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Two Small Species of *Cremohipparion* (Equidae, Mamm.) from Samos, Greece

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With 3 figures

Kurzfassung

Zwei kleinwüchsige Arten von *Cremohipparion* aus Samos, Griechenland (spätes Miozän, Turolium), werden beschrieben. Diese Arten sind *Cremohipparion matthewi* und *Cremohipparion nikosi* n. sp. Bei *Cremohipparion matthewi* reicht die Incisura nasalis bis zum Vorderende des P^2 zurück, bei *Cremohipparion nikosi* reicht sie weiter – bis zum Mesostyl der P^4 – zurück. Neben diesem Unterschied zeigt sich erstens: Zwei, wahrscheinlich mehr Taxa wurden bisher irrtümlich unter dem herkömmlichen Speziesnamen *„Hipparion" matthewi* beschrieben; zweitens: die beiden hier behandelten Arten sind Schwester-Taxa einer neuen, altweltlichen hipparionen Gattung *Cremohipparion* Qiu et al. und drittens: die Evolution hipparioner Zwergformen ist polyphyletisch.

Abstract

Evidence is cited here for two small species of *Cremohipparion* from Samos, Greece (Late Miocene, Turolian age). These species, *Cremohipparion matthewi* and *Cremohipparion nikosi* n. sp. are distinguished from one another by the former's rather shallow nasal notch incisure (to anteriormost P^2 only) and the other's sharply contrasting deeper nasal notch incisure (to mesostyle of P^4). These two species share the presence of a short preorbital bar with lacrimal closely approaching or touching the posterior rim of the preorbital fossa. These characters unite the two species with others belonging to the Old World hipparion genus *Cremohipparion*. Morphological comparisons with other eastern Mediterranean and southwest Asian late Miocene small hipparions verifies that small individuals have commonly been indiscriminately and unjustifiably grouped into the taxon "*Hipparion matthewi*". Our studies further show that dwarfing in hipparions was common, and by no means limited to a single lineage.

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Introduction

We characterize and diagnose here two small species of the genus *Cremohipparion* (formerly "*Hipparion*" Group 2 sensu Woodburne and Bernor, 1980, Bernor et al., 1980 and Bernor 1985; and *Hipparion (Cremohipparion)* sensu Qiu et al. 1987) from the Turolian of Samos, Greece: *Cremohipparion matthewi* and *Cremohipparion nikosi* n. sp. Small, Turolian aged hipparionines have long been known from the Perimediterranean region, one of the most common taxa recognized being "*Hipparion*" *matthewi*. Our current study demonstrates first that at least two, and potentially more small taxa have been erroneously included in traditional hypodigms of "*Hipparion*" *matthewi*, second that the two species here are sister taxa belonging to a newly recognized genus of Old World hipparionine, *Cremohipparion* (Qiu et al., 1987: 224; Bernor et al., in press), and third, the evolution of hipparionine dwarfing in the Old World was polyphyletic.

Abbreviations:

AMNH	– American Museum of Natural History, New York, USA.
BMNH	– British Museum of Natural History, London, England.
BSP	– Bayerische Staatssammlung für Paläontologie und historische Geologie, München, West Germany.
F:AM	– Frick: American Mammals (AMNH).
GIU	– Geological Institute, Utrecht. The Netherlands.
HLMD	– Hessisches Landesmuseum, Darmstadt, West Germany.
NHMW	– Naturhistorisches Museum, Wien, Austria.
PMMS	– Paleontological Museum of Mytilini, Samos.
UCR	– MMTT – University of California, Riverside Department of Earth Sciences Vertebrate Paleontological Collections.
UGR	– Ungarische Geologische Reichsanstalt, Budapest, Hungary.
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 rounded to tenth's of mm)
Ma	– megannum, millions of years ago.
var.	– measured variable

Definitions: Hipparionine or hipparion – any horse with an isolated protocone of the maxillary premolar and molar teeth, and, as far as known, tridactyl feet, including species of the following genera: *Hipparion, Neohipparion, Nannippus, Cormohipparion, Hippotherium, Proboscidipparion, "Sivalhippus", Pseudhipparion, 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. (1987), Bernor et al. (in press) and Woodburne (in press).

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. (in press) and Woodburne (in press) in restricting this nomen to a specific lineage of horses that have a facial fossa positioned high on the face. The posterior pocket becomes 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. (in press).

"*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. (in press): Old World hipparion horses with facial morphologies that differ from *Hipparion* s. s. (includes superspecific taxa listed above) and belong to distinct, separate lineages.

Systematic Paleontology

Order Perissodactyla Owen, 1848
Suborder Hippomorpha Wood, 1937
Superfamily Equoidea Hay, 1902
Family Equidae Gray, 1821
Subfamily Equinae Steinmann and Döderlein, 1890
Genus *Cremohipparion* Qiu, Weilong and Zhihui, 1987
(= Subgenus *Cremohipparion* Qui, Weilong and Zhihui, 1987)

Cremohipparion matthewi (Abel, 1926)
Fig. 1

Hipparion minus, Kormos, 1911
Hipparion matthewi, Abel, 1926, Fig. 273, pg. 430; pg. 432
Hipparion matthewi, Abel, 1927, Fig. 110, pg. 120
Hipparion matthewi, Sondaar, 1971, Pl. IV, Fig. a
"*Hipparion*" aff. ?*matthewi*, Bernor 1985, Fig. 18, pg. 220

Holotype: Male skull with associated lower jaw, UGR OK/557 originally figured by Kormos (1911, Fig. I and II), later by Abel (1926: 430, Fig. 273, 1927: 120, Fig. 110) and Sondaar (1971, Pl. IV, fig. a). However, none of these published figures clearly detail the facial and cheek tooth morphology of the type specimen.

Type Locality: Island of Samos Greece (no specific locality or horizon given).

Age: Turolian, ca. 8.5–5.7 Ma (Weidmann et al. 1984: 487), Sen (1986: 159) and Sen and Valet (1986: 173).

Geographic Distribution: Subparatethyan Province (sensu Bernor, 1983, 1984; Greece, Iran, Western U.S.S.R.).

Subgeneric characterization (as given by Qiu et al., 1987: 238 for their nomen *Hipparion [Cremohipparion]*): "*This subgenus is very distinctive in the snout and nasal structure. The lateral rims of the nasals turn down first, and then incurve into the nasal cavity. The preorbital fossa is very deep, close to the orbit. The subnasal fossa is also present. The nasal notch is retracted though less than in the subgenus Proboscidipparion.* The Samos *H. proboscideum* seems very close to this subgenus in its facial structure. Unfortunately, no adequate description is available to show whether the nasal bones have incurved lateral rims or not. Under *H. garezicum*, Meladze (1967) described some well preserved skulls from Arkneti, Caucasia. The Arkneti skulls are markedly different from the type of the species described by Gabunia in 1959. In our opinion the Arkneti sample may represent a member of the subgenus *Cremohipparion* in Caucasia."

