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Cranial variability in *Stephanorhinus hemitoechus* (Mammalia, Rhinocerotidae): A revision of Azzaroli's subspecies and the systematics of Middle-Late Pleistocene European rhinoceroses

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KEY WORDS - Stephanorhinus*, Rhinocerotidae, Quaternary, Morphology, Biochronology, Palaeoecology.*

ABSTRACT - Western European rhinoceroses have been the subject of several investigations in recent decades, but only a few studies have taken into account the broad morphological variability in extant rhinoceroses. The latter has given rise to doubts concerning the validity and variation of fossil species. Among the Pleistocene fossil rhinoceroses, Stephanorhinus hemitoechus *represents one of the most recorded and described species in Western Europe, being documented by well-preserved cranial remains. Moreover, in addition to the nominotypical subspecies, three further subspecies of* S. hemitoechus *were erected based on differences in cranial features, namely* Rhinoceros hemitoechus falconeri *Azzaroli, 1962,* Rhinoceros hemitoechus aretinus *Azzaroli, 1962 and* Dicerorhinus hemitoechus intermedius *Azzaroli in Anfossi & Cantaluppi, 1987. The validity of these subspecies and the cranial variability of* S. hemitoechus *are herein revised after consideration of the available morphological traits of the lectotype of the species, comparison with fossil cranial remains assigned to* S. hemitoechus *and the morphological variability in extant rhinoceroses. In both extant and fossil rhinoceroses, morphological features such as the shape and size of the occipital face and the position of the nasal notch and of the orbit are affected by ontogenetic patterns, revealing marked changes during the life cycle of an individual. Some other features of the cranium instead, such as the development of the nuchal crest, may have been affected by changes in feeding habitus or sexual dimorphism. Accordingly, the occurrences of subspecies of* S. hemitoechus *are herein rejected, both from a chronostratigraphic and geographic perspective. Finally, we suggest herein that an estimation of the age at death of the studied material and a more comprehensive comparison with the extant species be provided in future studies in order to arrive at a better understanding of fossil rhinoceroses and their taxonomic assignment.*

INTRODUCTION

Stephanorhinus Kretzoi, 1942 is an extinct genus of Rhinocerotidae that was widely distributed in Eurasia and North Africa during the Pleistocene (Guérin, 1980; Antoine et al., 2025). The origin of the genus is poorly known, pending the revision of the latest Miocene Rhinocerotini assigned to *Dihoplus* Brandt, 1878, i.e., *Dihoplus schleiermacheri* (Kaup, 1832) and "*Dihoplus*" *pikermiensis* (Toula, 1906), possibly phylogenetically related to *Stephanorhinus* (Antoine & Saraç, 2005; Pandolfi et al., 2021). Representatives of *Stephanorhinus* show a dolichocephalic double horned cranium, a partially ossified nasal septum, a ventrally-closed auditory pseudomeatus, absent or weakly developed incisors, and molarised upper premolars. *Stephanorhinus* became extinct at the end of the Pleistocene, leaving no representatives of the family in the Palearctic region except for *Coelodonta antiquitatis* (Blumenbach, 1799). In Western Europe, *Stephanorhinus* was seemingly represented by five partially coeval species: *S. jeanvireti* (Guérin, 1972) (Late Pliocene-Early Pleistocene); *S. etruscus* (Falconer, 1868) (earliest Pleistocene-Early/Middle Pleistocene transition); *S. hundsheimensis* (Toula, 1902) (latest Early Pleistocene-early Middle Pleistocene); *S. kirchbergensis* (Jäger, 1839) (early Middle Pleistocene-early Late Pleistocene); and *S. hemitoechus* (Falconer in Gaudin, 1859) (early Middle Pleistocene-late Late Pleistocene).

Stephanorhinus jeanvireti abruptly appeared in Western Europe during the Late Pliocene, following the extinction of representatives of the genus *Pliorhinus* (Guérin, 1980; Pandolfi et al., 2021). *Stephanorhinus jeanvireti* was a large-sized species, with an estimated body weight between 2,112 and 2,448 kg (Pandolfi et al., 2025), that persisted in Eastern Europe at least until the end of the middle Villafranchian (Pandolfi et al., 2019). *Stephanorhinus etruscus*, the smallest and probably the best-known member of the genus, is represented by conspicuous remains in the Upper Valdarno Basin (Italy) and at Senèze (France) (Pandolfi et al., 2017). It is a long-lived species, being recorded throughout the Early Pleistocene. *Stephanorhinus hundsheimensis* is a problematic species, partially synonymised with *Dicerorhinus etruscus brachycephalus* Schroeder, 1903 by Guérin (1980), and formally re-discovered during the 1990's (Fortelius et al., 1993). *Stephanorhinus kirchbergensis* is an Asian immigrant into Western Europe during the early Middle Pleistocene (Guérin, 1980; Lacombat, 2009; Pandolfi, 2023). The species is known by complete and well-preserved cranial material, and it is the sole species that yielded a complete *Stephanorhinus* mitochondrial genome sequence, recovered from a cranium discovered in the Chondon River valley in

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Yakutia, Russia (Kirillova et al., 2017). *Stephanorhinus hemitoechus* has been recorded from numerous Middle and Upper Pleistocene localities of Western Europe (Fig. 1), but it has been often misidentified with both *S. hundsheimensis* and *S. kirchbergensis*, leaving some doubts as to its diagnostic features and occurrences.

Azzaroli (1962) established two chrono-subspecies of *S. hemitoechus*, namely *Rhinoceros hemitoechus falconeri* from the Middle Pleistocene and *Rhinoceros hemitoechus aretinus* from the Late Pleistocene. According to Azzaroli (1962), the former subspecies was more gracile than the latter. A third subspecies, *Dicerorhinus hemitoechus intermedius* Azzaroli in Anfossi & Cantaluppi, 1987, was later named based on a cranium collected in northern Italy, from deposits referred to the Early/Middle Pleistocene transition.

Despite various attempts to describe the postcranial and cranial remains of *S. hemitoechus* (Guérin, 1980; Cerdeño, 1990; Fortelius et al., 1993; Lacombat, 2005; van der Made, 2010; Pandolfi & Tagliacozzo, 2015), a complete review of the lectotype of *S. hemitoechus* and its most representative Middle-Late Pleistocene specimens is still lacking. Herein, we re-describe the lectotype of *S. hemitoechus*, and compare it with crania belonging to the subspecies of *S. hemitoechus* erected by Azzaroli and then with other Middle and Late Pleistocene *Stephanorhinus* specimens from Western Europe.

MATERIAL AND METHODS

The material considered in this paper is housed in several museums and institutions and has been partially figured in published cited works (Supplementary Online Material [SOM]). The suprageneric classification follows Antoine et al. (2010) and Pandolfi et al. (2021). The anatomical terminology follows Guérin (1980) and Antoine (2002). The ontogenetic stages refer to the definition proposed by Groves (1967): 1, first permanent molar not visible; 2, first permanent molar erupting: no trace of a second molar; 3, second molar erupting: second and third premolars in process of replacement; 4, second molar in wear: fourth premolar in process of replacement; 5, third molar in evidence: all milk teeth replaced; 6, third molar fully erupted; 7, third molar in wear; 8, third molar in advanced wear. In the description of the position of some cranial features such as the rear border of the nasal notch, the position of the infraorbital foramen and that of the anterior border of the orbit, "anterior" is used when the observed character lies between the mesial side of the tooth and the paracone fold, "mid" is used when the character lies between the paracone and metacone folds, and "posterior" is used when the character lies between the metacone fold and the distal side of the tooth. The variability of the described morphological characters is tested on crania of both extant African and Asian species, except *Rhinoceros sondaicus* Desmarest, 1822, which is represented by a small number of crania within the studied collections. In addition, the crania of *Coelodonta antiquitatis* have also been considered to evaluate the variability in Quaternary fossil rhinoceroses. This species is indeed represented by a large number of crania, easily recognisable because of the peculiar morphology of both the teeth and the cranium. The specimens considered are listed in SOM.

Anatomical abbreviations

DP/dp, upper/lower deciduous premolar; M/m, upper/lower molar; P/p, upper/lower premolar.

Measurement abbreviations

MW, maximal width at the mastoids, occipital face view (this measure corresponds to n. 16 in Guérin, 1980); OB, width at the nuchal crest, occipital face view (this measure corresponds to n. 15 in Guérin, 1980); OH,

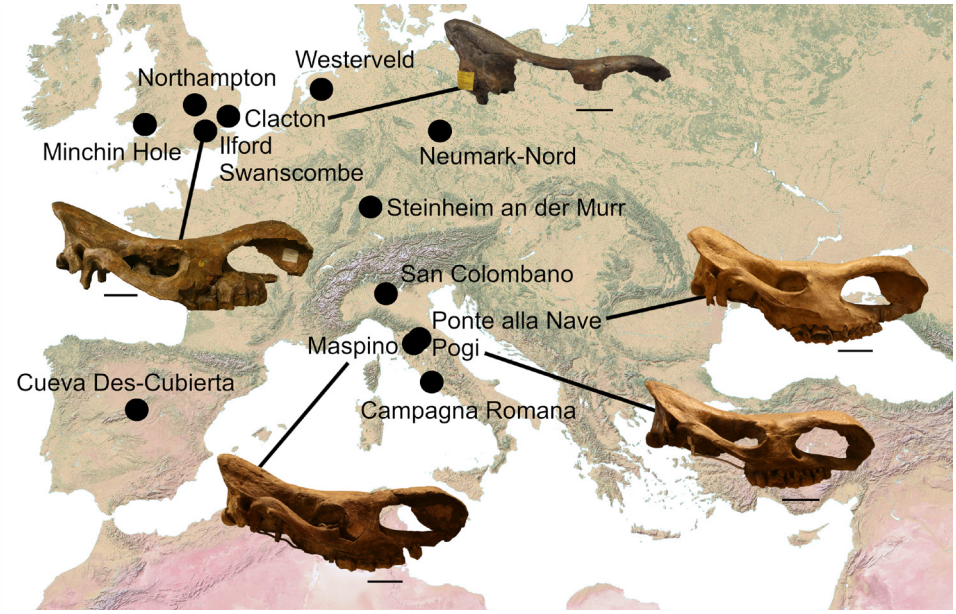

Fig. 1 - (color online) Location of fossiliferous localities with *Stephanorhinus hemitoechus* crania discussed in the text and SOM. Scale bars correspond to 10 cm.

occipital height measured from the dorsal border of the foramen magnum to the dorsal border of the nuchal crest, occipital face view (this measure corresponds to n. 23 in Guérin, 1980).

Institutional abbreviations

CNHM, Croatian Natural History Museum, Department of Geology and Paleontology, Zagreb, Croatia; DSSBC, Dipartimento di Scienze Storiche e dei Beni Culturali, Università di Siena, Siena, Italy; GRQ-SERP, La Guixera laboratory, Castelldefels, Spain; IfG, Institut für Geowissenschaften, Heidelberg, Germany; IGF, Museo di Storia Naturale dell'Università di Firenze, sezione di Geologia e Paleontologia, Florence, Italy; IQW, Senckenberg Forschungsstation für Quartärpaläontologie, Weimar, Germany; LHV, Landesmuseum für Vorgeschichte, Halle, Germany; MCSNB, Museo Civico di Scienze Naturali E. Caffi, Bergamo, Italy; MfN, Museum für Naturkunde, Berlin, Germany; MKSNP, Kosmos, Museo di Storia Naturale dell'Università di Pavia, Pavia, Italy; MPACSCL, Museo Civico "Virginio Caccia", San Colombano al Lambro, Italy; MPI, Museo Museo nazionale del Paleolitico, Isernia, Italy; MPAP, Museo Paleoantropologico di San Daniele Po, Cremona, Italy; MPP, Museo Paleontologico Parmense, Parma, Italy; MUST, Museo Universitario di Scienze della Terra, sezione di Paleontologia, Sapienza Università di Roma, Rome, Italy; MSNCC, Museo di Storia Naturale di Calci, Pisa, Italy; MZ, Muzeum Ziemi Polskiej Akademii Nauk, Warsaw, Poland; NAS, National Alliance of Shidlovskiy "Ice Age," Ice Age Museum, Moscow, Russia; NBC, Naturalis Biodiversity Center (in partim former Rijksmuseum van Geologie en Mineralogie), Leiden, Netherlands; NHMM, Naturhistorisches Museum, Mainz, Germany; NHMUK, The Natural History Museum, London, UK; NHMW, Naturhistorisches Museum, Wien, Austria; RMCA, Royal Museum for Central Africa, Tervuren, Belgium; SMNH, Shennongjia Museum of Natural History, Shennongjia, China; SMNK, Staatliches Museum für Naturkunde, Karlsruhe, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; UPWR, Uniwersytet Przyrodniczy we Wrocławiu, Wrocław, Poland; ZIN, Zoological Institute of the Russian Accademy of Sciences, St. Petersburg, Russia; ZSM, Zoologische Staatssammlung, Munich, Germany.

