A new species of rhinoceros from the site of Bethlehem: '*Dihoplus*' *bethlehemsis* sp. nov. (Mammalia, Rhinocerotidae)

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ABSTRACT

The Plio-Pleistocene fossil rhinoceroses of Eurasia are relatively well known, although their taxonomy and phylogeny are still debated. The fossil rhinoceros material collected at the Bethlehem site during the first half of the 20th century is revised and re-described. Based on morphological comparison of the Bethlehem material with the latest Miocene, Pliocene and Early Pleistocene Eurasian and African species, the specimens are assigned as Rhinocerotini indet., *Dihoplus* sp. and '*Dihoplus*' *bethlehemsis* sp. nov. The comparison revealed that the studied material displays more features in common with the genus *Dihoplus* than with the genus *Stephanorhinus*. Tooth microwear analysis revealed that the diet of Bethlehem rhinoceros was probably composed of leaves of trees, bushes, or part of dicots. The new species could be one of the latest representatives of the Miocene genus *Dihoplus* that survived in Eurasia until the end of the Pliocene. Thus again the site of Bethlehem being unique in its biogeographically setting, provides novel understanding of the 'Levantine Corridor' dispersal route.

1. Introduction

Three Rhinocerotidae species are currently distributed in limited areas of India and Southeastern Asia (*Rhinoceros unicornis* Linnaeus, 1758, *R. sondaicus* Desmarest, 1822 and *Dicerorhinus sumatrensis* (Fischer v. Waldheim, 1814)) and two species in Africa (*Ceratotherium simum* (Burchell, 1817) and *Diceros bicornis* (Linnaeus, 1758)). The five extant species, the wooly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799) and their closest relatives are usually grouped within the subtribe Rhinocerotina Gray, 1821 (*sensu* Antoine, 2003; Rhinocerotini Gray, 1821 *sensu* Heissig, 1996). During the Pliocene and the Early Pleistocene, the rhinoceros species were relatively well-distributed through Eurasia and Africa.

During the Pliocene, the genus *Dihoplus* Brandt, 1878 was represented in Western Europe by '*Dihoplus*' *megarhinus* (Guérin, 1980; Guérin and Sen, 1998; Fukuchi et al., 2009; Pandolfi, 2013; Pandolfi et al., 2015, 2016; Pandolfi and Rook, 2017) and three species belonging to the genus *Stephanorhinus* were recorded: '*Stephanorhinus*' *miguelcrusafonti* (Guérin and Santafé-Llopis, 1978: which is here provisionally retained within the genus *Stephanorhinus*, although cranial

remains of this species are unknown and its systematic position appears questionable; see Cerdeño, 1992; Pandolfi et al., 2016), *S. jeanvireti* (Guérin, 1972: details are reported in Guérin and Tsoukala, 2013, p. 454; Pandolfi et al., 2017, 2019) and *S. etruscus* (Falconer, 1868). '*Stephanorhinus*' *miguelcrusafonti* has a restricted geographic and chronological range; it has been recovered at a few Early Pliocene Spanish and French localities (Guérin and Santafé-Llopis, 1978; Guérin, 1980). *Stephanorhinus jeanvireti* has been frequently documented from Late Pliocene localities of France and Italy (Guérin, 1972, 1980; Pandolfi, 2013), Slovakia (Guérin, 1980; Ďurišová, 2004; Vlačiky et al., 2008; Šujan et al., 2013), and recently in Greece (Milia; Guérin and Tsoukala, 2013), and it has been dubitatively attributed (*Stephanorhinus* sp. cf. *S. jeanvireti*) in the Guadiz-Baza depression, at Baza-1 (around 4–4.5 Ma: Ros-Montoya et al., 2017). At the end of the Pliocene, and for almost the entire Early Pleistocene, *S. etruscus* occurred in several European localities (Guérin, 1980; Cerdeño, 1993; Mazo, 1995; Pandolfi, 2013; Pandolfi and Marra, 2015; Pandolfi et al., 2015, 2017) (Fig. 1).

In Central and East Asia, Pliocene rhinoceroses are not well documented and the species *S. yunchuchenensis* (Chow, 1963), *S. lantianensis*
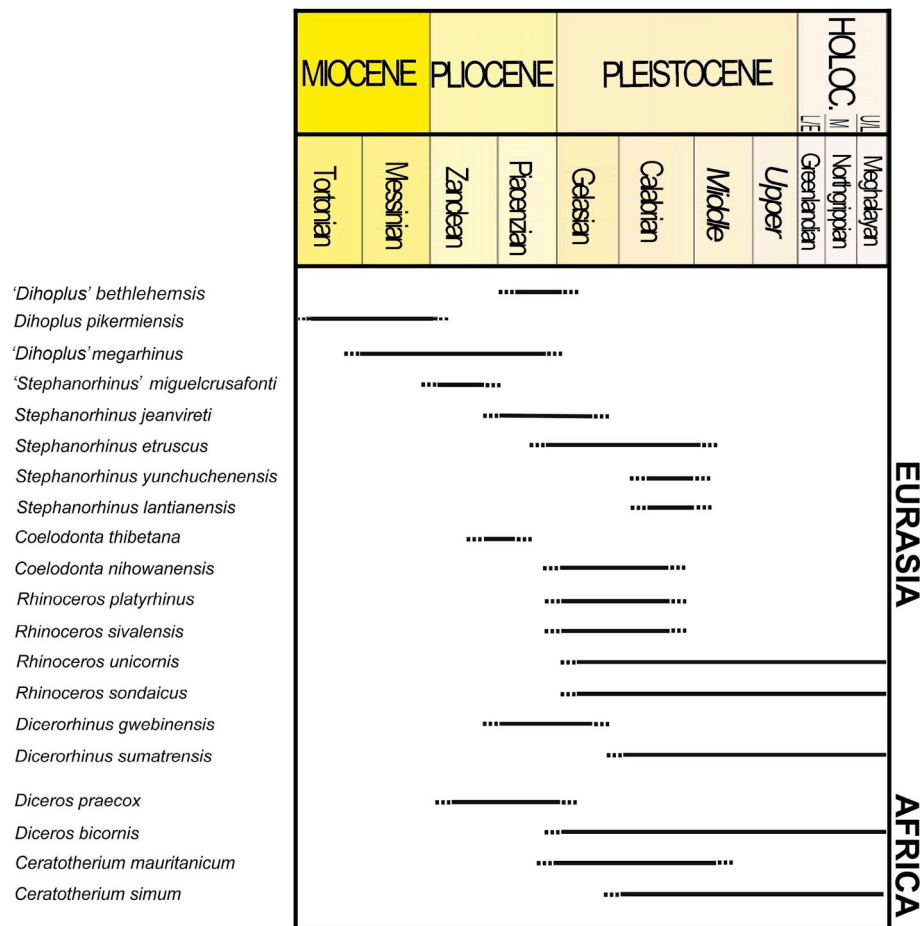
Fig. 1. Chronostratigraphic distribution of selected Pliocene and Pleistocene Eurasian and African rhinoceroses discussed in text.

(Hu and Qi, 1978) and *S. kirchbergensis* (Jäger, 1839) occurred only during the late Early Pleistocene (Tong, 2012) (Fig. 1). Among Rhinocerotina, the appearance of *Coelodonta thibetana* Deng et al. (2011), in the Pliocene of Tibet, and *C. nihowanensis* Kahlke (1969), during the Early Pleistocene in China, should be mentioned (Deng et al., 2011; Tong and Wang, 2014) (Fig. 1).

