

# On the Rhinocerotidae from the Miocene Manchar Formation, Sind, Pakistan

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**Abstract.**—The rhinocerotid remains from the Lower Manchar Formation, Sind (Pakistan), are studied herein. Four different forms are identified: *Hispanotherium matritense*, *Aprotodon fatehjangense*, *Brachypotherium perimense* and *Chilotherium cf. intermedium*. The association of these four rhinocerotids is known from the Early-Middle Miocene rhinocerotids from the Siwaliks in the Potwar Plateau.

**Key words:** Rhinocerotids, Manchar Formation.

## INTRODUCTION

The material studied is part of the collection recovered from the Manchar Formation (Sind, Pakistan), during 1981-1984, by a joint team of the Geological Survey of Pakistan, the Howard University (Washington, D.C.), and the University of Utrecht.

Preliminary investigations of the Manchar Formation (Khan *et al.*, 1984) suggested a Middle to Late Miocene faunal composition, and paleomagnetic data indicated an absolute age ranging from 15.2 to 9/10 Ma. However, further studies on the fossils recovered from the lower part of the Manchar Formation have established a correlation with the Kamlial Formation or the lower part of the Chinji Formation, that is Early or Middle Miocene (Jacobs *et al.*, 1990; Made and Hussain, 1992).

Some mammal groups from the Manchar Formation have already been studied, particularly rodents and artiodactyls (Bruijn and Hussain, 1984; Made and Hussain, 1992, 1994). This paper presents the study of the rhinocerotid remains from Howard University-Geological Survey of Pakistan Project. The specimens come from different localities, and they are catalogued as HGSP (=Howard University-Geological Survey of Pakistan Project), followed by a number which indicates the year of collection and the locality, and the specimen number (*e.g.* HGSP 8311/1737). Most localities yielded one or a few specimens. However, the localities 8108, 8205, and especially 8311 yielded relatively abundant specimens (22, 10 and 98, respectively).

## SYSTEMATICS

Comparative study of more than 300 specimens allowed the identification of four different rhinoceroses. However, the characterization was not easy, since most specimens are either fragmentary and/or not diagnostic enough to be identified at least at a specific level. For instance, especially abundant are the phalanges (93) that only can be separated by a clear difference of size, but seldom ascribed to one species. Therefore, a few specimens are accurately classified and described below.

Family RHINOCEROTIDAE Owen, 1845

Subfamily RHINOCEROTINAE Owen, 1845

Tribe RHINOCEROTINI Owen, 1845

Subtribe IRANOTHERIINA Kretzoi, 1943

*Hispanotherium matritense* (Prado, 1864)

**Material:** HGSP 8415/3588 and 3268, left and right P<sub>1</sub>; HGSP 8101/1013, right P<sub>2</sub>; HGSP 8311/895, right P<sub>3,4</sub>; HGSP 8414/3233, right P<sub>3</sub>; ?HGSP 8205/807, radius proximal fragment; HGSP 8311/1737, right scaphoid; HGSP 8108/1072, left semilunate; HGSP 8311/1620 and 1917, left and right pyramidals; HGSP 8311/1377, left unciform; HGSP 8311/1746, right navicular; HGSP 8129/649, 8207/893, 8311/1912 and 8121/305, 2 right and 2 left astragali; HGSP 8311/1679, right calcaneum;

HGSP 8311/1629, right McIII fragment; HGSP 8311/1438, 8311/1617, 8125/314 and 8108/1073, first central phalanges; HGSP 8311/1667, 8311/1689, 8311/1745, 8209/774, and 8314/1707, first lateral phalanges.

The teeth (Table I; Figs. 1-2) are characterized by the abundant presence of cement, well marked external groove, and metaconid lingually detached and backwardly directed. The protoconid of the  $P_3$  is rather acute. The carpal and tarsal bones (Figs. 8,11,16; Figs. 20,23) are small, and basically comparable to "*Caementodon oettingenae*" from the Siwaliks (Heissig, 1972; E.C.'s own data) and the *Hispanotherium* material from Spain (Cerdeno, 1989, 1992; Inigo and Cerdeno, 1996a) and Turkey (Heissig, 1976; E.C.'s own data). The scaphoid is slightly greater than the specimen 1956 II/373 from Kadirpur (Chinji, Siwaliks). The unciform has a relatively short posterior apophysis. The navicular is rather square in outline. The McIII fragment (Fig. 25) shows a large posterior lateral facet, that does not exceed the posterior edge of the epiphysis. Some phalanges ascribed to *H. matritense* are small and relatively slender; their dimensions (Table I) are very similar to the Spanish specimens from La Retama (Cerdeno, 1992).

*Hispanotherium matritense* was described upon some dental remains from the Middle Miocene of Spain (Prado, 1864; Crusafont and Villalta, 1947). Similar forms were later described as closely related to it (Heissig, 1972, 1976; Antunes and Ginsburg, 1983) in other close by and distant areas (Portugal, Chinji, Turkey). Following the recent cladistic analysis of the family Rhinocerotidae (Cerdeno, 1995), this group of Middle Miocene species is closely related with the genus *Iranotherium* (De Mecqueney, 1924) from the Upper Miocene of Maragha (Iran), but not with *Elasmotherium* (Fischer, 1809) from the Pleistocene of Asia (Europe?); consequently, they have been separated, and the former is considered as subtribe *Iranotheriina*. On the other hand, the taxonomic validity of these Middle Miocene forms has been often discussed, and mostly considered synonyms of *Hispanotherium* either at generic or even at specific level (Antunes and Ginsburg, 1983; Cerdeno, 1989; Inigo and Cerdeno, in press; Cerdeno, 1996a). In the area of Chinji, Heissig (1972) described the species *Caementodon oettingenae*, later synonymized with *H. matritense* (Cerdeno, 1989; Inigo and Cerdeno, in press).

The present knowledge of *Hispanotherium* - especially *H. matritense* from Spain - shows that it was widely distributed throughout Asia and Western Europe (Iberian Peninsula and poorly known in France); this geographical distribution led to postulate a migration route through the Mediterranean (Antunes, 1979). The oldest known remains of the genus so far known correspond to *H. matritense* from the early Middle Miocene Spanish site of Corcoles (Inigo and Cerdeno, in press), while the youngest ones would be the Chinese form from the late Middle Miocene of Tung-gur, *H. tungurensis* (Cerdeno, 1996a). The Pakistani material would be younger than Corcoles (biozone MN 4a), since some lower Manchar Formation localities have been correlated with the MN 5 (Made and Hussain, 1992).

