The Oldest Ethiopian Hipparion (Equinae, Perissodactyla) from Chorora: Systematics, Paleodiet and Paleoclimate

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Abstract

We report here a sample of 5 cheek teeth of a primitive hipparion from the early late Miocene Ethiopian locality of Chorora. This sample represents the oldest hipparion known from Ethiopia, and probably East and South Africa. The sample exhibits a number of distinctly primitive characters that suggest its provisional referral to "Cormohipparion" sp. The Chorora hipparion has none of the more advanced features typical of the latest Miocene-Pleistocene African hipparionine lineage *Eurygnathohippus*, maintaining a low crown height, lack of ectostylids and pli caballinids. The Chorora hipparion does exhibit a mesowear signal, suggesting that it was a mixed-feeder. The carbon isotope signal also suggests that it was a mixed-feeder that included both browse and C$_4$ grass in its diet.

Key words: Ethiopia, Equidae, Hipparion, mesowear, carbon isotopes, paleodiet

Zusammenfassung


Schlüsselworte: Äthiopien, Equidae, Hipparion, Mesowear, Kohlenstoffisotopie, Paläodiät
Introduction

The Chorora hipparion sample that we report upon here was initially announced by Sickenberg & Schönhfeld (1975) as the result of a German led geological and paleontological exploration program in the Afar Depression, Ethiopia (Pilger & Rosler 1975; fig. 1). The fauna is derived from the Chorora Formation which is composed mostly of limnic diatomite sediments and represents the oldest sediments of the southern Afar. The Chorora Formation is structurally situated between the Southeast Escarpment and the Afar Depression. These sediments are found between Awash Station and Afadem, over an area of 10–15 km wide and 100 km long, with an estimated original area of more than 1000 km² (Sickenberg & Schönhfeld 1975).

The Chorora Formation is stratigraphically preceded by the Bacca Basalt, which itself is covered by rhyolitic ignimbrites. The Chorora Formation stratigraphically succeeds these sediments and is itself stratigraphically succeeded by another ignimbrite accumulation. Kunz et al. (1975) reported K/Ar ages for the Bacca Basalts (sample M938) of 10.5 Ma., and the succeeding trachytic ignimbrites (sample M567) of 9.05 Ma. (Kunz et al. 1975: fig. 2, pp. 372). Swisher (in Woodburne et al. 1996) corrected these ages for current decay constants to 10.8 +/– 0.3 Ma. and 9.3 Ma. +/- 1.0 Ma. He further estimated that the Chorora hipparion indicated a likely age range of between 10.5 and 9.3 Ma. The stage-of-evolution of the Chorora hipparion was estimated by Bernor (in Woodburne et al. 1996) to be approximately that of Central European Pannonian D-E Hippotherium primigenium, known to occur in MN 9, circa 10.5–10 Ma.

Geraads et al. (2002) report on a recent French-Ethiopian expedition to Chorora. They have new results on the stratigraphy and dating of the Chorora Formation based on whole rock analysis of lava flows using conventional ⁴⁰K/⁴⁰Ar dating. Their fig. 1 is a 40 m. stratigraphic section of the upper member of the Chorora Fm., together with three volcanic units, from the base to the top of their section: CHO 11, CHO 13 and CHO 12. The oldest, CHO 11, was dated 11 +/-0.45 Ma, while CHO 13, was dated 10.10 +/-0.30 Ma and CHO 12 was dated 9.84 +/-0.30 Ma. The fossiliferous layers are found 10 m. above the lowest lava flow, CHO 11, while CHO 13 is located about 20 m. above the fossil-bearing horizons and is separated from these sedimentary beds by a minor stratigraphic unconformity. CHO 12 is apparently about 3 meters above CHO 11.

The original Sickenberg & Schönhfeld (1975) vertebrate paleontological sample is part of a small paleontological assemblage that includes poorly preserved plants (leaves and trunks of trees), fish scales and vertebrate remains including: Homotherium sp. (sic., likely Machairodus), "Masodon" (=? Gomphotherium) sp. of the longirostre group, "Hipparion primigenium" (our quotes), Stephanorhinus (=? Ceratotherium) sp., Suidae gen. indet., Hippopotamidae (gen. & sp. indet.), Giraffidae (Palaeotraginae?) and Bovidae gen. indet. Recently, Geraads et al. (2002) reported on their collection of fossil mammals from the Chorora Formation. These specimens are apparently from the same sandy horizon as the earlier German collection and includes the following fauna: Herpestides afarensis n. sp., Machairodus aphanistus, an early member of the Siegstratbelodon lineage, cf. Kenyapotamus sp.?, a sivathere giraffid, two bovid species, the chalicother, Ancylostherium, a rhinocerotid, and remains of hipparion, referred to by them to Hipparion sp. cf. H. primigenium. We have not studied this new fauna, and in fact were not made aware of this publication until after an earlier version of this manuscript was submitted for publication. Dr. Geraads (Paris) graciously supplied Bernor with reprints of this work allowing us to consider his team’s results on the hipparion sample for the present manuscript. Based on the geological and paleontological data, along with a biochronologic assessment of the fauna, Geraads et al. (2002) conclude that the Chorora fauna was 10.6-10.3 Ma. Hipparion has been first reported as appearing in Spain at 11.1 Ma. (Garcés et al. 1996), but is not known from either the very well dated sequences of Sinap, Turkey, (Bernor et al. 2003, Kappeelman et al. 2003), or the Potwar Plateau, Pakistan (J. Barry pers. commun.), prior to 10.7 Ma. We believe that the calibration of the Siswalk and Turkish Hipparion Datum is secure, and therefore believe that the Chorora Fm. fauna is best estimated as being between 10.7 and 10.1 Ma.