Four species belonging to the genus *Rhinoceros* were documented in southern Asia during the Plio-Pleistocene (Fig. 1): *Rhinoceros platyrhinus* Falconer and Cautley (1846), *R. sivalensis* Falconer and Cautley (1846), *R. unicornis* and *R. sondaicus*. *Rhinoceros platyrhinus* was only collected from the Siwalik Hills, in the surrounding areas of Yamuna River and nearby Mirzapur (northern India) (Pandolfi and Maiorino, 2016). *Rhinoceros sivalensis* was documented in the Siwalik Hills (India and Pakistan; Pandolfi and Maiorino, 2016), and Matthew (1929) recorded the species within the deposits of the Middle Siwaliks. Several faunal lists from Middle Pleistocene localities in Laos (Tam Nang and Tam Hang) included *R. sivalensis* and *R.* cf. *sivalensis* (Fromaget, 1936; Arambourg and Fromaget, 1938; Louys et al., 2007), but they were probably misidentified as *R. sondaicus* (see also Antoine, 2012). *Rhinoceros sondaicus*, currently represented in limited areas of western Java and southern Vietnam (Talukdar et al., 2008; Groves and Leslie, 2011), was widespread in several areas of South-East Asia and India in historical times. During the Pleistocene the species occurred in Java (Hooijer, 1964; Guérin and Faure, 2002; Antoine, 2012), in Malaysia (Hooijer, 1962), and other areas (Beden et al., 1972; Beden and Guérin, 1973; Bacon et al., 2004). Subfossil remains were collected from several localities on the Indo-Malaysian archipelago and southern China (Hooijer, 1948; Bacon et al., 2004; Rookmaaker, 2006; Groves and Leslie, 2011). *Rhinoceros unicornis* was recorded from the Early Pleistocene of Java, southern China, India and Pakistan and several Middle Pleistocene

localities in South-East Asia (Antoine, 2012 and references therein). During the Late Pleistocene *R. unicornis* occurred in China, Vietnam, southern India and Sri Lanka (Nanda, 2002; Antoine, 2012).

The genus *Dicerorhinus* occurred during the Pliocene-Early Pleistocene in Myanmar with *D. gwebinensis* (Zin-Maung-Maung-Thein et al., 2008, Fig. 1) and during the late Early Pleistocene in South China with *D. sumatrensis* (Tong and Guérin, 2009); the latter species later dispersed in South-East Asia (Antoine, 2012).

The systematics of African fossil species is still debated (cf. Geraads, 2010; Hernesniemi et al., 2011). The Plio-Pleistocene African Rhinocerotina (Fig. 1) seem to be limited only to four known species (Gerrads, 2010): *Ceratotherium mauritanicum* (Pomel, 1888), *Ceratotherium simum*, *Diceros praecox* (Hooijer and Patterson, 1972), and *Diceros bicornis*. In North Africa, *C. mauritanicum* is known from the Late Pliocene to the Late Pleistocene. During the Early Pleistocene, the extant *C. simum* occurred in East Africa (Geraads, 2005). *Diceros praecox*, previously included in *Ceratotherium* (see Geraads, 2005, 2010), first occurred during the Early Pliocene in East Africa (Lothagam, Kenya; Harris and Leakey, 2003) and is also known from the Plio-Pleistocene boundary in Kenya and Ethiopia (Geraads, 2010: Tab.34.I). According to Geraads (2010) the best early representative of the extant *D. bicornis* is from Koobi Fora (Kenya), dated to ca. 2.5 Ma, while older forms were referred as *D. praecox* (Geraads, 2010).

The temporal and spatial distributions of rhinoceros species are poorly documented in some geographic areas such as Anatolia, Caucasus and the Near East, which played an important role in faunal exchanges within Eurasia and between Eurasia and Africa (Hooijer, 1958, 1961; Guérin, 1986; Guérin and Faure, 1988; Pandolfi and Erten, 2017; Pandolfi et al., 2017).

In the southern Levant, some Pleistocene sites include rhinoceros' species mainly from archaeological sites (Fig. 2). The first record was
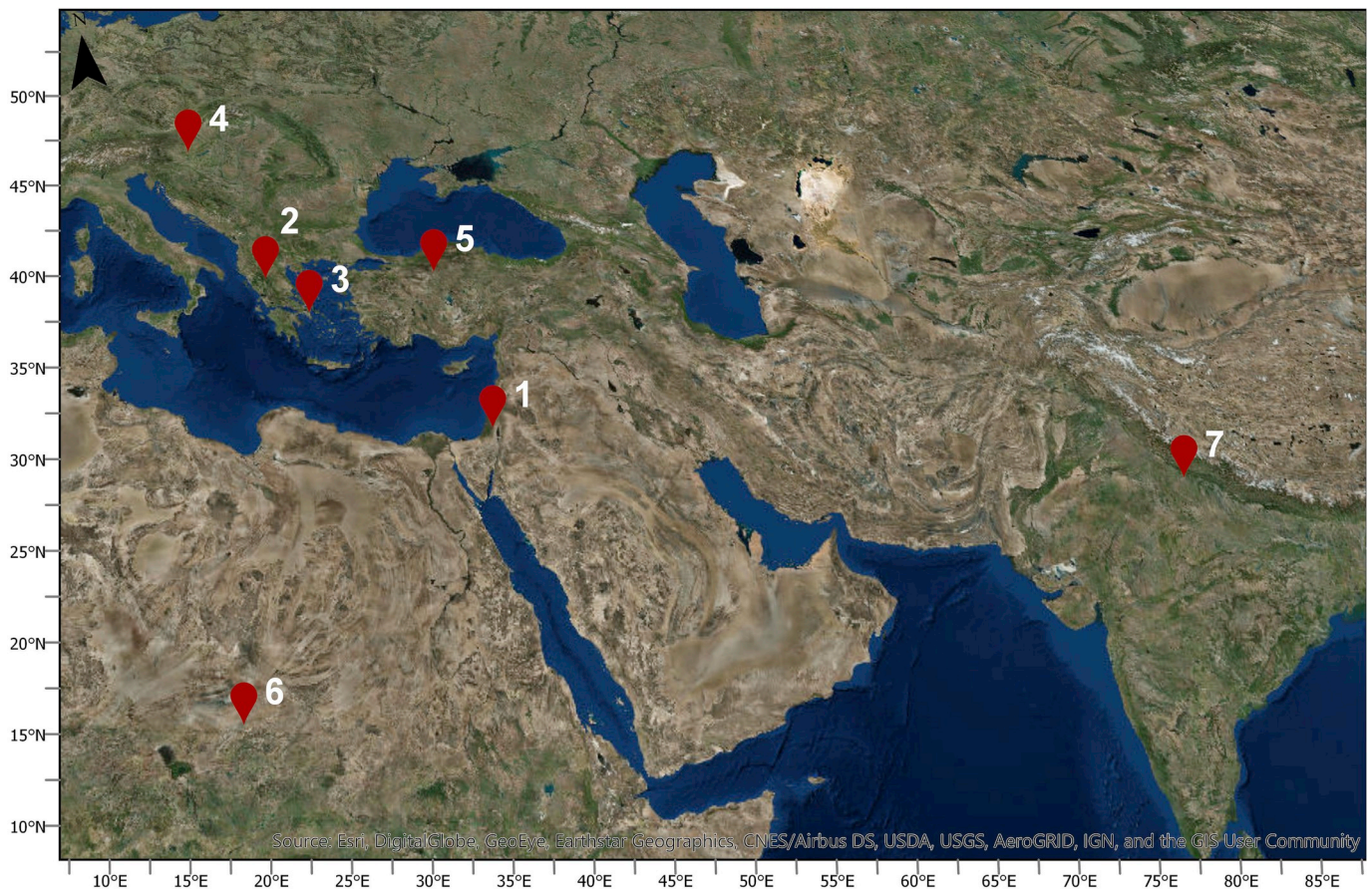
Fig. 2. Map showing selected localities mentioned in the text: 1. Bethlehem, Late Pliocene, Israel-Palestine; 2. Milia, Late Pliocene, Greece; 3.Pikermi, latest Miocene, Greece; 4. Kávás, latest Miocene, Hungary; 5. Çalta, Late Pliocene, Turkey; 6. Koro Toro 13, Late Pliocene, Chad; 7. Siwalik Formation, Late Pliocene-Early Pleistocene, Pakistan-India.

reported from the Early Miocene of the Negev (southern Israel), where scarce remains were assigned to ?*Dicerorhinus* sp. indet. (Tchernov et al., 1987). At Ubeidiya, Guérin (1986) recognised an evolved form of *S. etruscus*; the occurrence of this taxon has been confirmed by Pandolfi et al. (2017). Pleistocene rhinoceroses have been reported from at least 13 localities in the southern Levant; Guérin and Faure (1988) recorded the presence of *Dicerorhinus* cf. *mercki* (= *S.* cf. *kirchbergensis*?) at Oum Qatafa and Qafzeh and of *D. mercki* (= *S. kirchbergensis*?) at Ksar'akil. *Stephanorhinus hemitoechus* has been reported from Skhul, Naamé, Tabun C-D, but also from Dederiyeh Cave, Nadaouiyeh Aïn Askar, C-Spring, Ain Soda and Shishan Marsh (Griggo, 2004; Reynaud Savioz and Morel, 2005; Lister et al., 2013; Nowell et al., 2016) while *S.* cf. *hemitoechus* at Gesher Benot Ya'aqov and Geula (Guérin, 1980; Guérin and Faure, 1988; Guérin et al., 1993; Rabinovich and Biton, 2011). Other remains collected at Hayonim C, Kebara and Zuttiyeh have been assigned to an indeterminate dicerotine by Guérin and Faure (1988). Hooijer (1958) assigned several remains collected at Bethlehem to the Etruscan rhino; this attribution has been recently questioned by Pandolfi et al. (2017).

