

FOSSIL
VERTEBRATES
OF ARABIA

*With Emphasis on the Late Miocene Faunas,
Geology, and Palaeoenvironments of the
Emirate of Abu Dhabi, United Arab Emirates*

Edited by Peter J. Whybrow and Andrew Hill

*In collaboration with The Abu Dhabi Company for Onshore Oil Operations
The Ministry for Higher Education and Scientific Research, United Arab Emirates*

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Hipparions from the Late Miocene Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates

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VÉRA EISENMANN AND PETER J. WHYBROW

The names Baynunah Formation (Whybrow, 1989) and the Shuwaihat Formation (Whybrow et al., 1999; Bristow, 1999—Chapters 4 and 6) are given to deposits of mainly elastic, late Miocene sedimentary rocks outcropping in an area of about 16 000 km² in the Western Region of the Emirate of Abu Dhabi, United Arab Emirates. It is likely that the fossil-bearing Baynunah Formation is coeval with parts of the Agha Formation of Iraq (Thomas et al., 1980) and Iran (James and Wynd, 1965). From the most western fossil site, Jebel Barakah (fig. 19.1) to the most eastern (Tarif), a distance of about 150 km, and further east to Abu Dhabi city, the regional dip is merely 1° east. All sedimentary units are horizontally-bedded; there is no regional folding and therefore no complicated stratigraphy. The sedimentary associations are, however, complex and tremendously variable (Whybrow et al., 1999; Friend, 1999; Bristow, 1999—Chapters 4–6).

Except for a small collection (1982–83) made by Al Ain Museum and German archaeologists (Vogt et al., 1989) now in Al Ain Museum, Emirate of Abu Dhabi, fossil collections from the Western Region made since 1986 by The Natural History Museum/Yale University team are temporarily housed in the Department of Palaeontology, The Natural History Museum, London: material collected pre-1984 has BMNH numbers. A collection made by Andrew Hill and Walid Yasin in 1984 is stored in Al Ain Museum. All palaeontological material collected by the NHM/Yale team has reg-

istration numbers of the Emirate of Abu Dhabi (AUH). Comparative hipparion material is housed in the American Museum of Natural History, New York (AMNH), Muséum National d'Histoire Naturelle, Paris (MNHN), and Ungarische Geologische Reichsanstalt (UGR).

METHODS AND MATERIAL

Bone scraps can be found on the slopes of most of the Miocene exposures. The Natural History Museum/Yale University team has attempted to be nonselective in their collecting to reduce sampling problems (Hill, 1987). All hipparion fossils were collected by close examination of outcrop surfaces. The genus *Hipparion* is represented among the Abu Dhabi fossils by 41 specimens, including 13 upper cheek teeth, 14 lower cheek teeth, and 14 limb bones, nearly all fragmentary, collected at six localities (fig. 19.1). The sizes of bones and teeth show that two species are represented: one small or middle-sized, and one larger. What makes the sample most interesting is the presence of two mandibular fragments belonging to the smaller species. In size and proportions they differ from other *Hipparion* mandibles and warrant the description of a new species.

Mandibles and other bones and teeth were measured according to the recommendations of the New York International Hipparion Conference of 1981 (Eisenmann et al., 1988). Two new mandibular

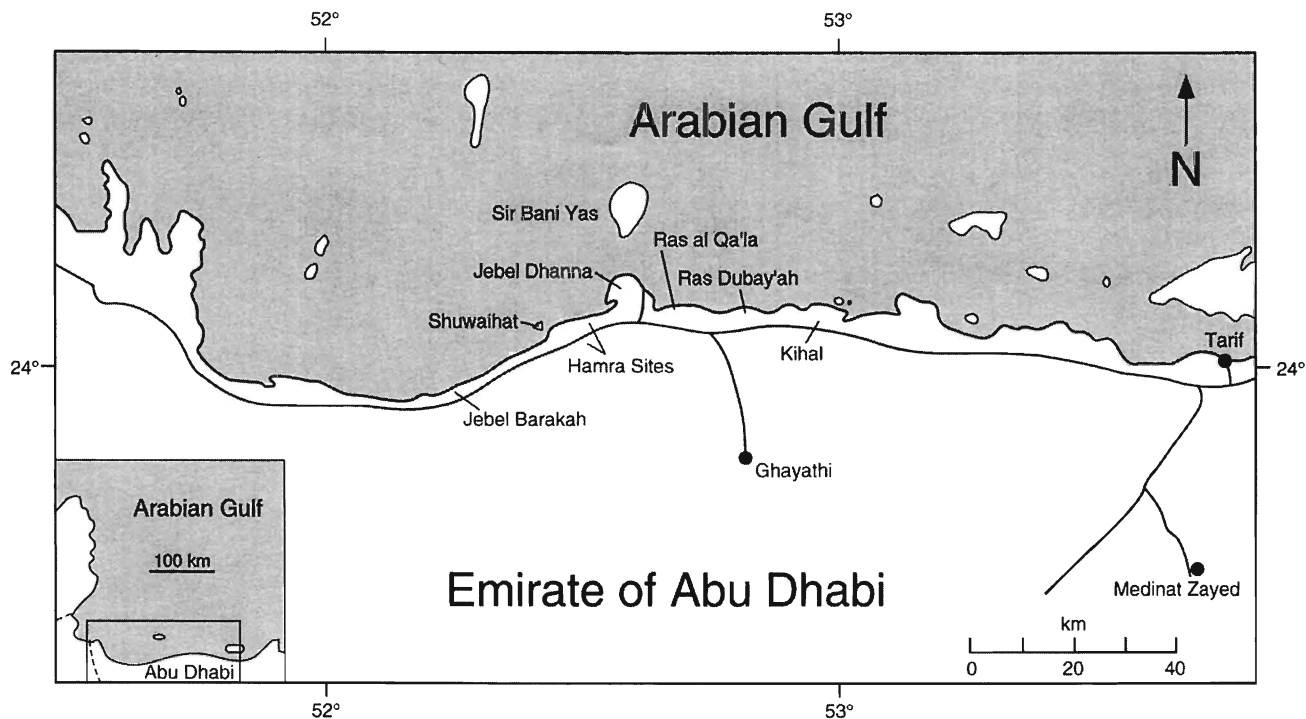


Figure 19.1. Map of the Western Region of the Emirate of Abu Dhabi, showing the locations (Shuwaihat, Hamra, Jebel Barakah, Jebel Dhanna, Ras Dubay'ah, and Kihal) where specimens of *Hipparion* have been found.

measurements were introduced to evaluate the length of a fragmentary muzzle. They are:

A = distance between infradentale (the point between the alveoli of the first incisors) and the symphyseal constriction (where the width of the symphysis is smallest); and

B = the distance between the symphyseal constriction and the second premolar.

The sum of A plus B is the muzzle length. A third measurement comes from the system used by Grovova (1952):

G3 = the distance between the mandibular angle and the front of the second premolar, which gives an idea of size independent of the muzzle length (muzzle length plus G3 is the maximal anteroposterior length of the mandible).

Simpson's ratio diagrams (Simpson, 1941) were used to compare the sizes and proportions of the Abu Dhabi *Hipparion* mandibles to others. Unworn or little worn cheek teeth were sectioned at mid-crown to provide evidence of the enamel pattern.

The ages of *Hipparion* localities given here are according to the updated European Land Mammal Zones (MN) of Mein (1990). Comparisons were made chiefly with hipparions for which the samples are good enough to give points of comparison (mandibles, cheek series), and where the age is at least approximately known. Because of the geographical position of the Emirate of Abu Dhabi in the Arabian Peninsula comparisons were also attempted with some African, Middle Eastern, and Asiatic hipparions.

