



General Palaeontology, Systematics, and Evolution (Vertebrate Palaeontology)

The latest Miocene Rhinocerotidae from Sahabi (Libya)

Les Rhinocérotidés du Miocène tardif de Sahabi (Libye)

Luca Pandolfi*, Lorenzo Rook

Dipartimento di Scienze della Terra, Università degli Studi di Firenze, Via G. La Pira, 4, 50121 Firenze, Italy

ARTICLE INFO

Article history:

Received 3 November 2018

Accepted after revision 1st March 2019

Available online 29 March 2019

Handled by Lars van den Hoek Ostende

Keywords:

Brachypotherium

Dicerotine

Morphology

Systematics

Northern Africa

ABSTRACT

The Rhinocerotidae material from the latest Miocene of Sahabi (Libya) is here revised in detail in order to clarify its systematic position and the paleobiogeographic implications. The family is represented by four specimens only at Sahabi, a phalanx, a mandible, a second upper molar (M2), and a second upper premolar (P2). Except for the phalanx, which can be only identified at the family level, the morphology and the dimensions of these specimens have revealed the presence of three taxa: *Aceratheriini* vel *Teleoceratina*, *Brachypotherium lewisi* and '*Diceros*' sp. The presence of the large-sized *B. lewisi* has been suggested in several papers, but without a detailed comparison or critical revision. The *Brachypotherium* from Sahabi also resembles *Brachypotherium heinzlini*, suggesting a probable synonymy between this species and *B. lewisi*. A P2 from Sahabi differs from several species belonging to *Ceratotherium*, including *Ceratotherium neumayri*, and it resembles the genus *Diceros*. The rhinoceros association (*Brachypotherium* and a dicerotine) recognized at Sahabi has been recorded at Lothagam (Kenya), suggesting a biogeographic affinity with the eastern Africa assemblage.

© 2019 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

R É S U M É

Le matériel de Rhinocérotidés récolté dans le Miocène tardif de Sahbi (Libye) est ici révisé en détail pour clarifier sa position systématique et les implications paléobiogéographiques qui en découlent. La famille est représentée par quatre spécimens seulement à Sahabi, à savoir une phalange, une mâchoire inférieure, une seconde molaire supérieure (M2) et une seconde prémolaire supérieure (P2). Excepté en ce qui concerne la phalange, qui ne peut être identifiée qu'au niveau de la famille, la morphologie et les dimensions de ces spécimens ont révélé la présence de trois taxa : *Acerathiini* vel *Teleoceratina*, *Brachypotherium lewisi* and « *Diceros* » sp. La présence de *Brachypotherium lewisi* de grande taille a été suggérée dans plusieurs articles, mais sans comparaison détaillée ou révision critique. Le *Brachypotherium* de Sahabi ressemble aussi à *Brachypotherium heinzlini*, suggérant une synonymie probable entre cette espèce et *B. lewisi*. Une P2 de Sahabi diffère de différentes espèces appartenant à *Ceratotherium*, incluant *Ceratotherium neumayri* et ressemble au genre *Diceros*. L'association de Rhinocéros (*Brachypotherium* et un Dicerotiné) reconnue à Sahabi, a été enregistrée à Lothagam (Kenya), suggérant une affinité biogéographique avec l'assemblage de l'Afrique orientale.

© 2019 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

* Corresponding author.

E-mail address: luca.pandolfi@unifi.it (L. Pandolfi).

1. Introduction

Sahabi (formally As Sahābī) is a very well-known latest Miocene vertebrate site in northern Libya. It is located 130 km south of Ajdabiya (Aǧdābiyā) in the hinterland of the Sirte Gulf (30°00′26″N and 20°47′46″E; Fig. 1A) and is located along the route going south into the Libyan Sahara to the Gialo and Kufra oases. In the 1920s and 1930s, there was an Italian army station (*ridotta militare*) at Sahabi with an airfield (*campo di aviazione*) for small airplanes (ruins of the Italian small fort and of the airfield are still visible at the site; Fig. 1B and C). Being on the road to various sites into the Libyan Desert, Sahabi was frequently crossed by caravans and explorers and was visited by eminent geologists such as Desio (1931) and Stefanini (1934).

The discovery of Sahabi as a large terrestrial vertebrate paleontological locality and the recovery of abundant vertebrate fossils from the site in early years are undoubtedly due to the efforts of Carlo Petrocchi (Rook, 2008). Italian soldiers and other Italian personnel assigned to the Sahabi fort collected fossils as curiosities, because they were so common around the military installation. In early 1934, a team of public health personnel realized the possible scientific importance of the fossil discoveries and reported them to the local authorities. Following these reports, Petrocchi was charged to study these fossil remains and to survey the Sahabi area. From 1934 to 1939, Petrocchi conducted several seasons of field survey and excavation, and undertook intensive laboratory work for the preparation of the collected material (Petrocchi, 1934, 1941, 1943). Despite Petrocchi's enthusiasm, continuing his work at Sahabi proved to be difficult. Petrocchi was left without sufficient support to continue his work at the site with no geologist or paleontologist charged to collaborate with him. Nonetheless, the activity of these years resulted in the assembly of a large fossil collection (consisting of about 1000 specimens) that was stored in Benghazi. When, in 1939, Petrocchi was appointed director of the Libyan Museum of Natural History, the Sahabi fossil material was transferred to Tripoli. At the beginning of 1940, Petrocchi was asked to organize a paleontological exhibition within the 1940 "Mostra Triennale d'Oltremare", to be held in Naples. For this purpose, Petrocchi travelled back to Italy carrying with him a cast of the *Stegotetabelodon syrticus* type cranium (at present kept within the Rome Civic Zoology Museum; Marangoni et al., 2017), as well as a number of original fossils among the Sahabi collection. The circumstances of the Italian participation in World War II made it impossible for him to come back to Tripoli, and Petrocchi was obliged to remain in Italy, where he was able to continue working on the small part of the Sahabi material that was "temporarily" transferred to this country (Petrocchi, 1951, 1954, 1956).

