

Aivaliki, a New Locality with Fossil Rhinoceroses near Alistrati (Serres, Greece)

by

Nikolaos K. SYMEONIDIS¹⁾, Ioannis X. GIAOURTSAKIS²⁾, Robert SEEMANN³⁾ & Vassileios I. GIANNOPOULOS⁴⁾

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Abstract

Aivaliki, a new fossiliferous locality near Serres (Greece), has yielded an adult and a juvenile mandible of a rhinoceros. The most striking feature of the material from Aivaliki, assigned to *Stephanorhinus cf. etruscus*, is the small size of the dentition with relative brachyodont and unspecialized teeth, especially the molars. The occurrence of small sized transitional rhino populations of the *etruscus*-group appears to be a characteristic element of some Early Pleistocene faunas across Europe associated probably with the changing climatic conditions. The known Plio-Pleistocene record of fossil rhinoceroses in Greece is briefly reviewed.

Keywords: *Stephanorhinus cf. etruscus*, Early Pleistocene, Aivaliki, Greece

Zusammenfassung

Aivaliki, eine neue Fossilfundstelle in der Nähe von Serres (Griechenland), hat einige Nashornreste erbracht, die einen erwachsenen und einen juvenilen Unterkiefer darstellen. Das auffallendste Merkmal des Materials von Aivaliki, das als *Stephanorhinus cf. etruscus* bestimmt wird, ist die kleinere Größe des Gebisses mit relativ brachyodonten und unspezialisierten Zähnen, besonders die Molaren. Das Auftreten von kleinen Übergangspopulationen der *etruscus*-Nashorngruppe scheint ein kennzeichnendes Element mehrere Alt-Pleistozänen Faunen in Europa zu sein, das vermutlich mit den verändernden klimatischen Verhältnissen verbunden ist. Die bekannten Plio-Pleistozänen Fundstellen mit fossilen Nashörnern in Griechenland werden kurz zusammengefaßt.

1. Introduction

During 25-30 August 2003, a multidisciplinary research project was carried out in the area of Alistrati, Serres Prefecture (N. Greece), by Prof. N. Symeonidis (University of Athens), Dr. R. Seemann (Naturhistorisches Museum Wien), Dr. V. Giannopoulos (Hellenic Ministry of Culture), S. Giannopoulou (Hellenic Ministry of Culture) and N. Diafas (Supervisor of Aggitis Cave, Prosotsani). Objectives of the project were the continuity of the excavations in the recently discovered "Orpheus Cave", as well as the exploration of new caves in the area. The results of the multidisciplinary research at Orpheus Cave (archaeology, geology, palaeontology) are currently under study by S. Giannopoulou-Konteli (Thesis in preparation). During the course of these investigations, Mr. Elias Kotsenoglou, a resident of the village of Nea Mpaфра, informed the research team that he has discovered bones of a large animal in a nearby locality known to locals as Aivaliki. The locality of Aivaliki is situated 1 km away from the village of Nea Mpaфра (Fig. 1, 2) and 6 km SE from Alistrati Cave. It is also located very near to the Canyon of the Aggitis River. A preliminary excavation was organized at the locality by the research team, which yielded several specimens of fossil rhinoceroses described in this paper.

¹⁾ Prof. Dr. Nikolaos K. SYMEONIDIS, National and Kapodistrian University of Athens, Faculty of Geology and Geoenvironment, Department of Historical Geology and Palaeontology, Panepistimiopolis, GR-15784 Athens, Greece, e-mail: symeonidis@geol.uoa.gr

²⁾ **Corresponding Author:** Dipl.-Geol. Ioannis X. GIAOURTSAKIS, Ludwig-Maximilians-Universität München, Department für Geo- und Umweltwissenschaften, Bereich Paläontologie, Richard-Wagner-Str. 10, D-80333 München, Germany, e-mail: i.giaourtsakis@lrz.uni-muenchen.de

³⁾ Dr. Robert SEEMANN, Naturhistorisches Museum Wien, Mineralogisch-Petrographische Abteilung, Burgring 7, A-1010 Wien, Austria, e-mail: robert.seemann@nhm-wien.ac.at

⁴⁾ Dr. Vassileios I. GIANNOPOULOS, Ephorate of Paleoanthropology - Speleology, Ministry of Culture, Arditou 34B, GR-11636 Athens, Greece.

