

Zeitschrift: Eclogae Geologicae Helvetiae
Herausgeber: Schweizerische Geologische Gesellschaft
Band: 88 (1995)
Heft: 3

Artikel: Pannonictis nestii (Carnivora, Mammalia) from the late Villafranchian of Pietrafitta (Umbria, Italy) : preliminary note
Autor: Rook, Lorenzo
DOI: <https://doi.org/10.5169/seals-167707>

Nutzungsbedingungen

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. [Mehr erfahren](#)

Conditions d'utilisation

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. [En savoir plus](#)

Terms of use

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. [Find out more](#)

Download PDF: 29.04.2026

ETH-Bibliothek Zürich, E-Periodica, <https://www.e-periodica.ch>

Pannonictis nestii (Carnivora, Mammalia) from the late Villafranchian of Pietrafitta (Umbria, Italy). Preliminary note

LORENZO ROOK¹

Key words: *Pannonictis*, Mustelidae, Carnivora, late Villafranchian, early Pleistocene, Pietrafitta, Italy

ABSTRACT

The lignite deposits of Pietrafitta (Perugia, Central Italy) contain a rich association of large mammals attributable to the Farneta faunal unit, early Pleistocene (late Villafranchian). This paper gives a preliminary description of some remains of the Galictinae mustelid *Pannonictis nestii*. The taxonomy and the palaeobiogeography of the Galictinae subfamily are briefly discussed. The genus *Pannonictis* is present in several localities in Eurasia but its alpha-taxonomy is still to be clearly defined. Its occurrence in the Italian peninsula before the Pietrafitta findings were limited to the Upper Valdarno.

RIASSUNTO

I depositi lignitiferi di Pietrafitta (Perugia) hanno restituito una ricca associazione di mammiferi fossili attribuibili alla unità faunistica Farneta, del Pleistocene inferiore (Villafranchiano superiore). In questo articolo viene fornita una descrizione preliminare del mustelide *Pannonictis nestii*. Viene brevemente discussa la tassonomia e la paleobiogeografia della sottofamiglia Galictinae. Il genere *Pannonictis* è presente in diverse località dell'Eurasia ma la sua tassonomia non è ancora ben definita. La sua documentazione nell'Italia peninsulare prima del ritrovamento di Pietrafitta era limitata al Valdarno Superiore.

1. Introduction

In 1931 Kormos described the remains of a very large mustelid from Villany and Beremend (Hungary) as the new genus and new species *Pannonictis pliocaenica*. Later (1933), the smallest individuals in the sample were recognised by the same author as a different species, *Pannonictis pilgrimi*.

The taxonomic position of this genus has been debated. Many authors considered it possibly identical to *Enhydriactis*, a genus erected by Forsyth Major (1901) for the Sardinian Pleistocene mustelid *E. galictoides*.

Viret (1954) studied the species *Mustela ardea* Bravard and *Pannonictis pilgrimi* Kormos. Comparing them with a mustelid skull from SaintVallier, he recognised the specific identity of these species, referred them to the genus *Enhydriactis* and included these fossils in the species *Enhydriactis ardea*. The synonymy established by Viret (1954) between

¹ Dipartimento di Scienze della Terra, via G. La Pira 4, I-50121 Firenze

the *Enhydriactis* skull from SaintVallier and the mandibles of *Mustela ardea* should be accepted as these mandibles have characters well adaptable to the skull (e.g. the narrow width of the ascending rami, and the narrow cranial region between glenoid fossa and M¹).

In the same paper, Viret (1954) synonymized the mandible of *Pannonictis pilgrimi* under the name *E. ardea* but, according to Ficarelli & Torre (1967), this is not correct. The Villany species in fact has a skull with a longer rostral length and an arched upper profile, and a mandible with a larger ascending ramus. This view was not accepted by some authors (Kurtén 1968; Rabeder 1976; Willemsen 1988). However, in addition to the characters given by Ficarelli & Torre (1967), *Pannonictis pilgrimi* and *Enhydriactis ardea* differ also in the stoutness of the mandibular body, that in *Pannonictis* is very strong.

Ficarelli & Torre (1967) recognized that a great resemblance exists between the fossils of *Pannonictis pilgrimi* from the localities Villany and Beremend (Hungary) and the mandible from Upper Valdarno (Italy) described by Martelli (1906) as *Proputorius nestii*, and proposed the combination *Pannonictis nestii* (Martelli).

The genus *Pannonictis* was present in Asia during Plio-Pleistocene times with the species *P. pachygnata*. This species is recorded in China, at Nihowan (Teilhard de Chardin & Piveteau 1930) and in the Yushe basin (Teilhard de Chardin & Leroy 1945), and in Mongolia, at Shamar (Sotnicova 1980). The genus *Pannonictis* occurs in Eurasia from the latest Miocene, the Mustelidae gen. indet. et sp. indet. of Zdansky (1927) from the *Hipparion* beds of China is in fact attributable to this genus (Pilgrim 1933; Schreuder 1935).

A taxon closely related with *Pannonictis* is known from the early Pleistocene of North America under the name *Trigonictis* Hibbard (1941). Synonymy of Old and New World forms has been suggested by some author (Repenning 1967; Thenius 1972; Kurtén & Anderson 1980). As pointed out by Ray et al. (1981) it is preferable to consider the two genera as separate, since *Trigonictis* shows some primitive characters that place the North American form closer to the Miocene genus *Trochictis* than to *Pannonictis* or *Enhydriactis*.

Tigonictis is thought to have reached North America as an immigrant from Eurasia in the early Blancan (late Pliocene) or earlier (Repenning 1967).

Fossil representatives of this group are documented also in the South American fossil record since the lower Pleistocene (Lund 1841; Reig 1957).