Generic Diagnosis (modified from Bernor et al., in press; characters in bold, underlined print are uniquely shared-derived characters of the group) – Hipparionine horses ranging from

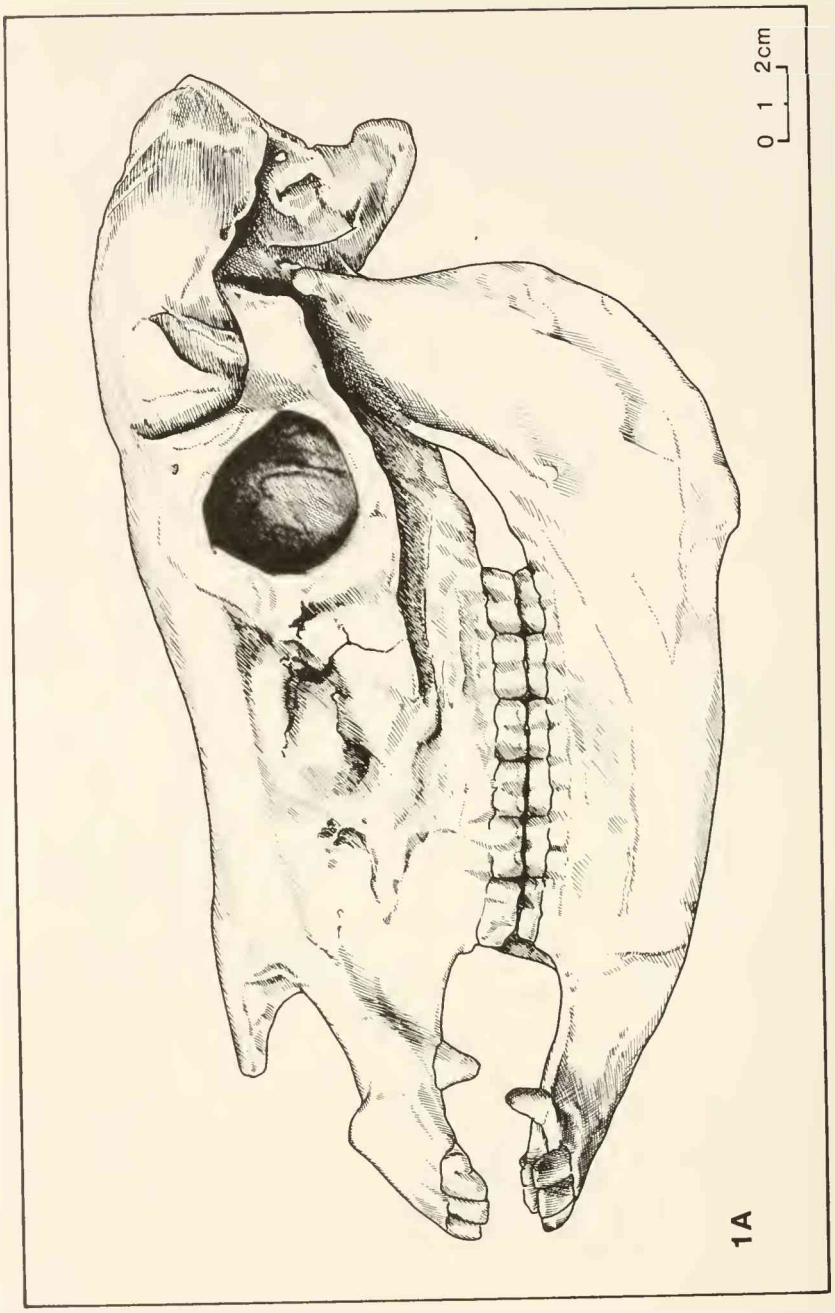
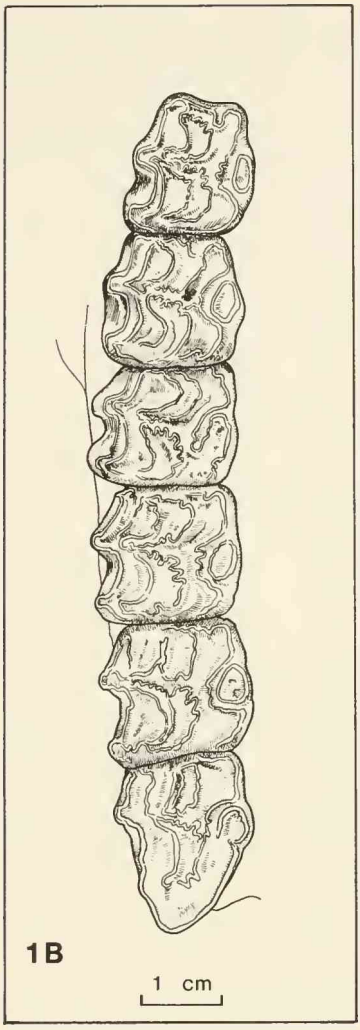
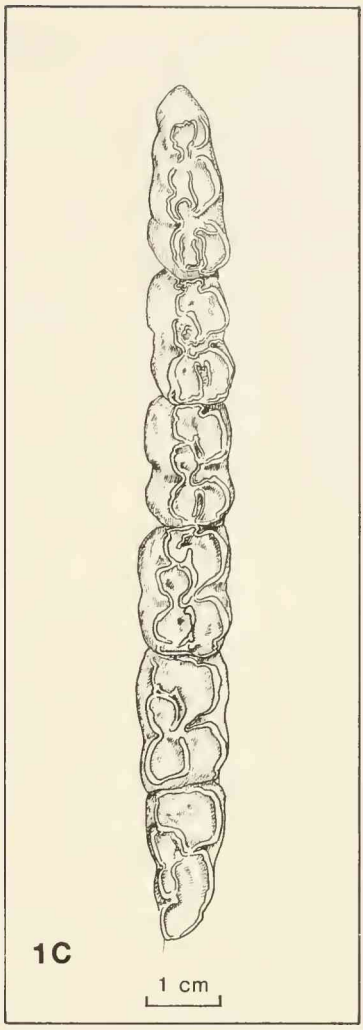


Figure 1: *Cremohipparion matthewi,* UGR OK/557. A. Skull and lower jaw, left lateral view; B. Left maxillary cheek tooth series; C. Left mandibular cheek tooth series.





small to large size with length of tooth row 105–170 mm; lacrimal foramen lacking, although it may be represented by a large depression: **preorbital bar short, with lacrimal usually touching or invading posterior limit of POF;** when present, POF subtriangular shaped and mostly anteroventrally oriented; posterior pocketing slight to absent, medial depth great to slight, **medial internal pits occur only in the most derived species,** *C. licenti;* peripheral outline strong to weakly defined, anterior rim distinct to absent; infraorbital foramen placed inferior to and encroaching upon the anteroventral border of POF; buccinator fossa distinct and unpocketed **except in** *C. licenti;* **caninus fossa present in some,** but not all species; malar fossa lacking except in *C. licenti;* nasal notch tends to become retracted in this lineage and may or may-not curve inward in species included within the group; no persistent and functional P^1; in adult, middle stage-of-wear individuals maxillary cheek teeth moderately curved to straight, with maximum crown height of 40–60 mm, fossette ornamentation complex to simple, posterior wall of postfossette always distinct; pli caballins may be double or single; hypoglyphs dee-

ply to shallowly incised; protocones may show some lingual flattening, but tend to become rounded, are clearly always isolated from protoloph, usually having no noticeable protoconal spur, and are lingually placed relative to the hypocone; P2 anterostyle/paraconid usually elongate, but become shortened in some species; in adult middle stage-of-wear individuals mandibular incisors not grooved, are curved, and I_3's not atrophied; cheek tooth metaconids/metastylids are generally rounded, not angled; ectoflexids do not separate metaconids and metastylids on the premolars, but do so on the molars; pli caballinids generally absent; protostylids may be present and frequent; ectostylids absent; linguaflexids V-shaped to shallow U-shaped; metapodials, when known are elongate and slender.