SYSTEMATICS

Order Perissodactyla Owen, 1848

Family Equidae Gray, 1821

Genus *Hipparion* de Christol, 1832

Hipparion sp., medium-large size

Referred Material (fig. 19.2.4–7, 9, 10)

Shuwaihat. Site S1, N 24° 06' 38", E 52° 26' 09": AUH 28, left metatarsal IV, distal; AUH 88, left astragalus; AUH 89, right tibia, proximal.

Hamra. Site H5, N 23° 06' 04", E 52° 31' 38": AUH 46, left P² (fragments); AUH 144, right, lower P (unworn and sectioned). Site H6, N 23° 06' 43", E 52° 31' 28": AUH 267, left posterior phalanx II.

Jebel Barakah. Site B2, N 24° 00' 13", E 52° 19' 35" (U.S. Marines Alpha-1 GPS survey point, 1990): BMNH M50664, left P² (fragment); BMNH M50667, left pelvis.

Jebel Dhanna. Site JD3, N 24° 10' 31", E 52° 34' 21": AUH 176, right metacarpal IV, proximal; AUH 177, right metacarpal IV, distal; AUH 246, left tarsal navicular. Site JD5, N 24° 10' 22", E 52° 34' 38": AUH 178, right P³ or right P⁴. Site JD4, N 24° 10' 42", E 52° 34' 12": AUH 265, right, lower P (unworn and sectioned).

Ras Dubay'ah. Site R2 (collected 1989, now a Defence Area): AUH 196, right astragalus (fragment); AUH 197, right cuneiform (fragment); AUH 203, right M¹ or right M² (sectioned); AUH 205, vestibular half of right P³ or right P⁴; AUH 208, left lower cheek tooth (unworn fragment); AUH 210, vestibular half of right P³ or right P⁴ (unworn); AUH 212, left M¹ or left M² (unworn); AUH 216, two lower cheek teeth (other teeth plus mandible fragments).

Description

Size medium to large. Moderately hypsodont teeth. Upper cheek teeth plicated; long protocone, lingually flattened, and with pointed ends (fig. 19.2.7). Left lower cheek teeth with a hipparionine double knot, and shallow ectoflexids on premolars (fig. 19.2.4, 10c).

Comments

The only character that deserves a short comment is the rather elongated, pointed, and flattened protocone. Despite exceptions like specimens from Seu de Urgell and some African forms, it may be said that Vallesian hipparions usually have shorter and more oval (not flattened) protocones. They also tend to have extremely plicated fossettes and multiple plis caballin. In contrast, Pliocene hipparions tend to have elongated, pointed and/or flattened

protocones. Both morphologies, however, occur in the Turolian.

The referred limb bones include two fragmentary and badly preserved tali (AUH 88 and 196) measuring about 50 mm (maximum height), a second phalanx (AUH 267) measuring 37.7 mm (maximum height), 28 mm (minimum width), and 33 mm (distal articular width). The distal articular surface of the metatarsal IV from Shuwaihat (AUH 28) is 20 mm long and 10 mm wide. On the metacarpal IV from Jebel Dhanna (AUH 176 and 177) the same measurements are 17.7 mm and 8 mm, respectively.

Hipparion abudhabiense sp. nov.

Holotype

Right mandibular fragment, AUH 270 (fig. 19.3.1a and 1b).

Etymology

From the Emirate of Abu Dhabi, United Arab Emirates.

Type Locality

Jebel Dhanna, site JD3, N 24° 10' 31", E 52° 34' 21"; Western Region of the Emirate of Abu Dhabi, United Arab Emirates.

Age and Geographic Distribution

Late Miocene, probably early to middle Turolian (European Mammal Age), Baynunah Formation of Abu Dhabi (Whybrow, 1989; Whybrow et al., 1990). Possibly related to the early Turolian *H. dietrichi* from Greece—Samos (QI and Andrianos) and Lower Axios Valley (Vathylakkos and Ravin des Zouaves); to the small early Turolian hipparion from Iraq (Jebel Hamrin); to the Algerian middle Turolian *H. sitifense*; to the Turolian medium-sized *H. cf. dietrichi* from Turkey (Kayadibi, Garkin, and Kinik) and Lebanon; but also resembling an early Pliocene form from La Gloria 4, Spain (Eisenmann and Mein, 1995).

