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On Pliocene tapirs from France and Italy

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ABSTRACT — *The Ruscinian and Villafranchian (Triversa f. u.) tapirs from Central-Western Europe and Italy are referred to Tapirus arvernensis. Scanty remains from Baccinello V3 and Casino are tentatively ascribed to this species. A specimen from Sarzanello is generically called Tapirus sp.*

T. arvernensis is easily distinguishable from the living South American species and Malayan tapir; it seems strictly related with the latter. It was smaller than the extant species, slenderly built and shows a fairly good level of specialization to cursoriality; it is one of the most cursorial species of the genus. Tentative reconstructions of the skull, of the arrangement of its muscles, and of some parts of the postcranial skeleton are proposed.

RIASSUNTO — [Osservazione sui tapiri pliocenici della Francia e dell'Italia] — *I resti fossili di tapiro rinvenuti in alcune località fossilifere rusciniane e villafranchiane (U.F. Triversa) dell'Europa centro-occidentale e dell'Italia sono riferiti a Tapirus arvernensis. Gli scarsi resti di Baccinello V3 e del Casino sono segnalati come Tapirus cf. arvernensis, mentre quelli di Sarzanello come Tapirus sp.*

T. arvernensis è facilmente distinguibile dalle specie sudamericane attuali e dal tapiro asiatico, col quale sembra essere strettamente imparentato. Era di taglia inferiore alle specie attuali, aveva corporatura snella e mostra un discreto grado di specializzazione per la corsa. Nell'ambito del genere, si tratta di una delle specie più cursoriali. Viene inoltre proposta una ricostruzione dei principali tratti del cranio, della sua muscolatura e di alcune porzioni dello scheletro postcraniale.

INTRODUCTION

The genus *Tapirus* L. seems to appear in Europe during the Early Miocene. In the Early and Middle Miocene, the genus widely dispersed as testified by its occurrence in several Western European sites (Guérin & Eisenmann, 1982).

The species which dispersed in Europe during the Pliocene and possibly in the Latest Miocene is *Tapirus arvernensis* Croizet & Jobert, 1828; it is reported from France, Italy, Germany, The Netherlands and Czechoslovakia (Fejfar, 1964; Guérin & Eisenmann, 1982).

HISTORICAL

Tapirus arvernensis was established by Croizet & Jobert in 1828 on fragments of mandibles and some isolated teeth of an adult and of a young individual. These specimen, were found, respectively, in the "... couche n° 24 du tableau, au ravin des Etouaires ..." and in the fossiliferous site "... Ardé, à quelques centaines de mètres du premier gisement, et à la meme élévation." (Croizet & Jobert, vol. 1, p. 162, Tapirs). The material was briefly described and figured (*ibid.*, pl. II, figs. 3 and 5, and pl. 12, figs. 4, 5 and 6); it

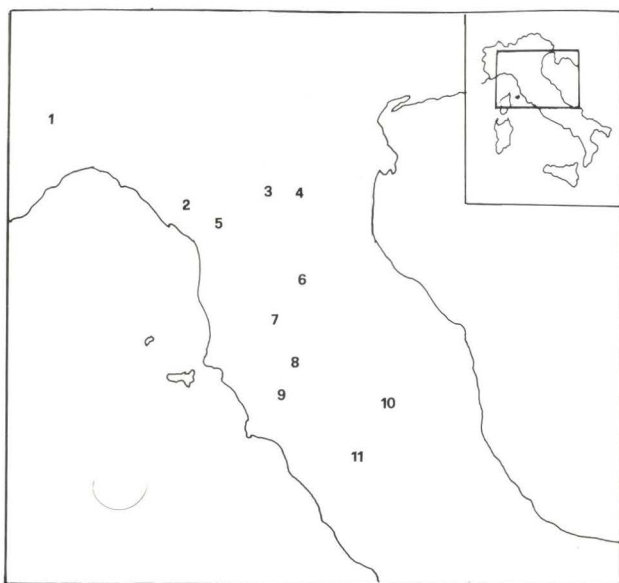
was referred to "... *tapir arvernensis*, pour le distinguer des autres espèces fossiles." (*ibid.*, p. 167, Résumé).

Formerly, tapir remains from the sandy fluvial levels of Mount Boulade, near Issoire, were described and figured by Devèze and Bouillet in 1827 (p. 50, pls. VI and VII). These Authors referred the specimens generically to *Tapirus*, but they stressed that it was smaller-sized than the living species known at that time.

Few years later, De Serres (1839) described new specimens found in the Early Ruscinian levels of Montpellier, establishing the species *Tapirus minor*. This species was accepted as valid by other authors, among whom Gervais (1859).

Describing a maxillary fragment found in the Rousillon, Depèret (1885) considered *T. minor* a synonym of *T. arvernensis*. Del Campana (1910) agreed with Depèret. However, *T. minor* is poorly represented and badly defined.

The specimens from the early Villafranchian levels (Triversa f. u.) of Viallette (Haute-Loire, France), now preserved in the Naturhistorisches Museum of Basel, were retrieved during 1937-1938 excavations; they are described in the following section. The specimens recovered in Italian sites (Text-fig. 1) are analysed further on.



Text-fig. 1 - Italian fossiliferous sites that provided tapir fossil remains: 1) Villafranca d'Asti; 2) Magra Valley; 3) Vignola; 4) Livergnana and Sasso di Glosina; 5) Garfagnana; 6) Upper Valdarno; 7) Casino; 8) Monticchiello; 9) Baccinello; 10) Spoleto; 11) Nera Montoro.

THE TAPIRS FROM VIALETTE

Heintz *et al.* (1974) provided an almost complete list of the fossil vertebrates found in the Early Villafranchian deposits of Vialette. In this paper, the tapir was referred to *Tapirus arvernensis*. The site was radiometrically dated to 3.3 ± 2.6 Ma by Couthures and Pastre (1983).

At Vialette, tapir remains dominate over those of other vertebrates. They belong to at least five specimens, three of which have the third lower molar in eruption.

Only the best preserved material was studied:

- uncatalogued, incomplete juvenile skull (Pl. 1, fig. 1; Text-fig. 7 A and B), with the last molars in eruption;
- two incomplete maxillaries and two mandibular horizontal rami attributed to an adult male because of their relatively small dimensions (VT 573) (Pl. 1, fig. 2; Pl. 2, fig. 2);
- fragmentary left mandible (VT 574) and uncatalogued incomplete mandible (Pl. 3, fig. 1) with erupting third molar;
- uncatalogued incomplete right maxillary;
- uncatalogued isolated teeth;
- two uncatalogued humeri (Pl. 4, fig. 2);
- five uncatalogued third metacarpals (Pl. 4, fig. 3);
- uncatalogued first phalanges of the third digit of the manus (Pl. 5, fig. 6);

- two uncatalogued femurs, one right (Text-fig. 7c; Pl. 5, fig. 1) and one left;
- four uncatalogued right tibia (Pl. 5, fig. 2);
- four uncatalogued third metatarsals (Text-fig. 9.2);
- uncatalogued first phalanges of the third digit of the pes (Pl. 5, fig. 6).

DESCRIPTION

Juvenile skull with mandible (uncatalogued, Museum of Basel) (Text-figs 5B, 7; Pl. 1, fig. 1).

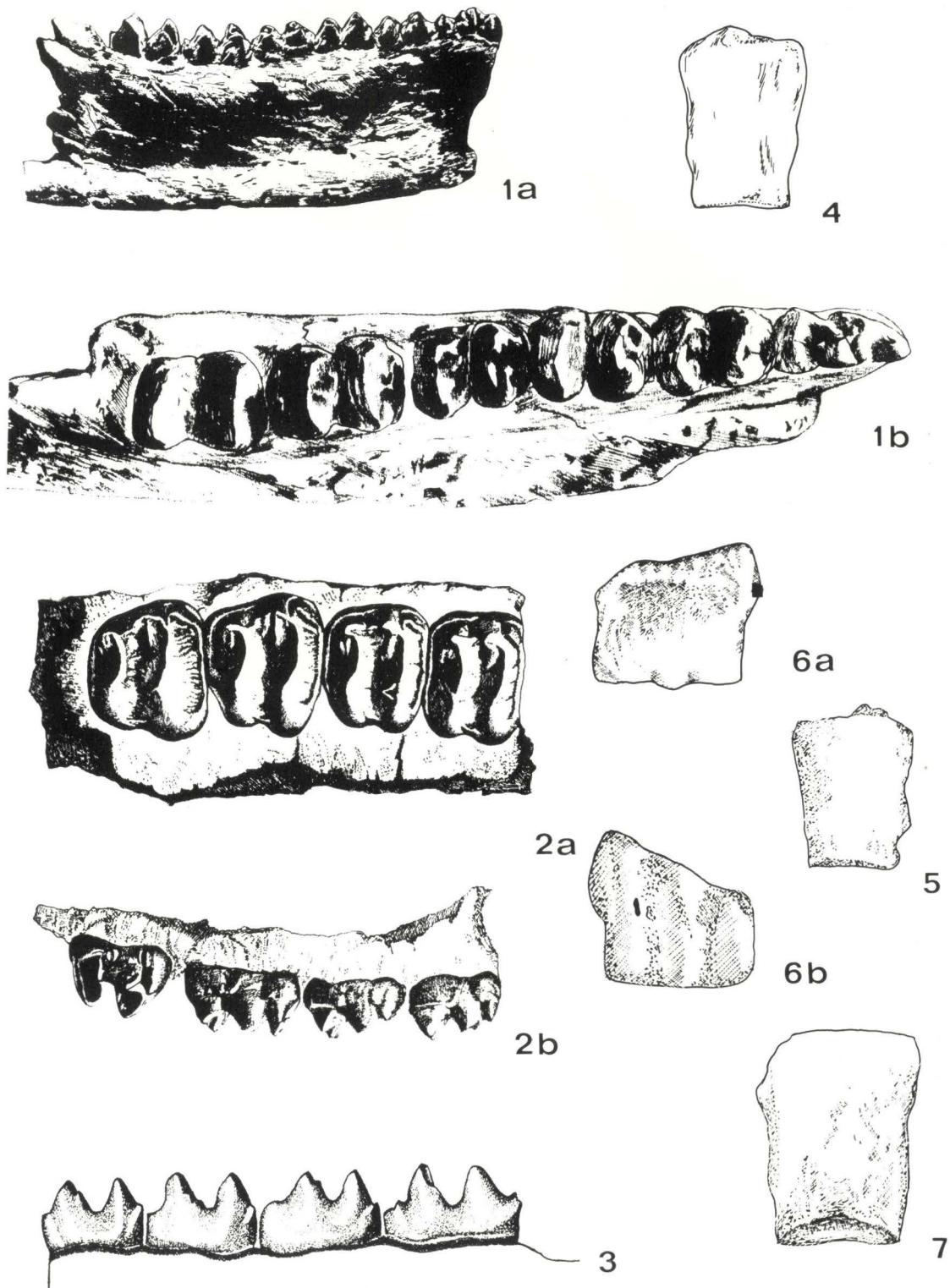
The skull is dorso-laterally crushed and its occipital region was lost. The prosthion-akrokranium length is approximately 335 mm. The morphology is typical of the genus: the neurocranium is more developed than the facial skeleton and the nasal bones are placed in high position and very short.

The neurocranium is relatively elongated and deep. The temporal lines are fairly developed; they reach the summit of the skull at the fronto-parietal suture starting from the lower margin of the nasal bones. The occiput is slightly inclined backwards and the occipital condyles are protruding. The fronto-parietal profile is straight and dips gently toward the nasal area; it interrupts at the Tubera Frontalis, which are slightly prominent. The orbits are fairly low and its fore rim overlies the M2/-M3/ commissure. Also the zygomatic arches are proportionally more robust and shifted in a relatively lower position than in other species. The greatest height of the zygomatic arch is 40,2 mm. The retroarticular process, is well developed. I1/ and I2/ are broad.

The facial skeleton is short and the premaxillae are reduced. The narial opening is wide: the narial notch is placed high and is deep, approximately extending over the 2nd half of the first upper molar. The nasal bones are short.

