Evolution of Old World Equus and origin of the zebra-ass clade

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Evolution of the genus Equus has been a matter of long debate with a multitude of hypotheses. Currently, there is no consensus on either the taxonomic content nor phylogeny of Equus. Some hypotheses segregate Equus species into three genera, Plesippus, Allohippus and Equus. Also, the evolutionary role of European Pleistocene Equus stenonis in the origin of the zebra-ass clade has been debated. Studies based on skull, mandible and dental morphology suggest an evolutionary relationship between North American Pliocene E. simplicidens and European and African Pleistocene Equus. In this contribution, we assess the validity of the genera Plesippus, Allohippus and Equus by cladistic analysis combined with morphological and morphometrical comparison of cranial anatomy.

Our cladistic analysis, based on cranial and postcranial elements (30 taxa, 129 characters), supports the monophyly of Equus, denies the recognition of Plesippus and Allohippus and supports the derivation of Equus grevyi and members of the zebra-ass clade from European stenonis horses. We define the following evolutionary steps directly relevant to the phylogeny of extant zebras and asses: E. simplicidens–E. stenonis–E. koobiensis–E. grevyi -zebra-ass clade. The North American Pliocene species Equus simplicidens represents the ancestral stock of Old World Pleistocene Equus and the zebra-ass clade. Our phylogenetic results uphold the most recent genomic outputs which indicate an age of 4.0–4.5 Ma for the origin and monophyly of Equus.

The Old World Equus Datum is a widely recognized biochronological event by geochronologists, correlative with the beginning of the Pleistocene, 2.58 Ma1–22. It is traditionally considered a significant event in the evolution of Old World mammalian faunas, represented by the immigration of the Pliocene North American Equus simplicidens into Eurasia across the Beringia land bridge3–6,8–11,17,18,21–24. This intercontinental dispersal is correlated with strong paleoclimatic variation documented in the terrestrial and marine records, driven by the beginning of a major glaciation pulse in the northern hemisphere25–28 (Fig. 1).

In the last century, evolution of the genus Equus was actively debated by biologists and paleontologists alike proposing a multitude of hypotheses1–12. Although most of the authors consider the North American E. simplicidens as the possible ancestor of the genus Equus1–6,11,18,22, there is no current consensus on either the taxonomic content nor phylogeny of Equus. In fact, Equus’ traditional taxonomy was upended when some investigators proposed segregating the genus into three genera7: North American Pliocene Plesippus13 (type species E. simplicidens), Pleistocene Eurasian and African Allohippus14 (type species E. stenonis) older than 1 Ma, and previously recognized species of Equus less than 1 Ma as being the sole members of the genus. The segregation into these three genera was based on cranial morphology and proportion7. Notably, some studies used ten metric characters to distinguish Plio–Pleistocene species and extant Equus8, whilst more recent studies used only a single character (size of the cranium, brain-box) to distinguish among Plesippus, Allohippus and Equus9. The morphology of the dentition and postcranial elements was never taken into account. The validity of North American Plesippus and the European Allohippus was supported by a recent morphological qualitative cladistic analysis15, whereas another cladistic study supported the hypothesis of E. simplicidens as possible common ancestor for species of the genus Equus16. During the last decades, the Chinese species Equus E. qingyangensis was included within the genus Plesippus (P. qingyangensis)17, whereas the Chinese species Equus sanmeniensis (Allohippus sanmeniensis)18, the European Early Pleistocene species Equus livenzovensis and Equus senezensis (Allohippus livenzovensis and Allohippus senezensis)19–21, and the African Early Pleistocene Equus koobiensis (Allohippus koobiensis)22 were assigned to the genus Allohippus. Furthermore, other authors23, regarded Allohippus as a subgenus of Plesippus for the European Early Pleistocene species Plesippus (Allohippus) livenzovensis and Plesippus (Allohippus) stenonis.

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Another controversial issue concerns European Pleistocene Equus stenonis role in the evolutionary history of Equus and the origin of the zebra-ass clade. Early studies suggested a relationship between Equus stenonis and extant Equus grevyi based on skull and dental morphology. A morphological similarity was further identified in the skull and dentition between E. stenonis, E. koobiforensis (Kenya, Africa, 1.9 Ma) and E. grevyi, suggesting that E. koobiforensis could be more closely related to European E. stenonis than the Chinese E. sanmeniensis. Furthermore, some similarities were highlighted in skull, mandible and dental morphology between E. stenonis and E. simplicidens, suggesting that E. stenonis exhibits an intermediate morphology between the North American E. simplicidens and the African E. koobiforensis. Nevertheless, other hypotheses identified E. stenonis as a branch of the E. simplicidens–E. sanmeniensis–E. koobiforensis–E. grevyi evolutionary lineage.

