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ONTOGENY AND VARIABILITY IN THE CHEEK REGION OF HIPPARIONS FROM THE LATE MIOCENE LOCALITY HADZHIDIMOVO-1, SOUTHWEST BULGARIA

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Abstract. A large number of hipparion skulls from Hadzhidimovo-1 (HD) are studied herein. The sample includes individuals of various ages that allow the investigator to study their ontogenetic development. Two species of hipparion are recognized, including *Hippotherium brachypus* Hensel, 1862 and *Cremohipparion mediterraneum* Roth & Wagner, 1855. A study of the lateral aspect of the face, including the maxillary and premaxillary regions were made with specific attention paid to the placement of the preorbital and subnasal (= intermediate) fossae. The morphology of these structures are found to be of taxonomic value. This study reveals that the most intensive growth of the cheek region in both species is the period during which the maxillary M2 erupts and that the two species have different modes of ontogenetic changes in the location of preorbital fossa. During ontogeny, the preorbital fossa of *Hippotherium brachypus* migrates further from the orbit, while in the *C. mediterraneum* samples the preorbital fossa does not migrate – it remains stationary into and throughout adulthood. This study documents intraspecific variability in preorbital fossa morphology, throughout the ontogeny for both species of hipparion under consideration.

Riassunto. In questo articolo vengono studiati numerosi crani di hipparion provenienti dalla località Hadzhidimovo-1 (HD). Il campione comprende individui di varie età, consentendo di studiare il loro sviluppo ontogenetico. Sono riconosciute due specie di hipparion, in particolare *Hippotherium brachypus* Hensel, 1862 e *Cremohipparion mediterraneum* Roth & Wagner, 1855. È stato compiuto uno studio dell'aspetto laterale del cranio, comprese le regioni mascellari e premascellari, con particolare attenzione alla posizione delle fossae preorbitali e subnasali (= intermedie). La morfologia di queste strutture ha valore tassonomico. Questo studio indica che la crescita più significativa della regione delle guance per entrambe le specie avviene durante l'eruzione del M2 mascellare e che le due specie mostrano differenti modalità di cambiamenti ontogenetici per quanto riguarda la posizione della fossa preorbitale. Durante l'ontogenesi, la fossa preorbitale di *Hippotherium brachypus* migra in avanti rispetto all'orbita, mentre in *C. mediterraneum* la fossa preorbitale non migra, rimanendo stazionaria per tutto lo stadio adulto. Questo studio documenta la variabilità intraspecifica nella morfologia della fossa preorbitale durante l'ontogenesi di entrambe le specie di hipparion qui considerate.

Introduction

Late Miocene locality Hadzhidimovo-1 (HD) is situated near the town of Hadzhidimovo on the Bulgarian-Greek border. Biochronologically this locality could be placed near the limit of Mammalian Neogene (MN) units MN11/MN12, and is somewhat older than Pikermi (Greece) (Spassov 2002). More than 30 mammal species are reported from this locality. The number of hipparion specimens from this locality is enormous – more than 3,000. There are many hipparion skulls with different preservation of the specimens. The locality formed in comparatively short time, as a result of seasonal water masses, typical for relatively open plains (Spassov 2002). This allows us to look at the hipparion remains as simultaneous. The other two localities (Hadzhidimovo - 2 (Hadzhidimovo - Tumbichkite) and Hadzhidimovo - 3) could have a slightly different age (Spassov 2002) and no hipparion skulls were found from them.

Until now, information about the preorbital fossa ontogeny of hipparions is very limited. Gromova (1952) discussed the question about young individuals from *C. moldavicum* and noticed that the semi-adult specimens had less developed preorbital fossa located highly above the facial crest compared to the adults. Sondaar (1971) wrote about *H. dietrichi* from Samos "there was no indication to suppose that the fossa changed with the age of the animal". MacFadden (1984) investigated the