The upper incisors and canines are deformed or lost. The cheek teeth are relatively short, broad and rectangular: the parastyle is well developed, especially in the molars. Cingula are strong anteriorly and posteriorly, weak lingually and extremely weak or completely absent buccally.

The mandible has slender horizontal rami with convex or slightly convex ventral profiles, backward projected ventral gonions and fairly massive ascending rami. The zygoma, the base of the skull and the mandible are structured so to suggest the existence of strong masseterine and pterygoid muscles. The sigmoidal incisures are shallow and the coronoid processes are moderately salient. The mandibular foramina open under the fore halves of the second premolars. The lower incisors are broad: the second lower incisor equal in size the first ones. The lower canines are laterally compressed with rather marked front and rear crests.



Text-fig. 2 - 1) *Tapirus arvernensis*, Upper Valdarno, IGF 917, incomplete left mandible; a) medial view about 1/2 nat. size; b) lateral view, about nat. size. 2) *Tapirus* sp. Sarzanello, IGF 177OV, cast, right upper fourth premolar and molar row; a) lateral view; b) occlusal view, about nat. size. 3) *Tapirus arvernensis*. Spoleto, modified from Del Campana (1910) fragment of the left mandible with the fourth premolar and the molar row, internal view, about nat. size. 4-7) *Tapirus* cf. *arvernensis*. Casino, AFS. 4) left manus, first phalanx of the fourth digit, dorsal view, about nat. size; 5) left manus, first phalanx of the fourth digit, dorsal view, about nat. size; 6) distal end of the left third metatarsal bone, a) dorsal view, b) plantar view, about nat. size; 7) right pes, first phalanx of the central digit, dorsal view, about nat. size.

All lower cheek teeth bear fairly well developed mesial and caudal cingula, while cingula are hardly developed, or completely lack, on the labial and lingual sides. The lobes of the first lower molars may be of the same size.

Postcranial skeleton (uncatalogued specimens preserved in the Museum of Basel, Text-fig. 6; Pl. 4, figs. 2, 3, 5; Pl. 5, figs. 1, 2, 4-6; Text-fig. 9.2).

The postcranial bones are slender and generally have narrow epiphyses.

In the humerus, the deltoid tuberosity is well developed; it is placed in a rather proximal position. The Teres major tuberosity is slightly prominent. A coronoïd foramen sometimes occurs in the distal epiphysis. The olecranic fossa is broad and deep (Pl. 4, fig. 2). The metacarpal are proportionally slender (Pl. 4, fig. 3) and the first phalanges of the third digit of the manus are dorso-ventrally flattened (Pl. 4, fig. 5).

The Caput Femori, is relatively small with a wide and deep legamentous fossette. The greater trochanter is salient, but not massive. The lesser trochanter is shifted proximally along the diaphysis; it is stretched proximo-distally. The third trochanter is well developed and slightly concave in its cranial face (Text-fig. 6C; Pl. 5, fig. 1).

The tibia is slender and has a sinuous diaphysis in dorsal and plantar view (Pl. 5, fig. 2).

The metatarsal are more slender than metacarpal (Text-fig. 9.2; Pl. 4, fig. 3).

The first phalanges of the third digits of the pes are dorso-ventrally flattened (Pl. 5, fig. 6) but are more slender than those of the manus (Pl. 4, fig. 5).

FOSSIL TAPIRS FROM ITALY

Villafranca d'Asti (Asti, Piedmont) (Pl. 1, fig. 3; Pl. 2, fig. 1; Pl. 3, fig. 2).

Several authors have quoted the mammals from this locality, among which Michaux (1970), Savage & Curtis (1970), Azzaroli (1970, 1977, 1980), Azzaroli *et al.* (1986, 1988), etc. The assemblage of this site, paleomagnetically dated 3.01 ± 3.05 Ma (Lindsay *et al.*, 1980) was selected to typify the oldest faunal unit of the Villafranchian (Azzaroli, 1977).

The tapir specimens from Villafranca d'Asti were collected by Mr. Masoero and are now kept at the Naturhistorisches Museum of Basel. Tapir remains are represented by an incomplete palate (Pl. 1, fig. 3), one incomplete mandible and two fragmentary hemimandibles (Pl. 2, fig. 1; Pl. 3, fig. 2) a first phalanx of the third digit of the manus and part of the diaphysis of a right humerus. All this material seems to belong to at least three individuals.

The specimens from Villafranca are distinguished from the ones from Viallette by having shorter pre-molar rows. In terms of morphology, the only significant difference is that in the upper premolars the lingual cusps are more shifted forwards than in all the other specimens studied. The metalophs of the second upper premolars are interrupted by a cleft which opens into the main valley between the lophs. In my opinion, these differences fall in the variability of *T. arvernensis* and therefore are not diagnostic.

Gaville and Santa Barbara, Upper Valdarno (Arezzo, Tuscany) (Text-fig. 2.1; Pl. 3, figs. 4, 5; Pl. 4, figs. 1, 6, 7; Pl. 5, fig. 3; Text-figs. 9.1, 3-6).

The oldest fossil vertebrates come from the Pliocene lignitiferous clays of the Castelnuovo dei Sabbioni Group (Merla & Abbate, 1967; Azzaroli, 1967, 1977, 1982; Azzaroli *et al.*, 1982, 1986). The faunal remains are poor and fragmentary; most were retrieved, together with plant remains typical of a warm and humid climate, in the clays over the main lignite levels, locally called "Stelliccione". Azzaroli (1977) correlated the assemblage with the Triversa f.u.

De Giuli (1983) provided a full list of mammals, which includes: *Ursus minimus*, *Mammuth borsoni*, *Anancus arvernensis*, *Tapirus arvernensis*, *Dicerorhinus* sp., a small- to middle-sized *Leptobos* sp. Rustioni (1987) tentatively referred the bovid to *Leptobos stenometopon* and observed that the rhinoceros seems to be closer to *Dicerorhinus jeanvireti* than to other species.

The Upper Valdarno tapir was first quoted by De La Beche (1833). Later on, new finds were reported by Blainville (1841), Strozzi (1858), Falconer (1868) and Stoppani (1873).

Del Campana (1910) referred two incomplete mandibles, some maxillary fragments and some isolated

EXPLANATION OF PLATE 1

- Figs. 1-2 - *Tapirus arvernensis*, Viallette, Naturhistorisches Museum of Basel;
 1) skull with mandible, young specimen, right lateral view, not to scale;
 2) VT 573, fragmentary skull, adult specimen; a) right lateral view, about 1/2 nat. size; b) right toothrow, occlusal view, about nat. size.
 Fig. 3 - *Tapirus arvernensis*, Villafranca d'Asti, NMB; a) fragment of the palate, adult specimen, left lateral view, about 1/2 nat. size; b) occlusal view, about 1/2 nat. size; c) detail of the left premolar row, not to scale; d) detail of the right premolar row, not to scale.



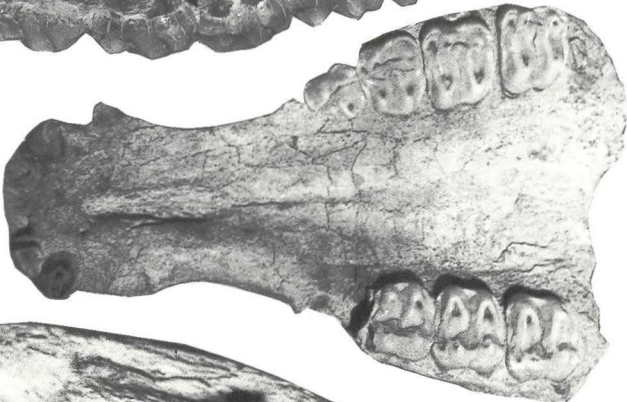
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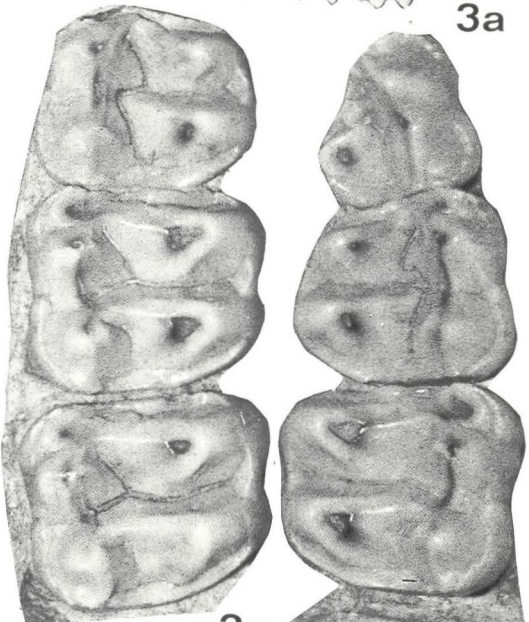
2a



3a



3b



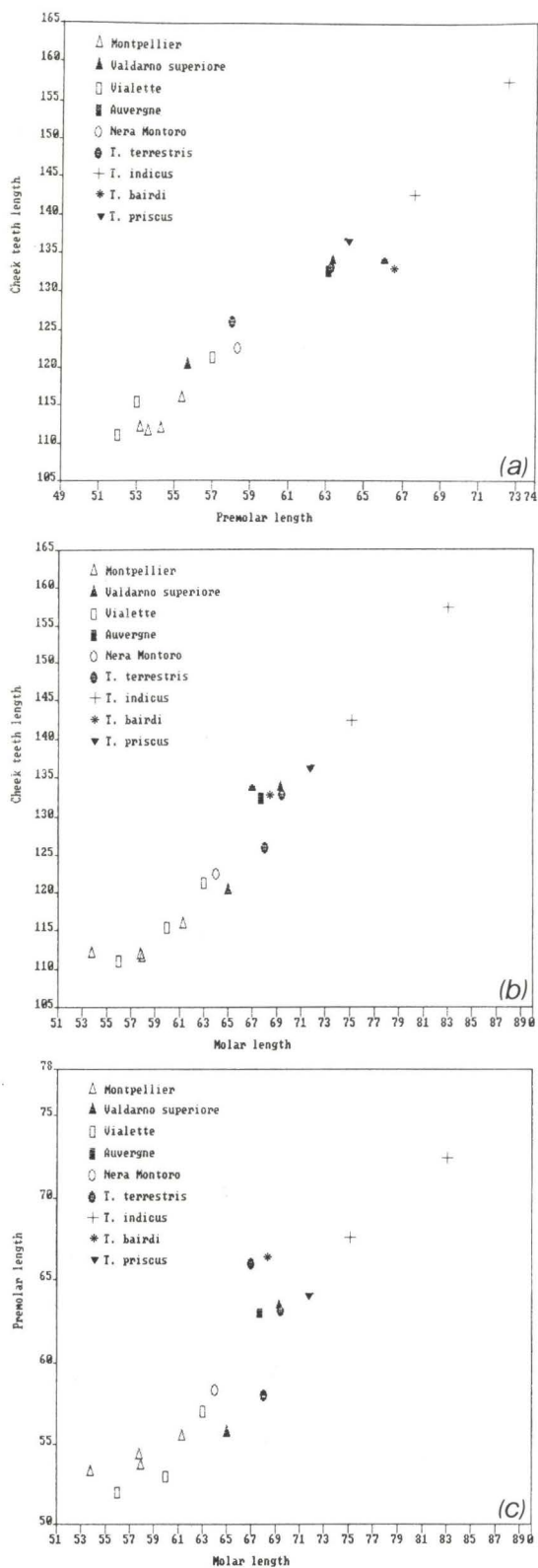
3c



2b



3d



Text-figs. 3 - Scatter diagram of the lower teeth: a) premolar length (LP) versus total length; b) molar length (LM) versus total length (LMP); c) molar length versus premolar length.

teeth to *T. arvernensis*. The same Author also reported and figured an incomplete juvenile skeleton, IGF 915, but did not described it.