After several decades of no field activity at Sahabi, a multidisciplinary research team, the International Sahabi Research Project (ISRP), developed intensive investigations in the area from the middle 1970's to early 1980's (Boaz et al., 1979, 1987). Later, in 2004, the efforts of several institutions (the Benghazi University and the International Institute for Human Evolutionary Research, Martinsville, Virginia) formally reorganized Sahabi research into a

renewed research initiative named the "East Libya Neogene Research Project" (ELNRP) (Boaz et al., 2008).

The Sahabi material "temporarily" transferred to Italy by Petrocchi in 1940 is still housed in this country, kept in different Institutions in Rome: the Museum of Paleontology/Earth Sciences, Department of the University "La Sapienza", and the Rome Civic Zoology Museum (where the collections of the former "Museo dell'Istituto Italo Africano" were entrusted in 1989; Marangoni et al., 2017). Since then and until recent years, these specimens were the object of descriptive papers or material revisions (Bonarelli, 1947; Delfino, 2008; D'Erasmus, 1954; Esu and Kotsakis, 1980; Leonardi, 1952; Maccagno, 1948, 1954; Rook and Martínez-Navarro, 2004; Sardella and Werdelin, 2007).

Within the framework of a general revision of the late Neogene Rhinocerotidae in the Perimediterranean area (Pandolfi, 2018; Pandolfi and Rook, 2017; Pandolfi et al., 2016), we report herein the Rhinocerotidae record from the famous latest Miocene locality of Sahabi. The Rhinocerotidae material from Sahabi is relatively scarce, but important as it represents one of the few latest Miocene localities of Northern Africa and one of the six localities "that yielded remains of Rhinocerotidae". This short note is aimed to clarify the number of specimens and the taxonomic position of the rhinoceroses recorded at Sahabi and their possible implications.

2. Material and methods

Only the following four Rhinocerotidae specimens have been collected at Sahabi.

- A large-sized M2 was initially assigned to the American genus *Teleoceras* (D'Erasmus, 1954) and later referred to the giant rhinoceros *Baluchitherium* or *Indricotherium* (= *Paraceratherium*) (Hooijer, 1968; Savage, 1971). The M2 collected by Petrocchi (1951) between January and February 1938 and published by D'Erasmus (1954) is currently missing. Our attempt to locate the specimen while revising the collection stored at the Rome Civic Zoology Museum, at the Museum of Paleontology of the University of Naples (where D'Erasmus was active, and where a small collection of marine vertebrates from Sahabi is still kept), and the Sapienza University in Rome did not allow us to recover the specimen. Thus, all our morphometric and morphological considerations are limited to the evaluation of D'Erasmus's figures.
- A mandible of rhinoceros has been briefly described by Petrocchi (1951: p. 27), but it is also considered to be lost, as this specimen cannot be located in the collections where Petrocchi's material is currently stored.
- A worn-out P2 collected during the 1980's was initially published by Heissig (1982) as cf. *Diceros neumayri* and by Bernor et al. (1987) as *D. neumayri*. Later, it was referred to different dicerotine taxa (cf. Geraads, 2010; Giauourtsakis et al., 2009).
- A second phalanx of the middle digit was also cited by Heissig (1982), but it was not mentioned or figured in other papers (e.g., Bernor et al., 1987).

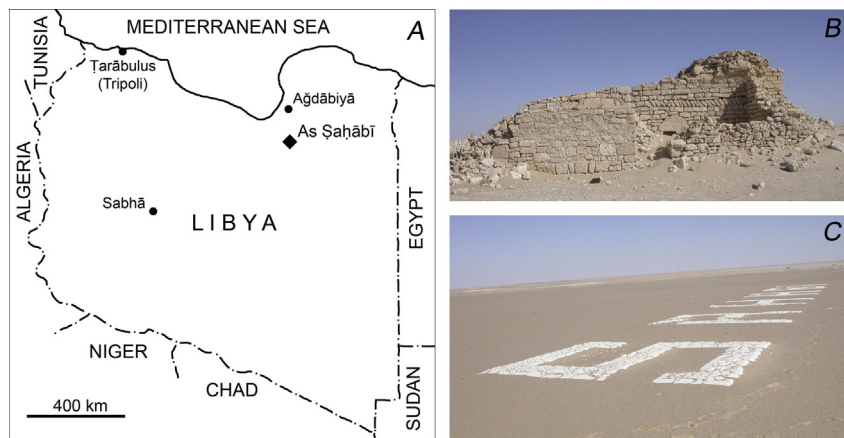


Fig. 1. Location map of the Sahabi site (A), with a view of the ruins of the Italian small fort (B) and of the airfield (C) (Photo taken by L.R. during the 2004 ELNRP field survey).

Fig. 1. Carte de localisation du site de Sahabi (A) avec vue des ruines du petit fort italien (B) et du champ d'aviation (C) (photo prise par L.R. pendant la campagne de terrain ELNRP de 2004).

The specimens were morphologically compared with the rhinocerotid material collected from selected Miocene African and European localities. The comparisons were based on direct observation of the material housed in several museums and institutions, as well as on data from literature. The dental terminology follows Antoine (2002); the morphometric methodology follows Guérin (1980). The suprageneric classification follows Antoine (2002).

3. Systematic paleontology

Family Rhinocerotidae Gray, 1821

Referred material: 96P16B, a second phalanx of the middle digit.

Description and comparison: According to Heissig (1982), the size of the specimen is comparable to that of *Ceratotherium neumayri*. However, phalanges of *Ceratotherium douariense* (= *Diceros douariensis*, see Geraads, 2010) and other late Miocene rhinoceroses are unknown. An attribution to the family level seems to be appropriate due to the absence of detailed morphological and morphometric studies on Neogene rhinocerotid phalanges.

Subfamily Rhinocerotinae Gray, 1821

Aceratheriini Dollo, 1885 vel Teleoceratina Hay, 1902

Referred material: A partially preserved mandible currently lost.

