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The Systematic Position of *"Plesiohipparion"* aff. *huangheense* (Equidae, Hipparionini) from Gülyazi, Turkey

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With 3 text-figures and 2 tables

Abstract

The Pliocene locality of Gülyazi, referred to European Mammal Neogene Zone (MN) 16b, has yielded limited material of an advanced, and provincially late occurring hipparionine horse, *"Plesiohipparion"* aff. *huangheense*. Morphologic characterization initially using 50 skull and mandible characters has led us to identify this hipparion as being a member of the *"Sivalhippus"* Complex (sensu lato). A cladistic analysis using 33 characters has yielded a single most parsimonious tree with a high consistency index (C. I. = 83), clarifying *"Plesiohipparion" huangheense'* systematic position. Results of the cladistic analysis lead us to hypothesize that the Gülyazi hipparion represents a medial Pliocene extension of an east Asian species into western Anatolia. Furthermore, our analysis suggests that species belonging to the *"Sivalhippus"* Complex ranged circa 9.5–1 Ma, and underwent 3 major intercontinental biogeographic extensions: the first, ca. 8–5.5 Ma (*"Sivalhippus" perimense* – *"Sivalhippus" turkanense* clade), including South Asia and East Africa; the second, ca. 5 Ma (*"Plesiohipparion" houfenense* / *"Plesiohipparion" rocinantis rocinantis* – *"Plesiohipparion" rocinantis crusafonti,* and potentially the *"Eurygnathohippus"* clade) and including Asia, Europe and Africa; the third, represented by the Gülyazi hipparion *"Plesiohipparion"* aff. *huangheense,* ca. 2.5 Ma, and representing the extension of an otherwise exclusively East Asian clade into western Anatolia.

I. Introduction

Gülyazi is located in western Anatolia, approximately 75 km southwest of Afyon, and 225 km east of Izmir. The locality was found during the joint Turkish-German lignite exploration program between 1965 and 1970. The fauna is extensive, including both small and large mammals derived from lacustrine and fluvio-lacustrine sediments with a molassic character (Sickenberg et al., 1975: 43). Included in this fauna are two equids, an *"Equus"* (sensu lato), *Allohippus stenonis* (written communication to Tobien), and an hipparionine, referred here to *"Plesiohipparion"* aff. *huangheense*.

The cooccurrence of *"Equus"* and an hipparionine in Europe or southwest Asia is rare, because hipparions diversify there explosively during the late Miocene (Bernor et al., 1989,

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1990a), then decline in species abundance and diversity at the end of the Miocene. *Equus* first occurs in Europe and southwest Asia circa 2.5 Ma, closely correlative with the Gauss/Matuyama boundary (LINDSAY et al., 1980) and the base of MN 16b (TOBIEN, 1981; VAN DER MEULEN and VAN KOLFSCHOTEN, 1986; MEIN, 1989; STEININGER et al., 1989).

STAESCHE (1975; in SICKENBERG et al., 1975) referred the Gülyazi hipparion to *H.* cf. *crusafonti* based on relatively close similarities to the Spanish form recognized by ALBERDI (*„H". rocinantis crusafonti;* 1972, 1974). We present evidence here that the Gülyazi hipparion is closely related to the Chinese Nihewan age species *"Plesiohipparion" huangheense. H. crusafonti* is believed to be a member of the same clade (sensu lato), but the exact nature of this relationship requires further study of both the Chinese and Spanish assemblages.

The Gülyazi fauna has been previously correlated with MN 16b on the basis of mammal species other than the equids. SICKENBERG et al. (1975) noted that the Gülyazi "faunengruppe" correlated well with Kvabebe based on joint occurrences of *Paracamelus* cf. *alexejewi, Canis odessanus, Stephanorhinus* (= *Dicerorhinus) megarhinus, Anancus* sp. and *Hipparion* cf. *crusafonti.* SICKENBERG et al. (1975) determined that Gülyazi's age correlation is most precisely made by the occurrence of *Paracamelus alexejewi,* characterized as a member of a rapidly evolving lineage occurring in a number of provincial medial MN16 assemblages. Amongst the small mammals, *Mimomys polonicus* and *Mimomys septimanus* are similarly thought to be sensitive biochrons. SICKENBERG et al. (1975: 124) have noted that these species are somewhat more evolved than *Mimomys stehlini,* and correlate Gülyazi with the "Older Villafranchian" localities of Rebielice (Poland), Seynes, Etouaires, Chagny II (France), Hajnacka (Czechoslovakia) and Tologoj (Transbaikal region). Information presented here and in other contributions to this volume serve to further substantiate an MN16b correlation, circa 2.5 Ma.

A recent report on late Turolian to early Biharian mammal faunas from Greece and Turkey by VAN DER MEULEN and VAN KOLFSCHOTEN (1986) suggest that the base of MN 16b correlates with a major regional environmental shift which substantially reduced the forest environment and led to a typical seasonal Mediterranean climate with marked summer drought (SUC and ZAGWIJN, 1983).

Abbreviations and Definitions:

AL – Afar locality, Museum of Natural History, Addis Abeba, Ethiopia
AMNH – American Museum of Natural History, New York, USA
HU – Howard University, Laboratory of Paleobiology, Washington D. C., USA
IVPP – Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China
KNM – Kenya National Museums, Nairobi, Kenya
LSNK – Landessammlungen für Naturkunde, Karlsruhe, Germany
PMU – Palaeontologiska Museet, Uppsala, Sweden
THP – Tianjin Natural History Museum, China

Taxonomic abbreviations used in text and Tables 1 and 2 (see also BERNOR et al., 1989 for a more detailed discussion of the taxa listed below):

Hpri (= *"Hipparion" primigenium* s. s.); TOBIEN (1986), BERNOR and HUSSAIN (1985); BERNOR et al. (1987b); BERNOR et al. (1988); BERNOR et al. (1990a; measurements)
Spla (= *"Sivalhippus" platyodus);* BERNOR et al. (1987); QIU et al., 1988; BERNOR et al. (1990b; measurements)

