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# Comparative anatomy of carpal and tarsal bones in three sympatric Turolian hipparions (Kryopigi, Chalkidiki, Greece)

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*KEY WORDS* - Hipparion, Cremohipparion, Hippotherium, *anatomy, carpals, tarsals.*

*ABSTRACT - The anatomy of carpal and tarsal bones in three sympatric hipparionine horses is studied in order to investigate the interspecific and intraspecific variation of non-metric variants, such as the presence and shape of articular facets and attachment sites of ligaments. The material comes from the Turolian Kryopigi locality (Chalkidiki, northern Greece) and includes about five hundred specimens, many of which are in articulation with other long bones and used as reference. Among four hipparion species identified in the locality, one is only briefly discussed here due to lack of material. Differences are indicated in the illustrations, and discussed in comparison to other hipparion species. Some additional articular facets are found to be present in Kryopigi hipparions with different frequencies, whereas others occur in a single species. The most striking characters of the wrist and the hock are given for the various Kryopigi hipparions. Most additional articular facets occur in the bones of the distal carpal and tarsal row and especially in the magnum and the cuneiforme 3, which articulate with the central metacarpal and metatarsal, respectively. Some morphological characters on the carpal and tarsal bones might be synapomorphic.*

*RIASSUNTO* - [Anatomia delle ossa carpali e tarsali a confronto in tre equidi tridattili turoliani simpatrici di Kryopinigi (Calcidica, Grecia)] - *Obiettivo di questo lavoro è lo studio dell'anatomia delle ossa carpali e tarsali di tre equidi tridattili simpatrici (*Hippotherium *cf.* H. brachypus*,* Hipparion phlegrae*,* Cremohipparion matthewi/nikosi*) per approfondire le variazioni interspecifiche e intraspecifiche di variabili non metriche, come la presenza e la morfologia delle faccette articolari e delle aree di inserzione muscolare. I fossili presi in esame fanno parte di una associazione a mammiferi turoliani proveniente dalla località di Kryopigi (Calcidica, Grecia settentrionale) e includono circa 500 resti, molti dei quali si presentano in connessione anatomica con ossa lunghe e usati quindi come riferimento. Nel presente studio saranno illustrate e discusse le differenze riscontrate tra i diversi esemplari ed i fossili di altri equidi tridattili. In questi animali sono state individuate alcune faccette articolari presenti con diversa frequenza nei differenti esemplari, mentre altre sono presenti solo in un'unica specie. Nel lavoro sono illustrati i caratteri più importanti relativi alle articolazioni del "polso" e della "caviglia" per i diversi equidi di Kryopigi. Nell'associazione faunistica greca* C. matthewi/nikosi *è in assoluto il taxon più piccolo per massa corporea. Questo equide presenta: magnum e trapezoide strettamente connessi; pisiforme allungato, morfologicamente molto prossimo a quello presente negli equidi monodattili; la faccetta caudale dello scafoide per il lunatum può non essere presente, in contrasto con quanto riscontrato per* H. phlegrae*; maggiori capacità di retroflessione rispetto alle altre specie e una articolazione radiocarpale flessibile. Il tarso presenta una ulteriore faccetta articolare tra il cuneiforme 3 e i cuneiformi 1+2. Sia nel carpo, sia nel tarso l'elemento centrale della linea distale (magnum e cuneiforme 3 rispettivamente) mostra una articolazione extra con l'osso che trasmette il peso al metapodiale mediale (rispettivamente trapezoide e cuneiforme 1+2). In* H. phlegrae *il magnum è più fortemente connesso con l'unciforme, mentre la connessione con il trapezoide è normale e priva di ulteriori faccette articolari. Il movimento relativo nell'articolazione intercarpale durante la flessione del carpo era notevole, come può essere dedotto dalla conformazione della testa articolare del magnum.* H. *cf.* H. brachypus *è rappresentato da materiale molto frammentario. Carpali e tarsali sono morfologicamente diversi da quelli degli altri due equidi tridattili di taglia minore provenienti da Kryopigi. Non è stata individuata in questa forma alcuna articolazione extra nei carpali e nei tarsali. Le differenze riscontrate nel confronto con le altre specie sono prevalentemente individuabili nello sviluppo di alcune aree di inserzione dei muscoli e dei legamenti, oltre che nella morfologia di alcune faccette articolari. La maggior parte delle faccette articolari addizionali è presente nella parte distale dei carpali e dei tarsali, in particolar modo nel magnum e nel cuneiforme 3, che si articolano rispettivamente con il metacarpale e il metatarsale centrale. Alcuni caratteri non sono presenti sempre in alcune specie (ad esempio, la faccetta articolare caudale del cuneiforme 1+2 è presente solo nel 26% degli esemplari di* C. matthewi/nikosi*), ma solo la scoperta di nuovi resti fossili potrà permettere di capire se tali caratteri possano essere considerati sinapomorfi.*

## INTRODUCTION

The limb structure of the equids is generally the same since they acquired a fore and aft type of locomotion during their evolution from the phenacodontid condylarths (Hussain, 1975). However, changes in the limbs, including the carpal and tarsal bones, during their evolution from plantigrade to digitigrades have been depicted for various equids (Gromova, 1952; Sondaar, 1968; Hussain, 1975; Thomason, 1986; Wood et al., 2010). Most of these studies concerned equids at the genus level and in most cases only certain species of each genus were used as representatives. In *Hipparion* s.l. the variation on the anatomy of the carpal and tarsal bones is rarely investigated per locality or even per species (e.g., Gromova, 1952; Gabunja, 1959; Sondaar, 1968; Hussain, 1975; Zhegallo, 1978; Theodorou, 1995; Bernor et al., 1997). Thus, *"due to the lack of systematically gathered data nothing can be said about the amount of interspecific, intraspecific, ontogenetic or sexual variation (...in the carpal and tarsal joints)"* (Tobien, 1992, p. 387).

In the Kryopigi (KRY) Turolian locality (northern Greece; N 40º 02.260´ E 023º 28.190´), four hipparion species have been recognized (Lazaridis, 2010): *Hippotherium* cf. *H. brachypus* Hensel, 1862 is represented by two mandibles and postcranial material, whereas ?*Cremohipparion* sp. cf. *C. mediterraneum* (Roth & Wagner, 1854) is represented only by poorly

preserved postcranial material. The most characteristic and common taxon of the Kryopigi hipparion assemblage is a small-sized hipparion that shares common characters with the small *Cremohipparion matthewi* Abel, 1926 and *Cremohipparion nikosi* Bernor & Tobien, 1989, referred here as *C. matthewi/nikosi*. The fourth hipparion species, *Hipparion phlegrae* Lazaridis & Tsoukala, 2014 is almost equally represented with the latter in the locality.

We study here the variation of the carpal and tarsal bone morphology from the above mentioned Kryopigi hipparion species, apart from ?*Cremohipparion* sp., which is poorly represented. The presence or absence of various articular facets and the shape and size are compared among the various species of Kryopigi and with those from other localities, when available data are known from the literature.

## MATERIAL AND METHODS

About five hundred carpal and tarsal bones are included in this study (stored in LGPUT: Laboratory of Geology and Paleontology, University of Thessaloniki). Several of them have been found articulated with long bones (i.e., metapodials). These findings were used as reference for the allocation of isolated specimens in different size-groups. *H. phlegrae* and the smallest *C. matthewi/nikosi* of Kryopigi were determined from cranial material and *H.* cf. *H. brachypus* from mandibles and metapodials. Few, mostly fragmented, specimens with intermediate size between *H. phlegrae* and *H.* cf. *H. brachypus* are attributed to ?*Cremohipparion* sp. The largest carpal and tarsal bones are attributed to the largest in size species *H.* cf. *H. brachypus* and similarly the smallest ones to *C. matthewi/nikosi*. *Hipparion phlegrae* and ?*Cremohipparion* sp. are the two intermediate in size species of Kryopigi with the former being smaller than the latter and better represented by hundreds dental and bone elements. Thus, from the two remaining size-groups of postcranial bones, the smallest and most numerous one is attributed to *H. phlegrae*.

Even though size overlapping is very limited in all bones studied, in some cases the smallest specimens of *H. phlegrae* may belong to large *C. matthewi/nikosi* individuals and vice versa. Careful observation of these specimens allows us to conclude that they did not show any special morphology that could have affected significantly our results on anatomical differences. Furthermore, ontogenetical bias is possible since there are no clear indications for the recognition of carpal and tarsal bones from young individuals except calcaneus, the tuber calcanei of which is not fused in young individuals. This is checked by comparisons with specimens found articulated with long bones that present not fused epiphyses. These specimens were excluded from the studied material.