The characteristics of *Hispanotherium* (subhypsodont teeth and slender skeleton) make it an indicator of open and rather dry climate. The abundance of *H. matritense* at several Spanish sites indicates a gregarious way of life for this species, as well as for other small and hornless rhinoceroses such as *Protaceratherium minutum* and *Alicornops simorreense* (Cerdeno and Neito, 1995).

Other faunal elements from Sind, such as the sanitheres (Suoidea), indicate a more tropical climate (Made and Hussain, 1992). However, the sanithere material comes from different fossiliferous localities than the *Hispanotherium* remains, and one could think that different local conditions are represented in the area. Slight temporal differences among the sites could also imply climatic variations.

#### Subfamily RHINOCEROTINAE Owen, 1845

##### Genus APROTODON Forster-Copper, 1915

##### *Aprotodon fatehjangense* (Pilgrim, 1910)

*Material:* HGSP 8114/?, germ of right  $P_2$ ; HGSP 8222a/1228, 8108/239, and 8311/1688, three right larger scaphoids; HGSP 8311/1896, 1735, 1883 and 8209/223, four (2 l./2 r.) smaller scaphoids; HGSP 8205/816 juvenile right scaphoid; HGSP 8311/1950, left semilunate; HGSP 8311/1443, 1575, 1885, 8108/60, and 8116/506, 3 left and 2 right pyramidal; ?HGSP 8311/1686, left pisiform; HGSP 8311/1465, left trapezoid; HGSP 8311/1647,

**Table I.- Dimensions of teeth and bones of *Hispanotherium matritense* from the Manchar Formation, Sind.**

Premolars 1:	8415/3588; L (17.2), W 12.0 8415/3268; L 18.6, W 11.2
Premolars 2:	8101/1013; L 27.3, W 18.2
Premolars 3-41:	8414/3233; L 33.0, W 17.7 8218/895; L 32.4, W 23.0
Scaphoid	8311/1737; TDm 37.9, APDm 61.1, Hm 53.3, prox.art.: TD 37.9, APD 38.0, dis.art.: TD, 23.0, APD 52.0
Semilunate	8108/1072; TDm 35.1, APDm 49.5, H 37.2, Hant 38.0
Pyramidal	8311/1917; TDm 36.0, APDm 37.3, Hm 45.1, APDpr 24.4 8311/1620; TDm 31.9, APDm 37.5, Hm 43.3, APDpr 25.7
Unciform	8311/1377; TD 53.8, H 40.7, Lab. 66.0, Lan 49.2
Navicular	8311/1746; TD 38.8, APD 45.7, Hm 26.5, Hmin 18.2
Astragalus	8129/649; TD 90.5, H 68.9, TDdis 78.2, dis.art.: TD 76.0, APD (41.0), DL 55.2, APDi 55.8 8207/893; TD 82.6, H 64.4, TDdis 70.0, dis.art.: TD 67.9, APD 37.5, DL 49.0, APDi 41.6 8311/1912; TD (84.0), H 72.0, TDdis (71.0), dis.art.: TD 68.7, APD (39.0), DL 55.0 8121/305; TD (75.4), H 62.8, TDdis 68.0, dis.art.: TD 62.1, APD (34.4), APDi 44.3
Calcaneum	8311/1679; tuber: TD 39.0, APD 64.7, beak: APD 61.5, sus: TD -, post: TD 31.6
Metapodial McIII	8311/1629; L -, prox.ep: TD 49.4, APD 38.3, prox.art: TD 46.0, APD 36.0, diaphysis: TD 40.2, APD 18.5, TDm dis.art.: TD -, APD -
1st central phalanx	8311/1438; TD 39.4, APD 39.5, H 30.5 8311/1617; TD 38.3, APD 26.0, H 34.6 8125/314; TD 40.0, APD 30.6, H 33.5
1st lateral phalanx	8311/1667; TD 31.5, APD 30.9, H 32.7 8311/1689; TD 29.2, APD 27.4, H 24.4 8311/1745; TD 29.0, APD 28.1, H 28.0 8209/774; TD 31.2, APD 25.2, H 25.5 8314b/1707; TD 27.0, APD 27.3, H 27.5

Abbreviations used: APD, anteroposterior diameter; APDi, internal anteroposterior diameter; APDm, maximum anteroposterior diameter; APDpr, proximal anteroposterior diameter; prox.art., proximal articulation; dis.art., distal articulation; dis.ep., distal epiphysis; D, milk molar; DL, distance between the astragalus lips; H or Hm, maximum height; Hant, anterior height; Hmin, minimum height; Hpost, posterior height; I, Incisor; L, length; Lab, absolute length; Lan, anatomical length; M, molar; Mc, metacarpal; Mt, metatarsal; P, premolar; prox.art., proximal articulation; prox.ep., proximal epiphysis; sus., sustentaculum; TD, transverse diameter; TDant, anterior transverse diameter; TDdis, distal transverse diameter; TDm, maximum transverse diameter; TDpost, posterior transverse diameter; W, width.



8311/1946, 8311/1468, 8108/237, 8311/1619, and 8413/3174, 4 left and 2 right unciforms; HGSP 8205/819, right patella; HGSP 8311/1573, 8311/1939, 8108/1062, 8311/1974, 3 right and 1 left astragali; HGSP 8302/1296, left astragalus fragment; HGSP 8111/114, right calcaneum; HGSP 8213/964, left cuboid; HGSP 8311/1722 and 1691, right and left McIII fragments; HGSP 8108/69, left McIV fragment; ?HGSP 8311/1935, Mc V fragment; HGSP 8116/514, 8108/869, 8311/1731, and 8311/1725, 4 right MtII fragments; HGSP 8311/1422, right MtIII; HGSP 8108/76 and 8311/1582, 2 left MtIII fragments; HGSP 8311/1440 and 8206/716, right and left MtIV fragments.

The P<sub>2</sub> is high and narrow, with a smooth but clear external groove (Fig. 3). The protoconid is well marked, and the metaconid is slightly directed backwards. It is similar to that figured by Heissig (1972, pl. 9, Fig. 10), and their dimensions are very close.

