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Original article

New *Alicornops* (Rhinocerotidae) remains from Lower and Middle Siwaliks, Pakistan

*Nouveaux restes d'*Alicornops *(Rhinocerotidae) des Siwaliks Inférieur et Moyen, Pakistan*

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Abstract

Unpublished rhinocerotid remains from the Lower and Middle Siwaliks of Pakistan are described in this paper and recognized as two species of *Alicornops*. *Alicornops complanatum* (Heissig) is identified in the Dhok Pathan Formation of the Middle Siwaliks and *Alicornops laogouense* Deng in the Kamlial Formation of the Lower Siwaliks. The Dhok Pathan Formation levels with *A. complanatum* are roughly correlated with the late Miocene-Pliocene European mammal zones MN10-15. In turn, levels with *A. laogouense* of the Kamlial Formation would correlate with the middle–late Aragonian (middle Miocene) European MN5. The recognition of the Chinese species *A. laogouense* in the Potwar Plateau represents the first discovery of this taxon in Pakistan and increases the geographical and stratigraphic distributions of this species, and adds to the rhinocerotid association from the Siwaliks. In turn, the presence of *A. complanatum* in the Siwaliks of Potwar Plateau also enlarges its geographic distribution in Pakistan, as it was previously known from the Bugti Hills of Balouchistan. The absence of *Alicornops* from the Siwaliks in the Chinji and Nagri formations (between late MN5 and MN9 zones) might be due to an inadequate fossil record, as other rhinocerotid species are known from Kamlial to Dhok Pathan formations. However, the two recorded species of *Alicornops* could also reveal two independent migration waves as supported by the appearance of other taxa in different formations. A summary of fossil Cenozoic rhinocerotids from different areas of Pakistan is also presented.

Keywords: Rhinocerotidae; *Alicornops*; Siwaliks; Pakistan

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Résumé

Dans la présente contribution sont décrits et analysés des restes inédits de rhinocérotidés provenant des Siwaliks Inférieur et Moyen du Pakistan. Deux espèces sont reconnues à savoir *Alicornops complanatum* (Heissig) de la Formation Dhok Pathan des Siwalik Moyen et *Alicornops laogouense* Deng de la Formation Kamlial des Siwalik Inférieur. Les niveaux de la Formation Dhok Pathan avec *A. complanatum* permettent sa corrélation avec les unités mammaliennes européennes MN 10-15 du Miocène supérieur au Pliocène. Au même temps, les niveaux avec *A. laogouense* de la Formation Kamlial correspondent à peu près à l'unité MN5 (Aragonien moyen à supérieur, Miocène moyen) en Europe. La reconnaissance de l'espèce chinoise *A. laogouense* dans le Plateau de Potwar représente la première découverte de ce taxon au Pakistan, augmente les distributions géographique et stratigraphique de cette espèce et ajoute un nouveau registre aux Rhinocerotidae des Siwalik. D'autre part, la présence d'*A. complanatum* dans cette région augmente aussi sa distribution au Pakistan, donc elle était connue à Bugti Hills, Balouchistan. L'absence d'*Alicornops* dans les Siwaliks aux Formations Chinji et Nagri (équivalent aux zones MN 5 à MN 9) pourrait être due à certain biais dans les fouilles, donc autres espèces de rhinocéros sont connues depuis la Formation Kamlial jusqu'à la Formation Dhok Pathan. Cependant, les deux espèces d'*Alicornops* pourraient rendre évident deux migrations indépendantes tel qu'il est supporté par d'autres taxons dans des formations différentes. Un résumé des rhinocérotidés cénozoïques des différentes régions du Pakistan est aussi présenté.

Mots clés : Rhinocerotidae ; *Alicornops* ; Siwaliks ; Pakistan

1. Introduction

In Pakistan, innumerable fossil vertebrates have been collected and described, amongst which rhinocerotoids are particularly plentiful and diversified. The Tertiary deposits of the Siwalik group in Potwar Plateau, Punjab, the Bugti Hills, Baluchistan, and the Manchar Formation in Sindh are the major sites of provenance of the fossil vertebrate fauna including rhinocerotids. The age of the Siwalik group ranges from late early Miocene to Pleistocene, including Kamlial, Chinji, Nagri, Dhok Pathan and Soan formations. The fossiliferous levels in the Bugti Hills document a long time range, spanning the Oligocene epoch and most of the Miocene times (Antoine et al., 2003c). The Manchar Formation, a middle and late Miocene fluvial sequence, is exposed in a narrow north-south belt in the Lower Indus Basin of Sindh. According to Raza et al. (1984), the basal and middle Manchar levels are probably older than the fauna from the Chinji Formation in its type area, and younger than the Dera Bugti fauna.

Recent revision of unpublished rhinocerotid remains from the Siwaliks has led to the recognition of three genera, *Alicornops*, *Gaindatherium*, and *Chilotherium*, coming from the Miocene formations of the Siwalik Group, outcropping at different localities around Dhok Pathan, Chinji and Ghabir River areas, Potwar Palteau (Khan, 2009). The material identified as *Chilotherium intermedium* was studied in detail by Khan et al. (2011). The present paper deals with the specimens recognized as genus *Alicornops* coming from the Dhok Pathan and Kamlial formations.

Alicornops is the most widespread rhinocerotid of the European middle and late Miocene (MN5-MN10) (Cerdeño and Sánchez, 2000). The type species *Alicornops simorrense* (Lartet, 1851) has been recovered from the middle Miocene of France (Ginsburg and Guérin, 1979), the late Miocene of Spain (Cerdeño and Sánchez, 2000), where it is better represented, and Romania (Codrea, 1992, 1996), the late Miocene of Moldova (Lungu, 1984), and the middle Miocene

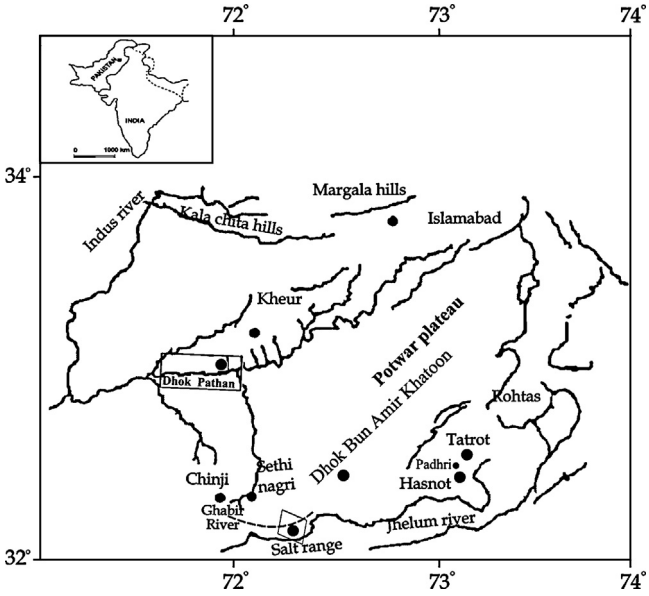

Fig. 1. Geographic location of the fossiliferous localities with *Alicornops*.
Localisation géographique des gisements fossilifères à Alicornops.

of Poland (Kubiak, 1981). Outside Europe it has been reported from the middle Miocene of Turkey (Heissig, 1976) and a similar form from the late Miocene of Pakistan (Guérin in Pilbeam et al., 1979; Guérin, 1980: 387). Ginsburg and Guérin (1979) identified some fossils from the lower Aragonian (MN3) of Wintershof, Germany, as *Alicornops* sp., previously considered as *Aceratherium* (*Mesaceratherium*) sp. by Heissig (1969). A second European species of the genus, *Alicornops alfambrense*, was reported from the late Miocene of Spain, France, and Germany (Cerdeño and Alcalá, 1989; Cerdeño, 1995, 1997; Cerdeño and Sánchez, 2000), although Antoine et al. (2003b) have questioned its assignment to *Alicornops* and proposed it belongs to *Acerorhinus*.

In Pakistan, *Alicornops* was already recognized by Antoine et al. (2003b) in the late Miocene locality of Sartaaf (Bugti hills, Baluchistan), based on the subspecies *C. intermedium complanatum* Heissig, 1972, and including the material considered cf. *A. simorrense* by Guérin (Pilbeam et al., 1979); they proposed the combination *Alicornorps complanatum* (Heissig, 1972) and provided an emended diagnosis of *Alicornops*. The Sartaaf locality has been correlated with the Dhok Pathan Formation of the Middle Siwaliks (Pilbeam et al., 1996). Another Asian species of *Alicornops* is *A. laogouense* Deng, 2004, described in Laogou, Linxia Basin, Gansu, China (Deng, 2004).