SYSTEMATIC PALAEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Perissodactyla Owen, 1848
Family Rhinocerotidae Gray, 1821
Subfamily Rhinocerotinae Gray, 1821
Tribe Rhinocerotini Gray, 1821

Genus *Stephanorhinus* Kretzoi, 1942

Stephanorhinus hemitoechus (Falconer in Gaudin, 1859) (Fig. 2)

1859 *Rhinoceros hemitoechus* Falconer - Gaudin, p. 131.
1867 *Rhinoceros leptorhinus* Owen - Dawkins, p. 215, Pl. 10.
1868 *Rhinoceros hemitoechus* Falconer, p. 323, Pl. 23, fig. 1; Pl. 24, figs 2-3.
1874 *Rhinoceros leptorhinus* Owen - Woodward, p. 398, Pl. 15.
1942 *Procerorhinus hemitoechus* (Falconer) - Kretzoi, p. 314, Fig. 1, n. 5-8.
1962 *Rhinoceros hemitoechus falconeri* Azzaroli, p. 27, Fig. 1, n. 2; Fig. 4, n. 3-4; Pl. 16, figs 1, 4; Pl. 17, fig. 2; Pl. 18, fig. 2; Pl. 19, figs 1, 3.
1962 *Rhinoceros hemitoechus aretinus* Azzaroli, p. 27, Fig. 1, n. 1, 3; Fig. 3, n. 1; Fig. 4, n. 1-2; Pl. 16, figs 2-3; Pl. 17, figs 1, 3; Pl. 18, figs 1, 3; Pl. 19, fig. 2; Pl. 20, figs 2-4.
1980 *Dicerorhinus hemitoechus* (Falconer) - Guérin, p. 624.
1993 *Stephanorhinus hemitoechus* (Falconer) - Fortelius et al., p. 66.

Lectotype - NHMUK 48953, neurocranial portion of cranium from the Late Pleistocene of Minchin Hole, Glamorganshire, UK, designated by van der Made (2010); figured in Falconer (1868).

Neodiagnosis - Representative of *Stephanorhinus*, with a posterior profile of the nuchal crest, in dorsal view, from slightly concave in young individuals to straight or slightly convex in senile individuals. A tubercle or exostosis in the mid of the nuchal crest (a sexually-dimorphic character) is present. Nasal bones slightly enlarged and/or anteriorly rounded. Anterior groove absent on the most anterior tip of the nasal bones. Occipital face generally subtrapezoidal, with a convex or straight dorsal border. Mastoids slightly wider than the nuchal crest. Nuchal crest slightly posteriorly protruding in lateral view, generally overhanging the occipital condyles. Occipital face normally vertical or slightly forward inclined. Posttympanic process normally short and massive. Area between the temporal and the nuchal crest flattened. Hypoglossal foramina generally small and anteriorly located on the condylar fossa. Sagittal crest present on the basilar process in adults. Postglenoidal process polygonal or curved. Nuchal tubercle little developed. Rear border of the nasal notch from the anterior side of P4 (stage <5) to anterior side of M1 (stage 7), and up to the posterior side of M2 in males (stage 8) or the mid of M1 in females (stage 8). Position of the anterior border of the orbit from the posterior side of P4 in juveniles to the anterior side or mid of M3 in adults.

Description of the lectotype NHMUK 48953 - The specimen preserves the neurocranial portion, slightly damaged at the nuchal crest. In lateral view (Fig. 2a), the specimen shows a massive posttympanic process, a wide auditory pseudomeatus, a flattened area between the temporal and the nuchal crests, a vertical occipital face (OH: 171.30 mm), and a nuchal crest protruding posteriorly overhanging the occipital condyles. In occipital view (Fig. 2b), the specimen has a subtrapezoidal face, slightly wider at the mastoids (WM: 261.95 mm) than at the nuchal crest (OB: 137.57 mm). In dorsal view (Fig. 2c), the frontal-parietal crests are barely visible but close to each other. In ventral view (Fig. 2d), the postglenoidal apophysis is broken but shows a subtrapezoidal cross-section, the hypoglossal foramina are relatively small and located anteriorly on the condylar fossa, and the occipital condyles are triangular with a straight internal border. The sagittal crest on the basilar process is barely visible and damaged.

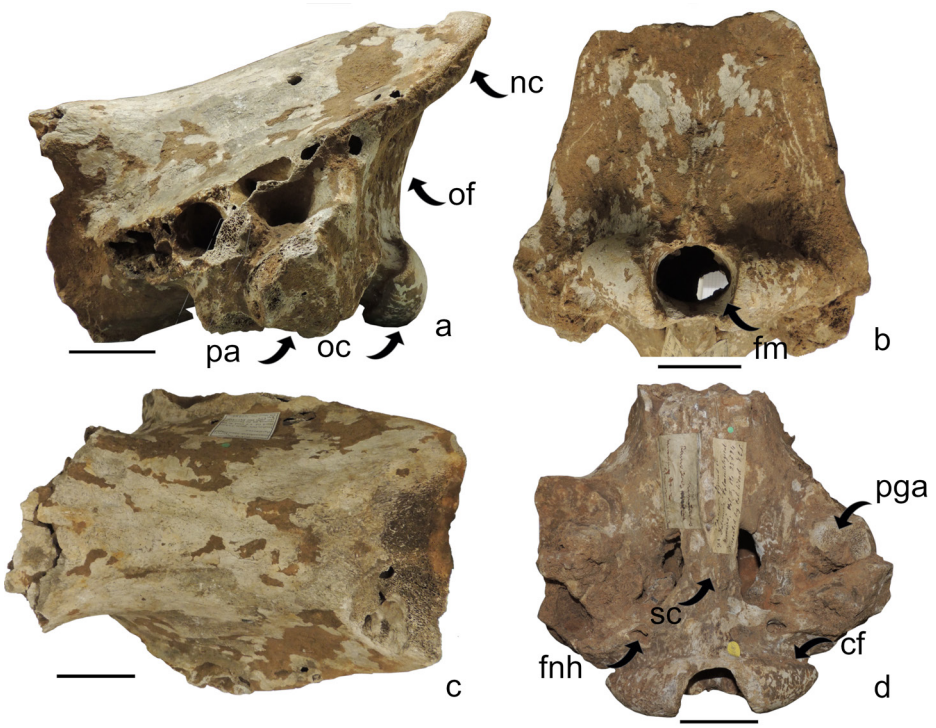

Fig. 2 - (color online) NHMUK 48953, lectotype of *Stephanorhinus hemitoechus*, neurocranial portion, Late Pleistocene of Minchin Hole, Glamorganshire, UK. a) lateral view, b) occipital face view, c) dorsal view, d) ventral view. Abbreviations: cf, condylar fossa; fm, foramen magnum; fnh, foramen nervi hypoglossi; nc, nuchal crest; oc, occipital condyles; of, occipital face; pa, paraoccipital apophysis; pga, postglenoidal apophysis; sc, sagittal crest. Scale bars correspond to 10 cm.

Remarks - Gaudin (1859, p. 131) first mentioned the species *Rhinoceros hemitoechus* explaining that it was named by Falconer, the name referring to its partially closed nasal septum, and that this species was associated with *Elephas antiquus* Falconer & Cautley, 1847 (=*Palaeoloxodon antiquus*) in the caves of the Glamorganshire (Wales) and also with *Hippopotamus major* Cuvier, 1824 (=*Hippopotamus antiquus?* Desmarest, 1822) at Gray's Thurrock and other deposits of the Thames River, England. Falconer (1868, pp. 323, 350) then described the specimen in greater detail, adding further material (maxilla, isolated teeth and fragmentary mandibles from Minchin Hole and various localities) to complete the description of the species. In this paper (included in a compilation of notes and memoirs edited by Charles Murchison), the author did not select a type specimen for the species, and later authors (Azzaroli, 1962; Loose, 1975) erroneously indicated a cranium from Clacton (Middle Pleistocene, UK, NHMUK 27836; described by Owen, 1846 as *Rhinoceros leptorhinus*) as lectotype of *Rhinoceros hemitoechus*. As firstly remarked by Gaudin (1859), the original specimens studied by Falconer came from several caves in Glamorganshire, and thus they are the syntypes of the species as stated by van der Made (2010, p. 478). The latter author, following A. Currant's personal opinion, formally designated the partial cranium NHMUK 48953 from Minchin Hole as lectotype of *R. hemitoechus*.

Occurrence - The earliest occurrences of the species are from the Middle Pleistocene of Europe at Campagna Romana (Italy, ca. 500 ka), Caune de l'Arago (France, ca. 450 ka), Ambrona (Spain, ca. 400 ka), Bilzingsleben (Germany, MIS11) and Clacton (UK, MIS11, ca. 424-374 ka). The species is recorded from numerous Middle and Upper Pleistocene localities in Europe (Guérin, 1980; Cerdeño, 1990; Fortelius et al., 1993; Lacombat, 2009; Pandolfi et al., 2013; Pandolfi & Tagliacozzo, 2015; Giaourtsakis, 2021), in the latest Middle Pleistocene of the Caspian area, but also in the Late Pleistocene of northern Africa and Middle East (Guérin, 1980). *Stephanorhinus hemitoechus* became extinct during the late Late Pleistocene, being lastly recorded before the Last Glacial Maximum at Cueva del Castillo (Spain, ca. 42-45 ka), Bachi Kiro Cave (Bulgaria, ca. 42 ka), Cava Muracci (Italy, ca. 40 ka), and Gruta da Figueira Brava (Portugal, ca. 30 ka) (Stuart & Lister, 2007).

Stephanorhinus hemitoechus falconeri (Azzaroli, 1962) (Fig. 3a)

1846 *Rhinoceros leptorhinus* Cuvier - Owen, p. 356, Figs 131, 138-140.
1868 *Rhinoceros hemitoechus* Falconer, p. 317-324, Pl. 15.
1980 *Dicerorhinus etruscus brachycephalus* (Schroeder) - Guérin, p. 628.
1980 *Dicerorhinus hemitoechus hemitoechus* (Falconer) - Guérin, p. 1043.
1987 *Dicerorhinus hemitoechus falconeri* (Azzaroli) - Anfossi & Cantaluppi, p. 467.
1993 *Stephanorhinus hemitoechus hemitoechus* (Falconer) - Fortelius et al., p. 64.

2010 *Stephanorhinus hemitoechus falconeri* (Azzaroli) - van der Made, p. 479.
2024 *Stephanorhinus kirchbergensis* (Jäger) - Pandolfi et al., p. 57.