Herein, we assess the validity of the genera Plesippus, Allohippus and Equus by means of our cladistic analysis. We define the evolutionary relationships of E. stenonis to other Old World Pleistocene and extant Equus and the origin of the zebra-ass clade.
Results

Phylogenetic analysis. The cladistic analysis includes 30 Operative Taxonomic Units (OTU, with 4 out-groups and 26 ingroups) and 129 characters and it has produced one most parsimonious tree (Fig. 2) (Tree Length = 398 steps, Consistency Index = 0.472, Retention Index = 0.705; Homoplasy Index = 0.528). The characters have been coded by direct observations on fossil collections combined with other published fossil specimens (see Methods below). The present phylogenetic tree clusters the family Equidae by node 57 with 13 unambiguous synapomorphies (Appendix 1) and, furthermore, the Miocene tridactyl genera Merychippus and Cormohippparion are segregated from the monodactyl genus Pliohippus by 6 unambiguous synapomorphies (Appendix 1). The species referred to the genera Merychippus, Hippidion and Dinohippus are clustered together as dichotomies, with Cormohippparion being sister to Merychippus.

The phylogenetic tree reveals outcomes for the Plio-Pleistocene species from North America and the Old World. Genus Equus is modeled as a single clade with node 52 being supported by 18 unambiguous synapomorphies, and 13 of these have a CI ≥ 0.500. The complete list is reported in Table 1.

The bootstrap tree supports the Equus clade with 99/100 replications (Appendix 1, bootstrap tree and UPGMA tree). The species previously included within the genera Plesiippus and Allohippus are not clustered from the Equus clade, identified by the node 52 (Fig. 2). This evidence is strongly supported by the bootstrap resampling analyses and tree, where the species included in the clade Equus are grouped as polytomies, except for 4 small clades (Appendix 1, bootstrap tree). These small clades cluster the North American species E. simplicidens with the Chinese E. qingyangensis (node 35; bootstrap values 95/100), the Equus sp. from Dmanisi (Georgia, Caucasus) with the fossil African E. oldowayensis (node 37; bootstrap values 77/100), the extant E. hemionus and E. kiang (node 44; bootstrap values 99/100) and E. przewalskii and E. ferus (node 44; bootstrap values 100/100). These subclades do not represent other genera in the Equus clade (node 52), but may indicate no relevant morphological difference between these species being scored with similar character states (Table S1). An analogous result was already highlighted in recent research applying Geometrics Morphometrics on cranial elements in extant species31.

Notably, E. simplicidens and E. qingyangensis differ only by a single character, the shape of palatine process (slender in the former and flat in the Chinese species), raising a question about the validity of E. qingyangensis. Another small clade including E. stenonis and E. senezensis in the parsimonious tree (node 36, Fig. 2) is not supported by the bootstrap resampling (Appendix 1).

Furthermore, the UPGMA tree based on the qualitative and quantitative characters described in the Table S1 may share new insights on the possible species relationships included in the Equus clade. The UPGMA well clusters the Equus clade from the other fossil genera of North and South America since the node 59 and, remarkably, separate the caballine horses (including E. przewalskii–E. ferus) from all other stenonine species (Appendix, UPGMA, node 58). This last cluster includes the entire fossil species from the New and the Old World and the extant zebras and asses. Noteworthy, the morphometric analyses based on the skull morphology show a similar result. The small clades within Equus evidenced by the most parsimonious tree and the bootstrap resampling are also present in the UPGMA tree (E. simplicidens–E. qingyangensis; Equus sp. from Dmanisi–E. oldowayensis (Orgeisaile); E. hemionus–E. kiang; E. przewalskii–E. ferus) thus supporting their morphological similarities. The Early Pleistocene Chinese species E. eisenmanna is grouped with the E. simplicidens–E. qingyangensis clade, whereas, as reported in Fig. 2, E. tivenovensis and E. stenonis are the closest relatives of E. koobiensis (Appendix 1, UPGMA tree). These relationships are reflected in the morphometric results on skulls, wherein E. koobiensis is found to be closely related to E. samenensis and E. stenonis (Fig. 3, S. text and Fig. S2). Equus sp. from Dmanisi (Equus aff. E. altidens) and E. oldowayensis are still closely related31.