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Hippotherium brachypus						
№	Age group	32	33	35	36	Orbit-P2
HD 10045	I	40	42	27	27	135.5
HD 10064	I	34	43.5	-	-	128
HD 10044	I	~38	-	-	~29	145
HD 10074	I	38.2	-	-	~35	132
HD 10003	II	35	44.8	30.5	36.5	134.2
HD 10059	II	32.3	46.7	-	30.5	137
HD 10055	II	30	58	-	27	143
HD 10011	II	37.3	52.5	-	31.3	143
HD 10066	III	41	-	-	~38	160
HD 10047	IV	44	-	-	37.5	160
HD 10031	IV	43	58	32	~41	176
HD 10039	IV	40.2	49.1	-	~38.7	160
HD 10012	IV	~50	60.5	-	32	-
HD 10020	IV	48.5	55	-	45	181
HD 10048	IV	52	-	40.5	37	-
HD 10053	IV	45.5	53	38.5	36	166.5
HD 10036	IV	47.8	54	~35	38.3	175.5
HD 10037	IV	42.7	60.3	33.4	~37	178
HD 10062	IV	45	-	-	35	-
HD 10093	IV	48	65	33.4	31	169
HD 10158	IV	44.3	155	41.5	36.5	-
HD 10038	IV	~50	-	-	-	184
HD 10033	IV	45.6	68	47	-	178

Tab. 1 - Number, age group and measurements of the specimens of *Hippotherium brachypus* from locality Hadzhidimovo-1: 32 - distance orbit - preorbital fossa; 33 - length of preorbital fossa; 35 - height of preorbital fossa; 36 - distance ventral border of preorbital fossa - crista facialis; orbit-P2 - distance anterior border of the orbit - anterior point of P2. All measurements are in millimetres.

influence of the sex and ontogeny on several features of skull morphology for *Hipparion tehonense* from the MacAdams Quarry, including the length of preorbital bar, length and height of the preorbital fossa. The arbitrary age classes are four and the youngest (juvenile-young adult) is that with slightly worn tooth row and M3 virtually unworn. In this case the individuals have already completed the process of lengthening of the cheek region and naturally the results from statistical analysis show that there are no significant differences among the four age classes.

Watabe & Nakaya (1991) gave some information about facial morphology of juvenile maxillae of *C. moldavicum* and *H. prostylum*. Unfortunately, the sample is limited and there is no exact information about the age of the specimens. The other problem is that the specimens are from different localities and can not be looked at as simultaneous.

Material and Methods

The rich hipparion material from Hadzhidimovo-1 is stored in the Paleontological Museum in Assenovgrad, branch of the National Museum of Natural History-Sofia. Number, age group and some measurements of the specimens from locality Hadzhidimovo-1 are given in the Tab. 1 and Tab. 2. The numbers with sign "~" are approximately value, but they are almost real. They differ from the probable true measurement less than 2 mm and were used for diagrams. All measurements are in millimetrs.

The names "hipparion" or "hipparionine" are used for horses with an isolated protocone on maxillary premolar and molar teeth and, as far as known tridactyl feet, including species of the following genera: *Cormohipparion*, *Neohipparion*, *Nannippus*, *Pseudohipparion*, *Hippotherium*, *Cremohipparion*, *Hipparion*, "*Sivahippus*", *Eurygnathohippus*, *Proboscidipparion*, "*Plesiohipparion*" (after Bernor et al. 1996, 1997).

The Hadzhidimovo-1 hipparion sample includes 35 (adult and young) specimens from the species *H. brachypus* and 37 (adult and young) specimens from *C. mediterraneum* (Hristova et al. 2002, 2003). Unfortunately, most of them are not well preserved – they are deformed and damaged, usually without a muzzle. This hindered us to observe other morphological features of the skull and, in particular the proportions between the facial fossae and the snout.