Lectotype - NHMUK 27836, portion of cranium from the Middle Pleistocene of Clacton, Essex, UK; figured in Falconer (1868) and Azzaroli (1962, fig. 1, n. 2, pl. 16, fig. 4, pl. 19, fig. 1).

Remarks - Azzaroli identified this subspecies based on the crania from Clacton (UK), Pogi (Bucine, Italy) and Mosbach (Germany). In turn, Guérin (1980) stated that Azzaroli had not designated a nominotypical subspecies (cf. ICZN, 1999, Article 47.1) and thus that *Dicerorhinus hemitoechus falconeri* should be substituted by *D. h. hemitoechus*; the latter author also questioned the identification of the cranium from Pogi as belonging to this subspecies (Guérin, 1980, p. 628). However, the concept of nominotypical taxon was introduced in the third edition of the ICZN (1985), whilst in the previous ones, in force when Azzaroli (1962) established the subspecies, the term "subordinate taxon" was used. On the other hand, the lectotype of the species (designated by van der Made, 2010), NHMUK 48953, was not assigned by Azzaroli to either of the two subspecies. Later, Anfossi & Cantaluppi (1987) identified a fragmentary cranium from Mezzana Rabattone (Italy) as belonging to *D. h. falconeri*, but they did not consider the suggestion by Guérin (1980).

The cranium NHMUK 27836 from Clacton (UK, MIS11c; Fig. 3a) was firstly discussed and figured by Owen (1846), who determined it as *Rhinoceros leptorhinus* Cuvier, 1822. Later, Falconer (1868) considered it as belonging to *Rhinoceros hemitoechus*, and Azzaroli (1962, fig. 1-n. 2, fig. 4-n. 4, pl. 27, fig. 4, pl. 19, fig. 1), Loose (1975), Guérin (1980) and van der Made (2010) also studied this cranium, being considered as type specimen (Loose, 1975, p. 13) or part of the syntypes (Guérin, 1980, p. 628) of *Stephanorhinus hemitoechus*. However, as noted by van der Made (2010, p. 479), this specimen does not come from the area of Minchin Hole and cannot be part of the original syntypes of the species, but it can be taken as lectotype of *S. h. falconeri*. In dorsal view (Owen, 1846, fig. 139), the Clacton cranium shows a narrow depression between the frontal-parietal crests, a boss in the mid of the nuchal crest, and completely fused nasal bones. In lateral view (Owen, 1846, fig. 138; Fig. 3a), the dorsal profile of the temporal-parietal bone is slightly convex, with the nuchal crest protruding posteriorly, but less than in the Minchin Hole cranium. The occipital face (Owen, 1846, fig. 140) is subtrapezoidal, wider at the mastoids (OB: 136.5 mm; MW: estimated 237 mm), but apparently lower than in the lectotype from Minchin Hole and the crania from Ilford and Swanscombe (UK) also assigned to *S. hemitoechus* (SOM). The nuchal crest, in dorsal view (Owen, 1846, fig. 139), displays a rather sinuous profile due to the presence of a tubercle in the mid-part. This feature is not documented in other crania from the UK but it is instead present in a cranium from Maspino (Italy; MSNCC I17769: Fig. 3b; a 3D model is freely available at https://sketchfab.com/MuseoStoriaNaturaleUnipi) and another one from Neumark-Nord (Germany; van der Made, 2010, pl. 5, pl. 6, fig. 1). Another specimen from Clacton (NHMUK M203694) is a basicranial fragment of a juvenile individual (presence of the suture line between the basisphenoid and the occipital bone) that shows relatively wide hypoglossal foramina, which occupy the most anterior portion of the condylar fossa, a subtrapezoidal cross section of the postglenoidal apophysis, and relatively massive posttympanic process. These characters can be detected on the cranium from Minchin Hole.

As said above, the cranium IGF 10792 from Pogi (Bucine, Italy; late Middle Pleistocene; Fig. 3b) was also considered by Azzaroli as belonging to the subspecies *R. hemitoechus falconeri* but then referred to as *Dicerorhinus etruscus brachycephalus* by Guérin (1980, p. 628) without any specific explanation. IGF 10792 is a relatively old individual, being the M3 worn-out (stage 7/8), but not as old as the specimens from Ilford (UK) and Neumark-Nord (Germany) (stage 8: SOM). In lateral view (Fig. 3b), the nuchal crests protrude posteriorly overhanging the occipital condyles, the occipital face is vertical, the area between the temporal and the nuchal crests is flattened, and the auditory pseudomeatus is wide. In dorsal view (Fig. 3b), the nuchal crest has a relatively straight posterior border (in Azzaroli, 1962, pl. 27, fig. 2), the nuchal crest seems to be slightly concave), the frontal-parietal crests are wide, and the nasal bones are completely fused anteriorly. In the basicranium, the hypoglossal foramina are anteriorly placed on the condylar fossa, and the sagittal crest on the basilar process is sharp. The dimensions of the occipital face (OB: 134 mm; MW: 212 mm) approximate those of the cranium from Ilford. The palate ends at the level of M2 metaloph, similar to the condition in the cranium of *S. hemitoechus* from Ponte alla Nave (Italy; SOM; Ugolini, 1906; Azzaroli, 1962), while it ends at M3 protoloph level in the crania (stage 8) from Ilford, Maspino (Italy) and Neumark-Nord and at the level of the M2 median valley in the crania (stage 7) from San Colombano (Italy) and Westerveld (Netherlands) (SOM). The rear border of the nasal notch and that of the infraorbital foramen lie above the anterior of M1 and the mid of M1, respectively, as in the specimens from Ponte alla Nave, San Colombano, and Westerveld, while both lie above the mid of M1 in the specimens from Ilford, Maspino and Neumark-Nord (SOM). The anterior border of the orbit on IGF 10792 lies above the posterior of M2, similarly to the specimen from San Colombano (stage 7, possibly female), but it is above the mid-M3 on Ilford, Maspino and Neumark-Nord (stage 8) and the anterior of M3 on Ponte alla Nave and Westerveld (stage 7, possibly males). It is possible that the detected differences are related to the age and sex of the specimens, as observed in extant rhinoceroses (see below). The cranium from Pogi was discovered in association with *Mammuthus primigenius* Blumenbach, 1799 and other taxa chronologically spanning from MIS6 to the latest Pleistocene (Napoleone et al., 2003) and it is therefore younger than that from Ilford (considered by Azzaroli as belonging to the younger subspecies *D. hemitoechus aretinus*).

Azzaroli (1962, p. 23) also included in *R. h. falconeri* a partially preserved cranium from Mosbach figured by Schroeder (1903, pl. 1, figs 1-1a, pl. 4), which is instead referable to as an individual at stage 7 of *S.*

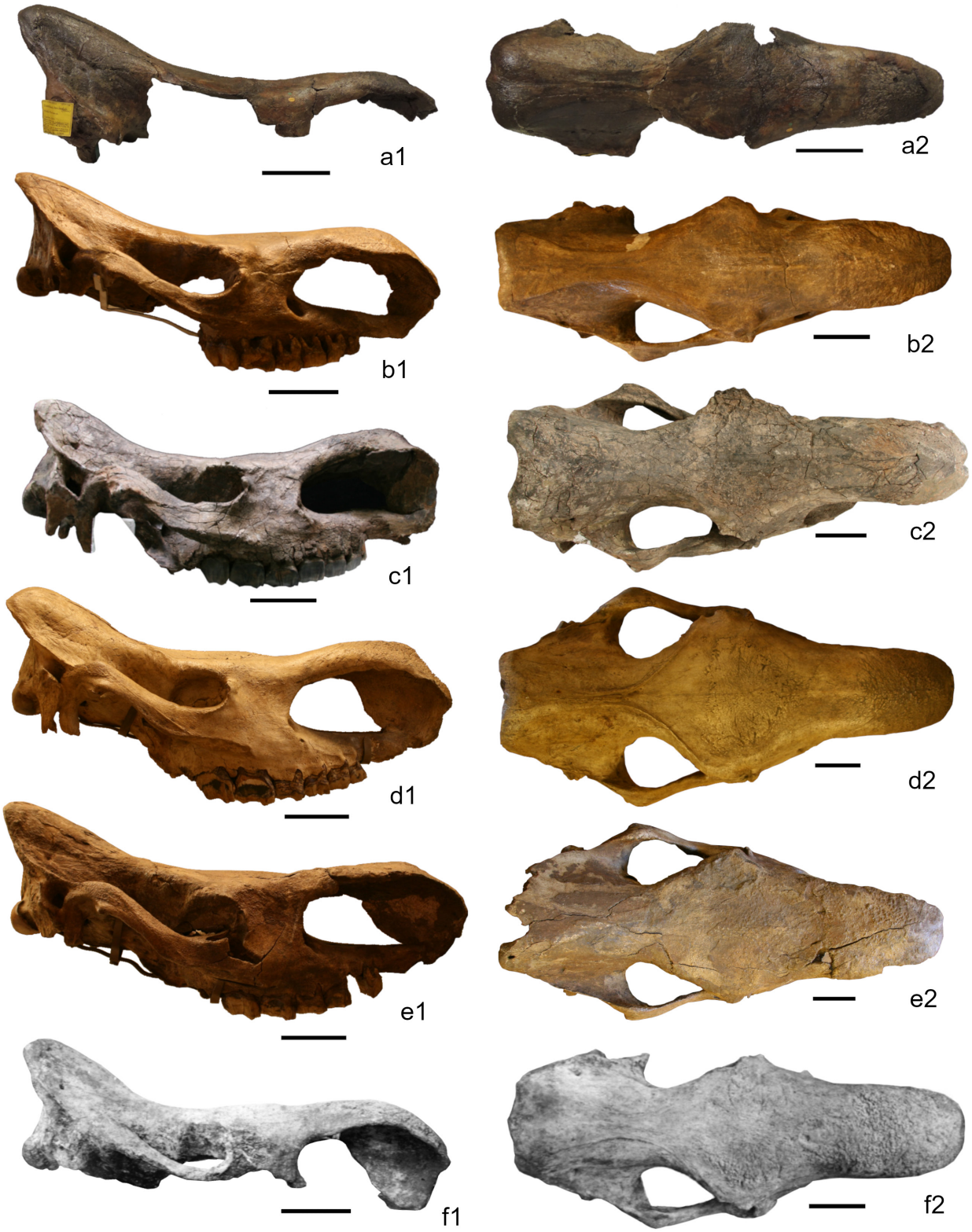

Fig. 3 - (color online) *Stephanorhinus* crania discussed in the text. a) NHMUK 27836, *S. hemitoechus* from Clacton. b) IGF 10792, *S. hemitoechus* from Pogi, Bucine. c) MPP VER_099, *S. hundsheimensis* from Torrente Stirone. d) IGF 1105, *S. hemitoechus* from Ponte alla Nave. e) IGF 1109, *S. hemitoechus* from Maspino. f) MSNCC I17769, *S. hemitoechus* from Maspino. 1) lateral view, 2) dorsal view. Scale bars correspond to 10 cm.

hundsheimensis. This cranium shows, in dorsal view (Schroeder, 1903, pl. 1, fig. 1), anteriorly-separated nasal bones, similarly to *S. hundsheimensis* crania from Mosbach (NHMM PW 1977-13, NHMM PW 1958-

764), Untermassfeld (Germany, IQW 2009/30270) and Torrente Stirone (Italy, MPP VER_099; Fig. 3c), and the anterior border of the orbit at the level of the mid-M2, similarly to the *S. hundsheimensis* crania from Isernia (Italy, MPI 33085), Untermassfeld (IQW 2009/30270) and Sussenborn (IQW Suss.1965/2513). Further, the upper premolars of the Mosbach cranium (Schroeder, 1903, pl. 4) bear a continuous lingual cingulum, a character documented in *S. hundsheimensis* (SOM).