The taxonomy of these forms has been debated for a long time. Pilgrim (1933, p. 848) first regarded such taxa as fossil representatives of the group of living South American Grisoninae Pocock 1921: "It seems that the genera *Tayra* (= *Eira*), *Grison* (= *Galictis*), *Enhydriactis*, *Pannonictis* and *Trochictis*, and, as Kormos (1931, p. 172) has surmised, the large Mustelid described by Zdansky (1927, p. 17, pl. i. fig. 26, pl. ii. figs. 1-3) under the name Mustelid gen. indet., sp. n., may be united into one group distinguished from the Melinae by the coexistence of a longer occiput and a short face, by the less backward extension of the protocone of P⁴, and by the reduction of the metacone and the postero-external root of M¹, accompanied by a moderate internal expansion antero-posteriorly of the same tooth. The face is probably rather longer in *Trochictis* than in the other genera of this group".

Although included in this group, Pilgrim notes that *Trochictis* is an unlikely ancestor of the other forms: "*Trochictis* is evidently a primitive somewhat generalised form, as shown by its narrow braincase, to be correlated by the nearness of the two bullae and the short meatal tube, and by the entire absence of any tendency to depression of the bulla. At the same time the anterior development of the auditory bulla, the advanced reduction of the metacone, and the internal expansion of M¹ as compared with *Enhydriactis*, *Panno-*

nictis, and Zdansky's Mustelidae gen. indet., sp. n., seem to prohibit us from placing *Trochictis* on the direct line to other genera of the group".

Ficarelli & Torre (1967), studying the structure of the bulla recognized a great affinity between *Enhydriactis*, *Pannonictis* and "*Grison*", and re-evaluated the subfamily Grisoninae established by Pocock. The same general view was expressed by Reig in 1957. This author described a fossil *Galictis* species from the late Pleistocene of Argentina, and erected the name Galictinae, replacing and expanding the Grisoninae of Pocock (1921). Pocock (1921) in fact restricts it to "*Grison*" and *Grisonella*, excluding *Eira*.

There is still no agreement in the taxonomical assessment at the subfamily level of these forms. Some researchers (Wolsan 1993; Wozencraft 1989a, b) in fact do not accept Galictinae, and include them in the subfamily Mustelinae. However, according to Reig (1957), Ray et al. (1981), and Martin (1989), the subfamily Galictinae includes the following genera: *Enhydriactis* and *Pannonictis* from the Turolian – Villafranchian of Eurasia, *Lyncodon*, *Trigonictis* and *Sminthosinis* from the Blancan of North America, and the living South American *Galictis*, and *Eira*.

2. The Pietrafitta locality and its local fauna

The lignites of Pietrafitta (Fig. 1) have been known since the second half of the past century. The systematic collection and conservation of fossils from the mine began in the

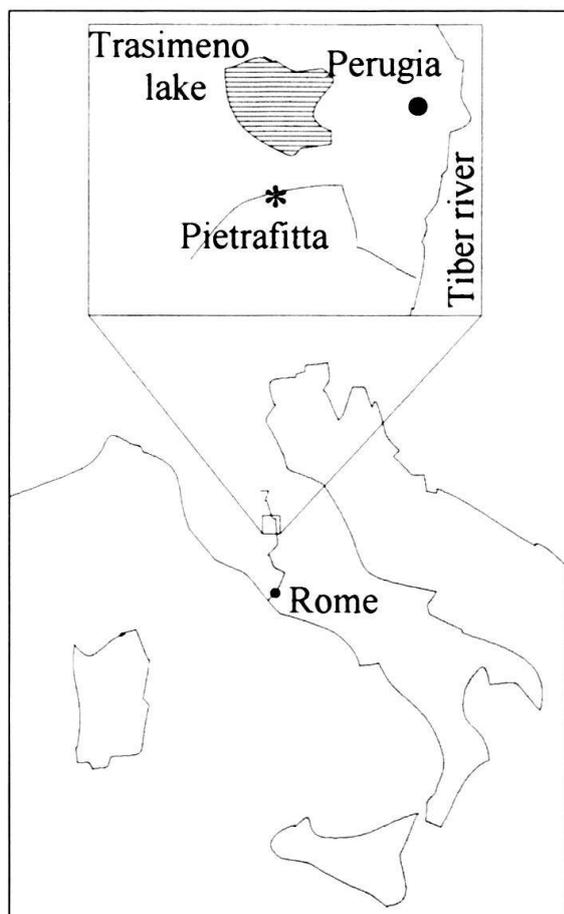


Fig. 1. Location of the Pietrafitta lignite mine.

1960's, thanks to the interest of some miners at Pietrafitta (especially Mr. Luigi Boldrini). Since the 1980's, these remains have been stored in the premises of the ENEL (the Italian National Electricity Company) mine, under the supervision of the Archaeological Superintendence of Umbria.

Many remains of large and small mammals together with other vertebrates, invertebrates and representatives of the macroflora have been found in Pietrafitta. The mammals have been the subject of many studies (Abbazzi 1991; Azzaroli & Mazza 1992, 1993; Ferretti 1993; Gentili et al. in press; Masini 1989; Masini & Torre 1990; Mazza et al. 1993; Rustioni & Mazza 1993). Up to now the following taxa have been identified: *Mammuthus meridionalis vestinus*, *Stephanorhinus* cf. *hundsheimensis*, *Equus* sp., *Leptobos* aff. *vallisarni*, *Megaceroides boldrini*, *Pseudodama farnetensis*, *Ursus etruscus*, *Panthera gombaszoegensis*, *Pannonictis nestii*, *Mustela* cf. *palerminae*, ? *Baranogale* sp., *Macaca* ex gr. *sylvana-florentina*, *Lepus etruscus*, *Castor plicidens*, *Microtus* (*Allophaiomys*) cf. *ruffoi*, *Microtus* (*Allophaiomys*) *chalconi*, *Mimomys pusillus*, *Sorex* sp. (small-sized) and *Talpa* sp.

The large mammal remains have made it possible to attribute the association to the Farnet faunal unit of the latest Villafranchian (early Pleistocene; Ambrosetti et al. 1987; Masini et al. 1994; Torre et al. 1992). The presence of some derived species characteristic of the latest Villafranchian, like *Mammuthus meridionalis vestinus*, *Stephanorhinus* cf. *hundsheimensis* and *Leptobos* aff. *vallisarni*, together with a primitive representative of the genus *Megaceroides*, indicate a faunal change that preceded the events which brought about a complete turnover, at the end of the Villafranchian and the beginning of the Galerian (Azzaroli 1983; Torre et al. 1992). The micromammal association is referable to the early Biharian (Gentili et al., in press).