Here we describe and compare the most distinctive anatomical characters (all bones illustrated as left side), whereas the general description of the bones and the anatomy nomenclature, especially for *Hipparion* s.l. can be found in Bernor et al. (1997). Scatter-plots of Kryopigi hipparion carpals and tarsals are given as online supplementary information, available at the journal website

## COMPARATIVE ANATOMY

*Carpals*

The bones that form the wrist are divided into two rows, the proximal and distal ones. Medially to laterally, the proximal row consists of the scaphoideum, the lunatum, the pyramidale and the pisiforme, whereas the distal row consists of the trapezium, the trapezoideum, the magnum and the unciforme. Carpal bones together form three articulations: the bones of the proximal row series proximally articulate with the distal articular facets of the radius and distally with the bones of the distal row, which distally articulate with the proximal articular facets of the metacarpals.

Scaphoideum (os scaphoideum, os carpi radiale, os naviculare manus, navicular, radiale): the tubercle for the attachment of the ligamentum obliquum volare portion of the ligamentum carpi volare profundum is narrower in *C. matthewi/nikosi* than in *H. phlegrae* and *H.* cf. *H. brachypus* where it is wide (Fig. 1A). In 15% of *C. matthewi/nikosi* this tubercle is developed toward the caudal side and not as commonly developed toward the medial side. The articular facet for the trapezium is relatively smaller in *C. matthewi/nikosi* than that in *H. phlegrae* and *H.* cf. *H. brachypus*. Especially in the latter, it is very large and of triangular shape (not shown in Fig. 1). At the caudal part of the medial border of the articular facet for the trapezoideum a notch in *H. phlegrae* is present in contrary to the other two species, where it is absent (Fig. 1B). The small caudal portion of the articular facet for medial portion of the radius in *C. matthewi/nikosi* is more transversally developed than in *H. phlegrae*, where it is less expanded to the lateral side (Fig. 1C).This is also related to small differences in the development of the articular facet for the trapezium. At the medial aspect, a sulcus is frequently better developed in *C. matthewi/nikosi* among the attachment sites for the ligaments than in the other two species.

Lunatum (os carpi intermedium, os lunatum, lunar, lunate, semilunar, intermedium): the ratio of the maximal anteroposterior diameter to the anterior maximal width is significantly different ($p=0.0006$) between the two small-sized species, *H. phlegrae* and *C. matthewi/nikosi*, the latter being more elongated. In cranial aspect, the proximo-lateral border of the bone is curved downward in *H. phlegrae* whereas it is more straight in *C. matthewi/nikosi* apart from few specimens, where it is slightly curved (Fig. 2A). The caudal extension of the articular facet for the radius is better and more frequently developed in *C. matthewi/nikosi* than in *H. phlegrae* (Fig. 2B). This facet is absent in 10% of the former species, whereas in the latter it is absent in 33%. The caudal distal articular facet for the scaphoideum (not shown in Fig. 2) is better developed and always clearly distinguished in *H. phlegrae* than in *C. matthewi/nikosi*. In 50% of the *C. matthewi/nikosi* specimens it has distinct contour and about same size of the cranial articular facet for the scaphoideum; in 25% there is a similar in shape rough area instead of the articular facet, whereas in the remaining 25% the bone surface is rough without contour. The distal articular facet for the pyramidale is larger and different in shape in *H.*

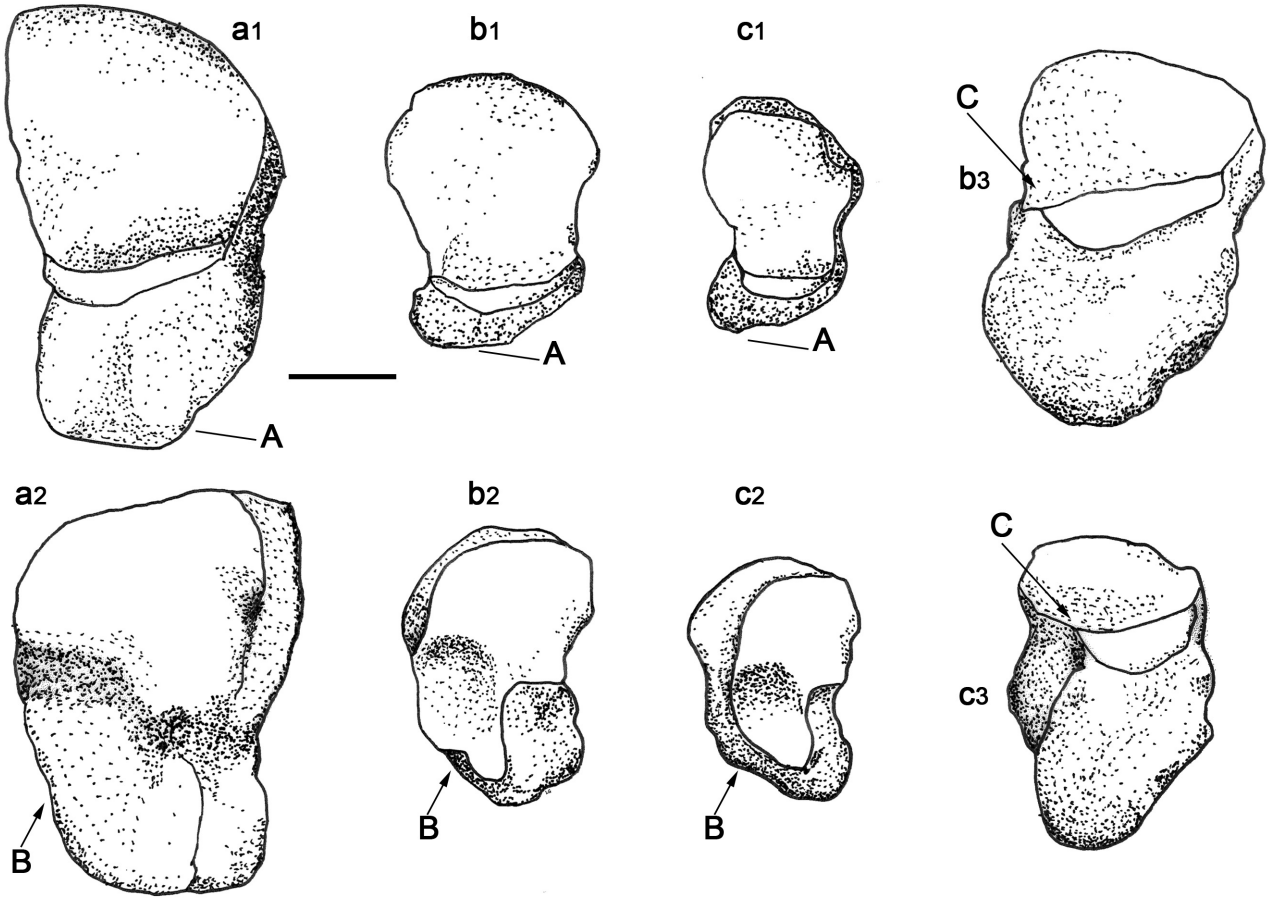


Fig. 1 - Scaphoideum. Proximal aspect (scale bar corresponds to 10 mm): a1: *H.* cf. *H. brachypus*, KRY4528; b1: *H. phlegrae*, KRY4177; c1: *C. matthewi/nikosi*, KRY6846. Distal aspect: a2: *H.* cf. *H. brachypus*, KRY4528; b2: *H. phlegrae*, KRY4177; c2: *C. matthewi/nikosi*, KRY6846. Oblique caudal view (not in scale): b3: *H. phlegrae*, KRY4177; c3: *C. matthewi/nikosi*, KRY6846. A: tubercle for the attachment of the ligamentum obliquum volare portion of the ligamentum carpi volare profundum; B: caudal part of the medial border of the articular facet for the trapezoideum; C: caudal portion of the articular facet for medial portion of the radius.

*phlegrae* (Fig. 2C). Differences are also noticed at the attachment site of the ligamentum carpi volare (cranial) profundum (Fig. 2D) and at the caudal end of the proximal articular facet for the radius, which is more prominent in *H. phlegrae*.