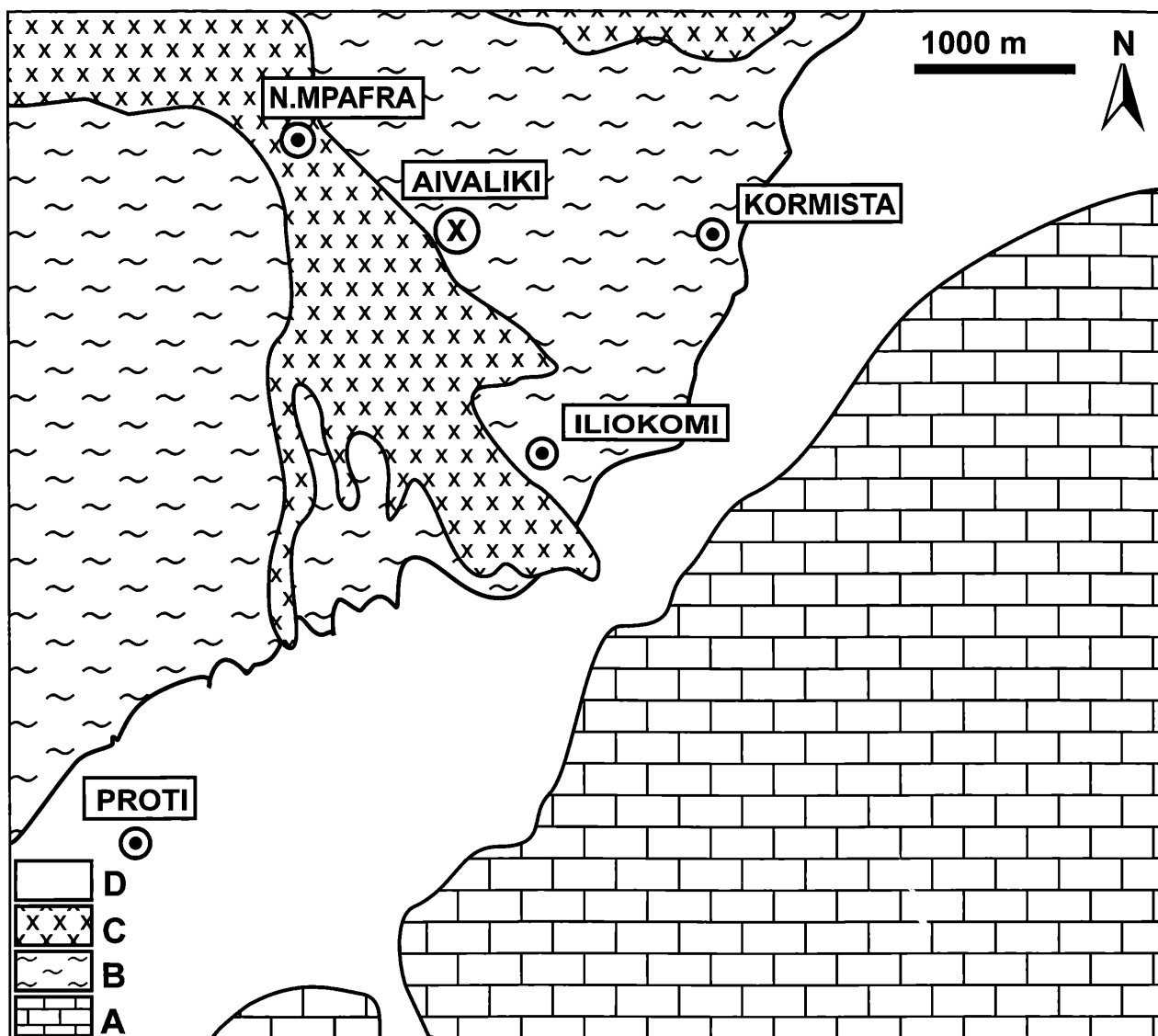


Figure 1: Geological map of the fossiliferous locality Aivaliki (modified after KRONBERG & SCHENCK, 1974). **Legend:** A: Pre-Neogene Basement: Massive or poorly bedded white marbles alternated with bands or lenses of thin well bedded grey marbles, B: Plio-Pleistocene lacustrine and continental deposits: marls, conglomerates, silts, sands and gravels, C: Pleistocene scree slope with or without clay. Terrestrial terrace: reddish sandy clay intermixed with rounded and angular marble pebbles, D: Pleistocene-Holocene continental deposits: blocks and unconsolidated conglomerates combined with fine-grained sands and reddish clay silicates. Alluvial fans with erosion material of marbles, gneiss, and granite locally brecciated.

The studied material is interesting, as our knowledge about the Pleistocene rhinoceroses of Greece remains quite limited. In the future, an intensive excavation research project is scheduled for discovery of additional fossil material and new localities in the area.

2. Material and Methods

The material from the locality of Aivaliki, near Alistrati, is stored in the collections of the Museum of Palaeontology and Geology of the National and Kapodistrian University of Athens (AMPG). It comprises three specimens of a fragmentary adult mandible (AMPG: AVL-1, 2, 3) that probably belong to the same individual and the right side of a juvenile mandible (AMPG: AVL-4). Dental measurements and terminology follow PETER (2002).