3. Systematics

Family	Mustelidae FISCHER DE WALDHEIM, 1817
Subfamily	Galictinae REIG, 1957
Genus	<i>Pannonictis</i> KORMOS, 1931

Pannonictis nestii (MARTELLI, 1906)

1889,	<i>Mustela</i> sp., Weithofer
1906,	<i>Proputorius nestii</i> , Martelli
1954,	<i>Enhydriactis ardea</i> , Viret
1967,	<i>Pannonictis nestii</i> , Ficcarelli & Torre

Holotype

Left mandible bearing P₃–M₂, from Upper Valdarno (Tuscany, Italy). It is housed in the "Museo di Geologia e Paleontologia" of the University of Florence and is labelled as IGF 916.

The Pietrafitta sample

In addition to several isolated bones, fragmentary mandibular branches and isolated teeth, a crushed skull (n. 1749) and associated right mandible (n. 1750) was recently recovered. These remains are housed in a special building in the premises of the ENEL mine.

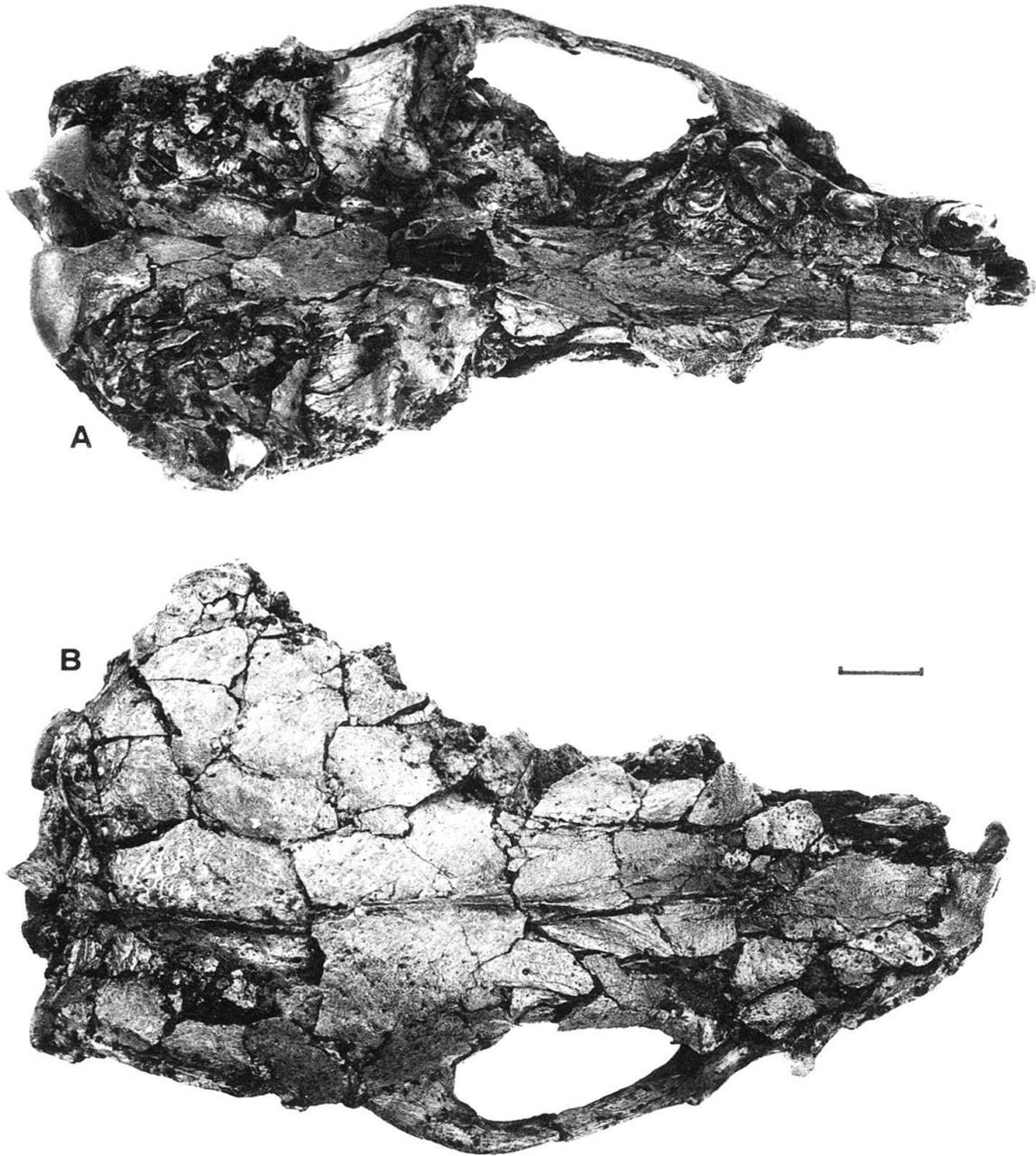


Fig. 2. *Pannonictis nestii* from Pietrafitta. Skull 1749. A: ventral view; B: dorsal view. Bar scale is 1 cm.

Skull: although compressed, the skull is almost complete, lacking only the left zygomatic arch and left maxillary bone (Fig. 2). The muzzle is short and robust, the post-orbital constriction relatively broad and placed very close to the post-orbital processes. Temporal and sagittal crests are well pronounced but not very much developed, the braincase is expanded, the palate large, the basioccipital relatively large. Elongated *bulla* with an anterior margin strongly protruding. Occurrence of fossa pre-orbitalis, and of rounded and large infra-orbital foramina.