Sper (= *"Sivalhippus" perimense);* MacFadden and Woodburne (1982); Bernor and Hussain (1985; measurements)
Stur (= *"Sivalhippus" turkanense);* Hooijer and Maglio (1974; measurements); Bernor and Hussain (1985)
Plhou (= *"Plesiohipparion" houfenense);* Flynn and Bernor (1987); Qiu et al. (1988)
Plaffhou (= *"Plesiohipparion"* aff. *houfenense);* MacFadden (1984); Flynn and Bernor (1987)
Plcru (= *"Plesiohipparion" rocinantis crusafonti);* Alberdi (1972, 1974; cheek tooth and metapodial distal articular measurements estimated from figures)
Plhua (= *"Plesiohipparion" huangheense);* Qiu et al. (1988)
Plaffhua (= *"Plesiohipparion"* aff. *huangheense)* this publication
Euafa (= *"Eurygnathohippus" afarense);* Eisenmann (1976, and Bernor, personal observation; measurements)
Prpat (= *"Proboscidipparion" pater);* Qiu et al. (1988; measurements)
Prsin (= *"Proboscidipparion" sinense);* Qiu et al. (1988; postcranial measurements); Bernor et al. (1990b; skull measurements)

Hipparionine or hipparion – horses with an isolated protocone on maxillary premolar and molar teeth and, as far as known, tridactyl feet, including species of the following genera: *Hipparion, Neohipparion, Nannippus, Cormohipparion, "Hippotherium", "Proboscidipparion", "Plesiohipparion", "Sivalhippus", Pseudhipparion, "Eurynathohippus"* (= senior synonym of *"Stylohipparion")* and *Cremohipparion.* Recent characterizations of these taxa can be found in MacFadden (1984), Bernor and Hussain (1985), Webb and Hulbert (1986), Hulbert (1987), Qiu et al. (1988), Bernor et al. (1989) and Woodburne (1989).

Hipparion s. s. – We follow MacFadden (1980, 1984: 53), Woodburne and Bernor (1980: 1329), Woodburne et al. (1981: 496), MacFadden and Woodburne (1982: 187), Bernor and Hussain (1985: 134), Bernor (1985: 180), Bernor et al. (1987: 46 and Fig. 4), Bernor et al. (1989: 298) and Woodburne (1989) in restricting this nomen to a specific lineage of horses that have a facial fossa positioned high on the face; the posterior pocket becoming reduced and eventually lost, and confluent with the adjacent facial surface (includes Group 3 of Woodburne and Bernor, 1980: 1329). We differ with some of the previous authors in the specific referrals of *Hipparion* s. s.; this issue has most recently been discussed in detail by Bernor et al. (1989).

"Hipparion" – following Woodburne and Bernor (1980: 1328), MacFadden and Woodburne (1982: 187), Bernor and Hussain (1985: 34), Bernor (1985: 180), Bernor et al. (1988: 428) and Bernor et al. (1989): Old World hipparion horses with facial morphologies that differ from *Hipparion* s. s. (includes superspecific taxa listed above) and belong to distinct, separate lineages.

DAW – Metapodial III distal articular width
MC III – metacarpal III
MT III – metatarsal III
POB – preorbital bar
POF – preorbital fossa
mm – millimeters (all measurements after AMNH recommendations as presented by Eisenmann et al., 1988 and rounded to tenth's of mm)
Ma – megannum, millions of years ago.
var = measured variable

Systematic Paleontology

Order Perissodactyla Owen, 1848
Suborder Hippomorpha Wood, 1937
Superfamily Equoidea Hay, 1902
Family Equidae Gray, 1821
Subfamily Equinae Steinmann and Döderlein, 1890

"*Plesiohipparion*" aff. *huangheense* Qiu, Weilong and Zhihui, 1988

Age: Early Villanyian, base MN 16b ca. 2.5 Ma, Lindsay et al., 1980; Mein, 1989; Steininger et al., 1989.

Geographic Distribution: Turkey

Description: The Gülyazi hipparion sample includes a left maxillary M^1 (HU 9101) and a left mandibular fragment (HU 9102) with P_3–M_3. The M^1 (Figs 1A and 1B) is in a medial stage-of-wear and complete except the anterolingual corner of the tooth. The tooth has a mesostyle crown height of 39.6 mm (Table 1), and occlusal enamel features are obscured by surface erosion. Nevertheless, the pre- and postfossettes appear to be complex (10B); the posterior wall of the postfossette is distinct; pli caballin although broken, can be seen under low power microscope to have been double (11A), with the anterior pli larger than the posterior one; hypoglyph enamel is broken internally, but appears to have been somewhat more than moderately incised (12B); the protocone's enamel is broken anteriorly, but appears to have been triangular-shaped (13B) and isolated, because the anterior portion is found curving strongly downward for its apparent connection with the protocone labial surface; protocone is clearly more lingually placed than the hypocone.

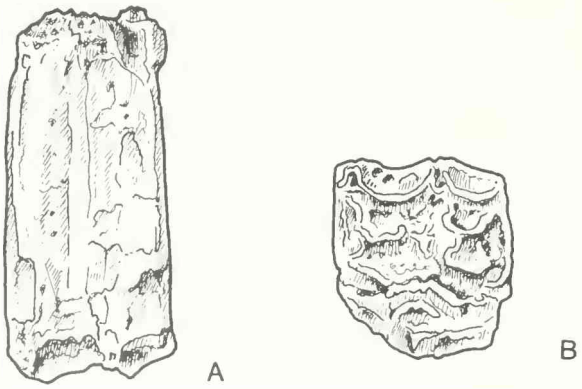

Fig. 1: "*Plesiohipparion*" aff. *huangheense*, left M^1 (HU 9101) in lateral view (A) and in occlusal view (B). Natural size.

The mandibular fragment (Figs 2A and 2B) has metaconid pointed on P_{3-4} (17C) and M_2 (18C), angular on distal surface only of M_1 (18B); metastylid is pointed on P_3–M_2 (19C and 21C), angular on the proximal surface of M_3 only (21B); premolar ectoflexids do not penetrate metaconid/metastylid, whereas in the molars they converge with the preflexid and postflexid to abutt against metaconids and metastylids (22B), contacting the deep border of