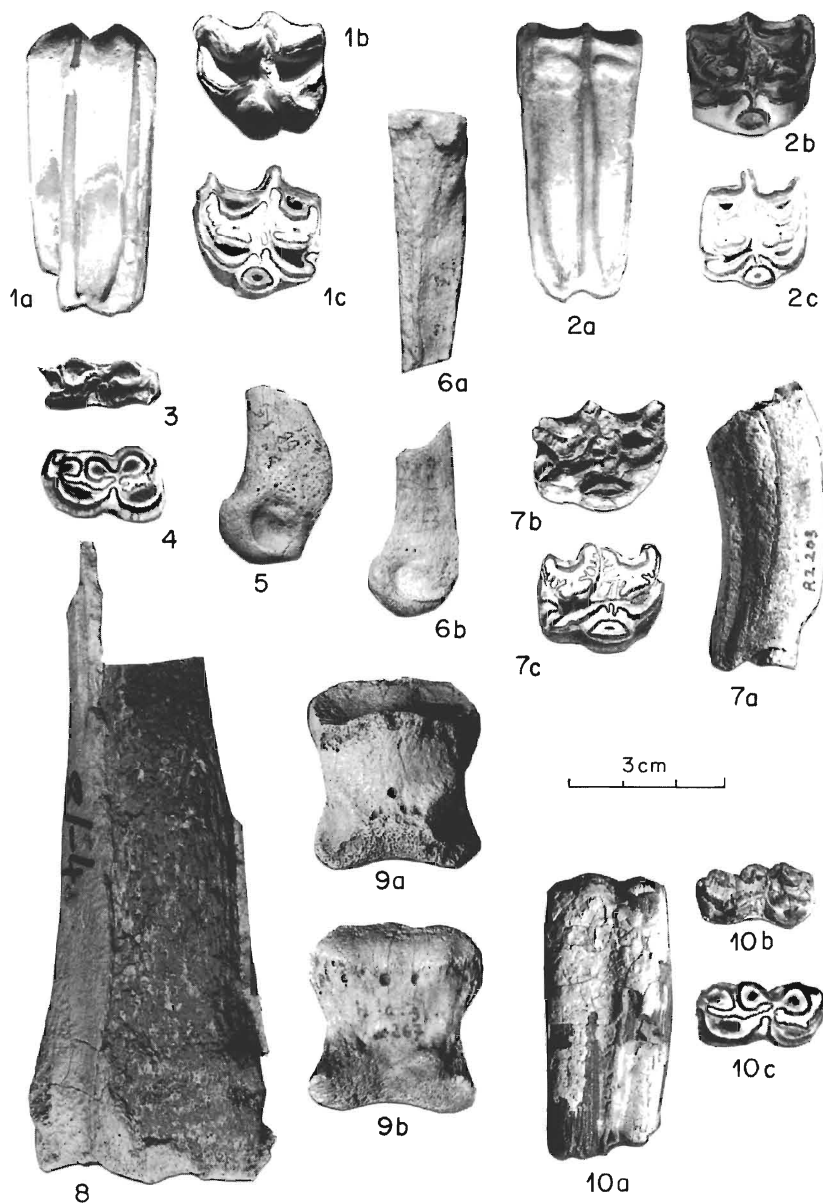


Figure 19.2. *Hipparion abudhabiense* (1, 2, 3, 8) and *Hipparion* sp. (4, 5, 6, 7, 9, 10). Left upper premolar, AUH 264: 1a, vestibular view; 1b, occlusal view; 1c, mid-crown section. Right upper molar, AUH 229: 2a, vestibular view; 2b, occlusal view; 2c, mid-crown section. 3, Right lower premolar, AUH 174; occlusal view. 4, Right lower premolar, AUH 265: mid-crown section. 5, Distal end of a left fourth metatarsal, AUH 28; lateral view. Right fourth metacarpal, medial view: 6a, AUH 176, proximal end; 6b, AUH 177, distal end. Right upper molar, AUH 203: 7a, mesial view; 7b, occlusal view; 7c, mid-crown section. 8, Distal end of left radius, BMNH M50665; dorsal view. Second phalanx of the third digit, AUH 267: 9a, dorsal view; 9b, ventral view. Right lower premolar, AUH 144: 10a, vestibular view; 10b, occlusal view; 10c, mid-crown section.

Diagnosis

Skull unknown. Size small or medium; lower cheek teeth series about 140 mm long. Mandibular ramus deep both in front of the second premolars (P_2) and between the premolars and molars (between P_4 and M_1). Broad symphysis at the constriction, probably indicating a broad muzzle. Very short distance between the second premolar and the symphyseal constriction probably indicating a short muzzle. The molar length nearly equals the premolar length. Teeth moderately hypsodont. Double-knot hipparionine. Ectoflexids deep on the molars and at least some premolars. No ectostylids. Frequent protostylids, either plis (P_3 , P_4 , M_1 , and M_2 of the holotype) or isolated columns (M_3 of the holotype). Protocones small (fig. 19.3.2) and rather rounded (fig. 19.2.1c, 2c). Plications and plis caballin are moderately developed.

Referred Material (figs 19.2.1–3, 8 and 19.3.1–5)

Shuwaihat. Site S1, N 24° 06' 38", E 52° 26' 09": AUH 23, left, lower M? (unworn, fragments); AUH 72, half anterior left, lower M; AUH 115, left M_1 or left M_2 ; AUH 164, phalanx I

distal (fragment); AUH 165, phalanx I half proximal; AUH 166, phalanx I half distal. Site S4, N 24° 06' 44", E 52° 26' 12": AUH 228, vestibular half of left, upper M; AUH 264, left, upper P (unworn and sectioned).

Hamra. Site H1, N 23° 06' 50", E 52° 31' 31": AUH 174, right, lower P, lingual fragment. Site H5, N 23° 06' 04", E 52° 31' 38": AUH 231a, left P_3 or left P_4 . Site 6, N 23° 06' 43", E 52° 31' 28": AUH 266a, left M_1 or left M_2 (fragment).
Jebel Barakah. Site B1, N 24° 00' 24", E 52° 19' 48": AUH 229, right M^1 or right M^2 (sectioned); AUH 230, left M^1 or left M^2 . Site B2, N 24° 00' 13", E 52° 19' 35" (U.S. Marines Alpha-1, 1990); BMNH M50661, left P_3 or left P_4 ; BMNH M50662, left P_2 (fragment); BMNH M50663, right, lower M (fragment); BMNH M50665, left distal radius.
Jebel Dhanna. Site JD5, N 24° 10' 22", E 52° 34' 38": AUH 452, right mandible.
Kihal. Site K1, N 24° 07' 23", E 53° 00' 27": AUH 260, right, upper M? (unworn fragment).

Description and Comparisons of *Hipparion abudhabiense*

Mandibles (tables 19.1 and 19.2)

The two mandibular fragments were collected at Jebel Dhanna. One (AUH 452) is a right ramus lacking most teeth and with very worn P_4 and M_1 , but conserving the proximal half of the symphysis. The holotype AUH 270, also a right ramus, lacks the symphysis but has well-preserved teeth. Both mandibles have a relatively deep ramus (fig. 19.3.1a and 5a). The specimen AUH 452 seems to have a short muzzle, or at least a short measurement B (fig. 19.3.5b). Specimen AUH 270 has relatively large molars (fig. 19.3.1b).

Table 19.1. Measurements (in mm) of some African and Eurasian hipparion mandibles (also see table 19.2)

Locality		Abu Dhabi	Abu Dhabi	Samos Q1	Samos Q?
Specimen		AUH 452	AUH 270	AMNH 20655	UGR OK 557
Species		<i>Hipparion abudhabiense</i>	<i>Hipparion abudhabiense</i>	<i>Hipparion dietrichi</i>	<i>Hipparion matthewi</i>
I ₁ -symph. constriction	A	—	—	50.0	41.0
P ₂ -symph. constriction	B	34.0	—	46.0	31.0
Height in front of P ₂	12	49.0	—	56.5	39.5
Alveolar length P ₂ P ₄	3	67.0	72.0	69.0	57.0
Alveolar length M ₁ M ₃	4	—	70.0	63.5	56.0
Height between P ₄ and M ₁	11	64.0	69.0	67.5	52.0
Width at symph. constriction	14	34.0	—	41.2	27.7
Length P ₂ to gonion	G3	—	225.0	215.0	208.0

Abbreviations: A = distance between the infradentale (between the alveoli of the first incisors) and the symphyseal constriction; B = distance between the symphyseal constriction and the second premolars (P_2); 12 = height of the mandibular ramus in front of P_2 ; 3 = length of the premolars; 4 = length of the molars; 11 = height of the mandibular ramus between P_4 and M_1 ; 14 = width at the symphyseal constriction; G3 = distance between the mandibular angle and the front of P_2 .