Study of the Sickenberg & Schönhfeld Chorora hipparion assemblage has thusfar been cursory. Given the importance of this sample as the oldest Hipparion in Ethiopia, and probably the oldest hipparion in all of East Africa, we believe that a complete study and report of this original sample is long overdue. Our work here will include a morphologic description and taxonomic assessment of the Chorora hipparion sample, as well as a brief comparison of this material to that described and figured by Geraads et al. (2002), which has not yet been studied by us. We will further report our results on the paleodietary preferences of the Chorora hipparion and its paleoclimatologic context as reflected by carbon isotopes. We will further discuss its likely evolutionary relationships and the consequences of this assessment for paleobiogeographic interpretations. We dedicate this work to Professor Dr. Fritz F. Steininger in celebration of his 65th birthday.

Materials and Methods

The material available consists of one maxillary M1 NL(B)CHOR 2) and 4 lower premolar and molar teeth NL(B)CHOR 1, 3, 5 and 6).

Abbreviations

NL(B) – Niedersächsisches Landesamt für Bodenforschung/Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover.

CHOR – for Chorora as applied to specimen numbers.
Fig. 1: Geographic location of the Vertebrate Locality of Chorora, Ethiopia (asterisk).

**Morphologic Description and Taxonomic Determination**

We measure the Chorora teeth following the conventions published by BERNOR et al. (1997), and provide them here in table 1 (see table 1 Legend for description of measurements). Because of the limited sample size, our statistical analysis is limited to bivariate plots of the maxillary M1 (fig. 2) and mandibular p4 (fig. 3) below. These plots were calculated using Systat 9.0 licensed to Kaiser. The 95% confidence ellipses were calculated using the Eppelsheim, Dinotheriensande, Germany, sample (BERNOR et al. 1999, KAISER et al. 2000b, BERNOR & HARRIS 2003, KAISER et al. 2003, KAISER & SOLOUNIAS 2003, KAISER 2003).

We also score each tooth using standard character state attributes published by BERNOR et al. (1997). We compare these states in particular to the primitive Central European species *Hippotherium primigenium* (BERNOR et al. 1997) and East African late Miocene representatives of *Eurygnathohippus* (BERNOR & ARMOUR-CHELU 1999, BERNOR & HARRIS 2003) to estimate its relative stage-of-evolution.

**Mesowear Analysis**

We apply here the mesowear methodology originally formulated by FORTELIUS & SOLOUNIAS (2000). FORTELIUS & SOLOUNIAS (2000) and KAISER et al. (2000b) found that the mesowear signal allows a reasonable scoring of paleodietary preference when the sample size is 10 dental specimens or greater. A statistically stable paleodietary signal can be expected when the sample size is 20-30 individuals. The sample size available to this study is much too small to obtain a statistically sound mesowear classification if the standard methodology is followed. In order to gain a reasonably accurate scoring of our sample, we abandon conventional practice here as follows: 1. tooth positions other than upper M2s are included, 2. lower teeth are included, 3. both labial cusps (anterior and posterior) are scored in the individual teeth, and 4. scoring is not restricted to the ectoloph in the one upper cheek tooth specimen (NL(B)CHOR 2), but the labial band of the postfossette is included. However, there is good reason to believe that the buccal bands of the prefossette and postfossette immediately lingualward of the ectoloph will produce a reasonably consistent mesowear signal. This is due to the longitudinal movement of the antagonistic teeth and the fact, that mesowear in upper cheek teeth is largely controlled by the occlusal morphology of the antagonistic (lower) tooth (KAISER & FORTELIUS 2003). In NL(B)CHOR 2 therefore scorings for these enamel bands are summed. Scorings of mandibular teeth are calibrated following calibration factors introduced by KAISER & FORTELIUS (2003) for the Eppelsheim sample of *Hippotherium primigenium*.

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**Table 1:** Measurements on Chorora hipparions. SPEC_ID = Niedersächsisches Landesamt für Bodenforschung/Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover, specimen accession number; TOOTH = tooth position (tx = maxillary tooth, tm = mandibular tooth, Measurements M1–M11 are in millimetres and follow BERNOR et al. (1997)).