Measurements were taken according to recommendations of the International Hipparion Symposium (Eisenmann et al. 1988; Bernor et al. 1997). We dispose with hipparion skulls (from both species) with different individual age – from specimens with unworn milk teeth to senile individuals with practically erased teeth. Several dimensions were used in this investigation: distance orbit – preorbital fossa (32); length of preorbital fossa (33); height of preorbital fossa (35); distance ventral border of preorbital fossa – crista facialis (36). Two dimensions can be used for information about cheek region length: distance anterior border of the orbit – back posterior limit of narial opening and distance anterior border of the orbit – anterior end of P2. Both of these dimensions have failings, due to the influence of the individual features of the specimens. The distance between the anterior border of the orbit – anterior end of P2 depends on the individual features over 1) individuality of the tooth row length and 2) individuality of the orbit location compared to the teeth. In adult individuals, location of the most anterior point of the orbit varies from the middle of the M3 to above 10 mm after its posterior end. In young specimens, however, orbit location varies on a small scale. The priority of this measurement is that it can be taken in most specimens. In the case of the distance between the anterior border of the orbit and the posterior limit of narial opening, the influence of the individual features is on the 1) individuality of the tooth row length, 2) individuality of the orbit location according to the teeth and 3) individuality of the end of the narial opening. The location of the end of the narial opening is not in the same place for each specimen. In *H. brachypus* it ends from anterior part of P2 to anterior half of the P3. In *C. mediterraneum* the nasal slit is deeper, ending in the limits between middle of P2 – middle of P3. Frequently the region above nasals is broken and it is impossible to take this measurement. Then we prefer to use the distance anterior border of the orbit – anterior point of P2 for evaluating how the cheek lengthens with the growth. Measurements of the length and especially height of the preorbital fossa are often difficult because of the deformation and destruction of the skulls and they are available in fewer skulls.

The cheek region of hipparions changes during the individual age of the animals. In the foals, the orbit is situated behind the unerupted M1. As they grow up it gradually moves back and makes room for the roots of the permanent teeth. In this way, the cheek region changes its dimension during the process of growth. That is why hipparion specimens are divided in four age groups (AG) according to the number of the cheek teeth in tooth series and the location of the orbit above them.

I AG – has only milk premolars (nursing period); orbit is above the end of unerupted M1 or just after it.

II AG – has milk premolars and constant M1 (frequently just erupted); orbit is above the posterior half of unerupted M2.

III AG – has milk premolars, M1 and M2 (just erupted); orbit is above the middle of M3 (unerupted) or after it.

IV AG – has constant premolars (in some cases P4 coming into occlusion) and all molars; orbit is above the posterior half of M3 or 10 mm posterior to it.

As we can judge from Tab. 3, there is no even distribution of specimens among the different groups. That is why it is not correct to apply statistical analysis – the results will not be true. In *H. brachypus* in III AG there is only one specimen. For *C. mediterraneum* in groups I AG and III AG there are two individuals on each. In III AG both specimens have broken tooth rows

Tab. 2 - Number, age group and measurements of the specimens of *Cremohipparion mediterraneum* from locality Hadzhidimovo-1: 32 - distance orbit - preorbital fossa; 33 - length of preorbital fossa; 35 - height of preorbital fossa; 36 - distance ventral border of preorbital fossa - crista facialis; orbit-P2 - distance anterior border of the orbit - anterior point of P2. All measurements are in millimetres.

Cremohipparion mediterraneum						
№	Age group	32	33	35	36	Orbit-P2
HD 10091	I	12	72	48	16	148
HD 10002	I	20	56.5	44	12	144.5
HD 10051	I	24	51.3	32.5	18	~142
HD 10050	II	16.4	65	-	15.5	143.5
HD 10152	II	22	-	-	17	146.5
HD 10104	II	~19	-	-	19.5	~148
HD 10105	II	16	71	53.4	15.5	-
HD 10015	II	18.5	-	-	16	146
HD 10058	II	16	51	-	14	-
HD 10054	III	29	-	-	14	extr. 165
HD 10014	III	25	-	-	20	-
HD 10017	IV	19.7	69	-	20	157
HD 10032	IV	22	74.5	42	20.5	179
HD 10001	IV	19	73	45	19.5	180.5
HD 10004	IV	18	79	-	~21	-
HD 10028	IV	22.5	63	43.5	~20	-
HD 10029	IV	23	81	45.5	15	~158
HD 10030	IV	16	-	-	~18	-
HD 10040	IV	16.5	73	51	-	169
HD 10043	IV	21	61	-	~28	161
HD 10046	IV	~14	-	-	21	-
HD 10007	IV	18	70	42.5	18.6	-
HD 10019	IV	29	55	41	~21	167
HD 10024	IV	23	57	53	22	-
HD 10049	IV	21	~76.5	44	-	168