Pyramidale (os carpi ulnare, os triquetrum, os cuneiforme, cuneiform, cubital, pyramidal): the small articular facet for the pisiforme is more developed and rounded in shape in *C. matthewi/nikosi* than in *H. phlegrae*, where it is more transversally developed, small and angular (Fig. 3A), following the differences noted also in the corresponding facet of the pisiforme. In one specimen of *H. phlegrae*, the large (Fig. 3B) and the small articular facets for the pisiforme are connected. The distal articular facet for the lunatum (Fig. 3C), in respect to the

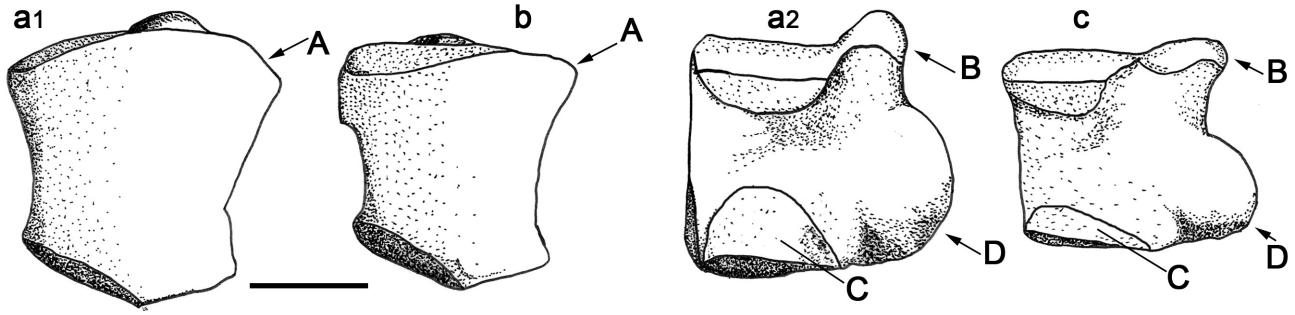


Fig. 2 - Lunatum. Cranial aspect (scale bar corresponds to 10 mm): a1: *H. phlegrae*, KRY4266; b: *C. matthewi/nikosi*, KRY3843. Lateral aspect: a2: *H. phlegrae*, KRY4266; c: *C. matthewi/nikosi*, KRY3844. A: lateral end of the proximal border of the cranial aspect; B: caudal end of the proximal articular facet for the radius; C: distal articular facet for pyramidale; D: attachment site of the ligamentum carpi volare (cranial) profundum.

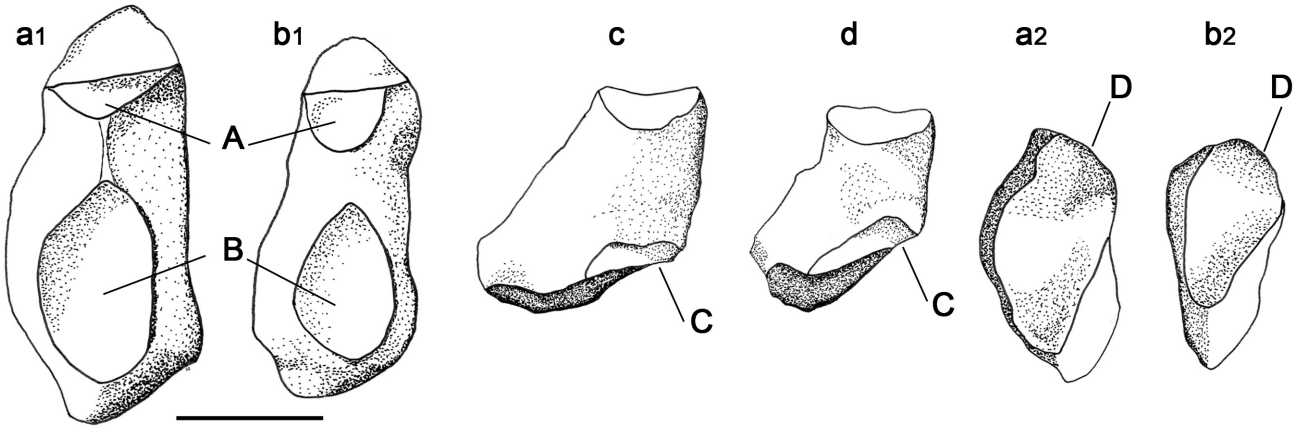


Fig. 3 - Pyramidale. Caudal aspect (scale bar corresponds to 10 mm): a1: *H. phlegrae*, KRY5402; b1: *C. matthewi/nikosi*, KRY5382. Medial aspect (not in scale): c: *H. phlegrae*, KRY6168; d: *C. matthewi/nikosi*, KRY2365. Distal aspect (not in scale): a2: *H. phlegrae*, KRY5402; b2: *C. matthewi/nikosi*, KRY5382. A: small articular facet for the pisiforme; B: large articular facet for the pisiforme; C: distal articular facet for the lunatum; D: articular facet for the unciforme.

proximal one, is more developed craniocaudally in *C. matthewi/nikosi* than in *H. phlegrae*, where they are almost equal. The bipartite articular facet for the unciforme (Fig. 3D) has a less developed caudal portion in *C. matthewi/nikosi*, thus a more triangular shape in comparison with *H. phlegrae*, where it is wider and more developed towards the large articular facet for the pisiforme.

Pisiforme (os carpi accessorium, os pisiforme, pisiform): the shape of the pisiforme tends to be more elongated in the smallest species *C. matthewi/nikosi*, while it is higher and less elongated in *H. phlegrae* and *H.* cf. *H. brachypus* (Fig. 4a1, b1, c1). The null hypothesis for same mean ratio of height/anteroposterior diameter for *C. matthewi/nikosi* and *H. phlegrae*, is rejected with t-test (p=0.0002).

In caudal aspect the small articular facet for the proximal portion of the lateral radius (ulnar) trochlea is frequently more developed towards the proximal margin in *H. phlegrae* than it is in *C. matthewi/nikosi* where it is always retracted (Fig. 4, see arrow). Furthermore, it is mediolaterally more expanded in the former than in the latter species. In *H.* cf. *H. brachypus* this articular facet is similar to *H. phlegrae* but relatively large and more proximodistally expanded. The shape of the smaller facet for the pyramidale is triangular in *H.* cf. *H. brachypus* whereas it is more mediolaterally extended in the other two species (Fig. 4c). In *C. matthewi/nikosi* this articular facet is frequently less developed and more curved in comparison with *H. phlegrae*.

Trapezium (os carpale I, os multangulum majus, distal carpal 1, os trapezium, os carpale primum): since only one specimen of *H. phlegrae* has been found, no comparisons are possible.

Trapezoideum (os carpale II, os multangulum minus, os trapezoideum, trapezoid, os carpale secundum, distal carpal 2): few specimens occur in the material

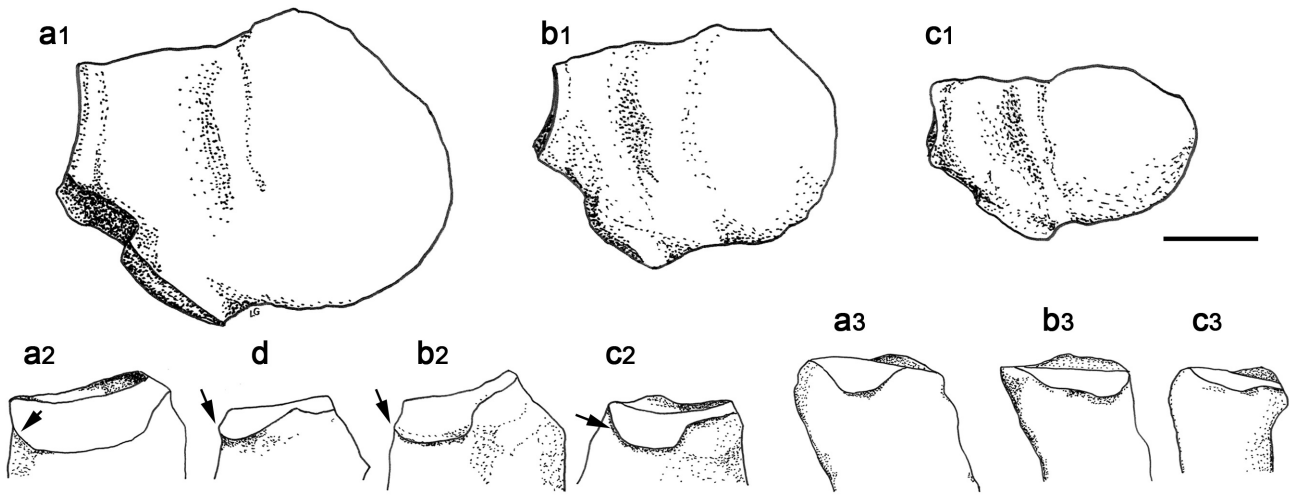


Fig. 4 - Pisiforme. Cranial aspect (scale is equal to 10 mm): a1: *H.* cf. *H. brachypus*, KRY3804; b1: *H. phlegrae*, KRY5733; c1: *C. matthewi/nikosi*, KRY2346. The small articular facet for the proximal portion of the lateral radius (ulnar) trochlea (caudal aspect, not in scale, see arrow): a2: *H.* cf. *H. brachypus*, KRY3804; d: *H. phlegrae*, KRY2850; b2: *H. phlegrae*, KRY5733; c2: *C. matthewi/nikosi*, KRY2346. The smaller facet for the pyramidale (distal aspect, not in scale): a3: *H.* cf. *H. brachypus*, KRY3804; b3: *H. phlegrae*, KRY5733; c3: *C. matthewi/nikosi*, KRY2346.

