

The Plio-Pleistocene artiodactyls (Vertebrata, Mammalia) of Macedonia 1. The fossiliferous site "Apollonia-1", Mygdonia basin of Greece

Dimitris S. KOSTOPOULOS

University of Thessaloniki, Department of Geology,
54006 Thessaloniki (Greece)

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ABSTRACT

The artiodactyls from the early Pleistocene locality of Apollonia-1 (APL) are described and compared. The cervid *Megaloceros* sp., as well as the bovids *Bison* (*Eobison*) sp., *Soergelia brigittae* n.sp., *Praeovibos* sp., *Pontoceros ambiguus mediterraneus* n.ssp. and a Caprinae indet. are recognized. A latest Villafranchian age (MNQ20) could be suggested for the locality of Apollonia-1. The environment, during that time, has been reconstructed as a warm and dry period with seasonal rainfalls.

RÉSUMÉ

Les artiodactyles du Pléistocène inférieur de la localité d'Apollonia-1 (APL) sont déterminés et discutés dans le présent article. Ce gisement a livré les restes du cervidé *Megaloceros* sp. ainsi que ceux des bovidés *Bison* (*Eobison*) sp., *Soergelia brigittae* n.sp., *Praeovibos* sp., *Pontoceros ambiguus mediterraneus* n.ssp., un Caprinae indet. est présent. L'âge Villafranchien terminal (MNQ20) peut être suggéré pour ce gisement fossilifère. Pendant cette période, l'environnement du site d'Apollonia aurait été caractérisé par la prédominance de saisons chaudes et sèches entrecoupées de violents orages.

KEY WORDS

Artiodactyls,
Cervidae,
Bovidae,
early Pleistocene,
Apollonia-1,
Greece.

MOTS CLÉS

Artiodactyles,
Cervidae,
Bovidae,
Pléistocène inférieur,
Apollonia-1,
Grèce.

INTRODUCTION

The fossiliferous site "Apollonia-1" (APL), found during the summer 1991 (Koufos *et al.* 1992), is situated 60 km NE to Thessaloniki, in the eastern part of the Mygdonia basin. The locality belongs to the Platanochori Formation (Premygdonian Group), consisting of fluvio-lacustrine sediments (Koufos *et al.* 1995).

The excellent preservation of the APL material allows a detailed description and a precise comparison. The systematic study of artiodactyls was a part of the Ph.D Thesis, completed by the author (Kostopoulos 1996) under the scientific supervision of Prof. G. Koufos. An extended summary of this work, with emphasis to the new or particular forms of artiodactyls, is given in the present article. Moreover, some new specimens, collected during summer 1996, are also described and compared. The association of artiodactyls from APL provides important palaeoecological and biochronological informations, already discussed by Kostopoulos (1996) and Kostopoulos & Koufos (in press).

SYSTEMATIC PALEONTOLOGY

Family CERVIDAE Gray, 1821

Genus *Megaloceros* Brookes, 1828

Megaloceros sp.

(Fig. 1, Tables 1-3)

Megaloceros (*Megaceroides*) sp. Kostopoulos *et* Koufos, 1994: 1270.

MATERIAL. — Frontlet, APL-212; proximal part of antler, APL-206, 357, 434; distal part of antler, APL-241, 489; part of maxilla with dP2-dP4, APL-326, 529; part of maxilla with dP3-M1, APL-482; part of maxilla with P2-M3, APL-243, 274, 325, 401; part of maxilla with P2-P4, APL-37; P3-P4 *in situ*, APL-506; M3 *in situ*, APL-483; P3, APL-152; M1, APL-141.

Part of mandibular ramus with dp2-dp4, APL-36, 327, 467; part of mandibular ramus with dp3-dp4, APL-507; part of mandibular ramus with p2-m3, APL-33, 384, 402, 491; m3 *in situ*, APL-28.

Distal part of humerus, APL-298; McIII+IV,

APL-334, 376, 385; radius + part of ulna, APL-576; proximal part of McIII+IV, APL-198, 230, 231, 312, 504; astragalus, APL-359; calcaneum, APL-216, 217, 255, 291, 292, 359; cubonaviclar, APL-219, 273, 296, 359; MtIII+IV, APL-199, 354; proximal part of MtIII+IV, APL-245, 271, 359; first phalanx, APL-253; third phalanx, APL-580.

DESCRIPTION

The skull is only known by a part of the frontals with the proximal segment of the antlers. The frontal region between the pedicels is flat (Fig. 1A). The interfrontal suture is slightly elevated in front of the antlers. In lateral view, the frontals form an angle of about 90°. The breadth of the skull posteriorly to the antlers is almost 120 mm. The supraorbital pits are double, situated in shallow depressions of the frontals. The pedicels are strong, cylindrical and relatively high. The divergence of the antlers reaches almost 90°. The proximal part of the antlers is almost straight, directed laterally and distally. The internal distance between the antlers (between the burrs) is 187 mm, indicating a wide separation. The burr is rounded-oval shaped. The proximal part of the beam, above the burrs, is cylindrical. The beam is slightly curved backwards at the level of the first appeared tine. At the same level, the beam is compressed laterally. The first appeared tine is inserted anteriorly and relatively far up to the burr (71.8 mm in a young individual and 121.5 mm in an adult one). Its section is subrounded at the base and becomes more compressed to the top. It is directed anteriorly and slightly laterally. The anterior part of the first appeared tine is bifurcated in the specimen APL-357, where it is completely preserved (Fig. 1B). In the same specimen, the maximal length of the first appeared tine is almost 240 mm. The distance between the first and the second tine exceeds 130 mm. The distal part of the beam should be partly palmate. The specimens APL-241, 489, originated from the distal part of the antlers, present a strong lateral compression and secondary bifurcations. The surface of the antlers is well grooved by fine longitudinal furrows.

The preorbital foramen is situated above P2. The length P2-M3 varies between 134.4 mm and 157.1 mm. The premolar row is relatively elon-

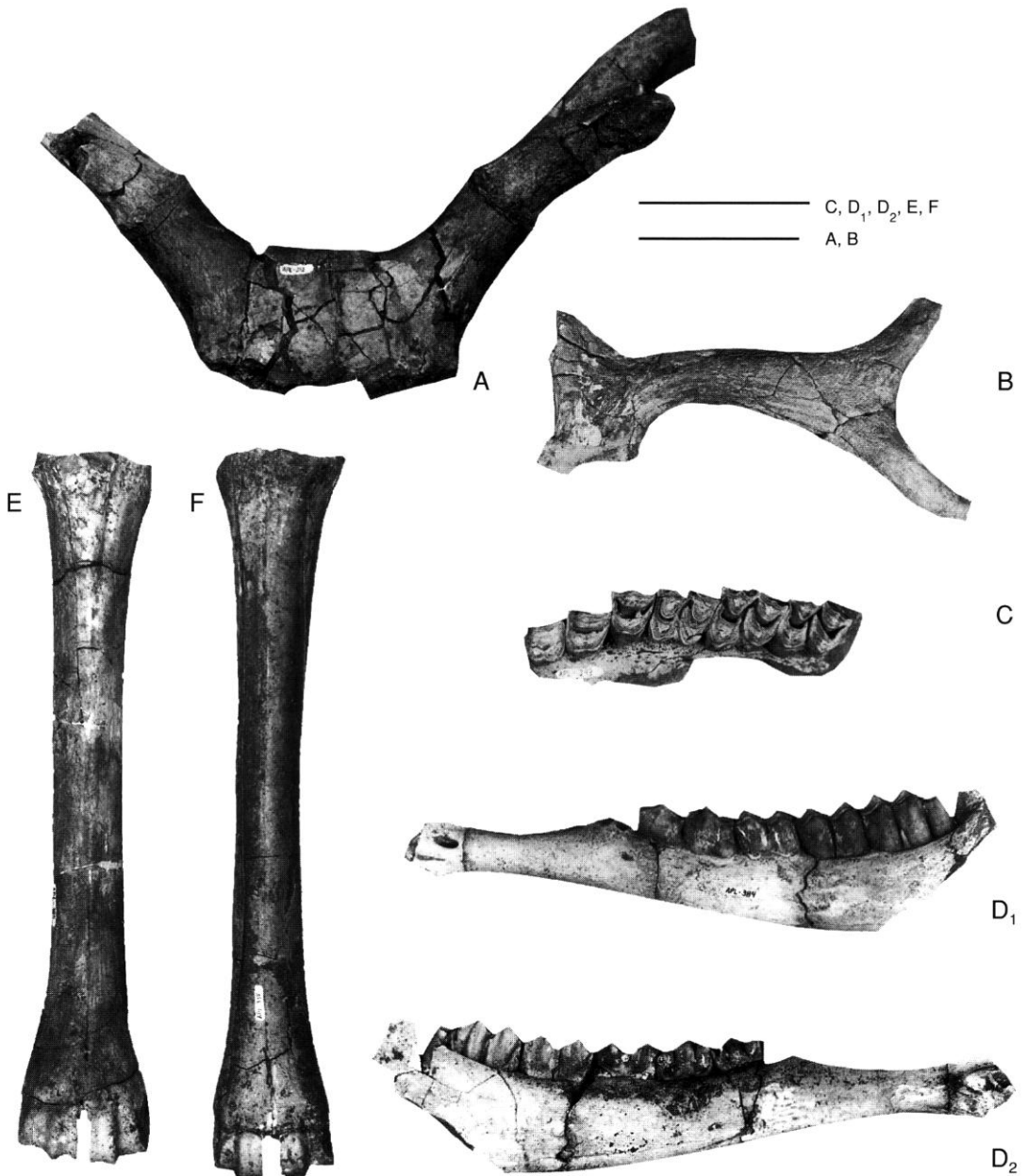


FIG. 1. — *Megaloceros* sp., Apollonia-1 (APL), Macedonia, Greece. **A**, APL-212, frontlet, anterior view; **B**, APL-357, first tine, lateral view; **C**, APL-243, right maxilla, occlusal view; **D₁**, APL-384, left mandibular ramus, labial view; **D₂**, APL-384, left mandibular ramus, lingual view; **E**, APL-385, metacarpal, anterior view; **F**, APL-334, metacarpal, anterior view. Scale bars: 10 cm.

gated comparatively to the molars one. The index " $LP2-P4 \times 100/LM1-M3$ " is 69.8-76.4. P2, 3 are molarized lingually. All the upper premolars present a strong hypoconal fold ("*éperon hypoconal*" according to Heintz 1970). The upper molars have strong pillars and styles. The unworn or slightly worn molars present a protoconal fold ("*pli protoconal*"). The M3 of the specimen APL-141 has a strong protoconal fold, as well as a weak anterior hypoconal fold ("*pli hypoconal*"). The "*éperon hypoconal*" is variably developed; it is present in the specimens APL-274, 483 but absent from the specimen APL-243. The development of the cingulum varies also but it is present in the majority of the molars.

The mandibular ramus is straight, shallow and relatively wide (Fig. 1D). The diastema i3-p2 is longer than 90 mm. A secondary mental foramen is situated below the posterior end of p2. The length p2-m3 is 162.7-182 mm. The index " $Lp2-p4 \times 100/Lm1-m3$ " is 64-72; p2 is relatively large. Its paraconid is connected with the parastylid, while the talonid is closed. The paraconid of p3 is distinguished from the parastylid in the unworn specimens. The second valley is open. The metaconid is strong and sub-triangular shaped. There is no labial furrow between the protoconid and the hypoconid. p4 presents some morphological variations. The unworn specimens APL-402, 491 have a closed trigonid and a lingually well curved metaconid. The specimens APL-33, 384 have an open second valley and an elongated metaconid directed distally. The third valley is always narrow and deep but remains open. The protoconid is distinguished from the hypoconid by a strong labial furrow. In general, p4 presents a closed trigonid (50%) and a closed talonid (100%). The lower molars have a strong cingulum and a well developed anterior fold ("*pli antérieur*" according to Heintz 1970). A slender basal pillar is also present between the lobes. It is double in m1 and single in m2, 3.

The radius is elongated and relatively slender. The coronoidal process is not very marked, while the radial tuberosity is strong. The metapodials are extremely elongated and relatively slender. The calcaneum is high. The cubonavicular presents a shallow disto-lateral projection. The index " $L \text{ metacarpal} / L \text{ radius}$ " is 0.93.

DISCUSSION

The origin and the systematic position of Megacerini (= Megalocerini) among the family Cervidae remain debatable. The late Miocene genera *Praesinomegaceros* and *Neomegaloceros* are considered as the first representatives of the tribe (Vislobokova 1990, 1992; Vislobokova & Changkang 1990), while the early Villafranchian species *Arvernoceros ardei* is considered as the first occurrence of the tribe in Europe (Heintz 1970; Vislobokova 1992). For the Pleistocene megaloceroses of Europe, the greatest problem concerns the nomenclature of the referred genera and species. The different generic names, proposed for the same or similar forms, as well as the different systematic divisions of the group of megaceres, provoke an incredible confusion (see Radulesco & Samson 1967; Azzaroli 1979; Vislobokova & Changkang 1990; Azzaroli & Mazza 1992...). Nevertheless, the majority of the researchers agree with the presence of two distinct groups within the tribe of European megaceres: the group *verticornis* and the group *giganteus*. In the present study, I prefer to use a simple nomenclature, based on the proposal of Azzaroli (1976) (*fide* Azzaroli 1979; Abbazzi 1991), to avoid a new confusion. Thus, I generally – but not dogmatically – accept the presence of a single genus *Megaloceros*, which is divided in two groups: the group *giganteus* [= *M. (Megaloceros) = Megaceres = Megaloceros = Dolichodoryceros*] and the group *verticornis* [= *M. (Megaceroides) = Megaceroides = Praemegaceres = Orthogonoceros*].

The species of *Megaloceros* are distinguished from *Eucladoceros* by: (1) the arrangement of the antlers, forming a divergence angle larger than 90° (< 90° in *Eucladoceros*); (2) the curving of the beam, which tends to be horizontal above the second tine; (3) the absent or rudimentary first tine in basilar position (close to the burr); (4) the insertion of the second tine on the upper surface of the beam; (5) the larger size; (6) the more robust metacarpals with robusticity index larger than 18 (< 17 in *Eucladoceros*) and (7) the low disto-lateral projection of the cubonavicular (according to Radulesco & Samson 1967; Abbazzi 1991).