2. Geological context

The studied remains from the Dhok Pathan Formation come from nearby south-west of Dhok Pathan Rest House and Dhok Resham (33° 06' N, 72° 20' E), while those from the Kamlial Formation were recovered nearby the Ghabir river (33° 15' N, 72° 30' E) (Fig. 1).

The sedimentological characteristics of the Dhok Pathan Formation, as well as its paleomagnetic and biostratigraphic correlations, were provided by Pickford (1988) and Barry et al. (2002), who obtained a temporal range from the latest Miocene to the late Pliocene for this formation.

This formation corresponds to the Middle Siwalik sequence, underlying the Soan Formation that is at the top of the sequence (Fig. 1).

The Kamlial beds of Pinfold (1918) have been formally established as Kamlial Formation by the Stratigraphic committee of Pakistan. The formation is equivalent to the "Kamlial Stage" of Pascoe (1963). The Kamlial Formation corresponds to the basal part of the Lower Siwalik sequence (Pilgrim, 1913), underlying the Chinji Formation. It is the second oldest Neogene biostratigraphic unit in southern Asia, but has a very poor fossil record, being one of the most poorly known of the Pilgrim's faunal zones. It is considered as transitional in faunal characters between the denominated Bugti fauna, with archaic rhinoceroses and anthracotheres, and the younger Siwaliks fauna with a rich diversity of ruminants, suids, and proboscideans (Raza et al., 1984).

3. Materials and methods

The studied material mainly comprises maxillary and mandibular fragments, as well as isolated teeth, which are detailed in the Systematic Paleontology section. The fossils are housed in the Dr. Abu Bakr Fossil Display and Research Center of the Department of Zoology, University of the Punjab, Lahore, Pakistan. The specimens are catalogued in two series: the first figure refers to the year of collection and the second figure denotes the serial number of the respective specimen.

The morphological and metrical study of the specimens was based on different papers on rhinocerotid systematics (Heissig, 1972; Guérin, 1980; Cerdeño and Sánchez, 2000; Antoine et al., 2003a, 2003b; Deng, 2004, among others). Suprageneric classification follows Antoine et al. (2003b). Measurements of the specimens are given in millimeters, and taken with the help of a metric Vernier Caliper. Tooth length and width were measured at maximum level.

Abbreviations (text and tables): **D/d**, upper/lower deciduous cheek tooth; **Fm**, Formation; **L**, length; **l**, left; **M**, upper molar; **m**, lower molar; **Ma**, million years ago; **P**, upper premolar; **p**, lower premolar; **PUPC**, Punjab University Palaeontological Collection; **r**, right; **W**, width.

4. Systematic palaeontology

Order PERISSODACTYLA Owen, 1848
Family RHINOCEROTIDAE Gray, 1821
Subfamily RHINOCEROTINAE Gray, 1821
Tribe RHINOCEROTINI Gray, 1821
Subtribe ACERATHERIINA Dollo, 1885
Genus ***Alicornops*** Ginsburg and Guérin, 1979
Type species: *Alicornops simorrense* (Lartet, 1851).

Generic diagnosis (translated from Antoine et al., 2003b: 581): Small Aceratheriina, with a mandibular corpus ventrally convex; weak presence of cement on cheek teeth; P2 with protocone less developed than hypocone; anticrochet always present in upper molars; lower cheek teeth with angular trigonid and talonid forming a sharp dihedral angle; lingual cingulum absent on lower molars; radius with deep depression for the insertion of the biceps brachii muscle.

Stratigraphic and geographical distribution: Middle and late Miocene; middle Aragonian-late Vallesian in Europe, Anatolian Peninsula (Turkey), China, Baluchistan, and the Siwalik

deposits in Punjab, Pakistan (Antoine et al., 2003b; Cerdeño and Sánchez, 2000; Deng, 2004; Guérin, 1980; Ginsburg and Guérin, 1979; Heissig, 1972, 1976; Kubiak, 1981; Lungu, 1984).

4.1. Alicornops complanatum *(Heissig, 1972) Antoine et al., 2003b*

Holotype: Associated cranium and mandible, BSP 1956 II 392 (Heissig, 1972).

Stratigraphic distribution: Dhok Pathan Formation (lower and upper levels), late Miocene (MN10-13; Pilbeam et al., 1996). Hypothetical presence in the late Miocene layers of Sethi Nagri Formation (MN9) (Heissig, 1972; Pilbeam et al., 1996).

Material studied: PUPC 02/110 and PUPC 10/25, right and left maxillary fragments of the same juvenile individual, with D2-D4 and anterior end of zygomatic arch; PUPC 07/143, isolated lD4; PUPC 10/26, isolated rD4; PUPC 10/28, isolated rM3; PUPC 00/98, mandibular fragment with ld2-m1 and rd3-m1; PUPC 02/131, mandibular fragment with right and left d2-m1.

Locality: Dhok Pathan Formation, Punjab, Pakistan.

Diagnosis (translated from Antoine et al., 2003b). *Alicornops* differing from the type species by the presence of a sometimes double crochet in P2-P4, mesostyle in D2, simple paralophid in d2; I1 absent; absence of anticrochet in P2-P3, of median fossette in P3-P4, of crista in P3 and upper molars; labial cingulum of lower premolars reduced; usual absence of anticrochet in P4; usual presence of lingual cingulum in upper molars; and small dimensions of p2 and d1.

4.2. *Description*

Upper dentition: The deciduous molars are hardly worn, molariform, with the lingual cusps well separated (Figs. 2–4). The ectoloph is undulate, with a very strong paracone rib and a strong parastyle. The metacone rib is less developed. The metastyle is also present. In D2 there is no anterior protocone groove, whereas in D3 and D4 this groove becomes well marked with wear (Fig. 2). The cingulum is present anteriorly and posteriorly, and forms a shelf, high above the base of the teeth, especially in D2. The lingual cingulum is better developed in D2, being reduced to a tubercle at the entrance of the median valley in D3-D4. The protoloph and metaloph are of different widths and their lingual surfaces are rounded. The crochet is long and can unite to the ectoloph with wear, enclosing part of the median valley as a fossette. The postfossette is very deep. Traces of cement are present in the valleys (Figs. 2 and 3).

The M3 PUPC 10/28 is triangular; its parastyle is strong, separated from the paracone fold by a relatively wide depression, which marks a great angle with the rest of the slightly convex ectometaloph (Fig. 4H-I). The protoloph is continuous, sigmoid with moderate anterior constriction and weakly developed anticrochet at the base of the crown. There is a double crochet as two spur-like enamel projections into the median valley, which extend throughout its height. The lingual side of the protocone is long and flat. At the entrance of the median valley there is a pillar-like tubercle. At the posterolingual corner of the ectometaloph there is a short, serrated cingulum projecting lingually. There is a broad and low anterior cingulum, from the parastyle to the anterolingual base of the protocone. The enamel is moderately thick.

Lower dentition: Both PUPC 02/131 (Fig. 5A) and PUPC 00/98 (Fig. 5B, C) are incomplete juvenile mandibles with d2-d4 and the first permanent molar erupting. The symphysis of PUPC 00/98 is thick, covered with compact sandstone. A horizontal crack is present on the posterior end of the symphysis, which indicates its actual posterior boundary at d3 level. The horizontal rami are moderately thick; the lower margin is flat and curves slightly upwards at the anterior part, which is broken below the symphysis. In dorsal view, the symphysis is moderately wide,