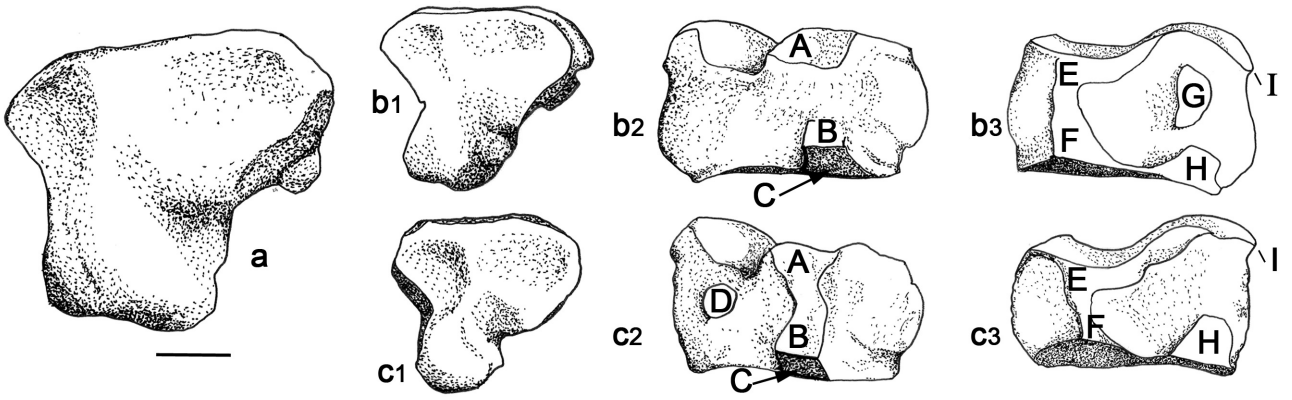


Fig. 5 - Magnum. Proximal aspect (scale bar corresponds to 10 mm): a: *H.* cf. *H. brachypus*, KRY4539; b1: *H. phlegrae*, KRY6664; c1: *C. matthewi/nikosi*, KRY3811. Medial aspect (not in scale): b2: *H. phlegrae*, KRY6664; c2: *C. matthewi/nikosi*, KRY3811. Lateral aspect: b3: *H. phlegrae*, KRY6664; c3: *C. matthewi/nikosi*, KRY3811. A: proximal articular facet for the trapezoideum; B: distal articular facet for the trapezoideum; C: articular facet for the McII; D: caudal articular facet for the trapezoideum; E: proximocranial articular facet for the unciforme; F: distocranial articular facet for the unciforme; G: proximocaudal articular facet for the unciforme; H: distocaudal articular facet for the unciforme; I: caudal articular head for the lunatum.

and although there is one specimen of *C. matthewi/nikosi* found articulated with the rest fore-leg and three specimens of *H. phlegrae*, morphological differences cannot be considered. On the other hand, following the differences found in the articular facets for trapezoideum in magnum, there must be analogous differences also in the trapezoideum. In its general shape the trapezoideum of *C. matthewi/nikosi* appears to be less wide than that of *H. phlegrae*.

Magnum (os carpale III, os carpale tertium, distal carpal 3, os capitatum): in *C. matthewi/nikosi* the articular facets for the trapezoideum (Fig. 5A, B) are confluent in about 20%. At the caudal part of the medial surface, a well developed third articular facet for the trapezoideum (Fig. 5D) is present in 13% of *C. matthewi/nikosi*. In several specimens of this species there is a rough prominent area in the same place instead of a distinct articular facet. It is noticeable that when such an articular facet is found in *C. matthewi/nikosi* the other two cranial articular facets for the trapezoideum are always confluent. In the other two species these characters do not occur in the studied material. At the lateral side, the proximal and distal articular facets for the unciforme (Fig. 5E, F) are confluent in *H. phlegrae* and frequently in *C. matthewi/nikosi*, whereas in *H.* cf. *H. brachypus* they are separated (not shown in Fig. 5, representing the typical hipparion morphology; see Bernor et al., 1997). In addition to these facets for the articulation of the unciforme there is a third caudal one (Fig. 5G) in two specimens of *H. phlegrae*.

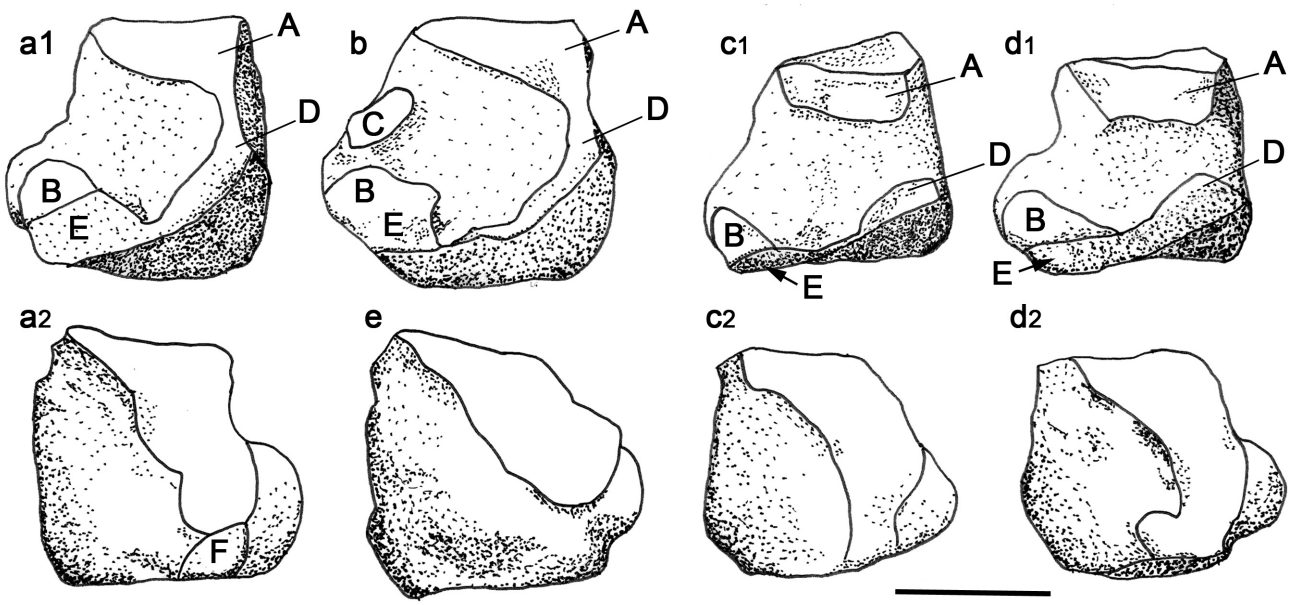


Fig. 6 - Unciforme. Caudal aspect (scale bar corresponds to 10 mm): a1: *H. phlegrae*, KRY3769; b: *H. phlegrae*, KRY2224; c1: *C. matthewi/nikosi*, KRY5844; d1: *C. matthewi/nikosi*, KRY2357. Cranial aspect: a2: *H. phlegrae*, KRY3769; e: *H. phlegrae*, KRY3771; c2: *C. matthewi/nikosi*, KRY5844; d2: *C. matthewi/nikosi*, KRY2357. A: proximal facet for the magnum; B: lateral articular facet for the magnum; C: additional articular facet for the magnum; D: medial articular facet for the third metacarpal; E: lateral articular facet for the third metacarpal; F: articular facet for the fifth metacarpal.