Concerning the partial cranium from Mezzana Rabattone (Pavia; MKSNP no inventory number) attributed to *D. h. falconeri* by Anfossi & Cantaluppi (1987), the specimen shows a subtrapezoidal occipital face, wider at the mastoids than at the nuchal crest, and with more oblique lateral borders of the face than the cranium from Minchin Hole and other mentioned crania of *S. hemitoechus*. In lateral view, the nuchal tubercle is developed and the nuchal crest does not protrude posteriorly overhanging the occipital condyles. The described characters are observed, instead, in the crania from the Chondon River (Russia; Kirillova et al., 2017, fig. 2), Irkutsk (Russia; Brandt, 1877, pls 1, 2, figs 1-3), Krapina (Croatia; Gorjanović-Kramberger, 1913, pl. 1, figs 1-3) and Warsaw (Poland; Borsuk-Białynicka & Jakubowski, 1972, pls 1-4) referred to *Stephanorhinus kirchbergensis* (SOM), which suggests that the Mezzana Rabattone cranium actually belongs to this species (Pandolfi et al., 2024).

In summary, out of the four crania assigned to *R. hemitoechus falconeri* by Azzaroli (1962), two can be discarded from belonging to the species *Stephanorhinus hemitoechus*, whereas the other two (from Clacton and Pogi) present similarities between them and with the lectotype of the species, such as the posteriorly protruding nuchal crest and the vertical occipital face, but also some minor differences, such as the sinuous posterior profile of the nuchal crest in dorsal view in the Clacton cranium (SOM).

Stephanorhinus hemitoechus aretinus (Azzaroli, 1962) (Fig. 3d)

1906 *Rhinoceros* (*Coelodonta*) *mercki* Jäger - Ugolini, p. 27-34, Pl. 1, figs 1-2; Pl. 3, fig. 2; Pl. 4, figs 1-2.
1980 *Dicerorhinus hemitoechus aretinus* (Azzaroli) - Guérin, p. 624.
1987 *Dicerorhinus hemitoechus aretinus* (Azzaroli) - Anfossi & Cantaluppi, p. 467.
1993 *Stephanorhinus hemitoechus aretinus* (Azzaroli) - Fortelius et al., p. 64.
2010 *Stephanorhinus hemitoechus hemitoechus* (Falconer) - van der Made, p. 479.

Lectotype - IGF 1105, cranium from the late Middle Pleistocene of Ponte alla Nave, Val di Chiana, Italy; figured in Ugolini (1906, pl. 1, figs 1-2, pl. 3, fig. 2, pl. 4, figs 1-2) and Azzaroli (1962, fig. 1 n. 2, pl. 16, fig. 4, pl. 19, fig. 1).

Remarks - Azzaroli (1962) recognised this second subspecies of *S. hemitoechus* based on the crania from Val di Chiana (Ponte alla Nave; Italy) and Arezzo (Botro Maspino; Italy) and probably that from Ilford (UK).

The two Italian crania from Ponte alla Nave (IGF 1105; Fig. 3d) and Botro Maspino (IGF 1109; Fig. 3e) were respectively interpreted as a male and a female. The two specimens have similar age at death (stage 7/8) and they share the following morphological features: the hypoglossal foramina are located on the anterior side of the condylar fossa, the sagittal crest is present on the basilar process, the anterior tip of the nasal bones is completely fused, the rear border of the infraorbital foramen is located above the mid of M1, the anterior border of the orbit is located above the anterior side of M3, and the area between the temporal and the nuchal crests is flattened (although the auditory pseudomeatus is wider in IGF 1109 than in IGF 1105). IGF 1109 displays polygonal-shaped postglenoidal process, but IGF 1105 shows variability between the left curved postglenoidal process and the right polygonal one. On the whole, the morphological characters shared by the two specimens exclude their attribution to *S. hundsheimensis* or *S. kirchbergensis* (SOM). However, in lateral view, the occipital face is slightly inclined forward in IGF 1105, while it is vertical in IGF 1109; on both specimens, the nuchal crest protrudes posteriorly overhanging the occipital condyles. In the occipital face, the cranium from Ponte alla Nave differs from that from Maspino in having a convex dorsal border of the nuchal crest, resulting in a subtriangular occipital face. The specimen IGF 1109 shares with the crania from Ilford and Neumark-Nord the position of the infraorbital foramen, the rear border of the nasal notch and the anterior border of the orbit; all these crania have a similar age at death.

Another cranium from Botro Maspino, housed at MSNCC, was described by Ugolini (1906) and referred as *Rhinoceros* (*Coelodonta*) *mercki* Jaeger in Meyer (1842). The specimen (Fig. 3f) shows, in lateral view, a slightly forwardly inclined occipital face, a flattened area between the temporal and the nuchal crests, and a nuchal crest overhanging the occipital condyles; further, in occipital view, the occipital face is high (higher than depicted by Ugolini, 1906, pl. 1, fig. 1), similar to that of IGF 1109, subtrapezoidal, and with a rather convex dorsal border due to the presence of an exostosis, similarly to the specimen from Clacton NHMUK 27836 (Fig. 3). Therefore, the MSNCC specimen can be considered as belonging to *S. hemitoechus*.

The cranium NHMUK 45205 from Ilford (UK, MIS7; Fig. 4a), firstly figured by Woodward (1874, pl. 15) and considered by Azzaroli as *R. hemitoechus aretinus*, belongs to a fully adult individual (M3 erupted and in advanced wear, stage 8) and displays a subtrapezoidal occipital face (Fig. 4a), similar to that of the lectotype from Minchin Hole, NHMUK 48953, and a straight nuchal crest (Fig. 4a). In lateral view (Fig. 4a), similarly to the Minchin Hole specimen, the nuchal crest protrudes posteriorly and the occipital face is vertical, the area between the temporal and nuchal crests is flattened, and the posttympanic process is massive. In ventral view, as in the cranium from Minchin Hole, the Ilford specimen bears two small hypoglossal foramina, located anteriorly on the condylar fossa. Accordingly, the specimen from Ilford does not differ from the lectotype from Minchin Hole and both can be assigned to the same taxon that, at subspecies level, should be the nominotypical subspecies *S. h.*

hemitoechus. However, a few differences exist between the specimen from Ilford and the other two from Italy. In the Ilford cranium (Fig. 4a), the position of the anterior border of the orbit is slightly more anteriorly placed than on specimens from Ponte alla Nave and Bucine (above the mid of M3 contra above the anterior of M3 in IGF 1105 and above the posterior of M2 in IGF 10792), the palate ends at the level of the M3 protoloph but at the level of M2 metaloph on the Italian specimens, and the occipital face is regularly subtrapezoidal but bell-shaped on IGF 1105 and narrower on IGF 10792. Dimensionally, the specimen from Ilford is longer and wider than those from Ponte alla Nave and Pogi.

In summary, among the specimens assigned by Azzaroli (1962) to *R. h. aretinus*, the cranium from Ilford is the closest to the lectotype of the species, while those from Italy present minor differences, as well as those referred to as *R. h. falconeri*. One cranium from Botro Maspino (MSNCC) resembles that from Clacton (NHMUK 27836), while the other one (IGF 1109) resembles the specimen from Pogi (IGF 10792). The Ponte alla Nave cranium, instead, shares some features with the lectotype NHMUK 48953, such as the anteriorly-located hypoglossal foramina, the polygonal postglenoidal apophyses, and the flattened area between the temporal and the nuchal crests, but it also displays some more differences, such as the forwardly-inclined occipital face and the almost subtriangular occipital face in posterior view.

Stephanorhinus hemitoechus intermedius (Azzaroli in Anfossi & Cantaluppi, 1987) (Fig. 3c)

1976 *Dicerorhinus hemitoechus* (Falconer) - Cigala Fulgosi, p. 61-65, Pl. 1.

1987 *Dicerorhinus hemitoechus intermedius* Azzaroli - Anfossi & Cantaluppi, p. 466.

1993 *Stephanorhinus hundsheimensis* (Toula) - Fortelius et al., p. 116.

2013 *Stephanorhinus hundsheimensis* (Toula) - Pandolfi et al., p. 53.

Lectotype - MPP VER_099, cranium from the early Middle Pleistocene of Torrente Stirone, Parma, Italy; figured in Cigala Fulgosi (1976, pl. 1).

Remarks - According to Anfossi & Cantaluppi (1987, p. 466), Azzaroli was working on an unpublished paper about Early and Middle Pleistocene rhinoceroses from Italy, where another subspecies of *Dicerorhinus hemitoechus* was going to be established. The latter, *D. h. intermedius*, was based on a cranium collected at Torrente Stirone (Parma, Italy; 0.89-0.7 Ma) and published by Cigala Fulgosi (1976). The cranium from Torrente Stirone (MPP VER_099; Fig. 3a) was assigned to *Stephanorhinus hundsheimensis* by Pandolfi et al. (2013) and Pandolfi (2023). The cranium is represented by an adult individual, similar in age at death to the Hundsheim type specimen (erupted but slightly worn M3, stage 7). However, contrary to the latter, the cranium from Torrente Stirone, in dorsal view, has a strong concavity in the mid of the posterior profile of the nuchal crest, and a more subtrapezoidal shape of the occipital face. Similarities between the two specimens include a depressed area between the temporal and nuchal crests, a forwardly-inclined occipital face, a developed nuchal tubercle, a wide condylar fossa, and a small posttympanic process (SOM). The Torrente Stirone cranium resembles the specimen MNHM PW1977-13 from Mosbach 2, and both have a similar age at death (erupted but slightly worn M3), similar geological age, and were referred to *S. hundsheimensis* (Pandolfi et al., 2013; Pandolfi, 2023). The detected differences between

Fig. 4 - (color online) Variability of cranial features in *Stephanorhinus hemitoechus* from the UK. a) NHMUK 45205, cranium from Ilford, P2-M3 in wear (stage 8). b) NHMUK 43937, cranial fragment from Swanscombe (stage <5). 1) lateral view, 2) occipital face view, 3) dorsal view. Scale bars correspond to 10 cm.

the shape of the nuchal crests in these two specimens could be probably related to intraspecific variability, as observed in extant rhinoceroses. This hypothesis can be supported by the cranium of *S. hundsheimensis* from Isernia La Pineta (0.6-0.5 Ma; MPI 33085; Sala & Fortelius, 1993, pl. 1). The latter shows a slightly concave posterior profile of the nuchal crest, similarly to MNHM PW1977-13 from Mosbach 2, but with the presence of an exostosis in the mid of the crest. Similarly to the specimens from Mosbach 2 and Torrente Stirone, the Isernia cranium displays a groove in the anterior tip of the nasal bones, a forwardly-inclined occipital face (even if dorsal-ventrally crushed), a depressed area between the temporal and nuchal crests, and a small and thin posttympanic process. In posterior view, the specimen from Isernia has a generally low and broad-subtrapezoidal occipital face, slightly wider at the mastoids, and with a convex dorsal border, similarly to other specimens referred to *S. hundsheimensis*. In conclusion, the subspecies *D. hemitoechus intermedius* is to be considered as a junior synonym of *S. hundsheimensis*.

Other crania of S. hemitoechus *from the UK* - The neurocranium NHMUK 20013 from Northampton (UK, MIS5) was figured in Falconer (1868, pl. 23, fig. 2, pl. 24, fig. 1) together with that from Minchin Hole, NHMUK 48953, in order to show similarities between them. The specimen from Northampton has a subtrapezoidal occipital face (OB: 132.73 mm; MW: 239.15 mm; HO: 151.5 mm), similarly to the Minchin Hole specimen, but it has a slightly concave posterior profile of the nuchal crest in dorsal view (Falconer, 1868, pl. 23, fig. 2, pl. 24, fig. 1). In lateral view, the occipital face is vertical, the posttympanic process is relatively massive and the area between the temporal and the nuchal crests is flattened, resembling the lectotype of *S. hemitoechus*. However, the cranium from Northampton probably belonged to a not fully adult individual, being characterised by the presence of suture lines between the postglenoidal and the paraoccipital apophyses, and between the temporal and the parietal bones. In lateral view, the profile of the parietals is slightly convex and the neurocranium seems to be slightly enlarged at the level of the temporals. These features could be related to the relatively young age at death of the animal as observed in extant rhinoceroses (see below).

