingual flattening (C23DE). The remaining maxillary cheek tooth characters are as in the Höwenegg hipparion sample (Supplementary Table 1). Although no postcranial elements were reported with the holotype skull, the new *Hi. weihoense* sample (Sun et al. 2022) shows striking differences in mc3s and mt3s Log10 ratio plots, when compared to the *Cormohipparion* and *Hippotherium* sample reported herein. This is particularly evident in the midshaft width, but also in the proximal and distal epiphyses (Figure 9b,). Supplementary Figure 4 compares the whole Sun et al. (2022) mc3 and mt3 sample with the mean values of *Hippotherium* from Europe. As shown in S. Figures 4(b,d) the Sun et al. (2022) sample exhibits much slenderer mc3 and mt3 dimensions, especially for the midshaft (M3) but also for the proximal and distal epiphyses than the *Hippotherium* or *Cormohipparion* samples. This could be because Sun et al. (2022) have synonymised the smaller '*Hipparion*' *chiai* sample with their concept of *Hi. weihoense*. The same hypothesis was previously proposed by Watabe (1992).

'*Hipparion*' *chiai* was nominated by Liu et al. (1978). Qiu et al. (1987) referred '*Hipparion*' *chiai* to '*Hipparion*' (*Hippotherium*) *chiai*. Qiu et al. (1987) recognised '*Hipparion*' *weihoense*, '*Hipparion*' *chiai* and '*Hipparion*' *xizangense* as being members of their subgenus *Hippotherium* because of their large sized, with well-defined preorbital fossae (conjectured for *'Hipparion' xizangense)*, strong plication and long protocone, etc. (Qiu et al., 1987, pp. 158 and 164). We compare (Figure 10 (,)) Höwenegg SMNK HoA and HLMD Ho485 *Hi. primigenium*, IVPP V3113-1 (Type *Hippotherium weihoense*) and IVPPV31170 (Type '*Hipparion*' *chiai*) skulls lateral view, and (Figure 11(a,d)) in occlusal view. The cheek tooth row length (M9) of '*Hipparion*' *chiai* is below the range of the Höwenegg *Hi. primigenium* and very far below that of the type *Hi. weihoense* (144.0 mm versus 168.5 mm; Supplementary Table 2). The type '*Hipparion*' *chiai* POB is broken, whereas length of the POF (M33) is long (59.3 mm) but shorter than the Höwenegg sample and the type *Hi. weihoense*. The POF height (M35) is shorter (30.2 mm) than both the Höwenegg sample range and *Hi. weihoense*. The distance from the ventral rim of the POF to maxillary crest (M36) is 31.2 mm which is greater than the Höwenegg sample but less than the type *Hi. weihoense*. The height of the POF (M38) is 81.2 mm and overlaps both the Höwenegg and type *Hi. weihoense*. With regard to facial characters, the Type '*Hipparion*' *chiai* has its POB broken distally but has the lacrimal clearly placed posterior to the POF (C1C); the POF is elongate and anteroposteriorly oriented (C4J); the POF is deeply posteriorly pocketed (C5A); the POF is medially deep (C6A); the POF peripheral outline is strongly