The morphological features of the APL cervid

TABLE 1. — Skull and antler measurements of several European Pleistocene Megacerini (*, measurements from Radulesco & Samson 1967): 1, circumference of the pedicel; 2, DT of pedicel; 3, DAP of pedicel; 4, internal distance between pedicels; 5, external distance between pedicels; 6, internal distance between burrs; 7, circumference of burr; 8, DT of burr; 9, DAP of burr; 10, circumference of the beam above the first tine (point 1); 11, DT at point 1; 12, DAP at point 1; 13, distance between first and second tine; 14, DT of the first tine; 15, DAP of the first tine; 16, distance between the burr and the first tine (according Heintz 1970); 17, distance between the burr and the base of the first tine (after Radulesco & Samson 1967, modified).

Antlers	<i>Megaloceros</i> sp. (APL) n (max) = 4	<i>M. arambourgi</i> (Roumania) Radulesco & Samson 1967	<i>P. mosbachensis</i> (Mosbach) Soergel 1927*	<i>Praemegaceros</i> sp. (Voigstedt) Kahlke 1958*
1	165-170	190-199	200	171-199.8
2	47.8-54.6	64.0-66.8	68.0	63.4-70.6
3	51.3-55.4	56.5-58.0	63.0	48.1-56.8
4	175	79.5-100	140	75.0-129.8
5	250	187.5-214	252	180.0-225.3
6	187	80.0-94.0	—	—
7	200-225	230-267	—	213-255
8	58-69	70.7-80.2	—	—
9	64.5-73.1	74.5-85.5	—	—
10	150-160	185-205	—	175-204
11	40-47	67.5-73.8	54.5	54.0-65.0
12	48.3-59.2	48.0-56.0	59	54.0-65.0
13	>130	100	—	—
14	24-44	50	30	37.0-44.0
15	39.6-55.3	47	41	43.0-52.0
16	72-121.5	—	—	—
17	—	—	—	—

Antlers	<i>P. cf. verticornis</i> * (Suessenborn) Kahlke 1956-1959	<i>P. soleilhacus</i> (Venta Micena) Menendez 1987	<i>Orthogonoceros</i> <i>verticornis</i> Melentis 1967 (one frontlet)	<i>Cervidae</i> indet. (Libakos) Steensma 1988 (one frontlet)
1	203-234	160.4-187.0	180-183	—
2	70.0-81.0	53.4-60.1	—	61.5-62.2
3	55.0-79.0	48.7-64.0	—	50.0-51.0
4	114-135	148.4	—	—
5	219.5-231.0	159.8	—	—
6	102-145	—	100	116
7	136-268	161.5-227.3	228-236	—
8	—	51.7-75.6	—	55.5-72.0
9	—	51.1-69.5	—	46.0-70.0
10	166-212	—	—	—
11	53.0-78.0	—	60.0-62.0	49
12	47.0-61.0	—	55.0-56.0	52.5
13	—	—	—	450
14	20.0-47.0	—	—	—
15	34.0-63.0	—	—	—
16	—	193.4	>70	121-130
17	—	—	60.0-63.0	—

such as the very large size, the strong divergence of the antlers (90°), the relatively robust metacarpals (robusticity index = 17.3-18.7) and the low disto-lateral projection of the cubonaviclar,

show great similarity with *Megaloceros* s.l.

The representatives of the *giganteus* group are characterized by concave frontals between the pedicels, horizontally extended beam, palmate or

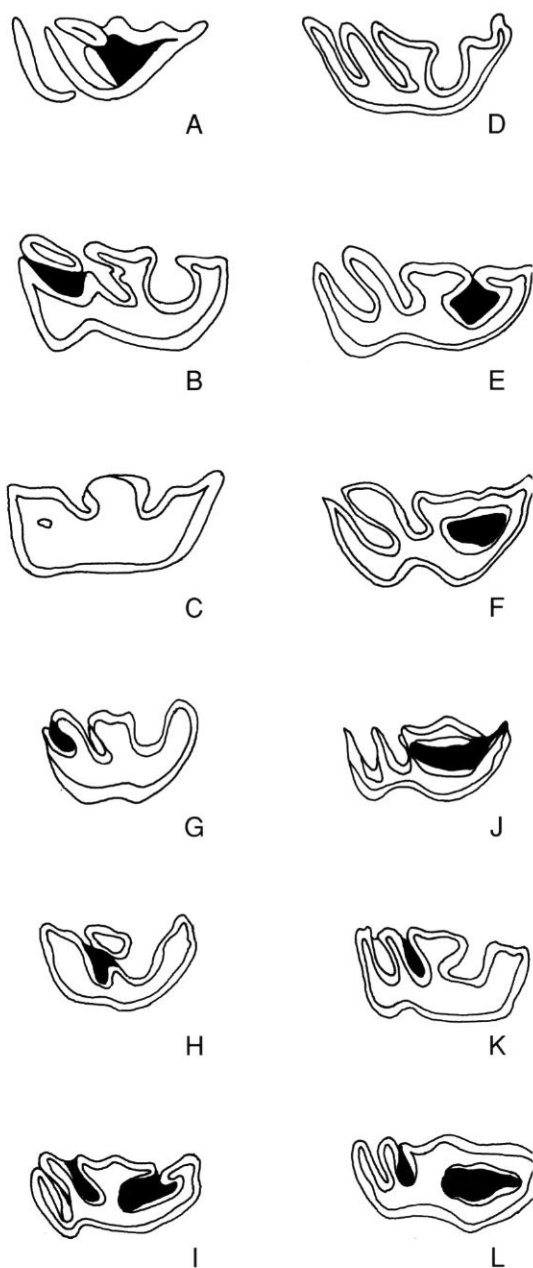


FIG. 2. — *Megaloceros* sp., APL, Macedonia, Greece. Comparison of the p4 structure of several European megaceros (data from Abbazzi 1991, modified): A, APL-491; B, APL-384; C, APL-33; D, *M. soleilhacus*, Venta Micena VM84 C3B8.30; E, *M. soleilhacus* VM84 C3L7.40; F, *M. soleilhacus* VM82 C60; G, *M. verticornis*, Süssenborn, Süss 7130; H, *M. verticornis*, Süssenborn, Süss 1965/2430; I, *Megaloceros* sp. Voigstedt, Voi.524; J, *M. süssenbornis*; K, *M. obscurus* (= "boldrinii"), Italy; L, *M. obscurus* (= "boldrinii"), Italy. Not to scale.

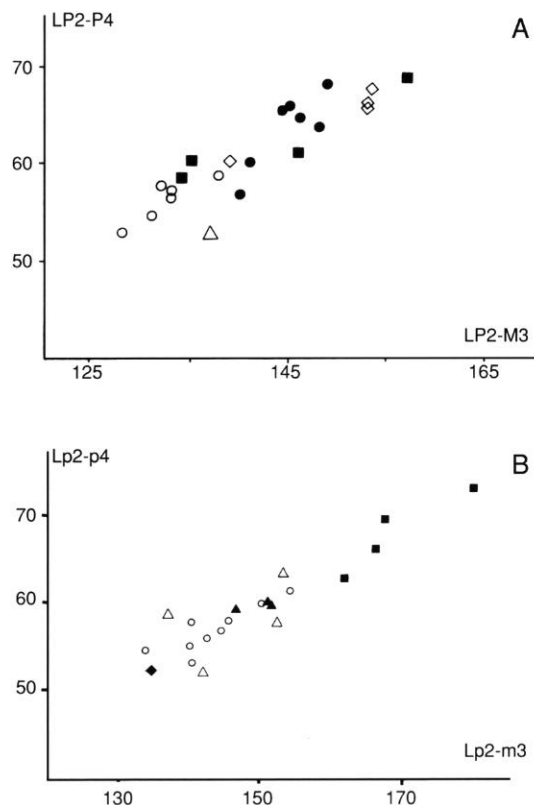


FIG. 3. — *Megaloceros* sp., APL, Macedonia, Greece. Scatter diagrams comparing the upper (A) and lower (B) tooththrow of several European megaceros (data from Menendez 1987; Abbazzi 1991, modified for A): ■, *Megaloceros* sp. APL; ◇, *Megaloceros giganteus*; ●, *M. giganteus* from Ofnet; ○, *Praemegaceros soleilhacus* from Venta Micena; △, *Megaceroides "boldrinii"* from Pietrafitta; ◆, *Megaloceros* sp. from Val di Chiana; ▲, *Praemegaceros* sp. from Voigstedt.

pteroïd first tine in basal insertion (close to the burr) and absence of the second tine. On the other hand, the forms included to the *verticornis* group are characterized by flat or convex frontals, small or rudimentary first tine and large second tine, descending to a proximal insertion, curved and not palmate (Radulesco & Samson 1967; Abbazzi 1991; Azzaroli & Mazza 1992). The flat frontals of APL-212 indicate that the studied cervid is closer to the forms of *verticornis* group. Nevertheless, the beam of the APL cervid is more straight than that of the typical forms of this group (*Praemegaceros verticornis*, *P. soleilhacus*) and it is directed laterally and distally but not horizontally. Moreover, the angle of divergence is

TABLE 2. — *Megaloceros* sp., APL, Macedonia, Greece. Dental measurements: **Lo**, occlusal length; **la**, breadth of anterior lobe; **lp**, breadth of posterior lobe; **lt**, breadth of talonid; **l**, maximal breadth; **s**, standard deviation; **v**, coefficient of variability.

	n	mean	min	max	s	v
Maxilla						
LPM	4	143.20	134.4	157.1	10.80	7.5
LP	5	63.03	58.5	69.0	4.40	7.0
LM	4	85.45	78.8	95.0	7.40	8.6
P2 Lo	3	22.50	21.2	23.3	1.14	5.0
P2 l	4	20.56	19.3	22.0	1.12	5.5
P3 Lo	5	22.40	20.8	23.8	1.41	6.3
P3 l	6	21.85	20.1	22.5	0.89	4.0
P4 Lo	5	20.95	20.0	23.0	1.23	6.0
P4 l	6	24.65	21.2	27.0	1.98	8.0
M1 Lo	5	30.16	27.5	31.9	1.97	6.5
M1 la	5	25.34	22.2	28.9	2.43	9.6
M1 lp	3	26.60	25.0	28.4	1.70	6.4
M2 Lo	2	32.90	32.5	33.3	—	—
M2 la	4	31.06	30.2	32.9	1.25	4.0
M2 lp	5	29.32	28.0	30.5	1.00	3.4
M3 Lo	3	30.90	30.3	31.4	0.55	1.8
M3 la	5	30.16	29.7	31.1	0.55	2.0
M3 lp	4	27.03	26.7	27.6	0.38	1.4
Mandible						
LPM	4	168.90	162.7	182.0	9.00	5.3
LP	4	68.11	63.3	73.6	4.50	6.6
LM	4	100.40	96.1	109.5	6.20	6.1
p2 Lo	3	16.53	16.0	17.0	0.50	3.0
p2 l	3	10.00	9.6	10.4	0.40	4.0
p3 Lo	4	23.10	21.9	25.0	1.34	5.8
p3 l	3	13.00	12.5	13.4	0.45	3.4
p4 Lo	4	24.93	24.3	26.1	0.79	3.2
p4 l	4	14.50	13.0	15.4	1.06	7.3
m1 Lo	3	28.60	27.5	30.5	1.70	5.8
m1 la	4	17.80	17.0	18.9	0.80	4.5
m1 lp	4	18.10	17.2	18.7	0.66	3.7
m2 Lo	4	31.10	30.0	32.0	0.92	3.0
m2 la	4	18.70	16.7	20.2	1.74	9.3
m2 lp	3	18.10	17.5	19.1	0.88	5.0
m3 Lo	5	39.64	36.9	42.1	2.43	6.1
m3 la	4	19.06	17.6	20.4	1.22	6.4
m3 lp	3	19.06	17.4	20.2	1.47	7.7
m3 lt	4	11.50	10.8	12.0	0.50	4.3

90° in APL, while it is larger in *Megaloceros* s.l. and smaller in *Eucladoceros*, indicating probably an intermediate character for the APL cervid.

As regards to the antler morphology of the studied cervid, the first tine, generally situated close to the burr, is totally missing. The first appeared tine of the APL antlers is strongly elongated, directed laterally and anteriorly, while it is not curved at its base. Moreover, it is compressed laterally and bifurcated (APL-357). These fea-

tures are far enough from those of the *verticornis* group. The bifurcation of this tine cannot be considered as a stable character, since it is observed only in one specimen.

Steensma (1988) notes that the insertion of the lowest tine on the anterior surface of the beam and its structure (strong, palmate) are evidence that it is a first tine. In *Praemegaceros* (= *Megaceroides*) the true first tine is rudimentary or absent. The lowest tine of the APL cervid is

TABLE 3. — *Megaloceros* sp., APL, Macedonia, Greece. Limb-bones measurements: 1, length (max); 2, DT proximal; 3, DAP proximal; 4, DT diaphysis; 5, DAP diaphysis; 6, DT distal (articular); 7, DAP distal (articular).

	n	mean	min	max	s	v
Radius						
1	1	408.00	—	—	—	—
2	1	90.70	—	—	—	—
3	1	82.50	—	—	—	—
4	1	52.00	—	—	—	—
5	1	33.00	—	—	—	—
6	1	82.80	—	—	—	—
7	1	58.00	—	—	—	—
McIII+IV						
1	3	379.60	372.3	385.0	6.56	1.7
2	8	63.36	56.7	68.5	4.10	6.5
3	7	42.45	36.4	49.5	5.59	13.1
4	3	38.40	38.0	39.2	0.69	1.8
5	3	38.96	37.9	39.6	0.93	2.4
6	3	68.33	66.7	69.7	1.52	2.2
7	3	43.90	42.6	45.0	1.21	2.8
MtIII+IV						
1	2	391.30	388.5	394.1	—	—
2	5	52.83	50.3	55.2	1.95	3.7
3	5	58.56	56.5	60.6	1.54	2.6
4	4	33.20	31.0	37.2	2.90	8.7
5	4	38.95	37.0	42.0	2.14	5.5
6	3	65.20	63.1	68.3	2.71	4.1
7	3	41.96	40.4	43.1	1.40	3.3
Phalanx I						
1	1	80.20	—	—	—	—
2	1	30.00	—	—	—	—
3	1	36.90	—	—	—	—
4	1	23.25	—	—	—	—
5	1	23.10	—	—	—	—
6	1	27.80	—	—	—	—
7	1	26.00	—	—	—	—

also strong, compressed, bifurcated and it descends to an anterior insertion, indicating that it is the first tine but not the second one. This feature differentiates the APL cervid from the group *verticornis*. A strong first tine, inserted anteriorly, characterizes *Eucladoceros*. Moreover, several species of the latter genus (*E. sedgwicki*, *E. dicranios*) present a bifurcated first tine as it happens in the APL cervid.