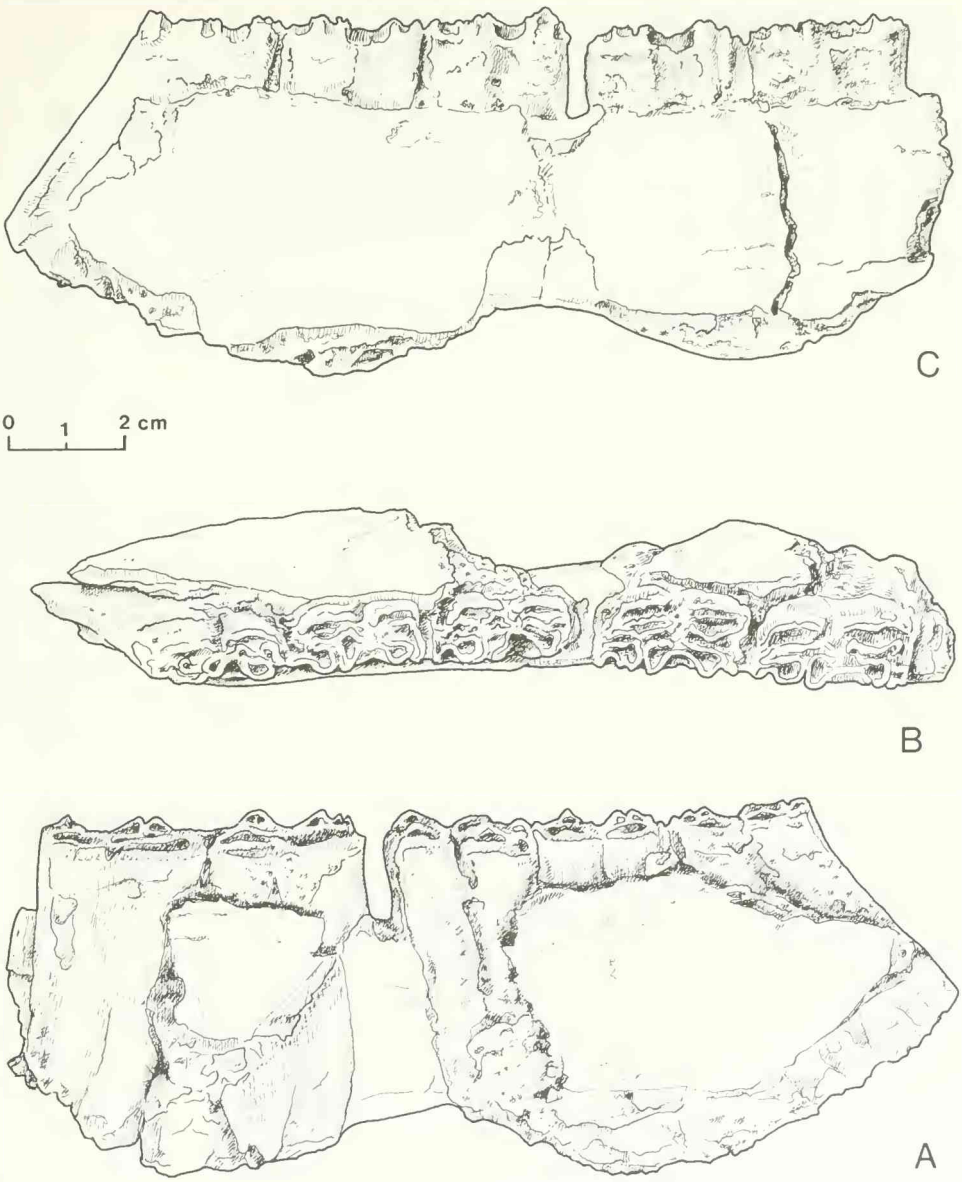

Fig. 2: *"Plesiohipparion"* aff. *huangheense*, left mandibular fragment with P_3–M_3 (HU 9102) in lateral view (A), occlusal view (B) and lingual view (C).

the linguaflexid on M_{1-3}; pli caballinids are single on P_3, M_{1-3} (23 B), strongly double on P_4 (23 A); the protostylids are an open loop (24 A) extending posterolabially on the tooth crown of P_{3-4}; M_2 (25 B), but only labially on M_1 (25 A; this may be wear-related), not present on M_3 (24 B); ectostylids are absent on all cheek teeth (26 A); linguaflexids are deep and have an extremely broad U-shape on P_3–M_2 (27 C and 28 C), not quite so broad and more V-shaped on the M_3 (28 B; probably wear-related here). Preflexids and postflexids have

simple margins (29B and 30B), and postflexids invade metaconid/metastylid by their anteriormost portion bending sharply lingually (31B). Protoconid enamel band is flat on all cheek teeth (32B).

Remarks: The Gülyazi specimens have a morphology consistent with a radicle of late Miocene – Plio-Pleistocene horses referred to the "*Sivalhippus*" Complex by Bernor et al. (1989: 302–307). Table 1 contains an updated list of character state distributions for this group and Table 2 gives some comparative measurements.

The maxillary cheek tooth's complex plication is shared here amongst all members of the "*Sivalhippus*" Complex (re: taxa and their abbreviations as used below have been listed above) except Plaffhou. The distinct posterior wall of the postfossette is typical for all Old World hipparionines. The pli caballin's bifid structure is found in all taxa here except Prsin, where the structure is derived to a highly complex state. The hypoglyph's moderately deep incision is unique for taxa belonging to this complex. Protocone's triangular shape is shared by Sper, Stur, Plhou, Plcru, Plaffhou, and Euafa. Protocone is isolated and lingually placed as in all taxa considered here.

The mandibular cheek teeth have a preponderence of lingually pointed metaconids and metastylids as reported only for "*Plesiohipparion*" *huangheense;* pointed metastylids only are present in "*Plesiohipparion*" aff. *houfenense*. The lack of premolar metastylid spurs is unlike Hpri, but typical for the entire "*Sivalhippus*" Complex. Premolar ectoflexids are as in all other taxa, not separating metaconid/metastylid. Molar ectoflexids are as in Plhua only in their convergence with preflexid and postflexid metaconid/metastylid (see: Qiu et al., 1988: pg. 61, fig. 24, ectoflexids do not separate metaconid/metastylid); this feature could potentially vary ontogenetically, and requires further study. The pli caballinids vary from being single to double/complex as is generally reported for all taxa in Table 1 except Spla which only inconsistently has pli caballinids, and Prpat and Prsin which lack pli caballinids altogether (Bernor et al., 1990b; re: type "*Proboscidipparion*" *sinense,* PMU M3925). The protostylid's occasional occurrence on the crown surface, but distinct intracementum location along the vertical axis of all cheek tooth anterolateral surfaces, is common for Plaffhou, Euafa, Prpat and Prsin; its propensity to extend posteriorly along the lateral occlusal surface of the tooth is found only in Plhua and Plaffhua. The presence of ectostylids in the permanent premolar and molar mandibular teeth is found only in the *Eurygnathohippus* clade (senior synonym of "*Stylohipparion*" from Plio-Pleistocene levels of Africa; see discussions by Hooijer, 1975; Eisenmann, 1976, 1979, 1983; Churcher and Richardson, 1978; Bernor et al., 1989). The premolar and molar ectoflexids are very deep and have a broad U-shape, nominally greater than all members of the "*Sivalhippus*" Complex.