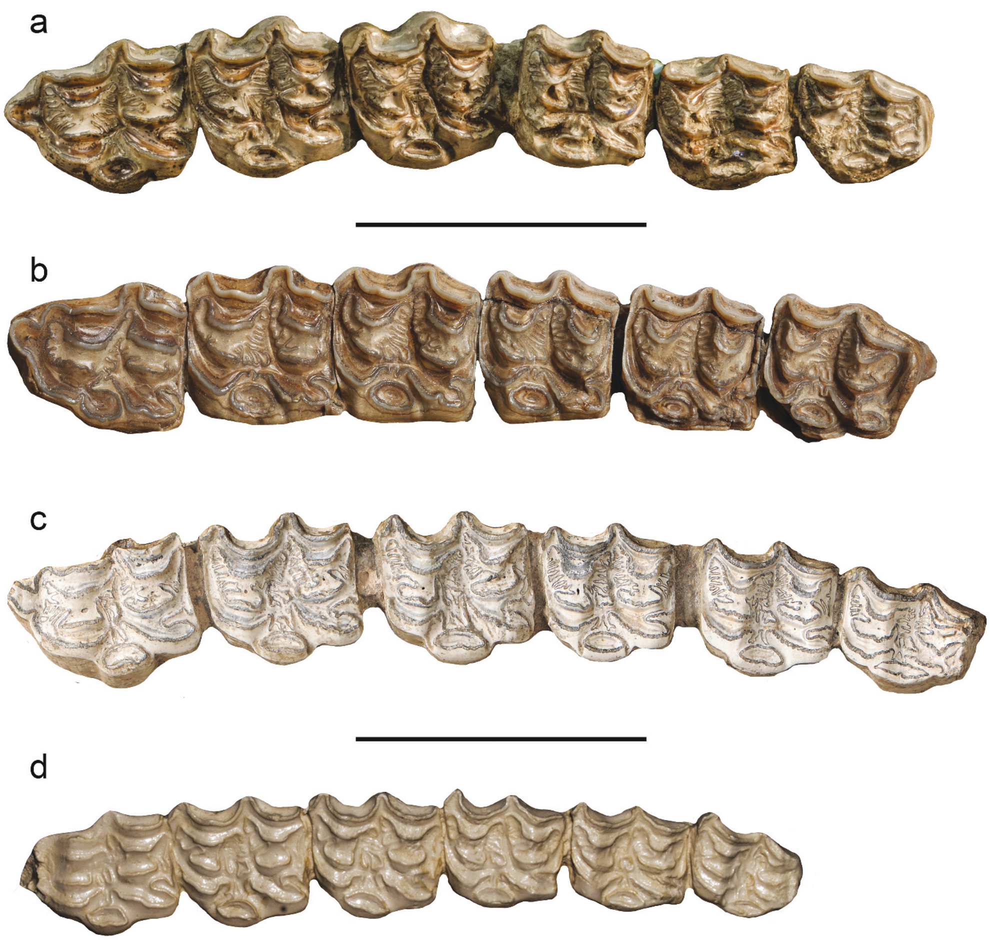

Figure 11. Morphological comparison of the Höwenegg *Hippotherium primigenium* SMNK HöA (a) and HLMD Hö485 (b), with the Chinese *Hippotherium weihoense* IVPP V3113-1 (c) and '*Hipparion*' *chiai* IVPPV31170 (d) Type maxillary cheek teeth occlusal view (a-d).

delineated around the entire boundary (C8A); anterior rim is present and strongly expressed (C9A); the nasal notch is not preserved (Figure 10). With regard to the cheek tooth characters, '*Hipparion*' *chiai* has a maximum crown height of between 40 and 60 mm (C18C); the maxillary cheek tooth ornamentation is moderately complex and not as extreme as in *Hippotherium* (C19B); there is no linkage of opposing borders of pre- and postfossettes (FLink = No); protocone is elongate oval with lingual flattening (C23DE); the protocone is isolated from the protoloph (C24B); a small protoconal spur is found on the P2 (C25B); the anterostyle is elongate (C28?) (Figure 11).

The *Cremohipparion moldavicum* type specimen is PIN 1256–3646, a skull from Taraklia, Moldova (Gromova 1952; vera-eisenmann.com) which we use to characterise the species. It is the smallest species in our Eurasian hipparion sample (Supplementary Table 2), in particular its P2-M3 measurement range (M9) and POB length (M32). The POF length (M33) and posterior height (M38) are relatively large and fall within the range of the Höwenegg *Hi. primigenium*. Measurements 9 and M32 are remarkably reduced overlapping North American *Co. quinni* (Figure 8). The POF height (M35) and POF distance of ventral rim to facial maxillary crest (M36) are likewise great, overlapping and exceeding the range of the Höwenegg hipparion in M35. These results (large POF, reduced POB and short UTR) are important cranial characters of *Cr. moldavicum* as reported by Bernor et al. (2021b). The short preorbital bar with lacrimal invading the POF (C1B) is a genus-level characteristic of *Cremohipparion*. POF morphology is primitively subtriangular shaped and anteroventrally oriented (C4D). POF posterior pocketing is reduced due to the short POB (C5B) while the remaining facial morphology is as in the Höwenegg hipparion. Maxillary cheek tooth ornamentation is only moderately complex (C19B), protocones are rounded (C23G), P2 anterostyle is short and rounded (C28B). In the mandibular cheek tooth, premolar and molar metaconids and metastylids are rounded (C32A, C33A, C34A, C36A) and premolar metastylid spurs do occur (C35A); remaining characters are as in the Höwenegg *Hi. primigenium*. Third metapodials are elongate and slender, slenderer than the X-Mas Quarry sample, *Co. sinapensis*, '*Co*'. *africanum* and *Hi. primigenium* (Figure 9(a,c)). This is evident in the midshaft width (M3), although the dimensions of the proximal and distal epiphyses are close to *Cormohipparion* (Figure 9(a,c)).