	H. brachypus	*C. mediterraneum*
I age group	4	2
II age group	4	6
III age group	1	2
IV age group	14	14

Tab. 3 - Number of the specimens in each group for both investigated species.

and it is impossible to take dimension of orbit-P2 distance. For one of them, HD 10054, the dimension of orbit-P3 (135 mm) is taken and it was extrapolated to approximately minimal value of the whole dimension orbit – P2 (165 mm).

Line drawings were made from photos of the best preserved specimens of different age groups for both species. Software "PAST" (Hammer et al. 2001) was used for graphics.

Results

Scatter diagrams show that ontogenetic changes in preorbital fossa location are different for each species. In *Hippotherium brachypus* there is a separation between two of the groups: one includes I and II AG and the other - III and IV AG. This can be observed in orbit-P2 distance (Fig. 1A). The second age group (II AG) covers the period from M1 eruption about 10-12

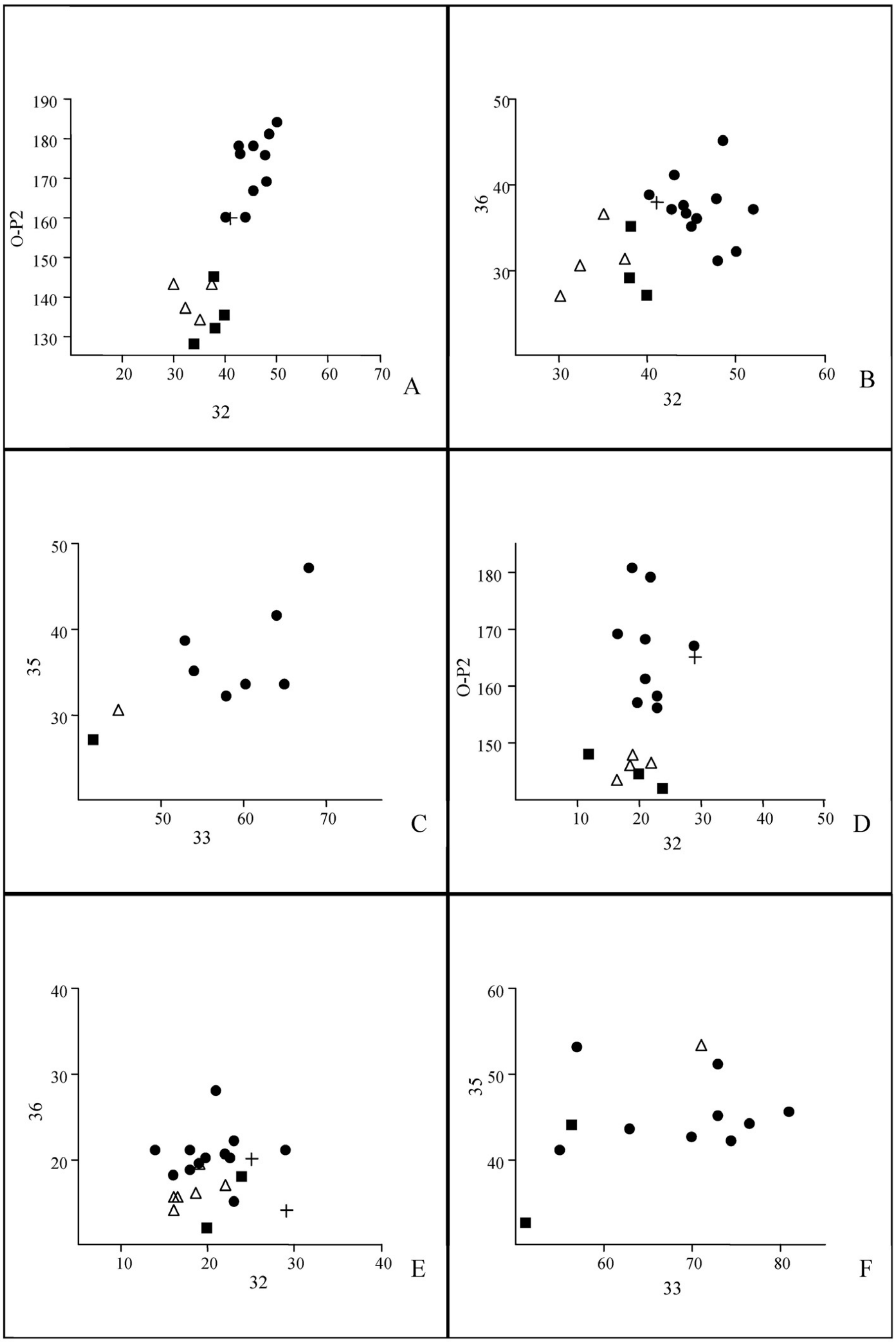

Fig. 1 - Bivariate plots of: A) preorbital fossa distance (32) and orbit-P2 distance in *Hippotherium brachypus*. B) orbit - preorbital fossa distance (32) and preorbital fossa - facial crest distance (36) in *Hippotherium brachypus*. C) length of preorbital fossa (33) and height of preorbital fossa (35) in *Hippotherium brachypus*. D) orbit - preorbital fossa distance (32) and orbit - P2 distance in *Cremohipparion mediterraneum*. E) orbit - preorbital fossa distance (32) and preorbital fossa - facial crest distance (36) in *Cremohipparion mediterraneum*. F) bivariate plot of length of preorbital fossa (33) and height of preorbital fossa (35) in *Cremohipparion mediterraneum*.
Legend: black square - I age group; triangle - II age group; cross - III age group; black dot - IV age group.

months to just before eruption of M2 about 24 months (after the data for recent horses). In the II AG M2 has not erupted, but already exist (this can be observed on the skulls with broken alveolar rim). The greatest lengthening of the cheek region in a hipparion's skull occurs between II and III AG (Fig. 1A). As a whole the length of the preorbital bar increases with age (Fig. 1B). The distances preorbital fossa - facial crest also increased and made room for the roots of the permanent teeth.