The pointed metaconids and metastylids would appear to be the most distinctive feature of the Gülyazi hipparion, clearly relating it to the Chinese species "*Plesiohipparion*" *huangheense* (Qiu et al., 1988: THP 10097, pg. 60 fig. 24). Metaconid-metastylid pointing may be functionally related to the greatly increased width of the linguaflexid, which results in "pinching" the metaconid and metastylid on their lingual borders). These features would seem to be progressive within the "*Plesiohipparion*" clade (sensu lato), and shared specifically with "*Plesiohipparion*" *huangheense*. Measurements provided in Table 2 reveal that Plhua and Plaffhua are similar in their size, and give further support to our referral.

Qiu et al. (1988: 207) have suggested that these interrelated features of metaconid/metastylid and linguaflexid morphology indicate that "*Plesiohipparion*" *huangheense* is a lineage distinct from "*Pl.*" *houfenense* – "*Pl.*" aff. *houfenense,* the latter best represented by F:AM 111820 (MacFadden, 1984: 188, Fig. 158; Bernor et al., 1989: 305, Fig. 7). We note here however that F:AM 111820 has distinct pointing of premolar and molar metastylids (but not metacon-

ids), supporting a closer phylogenetic relationship to the Plhua-Plaffhua clade than Plhou (Fig. 3). Moreover, Bernor (personal observation) has seen a similar pointed metaconid-metastylid morphology in portions of the Hadar, Ethiopia assemblage of "*Eurygnathohippus*" sp. (but not the material referred to here). The apparent relationships of this assemblage to the Plhua-Plaffhua assemblage require further study.

We presently retain the nomina "*Sivalhippus*", "*Plesiohipparion*", "*Proboscidipparion*" and "*Eurygnathohippus*" as taxonomic labels, and wish rather to emphasize the phylogenetic diversity, biogeographic and chronologic ranges of this nested series of species belonging to the "*Sivalhippus*" Complex. While we appreciate Qiu et al.'s (1988) caution in recognizing *Proboscidipparion* and *Plesiohipparion* as subgenera, neither can in our opinion be included within the genus *Hipparion* s. s.

Phylogenetic Relationships

Bernor et al. (1989) reported that a specific group of hipparionines, their "*Sivalhippus*" Complex, diverged in the late Miocene of Asia, diversified and subsequently extended their range into Europe, west Asia and Africa. The Gülyazi specimens would appear to belong to this radicle of hipparionine horses. Bernor et al. (1989) hypothesized that the "*Sivalhippus*" Complex (sensu lato) includes mostly large to very large hipparionines showing a trend to lose the preorbital fossa and increase cheek tooth crown height. The "*Sivalhippus*" Complex has thus far been recognized to include four superspecific taxa: "*Sivalhippus*", a stem-group including "*S.*" *platyodus* (also note the questionable inclusion of the Chinese late Miocene form "*S.*" *ptychodus* by Bernor et al., 1990b: 31, Figs 11 and 12), "*S.*" *perimense*, and "*S.*" *turkanense*; "*Plesiohipparion*", including "*Pl.*" *houfenense*, "*Pl.*" aff. *houfenense*, "*Pl.*" *crusafonti* and *Pl. huangheense*; "*Eurygnathohippus*", including "*Eu.*" *afarense*, and potentially "*Eu.*" *hasumense*, "*Eu.*" *cornelianum* (potentially the senior synonym of "*Eu*". *ethiopicum*) and "*Eu*". sp. B of Eisenmann (1983; although Eisenmann recognizes all of these as species of the genus *Hipparion*); and "*Proboscidipparion*", including "*Pr.*" *pater* and "*Pr.*" *sinense*.

Taxa believed to belong to the "*Sivalhippus*" clade occur in South Asia and Africa during the late Miocene only (ca. 9.5–5 Ma). "*Sivalhippus*" was asserted to be derived from some "Group 1" taxon such as "*Hipparion*" *primigenium* s. s. (sensu Bernor et al., 1988 and Bernor et al., 1989). This group was distinguished by the increase in preorbital bar length which presages loss of the preorbital fossa altogether; nasal notch which remains conservative in its retraction only at the anterior limit of P2; maxillary cheek teeth which lose their labiolingual curvature altogether, becoming very straight walled, and significantly higher crowned; protocones which transform from a lingually flattened-labially rounded morphology to a labiolingually compressed triangular shape; metaconids and metastylids which evolve angular facing borders and lose their premolar metastylid spurs; and linguaflexids which become a broader U-shape.

"*Plesiohipparion*" has included species reported from Eurasia circa 6–2 (or less) Ma (Qiu et al., 1988), and was believed to be further divergent from "*Sivalhippus*" by completing the loss of the preorbital fossa, either leaving only a faint medial depression or becoming entirely absent. While maxillary cheek tooth morphology would appear to remain complex in most taxa belonging to this group, it was believed to simplify in "*Plesiohipparion*" aff. *houfenense*, a large Nihewan age (ca. 2 Ma) species. The "*Plesiohipparion*" group evolved grooved incisors, the very late occurring taxon "*Pl.*" aff. *houfenense* evolved pointed metastylids; "*Pl.*" *huangheense* evolved both pointed metaconids and metastylids. Protostylids become reduced to

lost in this group, and *"Pl." huangheense* has the autapomorphy of a posteriorly projecting protoconid loop. The Gülyazi specimen has postflexids anteroposteriorly oriented, and do not curve labially at their anteriormost extent to invade metaconid/metastylid.

"Eurygnathohippus" was recognized as a group known only from Africa between 3.5–1 Ma (Eisenmann, 1976, 1979), although reference to Hooijer (1975) would seem to indicate that the persistent occurrence of ectostylids in adult mandibular dentitions (synapomorphy for this group) may have first appeared between 5 and 4 Ma. *"Eurygnathohippus"* shares characters of preorbital fossa reduction, increased crown height and noncurvature, and incisor grooving with *"Plesiohipparion"*. Its metaconid-metastylid morphology, as represented in Euafa specimen A. L. 177–21 (Eisenmann, 1976: 582, Pl. 5, Fig. A and Pl. 7, Fig. D), has character states including angular opposing borders without pointing, broad linguaflexids (although not as broad as seen in Plhua and Plaffhua). *"Eurygnathohippus"* is further distinct from other members of the *"Sivalhippus"* Complex in its evolution of hypertrophied I1–2 and atrophied I3 (particularly marked in later more advanced species such as *"E". cornelianum* and the potentially synonymous taxon *"E". ethiopicum;* Hooijer, 1975, Pl. 12, Figs 1–3; Eisenmann, 1983).