The dimensions of the antlers show that the APL cervid has a smaller pedicel and a more slender beam than the species *P. arambourgi*, *P. mosbachensis*, *P. sp.* (Voigstedt), *P. cf. verticornis* (Süssenborn), *O. verticornis* (Aliakmon, Greece) and Cervidae indet. (Libakos, Greece) (measure-

ments 1-10, Table 1). Additionally, the antler's divergence, expressed as the distance between the burrs (measurements 4, 6, Table 1) is significantly larger in APL than in the other forms.

The morphological features of the dentition cannot differentiate the APL cervid from the rest of the Megalocerini, because of the great morphological variation. However, the p4 of the APL cervid presents a particular morphology with generally advanced molarization, represented by two types, that of the Voigstedt megalocere and *P. soleilhacus* from Venta Micena (Spain; Fig. 2). Moreover the structure of the metaconid differentiates the APL p4 from the other species.

The length P2-M3 varies in APL from

134.4 mm to 157.1 mm. The maximal observed values are 137.6 mm in *P. soleilhacus* from Venta Micena and 144.6 mm in *M. "boldrini"* from Pietrafitta (Italy), while in fourteen specimens of *M. giganteus* this length varies between 140–156 mm (data from Bonifay 1981; Menendez 1987; Abbazzi 1991). The length p2-m3 is 162.7 mm–182 mm for the APL cervid, *vs* 133.1–154.4 mm ($n = 9$) for *P. soleilhacus* from Venta Micena, 143.5–144.2 mm ($n = 2$) for *P. verticornis* from Süssenborn, 149–154.4 mm ($n = 4$) for *P. sp.* from Voigstedt, 152.4–161 mm ($n = 4$) for *M. "boldrini"* from Italy and 155–166 mm for *M. giganteus* (data from Bonifay 1981; Menendez 1987; Abbazzi 1991). Obviously, the APL cervid has a clearly larger tooththrow than all the other known forms of European Pleistocene Megalocerotini (Fig. 3). Similar values are observed in the Asiatic genus *Sinomegaceros* (P2-M3 = 156 mm, p2-m3 = 171–173 mm; Sotnikova & Vislobokova 1990). The metapodials of the APL cervid (Table 3) are larger than those of *M. "boldrini"*, *M. cf. "boldrini"*, *Praemegaceros* sp. (Voigstedt), *P. verticornis* (Süssenborn), *M. verticornis* (Colle Curti, Italy), *P. gr. verticornis* (Petalona, Greece) and *P. soleilhacus* (Venta Micena). The more distinctive metrical differences concerns the length of McIII+IV and MtIII+IV as well as the height of the calcaneum (Fig. 4). Moreover, the proportions of the APL cervid are much larger than those of the known forms of European megaceros. Nevertheless, a single MtIII+IV from Venta Micena is close in size to that of APL.

In conclusion and according to all the available data, the following proposal can be made:

– The majority of the morphological and metrical characters of the APL antlers, tooththrows and limb bones show that the APL cervid could be attributed to the genus *Megaloceros* s.l. Nevertheless, some plesiomorphic (?) features of the antlers indicate affinities to *Eucladoceros*.

– The APL cervid is differentiated from the known species of European *Megaloceros* by its much larger size, the larger distance between the antlers, the more slender beam, the smaller pedicels, the arrangement and the structure of the first tine, the larger tooththrow, the moderate value of the index "length of premolar row/length of

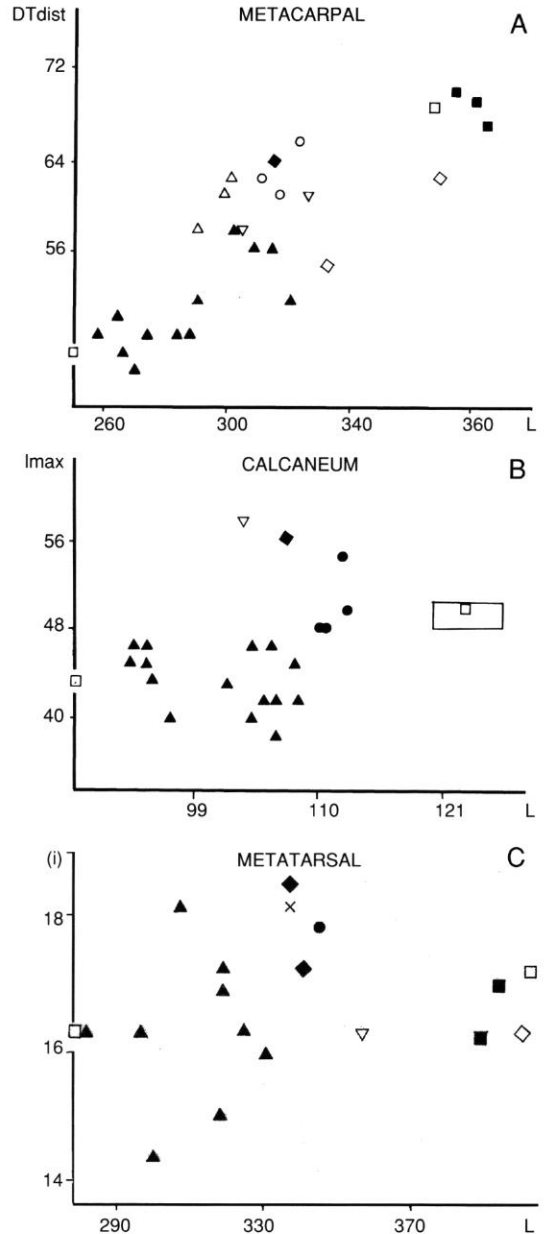


FIG. 4. — *Megaloceros* sp., APL, Macedonia, Greece. Scatter diagram comparing the proportions of the metacarpals (A), of the calcaneum (B) and of the metatarsals (C) of several European megaceros (after Abbazzi 1991; modified). ■, *Megaloceros* sp. APL (□ in B); ▲, *Eucladoceros*; □, *M. arambourgi* from Romania; ○, *Praemegaceros verticornis* from Süssenborn; ◇, *Praemegaceros soleilhacus* from Venta Micena; ◆, *Megaceroidea "boldrini"* from Pietrafitta; △, *M. gr. verticornis* from Petralona; ●, *M. verticornis* from Colle Curti; ×, *Praemegaceros* sp. from Voigstedt. Imax = maximal large (DT); (i) = "DTdistal × 100/L".

the molar row" (73.7 and 67.8 for the upper and lower toothrow respectively) situated between *Megaloceros* and *Eucladoceros*, the particular morphology of p4 and the strongly elongated and moderately robust metapodials and radius.

Since the systematic position of the APL cervid is not clear, and taking into account the great confusion among the Pleistocene megaloceres, I prefer – for the moment – to refer the APL cervid to *Megaloceros* sp., waiting for new data to refine its determination. Nevertheless, the extremely large dimensions of the APL form, as well as the particular morphology of its antlers and teeth, could support the erection of a new taxa, at specific level at least.

Family BOVIDAE Gray, 1821

Subgenus *Bison* (*Eobison*) Flerov, 1972

***Bison* (*Eobison*) n.sp.**

(Fig. 8, Tables 4-6)

MATERIAL. — Part of maxilla with dP2-M2, APL-145; part of maxilla with dP3-M2, APL-417; part of maxilla with dP2-dP4, APL-191, 418, 458; part of maxilla with dP3-M1, APL-32, 488, 492; part of maxilla with dP4-M2, APL-416; part of maxilla with dP4-M1, APL-29; part of maxilla with dP4, APL-473; part of maxilla with P2-M3, APL-269, 419; part of maxilla with P3-P4, APL-264; part of maxilla with M1-M3, APL-34, 270, 432, 433, 448, 488; part of maxilla with M1-M2, APL-505; part of maxilla with M2-M3, APL-487; P3, APL-442, 511, 512, 513; P4, APL-503, 510; M1, 2, APL-399, 472, 497; M3, APL-240, 263, 495.

Part of mandibular ramus with dp2-dp4, APL-240; part of mandibular ramus with dp3-dp4, APL-31, 38, 464; part of mandibular ramus with dP3-M1, APL-421, 504; part of mandibular ramus with dp2-m1, APL-422, 429; part of mandibular ramus with dp4-m1, APL-493; part of mandibular ramus with dp4-m2, APL-456; part of mandibular ramus with p2-m3, APL-478; part of mandibular ramus with p2-m1, APL-477; part of mandibular ramus with p3-m3, APL-297; part of mandibular ramus with p4-m3, APL-259.

Humerus, APL-575; distal part of humerus, APL-297, 501; proximal part of radius, APL-203, 288; distal part of radius, APL-373; carpals, APL-373; McIII+IV, APL-51, 95, 96, 196, 262, 373, 414, 446; proximal part of McIII+IV, APL-78, 144, 218, 221, 247, 279, 284, 285, 300a, 428, 455, 494; astragalus, APL-43, 46, 59, 65, 215, 273, 300b, 425, 453, 454; calca-

neum, APL-44, 146, 499; cubonavicular, APL-64, 85, 205, 220, 249; MtIII+IV, APL-41, 66, 94, 97, 192, 193, 194, 200, 249, 521; proximal part of MtIII+IV, APL-80, 101, 107, 207, 391; distal part of MtIII+IV, APL-79, 208; first phalanx, APL-128, 373s, 373d; second phalanx, APL-373s, 373d; third phalanx, APL-373s, 373d.

DESCRIPTION

The teeth are moderately hypsodont with a relatively strong presence of cement. The length P2-M3 is 135-137 mm with index " $LP2-P4 \times 100/LM1-M3$ " = 69.4-77.3. The hypsodonty index (height of parastyle $\times 100/L$ occlusal) is 126.5 for M1 (APL-458), 144.3 for M2 (APL-505) and 136.5-153.7 for M3 (n = 3). P2, 3 have a posterior hypoconal fold. The rear cavity of P4 does not have indentations and trends to form an inverse U. The enamel of the lingual face of the molars is well rippled, while the base of their crown is swollen. The styles are strong. The entostyle is also strong, high and wide; it is connected with the posterior lobe. The index "height of the entostyle $\times 100$ /height of the parastyle" is 70-81 for M3 (n = 3). In M2, 3 there is a variably developed posterior hypoconal fold. In M3 and in several M2 there is also a central islet.

The index " $Lp2-p4 \times 100/Lm1-m3$ " is 56, indicating a short premolar row. p2 is small. p3 is elongated and relatively narrow. The parastylid is strong, well separated from the paraconid. The metaconid is elongated and subparallel to the anteroposterior axis of the tooth. The second and third valleys are open, filled with cement. The protoconid is distinguished from the hypoconid by a shallow furrow. p4 is elongated and narrow. It is similar to p3 but its metaconid is more robust and parallel to the anteroposterior axis of the tooth. The second valley is deeper and narrower than in p3, while the third valley closes in advanced stages of wear. The hypoconid is stronger than in p3 and it is separated from the protoconid by a vertical furrow. The lower molars are prismatic and narrow. The parastylid and the entostylid are weak. There is no goat fold. The talonid of m3 is semicircular with flat internal wall. The ectostylid is slender, high and it is connected with the anterior lobe.

The preserved limb bones indicate a relatively

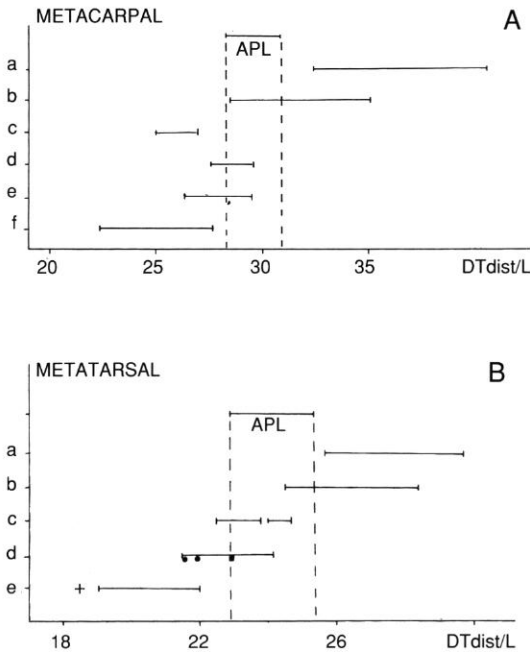


FIG. 5. — *Bison (Eobison)* n.sp., APL, Macedonia, Greece. Diagram comparing the distribution of the index "DTdistal/L" for the metapodials of several early Pleistocene Bovini (data from Moya-Sola 1987; Sala 1987; Masini 1989; Tsoukala 1989). **A**, metacarpal: APL (n = 6); **a**, *Bison priscus* (n = 8); **b**, *Bison schoetensacki* (n = 10); **c**, ? *Eobison* sp., Venta Micena (n = 13); **d**, *Eobison degiulii* (n = 7); **e**, "*Leptobos*" *vallisarni* (n = 4); **f**, *Leptobos etruscus* (n = 21). **B**, metatarsal: APL (n = 9); **a**, *Bison priscus* (n = 6); **b**, *Bison schoetensacki* (n = 2); **c**, *Eobison degiulii* (n = 4); **d**, ? *Eobison* sp., Venta Micena (n = 8); **e**, *Leptobos etruscus* (n = 21); **●**, *E. palaeosinensis*; **+**, "*L.*" *vallisarni*; **■**, *Leptobos* sp., Selvella (Italy).

delicate bovine. The humerus is elongated and robust. The humeral crest is well developed and the deltoid tuberosity is strong. The lateral epicondylar crest is weak. The tuberosities of the teres major and minor are well marked. The intertubercular sulcus and the coronoid fossa are deep. The trochlea is clearly more robust than the condyle and more elevated. The medial tuberosity of the condyle is strong. The metacarpals are divided metrically in two groups, representing males and females. In several metatarsals, the MtIII is more developed antero-posteriorly than the MtIV. The length of the anterior foot (humerus-third phalanx) is estimated at about 1 m.

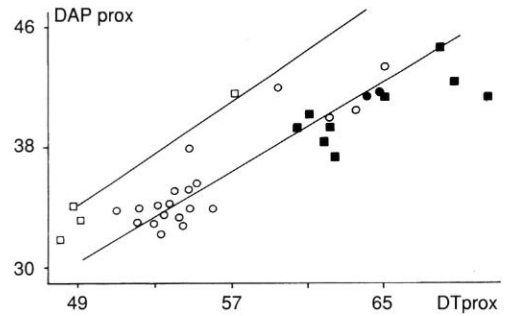


FIG. 6. — *Bison (Eobison)* n.sp., APL, Macedonia, Greece. Scatter diagram comparing the proportions of the proximal epiphysis of the metacarpal (after Moya-Sola 1987, modified): **■**, *Bison (Eobison)* n.sp. APL; **○**, ? *Eobison* sp., Venta Micena; **□**, *Leptobos etruscus*, Seneze; **●**, *Bison schoetensacki*, Durlfort (Brugal 1994).