The scaphoids (Fig. 9) are low and wide, with a large third posterior facet for the semilunate. Their proportions are not so wide as in *B. perimense*, fitting better with *A. fatehjangense* (Heissig, 1972), although there are some specimens clearly larger in size. The smaller specimens ascribed to *Aprotodon* (Table II) are closer in dimensions to those from the Siwaliks. Since there is only size difference, it could be considered as intraspecific variation, probably due to sexual dimorphism.

The semilunate is low and wide (Table II; Fig. 12), with a large posterior facet for the scaphoid; the inferior pyramidal facet is long. The morphology is also similar to *Chilotherium intermedium* (Heissig, 1972), but this species lacks the posterior scaphoid facet. The pyramidals (Fig. 14) in Table II show a slight variation concerning proportions, but their taxonomic separation is not clear. The lower semilunate facet is long, but not L-shaped. The pisiform (Fig. 15) is ascribed tentatively to *Aprotodon*, since no comparative material is available. The outline is subrectangular, with large articular zone and low posterior apophysis. The trapezoid is large (Table II; Fig. 13); the anterior face is low and wide, and the posterior one relatively high. Only two unciforms are complete, showing a broad and rather short posterior apophysis. The proximal facet is laterally narrowed.

The patella HGSP 8205/819 (Fig. 19) is tentatively ascribed to *Aprotodon*. It is broad, with strongly developed medial apophysis.

The astragalus (Table II) is broad, with inclined trochlea, the lateral lip much longer than the medial one; large separation between the trochlea and the distal articulations; distal facets with a marked angle between them; and projected medial tubercle (Fig. 24). The size is similar to *A. fatehjangense* from the Siwaliks, except that they are slightly higher. The specimen HGSP 8311/1939 has more concave facet 1 and larger facet 2. HGSP 8311/539 is larger than the others but morphologically similar.

- Fig. 1. *Hispanotherium matritense*; Right P<sub>2</sub>, HGSP 8101/1013, labial view.  
 Fig. 2. *Hispanotherium matritense*; Right P<sub>3</sub>, HGSP 8218/895, lingual view.  
 Fig. 3. *Aprotodon fatehjangense*; Left P<sub>2</sub>, HGSP 8129/658, labial view.  
 Fig. 4. *Aprotodon fatehjangense*; Right M<sub>3</sub>, HGSP 8427/3637, lingual view.  
 Fig. 5. *Brachypotherium perimense*; Right M<sup>2</sup>, HGSP 8424/3506, occlusal view.  
 Fig. 6. *Brachypotherium perimense*; Left P<sup>2</sup>, HGSP 8413/3185, occlusal view.  
 Fig. 7. *Brachypotherium perimense*; Left M<sub>3</sub>, HGSP 8412/3119, occlusal view.  
 Fig. 8. *Hispanotherium matritense*; Right scaphoid, HGSP 8311/1737, medial view.  
 Fig. 9. *Aprotodon fatehjangense*; Right scaphoid, HGSP 8311/1688, medial view.  
 Fig. 10. *Chilotherium cf. intermedium*; Left scaphoid, HGSP 8311/1612, lateral view.  
 Fig. 11. *Hispanotherium matritense*; Left semilunate, HGSP 8108/1072, medial view.  
 Fig. 12. *Aprotodon fatehjangense*; Left semilunate, HGSP 8311/1950, medial view.  
 Fig. 13. *Aprotodon fatehjangense*; Left trapezoid, HGSP 8311/1465, proximo-lateral view.  
 Fig. 14. *Aprotodon fatehjangense*; Left pyramidal, HGSP 8311/1443, medial view.  
 Fig. 15. *Aprotodon fatehjangense*; Left pisiform, HGSP 8311/1686, medial view.  
 Fig. 16. *Hispanotherium matritense*; Left unciform, HGSP 8311/1377, proximal view.  
 Fig. 17. *Aprotodon fatehjangense*; Left unciform, HGSP 8311/1946, proximal view.

Scales: 1-4, 5-7, 8-10, 11-15, and 16-17, respectively.

**Table II.- Dimensions of teeth and bones of *Aprotodon fatehjangense* from the Manchar Formation, Sind.**

Premolars 2:	8114/?; L 25.0, W (14.0) 8129/658; L 26.0, W 20.3 8311/1412; L 24.5, W 19.4 8319/2019; L 22.6, W 16.5
M / 1-2:	8415/3254; L (49.8), W (26.6)
M / 3:	8427/3637; L 56.0, W 30.5 8408/3032; L 53.6, W 29.7
Scaphoid	8222a/1228; TDm 59.5, APDm 93.2, Hm 68.9, prox.art.: TD 48.0, APD 55.1, dis.art: TD 40.8, APD 77.6 8108/239; TDm 52.0, APDm 83.0, Hm 65.4, prox.art.: TD 45.4, APD 55.3, dis.art: TD 35.6, APD 74.0 8311/1688; TDm 54.0, APDm 94.0, Hm 62.0, prox.art.: TD 48.2, APD 53.9, dis.art: TD 35.0, APD 75.7 8311/1883; TDm 54.6, APDm 78.2, Hm 60.4, prox.art.: TD 50.3, APD 46.0, dis.art: TD 33.4, APD 62.0 8311/1896; TDm 55.8, APDm 74.7, Hm 60.3, prox.art.: TD 46.4, APD 40.0, dis.art: TD 39.1, APD 65.0 8311/1735; TDm 47.3, APDm 75.3, Hm 59.7, prox.art.: TD 41.5, APD 42.3, dis.art: TD 35.0, APD 62.9 8209/223; TDm 52.1, APDm -, Hm -, prox.art.: TD 47.9, APD 40.5, dis.art: TD -, APD - 8205/816 juv.; TDm 42.6, APDm -, Hm 48.4, prox.art.: TD 39.0, APD, 36.0, dis.art.: TD -, APD -
Semilunate	8311/1950; TDm 49.0, APDm 64.3, H 42.8, Hant 45.2
Pyramidal	8311/1443; TDm 43.8, APDm 53.4, Hm 54.5, APDpr 33.5 8311/1575; TDm 41.4, APDm 47.3, Hm 48.5, APDpr 30.7 8311/1885; TDm 38.0, APDm 47.9, Hm 47.0, APDpr 31.1 8108/60; TDm 39.8, APDm 52.1, Hm 52.4, APDpr >29.7 8116/506; TDm -, APDm >47, Hm 52.3, APDpr 35.7
Pisiform	8311/1686; TDant 25.2, APD 60.9, Hant 31.2, Hpost 31.9, TDpost 17.8
Trapezoid	8311/1465; TD 40.0, APD 50.9, Hm 39.7, Hmin 25.6
Unciform	8311/1647; TD 67.4, H 50.4, Lab -, Lan - 8311/1946; TD 62.9, H 47.4, Lab 79.0, Lan 62.5 8108/237; TD 64.5, H 49.6, Lab -, Lan - 8311/1619; TD 59.2, H 47.5, Lab 80.4, Lan 64.1 8413/3174; TD 62.4, H 46.3, Lab -, Lan - 8311/1468; TD 59.2, H 44.5, Lab -, Lan -
Patella	8205/819; TD 87.7, APD 43.0, H 83.3
Astragalus	8311/1573; TD 95.6, H 75.0, TDdis 81.8, dis.art: TD 77.0, APD 47.2, DL 60.2, DAPi 51.0 8311/1974; TD 102.8, H 80.1, TDdis 85.7, dis.art: TD 80.0, APD 45.4, DL 61.5, DAPi 54.4 8311/1939; TD 91.0, H 71.5, TDdis 77.9, dis.art: TD 76.1, APD 42.0, DL 55.6, DAPi 48.6 8108/1062; TD 101.1, H 78.0, TDdis 86.5, dis.art: TD 80.3, APD 43.6, DL 61.7, DAPi 56.2
Calcaneum	?8111/114; H 142.0, tuber: TD 51.7, APD 66.0, beak: APD 69.2, sus.: TD -, post. TD 34.0

