

SYNOPSIS OF THE STRATIGRAPHICAL DISTRIBUTION OF THE VILLAFRANCHIAN EQUIDS, TAPIRIDS AND RHINOCERONTIDS OF WESTERN EUROPE *

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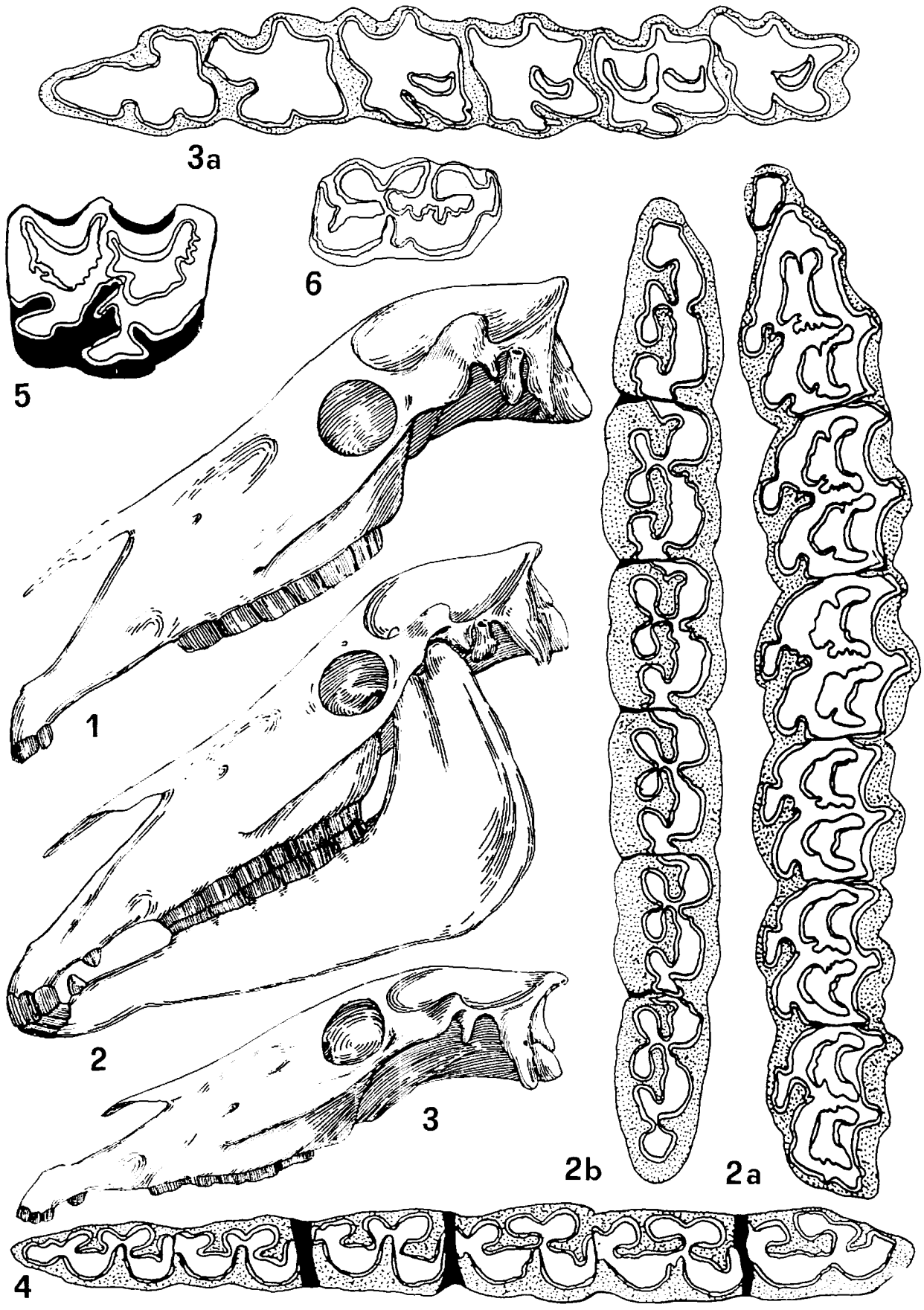
RIASSUNTO - Quadro riassuntivo sulla distribuzione stratigrafica degli equidi, tapiri e rinoceronti villafranchiani dell'Europa occidentale - Il Quaternario *Italian Journal of Quaternary Sciences*, 8(2), 1995, 357-366 - Quattro equidi caratterizzano le comunità fossili villafranchiane dell'Europa occidentale, *Equus livenzovensis*, *E. stenonis*, *E. stehlini* e *E. gr. bressanus-süssenbornensis*. *E. livenzovensis*, rappresentante di grande taglia, probabile discendente di *E. simplicidens* del Nord America, si diffuse in Eurasia all'incirca durante l'intervallo di circa 2.5-2.4 Ma (Unità Faunistica di Montopoli). *E. stenonis* è rappresentato per la prima volta nelle associazioni dell'Unità Faunistica di St. Vallier. Questa specie dette origine ad una varietà di sottospecie diffuse in Europa occidentale e distinte solo su base dimensionale. *E. stenonis* dette origine ad una specie asinina di taglia medio-piccola, *E. stehlini*, che apparve in Toscana al tempo dell'Unità Faunistica del Tasso e sembra anche rappresentato nell'associazione fossile di Vallonnet, transizionale alle faune galeriane. Un altro possibile discendente di *E. stenonis*, *E. gr. bressanus-süssenbornensis*, uno dei più grandi equidi d'Eurasia, caratterizza le comunità dell'ultimo Villafranchiano o del primissimo Galeriano. I tapiri villafranchiani dell'Europa occidentale sono rappresentati da una sola specie, *Tapirus arvernensis*. Sono note due sottospecie, *T. arvernensis minor*, di piccola taglia ed il più grande *T. arvernensis arvernensis*. Le relazioni filogenetiche di *T. arvernensis* sono ancora fonte di discussione. Resti di questa specie caratterizzano le comunità note dal tardo Turoliano al Villafranchiano inferiore. Quattro rinocerodonti, *Stephanorhinus jeanvireti*, *S. etruscus*, *S. hundsheimensis* e *S. hemitoechus*, si distribuirono in Europa occidentale durante il Villafranchiano. Al momento, le relazioni filogenetiche fra queste specie sono incerte. *Stephanorhinus jeanvireti* è una specie di grande taglia, cursoriale, del Villafranchiano inferiore, che apparentemente condivide un certo numero di caratteri craniali in comune con *S. hundsheimensis*. A tutt'oggi le più antiche testimonianze accertate di *S. etruscus* sono quelle di Città della Pieve (Perugia) e Montopoli (Pisa), del Villafranchiano inferiore; esso perciò convisse per un certo intervallo con *S. jeanvireti*. *S. etruscus* sembra essere scomparso al tempo del rinnovamento faunistico del Villafranchiano-Galeriano (1.0-0.7 Ma). Individui peculiari di piccola taglia con affinità di tipo *S. etruscus*-*S. hundsheimensis* sono noti in Olanda, Germania e Italia, da livelli datati alla fine del Pleistocene inferiore. Questi esemplari sembrano essere validi indicatori stratigrafici, data la loro limitata distribuzione verticale. Il più antico rappresentante di *S. hundsheimensis* caratterizza le comunità del tardo Villafranchiano superiore. La specie condivide numerosi caratteri dentari e postcraniali con *S. etruscus*, che dimostra una possibile discendenza da quest'ultima specie. Le prime testimonianze di *S. hemitoechus* sono stratigraficamente problematiche. Una mandibola incompleta è conosciuta da Croce dei Cappuccini (Valdarno superiore) ed un cranio incompleto, con affinità tipo *S. hemitoechus*, fu rinvenuto a Grezzano (Mugello). E' quindi possibile che la specie sia effettivamente comparsa in tempi leggermente precedenti a quanto comunemente accettato.