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Fig. 2: The Chorora Hipparion dental assemblage. A = NL(B)CHOR2 (txM1); B = NL(B)CHOR3 (tmm1); C = NL(B)CHOR5 (tmm2); D = NL(B)CHOR1 (tmp4); E = NL(B)CHOR6 (tmp3). 1 = buccal view; 2 = lingual view; 3 = occlusal view.
Hierarchical cluster analysis with complete linkage (furthest neighbours) is applied here following the standard hierarchical amalgamation method of HARTIGAN (1975). The algorithm of GRUVAEUS & WIEBER (1972) was then used to order the cluster tree using the three mesowear variables (% high, % sharp and % blunt). As a comparative dataset for dietary classification, we use 27 extant mammalian ungulate species reported as “typical” dietary categories by FORTELIUS & SOLOUNIAS (2000). As comparative datasets for fossil hipparionine horses, we include mesowear signatures of three North American taxa, *Merychippus insignis*, *Cormohipparion goorisi* and *Cormohipparion quinni* provided by FORTELIUS & SOLOUNIAS (2000). As a representative of the African Miocene hipparion fauna we include the mesowear signature of “Eurygnathohippus” cf. *baardi* from Langebaanweg (BERNOR & ARMOUR-CHELU 1999) as given by FRANZ-ODENDAAL et al. (2003). Two populations of the Central European late Miocene genus *Hippotherium* are represented by the Vallesian (MN9) population of *H. primigenium* from Höwenegg (Southern Germany) (after KAISER 2003) and the Turolian (MN11) population of *H. primigenium* from Dorn-Dürkheim (Southern Germany; BERNOR & FRANZEN 1997, KAISER et al. 2003). Systat 9.0 software was used to compute cluster statistics, using default settings.

Results and Discussion

Systematics

Order Perissodactyla OWEN 1848
Suborder Hippomorpha WOOD 1937
Family Equidae GRAY 1821
Subfamily Equinae STEINMANN & DODERLEIN 1890
“Cormohipparion” sp.

**Referred Specimens**: NL(B)CHOR 1, left p4; NL(B)CHOR 2, left M1; NL(B)CHOR 3, right m1; NL(B)CHOR 5, left m2; NL(B)CHOR 6, right p3.

**Localities**: Undesignated locality (ities) in the Chorora Formation, Ethiopia.

**Age**: Late Miocene, between 10.7 and 10.1 Ma.

**Geographic Location**: Ethiopia, Afar Triangle between the SE Plateau and Afar floor.

**Description of the Material**: NL(B)CHOR 2 – Left maxillary M1 (fig. 2A)

This specimen is a worn M1, mostly complete with broken distal mesostyle. It is in a middle stage-of-wear with a mesostyle height of 30.3 mm. The tooth is moderately curved; pre- and postfosssettes are complex, especially on the posterior wall of the prefossette and facing anterior wall of the postfossette (P, for primitive here and throughout the description); the posterior wall of the postfossette is distinct; the phl caballin is distinctly double (P); the hypoglyph is very deep nearly encircling the hypocone (P); protocone is broken on its lingual margin at the occlusal level, but can be seen to have been oval; there is no apparent protoconal spur; protocone is placed slightly lingual to the hypocone (P). There is a strong buccolingual groove coursing from mesostyle to protocone producing prominent buccolingual ridges across the middle of the prefossette and postfosssette. This feature produces a high-rounded ectoloph anteriorly and posteriorly and is usually indicative of a significant component of browse in this individual’s diet (BERNOR et al. 1999, KAISER et al. 2000b, FORTELIUS & SOLOUNIAS 2000). Measurements are included in table 1.

**NL(B)CHOR 6 Right mandibular p3 (fig. 2E)**

This specimen is an earlier stage-of-wear p3, mostly complete with some of the buccal margin broken and missing. The tooth is rather large and “blocky” in its outline, and has a height of 42.3 mm. The occlusal morphology suggests that this tooth was in an early stage-of-wear, and that maximum crown height would not likely have exceeded 50 mm (P). The tooth has the enamel margins of the metaconid and metastylid abraded, but would appear to be essentially...
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Fig. 3A–C: Bivariate Plots: A. Maxillary M1 Occlusal Length (M1) versus Occlusal Width (M3); B. Maxillary M1 Protocone Length (M10) versus Protocone Width (M11); C. Mandibular P4 Occlusal Length (M1) versus Width across Protoconid Enamel Band-Metaconid (M8). A = Middle Awash, Ethiopia; B = Baynunah, Abu Dhabi; C = Chorora (indicated by arrow); E = Eppelsheim, Germany; G = Samos, Greece; H = Höwenegg, Germany; K = Ekora, Kenya; L = Lothagam, Kenya; M = Maramena, Greece; N = Ngorora, Kenya; O = Bou Hanifa, Algeria; P = Indo-Pakistan localities; R = Hadar, Ethiopia; S = Sahabi, Libya; U = Nkondo, Uganda.

This tooth is an early stage-of-wear p4 with a crown height of 46.1 mm. Occlusal morphology reveals: rounded metaconid and metastyliid (P); ectoflexid does not separate metaconid-metastyliid; there is no pli caballinid (P), but a distinctive “rippling” of the enamel band; the mesiobuccal margin is broken where one would expect to see a protostyliid; there is no ectostyliid (P); the linguaflexid is shallow and occupied by the strongly developed metastyliid spur (P); the preflexid and postflexid are mostly simple, with the former having some plication on its mesial margin, while the latter has some plication on its buccal wall; the protococonid enamel band is distinctly rounded.

This is an m1 in a middle stage-of-wear. Much of the buccal and posterobuccal margin is broken, but preserves much of the pertinent occlusal morphology. The occlusal surface preserves the following morphology: the metaconid is rounded while the metastyliid is square-shaped.
(P); the isthmus connecting the metaconid and metastylid is very long; there is no metastylid spur; the ectoflexid extends far lingually, but falls short of actually projecting between the metaconid and metastylid; the buccal enamel band next to which the pli caballinid would rest is broken away; the mesiobuccal margin is broken, and with it any evidence of a protostylid; the area where an ectostylid could occur is likewise missing (P); the linguaflexid has a distinct V-shape (P); the preflexid has complex margins while the postflexid has simple margins; the protoconid enamel band is broken.