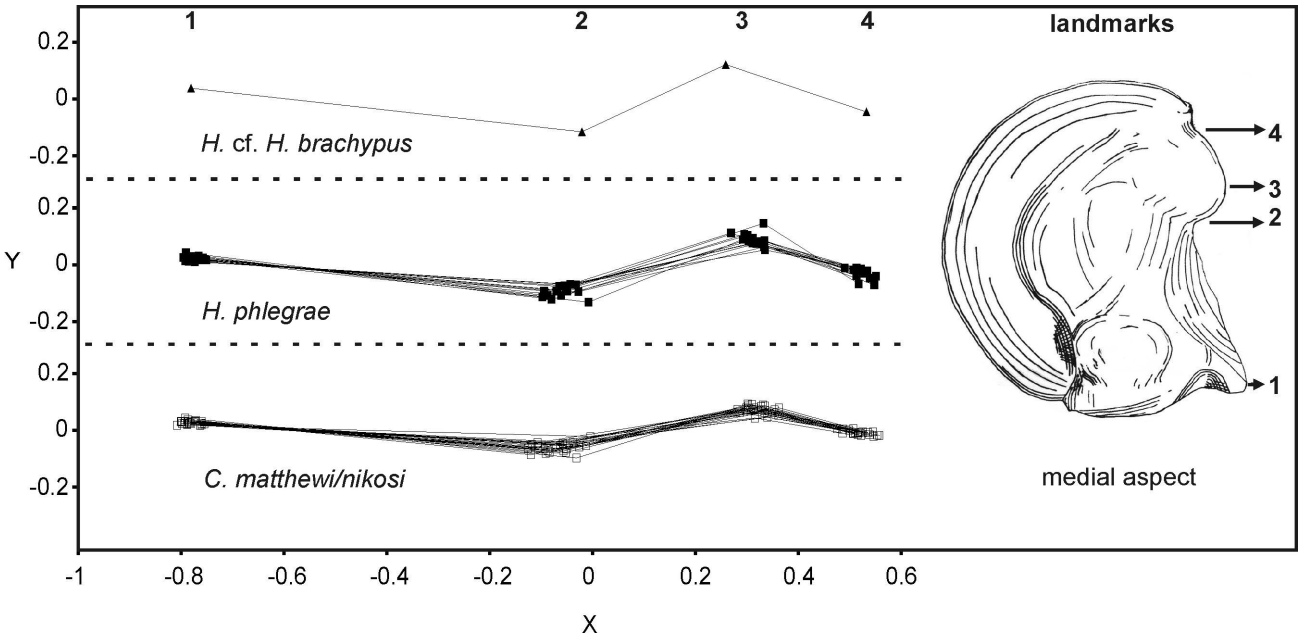


Fig. 7 - Landmark profile (1-4 landmarks) of the protuberance for the ligamentum colli medialis brevis on the medial aspect of the astragalus. Procrustes method used for data fitting.

This is consistent with the morphology found in the unciforme. The fossa synovialis of the articular facet for the third metacarpal is less developed in *C. matthewi/nikosi* than in the other two species. In *H. phlegrae* the caudal articular head for the lunatum is frequently more developed caudally than in *C. matthewi/nikosi*.

Unciforme (os carpale IV, os carpale quartum, hamate, distal carpal 4, os hamatum): in *H. phlegrae* it is higher in respect with the mediolateral diameter of the bone than that of *C. matthewi/nikosi* (p=0.0026). The proximal articular facet for magnum (Fig. 6A) and the medial articular facet for third metacarpal (Fig. 6D) are commonly confluent in *H. phlegrae* (56%), which is consistent with the morphology of the magnum. In *C. matthewi/nikosi* the medial (Fig. 6D) and lateral (Fig. 6E) articular facets for the third metacarpal are commonly confluent and the lateral one is commonly significantly smaller than the medial facet. In *H. phlegrae* they are almost equally developed and frequently separated. The angle between the medial articular facet for the third metacarpal and the distal articular facet for the fourth metacarpal is larger

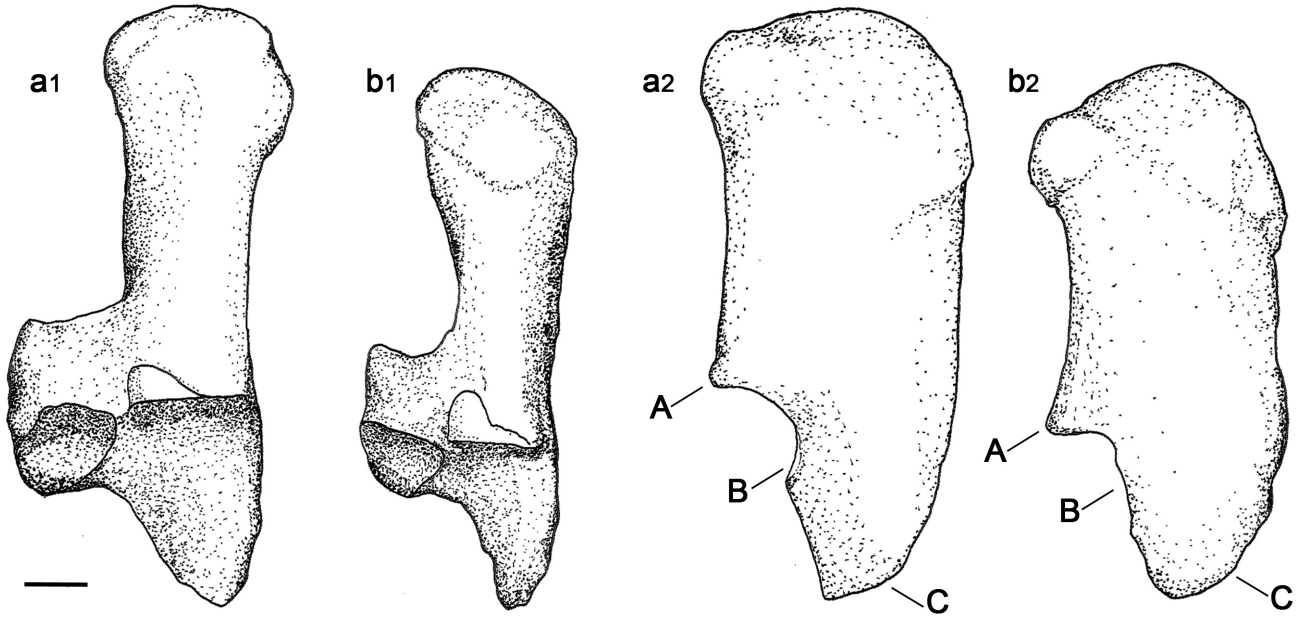


Fig. 8 - Calcaneum. Cranial aspect (scale bar corresponds to 10 mm): a1: *H. phlegrae*, KRY3907; b1: *C. matthewi/nikosi*, KRY2830. Lateral aspect: a2: *H. phlegrae*, KRY3907; b2: *C. matthewi/nikosi*, KRY2830. A: processus coracoideus; B: lateral articular facet for the magnum; C: distal end of the calcaneum.

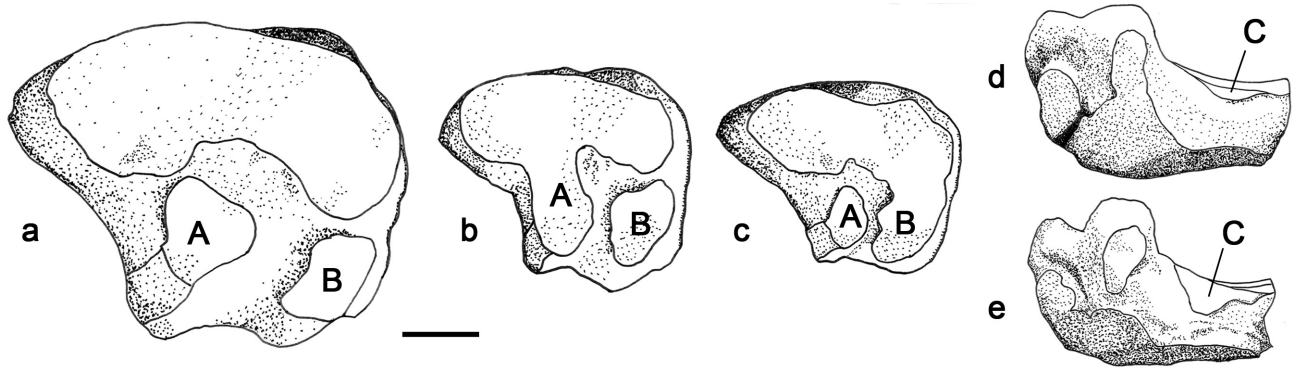


Fig. 9 - Naviculare. Distal aspect (scale is equal to 10 mm): a: *H.* cf. *H. brachypus*, KRY3862; b: *H. phlegrae*, KRY6303; c: *C. matthewi/nikosi*, KRY3648. Lateral aspect (not in scale): d: *H. phlegrae*, KRY3865; e: *C. matthewi/nikosi*, KRY3654. A: laterocaudal lanceolate process of the distal articular facet; B: mediocaudal articular facet for the cuneiforme 1+2; C: cranial articular facet for the cuboideum.

in *H. phlegrae* than in *C. matthewi/nikosi*, following the morphology of the third metacarpal (not shown in Fig. 6). An additional small elliptical articular facet for the magnum (Fig. 6C) between the other two facets (Fig. 6A, B) is found in two specimens of *H. phlegrae* and none in *C. matthewi/nikosi*. This is consistent with the morphology of the magnum. The articular facet for the fifth metacarpal (Fig. 6F) is well developed and distinct only in one specimen of *H. phlegrae*, while in the smaller species *C. matthewi/nikosi* it is commonly less developed and distinct.