ABSTRACT - Synopsis of the stratigraphical distribution of the Villafranchian equids, tapirids and rhinocerotids of Western Europe - Il Quaternario *Italian Journal of Quaternary Sciences*, 8(2), 1995, 357-366 - Four equids characterize the Villafranchian fossil communities of Western Europe, *Equus livenzovensis*, *E. stenonis*, *E. stehlini* and *E. gr. bressanus-süssenbornensis*. The large-sized *E. livenzovensis*, a probable offspring of the North American *E. simplicidens*, dispersed in Eurasia approximately during the interval spanning about 2.5-2.4 Ma (Montopoli Faunal Unit). *E. stenonis* is first represented in the St. Vallier F.U. assemblages. This species formed a variety of subspecies spread throughout Western Europe and distinguished only on dimensional basis. *E. stenonis* gave rise to a middle- small-sized asinine species, *E. stehlini*, which appeared in Tuscany at the time of the Tasso F.U. and seems to be also represented in the fossil assemblage of Vallonnet, transitional to the Galerian faunas. Another possible offspring of *E. stenonis*, *E. gr. bressanus-süssenbornensis*, one of the largest equids of Eurasia, characterizes the latest Villafranchian and earliest Galerian communities. The Villafranchian tapirids of Western Europe are represented only by one species, *Tapirus arvernensis*. Two subspecies are known, the small-sized *T. arvernensis minor* and the larger-sized *T. arvernensis arvernensis*. The phylogenetic relationships of *T. arvernensis* are still debated. Remains of this species characterize the Late Turolian to Lower Villafranchian communities. Four rhinocerotids, namely *Stephanorhinus jeanvireti*, *S. etruscus*, *S. hundsheimensis* and *S. hemitoechus*, distributed in Western Europe during the Villafranchian. The phylogenetic relationships between these species are presently unresolved. *Stephanorhinus jeanvireti* is a large-sized, cursorial, Early Villafranchian species that apparently shares a number of common cranial characters with *S. hundsheimensis*. At the moment, the first ascertained occurrences of *S. etruscus* are from the Lower Villafranchian localities of Città della Pieve (Perugia) and Montopoli (Pisa); it therefore co-occurred for a while with *S. jeanvireti*. *S. etruscus* apparently disappeared at the time of the Villafranchian-Galerian faunal turnover (1.0-0.7 Ma). Peculiar small-sized specimens with *S. etruscus*-*S. hundsheimensis* affinities are known, in the Netherlands, in Germany and in Italy, from levels dated to the end of the Early Pleistocene. These specimens seem to be good markers, given their sharp stratigraphic distribution. The most ancient *S. hundsheimensis* representatives characterize very late Villafranchian communities. The species shares a number of dental and postcranial features with *S. etruscus*, which attests to a possible descent from the latter species. Ancient occurrences of *S. hemitoechus* are stratigraphically problematic. A partial mandible is known from Croce-dei-Cappuccini (Upper Valdarno) and a partial skull, with *S. hemitoechus* affinities, was found at Grezzano (Mugello). It is therefore possible that the species actually made its first appearance in times slightly older than commonly accepted.