Width measurements include, however, the anterior (W_A) as well as the posterior (W_p) maximal width of each tooth, following FORTELIUS et al. (1993). Measurements ranging 0-150 mm were taken with a digital calliper to 0.01 mm and rounded to the nearest 0.1 mm. For larger measurements a linear calliper with a precision of 0.1 mm was applied. All measurements are given in millimetres (mm). Comparative studies with fossil and extant species were conducted at the collections of the Natural History Museum of Vienna (NHMW), the Natural History Museum of Paris (MNHN), the Bayerische Staatssammlung für Paläontologie und Historische Geologie München (BSPG) and the Staatliches Museum für Naturkunde Karlsruhe (SMNK). The sedimentological analysis was carried out at the laboratories of the Department of Mineralogy and Petrology of the Natural History Museum of Vienna.

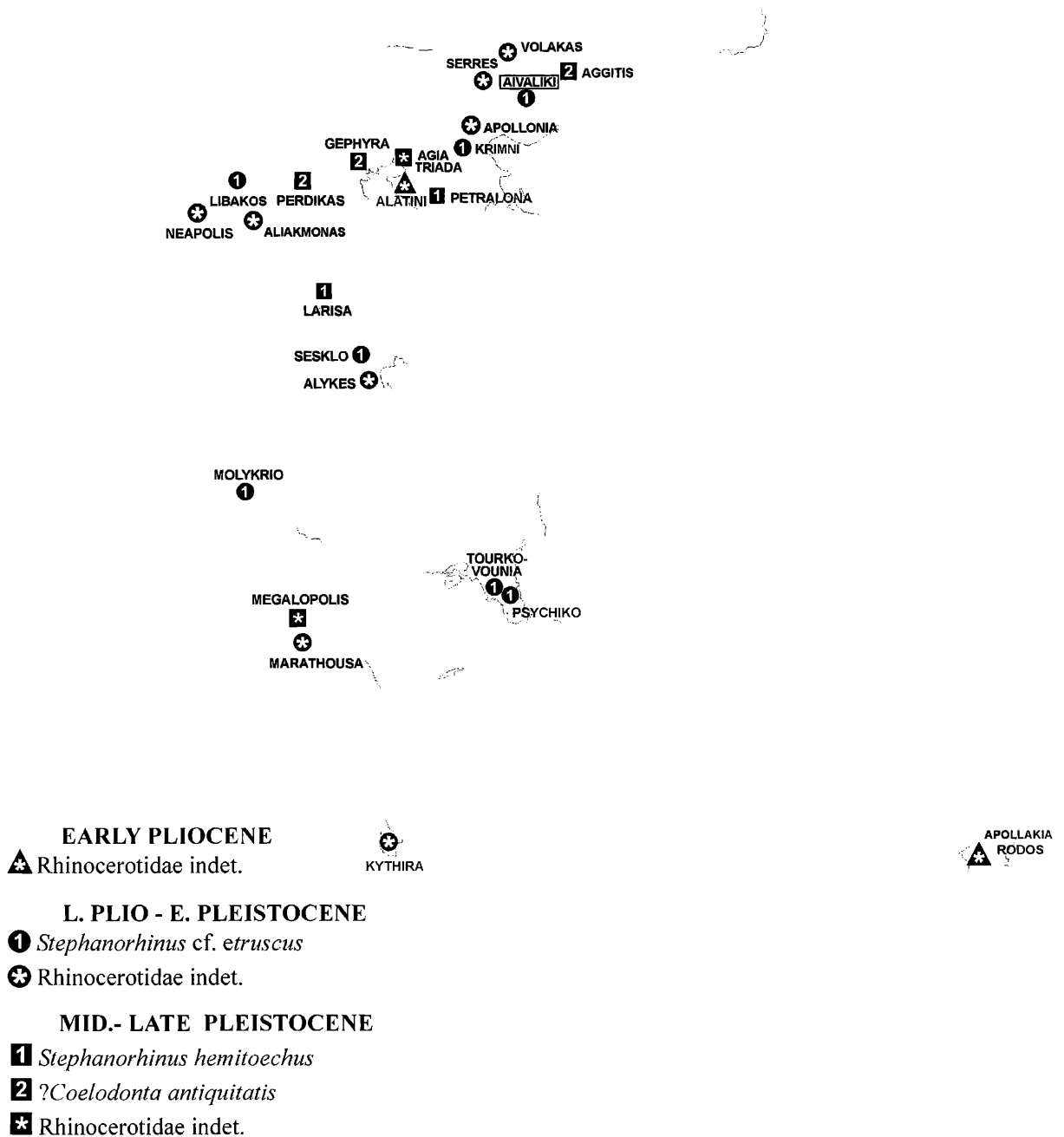


Figure 2: Distribution of the family Rhinocerotidae in Greece during the Pliocene and the Pleistocene.