Here we re-describe rhinoceros fossil material from the locality of Bethlehem (Fig. 3) published by Hooijer (1958), recently referred to an age older than 3 Ma (see Rabinovich and Lister, 2017). The locality is situated in the 'Levantine corridor' (Figs. 2-3), which is famous for its central location in the faunal exchange between Eurasia and Africa, but is actually quite poor in Pliocene localities.

2. The Bethlehem site

The Bethlehem site is located at the Israel-Palestine water divide in

the city of Bethlehem on Senonian chalk, at the highest point of the town, ca. 790 m a.m.s.l. (Fig. 3). Several excavation seasons took place at the site, directed in 1935–1937 by Gardner and Bate (Bate, 1934, 1941; Gardner and Bate, 1937) and in 1940 by Stekelis, when most of the large bones were exposed (Stekelis, 1940; Shindler, 2005). The excavations extended to a depth of some 11 m below the land surface, but after the last season in 1940 the pit was filled, and is now within the urban center of Bethlehem. The faunal, flint and some sediment samples were shipped to the Natural History Museum in London where they remain conserved.

The bone beds of Bethlehem are unique in their faunal composition (Bate, 1934, 1941; Gardner and Bate, 1937; Hooijer, 1958; Rabinovich and Lister, 2017). Although numerous caves have been found in SW Samaria (some 50 km NW of Bethlehem) (Frumkin et al., 2015), none have yet revealed such a faunal composition.

Information about the excavations was assembled from the interim reports, photos, excavation drawings and geological sections kept at the NHM Library, British Museum, and Wellcome Trust Library (all in London), and the Israel Antiquity Authority Archive (IAA) and Stekelis Archive at the Institute of Archaeology, The Hebrew University of Jerusalem (Israel). Consequently, we could allocate most faunal elements in the bone beds (Table 1).

There is currently no absolute dating for the Bethlehem site, so the approximate age is based on the geological setting and the fauna. The composition of the fauna at Bethlehem is unique in the southern Levant. Compared with faunas from Europe and the Siwaliks, Bate (1934) and Hooijer (1958) considered it to indicate a Villafranchian age (Late Pliocene to Early Pleistocene; Rook and Martinez-Navarro, 2010). Recent study on the elephantid material suggested a date of ca.
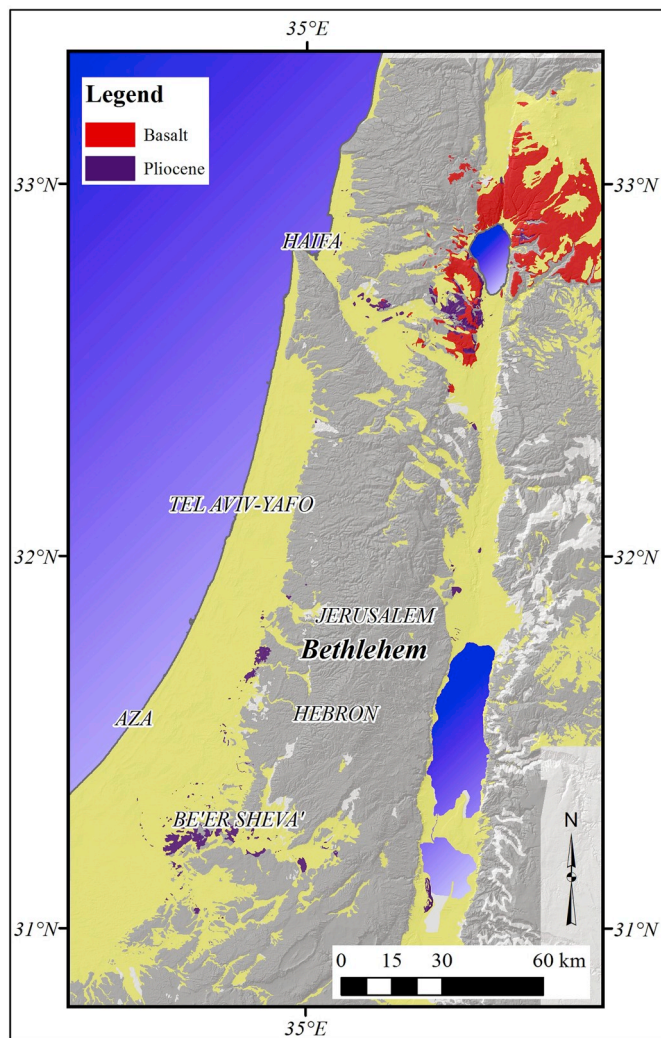
Fig. 3. Location map of the locality of Bethlehem.

Element	Elevation (m, MSL)	Square	No.	Year	Notes	Species
T (3 frag.)	ca.790			1934	M1 M18513	R. indet.
M				1935	M18564	R. indet.
P3			14	1937	M18577	*D.* sp.
P3-4*	ca. 782		20	1937	M18570	R. indet.
M1-2*	ca. 780		23	1937	M18563	*D.* sp.
M1				1937	M18562	*D.* sp.
T (1 frag.)		Dump		1937	M18572	R. indet.
m				1937	M18574	
t (2 frag.)	778	A1	12	1940	M18514	R. indet.
Skull	773	C2	34	1940	M18542	'*D.*' *bethlehemsis*
Mandible F	772	A2	43	1940	M18558	'*D.*' *bethlehemsis*
T (2 frag.)	771.5	B2	58	1940	M18549	R. indet.
T (1 frag.)					M18571	R. indet.

burial, when powerful sediment compaction crushed and distorted the bones, and was further damaged during exposure and excavation while wet and soft. Based on the interim reports, and the nature and scale of the damage in some cases, we can conclude that some of the deformation had occurred prior to excavation. Examples include flints embedded in tooth dentine, and the powerful compaction of the rhinoceros skull (M18542, *'Dihoplus' bethlehemsis* sp. nov.) found in the vicinity of the large elephantid remains, which was completely flattened into one dimension (Figs. 6–7).

We identified three rhinoceros taxa at Bethlehem, mainly due to the lack of identifiable characteristics. It is most plausible that only one species is represented, the newly identified species *'Dipholus' bethlehemsis*. For example the fragments of a maxillary teeth (M18570, M18563) might belong to the same specimen, though they were found at different depths (i.e. Table 1), and the skull (M19542) might be associated with the mandible fragment (M18558). It is worth noting that rhinoceroses occur along the entire sequence. As specified elsewhere (Rabinovich and Lister, 2017), the accumulation might have included several events or mass-movements of collapse, while the subsequent crushing and deformation of the bones was probably due to post-depositional sediment compaction.

The rhinoceros remains collected at Bethlehem are currently housed at NHMUK. The material includes a crushed skull (NHMUK M18542); a fragment of maxilla with M1 and M2 (NHMUK M18563); an isolated M1 (NHMUK M18562); a fragment of an upper premolar (NHMUK M18564); an ectoloph fragment of a P3 (NHMUK M18577); a fragment of mandible with m3 (NHMUK M18558); a fragment of maxilla with roots of upper premolars (NHMUK M18570); three fragments of upper teeth (NHMUK M18513); two fragments of upper teeth (NHMUK M18549); two fragments of lower teeth (NHMUK M18514); a fragment of an indeterminate tooth (NHMUK M18571) and a fragment of an upper tooth with the postfossette (NHMUK, 18572).

3.5–3.0 Ma, while an earlier age for the Bethlehem remains is plausible, if not currently certain (Rabinovich and Lister, 2017).

3. Material and methods

3.1. Material

The Bethlehem animal bones were in a poor state of preservation when exposed in the wet gravel, requiring extensive *in situ* treatment in addition to plastering before removal. A very thin solution of celluloid with acetone and amyl acetate was infiltrated into the bones (Stekelis, 1940; Shindler, 2005, p. 251).