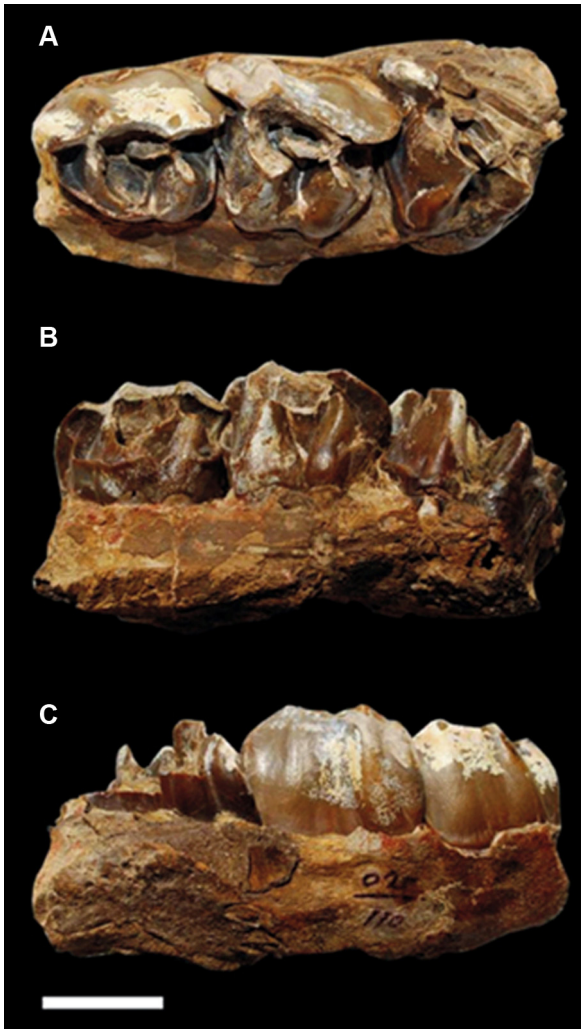

Fig. 2. *Alicornops complanatum* (Heissig, 1972). PUPC 02/110, D2-4. **A**, occlusal view, **B**, lingual view, **C**, labial view. Scale bar = 30 mm.
Alicornops complanatum. *PUPC 02/110, D2-4. **A**, vue occlusale, **B**, vue linguale, **C**, vue labiale. Échelle = 30 mm.*

with its anterior region narrower than the posterior one. The symphysis is broken anteriorly and it cannot be confirmed whether the incisors are present or not. The vertical ramus is inclined outwards.

The tooth crowns are relatively high. There are no traces of cement on the teeth. The trigonids are angular. The paralophid of d2 is slightly constricted and directed forward with a wide shallow groove. The paralophid is short; the metalophid forms a marked labial angle at the level of the protoconid. The hypolophid is oblique and short. The labial groove between trigonid and talonid is well marked. A discontinuous labial cingulum is present in PUPC 02/131 and PUPC 00/98. A ridge-like enamel projection corresponding to the lingual cingulum is present along the lingual

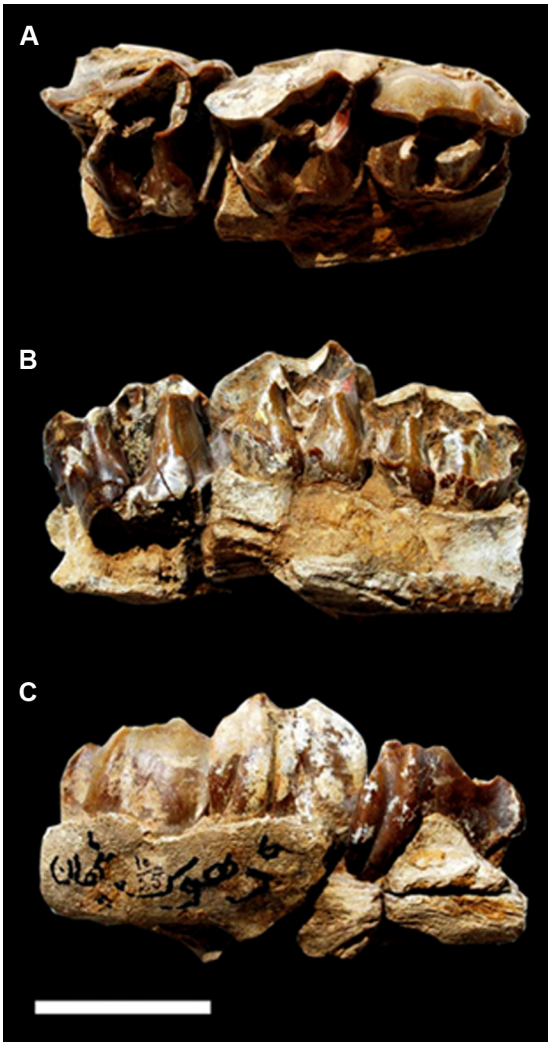

Fig. 3. *Alicornops complanatum* (Heissig, 1972). PUPC 10/25, D2-4. **A**, occlusal view, **B**, lingual view, **C**, labial view. Scale bar = 30 mm.
Alicornops complanatum. *PUPC 10/25, D2-4. **A**, vue occlusale, **B**, vue linguale, **C**, vue labiale. Échelle = 30 mm.*

side of the paralophid of d2 and the base of the posterior valley of d4 in PUPC 02/131. The anterior and posterior cingula are well developed. There is no constriction on metaconid or entoconid. A tubercle is present at the entrance of the posterior valley of d4 in PUPC 02/131 and PUPC 00/98. The valley of the talonid is deep, open lingually.

The m1 have the paralophid almost as long as the metalophid. The anterior valley is V-shaped and the posterior valley is U-shaped (Fig. 5B). The posterior cingula are visible in both m1, whereas the presence of cingulum on the other walls is not observable, as these teeth are not fully erupted. The enamel is thick and wrinkled. The labial groove is narrow and deeply V-shaped down to the base (Fig. 5).

Mandibular and dental measurements are provided in Tables 1 and 2.

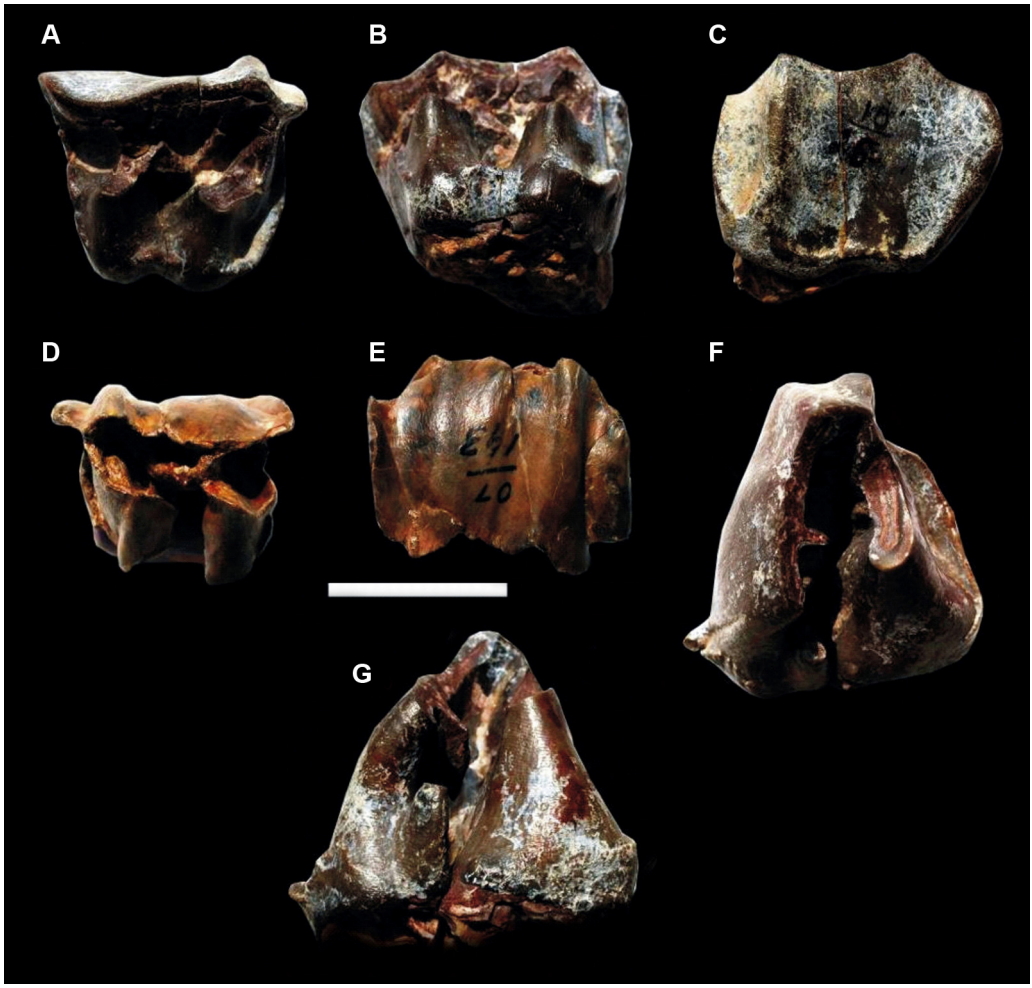

Fig. 4. *Alicornops complanatum* (Heissig, 1972). **A**–**C**. PUPC 10/26, rD4. **D**–**E**. PUPC 07/143, rD3. **F**–**G**. PUPC 10/28, rM3. **A**, **D**, **F**, occlusal view; **B**, **G**, lingual view; **C**, **E**, labial view. Scale bar = 30 mm.
Alicornops complanatum. ***A–C****. PUPC 10/26, D4 droite.* ***D–E****. PUPC 07/143, D3 droite.* ***F–G****. PUPC 10/28, M3 droite.* ***A****,* ***D****,* ***F****, vue occlusale ;* ***B****,* ***G****, vue linguale ;* ***C****,* ***E****, vue labiale. Échelle = 30 mm.*

Table 1
Measurements (mm) of the mandibular ramus PUPC 00/98 of *Alicornops complanatum*.
*Dimensions de la branche mandibulaire PUPC 00/98 d'*Alicornops complanatum.