Emended Species Diagnosis: A small species of *Cremohipparion* (P^2-M^3 dimension about 110–120 mm) with preorbital bar and lacrimal as for genus; POF is reduced in medial depth and peripheral outline, no anterior rim, but retains an approximately anteroventral orientation; lacks a caninus fossa; nasal notch retracted only to anterostyle of P^2; fossette ornamentation has moderate complexity; pli caballins variably double or single; hypoglyphs moderately deeply incised; P2 anterostyle/paraconid shortened; mandibular incisor and cheek teeth are as for genus. Metapodials are elongate and slender.

Description: the type specimen of *Cremohipparion matthewi* is an old adult male individual, including a nearly complete skull and mandible (Fig. 1). Since its original collection, the skull has deteriorated badly, having lost both posterior orbits, zygomatic arches, incisors and canine teeth. The snout has been broken and remodelled. Likewise, the mandible has been partially destroyed since collection, having lost both rami, left I_3 and C.

The skull is small for this genus. It preserves a roughly subtriangular, anteroventrally oriented POF, and its anteriormost limit is abruptly interrupted by a large infraorbital foramen. The POF is moderately deep, it is not pocketed posteriorly, but has a large, triangular-shaped lacrimal bone which distinctly invades the posterior 17,5 mm of the POF. The POF lacks any posterior pocketing, but the preorbital bar remains distinct, and is short (= 21.2 mm). The peripheral border of the POF is moderately well delineated, its strongest border being the ventral one. There is a strong, dorsoventrally oriented ridge at the posterior extent of the POF which is touched posteriorly by the anteriormost lacrimal. There is no caninus fossa (= intermediate fossa of Woodburne and Bernor, 1980: 1329 and subsequent publications) between the POF and the buccinator fossae. The nasal notch is retracted only to the anterior border of P^2. There are a pair of dorsal premaxillary tubercles that are large and very prominent. The I^2's and I^3's have large, mediolaterally elongate infundibula. The canine roots are large and suggest that this individual was a male. The cheek teeth are in an advanced stage-of-wear, but still preserve some important occlusal features. P^2 anterostyle is shortened (synapomorphy with *"H". aff. moldavicum;* Middle Maragheh, Iran, ca. 8 Ma). Protocones are rounded on the premolars, and slightly more elongate on M^{1-3}; P^2 and M^1 protocones are connected with the protoloph due to very late wear-stage. When preserved, the pli caballins are short, but distinctly double. The pre- and postfossettes are heavily worn, but still consistently show complex, very finely banded plication on both anterior and posterior surfaces. The hypoglyphs are obliterated on P^{2-3} and M^{1-2}; on P^4 only a shallow hypoglyph is preserved, while M^3's hypoglyphs have moderate depth.

The mandible is likewise small and has a highly worn incisor and cheek tooth dentition. I_{1-2} have highly worn, rounded infundibula; I_3's infundibulum is more mediolaterally elongate. The right canine is preserved and maintains a stout morphology with a strong central lingual pillar, indicative of a male individual. All cheek teeth are heavily worn. The metaconids and metastylids are generally rounded with slightly angular facing borders. Fully encircled protostylids are absent, except for a small one on the left M_3. The pre- and postflexids are heavily worn,

but generally preserve a short and buccolingually narrow morphology. The linguaflexid is obliterated on P_2, distinctly V-shaped on P_{3-4}, and becomes progressively more U-shaped serially from M_{1-3}. The ectoflexid does not separate metaconid/metastylid on the premolars, while it does separate them on the molars.

Remarks: *Cremohipparion matthewi* constitutes perhaps one of the most complex taxonomic muddles of Old World hipparionines. This can be attributed to many past workers using principally size and presumed limb slenderness to distinguish this species. As we discuss below, there are a range of skull, mandibular and postcranial characters which support our assertion that there is certainly more than one species of small horse from the eastern Mediterranean and southwest Asia, necessitating their future complete revision.

Pavlow (1890) identified a small hipparion MC III fragment from Sebastopol and referred it to a new species *Hipparion minus*. In his catalogue of Samos fossils, Forsyth Major (1894: 5 and 32) referred small, very worn upper right molar from Andriano to *Hipparion minus* Pavlow. Studer (1911: Fig. 4, pg. 196) figured a fragmentary MT III from Samos, and followed previous authors in applying the nomen *Hipparion minus*. Kormos (1911: Fig. 1, plate at end of text; UGR OK 557, Fig. 1 here) figured a complete skull and lower jaw from Samos retaining the nomen *Hipparion minus*. Antonius (1913: 244; 1919: 285–287) perpetuated the referral of Samos small hipparions further to the southwest Russian species of Pavlow, and in the 1919 publication remarked that "*Hipparion minus*" was morphologically quite similar to the North American horse *Neohipparion withneyi* Gidley, except for the North American form's more poorly developed "Wangengrube" (POF).

Abel (1926) cited the inappropriateness of using Pavlow's type for "*Hipparion*" *minus* to characterize any hipparion species, and proposed that the name be considered a nomen nudum. Abel (1926: 430 Fig. 273; 432) then citing the skull and mandible figured by Kormos (1911: Fig. 1), elected it as the type of a new species, *Hipparion matthewi* named in honor of W. D. Matthew. Abel (1927: Fig. 110, pg. 120) figured this same specimen once again.

Wehrli (1941) made an extensive review of Samos hipparion systematics. He nominated a new genus for all the Samos hipparions he recognized, raising them to a distinct generic rank, *Hemihipparion*. Wehrli's (1941) Samos species included: *Hemihipparion proboscideum* (Studer), *Hemihipparion dietrichi* n. sp. and *Hemihipparion matthewi* (Abel). The nomen *Hemihipparion* would be a synonym senior to *Cremohipparion* except Wehrli (1941: 374) nominated *Hipparion dietrichi* as the genotype species. Woodburne and Bernor (1980: 1329), Bernor (1985: 205) and Bernor et al. (in press) have cited the specific reasons why *H. dietrichi* should be considered as belonging to a clade (= a member of the *Hipparion* s. s. clade; Bernor et al., in press) quite distinct from *Cremohipparion* (= Group 2 hipparions of earlier work).

Gromova (1955: 231) recognized Abel's nomen *Hipparion matthewi* from Samos, and gave it an extensive diagnosis. Some of the more important points in her diagnosis were: range of maxillary cheek tooth length = 102.4–113.5 mm (far less of a range than given by most subsequent authors); short muzzle; single preorbital fossa, short and deep; nasal notch shallowly incised; extremities slender. Gromova (1952: 232) cited only Kormos's (1911) skull and mandible specimen in her characterization of facial morphology, and apparently did not have the München specimen of *Cremohipparion nikosi* available to her for study. She included Tobien's (1938: Taf. 1) and Wehrli's (1941) measurements in her diagnosis of cheek tooth dimensions, and in so doing mixed the hypodigms of *Cremohipparion matthewi* and *Cremohipparion nikosi*. She cited the rarity of well known *C. matthewi* postcranials, but utilized the collection described by Wehrli (1941) in her diagnosis of "*Hipparion*" *matthewi*. Gabunja (1959: 222) and Forsten (1968: 53) essentially followed Gromova's (1952) concept of "*Hipparion*" *matthewi*, applying it to small horses from the eastern Mediterranean and southwest Asia.