DISCUSSION

The family of Bovidae presents several taxonomical problems, concerning the phylogenetic relationships of the different forms as well as their systematic (Moya-Sola 1987). This fact becomes extremely intense in regard to the early Pleistocene representatives of Bovini. Flerov (1972) (*vide* Flerov 1976) divides the genus *Bison* in two subgenera: *Bison (Eobison)* for the primitive forms and *Bison (Bison)* for the advanced forms of the genus. Masini (1989) describes the new species *Eobison degiulii* from the early Pleistocene locality of Pietrafitta (Italy), considering *Eobison* as a distinct genus. Nevertheless, the affinities of *E. degiulii* to the typical species of this genus (or subgenus), *E. palaeosinensis* are not so clear (Brugal pers. comm.). The absence of skull and/or horn-cores from the studied material does not allow an investigation of the systematic position of the APL large bovid. However, the numerous dental and postcranial remains are suitable for detailed comparison with the most common Plio-Pleistocene genera, such as *Leptobos*, *Bison (Eobison)*, *Bison (Bison)* and *Bos*. The degree of hypsodonty, the important presence of cement, the connection of the ectostylid with the anterior lobe of the lower molars, the absence of internal basal pillars on the lower molars, the absence of anterior constriction on the lobes of the molars, the strong and distally projected metastylid of m3, the strong entostylid

TABLE 4. — *Bison (Eobison)* n.sp., APL, Macedonia, Greece. Dental measurements: Lo, occlusal length; la, breadth of anterior lobe; lp, breadth of posterior lobe; lt, breadth of talonid; I, maximal breadth.

	n	mean	min	max	s	v
Maxilla						
LPM	2	136.00	135.0	137.0	—	—
LP	2	57.50	57.0	58.0	—	—
LM	8	81.86	75.0	94.4	5.68	6.9
P2 Lo	2	19.35	19.2	19.5	—	—
P2 I	2	13.80	13.0	14.6	—	—
P3 Lo	8	19.68	18.3	22.3	1.29	6.5
P3 I	8	17.73	15.3	19.3	1.29	7.3
P4 Lo	6	17.65	16.2	18.2	1.14	6.4
P4 I	7	21.13	20.5	22.0	0.61	2.9
M1 Lo	14	31.92	26.8	34.2	2.07	6.5
M1 la	20	21.75	17.8	26.8	3.53	16.2
M1 lp	17	23.06	16.1	28.0	4.01	17.4
M2 Lo	7	32.40	29.3	34.3	1.56	4.8
M2 la	14	24.69	17.7	28.4	4.09	15.6
M2 lp	12	24.85	17.8	29.2	3.81	15.3
M3 Lo	11	31.70	29.3	35.9	1.79	5.6
M3 la	12	25.57	21.5	27.7	1.62	6.4
M3 lp	12	23.62	18.5	27.3	2.19	9.2
Mandible						
LPM	1	143.00	—	—	—	—
LP	2	53.60	51.0	56.2	—	—
LM	2	90.75	90.5	91.0	—	—
p2 Lo	—	—	—	—	—	—
p2 I	2	8.75	8.4	9.1	—	—
p3 Lo	4	19.07	18.0	20.9	1.26	6.6
p3 I	4	11.20	10.7	11.6	0.40	3.5
p4 Lo	4	22.00	20.4	22.0	1.30	5.9
p4 I	5	13.36	12.5	15.2	1.10	8.3
m1 Lo	10	30.33	24.0	32.6	3.16	10.4
m1 la	8	14.50	13.2	15.9	1.04	7.2
m1 lp	8	14.80	13.0	17.0	1.50	10.2
m2 Lo	3	30.50	27.2	35.5	4.36	14.3
m2 la	4	16.73	14.9	18.0	1.53	9.2
m2 lp	4	16.93	14.9	18.6	1.90	11.2
m3 Lo	3	39.10	38.8	39.7	0.51	1.3
m3 la	3	16.70	15.0	17.7	1.53	9.1
m3 lp	3	16.40	15.1	18.1	1.53	9.3
m3 lt	3	9.86	8.0	12.6	2.42	24.5

of m3, the lateral projection of the external articular surface of the metacarpals, the great transverse diameter of the distal epiphysis of the metapodials and the outline of the proximal epiphysis of the metapodials (Fig. 8) are characteristics, and differentiate the APL bovid from *Leptobos*; they approach him to the primitive forms of *Bison* (Teilhard & Piveteau 1930; Moya-Sola 1987; Masini 1989; Brugal 1994).

Sala (1987) and Brugal (1994) give an important number of distinctive characters, which separate

the genera *Bos* and *Bison*. The comparison of the APL dental and postcranial remains with both genera indicates that the morphological features of the studied form are closer to the genus *Bison*. Thus, the basal swelling and the angular rear cavities of the upper molars, the presence of a central islet, the accute angle between the second and the third lobe of m3, the flat internal wall of the third lobe of m3, the low posterior relief of the proximal epiphysis of the radius, the lower situation of the lateral tuberosity of the radius,

TABLE 5. — Comparison of the toothrow's dimensions of several early Pleistocene Bovini.

	APL	<i>E. degiulii</i> Masini 1989	<i>Eobison</i> sp. (V. Micena) Masini 1989	<i>E. palaeosinensis</i> Teilhard & Piveteau 1930
	n = 1-2	n = 2	n = 1	n = 1
Lp2-m3 (1)	143	123.2-128.0	157.0	148
Lp2-p4 (2)	51.0-56.2	46.5-49.0	57.5	58.5
Lm1-m3 (3)	90.5-91.0	73.5-78.0	96.4	88.5
(2)/(3) × 100	56.3	59.6-66.6	59.6	66.1
(2)/(1) × 100	35.6	36.3-39.7	36.6	395
(3)/(1) × 100	63.2	59.6-60.9	61.4	59.8
	n = 2	n = 4		n = 3
L P2-M3 (4)	135.0-137.0	—		131-134
L P2-P4 (5)	57.0-58.0	—		54.0-60.0
L M1-M3 (6)	75.0-94.4	67.0-76.1		77.0-84.0
(5)/(6) × 100	73.3	—		61.1-72.2
(5)/(4) × 100	42.3	—		40.8-41.9
(6)/(4) × 100	57.8	—		58.0-59.1
	<i>Eobison</i> sp. (Soleilhac) Masini 1989	<i>L. etruscus</i> Masini 1989	<i>L. etruscus</i> Duvernois 1990	<i>Bison priscus</i> Tsoukala 1989
	n = 1	n = 12	n > 30, mean	n = 1
Lp2-m3 (1)	148	132.5-146.0	139.8	158.6
Lp2-p4 (2)	56.0	44.0-53.0	50.9	57.1
Lm1-m3 (3)	92.0	80.2-88.6	88.5	101.8
(2)/(3) × 100	60.8	53.5-65.3	57.5	56.0
(2)/(1) × 100	37.8	33.0-39.7	36.4	36.0
(3)/(1) × 100	62.1	56.2-63.4	63.3	64.2
		n = 4	n > 10, mean	
L P2-M3 (4)		110-128	132.9	
L P2-P4 (5)		50.5	52.1	
L M1-M3 (6)		76.0-78.3	79.0	
(5)/(6) × 100		66.4	65.9	
(5)/(4) × 100		39.4	39.2	
(6)/(4) × 100		59.3	59.4	

the strong anterior crests of the distal part of the radius diaphysis, the strongly concave proximal articular surface of the scaphoid, the posteriorly projected crest which divides the two proximal facets of the metacarpals, the concave postero-medial surface of the metacarpal proximal epiphysis, the dissymetrical sustentaculum tali of the calcaneum, the shallow groove of the distal trochlea of astragalus and the oblique arrangement of the lateral borders of the metapodials are morphological features which indicate great similarity between *Bison* and the APL bovid.

The dimensions of the toothrow (Tables 4, 5)

show that the studied form is larger than *Eobison degiulii* and *Leptobos etruscus* (Table 5) and closer to *E. palaeosinensis*. The lower premolar row is 51-56.2 mm in APL, similar to that of *Eobison* s.l. and slightly larger than that of *Leptobos* (Table 5).

The comparison of the metapodials provides more information (Fig. 5). The index "DTdistal × 100/L" of the metapodials shows that the APL bovid is situated between the samples of *Leptobos etruscus* and *Bison priscus*. The index seems to increase more or less gradually from the Villafranchian *Leptobos* to the late Pleistocene

TABLE 6. — *Bison (Eobison)* n.sp., APL, Macedonia, Greece. Limb-bones measurements: 1, length (max); 2, DT proximal; 3, DAP proximal; 4, DT diaphysis; 5, DAP diaphysis; 6, DT distal (articular); 7, DAP distal (articular); 8 (humerus), height (min) troclaea.

	n	mean	min	max	s	v
Humerus						
1	1	382.00	—	—	—	—
2	1	126.00	—	—	—	—
3	1	127.00	—	—	—	—
4	3	54.00	45.8	63.5	—	—
5	1	63.5	—	—	—	—
6	3	104.23	91.3	118.0	—	—
7	3	95.30	90.5	100.6	—	—
8	2	47.35	45.2	49.5	—	—
Radius						
1	1	> 300	—	—	—	—
2	2	84.30	80.6	88.0	—	—
3	2	47.80	44.8	50.8	—	—
4	2	48.00	47.7	48.3	—	—
5	2	30.75	30.5	31.0	—	—
6	1	79.70	—	—	—	—
7	1	47.00	—	—	—	—
McIII+IV						
1	7	237.60	226.0	245.6	7.06	2.9
2	11	68.05	57.7	77.5	5.85	8.6
3	10	39.65	33.9	44.5	2.95	7.4
4	10	40.40	31.7	49.1	5.61	13.9
5	10	29.14	23.4	34.1	3.16	10.8
6	8	72.44	66.5	88.5	7.19	9.9
7	9	39.66	34.4	48.2	4.10	10.3
Tibia						
1	—	—	—	—	—	—
2	—	—	—	—	—	—
3	—	—	—	—	—	—
4	4	47.22	43.6	52.9	4.50	9.5
5	4	36.31	34.6	38.3	1.74	4.8
6	12	75.74	61.0	92.4	7.98	10.5
7	13	56.76	51.0	67.0	4.51	7.9
MtIII+IV						
1	10	274.18	261.2	287.0	8.34	3.0
2	15	54.68	51.4	63.2	3.13	5.7
3	15	54.08	51.8	59.8	2.15	4.0
4	11	33.83	30.6	37.8	2.45	7.2
5	11	35.47	32.8	40.7	2.25	6.3
6	11	65.07	62.0	71.4	2.46	3.8
7	12	39.09	37.0	41.1	1.51	3.8

Bison. The estimated values for the APL bovid are similar to those of "*Leptobos*" *vallisarni*, *Eobison degiulii*, *Eobison* sp. from Venta Micena (= *Bubalus* sp. according to the revision of

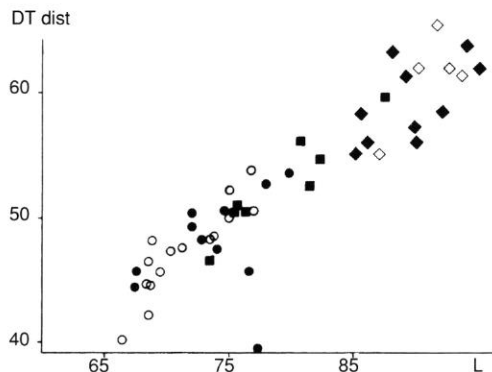


FIG. 7. — *Bison (Eobison)* n.sp., APL, Macedonia, Greece. Scatter diagram comparing the proportions of the astragalus of several early Pleistocene Bovini: ■, *Bison (Eobison)* n.sp. APL; ○, ? *Eobison* sp., Venta Micena; ●, *Eobison degiulii*; ◆, *Bison schoetensacki*, Mauer; ◇, *Bison schoetensacki*, Isernia la Pineta (data from Sala 1987; Moya-Sola 1987; Masini 1989).

Martinez 1992), as well as to the minimum values of *Bison schoetensacki* (Fig. 5). In the diagram "DAP/DT" of the proximal epiphysis of the metacarpals (Fig. 6), the APL sample is placed along the same axis as the Venta Micena bovid and it is divided in two dimensional groups, which correspond to male and female individuals. The dimensions of the astragalus lead to the same conclusion (Fig. 7).

According to the above mentioned data, it is obvious that the APL large bovid can be placed among the primitive forms of *Bison*, which are generally referred to as *Eobison* or better as *Bison (Eobison)* Flerov, 1972. The APL *Eobison* is situated between *Eobison degiulii* and *Bison schoetensacki*. Brugal (1994) notes that the material from Pirro Nord, Sainzelles, Casa Frata and Apollonia indicates the presence of a large sized bovid, intermediate between *Leptobos* and *Bison schoetensacki* in Mediterranean Europe. This idea becomes more clear after the previous comparison. Although the skull is absent, the APL sample is one of the most well known, as well as one of the most important, in number of specimens as in individuals (> 10); for these reasons it could be considered as a distinct species. Nevertheless, the systematic problems of the primitive bisons cannot permit a precise determination and thus the APL form is referred at the moment to *Bison (Eobison)* n.sp.