Although there are only two young specimens with well preserved preorbital fossae (one from I and one from II AG), obviously in *H. brachypus* its dimensions increase from younger to older individuals (Fig. 1C). Young specimens are clearly separated from adults ones.

Preorbital bar is long (Fig. 2). As in hipparions from *Hippotherium* (Group 1), the lacrimal's most anterior projection is posterior to the preorbital fossa (Woodburne & Bernor 1980). The anterior edge of the lacrimal placed more than half the distance from the anterior orbital rim to the posterior rim of the fossa (hipparionine state character 1 C, Bernor et al. 1997). This is clearly visible in the specimens HD 10055, HD 10074, HD 10033, HD 10053, and HD 10158. Preorbital fossa in the specimens (juveniles and adults) is subtriangularly shaped and its long axis is with anteroventral orientation (hipparionine state character 4 D, Bernor et al. 1997). Posterior pocketing (in adult individuals) varying from moderate to slight depth (hipparionine state character 5 B, Bernor et al. 1997) to not pocketed but with a posterior rim (5 C, Bernor et al. 1997). The adult specimens have well delineated posterior and ventral borders, but some of the specimens have weakly defined anterior or dorsal rim. In some cases inside the dorsal rim there is slight inner (in the dorsal part) rim (Fig. 2D). In preserved skulls of very young specimens (I AG) preorbital fossa is shallower, without posterior pocket, with less developed peripheral borders, especially anterior and dorsal ones. Infraorbital foramen is elliptic and has strongly anterior orientation of its opening. It is situated to the anteroventral border of the preorbital fossa (10 B, Bernor et al. 1997). Even in the young individuals infraorbital foramen is about 3-5 mm from it. Its location above the tooth varying from posterior half of the dP2 to anterior half of the dP4 in young individuals to posterior half of the P4 in adults. Nasal notch ends above P2 (15 D, Bernor et al. 1997).