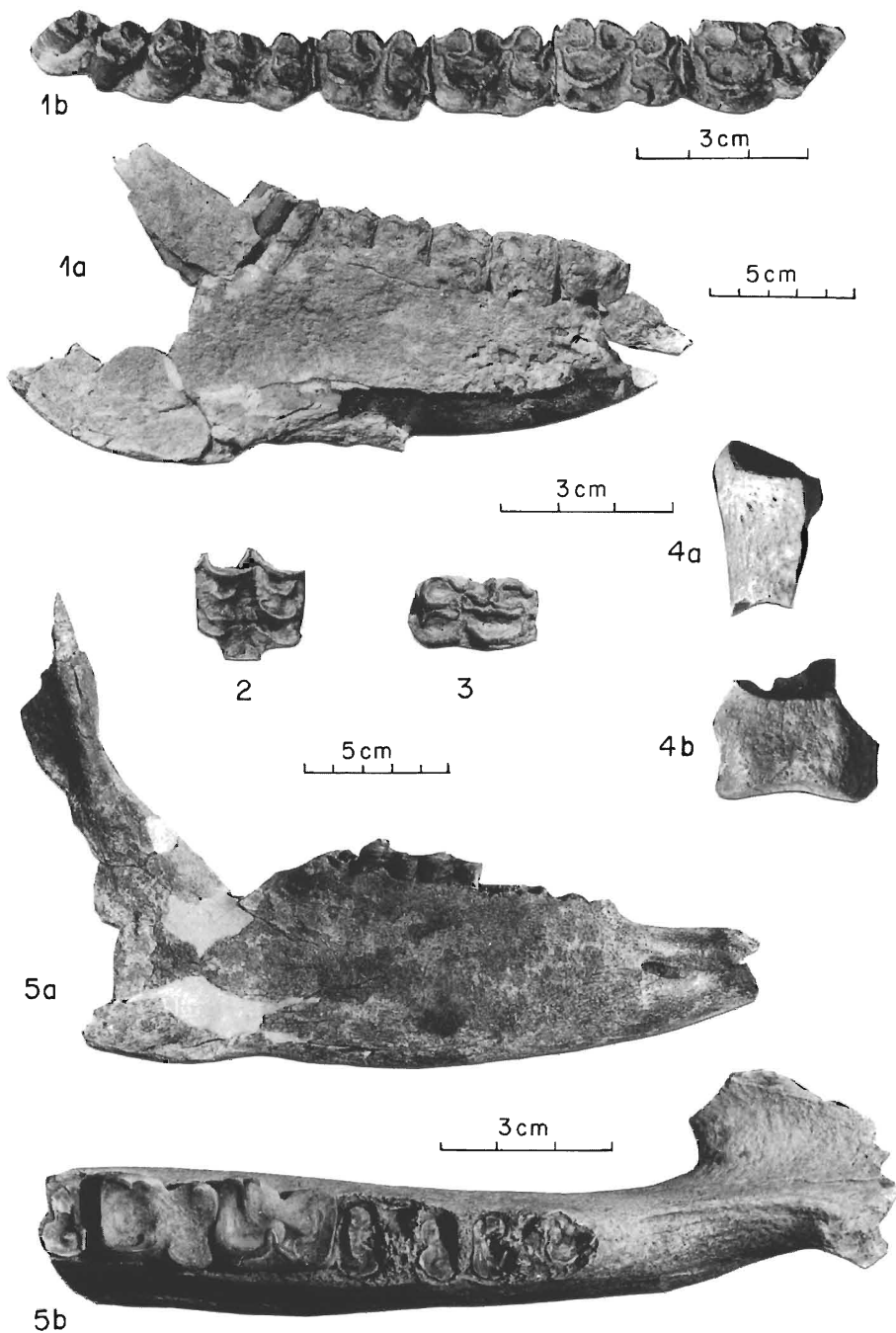


Figure 19.3. *Hipparion abudhabiense*, sp. nov. Holotype. Right mandibular ramus, AUH 270: *1a*, lateral view; *1b*, occlusal view. 2, Left upper molar, AUH 230; occlusal view. 3, Left lower premolar, BMNH M50661; occlusal view. Proximal phalanx of the third digit, dorsal view: *4a*, AUH 165, proximal fragment; *4b*, AUH 164, distal fragment. Right mandibular ramus, AUH 452: *5a*, lateral view; *5b*, occlusal view.

A ratio diagram (fig. 19.4) shows the differences in sizes and proportions between the two mandibles of *H. abudhabiense*, the average of two mandibles of *H. africanum* (reference zero line), and the mandibles most resembling *H. abudhabiense*: the type mandible of *H. matthewi* (Samos, quarry unknown), one mandible of *H. dietrichi* AMNH 20665 from Samos, Q1 (Sondaar, 1971), and the average of 8–16 mandibles of *H. dietrichi* from the Thessaloniki area of Greece: Vathylakkos (Koufos, 1988), Ravin des Zouaves (RZO, Koufos, 1987), and “Saloniki” (MNHN 290a and others).

Judging from the mandibular length excluding the muzzle (measurement G3) all mandibles are smaller than in the Vallesian reference specimen of *H. africanum*; all have relatively short muzzles (measurements A and/or B), relatively high rami (12 and 11), relatively broad symphyses (14), and relatively large molar lengths (4) compared with the premolar lengths (3). The Jebel Dhanna mandibles, however, cannot be referred to any of these *Hipparion* species. *Hipparion matthewi* is much smaller but has a relatively longer distance between the P₂ and the symphyseal constriction (B). The last character also distinguishes *H. abudhabiense* from other hipparion species.

Another ratio diagram (fig. 19.5) compares the average of the two mandibles of *H. abudhabiense* with Turkish mandibles referred to *H. mediterraneum* and to *H. matthewi* (Koufos and Kostopoulos, 1994). Only the better preserved and figured material (mandibles D 532 and D 533 from Kemiklitepe D, and mandible A 537 from Kemiklitepe A) has been used so that measurements A, B, and G3 could be estimated on the plates. According to the ratio diagram, neither the mandibles referred to as *H. mediterraneum* (D 532 and 533) nor the mandible referred to as *H. matthewi* (A 537) resemble the mandible of *H. abudhabiense*. The Arabian species has a much higher horizontal ramus (measurements 12 and 11).

Lower Cheek Teeth (tables 19.3–19.5)

The lower cheek teeth have a banal, hipparionine, double knot. This kind of morphology has no biostratigraphical significance outside Africa. It is only in Africa that hipparionines with double knots

are no longer found after 6 million years (Ma), being completely replaced at that time (or perhaps even earlier) by more evolved patterns—first the caballoid, then the caballine double knot (Eisenmann, 1995a). In Eurasia, the caballine double knot appears only in MN 15–16 at Villaroya (Spain), Kvabebi (Georgia), Beregovaja (Russia), and Shamar (Mongolia). Even then, it does not replace the hipparionine pattern, which is still found in MN 15 zone at Layna (Spain), Perpignan (France), and Çalta (Turkey), and co-occurs with the caballine pattern at Shamar and Beregovaja. Peculiarly, the lower cheek teeth from Kemiklitepe D (Koufos and Kostopoulos, 1994, pl. III, figs 3 and 4) are rather caballoid, although they belong to an early Turolian hipparion.

Usually protostylids are present in hipparions, especially in moderately worn or very worn teeth. Their occurrence is so commonplace that they hardly have any systematic significance. They are present on the early Pliocene cheek teeth from La Gloria 4 and on the Kemiklitepe lower cheek teeth (Koufos and Kostopoulos, 1994). Protostylids are also said to be present but not strong in *H. dietrichi* from Samos Q1 (Sondaar, 1971), average in *H. dietrichi* from Andrianos Quarry in Samos, and double in very worn teeth (Koufos and Melentis, 1984). They are moderate and rarely isolated in *H. dietrichi* from Ravin des Zouaves and Vathylakkos (Koufos, 1987, 1988).

More important is another character: the deep development of the ectoflexid (vestibular groove) seen not only on the molars but at least on some premolars, such as the P₄ of the holotype and a fragmentary premolar from Hamra (fig. 19.2.3). Deep ectoflexids are the rule on *Hipparion* molars, even if they have a tendency to become shallower as in the evolved African *Hipparion* species (Eisenmann, 1977). But on *Hipparion* premolars, short ectoflexids are the rule, even though they may be deep on very worn teeth, as in some Vallesian species such as *H. depereti* of Montredon (Eisenmann, 1988).