In lateral view, the unpublished specimen NHMUK 43937 from Swanscombe (UK, MIS11; Fig. 4b) resembles the neurocranial portion from Minchin Hole in having a massive posttympanic process, a wide auditory pseudomeatus, a vertical occipital face, a nuchal crest protruding posteriorly, and a flattened area between the temporal and the nuchal crests (Fig. 4b). In occipital face view (Fig. 4b), the two specimens share a subtrapezoidal face, slightly wider at the mastoids than at the nuchal crest. In size, the specimen from Swanscombe (NHMUK 43937, OB: 131.7 mm; MW: 229.7 mm; HO: 148 mm) resembles that from Northampton. In dorsal view (Fig. 4b), the posterior border of the nuchal crest is slightly concave in NHMUK 43937, whereas it is apparently straight in the lectotype. However, this difference could be related to ontogeny, as the Swanscombe cranium seems to belong to a not fully adult individual (frontal-parietal crests barely visible, presence of suture lines between the lachrymal and the frontal bones).

Comparison between NHMUK 48953 and Rhinoceros hundsheimensis *Toula, 1902 from Hundsheim* - In lateral view, the posttympanic process is massive on the Minchin Hole specimen and less developed in the holotype from Hundsheim (NHMW 2013/0282/0001; Fig. 5a). The auditory pseudomeatus is elliptical and dorsoventrally oriented in the Hundsheim specimen, while it is larger and rounded in the Minchin Hole cranium (Fig. 5b). Furthermore, the area between the temporal and nuchal crests is flattened in the latter and depressed in that from Hundsheim. In lateral view, the occipital face is vertical in NHMUK 48953 and forwardly inclined in NHMW 2013/0282/0001 (Fig. 5a). In ventral view, the postglenoidal apophysis is massive and with a subtrapezoidal cross-section on the specimen from Minchin Hole, while curved and laterally flattened in the specimen from Hundsheim (Fig. 5a). The hypoglossal foramen is wider in the Hundsheim rhinoceros, occupying, anteroposteriorly, more than a half of the condylar fossa (Fig. 5a). The occipital condyles are triangular in the Minchin Hole cranium and elliptical in the Hundsheim cranium, but this difference can be related to the different age at death of the two specimens. In occipital view, the Hundsheim cranium has a subtrapezoidal occipital face, with slightly convex lateral borders (Toula, 1902, pl. 3, fig. 2), while that from Minchin Hole is subtrapezoidal with straight lateral borders (Fig. 2b). In the former, the nuchal crest is wider (OB: 146.9 mm), the mastoids are shorter (MW: 218.5 mm), and the occipital face is shorter (OH: 145.5 mm). The values of the Hundsheim cranium proportionally approximate those of the crania of *S. hundsheimensis* from Mosbach (NHMM PW 1958-764; OB: 152 mm; MW: 218 mm) and Mauer (IfG no code; OB: 143 mm; MW: 230 mm; OH: 151 mm).

Comparison between NHMUK 48953 and crania of Stephanorhinus kirchbergensis *(Jäger, 1839) - Rhinoceros kirchbergensis* was erected on a few isolated teeth (SMNS 34000.1, 34000.2, 34000.3, p3, M3 and M2, respectively) from the late Middle Pleistocene locality of Kirchberg (Germany). A direct comparison between this type material and NHMUK 48953 is therefore prevented and thus we compare cranial features with published data on other specimens referred to *S. kirchbergensis* (SOM). Contrary to the neurocranium from Minchin Hole, these specimens are generally characterised by a broad V-shaped nuchal crest in dorsal view (e.g., Chondon cranium, Russia, Kirillova et al., 2017, fig. 2; Warsaw cranium, Poland, Borsuk-Białynicka & Jakubowski, 1972, pl. 1; Neumark Nord, Germany, van der Made, 2010, pl. 1, fig. 1a). In the cranium from Daxlanden, Germany (SMNK PAL4254, type of *Rhinoceros mercki var. brachycephala* Schroeder, 1903), the nuchal crest is slightly concave (Loose, 1975, pl. 6, fig.1), similarly to that from Irkutsk (Russia, Brandt, 1877, pl. 1, fig. 1), and Krapina (Croatia; Gorjanović-Kramberger, 1913, pl. 1, fig. 2). Furthermore, the skulls of *S. kirchbergensis* display, in ventral view, a curved postglenoidal apophysis, and hypoglossal foramina located in the mid of the condylar fossa (e.g., Schroeder, 1903, pl. 3, figs 1-2; Gorjanović-Kramberger, 1913, pl. 1, fig. 3; Borsuk-Białynicka & Jakubowski, 1972, pl. 3; Loose, 1975, pl. 8, fig. 3; van der Made, 2010, pl. 1, fig. 1c). The nuchal tubercle is normally developed

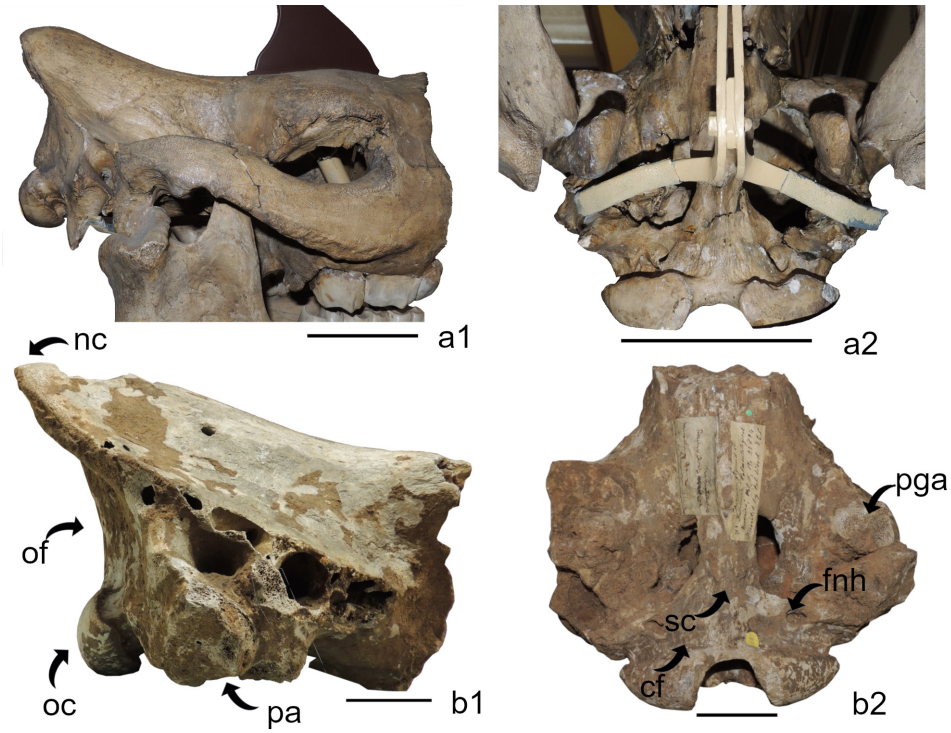

Fig. 5 - (color nline) a) NHMW 2013/0282/0001, holotype of *Stephanorhinus hundsheimensis*, cranium from the Middle Pleistocene of Hundsheim, Austria. b) NHMUK 48953, lectotype of *Stephanorhinus hemitoechus* from the Late Pleistocene of Minchin Hole, Glamorganshire, UK. 1) lateral view, 2) ventral view. Abbreviations: cf, condylar fossa; fnh, foramen nervi hypoglossi; nc, nuchal crest; oc, occipital condyles; of, occipital face; pa, paraoccipital apophysis; pga, postglenoidal apophysis; sc, sagittal crest. Scale bars correspond to 10 cm.

in adult individuals of *S. kirchbergensis* and the area between the temporal and the nuchal crests is depressed (e.g., Schroeder, 1903, pl. 2, figs 1-2; Borsuk-Białynicka & Jakubowski, 1972, pl. 2; Persico et al., 2015, pl. 2, fig. b), contrary to the condition in the Minchin Hole specimen.

Variability of the described cranial characters in extant rhinoceroses and the woolly rhinoceros Coelodonta antiquitatis - In order to better evaluate the cranial differences described above, we examined the observed variations in extant species, as well as in the well-known Late Pleistocene woolly rhinoceros. The morphology of the postglenoidal process is relatively stable in extant rhinoceroses: it is convex in *Diceros bicornis* (Linnaeus, 1758), in both juvenile and adult individuals (Fig. 6), and thus not affected by ontogenetic stages. However, in *Ceratotherium simum* (Burchell, 1817) this process is curved or polygonal; the two morphologies are even displayed at the same time by the same individual (e.g., RMCA 8655, stage 7). In *Coelodonta antiquitatis*, the postglenoidal process is polygonal (e.g., MfN MbMa672, stage 8; Fig. 7a) or curved (e.g., MfN MbMa666, stage 8, Fig. 7b) and in *Rhinoceros* it is curved (Fig. 7c, d).

The development and position of the hypoglossal foramina are also relatively stable in extant rhinoceroses (Fig. 6). In African species (*Ceratotherium simum*, *Diceros bicornis*), these foramina have a similar position in both juveniles (stage < 6) and adults (stage > 6) (Fig. 6). In juvenile specimens of *Di. bicornis* the hypoglossal foramina are normally wider than in old adults (stage 8), whereas in both juveniles and adults of *C. simum* these foramina are generally wide and located in the mid of the condylean fossa. In *Co. antiquitatis*, the hypoglossal foramina are generally located in the mid of the condylean fossa but in some cases they are anterior-externally located (e.g., MfN MbMa673).

The presence and development of a sagittal crest on the basilar process is affected by the age of the animal (e.g., in *Di. bicornis*; Fig. 6), being present in individuals with erupting and erupted M3, but absent in juveniles (stage < 5).

The shape of the occipital condyles, in ventral view, changes during ontogeny; it is sub-triangular in adult and elliptical in juvenile of *Di. bicornis* (Fig. 6). Furthermore, the condyles protrude anteriorly over the condylar fossa in old individuals of *Di. bicornis* (Fig. 6d), with a convex border in juveniles and a straight border in adults (with erupted M3). These variations can be also detected in *Ceratotherium* Gray, 1868 and *Rhinoceros* Linnaeus, 1758 (Fig. 7c, d).

In occipital view, individuals of *Di. bicornis* with deciduous teeth (e.g., RMCA 7974, DP1-M1, erupting M2) show a straight dorsal profile of the nuchal crest and strongly convex lateral borders, while individuals with erupting permanent premolars (e.g., RMCA 2133; DP1, P2-P3 erupting, DP4, M1-M2) show a strongly concave dorsal profile of the nuchal crest that protrudes laterally overhanging the mastoids. In full-adult individuals of *Di. bicornis* (e.g., RMCA 1259, P2-M3 in wear) the occipital face is generally subtrapezoidal, wider at the mastoids, barely convex at the lateral borders, and with a slightly concave dorsal profile of the nuchal crest.