Key words: Perissodactyla, Mammalia, Plio-Pleistocene, Europe
Parole chiave: Perissodattili, Mammiferi, Plio-Pleistocene, Europa

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1. INTRODUCTION

Perissodactyls are frequently encountered in Western European terrestrial fossil communities, and many times they are quite well represented. These animals often provide invaluable stratigraphical and ecological information. For this reason, an overview of the results of up-to-date investigations on this important group of ungulates seems particularly useful.

2. EQUIDS

At least four species are recognized in the Villafranchian faunal contexts of Europe: *Equus livenzovensis*, *E. stenorionis*, *E. stehlini* and *E. gr. bressanus-süssenbornensis*.

The species *Equus livenzovensis* (Fig. 1) was established on remains found at Livenzovka and Khapry (Southern Russia) (Bajgusheva, 1978), which are the oldest known occurrences of the species in Eurasia. The assemblages from these two localities are attributed to the Montopoli Faunal Unit; *E. livenzovensis* seems limited to

the latter faunal contexts. In Italy the species is slightly represented; it is reported only from Montopoli, Lower Valdarno. *E. livenzovensis* is a large-sized representative (about 1.60 m at the shoulder), closely related with *E. stenorionis* with which it shares several common post-cranial characters.

E. stenorionis (Fig. 1) appeared at the end of the Late Pliocene in Middle Villafranchian assemblages. It may represent a European offspring from *E. livenzovensis*. However, recently a new subspecies of *E. stenorionis* (*E. stenorionis anguinus*) from some Pliocene sites of North America open new problems on the origin of this species. The most significant occurrences of Europe are from Saint Vallier, La Puebla de Valverde, Senèze, Chilhac, Venta Micena and Mygdonia. Several authors (Prat, 1964; 1980; Boeuf, 1986; Marin, 1987; Koufos, 1992; etc.) recognized several subspecies with stratigraphic significance. However the characters used for separating the various subspecies seem rather to have geographical significance. In Italy the species is well represented in the faunal assemblages from Olivola (Magra Valley), Matassino and Terranova Bracciolini (Upper Valdarno), Selvella (Chiana Valley) and Pirro (Apulia). From the oldest representatives in Italy, those from Olivola and Matassino (Olivola Faunal Unit), to the most recent ones from Pirro (transitional Villafranchian-Galerian faunas) the limbs grow progressively more slender, as shown by the astragali and metapodial bones (Figs. 2 and 3). Also the size seems to improve parallelly. The specimens from Saint Vallier and La Puebla seem to be very similar to those from Olivola and Matassino, while the ones from Venta Micena and Mygdonia to those from Selvella and Pirro. The reduced dimensions of the Pliocene population from Senèze are linked with local adaptations. *E. stenorionis* became extinct between the Early and Middle Pleistocene.

The type specimen of *E. stehlini*, IGF 563 (Fig. 1) was found near Terranova Bracciolini, Upper Valdarno, but its exact stratigraphic provenance is indetermined. The Casa Frata fauna (Borselli *et al.*, 1980; De Giulii & Masini, 1987), which is referred to the Tasso Faunal Unit, yielded several remains of *E. stehlini*. Although similar to *E. stenorionis*, the species is easily recognizable for its reduced size (about 1.15 m at the shoulder), for the asinine characters of the skull (the premaxillary spine and the prominent and forward-faced orbital cavities), which otherwise recalls that of *E. stenorionis*. The first upper premolar lacks in the upper cheek tooththrow, while it is always present in *E. stenorionis*. According to Azzaroli (1965) and Privat-Defaus (1985), *E. stehlini* derived from *E. stenorionis* by sympatrical speciation during the Early Pleistocene. However, no case of sympatrical speciation is known at present among mammals. In Europe only the poor material from Vallonnet (Southern France), which provided remains of a transitional Villafranchian-Galerian fauna, could be referred to *E. stehlini*. If the latter attribution will be confirmed by further studies, the species

Fig. 1 - (1) *Equus livenzovensis* (Eurasia, Late Pliocene): tentative reconstruction of the skull, left lateral view. Condilo-basal length: about 600 mm. (2, 2a-2b) *Equus stenorionis* (North America, Eurasia, Late Pliocene-Early Pleistocene): IGF 560 from the Upper Valdarno, type skull, left lateral view. Condilo-basal length: about 590 mm; (2a) IGF 560 from the Upper Valdarno, type skull: left upper tooththrow, occlusal view, about natural size; (2b) IGF 560 from the Upper Valdarno, type specimen: right lower tooththrow, occlusal view, about natural size. (3-3a & 4) *Equus stehlini* (Italy, France?, Early Pleistocene): IGF 563 from the Upper Valdarno, type skull, left lateral view. Condilo-basal length: about 495 mm; (3a) IGF 563 from the Upper Valdarno, type skull: left upper tooththrow, occlusal view, about natural size; (4) IGF 562 from the Upper Valdarno: left lower tooththrow, occlusal view, about natural size. (5-6) *Equus gr. bressanus-süssenbornensis* (France, Great Britain, Italy, Early Pleistocene): IGF 11559 from Bucine, Upper Valdarno: right upper premolar, occlusal view, about natural size; (6) Uncatalogued from Chiugiana (Perugia): left lower premolar, occlusal view, about natural size.