In *H. abudhabiense* the deep ectoflexid on moderately worn premolars is associated with a high (deep) mandibular ramus and a short muzzle. This association of characters was investigated in other hipparions. Unfortunately, the mandible of *H. depereti* (MN 10) is unknown, but Vallesian mandibles seem to have much

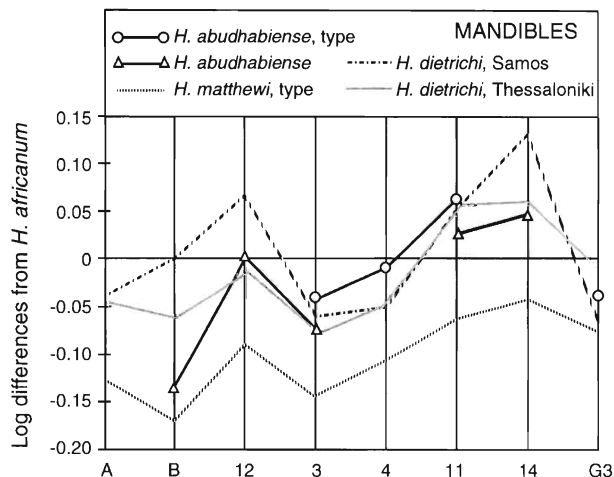


Figure 19.4. Ratio diagrams comparing the mandibles of *Hipparion abudhabiense* of Jebel Dhanna (type specimen AUH 270, and AUH 452), the type mandible of *H. matthewi* from Samos, and the early Turolian *H. dietrichi* from Samos Quarry 1 and the Thessaloniki area (Vathylakkos, Ravin des Zouaves, and specimen MNHN 290a from “Salonique”). The average of two mandibles of the Vallesian *H. africanum* from Bou Hanifa is the reference line. Key: A, distance between the infradentale (between the alveoli of the first incisors) and the symphyseal constriction; B, distance between the symphyseal constriction and the second premolars (P₂); 12, height of the mandibular ramus in front of P₂; 3, length of the premolars; 4, length of the molars; 11, height of the mandibular ramus between P₄ and M₁; 14, width at the symphyseal constriction; G3, distance between the mandibular angle and the front of P₂.

Table 19.2. Measurements (in mm) of some African and Eurasian hipparion mandibles (also see table 19.1)

Locality		Bou Hanifia	Salonique	Ravin Zouaves	Vathylakkos	Thessaloniki
Number		$n = 2$	MNHN 290a	RZO 44 and 76	$n = 2-5$	$n = 3-8$
Species		<i>H. africanum</i>	<i>H. dietrichi</i>	<i>H. dietrichi</i>	<i>H. dietrichi</i>	<i>H. dietrichi</i>
I ₂ -symph. constriction	A	55.0	48.0	50.0	—	49.3
P ₂ -symph. constriction	B	46.0	41.0	39.0	—	40.0
Height in front of P ₂	12	48.5	49.0	48.4	43.6	47.0
Alveolar length P ₂ P ₄	3	79.5	66.0	64.0	68.0	66.0
Alveolar length M ₁ M ₃	4	71.5	65.0	61.5	64.0	63.5
Height between P ₄ and M ₁	11	60.0	66.0	73.0	65.7	68.2
Width at symph. constriction	14	30.5	35.0	35.0	—	35.0
Length P ₂ to gonion	G3	248.0	—	—	241.5	241.5

Note: For abbreviations see table 19.1.

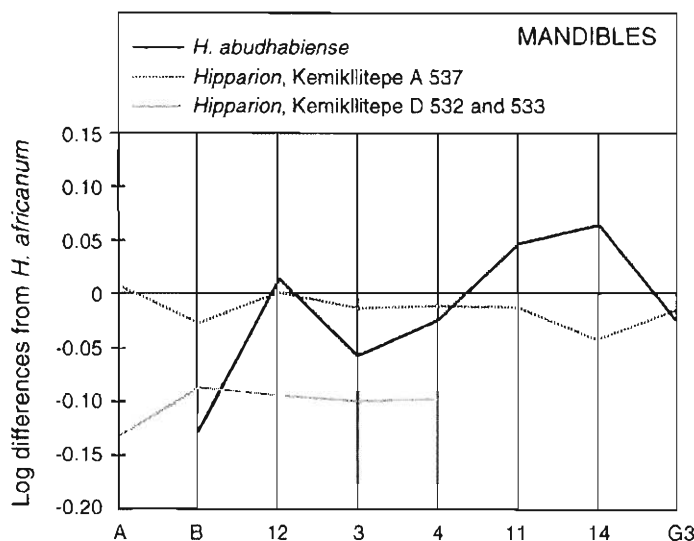


Figure 19.5. Ratio diagrams comparing the average of two mandibles of *Hipparion abudhabiense* of Jebel Dhanna, the average of two mandibles (D 532 and D 533) from Kemiklitepe D, and one mandible (A 537) from Kemiklitepe A. The average of two mandibles of the Vallesian *H. africanum* from Bou Hanifa is the reference line. Data on Kemiklitepe from Koufos and Kostopoulos, 1994). Abbreviations as in legend to figure 19.4.

Table 19.3. Measurements (in mm) of the lower cheek teeth of the type mandible of *Hipparion abudhabiense*, with mode of protosylids and occurrence of plis caballinid

	P ₂	P ₃	P ₄	M ₁	M ₂	M ₃	
Wear stage	IV	III	III	III	III	II	
Height	17.0	23.0	—	—	—	31.0	
	Length	28.0	23.0	22.0	19.5	20.2	25.0
	L. Ant Foss	5.0	7.0	6.2	5.1	6.3	6.5
Occlusal	L. Double K	10.0	12.5	12.0	11.0	10.2	9.7
	L. Post Foss	11.5	12.7	9.2	7.7	8.6	7.2
	Width	13.0	12.0	12.2	12.0	10.0	9.0
Protostylid	—	Pli	Pli	Pli	Pli	Isolated	
Pli caballinid	0	0	0	0	0	0	

Abbreviations: L = length; Ant Foss = anterior fossette; Double K = double knot; Post Foss = posterior fossette.

lower rami than *H. abudhabicus*. From an unknown Turolian level of Samos, the type *H. mathewi* has shallow ectoflexids on the premolars, although the teeth are very worn. The situation is unclear for *H. dietrichi* Mandibles from Samos Q1 (MN 11), which do have short muzzles and high rami, may have deep ectoflexids on very worn premolars (Sondaar, 1971: pl. II, fig. c) and even moderately worn ones (Wehrli, 1941: pl. 23, fig. 6), but at the Andrianos Quarry (also MN 11) the ectoflexid is shallow on premolars (Koufos and Melentis, 1984: pl. VI, fig. 1). The state of this character is unknown for the Lower Axios Valley *H. dietrichi* (MN 11). Only one lower series is figured from the Ravin des Zouaves (Koufos, 1987: fig. 8d); it has deep ectoflexids

but is very worn. No lower cheek series is figured from Vathy-lakkos, and the description states only that ectoflexids are deeper on molars (Koufos, 1988: 17). Among the "Saloniki" material of the MNHN (Paris), only very worn premolars of *H. dietrichi* have deep ectoflexids.

Deep ectoflexids are also seen in the rather worn P₃ and P₄ (but not on the P₂) of a lower cheek series from La Gloria 4, Spain, belonging in the MN 14 zone (Eisenmann and Mein, 1995). Thus, judging from the characters of the mandible, *H. abudhabiense* resembles *H. dietrichi* from Greece (MN 11 zone) while the same kind of deep ectoflexid on premolars is present in *Hipparion* sp. from Spain (MN 14 zone).

Upper Cheek Teeth (tables 19.6 and 19.7)

Three characters are usually considered: the shape of the protocone, the degree of enamel plication, and size. Interpretation of these characters is, however, made difficult by the wide range of variation, intraspecific and interspecific, which does not seem to have any clear biostratigraphical significance. We have nevertheless compared the upper cheek teeth of *H. abudhabiense* with those of hipparions that resemble it most in mandibular and lower cheek teeth characters.