In our parsimonious tree (Fig. 2), E. quagga is regarded as a sister species of the E. hemionus–E. kiang clade. This result seems to be in contrast with the most recent molecular phylogenies32–34, wherein plain zebras and wild (PC1 = 54.0% and PC2 = 17.3%). The loadings’ distribution is shown in Figure S3 and reported in Table S2. PC1 separates species by maximum length (M6 and M23) from negative to positive values (more to less elongated), whereas PC2 mostly clusters species by M3 and M31 in positive values, and M4 and M5 negative values. The opposite development of the vomerine length (M3) and post vomerine length (M4) shown in the PCA is given whereas PC2 mostly clusters species by M3 and M31 in positive values, and M4 and M5 negative values. The opposite development of the vomerine length (M3) and post vomerine length (M4) shown in the PCA is given also in the Log10 Ratio diagrams outcomes (Figure S2): even if E. simplicidens, E. stenonis and E. grevyi show the same skull length, E. simplicidens is separated from E. stenonis and E. grevyi by its greatly elongated vomerine length (M3) and a reduced post vomerine length (M4), whereas E. stenonis and E. grevyi show a longer development of the post vomerine length (M4) and a reduced vomerine length (M3). M30 and M31 cluster E. simplicidens and E. stenonis, with E. grevyi which occupies an intermediate morphospace between these species. This evidence is supported also by the Log10 Ratio diagrams (Figure S2), with E. grevyi showing a skull basal morphology similar to E. stenonis, and the lateral, naso-incisival notch, and cheek tooth length being similar to E. simplicidens. The Old World Equus species exhibit a longer naso-incisival notch dimension when compared to E.
Figure 2. Most parsimonious tree of the cladistic analysis (30 taxa; 129 characters; Length = 398; CI = 0.472; RI = 0.705; HI = 0.528) recovered by PAUP 4.0β1047 and edited by Adobe Photoshop CC2017. Grey numbers report the Bootstrap values, whereas numbers included in circles represent the nodes discussed in the text. Terminal color branches indicate the following different genera identified by the cladistic analysis: yellow, *Merychippus*; Cyan, *Cormohipparion*; grey, *Pliohippus*; purple, *Hippidion*; green, *Dinohippus*; dark red to orange, *Equus*. On the right, red color box indicates the genus *Equus*, black box Zebras, dark green box Asses and blue box Modern Horses. Black circles indicate the previous genus attribution to *Plesippus*, whereas black squares *Allohippus*. The detailed analyses are reported in Appendix 1.
Table 1. List of unambiguous synapomorphies of the Equus clade (node 52 in Fig. 2).

| Character description          | Character number | Character state | Character state description                  | Consistency Index |
|-------------------------------|------------------|-----------------|---------------------------------------------|------------------|
| Length of the skull           | 1                | 3               | Between 500 and 550 mm                      | 0.385            |
| Lateral outline of skull      | 2                | 0               | Linear                                      | 0.500            |
| Buccinator fossa              | 21               | 1               | Absent or poorly developed                  | 1.0              |
| Orbits position related to the upper third molar | 27               | 3               | Well behind the upper third molar           | 0.375            |
| Lingual margin of the protocone | 55              | 2               | Shallow depression on its medial aspect     | 0.500            |
| Protocone shape of the upper second premolar | 60              | 1               | Squared                                     | 0.500            |
| Hypocone shape of the upper third and fourth premolar | 61              | 1               | Squared                                     | 0.167            |
| Pli caballin shape of the upper third and fourth premolar | 62              | 2               | Present and elongated                       | 1.0              |
| Protocone shape of the upper third and fourth premolar | 63              | 1               | Squared                                     | 0.667            |
| Upper premolar cheek teeth length | 71              | 2               | Between 100 and 110 mm                      | 0.375            |
| Morphology of the metaconid-metastylid complex | 91              | 2               | V-shaped                                    | 1.0              |
| Morphology of the lingual side of the metastylid | 92              | 2               | Squared                                     | 1.0              |
| Functional morphology of foot | 114              | 2               | Hoof without soft pad, 3rd phalanx is strong and broad | 0.500            |
| Elongation of the lateral second metacarpal | 116              | 3               | Reduced up to the diaphysis and the proximal epiphysis of the third metacarpal | 0.750            |
| Elongation of the lateral fourth metacarpal | 118              | 3               | Reduced up to the diaphysis and the proximal epiphysis and the third metacarpal | 0.750            |
| Elongation of the lateral second metatarsal | 122              | 3               | Reduced up to the diaphysis and the proximal epiphysis of the third metatarsal | 1.0              |
| Elongation of the lateral fourth metatarsal | 124              | 3               | Reduced up to the diaphysis and the proximal epiphysis of the third metatarsal | 1.0              |