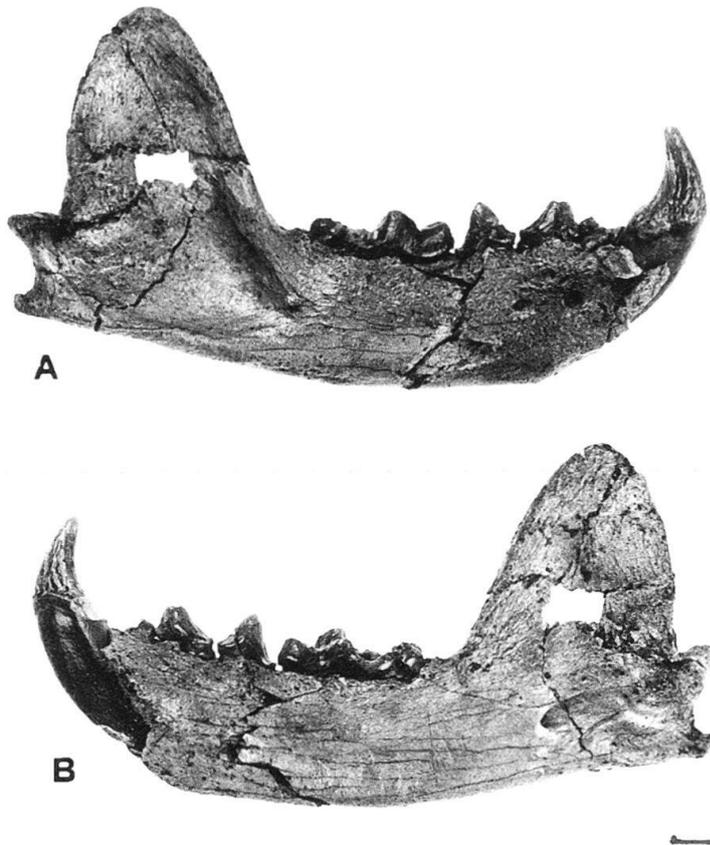


Fig. 3. *Pannonictis nestii* from Pietrafitta. Right mandible 1750. A: labial view; B: lingual view. Bar scale is 1 cm.

Upper dentition (Tab. 1): P^1 is single rooted and very reduced; P^4 is triangular in occlusal view, with large, strong, conical paracone and well developed lingual cingulum that forms a wide shelf extending from deuterocone to posterolingual base of metacone; the labial cingulum is almost absent. M^1 is rectangular in outline with no distinct waist, and with a labial cingulum.

Mandible: the right mandible is relatively short (Fig. 3), very massive and with a short angular process. The ventral margin is weakly curved. The deep masseteric fossa terminates posterior to the M_2 alveolus. The coronoid process is relatively small. Mental foramina 2 and 3 are present.

Lower dentition (Tab. 2): the lower canine is wrinkled by thin grooves. P_2 , P_3 and P_4 without accessory cusplets or strong cingulum. M_1 is relatively large, with a stout metaconid; the talonid of M_1 , that is almost $\frac{1}{3}$ of the tooth, is broad, basined, and with hypoconid moderately developed. The M_2 is rounded.

Comparisons

The specimens from Pietrafitta were compared directly with the type material of *Pannonictis nestii* (IGF 916) and with Hungarian populations of *P. pliocaenica* from Villany-Kalkberg and of *Pannonictis pilgrimi* from Villany-Kalkberg and Beremend (specimens of both species housed in the collections of the "Naturhistorisches Museum", Basel), and with the fossils referred to *P. arzilla* from Monte Pellegrino (Sicily), kept in the "Museo Geologico G.G. Gemellaro" of the University of Palermo. Further comparisons were made with data from the literature.

Tab. 1. Measurements, in millimetres, of upper dentition of different *Pannonictis* species. Bl = Basal length. A) from Kormos 1931.

			P1L	P1B	P2L	P2B	P3L	P3B	P4L	P4B	M1L	M1B	C-M1	Bl
<i>Pannonictis nestii</i>	Pietrafitta	1749	3.20	1.85	4.45	3.10	6.60	3.80	10.45	5.90	5.00	9.00	36.00	114.40
<i>Pannonictis pilgrimi</i>	Beremend	U.P. 606					6.30		10.50		5.55		31.50	
<i>Pannonictis pliocaenica</i>	Villany	OB 3594	2.10	1.70	5.50	3.50	7.70	4.50	13.20	8.30	6.80	12.80	39.60	122.60 A
<i>Pannonictis pliocaenica</i>	Villany-Kalkberg	U.P. 766			5.20	3.00	6.90	3.70	10.70	7.80				
<i>Pannonictis pliocaenica</i>	Villany-Kalkberg	U.P. 129							11.50		6.50		36.70	
<i>Pannonictis pliocaenica</i>	Villany-Kalkberg	U.P. 765			5.30	3.05	7.35	3.85	11.20	7.25	6.20	9.35	40.00	117.00
<i>Pannonictis pliocaenica</i>	Villany-Kalkberg	U.P. 149							12.00	7.60				
<i>Pannonictis pliocaenica</i>	Villany-Kalkberg	U.P. 132					7.25	4.15	12.55	8.70	7.25	12.05		

Tab. 2. Measurements, in millimetres, of lower dentition of different *Pannonictis* species. HMa = Height of mandibular body at M₁; Bma = Breadth of mandibular body at M₁. A) from Kormos 1931; B) from Teilhard de Chardin & Piveteau 1930; C) from Teilhard de Chardin & Leroy 1945; D) from Sotnicova 1980.