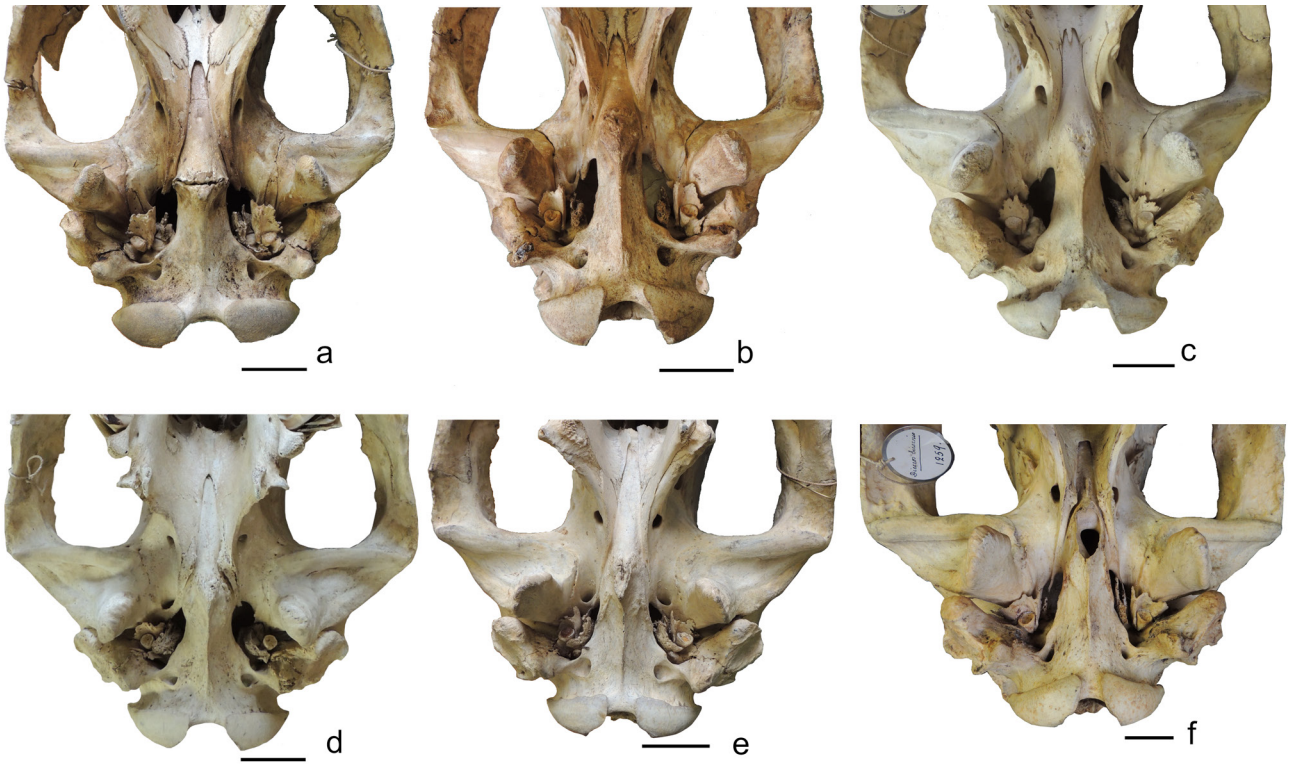

Fig. 6 - (color online) Variability of basicranial features in extant *Diceros bicornis*. a) RMCA 1173, individual with DP1-DP4 and erupting M1. b) RMCA 2133, individual with DP1, P2-P3, DP4 and erupted M1. c) RMCA 7974, individual with P2-M2. d) RMCA 7349, individual with DP1, P2-M2 and erupted M3. e) RMCA 7990, individual with DP1, P2-M2 and erupting M3. f) RMCA 1259, individual with DP1, P2-M3 in wear. Scale bars correspond to 10 cm.

The posterior profile of the nuchal crest, in dorsal view, varies from straight (NHMUK 1907.2.26.1) to slightly concave (NHMM 1965-1129, 1996-2520) or broad V-shaped (NHMUK 1927.7.6.6) (Fig. 8). The breadth of the occiput is wide in the nominotypical subspecies of the black rhinoceros, *Di. bicornis bicornis* (Linnaeus, 1758) (OB: 218.8±23.6 mm), and narrower in *Di. bicornis brucii* (Lesson, 1842) (OB: 182.5±10.6 mm) (Groves, 1967, tab. 2). The shape of the nuchal crest is different among subspecies of *Dicerorhinus* Gloger, 1841, such as *Dicerorhinus sumatrensis lasiotis* (Buckland, 1872) (e.g., NHMUK 1931.5.28.1, NHMUK 1.1.22.1), which shows a wide nuchal crest with a straight posterior border in dorsal view, and *Dicerorhinus sumatrensis sumatrensis* (Fischer v. Waldheim, 1814) (e.g., NHMUK 21.2.8.3, NHMUK 1949.1.11.1), with a narrower nuchal crest with a concave posterior border and a lower occipital face (Groves, 1966; Pandolfi, 2023). In *Rhinoceros unicornis* Linnaeus, 1758, the nuchal crest varies from deeply concave to sinuous to slightly concave (Fig. 8), irrespective of the age and sex of the animal. In grazer species such as *C. simum* and *Co. antiquitatis*, the nuchal crest and the shape of the occipital face varies during ontogeny, but in adult individuals it is rather stable, showing a broad or narrow V-shaped posterior profile in the former, with the nuchal crest wider than the mastoids, and a rather convex posterior profile in the latter, with the nuchal crest slightly narrower than the mastoids. However, in adult individuals of *C. simum*, the occipital breadth is sexually dimorphic, second only to the nasal breadth, as well as the occipital height (Groves et al., 2010), and females of the northern white rhinoceros display a smaller occipital breadth than those belonging to the southern white rhinoceros.

The inclination of the occipital face, in lateral view, is a relatively stable character within the grazer species, at least in individuals with permanent dentition. In *Di. bicornis* (Fig. 9a-c), the occipital face is generally vertical, but in several cases it is inclined forward. In extant Asian rhinoceroses, the occipital face is generally inclined forward, with little variation (Fig. 9d-f).

Additional variable characters in rhinoceroses include the morphology of the teeth, the length of the tooth row and the dorsal outline of the cranium. The southern white rhinoceros, *C. simum simum* (Burchell, 1817), displays a protoloph that runs more distally than lingually with respect to the northern subspecies *C. simum cottoni* (Lydekker, 1908), and a deeper concavity of the dorsal outline, particularly in males. In the former, adult females display a flattened dorsal outline of the cranium and a shorter toothrow than males (Groves et al., 2010). The ends of the palatine and the incisive foramen have been used to discriminate between *C. simum simum* and *C. simum cottoni* (Groves et al., 2010); in the latter, both the palatine and the incisive foramen end more anteriorly than in the former (see the comparison section). This character has not been tested in other species and is here considered for the first time in fossil rhinoceroses, to our knowledge (SOM). In *Di. bicornis*, the length of the toothrow varies among the different subspecies, being longer in the nominotypical subspecies and

shorter in *Di. bicornis michaeli* Zukowsky, 1964 and *Di. bicornis brucii* (Groves, 1967). As to *D. sumatrensis*, *D. sumatrensis lasiotis* displays larger teeth than the other subspecies.

To sum up, extant rhinoceroses exhibit a wide range of craniodental phenotypical plasticity, affected by ontogeny, lifestyle, sexual maturity, and gene flow. As previously reported by Groves (1982), some features of the cranium in extant Asian rhinoceroses are modified by their feeding behavior, suggesting that environmental conditions may act as a driving force in shaping morphological characters such as the zygomatic arches, the nuchal crest, and the temporal area, all of them related to the action of the masseter and temporal muscles. However, it seems that these modifications mainly occur in browser and mixed-feeder species (such as *R. sondaicus, D. sumatrensis* and *Di. bicornis*), whereas grazers are probably not affected by such changes (*C. simum*, *Co. antiquitatis*). Some features of the occipital face are subject to modifications during ontogeny and sexual maturity in extant Asian rhinoceroses (see discussion in Groves, 1966, 1982; Groves & Kurt, 1972; Pandolfi, 2023), but also in African species (Groves, 1967; Groves et al., 2010) (Fig. 8), such as the posterior and dorsal profile of the nuchal crest, and the general shape of the occipital face and its inclination. Nevertheless, these features have been generally used as discriminant characters in fossil rhinoceroses. Additional cranial features, such as the position of the nasal notch, the infraorbital foramen, and the orbit, are also affected by ontogenetic development and sexual maturity; it is therefore necessary to estimate the age at death of the individuals before carrying on comparative studies.

DISCUSSION

Morphological characters in rhinocerotid crania are subject to modification during the life span of the individual, and only a combination of such characters may really help to define and distinguish a fossil species from others.

At the species level, the lectotype NHMUK 48953 of *Stephanorhinus hemitoechus* is characterised by some features that cannot be currently detected in other Middle and Late Pleistocene rhinoceroses. It is well differentiated from the type of *S. hundsheimensis* by the posteriorly protruding nuchal crest, the vertical occipital face, the flattened area between the temporal and the nuchal crests, and the anteriorly placed hypoglossal foramina. In turn, NHMUK 48953 also differs from referred specimens of *S. kirchbergensis* mainly by the posteriorly protruding nuchal crest, the flattened area between the temporal and the nuchal crests, and the poorly developed nuchal tubercle.

Few earlier works on cranial material of fossil rhinoceroses have addressed an exhaustive comparison with the morphological variation in extant species (e.g., Toula, 1902; Loose, 1975; Guérin, 1980). Most of the fossil species have been identified on the basis of some features of the occipital face, such as the development of the nuchal crest or the shape of the occiput, but without considering the extreme variability of this area of the cranium. For instance, the differences in size and shape of the nuchal crests and of the occiput in the Sumatran rhinoceros are remarkable between populations of the mainland and those of the Borneo or Sumatran islands (Groves, 1966, 1982). Further, a certain degree of variability is

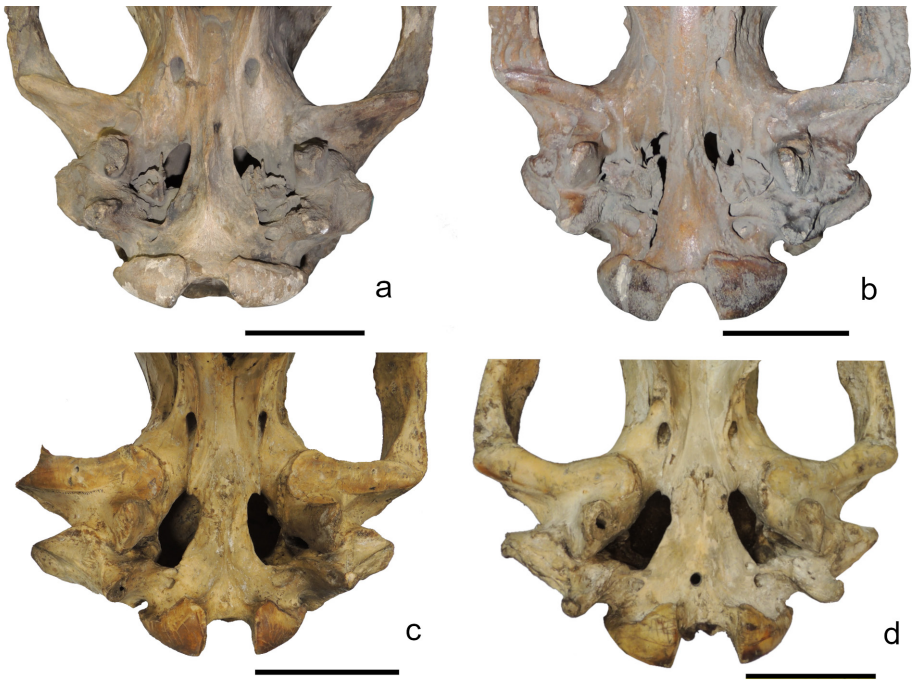

Fig. 7 - (color online) Variability of basicranial features in *Coelodonta antiquitatis* (a, b) and *Rhinoceros sondaicus* (c, d). a) MfN 672, individual with P2-M3 (stage 8), polygonal postglenoidal process. b) MfN 666, individual with P2-M3 (stage 8), curved postglenoidal process. c) DSSBC no inventory number, individual with P2-M3 (stage 8). d) UPWR no inventory number, individual with P2-M3 (stage 8). Scale bars correspond to 10 cm.

documented in other areas of the cranium, such as the development of the paraoccipital process, the nuchal tubercle and the zygomatic arches (see description above). These characters are also partially affected by sexual dimorphism, at least in Asian rhinoceroses, and ontogeny. A few studies and direct observations also suggest that feeding behavior and environmental conditions may affect shape and size of some cranial features (Groves, 1982; Pandolfi, 2023). Accordingly, it is very difficult to detect really useful morphological characters to discriminate among the fossil species and recognise the presence of chrono- or geographic subspecies.