Sondaar (1971: 423) reviewed the American Museum collection of Samos hipparionines. He recognized and refigured the type skull and lower jaw of *"Hipparion" matthewi* (UGR OK/557; Sondaar, 1974: Plate IV, Fig. a) and subsequently referred all AMNH Samos hipparions of small size (P^2-M^3 = 100–130 mm; P_2-M_3 = 110–135 mm), with slender limbs (MT III length = 211–242 mm, proximal width = 27–34 mm), with simple enamel plication, oval to nearly rounded protocone and slightly developed POF, to *„Hipparion" matthewi*. Of this Samos hypodigm, he figured two Quarry 5 specimens: a skull, AMNH 22936 (Plate 1a, b) and palate AMNH 22888 (Plate 1c). Sondaar (1971) noted that the type specimen of *"H". matthewi* had a shorter muzzle than the AMNH material in his hypodigm.

Although AMNH 22936 is a virtually complete adult male specimen, the nasal notch area is destroyed, disallowing any certain referral to either *C. matthewi* or *C. nikosi*. However, AMNH 22936's preorbital fossa morphology, short POB length and P^2-M^3 length do conform well with either of these two *Cremohipparion* small species, and may reasonably be considered as being a species of that genus. Of the remaining AMNH Samos skull material referred by Sondaar (1971: Tab. 1) to *"Hipparion" matthewi* (AMNH 22888, 22936, 20788 (here two distinct specimens), 20787, 22907), AMNH 22888 **may** have a somewhat longer P^2-M^3 dimension (i. e. 129.4 mm) than would be expected for either *C. matthewi* or *C. nikosi*. Likewise, the extensive mandibular series referred by Sondaar (1971, Tab. II) to *"Hipparion" matthewi* includes at least two specimens, AMNH 20791 (P_2-M_3 = 131 mm) and AMNH 22928 (P_2-M_3 = 134 mm) that may be larger than expected for either *C. matthewi* or *C. nikosi*. As a result of our evaluation, it is not presently clear which, if any, of the AMNH material is referrable to either *Cremohipparion matthewi* or *Cremohipparion nikosi*.

Bernor (1985: 220, Fig. 18) referred a skull fragment, some isolated maxillary and mandibular cheek teeth and postcranial fragments to *"Hipparion" ?matthewi*. The skull fragment was the most definitive specimen, being small sized (P^2-M^3 = 121.9 mm) with POF and POB morphologies agreeing well with the type of *Cremohipparion matthewi*. Although there is no snout or nasal notch preserved, the skull specimen, GIU P100–1958, is broken at the level of P^2 mesostyle, and therefore would not have nasals as retracted as *C. nikosi*. A referral of this specimen to *C.* aff. *matthewi* would presently be acceptable.

Lehmann (1984: 152 and Taf. VII) briefly described a virtually complete skull (Nr. 3002), an unassociated lower jaw (Nr. 3005) and MT II–IV elements (no numbers given) of *"Hipparion" matthewi*. The skull is quite interesting in that Lehmann's Taf. 8, Fig. 1 shows the POB as being short, with lacrimal invading posterior rim of the POF, and POF essentially has a morphology consistent with *C. matthewi* and *C. nikosi*. However, the nasals would appear to be somewhat retracted compared to the holotype of *C. matthewi* (posterior aspect of P^2), but certainly not as far as seen in *C. nikosi* (mesostyle of P^4). Maxillary cheek tooth morphology would appear to be consistent with that found in *C. matthewi* and *C. nikosi,* and MT III length (= 223 mm) and diaphysial width (22.2 mm.; Lehmann, 1984: 152) is consistent with the range of variation reported for Samos small horses here. It would appear that this specimen exhibits somewhat intermediate characters between *C. matthewi* and *C. nikosi* in the degree of its nasal incisure. We believe that despite this intermediate nature, the difference between *C. matthewi* and *C. nikosi* is too great (see description for the latter below) to be explained as variability in a single species.

Koufos (1984, 1986, 1987a, b) has recently cited the occurrence of some small horses from Macedonia. Koufos (1984) named a new species of small horse, *H. macedonicum* from Ravin de Pluie 1 (RPL 1). He stated that *"Hipparion" matthewi* differs from *H. macedonicum* in its shorter snout, longer mandibular symphysis, simpler enamel plications, rounded protocone connecting to protoloph (sic., only in later wear), small-rudimentary pli caballin, less developed protostylid, simple enamel in the flexids, as well as having single column ectostylids in the lower

milk teeth. The differences in the adult dentition reveal a generally more primitive morphology typical of older European species. It is uncertain however what the juvenile dental morphology would be for *Cremohipparion matthewi*, since the type specimens of both *C. matthewi* and *C. nikosi* are adult individuals.

Koufos (1984: 313) cited that the character which most distinguished *H. macedonicum* from other small Turolian horses (*"H". matthewi*, *"H". gromovae*, *"H". periafricanum* and *"H". elegans)* was its greater molar row length/premolar length ratio (greater than 100 in *H. macedonicum*, less than 100 in all others; 84.0 in the type maxilla and 92.9 in the type mandible of *Cremohipparion matthewi;* 84.8 in the type maxilla of *Cremohipparion nikosi).* He included in this distinction the younger Ravin de Zouaves samples of small hipparion which showed lower (less than 100) length molar series/length premolar series ratios. However, since citing lower molar length/premolar length ratios in the younger Macedonian Ravin des Zouaves (RZO) series, Koufos (1987a: 304) referred two of three RZO specimens (RZO 38 and RZO 44, with ratios of 90 and 94.5 respectively) to *H. macedonicum.* It is presently not clear whether Koufos (1987a) believes that the ratio change within the "late Vallesian – Turolian" aged Macedonian series is insignificant, and *"H". macedonicum* has members with length molar/length premolar series both above and below 100, or whether it is possible that more than one species of small hipparion is included in the hypodigm of *"H". macedonicum*, or if these differences are ontogenetically (= wear) related. If the differences in length molar/length premolar ratio prove to be significant at the species level as Koufos (1984: 313) claimed, then his (1987a) hypodigm would necessarily include more than one species of small horse.

Koufos' (1986: 71, Tab. 9) report on new material of *H. macedonicum* included discussion of MT III material which he cited as differing from *"H". matthewi* in its longer (var. 1 = 239.0 mm), more slender diaphysis (var. 11 = 26.6). Of course there are no articulated skeletons of *Cremohipparion matthewi*, making referrals of postcrania to the type uncertain. Indeed, the measurements of AMNH Samos small horse MT III's that we record here in Table 5 include one Quarry 5 specimen that is quite close to Koufos' (1986: Tab. 9) dimensions (i. e. F:AM Q5 22893, var. 1 = 239.4 mm, var. 11 = 25.9 mm). The other Samos individual (F:AM Q5) has quite a shorter length MT III (var. 1 = 213.7 mm), and slightly shorter DAW dimension (var. 11 = 24.2 mm). These individuals are included here in Fig. 3.