Description and comparison: Petrocchi did not figure the remains and only reported a very short description, giving some details about the state of preservation. According to Petrocchi (1951), the horizontal ramus of the mandible preserved a large-sized incisor. Unfortunately, no information about the orientation of i2s (parallel or diverging rostrally) was reported by Petrocchi. During the latest Miocene, large-sized incisors are only documented in aceratheres (Aceratheriini; e.g., *Chilotherium*) and brachypotheres (Teleoceratina; e.g., *Brachypotherium*). Dicerotines (Rhinocerotina) lack well-developed and large lower incisors.

Tribe Rhinocerotini Gray, 1821

Subtribe Teleoceratina Hay, 1902

genus *Brachypotherium* Roger, 1904

Brachypotherium lewisii Hooijer & Patterson, 1972

(Fig. 2A)

Referred material. One second upper molar figured by D'Erasmus (1954, figs. 1–3), currently missing.

Description and comparison. The upper molar from Sahabi was originally described and compared by D'Erasmus (1954). The greatest width of 99 mm reported by this author led Savage (1967, 1971) and Hooijer (1968) to consider this tooth as belonging to a baluchitherine (*Indricotherium* or *Baluchitherium* = *Paraceratherium*, family Hyracodontidae, subfamily Indricotheriinae). Indricotheriinae occurred from the middle Eocene to the late Oligocene in Eurasia and this group seemingly never reached the Afro-Arabian continent (Antoine et al., 2004, 2008 and references therein). The greatest width of Sahabi's tooth is most probably overstated by differences in the method of measuring; considering the size reported in the original figure, the greatest width of the tooth is approximately 91 mm, whereas the length of 78 mm seems to be correct (Table 1). As correctly depicted by D'Erasmus (1954), the tooth displays a large and robust crochet, a prominent antecrochet, and a buccal cingulum in the posterior side of the ectoloph, which is rather flat. Protoloph and metaloph are relatively parallel (Fig. 2A). The author also reported the presence of a tubercle at the entrance of the medisinus and a narrow and buccal-lingually elongated postfossette.

Contrary to Sahabi's tooth, the M2 of *Paraceratherium* lacks a crochet, and the buccal cingulum is strong and continuous (e.g., Antoine et al., 2004, fig. 3A; Fooster-Cooper, 1924; fig. 11). The European *Brachypotherium brachypus* (which is doubtfully distinct from *B. goldfussi*) shows a well-developed crochet and an antecrochet on M2 (Cerdeño, 1993) as found in the studied specimen, but the dimensions are considerably smaller compared with those of the

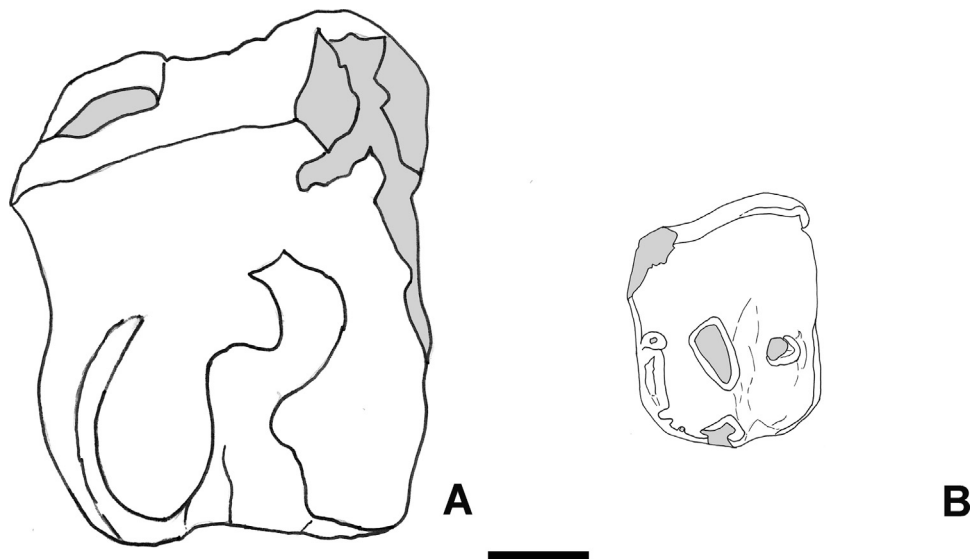


Fig. 2. Latest Miocene Rhinocerotidae from Sahabi, occlusal view. Right M2 of *Brachypotherium lewisi* (A) (redrawn from D'Erasmus, 1954). Left P2 of “*Dicerops*” sp. (B) (redrawn from Bernor et al., 1987). Scale bar corresponds to 2 cm.

Fig. 2. Rhinocérotidé du Miocène terminal de Sahabi, vue occlusale. Molaire M2 droite de *Brachypotherium lewisi* (A) (redessinée à partir de D'Erasmus, 1954). Prémolaire P2 gauche de « *Dicerops* » sp. (B) (redessinée d'après Bernor et al., 1987). Barre d'échelle = 2 cm.

Table 1

Measurements (in mm) of the M2 of *B. lewisi* from Sahabi (Libya) compared with those of *B. brachypus* (Cerdeño, 1993), *B. minor* (from Geraads and Miller, 2013), ‘*A. campebelli*’ (from Hamilton, 1973), *B. snowi* (from Guérin, 2000), *B. lewisi* (from Hooijer and Patterson, 1972), *B. lewisi* (from Harris and Leakey, 2003), *B. heinzlini* (from Hooijer, 1968), and *B. perimense* (from Heissig, 1972). Measurements (in mm) of the P2 of ‘*Dicerops*’ sp. from Sahabi (Libya) compared with those of *C. simum* (from Guérin, 1980), *D. bicornis* (from Guérin, 1980), *C. douariense* (from Guérin, 1966; Giaourtsakis et al., 2009), *C. neumayri* (Geraads, 1988; Antoine and Saraç, 2005; Geraads and Spassov, 2009; Giaourtsakis et al., 2009; Antoine et al., 2012). L: length; B: breadth.