In the bone-bearing beds of Bethlehem, Bate reported among other species the presence of *Rhinoceros*, stating that: 'The Bethlehem *Rhinoceros* has been compared with *R. etruscus*, since some of the upper cheek teeth appear to be similar; the height of the crown is, if anything, slightly shorter in the Palestine specimens' (Gardner and Bate, 1937, p. 431). Therefore, she assigned it to *Rhinoceros* cf. *etruscus*. Hooijer (1958) described the entire available Bethlehem fauna after Bate's tragic death, and assigned the remains to *Dicerorhinus etruscus*.

Based on the elephant remains, several scenarios were suggested for the accumulation of the bones at the pit: a natural trap, a fluviatile accumulation or a collapsed cave (Rabinovich and Lister, 2017). Unfortunately, the limited rhinoceros elements, mainly teeth, do not contribute much to the debate. The faunal material suffered after

3.2. Methods

The examined specimens were morphologically compared with the rhinocerotid material collected from several latest Miocene, Pliocene and Early Pleistocene localities from Eurasia and Africa (Table S1). The

comparisons were based on direct observations of the material housed in several institutions and museums as well as on published data (Table S1). The classification above genus level follows Antoine et al. (2010). The dental terminology and the morphometric methodology follow Antoine (2002) and Guérin (1980), respectively. The studied specimens were measured using a digital caliper.

Tooth microwear patterns were analysed on two upper teeth (a M1 and a fragment of premolar) using the light stereomicroscope technique established by Solounias and Semprebon (2002). Sample size is small (N = 2) but the microwear will provide an approximation of the diet. The microwear was quantified through direct observation at a magnification of 35x on a 0.16 mm^2 area. The numbers of pits (NP) and scratches (NS) were quantified in two areas of the occlusal surface and then averaged. Other variables were qualitatively scored: presence/absence of large pits (LP), gouges (G) i.e., circular features with irregular shape, cross scratches (XS) i.e., scratches oriented differently than the majority of scratches, and hyper-coarse scratches (HC) i.e., very large scratches, and puncture pits (PP). The width of the scratches was assessed through the Scratch Width Score (SWS) where 0 correspond to fine scratches, 1 to mix of fine and coarse, and 2 to coarse scratches.

Institutional Abbreviations - **HNHM**, Hungarian Natural History Museum, Budapest, Hungary; **IGF**, Museo di Storia Naturale, sezione di Geologia e Paleontologia, Florence, Italy; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; **MNCN**, Museo Nacional de Ciencias Naturales, Madrid, Spain; **MNHN**, Musèum National d'Histoire Naturelle, Paris, France; **NHMUK**, Natural History Museum, London, England; **NMB**, Naturhistorisches Museum, Basel, Switzerland.

Anatomical Abbreviations- **L**, length; **M/m**, upper/lower molar; **P/p,** upper/lower premolar.

4. Systematic paleontology

Order Perissodactyla Owen, 1848.
Family Rhinocerotidae Gray, 1821.
Subfamily Rhinocerotinae Gray, 1821.
Tribe Rhinocerotini Gray, 1821.

4.1. RHINOCEROTINI indet

Referred material - NHMUK M18564, NHMUK M18513, NHMUK M18549, NHMUK M18514, NHMUK M18571, NHMUK 18572, NHMUK M18558.

Description and comparison - NHMUK M18564, fragment of an upper premolar (Fig. 4A). The protocone is large and anteriorly constricted. A mesial cingulum is present and a reduced lingual cingulum occurs at the entrance of the medisinus, which is very narrow. Internal folds are not observable.

NHMUK M18513, three fragments of upper teeth (Fig. 4B).
NHMUK M18549, two fragments of upper teeth (Fig. 4C).
NHMUK M18514, two fragments of lower teeth (Fig. 4D).
NHMUK M18571, a fragment of tooth (Fig. 4E).
NHMUK 18572, a fragment of an upper tooth with the medifossette (Fig. 4F).

The listed specimens do not display useful morphological characters for a detailed taxonomic attribution. The few characters described for NHMUK M18564 are observable in different Pliocene and Early Pleistocene species.

NHMUK M18558, fragment of mandible with m3 (Fig. 5). The specimen is badly preserved. The ventral border of the horizontal ramus is rather straight below m3. The posterior lingual valley on m3 is broad V-shaped.

The few characters described for NHMUK M18558 are observable in several Pliocene and Early Pleistocene species. Broad V-shaped lingual valleys are present on the m3 of *'S.' miguelcrusafonti*.
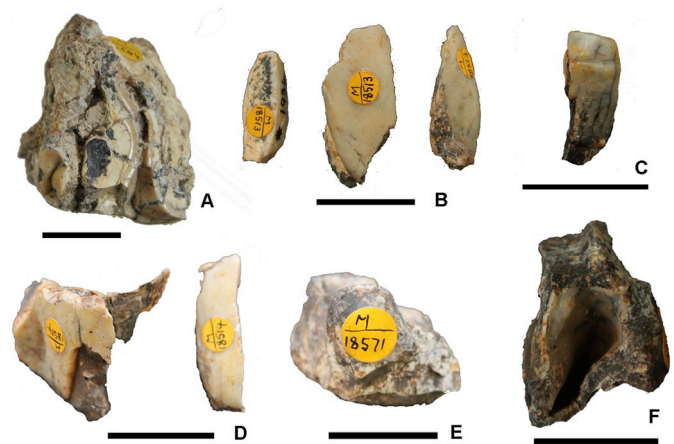

Fig. 4. Rhinocerotini indet. from Bethlehem. A, NHMUK M18564, fragment of an upper premolar in occlusal view; B, NHMUK M18513, three fragments of upper teeth; C, NHMUK M18549, one of the two fragments of upper teeth in lingual view; D, NHMUK M18514, two fragments of lower teeth; E, NHMUK M18571, a fragment of tooth; F, NHMUK 18572, a fragment of an upper tooth with the medifossette in occlusal view. Scale bar equals 2 cm.

Fig. 5. Rhinocerotini indet. from Bethlehem. NHMUK M18558, fragment of mandible with m3 in buccal (A) and lingual (B) view. Scale bar equals 2 cm.

4.2. Subtribe RHINOCEROTINA Gray (1821)

Genus *Dihoplus* Brandt, 1878.

Type species - *Rhinoceros schleiermacheri* Kaup (1832) from the Late Miocene of Eppelsheim, Germany (Kaup, 1832: tab. X, Fig. 1; Giaourtsakis and Heissig, 2004: Fig. 1.4).

Other species – *'Dihoplus' megarhinus* (de Christol, 1834), *D. pikermiensis* (Toula, 1906). *Dihoplus ringstroemi* (Arambourg, 1959) is considered a junior synonym of *'D.' megarhinus* by Pandolfi et al. (2015).

Dihoplus sp.

Referred material - NHMUK M18563, NHMUK M18570, NHMUK M18562, NHMUK M18577.
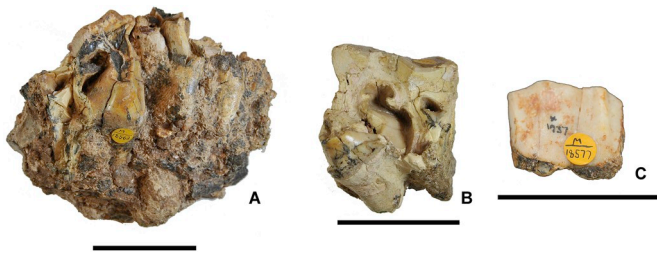
Fig. 6. *Dihoplus* sp. from Bethlehem. A, NHMUK M18563, fragment of maxillae with M1 and M2, occlusal-lingual view; B, NHMUK M18562, isolated M1 in occlusal view; C, NHMUK M18577, ectoloph fragment of a P3 in buccal view. Scale bar equals 2 cm.
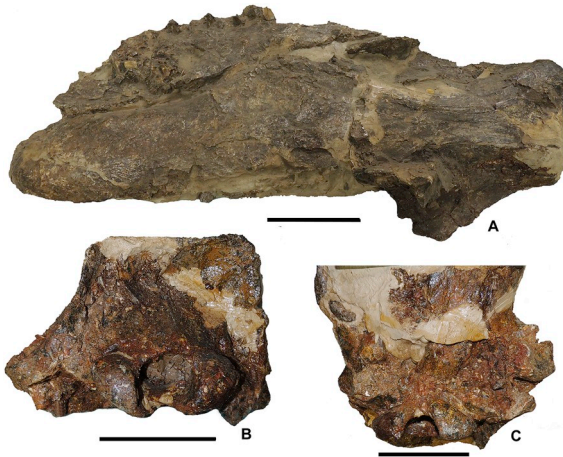

Fig. 7. *'Dihoplus' bethlehemsis*sp. nov. from Bethlehem. NHMUK M18542, crushed skull in dorsal (A), occipital (B) and basal-occipital (C) views. Scale bar equals 5 cm.