Koufos (1987b: 347, Fig. 8) figured for the first time a skull of *H. macedonicum*, PXM 20. No raw measurements were given for POF and POB, but the shape of the former is consistent with *C. matthewi*, and the length of the POB has been reported by the author as being short. The nasal notch can clearly be seen in this figure to be retracted no further than the anteriormost portion of P^2, as is seen in *C. matthewi.*

Cremohipparion nikosi n. sp.
Fig. 2

Hipparion matthewi, Tobien, 1938
Hipparion matthewi, Gromova, 1952, in part

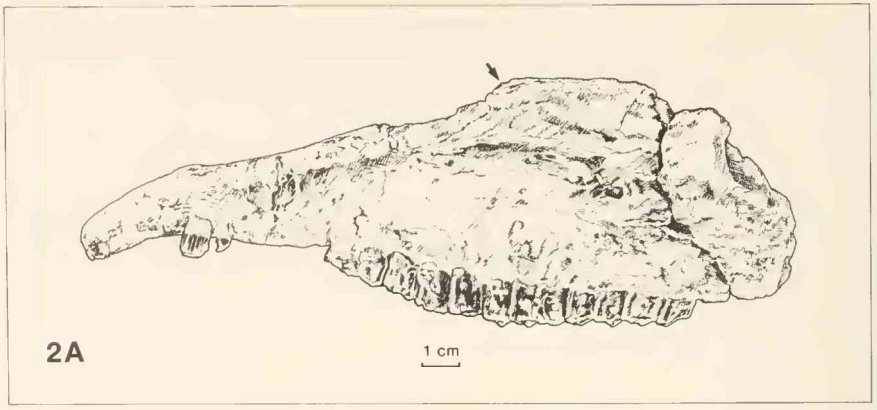
Holotype: Male skull fragment, BSP 1899 VII 31b.

Type Locality: Island of Samos (Greece, without locality).

Etymology: Named in honor of Dr. Nikos Solounias as a tribute to his long and exhaustive work on the stratigraphy and paleontology of Samos.

Age: Turolian, ca. 8.5–5.7 Ma.

Geographic Distribution: Greece.



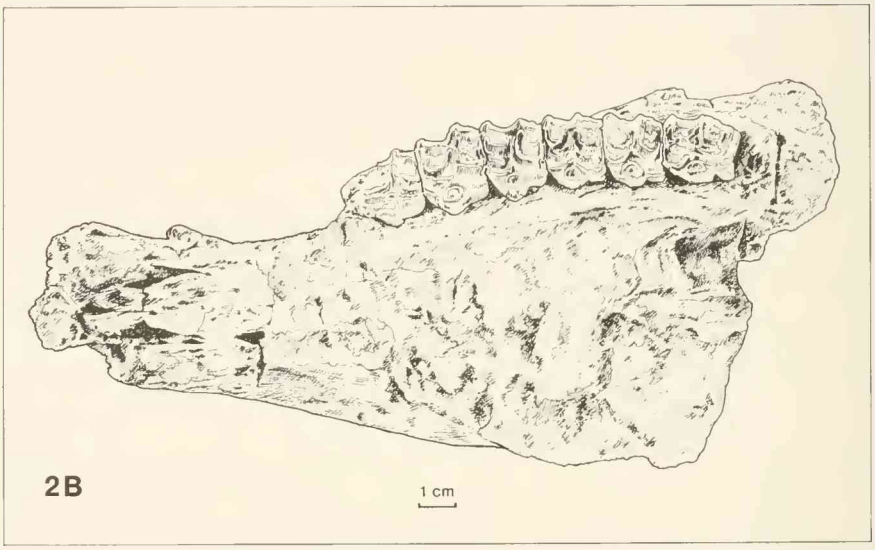


Figure 2: *Cremohipparion nikosi* n. sp., BSP 1899 VII 31 b. A. Skull fragment, left lateral view; B. Left maxillary cheek tooth series.

Diagnosis: As for *Cremohipparion matthewi* except that the nasals are strongly retracted to the mesostyle of P^4. Lower jaws are not known for this species.

Description: The type specimen of *Cremohipparion nikosi* n. sp. (Fig. 2) is an old adult male individual including the snout, nasals, maxilla and anteroventral aspect of the orbits, both canines and left P^2-M^3.

As with the holotype of *C. matthewi,* this is a small species. The specimen preserves an approximately subtriangular, anteroventrally oriented POF with a large anteroventrally placed infraorbital foramen. The POF is less than 10 mm deep medially, has no posterior pocketing, preorbital bar is quite short (19.2 mm) and while not clear, the lacrimal most probably invaded the posterior aspect of the POF because of the POB's very short length. As with *C. matthewi,* there is no visible caninus fossa. The nasal notch is clearly very strongly retracted to mesostyle

of P^4. The dorsal premaxillary tubercles are far less developed in this specimen than in *C. matthewi*. The canines are large and quite robust, and suggest, that it was a male individual. The cheek teeth are in an advanced stage-of-wear, suggesting that this was an old individual. P^2 anterostyle is shortened. Protocones are rounded on all cheek teeth; P^2's protocone is connected with the protoloph due to its late wear-stage. When preserved, pli caballins are short, but either single or double. The pre- and postfossettes are heavily worn, but reveal that the individual had shallow amplitude, moderately complex plications of the cheek teeth. However, wear is too advanced to reliably account for how many plications the younger middle stage-of-wear adults had. The hypoglyphs are essentially obliterated on P^{2-3}, shallow on P^4-M^2, and deep on M^3.

Remarks: The only previous citations of the type specimen, BSP 1899 VII 31b, were Tobien (1938: Taf. 1) and Gromova (1952), both of whom referred it to *Hipparion matthewi*, based on its size.

This species is remarkably similar to *C. matthewi* in its size and morphology, except for the strong retraction of the nasal bones. This single contrast is significant, in that the ratio of measurement 30 versus 31 (length of the naso-incisival notch from prosthion to the back of the narial opening versus the length of the narial opening to the anteriormost limit of the orbit; re: Eisenmann et al., 1988: Fig. 3a) is 136.0/74.9 (= 181.6) in *Cremohipparion nikosi* versus 99.1/110.6 (= 89.7) in *Cremohipparion matthewi*. Moreover, we know of no case where a single species of hipparion exhibits a variability in nasal retraction ranging from anterior limit of P^2 to mesostyle of P^4.