			P2L	P2B	P3L	P3B	P4L	P4B	M1L	M1B	Trigonid	M2L	M2B	C-M2	HMa	BMa
<i>Pannonictis nestii</i>	Upper Valdarno	IGF 916			6.05	3.25	6.55	3.35	11.75	5.20	8.00	3.85	3.80	40.15	14.80	6.35
<i>Pannonictis nestii</i>	Pietrafitta	1745							12.60	5.55	8.05				13.25	6.70
<i>Pannonictis nestii</i>	Pietrafitta	1776	4.60	2.90			6.25	3.35	11.50	4.80	7.70				11.95	5.35
<i>Pannonictis nestii</i>	Pietrafitta	1750		2.65	6.20	3.65	6.85	3.65	12.50	5.25	8.20	3.25	3.30	42.95	14.50	7.05
<i>Pannonictis pilgrimi</i>	Villany-Kalkberg	U.P. 135							13.50	5.35	8.50				13.15	7.05
<i>Pannonictis pilgrimi</i>	Villany-Kalkberg	U.P. 768	4.75	2.85	6.20	3.85	7.25	4.00	13.55	5.35	8.85	4.25	4.25	45.15	14.55	7.55
<i>Pannonictis pilgrimi</i>	Beremend	U.P. 606			6.10		6.40		11.80					38.90	13.30	6.25
<i>Pannonictis pliocaenica</i>	Villany	OB 3596	5.50	3.20	6.70	4.00	7.70	4.20	15.30	6.80	9.70			50.00	15.90	A
<i>Pannonictis pliocaenica</i>	Villany	OB 3600			6.70	4.30	8.20	4.30	15.40	6.30	10.70					A
<i>Pannonictis pliocaenica</i>	Villany-Kalkberg	U.P. 129			7.15		7.35		15.90					50.40	13.65	
<i>Pannonictis pliocaenica</i>	Villany-Kalkberg	U.P. 769			7.00	4.50			15.70	6.60	10.85	6.10	5.00	53.60	16.40	9.00
<i>Pannonictis pliocaenica</i>	Villany-Kalkberg	U.P. 767	5.65	3.55	6.65	4.75	8.90	4.75	15.95	6.55	11.05			54.00	17.90	9.55
<i>Pannonictis pliocaenica</i>	Villany-Kalkberg	U.P. 134					8.85	4.50	15.45	6.35	10.00				18.35	9.70
<i>Pannonictis pachygnata</i>	Shamar		5.50	4.70	6.80	4.70	8.50	5.00	16.40	7.50	11.70	4.30	5.40	54.00	18.00	10.00 B
<i>Pannonictis pachygnata</i>	Yushe		5.00		8.50		9.00		16.70					51.00	17.00	C
<i>Pannonictis pachygnata</i>	Nihewan		6.20	3.40	7.20	3.80	8.70	4.40	15.10	6.60					17.80	9.90 D

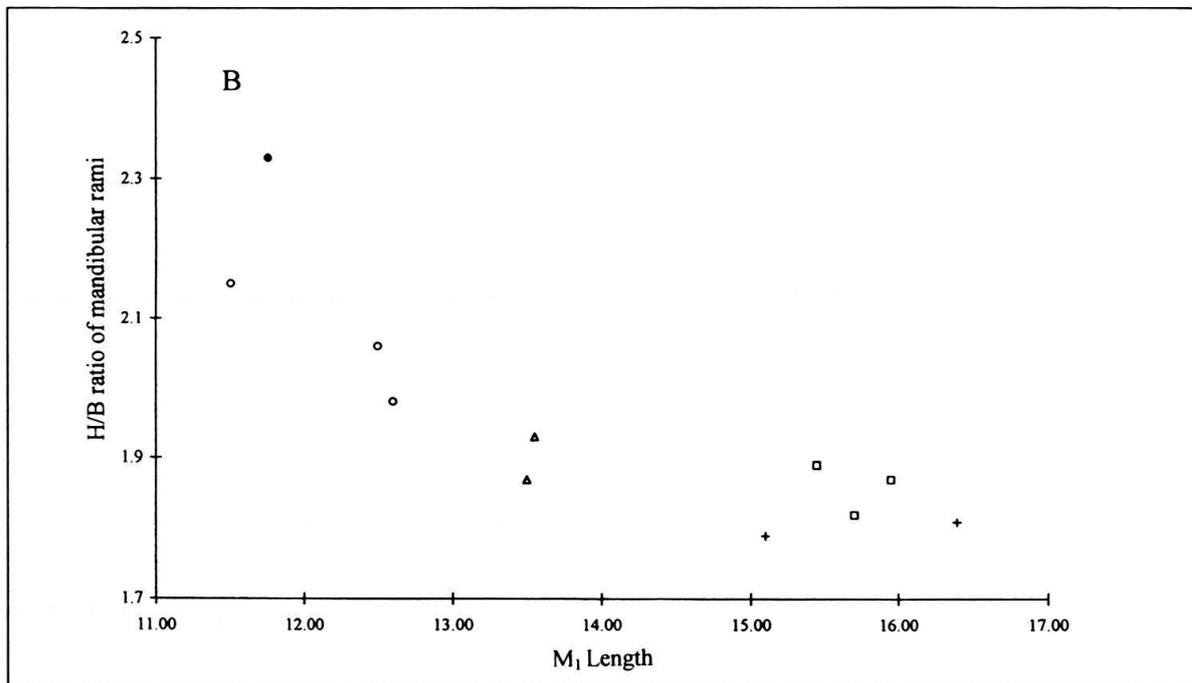
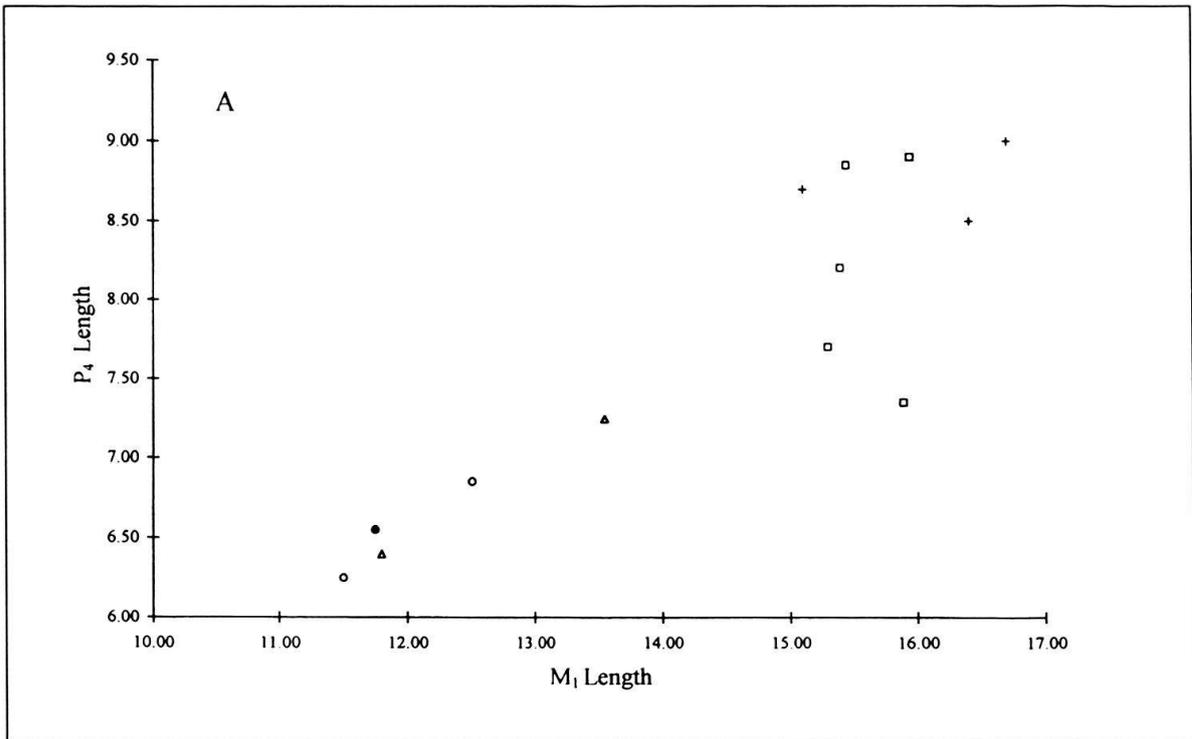