*Tarsals*

Astragalus (os tarsi tibiale, talus tibiale): among the *Hipparion* species of Kryopigi there are differences in respect to the shape and the dimensions of the astragalus. The largest *H.* cf. *H. brachypus* is relatively wider than the two smaller species. *H.* cf. *H. brachypus* and *H. phlegrae* have better developed proturberance for the ligamentum colli medialis brevis than *C. matthewi/nikosi* (Fig. 7).

Calcaneum (os tarsi fibulare, os calcis, calcaneus): the articular facet for the astragalus at the distal aspect of the sustentaculum tali is flatter in *C. matthewi/nikosi* than in *H. phlegrae*, where it is curved toward the processus coracoideus (Fig. 8A). The smaller distal articular facet for the astragalus is laterally more straight in *C. matthewi/nikosi* than in *H. phlegrae*, whereas in the latter it has a laterally semi-circular contour (Fig. 8B). The distal end of the calcaneum is more pointed in *C. matthewi/nikosi* than in *H. phlegrae* where it is flatter due to differences in the development (curvature) of the lateral contour of the distal articular facet for the cuboideum (Fig. 8C).

Naviculare (os tarsi centrale, os naviculare pedis, navicular, scaphoideum, centrale): on the distal aspect, the laterocaudal lanceolate process of the distal articular facet (Fig. 9A) as well as the mediocaudal articular facet for the cuneiform 1+2 (Fig. 9B) are in *H.* cf. *H. brachypus* isolated from the cranial portion of the distal articular facet. In *H. phlegrae* the mediocaudal articular facet for the cuneiform 1+2 is isolated in 27%, whereas in *C. matthewi/nikosi* it is always confluent with the distal articular facet. Furthermore, in 13% of *C. matthewi/nikosi* the laterocaudal lanceolate process of the distal articular facet is isolated, but never in *H. phlegrae*.

At the lateral surface of the bone, in 50% of the *C. matthewi/nikosi* specimens the caudal part of the proximal articular facet for the cuboideum is extending distally

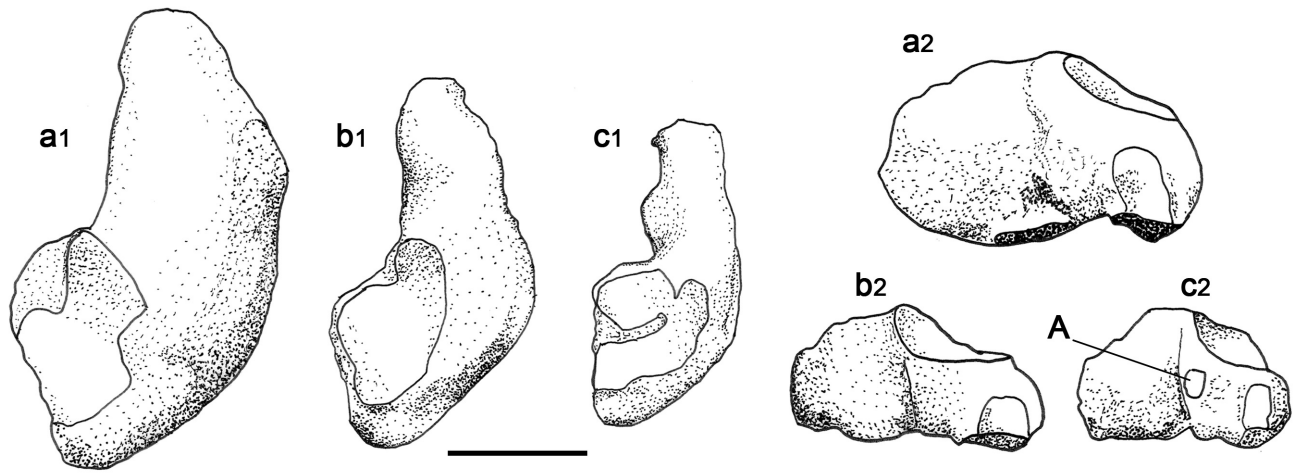


Fig. 10 - Cuneiforme 1+2. Proximal aspect (scale bar corresponds to 10 mm): a1: *H.* cf. *H. brachypus*, KRY6929; b1: *H. phlegrae*, KRY3777; c1: *C. matthewi/nikosi*, KRY3775. Craniolateral aspect (not in scale): a2: *H.* cf. *H. brachypus*, KRY6929; b2: *H. phlegrae*, KRY3777; c2: *C. matthewi/nikosi*, KRY3775. A: articular facet for the cuneiforme 3.

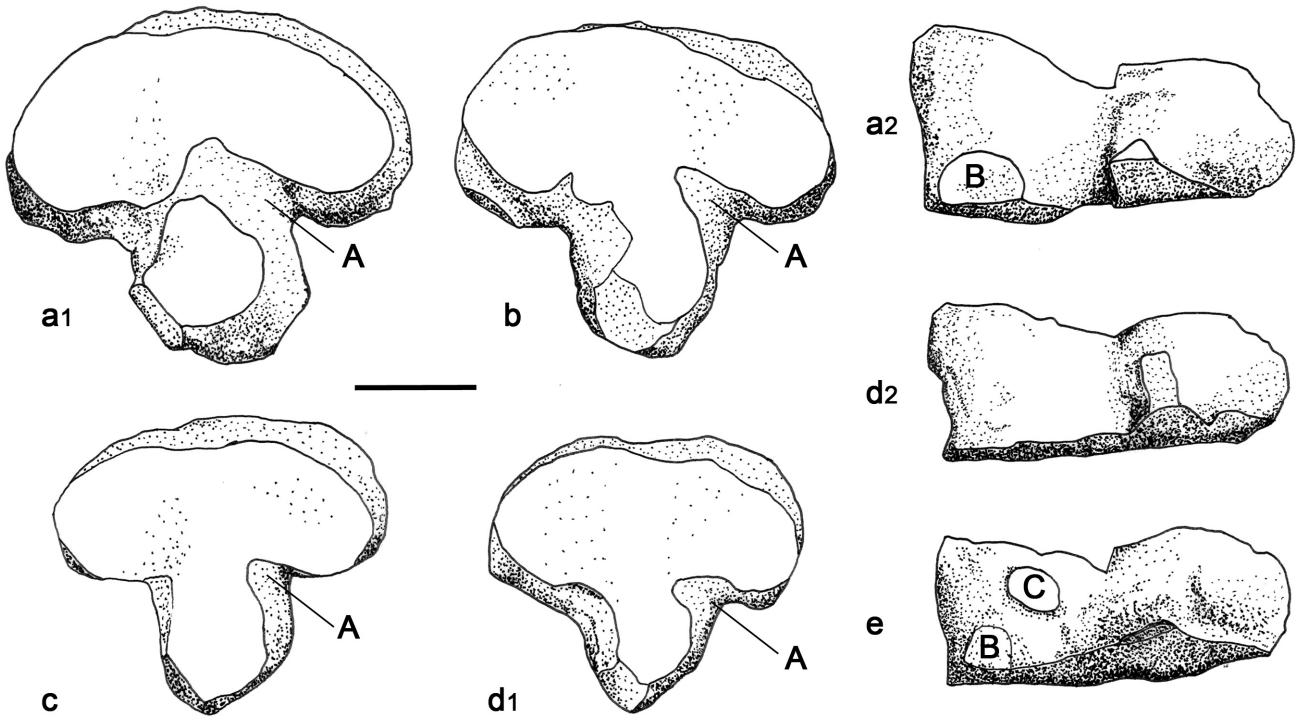


Fig. 11 - Cuneiforme 3. Proximal aspect (scale bar corresponds to 10 mm): a1: *H. phlegrae*, KRY1766; b: *H. phlegrae*, KRY1854; c: *C. matthewi/nikosi*, KRY3665; d1: *C. matthewi/nikosi*, KRY3666. Medial aspect (not in scale): a2: *H. phlegrae*, KRY1766; d2: *C. matthewi/nikosi*, KRY3666; e: *C. matthewi/nikos*i, KRY4265. A: fossa synovialis of the proximal articular facet; B: articular facet for the second metatarsal; C: caudal articular facet for the cuneiforme 1+2.