(Continued)



Cuboid	8213/964; TDm 39.0, TDant 37.8, APD 52.8, Hm 45.3, Hant 30.3, prox.art.: TD 33.5, APD 39.1
Metapodial McII	8311/1722; prox.ep: TD 60.6, APD 50.0, prox.art.: TD 58.6, APD 47.0 8311/1691; prox.ep: TD 58.0, APD 48.0, prox.art.: TD 54.1, APD 41.0
Metapodial McIV	8108/69; prox.ep: TD 39.9, APD 42.4, prox.art.: TD 34.7, APD 36.0
Metapodial McV	8311/1935; TDm 31.6, dis.art.: TD, 27.0, APD 23.4
Metapodial MII	8116/514; prox.ep: TD 29.5, APD 43.5, prox.art.: TD 19.2, APD 40.0 8108/869; prox.ep: TD 30.6, APD 41.1, prox.art.: TD 17.4, APD 37.0 8311/1731; prox.ep: TD 30.0, APD (41.0), prox.art.: TD 23.8, APD- 8311/1725; prox.ep: TD 28.8, APD 42.4, prox.art.: TD 19.0, APD 33.4
Metapodial MIII	8311/1422; L 151.4 prox.ep: TD 50.3, prox.art.: TD 45.3, diaphysis: TD 39.6, APD 19.7, TDm 52.7, dis.art.: TD 47.5, APD 39.0 8108/76; prox.ep: TD 49.2, APD 42.7, prox.art.: TD 46.6, APD (34.8) 8311/1582; prox.ep: TD 50.0, APD 42.7, prox.art.: TD 46.0, APD 37.0
Metapodial MtIV	8311/1440; prox.ep: TD 40.4, APD 42.4, prox.art.: TD 30.4, APD 40.3, diaphysis: TD 26.3, APD 21.0 8206/716; prox.ep: TD 42.8, APD 42.7, prox.art.: TD 38.2, APD 38.0

Abbreviations used: APD, anteroposterior diameter; APDi, internal anteroposterior diameter; APDm, maximum anteroposterior diameter; APDpr, proximal anteroposterior diameter; prox.art., proximal articulation; dis.art., distal articulation; dis.ep., distal epiphysis; D, milk molar; DL, distance between the astragalus lips; H or Hm, maximum height; Hant, anterior height; Hmin, minimum height; Hpost, posterior height; I, Incisor; L, length; Lab, absolute length; Lan, anatomical length; M, molar; Mc, metacarpal; Mt, metatarsal; P, premolar; prox.art., proximal articulation; prox.ep., proximal epiphysis; sus., sustentaculum; TD, transverse diameter; TDant, anterior transverse diameter; TDdis, distal transverse diameter; TDm, maximum transverse diameter; TDpost, posterior transverse diameter; W, width.

The calcaneum HGSP 8111/114 could correspond to *Aprotodon*. It is a large, high bone, with wide and short tuber, with marked unevenness; a tibial facet seems to have existed. The cuboid (HGSP 8213/964) is clearly smaller (Table II) than the other two specimens ascribed to *Brachypotherium* (Table III), although the ratio TD/APD is similar to HGSP 8129/546. The former is close to the cuboids of *Aprotodon* from the Siwaliks (Heissig, 1972).

The MtIII HGSP 8311/1422 (Figs. 32-33) is the only almost complete metapodial of the sample. It is rather slender but with enlarged epiphyses. The proximal facet of MtIV (Fig. 35) is longer (APD) than wide. The MtII (Figs. 27, 28) has a large entocuneiform facet. The McIII fragments show a well-marked proximal crest, shorter than on HGSP 8311/1376 of *B. perimense*. The McIV fragment (Fig. 34) has a broad, trapezoidal proximal facet. A distal fragment of a well-developed McV is tentatively ascribed to *Aprotodon*. The other identified genera

have a reduced McV. In size, this distal fragment of McV is very similar to the McV of *Diaceratherium aurelianense* from Artenay, France (Cerdeno, 1993).

*Aprotodon* was included in the tribe Teleoceratini (Subfamily Aceratheriinae) (Heissig, 1972; Prothero and Schoch, 1989), but it has been recently excluded from it (Cerdeno, 1995), since the cladistic analysis of the family shows that it shares the synapomorphies of the Rhinocerotinae. A number of characters (mainly from the skull and teeth) are still unknown for this genus (further details in Cerdeno, *op.cit.*); a few postcranial elements have been described. Heissig (1972) included in this genus the type species *A. smith-woodwardi* Forster-Cooper, 1915, and *A. fatehjangense*. Within this latter, he considered some remains of *Chilotherium blanfordi* (Colbert, 1935) as synonym. *A. fatehjangense* has been reported from the different levels of the Chinji Formation (Heissig, 1972).