Fig. 4. Scatter diagrams of lower dentition of different *Pannonictis* species. Solid circle: *Pannonictis nestii* (type specimen); Open circle: *Pannonictis nestii* from Pietrafitta; open triangle: *Pannonictis pilgrimi*; open square: *Pannonictis pliocaenica*; cross: *Pannonictis pachygnata*. Scale in millimetres.

A) P₄ length versus M₁ length;

B) Height/Breadth ratio of mandibular rami versus M₁ length.

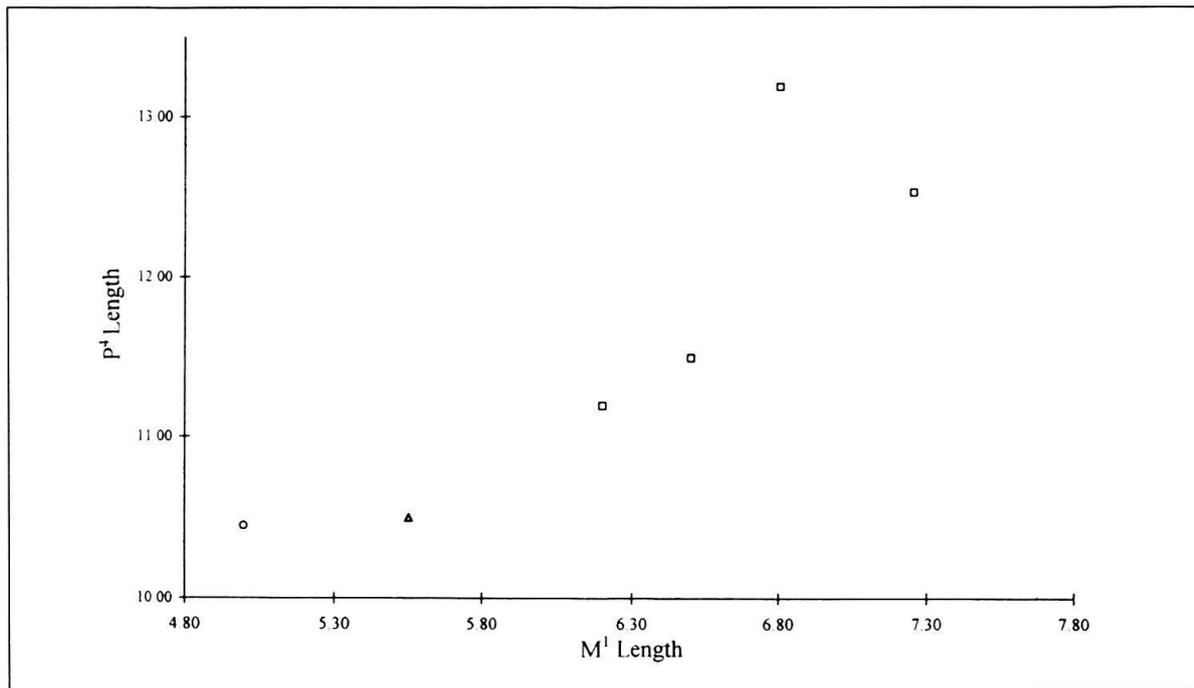


Fig. 5. Scatter diagrams of P⁴ length versus M¹ length of different *Pannonictis* species. Symbols and scale as in Figure 4.

Dimensionally and morphologically the Pietrafitta specimens are comparable with the type specimen of *Pannonictis nestii* from the Upper Valdarno. *Pannonictis nestii* and *P. pilgrimi* are two very closely related species, clearly distinguishable from both *P. pachygnata* and *P. pliocaenica* by size, by a stout mandibular body relative to M₁ length and by a relatively larger P₄ (Fig. 4). In the upper dentition two specimens from Villany-Kalkberg labelled as *P. pliocaenica* are metrically intermediate between the two groups (Fig. 5). Kormos (1933) found that the *Pannonictis* sample from Hungary fall into three groups for the M₁ length; the largest specimens were attributed to males of the species *P. pliocaenica*, the intermediate ones to females of the same species and the smallest ones to the species *P. pilgrimi*. A more precise systematic assessment for the alpha-taxonomy of *Pannonictis* is however impossible, given by the small sample at disposal for the present study. Further comparisons with the rich material from Hungary will be of great help in solving this problem. For the moment, the specific name *P. nestii* is maintained here for the Italian form.

A form very close to *P. nestii* is recorded in the endemic fauna of Monte Pellegrino (Palermo, Sicily). In 1886 De Gregorio described a mustelid which he named *Mustela arzilla*. Recently the material was revised by Burgio & Fiore (1994) who recognized it as belonging to the genus *Pannonictis*. The Monte Pellegrino sample is very close to *P. nestii*, although, some morphological features allowed the authors to retain a distinct specific name, *Pannonictis arzilla*, for the Sicilian fossil.