"Proboscidipparion" was recognized as being a distinctly southeast Asian clade reported to occur circa 5–2 Ma, and including two species: *"P." pater* and *"P." sinense* (Qiu et al., 1988; Bernor et al., 1989; Bernor et al., 1990b).

"Proboscidipparion" shares a number of characters with more advanced members of the *"Sivalhippus"* Complex including: loss of the preorbital fossa, strong increase in crown height, presence of grooved incisors, angular metaconids/metastylids, and broad linguaflexids. *"Proboscidipparion"* is divergent from all other members of the *"Sivalhippus"* Complex in the very strong retraction of the nasals: to M1 in *"Pr." pater* (Qiu et al., 1988), and to the anterior border of the orbits in *"Pr." sinense* (Bernor et al., 1990b). *"Pr." pater* exhibits a relatively primitive morphology in its lingually flattened-labially rounded protocones (as in *"H". primigenium* and *"Sivalhippus" platyodus* but may be wear-related), whereas *"Pr." sinense* evolved elongate-triangular protocones. *"Pr." sinense* also exhibits very complex enamel ornamentation of maxillary pre- and postfossettes, and mandibular pre- and postflexids. Metaconids and metastylids remain as in other members of the *"Sivalhippus"* Complex except for *"Pl." huangheense, "Pl."* aff. *huangheense* and *"Pl."* aff. *houfenense*. Likewise, no ectostylids occur on permanent cheek teeth, and linguaflexids remain broad U-shaped.

A cladistic analysis was made including 11 members of the *"Sivalhippus"* Complex. Table 1 presents the 32 characters used in our analysis. These are the relevant subset of a larger 50 character set including 40 cited in Bernor et al. (1989), and 10 added as the result of this study. Character polarity was determined by the occurrence of states in an outgroup, *"Hipparion" primigenium*. Order of multistate characters was made by morphocline analysis (Maslin, 1952), and these characters were also analysed nonadditively (= unordered). All cladistic analyses were done with the implicit enumeration command of Hennig 86. All analyses gave the same single cladogram (Fig. 3). This tree has a consistency index of 83 and a retention index of 83 with homoplasy occurring in just 5 of the 32 characters. The character states are optimized onto the branches in figure 3 under the ordered hypothesis of character state change (given in legend of Table 1).

The cladistic relationships of the *"Sivalhippus"* Complex given in figure 3 should be considered to be provisional and represent our current hypothesis of phylogenetic relationship. The cladogram supports a more complex evolutionary history for the group than previously recognized (Bernor et al., 1989; and statements above). *"Sivalhippus"* Complex monophyly is supported by derived states of eight characters: 3B, 4B, 8B, 17B, 18B, 19B,

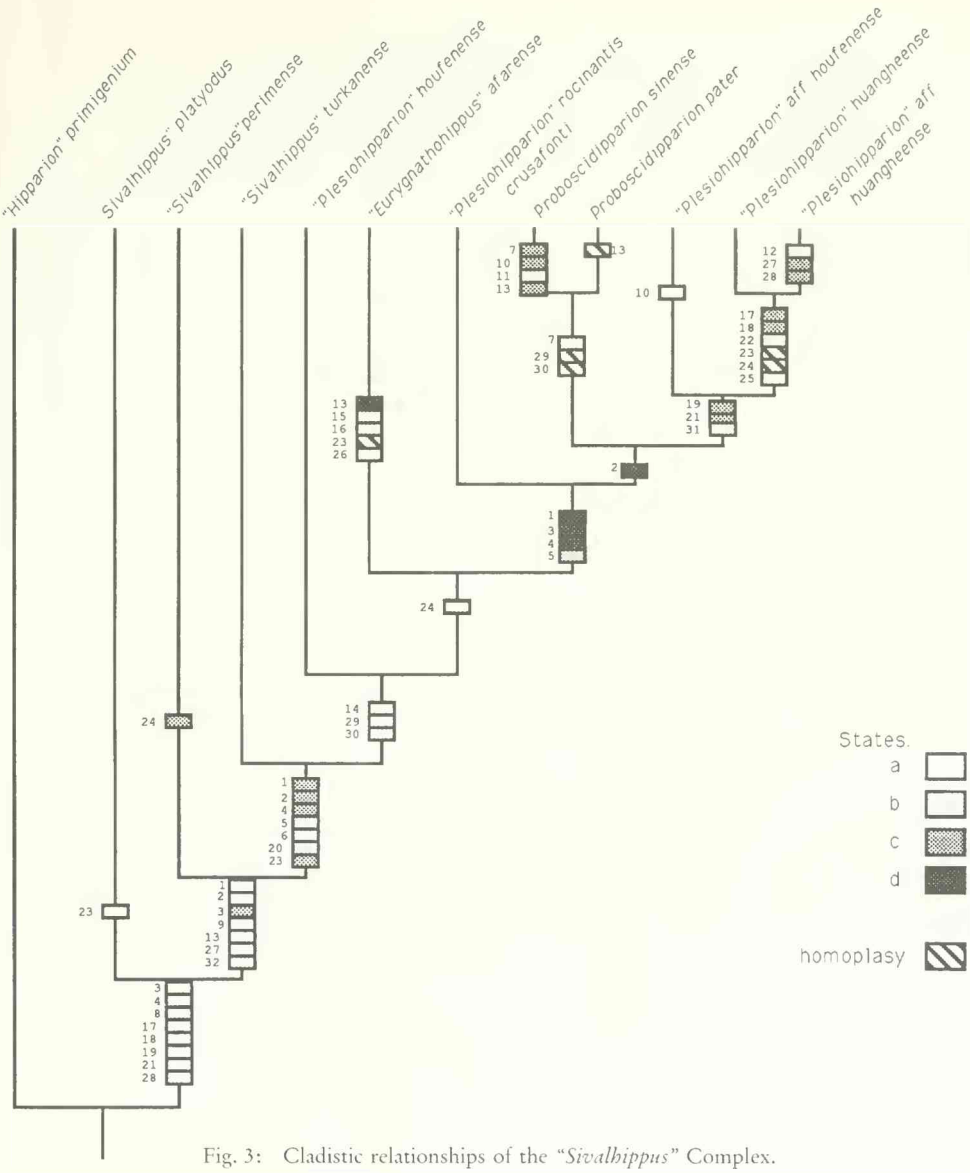

Fig. 3: Cladistic relationships of the "*Sivalhippus*" Complex.