Most tapir specimens are preserved in the Museum of Geology and Paleontology of Florence. Leaving aside the young individual mentioned above, at least three adult specimens are present in collection, IGF 917, IGF 918 and IGF 1939V. IGF 917 comes from Gaville; it is represented by a third right upper molar (Pl. 3, fig. 4), an incomplete horizontal ramus of left mandible, without the portion in front of P/2 (Text-fig. 2.1), and by the metalophid of the second right lower molar; IGF 918 by a wonderfully preserved third right upper molar (Pl. 3, fig. 5); IGF 1939V by part of the mandible and some postcranial elements, among which a distal fragment of right humerus, two anterior phalanges (Pl. 4, figs. 6, 7) a proximal fragment and trochlea of the left femur (Text-fig. 9.1), the Caput femoris and the medial condyle of the right femur, a fragment of the proximal end of the right tibia (Pl. 5, fig. 3), three fragmentary metatarsal bones (Text-fig. 9.3, 4) and four posterior phalanges (Text-fig. 9.5, 6). IGF 917 is the largest specimen from Italy and has a size comparable with the large specimens from Auvergne (cast IGF 1268V) and Hajnacka (Fejfar, 1964). The teeth are narrow, rectangular; the second premolar has a robust paraconid, the protoconid is decidedly shifted forwards with respect to the metaconid and the talonid is latero-medially compressed. The molar IGF 918 is characterized by a strong parastyle. IGF 1939V is middle-sized and slender.

Two incomplete lower tooththrows of an adult specimen (M 25) (Pl. 4, fig. 1), still bedded in lignite of the Santa Barbara mine, are preserved in the Paleontological Museum of Montevarchi.

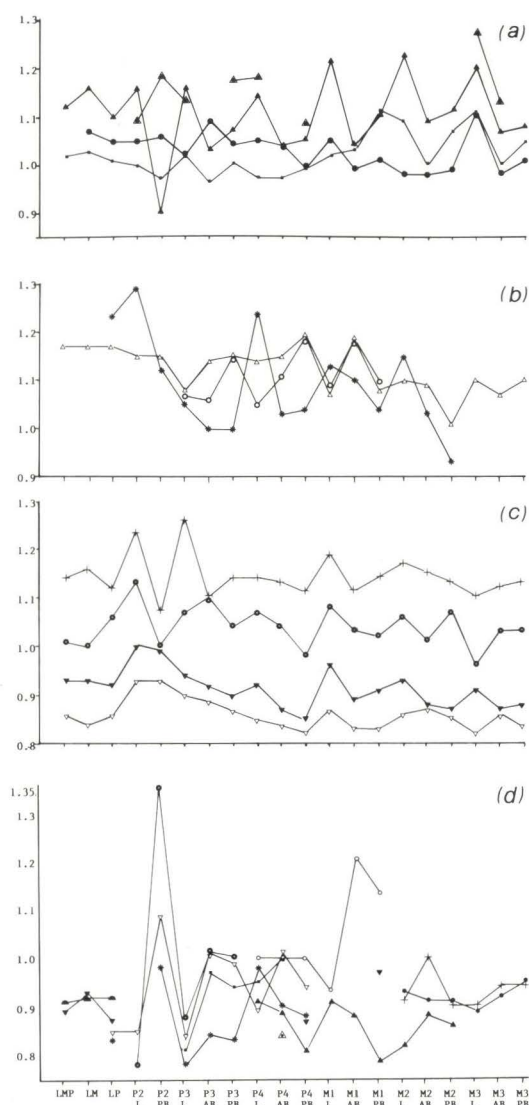
All these specimens are morphologically similar to those from Viallette; differences are slight and fall in the variability of *T. arvernensis*.

Spoleto (Terni, Umbria) (Text-fig. 2.3)

The faunal assemblage, composed by *Anancus arvernensis*, *Mammuth borsoni* and *Tapirus arvernensis*, is correlatable with the Triversa f. u..

Few molars of *Anancus arvernensis* from this site were first reported by Capellini (1879). Pantanelli (1886) referred an incomplete left mandible of tapir (Text-fig. 2.3) to *T. arvernensis*. The same Author tentatively attributed to this species also some postcranial bones from this site. Del Campana (1910) confirmed Pantanelli's specific attribution.

Casts of a fourth right lower premolar and of a first right lower molar, IGF 838V, were studied. The protolophid and metalophid of the first molar are the largest ever observed in the specimens studied.



Text-fig. 4 - Ratio diagram, lower teeth. Standard: specimens of Montpellier (n. min. LP = 3, n. max. M1 = 7)
 a) ● Viale; ▲ Hajnacka (data from Fejfar, 1964); ■ Villafranca d'Asti; ▲ Upper Valdarno
 b) ▲ Auvergne (IGF 1268V); ○ Les Vans (MUL n° 210010, Sala *et al.*, 1990; ☆ Perrier (Les Etouaires, Sala *et al.*, 1990). The sample of Montpellier was partly enriched with data from Sala *et al.*, 1990.
 c) Standard: *Tapirus terrestris*, data from Simpson (1945); + *Tapirus indicus*; ○ *Tapirus bairdi* (data from Simpson, 1945, one specimen); ▼ *Tapirus arvernensis*; ▽ *Tapirus arvernensis* (Montpellier).
 d) Ratio diagram, lower teeth. Standard: incomplete mandible IGF 917, see Text-fig. 2, fig. 1. (Gaville, Upper Valdarno); ▲ Baccinello; ○ Casino; ▲ Vignola; ● Sasso di Glosina; ☆ Monticchiello; ● Nera Montoro; ▽ Ponzano Magra; + Garfagnana; ▼ Upper Valdarno (incomplete lower teeth, M25); ● Spoleto.

Garfagnana (Lucca, Northern Tuscany) (Pl. 2, fig. 3; Pl. 3, figs. 6, 7).

Two small lacustrine basins, near Barga and Pieve Fosciana, yielded fossil vertebrates of warm and humid climate (Azzaroli, 1947, 1970). The mammals of these localities include elements typical of the Early Villafranchian (Triversa f.u.) (Azzaroli, 1977).

Meneghini (1880) first reported the occurrence of tapir in the Garfagnana basin. Later on, *Tapirus* was cited by De Stefani (1887) together with other vertebrates. In 1889 the same Author referred some remains from Barga to *Tapirus* sp. Ugolini (1902) ascribed to *T. arvernensis* an isolated left upper premolar from Barga. Del Campana (1910) described and figured the fossils from Garfagnana and confirmed the occurrence of *T. arvernensis*.

All the specimens from the Garfagnana basin are preserved in the Museum of Florence. Tapirs are represented by mandible fragments (Pl. 2, fig. 3) several isolated teeth (Pl. 3, figs. 6, 7) several maxillary fragments, part of a mandibular symphysis, a fragment of a right humerus, a fragment of a right radius, part of the diaphysis of a right tibia, and fragments of a pelvis. At least three individuals seem to be present.

The second left lower premolar IGF 1270V is characterized by the occurrence of accessory cusplids on its lingual side (Pl. 3, fig. 6). The lower molars generally show a small secondary cingulum at the bases of their antero-lateral edges. The small labial ridge which connects the two lophs is very reduced.

Val di Magra (Massa Carrara, Northern Tuscany) (Text-fig. 2.2; Pl. 3, fig. 3).

Pliocene fossil vertebrates are known from two localities, Sarzanello and Ponzano Magra, near Sarzana. The Sarzana basin is a typical fluvio-lacustrine deposit composed of lignitiferous clays at the base, overlain by sands and conglomerates.

Gaudin (1857) reported the occurrence of tapir, deer and suid remains from Sarzanello. Capellini (1881) referred the tapir to a generic *Tapirus* sp. In a following paper, Capellini (1913) published a study of the fauna from Ponzano Magra, identifying *Tapirus capellini*, *Rhinoceros megarhinus*, *Machairodus* sp. (*M. cultridens*?) and *Sus* sp. In more recent times Federici (1972) and Senesi (1991) referred the deposits of the Sarzana basin to the Early Villafranchian on the basis of data from geomorphology and tectonics, but most of all on paleontological evidence.

I recently revised the fauna from Ponzano Magra, now preserved at the Museum of Paleontology of Bologna; it includes *Tapirus arvernensis*, *Dicerorhinus jeanvireti*, *Sus* cf. *minor*, *Ursus* cf. *minimus*, which might be referred to the Triversa f. u.

The tapir remains from Ponzano Magra are represented by a fragmentary left mandible with its complete premolar row and the protolophid of the first molar still preserved (Pl. 3, fig. 3) and some isolated teeth (the third upper incisors, the left first and second lower incisors, the left first and second molars). All these specimens likely belong to a single adult individual.

The lower third and fourth premolars and the molars bear small, slightly developed accessory cusplids on their labial cingula. The size and morphology of the rectangular-shaped lower cheek teeth are typical of *T. arvernensis*.

The tapir of Sarzanello is represented by the third and fourth premolars and all the molars of the right upper tooththrow (Text-fig. 2.2). Only the casts of these specimens are known, IGF 1770V and 1771V.

The basal cingula are slightly prominent and on the labial sides of the anterior cingula there is a small accessory cusplid. The parastyles are antero-posteriorly compressed and are fairly depressed. Guérin and Eisenmann (1982) ascribed the tapir from Sarzanello to *Tapirus priscus*. In my opinion, the scantiness of the sample prevents a sure specific attribution; I am thus inclined to identify the tapir from Sarzanello as *Tapirus* sp.

Vignola (Modena, Emilia Romagna, Northern Italy).

A tapir mandible, recently found in marine sediments near the Panaro river (Vignola, Modena), has been described and figured by Sala *et al.* (1990), who attributed it to *T. arvernensis*. The Authors observe that European tapirs became progressively larger through time. From this standpoint, the specimen from Vignola was referred to the Early Villafranchian only on the basis of its dimensions; according to Sala *et al.* (1990) micropaleontological evidence apparently confirms this datum.

I personally agree with the specific attribution to *T. arvernensis*. On the contrary, I first of all contest a stratigraphical allocation based on the size of the specimens, inasmuch as I have not observed any significant size growth through time in the fossil tapirs

that I have studied, as is evidenced in the scatter and ratio diagrams (Text-figs. 3, 4). Furthermore, I find that only one specimen is too poor to decide between an attribution to the Ruscinian or the Early Villafranchian.

Livergnana and Sasso di Glosina (Bologna, Northern Italy).

Also the tapirs from these two localities were ascribed to *T. arvernensis* by Capellini (1911), who erroneously referred to this species also an incomplete humerus, which most probably belongs to a suid.

The deposits that yielded this material are comprised in the *Globorotalia puncticulata* Zone; however the Sasso section also extends to the *Globotalia aemiliana* Zone (Vai, 1988, and personal communication). The two localities are thus to be referred to the Late Ruscinian - Early Villafranchian interval of the mammal age scale.

The specimens are presently kept in the Museum of Paleontology of Bologna.

Livergnana provided remains of two individuals, an adult and a calf. The adult is represented by an incomplete third right upper molar (n. 7923), while the juvenile specimen by part of the left maxillary with deciduous and definitive teeth (n. 7921) and by some fragments of upper definitive (n. 7930) and milk teeth (n. 7931). The morphology and size of the third upper molar are typical of *T. arvernensis*. The calf is smaller than IGF 975 from Gaville (Upper Valdarno).

Only a fragment of a left mandible (n. 7928), with the second and third molar still preserved, was found at Sasso. This specimen is morphologically and dimensionally similar to the tapir of Villafranca d'Asti.

Monticchiello (Siena, Tuscany).