Length of horizontal ramus from d2 to coronoid process	182
Total length of horizontal ramus	235
Distance between posterior border of symphysis and ascending ramus	135
Height of horizontal ramus in front of m2	53.6
Distance between horizontal rami in front of m1	52
Length of symphysis	75

Fig. 5. *Alicornops complanatum* (Heissig, 1972). **A**. PUPC 02/131, mandible with rd3-m1 and ld2-m1, occlusal view. **B–C**. PUPC 00/98, mandible with r/ld2-m1. **B**, occlusal view; **C**, labial view. Scale bar = 30 mm.
Alicornops complanatum. ***A***. *PUPC 00/98, mandibule présentant d2-m1 droites et d3-m1 gauches en vue occlusale.* ***B–C***. *PUPC 02/131, mandibule présentant d3-m1 droites et d2-m1 gauches.* ***B***, *vue occlusale ;* ***C***, *vue labiale. Échelle = 30 mm.*

4.3. Comparison

The present material from the Dhok Pathan Formation shows similarities with the deciduous and permanent dentition described by Heissig (1972) as *C. intermedium complanatum* (= *A. complanatum* after Antoine et al., 2003b) from the same formation in Punjab, Pakistan. Milk molars bear strong parastyle and paracone fold, and a long crochet. Antoine et al. (2003b) indicated as a diagnostic character of this species the presence of a mesostyle in D2. However, the deciduous dentition figured by Heissig (1972: pl. 7, fig. 13) does not show a clearly developed mesostyle but a smooth convexity that is also observed in the specimen PUPC 10/25 (Fig. 3A, C); this convexity can be also present in the molars of the type species *A. simorrense* (Cerdeño and Sánchez, 2000: 284). The M3 PUPC 10/28 is rather similar to those of the holotype of *A. complanatum*, although the posterolingual cingulum is less developed, but also detached from

Table 2
Comparative dental measurements of *Alicornops complanatum* from the Dhok Pathan Formation.
*Dimensions comparées des dents d'*Alicornops complanatum *de la Formation Dhok Pathan.*

Number	Nature	L	W	H
PUPC 02/110	D2	36.0	28.0	
	D3	38.4	32.4	
	D4	43.0	35.4	
PUPC 07/143	D3	35.0	30.0	31.0
PUPC 10/26	D4	41.0	36.0	32.0
PUPC 10/88	M2	55.0	43.0	
PUPC 10/28	M3	44.0	47.5	LD 50.0
1956 II 394[a]	D2	34.0	29.0	
	D3	34.0	32.0	
	D4	44.0	35.0	
1956 II 392[a]	M2	48.0	43.0	
1956 II 393[a]	M3	45.0	48.0	LD 53.0
MNCN 16020[b]	P2	31.1	35.7	
	P3	35.6	42.9	
	P4	37.8	46.2	
PUPC 00/98	d2	28.5	19.7	
	d3	34.0	21.0	
	d4	37.3	21.4	
	m1	39.5	23.7	
PUPC 02/131	d2	29.2	14.0	
	d3	33.0	19.0	
	d4	35.6	19.3	
	m1	39.0	24.0	
1956 II 396[a]	p2	27.0	14.0	
1956 II 398[a]	d3	34.0	19.0	
	d4	35.0	22.0	
1956 II 392[a]	m1	35.0	24.0	
MNHN-MHNT[c]	p2	30.0	20.0	
Pak.1606[c]	p3	34.5	21.5	
	p4	35.0	21.0	
	m1	40.5	23.5	
MNCN 31856[b]	p2	21.5	16.2	
	p3	27.5	21.4	
	p4	30.5	24.0	
	m1	33.8	23.6	

[a] Heissig (1972), *Alicornops complanatum*.
[b] Cerdeño and Sánchez (2000), *A. simorrense*.
[c] Antoine et al. (2003b), *A. complanatum*.

the tooth wall. It is not clear from the figure in Heissig (1972) if the right M3 has also a lingual tubercle. In *A. simorrense*, the lingual cingulum can be sometimes reduced to a small tubercle (Cerdeño and Sánchez, 2000: 281).

The lower deciduous teeth from Dhok Pathan (Fig. 3) seem somewhat different from those figured by Heissig (1972: pl. 8, fig. 3), where d3 has an apparently more elongated, bifurcated paralophid. However, these differences may be due to the almost unworn condition of that specimen. The bifurcation could disappear with wear. This feature has been observed in some d2 of *A. simorrense* (Cerdeño and Sánchez, 2000).

With respect to *A. complanatum* from Sartaaf (Antoine et al., 2003b), homologous teeth are reduced to the m1, and this tooth is incomplete in the Sartaaf specimen, but the studied material share the molar characters described by Antoine et al. (2003b): transversely long paralophid, oblique hypolophid, and entoconid without groove. The age of the layers of Sartaaf is comparable to that of Dhok Pathan Formation (Antoine et al., 2003b) from where the present specimens come from.

These similarities allow the identification of the studied material as *A. complanatum*. Antoine et al. (2003b), on the basis of phylogenetic studies, considered *A. complanatum* as the sister group of the type species *A. simorrense*, both included within the subtribe Aceratheriina, while "*Chilotherium intermedium*" belongs to Teleoceratina.

According to Heissig (1972), other rhinocerotid species recorded in the Dhok Pathan Formation, and therefore coeval with *A. complanatum*, are *C. intermedium* and *Brachypotherium perimense*.

4.4. Alicornops laogouense *Deng, 2004*

Holotype: An adult skull without the occipital surface, HMV 0982 (Deng, 2004).

Stratigraphic distribution: Middle Miocene (equivalent to MN 6 in Europe) at Laogou, Gansu, China (Deng, 2004); Kamlial Formation (late early Miocene), Siwaliks, Pakistan (present study).

Material studied: PUPC 07/46, left maxillary ramus with P3-M3; PUPC 07/47, right maxillary ramus with P2-M2; PUPC 07/48, left mandibular ramus with m1-m2.

Locality: Kamlial Formation (late early Miocene) of the Siwaliks, northern Pakistan.

Diagnosis (after Deng, 2004): Mid-sized skull, about 30% smaller than that of extant *Rhinoceros unicornis*, but larger than other known species of the genus *Alicornops* (*A. simorrense* and *A. alfambrense*). There is no horn on the nasals or the frontal. It differs from *A. simorrense* in the following ways: (1) the nasals are 1.7 times as long as wide, but the width of the nasal base is narrower; (2) the skull is much higher; (3) the skull roof is lozenge-shaped, with a narrower maximal frontal width; (4) the frontal bone narrows posteriorly, but less strongly; (5) the surface between the parietal crests is slightly wider with a minimum width of 25 mm; (6) the nasal notch is situated at the level of the middle of P3, shallower than that of *A. simorrense* at the level of P4; (7) the postorbital process is much weaker; (8) the anterior margin of the orbit is situated at the level of the anterior part of M1, more anterior than that of *A. simorrense* at the level of the M1/M2 boundary or anterior part of M2.