Some similarities occur in the *Cremohipparion mediterraneum* sample. Although there is a fewer number of juvenile individuals in this portion of the sample, the orbit – P2 distance (Fig. 1D) exhibits a separation between I and II AG from one side and to III and IV AG from other can be observed, like in *H. brachypus* sample. With regard to the preorbital bar length the situation is different: it does not depend on the individual age of animals (Fig. 1D, E). That means that in this species the cheek region lengthening does not influence the length of the preorbital bar, i.e. it probably depends on the idiosyncrasy. Likewise, in *H. brachypus* the preorbital fossa is comparatively closer to the crest in younger individuals and with development of the permanent teeth it is moved higher on the cheeks (Fig. 1E).

About preorbital fossa dimensions in species *C. mediterraneum* the situation is not clear (Fig. 1F) - there is not enough data about undoubted conclusion. One of the specimens (II AG) has big preorbital fossa, as in the adults.

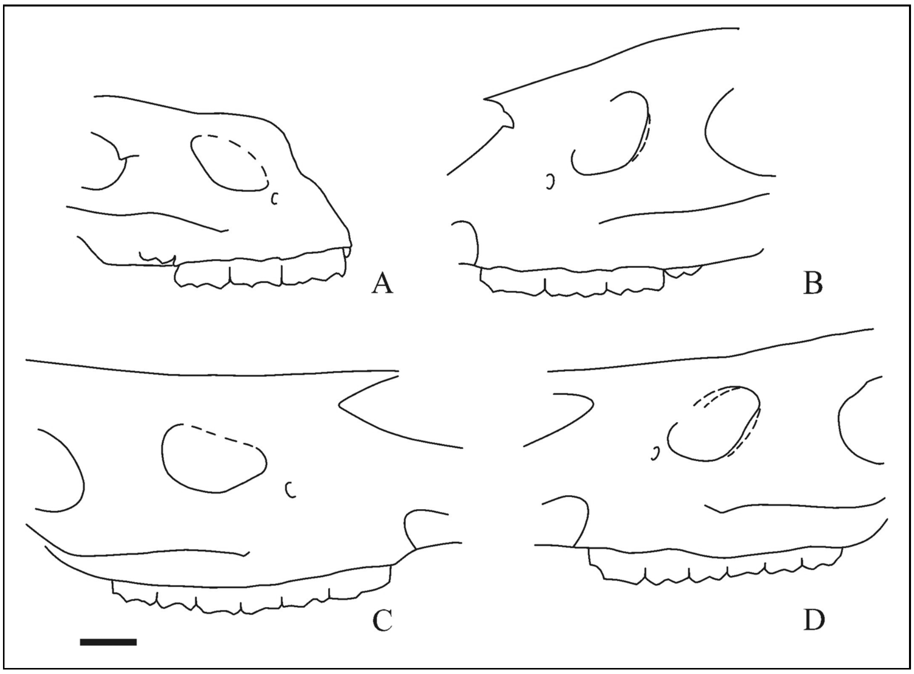

Fig. 2 - Outline drawings of *Hippotherium brachypus* Hensel, 1862; skulls: A) HD10045 - I age group; B) HD10003 - II age group; C) HD10020 - IV age group; D) HD 10093 - IV age group. Scale bar - 3 cm.