greyvi. Equus koobiforensis plots between E. stenonis, E. sammeniensis and E. eisenmannae, even if the basal morphology of the skull appears to be more related to E. stenonis and E. sammeniensis rather than E. eisenmannae. Nevertheless, its position in this diagram is influenced by the total maximum length (M6) and the upper cheek tooth row length (M7, M8, M9) which are slightly longer than E. stenonis and E. greyvi (see the original raw data in Table S3). The Chinese species E. eisenmannae and E. huanghoensis appear to be more closely related to E. simplicidens than E. stenonis. PC1 and PC3 account for most of the variance with 63.4% of the total variance (PC1 = 54.0% and PC3 = 9.4, Fig. 3b; the loadings’ distribution is shown in Figure S3b and reported in Table S2). PC1 separates species by M4 in positive values and maximum lengths (M6 and M23) in negative values (more to less elongated), whereas PC2 mostly clusters species by M5 and M31 with negative values (more to less elongated). In this diagram, E. simplicidens, E. stenonis and E. greyvi are closely clustered, overlapping some portions of their morphospaces. Equus koobiforensis plots between E. stenonis, E. sammeniensis and E. eisenmannae, whereas E. huanghoensis is well separated from the entire sample by its reduced M5 and its elongated M2.

The PCA results on the basal skull measurements (Fig. 3c,d) do not include maximum skull length (M6). We have excluded this measurement in order to investigate the evolution of the basal skull morphology. PC1 and PC2 account for most of the variance with 74.7% (PC1 = 43.2% and PC2 = 31.5%, Fig. 3c; the loadings’ distribution is shown in Figure S3c and it is reported in Table S2). PC1 separates species by M1 (ventral length of the muzzle) and M2 (palatal length), from negative to positive values (more to less elongated), whereas PC2 mostly clusters species by M3 in positive and M4–M5 in negative values. These results are congruent with the previous clustering pattern (Fig. 3a). Equus simplicidens and E. huanghoensis are clustered by their longer M3 length, whereas E. greyvi and E. stenonis show higher values for M4. Nevertheless, E. stenonis overlaps with E. greyvi’s morphospace, providing additional support of the evidence shown in the Log10 Ratio diagram (Figure S2b). Equus koobiforensis is placed closer to E. stenonis and extant E. greyvi, whereas the Chinese species E. eisenmannae is the largest horse of the entire sample and E. sammeniensis is placed between E. eisenmannae and E. stenonis. PC1 and PC3 account the 60.6% of the total variance (PC1 = 43.2% and PC3 = 17.4%, Fig. 3d; the loadings’ distribution is shown in Figure S3d and reported in Table S2). PC1 separates species by M4 with positive values and M1 and M3 with negative values (more to less elongated), whereas PC3 clusters species by M2 with positive values and M5 with negative values (more or less elongated). Equus stenonis and E. greyvi overlap extensively in their morphospaces which likewise include E. koobiforensis. Also, the E. simplicidens sample is placed close to E. stenonis, even if separated by the latter by its longer vomerine length (M3), and it includes E. sammeniensis in its morphospace. Equus eisenmannae is more closely related to E. simplicidens than E. stenonis, supporting observations of the Log10 ratios diagrams (Figure S2a). Equus huanghoensis still remains separated from the entire sample by its reduced M5 and its elongated M2.