4.5. Description

Upper dentition: The material is partially damaged and many cracks are present, but the crown morphology is visible (Figs. 6 and 7). The labial cingulum is absent in all upper cheek teeth; the parastyle is sharply projected; the paracone fold is prominent; a weakly developed mesostyle is present. The labial wall of the ectoloph is undulated. In P2-P4, the anterior and posterior cingula are well developed, although the lingual cingulum is weaker and discontinuous in PUPC 07/47 (Fig. 7B). The protoloph and metaloph are of different width and their lingual surfaces are rounded. The P3 has a lingual bridge between protoloph and metaloph; both lophs appear already fused in the P3 of PUPC 07/47 (more worn than PUPC 07/46, M3 still unworn) closing the median valley; in the P4 it is a ridge placed deeper, projecting from the protoloph. The protoloph of P3-P4 at the occlusal surface is rather straight with parallel sides to its lingual

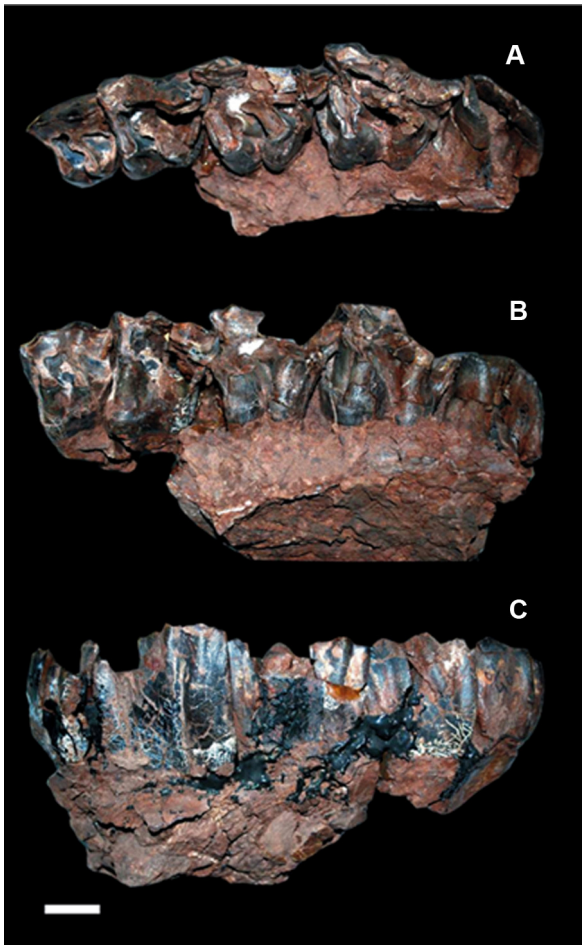

Fig. 6. *Alicornops laogouense* Deng, 2004. PUPC 07/46, left maxillary ramus with P3-M3. **A**, occlusal view; **B**, lingual view; **C**, labial view. Scale bar = 30 mm.
Alicornops laogouense*. PUPC 07/46, maxillaire gauche présentant P3-M3. **A**, vue occlusale ; **B**, vue linguale ; **C**, vue labiale. Échelle = 30 mm.*

end; however, there is a posterolingual groove that, with wear, delimits the protocone, especially in P4. A well-developed crochet and a weak crista are present in premolars, which are connected in the right P2 and P3 enclosing a fossette (Fig. 7A). The postfossette is large and triangular in all teeth. The M1 of PUPC 07/46 presents a metacone fold (Fig. 6); in M2, a second fold appears posterior to the paracone fold, but too anteriorly placed to be a metacone fold. The median valley is open, but some tubercles are at the entrance of M1 in both specimens. The crochet is strong in molars, as well as the anticrochet. The protocone is wide and rounded, clearly constricted by anterior and posterior grooves; the constriction increases with wear. The hypocone of M1-M2 of PUPC 07/47 has an anterior groove, but below the occlusal surface (Fig. 7A,B). The anterior and posterior cingula are strongly developed in premolars and molars. The M3 of PUPC 07/46 has a smoothly convex ectometaloph (Fig. 6); its protocone expands gradually towards the base, and

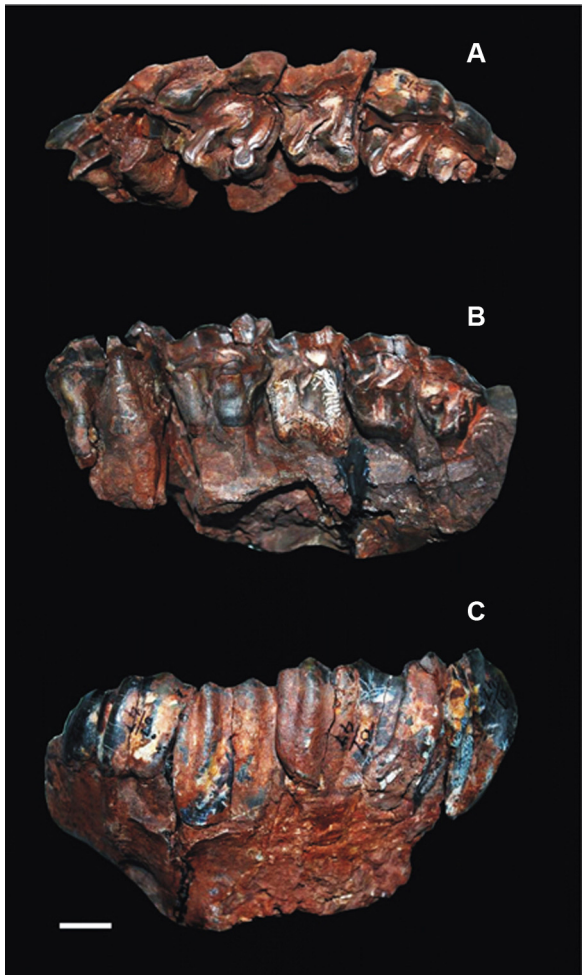

Fig. 7. *Alicornops laogouense* Deng, 2004. PUPC 07/47, right maxillary ramus with P2-M2. **A**, occlusal view; **B**, lingual view; **C**, labial view. Scale bar = 30 mm.
Alicornops laogouense. *PUPC 07/47, maxillaire droit présentant P2-M2.* ***A****, vue occlusale ;* ***B****, vue linguale ;* ***C****, vue labiale. Échelle = 30 mm.*

the crochet is present, but broken; no cingulum is still visible as the tooth is not yet completely erupted (Fig. 6A).

Lower dentition: PUPC 07/48 (Fig. 8) preserves the m1-m2 very little worn, which indicates a rather young individual that should still have its milk dentition in use. The tooth crowns are relatively high. Irregular and thin traces of cement are present at various places on the teeth. The labial groove is well developed; the protoconid marks an acute angle on the trigonid; the hypolophid is instead smoothly convex. The anterior and posterior cingula are present, as well as lingual tubercles along the base of the anterior valley of the m1-m2. The anterior and posterior valleys are V-shaped. The labial cingulum is serrated and absent at the level of the labial groove in both teeth (Fig. 8C).

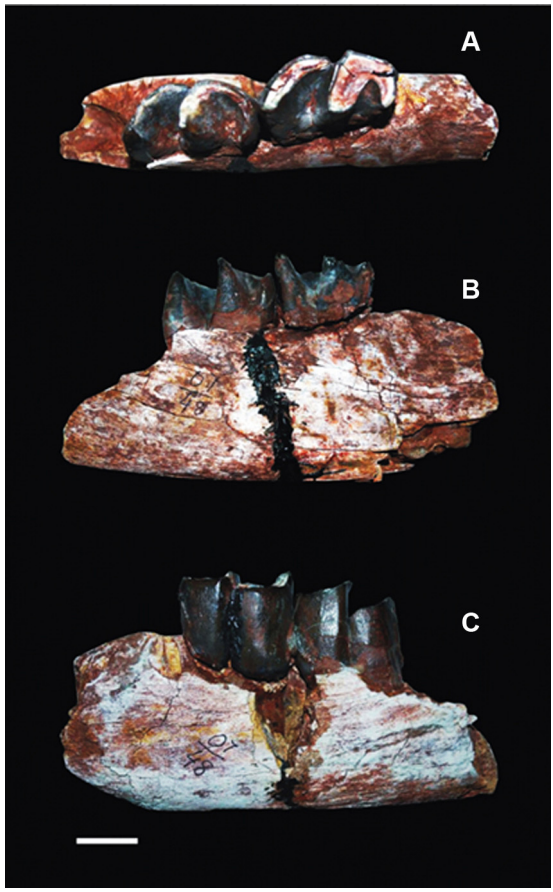

Fig. 8. *Alicornops laogouense* Deng, 2004. PUPC 07/48, left mandibular ramus with m1-m2. **A**, occlusal view; **B**, lingual view; **C**, labial view. Scale bar = 30 mm.
Alicornops laogouense. *PUPC 07/48, mandibule gauche présentant m1-m2.* ***A****, vue occlusale ;* ***B****, vue linguale ;* ***C****, vue labiale. Échelle = 30 mm.*

4.6. Comparison

The dental characters of the rhinocerotid material from the Kamlial Formation are fairly similar in dimensions and morphology to *A. laogouense* described by Deng (2004) in China. The upper premolars are similar in having high, well-developed anterior, lingual, and posterior cingula; hardly constricted protocone; dissimilar width of the protoloph and metaloph; posterior fossette triangular; and projecting parastyle. The lingual surfaces of the protocone and hypocone are also similar, maybe slightly less rounded in our specimens. The union of crochet and crista observed in the P3 of PUPC 07/47 resembles that present in the P2 of the holotype (Deng, 2004, pl. 1). The upper molars resemble *A. laogouense* by the protocone markedly constricted, strong crochet and anticrochet, absence of crista, flattened lingual surface of the protocone, open entrance of the median valley, with a lingual tubercle in M1, and anterior and posterior cingula well developed. Deng (2004, p. 1431) also stated that upper M1-M2 have a wide metacone fold; however, after the figure, the ectoloph is similar to that of our specimens, with a developed paracone fold and a

smooth convexity in the middle of the labial wall, which would correspond to the mesostyle, not to the metacone.