It is here possible to assert that the posterior profile of the nuchal crest of *S. hemitoechus*, in dorsal view, varies from slightly concave in relatively young individuals to straight or slightly convex in relatively old individuals. A few specimens display a tubercle or exostosis in the mid of the nuchal crest; this character could be probably related to the age of the animal and an ossification of tendons, being documented in specimens with fully erupted and worn-out M3, or it could be a sexually dimorphic character. It is indeed present in cranium NHMUK 27836 from Clacton (Fig. 3), in one MSNCC from Maspino (Fig. 3), but also in cranium LHV 189 - HK 88 from Neumark Nord (van der Made, 2010, pl. 5, fig. 1a), and it is partially developed in the specimens from Westerveld (Loose, 1961, fig. 3), Ilford (Fig. 4a), and another one from Neumark Nord (van der Made, 2010, pl. 7, fig. 1a-b). All these crania are characterised by slightly enlarged and/or anteriorly rounded nasal bones, as in the specimens from Ponte alla Nave and in contrast to those from Botro Maspino, San Colombano, and Pogi, which show anteriorly narrower nasal bones. The presence of tubercles or exostoses in the mid of the nuchal crest is documented in other fossils (e.g., *Coelodonta antiquitatis*, IGF 1040; *S. hundsheimensis*, MPI 33085) and extant species (e.g., *D. sumatrensis*, NHMUK 1879-6-14-2; *Di. bicornis* MZUF 7525, NHMUK 48-1-14-3), but of unknown sex, making difficult a clear identification of it as a dimorphic character. The occipital face is generally subtrapezoidal in *S. hemitoechus*, with a convex or straight dorsal border, and with the mastoids a little wider than the nuchal crest (see Loose, 1975). In juvenile individuals (e.g.,

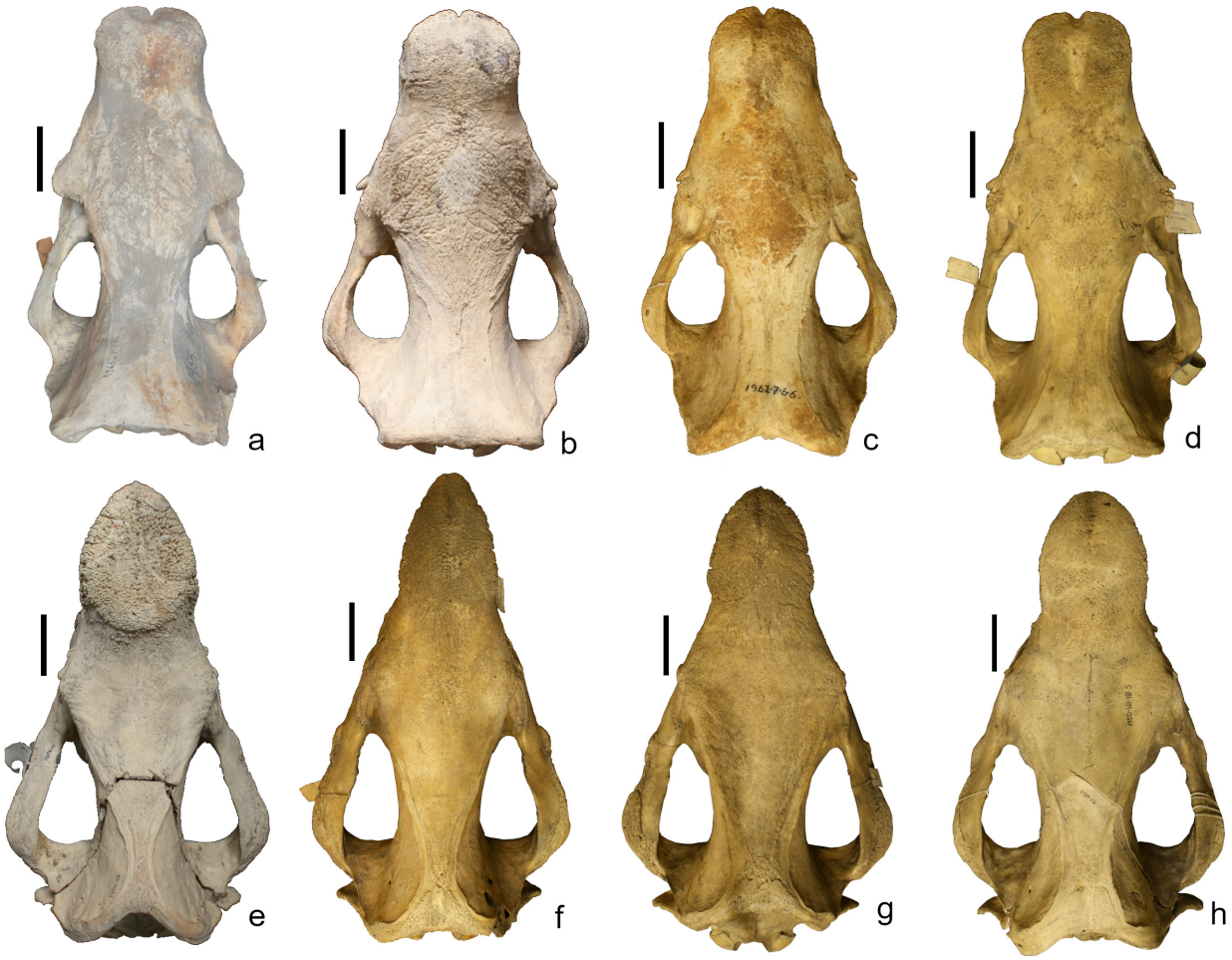

Fig. 8 - (color online) Variability in dorsal cranial features of the extant *Diceros bicornis* and *Rhinoceros unicornis*. a-d) *Diceros bicornis*: a) NHMM P1965-1127, with DP1, P2-M3 in wear (stage 8). b) SMF 22 260,with DP1, P2-M3 in wear (stage 7). c) NHMUK 1962-7-6-6,with DP1, P2-M3 in wear (stage 7/8). d) NHMUK 2-11-18-6,with DP1, P2-M2 in wear and M3 erupted (stage 6/7). e-h) *Rhinoceros unicornis*. e) NHMM P1960-59, with P1-M3 in wear (stage 8). f) NHMUK 72-12-30-1,with P1-M3 in wear (stage 8). g) NHMUK 72-739,with P1-M3 in wear (stage 7). h) NHMUK 1950-10-18-5,with P1-M2 in wear, M3 erupted (stage 6). Scale bars correspond to 10 cm.

Swanscombe), the lateral borders of the face are slightly convex, but normally straight in adults.

The subtriangular occipital face in the specimen from Ponte alla Nave deserves instead a short discussion. It could fall within the intraspecific variability of *S. hemitoechus* or be affected by the feeding behavior of the animal, rather than coinciding with a dimorphic character as maintained by Azzaroli (1962). The Ponte alla Nave individual is indeed characterised by the presence of sub-quadrangular M3, with a deep posterior groove, and by a short gap between the alveolus of the M3 and the posterior maxillary tuberosity, contrary to other studied crania that show instead a sub-triangular M3 and long distance between the alveolus and the posterior maxillary tuberosity. Further, the Ponte alla Nave cranium displays a linear healing on the left zygomatic arch and a relatively deep healed groove on the left side of the occipital face. These characteristics probably affected in some way the feeding mode of the animal, resulting in an "uncommon" shape of the occipital face, as observed in extant rhinoceroses feeding in severe or unfavorable conditions (Groves, 1982).

In lateral view, the nuchal crest in *S. hemitoechus* slightly protrudes posteriorly, generally overhanging the occipital condyles (cf. Guérin, 1980), and the occipital face is normally vertical or slightly inclined forward. The posttympanic process is normally short and massive, and the area between the temporal and the nuchal crest is flattened. The latter area is well developed in some specimens such as those from Ilford, Neumark-Nord, San Colombano and Westerveld, and little developed in those from Pogi and Ponte alla Nave. At Maspino, the specimen MSNCC, assigned to a male, displays a well-developed flattened area, but IGF 1109, assigned to a female, has a little developed area; this character could be therefore dimorphic, similarly to the development of the median boss on the nuchal crest. In the basicranium, the hypoglossal foramina are generally small and anteriorly located on the condylar fossa, the sagittal crest on the basilar process is present only in adults, and the postglenoidal process is polygonal or curved. The shape of the occipital condyles varies among the individuals and their ontogenetic stages. The nuchal tubercle is not particularly developed and there is no incision on the most anterior tip of the nasal bones. The position of the rear border of the nasal notch, the infraorbital foramen, and the anterior border of the orbit changes during the growth of the animal. The rear border of the nasal notch moves from the anterior side of P4 (stage < 5) to the posterior side of P4 (stage 5), to the anterior side of M1 (stage 7), and till the posterior side of M2 in males (stage 8) or the mid of M1 in females (stage 8). The position of the anterior border of the orbit moves from the posterior side of P4 in juveniles to the anterior side or mid of M3 in adults. Therefore, the variability detected by Guérin (1980) concerning the position of the above-mentioned features is primarily affected by the age of the animal. Further, the position of the palate changes during the growth of the individual; it is located at the level of M3 at stage 8, but at the level of the metaloph at stage 7 and more anteriorly in younger specimens.

Taking into account the mentioned variations, the validity of different subspecies of *S. hemitoechus* is difficult to assess. The lectotype from Minchin Hole can be considered by its morphology in a group together with the crania from Northampton, Ilford, Westerveld, and Neumark-Nord, whilst the cranium from Clacton, designated as lectotype of the species *Rhinoceros hemitoechus* and included within the subspecies *R. h. falconeri* by Azzaroli (1962) gathers with the specimens from Swanscombe, San Colombano, Pogi, Botro Maspino and to a certain degree Ponte alla Nave. In this context, neither group corresponds to the subspecies proposed by Azzaroli (1962), as the author separated the crania from Clacton and Pogi (*R. h. falconeri*) from those from