In most of the specimens the lacrimal is large, rectangularly shaped, invades medial wall and posterior aspect of preorbital fossa (hipparionine state character 1 A, Bernor et al. 1997), but in specimen HD 10017 (adult one) the lacrimal suture approaches but does not touch the posterior rim of the fossa (Fig. 3E). The preorbital fossa is subtriangularly shaped and anteroventrally oriented (4 D, Bernor et al. 1997), medially deep (6 A, Bernor et al. 1997). Pocketing in the adults is reduced, moderate to slight depth (5 A, Bernor et al. 1997). Morphology of the posterior rim varying from slightly curved to curved, with ventral part which juts out over the preorbital fossa. In the first cases the preorbital bar is comparatively longer (Fig. 3B, D); in the second the preorbital bar is narrower at the dorsal part of the posterior rim (Fig. 3A, C, F). The mode of the posterior border (slightly curved or curved) does not depend on the individual's ontogenetic stage of development (there are juvenile and adult specimens with both types of posterior rim) or on the presence/absence of the caninus (= intermediate) fossa (Fig. 3). The anterior border of the fossa is well developed, especially in specimens with caninus fossa. The dorsal rim is usually weakly defined; in most specimens it represents slight curvature of the cheek bone (Fig. 3B, F). In some specimens there is a faint dorsal rim, as in *H. brachypus* (Fig. 3A, C, F). The preorbital fossa in young specimens is slightly shallower than in the adult one, but with well developed posterior, anterior and ventral borders. The infraorbital foramen in most cases has a triangular outline, rarely oval, with antero-lateral to lateral orientation of its opening and is situated on the anteroventral border of the preorbital fossa (10 B, Bernor et al. 1997). As in *H. brachypus*, its location varies from the posterior half of the dP2 to anterior half of the dP4 in young individuals to posterior half of the P4 in adults.

In some specimens a caninus fossa is found anterior to the preorbital fossa (13 B, Bernor et al. 1997) (Fig. 3A, F). It is separated from preorbital fossa about 15-20 mm width bar. It is well defined posteriorly, while anteriorly it is open, not connected with the buccinator fossa. The canine fossa is represented at all ages in hipparion skulls. The nasal notch varies: it extends from the mesostyle of P2 to the mesostyle of the P3 (15 D, E, Bernor et al. 1997).

Discussion

Hippotherium brachypus Hensel, 1862 and *Cremohipparion mediterraneum* Roth & Wagner, 1855 originate from one locality - Hadzhidimovo-1 where the