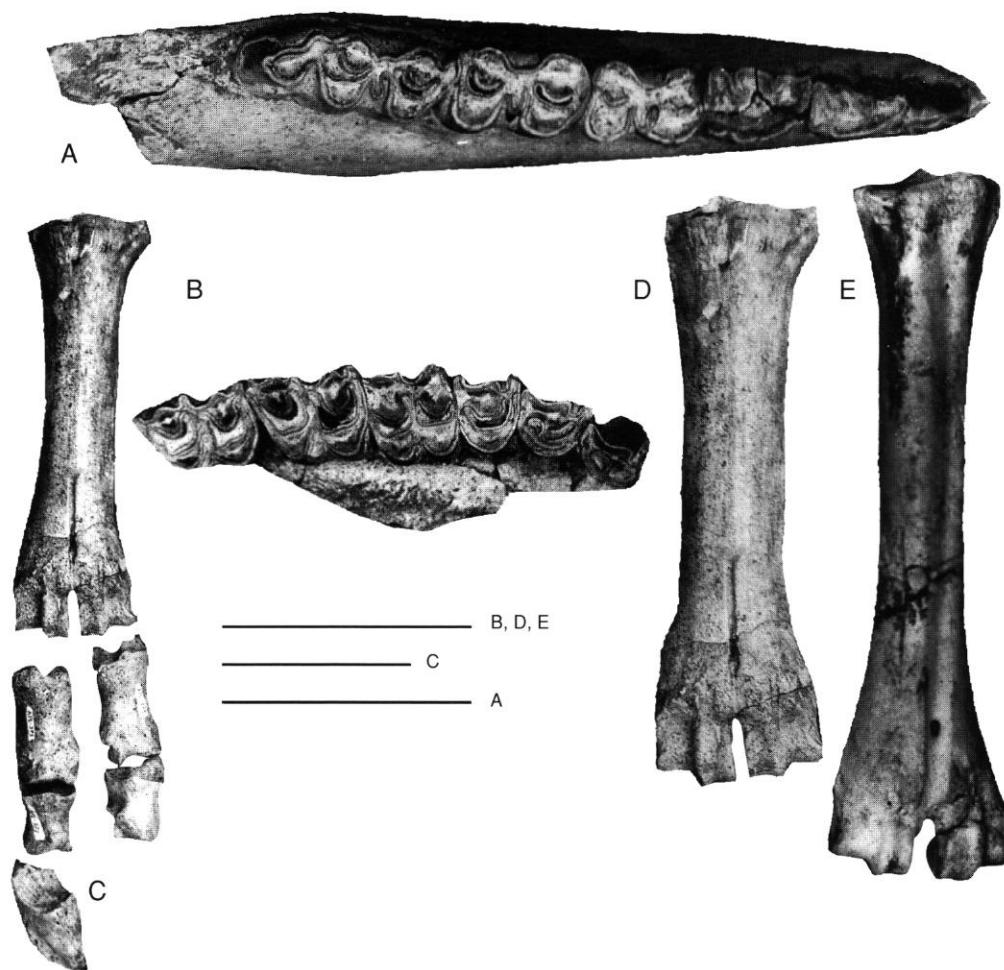


FIG. 8. — *Bison (Eobison)* n.sp., Apollonia (APL), Macedonia, Greece. **A**, APL-478, right mandible, occlusal view; **B**, APL-34, right maxilla, occlusal view; **C**, APL-373, left acropode, anterior view; **D**, APL-26, metacarpal, anterior view; **E**, APL-66, metatarsal, anterior view. Scale bars: A, 5 cm; B-E, 10 cm; A complete series of pictures is given by Kostopoulos (1996).

Genus *Soergelia* Schaub, 1951

Soergelia brigittae n.sp.

(Fig. 9, Tables 7-10)

TYPE SPECIMEN. — Part of mandibular ramus with P_2 - M_3 , APL-383.

MATERIAL. — Part of horn-core, APL-310; M_2 - M_3 *in situ*, APL-245P.

Part of mandibular ramus with p_3 - m_3 , APL-25, 244. $McIII$ + IV , APL-246; $MtIII$ + IV , APL-58, 356.

TYPE LOCALITY. — "Apollonia-1" (APL), Macedonia, Greece.

AGE. — Latest Villafranchian, Early Pleistocene.

DERIVATIO NOMINIS. — To the honour of my mother, Brigitte.

DIAGNOSIS. — Size similar to that of *S. elisabethae* and larger than *S. minor*. Dimensions of horn-cores and metapodials between those of the previous species. More elongated tooththrow than *S. elisabethae*. p_3 with anteriorly extended paraconid-parastyloid. p_4 with open third valley and closed trigonid. Third lobe of m_3 semicircular shaped. Angular palmar tuberosity of $MtIII$ + IV .

DESCRIPTION

The horn-core morphology is known only by a single specimen (Fig. 9G), consisting of a small part of the frontal bone and the base of the horn-core. The horn-core seems to be inserted laterally on the frontals. Directed anteriorly and laterally, the horn-core is slightly torsioned in its preserved proximal part. Its surface is well grooved. The preserved part of the frontal has several sinuses. The horn-core's dimensions at the base are: maximum diameter = 54 mm, minimum diameter (perpendicular to the previous one) = 47.5 mm.

The protocone of M3 is well developed, relatively wide and angular lingually. As it, the hypocone is equally, but not angular. The metastyle is strong, directed distally. The mesostyle is strong and fine. The paracone and the metacone are slightly convex.

The length p2-m3 is 156.8 mm (APL-383) with short premolar row comparatively to the molars (index "Lp2-p4 × 100/Lm1-m3" = 52.7). p2 has

a clear parastylid. The metaconid is directed distally, while the entoconid and the entostylid are well developed. The paraconid is missing and the first and the second valleys are confused. The third and the fourth valleys are elongated and narrow. The presence of a rudimentary hypoconid is clear. p3 is slightly molarized with rudimentary, angular hypoconid and slightly convex protoconid (Fig. 10). The parastylid and the paraconid are distinguished in the upper part of the crown. However, they are connected below the middle of the crown's height, forming an elongated sub-squarish stylid, which is vertical to the anteroposterior axis of the tooth. The first valley is very shallow forming a vertical groove between the paraconid and the parastylid. The metaconid is elongated, elliptical and parallel to the anteroposterior axis of the tooth. It is connected with the entoconid from the first stage of wear. The second valley is V-shaped and closes above the base of the crown. The entoconid and the entostylid are elongated and vertical to the

TABLE 7. — *Soergelia brigittae*, APL, Macedonia, Greece. Dental measurements: Lo, occlusal length; la, breadth of anterior lobe; lp, breadth of posterior lobe; lt, breadth of talonid; l, maximal breadth.

	n	mean	min	max	s	v
Mandible						
LPM	3	149.93	143.0	156.8	6.90	4.6
LP	3	52.40	50.3	54.0	1.94	3.7
LM	3	57.36	92.6	102.5	4.96	5.1
p2 Lo	1	13.10	—	—	—	—
p2 La	1	11.40	—	—	—	—
p2 l	1	9.20	—	—	—	—
p3 Lo	3	15.53	14.6	17.1	1.36	8.8
p3 La	3	15.20	14.2	16.8	1.41	9.2
p3 l	3	11.25	11.0	11.4	0.18	1.6
p4 Lo	3	22.03	22.0	22.1	0.06	0.2
p4 La	3	21.75	20.9	23.0	1.11	5.1
p4 l	3	12.35	12.3	12.5	0.13	1.0
m1 Lo	3	23.73	21.9	27.3	3.09	13.0
m1 La	3	21.88	20.2	25.1	2.78	12.7
m1 la	3	14.60	14.2	15.0	0.40	2.7
m1 lp	3	15.36	14.6	16.2	0.77	5.0
m2 Lo	3	28.60	27.2	31.1	2.17	7.6
m2 La	3	28.40	27.6	30.0	1.38	4.8
m2 la	3	16.40	16.1	16.8	0.32	1.2
m2 lp	3	16.05	15.6	16.3	0.39	2.4
m3 Lo	3	37.40	34.1	39.2	2.85	7.6
m3 La	3	40.46	40.0	41.0	0.50	1.2
m3 la	3	14.83	13.0	16.2	1.65	11.1
m3 lp	3	14.71	13.0	16.0	1.55	10.5
m3 lt	3	8.63	8.0	9.4	0.71	8.2

anteroposterior axis of the tooth, connected to each other from the first stage of wear. The third and fourth valleys are closed. Finally, p3 has an open trigonid and a closed talonid. p4 is strongly molarized (Fig. 10) with closed trigonid and talonid. The parastylid is strong, while the entostylid is weak. The third valley is deep and oblique. The metaconid is well curved lingually. The protoconid and the hypoconid are well developed and they are distinguished by a relatively deep vertical furrow. The lower molars are moderately elongated. The protoconid and the hypoconid are equally developed and more angular in m1 than in m3. The parastylid is lingually projected and increases from m1 to m3. The metaconid and the entoconid are slightly curved

lingually and they are separated by a wide central furrow. The entostylid is weak in m1, 2, stronger in m3. There are no traces of metastylid in m1, 2, while in m3 the metastylid is weak but observable. The third lobe of m3 is semicircular with a disto-lingual rudimentary stylid. The molars have a very weak goat fold in their anterior wall. The ectostylid is absent. In occlusal view the unworn m3 has a weak "protoconal fold" and a moderate "hypoconal fold".

The metacarpals are short and relatively robust. The robusticity index ($DT_{diaphysis} \times 100/L$) is 17.9. The distal epiphysis of the metacarpal is well developed. The groove of coossification is very weak and the intertrochlear incision is wide. The posterior face of the diaphysis is flat. The

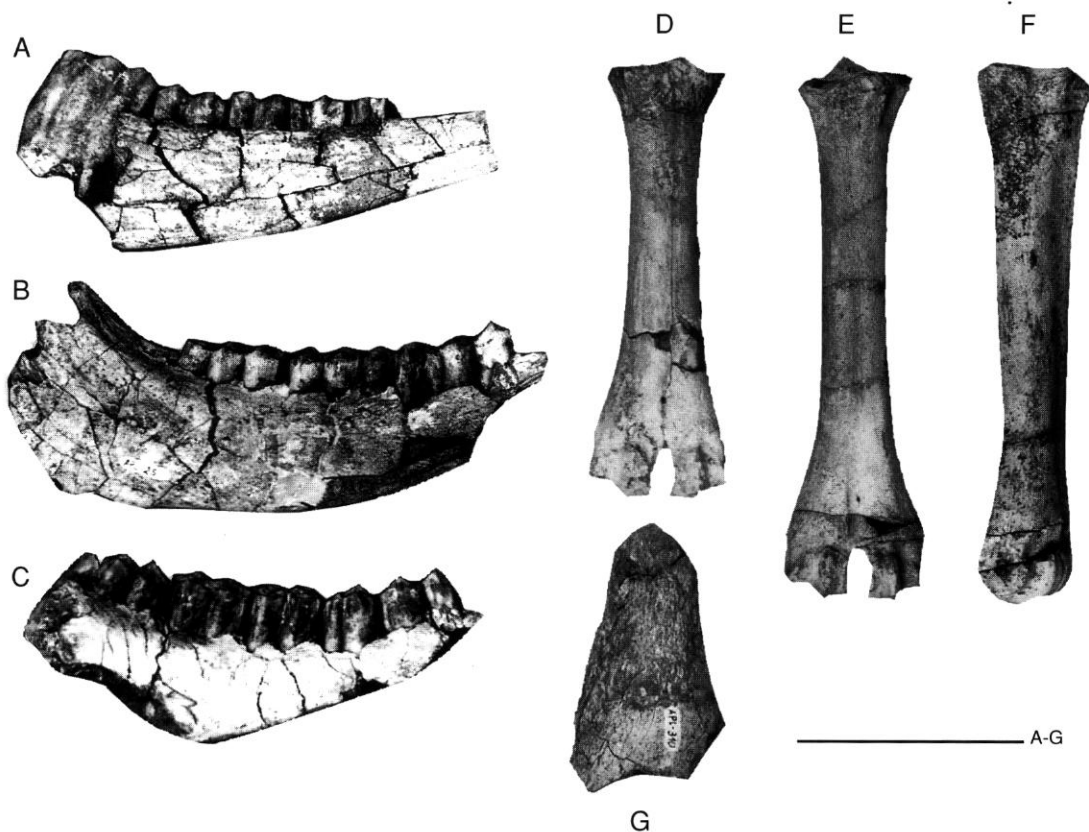


FIG. 9. — *Soergelia brigittae* n.sp., Apollonia (APL), Macedonia, Greece. **A**, APL-244, left mandible, lingual view; **B**, APL-25, right mandible, labial view; **C**, APL-383, right mandible, labial view; **D**, APL-246, metacarpal, anterior view; **E**, APL-58, metatarsal, anterior view; **F**, APL-356, metatarsal, lateral view; **G**, APL-310, part of horn-core, lateral view. Scale bar: 10 cm.

DTproximal is smaller than the DTdistal. The metatarsals are robust and short, but more elongated than the metacarpals. Their proximal epiphysis is almost rounded. The articular facet for the cubonavicular is situated higher than that for the magnum. The palmar tuberosity is angular and well developed. The groove of coossification is observable but shallow and wide. The posterior face of the diaphysis is flat along the bone. In the posterolateral face of the proximal epiphysis there is a clear tuberosity, corresponding to the fifth metatarsal. In the proximal part of the diaphysis, the MtIII is more developed anteroposteriorly than the MtIV. The keels of the distal epiphysis are strong.

DISCUSSION

The hypsodonty, the elongated lower premolars, the elongated-stylomorph lower molars, the absence of ectostylid, the strongly molarized P4, the distally projected metaconid of p3, the relatively small p2 and the robust metapodials are features regarded as typical for Ovibovini (Moya-Sola 1987).

Moreover, the following morphological characters of the McIII+IV and MtIII+IV are also features regarded as typical for Ovibovini (De Giuli & Masini 1983):

- the subparallel medial and lateral borders of the diaphysis in the upper third of the bone;
- the larger distal epiphysis comparatively to the proximal one;
- the weak groove of coossification, observable in the lower and upper third of the bone and almost absent in the central part;
- the slightly convex anterior face of the diaphysis comparatively to the flat posterior one;
- the elliptical, narrow and closed sinovial fossa;
- the slightly concave articular facet of the McIII+IV;
- the wide intertrochlear incision, especially in the posterior surface;
- the well developed medial and lateral tuberosities.

The most common Plio-Pleistocene representatives of medium sized Ovibovini are: *Soergelia*, *Megalovis*, *Pliotragus* (= *Hesperoceras* = *Hesperidorcas* = *Deperetia*), *Praeovibos* and *Ovibos*

(De Giuli & Masini 1983; Moya-Sola 1987; Duvernois & Guérin 1989). The systematic position and the relationships of some of these genera are still discussed; several authors place them in Caprini (e.g. Schaub 1951). The genus *Soergelia* is described for the first time from Süssenborn by Schaub (1951). Later it is recorded from the middle Pleistocene of Romania (Radulesco & Samson 1965), Germany (Kahlke 1969), Bulgaria (Spasov pers. comm.) and former Soviet Union (Sher 1986). Gentry (1970) considers *Soergelia* as an Ovibovini, supposing a close relationship between *Hesperidoceras*, *Deperetia*, *Megalovis* and *Soergelia*. De Giuli & Masini (1983) divide the Ovibovini in three distinct groups: the “group of *Ovibos*”, the “group of *Praeovibos*” and the “group of *Megalovis*”. These authors place also in the latter group *Hesperidorcas* and *Soergelia*. Duvernois & Guérin (1989) synonymize *Deperetia*, *Hesperoceras* and *Hesperidoceras* with *Pliotragus*.