The stratigraphy of the area was recently studied by Poggi (in progress). From the bottom to top the sequence consist of basal conglomerates, clays, sands with lignite lens conglomerates and lacustrine limestones, clays, sands. The lignitiferous levels are 10 to 30 cm thick. Most of the sequence is comprised in the *Globorotalia puncticulata* biozone. This biozone is cor-

EXPLANATION OF PLATE 2

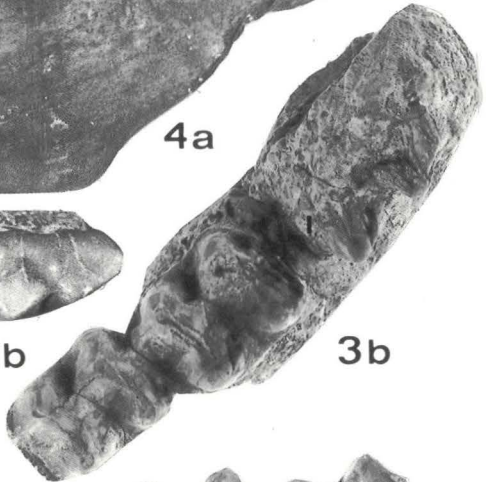
Figs. 1-2 - *Tapirus arvernensis*, Naturhistorisches Museum of Basel.

1) Villafranca d'Asti, uncatalogued right mandible; a) lateral view, about 2/3 nat. size; b) occlusal view, nat. size.

2) Viale, VT 573, fragment of the right mandible; a) lateral view, about 1/2 nat. size; b) occlusal view, about nat. size;

Fig. 3 - Museum of Geology and Paleontology of Florence, IGF 1689V, Fornaci di Pievefosciana, fragment of right mandible; a) lateral view, about nat. size; b) occlusal view, about nat. size.

Fig. 4 - *Tapirus priscus*, Eppelsheim, cast kept in the Museum of Geology and Paleontology of Florence, IGF 13746; a) incomplete left mandible, lateral view, about 1/2 nat. size; b) tooththrow, occlusal view, about nat. size.



relatable with the Ruscinian Mammal Age scale (Steininger *et al.*, 1990).

Besides some rhinoceros remains, which seem to have gone lost, and others of *Anancus arvernensis* reported by Barbiani (1908), scanty tapir specimens are known from this locality. These were partly described by Simonelli (1922) and later on donated to the Museum of Paleontology of Bologna, in which they are now preserved (n. 7929).

The specimens are represented by a right lower premolar row and the protolophid of a first lower molar. The basal cingula are proportionally well developed anteriorly and posteriorly in all the teeth. The morphology is typical of *T. arvernensis*, although this is the smallest representative of the species in Italy.

Nera Montoro (Rome, Latium).

T. arvernensis and *A. arvernensis* are also reported from the lignite mine of Castel San Pietro, few Kms from Poggio Mirteto. The specimens were collected by Maxia in 1948, they were then quoted by other Authors, among which Ambrosetti *et al.* (1972), Arias *et al.* (1976), Azzaroli (1980), etc. Unfortunately the tapir specimens from Poggio Mirteto seem to have gone lost. As a matter of fact the incomplete and deformed mandible kept in the Paleontological Museum of Rome, figured by Azzaroli (1980), seems to come from Montoro, near the Nera river, as attested by the label on the specimen. This locality was already known to have provided mastodont remains (Maxia, 1948). In the same paper the Author reports only mastodont and rhinoceros, and no tapir, from the quarry of Castel San Pietro.

Besides the already mentioned mandible, three tapir teeth of uncertain provenance (cf. Portis 1886, vol. II, p. 113) which were preserved in the Museum of Rome, are gone lost.

The two mandible rami are still embedded in the lignite; they lack their ascending rami and symphyses and are very deformed and crushed. Anyhow, the morphology of the few teeth still preserved is typical of *T. arvernensis*. In my opinion, data are too scarce for a sure attribution of the fossils to the Ruscinian or to the Early Villafranchian.

Baccinello V3 (Grosseto, Tuscany).

Hürzeler was the first to study this site in 1976. The Author quoted *Tapirus* among the species represented at Baccinello V3 on the basis of some fragmentary definitive teeth now kept in the NMB. This material (cast preserved in the Museum of Florence, IGF 4017V) and some fragments of deciduous teeth recently found at the Baccinello V3 level by Malpassi (IGF 4018V, 4019V and 4020 V), was described by

Rook and Rustioni (1991) and was tentatively referred to *T. arvernensis*.

There is still much debate on the stratigraphic position of this site. Recently Engesser (1989) and Rook *et al.* (1991), proposed to refer the V3 level to the Late Turolian. I personally think that evidence is still insufficient for a sure datation to the Late Turolian rather than to the Early Ruscinian. We must also consider that it would be the first time that *T. arvernensis* is reported in a Late Turolian faunal context. The only sure aspect of the assemblage is that it "... rappresenta la fine delle condizioni di endemismo della Toscana meridionale e il collegamento definitivo all'area continentale europea." (De Giuli *et al.*, 1983).

Il Casino (Siena, Tuscany) (Text-figs. 2.4-7).

The Casino fluvio-lacustrine basin is characterized by two distinct sedimentary cycles, both lignitiferous. The oldest is Late Tortonian-Messinian in age; the most recent is Late Messinian to Early Pliocene (Lazzarotto & Sandrelli, 1979). The mammal faunas come from the deposits of the second sedimentary cycle; it has been referred by De Giuli *et al.* (1983), Azzaroli *et al.* (1988) and Azzaroli (1990), to the Early Ruscinian. Recent studies (Rook in press) propose a more ancient age for this fauna even because of the presence of *Hexaprotodon*. The latter actually characterized the Turolian levels of Gravitelli, in Sicily, and Messinian deposits of Spain; however, in my opinion, the occurrence of *Hexaprotodon* at Casino is not diagnostic, because it might be a Turolian holdover in a Ruscinian assemblage. Conversely, in agreement with De Giuli *et al.* (1983), Azzaroli *et al.* (1988) and Azzaroli (1990), the relative abundance of the tapir, of the suid and the occurrence of scanty remains referable to *Parabos?* sp., could be sufficient to refer the assemblage to the Early Ruscinian.

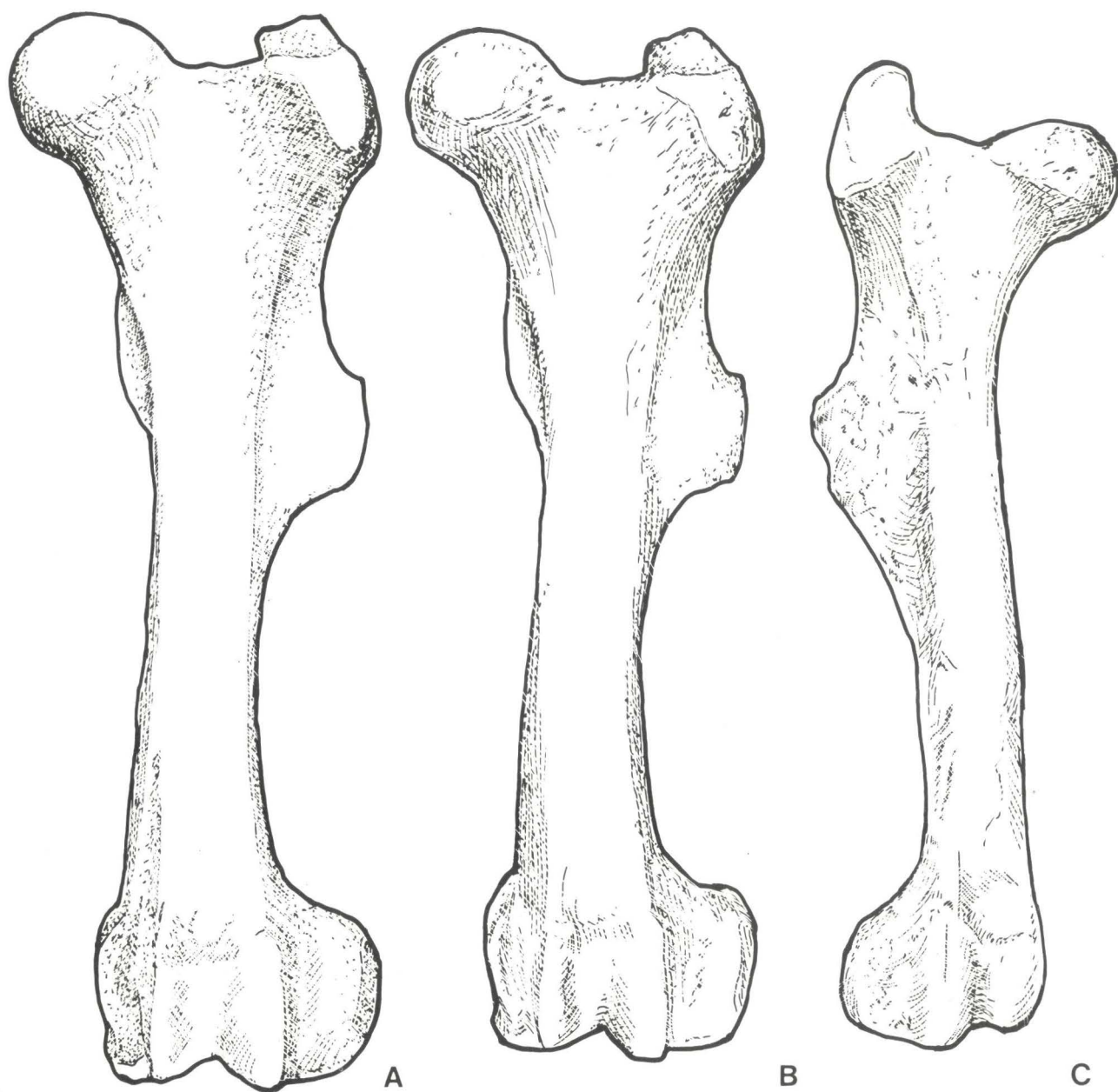
The tapir was first mentioned among the mammal, from Casino by Major (1875). Later on it was reported also by Capellini (1872), Rüttimeyer (1876) and Pantanelli (1878-79). The latter Author referred the tapir remains to *T. priscus*. On the contrary Del Campana (1910) and Gori (1920) called it *T. arvernensis*.

The material studied and figured by Del Campana included isolated upper and lower teeth, while Gori described also postcranial elements.

Most specimens are now kept at the Accademia dei Fisiocritici at Siena. At least two adult individuals are represented. A badly preserved fragment of left mandible (AFS 4957) does not seem to come from Casino; the different kind of fossilization may support this opinion. A fourth left upper premolar (n. 7925) and a first left lower molar (n. 7920) are preserved in the Museum of Geology and Paleontology of Bologna.



Text-fig. 5 - Skulls: A) *Tapirus indicus*; B) *Tapirus arvernensis*; C) *Tapirus terrestris*; D) *Tapirus pinchaque*; E) *Tapirus bairdi*.



Text-fig. 6 - Femurs, specimens preserved in the Naturhistorisches Museum of Basel, cranial view: A) *Tapirus indicus*, left femur; B) *Tapirus terrestris*, left femur; C) *Tapirus arvernensis*, right femur.

EXPLANATION OF PLATE 3

Figs. 1-2 - *Tapirus arvernensis*, Naturhistorisches Museum of Basel;

1) Vialette, uncatalogued, right mandible of young specimen; a) lateral view, about 2/3 nat. size; b) toothrow, occlusal view, about 2/3 nat. size;

2) Villafranca d'Asti, uncatalogued, fragment of mandible; a) right lateral view, about 2/3 nat. size; b) toothrow, occlusal view, about 2/3 nat. size; c) detail of the incisors and canines, about nat. size; d) detail of the left toothrow, occlusal view, about nat. size.