NL(B)CHOR 5, Left mandibular m2 (fig. 2C).

A late wear m2 that has been rolled, but still preserves some important occlusal detail; the occlusal morphology of the metaconid and metastylid are broken, but the round morphology of both can be seen subocclusally; there is no evidence of a metastylid spur; the ectoflexid extends deeply lingualward intervening between the metaconid and metastylid; there is no pli caballinid (P); there is no evidence of an ectostylid (P); the mesiobuccal wall of the tooth is damaged disallowing evaluation of a protoconid; pre- and postflexids have simple margins; the protoconid enamel band is damaged, but would appear to have been rounded (P).

**Bivariate Plots**

Fig. 3a is a bivariate plot of occlusal length (M1) versus occlusal width (M3) for the Chorora M1 NL(B)CHOR 2 specimen compared to a number of Eurasian and African late Miocene and early Pliocene hipparions (refer to Legend, fig. 3). We use here, as well as in the subsequent bivariate plots (figs 3b, 3c) the Eppelsheim sample to plot a 95% confidence ellipse. NL(B)CHOR 2 (marked by an arrow) plots just below the central portion of the ellipse and indicates that this tooth is relatively small, particularly in comparison to the Hadar (indicated by R), Ethiopia sample that has many specimens plotting above the ellipse. NL(B)CHOR 2 compares most closely in these dimensions to specimens of small species from late Miocene horizons from the Middle Awash and Lothagam. Fig. 3b plots protocone length (M10) versus protocone width (M11) for NL(B)CHOR 2 left of the center of the plot, and indicates a relatively short, but not narrow protocone. These values are smaller than all Ethiopian hipparions. They most closely compare to primitive early late Miocene (MN 9) *Hipparium primigenium* from Eppelsheim (E) and Höwenegg (H), and the small species from Lothagam, *Eurygnathohippus feibeli* (BERNOR & HARRIS 2003). Fig. 3c plots occlusal length (M1) versus occlusal width (M8) for the Chorora mandibular p4, NL(B)CHOR 1. Here, NL(B)CHOR 1 plots approximately right of center and would not appear to be particularly large, or small.

**Remarks:** The Chorora dental sample exhibits a number of primitive characteristics for Old World hipparionine horses in general, but more importantly African hipparionine horses, specifically. While there are no unworn teeth in our sample, the relatively early wear p4, NL(B)CHOR 1, has a crown height of 46.1 mm suggesting that its maximum height would not likely much exceeded 50 mm. Late Miocene African hipparions exceed 60 mm in maximum crown height, while later Plio-Pleistocene species evolve maximum crown heights from 70+ mm to nearly 90 mm (BERNOR & ARMOUR-CHELU 1999).

Another prominent pair of features include the lack of either a strong pli caballinid or ectostylid. BERNOR & HARRIS (2003) demonstrated that ectostyldids appear as variable, weakly developed features in the Lower Nawata of Lothagam, 7+ Ma. ago. These are likewise seen as more prominent features in the latest Miocene and earliest Pliocene portion of the Middle Awash sequence. Often, primitive ectostyldids are accompanied by very prominent, single pli caballinids. EISENMANN (1994: pl. II, fig. 5) has illustrated exactly an example of this association in a specimen of *“Hipparion” (= Eurygnathohippus of BERNOR & HARRIS 2003)* “*turkanense*” from the Nkondo Formation (locality NK 58), Uganda. While EISENMANN (1994) has claimed that the small circular structure on the buccal margin of the tooth is not an ectostylid, Bernal has observed that this is exactly the morphology seen in primitive adult cheek tooth ectostyldids, and frequently in association with the strong pli caballinid seen in this specimen. These primitive hipparions do not have ectostyldids rising the full height of the tooth, and often are restricted to very short, small, vertically oriented swellings on the buccal side of the crown. When the tooth is sufficiently worn, these structures are expressed as small enamel rings on the occlusal surface of the tooth. As the *Eurygnathohippus* lineage evolved, ectostyldids became larger in their length and width dimensions, and rose higher on the labial side of the crown. We believe that ectostyldids evolved as structures that provide stability to the cheek teeth during extreme buccolingually directed forces associated with the masticatory cycle.

Yet other primitive features of the NL(B) Chorora sample include: complex pre- and postfossettes, double pli caballin, and very deep hypoconal groove in the upper cheek tooth; lack of a pli caballinid, strongly developed metastylid spur, rounded metaconid and rounded-to-square metastylid in the lower cheek teeth. Later African hipparions tend to evolve single pli caballins, shallower hypoconal grooves, they lose their metastylid spurs and evolve, by the latest Miocene, very angular-to-pointed metaconids and metastylids.