Koufos and Melentis (1984) described an important and previously poorly known collection of Samos hipparions from the PMMS, Samos, Greece. This collection originates from the Stefanidis or Andrianos Ravine, and is believed by the authors to be identical to Quarry 1 of the AMNH collection (Brown, 1927). Koufos and Melentis (1984) describe a smaller horse in this which they referred to *Hipparion* sp. II; the most complete specimen being a skull, PMMS 9 (Plate II, pg. 69; Plate III, pg. 70). They characterize this taxon as being (Koufos and Melentis, 1984: 66): "size middle; moderate developed preorbital fossa, situated near the orbit; long muzzle; short tooth series, closed (= close to) *H. matthewi;* simple enamel plication; protocone connected to the protoloph; moderate protostylid". The cheek tooth characters are most probably not diagnostic because of their later wear-stage. Length of the cheek tooth series is somewhat greater (P^2-M^3 length = 122.1 mm), than the type *C. matthewi* (= 111.8 mm) and *C. nikosi* (= 105.5 mm). Preorbital bar length for PMMS 9 (= 29 mm; Table 1: 54) falls within the uppermost portion of the range of length for *Cremohipparion* species (Bernor, 1985: 264, Tab. 14; *C.* aff. *moldavicum* from Middle Maragheh has one of the highest ranges for this lineage, = 23.6–29.8 mm). Also, reference to Table 1 here reveals that the values for measurements 30 (= 142 mm) and 31 (= 135 mm) are greater overall than *C. matthewi* and *C. nikosi*, while its ratio of these measurements (= 105.2) is somewhat different than *C. matthewi* (= 89.6 mm), and much different than *C. nikosi* (= 181.6 mm). This feature of *Hipparion* sp. II suggests a relatively intermediate snout length/nasal retraction.

It is presently difficult to determine what the evolutionary relationships of "*Hipparion*" sp. II are. The length of preorbital bar is within the range of variation for *Cremohipparion* aff. *moldavicum* from Maragheh, as is the length of the maxillary cheek tooth row (= 120.0–141.3 for *C.* aff. *moldavicum;* Bernor, 1985: 264, Tab. 14) especially given the fact that PMMS 9 is an old individual. However, PMMS's POF would not appear to be as strongly developed in its medial depth and peripheral rim as *Cremohipparion moldavicum*. Therefore, there is no apparent basis to refer PMMS 9 to either *C. matthewi* nor *C. nikosi*, and it may or may not prove to be a member of the *Cremohipparion* lineage. However, further details on POF, lacrimal and caninus fossa morphology are particularly needed to determine its phylogenetic affinities.

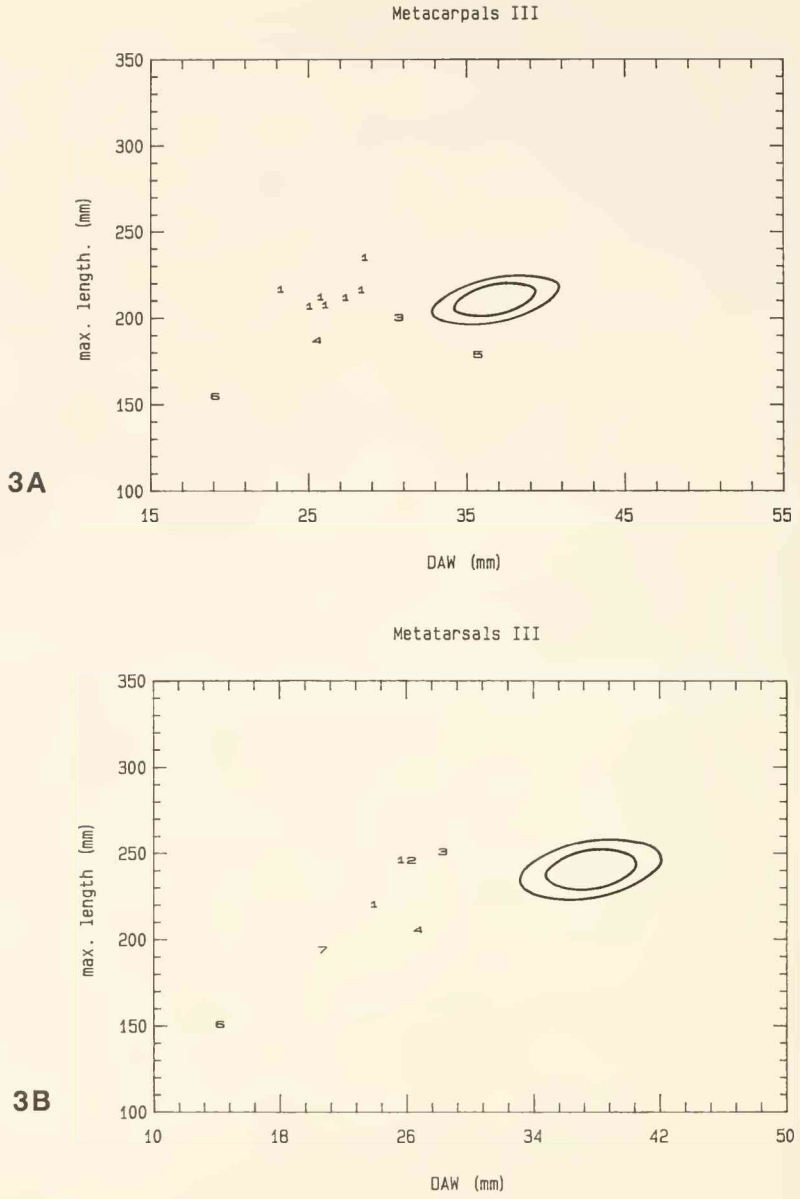


Figure 3: Comparison of Samos "*Cremohipparion matthewi*" species with selected later Miocene Holarctic and Ethiopian smaller horses. A. MC III maximum length (ML) versus distal articular width (DAW). B. MT III ML versus DAW. 1 = "*Cremohipparion matthewi*" (Samos; AMNH: 23054 b–e, 22933, 23054, Q5 no numbers, 22893; BERNOR, personal observation); 2 = "*Hipparion macedonicum*" (Ravin de Pluie, Greece; RPL 38; KOUFOS, Table 9 – insert); 3 = "*H*". *sitifense* (Sahabi, Libya; 27P25B, MC III; 1P25B, MT III; BERNOR et al., 1987); 4 = "*H*". *gromovae* (La Fontana, Spain; TOBIEN, personal observation); 5 = "*S*". *platyodus* (China; QIU et al., 1987: 95); 6 = *Calippus* (XMAS Quarry, Nebraska AMNH 98 (BERNOR, personal observation); 7 = *Pseudhipparion* sp., XMAS Quarry AMNH 202 (BERNOR, personal observation).

The AMNH houses some small horse postcranials from Samos. Measurements for metapodials (Table 5), humerus (Table 6) radius (Table 7), ulna (Table 8) and astragalus (Table 9) are given here. Figure 3 compares the proportions of metacarpal III and metatarsal III maximum length (var. 1) versus distal articular width (= DAW; var. 11) in comparison with 95% and 99% confidence ellipses for the Höwenegg hipparions (Bernor et al., in press). This figure illustrates that there were a number of different species, belonging to distinctly different later Miocene equid lineages that decreased size. The two species of *Cremohipparion* reported here are amongst the more elongate and slender species, and contrast most sharply with *"Sivalhippus" platyodus* from China (Qiu et al., 1987: 94–95; Tab. 10), which had relatively short and broad proportions (and indeed was not a true dwarf form as is seen from its skull dimensions). These observations reinforce our assertions that size cannot be used alone in defining a hipparion species, nor can it alone support assertions of phylogenetic relationship and time correlation.