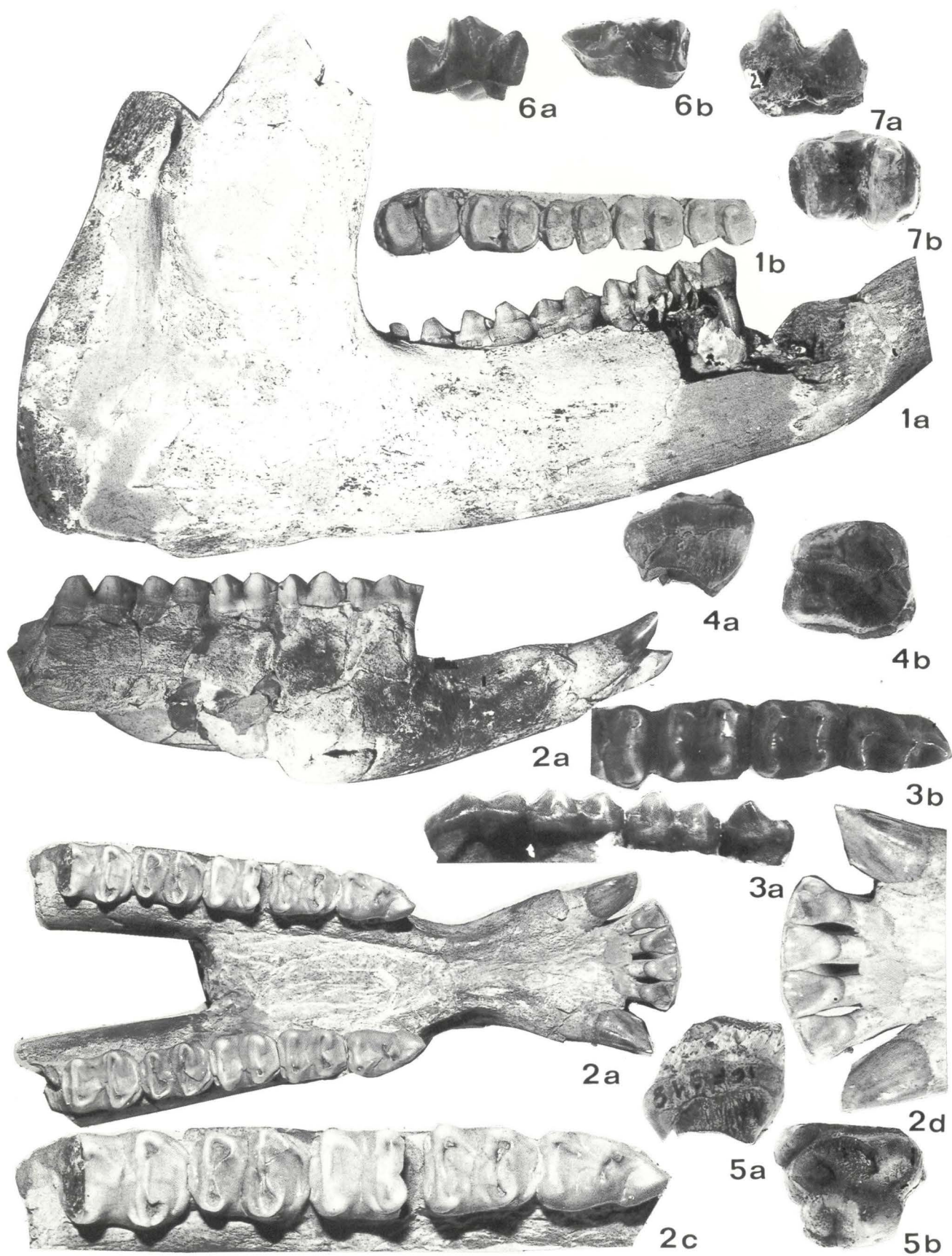
Fig. 3 - Capellini Museum of Bologna, Ponzano Magra, uncatalogued, fragment of the left mandible with the premolar row and protolophid of the first molar: a) lateral view; b) occlusal view, nat. size.

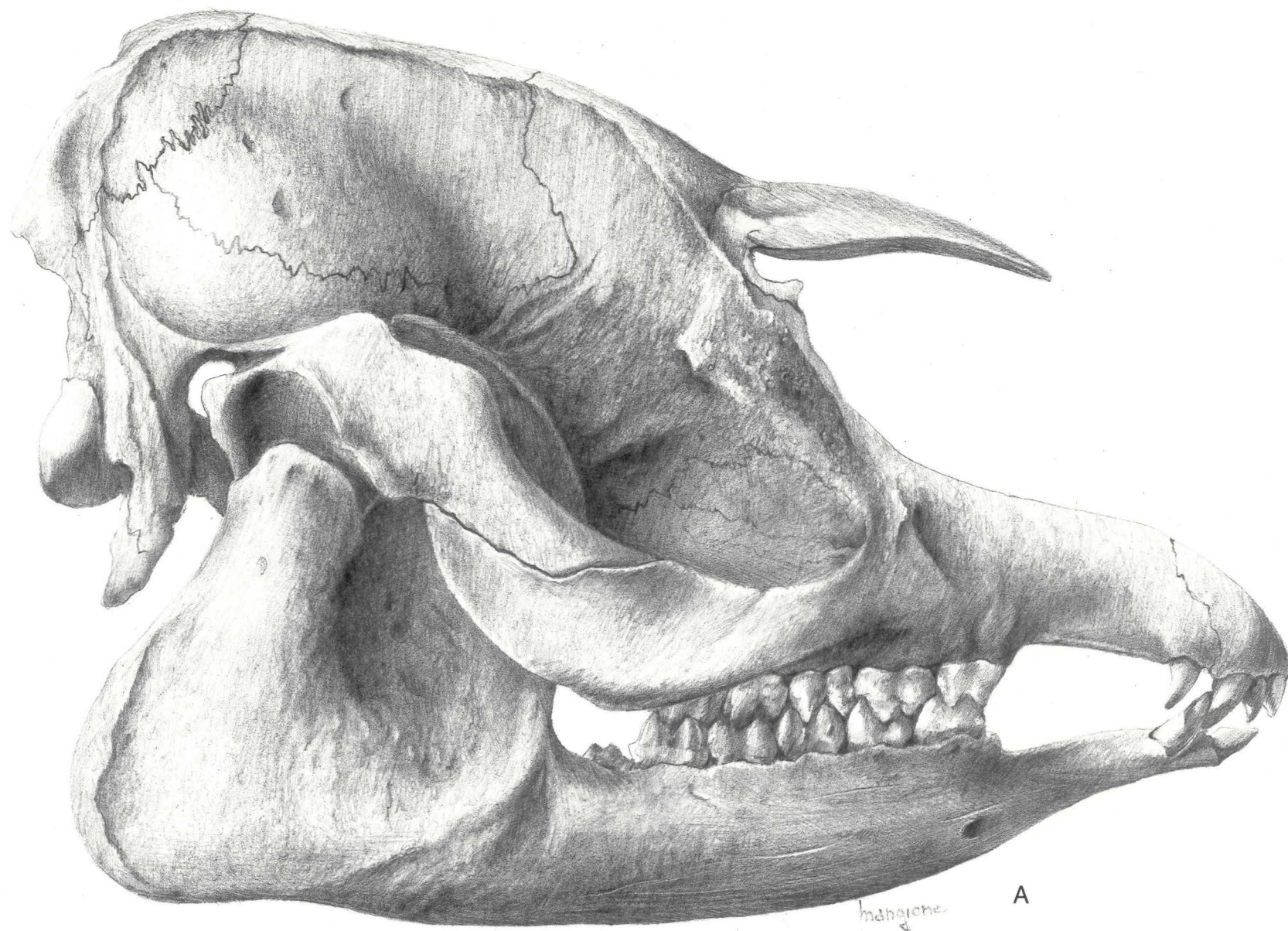
Figs 4-7 - Museum of Geology and Paleontology of Florence: 4) Gaville, IGF 917, right third upper molar: a) occlusal view, about nat. size; b) anterior view about nat. size;

5) Gaville, IGF 918, right third upper molar; a) occlusal view, about nat. size; b) anterior view about nat. size;

6) IGF 1270V, Ponte dei Sospiri (Garfagnana), left second lower premolar; a) lingual view, about nat. size; b) occlusal view, about nat. size;

7) IGF 1692, Fornaci di Pievofosciana (Garfagnana), right third lower molar; a) lingual view, about nat. size; b) occlusal view, about nat. size.



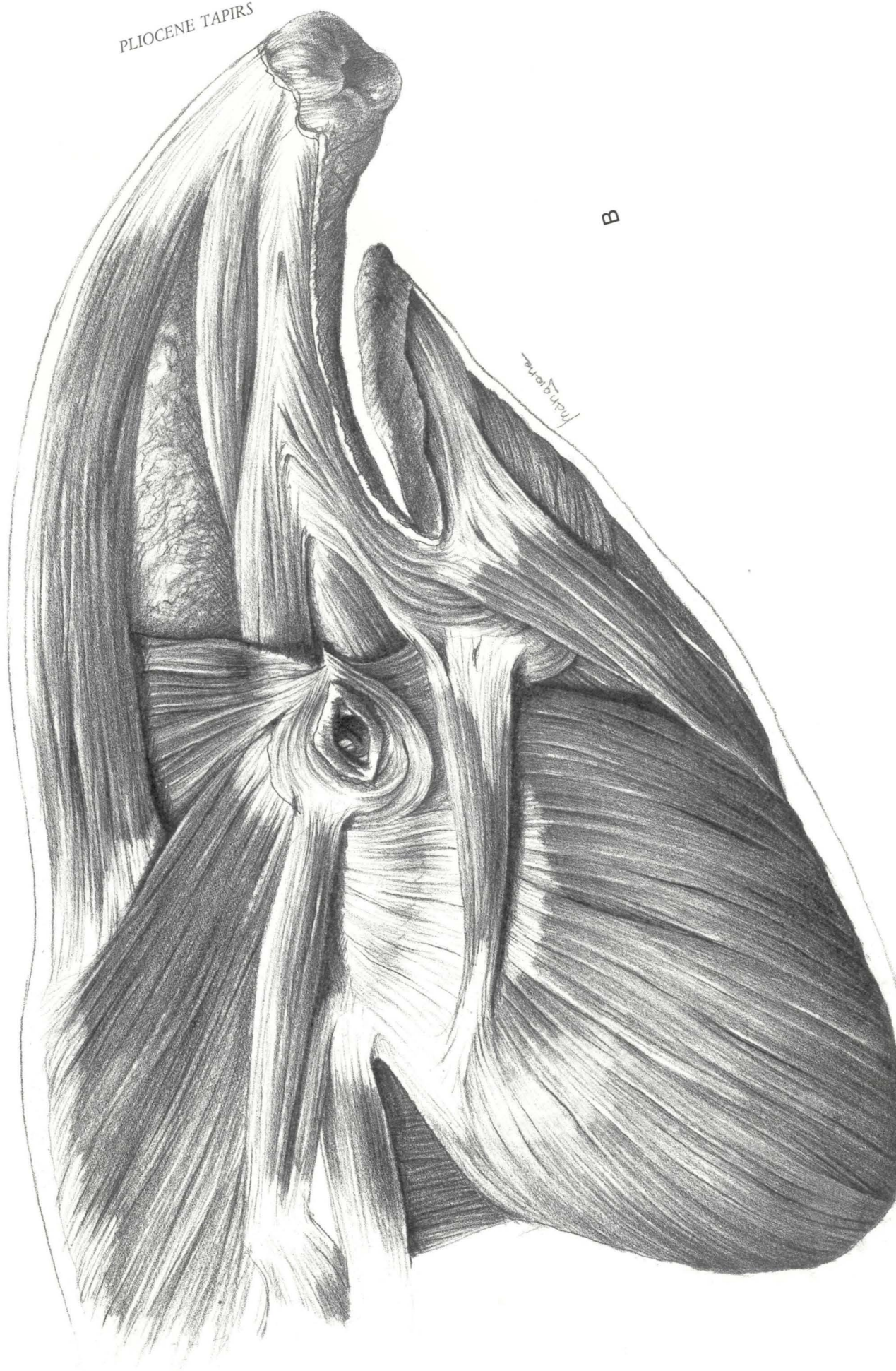


Text-fig. 7 - *Tapirus arvernensis*, uncatalogued specimen from Vialette, see plate 1, fig. 1.; tentative restoration of the skull (A) and of its muscles (B).

PLIOCENE TAPIRS

B

palatine



The occlusal morphology is typical of *T. arvernensis*, and its dimensions are close to those of the specimens, from Villafranca d'Asti. The second right lower molar (AFS 4958) bears an exceptionally large talonid.