Discussion

Cormohipparion datum and the Old World dispersal event

The '*Hipparion*' Datum was advanced by Berggren and Van Couvering (1974) based on their interpretation that a North American '*Hipparion*' made an instantaneous prochoresis across the Old World 12.5 Ma. Their datum was secured by a K/Ar age of 12.4 ±1.1 Ma on volcanic rocks at the Höwenegg locality (Lippolt et al. 1963). A review of the geology at Höwenegg by Woodburne et al. (1996) and redating the volcanics by Swisher (1996) using the single crystal argon methodology, yielded a revised date of 10.29 ±

0.07 Ma, corroborated by three magnetostratigraphic determinations within the Höwenegg section. Woodburne et al. (1996) recognised that older strata in Europe, namely the Pannonian C hipparions occurred in the Vienna Basin. Woodburne (2009) undertook a study of the Atzelsdorf Pannonian C hipparions from the Vienna Basin and was followed by Bernor et al. (2017) who undertook a study of all Pannonian C hipparions from Atzelsdorf, Gaiselberg and Mariathal (Austria). Both Woodburne (2007, 2009) and Bernor et al. (2017) found a broad agreement that the Pannonian C hipparions, dating between 11.4 and 11.0 Ma were more primitive than the Höwenegg hipparions but referable to *Hippotherium* sp.

In Spain, Agustí et al. (1997) reported a correlation of the '*Hipparion*' Datum with Chron C5r.1 n (11.188–11.146). More recently, Alba et al. (2019) correlated the '*Hipparion*' Datum in the Vallès-Penedès Basin from the localities of Castell de Barberà and Creu de Conill 20 with Chron C5r.1 n (11.188–11.146 Ma), suggesting an age of ca. 11.2–11.1 Ma for both localities. Sen (1997) summarised data from a number of Western Eurasian localities citing the occurrence of earliest local hipparions with C5n.2 n, 11.05–9.98 Ma.

The first occurrence of the hipparionin horses in China is controversial. Qiu and Xie (1997) erected a new species, '*Hipparion*' *dongxiangense* for some isolated teeth from the Vallesian correlative locality Dongxiang (Gansu, Linxia Basin, China). As reported by Qiu and Xie (1997), this species differs from other Chinese species, such as *Hi. weihoense*, in its morphology and very small size. Qiu and Xie (1997) highlighted some plesiomorphic features of the occlusal morphology of the teeth close to the North American *Cormohipparion* species, supporting an early Bahean age for '*Hipparion*' *dongxiangense*. Qiu et al. (2013) reported the earliest occurrence of '*Hipparion*' in the Linxia Basin from the Guonigou locality in Nalesi, Dongxiang County, with localities falling within the base of C5n.2 n, 11.05 Ma or within C5r.1 r, 11.14–11.05 Ma. Qiu et al. (2013, pp. 60–61, fig. 1.7), Woodburne et al. (2013, p. 106) and Deng et al. (2013: pp. 255–267, fig. 9.3) concluded that the '*Hipparion*' Datum should be considered to be around 11 Ma in China. Deng et al. (2013) defined the chronologic range for the Early Bahean (= Early Vallesian, MN9) species in the Linxia Basin, including '*Hipparion*' *dongxiangense* in the Guonigou Fauna (11.1–9.8 Ma). Deng et al. (2013) further cited the occurrence of *Hi. weihoense* in the Guonigou (11.1–9.8 Ma) and Dashegou Fauna (9.8–8.7 Ma) and '*Hipparion*' *chiai* in the Dashegou Fauna (9.8–8.7 Ma) (Deng et al. 2013; fig. 9.3). Therefore, Qiu et al. (2013), Woodburne et al. (2013) and Deng et al. (2013) correlated the first appearance of hipparions in China at ca. 11.1 Ma.