Discussion

Origin and early evolution of the Equus greyvi clade. Our phylogenetic and morphometric analyses, within the systematic position of Equus stenonis, provide novel insights into the phylogenetic relationships of the Old World Equus and the origin of the zebra-ass clade based on paleontological evidence.2–4,7,11,12,15,18–22,36,37. As reported in the outcomes shown by the morphometric analyses, the Early Pleistocene Chinese species E.
eisenmannae, E. qingyangensis and E. huanghoensis have more primitive skull traits than E. stenonis that compare best with North American E. simplicidens, whereas the African E. koobiforensis and the extant E. grevyi are more closely related to E. stenonis and E. sanmeniensis. Nevertheless, Equus grevyi has a reduced muzzle when compared to the fossil species (Fig. 4l). The E. simplicidens skull is characterized as having a longer vomer length and a reduced post vomerine length (Fig. 4a,c), whereas E. stenonis, E. koobiforensis and E. grevyi have a reduced vomer length and a longer post vomerine length (Figs. 4e,g,i,k). In lateral view, E. simplicidens (Fig. 4b,d) has an elongated skull with a linear dorsal outline and a deep incision of the narial notch, whereas the skulls of E. stenonis (Fig. 4f,h) and E. koobiforensis (Fig. 4j) have a concave dorsal skull outline, akin to E. grevyi (Fig. 4l).

Furthermore, this skull development could be related to the mandibular profile. Equus simplicidens has the mandibular ramus angled posteriorly, whereas that of E. stenonis is vertically oriented (Fig. 5a–d). There is no mandible associated with E. koobiforensis. Equus grevyi has a mandible shaped more like E. stenonis, with a steep vertical ramus and a large and round posterior angle of the mandible (Fig. 5e–f).

The preorbital fossa (POF) underwent progressive reduction in Equus species related to the increase in cheek tooth crown height7,11–14. Figure S4 summarizes POF evolution in E. simplicidens, E. eisenmannae, E. stenonis, E. koobiforensis and E. grevyi, in the lateral morphology of the skull by its perpendicular maximum height (M35), by distance between POF and the facial maxillary crest (M36) and by its height of the back of the POF above
the alveolar border (M38). The POF is larger in *E. simplicidens*, *E. eisenmannae* and *E. stenonis* (M35) but it is placed higher on the maxilla (M36 and M38) in *E. stenonis*, *E. koobiforensis* and *E. grevyi*. *Equus stenonis* exhibits both plesiomorphic characters as does *E. simplicidens* and *E. eisenmannae* (M35), and more derived characters as seen in *E. koobiforensis* and *E. grevyi* (M36, M38) (S. text and Figure S4).

Recent research cites *Equus*’ distinction as having the greatest crown height of all Equidae. In turn, increased hypsodonty is hypothesized to be an adaptation to more arid environments in the Early Pleistocene (a generalized Neogene trend in ungulates). Horses became more adapted to grazing during the Pleistocene with a higher degree of hypsodonty and, as a consequence, increased hypsodonty also affected both the development of the lateral shape of the skull and the expression of the POF. Such evidence is provided by the evolution of the preorbital fossae (Fig. 3 and Figure S4), which is strongly reduced in *E. grevyi* and *E. koobiforensis* when compared to *E. simplicidens*.

Furthermore, there are important and consistent traits of the cheek tooth dentitions in *Equus*. The lingual margin of the protocone has a shallow depression on its medial aspect in *E. simplicidens* and *E. stenonis*, and it is more evident in *E. koobiforensis* and *E. grevyi* (S. text and Figure S5a–d; Ch. 55 in Table S1). In the lower cheek tooth row, the typical V-shaped linguaflexid and stenonine metaconid-metastylid morphology is precociously

Figure 4. Comparisons of skulls, ventral and lateral views: *E. simplicidens* (USNM12573 and USNM12542, (a–d), *E. stenonis* (NHML20.163360 and IGF560 (e–h), *E. koobiforensis* (KNM-ER1284, i–j) and *E. grevyi* (USNM163228 k–l). Scale bar 10 cm.
present in *E. simplicidens* (S. text and Figure S5f–h; Ch. 91 in Table S1). However, the remarkable squared morphology of the lingual margin of the metastylid is found in *E. stenonis*, *E. koobiforensis* and extant *E. grevyi*, and it is present, even if less clear, in *E. simplicidens* (S. text and Figure S5f–h; Ch. 92 in Table S1).

**Evolutionary remarks.** The various analyses provided herein have shown that the evolution of the head morphology occurred in the evolutionary steps *E. simplicidens*–*E. stenonis*–*E. koobiforensis*–*E. grevyi*+ zebra-ass clade (Fig. 6) including: (i) the reduction of the vomerine length; (ii) elongation of the post vomerine length; (iii) reduction of the length of the naso-incisival notch; (iv) progressive reduction of the POF, from a large and more developed structure to a reduced and shallow morphology, which is still present in the extant zebras; (v) progressively more vertically oriented mandibular ramus; (vi) a more derived morphology of the lingual margin of the protocone; (vii) the advanced squared shape of the metastylid and persistent V-shaped linguaflexid.