The morphology of the postcranial bones (Text-figs. 2.4-7) is similar to the Upper Valdarno specimen IGF 1939V (Pl. 4, figs. 6, 7; Text-figs. 9.3-6). The dimensions and proportions, however, are larger. This is particularly evident in the distal articulation of a left humerus (AFS 2852). The articular heads of the femurs, right (AFS 3764) and left (AFS 3765), are more robust and bear wider and deeper legamentous fossettes than the Upper Valdarno specimens. The first phalanx of the third digit of the pes (AFS 2844, Text-fig. 2.7) is dimensionally similar to some specimens of *T. arvernensis* from Hajnacka I.

The characters described recall *T. arvernensis* rather than *T. priscus*. However the scantiness and fragmentariness of the sample prevent a secure taxonomic attribution. For this, the remains are tentatively referred here to *T. arvernensis*.

COMPARISON

The Vallesian *Tapirus priscus* Kaup, 1832 is larger and more massive than *T. arvernensis*.

The upper teeth of *T. arvernensis* are relatively short, broad and rectangular-shaped as opposed to the more square-shaped ones of the Late Miocene *T. priscus*. In this character *T. priscus* is more similar to *T. indicus* than to *T. arvernensis*.

The first upper premolars seem to be more advanced than those of *T. priscus* for the presence of a small meso-lingual cuspule. Furthermore, the Pliocene tapir is easily distinguishable from *T. priscus* (Pl. 2, fig. 4) in the shape of the mandible.

In the structure of neurocranium the Pliocene tapir recall the extant Asian species *Tapirus (Acrocodia) indicus* Desmarest, 1829, and is markedly distinct from the American species (Text-fig. 5). In particular, the structure of the fronto-parietal region of the Pliocene tapir is very similar to that of the living Asian tapir.

However other features distinguish the two forms. *T. arvernensis* shows the following differences from the larger and more massive *T. indicus*:

- less prominent Tubera frontalis;
- the temporal fossae are narrower and the zygomatic arches are stronger and placed in a lower position. These characters suggest a different proportional development of the temporal and masseterine muscles in the two species;
- stronger cingula and a higher number of small accessory cuspules, especially in the second lower premolars;
- stronger parastyles, especially in the third upper molar;
- first upper premolars made more complex by the presence of an antero-lingual cuspule; this character gives the tooth a trapezoidal outline which is more complex and more advanced towards molarization than the triangular-shaped first upper premolar of the Malayan tapir;
- more slender horizontal rami, with ventral gonions more extended backward and rear profiles of the ascending rami quite more incline forward;
- the first and second lower incisors are of the same size; in the Malayan tapir the incisors become progressively smaller, from the first to the third;
- more rectangular-shaped lower cheek teeth;
- more slender rear limb bones, with ratios between the segments that suggest a higher cursoriality.

The parastyles, especially the ones of the molars, are more developed than in other fossil and extant species.

The general morphology and the values of the posterior limb bones ratio are peculiar to this species. *T. indicus*, *T. terrestris* and *T. bairdi*, have more massive limb bones; the femur/tibia/metatarsal ratios usually are higher (see table at the end of the paper).

As a whole *T. arvernensis* seems to be more specialized than *T. indicus*. Although the relationship between the two species is hard to establish at the present state of the knowledge, the European Pliocene tapir and the extant *T. indicus* probably represent two distinct phylet-

EXPLANATION OF PLATE 4

- Fig. 1 - *Tapirus arvernensis*;
Paleontological Museum of Montevarchi, M 25, S. Barbara lignite mine, incomplete lower tooththrows, about nat. size.
- Figs. 2-5 - Naturhistorisches Museum of Basel;
2) Viallette, uncatalogued right humerus; a) cranial view, about 1/2 nat. size; b) caudal view, 1/2 nat. size;
3) Viallette, uncatalogued right third metacarpal bone; a) dorsal view, about nat. size; b) palmar view, about nat. size;
4) Montpellier, MP 850; left third metatarsal bone dorsal view, about nat. size;
5) Viallette, right manus, uncatalogued first phalanx of the central digit; a) dorsal view, about nat. size; b) palmar view, about nat. size.
- Figs. 6-7 - Museum of Geology and Paleontology of Florence, IGF 1939V, S. Barbara lignite mine;
6) right manus, first phalanx of the central digit; a) dorsal view, about nat. size; b) medial view, about nat. size; c) palmar view, about nat. size;
7) left manus, first phalanx of the fourth digit; a) dorsal view, about nat. size; b) palmar view, about nat. size.



ic lines adapted to two different kinds of woodlands, characterized by a respectively more or less thick underbrush. Both species might even have evolved from a common ancestor which lived in Eurasia during the Miocene.

CLOSING REMARKS

The genus *Tapirus* is characteristically uniform in its dentition and postcranial skeleton; only some peculiarities of the teeth, such as the morphology of the first and second upper premolars, may be diagnostic. The most significant differences between the species can be observed in the skulls. However, also differences in overall size and in the proportions of the limb bones may sometimes be significant.

The teeth of *T. arvernensis* differ from those of *T. priscus*. Although very similar to the present day Asian tapir in the fronto-parietal neurocranium, several other skeletal characters make the Pliocene European tapir distinct.

T. arvernensis is middle to small-sized and shows all the conservative characters that distinguish the genus. Comparative analyses with limb bones of extant species seem to indicate that the morphology and the proportions of the postcranial elements are typical of a relatively cursorial animal; perhaps it is one of the most cursorial species of the genus.

The morphological and dimensional differences between the specimens of *T. arvernensis* studied here do not seem to be diagnostic and seem to fall in the intraspecific variability of the species. However, some characters may be adaptations to peculiar environmental conditions; Simpson (1945) and Hooijer (1947) have observed a marked morphological and dimensional variability in some fossil and living species. The Early Ruscinian tapirs from Casino are similar in size to the ones from some Villafranchian localities of Europe, but are larger than the ones from Montpellier. The third left metatarsal from Montpellier (MP 850), preserved in the Naturhistorisches Museum of Basel (Pl. 4, fig. 4) is longer and more slender than the specimens from Viallette and bears a distal epiphysis similar to those

from Upper Valdarno (IGF 1939V) (Text-fig. 9.3) and smaller than the ones from Casino (AFS 3763, AFS 3762) (Text-fig. 2.6). The presently available data (Text-figs. 3, 4) do not permit to establish evolutionary trends for biochronological purposes; its occurrence is at most significant for climatical and environmental reconstructions.

In my opinion, not more than one species is hitherto represented in the Pliocene material of Europe.

T. priscus, which is said to be strictly related to *T. arvernensis* (Eisenmann & Guérin, in press), is only reported in Vallesian faunal contexts.

T. arvernensis first occurs in Europe together with faunas of the Early Ruscinian, or perhaps of the latest Turolian, and characterizes the Early Villafranchian faunal context (Triversa f. u.). Its LOD is placed at the transition from the Triversa to the Montopoli f. u. In Western Europe, the species is reported for the last time at the Middle Villafranchian site of Tegelen, in the Netherlands. However the occurrence of tapir remains in the mammal list published by Freudenthal *et al.* (1976) is doubtful (Azzaroli *et al.*, 1988). Furthermore, of the stratigraphy of the latter locality is still uncertain; more than one level may be present in the site.

The Czechoslovakian site of Hajnacka I, which can be correlated with the Triversa f. u., yielded the largest specimens of *T. arvernensis* ever known in Europe.

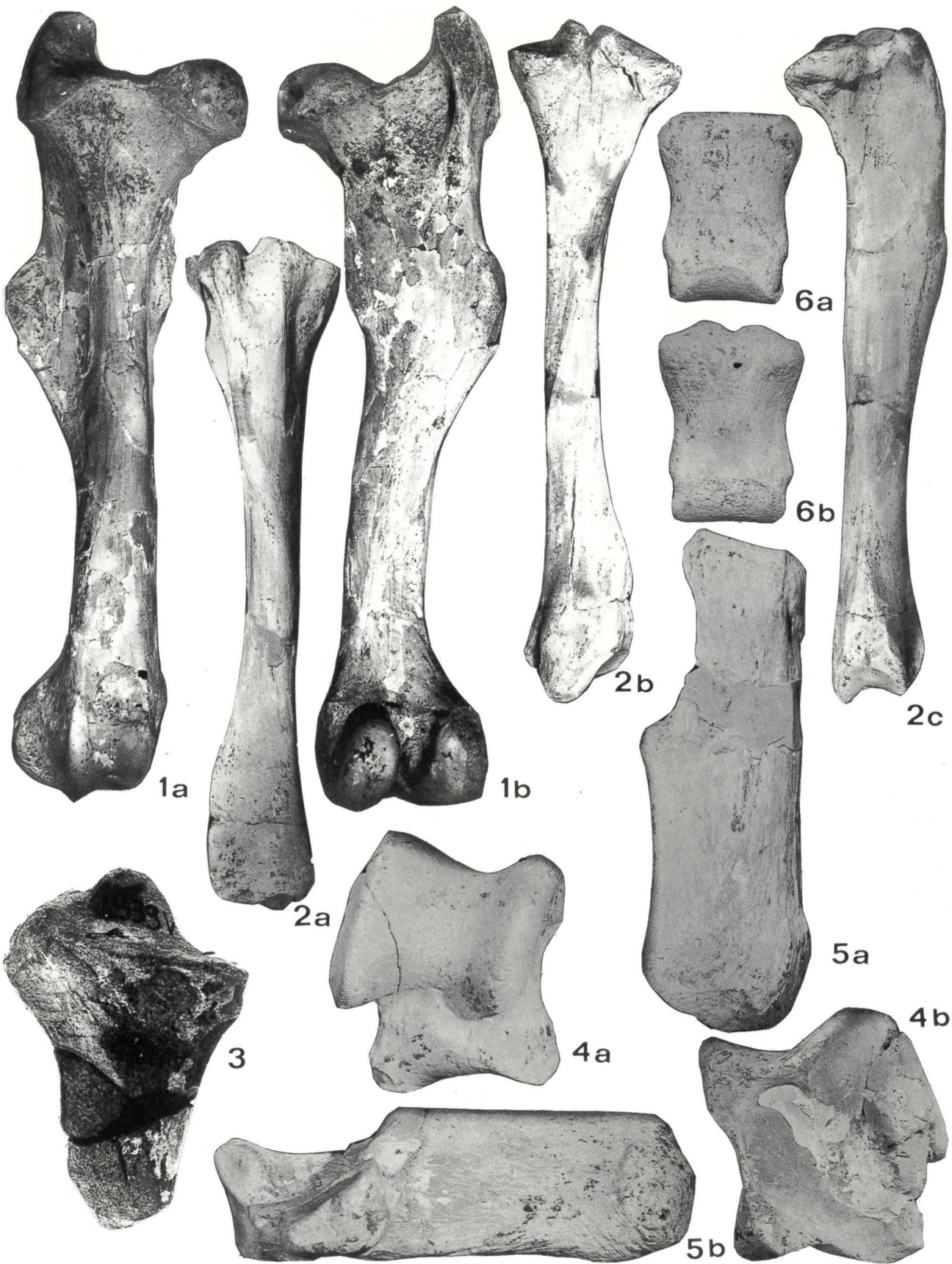
The sites that provided tapir remains in Italy are distributed from Piedmont to Northern Latium. In the present paper, most of these specimens are referred to *T. arvernensis*; only the scanty and fragmentary specimens from Baccinello V3 and Casino are tentatively attributed to this species. The finds from Sarzanello are referred to here as *Tapirus* sp.