More recently, Fang et al. (2016) and Sun et al. (2022) have made new interpretations on the China Hipparion FAD. Fang et al. (2016) provided a revision of the magnetostratigraphy of the Linxia Basin (China), correlating the base of the lowermost level of the lithostratigraphic unit yielding the '*Hipparion*' Fauna to the Chron C5r.2 r–C5r.1 r, dated at 11.5–11.1 Ma. Sun et al. (2022) have developed further information on the Linxia Basin hipparions citing an 11.5 Ma age for their *Hippotherium* Datum asserting that the genus originated in East Asia. The assignment of earliest occurring hipparion in the section to *Hi. weihoense* is contrary to Qiu and Xie (1997) report of the very small '*Hipparion*' *dongxiangenese* in this very section. Sun et al. (2022) reported the new basal age for the Gounigou Fauna at 11.5 Ma and described a remarkable *Hi. weihoense* sample from the localities of Houshan, Shuanggongbei and Niugou (Gansu, Linxia Basin) of the Dashengou Fauna (9.8–8.7 Ma). Sun et al. (2022) also reported an unprepared incomplete cranium with sediment still attached (Sun et al. 2022, p. 3, supplementary figs. 6i) from the Bantu locality, correlated with the Guonigou Fauna (11.1–9.8 Ma in Qiu et al. 2013; Woodburne et al. 2013; Deng et al. 2013, p. 11.5–9.8 Ma in Fang et al. 2016; Sun et al. 2022), referred to *Hi. weihoense*. They also reported an isolated M3 from Guonigou locality that they argue resembles *Hi. weihoense*. Based on these lines of evidence, Sun et al. (2022) reported that *Hi. weihoense* is the first appearing hipparionin equid in China and the basis for their recognising an Old World *Hippotherium* Datum. Moreover, Sun et al. (2022) have synonymised '*Hipparion*' *chiai* with *Hi. weihoense*.

We have characterised here, in detail, the morphology of Central European *Hippotherium primigenium* and *Hippotherium* sp. based on cranial, dental and postcranial material. Sun et al.'s (2022) synonymy of '*Hipparion*' *chiai* with *Hi. weihoense* is problematic because of the former' smaller size, POF being short in its dorso-ventral dimension, the highly derived mean third metapodial Log10 ratio diagrams for their sample (Figure 9b,) and the clear diversity of third metapodial Log10 ratio diagrams of the individual bones (Supplementary Fig. 4). The shape and size of the third metapodials do not conform to Central European *Hippotherium*. We find that the assertion of a 11.5 Ma *Hippotherium* Datum in the Linxia Basin is not certain on stratigraphic, chronologic or taxonomic grounds and comparisons to Central European *Hippotherium*, where the type of *Hi. primigenium* originates (Eppelsheim, Germany) are entirely lacking.

Bernor et al. (2003, 2017) found that *Co. occidentale* was a suitable source of an Old World *Cormohipparion* (replacing the *Hipparion* and *Hippotherium*) Datum. Woodburne (2009) favoured a slightly more primitive form *Cormohipparion* sp. (LACM150080, Figure 3L; Woodburne 2009, p. 591) from the Punchbowl Fm., ca. 11.5 Ma California, as a potential source for the *Cormohipparion* Datum. However, the combination of cranial, maxillary dental characters and third metapodial morphology has made *Co. occidentale* (12.7–9.95 Ma, Late Barstovian – Early Claredonian; Woodburne et al. 1981; Woodburne 1996, 2007) a plausible source for first occurring Eurasian *Co. sinapensis* (10.8 Ma; Sinap, Turkey; Bernor et al. 2003).