Tableau 1

Mesures (en mm) de la M2 de *B. lewisi* de Sahabi (Libye) comparée à celles de *B. brachypus* (Cerdeño, 1993), *B. minor* (d'après Geraads et Miller, 2013), « *A. campebelli* » (d'après Hamilton, 1973), *B. snowi* (d'après Guérin, 2000), *B. lewisi* (d'après Hootjer et Patterson, 1972), *B. lewisi* (d'après Harris et Leakey, 2003), *B. heinzlini* (d'après Hooijer, 1968) et *B. perimense* (d'après Heissig, 1972). Mesures (en mm) de la P2 de « *Dicerops* » sp. de Sahabi (Libye) comparée à celles de *C. simum* (d'après Guérin, 1980), *D. bicornis* (d'après Guérin, 1980), *C. douariense* (d'après Guérin, 1966; Giaourtsakis et al., 2009), *C. neumayri* (d'après Geraads, 1988; Antoine et Saraç, 2005; Geraads et Spassov, 2009; Giaourtsakis et al., 2009; Antoine et al., 2012). L : longueur ; B : largeur.

Measurement	Sahabi	<i>B. brachypus</i>	<i>B. minor</i>	' <i>A. campbelli</i>	<i>B. snowi</i>	<i>B. heinzellini</i>	<i>B. lewisi</i>	<i>B. lewisi</i>	<i>B. perimense</i>
M2 L	78	57.3–(71.5)	48.3–56.6	61–62	63–71	63	ca. 70	63.59–80.58	55–72
M2 B	91	56.4–73	50.6–58.4	75–79	74–79	77	86–87	65.78–90.34	67–83
Measurement	Sahabi	<i>C. simum</i>		<i>D. bicornis</i>		<i>C. douariense</i>		<i>C. neumayri</i>	
P2 L	34	36–46		30–41.5		30–38.5		36.1–41	
P2 B	43	36–44		31.5–45		38–47.6		41.8–44	

Sahabi tooth (Table 1). Late Miocene *Brachypotherium* sp. from Bulgaria (Geraads and Spassov, 2009; pl. I, fig. F) has a weak and double crochet, a less prominent antecrochet than in the studied specimen and a backwards-directed metaloph. The dimensions of the M2 of *B. perimense* from Asia reported by Heissig (1972) are slightly smaller than those of the specimen from Sahabi (Table 1). The M2 figured by Heissig (1972: Pl. 10, fig. 9) displays a longer crochet, a shorter metaloph, and a backward directed protoloph and metaloph with respect to Sahabi's tooth. The latter features are present on the worn-out M2 from the Siwaliks of Burma (Lydekker, 1884: pl. 1, fig. 5); this tooth also displays lingual pillars at the entrance of the medisinus, similarly to the specimens from Punjab (Lydekker, 1881: pl. 2, fig. 1; pl. 3, fig. 3) and Perim Island (Lydekker, 1881: pl. 2A). The worn-out M2 of *B. perimense* figured by Colbert (1935: fig. 89) differs from the studied specimen by having

a constricted metaloph, a larger postfossette and by being smaller ($L = 69$ mm; $B = 78$ mm; Colbert, 1935: p. 198); nevertheless, the specimen AM19470 from Pakistan (Colbert, 1935: fig. 88) has larger size ($L = 87$ mm; $B = 94$ mm).

Compared with the M2 from Sahabi, the middle Miocene *B. minor* (Geraads and Miller, 2013) has smaller crochet and antecrochet, a slightly concave posterior part of the ectoloph and smaller dimensions (Table 1). The M2 of ‘*Aceratherium*’ *campbelli* from the early Miocene of Jebel Zelten (Libya) has a smaller size, smaller crochet and antecrochet with respect to the Sahabi tooth and a slightly concave posterior part of the ectoloph. A weak and reduced labial cingulum occurs on the posterior side of the ectoloph on M2 of *B. snowi* (Hamilton, 1973). In *Brachypotherium heinzlini* from Sinda (Zaire), the M2 displays a rather flat ectoloph, the crochet and the antecrochet are well developed and the lingual cingulum is reduced

to a tubercle (Hooijer, 1963; pl. VIII, figs. 4, 6). A labial cingulum occurs on the posterior half of the ectoloph on the molars of *B. lewisi* from Lothagam (Kenya) (Hooijer and Patterson, 1972: p. 5); the M2 of this species displays crochet and antecrochet, a lingual cingulum reduced to a tubercle at the entrance of the medisinus, and a flattened ectoloph profile behind the paracone style. The anterior width of M2 of *B. lewisi* from Lothagam (KNM LT 100) reaches ca. 90 mm (Hooijer and Patterson, 1972: p. 13); Harris and Leakey (2003) also reported an anterior width of more than 90 mm (Table 1).

Subtribe Rhinocerotina

Genus '*Diceros*' sp.

(Fig. 2B)

Referred material: 445P34A, a second upper premolar figured by Bernor et al. (1987, fig. 15).

Description and comparison: the tooth is very worn; the anterior width is less than the posterior one, resulting in a trapezoidal shape of the occlusal surface of the tooth (Fig. 2B). The buccal profile of the tooth displays a concavity in the middle; the postfossette is circular, the medisinus is buccal-lingually elongated and does not reach the lingual side of the tooth at this stage of wear (Fig. 2B). A lingual cingulum is expressed by an enamel fold on the lingual side of the tooth; a prefossette is evident on the anterior side of the protoloph. Protocone and hypocone are similar in size and fused at this stage of wear; every constriction on the metaloph and protoloph is absent.