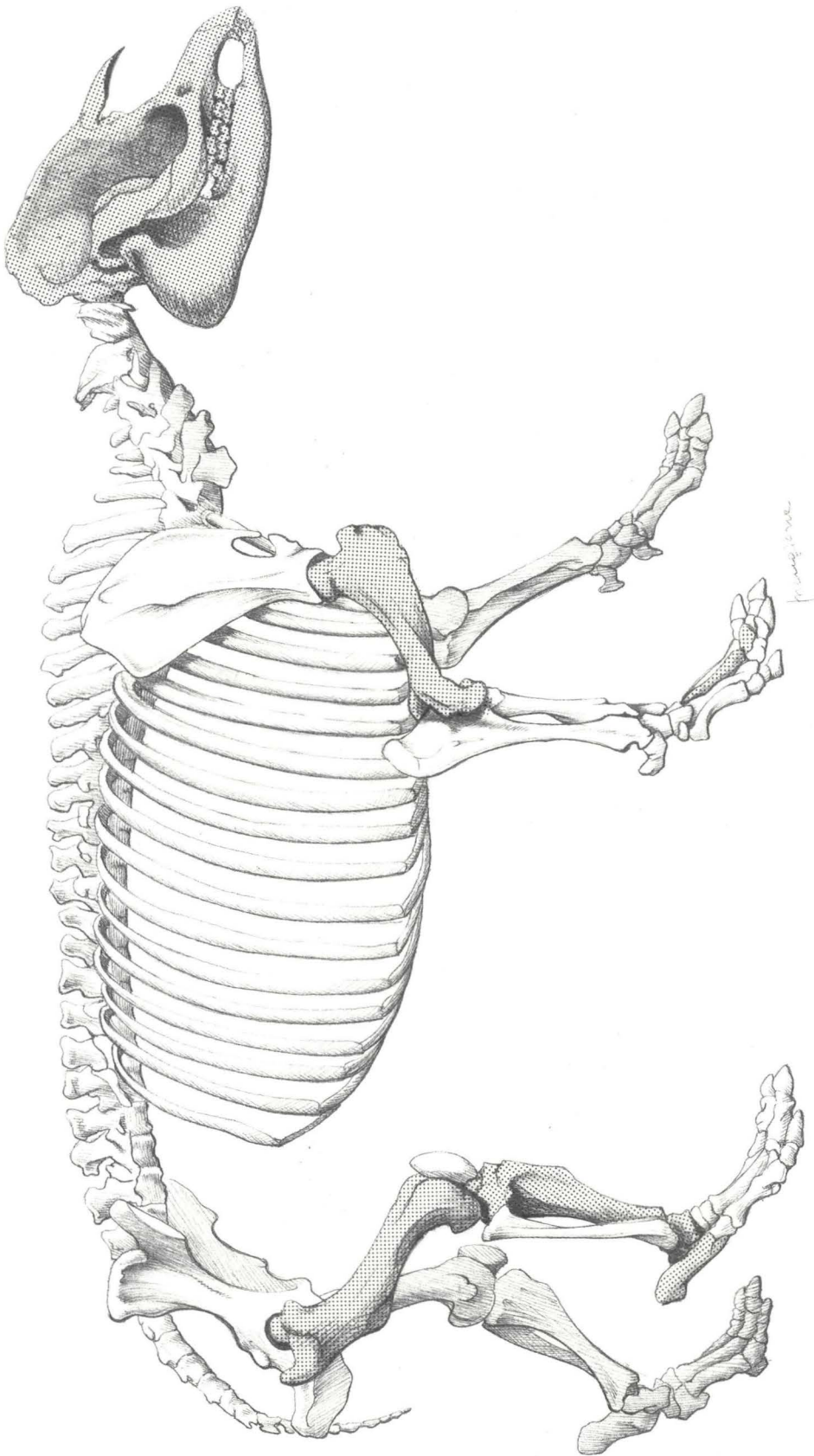
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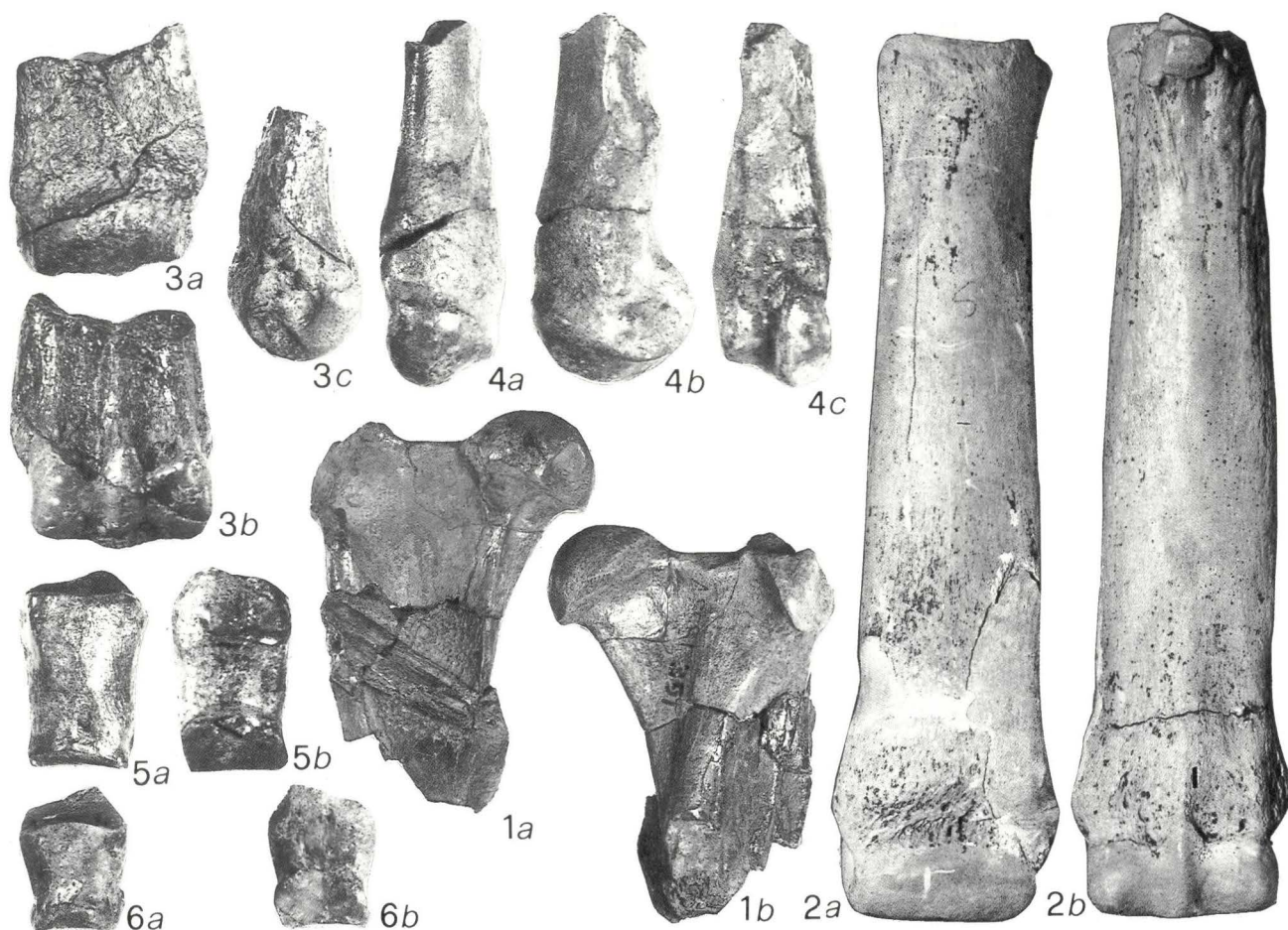
EXPLANATION OF PLATE 5

- Figs. 1-2 - *Tapirus arvernensis*, Naturhistorisches Museum of Basel, Viallette, uncatalogued;
 1) right femur; a) cranial view, about 1/2 nat. size; b) caudal view, about 1/2 nat. size;
 2) right tibia; a) dorsal view, about 1/2 nat. size; b) lateral view, about 1/2 nat. size; c) plantar view, about 1/2 nat. size.
 Fig. 3 - Museum of Geology and Paleontology of Florence, IGF 1939V, S. Barbara lignite mine, right tibia, proximal end, medial view, about nat. size.
 Fig. 4-6 - Naturhistorisches Museum of Basel, Viallette, uncatalogued;
 4) right astragalus; a) dorsal view, about nat. size; b) plantar view, about nat. size;
 5) right calcaneus; a) lateral view, about nat. size; b) medial view, about nat. size;
 6) right pes, first phalanx of the central digit; a) dorsal view, about nat. size; b) plantar view, about nat. size.





Text-fig. 8 - *Tapirus armenensis* from Viallette; tentative restoration of the postcranial skeleton.



Text-fig. 9 - *Tapirus arvernensis*, Museum of Geology and Paleontology of Florence, IGF 1939V, S. Barbara lignite mine [Figs. 1, 3-6]; 1) left femur, proximal end; a) cranial view, about 1/2 nat. size; b) caudal view, about 1/2 nat. size. 2) Naturhistorisches Museum of Basel, left third metatarsal bone; a) dorsal view, about nat. size; b) plantar view, about nat. size. 3) distal end of left third metatarsal bone; a) dorsal view, about nat. size; b) lateral view, about nat. size; c) plantar view, about nat. size; 4) fragment of left fourth metatarsal bone; a) dorsal view, about nat. size; b) lateral view, about nat. size; c) plantar view, about nat. size; 5) right manus, first phalanx of the fourth digit (?); a) dorsal view, about nat. size; b) palmar view about nat. size; 6) right pes, second phalanx of the fourth digit (?); a) dorsl view, bout nat. size; b) plantar view, about nat. size.

indebted to dr. M. Borri, dr. P. Agnelli and dr. M. Poggesi for granting me access to the skulls kept in La Specola Museum of Florence. The drawings were made by dr. F. Vianello, Mrs. M. C. Andreani and Mr. F. Landucci. I am particularly grateful to Mr. A. Mangione for the care shown in making the reconstructions included in the paper. Finally many thanks to prof. A. Azzaroli, prof. G. Ficcarelli and prof. D. Torre for the critical reading of the manuscript. Work supported by a M.U.R.S.T. grant.

SYMBOLS OF THE MUSEUM AND OF THE SPECIMENS

NMB - Naturhistorisches Museum of Basel (VT = specimens from Viallette and MP = specimens from Montpellier)
 IGF - Museum of Geology and Paleontology of Florence
 MPM - Museum of Paleontology of Montevarchi, some specimens are catalogued with the letter M
 MCB - Capellini Museum of Bologna
 AFS - Museum of Accademia dei Fisiocritici di Siena
 MUL - University Museum of Lyon

APPENDIX

LIST OF THE SPECIMENS

- 1 - Mus. of Vignola, Vignola
- 2 - Mus. of Basel, VT 573
- 3 - Mus. of Basel, Viallette, uncat.
- 4 - Mus. of Basel, Viallette, uncat.
- 5 - Mus. of Basel, Villafranca d'Asti, uncat.
- 6 - Mus. of Basel, Villafranca d'Asti, uncat.
- 7 - Mus. of Basel, Villafranca d'Asti, uncat.
- 8 - Auvergne, cast IGF 1268V
- 9 - 10, data from Fejfar, 1964
- 11 - 16, data from Sala *et al.*, 1990
- 17 - Upp. Valdarno, IGF 1939V
- 18 - Il Casino, AFS 2852
- 19 - Mus. of Basel, Viallette, uncat.
- 20 - 27, data from Fejfar, 1964
- 28 - Mus. of Basel, Viallette, uncat.