Following Azzaroli and Voorhies5, we find that North American Pliocene *Equus simplicidens* represents the likely ancestral stock for the origin of Eurasian stenonine horses and ultimately African *E. grevyi*, and the zebra-ass clade1–6,9,11,18,41. Our phylogenetic results support *Equus* as being a single clade, with *Dinohippus* as the sister taxon. Our results do not support *Plesippus* and *Allohippus* at either the generic or subgeneric ranks. Our phylogenetic outcomes support the most recent genomic outputs9,33, which have found evolutionary rates for the *Equus* most common recent ancestor living 3.6–5.8 Ma. Ancient DNA analyses have shown slower mutation rates in horses than humans9 implying a minimal date of 4.07 Ma for *Equus*’ most common recent ancestor, proposing an age of 4.0–4.5 Ma for the origin of *Equus*. The concurrent evidence of our phylogenetic and the genomic results9 can be correlated with the most recent paleontological findings in Central America21,36, which have proved the occurrence of the primitive *Equus* morphologies9,36 at the Hemphillian–Blancan boundary at ca. 4 Ma21,36 correlative with the onset of Pliocene global warming11,19,36,42.

**Methods**

**Phylogenetic analysis.** Our cladistic analysis uses 30 Operational Taxonomic Units (OTUs) and 129 characters (72 cranial, 40 mandibular and 17 on autopodia), including 26 equid taxa and 4 outgroups, *Tapirus terrestris*, *Hyrachyus extimus*, *Trigonias osborni* and *Merychippus insignis* (Appendix 1 and Table S1). The complete
sample of the specimens coded in the cladistic matrix is reported in S. text. The matrix used in this cladistic analysis includes 68 novel characters, combined with the most recent matrices for equids and perissodactyl cladistic analyses\textsuperscript{12,20,34–46} (Table S1). The characters have been coded by direct observations. 24 characters are ordered (2, 5, 9, 10, 11, 12, 13, 14, 16, 22, 23, 42, 43, 52, 78, 91, 92, 113, 114, 116, 118, 121, 123, 129) and 105 characters unordered. All characters were equally weighted. The phylogenetic analysis was undertaken using PAUP 4.0\textsuperscript{1047}, under parsimony using Heuristic Search with the TBR (tree bisection reconnection) branch-swapping algorithm, 1000 bootstrap replications with additional random sequence, gaps treated as missing.

**Morphometric analysis.** We have undertaken statistical analyses (Log10 ratio diagrams, PCA, and box-plots) on selected skull, mandible and dental morphologies and measurements (S. text) to evaluate our cladistic analysis of Plio-Pleistocene Holarctic and African Equus evolution. We use international equid measurement standards\textsuperscript{48,49}. Plots were generated primarily using the R Studio Software v.1.4.103 2020\textsuperscript{50} packages ggplot2() v.3.3.3 and prcomp() v.3.6.2, using the function (scale = T). Following previous analytical studies\textsuperscript{7}, we have selected skull length measurements, avoiding medio-lateral deformation which would adversely influence our results. The complete database used in the Morphometric analyses is reported in Table S3, including personal and other published available data\textsuperscript{51–56}.

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Figure 6. Evolutionary framework of the extant zebras Equus grevyi since the oldest common ancestor Equus simplicidens, and through the European Equus stenonis and the African Equus koobiensis. The present figure aims to represent the dispersal of the genus Equus in the Old World by E. simplicidens at the beginning of the Pleistocene, and the origin of the extant zebras E. grevyi through the E. stenonis and E. koobiensis lineage. Artwork O. Cirilli (map edited from row data of QGIS v.3.18.1 (https://www.qgis.org/it/site/), zebras in background edited from Nina Marie Photography (https://ninamarievisuals.com/)).
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Author contributions
O.C., L.P., L.R. and R.L.B. conceived the paper; O.C. and R.L.B. acquired data; O.C. developed the morphometric analyses; O.C., L.P. and R.L.B. developed the cladistic analysis; all authors discussed and interpreted the results and equally contributed to finalize the manuscript.

Competing interests
The authors declare no competing interests.

Additional information
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