(1) *Equus livenzovensis* (Eurasia, Pliocene superiore): tentativo di ricostruzione del cranio, norma laterale sinistra. Lunghezza condilo-basale: circa 600 mm. (2, 2a-2b) *Equus stenorionis* (Nord America, Eurasia, Pliocene superiore-Pleistocene inferiore): IGF 560 dal Valdarno Superiore, cranio tipo, norma laterale sinistra. Lunghezza condilo-basale: circa 590 mm; (2a) IGF 560 dal Valdarno Superiore, cranio tipo: serie dentaria sinistra, norma occlusale, circa dimensioni naturali; (2b) IGF 560 dal Valdarno Superiore, esemplare tipo: serie dentaria inferiore destra, norma occlusale, circa dimensioni naturali. (3-3a & 4) *Equus stehlini* (Italia, Francia?, Pleistocene inferiore): IGF 563 dal Valdarno Superiore, cranio tipo, norma laterale sinistra. Lunghezza condilo-basale: circa 495 mm; (3a) IGF 563 dal Valdarno Superiore, cranio tipo: serie dentaria sinistra, norma occlusale, circa dimensioni naturali; (4) IGF 562 dal Valdarno Superiore: serie dentaria inferiore sinistra, norma occlusale, circa dimensioni naturali. (5-6) *Equus gr. bressanus-süssenbornensis* (Francia, Gran Bretagna, Italia, Pleistocene inferiore): IGF 11559 da Bucine, Valdarno Superiore: premolare superiore destro, norma occlusale, circa dimensioni naturali; (6) non catalogato da Chiugiana (Perugia): premolare inferiore sinistro, norma occlusale, circa dimensioni naturali.



would not be stratigraphically and geographically confined within the Late Villafranchian of Tuscany.

At the end of the Early Pleistocene the *E. stenonis* lineage seems to have given rise to the largest-sized equid known until now (1.70+1.80 m at the shoulder). The species is characterized by peculiar morphologies, such as, in many cases, the exceptionally complex folding of the enamel. Many authors recognized two different large-sized species, one typical of Late Villafranchian faunal contexts, *E. bressanus*, and the other characteristic of Early Galerian assemblages, *E. süssenbornensis*. Nevertheless, the characters used to separate the two species are considered insufficient here, and therefore the large-sized Late Villafranchian-Early Galerian equids of Europe are referred here to *E. gr. bressanus-süssenbornensis* (Fig. 1). The most significant finds in Europe are rare and fragmentary. They come from Chagny and Senèze (France), East Runton (Great Britain), Pietrafitta, Galleria-di-Bucine and other sites near Verona (Italy).

3. TAPIRIDS

The genus *Tapirus* seems to have appeared in Europe during the Early Miocene. It reached its highest grade of diversification and diffusion during the Middle Miocene. Between the end of the Middle Miocene and the Late Miocene the genus rapidly declines. During the Pliocene, and perhaps already during the latest Late Miocene, only one species is reported, *Tapirus arvernensis* (Fig. 4). This species is easily distinguishable from the extant South American and Asian ones. *Tapirus arvernensis* seems relatively more closely related with the latter.

The Pliocene tapir of Europe was smaller-sized, more slender and had limbs quite more cursorially struc-

tured than present day representatives.

The oldest evidence of the species seems that from Baccinello V3, a site characterized by a Late Turolian association (Rook & Rustioni, 1991; Rustioni, 1992). However, the oldest representatives in Central Europe are from the Ruscinian levels of Montpellier, which, together with those from Vialette, are the smallest-sized individuals hitherto known. On the other hand, the specimens from Hajnacka I, a site correlated with Early Villafranchian Faunal Unit Triversa, together with those from Auvergne, Les Etouaires and the Upper Valdarno, are the largest-sized representatives known at present. The dimensions and few other morphological traits permit to group the Pliocene tapirs of Europe into two subspecies: *Tapirus arvernensis minor* and *Tapirus arvernensis arvernensis*. *T. arvernensis* disappeared during the Middle Pliocene, at the time of the great faunal turnover that wiped away all the typical forest-dwelling animals characteristic of the Triversa Faunal Unit. The few remains reported from Tegelen are attributed with doubt to the Middle Villafranchian because of the uncertain stratigraphic provenance of the specimens (Azzaroli *et al.*, 1988; Rustioni, 1992).