Woodburne's observation (2007, 2009) that a more primitive North American *Cormohipparion, Co. quinni* (14–12.5 Ma, Middle-Late Barstovian; Woodburne 1996, 2007) may have been the source of the Old World *Cormohipparion* Datum has some support here from our own observations on the morphology of *Cr. moldavicum*, but there is no stratigraphic-chronologic record of this taxon approaching the antiquity of *Hi. primigenium*. We believe that the holotype *Hi. weihoense* is a valid referral to the genus, but its biochronologic range (Guonigou and Dashegou Fauna) does not certainly extend as early in time as 11.5 Ma as asserted by Sun et al. (2022). We therefore follow the original attribution to ca. 11.1 Ma for the Guonigou fauna as reported by Qiu et al. (2013), Woodburne et al. (2013) and Deng et al. (2013), underlying the importance of '*Hipparion*' *dongxiangese* as one of the most primitive species found in the Linxia Basin (Qiu and Xie 1997; Deng et al. 2013).

Hippotherium primigenium's place in Old World hipparion evolution

We have presented detailed information on the environmental context of the Höwenegg *Hi. primigenium* population being a subtropical forested environment. This concurs with the Vallesian MN9 populations of the Vienna Basin which had the same forested conditions (Bernor et al. 1988). Sun et al. (2022) have interpreted the Linxia, China habitats as having been more open country habitats than other Central European localities. The contrast between Central and Western European MN9 forested terrestrial environments with *Hippotherium* spp. and pan-Asian localities with *Hippotherium, Sivalhippus* and *Cormohipparion* drier habitats has been illustrated by Bernor et al. (2021a).

The Höwenegg *Hi. primigenium* sample is primitive for the Old World hipparion radiation (Bernor et al. 1989, 1996, 2021a). The description of the Höwenegg sample reported herein and in Bernor et al. (1997) demonstrated that it was a hipparion of about 1 metre height at the withers, had a primitive facial and dental morphology, the vertebral column had long spinous processes, weakly developed vertebral zygapohyses, an elongate and slender sacrum and elongate-slender limbs (Bernor et al. 1997). Yet, compared to many of the late Miocene Eurasian and African hipparions it was more robustly built, with larger metapodials, but surpassed in size by some of the Old World Plio-Pleistocene lineages (Bernor et al. 2021a). The large sample size of postcrania, in particular, has been permissive of robust statistical analyses because it has been demonstrated that the Höwenegg hipparion sample is of a single species accumulated over a short duration. Study of the North American *Cormohipparion* sequence by Woodburne (2007), Sinap MN 9 hipparion record (Bernor et al. 2003) and the Pannonian C (early MN9) population of *Hippotherium* sp. (Woodburne 2009; Bernor et al. 2017) have provided new perspectives on the evolutionary history of the origins of Old World hipparions.

Relative to Höwenegg *Hi. primigenium*, North American *Co. occidentale* exhibits overlapping P2-M3 dimensions (M9), POB length (M32) and all other facial dimensions (M33, M35, M36 and M38) while be smaller overall. The dimensions of the third metapodials are overall slenderer than the Höwenegg hipparion, and cheek teeth have less complex plications (C19B) and a propensity for linking opposing borders of the pre- and postfossettes. At the present time, we do not know what the mandibular cheek tooth characters are for *Co. occidentale.*

The Sinap *Co. sinapensis* is first documented at 10.8 Ma and exhibits close similarities to North American *Co. occidentale* in facial and cheek tooth characters having a somewhat less defined peripheral rim (C8B), linkage of opposing borders of pre- and postfossettes on P2 (Flink = Yes), protocones that are oval with flat lingual surfaces (C23CE) and anterostyles that are short and rounded, as in *Co. quinni* (C28B). In these regards, *Co. sinapensis* is more primitive than Höwenegg *Hi. primigenium*. Inzersdorf *Hi. primigenium* is very similar to Höwenegg *Hi. primigenium* but has postcrania that are slenderer and like *Co. sinapensis* (Bernor et al. 2003).