Two species of *Soergelia* are known: *Soergelia elisabethae* from the early-middle Pleistocene of Central-Western Europe (Kahlke 1969) and *Soergelia minor* from the early Pleistocene of Spain (Moya-Sola 1987).

The horn-core APL-310 is very badly preserved for adequate comparison. Its insertion on the cranial roof as well as its morphology fit well with those referred to *Soergelia*: horn cores inserted laterally, robust at their base and slightly torsioned (Schaub 1969; Moya-Sola 1987). The maximum diameter of the horn-core's base is 73-77 mm in *S. elisabethae*, 43-47.5 mm in *S. minor* and 54 mm in the APL specimen, indicating an intermediate position (measurements from Kahlke 1969; Moya-Sola 1987). The index “minimum diameter × 100/maximal diameter at the base” is 88 for APL-310, vs 73-80.5 for *Soergelia minor*, 86 for *Pliotragus ardeus* and 62.5 for *Praeovibos priscus* (measurements from Kahlke 1964; Moya-Sola 1987; Duvernois & Guérin 1989). These values indicate that the horn-core is less compressed laterally in *Soergelia*, *Pliotragus* and APL-310 than in *Praeovibos*.

p3 of the Apollonia bovid has an elliptical metaconid, which runs parallel to the anteroposterior axis of the tooth and is connected with the complex entoconid + entostylid. The p3 of *Soergelia*

TABLE 8. — Comparison of the lower tooththrow's dimensions of several early Pleistocene Ovibovini (data from Kahlke 1969; Cregut & Guérin 1979; Duvernois & Guérin 1989). *, personal measurements on casts; **, partly from photographs.

	<i>S. brigittae</i> APL	<i>S. elisabethae</i> *	<i>S. minor</i> *	<i>Pliotragus</i> **	<i>Praeovibos</i> Caune d'Arago
Lp2–m3 (1)	143.0–156.8	138.8	116.0	(117.4)	144
Lp2–p4 (2)	50.3–54.0	46.5	43.0	(39.9)	—
Lm1–m3 (3)	92.6–102.5	87.8	74.5	77.5	—
(2)/(3) × 100	53.65	53.0	57.7	(51.5)	—
(2)/(1) × 100	34.90	33.5	37.0	(34)	—

minor has a similar morphology (Fig. 10) but the parastylid and the paraconid are more vertical to the anteroposterior axis, while the hypoconid is less developed than in Apollonia. p3 of *Pliotragus* has a more squarish and less distally projected metaconid, a less developed hypoconid and more vertical situated paraconid and parastylid (Fig. 10). The p3 of *Praeovibos priscus* has a metaconid vertical to the anteroposterior axis of the tooth, while the second and third valleys are open, indicating a more primitive morphology than that of Apollonia.

p4 of the APL bovid is moderately elongated with clear parastylid, lingually convex metaconid, well developed hypoconid and deep third valley, situated obliquely in relation to the anteroposterior axis of the tooth. The p4 of *S. elisabethae* is shorter with less developed hypoconid and continuous internal wall (closed third valley, flat metaconid) (Fig. 10). p4 of *Soergelia minor* is similar to that from Apollonia but the third valley is closed. Thus, the p4 of the APL bovid seems to be more primitive than those of *S. minor* and *S. elisabethae*. *Pliotragus ardeus* has a more similar morphology to that of the studied bovid (Fig. 10). The p4 of *Praeovibos priscus* has a shallow third valley and a rudimentary hypoconid, characters which differ from those of the APL bovid.

In the APL bovid, the talonid of m3 is semicircular with flat internal wall and a disto-lingual stylid. This morphology fits well with that of *Soergelia*, but in *Soergelia minor* the talonid is more rounded and the stylid shorter. The talonid's internal wall of *Pliotragus ardeus* is not flat but clearly convex. In *Praeovibos priscus* from Caune d'Arago the talonid of m3 is quadran-

gular, because of the presence of two distal stylids (Cregut & Guérin 1979; Duvernois & Guérin 1989). The dimensions of the Apollonia m3 are closer to those of *Soergelia elisabethae*. The m3 of *S. minor* and *Pliotragus ardeus* is smaller, while

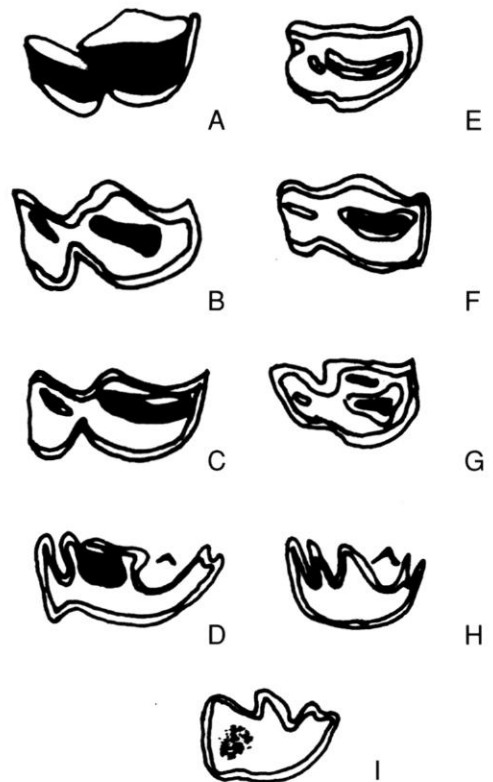


FIG. 10. — Comparison of the p3 and p4's morphology of several Ovibovini: A–C, p4, *Soergelia brigittae*, Apollonia, Macedonia, Greece; D, p3, *idem*; E, p4, *Soergelia elisabethae*; F, p4, *Praeovibos priscus*; G, p4, *Pliotragus ardeus*; H, p3, *Soergelia minor*; I, p3, *Pliotragus ardeus*. Not to scale.

TABLE 9. — Comparison of the metacarpal's dimensions of several Pleistocene *Ovibovini*: 1, length (max); 2, DT proximal; 3, DAP proximal; 4, DT diaphysis; 5, DAP diaphysis; 6, DT distal (articular); 7, DAP distal (articular); (data from Radulesco & Samson 1962; Kahlke 1969; De Giuli & Masini 1983; Moya-Sola 1987; Duvernois & Guérin 1989).

McIII+IV	APL-246	<i>S. elisabethae</i> Süsssenborn n = 1	<i>S. Minor</i> V. Micena mean	<i>Pliotragus</i> Duvernois & Guérin 1989 n = 1
1	174.3	180.6	168.4	190
2	46	49.8	43.6	47
3	30.6	32.1	28.4	—
4	31.2	29.3	26.7	32
5	20.7	21.6	19.2	—
6	55.9	56.6	49.0	49
7	29.3	29.3	25.8	—
(2) × 100/(1)	26.4	27.6	25.9	24.7
(4) × 100/(1)	17.9	16.2	15.8	16.8
(6) × 100/(1)	32.0	31.3	29.1	25.8
(4) × 100/(6)	55.9	51.8	54.4	65.3

McIII+IV	<i>Megalovis</i> De Giuli & Masini 1983 n = 6	<i>Praeovibos</i> De Giuli & Masini 1983 n = 4	<i>Ovibos</i> <i>moschatus</i> n = 1	cf. <i>Praeovibos</i> Casa Frata n = 1
1	190.5 (192-204)	184.1 (172-194.5)	188	188
2	55.5 (51-58.7)	53.5 (49-58.5)	61.9	61.7
3	38.0 (36.8-39.2)	35.3 (33-38.5)	36.7	36.4
4	35.5	39.4 (35.3-46)	44.0	42.9
5	24.6 (24.3-24.8)	23.4 (22.8-23.8)	22.3	27.2
6	59.5 (54-64)	65.5 (62-67.4)	69.9	66.0
7	33.4 (32.5-34.4)	35.1 (33-37)	35.2	37.0
(2) × 100/(1)	28.2 (26.5-29.4)	29.6 (26.4-31.7)	32.6	32.8
(4) × 100/(1)	18.1 (17.1-19.2)	21.3 (20.2-23.6)	23.3	22.8
(6) × 100/(1)	30.3 (28.1-33.3)	36.1 (35.3-36.5)	37.0	35.5
(4) × 100/(6)	59.9 (55.8-64.5)	57.1 (55.5-59)	62.9	65.0

that of *Praeovibos priscus* is clearly larger than that from Apollonia (Fig. 11).

The index " $Lp2-p4 \times 100/Lm1-m3$ " is 53.7 in APL, similar to that of *S. elisabethae* and relatively smaller than that of *S. minor*. Nevertheless, the absolute dimensions of the Apollonia's lower toothrows are significantly larger than those of

S. elisabethae, *S. minor*, *Pliotragus ardeus* and *Praeovibos* (Table 8).

As regards to the premolars, the studied bovid differs from *Praeovibos* because, in the latter genus, the index (breadth/length) is usually larger than 100, while it is smaller than 100 in *Soergelia*, *Pliotragus* and in the APL bovid.

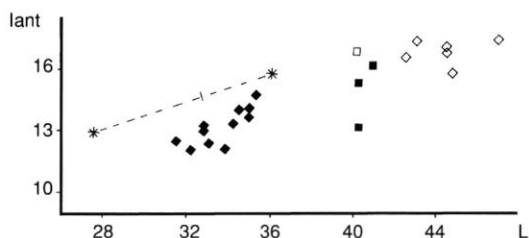


FIG. 11. — *Soergelia brigittae*, APL, Macedonia, Greece. Scatter diagram comparing the m3 dimensions of several Ovirovini (after Moya-Sola 1987, modified; data from Kahlke 1964; Duvernois & Guérin 1989): ■, *Soergelia brigittae*, APL; ◆, *Soergelia minor*, Venta Micena; □, *Soergelia elisabethae*, Süssenborn; ◇, *Praeovibos priscus*; *, *Pliotragus ardeus*.

The metacarpal of the APL bovid is smaller than those of *Megalovis*, *Praeovibos*, *Ovibos moschatus* and cf. *Praeovibos* from Casa Frata, Italy (Table 9). Moreover, the studied metacarpal is shorter and less widened distally than that of *Pliotragus* (Table 9). The absolute dimensions of the APL metacarpal are situated closer to *Soergelia* and between *S. elisabethae* and *S. minor* (Table 9). The proportions of the transverse diameters, comparatively to the length of the bone, show that the metacarpals of *Praeovibos* and *Ovibos* are more robust than those of the APL bovid, *Soergelia*, *Pliotragus* and *Megalovis*. The APL metacarpal is situated in the "Megalovis group" of De Giuli & Masini (1983) and close to the representatives of *Soergelia* (Fig. 12).

The morphological features of the studied metatarsal are similar to those referred to *Soergelia elisabethae* (Schaub 1951; Samson & Radulesco 1965). Nevertheless, the APL metatarsal has an angular palmar tuberosity, similar to that of *S. minor* (Moya-Sola 1987). The APL metatarsal is metrically similar to that of *S. elisabethae*, while its proportions are similar to those of *S. elisabethae* and *S. minor* (Table 10).

Taking into account the available data, the studied bovid is determined as *Soergelia*. Although the material is not very abundant, the APL *Soergelia* presents some particularities in body size and teeth morphology, which indicate a more primitive form than *S. elisabethae* and a larger form than *S. minor*. Moreover, the p4's morphology of the APL *Soergelia* presents certain

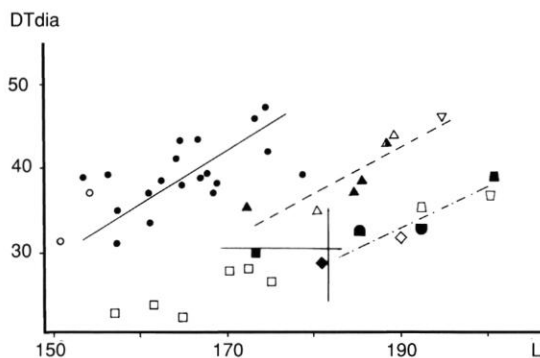


FIG. 12. — *Soergelia brigittae*, APL, Macedonia, Greece. Scatter diagram comparing the proportion of metacarpals of several Ovirovini (after De Giuli & Masini 1983, modified): ■, *Soergelia brigittae*, APL; □, *S. minor*, Venta Micena; ◆, *S. elisabethae*, Süssenborn; ◇, *Megalovis*, Senèze; ○, *Megalovis*, Olténie; ●, *Megalovis*, Nihowan; ◐, *Megalovis*, Honan; ◑, *Megalovis*, Chao Chuang; ◇, *Hesperoceras*, Villaroya; ▽, *Praeovibos*, Bad Frankenhausen; ▲, *Praeovibos*, Kolya; △, *Ovibos moschatus*, Süssenborn; ●, *Ovibos pallantis*, E. Siberia; ○, *Ovibos moschatus*, Greenland; ▲, cf. *Praeovibos*, Casa Frata.

affinities to the earlier form *Pliotragus ardeus*, supporting the idea of a close phylogenetic relationship between the two genera. These considerations allow us to propose a new specific name for the APL *Soergelia*: *S. brigittae* n.sp.

Genus *Praeovibos* Staudinger, 1908

Praeovibos sp.

(Table 11)

MATERIAL. — M3, APL-211.

DESCRIPTION — COMPARISON

There is only a worn M3. The presence of cement is strong. The protocone is well developed, more projected and more angular than the hypocone. The parastyle is strong, directed anteriorly and connected with the paracone at the base of the crown. The paracone is strongly curved labially. The valley between the paracone and the mesostyle is U-shaped and not very deep. The metastyle is strongly developed with squarish occlusal shape. It is distally directed, forming an extension in the disto-labial face of the tooth. The cingulum is present in the lingual side of the

TABLE 10. — Comparison of the metatarsal's dimensions of several early Pleistocene Ovibovini: 1, length (max); 2, DT proximal; 3, DAP proximal; 4, DT diaphysis; 5, DAP diaphysis; 6, DT distal (articular); 7, DAP distal (articular); (data from Radulesco & Samson 1962; Kahlke 1969; Moya-Sola 1987).