4. RHINOCERONTIDS

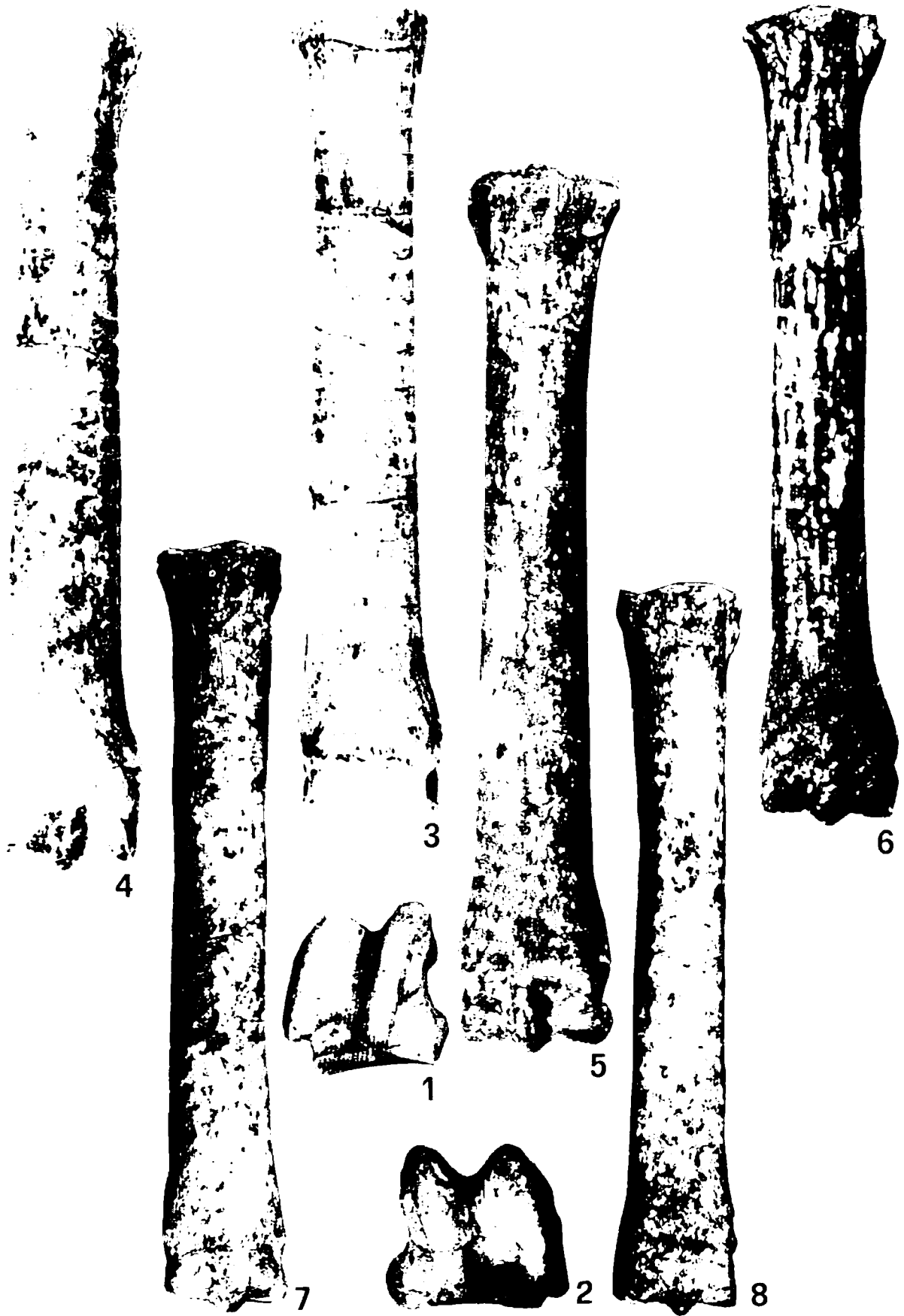
Four species settled in Western Europe during the time spanning the Middle Pliocene-Early Pleistocene interval, *Stephanorhinus jeanvireti*, *S. etruscus*, *S. hundsheimensis* and *S. hemitoechus*. At the moment, the phylogenetic relationships between these species is still controversial, but this topic goes beyond the scope of the present paper. Pending an up-to-date revision of the phylogeny of European rhinoceroses, since all four the named species are morphologically fairly uniform and share common dental features, they may provisionally be placed in one clade.

Stephanorhinus jeanvireti (Fig. 5A) makes its appearance in the Western European theater approximately 3 Ma ago as attested by the Early Villafranchian finds from Vialette, Les Etouaires and Dusino (Villafranca d'Asti). Recently a particularly large-sized representative was found at Roatto (Villafranca d'Asti) (B. Sala, pers. comm.). *S. jeanvireti* was a large-sized rhinoceros, with relatively slender, cursorially structured limbs. It is distinct, in morphology and proportions, from *S. etruscus*, while it apparently shares a number of cranial characters in common with *S. hundsheimensis*, although the only known skulls of *Stephanorhinus jeanvireti*, two specimens (Vt. 627, holotype of the species, and Vt. 621) from Vialette, both preserved at the *Naturhistorisches Museum* of Basel, are largely restored in plaster, with only few original parts.

Guérin (1980) reported the most ancient *S. etruscus* (Fig. 5B) representatives from the Lower Villafranchian sites of Les Etouaires, Villafranca d'Asti, Montopoli and Villaroya. Mazza (1988) considered this record too poorly

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Fig. 2 - (1) *Equus stenonis* (Olivola, Magra Valley, northern Tuscany): IGF 11272, left metacarpal, dorsal view, about 1/2 natural size. (2-3) *Equus stenonis* (Upper Valdarno, central Tuscany): (2) IGF 11042, left metacarpal, dorsal view, about 1/2 natural size; (3) IGF 11041, right metacarpal, dorsal view, about 1/2 natural size. (4-5) *Equus stenonis* (Selvella, central Tuscany): (4) IGF 14092, right metacarpal, dorsal view, about 1/2 natural size; (5) IGF 14333, left metacarpal, dorsal view, about 1/2 natural size. (6-7) *Equus stenonis* (Pirro, Apulia): (6) IGPB 11, right metacarpal, dorsal view, about 1/2 natural size; (7) IGPB PP27, right metacarpal, dorsal view, about 1/2 natural size.