The maxillary and mandibular cheek teeth figured by GERAADS (2002, fig. 4, 1–7) are strikingly similar to our sample. Two upper cheek teeth (GERAADS 2002, fig. 4, 2, 4) are remarkable for their multiple pli caballins (rather than double) and highly ornamented pre- and postfossettes. Fig. 4.3 (GERAADS 2002) is an upper cheek tooth, apparently in early wear, that preserves a mesial pli on the protocone.
This is a primitive feature for Old World hipparions. All lower cheek teeth (GRAAADS 2002, figs 4.5–7) have deep ectoflexids and rounded metaconids/metastylids, which are also primitive characters for African hipparions.

All of these characters support our interpretation (GRAAADS et al. 2002) that the Chorora hipparion is very primitive, and correlative with MN 9 of Europe.

The Chorora hipparion exhibits an extensive suite of primitive characters that in toto deny its taxonomic assignment either to the African clade, Eurygnathohippus, or its sister South Asian clade, Sivalhippus (BERNOR & LIPSCOMB 1995). Primitive characters of both the upper and lower dentition suggest that the Chorora hipparion is not readily referable to either Hipparion s.s. or Creomohipparion (BERNOR et al. 1996). However, the distinction between Hippotherium and Cormohipparion cannot be made on teeth alone. A recent detailed study of the Sinap, Turkey late Miocene sequence, from basal MN9 – MN12, and including the so-called “Hipparion Datum” has revealed that the first occurring hipparion there is best referred to the North American Genus, Cormohipparion, and not Hippotherium based on associated cranial, dental and particularly postcranial material. BERNOR et al. (1996, 2003) concluded that Hippotherium primigenium is principally a Central and Western European clade, and derived particularly in its postcranial morphology. In fact, there is no critical morphological data to support claims that Hippotherium primigenium populated Africa, although this possibility cannot be absolutely ruled out. What is sorely needed is complete postcranial data from Chorora and other East African early late Miocene localities, and in particular, complete metapodials, to resolve this issue (BERNOR & SCOTT 2003).

North American Cormohipparion was the ancestral stock from which all Vallesian hipparion (at least) are derived. Given the overall primitive characters of the Chorora hipparion dentition, combined with the demonstrated antiquity of the sample and our current understanding of early Vallesian hipparion morphology and biogeography, we believe that its most prudent taxonomic referral is to “Cormohipparion” sp. We believe that the current evidence further suggests that the Chorora hipparion was likely derived from the initial “Hipparion Datum” event, ca. 10.7+ Ma. (BERNOR et al. 2003).

Paleodietary Reconstruction

Introductory Considerations

The mesowear method, initially developed by FORTELIUS & SOLOUNIAS (2000) has proven to be a powerful tool for reconstructing paleodietary adaptations (KAISER et al. 2000b). The mesowear method is based on facet development of cheek tooth occlusal surfaces. The degree of facet development reflects the relative proportions of tooth-to-tooth contact (attrition) and food to tooth contact (abrasion). Attrition creates facets while abrasion obliterates them. The entire exposed surface of a tooth is affected by wear, but mesowear analysis so far has focused on the cutting edges of cheek tooth enamel surfaces where the buccal wall (ectoloph in perissodactyls) meets the opposing occlusal plane.

**Table 3: Absolute and calibrated mesowear scorings (datasets 1–6).** DS = # of dataset, tx = maxillary tooth, tm = mandibular tooth, 1 = low occlusal relief, h = high occlusal relief, s = sharp cusp, r = round cusp, b = blunt cusp. DS1 = absolute mesowear counts maxillary teeth, DS2 = absolute mesowear counts mandibular teeth, DS3 = Calibration factor for lower of hipparionines (CFHp) as established in Hippotherium primigenium by KAISER & FORTELIUS (2003). DS4 = absolute mesowear counts mandibular teeth calibrated by CFHp, DS5 = sum of calibrated counts in upper and lower teeth, DS6 = calibrated frequency (percentage) used for cluster analysis (fig. 4).

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<td>7</td>
<td>tx+tm (CFHp) [%]</td>
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KAISER & SOLOUNIAS (2003) extended the mesowear method to four upper cheek teeth (P4-M3), and thus expanded the methodology to intrinsically larger sample sizes. The mesowear method was tested and applied to hipparionine horses by BERNOR et al. (1999), KAISER et al. (2000a, b), KAISER et al. (2003), and KAISER (2003). A replication test using different samples of some species originally studied by FORTELIUS & SOLOUNIAS (2000) gave highly congruent results (DAMUTH, personal communication 2002).

The “extended” mesowear method (KAISER & SOLOUNIAS 2003) was applied to maxillary premolar and molar teeth. KAISER & FORTELIUS (2003) further extended the mesowear method to lower equid cheek teeth, and investigated the mesowear profile at the buccal enamel band of both lower and upper teeth. Implicit in this methodology is that the buccal enamel band remains undamaged. In the Chorora sample, this is the case with only a single lower premolar tooth (NL(B)CHOR 1). KAISER & FORTELIUS (2003) further investigated the functional relationships

![Hierarchical Cluster Diagram](image)

Fig. 4: Hierarchical cluster diagram comparing a set of 27 “typical” extant species from FORTELIUS & SOLOUNIAS (2000) with the Chorora sample [NL(B) CHOR] of dental specimens, and 6 fossil populations of North American, African and European Hipparions. NED = normalized Euclidean distance (root-mean-squared difference). Circle = extant browser, rectangle = extant mixed-feeder, triangle = extant grazer. Fossil species (printed in bold) are “Eurygnathohippus” cf. baardi from the Pelletal Phosphate Member (PPM) of Langebaanweg, South Africa (~ 5 Ma), Cormohipparion goorisi and Cormohipparion quinni from North America (data from FORTELIUS & SOLOUNIAS 2000), and Hippotherium primigenium from the MN 10 Locality of Dorn-Dürkheim, Germany (data after KAISER et al. 2003) and the MN 9 of the Höwenegg, Germany (data after KAISER 2003).
between the distribution of dental tissues and the mesowear profile in occluding pairs of equid teeth. They found that the mesowear signal is more closely related to the distribution of enamel areas at the antagonistic occlusal surface rather than at the occlusal surface of the tooth under consideration.