The lower dentition also shares many morphological characteristics with *A. laogouense*. In molars, anterior and posterior valleys are V-shaped; the posterior valley is deep; and there is a serrated labial cingulum. The labial cingulum of PUPC 07/48 is less developed than that of the molars of *A. laogouense* from China; however, it must be considered that our specimen is a very young individual, and the base of the teeth is observed because of the lack of some mandibular bone; maybe the cingulum would become more developed when the molar was fully erupted.

Compared with other *Alicornops* species, our material differs from *A. complanatum* from Dhok Pathan and Sartaaf (Heissig, 1972; Antoine et al., 2003a, 2003b, 2003c) in the P2 with the hypocone larger than the protocone; the absence of a continuous labial cingulum in lower molars; and the presence of lingual tubercles at the base of the anterior valley. With respect to *A. simorrense*, these remains differ in the presence of a lingual connection between protoloph and metaloph in the upper premolars; discontinuous lingual cingulum in the upper premolars; and less convex ectometaloph in M3.

The specimens from the Kamlial Formation are relatively longer than those of *A. laogouense* from China (Table 3). They are larger than those of *A. complanatum* from the Dhok Pathan Formation (Tables 2 and 3), as well as larger than *A. simorrense* from France and Spain (Cerdeño and Sánchez, 2000; see also Table 3).

Aprotodon blanfordi has been described from similar strata (transitional boundary between the Kamlial and the Chinji formations) by Colbert (1935). Comparing with this species, *A. laogouense* shares only a sharply constricted protocone. *Ap. blanfordi* differs by the absence of heavy cingula, prominent crista, undulate ectoloph, well-developed paracone fold, and strongly projecting parastyle. Moreover, the protoloph of the third upper molar is shorter than the ectometaloph in our material, while *Ap. blanfordi* have these crests of almost equal length (Colbert, 1935).

5. Final remarks

Originally erected as a species of the genus *Rhinoceros* from Simorre, France (Lartet, 1851), the species *R. simorrensis* changed successively its generic position, firstly referred to *Aceratherium* (Hooijer, 1966) and later to *Dromoceratherium* (Ginsburg, 1974) or *Mesaceratherium* (Heissig, 1976). Afterwards, Ginsburg and Guérin (1979) created the subgenus *Alicornops*, within *Aceratherium*, to allocate this species, *A.* (*Alicornops*) *simorrense*. Finally, Yan and Heissig (1986) elevated *Alicornops* to generic level, which was generally accepted by later authors (Heissig, 1989; Prothero et al., 1989; Cerdeño, 1992, 1995). The genus (*Alicornops* sp.) was recognized in the early Miocene (MN 3) of Europe by Ginsburg and Guérin (1979), based on a few upper molars from Germany with developed crochet and anticrochet; these teeth were previously identified by Heissig (1969) as the subgenus *Mesaceratherium*, including a P2 that was not considered later by Ginsburg and Guérin (1979); the specific determinaton of these teeth remains unresolved. Cerdeño and Alcalá (1989) established the species *A. alfambrense* from the late Miocene of Spain, also documented later in France and Germany (Cerdeño, 1997). However, Antoine et al. (2003b) considered *A. alfambrense* as a member of the genus *Acerorhinus*, an Asian genus in which Cerdeño (1996) included the European *A. tetradactylum*. According to Antoine et al. (2003b), *Alicornops* would just include the species *A. simorrense* and *A. complanatum*.

Among the Siwaliks rhinocerotids, Heissig (1972) recognized two successive subspecies of *C. intermedium*: *C. i. intermedium*, restricted to the Chinji and Nagri formations (middle Miocene and the base of the late Miocene), and *C. i. complanatum* from the Dhok Pathan Formation (late

Table 3
Comparative dental measurements of *Alicornops laogouense* from the Kamlial Formation.
*Dimensions comparées des dents d'*Alicornops laogouense *de la Formation Kamlial.*

Taxa	Formations	Number	Nature	Length	Width
A. laogouense	Kamlial	PUPC 07/46	P3	42.0	48.0
			P4	50.0	56.0
			M1	–	55.6
			M2	63.0	58.0
			M3	46.7	42.5
	Kamlial	PUPC 07/47	P2	30.0	36.0
			P3	41.0	50.0
			P4	46.0	59.0
			M1	59.0	57.0
			M2	61.0	60.0
A. laogouense[a]	Laogou, China	HMV0982	P2	32.0	39.0
			P3	39.5	49.0
			P4	42.0	57.0
			M1	52.5	57.5
			M2	52.0	57.0
			M3	50.0	49.0
A. simorrense[b]	Spain	MNCN16020	P2	31.1	35.7
			P3	35.6	42.9
			P4	37.8	46.2
			M1	45.4	47.9
			M2	48.9	49.5
			M3	39.5	44.0
A. complanatum[c]	Dhok Pathan	1956 II 392	P2	26.0	34.0
			P3	29.0	46.0
			P4	34.0	47.0
			M1	38.0	45.0
			M2	45.0	42.0
			M3	45.0	53.0
A. blanfordi[d]	Chinji (lower)	AMNH 19408	M1	52.0	64.0
			M2	64.0	66.0
			M3	56.0	61.0
B. fatehjangense[e]	Chinji	U CHH2	P3	38.0	47.0
		U CH1	M2	–	63.0
		U CHJ9	M3	52.0	57.0
	Kamlial	U KM1	M3	54.0	58.0
A. laogouense	Kamlial	PUPC 07/48	p4	49.0	24.0
			m1	45.0	27.0
A. laogouense[a]	Laogou (China)	HMV0983	p4	41.5	31.0
			m1	44.5	29.0
A. simorrense[b]	Spain	MNCN7942	p4	32.9	23.2
			m1	35.6	21.9

[a] Deng, 2004 (*Alicornops laogouense*).
[b] Cerdeño and Sánchez (2000), *A. simorrense*.
[c] Heissig (1972), *Alicornops complanatum*.
[d] Colbert (1935), *Aprotodon blanfordi*.
[e] Heissig (1972), *Brachypotherium fatehjangense*.

Miocene and the base of Pliocene). However, as said before, the latter was recently identified as a species of *Alicornops* by Antoine et al. (2003b), *A. complanatum*. Previously, the presence of *Alicornops* in this formation was mentioned by Guérin (in Pilbeam *et al.*, 1979) as ?*Aceratherium* sp. cf. *A. simorrense*, although Antoine et al. (2003b: 594) considered it synonymous of *A. complanatum*.

More recently, Deng (2004) defined another Asian species of *Alicornops*, *A. laogouense* from Laogou, Linxia Basin, Gansu, China, being the largest species of this genus. The fossiliferous levels with *A. laogouense* were correlated with the Chinese middle Miocene fauna of Tongxin, Ningxia, corresponding to the European MN6 mammal zone (Qiu et al., 1999; Deng, 2004, 2006). After the discovery of *A. laogouense* in Linxia Basin, it appears that the genus *Alicornops* migrated from Western through Eastern Europe, Western and Southern Asia to the Far East. During MN6 times, its distribution was relatively widespread throughout Eurasia (Deng, 2004). The present material of *A. laogouense* from the late middle Miocene of the Siwaliks roughly corresponds to the European late MN5 and early MN6 zones. This discovery is the first occurrence of *Alicornops* in the Kamlial Formation of the Siwaliks.

According to Guérin (1980), *A. simorrense* lived in Western Europe in open woodland with associated lakes and swamps. The short limb bones and robust metapodials of *A. simorrense* were adapted for life on soft soils in contrast to the long and straight metapodials of other rhinoceroses (Cerdeño, 1998). Such kind of environment can be predicted for the Siwalik *Alicornops*. In China, *A. laogouense* lived together with *Hispanotherium matritense* in a warm environment (Deng and Downs, 2002). A large number of the fossils of Amebelodontidae, adapted to live in habitats near water, have been found associated with *A. laogouense* in the Linxia Basin, indicating that lakes and rivers were abundant in the environment in which this species lived (Deng, 2004). *A. laogouense* comes from the upper strata of the Kamlial Formation at the transition zone between the upper Kamlial and the lower Chinji formations of the Siwaliks, which represent a warm and humid open woodland environment with abundant rivers and lakes.