The upper cheek teeth referred to *H. abudhabiense* have a rather small protocone, flattened on the lingual side (fig. 19.3.2) or rounded (fig. 19.2.1c and 2c). The enamel plication is moderate. In the Pliocene hipparion from La Gloria 4, the enamel plication is also moderate but the protocone is long and elliptical. In *H. dietrichi*, the enamel plication is again moderate, and the protocone is said to be elliptical or oval (Wehrli, 1941; Sondaar, 1971; Koufos and Melentis, 1984; Koufos, 1987, 1988). On the upper cheek teeth of Kemiklitepe referred to *H. mediterraneum* and to *H. matthewi* (Koufos and Kostopoulos, 1994: pl. III, fig. 2; pl. IV, fig. 3) protocones are small and rounded but the enamel plication seems stronger than in *H. abudhabiense*.

Figure 19.6 compares the sizes of the upper premolars (P^3 and P^4) and molars (M^1 and M^2). Only measurements of moderately-worn teeth (stages II and III) were considered valid: occlusal or mid-crown lengths in *H. abudhabiense* and *Hipparion* sp. (the other hipparion from Abu Dhabi), and *H. dietrichi* from the MN 11 zone of Greece. The data on the Greek forms were published by Koufos (1987, 1988). *Hipparion abudhabiense* seems to have slightly larger teeth than the average of *H. dietrichi* from Vathy-lakkos and Ravin des Zouaves. Its teeth are smaller than in *H. mediterraneum* from Kemiklitepe D and larger than in *H. matthewi* from Kemiklitepe A and B (Koufos and Kostopoulos, 1994: tables 6 and 9).

Limb bones

No complete limb bones have been found, so there is no way to calculate gracility. The distal radius fragment (BMNH M50665) has a distal articular width of 46.5 mm and a distal articular anteroposterior diameter of 26 mm. The first phalanx (AUH 164 and 165) fragments seem to have the same size as *H. dietrichi* from Vathy-lakkos (Koufos, 1988): the distal supra-articular width is 28.5 mm, the distal articular width is 29 mm, and the distal articular anteroposterior diameter is 18 mm.

RELATIONSHIPS WITH AFRICAN, MIDDLE EASTERN, AND ASIATIC HIPPARIONS

Africa

Algeria

There is only one species of hipparion, *H. africanum*, at Bou Hanifia, represented by skulls, mandibles, and limb bones. The mandible (reference line in fig. 19.4) has a longer muzzle and a lower ramus than in *H. abudhabiense*. Moderately worn upper cheek teeth have longer and oval protocones. Ectoflexids are shallow on lower premolars. The age of the hipparion level at Bou Hanifia (MN 9) is estimated at little more than 10.5 Ma (Sen,

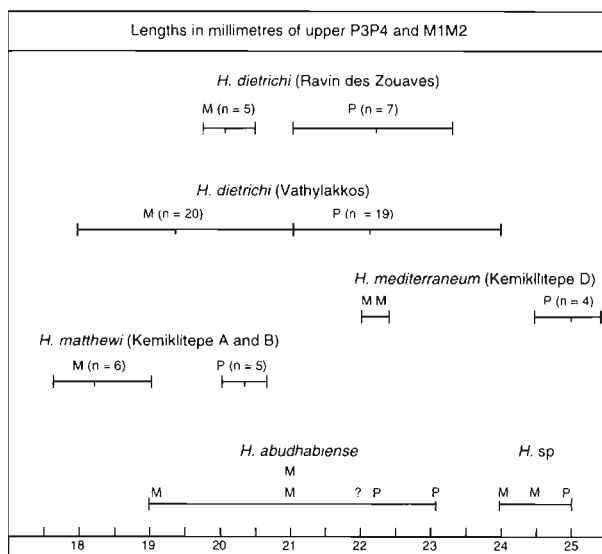


Figure 19.6. Lengths of upper cheek teeth in hipparions from Greece, Turkey, and the United Arab Emirates. The horizontal lines show the observed ranges.

Table 19.4. Measurements (in mm) of the lower cheek teeth of Abu Dhabi hipparions, with mode of protostylids and occurrence of plis caballinid (see also table 19.5)

		<i>Hipparion abudhabiense</i>	<i>Hipparion abudhabiense</i>	<i>Hipparion abudhabiense</i>	<i>Hipparion abudhabiense</i>	<i>Hipparion abudhabiense</i>	<i>Hipparion abudhabiense</i>	<i>Hipparion abudhabiense</i>
Tooth		P ₂	p	m	m	p	m	m
Specimen		M 50662	M 50661	AUH 23	M 50663	AUH 174	AUH 115	AUH 72
Wear stage		II	II	I	III	II	II	II
Height		30.0	36.0	50.0	33.0	44.0	39.0	37.5
	Length	21.5+	22.0	(23)	—	(25.5)	(21)	—
Occlusal	L Ante foss	7.2	7.0	9.0	—	7.0	6.8	7.0
	L Double K	12.1	12.0	14.0	—	16.0	12.0	—
	L Post foss	(12)	11.0	10.5	10.0	13.0	9.0	—
	Width	(17)	12.6	—	(12.5)	—	11.0	10.5
	Length	—	21.0	—	—	—	(20)	—
Mid-crown	L Ante foss	—	—	—	—	—	—	—
	L Double K	—	—	—	—	—	—	—
	L Post foss	—	—	—	—	—	—	—
	Width	—	13.7	—	—	—	(12)	—
At 1 cm	Length	—	21.0	—	—	—	—	—
	Width	—	13.7	—	—	—	—	—
Protostylid		—	0	—	—	—	—	—
Pli caballinid		—	0	—	0	0	0	—

Note: For abbreviations see table 19.3. Measurements in parentheses are approximate.

Table 19.5. Measurements (in mm) of the lower cheek teeth of Abu Dhabi hipparions, with mode of protostylids, and occurrence of plis caballinid (see also table 19.4)

		<i>Hipparion</i> sp.	<i>Hipparion</i> sp.	<i>Hipparion</i> sp.	<i>Hipparion</i> sp. ?	<i>Hipparion</i> sp. ?	<i>Hipparion</i> <i>abudhabicnse</i>	<i>Hipparion</i> sp. ?
Tooth		p	p	p?	p?	m?	m	ml
Specimen		AUH 144	AUH 265	AUH 208	AUH 216	AUH 216	AUH 266a	AUH 677
Wear stage		I	0–I	I	I	0	II–III	0
Height		55+	56.0	48.0	48.0	51.0	23.0	52.0
	Length	25.5	27.0	(26)	26.0	25.0	—	—
Occlusal	L Ante Foss	8.0	11.0	7.5	8.3	—	6.0	—
	L Double K	—	12.3	(13)	13.0	—	11.2	—
	L Post Foss	13.0	11.8	—	11.2	—	8.0	—
	Width	14.0	11.0	—	—	10.0	11.8	—
	Length	26.0	25.0	—	22.5	22.3	—	22.5
Mid-crown	L Ante Foss	7.8	7.0	—	—	—	—	6.7
	L Double K	15.0	13.0	—	—	—	—	14.0
	L Post Foss	13.8	11.0	—	—	—	—	7.5
	Width	13.0	12.5	—	—	11.2	—	12.0
At 1 cm	Length	—	23.5	—	22.0	21.0	—	—
	Width	—	14.0	—	—	11.0	—	—
Protostylid		0	Isolated	—	—	Pli	Isolated	—
Pli caballinid		0	0	—	—	—	0	0

Note: For abbreviations see table 19.3. Measurements in parentheses are approximate.