(1) *Equus stenonis* (Olivola, Val di Magra, Toscana settentrionale): IGF 11272, metacarpo sinistro, norma dorsale, circa 1/2 della dimensione naturale. (2-3) *Equus stenonis* (Valdarno Superiore, Toscana centrale): (2) IGF 11042, metacarpo sinistro, norma dorsale, circa 1/2 della dimensione naturale; (3) IGF 11041, metacarpo destro, norma dorsale, circa 1/2 dimensione naturale. (4-5) *Equus stenonis* (Selvella, Toscana centrale) (4) IGF 14092, metacarpo destro, norma dorsale, circa 1/2 della dimensione naturale; (5) IGF 14333, metacarpo sinistro, norma dorsale, circa 1/2 della dimensione naturale. (6-7) *Equus stenonis* (Pirro, Puglia) (6) IGPB 11, metacarpo destro, norma dorsale, circa 1/2 della dimensione naturale; (7) IGPB PP27, metacarpo destro, norma dorsale, circa 1/2 della dimensione naturale.



documented and thus gave scarce credit to it. Nevertheless, the specimens from marine Pliocene sediments reported by Cuscani Politi (1963; 1971) and some specimens (a juvenile skull and astragalus) from Montopoli, revisited for the present study and a mandible recently found at Città della Pieve (Perugia) (Fortelius *et al.*, 1993) indubitably confirm the occurrence of *S. etruscus* in Early Villafranchian faunal contexts. Mazo & Torres (1989-1990) reported the occurrence of *S. cf. etruscus* from Pozo de Piedrabuena, a Middle Pliocene locality of Spain. A. Mazo personally informed us that other significant rhinoceros material was recently retrieved from this site. It thus seems that *S. etruscus* is actually one of the new arrivals that mark the Ruscinian to Early Villafranchian faunal turnover. Remains of this lightly built, cursorial rhinoceros are then found in most of the Middle to Late Villafranchian (2.5-1.0 Ma) sites of Western Europe. It is one of the most characteristic elements of the Villafranchian, like *Equus stenonis* is among equids. *S. etruscus* apparently disappeared at the time of the Villafranchian-Galerian turnover (1.0-0.7 Ma). However, in the latest Villafranchian communities *S. etruscus* seems to be accompanied, or even replaced, by peculiar small-sized specimens with *S. etruscus*-*S. hundsheimensis* affinities. These characteristic elements were found at Pirro (Gargano, Southern Italy), Loreto (Venosa, Southern Italy), Westerhoven (Brabant, The Netherlands) and Wissel (Kalkar, Germany), only in levels dated to the end of the Early Pleistocene (Mazza *et al.*, 1993; Fortelius *et al.*, 1993). They therefore seem to be good markers, given their sharp stratigraphic distribution.

S. hundsheimensis (Fig. 1C) is the typical Middle Pleis-

tocene representative indicated in the passed literature with several names, such as the massive or large-sized etruscan rhinoceros, *Dicerorhinus etruscus brachycephalus*, *D. etruscus heidelbergensis*, *D. hemitoechus intermedius*, and so on. The most ancient representatives of this species characterize very late Villafranchian communities. Besides the already mentioned dubious cranial resemblance to *S. jeanvireti*, *S. hundsheimensis* shares a number of dental and postcranial features with *S. etruscus*, which attests to a possible descent from the latter species.

Nevertheless, the true ascendance of the species is still unresolved. *S. hundsheimensis* was more massively built than *S. etruscus*, but had cursorially structured limbs. It apparently disappeared during the Middle Pleistocene, since the last ascertained occurrence of *S. hundsheimensis* is from Mosbach-2 (*sensu* Koenigswald & Tobien, 1987).