Worn P2s of *Ceratotherium simum* have a trapezoidal shape (e.g., Fig. 3A), but the lingual length is shorter than the buccal one; the medifossette is usually evident also at an advanced stage of wear, the medisinus is generally elongated anterior-posteriorly, protocone and hypocone appear completely fused, and the lingual cingulum is absent. Worn-out P2s of *Diceros bicornis* have a rectangular shape (e.g., Fig. 3B–E), with the anterior width slightly smaller than the posterior one. Protocone and hypocone appear separated also in an advanced stage of wear; the postfossette is subcircular and the medisinus is buccal-lingually elongated. A small prefossette is sometimes present as well as the lingual cingulum (Fig. 3B–E). Worn-out P2s of *Ceratotherium effricax* (= *Ceratotherium mauritanicum* according to Geraads, 2005) differ from the Sahabi specimens by having an anterior-posteriorly elongated medisinus, a lingual-distally directed protoloph, and protocone and hypocone completely fused (selected tooth reported in Fig. 3F). The P2s of *Ceratotherium douariense* from Douaria (Guérin, 1966; figs. 6, 7) are less worn than that from Sahabi; they have a rectangular shape, a subcircular postfossette, a buccal-lingually elongated medisinus and a lingual cingulum as found in the studied specimen. Contrary to the studied P2, however, protocone and hypocone are separated on the Douaria's specimen, apparently, until their bases; the anterior width is larger than the posterior one, the protoloph is narrower and the metaloph is constricted in respect to Sahabi's tooth. The latter is slightly larger than the P2s from Douaria (Table 1). The P2 of *C. douariense* from the Middle Awash (Giaourtsakis et al., 2009; fig. 14.2 A) is less worn than that from Sahabi

and displays a circular postfossette, a prefossette, a lingual cingulum, a buccal-lingually elongated medisinus. However, the Middle Awash tooth differs from that from Sahabi by having a crochet, a constricted metaloph, a protocone and a hypocone well separated until their bases and a narrower protoloph. The P2 from the Middle Awash is larger than the type material from Douaria and slightly wider than that from Sahabi (Table 1). A relatively worn P2 of *C. neumayri* from Mytilinii (Giaourtsakis et al., 2009; pl. IV, fig. 1) displays protocone and hypocone completely fused, similar to *C. simum*, lingual length shorter than buccal length, and a lingual-distally directed protoloph. Protocone and hypocone are separated until the dorsal surface of the lingual cingulum on P2 of *C. neumayri* from Karacaşar (Turkey), which also displays a constricted metaloph, a narrow protoloph, and protocone smaller than hypocone (Antoine et al., 2012; fig. 3.b). The latter two characters are also evident of P2 from Akkaşdağı (Turkey) as well as a lingual length smaller than the buccal one (Antoine and Saraç, 2005; fig. 2A); all of them can be recognized on a worn-out P2 from Mytilinii.

4. Discussion and conclusions

Late Miocene Rhinocerotidae remains are relatively scarce and poorly represented in North Africa and, excluding Sahabi, they have been collected in other five localities:

- Douaria (Tunisia, considered latest Miocene in age by Geraads, 2010, whereas Guérin, 2000 suggested an age around 9.5 Ma), which yielded a partial adult skull with associated mandible and a partial juvenile skull assigned to *C. douariense*;
- Djebel Krechem (Tunisia, around 10 Ma; Geraads, 1989), where a few isolated teeth and a juvenile astragalus were assigned as cf. *C. douariense*, mostly on the basis of geographic proximity at Douaria (Geraads, 2010) and an isolated deciduous tooth was referred as cf. *B. lewisi*;
- Bou Hanifia (Algeria, around 10 Ma; Arambourg, 1959), where a partial juvenile skull and a few associated remains were assigned as *Ceratotherium? primaevum* (= *Dicerorhinus primaevus* in Arambourg, 1959);
- Béni Mellal (Morocco, early late Miocene; Guérin, 1976), which yielded two isolated upper teeth, a fragment of a tooth and a great cuneiform assigned to cf. *Paradicerus mukirii*;
- Tizi N'Tadderht (Morocco, late Miocene; Zouhri et al., 2012); a few collected remains have been referred as cf. *Ceratotherium* sp. and an isolated tooth has been assigned as aff. *Chilotherium* sp.

Ceratotherium douariense is doubtfully distinct from *C. neumayri* according to Geraads (2010) and the paratype of the Douaria's rhinoceros, a partial juvenile skull, morphologically resembles a non-dicerotine taxon, probably a teleoceratine (Geraads and Miller, 2013). The systematic affinities of the partial juvenile skull from Bou Hanifia, at first referred to the genus *Dicerorhinus*, are still doubtful (Geraads, 1986, 2010). Within this framework, any contribution on late Miocene Northern African Rhinocerotidae

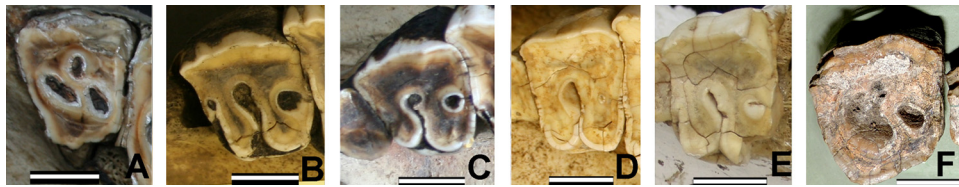


Fig. 3. Selected Dicerotines P2s at different stages of wear, in occlusal view. Left P2 of *Ceratotherium simum* (A) (MNHN 1928-310). Left P2 of *Diceros bicornis* (B) (NHMUK 1967-8-31-8). Left P2 of *D. bicornis* (C) (SMF 22.260). Left P2 of *D. bicornis* (D) (NHMUK 1962-7-6-6). Right P2 of *D. bicornis* (E) (NHMUK ZSM no_code). Left P2 of *Ceratotherium effcax* (F) (MfN MB.Ma. 42009). Scale bars correspond to 2 cm.