21B, and 28B. Species included in the taxon "*Sivalhippus*" represent three distinct branches on the tree: Spla (shares 8 synapomorphies with all other members of the "*Sivalhippus*" Complex [listed above], as well as having one autapomorphy [23B]); Sper (shares 7 synapomorphies with remaining members of the group [1B, 2B, 3C, 9B, 13B, 27B, 32B], and 1 autapomorphy [24C]); Stur (shares 7 synapomorphies with remaining members of the group [1C, 2C, 4C, 5B, 6B, 20B, 23C]). Cladistic relationships of species belonging to the genus "*Sivalhippus*" (sensu lato, here clearly a paraphyletic group) support Bernor et al.'s (1989) assertion that earliest reported members of the "*Sivalhippus*" Complex occur in Asia (first occurrences: Spla, 9.5 Ma, Qiu et al., 1988; Sper, 8 Ma, Bernor and Hussain, 1985), with an

Table 1: Character State Distribution of Gülyazi and Related Old World Hipparionines belonging to the "*Sivalhippus*" Complex sensu lato.

TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1) Hpri Eu, 11–8 Ma	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
2) Spla EAs, 9.5–9 Ma	A	A	B	B	A	A	A	B	A	A	A	A	A	A	A	A	B	B	B	A	B	A	B	A	A	A	A	B	A	A	A	A
3) Sper SAs, 8 Ma	B	B	C	B	A	A	A	B	B	A	A	A	B	A	A	A	B	B	B	?	B	A	A	C	?	A	B	B	A	A	A	B
4) Stur EAf, 5 Ma	C	C	C	C	B	B	A	B	B	A	A	A	B	?	?	?	B	?	B	B	?	?	C	?	?	A	B	?	A	A	A	B
5) Plhou EAS, 6–2.5 Ma	C	C	C	C	B	B	A	B	B	A	A	A	B	B	A	A	B	B	B	B	B	A	C	A	A	A	B	B	B	B	A	B
6) Plaffhou EAs, 2 Ma	D	D	D	D	C	B	A	B	B	B	A	A	B	B	A	A	B	B	C	B	C	A	C	B	A	A	B	B	B	B	B	B
7) Plcru Eu, 3 Ma	D	C	D	D	C	B	A	B	B	A	A	A	B	B	A	A	B	B	B	?	B	A	?	?	?	A	B	B	?	?	?	B
8) Plhua EAs, ca. 2.5 Ma	?	?	?	?	?	?	?	?	?	?	?	?	?	B	A	A	C	C	C	B	C	B	B	A	B	A	B	B	B	B	B	B
9) Plaffhua SWA, ca. 2.5 Ma	?	?	?	?	?	?	?	?	?	A	A	B	B	?	?	?	C	C	C	B	C	B	B	A	B	A	C	C	B	B	B	B
10) Euafa EAf, 3.5 Ma	C	C	C	C	B	B	A	B	B	A	A	A	D	B	B	B	B	B	B	B	B	A	A	B	A	B	B	B	B	B	A	B
11) Prpat EAs, 5–2 Ma EA, 5–2 Ma	D	D	D	D	C	B	B	B	B	A	A	A	A	B	A	A	B	B	B	B	B	A	C	B	A	A	B	B	A	A	A	B
12) Prsin EAs, 3–2 Ma	D	D	D	D	C	B	C	B	B	C	B	A	C	B	A	A	B	B	B	B	B	A	C	B	A	A	B	B	A	A	A	B

LEGEND

Eu = Europe; SWA = Southwest Asia (includes Turkish localities); SAs = South Asia; EAs = East Asia; EAf = East Africa.

1) Relationship of lacrimal to the preorbital fossa: a (c) = preorbital bar (POB) long with the anterior edge of the lacrimal placed more than ½ the distance from the anterior orbital rim to the posterior rim of the fossa; b (g) = POB very long with anterior edge of lacrimal placed less than ½ the distance from the anterior orbital rim to the posterior rim of the fossa; c (e) = POB vestigial; d (h) = POB absent (# 1; order: a-b-c-d).
2) Preorbital fossa morphology: a (b) = subtriangular and anteroventrally oriented; b (d) = egg-shaped and anteroposteriorly oriented; c (f and g, in part) = vestigial; d (g in part) = absent (# 3; order: a-b-c-d).
3) Fossa posterior pocketing: a (a) = deeply pocketed, greater than 15 mm. in deepest place; b (b/c) = pocketing extremely reduced but can be detected; c (c and d) = not pocketed, may or may not have remnant depression; d (e) = absent (neither a rim nor a depression) (# 4; order: a-b-c-d).
4) Fossa medial depth: a (a) = deep, greater than 15 mm. in deepest place; b (b) = moderate depth, 10–15 mm. in deepest place; c (c) = shallow depth, less than 10 mm. in deepest place; d (d) = absent (# 5, order: a-b-c-d).
5) Fossa peripheral border outline: a (a) = strongly delineated around entire periphery; b (d) = absent with a remnant depression; c (e) = absent, no remnant depression (# 7; order: a-b-c).
6) Anterior rim morphology: a (a) = present; b (b) = absent. (# 8; order: a-b).
7) Nasal notch position: a (c) = at or near the anterior border of P2; b (g) = above M1; c (h) = posterior to M1 (# 14; order: a-b-c).
8) Curvature of maxillary cheek teeth: a (b) = moderately curved; b (c) = straight (# 16; order: a-b).
9) Maximum cheek tooth crown height: a (c) = 40–60 mm; b (d) = > 60 mm. maximum crown height (# 17; order: a-b).
10) Maxillary cheek tooth fossette ornamentation: a (a) complex with several deeply amplified plications; b (b) = moderately complex with fewer, more shortly amplified, thinly banded plications; c (a+) very complex, with very many plications (# 18; order: a-b, c)