- 39 - 44, Mus. of Basel, Viallette, uncat.
 45 - 48, Mus. of Basel, Viallette, uncat.
 49 - Mus. of Basel, MP 850
 50 - Il Casino, AFS 3763
 51 - Il Casino, AFS 3762
 52 - Upp. Valdarno, IGF 1939V
 53 - 55, data from Fejfar, 1964
 56 - 60, Mus. of Basel, Viallette, uncat.
 61 - Il Casino, AFS 2844
 62 - 65, data from Fejfar, 1964
 66 - Mus. of Bologna, Monticchiello. n. 7929
 67 - Mus. of Bologna, Ponzano Magra, uncat.
 68 - Upp. Valdarno, IGF 917
 69 - Upp. Valdarno, M 25
 70 - Univ. Lyon, Viallette, data from Sala *et al.*, 1990
 71 - Mus. of Basel, Montpellier, uncat.
 72 - 73 - Il Casino (?), Acc. dei Fisiocritici, Siena
 74 - Mus. of Rome, Nera Montoro, uncat.
 75 - Eppelsheim, cast IGF 13746

FAUNAL LIST

BACCINELLO V3 (Rook, in press) - *Dicerorhinus* sp., *Tapirus* cf. *arvernensis*, *Hipparion* sp. (two forms), *Korynochoerus provincialis*, Bovidae indet. (two forms), *?Procapreolus*, *Machairodus* ex gr. *giganteus*, *Metailurus major*, *Plesiogulo crassa*, *Viverra* sp., Hyaenidae sp., *Mesopithecus pentelici*, cf. *Hypolagus*, *Prolagus* sp., *Hystrix* sp., *Antracomys lorenzi*, *Apodemus etruscus*, *Castor* cf. *preafiber*, *Muscardinus* sp., *Kowalskia nestori*, Erinaceidae indet.

CASINO (Rook, in press) - *Tapirus arvernensis*, *Hipparion* sp., *Sus* cf. *minor*, *Hexaprotodon pantanellii*, *Euprox?* (*Cervus*) *elsanus*, *Parabos?* sp., *?Mesopithecus*, *Prolagus* sp.

VIGNOLA - *Tapirus arvernensis*

LIVERGNANA - *Tapirus arvernensis*, *?Sus* sp.

SASSO DI GLOSINA - *Tapirus arvernensis*

MONTICCHIELLO - *Anancus arvernensis*, *Dicerorhinus* sp., *Tapirus arvernensis*

NERA MONTORO - *Anancus arvernensis*, *Tapirus arvernensis*

VILLAFRANCA D'ASTI (Fornace RDB, Savage & Curtis, 1970) - cf. *Macaca florentina*, cf. *Semnopithecus monspessulanus*, *Castor* sp., Felidae gen. indet., *Acinonyx* sp., *Viverra* cf. *pepraxti*, *Euryboas lunensis*, *Hyena* sp., *Mammuth borsoni*, *Anancus arvernensis*, *Dicerorhinus jeanvireti*, *Tapirus arvernensis*, *Sus* cf. *minor*, Cervidae (small size, cf. *Cervulus* or *Elaphodus*), Cervidae (large size)

SARZANELLO - *Tapirus* sp., *Sus* sp., Cervidae gen. indet.

PONZANO MAGRA - *Tapirus arvernensis*, *Dicerorhinus jeanvireti*, *Ursus* sp. (cf. *minimus*), *Sus* cf. *minor*

BARGA - *Anancus arvernensis*, *Dicerorhinus* sp., *Tapirus arvernensis*, Cervidae (cf. *Cervus pardinensis*)

PIEVEFOSCIANA - *Anancus arvernensis*, *Dicerorhinus* sp., *Tapirus arvernensis*, *Cervus* sp., *Sus minor*, *Lynx issiodorensis*, *Meganthereon cultridens*, *Vulpes alopecoides*, Carnivora indet.

VALDARNO SUPERIORE ("Castellnuovo dei Sabbioni group", De Giuli, 1983; Rustioni, 1987) - *Ursus minimus*, *Mammuth borsoni*, *Anancus arvernensis*, *Tapirus arvernensis*, *Dicerorhinus* sp. (large size), *Leptobos* cf. *stenometopon*

SPOLETO (Ambrosetti, personal communication, 1989) - *Mammuth borsoni*, *Anancus arvernensis*, *Tapirus arvernensis*, *Castor* sp., Cervidae.

Characters used in tables and in diagrams

- LF - greatest length of the femur
 LT - greatest length of the tibia
 LMT - greatest length of the metatarsal bone

MANDIBLE

- LIC - infradentale-condyle length
 LIap - infradentale-angular process length
 LD - diastema length
 BDmin - least breadth of the mandibular symphysis
 BDUmin - least breadth between the upper borders of the symphysis
 HMI-M2 - height of the horizontal ramus between M1 and M2
 HM2-M3 - height of the horizontal ramus between M2 and M3
 Ba - anterior breadth of the horizontal ramus, measured between M1 and M2
 Bp - posterior breadth of the horizontal ramus, measured between M2 and M3

TEETH

- LMP - length of the cheek toothrow
 LP - length of the premolar row
 LM - length of the molar row
 P2L - length of the second premolar
 P2PB - posterior breadth of the second premolar
 P3L - length of the third premolar
 P3AB - anterior breadth of the third premolar
 P3PB - posterior breadth of the third premolar
 P4L - length of the fourth premolar
 P4AB - anterior breadth of the fourth premolar
 P4PB - posterior breadth of the fourth premolar
 M1L - length of the first molar
 M1AB - anterior breadth of the first molar
 M1PB - posterior breadth of the first molar
 M2L - length of the second molar
 M2AB - anterior breadth of the second molar
 M2PB - posterior breadth of the second molar
 M3L - length of the third molar
 M3AB - anterior breadth of the third molar
 M3PB - posterior breadth of the third molar

HUMERUS

- L - greatest length
 PL - physiological length
 BP - proximal breadth
 BSmin - minimum breadth of the shaft
 BD - distal breadth

HUMERUS, FEMUR and TIBIA

- L - greatest length
 PL - physiological length
 BP - proximal breadth
 BPAa - antero-posterior diameter of the proximal articular surface
 BPLa - latero-medially diameter of the proximal articular surface
 BD - distal breadth

THIRD METATARSAL BONE and FIRST PHALANX

- L - greatest length
 BP - proximal breadth
 DP - proximal depth
 BSmin - minimum breadth of the shaft
 DSmin - minimum depth of the shaft
 BD - distal breadth of the articular surface
 DD - distal depth of the articular surface

RATIO OF THE POSTERIOR LIMB BONES

spec.	Tapiirus terrestris					Tapiirus indicus				Tapiirus bairdi	Tapiirus excelsus	Tapiirus arvernensis
	A	B	C	D	E	F	G	H	I	L	M	N
LF	252.3	254.0	315.7	300.9	307.7	348.0	342.0	330.0	319.1	289.0	324.2	282.1
LT	208.0	213.0	253.3	245.1	242.0	280.0	285.3	282.0	258.7	235.0	280.0	249.0
LMT	100.0	94.0	123.0	113.9	109.9	124.0	/	120.9	113.0	110.0	128.0	112.5
LF/LT	1.21	1.19	1.24	1.22	1.27	1.24	1.19	1.17	1.23	1.22	1.15	1.13
LF/LMT	2.52	2.70	2.56	2.64	2.79	2.80	/	2.72	2.83	2.62	2.53	2.50
LT/LMT	2.08	2.26	2.05	2.15	2.20	2.25	/	2.33	2.29	2.13	2.18	2.21
LF/L(T+MT)	0.80	0.82	0.83	0.83	0.78	0.86	/	0.81	0.85	0.83	0.79	0.78

A and B, data by Simpson (1945); C, n° 3761 male, NMB; D, n° 5691 female, NMB; D, n° 9938 female, NMB; F, data by Simpson (1945); G, NMB; H, n° 8125 female, NMB; I, n° 8917 male, NMB; L and M, data by Simpson (1945); N, Vialette, uncatalogued NMB.

MANDIBLE

spec.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
LIC	/	/	244.0	253.0	/	/	/	/	/	/	/	/	/	/	/	/
LIap	302.0	/	272 ?	290.0	/	/	/	/	/	/	/	/	/	/	/	/
LD	43.8	/	/	/	/	/	/	49.8	/	/	/	/	/	/	/	/
BDmin	30.2	/	/	/	30.7	/	/	29.9	29.1	34.8	/	/	/	/	/	/
BDUmin	20.0	/	/	/	22.4	/	/	23.8	/	/	/	/	/	/	/	/
HM1-M2	49.5	40.0	48.2	/	47.0	48.0	48.5	48.3	/	/	51.0	44.4	46.2	52.0	52.0	/
HM2-M3	/	40.5	49.0	/	/	/	/	49.5	/	/	/	/	/	/	/	/
Ba	/	/	/	/	/	/	/	28.5	/	/	24.9	29.5	26.5	25.0	29.4	29.4
Bp	/	26.0	28.7	/	31.0	30.5	30.9	29.9	/	/	/	/	/	/	/	/

LOWER TEETH

spec.	66	67	68	69	5	6	7	2	3	4
LMP	/	/	133.6	120.2	/	/	/	115.5	121.3	111.0
LP	53.0	54.0	63.3	55.7	56.4	/	/	53.0	57.0	52.0
LM	/	/	69.3	65	/	61.5	62.4	60.0	63.0	56.0
spec.	70	71	11	12	14	72	73	74	8	75
LMP	/	/	111.7	115.7	111.8	/	/	122.5	132.5	136.0
LP	55.0	/	54.3	55.4	53.2	57.6	58.0	58.3	63.1	64.0
LM	/	57.0	57.8	61.3	53.8	/	/	64.0	67.7	72.0

HUMERUS

spec.	17	18	19	20	21	22	23	24	25	26	27
L	/	/	218.0	/	/	/	/	/	/	/	/
PL	/	/	200.0	/	/	/	/	/	/	/	/
BP	/	/	59.0	/	/	/	/	/	/	/	/
BSmin	/	/	23.0	34.0	34.0	/	33.0	/	/	/	/
BD	57.0	60.0	50.0	65.3	66.5	63.0	64.5	62.0	65.6	58.7	64.0

FEMUR

spec.	28	29	30	31	32	33	34	35	36	37	38
L	282.0	/	/	/	/	/	/	/	/	/	/
PH	264.0	265.2	/	/	/	/	/	/	/	/	/
BP	82.0	/	78.8	/	/	/	/	/	/	/	/
BPAa	33.5	/	30.0	40.0	38.5	38.8	40.0	38.0	38.7	37.8	39.3
BPLa	37.5	/	35.5	42.7	40.7	41.6	42.0	43.0	43.0	42.8	41.9
BSmin	25.1	/	/	/	/	/	/	/	/	/	/
BD	60.3	60.0	/	/	/	/	/	/	/	/	/

TIBIA

spec.	39	40	41	42	43	44
L	245.0	239.0	248.0	249.0	246.0	/
PL	227.0	220.0	233.0	231.0	225.0	/
BP	/	63.3	68.4	/	64.6	65.0
BSmin	22.9	19.5	24.0	24.9	19.2	20.0
BD	41.3	39.1	40.3	41.8	39.1	/

THIRD METATARSAL BONE

spec.	45	46	47	48	49	50	51	52	53	54	55
L	/	115.0	112.5	/	125.0	/	/	/	/	/	/
BP	/	23.0	22.7	/	27.0	/	/	/	26.8	26.0	28.4
DP	/	23.0	23.8	/	26.8	/	/	/	25.7	/	26.0
BD	25.0	25.0	24.9	25.1	25.8	27.5	27.4	25.2	/	/	/
DD	18.0	18.4	18.1	18.1	19.0	21.1	22.4	17.0	/	/	/

PES, FIRST PHALANX OF THE THIRD DIGIT

spec.	56	57	58	59	60	61	62	63	64	65	17
L	35.0	34.2	36.9	36.0	33.0	37.4	40.7	38.0	39.6	41.4	29.8
BP	26.0	26.0	/	/	28.0	30.6	29.4	30.6	28.8	31.0	22.2
DP	16.3	16.4	18.8	16.8	16.9	20.0	19.1	19.6	19.6	20.6	17.2
BSmin	19.9	20.0	21.5	22.0	23.9	25.2	/	/	/	/	21.9
DSmin	9.9	11.0	13.0	12.0	12.1	10.3	/	/	/	/	7.2
BD	19.6	20.0	21.5	21.0	21.0	23.2	25.4	25.0	24.6	26.6	21.5
DD	10.3	10.9	10.9	11.0	10.3	11.8	11.7	13.2	12.4	12.8	10.0

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