Results: Applying the extended methodology used by Kaiser & Solounias as 2003 to the NL(B)CHOR 1 specimen (left p4), OR is “high” and CS in both cusps is “round”. In the NL(B)CHOR 2 specimen (left M1), no ectoloph is preserved and the second enamel band (buccal band of the fossettes) was scored instead. The anterior cusp of this tooth is “round”, while the posterior cusp is “sharp”. NL(B)CHOR 3 (right m1) has no buccal enamel band preserved and in NL(B)CHOR 5 (left m2) both buccal cusps are severely eroded by weathering. Due to poor preservation and no comparative data available, NL(B)CHOR 3 and NL(B)CHOR 5 need to be ruled out for any kind of mesowear investigation. NL(B)CHOR 6 would appear to have suffered from chemical erosion to the occlusal surface, however both buccal cusp apices are preserved and allow scoring. The anterior cusp is “sharp”, the posterior one is “round”.

Mesowear scorings on individual tooth specimens are given in table 2. Frequencies of mesowear variables and calibration factors are given in table 3 following the methodology of Kaiser & Fortelius (2003). Our analysis positions the Chorora hipparion (NL(B)CHOR) in a cluster with the extant African mixed-feeders Taurotragus oryx (eland) and Tragelaphus scriptus (bushbuck), and in close proximity to the mixed feeding wapiti (Cervus canadensis) and the Sumatra serow (Capricornis sumatraensis) (fig. 4).

The same cluster also includes the Dorn Dürkheim (DD) population of Hippotherium primigenium and at the level of NED = 23 it is linked to the two North American hipparions Merychippus insignis and Cormohipparion quinni. Those species however are at the abrasion dominated end of the mixed feeding edifice, while “Eurygnathohippus” cf. baardi from South Africa clusters as a grazer (Franz-Odendaal et al. 2003), and the Höwenegg population of H. primigenium (HO) was shown to have a browsing mesowear signal (Kaiser 2003).

Additional evidence for dietary behavior can be gained from the morphology of the buccal-lingual groove, developed in the one maxillary M1 specimen (NL(B)CHOR 2) available. The groove in this specimen is characterized as being particularly deeply incised and having steeply inclined flanks (fig. 5). In addition, the buccolingual oriented view of this groove is clearly deeply U-shaped. The combination of a deep and U-shaped buccolingual grooving is not frequently observed in hipparions. In most dental specimens of Old World hipparions investigated thusfar (e.g. Bernor et al. 1999, Kaiser et al. 2000b, Bernor et al. 2003, Kaiser 2003), the buccolingual groove is usually shallower and broader, or in African latest Miocene-Pliocene hipparions nearly or absolutely flat. However, there are a few observations of deep occlusal grooving such as found in MAFIV13266D-7, an M1 of a small sized hipparion species from Sümeg (Hungary; MN 10, ca. 9.7-8.7 Ma.; Bernor et al. 1999), as well as in several dental specimens of H. primigenium from Höwenegg, Germany, MN9, ca. 10.3 Ma. (e.g. P4, HLMD-HO-58V2), and Bacchinello V3, Italy (MN12/13, ca. 7-6 Ma.).

The mesowear signal suggests that the Chorora hipparion was likely a typical mixed-feeder, and is closely linked to the extant eland and the bushbuck, both of which are classified mixed-feeders by Fortelius & Solounias (2000). The bushbuck is even considered a browser by Janis & Erhardt (1988) and Hofmann (1989). The small number of observations, however, does not allow for a statistically significant statement. The results presented here must be treated as the best estimate possible based on mesowear for the Chorora hipparion assemblage. The morphology of occlusal grooving in NL(B)CHOR 2, however, may give some additional evidence that supports this classification. The steepness of grooving is partly mapped by the occlusal relief parameters of the mesowear convention. However, no distinction is made of extreme grooving as is observed in NL(B)CHOR 2. Deep grooving is never found in dedicated grazers, and in hipparions has thusfar only been reported in the Höwenegg population of H. primigenium, which was shown to have a browsing dietary signal by Kaiser (2003). Together with the observations by Kaiser & Fortelius (2003) this leads us to the conclusion that the NL(B)CHOR 2 tooth does not reflect a grass-dominated diet. However, because of small sample sizes, we cannot statistically confirm this interpretation.
Carbon Isotope Studies

Background to Chorora Hipparion Study

Stable isotopic analyses of tooth enamel provide a useful means for reconstructing diets, habitats, and paleoclimates. Fossilized tooth enamel records the carbon isotopic compositions of vegetation eaten during enamel development (CERLING et al. 1997, LEE-THORP et al. 1989). Four Chorora Hipparion teeth were analyzed for stable carbon isotopes in order to interpret the diet and habitat of these equids. The Chorora equid sample yields some of the oldest evidence for substantial grazing on C4 grasses.