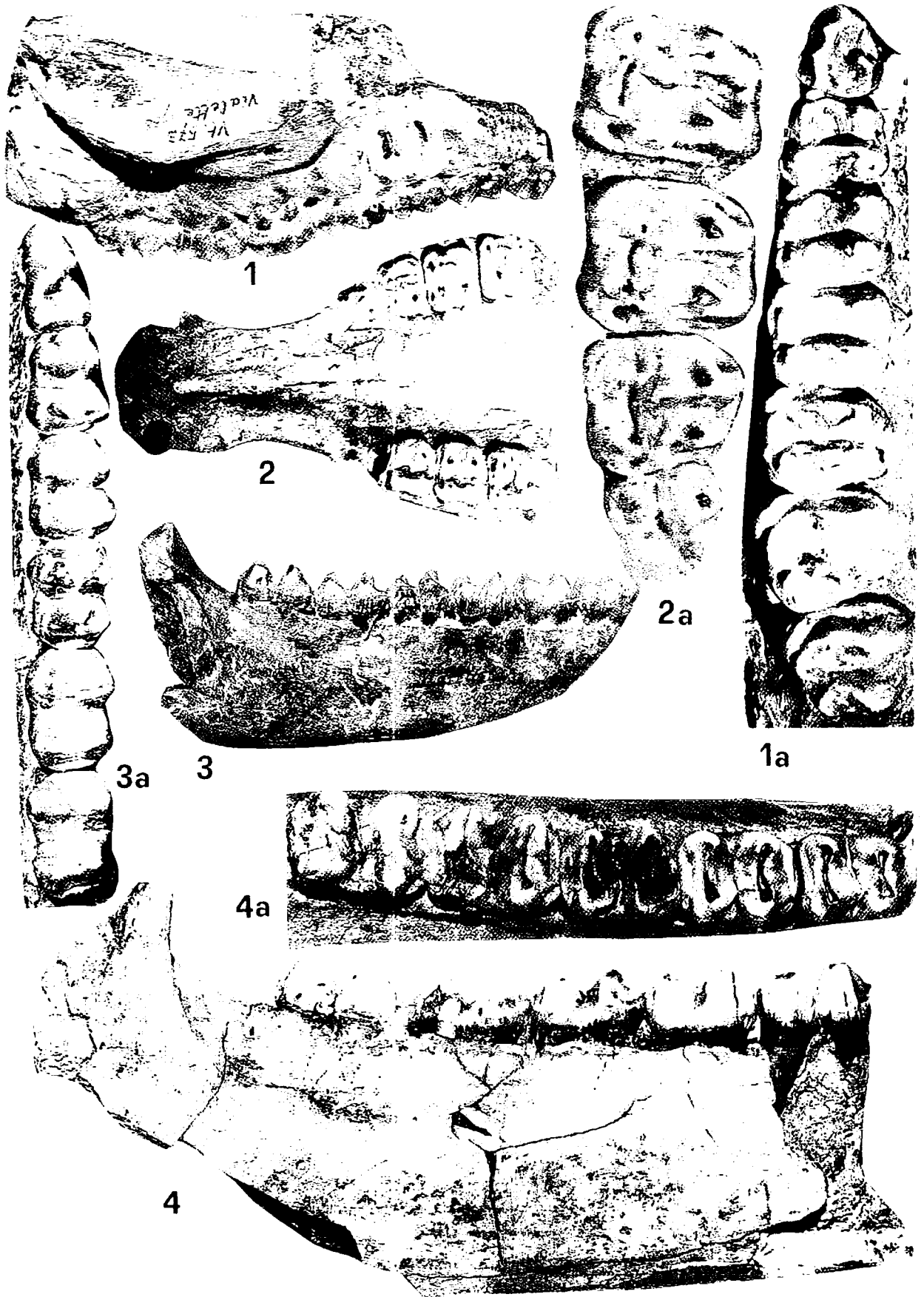
S. hemitoechus (Fig. 5D) is a typical representative of Middle and Late Pleistocene mammal assemblages. However, the first occurrence of the species is doubtful, because the most ancient specimens attributable to *S. hemitoechus* are of stratigraphically problematic provenance. Leaving aside two mandibles of *S. hemitoechus* found at Bacton, in East Anglia, which may actually come from Late Pleistocene deposits, three specimens, a complete mandible from Serravalle d'Arbia (Siena), a partial mandible from Croce dei Cappuccini (Upper Valdarno) (Fortelius *et al.*, 1993) and a partial skull from Grezzano (Mugello) (Mazza, 1988) show clear *S. hemitoechus* affinities. Although these specimens make part of historical collections and therefore lack clear stratigraphic references, these scattered remains from areas famous for Late Villafranchian finds make us suspect that *S. hemitoechus* may have appeared in Europe in times slightly older than commonly accepted. *S. hemitoechus* was a short-limbed, graviportally structured sturdy grazer, characterized by hypsodont molars, a down-slung cranium and stocky metapodials. *S. hemitoechus* probably was the ecological equivalent, in the steppe environment, of the tundra rhinoceros *Coelodonta antiquitatis* (Fig. 5E), with which it shares a number of analogies.

REFERENCES

Fig. 3 - (1) *Equus stenonis* (Pirro, Apulia): IGPB PP42, right astragalus, dorsal view, about 1/2 natural size. (2-3) *Equus stenonis* (Olivola, Magra Valley, northern Tuscany): (2) IGF 11244, left astragalus, dorsal view, about 1/2 natural size; (3) IGF 11268, left metatarsal, dorsal view, about 1/2 natural size. (4) *Equus stenonis* (Matassino, Upper Valdarno, central Tuscany): IGF 12833, left metatarsal, dorsal view, about 1/2 natural size. (5-6) *Equus stenonis* (Selvella, central Tuscany): (5) IGF 14190, left metatarsal, dorsal view, about 1/2 natural size; (6) IGF 14187, left metatarsal, dorsal view, about 1/2 natural size. (7-8) *Equus stenonis* (Pirro, Apulia): (7) IGPB 13, left metatarsal, dorsal view, about 1/2 natural size; (8) IGPB 2, left metatarsal, dorsal view, about 1/2 natural size.