11) Pli caballin morphology: a (a) = double; b (c) = complex (#20; order: a-b).
12) Hypoglyph: a (b) = deeply incised, may occasionally close and isolate hypocone; b (c) = moderately deeply incised (#21; order: a-b).
13) Protocone shape: a (b) = lingually flattened – labially rounded; b (e) = triangular; c (f) = triangular-elongate; d (h) = triangular with rounded corners (#22; order: a-b-c, d).
14) Mandibular incisor morphology: a = not grooved; b = grooved (#27; order: a-b).
15) Mandibular incisor curvature: a = curved; b = straightened (#28; order: a-b).
16) I3 lateral aspect: a (a) = elongate, not transversely constricted; b (b) = very elongate, transversely constricted (#29; order: a-b).
17) Premolar metaconid: a (a) = rounded; b (c) = angular on distal surface; c (f) = pointed (#30; order: a-b-c).
18) Molar metaconid: a (a) = rounded; b (c) = angular on distal surface; c (f) = pointed (#31; order: a-b-c).
19) Premolar metastylid: a (a) = present; b (c) = angular on distal surface; c (f) = pointed (#32; order: a-b-c).
20) Premolar metastylid spur: a = present; b (c) = absent (#32; order: a-b).
21) Molar metastylid: a (a) = rounded; b (c) = angular on proximal surface; c (f) = pointed (#33; order: a-b-c).
22) Molar ectoflexid: a (b) = separates metaconid and metastylid; b (c) = converges with preflexid and postflexid to abutt against metaconid and metastylid (#35; order: a-b).
23) Pli caballinid: a (a) = complex; b (b) = rudimentary or single; c (c) = absent (#36; order: a-b-c).
24) Protostylid: a (a) = present on occlusal surface; b (b) = usually absent on occlusal surface, but may be on side of crown buried in cement; c (c) = strong, columnar (#37; order: a-b, c).
25) Protostylid orientation: a (c) = vertically placed, lies flush or slightly lateral to protoconid enamel band; b (e) = open loop extending posterolabially (#37; order: a-b).
26) Ectostylids: a (b) = absent; b (a) = present (#38; order: a-b).
27) Premolar linguaflexid: a (a) = shallow; b (d) = deep, broad U-shape; c (e) = very broad and deep U-shape (#39; order: a-b-c).
28) Molar linguaflexid: a (b) = V-shaped; b (d) = deep, broad U-shape; c (e) = very broad and deep (#40; order: a-b-c).
29) Preflexid morphology: a (b) = complex margins; b (a) = simple margins (#41; order: a-b).
30) Postflexid morphology: a (b) = complex margins; b (a) = simple margins (#42; order: a-b).
31) Postflexid invades metaconid/metastylid by anteriormost portion bending sharply lingually: a (a) = no; b (b) = yes (#43; order: a-b).
32) Protoconid enamel band morphology: a = rounded; b = flat (#44; order: a-b).

Note: After each character state we give in parentheses the state registered in BERNOR et al., (1989), and at the end of each character description in parentheses we give the number that this character cross-indexes to in BERNOR et al. (1989; characters 1–40), as well as additional characters (such as 33', 41–44 etc.) recognized since the publication of that study. Also included in parentheses are the character orders recognized for generation of the cladogram (Fig. 3).

extension of a taxon related to the Sper-Stur clade into East Africa sometime between 8 and 5.5 Ma.

"Plesiohipparion" houfenense is the sister-taxon of all remaining members of the *"Sivalhippus"* Complex, including all species of *"Plesiohipparion"*, *"Eurygnathohippus"* and *"Proboscidipparion"*. Of these last three taxa, *"Plesiohipparion" houfenense* is known to occur only in China and Mongolia (Flynn and Bernor, 1987), and has the oldest known first occurrence (ca. 6 Ma, Qiu et al., 1988). *"Plesiohipparion" houfenense* shares characters 14B, 29B and 30B with all other members of the complex. Euafa, Plcru, Prsin, Prpat, Plaffhou, Plhua and Plaffhua are united here as a group by a single character (24B; diminished occurrence of protostylid). *"Eurygnathohippus" afarense* exhibits a number of autapomorphies (characters 13D, 15B, 16B, 23A and 26B), of which character 26, presence of ectostylids in adult cheek tooth dentitions, is known to be shared exclusively with other species of *"Eurygnathohippus"* and 23A is recognized as a reversal. Plcru, Prsin, Prpat, Plaffhou, Plhua and Plaffhua are united by characters 1D, 3D, 4D and 5B; Prsin, Prpat, Plaffhou, Plhua and Plaffhua are united by character 2D; Prsin and Prpat are united by characters 7B, 29A and 30A (last two being reversals); Plaffhou, Plhua and Plaffhua by characters 19C, 21C and 31B; Plhua and Plaffhua by characters 17C, 18C, 22B, 23B, 24A, and 25B (23B and 24A being reversals).

The cladistic relationships of Plhou, Euafa, Plcru, Prsin, Prpat, Plaffhou, Plhua and Plaffhua is remarkably congruent with the known age of their known first stratigraphic occurrence. *"Plesiohipparion" houfenense* is reported by Qiu et al. (1988) as first occurring in China ca. 6 Ma. As discussed above, the earliest African hipparions exhibiting ectostylids on adult cheek teeth occur approximately 5 to 4 Ma (re: Hooijer, 1975). Alberdi (1972, 1974) reports the first occurrence of the *"Plesiohipparion" rocinantis rocinantis* – *"Plesiohipparion" rocinantis crusafonti* lineage in the early Pliocene (ca. 5 Ma). This would suggest that there was a secondary geographic extension of the *"Sivalhippus"* Complex which included Asia, Africa and Europe during the terminal Miocene (ca. 5 Ma). This interval, a period of global sea-lowering, has already been heralded as being a time of extinction for some hipparionine lineages, and biogeographic extension of others (Bernor et al., 1989). Differentiation of the *"Eurygnathohippus"*, *"Proboscidipparion"* (including Prpat and Prsin) and *"Plesiohipparion"* aff. *houfenense* – *"Pl." huangheense* (including Plaffhua) clades would have had to have occurred no later than ca. 5 Ma (= first known occurrence of Prpat, the oldest known member of this radicle of the *"Sivalhippus"* Complex; Qiu et al., 1988: Text Fig. 69, pg. 171). The clade including Prpat Prsin, Plaffhou, Plhua is known only from China; the Gülyazi specimen Plaffhua would appear to represent the only known member of this clade to have extended its range outside of east Asia, and represents a third independent biogeographic extension of the *"Sivalhippus"* Complex.

Table 2: Comparitive Measurements of Gülyazi and other Related Hipparionine Mandibular Cheek Tooth Measurements.