## Subfamily ACERATHERIINAE Dollo, 1885

## Tribe TELEOCERATINI Hay, 1902

*Brachypotherium perimense* (Colbert, 1935)

**Material:** HGSP 8412/3285, left P<sup>1</sup>; HGSP 8311/2065, right D<sup>4</sup>; HGSP 8424/3506 and 8427/3638, right and left M<sup>2</sup>; HGSP 8412/3118, right M<sup>1-2</sup> fragment; HGSP 8420/3452, right I<sub>2</sub> fragment; HGSP 8124/588, right D<sub>2</sub>; HGSP 8102/1013, right P<sub>2</sub>; HGSP 8127/448, 8114/1153, and 8425/3517, three (1 r./ 2 l.) P<sub>3</sub>; HGSP 8409/3040, left M<sub>1,2</sub> fragment; HGSP 8412/3119, left M<sub>3</sub>; HGSP 8222/1200, radius distal fragment; HGSP 8107a/44 and 8108/81, left and right patellae; HGSP 8129/539, left astragalus; HGSP 8311/1969, 8311/1675, 8314/1705, and 8311/1604, 3 left and 1 right calcanei; HGSP 8129/546 and 8311/1517, left and right cuboids; HGSP 8311/1376, right McIII fragment; HGSP 8108/71, left MtIV fragment.

This is a large species. Lower teeth are characterized by the smooth external groove, hardly marked, as it is in other teleoceratines. The tooth morphology (Figs. 5-7) is similar to *B. perimense* from the Siwaliks (Heissig, 1972). Concerning size, the P<sup>1</sup>/ is wider and the M<sup>2</sup>/ narrower (Table III); the lower teeth have closer dimensions.

The radius fragment and the patellae have dimensions (Table III) similar to the European *Brachypotherium brachypus* (Cerdeno, 1993, p. 54-55). No data are available for *B. perimense* from Siwaliks.

The astragalus is very large (Table III), close in size to the specimen HGSP 8311/1974 (*Aprotodon*, see above), but with different morphology. The trochlea has a wider medial lip and a shorter lateral lip; the distal groove is broader, and the distal facets form a greater angle. The calcaneum facet 2 is very flat and obliquely placed. Two large and strong calcanei can be ascribed to *B. perimense*, as well as several smaller fragments (Table III). The tuber is irregularly outlined, and laterally directed. Their dimensions are smaller than on the Siwaliks specimen (Heissig, 1972). The cuboids are low and wide. The specimen HGSP 8311/1571 (Fig. 21) has the anterior face relatively lower and wider than HGSP 8129/546. The posterior apophysis is little backwardly projecting, consequently the length of the bone (Table III) is smaller than on the specimens from the Siwaliks (Heissig, 1972, tab. 40). Two large McIII and MtIV fragments (Figs. 26, 30) are identified as *B. perimense*. The former has a high proximal crest, and the latter has rounded proximal epiphysis and facet.

In general, this material is smaller than the Siwaliks *B. perimense* described by Heissig (1972). This could be due to the older age of the Sind specimens; they would correspond to the Lower Chinji Formation, and all the compared bones described by Heissig come from Middle and Upper Chinji, Nagri, or Dhok-Pathan Formations. An increase of size through time could be expected.

Compared with the type species *B. brachypus*, most elements have a similar size than the

- Fig. 18. *Brachypotherium perimense*; Left patella, HGSP 8107a/44, posterior view.  
 Fig. 19. *Aprotodon fatehjangense*; Right patella, HGSP 8205/819, posterior view.  
 Fig. 20. *Hispanotherium matritense*; Right navicular, HGSP 8311/1746, proximal view.  
 Fig. 21. *Brachypotherium perimense*; Right cuboid, HGSP 8311/1571, proximal view.  
 Fig. 22. *Chilotherium cf. intermedium*; Right ectocuneiform, HGSP 8311/1445, distal view.  
 Fig. 23. *Hispanotherium matritense*; Left astragalus, HGSP 8207/893, anterior view.  
 Fig. 24. *Aprotodon fatehjangense*; Left astragalus, HGSP 8311/1974, posterior view.  
 Fig. 25. *Hispanotherium matritense*; Right McII, HGSP 8311/1629, anterior view.  
 Fig. 26. *Brachypotherium perimense*; Right McIII, HGSP 8311/1376, anterior view.  
 Fig. 27. *Aprotodon fatehjangense*; Right MtII, HGSP 8311/1725, postero-lateral view.  
 Fig. 28. *Aprotodon fatehjangense*; Right MtII, HGSP 8108/869, proximal view.  
 Fig. 29. *Chilotherium cf. intermedium*; Left MtII, HGSP 8108/1076, proximal view.  
 Fig. 30. *Brachypotherium perimense*; Left MtIV, HGSP 8108/71, proximal view.  
 Fig. 31. *Chilotherium cf. intermedium*; Left MtIII, HGSP 8311/1439, anterior view.  
 Fig. 32. *Aprotodon fatehjangense*; Right MtIII, HGSP 8311/1422, anterior view.  
 Fig. 33. *Aprotodon fatehjangense*; Left MtIII, HGSP 8311/1582, proximal view.  
 Fig. 34. *Aprotodon fatehjangense*; Left McIV, HGSP 8108/69, proximal view.  
 Fig. 35. *Aprotodon fatehjangense*; Right MtIV, HGSP 8311/1440, proximal view.

Scales: 18-19, 20-22, 23-24, 25-26, 27-30, 31-33, and 34-35, respectively.