(Fig. 9C). The remaining specimens lack this extension like in *H. phlegrae* and *H.* cf. *H. brachypus*. The medial and lateral processes of the naviculare are more symmetrical in the large species *H.* cf. *H. brachypus*, while in the other two smaller species the medial one is more prominent.

Cuneiforme 1+2 (os tarsale I+II, small cuneiforme, os tarsale primum & secundum, os cuneiforme mediale & intermedium, mesocuneiform+entocuneiform, mesentocuneiform): a small elliptical articular facet for the cuneiforme 3 (Fig. 10A) is present at the craniolateral aspect of the bone in one specimen of *C. matthewi/nikosi* (17%). The articular facet for the cuboideum is less convex and the articular facets for the second metatarsal are closer to each other in *C. matthewi/nikosi* than the other two species. In *H.* cf. *H. brachypus* the fossa synovialis invades the caudomedial articular facet for the second metatarsal (not shown in Fig. 10).

Cuneiforme 3 (os tarsale III, large cuneiforme, os tarsale tertium, os cuneiforme laterale, os cuneiforme tertium, ectocuneiform): in two specimens (20%) of *H. phlegrae* the fossa synovialis (Fig. 11A) in both the proximal and the distal surfaces extends mediolaterally separating in two parts the articular facets for the naviculare and the third metatarsal, respectively. In *C. matthewi/nikosi* the incisions of the fossae synovialis are less developed. An articular facet for the second metatarsal (Fig. 11B) is developed at the caudal part of the medial surface of the bone in 90% of the *H. phlegrae* specimens and only in 32% of *C. matthewi/nikosi*. In the latter, when this articular facet is present it is less developed. The caudal articular facet for the cuneiforme 1+2 (Fig. 11C)

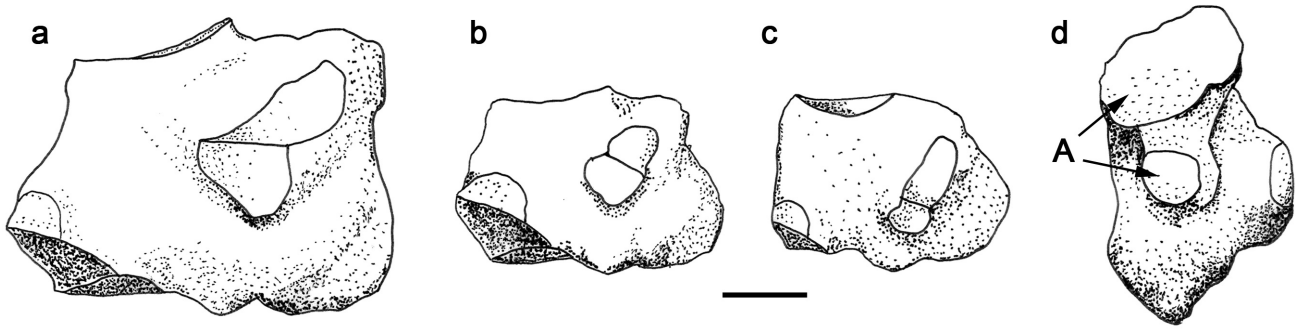


Fig. 12 - Cuboideum. Medial aspect (scale bar corresponds to 10 mm): a: *H.* cf. *H. brachypus*, KRY3845; b: *H. phlegrae*, KRY6304; c: *C. matthewi/nikosi*, KRY1991. Distal aspect (not in scale): d: *H. phlegrae*, KRY2865. A: articular facet for the fourth metatarsal.

is found only in 26% of the *C. matthewi/nikosi* specimens and in none of *H. phlegrae.* Only in two specimens of *C. matthewi/nikosi* it co-exists with the articular facet for the second metatarsal (10%).

Cuboideum (os tarsale IV, os tarsale quartum, os cuboideum): the larger caudal tuberosity for the attachment of the ligamentum collaterale tarsi longum plantare is more strongly developed in *H. phlegrae* and *H.* cf. *H. brachypus* than in *C. matthewi/nikosi*. The posterior articular facet for the naviculare and the cuneiforme 3 are narrower in *C. matthewi/nikosi* than in the other two species. The articular facet for the fourth metatarsal is more frequently separated in two almost equal parts in *H. phlegrae* (50%) than in *C. matthewi/nikosi* (30%) (Fig. 12A).

## DISCUSSION

The carpals and tarsals of the Kryopigi hipparion species exhibit several anatomical differences. Many of these observations have also been noticed in other hipparion species from various localities or in the extant *Equus*.

In the carpus, the magnum of *C. matthewi/nikosi* is more tightly connected with the trapezoideum, whereas in *H. phlegrae* the magnum is more tightly connected to the unciforme since the latter may present a third articular facet for the magnum. This facet has been illustrated by Zhegallo (1978) in *H. theobaldi mogoicum* Zhegallo, 1978, where in the figured specimen the proximal articular facet for the magnum and the medial articular facet for the third metacarpal are confluent, as similarly noted in *H. phlegrae*. Furthermore, in this subspecies the lunatum shows a caudal elevation at the posterior of the proximal articular facet for the radiocarpal joint, which was also illustrated by Zhegallo (1978). This elevated morphology is considered by Bernor et al. (1997) to be related with enlarged retroflexion ability of the radiocarpal joint. In the Höwenegg *H. primigenium* lunatum, the articulation radiocarpea also shows increased retroflexion ability. In *H. phlegrae* this extension is often absent (33%), whereas in *C. matthewi/nikosi* it is commonly present (90%). In *H. phlegrae* significant flexion seems to take place on the intercarpal joint due to the well developed caudal articular head of the magnum, whereas in *C. matthewi/nikosi* the intercarpal joint is not so flexible. In lunatum, the caudal facet for the scaphoideum is well developed in Höwenegg *H. primigenium* von Meyer, 1833 and in Kryopigi *H. phlegrae*, whereas in the smallest species from the Kryopigi it may be absent. In *H. primigenium* the caudal facet for the scaphoideum and the caudal extension of the proximal articular facet are always present, in contrast to Recent *Equus* where both are absent. In *H. phlegrae* the extension is frequently absent, whereas the caudal facet for the scaphoideum is always present. In *C. matthewi/nikosi* the extension is absent only in 10% and the caudal articular facet for the scaphoideum is absent in at least 25%.

In unciforme, medial and lateral articular facets for the third metacarpal are commonly confluent in *C. matthewi/nikosi*. Especially the lateral one may be of limited development in respect with the medial articular facet. This lateral facet for the third metacarpal is absent in *Neohipparion*, which is an evolved cursorial tridactyl and considered functionally monodactyl horse by Sondaar (1968). In *H. phlegrae* unciforme, the proximal articular facet for the magnum and the medial articular facet for the third metacarpal are commonly confluent. The medial and lateral articular facets for the third metacarpal are almost equally developed and frequently separated by a fossa synovialis. These characters give evidence for tight connection of the unciforme to the magnum and the third metacarpal. In *H. primigenium*, the unciforme presents isolated proximal articular facet for magnum, confluent medial and lateral articular facets for the third metacarpal, whereas the third additional articular facet for the magnum, which is noted in *H. phlegrae*, is absent (Bernor et al., 1997). The articular facet for the fifth metacarpal is exceptionally clearly developed in one specimen of *H. phlegrae*. This articular facet is indistinct in *H. primigenium* from Höwenegg according to Bernor et al. (1997).

In magnum, the third articular facet for the trapezoideum, at the caudal part of the medial surface, is considered by Sondaar (1968) as characteristic in advanced monodactyl horses, indicating tighter connection of these bones. The articular facet figured by Sondaar (1968) in *Pliohippus* is placed more distally, in touch with the distal articular surface. Thus, it differs from that reported here, which however is identical with that of *H. longipes* Gromova, 1952 figured by Gromova (1952). Moreover, she reported that in *H. longipes*, this articular facet for the trapezoideum is present in two out of four specimens and in *H. elegans* Gromova, 1952 it was found only in a single one of 139 specimens. In *Equus* it is absent in about 3% (in 33 specimens it was found in 30, in two a rough prominent area existed and in one it was definitely absent) and there is always in zebras and hemiones. According to Kovalevsky (in Gromova, 1952) it is absent in Pikermi hipparions. In *C. matthewi/nikosi* it is present in 13% and when it occurs the other two articular facets for the trapezoideum are confluent. The other two hipparion species from Kryopigi do not show this articular facet. Its presence may be related to more cursorial pattern of locomotion since it is commonly developed more frequently in the more cursorial tridactyl (i.e., *H. longipes*) or monodactyl horses.