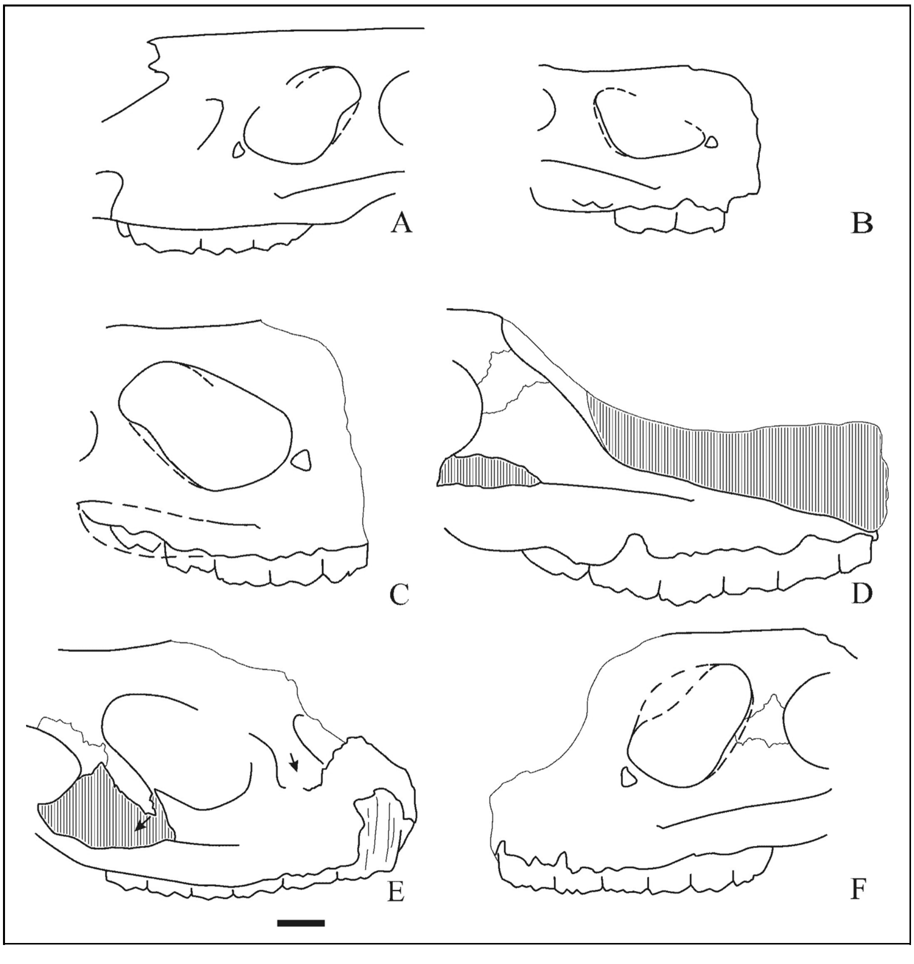

Fig. 3 - Outline drawings of *Cremohipparion mediterraneum* Roth et Wagner, 1855; skulls: A) HD 10091 - I age group; B) HD10051 - I age group; C) HD 10105 - II age group; D) HD 10054 - III age group (preserved only dorsal and ventral borders of the preorbital fossa); E) HD 10017 - IV age group; F) 10001 - IV age group. Scale bar - 3 cm.

material is especially abundant and in good preservation, giving the unique opportunity to observe the individual development with the age.

In the foetus of extant horses M1 begins its development and is represented by a "jelly-like amorphous body within the alveolar cavity" at about 275^{th} day of development (Soana et al. 1999) and its mineralization starts around two weeks after birth (Hoppe et al. 2004). The ontogenetic timing of M1 can be assumed to be similar in hipparions. In the specimens from the I age group with damaged alveolar rim after dP4, the enamel of the M1 is always visible. In all hipparion skulls from this group the orbit is above or after unerupted M1, even in the individuals with almost unworn deciduous teeth (there are not preserved skulls from new-born individuals). The period just before M2 eruption is the period when P2 and P3 already started their mineralization and have a well formed body, while P4 is just beginning its development (Hoppe et al. 2004). The most intensive growth of the cheek region in both species is the period about M2 eruption, i.e. the time when in recent horses P4 forms its body and starts moving to the alveolar surface and M3 starts its development and mineralization. The facts that III and IV AG form a group (Fig. 1A, D) and that the location of the anterior orbital rim is about the middle of unerupted M3 or after it, as in the adults, show that possibly after eruption of the M2, the changes of cheek region length are minor or absent. Unfortunately, there are only two comparatively well preserved skulls from III AG (one from *H. brachypus* and one from *C. mediterraneum*) which can be used to measure the distance orbit-P2. This is not enough for a firm conclusion. It has to be verified in samples with rich material from all age groups. If future investigation confirms it, this will provide a possibility to use (of course with great caution) specimens with erupted M2 for taxonomy, if there are no preserved adult ones.

Hippotherium brachypus and *Cremohipparion mediterraneum* are representatives of two different genera *Hippotherium* Kaup and *Cremohipparion* Qui, Huang et Guo (Bernor et al. 1990; Bernor et al. 1996; Zouhri et al. 2005). The investigations of the individual skull development shows ontogenetic differences (in the development of the preorbital bar), which can be interpreted as additional argument, confirming that these hipparions species belongs to different genera. It would be interesting to verify these observations in other species of these genera as well as in other ones. Woodburne & Bernor (1980) noted the morphological differences between their Group 1 (*Hippotherium* in more recent works) and their Group 2 (*Cremohipparion*). *Cremohipparion* is a particularly diverse lineage of hipparions including the following species (Bernor et al. 1996): *Cremohipparion moldavicum, C. mediterraneum, C. proboscideum, C. nikosi, C. matthewi, C. forstenae*, and *C. licenti.* This clade of hipparions ranged from as far west as Greece and Bulgaria, eastward to China and as far south as North Africa. *Hippotherium* was less diverse and included taxa limited in their distribution to Central Europe, Ukraine, Greece, Turkey and Iran: *Hippotherium primigenium, H. giganteum* and *H. brachypus.* The ontogenetic arguments developed here can, with sufficient sample sizes, be extended to other genera of hipparions such as *Plesiohipparion, Proboscidipparion, Eurygnathohippus,* and *Hipparion* s.s. (Bernor et al. 1996).

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