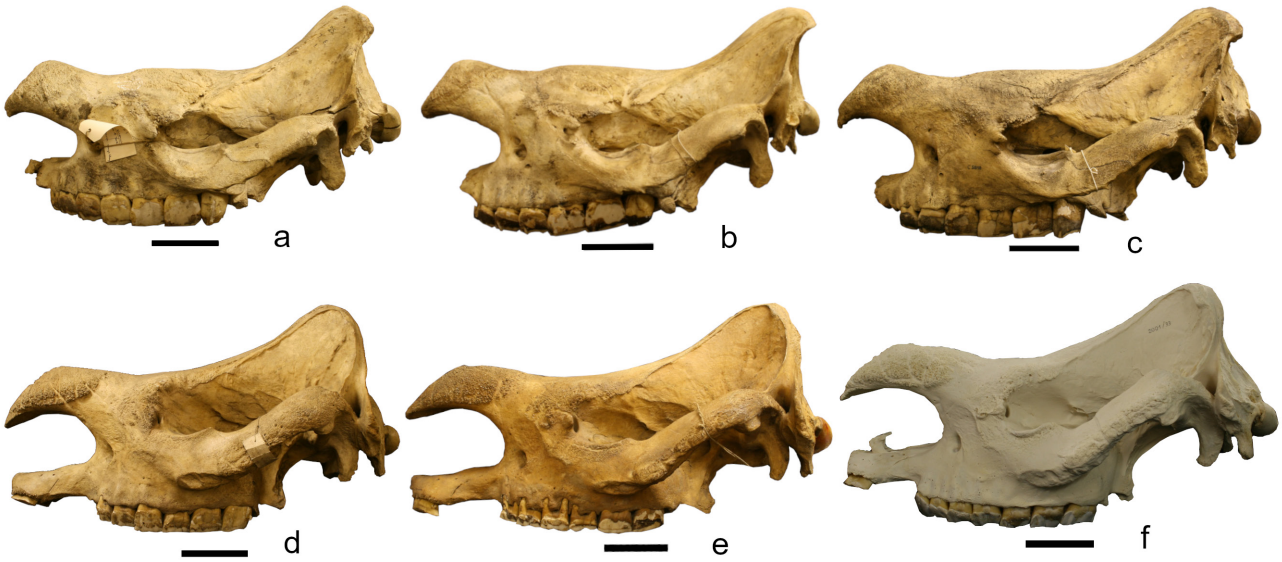

Fig. 9 - (color online) Variability of the occipital face in lateral view in extant *Diceros bicornis* (a-c) and *Rhinoceros unicornis* (d-f). a) NHMUK 25-7-6-1, individual with DP1, P2-M3 (stage 6). b) NHMUK 2-11-18-7, individual with DP1, P2-M3 (stage 7). c) NHMUK 1967-8-31-8, individual with DP1, P2-M3 (stage 7). d) NHMUK 72-739, individual with DP1, P2-M3 (stage 7). e) NHMUK 72-12-30-1, individual with DP1, P2-M3 (stage 8). f) ZSM 2001-33, individual with DP1, P2-M3 (stage 8). Scale bars correspond to 10 cm.

Ilford and the Italian sites (*R. h. aretinus*). The presently differentiated groups, if recognised as subspecies, should be split into the nominotypical one, *S. h. hemitoechus*, in which the lectotype of the species is included by definition (ICZN 1999, Art. 47.1), and another subspecies for which the name *S. h. falconeri* would be valid, considering the inclusion of the Clacton cranium in it. However, this subspecific differentiation is not so clear, as most of the established differences could be related to different ages of the specimens at death and/or to sexual dimorphism. The chronological distinction of two subspecies, as considered by Azzaroli (1962), is as well not supported. The lectotype from Minchin Hole corresponds to the MIS5 and the closest crania (Ilford and Neumark-Nord) to MIS7, whereas the crania from Clacton and Swanscombe correspond to MIS11 (SOM). Even if this difference could seem to be enough to separate them chronologically, the similarities of the two latter specimens with those from Italy assigned to MIS6? (Pogi and Ponte alla Nave) or MIS6-4 (Botro Maspino) (SOM) allow us to reject this hypothesis. At this point, taking into account the mentioned morphological variation in other fossil and extant species, and the lack of clear chronological separation of the fossils recognised as *Stephanorhinus hemitoechus*, we discard the validity of the previously established subspecies of this taxon.

On the other hand, the differentiation of geographic subspecies of extant rhinoceroses is based on the

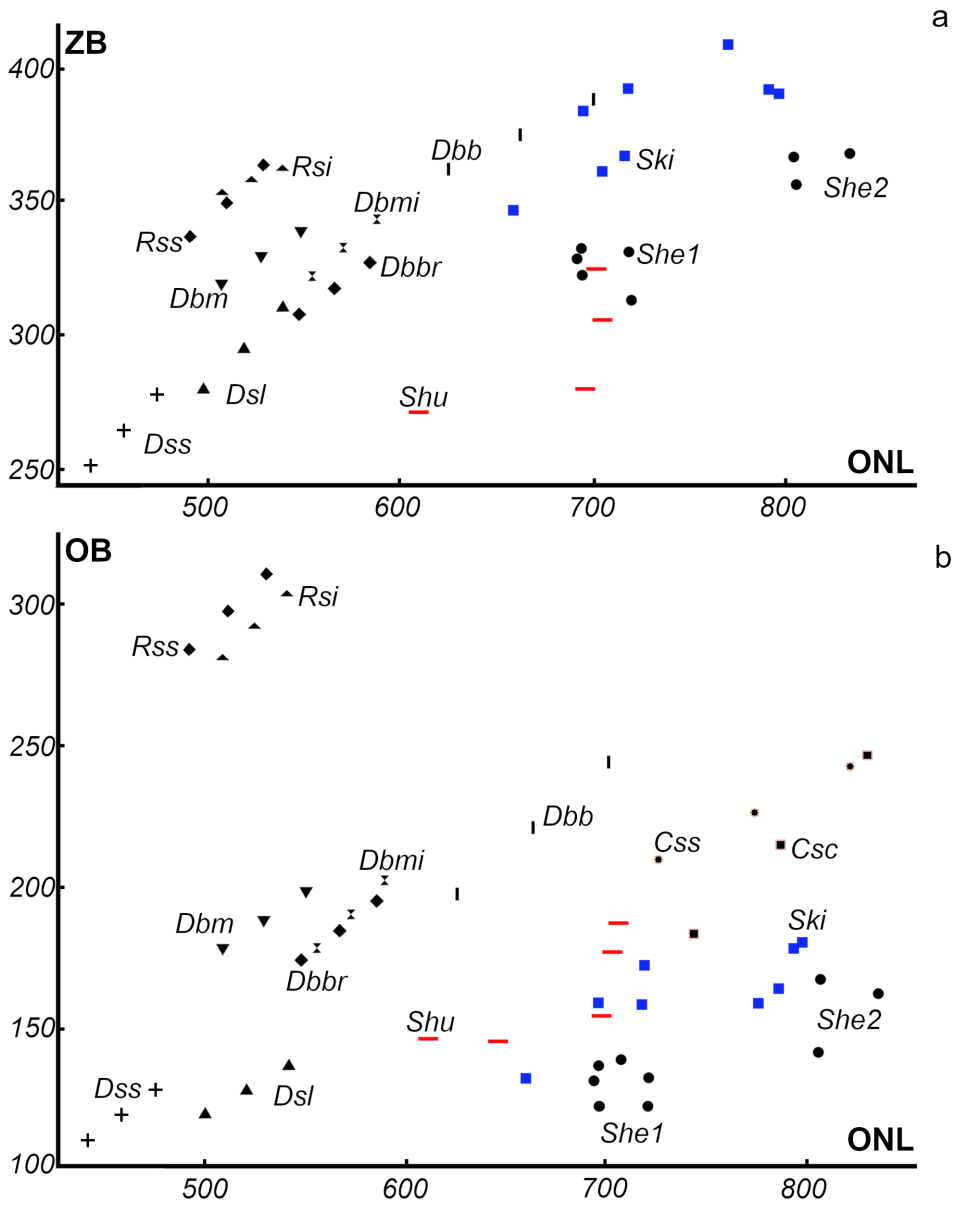

Fig. 10 - (color online) Morphometric variability in selected extant rhinoceroses (minimal, mean and maximal values) and fossil *Stephanorhinus*. a) Occipital-Nasal Length (ONL) vs Zygomatic breadth (ZB). b) Occipital-Nasal Length (ONL) vs Occipital breadth (OB). Data and data sources are reported in SOM. Csc, *Ceratotherium simum cottoni*; Css, *C. s. simum*; Dbb, *Diceros bicornis bicornis*; Dbbr, *Di. b. brucii*; Dbm, *Di. b. michaeli*; Dbmi, *Di. b. minor*; Dsl, *Dicerorhinus sumatrensis lasiotis*; Dss, *D. s. sumatrensis*; Rsi, *Rhinoceros sondaicus inermis* Lesson, 1838; Rss, *R. s. sondaicus* Desmarest, 1822; Shu, *Stephanorhinus hundsheimensis*; Ski, *S. kirchbergensis*; She1, *S. hemitoechus* (Ponte alla Nave, Maspino, San Colombano, Pogi, Clacton); She2, *S. hemitoechus* (Westerveld, Neumark-Nord, Ilford).

relationship of various morphometrical features such as the Occipital-Nasal Length (ONL) and the Zygomatic Breadth (ZB), in particular among *Dicerorhinus sumatrensis sumatrensis* and *D. s. lasiotis*, *Diceros bicornis bicornis* and *Di. b. minor* (Drummond, 1876) (Fig. 10a). Applying this method to the considered crania of *S. hemitoechus*, they show a bimodal distribution (mostly concordant with the morphological groups mentioned above), with the specimens from Ilford, Westerveld and Neumark-Nord located on the right-upper corner of the graph (She2) and the specimens from Italy (Pogi, Botro Maspino, Ponte alla Nave, San Colombano) located on the left-down side of the graph (She1; Fig. 10a; the Clacton cranium lacks the ZB value). Similarly, the ONL vs. the Occipital Breadth (OB) allows discriminating between *D. s. sumatrensis* and *D. s. lasiotis*, and between *Di. bicornis bicornis* and *Di. b. minor* (Fig. 10b), but also highlights a bimodal distribution for *S. hemitoechus*, separating the three crania from northern Europe from those from Italy plus the cranium from Clacton. These differences cannot be related to the age of the specimens or to sexual dimorphism (see the discussion above), and cannot reflect a geographical separation due to the close placement of Ilford and Clacton. Indeed, further detailed analyses and more complete material are needed to better understand the population dynamics and replacement in Quaternary rhinoceroses.

CONCLUSIONS

During the past decades, several attempts have been made in order to refine the alpha-taxonomy of Eurasian fossil rhinoceroses, often without considering the intraspecific variability shown by extant species. In the extant *Dicerorhinus sumatrensis*, *Diceros bicornis* and *Rhinoceros unicornis*, the neurocranium is somehow affected by changes during ontogeny and some characters, potentially considered as diagnostic in fossil species, may reflect feeding behavior, available resources and inter-populational variability. In fossil species, the variability of some characters in the cranium is still poorly investigated, as well as changes related to ontogenetic patterns and sexual maturity. In the present paper, the re-description of the lectotype and the most iconic and well-preserved crania of *Stephanorhinus hemitoechus* enables us to recognise changes of some cranial features during ontogeny, in particular related to the development of the nuchal crest. Interestingly, the latter is particularly variable in extant mixed-feeder and browser species, being affected by changes in feeding behavior of the animals. The cranium from Ponte alla Nave could represent an example of this hypothesis. Further, a kind of sexual dimorphism can be detected in *S. hemitoechus* considering the shape and size of the nasal bones in adult individuals (stage >7) and by the presence of an exostosis in the mid of the nuchal crest. This feature is also observed in some crania of extant rhinoceroses, unfortunately without indication of sex/gender, hence limiting the support of the proposed hypothesis. Finally, a few characters of the basicranium are here detected to discriminate among fossil species. These characters show a limited variability with respect to other features, such as the nuchal crest, allowing a more robust systematic attribution. To sum up, the detected variability does not support the subspecific differentiation of *S. hemitoechus* at morphological or chronological level, and therefore the validity of the chrono-subspecies erected by Azzaroli (1962) is here rejected. Accordingly, any research involving rhinoceros crania must initially consider the age at which the animal died (through dental wear), as well as its sex (if possible), prior to proceeding with systematic identification. The revision of diagnostic characters, proved to be highly variable, could likely modify the current established taxonomic diversity of Pleistocene rhinoceroses, which will probably decrease in the near future. The investigation on through-life changing patterns of some cranial features will be helpful to better understand the palaeoecology of fossil rhinoceroses and their palaeoenvironment.

SUPPLEMENTARY ONLINE MATERIAL

Supplementary data are available on the BSPI website at: https://www.paleoitalia.it/bollettino-spi/bspi-vol-641/

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