Table 19.6. Measurements (in mm) of the upper cheek teeth of Abu Dhabi hipparions, with number of plications (see also table 19.7)

		<i>Hipparion</i> sp.	<i>Hipparion</i> sp.	<i>Hipparion</i> sp.	<i>Hipparion</i> sp.	<i>Hipparion</i> sp.	<i>Hipparion</i> sp.
Tooth		p ²	p ²	P	M	M	P
Specimen		AUH 46	M50664	AUH 210	AUH 212	AUH 203	AUH 205
Wear stage		II–III	II–III	0–I	0	1	?
Height		42.0	40.0	50.0	51.0	54.0	—
Occlusal	Length	—	—	26.0	26.0	26.0	25.0
	Width	(34)	—	—	—	—	—
	Protocone L	—	—	—	—	9.0	—
	Protocone W	—	—	—	—	4.0	—
Mid-crown	Length	—	—	25.0	24.5	24.0	—
	Width	—	—	—	—	—	—
	Protocone L	—	—	—	—	8.1	—
	Protocone W	—	—	—	—	4.1	—
At 1 cm	Length	—	—	23.0	—	24.0	—
	Width	—	—	—	—	—	—
Plis fossette		Few	6–3	—	—	11–10	?–4
Plis caballin		—	—	—	—	2	—

Note: measurements in parentheses are approximate.

Table 19.7. Measurements (in mm) of the upper cheek teeth of Abu Dhabi hipparions, with number of plications (see also table 19.6)

		<i>Hipparion abudhabiense</i>	<i>Hipparion abudhabiense</i>	<i>Hipparion abudhabiense</i>	<i>Hipparion abudhabiense</i>	<i>Hipparion abudhabiense</i>	<i>Hipparion abudhabiense?</i>
Tooth		P	P	?	M	M	M2
Specimen		AUH 264	AUH 231a	AUH 260	AUH 229	AUH 230	AUH 676
Wear stage		0	III-IV	0	I	II	I
Height		55.0	22.0	48+	50.0	47.0	54.0
Occlusal	Length	26.0	22.3	25.0	24.2	20.0	23.0
	Width	23.0	—	—	23.0	20.1	—
	Protocone L	—	—	—	6.5	6.0	—
	Protocone W	—	—	—	4.1	3.0	—
Mid-crown	Length	24.0	—	22.0	21.1	19.0	21.0
	Width	24.0	—	—	23.0	21.0	—
	Protocone L	7.0	—	—	7.0	—	—
	Protocone W	5.0	—	—	4.5	—	—
At 1 cm	Length	22.0	22.3	—	20.7	18.0	20.5
	Width	22.6	—	—	23.2	20.3	—
Plis fossette		14-9	15-3	7-6	9-7	8?-3	—
Plis caballinid		1	—	—	1	0	—

1990), or about 10.85 Ma by extrapolation based on the sedimentation rate. The morphology of the skull, teeth, and limb bones of *H. africanum* is, however, much more evolved than in the usual Vallesian *H. primigenium*.

Hipparions from the middle Turolian (MN 12) may represent *H. sitifense*. The scanty material possibly belonging to *H. sitifense* was previously figured and discussed in detail by Eisenmann (1980). The type material is lost, and the material collected later at the same locality of Saint-Arnaud is limited to a badly preserved lower cheek tooth and a distal fragment of MT III. The age of the material is unknown. At present, our limited knowledge indicates that *H. sitifense* was a primitive form, with rather short and curved crowns and a rounded protocone (Pomel, 1897: pl. 1), smaller than *H. africanum* but not by much. More teeth were collected later in Algeria and referred to *H. sitifense*, although some of them could as well be referred to *H. africanum* if their morphology and not their age was considered. A few teeth come from Amama 2 (collected by J.-J. Jaeger), others probably from Amama 2 level "lower site of Kef el Amama" (collected by L. Ginsburg). According to Ameur-Chehbeur (1991), Amama 2 is Turolian. Some teeth come from Chabet el Maatga (old collections, and new collections by Mr and Mrs. Coiffait, who believe that the age of Chabet el Maatga is close to that of Amama 2). The whole sample is unsatisfactory because of its small size and the poor preservation of the teeth. It does appear, however, that, as at Abu Dhabi, two hipparions may be present, and that one small upper premolar has a small and rounded protocone. Consequently, there is a certain resemblance between *H. sitifense* of the middle Turolian of Algeria and *H. abudhabiense*.

East Africa

The *Hipparion primigenium*, described by Hooijer (1975), from the Ngorora Formation, Kenya, is represented by a few teeth and limb bones. It is larger than *H. africanum*, and does not resemble *H. abudhabiense* at all. There are no hipparion fossils in the type section of the Ngorora Formation, only in younger sites; their age is between 9.0 and 8.5 Ma (A. Hill, personal communication), cer-

tainly younger than 10 Ma (Hill et al., 1986), and they probably belong in the MN 11 zone.

From the Namurungule Formation, Samburu Hills, Kenya, Nakaya and Watabe (1990) describe *Hipparion* aff. *africanum*. Even if the skull and some other fossils are related to *H. africanum*, it is clear that the variation within the Samburu sample is too great for a single species. For example, one metacarpal (12272) is much larger than the others, and compares well with the large *H. koenigswaldi* from Nombrevilla, Spain (MN 10). According to the published measurements, the big upper cheek teeth of Samburu are larger than in *H. africanum*, but compare well with teeth from Nombrevilla. It is only the small teeth of Samburu that may be referred to the Bou Hanifa species (Eisenmann, 1995a). The large teeth from Samburu are similar in size to the large species of Abu Dhabi, but the morphology is very different: the figured upper cheek teeth have very plicated enamel, multiple plis caballin, and oval protocones. The small teeth from Samburu have longer protocones than *H. abudhabiense*. The age of the Samburu hipparions is estimated at 9 Ma.

The presence of two species of hipparion at one site was classically considered as an indication of Turolian rather than Vallesian age. Recent studies have shown, however, that there is no monotypy of Vallesian hipparions (Eisenmann, 1995b). In consequence, the presence of two hipparions at Samburu is no longer unique nor surprising.

A primitive, large *Hipparion* was described at Nakali, Kenya (Aguirre and Alberdi, 1974). From its size and morphology, it appears very close to the large *Hipparion* from Samburu. The ages are probably also close, since Nakali is believed to be possibly a little younger than 9 Ma (Hill, 1987).

Another primitive form, *H. macrodon* has been described from the Kakara Formation of Uganda (Eisenmann, 1995a) situated in the base of the Upper Miocene (Pickford et al., 1993). The upper premolars are larger than any of the known species of hipparion. Morphology and size differ completely from those of *H. abudhabiense*.

Between 6.5 and 4 Ma ago there are several East African hipparion localities: Mpesida Beds, Lukeino Formation, Lothagam 1, and lower units

of the Chemeron Formation (Hill, 1987; Hill and Ward, 1988). From the literature it is not always clear if the fossils come from these or from younger units (Hill et al., 1992): Lothagam 3 (about 4 Ma) or the upper units of Chemeron (about 4–1.6 Ma). Some of the material was published by Aguirre and Alberdi (1974), Hooijer and Maglio (1974), and Hooijer (1975). In the literature, the hipparion cheek teeth are poorly represented. The material consists of small samples: one tooth at Mpesida, probably no teeth from the lower levels of Chemeron, and very worn teeth in the skull of *H. turkanense* of Lothagam. It is nevertheless clear that, in the East African Miocene—for example, at Lukeino—the first hipparions with a caballoid pattern on the lower cheek teeth appear. This pattern becomes common and more pronounced—“caballine”—later and is made still more original by the development of ectostylids. Whatever their size, these hipparions lack primitive characters and cannot be closely related to *H. abudhabiense*. Since these publications, larger collections have been made from sites in the Mpesida, Lukeino, and Chemeron units by Andrew Hill and colleagues, and from Lothagam by Meave Leakey’s team. So far this material is unpublished.