Description and comparison - NHMUK M18563 (Fig. 6A), is a fragment of maxillae with M1 and M2. M1 only preserves a distal portion of the tooth with a mesio-distally elongated postfossette. M2 displays a mesial cingulum, a slightly constricted protocone, a large and single crochet, a well-developed parastyle, a narrow parastyle fold, a narrow and prominent paracone fold. The postfossette is circular.

In comparison to the studied M2s of *S. etruscus* (Table S1), the M2 of NHMUK M18563, has a less prominent paracone fold and a faint parastyle fold. The specimen morphologically resembles the M2s of *D. pikermiensis* and *'D.' megarhinus*.

NHMUK M18570, fragment of maxilla with roots of upper premolars, possibly same specimen of M18563.

NHMUK M18562 is an isolated M1 (Fig. 6B). The tooth displays a very large protocone and a wide protoloph; the metaloph is narrow and shorter than the protoloph, the hypocone (even if slightly damaged) is much smaller than the protocone. A small antecrochet, a small crochet and a faint crista are present. The postfossette is mesio-distally elongated. The parastyle and the paracone fold are not preserved, the mesostyle is very faint and the posterior profile of the ectoloph is slightly concave. A mesial cingulum seems to be present.

Crista and antecrochet are absent on the M1s of *S. jeanvireti* and *'S.' miguelcrusafonti* (Guérin, 1980) as well as on *S. yunchuchenensis*, *C. thibetana* and *C. nihowanensis* (Chow, 1963; Deng, 2008; Deng et al., 2011). In *S. etruscus* the crista is generally absent whilst the antecrochet is rare (Guérin, 1980). Lacombat (2006) mentions that the antecrochet is absent and the crista is rare on M1s of *S. etruscus* (the author studied a few specimens from Senèze and Upper Valdarno but he did not specify from which site or specimens he observed those characters). Antecrochet and crista have been never observed on the sample of *S. etruscus* studied by one of us (LP; see Table S1).

The crista is usually present on M1s of *'D.' megarhinus* whilst the antecrochet is rare (Guérin, 1980); this species also displays a faint mesostyle. These features (crista, antecrochet and faint mesostyle) occur on M1s of *D. pikermiensis* (e.g., right M1 NHMUK M10142).

NHMUK M18577 is an ectoloph fragment of a P3 (Fig. 6C). The enamel is rough; in occlusal view the parastyle fold is marked, the paracone fold is prominent, the mesostyle is very faint and the metacone fold is present.

The profile of the ectoloph resembles the P3s of *D. pikermiensis* (e.g., NHMUK M10144). The described features have been never observed in *S. jeanvireti*, *S. etruscus* and *S. yunchuchenensis* (Chow, 1963; Guérin, 1980). The P3s of *'S.' miguelcrusafonti* and *'D.' megarhinus* display a more convex ectoloph with a faint metacone fold (Guérin, 1980). *Coelodonta thibetana* and *C. nihowanensis* display a wavy ectoloph profile (Deng, 2008; Deng et al., 2011).

4.3. 'Dihoplus' bethlehemsis sp. nov

Holotype - NHMUK M18542 (Figs. 7-8), a crushed skull housed at the Natural History Museum of London, United Kingdom.

Type Locality and Horizon - From the site of Bethlehem, located at the Israel-Palestine water divide, in the city of Bethlehem on Sennonian chalk, probably Late Pliocene; no younger than 3 Ma according to Rabinovich and Lister (2017).

Etymology - After the name of the city of Bethlehem, the Nativity locality.

Diagnosis - Medium sized two horned rhinoceros, characterized by: absence of ossified nasal septum; long and narrow nasal bones; straight posterior border of the nuchal crest; foramen infraorbitalis behind the nasal notch; external auditory pseudomeatus fully closed; occipital face squared; closed medifossette and rough enamel on all the upper teeth; P2 with protocone and hypocone lingually separated and of the same size; P3 and P4 with a reduced lingual cingulum, metacone fold and metaloph constriction.

The species displays some common features of the genus *Dihoplus* (e.g., absence of ossified nasal septum, absence of P1). It differs from *D. pikermiensis* by having a more posterior position of the nasal notch; from *'D.' megarhinus* by having both protocone and hypocone of the same size on P2 and from both *D. pikermiensis* and *'D.' megarhinus* by having a straight posterior profile of the nuchal crest in dorsal view, a lower occipital face and a closed medifossetta on the upper teeth. *'Dihoplus' bethlehemsis* differs from the Miocene *D. schleiermacheri* by lacking the upper incisors, by lacking the DP1, by having a more posterior position of the nasal notch and a closed medifossetta on the upper teeth.

Description - NHMUK M18542: A skull of a medium-size rhinoceros was found at the site of Bethlehem. The skull was found crushed and teeth penetrated through, flints are embedded in the bone. The entire
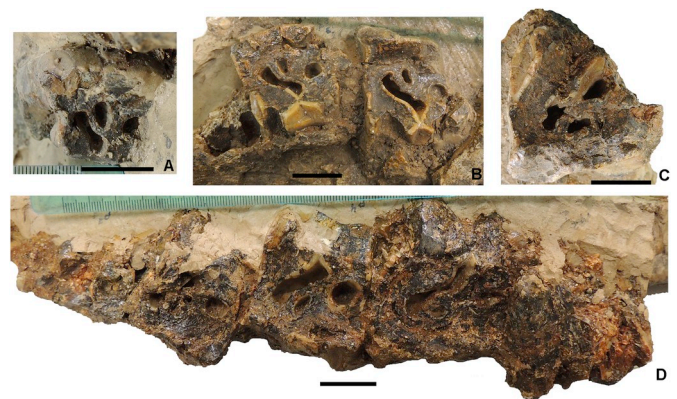

Fig. 8. *'Dihoplus' bethlehemsis* sp. nov. from Bethlehem. NHMUK M18542, upper teeth associated with the skull in occlusal view. A, left P2; B, left P3–P4; C, right M2; D, right P3-M1. Scale bar equals 2 cm.

Table 2
Resumed table of selected distinguished characters between *'Dihoplus' bethlehemsis* and several Rhinocerotidae species.

Taxon	Nasal bones: rostral end	Nasal bones: fusion	Nasal septum: ossification	Nasal rostral end/praemaxilla	Frontal: post-orbital process	External auditory pseudomeatus	Occipital side	Nuchal crest: posterior profile	P1 in adults	P2: protocone and hypocone	P2: protoloph and ectoloph	Medifossette on premolars	Medifossette on molars	Lingual cingulum: premolars
'Dihoplus' bethlehemsis	large	fused	never	separated	present	closed	vertical	straight	absent	weakly joined	weakly joined	present	present	present and reduced
Ceratotherium simum	very large	anteriorly separated	never	separated	absent	opened	inclined	forked	absent	lingually joined	joined	present	present	usually absent and reduced
Diceros bicornis	very large	anteriorly separated	never	separated	absent	opened	vertical	straight	sometimes present	separated	joined	present	usually absent	present and continuous
Rhinoceros sondaicus	large	anteriorly separated	sometimes present but incomplete	separated	present	closed	inclined	straight	sometimes present	separated	joined	usually absent	absent	present and reduced
Rhinoceros unicornis	large	anteriorly separated	sometimes present but incomplete	separated	present	closed	inclined	concave	sometimes present	separated	joined	absent	present	absent
Dicerorhinus sumatrensis	large	anteriorly separated	sometimes present but incomplete	separated	present	opened	inclined	concave	sometimes present	separated	joined	usually absent	absent	usually present and reduced
Dihoplus pikermiensis	large	fused	never	separated	present	closed	inclined	concave	absent	joined	separated	rare	rare	usually present and reduced
'Dihoplus' megarhinus	large	fused	never	separated	present	closed	vertical	concave	absent	joined	separated	rare	rare	usually absent and reduced
'Stephanorhinus' miguelcrusafonti	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO	absent	absent	present and continuous
Stephanorhinus jeanvireti	large	fused	always present	joined	present	closed	inclined	concave	absent	separated	joined	rare	rare	present and continuous
Stephanorhinus yunchuchenensis	very large	fused	always present	joined	present	closed	vertical	NO	absent	separated	joined	absent	absent	absent
Stephanorhinus lantianensis	narrow	fused	always present	joined	present	closed	vertical	concave	NO	NO	NO	NO	NO	NO
Stephanorhinus etruscus	large	fused	always present	joined	present	closed	vertical	concave	absent	separated	separated	rare	rare	usually absent and reduced
Coelodonta sp.	very large	fused	always present	joined	present	closed	inclined	straight	sometimes present	separated	joined	present	present	usually absent and reduced

skull was covered with glue (details in Bate records) and its base by cement (Stekelis, 1940; Hooijer, 1958).