Discussion: Woodburne and Bernor (1980: 1328) first recognized that those Old World hipparionine species with short preorbital bars and three facial (preorbital, intermediate and buccinator) fossae belonged to a single monophyletic group (their "Group 2"). The species they included in this group were the Greek Turolian age species *"H". mediterraneum* and *"H". proboscideum*. Bernor (1985: 222) suggested that *"H.". matthewi*, tentatively referred by Woodburne and Bernor (1980: 1331) to their "Group 4", may also belong to "Group 2", based upon material from Maragheh, Iran. Qiu et al. (1987: 207) recognized two Chinese species belonging to this clade and erected a new subgenus, *Hipparion (Cremohipparion)* to accomodate them *(H. [Cremohipparion] forstenae* and *H. [Cremohipparion] licenti)*. Most recently, Bernor et al. (in press), arguing that *Cremohipparion* is a clade quite distinct from *Hipparion* sensu strictu, chose to raise this taxon to genus rank, *Cremohipparion*.

Cremohipparion matthewi and *Cremohipparion nikosi* would appear to be sister-taxa. While *C. matthewi* is more primitive than *C. nikosi*, and the Samos faunas have most recently been interpreted as having a significant chronologic range (8.5 and 7 Ma by Weidmann et al. 1984: 487; whereas Sen, 1986: 159, Sen and Valet, 1986: 173, and personal communication, interprets the age for the upper "main bone beds", not including the stratigraphically lower Quarry X of Weidmann et al., 1984, to range between 6.8 and 5.7 Ma), it is currently not possible to establish these as being time-successive species since there is no clear provenance data on these specimens. *Cremohipparion matthewi* and *C. nikosi* are most closely related to *C. moldavicum*, ostensibly the most primitive member of the *Cremohipparion* clade (Bernor et al., in press). They are primitive compared to *C. moldavicum* in their retention of an anteroventrally oriented POF, but derived in their reduction of the POF, sharply reduced size and shortened anterostyle. Other members of the *Cremohipparion* lineage: *C. mediterraneum* (Pikermi, Greece, ca. 8.5–8 Ma; Bernor et al., 1980: 729, Fig. 8), *C. proboscideum* (Samos, Greece; ca. ?8.5–5.7 Ma; Weidmann et al., 1984; Sen, 1986: Sen and Valet, 1986), *C. forstenae* (China, ca. 9–7.5 Ma; Qiu et al., 1987: 171, Fig. 69); *C. licenti* (China, ca. 5+–3 Ma; Qiu et al., 1987: 171, Fig. 69) all have the shared derived character of a well delineated caninus (= intermediate) fossa not found in *C. moldavicum, C. matthewi* and *C. nikosi*. These taxa all show a trend to lengthen the nasals, which becomes very extreme in *C. licenti* (to mesostyle of M^1).

Bernor et al. (1987: 48, Fig. 3) and Bernor et al. (in press) have documented the biogeographic and geochronologic ranges of the *Cremohipparion* lineage. These taxa ranged in age from about 9 to 3 Ma., with the Chinese species *C. licenti* surviving at least two million years longer than all other taxa (Qiu et al., 1987: 171, Fig. 69). Geographically they are found as far west as Greece, and range through the Eastern Paratethys bioprovince, northwest Iran, and eastward to China. The occurrence of *C. mediterraneum* in both Greece and China (Bernor et al., in press) suggests an initial period of biogeographic extension of this clade which appears to have

been succeeded by vicariance, with Chinese and eastern European taxa evolving in isolation from one another.

Conclusions

We recognize a minimum of two small species of *Cremohipparion* from the late Turolian locality of Samos, Greece: *C. matthewi* and *C. nikosi* n. sp. These two species differ in their relative degree of nasal notch incisure: *C. matthewi*'s being only to the anterior limit of P^2, *C. nikosi*'s being to P^4 mesostyle. This gives a significant difference in the ratio of naso-incisival notch length from prosthion to back of the narial opening (measurement 30) versus length of the narial opening to the anteriormost limit of the orbit (measurement 31): *C. matthewi* is 89.6, *C. nikosi* is 181.6. The intermediate degree of retraction in Lehmann's skull specimen Nr. 3002 (1984: 152 and Taf. VII) suggests the possibility that the shift in nasal notch incisure from anterior P^2 to mesostyle P^4 may have been made in gradual steps; this is feasible in light of our current understanding of the long chronologic range of the Samos faunal sequence. Amongst all other species of *Cremohipparion* recognized by Bernor et al. (in press), *C. matthewi* and *C. nikosi* are most similar to *C. moldavicum* in their lack of a caninus fossa. However, all *Cremohipparion* species share the combined presence of a short preorbital bar with lacrimal closely approaching or touching the POF, shallow POF posterior pocketing and infraorbital foramen placed at, or invading, anteroventral aspect of the POF. Bernor et al. (in press) have cited two possible phylogenetic origins for the *Cremohipparion* group, including a more primitive form of North American *Cormohipparion*, not dissimilar to *Cormohipparion sphenodus*, and alternatively an Old World "Group 1" taxon, not dissimilar to *"Hipparion" primigenium*. *Cremohipparion* species are cited here as having first occurred in the earliest Turolian of eastern Europe and southwest Asia, and diversified across much of northern Asia. The genus is not known from Central and Western Europe, south Asia or Africa.

Our review of more recent literature of small eastern Mediterranean and southwest Asian hipparions reveals that their evolution may be more complex than presently recognized. Koufos' (1984, 1986, 1987a, b) and Koufos and Melenti's (1984) recognition of *"H". macedonicum* from Thessaloniki may include more than one species, which may or may not be referrable to *Cremohipparion*. It remains to be demonstrated exactly how many valid small hipparions are known from the eastern Mediterranean – southwest Asian areas, what their phylogenetic interrelationships may be, and their relationships to other small hipparions from throughout Eurasia and Africa.

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Table 1: Skull Measurements

	C. matthewi OK 557	*C. nikosi* BSP 1899 VII 31b	*C.* aff. *matthewi* GIU P 100/1958	*C.* aff. *moldavicum* BMNH M3924	„*H*". sp. II PMMS 9*)
1)	80.9	~ 85		91.0	124
2)	88.5		92	96.5	106
3)	70.2				
4)	80.0				
5)	150.4				
6)	318.7				
7)	60.7	58.4	66.9	80.3	66.0
8)	51.0	49.5	55.5	66.3	56.4
9)	111.8	105.5	121.9	141.3	122.1
10)	56.1				
11)	~ 17.9				
12)	~ 19.4			~ 22	
13)	33.5		41.9	51.2	
14)		~ 28		29.4	35.0
15)	42.3	~ 37		41.3	54.0
16)					
17)	83.4				
18)					
19)					
20)	67.6				
21)					
22)	53.2				
23)	~246.8			271.8	
24)	~118.5	~ 49			
25)	67.2			77.5	97.5
26)	74.7				
27)					
28)				~ 48	
29)	48.7			~ 50	97.5
30)	99.2	136.0		111.5	142
31)	110.6	74.9		132.2	135
32)	21.2	19.2	26.9	25.8	29
33)	57.4	55.5	58.1	64.4	
34)	54.1	52.0	48.4		
35)	32.0		35.6	48.5	
36)	21.8		22.5	21.2	
37)	36.2	39.4	30.5	39.3	
38)	72.0	51.4	44.6	46.0	

*) measurments from KOUFOS and MELENTIS, 1984

RATIO Length molars (measurement 8)/length premolars (measurement 7) × 100: *C. matthewi* = 84.0; *C. nikosi* = 84.8; *C.* aff. *matthewi* = 82.2; *C.* aff. *moldavicum* = 82.6; „*H*". sp. = 85.5.