The best faunal record of the Indian subcontinent corresponds to Pakistan. The rhinocerotid fauna in Pakistan is abundant and diverse, and distributed among three distinct biogeographic regions: Bugti Hills in Baluchistan, Manchar Formation in Sindh, and the Siwaliks in northern Pakistan. During the pre-Siwalik period, *Epiaceratherium* cf. *magnum* was recorded in the early Oligocene of central Baluchistan (Marivaux et al., 1999; Welcomme et al., 2001; Métais et al., 2009), and the *Brachyodus* dispersal event into the Indian subcontinent, about 21 Ma ago (early Miocene), includes the rhinocerotids "*Aceratherium*", *Chilotherium*, and *Brachypotherium* (Made, 1999).

The contemporaneous presence of *Aprotodon* in Kazakastan, Pakistan, and China (Qiu and Xie, 1997) at both sides of the Himalayas and the Tibet Plateau evidences that both ranges played a minimized role in the distribution and dispersal of rhinocerotids between Asia and the subcontinent throughout the Oligocene (Antoine et al., 2003c). The fauna of the south Asia has probably been distinct regionally since before the beginning of the Miocene. The Siwalik fauna maintained a certain resemblance to the modern fauna of Southeast Asia (Jacobs, 1980). The Siwaliks have yielded lineages leading to characteristic high diversity of rhinoceroses different from those of Europe and Africa. The peculiar Siwalik fauna clearly had its origin with the shift from the Bugti type of fauna to that in the basal Manchars. About one fourth of the Chinji species are directly related to Bugti forms, while the remainders are presumably immigrants (Raza et al., 1984). The rhinocerotid fauna from each biogeographic area in Pakistan is summarized below and in Fig. 9.

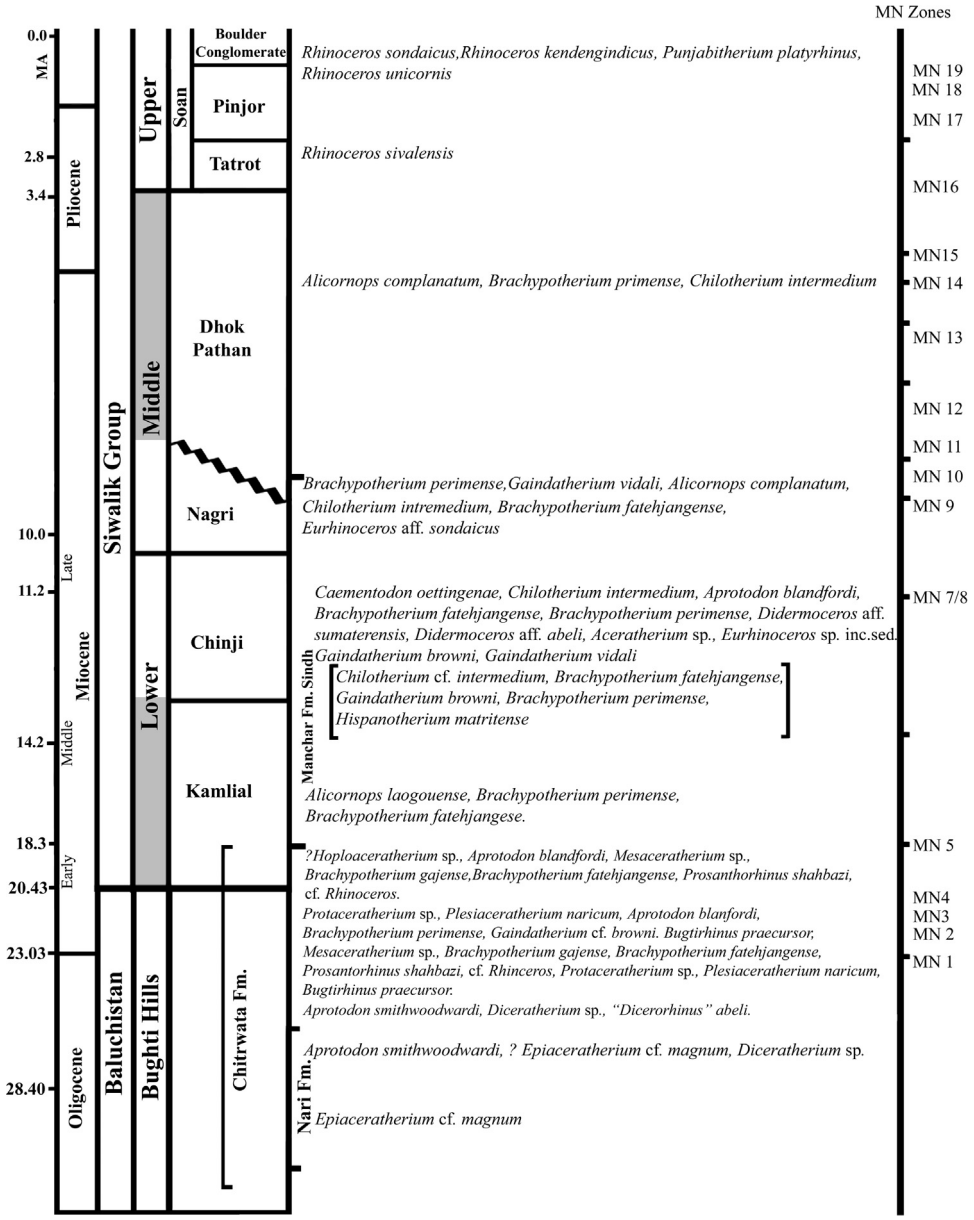

Fig. 9. Chronological distribution of the Mio-Pliocene rhinocerotids in Pakistan. Synthetic biostratigraphic sections from Barry et al., 2002, Welcomme et al., 2001 and Raza et al., 1984. Rhinocerotid data after Welcomme et al., 1997, 1999, 2001, Welcomme and Ginsburg, 1997, Marivaux et al., 1999, Antoine and Welcomme, 2000, Heissig, 1972 and Khan, 2009. (*) Species from Manchar Formation.

Distribution chronologique des rhinocérotidés mio-pliocènes du Pakistan. Sections biostratigraphiques d'après Barry et al., 2002, Welcomme et al., 2001 et Raza et al., 1984. Données sur les rhinocérotidés d'après Welcomme et al., 1997, 1999, 2001, Welcomme et Ginsburg, 1997, Marivaux et al., 1999, Antoine et Welcomme, 2000, Heissig, 1972, Khan, 2009. (*) Espèces connues à la Formation Manchar.

5.1. Bugti Hills

Tertiary continental layers from the Bugti Hills (Baluchistan) have yielded many fossil rhinoceroses (Fig. 9). They have been collected and studied since the beginning of the 20th century (Lydekker, 1881, 1884; Pilgrim, 1910, 1912; Forster-Cooper, 1924, 1934; Heissig, 1972; Flynn et al., 1995; Antoine et al., 2010). Within the Dera Bugti fauna, Forster-Cooper (1934) documented two species attributed to the genus *Aceratherium* (*A. blandfordi* and *A. abeli*) and one to *Chilotherium* (*C. smithwoodwardi*). Following recent investigations (Antoine et al., 2003a, 2004), early Oligocene strata in the Bugti Hills (Chitarwata Formation, lower Bugti Member) have yielded the rhinocerotid *Epiaceratherium* cf. *magnum*; in turn, late Oligocene levels (Chitarwata Formation, upper Bugti Member) have provided remains of the rhinocerotid *Aprotodon smithwoodwardi* together with two other rhinocerotoid taxa, *Paraceratherium bugtiense* (Indricotheriidae) and *Cadurcotherium indicum* (Amynodontidae).

The early Miocene levels (Welcomme et al., 2001) show a marked faunal turnover, including elasmotheriine rhinocerotids, deinotheres, bovids, and listriodontine suids (Antoine et al., 2004). Antoine et al. (2010) recognized two European genera in Bugti Hills (upper member of Chitarwata Formation and base of Vihowa Formation), with the species *Pleuroceros blanfordi* and *Mesaceratherium welcommi*; they are part of a great diversity of rhinocerotids (*Bugtirhinus praecursor*, *Protaceratherium* sp., *Plesiaceratherium naricum*, *Brachypotherium gajense*, *Gaindatherium* cf. *browni*, *Prosantorhinus shahbazi*, and cf. *Rhinoceros*), which can reach up to nine species in a single locality. In addition, this high rhino diversity is associated to a great number of other herbivorous species, from proboscideans and antracotheres to chalicotheres and ruminants (Métais et al., 2009), which implies the existence of an enormous food supply in the area (Antoine et al., 2010).