4. Concluding remarks

The genus *Pannonictis* is present in several localities in Eurasia but its alpha-taxonomy is still to be clearly defined. Its occurrence in the Italian peninsula before the Pietrafitta findings were limited to the Upper Valdarno. In contrast, the other Galictinae genus (*Enhydriactis*), apart from the rich sample from Sardinia, is reported at Arondelli (Villafranca d'Asti; early Villafranchian, Berzi et al. 1970), in the Olivola basin (Val di Magra, late Villafranchian, Ficarelli & Torre 1967) and in Mugello (Val di Sieve, late Villafranchian; cfr. Abbazzi et al. in press). Ecological inferences for the fossil Galictinae can be made based on the living species. These forms favour humid forest habitats, although they also occur in open landscapes. They are recorded as being good swimmers and are usually found near rivers and wet lands, where they feed principally on small mammals and birds, fishes, eggs and large insects (cfr. Leopold 1959).

An aquatic adaptation was recognised for the Sardinian form *Enhydriactis galictoides* (Forsyth Major 1901; Ficarelli & Torre 1967), and probably was common to all the fossil representative of the group. The occurrence of a form very close to *Pannonictis nestii* (*Pannonictis arzilla*) in the endemic fauna of Monte Pellegrino (Palermo, Sicily) support this hypothesis. This form could have reached Sicily by swimming, probably during a time of low stand of sea level, as occurred in the case of the colonisation of Sardinia by *Enhydriactis*.

Acknowledgements

I am particularly indebted to prof. P. Ambrosetti (University of Perugia), for granting the access to the material of Pietrafitta, and to Eng. Dr. R. Capurso and Eng. Dr. V. De Maria (Chief Executives of ENEL Umbria Power Plans) for supporting the field research in the mine. I greatly appreciated the generous help of Mr. L. Boldrini, Dr. S. Gentili, Mr. A. Bocciarelli, Mr. G. Bruni, and M. Rotoni. For access to collections under their care I wish to thank Dr. E. Burgio (Palermo), Mr. A. Curren (London), Dr. B. Engesser and Dr. F. Wiedemayer (Basel), and Dr. M. Sotnicova (Moscow). I am grateful to prof. D. Torre (Florence), Dr. A. Turner (Liverpool), and an anonymous reviewer for instructive comments and suggestions. I am also grateful to Mr. F. Cozzini ("Museo di Geologia e Paleontologia", University of Florence) for the photographs in Figs. 2 and 3. Research financially supported by contributions of ENEL (D.C.O. of Rome, and "Gruppo Impianti Umbria") and by grants of "Ministero dell'Università e della Ricerca Scientifica e Tecnologica" (M.U.R.S.T.) and "Consiglio Nazionale delle Ricerche" (C.N.R.).

REFERENCES

- ABBAZZI, L. 1991: Il grande cervide del giacimento Villafranchiano di Pietrafitta (Umbria). Unpublished dissertation, 170 pp., University of Florence.
- , BENVENUTI, M., ROOK, L. & MASINI, F. in press: Biochronology of the Mugello intermountain basin (northern Apennines, Italy). *Il Quaternario*.
- AMBROSETTI, P., FARAONE, A. & GREGORI, L. 1987: Pietrafitta: un Museo di Paleontologia in Umbria. *Museol. Sci.* IV/1–2, 99–118.
- AZZAROLI, A. 1983: Quaternary Mammals and the End-Villafranchian Dispersal Event – a turning point in the history of Eurasia. *Palaeogeogr., Palaeoclim., Palaeoecol.* 44, 117–139.
- & MAZZA, P. 1992: On the possible origin of the Giant Deer *Megaceroides*. *Rend. Fis. Acc. Lincei.* s. 9, 3, 23–32.
- 1993: Large early Pleistocene deer from Pietrafitta lignite mine, central Italy. *Palaeontogr. Ital.* 80, 1–24.