**Table III.- Dimensions of teeth and bones of *Brachypotherium perimense* from the Manchar Formation, Sind.**

Premolar 1:	8412/3285; L 25.7, W 24.2
Premolar 2:	8413/3185; L 32.5, W 40.8
Molar 2	8424/3506; L 64.7, W 63.7 8427/3638; L 64.2, W >59 8412/3118; L 66.0, W -
Milk molar (D4)	8311/2065; L 51.1, W -
Premolar 3:	8425/3517; L 39.0, W 28.6 8425/1153; L 39.0, W 30.6 8127/448; L 40.2, W 30.2
Molar 1-2:	8409/3040; L -, W 33.0
Molar 3:	8412/3119; L 57.5, W 31.2
Milk molar (D2)	8124/588; L 29.7, W 15.6
Radius	8222/1200; dis.ep.: TD 104.2, APD 62.6, dis.art.: TD 90.7, APD 44.5
Patella	8107a/44; TD 108.9, APD 59.8, H 111.6 8108/81; TD 96.6, APD 47.2, H 107.4
Astragalus	8311/539; TD 106.2, H 80.8, TDdis 88.2, dis.art.: TD 83.7, APD 50.7, DL 67.0, APDi >54
Calcaneum	8311/1969; H 127.9, tuber: TD 50.0, APD 72.7, beak: APD 60.0, sus. TD -, post. TD 39.2 8311/1675; H -, tuber: TD 45.1, APD 66.3, beak: APD 61.0, sus. TD -, post. TD 33.2 8311/1604; H 123.7, tuber: TD 46.8, APD -, beak: APD 60.5, sus. TD -, post. TD 39.4 8314/1705; H -, tuber: TD 42.5, APD -, beak: APD (61.0), sus. TD -, post. TD 34.6
Cuboid	8311/1571; TDm 55.1, TDant 50.2, APD 67.4, Hm (52.8), Hant 33.6, prox.art: TD 48.7, APD 45.7 8129/546; TDm 53.0, TDant -, APD 72.0, Hm 50.6, Hant 42.2, prox.art: TD 44.5, APD 47.2
Metapodial McIII	8311/1376; L -, prox.ep. TD 69.8, APD -, prox.art: TD 67.6, APD 41.5, diaphysis: TD 54.4, APD 22.4
Metapodial MtIV	8108/71; L -, prox.ep. TD 48.0, APD 50.0, prox.art: TD 33.4, APD 41.7

Abbreviations used: APD, anteroposterior diameter; APDi, internal anteroposterior diameter; APDm, maximum anteroposterior diameter; APDpr, proximal anteroposterior diameter; prox.art., proximal articulation; dis.art., distal articulation; dis.ep., distal epiphysis; D, milk molar; DL, distance between the astragalus lips; H or Hm, maximum height; Hant, anterior height; Hmin, minimum height; Hpost, posterior height; I, Incisor; L, length; Lab, absolute length; Lan, anatomical length; M, molar; Mc, metacarpal; Mt, metatarsal; P, premolar; prox.art., proximal articulation; prox.ep., proximal epiphysis; sus., sustentaculum; TD, transverse diameter; TDant, anterior transverse diameter; TDdis, distal transverse diameter; TDm, maximum transverse diameter; TDpost, posterior transverse diameter; W, width.

homologous French specimens (Cerdeno, 1993); only the calcanei are specially short; the teeth present the same differences that with respect to the Siwaliks material.

*Chilotherium cf. intermedium* (Lydekker, 1884)

**Material:** HGSP 8311/1538, right D<sup>2</sup>; HGSP 8108/1060, 8311/1612 and 8215/9017, 1 left/ 2 right scaphoids; HGSP 8311/1890, left pyramidal; HGSP 8213/964, left cuboid; ?HGSP 8311/1444 and 1445, left and right ectocuneiforms; HGSP 8108/1067, right McIII fragment; HGSP 8108/1076, left MtII fragment; HGSP 8311/1439, right MtIII fragment; HGSP 8111/95, left MtIV fragment.

The scaphoids (Fig. 10) have certain general similarity with those of *Aprotodon*, but they differ, particularly HGSP 8311/1612, in having a more triangular and less concave proximal facet, less developed lateral tuberosity, larger trapezium facet, and without posterior semilunate facet. Dimensions are similar in both species (Tables II and IV).

The pyramidal HGSP 8311/1890 (Table IV) differs from the other already described. The posterior border of the proximal facet is narrower than the anterior one. The bone is less massive than those of *Aprotodon*. The pisiform facet is broad and clearly concave. The inferior medial facet forms a marked L. The distal articulation is rather triangular outlined. It is relatively higher than the *Aprotodon* specimens.

Some doubts arise concerning the taxonomic ascription of the ectocuneiforms (Fig. 22), since we have no comparative data of *C. intermedium*. Their dimensions are close to those of the navicular (with which the ectocuneiform articulates) of this species (Heissig, 1972). Both the proximal and the distal facets of the ectocuneiform are L-shaped; the former longer than wide, and the latter wider than long.

The McIII HGSP 8108/1067 is tentatively ascribed to *Chilotherium* (Table IV). This fragment is slightly smaller than those of *Aprotodon*; it shows relatively shorter facets; the proximal crest is high. The MtIII (Fig. 31) also has a shorter proximal facet. Similarly, the MtIV has more rounded proximal epiphysis and facet. The anterior medial facet is large, while the posterior one is reduced. The transverse diameter of this fragment (Table IV) is intermediate between the two quite different dimensions given by Heissig (1972: tab. 33); the APD is very close on the three specimens. The dimensions

of the MtII fragment (Fig. 29) are different from Heissig's measurements; even though the way of measuring is different (probably the TD and APD are the contrary; Cerdeno, 1989). The Siwaliks specimen seems to be too narrow.

*Chilotherium* was defined by Ringstrom (1924) based on several species from the *Hipparion*-faunas of China. It was later recognized in other Asian areas, as well as in Eastern Europe. Its presence in the Iberian Peninsula (Antunes, 1972; Crusafont *et al.*, 1966; Crusafont and Quintero, 1970) is very doubtful, and previously refuted in some sites (Santaf *et al.*, 1982; Cerdeno, 1989: p. 18). Concerning *Chilotherium intermedium* from the Siwaliks, Heissig (1972: p. 61) considered two subspecies: *C. i. intermedium*, from the Chinji and Nagri Formations, and the younger *C. i. complanatum*, from the Dhok-Pathan Formation. Diagnostic differences concern some dental characters, and the description of the postcranial skeleton is presented for the entire species. Our material would correspond to *C. i. intermedium* considering the age of the Manchar Formation. In fact, the type material of the species comes from the same area, Sind (see Heissig, 1972: p.60).