In dorsal view (Fig. 7A), the nasals are long and fused, they display a slight rugosity which indicates the presence of a small nasal horn. A slight rugosity also occurs on the frontals. The frontal-parietal crests are separated. The orbits are not projected. The posterior border of the nuchal crest is straight. The foramen infraorbitalis is behind the nasal notch, at the level of the anterior border of P4. The anterior border of the orbit is at the level of the anterior border of M2. The processus post-tympanicus is fused with the post-glenoid process and the external auditory pseudomeatus is fully closed. The dorsal profile of the skull was probably rather flat. The post-orbital process is absent on the zygomatic arch. A small post-orbital process occurs on the frontal bone (Fig. 7A). The absence of the ossified nasal septum reported by Hooijer (1958) is confirmed here.

In occipital face view (Fig. 7B), the occipital face is slightly deformed and it appears squared in shape. In this view (Fig. 7B), the processus post-tympanicus and the processus paraoccipitalis are separated and both are well developed. The nuchal tubercle is little developed. The foramen magnum is circular.

The basal portion of the specimen is covered by cement, except for its neurocranial portion. The post-glenoid apophysis is latero-medially flat (Fig. 7C). The sagittal crest on the basilar process seems to be present.

The maxillae are shifted in respect to their original position and are placed on the right side of the skull (Fig. 7A). All the upper teeth display a closed medifossette and the preserved enamel is rather rough (Fig. 8). The left P2 (Fig. 8A) has a rather straight ectoloph profile, a subcircular postfossette, a straight and partially constricted protoloph, a transverse metaloph, protocone and hypocone, of the same size and weakly joined lingually.

The left P3 and P4 (Fig. 8B–D) display evidences of a lingual cingulum located at the entrance of the medisinus. The protocone and hypocone are weakly joined. The postfossette is circular. P3 also displays a mesial cingulum. The ectoloph is damaged on both the premolars but on P3 it shows a faint mesostyle and a portion of a metacone fold.

The lingual and vestibular sides of the right P3 and P4 are badly preserved. Both the premolars display a closed medifossette (double on P3) and a circular postfossette. The metaloph is also constricted as on the left premolars.

On M1 (Fig. 8C and D) the protoloph bends lingual-distally, the protocone is relatively close to the hypocone and a faint mesostyle is present. M2 (Fig. 8C) displays a mesial cingulum, a slightly anteriorly constricted protocone, a very small antecrochet, and a crochet and crista that are very close to each other, just forming a medifossette.

5. Comparison between *'Dihoplus' bethlehemsis* and Eurasian and African Plio-Pleistocene Rhinocerotidae

5.1. Comparison with *Ceratotherium* and *Diceros*

The Plio-Pleistocene species assigned to *Ceratotherium* (e.g., *C. mauritanicum*, *C. simum*) are characterized by hypsodont teeth with more complex enamel folding than in *'D.' bethlehemsis*, a longer skull with an inclined occipital face in lateral view, a higher occipital face, shorter nasal bones laterally expanded and anteriorly separated compared to *'D.' bethlehemsis* (cf. Pomel, 1888, 1895; Geraads, 2005, 2010; Table S1). In *Diceros* (e.g., *D. praecox*, *D. bicornis*) the dorsal profile of the skull is much more concave than in *'D.' bethlehemsis*, the orbits are more anteriorly placed and close to the nasal notch, the nasals are shorter; the upper teeth of *Diceros* lack the medifossette and the crista is absent (Hooijer and Patterson, 1972: Fig. 10B; Table 2, Table S1).

5.2. Comparison with *Rhinoceros*

The species of the genus *Rhinoceros* (Table 2, Table S1) differ from *'D.' bethlehemsis* by having shorter and curved nasals and a more concave dorsal profile of the skull (even if distorted in *'D.' bethlehemsis* it was not so concave as in the *Rhinoceros* species). In *R. unicornis*, *R. sondaicus* and *R. sivalensis* the occipital face is anteriorly inclined in lateral view. The upper teeth of *R. sondaicus* and *R. sivalensis* generally differ from *'D.' bethlehemsis* by having protocone and hypocone well separated on the premolars, by lacking lingual cingulum, crista and medifossette. *R. unicornis* and *R. platyrhinus* display more hypsodont teeth.

5.3. Comparison with *Dicerorhinus*

Contrary to *'D.' bethlehemsis*, the Plio-Pleistocene species securely attributed to *Dicerorhinus* (Table 2, Table S1) are characterized by the presence of a single crochet on the molars, sometimes by a small crochet on the premolars and the presence of separated protocone and hypocone on the premolars. In comparison to *'D.' bethlehemsis*, the occipital face in *Dicerorhinus* is proportionally higher than wider and the nuchal crest, in occipital face view, is less laterally expanded.

5.4. Comparison with *Dihoplus pikermiensis*

In the Pliocene of Europe, the absence of the ossified nasal septum is a typical character of species belonging to the genus *Dihoplus* (Table 2, Table S1). The skulls of *D. pikermiensis* differ from that of *'D.' bethlehemsis* by having the rear border of the nasal notch at the level of P2 or P2–P3 boundary, a concave posterior profile of the nuchal crest in dorsal view and by a higher occipital face compared to *'D.' bethlehemsis*. In dorsal view, the nasal bones of *D. pikermiensis* resemble those of *'D.' bethlehemsis*. Only one skull of *D. pikermiensis* (NHMW, 2009z-0085-0001) shows a larger insertion for the nasal horn in respect to *'D.' bethlehemsis*. The angle between the dorsal and anterior surfaces of the nasals is more obtuse in *D. pikermiensis* than in *'D.' bethlehemsis*.

The upper teeth of the type skull of *D. pikermiensis* display a lingual cingulum on the premolars, well-evident at the base of the protocone as well as on some other skulls of *D. pikermiensis*, while in *'D.' bethlehemsis* the lingual cingulum is less developed (Fig. S1). In *D. pikermiensis*, the postfossette on the premolars is generally wider, and opened posteriorly in comparison to *'D.' bethlehemsis*. Contrary to *'D.' bethlehemsis*, premolars and molars in *D. pikermiensis* usually have an opened medifossette. Closed medifossettes are rare indeed and occur on only one or two teeth.

5.5. Comparison with *'Dihoplus' megarhinus*

The ossified nasal septum is absent in *'D.' megarhinus* (Table 2, Table S1). The morphology of the nasal bones of *'D.' bethlehemsis* resembles that of *'D.' megarhinus* from Palaia (Pliocene, Italy) except for the angle between the dorsal and anterior borders of the nasals, which is more acute in the studied specimen. In the skull from Lens Lestang (Pliocene, France: NMB FP16), the rear border of the nasal notch is at the level of P4 as in *'D.' bethlehemsis*, but the posterior profile of the nuchal crest is concave and the occipital face is higher and subtrapezoidal in shape, as in the specimen from Saint-Laurent (Pliocene, France), Montpellier (Pliocene, France) and Kávás (latest Miocene, Hungary). The lingual cingulum is absent on the premolars of *'D.' megarhinus* from China (Ringström, 1924: Figs. 1–2; Deng, 2006: Fig. 3), Saint-Laurent (Guérin et al., 1969: 111) and Kávás (Pandolfi et al., 2015), and reduced on the premolars from Lens Lestang (Fig. S1). The presence of the lingual cingulum on the upper premolars is a variable character on the specimens from Montpellier (Guérin et al., 1969:112). The P2 protocone is less developed than the hypocone in *'D.' megarhinus* in comparison to the Bethlehem skull. Guérin (1980) reported several observations of

closed medifossette on premolars and molars of *'D.' megarhinus* from the Pliocene of Western Europe. Most of the measurable characters of *'D.' bethlehemsis* are smaller than those of *'D.' megarhinus* (Table S2).