RATIO Length of naso-incisival notch from prosthion to the back of the narial opening (measurement 30)/ length of the narial opening to the anteriormost limit of the orbit (measurement 31) × 100: *C. matthewi* = 87.7; *C. nikosi* = 181.6; *C.* aff. *moldavicum* = 84.3; „*H*". sp. II = 105.2.

Table 2: Measurements and morphological observations on maxillary Teeth of *Cremohipparion matthewi* and *Cremohipparion nikosi*

Specimen No.	Element	Length	Width	Protocone			Prefossette		Postfossette		Pli	Hyp
				Shape	Length	Width	A	P	A	P		
1) OK 557	I^1											
	I^2	11.3	8.8									
	I^3	12.1	7.2									
	C	10.6	6.0									
	p^2	24.4	17.5	round	5.3	4.3	6	5	3	0	2	
	p^3	17.6	21.6	round	6.1	4.6	0	7			2	
	p^4	18.2	20.5	round	6.1	4.3		8	5	1	2	D
	M^1	15.5	18.9	round	6.0	4.2		7	4		2	
	M^2	16.2	17.3	round	5.2	3.8		9	6		2	
	M^3	18.4	16.3	round	5.7	3.6	2	8	3	4	2	B/C
2) BSP 1899 VII 31b	C	8.0	6.0									
	p^2	22.2	18.6	round	6.6	4.6					0	
	p^3	18.0	21.7	round	6.1	4.5					0	
	p^4	17.0	19.9	round	5.9	4.7					1	D
	M^1	15.6	17.9	round	5.3	4.2					1	D
	M^2	15.9	17.7	round	5.5	3.9					0	D
	M^3	18.0	16.2	round	5.6	4.0					2	B

Explanation
Element: tooth
Length: maximum length of tooth
Width: maximum width of tooth
Protocone – shape = round; length: maximum length of structure; width: maximum width of structure
Prefossette – A: number of plis on anterior wall; P: number of plis on posterior wall
Postfossette – A: number of plis on anterior wall; P: number of plis on posterior wall
Pli – number of pli caballins
Hyp – depth of hypoglyph: A – very deep, encircling hypocone; B – very deep, but not encircling hypocone; C – moderately deep; D – shallow.

Table 3: Mandibular Measurements on *Cremohipparion matthewi* (as published by EISENMANN et. al., 1988)

	OK 557
1)	
2)	66.1
3)	57.7
4)	53.6
5)	111.9
6)	
7)	38.7
8)	
9)	
10)	61.5
11)	52.1
12)	34.6
13)	~ 62
14)	28.0

Table 4: Measurements and morphological observations on mandibular teeth

Specimen Number	Element	Length	Width	MCD	MSTD	PRO	PREF	PSTF	LING	ECT
1) OK 557	I_1	9.5	9.6							
	I_2	9.8	10.0							
	I_3	10.2	8.0							
	C	8.1	5.5							
	P_2	20.3	9.1	A	A/C	B		A		A
	P_3	18.1	11.7	A	A/C	B	A	A	B	A
	P_4	17.8	11.8	A	A/C	B	A	A	B	A
	M_1	16.5	10.0	A/C	A/C	B	A	A	B/C	B
	M_2	17.0	9.0	A/C	A/C	B	A	A	B/C	B
	M_3	21.6	8.1	A	A	A	A	A	C	B

Explanation
Length: maximum length taken at occlusal level
Width: width taken across metaconid/metastylid interface and ectoflexid
MCD: metaconid; A = rounded, C = angular
MSTD: metastylid; A = rounded, C = angular
PRO: protostylid; A = present, B = absent
PREF: preflexid; A = short and narrow, B = elongate and narrow
PSTF: postflexid; A = short and narrow, B = elongate and narrow
LING: linguaflexid; A = shallow; B = V-shaped; C = U-shaped
ECT: ectoflexid; A = does not separate metaconid/metastylid, B = does separate metaconid/metastylid

Table 5: Measurements on metapodial III

Metacarpals III Specimen No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1) FA:M 23054c	205.4	198.3	22.2	17.3	29.3	19.5	30.9		3.8	27.9	26.0	22.0	18.5	20.2
2) FA:M 23054d	200.8	197.9	20.1	17.1	30.4	18.9	28.3	7.7		26.4	26.3	22.4	18.8	20.5
3) FA:M 23054b	200.1	196.1	19.3	18.5	28.9	21.1	25.6	9.1	2.7	26.2	25.3	22.1	19.4	20.4
4) FA:M 23054e	205.0	199.0	25.7	18.4	33.5	22.0				25.6	27.6	23.6	20.9	21.7
5) FA:M 22933	209.9	204.6	18.9	19.2		17.9	23.7		3.4	25.6	23.5	21.2	17.5	19.5
6) FA:M 23054	209.4	203.8	25.3	19.3	32.8	22.8	28.6	10.1	4.6	29.7	28.6	24.2	20.9	20.7
7) FA:M Q5 Lg Form	228.3	224.6	22.3	19.2	34.8	25.4	34.4		5.8	30.3	28.8	26.6	22.0	23.8
*8) RP1 44			21	17	32.3		28	7						
Metatarsals III														
1) FA:M 22893	213.7	210.5	18.7	21.0	28.7	24.5	26.3	8.6	4.7		24.2			
2) FA:M Q5 Lg Form	239.4	236.5	22.0	22.0	26.3					27.8	25.9	26.2	20.5	22.4
*3) RP1 38	239.0	235.0	19.5	22.0	30.0	25.5	28.5	6.2	4.5	28.0	26.6	24.1	20.4	23.3

*measurements from KOUFOS, 1986.

Table 6: Measurements on Humerus

Specimen No.	1	2	3	4	5	6	7	8	9	10	11
HLMD SS–2	201.0	188.0	21.7	34.4		75.4	~ 50	55.2	35.9	27.7	33.0

Table 7: Measurements on radius

Specimen No.	1	2	3	4	5	6	7	8	9	10	11	12
1) FA:M Q5	215.0	212.3	25.7	18.0	43.2	22.5	43.4	35.9	16.1	39.6	14.2	16.2

Table 8: Measurements on ulna

Specimen No.	1	2	3	4	5
1) FA:M Q5			24.3		36.7

Table 9: Measurements on astragalus

Specimen No.	1	2	3	4	5	6	7
1) FA:M 22893	41.1	39.4	17.9	38.2	32.6	21.2	

Note added in proof

In a communication dated 12-6-1989 to Bernor from Professor Dr. Lehmann, Geolog.-Paläontolog. Institut, Hamburg, the following information on Samos skull specimen Nr. 3002 was given:

1) „The nasal notch is fairly well visible at the right side of the skull, it is incised to a level of the anterior end of P^2". This feature conforms exactly with the type *Cremohipparion matthewi*, and makes it quite distinct from *Cremohipparion nikosi*.
2) „The lacrimal bone invades the posterior rim of the preorbital fossa". This feature is a shared-derived feature for all *Cremohipparion* species.
3) Measurements:
   30– 98 mm
   31–112 mm
   32– 50 mm (this high value may be due to crushing or a measurement error)
   33– 50 mm
   35– 22 mm (this low value may be due to crushing)

Prof. Lehmann concludes that there is indeed crushing of the specimen which may adversely affect the accuracy of measurements.