## REMARKS AND CONCLUSIONS

The rhinoceros remains from Sind are a mostly fragmentary sample in which complete teeth are poorly represented. Bones are more abundant, but most of them are also incomplete. The anatomical identification of 304 remains is the following: 46 teeth (plus over 70 small fragments), 2 vertebrae, 18 long bones, 4 patellae, 35 carpal bones, 8 metacarpals, 37 tarsal bones, 19 metatarsals, 38 metapodial fragments (Mc/Mt), 4 sesamoids, and 93 phalanges. Only the above described specimens were taxonomically identified: 27 of *Hispanotherium matritense*; 44 of *Aprotodon fatehjangense*, 25 of *Brachypotherium perimense*, and 12 of *Chilotherium cf. intermedium*.

The fragmentary state, together with the eroded condition of many elements and the abundance of phalanges, points to taphonomic characteristics such as aerial alterations, extensive preburial transportation, and size selection. Besides, many specimens constitute more or less isolated finds, which indicates a great dispersion of the skeletons before fossilization.

**Table IV.- Dimensions of teeth and bones of *Chilotherium intermedium* from the Manchar Formation, Sind.**

Milk molar/ (D2)	8311/1538; L 34.0, W 32.0
Scaphoid	8311/1612; TDm (45.5), APDm 78.0, Hm 58.0, prox.art: TD 43.6, APD 43.5, dis.art: TD 32.0, APD 63.4 8108/1060; TDm 50.0, APDm 72.2, Hm 54.5, prox.art: TD 45.5, APD 42.8, dis.art: TD -, APD 60.4 8215/9017; TDm -, APDm -, Hm 57.5, prox.art: TD -, APD 43.4, dis.art: TD 28.0, APD -
Pyramidal	8311/1890; TDm 41.2, APDm 44.7, Hm 49.1, APDpr 31.7
Magnum	8205/823; TD (41.5), APD 79.7, H 53.8, Hart 52.6 8311/1643; TD 45.2
Ectocuneiform	8311/1444; TD 50.6, APD 49.7, H 26.3, Hmin 19.8 8311/1445; TD 50.6, APD 50.1, H 24.8, Hmin 17.8
	prox.ep. prox.art. diaphysis dis. art. L TD APD TD APD TD APD TDm TD APD
Metapodial McIII	8108/1067; L -, prox.ep.: TD 54.0, APD (38.5), prox.art: TD 51.0, APD (33.5)
Metapodial MtII	8108/1076; L -, prox.ep.: TD 28.5, APD 42.1, prox.art: TD 19.9, APD 36.6
Metapodial MtIII	8311/1439; L -, prox.ep.: TD 53.9, APD 48.0, prox.art: TD 47.8, APD 41.7
Metapodial MtIV	8111/95; L -, prox.ep.: TD 38.3, APD 37.0, prox.art: TD 32.2, APD 32.8, diaphysis: TD (24.7), APD (19.0)

Abbreviations used: APD, anteroposterior diameter; APDi, internal anteroposterior diameter; APDm, maximum anteroposterior diameter; APDpr, proximal anteroposterior diameter; prox.art., proximal articulation; dis.art., distal articulation; dis.ep., distal epiphysis; D, milk molar; DL, distance between the astragalus lips; H or Hm, maximum height; Hant, anterior height; Hmin, minimum height; Hpost, posterior height; I, Incisor; L, length; Lab, absolute length; Lan, anatomical length; M, molar; Mc, metacarpal; Mt, metatarsal; P, premolar; prox.art., proximal articulation; prox.ep., proximal epiphysis; sus., sustentaculum; TD, transverse diameter; TDant, anterior transverse diameter; TDdis, distal transverse diameter; TDm, maximum transverse diameter; TDpost, posterior transverse diameter; W, width.

On the other hand, different fossiliferous sites which yielded the studied material may reflect different temporal deposits within the Lower Manchar Formation. The study of the entire faunal association of each site could make evident differences among them that could, in turn, reflect local variations in environmental conditions. A careful analysis of the sedimentological, taphonomical and taxonomical characteristics of Sind, such as it was carried out for the Khaur area (Badgley and Behrensmeier, 1980), would allow the reconstruction and characterization of the paleoenvironments and paleocommunities of the Sind region during the Early-Middle Miocene.

Concerning the rhinocerotid association from Sind, the four identified species, *H. matritense*, *A. fatehjangense*, *B. perimense*, and *C. cf. intermedium*, are well known from the Siwaliks (Heissig, 1972).

Heissig established the presence of another well represented genus, *Gaindatherium* (Colbert, 1934) in the Lower and Middle Miocene deposits. However, it is only identified by skull and teeth, and no postcranial skeleton has been associated with it (postcranial bones from Portuguese Miocene sites ascribed to *Gaindatherium* -Antunes and Ginsburg, 1983- have been later identified as *Prosantorhinus* -Cerdeno, 1989, 1993, 1996b). Since the Manchar sample consists of mostly postcranials, it is difficult to identify that genus in Sind.

From a paleoenvironmental point of view, rhinoceroses provide some good data. Among these four species, two can be considered as good indicators. On one hand, *H. matritense* is associated to a dry and arid climate. Its subhypsodont teeth, with much cement, and its very slender postcranial skeleton indicate it as a grazer and open habitat



dweller that would have a gregarious behaviour (Cerdeno and Nieto, 1995).

On the other hand, *B. perimense* is one of the teleoceratine rhinoceroses which have been classically associated with a swampy habitat. Its short and massive legs together with its very large size points to a hippopotamus-like general aspect and behaviour. Therefore, this species would need more humid conditions than *Hispanotherium*, that could be represented by local areas with swamps.

*Aprotodon* and *Chilotherium* would not have so defined requirements. The former is a relatively large rhinoceros, with robust but not massive limbs. It would be a browser, occasionally mixing grasses, living in open woodlands. *C. cf. intermedium* presents a similar or slightly smaller size than *A. fatehjangense*, but its bones are relatively more slender. Teeth of *Chilotherium* species are rather hypsodont, and it can be presumed that *C. cf. intermedium* would be mainly a grazer, may be in a lesser degree than *Hispanotherium*.