(1) *Equus stenonis* (Pirro, Puglia): IGPB PP42, astragalo destro, norma dorsale, circa 1/2 dimensione naturale. (2-3) *Equus stenonis* (Olivola, Val di Magra, Toscana settentrionale): (2) IGF 11244, astragalo sinistro, norma dorsale, circa 1/2 della dimensione naturale; (3) IGF 11268, metatarso sinistro, norma dorsale, circa 1/2 della dimensione naturale. (4) *Equus stenonis* (Matassino, Valdarno Superiore, Toscana centrale): IGF 12833, metatarso sinistro, norma dorsale, circa 1/2 della dimensione naturale. (5-6) *Equus stenonis* (Selvella, Toscana centrale): (5) IGF 14190, metatarso sinistro, norma dorsale, circa 1/2 della dimensione naturale; (6) IGF 14187, metatarso sinistro, norma dorsale, circa 1/2 della dimensione naturale. (7-8) *Equus stenonis* (Pirro, Puglia): (7) IGPB 13, metatarso sinistro, norma dorsale, circa 1/2 della dimensione naturale; (8) IGPB 2, metatarso sinistro, norma dorsale, circa 1/2 della dimensione naturale.

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Fig. 4 - (1-1a) *Tapirus arvernensis*: VT 573 from Vialette, "Naturhistorisches Museum Basel": fragmentary skull, adult specimen: (1) right lateral view, about 1/2 natural size; (1a) right toothrow, occlusal view, about natural size. (2-2a) Not catalogued from Villafranca d'Asti, "Naturhistorisches Museum Basel": fragment of palate, adult specimen: (2) ventral view, about 1/2 natural size; (2a) detail of the right premolar row, occlusal view, not to scale. (3-3a) VT 573 from Vialette, "Naturhistorisches Museum Basel": fragment of right mandible: (3) right lateral view, about 1/2 natural size; (3a) right toothrow, occlusal view, about natural size. (4-4a) Not catalogued from Villafranca d'Asti, "Naturhistorisches Museum Basel": fragment of right mandible: (4) right lateral view, about 2/3 natural size; (4a) detail of the right toothrow, occlusal view, about nat. size.

(1-1a) *Tapirus arvernensis*: VT 573 da Vialette, "Naturhistorisches Museum Basel": cranio frammentario, individuo adulto: (1) norma laterale destra, circa 1/2 della dimensione naturale; (1a) serie dentaria destra, norma occlusale, circa dimensioni naturali. (2-2a) Non catalogato da Villafranca d'Asti, "Naturhistorisches Museum Basel": frammento di palato, individuo adulto: (2-) norma ventrale, circa 1/2 della dimensione naturale; (2a) dettaglio della serie premolare, norma occlusale, non in scala. (3-3a) VT 573 da Vialette, "Naturhistorisches Museum Basel": frammento di mandibola destra: (3) norma laterale destra, circa 1/2 della dimensione naturale; (3a) serie dentaria destra, norma occlusale, circa dimensioni naturali. (4-4a) Non catalogato da Villafranca d'Asti, "Naturhistorisches Museum Basel": frammento di mandibola destra: (4) norma laterale destra, circa 2/3 dimensione naturale; (4a) dettaglio della serie dentaria destra, norma occlusale, circa dimensioni naturali.

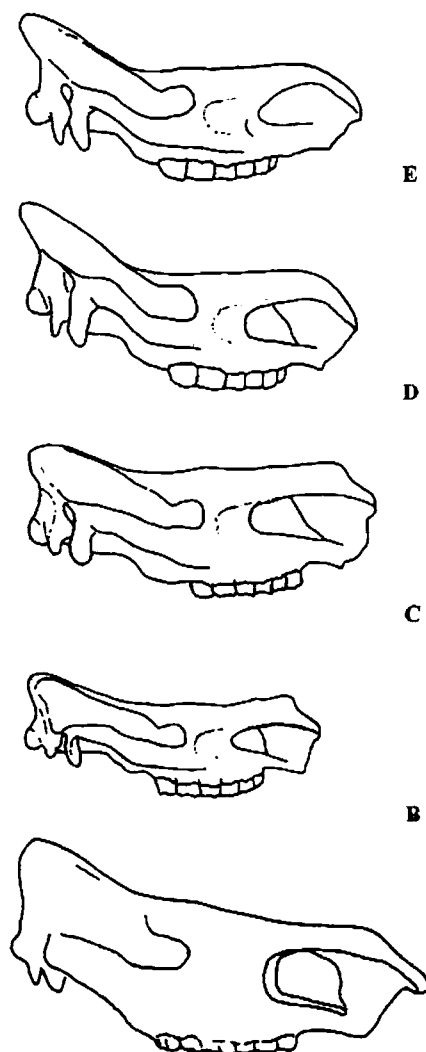


Fig. 5 - Right lateral views of the skulls of: (A) *Stephanorhinus jeanvireti*; (B) *Stephanorhinus etruscus*; (C) *Stephanorhinus hundsheimensis*; (D) *Stephanorhinus hemitoechus*; (E) *Coelodonta antiquitatis*. All figures are about 1/9 natural size.

Norma laterale destra dei crani di: (A) *Stephanorhinus jeanvireti*; (B) *Stephanorhinus etruscus*; (C) *Stephanorhinus hundsheimensis*; (D) *Stephanorhinus hemitoechus*; (E) *Coelodonta antiquitatis*. Tutte le figure sono circa 1/9 delle dimensioni naturali.

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