Fig. 3. Prémolaires P2 de Dicérotinés, sélectionnées à différents stades d'usure, en vue occlusale. Prémolaire P2 gauche de *Ceratotherium simum* (A) (MNHN 1928-310). Prémolaire P2 gauche de *Diceros bicornis* (B) (NHMUK 1967-8-31-8). Prémolaire P2 gauche de *D. bicornis* (C) (SMF 22.268). Prémolaire P2 gauche de *D. bicornis* (D) (NHMUK 962-7-6-6). Prémolaire P2 droite de *D. bicornis* (E) (NHMUK ZSM no_code). Prémolaire P2 gauche de *Ceratotherium effcax* (F) (MN MB.ma. 42009). Barres d'échelle = 2 cm.

would be helpful to better understand the biogeographic patterns and the affinities between the faunal assemblages.

Unfortunately, most of Petrocchi's Sahabi collection is missing. This is, for instance, the case of rhinoceros material collected during the 1930s. A mandible with a large-sized lower incisor would belong to either a brachypothere or an acerathere although the latter group is recorded only doubtfully in northern Africa (one uncertain record from Tizi N'Tadderht). The M2 from Sahabi described by D'Erasmus (1954) concurs well, morphologically and dimensionally, with a referral to *B. lewisi* from Lothagam. The tooth also resembles in morphology the M2 of *B. heinzlini* published by Hooijer (1963) as *Aceratherium* cf. *tetradactylum* and was later included within the new species of the brachypothere he established (Hooijer, 1968). Geraads (2010) and Geraads and Miller (2013) recently recommended restricting the nomen *B. heinzlini* only to the material collected from the type locality of Sinda 15 (Democratic Republic of the Congo) and reported the probable synonymy of *B. heinzlini* to *B. lewisi*. The morphological similarities between the M2s of the two species and the dimensions of *B. heinzlini*, which falls within the range of *B. lewisi*, would support this hypothesis, even if the material from Sinda is too scarce for any conclusion.

The P2 from Sahabi resembles *Diceros*, sharing some characters with *Diceros bicornis*, which never occurred north of the Sahara area. The tooth from Sahabi differs from worn-out P2s of *C. simum*, *C. effcax*, and *C. neumayri*. The presence of the eastern Mediterranean rhinoceros *C. neumayri* in northern Africa is therefore not confirmed. Considering the ambiguous generic status of several African dicerotines (alternatively assigned to *Ceratotherium* or *Diceros*), a provisional attribution to "*Diceros*" sp. is here proposed for the Sahabi dicerotine, pending the discovery of more preserved material.

A Rhinocerotidae association similar to that reported at Sahabi, with *Brachypotherium* and a dicerotine, is at present recorded only in Kenya, at Lothagam, upper and lower Nawata, and at Mpesida (Hooijer, 1973; Harris and Leakey, 2003; Geraads, 2010), suggesting a strict East African affinity of the rhinoceros assemblage from Sahabi.

Acknowledgements

We thank P.-O. Antoine and an anonymous reviewer for their insightful and useful suggestions and comments; we also thank Lars van den Hoek Ostende for a critical revision of the manuscript. We thank Carla Marangoni and Massimo Capula ("Museo Civico di Zoologia di Roma"), Mariella del Re ("Museo di Paleontologia, Centro Musei delle Scienze Naturali dell'Università di Napoli Federico II"), Riccardo Manni and Linda Rita ("Dipartimento di Scienze della Terra, La Sapienza Università di Roma") offered precious help on searching/exploring the Sahabi fossil vertebrate collections kept in their Institutions. Tasos Kotsakis ("Dipartimento di Scienze, Università di Roma III"), Noel T. Boaz (International Institute for Human Evolutionary Research, Martinsville), and Raymond L. Bernor (Howard University, Washington DC) were kindly available to critically read a preliminary version of the manuscript providing constructive criticism and advice. This contribution is framed within a wider project on late Neogene vertebrate evolution at the University of Florence, Italy (coordinator LR). LP thanks the European Community Research Infrastructure Action, EU-SYNTHESYS project AT-TAF-2550, DE-TAF-3049, GB-TAF-2825, HU-TAF-3593, ES-TAF-2997; part of this research received support from the SYNTHESYS Project <http://www.synthesys.info/which> is financed by European Community Research Infrastructure Action under the FP7 "Capacities" Program.

References

- Antoine, P.-O., 2002. *Phylogénie et évolution des Elasmotheriina (Mammalia, Rhinocerotidae)*. Mem. MNHN 188, 1–359.
- Antoine, P.-O., Savaş, G., 2005. *Rhinocerotidae (Mammalia, Perissodactyla) from the late Miocene of Akkaşdağı, Turkey*. In: Sen, S. (Ed.), *Geology, mammals and environments at Akkaşdağı, late Miocene of central Anatolia*. *Geodiversitas*, 27, pp. 601–632.
- Antoine, P.-O., Karadenizli, L., Savaş, G., Sen, S., 2008. *A giant rhinocerotoid (Mammalia, Perissodactyla) from the Late Oligocene of North-central Anatolia (Turkey)*. *Zool. J. Linn. Soc.* 152 (3), 581–592.
- Antoine, P.-O., Shah, S.M.I., Cheema, I.U., Crochet, J.Y., De Franceschi, D., Marivaux, L., Métais, G., Welcomme, J.L., 2004. *New remains of the baluchitherid Paraceratherium bugtiense (Pilgrim, 1910) from the late/latest Oligocene of the Bugti Hills, Balochistan, Pakistan*. *J. Asian Earth Sci.* 24, 71–77.