Specimen		L	LB	MM	PRE	PST	W1	WB	W2	W3	HT
Hpri (Ho A)	P2	28.3		11.7	7.1		13.7	16.9	10.9	13.3	
	P3	25.9		14.8	7.9		12.2	16.9	13.4	14.2	
	P4	25.9		13.8	6.9		12.2	17.4	13.0	13.2	
	M1	24.0		14.4	6.4		9.4	15.0	11.6	10.4	
	M2	24.8		12.9	6.4		9.8	14.3	10.6	9.4	
	M3	27.5		11.3	6.1		9.2	12.2	9.7	8.5	
Spla (V8201)	P2	26.3		9.8			10.4				
	P3	22.0		13.7			12.3				

Specimen		L	LB	MM	PRE	PST	W1	WB	W2	W3	HT
	P4	22.0		13.0			12.4				
	M1	18.7		11.2			11.2				
	M2	20.2		11.7			10.5				
	M3	24.0		11.2			10.0				
	P2–M3	141.7									
Type: PMU 3961	P2–M3	146.0									
	P2–P4	77.5									
	M1–M3	69.0									
Sper	P2										
	P3										
	P4										
	M1										
	M2										
	M3										
Stur	P2										
	P3										
	P4										
	M1										
	M2										
	M3										
Plhou	P2	29.0		13.5			13.1				
(THP 1073)	P3	23.6		14.7			14.2				
	P4	22.6		14.3			13.0				
	M1	21.4		13.2			12.0				
	M2	22.0		13.2			11.9				
	M3	25.3		11.9			10.7				
	P2–M3	145.7									
Plaffhou	P2	33.7		14.5	7.2	14.3	15.5		12.2	13.6	
AMNH 111820	P3	28.7		15.6	10.4	14.2	14.0		13.9	14.5	
	P4	25.0		16.7	9.1	13.8	17.5		14.3	13.6	
	M1	25.1		13.0	7.0	9.8	16.1		13.5	12.3	
	M2	25.6		13.1	7.1	10.4	16.2		12.2	12.0	
	M3	28.5		12.2	7.5	13.0	12.9		11.2	10.4	
	P2–M3	164.5									
	P2–P4	88.5									
	M1–M3	79.2									
Plcru	P2										
	P3										
	P4										
	M1										
	M2										
	M3										
Plhua	P2	28.8		14.2			13.0				
TZP 10097	P3	24.0		16.0			13.5				
	P4	25.0		14.6			13.4				
	M1	22.7		13.8			12.3				
	M2	22.3		13.7			11.7				
	M3	23.7		11.4			10.0				

Specimen		L	LB	MM	PRE	PST	W1	WB	W2	W3	HT
Plaffhua	P2										
(HU 9102)	P3	25.8	20.8	13.9	11.0	14.3	13.2		11.5	12.2	46.4
	P4	26.8	22.7	13.6	9.4	13.5	12.9		11.8	11.6	50.4
	M1	24.6		13.3	7.8	9.3	9.5		9.4	9.7	45.7
	M2	22.9		12.6	7.2	9.4	9.3		9.5	10.0	
	M3	22.8	25.0	11.4	8.2	8.3	8.5		9.5	6.3	53.1
	M1–M3	73.1									
Euafa Al 177–21	P2	32.9		12.2	9.5	16.4	12.8		11.2	12.0	
	P3	29.4		16.4	11.9	15.3	14.4		13.5	14.1	
	P4	26.1		14.5	9.4	13.0	14.5		12.2	11.7	
	M1	25.1		15.4	9.0	11.3	11.7		10.7	10.0	
	M2	27.8		14.8	8.2	12.6	11.9		10.1	10.1	
	M3										
Prpat	P2	30.0		12.5			12.2				
THP 14312	P3	27.0					14.0				
	P4	25.2					11.4				
	M1										
	M2	25.4		12.6			9.9				
	M3	19.3		10.0			8.6				
	P2–M3	153.0									
Prsin PMU 3925	P2										
	P3										
	P4										
	M1										
	M2										
	M3										
	P2–M3	171.6									
	P2–P4	88.1									
	M1–M3	81.7									

Legend:

Hpri – *"Hipparion" primigenium*, HoA skeleton, Höwenegg, Germany (Vallesian age, ca. 11 Ma)
Spla – *"Sivalhippus" platyodus*, IVPP V8201, Qiu et al., 1988, pg. 43 and Pl. XX, fig. 1; also, measurements provided for PMU M3961, Bernor et al., 1990.
Sper – original measurements
Stur – *"Sivalhippus" turkanense*, KNM LT-136, Hooijer and Maglio, 1974, pg. 8; individual mandibular cheek teeth Pl. 7, figs 1–6.
Plhou – *"Plesiohipparion" houfenense*, THP 10733, Qiu et al., 1988 pg. 42 and Pl. VIII, figs 2, 3,.
Plaffhou – *"Plesiohipparion"* aff. houfenense, AMNH 111820, Bernor et al., 1989, pg. 305 and fig. 7.
Plcru – *"Plesiohipparion" rocinantis crusafonti*, Alberdi, 1974 and Bernor et al., 1989.
Plhua – *"Plesiohipparrion"* huangheense, Qiu et al., 1988, THP 10097, pg. 61, fig. 24.
Plaffhua – *"Plesiohipparion"* aff. huangheense, HU 9102, specimen reported here.
Euafa – *"Eurygnohippus" afarense*, AL 177–21, Eisenmann, 1976, pg. 582 and Pl. VII, fig. D, and Bernor et al., 1989, pg. 306, and fig. 7.
Prpat – *Proboscidipparion pater*, THP 14312, Qiu et al., 1988, pg. 42 and Pl. II, figs 2 and 3; and Bernor et al., 1989, pg. 306 and fig. 7.
Prsin – *Proboscidipparion sinense*, PMU M 3925, Sefve, 1927: 55, Pl. VI, figs 22–24, Pl. VII, figs 25 and 26; and Bernor et al., 1990, pg. 48 and figs 17 and 18.

Conclusions

The Gülyazi hipparionine, *"Plesiohipparion"* aff. *huangheense,* has been found to belong to the species diverse *"Sivalhippus"* Complex (sensu Bernor et al., 1989). Morphological characterization, cladistic analysis, and previously reported chronologic and biogeographic ranges of species belonging to this group have led us to hypothesize that the Gülyazi hipparion represents a medial Pliocene extension of the east Asian species, *"Plesiohipparion" huangheense,* into Anatolia. An explicit cladistic analysis of the *"Sivalhippus"* Complex, rooted with the Central European early late Miocene species *"Hipparion" primigenium,* suggests a greater diversity of superspecific taxa than previously proposed by Bernor et al. (1987, 1989, 1990b) and Qiu et al. (1988). *"Sivalhippus"* Complex species relationships are presented here as being provisional and in need of further detailed morphologic and phylogenetic study.

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