5.6. Comparison with 'Stephanorhinus' miguelcrusafonti

Compared with the studied specimen, the M2 of *'S.' miguelcrusafonti* from Layna (Pliocene, Spain) displays well-developed crochet and crista, which are rather close to each other, forming a semi-closed medifossetta whilst the M1 displays a single crochet (Table 2, Table S1). Contrary to the P3 of *'D.' bethlehemsis*, the P3 of *'S.' miguelcrusafonti* is characterized by the presence of double crochet and crista and a wide postfossette with several internal folds.

5.7. Comparison with Stephanorhinus jeanvireti

Compared with *'D.' bethlehemsis*, the skull of *S. jeanvireti* displays a concave posterior border of the nuchal crest in dorsal view (Table 2, Table S1). In *S. jeanvireti* the nasals are larger than in *'D.' bethlehemsis*, and have a partially ossified nasal septum. Contrary to *'D.' bethlehemsis*, *S. jeanvireti* displays a continuous lingual cingulum on the premolars, a rare medifossette on P2 and P3 and absence of medifossette on M1 and M2 (Guérin, 1972, 1980). The dimensions of *'D.' bethlehemsis* are smaller than those of *S. jeanvireti,* except for the width of the occiput (Table S2).

5.8. Comparison with Stephanorhinus yunchuchenensis

The skull of *S. yunchuchenensis* (IVPP V2879) differs from Bethlehem by being more massive and by having very broad nasal bone and a partially ossified nasal septum (Table 2, Table S1). In addition, on the skull IVPP V2879 the rear border of the nasal notch is at the level of P3–P4 boundary and a semi-closed medifossette occurs on M1s and the right M2. *'D.' bethlehemsis* is a little bit smaller than *S. yunchuchenensis* (Table S2).

5.9. Comparison with Stephanorhinus lantianensis

The skull of *S. lantianensis* (IVPP V5413) differs from *'D.' bethlehemsis* by having shorter nasal bones, a partially ossified nasal septum, a concave posterior border of the nuchal crest and parallel metalophs and protolophs on P3-M3 (Table 2, Table S1).

5.10. Comparison with Stephanorhinus etruscus

According to Hooijer (1958) the morphological and morphometric characters of the skull (including the teeth) closely resembles those of *Dicerorhinus etruscus* except for the absence of the nasal septum.

The position of the foramen infraorbitalis and the rear border of the nasal notch are similar to that observed in *S. etruscus* (respectively at the level of P4 or P3–P4 boundary). The posterior border of the nuchal crest is slightly concave in *S. etruscus*, but rather straight in the studied specimen. The studied specimen is rather squared similar to that observed on *S. etruscus* from Upper Valdarno (Early Pleistocene, Italy; IGF756). The dimensions of the Bethlehem skull fall within the range of *S. etruscus* given by Guérin (1980) (Table S2).

In *S. etruscus* the nasal bones, in lateral view, are longer, and projected anteriorly and downwards compared to the studied specimen. The angle between the dorsal and anterior borders of the nasals is more acute in the studied specimen than in *S. etruscus*. In addition, in dorsal view, the nasals in *S. etruscus* are wider compared to those of the studied specimen and the rugosity for the nasal horn is much more marked. The nasal septum (or trace of it) is completely absent on the skull NHMUK M18542 whilst it is present in the skulls of *S. etruscus* from Upper Valdarno and several other from Senèze (e.g., NMB Se1703). Two skulls collected at Senèze and usually referred as *S.*

etruscus (NMB Se548 and Se1758) lack the partially ossified nasal septum. Nevertheless, these skulls are quite different from the material collected from the type locality of Upper Valdarno. The nuchal crest, in lateral view, is much more posteriorly projected in Se548 and Se1758 with respect to the skulls from Upper Valdarno and the skulls NMB Se566, Se743, Se1703, Se1706, MNHN 1923–4, 1970–75 from Senèze. According to Thenius (1955), skulls without nasal septum could be associated with female specimens. Nevertheless, the skull NMB Se548 displays a larger insertion for the nasal horn (usually indicates a male character) compared to Se1758 and a nasal septum has been observed in all the complete skulls belonging to the Eurasian Pleistocene *Stephanorhinus* studied (see Table S2 in Pandolfi and Maiorino, 2016), except on the two above mentioned skulls and the specimen from Bethlehem. A juvenile skull from Senèze (MNHN, 1922–15) also lacks of the ossified nasal septum. A detailed revision of the material from Senèze is beyond the scope of this paper but is, obviously, required.

According to Hooijer (1958) the particular morphological characters of the teeth pointing to *S. etruscus* (=*Dicerorhinus etruscus* in Hooijer, 1958) at Bethlehem, in particular were: the small or absent crown cement, the high and wide entrance of the medisinus, the prominent and slightly upwardly inclined anterior cingulum and the P3 lingual cingulum. The presence of a medifossette on all the teeth was considered by Hooijer (1958) as an individual peculiarity that is apparently rare in *S. etruscus*.

The morphology of the upper teeth of *'D.' bethlehemsis* is unusual for Pliocene and Early Pleistocene *Stephanorhinus*. The observed specimens of *S. etruscus* from Senèze (Table 2, Table S1) lack closed medifossette on premolars and molars and the postfossette is rather elliptical in shape; the lingual cingulum is missing (Fig. S1). The observed specimens usually display a single crochet or lack of internal folds. Sometimes a faint lingual cingulum is present. The upper teeth of the skull NMB Se548 display crista, double crista, crochet and double crochet; M1 and M2 also have an antecrochet. A well-developed lingual cingulum is observable on the premolars of the specimen NMB VAnc from Upper Valdarno. P2 has an isolated protocone and a closed medifossette whilst P3 and P4 have faint and undistinguished internal folds on the rear side of the medisinus. M1 display a single antecrochet. Isolated protocone on P2, lingual cingulum on the premolars and opened medifossette or complicated internal folds are observable on specimen NMB VA953 (Fig. S1). Other specimens from Upper Valdarno do not display a closed medifossette on the upper teeth and the lingual cingulum is usually absent or faint on the premolars. In a few cases, Guérin (1980) mentioned the occurrence of a closed medifossette on the premolars and on rare cases on the molars, but they never occur on the same specimen. According to Guérin (1980) the lingual cingulum on P3 is generally present and sometimes (12 cases on 18) is more noticeable. According to Lacombat (2006), the medifossette is always open on the premolars and M1 of *S. etruscus*.

The overall morphology of the NHMUK M18542 teeth does not correspond to the *S. etruscus* teeth.

5.11. Comparison with Coelodonta thibetana

Coelodonta thibetana differs from *'D.' bethlehemsis* by having a partially ossified nasal septum, very broad nasals and the anterior border of the orbit above the M2-M3 boundary (Table 2, Table S1). In addition, in basi-occipital view, the post-glenoid apophysis is a dihedron in cross section. A closed or semi-closed medifossette occurs on the premolars and the right M2 of *C. thibetana* and the protocone and hypocone are well-joined on P3 and P4. The dimensions of *'D.' bethlehemsis* are smaller than *C. thibetana* (Table S2).

5.12. Comparison with Coelodonta nihowanensis

The skull of *C. nihowanensis* (Deng, 2002: Fig. 2), unlike *'D.' bethlehemsis*, is characterized by a well-ossified nasal septum, broad nasal

Table 3
Raw microwear data. Average numbers of pits (NP) and scratches (NS), scratch width score (SWS) and presence/absence of large pits (LP), gouges (G), cross scratches (XS), hyper-coarse scratches (HC), puncture pits (PP).

Specimen #	NP	NS	SWS	LP	XS	G	HC	PP
M18562	23.5	13.5	0	0	1	0	0	0
M18564	26	13	1	0	1	0	0	0

bones and a well-developed nuchal crest (Table 2, Table S1). The upper teeth are similar to those of *C. thibetana* but also display a firmly closed medifossette on M1. *'Dihoplus' bethlehemsis* is dimensionally smaller than *C. nihowanensis* (Table S2).

6. Tooth microwear analysis

The microscopic observation revealed that the enamel of the occlusal surface is well preserved and the two teeth (specimens NHMUK M18562 and NHMUK M18564) are suitable for the quantitative microwear analysis.