Regarding pisiforme, it is more elongate and shorter in extant *Equus* than in *Hipparion*; it presents a deeper furrow for the musculus extensor carpi ulnaris (Gromova, 1952; Sondaar, 1968; Bernor et al., 1997). Moreover, the articular facets for the pyramidale and for the lateral ulnar radius trochlea are closer in *Equus* than in *Hipparion*. Sondaar (1968) considered this character as a potential general trend for the lineage *Mesohippus-Equus*. In *C. matthewi/nikosi* there is a stronger tendency for shorter distance between these two articular facets, unlike other Kryopigi hipparions.

In pyramidale the distal portion of the articular facet for the unciforme is longer in *H. primigenium* from Höwenegg than in extant *Equus* (Bernor et al., 1997). In *H. phlegrae* this distal portion is more developed than in *C. matthewi/nikosi*.

The magnum, the trapezoideum and the unciforme are found to exhibit varying morphology between *H. phlegrae*

and *C. matthewi/nikosi*. In younger horses the distal row bones are commonly well articulated and probably act together with limited movements between them (Sondaar, 1968). *H. phlegrae* shows relatively limited movement between the magnum and the unciforme, which transmits the weight to the fourth and the third metacarpals. The magnum in *C. matthewi/nikosi* is tightly connected to the trapezoideum, which transmits the weight to the second metacarpal.

The astragalus and the calcaneus of the Kryopigi hipparions present differences in the shape of the protuberance for ligamentum colli medialis brevis and the articular facet for the astragalus and the cuboideum, respectively. The cuneiformes show tighter connection to each other in the Kryopigi *C. matthewi/nikosi*. The small elliptical articular facet for the cuneiforme 3 at the craniolateral aspect of the cuneiforme 1+2 and the corresponding one in the cuneiforme 3 have also been reported in *C. moldavicum* Gromova, 1952 from Taraklyia (Gromova, 1952). These two hipparions are considered phylogenetically related and the presence of this articulation might be a synapomorphic character for the *Cremohipparion* lineage. However, more data are needed to check this hypothesis.

In cuneiforme 3 the articular facet for the second metatarsal, developed in caudal part of the medial surface of the bone is more frequently present in *H. phlegrae* than it is in *C. matthewi/nikosi* and has also been reported in Pavlodar *H. elegans* (Gromova, 1952). On the other hand, *H. primigenium* shows no evidence for the presence of this articular facet and the one for the second cuneiforme (Bernor et al., 1997). The mediolaterally extending fossa synovialis found in *H. phlegrae* is similarly developed in *Equus* (Tobien, 1992). In *H.* cf. *H. brachypus* naviculare, the fossa synovialis is better developed than in *H. phlegrae* and *C. matthewi/nikosi*. In the latter two this fossa is of similar size. It is more frequently found in *H. phlegrae*, which is larger in body-mass. In *H. phlegrae* cuboideum, distal articular facet for the fourth metatarsal is frequently divided by fossa synovialis.

The bones of the distal carpal and tarsal row (especially the magnum and the cuneiforme 3) have additional articular facets more frequently than those of the proximal row.

## CONCLUSIONS

Several morphological characters appear in carpals and tarsals with various frequencies among the different Kryopigi hipparion species. Thus, the presence or absence of a particular character in a single specimen is not always of taxonomical use. Nevertheless, some characters are present or absent in certain species (e.g., the caudal articular facet for the cuneiforme 1+2 is present only in 26% of *C. matthewi/nikosi* specimens). These characters might reveal to be synapomorphic when more data will be available. The distal carpal and tarsal row and especially the magnum and the cuneiforme 3 are the most varying in respect with the presence/absence of additional articular facets.

According to the lunatum morphology of *H. primigenium, H. phlegrae, C. matthewi/nikosi* and *Equus*, the coexistence of the caudal extension of the proximal articular facet and the caudal facet for the scaphoideum probably has weak or even no correlation to each other and may be related to different functions.

*C. matthewi/nikosi* is the smallest in body-mass of the Kryopigi hipparion assemblage. It presents: tightly connected magnum to trapezoideum; elongated pisiforme that is closer morphologically to the monodactyl horses; the caudal facet for the scaphoideum in lunatum may be absent in contrast to *H. phlegrae*; increased retroflexion ability and a flexible radiocarpal joint. Tarsus presents an additional articulation between the cuneiforme 3 and the cuneiforme 1+2. In both carpus and tarsus, the central bone of the distal row (magnum and cuneiforme 3 respectively) shows an extra articulation with the bone which transmits the weight to the medial metapodial (trapezoideum and cuneiforme 1+2 respectively).

In *H. phlegrae* the magnum is more tightly connected with the unciforme, whereas its connection with the trapezoideum is normal, without any additional articular facets. Due to the shape of the articular head of the magnum, it can be concluded that relative movement in intercarpal joint was significant during the carpus flexion.

*H.* cf. *H. brachypus* is represented by scarce material. Carpals and tarsals are morphologically different from those of the other two smaller Kryopigi hipparions. No additional articulations among the various carpal and tarsal bones have been noticed. The differences from other species occur mainly in the development of some attachment sites for ligaments and muscles and the shape of some articular facets.

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## REFERENCES

Abel O. (1926). Die Geschichte der Equiden auf dem Boden Nordamericas. *Verhandlungen der Zoologisch-Botanischen Gesellschaft*, 74: 159-164.

Bernor R.L. & Tobien H. (1989). Two small species of *Cremohipparion* (Equidae, Mamm.) from Samos, Greece. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie,* 29: 207-226.

Bernor R.L., Tobien H., Hayek L.-A.C. & Mittmann H.-W. (1997). *Hippotherium primigenium* (Equidae, Mammalia) from the late Miocene of Höwenegg (Hegau, Germany). *Andrias*, 10: 1-230.

Gabunja L. (1959). Histoire du genre *Hipparion*. Moscow: Academie Science Géorgie Institut Paléobiologie. 425 pp. (in Russian).

Gromova V. (1952). Gippariony (Rod *Hipparion*). *Trudȳ Paleontologičeskogo instituta. Akademiá nauk SSR*, 36. 478 pp. (in Russian).

Hensel R. (1862). Über die Reste einiger Säugetierarten von Pikermi in der Münchener Sammlung. *Monatsberichte der Akademie der Wissenschaften*, 27: 560-569.

Hussain S.T. (1975). Evolutionary and functional anatomy of the pelvic limb in fossil and recent Equidae (Perissodactyla, Mammalia). *Anatomia, Histologia, Embryologia*, 4: 179-222.

Lazaridis G. (2010). Contribution to the study of the Neogene Perissodactyles from Kryopigi (Kassandra, Chalkidiki, Greece). *M.Sc. thesis, Geology School, Aristotle University of Thessaloniki*. 365 pp. (in Greek with English summary).

Lazaridis G. & Tsoukala E. (2014). *Hipparion phlegrae* sp. nov. (Mammalia, Perissodactyla): A new species from the Turolian locality of Kryopigi (Kassandra, Chalkidiki, Greece). *Journal of Vertebrate Paleontology*, 34: 164-178.

Meyer H. von (1833). Beiträge zur Petrefactenkunde, Fossile Säugethiere. *Nova acta Academie caesarense Leopoldino-Carolinae germanicae naturae curiosum*, 16: 423-516.

Roth J.R. & Wagner A.J. (1854). Die fossilen Knochen-Ueberreste von Pikermi in Griechenland. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Physikalische Klasse*, 7: 371-464.

Sondaar P. (1968). The osteology of the manus of fossil and recent Equidae with special reference to phylogeny and function. *Eerste Reeks, Deel* XXV, 1.75 pp.

Theodorou E.G. (1995). Observations on the carpus and tarsus of *Hipparion* from Pikermi (Attica, Greece). *Annales Géologiques des Pays Helléniques*, 37: 921-980.

Thomason J.J. (1986). The functional morphology of the manus in tridactyl equids *Merychippus* and *Mesohippus*: paleontological inferences from neontological models. *Journal of Vertebrate Paleontology*, 6: 143-161.

Tobien H. (1992). On the fossae nudatae in the basipodia of *Equus* and of some fossil tridactyl horses (Equidae, Mammalia). *Annales zoologici Fennici*, 28: 381-400.

Wood A.R., Bebej R.M., Manz C.L., Begun D.L. & Gingerich P.D. (2010). Postcranial functional morphology of *Hyracotherium* (Equidae, Perissodactyla) and locomotion in the earliest horses. *Journal of Mammalian Evolution*, 18: 1-32.

Zhegallo V.I. (1978). The hipparions of Central Asia. *Joint Soviet-Mongolian Paleontological Expedition, Transactions,* 7: 1-141 (in Russian).

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