- Antoine, P.-O., Orliac, M.J., Atici, G., Ulusoy, I., Sen, E., Çubukçu, H.E., Albayrak, E., Oyal, N., Aydar, E., Sen, S., 2012. A Rhinocerotid Skull Cooked-to-Death in a 9.2-Ma-Old Ignimbrite Flow of Turkey. *PLOS ONE* 7 (11), e49997.
- Arambourg, C., 1959. Vertébrés continentaux du Miocène supérieur de l'Afrique du Nord. Service de la carte géologique de l'Algérie, Mem. 4, 5–159.
- Bernor, R.L., Heissig, K., Tobien, H., 1987. Early Pliocene Perissodactyla from Sahabi, Libya. In: Boaz, N.T., El-Arnauti, A., Gaziry, A.W., de Heinzelin, J., Boaz, D.D. (Eds.), *Neogene Paleontology and Geology of Sahabi*. Alan R. Liss, New York, pp. 233–254.
- Boaz, N.T., Gaziry, A.W., El-Arnauti, A., 1979. New fossil finds from the Libyan Upper Neogene site of Sahabi. *Nature* 280, 137–140.
- Boaz, N.T., El-Arnauti, A., Gaziry, A.W., de Heinzelin, J., Dechant Boaz, D., 1987. *Neogene Paleontology and Geology of Sahabi*. Alan R. Liss, New York, pp. 1–401.
- Boaz, N.T., El-Arnauti, A., Pavlakis, P., 2008. A brief history of As Sahabi Research and Collections. *Garyounis Sci. Bull. Spec. Issue* 5, 1–11.
- Bonarelli, G., 1947. Dinosaurio fossile del Sahara Cirenaico. *Riv. Biol. Coloniale* 8, 23–33.
- Cerdeño, E., 1993. Étude sur *Diaceratherium aurelianense* et *Brachypotherium brachypus* du Miocène moyen de France. *Bull. Mus. Nat. Hist. Natur. Paris, Ser. 4* (15), 25–77 (C 1–4).
- Colbert, E.H., 1935. Siwalik Mammals in the American Museum of Natural History. *Trans. Am. Phil. Soc. N. Ser.* 26, 1–401.
- Delfino, M., 2008. Late Neogene crocodylian faunas from Libya and the Mediterranean area. In: Salem, M.J., El-Arnauti, A., El Sogher Saleh, A. (Eds.), *The Geology of East Libya*, 3, pp. 291–296.
- D'Erasmo, G., 1954. Paleontologia di Sahabi (Cirenaica). Sopra un molare di *Teleoceras* del giacimento fossilifero di Sahabi in Cirenaica. *Rend. Accad. Naz. dei XL Ser.* 4, 89–102.
- Desio, A., 1931. Osservazioni geologiche e geografiche compiute durante un viaggio nella Sirtica. *Boll. R. Soc. Geogr. Ital., Ser. 6* 8, 275–299.
- Esu, D., Kotsakis, T., 1980. *Ichthytherium arkesilai* sp. n. (Hyaenidae, Carnivora) del Terziario superiore di Sahabi (Cirenaica, Libia). *Riv. Ital. Paleontol. Stratigr.* 86, 241–250.
- Fooster-Cooper, C., 1924. On the skull and dentition of *Paraceratherium bugtiense*: a genus of aberrant rhinoceros from the lower Miocene deposits of Dera Bugti. *Phil. Trans. Roy. Soc. London (B)* 212, 369–394.
- Geraads, D., 1986. Sur les relations phylétiques de *Dicerorhinus primaevus* Arambourg, 1959, rhinocéros du Vallésien d'Algérie. *C. R. Acad. Sci. Paris, Ser. II* 102 (13), 835–837.
- Geraads, D., 1988. Révision des Rhinocerotidae (Mammalia) du Turolien de Pikermi : Comparaison avec les formes voisines. *Ann. Paleontol.* 74, 13–41.
- Geraads, D., 1989. Vertébrés fossiles du Miocène supérieur du Djebel Krechem el Artsouma (Tunisie centrale). Comparaisons biostratigraphiques. *Geobios* 22, 777–801.
- Geraads, D., 2005. Pliocene Rhinocerotidae (Mammalia) from Hadar and Dikika (lower Awash, Ethiopia), and a revision of the origin of modern African rhinos. *J. Vert. Paleontol.* 25 (2), 451–461.
- Geraads, D., 2010. Rhinocerotidae. In: Werdelin, L., Sanders, W.J. (Eds.), *Cenozoic Mammals of Africa*. University of California Press, Berkeley, CA, USA, pp. 669–683.
- Geraads, D., Spassov, N., 2009. Rhinocerotidae (Mammalia) from the late Miocene of Bulgaria. *Palaeontogr. Abt. A* 287, 99–122.
- Geraads, D., Miller, E., 2013. *Brachypotherium minor* n. sp., and other Rhinocerotidae from the early Miocene of Buluk, northern Kenya. *Geodiversitas* 35 (2), 359–375.
- Giaourtsakis, I.X., Pehlevan, C., Haile-Selassie, Y., 2009. Rhinocerotidae. In: Haile-Selassie, Y., Wolde-Gabriel, G. (Eds.), *Ardeipithecus kadabba*, Late Miocene Evidence from the Middle Awash, Ethiopia. University California Press, Oakland, pp. 429–468.
- Guérin, C., 1966. *Diceros douariensis* nov. sp., un Rhinocéros du Mio-Pliocène de Tunisie du Nord. *Doc. Lab. Geol. Fac. Sci. Lyon* 16, 1–50.
- Guérin, C., 1976. Les restes de Rhinocéros du gisement miocène de Béni Mellal, Maroc. *Geol. Méditerranéenne* Marseille 3 (2), 105–108.
- Guérin, C., 1980. Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pleistocène supérieur en Europe occidentale : comparaison avec les espèces actuelles. *Doc. Lab. Geol. Fac. Sci. Lyon* 79, 1–1182.
- Guérin, C., 2000. The Neogene rhinoceroses of Namibia. *Palaeontol. Afr.* 36, 119–138.