Carbon isotopes are informative for both paleodiets and paleohabitat reconstructions due to differences in carbon assimilation between different plants. Most terrestrial plants assimilate atmospheric CO2 by one of two photosynthetic pathways, termed C3 and C4. C3 plants include almost all trees and shrubs, and only those grasses favored by cool, wet growing seasons. C4 plants include exclusively grasses and sedges growing in hot, dry habitats. These two photosynthetic pathways yield greatly different δ13C values (δ13C is the ratio of 13C to 12C relative to a standard, in this case Pee Dee Belemnite or PDB), with C4 plants falling between −22 and −35‰ (per mil), and C3 plants ranging between −10 and −15‰ (BENDER 1971, VOGEL 1980).

The non-overlapping δ13C values of C3 versus C4 plants allows discrimination of browsing versus grazing diets from analyses of tooth enamel. Enamel bioapatite records the carbon signal obtained from vegetation eaten, with an enrichment in δ13C due to fractionation from metabolic processes. The enrichment factor for all taxa analyzed in this Chorora study is assumed to be 14‰, as found by CERLING & HARRIS (1999) in an extensive analysis of ungulates. Thus, enamel with a δ13C of −14‰ for any Chorora equid is taken to indicate a diet of plants averaging −28‰, or C3 browse. Carbon isotopic values can be interpreted based upon certain cutoff values for diets of C3 versus C4. The δ13C values for tooth apatite for pure C3 modern diets in general range from approximately −20 to −8‰, with the extremes representing distinctive habitats, depleted very closed canopy rainforest and enriched very open habitat (CERLING et al. 1997). A pure C4 diet, on the other hand, yields δ13C values from +1 to +4‰. Modern δ13C values are depleted by 1.5‰ relative to Miocene values due to a shift in atmospheric carbon isotope ratios since the industrial revolution due to the burning of fossil fuels. Therefore, a value of −8‰ today, or the most enriched pure C3 diets, is comparable to a Miocene value of −6.5‰. For the purposes of this analysis, a cutoff δ13C value of −7.5‰ is used to distinguish evidence of at least some C4 in the diet.

The C3/C4 distinction is useful for paleoenvironmental as well as dietary inferences, for the C4 photosynthetic pathway is energetically expensive compared to the C3 pathway and is only competitively advantageous in hot, dry climates (EHLERINGER et al. 1991). Carbon dioxide enters a leaf through its stomata, but stomata must remain closed much of the time to conserve water in hot, dry climates. The enzyme used by C4 plants has a higher affinity for CO2 than does the C3 enzyme, thus allowing the plant to take up more CO2 when the stomata are open (EHLERINGER et al. 1991). Furthermore, this concentrated version yields a ratio of CO2 to O2 high enough that little CO2 is lost to photorespiration. These energetically expensive adaptations allow C4 plants to function better than C3 plants under high moisture stress during warm/hot growing seasons. However, because of the energetic tradeoff, C4 plants are restricted to warm, relatively dry regions, with C3 plants competitively superior in all other habitats.

The C4 photosynthetic pathway evolved multiple times during the Middle Miocene (EHLERINGER et al. 1997), with extensive C4 grasslands appearing in North and South America, Asia, and Africa by 7 Ma (CERLING et al. 1997). The first appearances of C4 plants around the globe have largely been determined based upon isotopic evidence from fossil tooth enamel and paleosols in addition to plant macrofossils, as summarized by JACOBS et al. (1999). The earliest potential evidence for a slight C4 dietary component comes from North America, with a 15.5 Ma camelid specimen yielding a δ13C value of −7.4‰, and two camels at 10.7 Ma yielding δ13C values as enriched as −7.1‰ (LATORRE et al. 1997). However, it was not until 7.0 Ma in North America that C4 plants become a significant proportion of diets (CERLING et al. 1997, MACFADDEN & CERLING 1994, WANG et al. 1994). Within South America, two 10 Ma notoungulate specimens yield δ13C values as enriched as −5.5‰, indicative of substantial C4 in the diet (MACFADDEN et al. 1994), but again, it is not until 7.3 Ma that C4-dominated diets and paleosols occur regularly (LATORRE et al. 1997).

In Asia, Pakistani Siwalik equids first incorporated significant proportions of C4 graze in their diets at 8.7 Ma, yielding values as enriched as −3.1‰ (NELSON in press). Furthermore, multiple intra-tooth isotopic sampling of Siwalik teeth demonstrates that C4 is a dietary component throughout a tooth’s development, which takes about a year, rather than being a seasonal dietary component (NELSON 2003). However, no Siwalik suids or bovids sampled yield a C4 signal by 8.0 Ma, and there is no paleosol evidence for C4 habitats until 8.1 Ma (BARRY et al. 2002). Paleoecological evidence suggests that the first C4-dominated habitats, or extensive grasslands occurred in Pakistan at 7.4 Ma, coinciding with the first C4-dominated habitats in North and South America.