Towards the end of the middle Miocene there is a strong decline of the rhinocerotid diversity in Bugti Hills. The locality of Sartaaf, with the record of *A. complanatum*, evidences the presence of late Miocene levels in the area of Bugti Hills (Antoine et al., 2003b).

5.2. Manchar Formation, Sindh

The early reports on the palaeontology of the Manchar Formation have largely been found in the records and memoirs of the Geological Survey of India. Major references are those published by Falconer (1868), Lydekker (1876, 1878, 1883, 1884), Blanford (1883), Colbert (1935), Pilgrim (1910, 1912, 1913, 1917, 1932), Forster-Cooper (1913, 1923, 1924, 1934), Matthew (1929), Osborn (1936), Sahni and Tripathi (1957), Pascoe (1963), and Heissig (1972). The Manchar Formation has been the source of type specimens of several Lydekker's and Pilgrim's species, such as *C. intermedium*, coming from the top of the Gaj Formation (Lydekker, 1884). The Manchars are very important as a potential source of topotypic material for many poorly known mammalian forms. Concerning rhinos, Cerdeño and Hussain (1997) described some remains, mainly postcranial, from different localities in the Sindh area, recognizing *H. matritense*, *Aprotodon fatehjangense*, *Chilotherium* cf. *intermedium*, and *B. perimense* (Fig. 9). In that paper, the authors compared the *H. matritense* remains with those of *Caementodon oettingenae* from Chinji Formation (Heissig, 1972) as they considered both species to be synonyms, a previous proposal (Íñigo and Cerdeño, 1997) that is not shared by other authors (Antoine, 2003).

According to Pilgrim (1917), the presence of archaic rhinocerotids, anthracotheres, very few suids and giraffes, and the absence of bovids and tragulids are indicative of an age for the Bugti fauna older than that of the basal Manchar Formation. Investigations carried out

by Khan et al. (1984), Raza et al. (1984) or Made and Hussain (1992), among others, have established correlations between the Manchar Formation and the Kamlial or the lower Chinji formations of the Siwaliks. According to Made and Hussain (1992), based on sanitheres (Suoidea), the fauna from Lower Manchar Formation can be correlated with European localities of the MN 5 mammal zone, that is the latest early Miocene or early middle Miocene (Métais et al., 2009: fig. 5). In a more recent paper, Brohi et al. (2009) stated that the Manchar Formation ranges from middle Miocene to Pliocene, but they did not comment on its paleontological record.

5.3. Siwaliks, Potwar Plateau

5.3.1. Kamlial Formation

Pilgrim (1917) named the lower Siwaliks as "Kamlial Zone" on the basis of its correlation to the basal Manchar Formation. The Kamlial Formation has a very poor fossil record and has always been one of the most poorly known of the Pilgrim's faunal zones. However, it is the second oldest Neogene biostratigraphic unit in Southern Asia and is considered as transitional in faunal characters between the Bugti fauna —with archaic rhinoceroses and anthracotheres— and the younger Siwaliks fauna with rich diversity of ruminants, suids, and proboscideans (Raza et al., 1984). Reports of the Geological survey of Pakistan have indicated that the fauna from the Kamlial Formation is in fact surprisingly diverse and includes many species which were not previously recorded there.

Concerning rhinoceroses, Colbert (1935) had recognized the presence of *B. perimense* in the Chinji, Nagri, and Dhok Pathan formations, but was Heissig (1972) who recorded it in the Kamlial Formation, as well as *A. fatehjangense*. The present recognition of *A. laogouense* in the Kamlial Formation, equivalent in age to the European MN5 unit (Métais et al., 2009), implies the temporal extension of this species in Asia, previously recorded in levels correlated with the MN6 mammal unit in China (Deng, 2004), although the genus *Alicornops* has a longer distribution in both Europe and Asia (Cerdeño and Sánchez, 2000; Antoine et al., 2003b).

5.3.2. Chinji Formation

The Chinji Formation in the lower Siwaliks of Pakistan has yielded numerous remains of fossil rhinoceroses (Colbert, 1935; Heissig, 1972). Recently, Antoine et al. (2010) recognized the material assigned to *A. blanfordi* as two different taxa, *Pleuroceros blanfordi* and *Mesotherium welcommi*. According to Heissig (1972), four rhinoceros species are common in the Chinji Formation: *B. perimense*, *A. fatehjangense*, *C. intermedium*, *Caementodon ottingenae*, and *Rhinoceros* (*Gaindatherium*) *browni*. More recently, Heissig (2003) reported four of them (at generic level) in Middle and Upper Chinji: *Aprotodon*, *Brachypotherium*, *Caementodon*, and *Rhinoceros* (*Gaindatherium*), indicating *Chilotherium* (*Subchilotherium*) just for the Nagri and Dhok Pathan formations. Antoine (2003), in turn, has considered *Aprotodon* as a probable synonym of the genus *Brachypotherium*, and *Gaindatherium* is treated at generic level, as originally established, in different papers (Antoine et al., 2003a, 2003b, 2003c).

Two of the mentioned species, *B. perimense* and *C. intermedium* are also present in late Miocene formations, and *Gaindatherium* is represented then by a different species (Colbert, 1934; see below).

5.3.3. Nagri Formation

The rhinoceroses from the Nagri Formation (Fig. 9) are not very well documented. Nevertheless, earlier researchers such as Colbert (1935) or Heissig (1972), among others, reported various rhinoceros taxa in this formation; they imply continuity from the underlying Chinji Formation with *C. intermedium, A. fatehjangense, C. oettingenae*, and *B. perimense*, as well as with a different species of *Gaindatherium*, *G. vidali* (Heissig, 1972). This author also mentioned some remains assigned to *Eurhinoceros* aff. *sondaicus* (*Rhinoceros sondaicus*).

5.3.4. Dhok Pathan Formation

Colbert (1935) reported *Aceratherium perimense*, *Aceratherium lydekkeri*, and *C. intermedium* from different levels of the Dhok Pathan Formation. Later Heissig (1972) just recognized two rhinoceros species from this formation: *C. intermedium complanatum*, recently renamed as *A. complanatum* (Antoine et al., 2003b) as explained above, and *B. perimense*. The presence of *A. complanatum* in the Dhok Pathan Formation is confirmed in the present study.

5.3.5. Soan Formation

Information regarding the fossil rhinoceroses from the Upper Siwaliks (Fig. 9) is scanty and goes back to Colbert (1935), who recognized two species, *Coelodonta platyrhinus* (originally defined as *Rhinoceros*) and *Rhinoceros sivalensis*, firstly reported from the Upper Siwaliks of Chandigarh in India. Later Khan (1971) erected the genus *Punjabitherium* for the species *P. platyrhinum*, based on a skull collected from the Upper Siwaliks of India near the base of the Pinjor stage (Fig. 9). Also, Sarwar (1971) reported an isolated premolar of *Rhinoceros kendengindicus* from the Pinjor Zone of Mirpur, Azad Kashmir, Pakistan; this species is considered by Antoine (2012) as one of the Pleistocene forms that would belong to *R. unicornis*. In addition, *R. sondaicus* and *R. unicornis* have been recovered from the Soan Formation of Sardhok, Jhelum, Pakistan (unpublished data).

6. Conclusion

The study of unpublished rhinocerotid remains from the Siwaliks has led to the recognition of two species of the genus *Alicornops*. The specimens from the Kamlial Formation (late early Miocene) are recognized as *A. laogouense*, and those from the Dhok Pathan Formation (late Miocene–early Pliocene) as *A. complanatum*. These materials add to the widespread record of *Alicornops* through the middle and late Miocene of Eurasia.

A. laogouense in the Kamlial Formation increases the so far known geographic and stratigraphic distributions of the species, previously recorded in China (Laogou, MN6). It appears as an Eurasian immigrant to the Siwaliks in MN5 times. The presence of *A. complanatum* in the Siwaliks of Potwar plateau also enlarges its geographic distribution in Pakistan, previously known from the Bugti Hills of Baluchistan. The absence of the genus *Alicornops* from the Siwaliks in levels equivalent to late MN5–MN9 zones might be due to a biased record in previous collections from the Chinji and Nagri formations. The rhinocerotid record throughout the Siwalik sequence shows the permanence of several species along different formations (i.e., *B. perimense* or *C. intermedium* from Kamlial to Dhok Pathan levels), together with the appearance of other taxa in one or another formation with different biochrons (Fig. 9). Only future findings could reveal a continuity of the *Alicornops* lineage throughout the geological sequence or if these two species represent two independent migration waves from Eurasia to the Siwaliks.

Disclosure of interest

The authors declare that they have no conflicts of interest concerning this article.

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