The Pannonian C *Hippotherium* sp. sample is the most primitive of all our Eurasian and African sample in cheek tooth morphologies. While the Gaiselberg and Mariathal samples have complex plications of the pre- and postfossettes, as in the Höwenegg and Inzersdorf samples, these Pannonian C hipparions demonstrate primitive retention of metastylid spurs (C35A), extension of premolar ectoflexid (C38B), persistent pli caballinids (C40B) and ectostylids (C43A). The relatively high occurrence of ectostylids in this assemblage is due to the lack of dentine on the labial surface of the crowns wherein the ectostylids are welded to the enamel wall and usually short and expressed as a small, pointed feature on the labial side of the hypoconal enamel band. Ectostylids only rarely occur (HLMD Ho486) in the Höwenegg and only evolve becoming higher, longer and wider in the African *Eurygnathohippus* lineage (Bernor et al. 2020, 2021a).

The China type *Hi. weihoense* is a large, early Turolian correlative of *Hi. primigenium* having a long cheek tooth row but overall somewhat smaller POF than the Höwenegg *Hippotherium* sample. The Sun et al. (2022) sample of *Hi. weihoense* includes '*Hipparion*' *chiai* which results in statistics that have smaller dimensions of facial morphology and much more slender metapodial dimensions than Höwenegg and Inzersdorf *Hi. primigenium.*

China type '*Hipparion*' *chiai* is a medium-sized Turolian equivalent age enigmatic taxon. Contrary to Sun et al. (2022) it is smaller than the type specimen of *Hi. weihoense* and while it has a well-developed POF, it is restricted higher on the face than any *Hippotherium*, and in particular *Hi. primigenium* and *Hi. weihoense*, while being anteroposteriorly oriented and very long (C4J), with deep posterior pocketing (C5A), medially deep (C6A), with a strongly developed POF peripheral rim (C8A) and strong anterior rim (C9A). The cheek teeth are not as heavily plicated (C19B) as in *Hi. primigenium*, while the protocones are elongate and lingually flattened (C23DE). We believe that '*Hipparion*' *chiai* is a lineage independent of *Hippotherium* and has not yet been recognised outside of China. We believe that Sun et al.'s (2022) synonymising of '*Hipparion*' *chiai* with *Hi. weihoense* has confused the hypodigm of

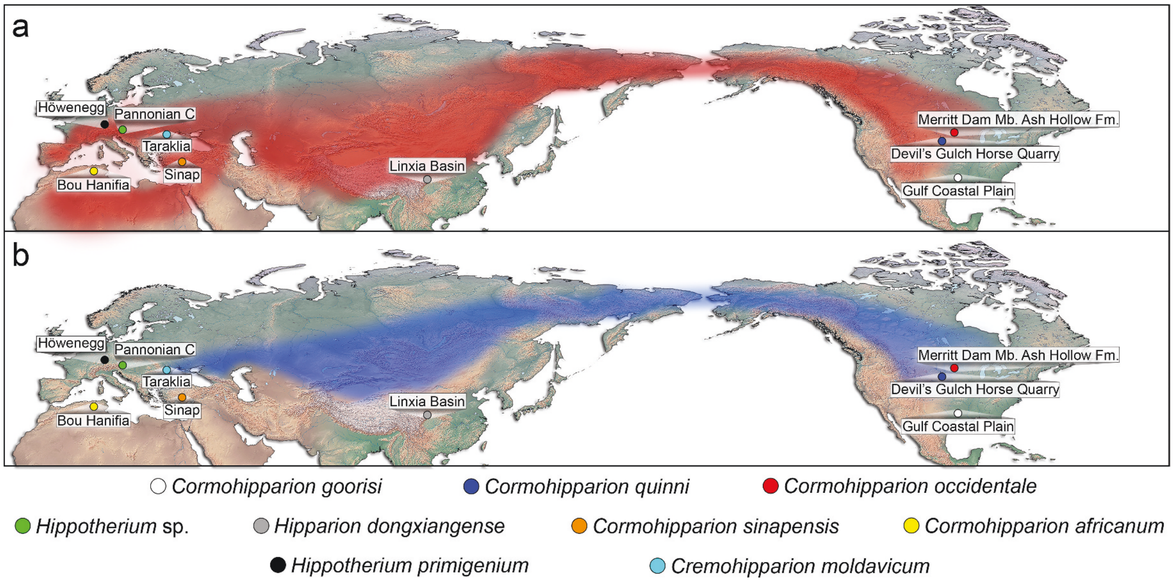

Figure 12. Geographical map showing the dispersal event of *Cormohipparion occidentale* (a) and the alternative dispersal of *Comohipparion quinni* (b) from North America into Eurasia and Africa. Colours indicate species and the main localities where the species originate.