The low numbers of scratches, moderate number of pits, as well as the presence of cross-scratches place these two specimens within the confidence ellipse for the extant leaf browsers (Table 3; Fig. 9). The two specimens, assigned to *Dihoplus* sp. and Rhinocerotini indet., recorded similar microwear patterns which suggest that their diet was very similar. This result is supporting the hypothesis that a single species is present at Bethlehem. The absence of large pits, hyper-coarse scratches, gouges, and puncture pits permit to discard the consumption of fruits and seeds, as well that of bark or twigs. The diet of these two individuals at the time of death was probably composed of leaves of trees, bushes, or part of dicots.

7. Discussion

The faunal assemblage of Bethlehem was previously considered of Villafranchian age; Rabinovich and Lister (2017) suggested an age older

than ca. 3.0 Ma, therefore ascribable to the earliest Villafranchian or at least to Ruscinian age (MN 16 to MN 14). The morphological features of *'D.' bethlehemsis* and the geographical and chronological assessment of Pliocene rhinocerotines in Eurasia would confirm a Pliocene age for this locality.

Dihoplus and *Stephanorhinus* have been never recorded from the same locality; and the latter genus seems to replace the first one during the Late Pliocene (Fig. 1).

The latest representative of the genus *Dihoplus* in Eurasia was the large-sized *'D.' megarhinus* which last occurred in Europe during the Late Pliocene (MN14 and MN15) (Guérin, 1980; Pandolfi, 2013; Pandolfi et al., 2015, 2016), in Anatolia during the second half of the Pliocene (Çalta, MN15: Guérin and Sen, 1998) and in Russia during the latest Pliocene (MN15-MN16a; Fukuchi et al., 2009).

The earliest representative of the genus *Stephanorhinus* could be the Early Pliocene *'Stephanorhinus' miguelcrusafonti*, although cranial remains of this species are unknown. This species, as mentioned above, occurred in a few localities of Western Europe. Cerdeño (1992) raised some doubts on the validity of this taxon, suggesting that a better knowledge of *'S.' miguelcrusafonti*, and possibly additional and well-preserved material, could lead to its confirmation as different species or as *'D.' megarhinus*. Two Late Pliocene *Stephanorhinus* species from Europe are known, *S. jeanvireti* and *S. etruscus*. The first one retained only a few plesiomorphic features, such as the presence of upper and lower incisors (Guérin and Tsoukala, 2013); the teeth of *S. jeanvireti* differ from those of *'S.' miguelcrusafonti*, which are characterized by several enamel folds. Both *S. jeanvireti* and *S. etruscus* display a partially ossified nasal septum and a relatively less evolved morphology of the upper teeth (e.g., simple crochet; usually absence of crista; medifossette rare or absent) in respect to *'D.' bethlehemsis*. *'Dihoplus' bethlehemsis* most probably represents an evolved *Dihoplus*. The new species retained plesiomorphic features such as the lack of ossification of the nasal septum, long and straight nasal bones, protoloph partially separated from the ectoloph on P2, protocone and hypocone joined on the premolars, presence of a lingual cingulum on P3 and P4, presence of a metacone fold on the premolars, which resemble some specimens of
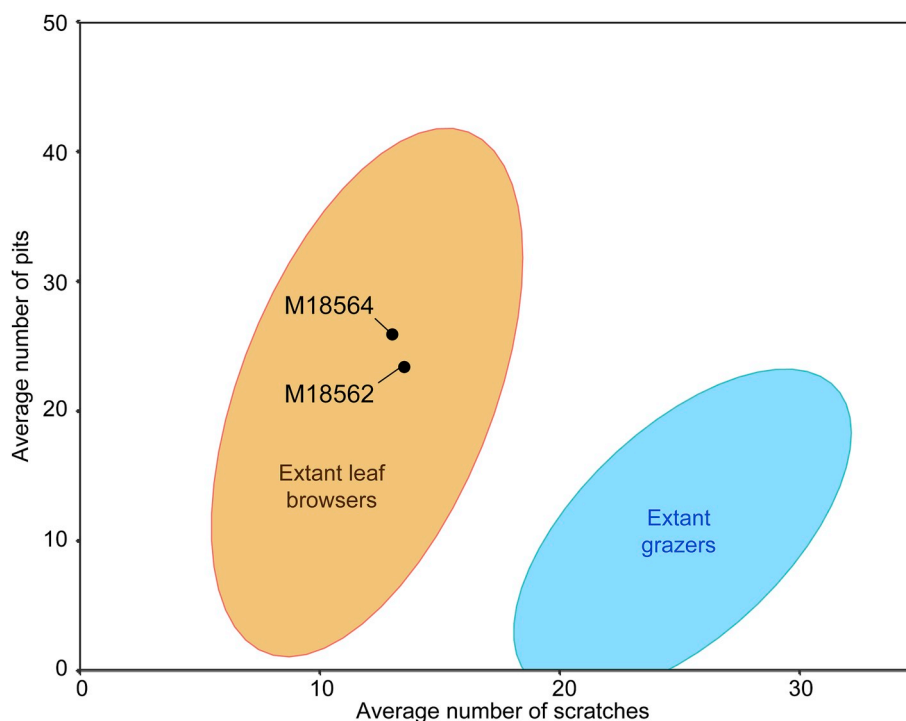

Fig. 9. Bivariate plot of the average numbers of pits and scratches. Coloured areas correspond to the Gaussian confidence ellipses ($p = 0.95$) on the centroid for the extant leaf browsers and grazers from Solounias and Semprebon (2002) and Rivals et al. (2010).

Dihoplus rather than *Stephanorhinus*. On the other hand, the combination of plesiomorphic and peculiar characters (e.g., morphology of the occipital face, presence of medifossette on all the teeth) enabled identification of the Bethlehem rhino as a new and different species.

At present, it is not possible to verify the occurrence of this new taxon in other areas, such as in northern Africa. A Pliocene rhinoceros collected from Lake Ichkeul (Tunisia), claimed to be intermediate in size between *S. etruscus* and *D. sumatrensis*, has been assigned to a new species named *Dicerorhinus africanus* by Arambourg (1970). This taxon is represented by scanty remains: an atlas, an M3, a fragment of mandible and an isolated lower molar. In agreement with Arambourg (1970), the morphology of M3 resembles *S. etruscus* (e.g, the specimen NMB Va4 from Upper Valdarno) and the presence of a double crochet (which is not common in the Plio-Pleistocene rhinoceroses of Europe; Guérin, 1980) can also be detected on an M3 from a maxilla collected at Senèze (NMB Se187). The lower molars (two in the mandible fragment and one isolated) display morphological characters that can be evidenced in several species. The lingual valley (even if a lingual view is not provided by Arambourg, 1970) seems to have a V-shaped morphology, which is common in *S. etruscus*. Contrary to Arambourg (1970), the material from Lake Ichkeul falls within the dimensional range of *S. etruscus* reported by Guérin (1980). Most likely, the species from Tunisia is a synonym of *S. etruscus*, but further discoveries are needed to support this hypothesis. A *Stephanorhinus* was also reported from Koro Toro 13 (Chad) aged between 3 and 3.5 Ma (Geraads, 2010) but the material has not been published. Thus, at this stage, it is impossible to confirm this record and to compare it with '*D.*' *bethlehemsis*.

Accordingly, considering the chronological and geographical distributions of *Dihoplus* and *Stephanorhinus* (Fig. 1) and the evolutionary stage of '*D.*' *bethlehemsis*, we suggest an age ranging from MN14 to MN15 (4.2–3.2 Ma) for the site of Bethlehem.

8. Conclusion

Due to its geographic position along the Levantine Corridor, the site of Bethlehem represents a focal locality along the exchanges route between Eurasia and Africa. The site was excavated at the beginning of the last century and, unfortunately, requires a combined effort from many disciplines to reconstruct the site formation and provide a final report. An effort is being made to publish the fauna and the history of the site (e.g., Rabinovich and Lister, 2017), and this paper on the rhinoceros remains is another step in that direction.

The revision of the rhinoceros revealed the presence of an evolved form of the Late Miocene-Pliocene genus *Dihoplus,* which is morphologically distinct from the known Eurasian and African species. We suggest an origin from the South-East European and Anatolian *D. pikermiensis*, however a new phylogenetic analysis of all Miocene and Plio-Pleistocene species of the group is needed (e.g. Cappellini et al., 2019). The rhinoceros from Bethlehem was a browser with a diet probably composed of leaves of trees, bushes, or part of dicots.

The revision of North African Pliocene material will contribute to better understanding the dispersal pattern of Eurasian rhinoceroses and possibly will add new data about this new described taxon, here named '*Dihoplus*' *bethlehemsis*.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quaint.2020.01.011.

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