Within East Africa, isotopic analyses of paleosols indicate the first C4 vegetation was present by 9.4 Ma but was only a small proportion of the total biomass (CERLING 1992). A 15.3 Ma rhino tooth with a δ13C value of −7.4‰ suggests the earliest diet with a very small C4 component (MORGAN et al. 1994), but isotopic analyses previous to the Chorora study suggest that a significant shift in elephant and equid diets from C3 to C4 did not occur until 8-7 Ma (CERLING et al. 1997).
Several hypotheses concerning why C₄ plants gained dominance in the late Miocene, when the first extensive C₄ grasslands occurred, have been proposed, including a global decrease in atmospheric CO₂ levels, for C₄ plants are competitively advantageous at lower atmospheric CO₂ levels (CERLING et al. 1993, 1997, EHLERINGER et al. 1991, 1997). However, timing across continents may not have been synchronous for first appearances of C₄ patches that were not extensive but were still sufficiently available both spatially and temporally for incorporation into faunal diets. Isotopic analyses of Chorora equids will add to the investigation of the spread of C₄ plants in Africa.

Results: All four Chorora equid teeth sampled yield carbon values indicating a significant proportion of C₄ grasses in their diets, with δ¹³C values ranging between −7.5‰ to −4.6‰ (fig. 6). Furthermore, within the two teeth sampled multiple times along their lengths, δ¹³C values of each sample indicates a C₄ dietary component, suggesting that C₄ grasses were present year-round rather than being a seasonal component of the diet, comparable to the pattern seen in Pakistan Siwalik equids. These δ¹³C values are consistent with an open, dry habitat exploitation by the Chorora equids.

These results mark the oldest evidence to date for a significant C₄ dietary component in East Africa, predating comparable African δ¹³Cvalues by as much as two million years. These values are similar to those of South American notoungulates of the same age, and they predate comparable values in Asia by about 1.3 Ma and North American values by about 3 Ma. These results suggest an earlier appearance of C₄ grass patches in equatorial Africa and the southern hemisphere than in the northern hemisphere, and they suggest that C₄ grassland expansion occurred in stages. While evolution of C₄-dominated habitats, or extensive C₄ grasslands, appears to have occurred roughly simultaneously across North and South America, Asia, and Africa around 7.5-7.0 Ma, the initial stages, such as first C₄ plants on the landscape and first significant C₄ grass patches, appears to have occurred at different times both between and within continents. Given the asynchrony of C₄ grass appearances even within Africa, these earlier increases in C₄ abundance are likely to have been the result of local changes in climate, such as increasing aridity or increasing seasonality of rainfall, rather than resulting from global shifts in CO₂ levels. These results do not, however, preclude a global climate explanation for the later expansion of extensive C₄ grasslands that occurred circa 7.5-7.0 Ma.

Conclusions

The Chorora equid sample represents the oldest known hipparion in Ethiopia, and probably all of East and South Africa. The small cheek tooth sample exhibits a number of primitive discrete characters and no clearly advanced features known for latest Miocene and Plio-Pleistocene East African hipparions. The size of this hipparion was not large, and together with the morphology we have reported here, is apparently a primitive Old World hipparion. The morphologic evidence best compares with early hipparions known from early MN9 of Turkey and leads us to cautiously refer this sample to “Cormohipparion” sp. We follow data presented in WOODBURREN et al. (1996), BERNOR et al. (1996, 2003) and GERADS et al. (2002) in estimating the Chorora hipparion sample as being circa 10.7-10.1 Ma., based on its stage-of-evolution and recent radiometric dates bracketing the Chorora Formation. (GERADS et al. 2002).

Gross tooth morphology, along with mesowear and carbon isotope evidence presented here, reveals an interesting paleodietary and paleohabitat signal. The presence of a deep, buccolingual groove across the mesostyle-protocone of the M1 (NL(B)CHOR2), accompanied by lavishly developed plications of the pre- and post fossettes, are features in common with Central European Hippotherium primigenium. The occurrence of lavish enamel ornamentation of hipparion cheek tooth occlusal surfaces is not limited to Hippotherium primigenium, but is found in a number of hipparion lineages: this character likely reflects paleodietary adaptation and cannot be used in isolation for taxonomic discrimination. Given our current state of knowledge about Old World hipparion evolution, we cautiously refer the Chorora hipparion to Cormohipparion sp. The carbon isotope signal, together with the mesowear signal, suggest that the Chorora hipparion had a mixed graze-browse diet, and that the graze component included a significant portion of C₄ grass. It would appear from these results that the Chorora hipparion were adapted to the same known dietary regime of earliest Old World hipparion: these hipparion were neither specialized in the

Fig. 6: Four Chorora equid teeth were sampled for carbon stable isotopes, and all yield values consistent with a substantial proportion of C₄ graze in their diets. Two teeth were sampled multiple times along their length to provide evidence of diet throughout the year. These teeth indicate that C₄ grasses were a component of the diet year-round.
direction of browsing or dedicated grazing (e.g. Kaiser 2003). Whether the “Cormohipparion” clade gave rise to the pan-South Asian-African late Miocene “Sivalhippus” Complex, including multiple species of Sivalhippus and Eurygnathohippus, is currently unknown, and will take an intensive study of fossil materials in the 10.7-7 Ma. temporal interval to determine.

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