MtIII+IV	APL-58	APL-356	<i>S. Minor</i> V. Micena	<i>Praeovibos</i> V. Micena
1	214.1	215.3	185.3	185.5
2	44.5	44.5	34.8	41.0
3	42.4	44.5	34.7	37.7
4	28.8	29.3	23.4	30.0
5	26.5	27.4	24.2	24.7
6	58.0	58.4	45.1	51.0
7	32.2	33.7	25.8	28.3
(2) × 100/(1)	20.7	20.6	18.8	22.1
(4) × 100/(1)	13.5	13.6	12.8	16.2
(6) × 100/(1)	27.1	27.1	24.4	27.5
(4) × 100/(6)	49.6	50.1	51.8	58.8

MtIII+IV	<i>S. elisabethae</i> D373 Süssenborn	<i>S. elisabethae</i> 1965/2569 Süssenborn	<i>S. elisabethae</i> Roumania
1	217.5	(210)	—
2	43.7	39.8	39.6
3	—	—	42.2
4	27.0	27.0	25.7
5	—	—	25.5
6	56.1	—	—
7	—	—	—
(2) × 100/(1)	20.1	(19)	—
(4) × 100/(1)	12.4	(12.8)	—
(6) × 100/(1)	25.8	—	—
(4) × 100/(6)	48.1	—	—

anterior lobe. In occlusal view, there is a well developed central islet, connected with the posterior rear cavity.

The general morphological features of the studied M3 are typical for Ovibovini or Caprini. The presence of cement, the strong central islet and the structure of the metastyle are different from the teeth of *Soergelia* and similar to those of *Praeovibos* and *Ovibos*. The morphological (Fig. 13) and metrical (Table 11) comparisons indicate that the characters of the studied specimen approach better those of *Praeovibos*. For that reason it is referred as *Praeovibos* sp.

Genus *Pontoceros* Veresgagin *et al.*, 1971
Pontoceros ambiguus Veresgagin *et al.*, 1971
Pontoceros ambiguus mediterraneus n.ssp
 (Fig. 14, Tables 12-14)

Antilopinae gen. and sp. indet. A, Steensma 1988: 260-263.

TYPE SPECIMEN. — Frontlet, APL-39.

MATERIAL. — Left and right horn-cores, APL-190a, b; part of horn-core, APL-222, 305; part of maxilla with P2-M3 dext and P3-M3 sin, APL-322; P4, APL-515; M2, APL-126; M3, APL-71.

TABLE 11. — Comparison of the M3 dimensions of several Pleistocene Ovibovini (data from Schaub 1937; Kahlke 1963, 1964, 1969).

M3	APL-211	<i>Praeovibos</i> Frankenhausen n = 1	<i>Ovibos</i> Suessenborn n = 3	<i>Soergelia</i> <i>elisabethae</i> n = 1	<i>Megalovis</i> n = 1
L occlusal	38.35	—	—	—	—
L alveolar	41.15	46.80	32.3–33.1	31.2	31.0
l anterior	25.15	26.40	22.4–24.5	23.2	—
l posterior	22.55	20.80	20.9–22.9	—	—
la × 100/La	61.12	56.40	69.3–74.0	74.6	—

Part of mandibular ramus with p3-m3, APL-35.

Distal part of humerus, APL-102, 150; radius, APL-403; carpals, APL-540; McIII+IV, APL-99, 100, 188; proximal part of McIII+IV, APL-335; distal part of tibia, APL-289, 290; proximal part of MtIII+IV, APL-106; first phalanx, APL-109, 110, 111, 112, 113; second phalanx, APL-114, 115, 320, 321, 490; third phalanx, APL-116, 117.

TYPE LOCALITY. — Apollonia-1, APL, Macedonia, Greece.

OTHER LOCALITY. — Libakos (Grevena basin, Greece).

AGE. — Early Pleistocene (MNQ20).

DERIVATIO NOMINIS. — From the Latin “*mediterraneus*”, indicating the living area of the animal.

DIAGNOSIS. — Horn-cores more massive than those of the type-subspecies, less torsioned and more strongly divergent from the base to the top. Their cross section is more elliptical-rounded than that of the typical form. The contact between the horn-core and the pedicel is not observable. The keels are less sharp than those of the typical form. Presence of a main antero-lateral foramen and of two secondary ones. Elongated toothrow with short-moderate premolar row. P2, 3 and p4 strongly molarized. p3 with independent metaconid. Presence of goat fold on the lower molars. Limb bones elongated and slender.

DESCRIPTION

The anterior part of the frontals is strong with numerous small sinuses. The frontal bones are slightly convex along the interfrontal suture. The fronto-parietal suture is Y-shaped. The posterior face of the horn-core's base is situated directly in front of the fronto-parietal suture.

The horn-cores are situated above the orbits and on the lateral borders of the frontals. Their separation is 37.5 mm medially and 122 mm lateral-

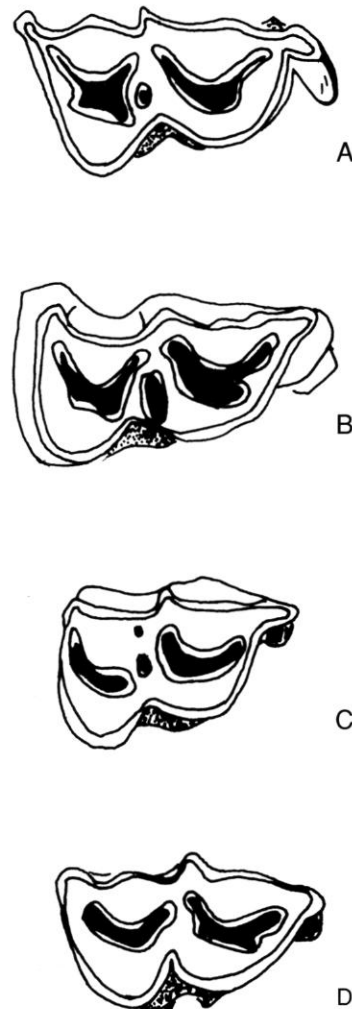


FIG. 13. — *Praeovibos* sp., APL, Macedonia, Greece. Comparison of the M3 morphology of several Pleistocene Ovibovini: A, *Praeovibos* sp., APL; B, *Praeovibos priscus*; C, *Ovibos moschatus sussenbornensis*; D, *Ovibos moschatus moschatus*. Not to scale.

ly. The horn-cores are strongly directed and inclined backwards, forming an angle of about 30-40° with the cranial roof. The pedicels are not observable. The horn-cores are elongated enough and inverse spiralled, forming a complete gyre. Their maximum length is estimated at about 230 mm. They present three well developed keels: anterolateral, anteromedial and posteromedial (distal) keel, according to their descending point. The anterolateral keel is the strongest one. At its base, there is a well developed foramen, associated with two rudimentary ones. Along the anterolateral keel there is a well marked furrow, which starts 50 mm above the base and disappears 125 mm from the base of the horn-core. The anteromedial keel is less developed than the previous one in the proximal part of the horn-core, but it becomes stronger in the distal part. The distal keel is weak, and associated with a clear furrow. All the keels are not sharp, except the anterolateral keel, which is sharply projected in the specimen APL-190a. Fine longitudinal grooves run across the surface of the horn cores. The cross-section of the horn-cores is elliptical-subrounded from the base to the middle of their height (Fig. 15). The index "DT × 100/DAP" is 90.3-94 at the base and 93-105.3 at 7 cm from the base. The internal part of the horn-cores presents a porous central region and a compact district zone. The horn-core dimensions are given in table 12.

The length P2-M3 is 99.7 mm, with short to moderate premolar row (index LP2-P4 × 100/LM1-M3 = 61). The teeth are meso-hypsodont with flat enamel. The breadth of the palate is 53 mm between P4-M1 and 57.5 mm behind M3. The premolars are slightly molarized, especially the P2, 3. M2 seems to predominate between the molars. The metastyle of M3 is directed distally. The posterior lobe of the molars is wider than the anterior one. In occlusal view there is a hypoconal fold.

The width of the mandible is 20 mm between m2-m3, while its height at the same point is 66 mm, indicating a relatively shallow and robust mandibular ramus. The length p3-m3 is 90 mm. p3 has a slightly convex protoconid and a clear but rudimentary hypoconid. The parastylid is separated from the paraconid and direc-

ted anteriorly. The paraconid is almost vertical to the anteroposterior axis of the tooth. The metaconid is strong, obliquely situated in comparison to the antero-posterior axis of the tooth. It is independent from the entoconid. The second valley is V-shaped and deep. The entoconid is elliptical and connected with the entostylid. The third valley is U-shaped, while the fourth valley is closed. In p4 the protoconid and the hypoconid are equally developed but the first one is wider. The internal wall of p4 is continuous, with strongly projected parastylid. The entostylid is also observable. The lower molars have no parastylid and metastylid (except m3), while the entostylid is weak. The presence of a goat fold is clear in m2, 3. The talonid of m3 is semi-circular shaped with a disto-lingual rudimentary stylid. The teeth measurements are given in table 13.

The radius, McIII+IV and MtIII+IV, are elongated and slender, indicating a medium-sized, delicate "antelope". The limb-bones measurements are given in table 14.

COMPARISON

The presence of the spiral horned "antilopes" in the early Pleistocene faunas is rather rare. Moreover, the only Pleistocene "antelope" with inverse torsioned horn-cores is the species *Pontoceros ambiguus* known from the Plio-Pleistocene deposits of Azov Sea (Ukraine), as well as from the faunal complex of Tiraspol (Ukraine; Veresgagin & David 1968; Veresgagin *et al.* 1971). These discoveries were initially described as *Capra Suleman kiakhtensis* (Pavlov 1911) or as *Spirocercus kjakhtensis* (Veresgagin & David 1968), but later transferred to the new genus and species *Pontoceros ambiguus* (Veresgagin *et al.* 1971). Nevertheless, and according to my knowledge, till today, only the morphology of its horn-cores is known.

The general morphological features of the APL horn-cores, such as the lateral insertion of the horns in the cranial roof, the angle between the horn-cores and the cranial roof (30-40°), the moderately elongated and inversely torsioned horn-cores, the presence of three keels associated with longitudinal furrows and the triangular to elliptical cross section of the horn-cores are similar to the characters referred to *Pontoceros* (Veresgagin *et al.* 1971).

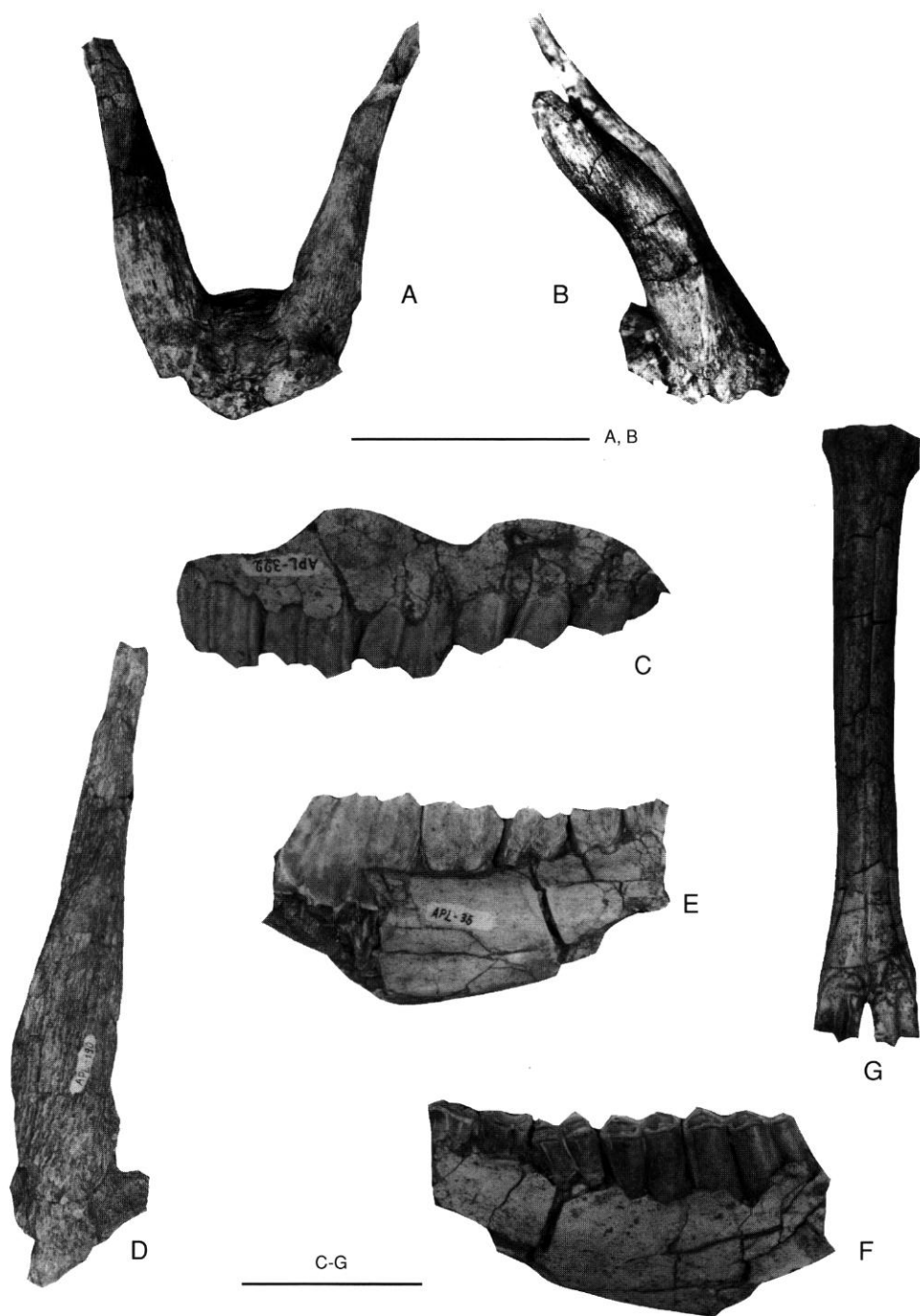


Fig. 14. — *Pontoceros ambiguus mediterraneus* n.ssp., Apollonia (APL), Macedonia, Greece. **A**, APL-39, frontlet, anterior view; **B**, APL-39, frontlet, lateral view; **C**, APL-322, right maxilla, labial view; **D**, APL-190, left horn-core, lateral view; **E**, APL-35, left mandible, lingual view; **F**, APL-35, left mandible, labial view; **G**, APL-188, metacarpal, anterior view. Scale bars: A, B, 10 cm; C-G, 5 cm.

TABLE 12. — *Pontoceros ambiguus mediterraneus*, APL, Macedonia, Greece. Horn-cores measurements and comparison with other forms of the species (data from Veresgagin *et al.* 1970; Steensma 1988).