- BERZI, A., MICHAUX, J., HUTCHINSON, J. H. & LINDSAY, E. 1970: The Arondelli local fauna, an assemblage of small vertebrates from the Villafranchian stage near Villafranca d'Asti, Italy. *Giorn. Geol.*, Ser. 2, 35/1, 133–136.
- BURGIO, E. & FIORE, M. 1994: *Pannonictis arzilla* (De Gregorio, 1886) a "Villafranchian" element in the fauna from Monte Pellegrino (Palermo, Sicily). Abstract in "Il significato del Villafranchiano nelle successioni Plio-Pleistoceniche" AIQUA-CNR, Peveragno (CN), 20–24 giugno 1994, 15.
- DE GREGORIO, A. 1886: Intorno a un deposito di roditori e di carnivori sulla vetta di Monte Pellegrino. *Atti Soc. Tosc. Sci. Nat.* 8/1, 1–39.
- FERRETTI, M. P. 1993: Le forme europee del genere *Mammuthus* (Proboscidea, Elephantidae). Studio sistematico. Unpublished dissertation, 91 pp., University of Bologna.
- FICCARELLI, G. & TORRE, D. 1967: Il mustelide *Enhydriectis galictoides* del Pliocene della Sardegna. *Palaeontogr. Ital.* 33, 139–160.
- FORSYTH MAJOR, C. I. 1901: On *Enhydriectis galictoides*, a new fossil mammal from Sardinia. *Proc. Zool. Soc. London* 2, 625–628.
- GENTILI, S., ABBAZZI, L., MASINI, F., AMBROSETTI, P. L. & TORRE, D. in press: *Microtus* (Allophaiomys) *chalinei* and other voles from the early Pleistocene of Pietrafitta (Central Italy, Perugia). *Acta zool. Cracov.*
- HIBBARD, C. W. 1941: Mammals from the Rexroad fauna from the upper Pliocene of southwestern Kansas. *Amer. Midl. Nat.* 26/2, 337–368.
- KORMOS, T. 1931: *Pannonictis pliocaenica* n.g., n.sp., a new giant Mustelid from the Late Pliocene of Hungary. *Ann. Inst. Reg. Hung. Geol.* 29/3, 167–177.
- 1933: Neue und wenig bekannte Musteliden aus dem ungarischen Oberpliozan. *Folia Hydrobiol.*, Riga 5/2, 129–158.
- KURTÉN, B. 1968: Pleistocene mammals of Europe. Weidenfield & Nicolson, London, 317 pp.
- & ANDERSON, E., 1980: Pleistocene mammals of North America. Columbia Univ. Press, New York, 442 pp.
- LEOPOLD, A. S. 1959: Wildlife in Mexico: The Birds and Mammals. Univ. of California Press, Berkeley, 586 pp.
- LUND, P. W. 1841: Blik paa Braziliens Dyreverden for sidste Jordomvaeltning V (Om de nulevende og uddode Arter af Povdyrenes Familie). *Kon. Danske Vidensk. Selsk., Naturv. Afh.* 11, 1–82.
- MARTELLI, A. 1906: Su due mustelidi ed un felide del Pliocene toscano. Roma.
- MARTIN, L. D. 1989: Fossil history of the Terrestrial Carnivora. In: *Carnivore behavior, ecology, and evolution* (Ed. by GITTLEMAN, J. L.). Cornell Univ. Press, Ithaca, 536–568.
- MASINI, F. 1989: I Bovini villafranchiani dell'Italia. Doctoral dissertation, 152 pp. Modena–Bologna–Firenze–Roma "la Sapienza" Universities.
- , ROOK, L., ABBAZZI, L., AMBROSETTI, P., AZZAROLI, A., FICCARELLI, G., GENTILI, S., KOTSAKIS, T., SALA, B. & TORRE, D. 1994: Mammalian Faunas of selected Villafranchian localities of Italy. Communicated at "Il significato del Villafranchiano nelle successioni del Plio-Pleistocene", AIQUA-CNR, Peveragno (CN), 20–24 giugno 1994.
- & TORRE, D. 1990: Review of the Villafranchian arvicolidids of Italy. *Int. Symp. Evol. Phyl. Biostr. Arvicolidids*, 339–346, Praha.
- MAZZA, P., SALA, B. & FORTELIUS, M. 1993: A small latest Villafranchian (late Early Pleistocene) rhinoceros from Pietrafitta (Perugia, Umbria, Central Italy), with notes on the Pirro and Westerhoven rhinoceroses. *Palaeontogr. Ital.* 80, 25–50.
- PILGRIM, G. 1933: The genera *Trochictis*, *Enhydriectis*, and *Trocharion*, with remarks on the taxonomy of the Mustelidae. *Proc. Zool. Soc. London* 1932/4, 845–867.
- POCOCK, R. I. 1921: On the External Characters and Classification of the Mustelidae. *Proc. Zool. Soc. London* 1921, 803–837.
- RABEDER, G. 1976: Die Carnivoren (Mammalia) aus dem Altpleistozan von Deutsch-Altenburg 2. *Beitr. Paläont. Österr.* 1, 5–119.
- RAY, C.E., ANDERSON, E. & WEBB, S. D. 1981: The Blancan Carnivore *Trigonictis* (Mammalia: Mustelidae) in the Eastern United States. *Brimleyana* 5, 1–36.
- REIG, O. 1957: Un mustelido del genero *Galictis* del Eocuartario de la Provincia de Buenos Aires. *Ameghiniana* 1/1-2, 33–47.
- REPENNING, C. 1967: Paelearctic-Nearctic mammalian dispersal in the late Cenozoic. In: *The Bering Land Bridge* (Ed. by HOPKINS, D. M.). Stanford Univ. Press, Stanford, 288–311.
- RUSTIONI, M. & MAZZA, P. 1993: The Late Villafranchian bear from Pietrafitta (Perugia, Central Italy). *Palaeontogr. Ital.* 80, 51–62.

- SCHREUDER, A. 1935: A note on the Carnivora of Tegelen clay, with some remarks on the Grisoninae. Arch. Ned. Zool. 2/1, 73–94.
- SOTNICOVA, M. V. 1980: Late Pliocene Mustelidae from Shamar (Mongolia). Bull. Kom. Iz. Chertv. Period. 50, 138–145 [in Russian].
- TEILHARD DE CHARDIN, P. & LEROY, P. 1945: Les Mustélidés de Chine. Inst. Géobiol. Peking 12, 1–56.
- & PIVETEAU, J. 1930: Les mammifères fossiles de Nihewan (Chine). Ann. Paleont. 19, 1–134.
- THENIUS, E. 1972: Grundzüge der Verbreitungsgeschichte der Säugetiere. Eine historische Tiergeographie. Gustav Fischer, Stuttgart, 345 pp.
- TORRE, D., FICCARELLI, G., MASINI, F., ROOK, L., SALA, B. 1992: Mammal Dispersal events in the Early Pleistocene of Western Europe. Courier Forsch.-Inst. Senckenberg 153, 51–58.
- VIRET, M. J. 1954: Le loess à bancs durcis de Saint-Vallier (Drome) et sa faune de mammifères villafranchiens. Nouv. Arch. Mus. Hist. Nat. Lyon 4, 1–197.
- WEITHOFER, K. A. 1889: Über die tertiären Landsäugetiere Italiens. Jahrb. Geol. Reichsanst. 39, 55–82.
- WILLEMSEN, G. F. 1988: *MUSTELA* and *Enhydriactis* (Carnivora, Mustelidae) from Tegelen (the Netherlands). Proc. Ned. Ak. v. Wet. B 91/3, 311–320.
- WOLSAN, M. 1993: Phylogeny and classification of early European *Mustelida* (Mammalia: Carnivora). Acta Teriol. 38, 345–384.
- WOZENCRAFT, W. C. 1989a: The Phylogeny of the Recent Carnivora. In: Carnivore behavior, ecology, and evolution (Ed. by GITTLEMAN, J. L.). Cornell Univ. Press, Ithaca, 495–534.
- WOZENCRAFT, W. C. 1989b: Appendix: Classification of the Recent Carnivora. In: Carnivore behavior, ecology, and evolution (Ed. by GITTLEMAN, J. L.). Cornell Univ. Press, Ithaca, 569–593.
- ZDANSKY, O. 1927: Weitere Bemerkungen über fossile Carnivoren aus China. Paleont. Sinica C 4/4, 1–30.

Manuscript received January 3, 1995

Revision accepted March 20, 1995