- Hamilton, W.R., 1973. North African Lower Miocene Rhinoceroses. *Bull. Brit. Mus. (Nat. Hist.) Geol.* 24, 351–395.
- Harris, J.M., Leakey, M.G., 2003. Lothagam Rhinocerotidae. In: Leakey, M.G., Harris, J.M. (Eds.), *Lothagam: The dawn of humanity in eastern Africa*. Columbia University Press, New York, pp. 371–385.
- Heissig, K., 1972. Paläontologische und geologische Untersuchungen im Tertiär von Pakistan, 5. Rhinocerotidae (Mamm.) aus den unteren und mittleren Siwalik-Schichten. *Bayer. Akad. Wissensch. Mathematisch-Naturwissenschaft. Klasse. Abhandl. Neue Folge* 152, 1–112.
- Heissig, K., 1982. Note on Sahabi Rhinocerotidae. In: Boaz, N.T., De Heinzelin, J., Gaziry, A.W., El-Arnauti, A. (Eds.), *Results from the International Sahabi Research Project. Special issue 4*, Garyounis Scientific Bull. University of Garyounis, Benghazi (85 p.).
- Hooijer, D.A., 1963. Miocene Mammalia of Congo. *Ann. Mus. Roy. Afr. Centrale, Sci. Geol.* 46, 1–150.
- Hooijer, D.A., 1968. A rhinoceros from the late Miocene of Fort Ternan, Kenya. *Zool. Med.* 43 (6), 77–92.
- Hooijer, D.A., 1973. Additional Miocene to Pleistocene rhinoceroses of Africa. *Zool. Med.* 46, 149–178.
- Hooijer, D.A., Patterson, B., 1972. Rhinoceroses from the Pliocene of North-western Kenya. *Bull. Mus. Compar. Zool. Harvard Univ.* 144 (1), 1–26.
- Leonardi, P., 1952. Resti fossili di *Sivachoerus* del giacimento di Sahabi in Cirenaica (Africa settentrionale). *Atti Acc. Naz. Lincei Rend.* 8, 166–169.
- Lydekker, R., 1881. Siwalik Rhinocerotidae. *Mem. Geol. Surv. India.-Pal. Ind. Ser.* 10 (2), 1–62.
- Lydekker, R., 1884. Additional Siwalik Perissodactyla and Proboscidea. *Mem. Geol. Surv. India.-Pal. Ind. Ser.* 10 (3), 1–34.
- Maccagno, A., 1948. Descrizione di una nuova specie di *Crocodylus* del giacimento di Sahabi (Sirtica). *Mem. Atti Acc. Naz. Lincei Ser.* 8 (1) (4), 63–96.
- Maccagno, A., 1954. I coccodrilli di Sahabi. *Rend. Acc. Naz. Quar.* 4/5, 77–117.
- Marangoni, C., Rook, L., Desio, M.A., 2017. L'esemplare tipo di *Stegotribelodon syrticus* Petrocchi, 1941, un reperto sopravvissuto alle vicissitudini belliche? *Museol. Sci., Mem.* 17, 71–75.
- Pandolfi, L., 2018. Evolutionary history of Rhinocerotina (Mammalia, Perissodactyla). *Fossilias* 2018, 26–32.
- Pandolfi, L., Rook, L., 2017. Rhinocerotidae (Mammalia, Perissodactyla) from the latest Turolian (MN13; late Miocene) of central and northern Italy. *Boll. Soc. Paleontol. Ital.* 56, 45–56.
- Pandolfi, L., Gasparik, M., Magyar, I., 2016. Rhinocerotidae from the upper Miocene deposits of the Pannonian Basin (Hungary): implications for migration routes and biogeography. *Geol. Carpath.* 67 (1), 69–82.
- Petrocchi, C., 1934. I ritrovamenti faunistici di as-Sahabi. *Riv. Colonie Ital.* 7, 733–742.
- Petrocchi, C., 1941. Il giacimento fossilifero di Sahabi. *Boll. Soc. Geol. Ital.* 40, 107–114.
- Petrocchi, C., 1943. Il giacimento fossilifero di Sahabi. *Coll. Sci. Doc. Ministero dell'Africa Italiana, Verbania*, pp. 1–162.
- Petrocchi, C., 1951. Notizie generali sul giacimento fossilifero di Sahabi. *Storia degli Scavi-Risultati. Rend. Accad. Naz. dei XL Roma*, 1–33.
- Petrocchi, C., 1954. I Proboscidi di Sahabi. *Rend. Accad. Naz. Quar.* 4/5, 1–76.
- Petrocchi, C., 1956. I *Leptobos* di Sahabi. *Boll. Soc. Geol. Ital.* 75, 1–36.
- Rook, L., 2008. The discovery of Sahabi site: Ardito Desio or Carlo Petrocchi? *Garyounis Sci. Bull. Spec. Issue* 5, 13–21.
- Rook, L., Martínez-Navarro, B., 2004. *Viverra howelli* n. sp., a new viverrid (Carnivora, Mammalia) from the Baccinello-Cinigiano basin (latest Miocene, Italy). *Riv. Ital. Paleontol. Stratigr.* 110, 719–723.
- Sardella, R., Werdelin, L., 2007. *Amphimachairodus* (Felidae, Mammalia) from Sahabi (latest Miocene-earliest Pliocene, Libya), with a review of African Miocene Machairodontinae. *Riv. Ital. Paleontol. Stratigr.* 113, 67–77.
- Savage, R.J.G., 1967. Early Miocene mammal faunas of the Tethyan region. *Syst. Assoc. Publ.* 7, 247–282.
- Savage, R.J.G., 1971. Review of the fossil mammals of Libya. In: Gray, C. (Ed.), *Symposium on the Geology of Libya*. Faculty of Science, University of Libya, Tripoli, pp. 215–225.
- Stefanini, G., 1934. Sulla scoperta di resti fossili di vertebrati nella Sirtica orientale. *Boll. Geogr. Gov. Tripolitana e Cirenaica* 5/6, 152–157.
- Zouhri, S., Geraads, D., El Boughabi, S., El Harfi, A., 2012. Discovery of an Upper Miocene Vertebrate fauna near Tizi N'Tadderht, Skoura, Ouazazate Basin (Central High Atlas, Morocco). *C. R. Palevol* 11, 455–461.