Horn-cores	L	DAP × DT base	DAP/DT base	DAP base/L
APL-39 s	205+	40.5 × 43.2	94	(20)
APL-39 d	175++	41.3 × 44.6	92.6	—
APL-190 s	190++	—	—	—
APL-190 d	225	—	—	—
APL-305 d	—	38.1 × 42.2	90.3	—
Libakos	—	40.5 × 43.9	93.2	—
Nogaïsk	297	46 × 48	95.8	16.1
Margaritovo	300	46 × 53	86.8	17.6
Tiraspol	280	42 × 46	91.3	16.4

TABLE 13. — *Pontoceros ambiguus mediterraneus*, APL, Macedonia, Greece. Dental measurements: Lo, occlusal length; la, breadth of anterior lobe; lp, breadth of posterior lobe; lt, breadth of talonid; l, maximal breadth.

	n	mean	min	max	s	v
Maxilla						
LPM	1	99.70	—	—	—	—
LP	1	37.00	—	—	—	—
LM	2	89.95	59.6	60.7	—	—
P2 Lo	1	10.60	—	—	—	—
P2 l	1	8.20	—	—	—	—
P3 Lo	2	10.92	10.7	11.2	—	—
P3 l	2	9.75	9.5	10.0	—	—
P4 Lo	2	11.42	10.8	12.1	—	—
P4 l	3	12.55	12.2	13.0	0.43	3.4
M1 Lo	2	18.45	18.1	18.8	—	—
M1 la	2	15.95	15.2	16.5	—	—
M1 lp	2	14.90	14.8	15.0	—	—
M2 Lo	3	21.56	21.0	21.9	0.49	2.3
M2 la	3	16.46	15.6	18.0	1.33	8.0
M2 lp	3	15.43	12.9	19.5	3.56	23.0
M3 Lo	3	20.66	19.5	22.5	1.61	7.8
M3 la	3	14.50	13.2	16.3	1.61	11.1
M3 lp	3	11.70	9.5	14.5	2.55	21.8
Mandible						
LM	1	66.00	—	—	—	—
p3 Lo	1	12.00	—	—	—	—
p3 l	1	6.60	—	—	—	—
p4 Lo	1	12.90	—	—	—	—
p4 l	1	7.50	—	—	—	—
m1 Lo	—	—	—	—	—	—
m1 la	1	9.25	—	—	—	—
m1 lp	1	10.15	—	—	—	—
m2 Lo	1	21.00	—	—	—	—
m2 la	1	11.25	—	—	—	—
m2 lp	1	11.20	—	—	—	—
m3 Lo	1	27.50	—	—	—	—
m3 la	1	11.20	—	—	—	—
m3 lp	1	10.90	—	—	—	—
m3 lt	1	5.50	—	—	—	—

The species *Pontoceros ambiguus* is characterized by elongated spiral horn-cores, which form more than one complete gyre (one and quarter). Their cross section is triangular at the base, becoming elliptical to the top. Three well developed and rather sharp keels are present, associated with three strong furrows. The stronger keel is descending to an anterolateral insertion, where three well developed foramina are present. The horn-cores of *Pontoceros ambiguus* run parallel in their proximal part. The frontals are slightly convex between the horn's bases, while the supraorbital foramina are strong.

The morphological characters of the APL "antelope" fit well with those mentioned for *Pontoceros ambiguus* (Veresgagin *et al.* 1971). Nevertheless, there are some secondary differences, which distinguish the Greek form.

1. The horn-cores of the typical *P. ambiguus* are more elongated than those from APL (Table 12).
2. The index "maximum diameter at the base × 100/length of the horn-core" is about 20 for APL, vs 16-18 for the typical *P. ambiguus*. These values indicate that the APL bovid has more massive horn-cores than the typical form of the species.
3. The keels of *P. ambiguus* are sharp, while those of the APL bovid are more smoothly developed.
4. The torsion of the APL horn-cores forms a complete gyre from the base to the top. The torsion of the typical *P. ambiguus* forms more than one complete gyre.
5. The cross section of the horn's base is more triangular in *P. ambiguus*, while it is more elliptical-rounded in APL.
6. The anterolateral keel is associated with three

TABLE 14. — *Pontoceros ambiguus mediterraneus*, APL, Macedonia, Greece. Limb-bones measurements: 1, length (max); 2, DT proximal; 3, DAP proximal; 4, DT diaphysis; 5, DAP diaphysis; 6, DT distal (articular); 7, DAP distal (articular).

	n	mean	min	max	s	v
Radius						
1	1	237.30	—	—	—	—
2	1	42.00	—	—	—	—
3	1	21.80	—	—	—	—
4	1	23.60	—	—	—	—
5	1	16.20	—	—	—	—
6	1	34.30	—	—	—	—
7	1	21.80	—	—	—	—
McIII+IV						
1	3	224.20	216.8	229.2	6.53	3.0
2	4	36.10	34.5	37.7	1.44	4.0
3	4	25.78	22.6	27.9	2.26	8.8
4	3	20.43	19.2	22.5	1.80	8.8
5	3	19.30	17.7	21.0	1.65	8.6
6	3	36.06	33.5	38.6	2.55	7.0
7	3	24.20	22.6	25.0	1.38	6.0
MtIII+IV						
1	—	—	—	—	—	—
2	1	30.00	—	—	—	—
3	1	33.50	—	—	—	—
Phalanx I						
1	5	59.22	55.3	61.6	2.40	4.0
2	6	17.41	17.0	18.0	0.34	2.0
3	6	21.50	20.4	22.0	0.58	3.0

equally developed foramens in the typical *P. ambiguus*, while it is associated with an important and two secondary foramens in APL.

7. The horn-cores of the typical *P. ambiguus* are parallel in their proximal part, while those from APL diverge from their base.

8. The contact between the horn-core and the pedicel is more clear in the typical form, while it is not developed in APL.

The differences mentioned above are not sufficient for a specific distinction, but they seem to be important to separate the two forms in sub-specific level. Thus, the APL *P. ambiguus* was considered as a new subspecies, named *P. ambiguus mediterraneus* n.ssp.

The possible presence of the species *P. ambiguus* in the Mediterranean region is mentioned for the first time by Moya-Sola (1987) and later by Steensma (1988). The latter author has described, from the locality of Libakos (Macedonia, Greece), a bovid, referred to as Antilopinae gen. and sp. indet. A, which shows great similarities

with *P. ambiguus* (Steensma 1988). The comparison of the Libakos sample with that from APL (Fig. 15, Table 12) shows that the two forms are very similar, in dimensions as in morphology. Consequently, the Libakos Antilopinae is included to the new subspecies. The available data allow to revise the systematic of the genus *Pontoceros* as following:

Genus *Pontoceros* Veresgagin et al., 1971

TYPE SPECIES. — *Pontoceros ambiguus* Veresgagin et al., 1971.

OTHER REFERENCES. — *Capra Suleman kiakhtensis* Pavlow, 1911; *Spirocerus kjakhtensis* Veresgagin et David, 1968; *Antilopinae* gen. and sp. indet. A, Steensma, 1988.

TYPE LOCALITY. — Nogaisk, Azov Sea, Ukraine.

OTHER LOCALITIES. — Margaritovo, Tiraspol, Apollonia-1 and Libakos.

AGE. — Latest Pliocene-early Pleistocene.

EMENDED DIAGNOSIS. — Medium sized “antelope” (probably related to Ovibovini) with straight spiralled and inverse torsioned horn-cores, situated above the orbits and in the lateral borders of the frontals. The horn-cores are strongly inclined backwards (30–40°) and variable laterally. They have three well developed keels, associated with equal number of furrows. In the anterolateral face of the horn's base, there are three well developed foramens of various size. The fronto-parietal suture is Y-shaped. The teeth are rather mesohypsodont. The premolar row is rather short comparatively to the molars. p4 is completely molarized with continous internal wall. The limb bones are elongated and slender.

Pontoceros ambiguus ambiguus
Veresgagin *et al.*, 1971

Pontoceros ambiguus ambiguus Veresgagin *et al.*, 1971: 167–169, fig. 61.

Spirocerus kjakhtensis Veresgagin *et* David, 1968: 391–397.

TYPE LOCALITY. — Nogaïsk, Azov Sea, Ukraina.

OTHER LOCALITIES. — Margaritovo, Tiraspol.

AGE. — Latest Pliocene-Early Pleistocene.

EMENDED DIAGNOSIS. — Typical form of the species. Horn-cores strongly inclined backwards and parallel to each other in their proximal part. Cross-section of the horn-cores, triangular at the base to elliptical at the top. Abrupt contact between horn-core and pedicel. Sharp keels. Anterolateral foramens equally developed.

***Pontoceros ambiguus mediterraneus* n.ssp.**

Antilopinae gen. indet. sp. A. Steensma, 1988: 260–263, fig. 81.

TYPE LOCALITY. — Apollonia-1, APL, Macedonia, Greece.

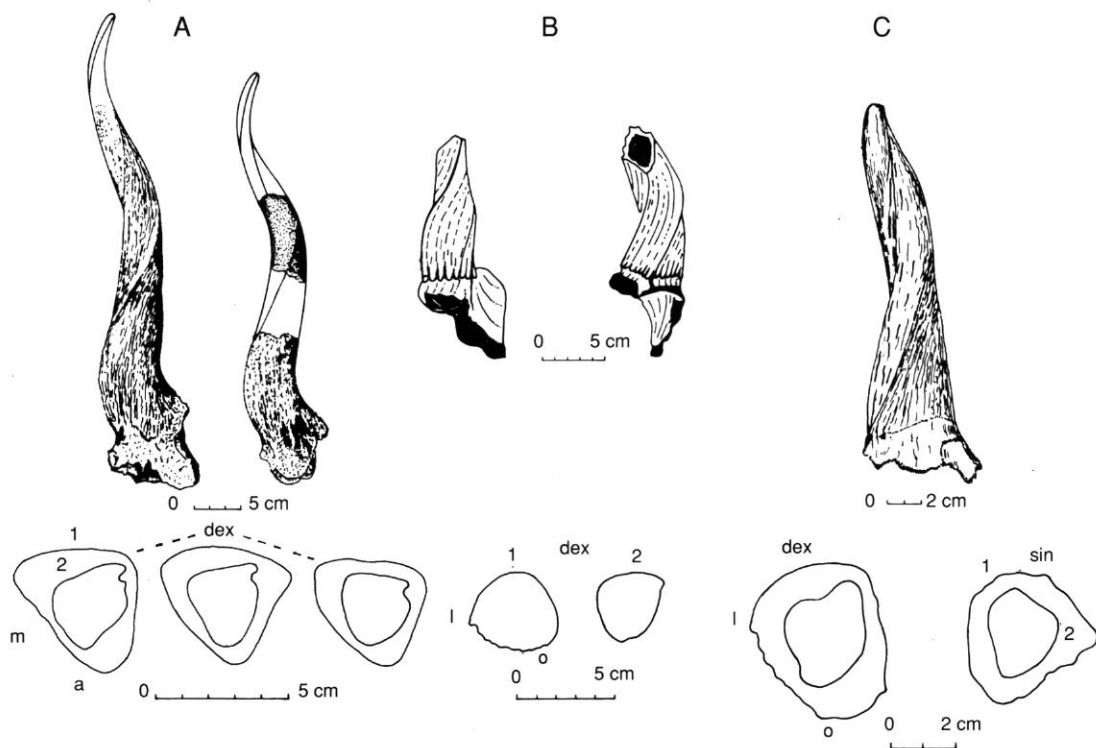


FIG. 15. — *Pontoceros ambiguus mediterraneus*, APL, Macedonia, Greece. Comparison of the horn-core morphology and of the transverse sections, of several forms of *Pontoceros* (data from Veresgagin *et al.* 1971; Steensma 1988): **A**, *P. ambiguus ambiguus*, Nogaïsk (former Soviet Union); **B**, *P. ambiguus mediterraneus*, Libakos-Greece; **C**, *P. ambiguus mediterraneus* APL-Greece; **m**, median side; **a**, posterior side; **l**, lateral side; **o**, anterior side; **1**, cross-section at the base; **2**, *id.* at the middle.

OTHER LOCALITY. — Libakos (Grevena basin, Greece).

AGE. — Early Pleistocene (MNQ20).

DIAGNOSIS. — See above.

Caprinae gen. *et* sp. indet.

Among the fossil material from APL there is a mandibular ramus with p2-m3, a M3 and some limb bones of a medium-sized bovid, clearly different from *Pontoceros ambiguus*. The teeth are very hypsodont with rippled enamel. p3, 4 are molarized. The goat fold of the lower molars is strong. The limb bones are relatively elongated but clearly robuster than those of *Pontoceros*. The robusticity index for the radius is 11.5, 12.7 for the metacarpal.

The general morphological features of the studied specimens are close to those referred for Caprini. Nevertheless, the scarce material cannot allow a certain determination. The APL Caprinae is larger than *Capra alba* Moya-Sola, 1987, *Capra primaeva* Arambourg, 1979 and *Hemitragus bonali* Harle *et* Stehlin, 1914, while it shows similarities with the middle-late Pleistocene *Capra ibex*.

CONCLUDING REMARKS

The study of the artiodactyl material from APL showed the presence of six different forms (one cervid and five bovids). Among them, there are one new species (*Soergelia brigittae*), one new subspecies (*Pontoceros ambiguus mediterraneus*) and a possible new species [*Bison* (*Eobison*) n.sp.]. *Soergelia*, *Praeovibos* and *Eobison* are described for the first time from Greece, while *Pontoceros* is certainly occurring for the first time in the Mediterranean Europe. *Eobison* and *Megaloceros* from APL are two faunal elements of great interest as regards to the origin, the systematic and the palaeogeography of primitive bisons and megaloceros respectively.

The artiodactyls from Apollonia-1, and especially the primitive *Bison*, *Soergelia*, *Pontoceros* and *Megaloceros* suggest an early Pleistocene age for

the locality (Kostopoulos & Koufos 1994; Kostopoulos 1996). This age fits well with the biochronological data obtained from the study of carnivores (Koufos 1993) and equids (Koufos *et al.* 1992).

The association of artiodactyls from APL is similar to that of Venta Micena (Spain), Farneta, Pirro Nord (Italy) and Sainzelles (France). The fauna of APL could be placed in the MNQ20 zone of Guérin (1990) or in the Farneta Faunal Unit of Torre *et al.* (1992).

The association of artiodactyls from APL indicates a "savanna grassland" environment (Kostopoulos & Koufos 1995 in press; Kostopoulos 1996) reconstructed as warm and dry with seasonal rainfalls. The tendency towards an increase of wetness is supported by the fauna characterizing the Platanochori Formation in which the occurrence of fresh-water mollusks, fish otolites and hippopotamids support this opinion.

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