Middle East

Turkey

Staesche and Sondaar (1979) have correlated the Turolian localities of Garkin and Kinik, respectively, with Samos Quarries 1 and 4 (MN 11 zone) and Samos Quarry 5 (MN 13 zone), and found that the medium-sized hipparion remains from Kayadibi, Garkin, and Kinik resembled *H. dietrichi* in various characters. At Kayadibi and Garkin, there is a larger form that makes the comparison with the two hipparions of Abu Dhabi especially interesting. The upper cheek teeth of the Turkish *H. cf. dietrichi* are the size of those in *H. abudhabiense* and also have rounded protocones. But the larger Turkish species also has rounded protocones that do not resemble those of *Hipparion* sp. of Abu Dhabi.

Koufos and Kostopoulos (1994) have described several hipparions from the localities of Kemiklitepe. The lower level (Kemiklitepe D) has yielded early

Turolian or even Vallesian Carnivora (Bonis, 1994) and Proboscidea (Tassy, 1994). According to our ratio diagrams, the hipparion mandibles from this lower level of Kemiklitepe are not very different from those of *H. africanum* from Bou Hanifa (fig. 19.5). The upper levels of Kemiklitepe are believed to belong in the MN 12 or 13 zone. According to our (unpublished) ratio diagrams, the mandibles from the upper levels resemble not the typical *H. matthewi* from Samos, but the small hipparions from Ravin de la Pluie and Dytiko. Neither the upper nor the lower level hipparions resemble *H. abudhabiense*.

Lebanon

Malez and Forsten (1989) have published some material from the Bekaa Valley. The artiodactyls indicate a Turolian age. Two hipparions are present, the dimensions of which fit well with the two forms from Garkin. Morphology and size also appear to fit well with the Abu Dhabi hipparions: protocones tend to be pointed and flattened on the larger teeth, rounded on the smaller. At least one small premolar has a deep ectoflexid. It is possible that both the smaller form (*H. cf. dietrichi*?) and the larger one are related to the Abu Dhabi forms.

Iraq

From the Agha Jari Formation of Jebel Hamrin, Thomas et al. (1980) have described a fauna with two hipparions: a medium-sized *H. mediterraneum* and a larger *H. cf. primigenium*. The fauna was believed to be close in age to the Vallesian–Turolian boundary. A well-preserved skull of *Prostrepsiceros zitteli* was found later in the same area, indicating an early Turolian age (Bouvrain and Thomas, 1992).

The smaller upper cheek teeth, with their small and rounded or flattened protocones, fit well with *H. abudhabiense*, but out of five small lower premolars, only one shows a tendency to a deep ectoflexid like the fragmentary premolar of Hamra (fig. 19.2.3). The larger upper cheek teeth have elongated protocones as in *Hipparion* sp. of Abu Dhabi, but with more plicated enamel (Thomas et al., 1980: pl. I, fig. 3). The larger lower cheek teeth (Thomas et al., 1980: pl. I, fig. 1) have a

somewhat caballoid pattern, similar to the medium-sized hipparion from Kemiklitepe D. These characters and the relative hypsodonty of both small and large teeth are surprising in Vallesian or early Turolian forms.

Asia

Siwaliks

The upper cheek lengths of hipparions from Abu Dhabi fall inside the ranges of variation given by Hussain (1971) for *H. antilopinum* and *H. thcobaldi*. All the upper cheek teeth figured by Hussain, however, have much more plicated enamel than the hipparions from Abu Dhabi and none has the small and rounded protocones of *H. abudhabiense*. Rounded protocones are present in the type of *H. feddeni* from the "middle Siwalik group of Perim Island" (Lydekker, 1884; MacFadden and Woodburne, 1982: fig. 9) but the teeth seem to be larger in *H. feddeni* than in *H. abudhabiense*. Bernor and Hussain (1985) state that one difference between the genera *Cormohipparion* and *Hipparion* is the shape of the protocone: elongate in *Cormohipparion*, rounded (at medium wear) in *Hipparion*. They do not illustrate, however, any Siwalik "Hipparion" with rounded protocones. Moreover, they seem to refer the type of *H. feddeni* (with rounded protocones) to *Cormohipparion perimense*, which is supposed to have elongate protocones.

Iran

There is no mandible—at least in the material of the Muséum National d'Histoire Naturelle, Paris, that has a muzzle as short as *H. abudhabiense*. At least two skulls (MNHN 18 and 359) belong to the short-muzzled *H. dietrichi* type, however, so that it is not unlikely that *H. abudhabiense* has affinities with some Maragheh hipparions (Bernor, 1985).

DISCUSSION

Several observations can be made about the Abu Dhabi hipparion material. Two species of *Hipparion* are represented: they are a small to medium-sized *H. abudhabiense* and a medium-sized to large

Hipparion sp. They differ not only in size, but in the shape of the protocone—very small and rather rounded in the former and elongate in the latter—and by the depth of the ectoflexid on the lower premolars, which tend to be deep in *H. abudhabiense*. The larger hipparion from the Baynunah Formation is poorly represented so that its affinities are not clear. *Hipparion abudhabiense* compares well with *H. dietrichi* from the MN 11 zone of Greece (Samos and Thessaloniki area) but it may have had an even shorter muzzle. Morphologically similar upper and/or lower cheek teeth may also be present in North Africa (*H. sitifense*), and Turkey, Lebanon, Iraq, and Piram (formerly Perim) Island.

Hipparion abudhabiense probably had a very short and broad muzzle, suggesting grazing rather than browsing habits. This species also shows two apparently contradictory characters: a relatively deep mandibular ramus, suggesting hypsodonty, and deep ectoflexids on some premolars, a primitive character interpreted by Gromova (1952: 92) as a poor adaptation to abrasive food. A Pliocene hipparion from Spain (La Gloria 4) associates deep ectoflexids on some premolars with an extremely slender metatarsal. Here again, there is an apparent contradiction between the dry environment suggested by the metatarsal and the soft food suggested by the primitive teeth.

Because of their geographical location, resemblances between the hipparions from Abu Dhabi and those from Africa and Asia might be expected, and we have already discussed the characters that may indicate relations with North African and Siwalik hipparions. Our best point of comparison, however, remains with *H. dietrichi*, a European species. Three possibilities may explain this. First, in East Africa there is a gap between the Nakali-Samburu faunas (which are probably too old to compare with the fauna from Abu Dhabi) and late Turolian sites (which are probably too young). It is possible that the fauna from Abu Dhabi falls into this gap. Second, in North Africa the Turolian hipparion material is too poor for adequate comparison. Finally, for Siwalik specimens, the problem is a little different as most of the material is unpublished. Skulls have been discussed at length and repeatedly, but there are no data on the mandibles,

not enough data on the limb bones, and not enough figures of the cheek teeth. When the Indian and Pakistani hipparions are better known, their relationship to the hipparion fauna from Abu Dhabi may become clear.

A final point should be made. We have already noted that the Vallesian *H. africanum* looks more "evolved" than classical Vallesian hipparions. Evolved characters (caballoid double knots, hypsodonty) may also be observed in Vallesian or early Turolian hipparions from Turkey (Kemiklitepe D) and Iraq (Jebel Hamrin). Do all these discrepancies indicate that age evaluations are wrong, or should biostratigraphic correlations be made only when the palaeoecological conditions are similar?

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