Hi. weihoense which is further evidenced by the Log10 ratio analyses on third metapodials which exhibit hyper-slender limbs and the likely occurrence of a mixed sample (Supplementary Figure 4).

Moldovan *Cr. moldavicum* is strikingly different in its short POB (C1B) and very large POF with resulting reduced posterior pocketing (C5B). Maxillary cheek teeth have rounded protocones (C23G) which are occasionally linked to the protoloph (C24A/B). Mandibular cheek teeth metaconids and metastylids are persistently round (C32A, C33A, C34A and C36A); pli caballinids are absent (C40C); ectostylids are not reported (C43B). Whereas Bernor et al. (2003) and Răţoi et al. (2022) have suggested that *Cr. moldavicum* could have been derived from *Hippotherium* by reduction of the preorbital bar, Woodburne (2007, 2009) has suggested an alternative plausible hypothesis that *Cr. moldavicum* was derived from a more primitive North American *Cormohipparion* with a short POB such as *Co. quinni*. Our analyses of cranial and postcranial elements support this alternative hypothesis, albeit the lack of fossil evidence for the genus *Cremohipparion* during the MN9 in the Old World suggests to consider this hypothesis still hypothetical rather than conclusive.

Figure 12 provides our alternative hypotheses of the *Cormohipparion* Datum. Figure 12a is the younger, 11.4–11.1 Datum with *Cormohipparion* sp. or *Co. occidentale* being the initial source for the Old World Datum, while Figure 12b suggests that there was an earlier (older), yet to be documented stratigraphically, Datum with *Co. quinni* being a plausible source and *Cremohipparion* being the most primitive Old World hipparions. In either case, a species of *Cormohipparion*, not *Hippotherium*, was the source of an Old World *Cormohipparion* Datum.

Conclusions

We have provided a detailed description of the Höwenegg *Hippotherium primigenium* sample publishing for the first time photographic images of the crania, mandibles and dentitions for comparisons with a suite of Eurasian and North African primitive members of the *Hippotherium, Cormohipparion, Cremohipparion* and *'Hipparion'* species. Whereas the Höwenegg *Hippotherium* sample is primitive in a number of its skeletal features, it shows advanced features of its facial morphology and cheek teeth compared to North American *Co. occidentale* and Sinap *Co. sinapensis* and cheek tooth characters of Pannonian C hipparions. The oldest hipparions of our sample are derived from the Pannonian C (11.4–11.0 Ma) exhibiting primitive cheek tooth morphologies compared to the Inzersdorf (Pannonian D-E) and Höwenegg *Hippotherium primigenium*. Sinap *Co. sinapensis* is older than the Höwenegg sample but younger than the Pannonian C. However, as discussed in the present work, it strikes close similarities with the North American *Co. occidentale* in its cranial and postcranial morphology. The definition provided by Sun et al.'s (2022) of *Hi. weihoense* claims uncertain assertions that this species first occurred at 11.5 Ma. Sun et al.'s (2022) synonymising '*Hipparion*' *chiai* with *Hi. weihoense* has produced a questionable taxonomy that results in recognising hyper-slenderised metapodials which cannot in themselves be referred to *Hippotherium*.

Bernor et al. (2017, 2021a) have asserted that the first occurring Old World hipparion was a member of the *Cormohipparion* clade (sensu Woodburne 2007). Whereas the oldest Eurasian *Cormohipparion* is from Sinap, Turkey not the Vienna Basin where *Hippotherium* is recognised as an early divergent lineage, we have previously found support that *Cormohipparion* not *Hippotherium* was the genetic pool from which subsequent members of the Old World hipparionini, including *Hippotherium* were derived. There is no *Hippotherium* reported in the North American record, and hence it cannot be considered a source for Old World *Hippotherium* in itself. We therefore recognise the *Cormohipparion* Datum rather than a *Hippotherium* Datum for Eurasia and Africa.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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