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#### REFERENCES

- ANTUNES, M.T., 1972. Notes sur la Geologie et la Paléontologie du Miocene de Lisbonne XI - Un nouveau Rhinocerotide. *Chilotherium ibericus* n. sp. *Bol. Museu Lab. Min. Geol. Fac. Sci. Lisboa*, 13: 25-33.
- Antunes, M.T., 1979. *Hispanotherium* fauna in Iberian Middle Miocene; its importance and paleogeographical meaning. *Ann. Geol. Pays Hellen. VII Inter. Congr. Medit. Neog.*, Athens: 19-26.
- ANTUNES, M.T. AND GINSBURG, L., 1983. Les rhinocerotides du Miocene de Lisbonne-systematique, ecologie, paleogeographie, valeur stratigraphique. *Ciencias da Terra (UNL)*, 7: 17-98.
- BADGLEY, C. AND BEHRENSMEYER, A.K., 1980. Paleocology of Middle Siwalik sediments and faunas, Northern Pakistan. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 30: 133-155.
- BRULJN, H. De, AND HUSSAIN, S.T., 1984. The succession of rodent faunas from the Lower Manchar Formation, Southern Pakistan, and its relevance for the biotratigraphy of the Mediterranean Miocene. *Paobiol. continent.*, 14: 191-204.
- CERDENO, E., 1989. *Revision de la sistemica de los rinocerontes del Neogeno de Espana*. Edit. Universidad Complutense de Madrid. Col. Tesis Doctorales no. 306/89: 429 p., 64 t., 51 l.
- CERDENO, E., 1992. New remains of the rhinocerotid *Hispanotherium matritense* at La Retama site: Tagus basin, Cuenca, Spain. *Geobios*, 25: 671-679.
- CERDENO, E., 1993. Etude sur *Diaceratherium aurelianense* et *Brachypotherium brachypus* (Rhinocerotidae, Mammalia) du Miocene moyen de France. *Bull. Mus. Natl. Hist. Nat.*, 15: 25-77.
- CERDENO, E., 1995. Cladistic analysis of the Family Rhinocerotidae. *Am. Mus. Novitates*, 3134: 25 pp.
- CERDENO, E., 1996a. Rhinocerotidae from the Middle Miocene of the Tung-gur Formation, Inner Mongolia (China). *Am. Mus. Novitates*, 3184: 43 pp.
- CERDENO, E., 1996b. *Prosantorhinus*, the small teleoceratine rhinocerotid from the Miocene of Western Europe. *Geobios*, 29: 111-124.
- CERDENO, E. AND NIETO, M., 1995. Changes on Western European Rhinocerotidae related to climatic variations. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 114: 325-338.
- COLBERT, E.H., 1934. A new rhinoceros from the Siwalik beds of India. *Am. Mus. Novitates*, 749: 1-13.
- COLBERT, E.H., 1935. Siwalik mammals in the American Museum of Natural History. *Trans. Am. Phil. Soc.*, 26: 1-402.
- CRUSAFONT, M. AND QUINTERO, I., 1970. Noticia preliminar acerca de un nuevo yacimiento de mamiferos fosiles de la provincia de Guadalajara. *Acta Geol. Hispanica*, 5: 102-104.
- CRUSAFONT, M., TRUYOLS, J. AND RIBA, O., 1966. Contribucion al conocimiento de la estratigrafia del Terciario continental de Navarra y Rioja. *Notasy Comunic. I.G.M.E.*, 90: 53-76.
- CRUSAFONT, M. AND VILLALTA, J.F., 1947. Sobre un interesante rinoceronte (*Hispanotherium*) del Mioceno del Valle del Manzanares. *Las Ciencias*, 12: 869-883.
- FISCHER, G. 1809. Sur l'*Elasmotherium* et le *Trogotherium*. *Mem. Soc. Imp. Natural. Moscou*, 2.
- FORSTER-COOPER, M.A., 1915. New genera and species of mammals from the Miocene deposits of Baluchistan. Preliminary notice. *Annls Mag. Nat. Hist.*, 16: 404-410.
- HEISSIG, K., 1972. Palaontologische und geologische Untersuchungen im Tertiär von Pakistan; 5: Rhinocerotidae aus den unteren und mittleren Siwalik-

- Schichten. *Abh. Bayer. Akad. Wissen. math. naturw. Kl.*, 152: 1-112.
- HEISSIG, K., 1976. Rhinocerotidae (Mammalia) aus der *Anchitherium*-Fauna Anatoliens. *Geol. Jb.*, 19: 1-121.
- INIGO, C. AND CERDENO, E. (in press). The *Hispanotherium matritense* (Rhinocerotidae) from C rcoles (Guadalajara, Spain): its contribution to the systematics of the Miocene Elasmotheriini. *Geobios*.
- JACOBS, L.L., FLYNN, L.J., DOWNS, W.R. AND BARRY, J.C., 1990. *Quo vadis Antemus?* The Siwalik mureoid record. In: *European neogene mammal chronology* (eds. E.H. Lindsay et al.), pp. 573-586. Plenum Press, New York.
- KHAN, M.J., HUSSAIN, S.T., ARIF, M. AND SHAHEED, H., 1984. Preliminary paleomagnetic investigations of the Manchar Formation, Gaj river section, Kirthar range, Pakistan. *Geol. Bull. Univ. Peshawar*, 17: 145-152.
- MADE, J. VAN DER, AND HUSSAIN, S.T., 1992. Sanitheres from the Miocene Manchar Formation of Sind, Pakistan, and remarks on sanithere taxonomy and stratigraphy. *Proc. Kon. Ned. Akad. v. Wetensch.*, 95: 81-95.
- MADE, J. VAN DER, AND HUSSAIN, S.T., 1994. Horn cores of *Sivoreas* (Bovidae) from the Miocene of Pakistan and utility of their torsion as a taxonomic tool. *Geobios*, 27: 103-111.
- DE MECQUENEN, R., 1924. Contribution a l'etude des fossiles De Maragha. *Ann. Palont.*, 13: 1-64.
- PRADO, C. De., 1864. *Descripcion fisica y geologica de la provincia de Madrid*. Junta General de Estadistica. 219 pp.
- PROTHERO, D.R. AND SCHOCH, R.M., 1989. Classification of the Perissodactyla. In: *The evolution of Perissodactyls* (eds. D.R. Prothero and R.M. Schoch), pp. 530-537. Oxford University, Press.
- RINGSTROM, T.J., 1924. Nashorner der *Hipparion*-fauna Nord Chinas. *Paleont. Sinica*, 1: 1-159.
- SANTAFE, J.V., CASANOVAS, M.L. AND ALFEREZ, F., 1982. Presencia del Vallesiense en el Mioceno continental de la Depresion del Ebro. *Rev. Real Acad. C. Exac., Fisicas y Nat.*, 76: 277-284.

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