3. Geological setting

The pre-Neogene basement of the area belongs to the geotectonic Zone of the Rhodope Massif. The Rhodope Massif is characterized by extensive outcrops of high-grade Paleozoic and Mesozoic metamorphic rocks (mainly marbles, amphibolites, gneisses and mica schists), which are intruded by Tertiary Alpine granitoids (KRONBERG et al., 1970; DINTER, 1994; KILIAS & MOUNTRAKIS, 1998). The metamorphic basement is covered by Neogene and Quaternary sediments and alluvium deposits (Fig. 1), which have been accumulated in the basin of Drama to the east and in the basin of Serres to the west of Alistrati. The sediment directly adherent to the surface of the fossil

bones is a rather inhomogeneous and poorly sorted deposit. At a first glance it looks like a compact and uniform fine-grained matrix. In fact, it is a heterogeneous mixture of minor amounts of completely unsorted mm-sized grains (sub-rounded to angular quartz and local rock fragments) set in a matrix of fine silt and clay. The colour is greenish grey to yellowish, depending on the stage of oxidation. The general mineral composition of the dominating fine-grained part of the sediment is characterized by:

- Calcite (CaCO₃): about 50-60%
- Chlorite (clinochlore) ([Mg,Fe,Al]₃ [(OH)₂/AlSi₃O₁₀].Mg₃(OH)₆): about 20-30%
- Quartz (SiO₂) and Biotite (mainly chloritized): about 1-5%

Mineral composition and chemistry classify the sediment

as carbonate rich silty clay (marl). Remarkable are small brownish to black dendritic formations (Fe- and Mn-oxihydrates), typical for weak diagenetic processes. The enrichment zones are close to the surface of the embedded fossil bones. In addition, small nodular phosphate concretions (dahllite: carbonate-hydroxyapatite) were formed by secondary processes nearby or even on the bone fragments. The fine grained sediment is typical for a shallow-water deposit or flood plain deposit. The much less abundant coarse grained part of the matrix sediment consists mainly of debris of quartz (vein quartz), feldspar, mica flakes, in part oxidized ore (hematite, pyrite, magnetite), and of fragments of local rocks (quartzite, gneiss and mica schists). Given the shape and low degree of roundness (sphericity) of fragments the distance to the source area cannot be very far. The only possible source material close enough for discussion is the pre-Mesozoic Rhodope Crystalline –either in shortest distance from the Pangeon/Simvolon Mountains in the South or, assuming a former exposure, with more probability from the North, from the Menikion or Phalakron Area. The available rocks from both sides are mainly marble, quartzites, gneisses, mica schists, amphibolites as well as granites and granodiorites. The peculiarity of this inhomogeneous sedimentation seems to be a result of rhythmic deposition of thin layers of coarse and fine grained material in a flood plain in basins in-between the southern spurs of the Rhodope Massif. An area influenced by river activity and in part with shallow water. Relict gravels, including bones, were infiltrated (and covered) by silt and clay providing the conditions to preserve even the biogenic relicts.

4. Systematic Palaeontology

Classis Mammalia LINNAEUS, 1758

Ordo Perissodactyla OWEN, 1848

Familia Rhinocerotidae OWEN, 1845

Subfamilia Rhinocerotinae OWEN, 1845

Tribus Dicerorhinini RINGSTRÖM, 1924

Genus *Stephanorhinus* KRETZOI, 1942

Stephanorhinus cf. etruscus (FALCONER, 1868)

Description of adult mandible: Three adult mandibular specimens have been recovered from Aivaliki. The identical size and stage of wear, as well as the proximity of the findings, indicate that they must belong to the same individual. AMPG:AVL-1 consists of the left mandibular corpus with the complete lower dentition p2-m3 (Pl. 1, figs. 2-4). It shows mediolateral compression slightly deforming its morphology. The ventral border of the mandibular corpus appears to be straight or slightly concave. It shallows anteriorly towards the symphysis, which is barely preserved. There are no traces of incisor alveoli and the posterior margin of the symphysis lies in front of the p2. The ascending ramus and the mandibular angle are not preserved. AMPG:AVL-2 is a fragment of the right man-

dibular corpus bearing the three molars m1-m3 (Pl. 1: fig. 1). The third specimen, AMPG:AVL-3, consists only of the right p3 with parts of its roots. The description of the dentition is primarily based on the complete left tooth row of AMPG:AVL-1.

The second lower premolar has a reduced trigonid as is common in advanced rhinocerotids. The paralophid is straight and single. A shallow anterior groove is developed on the labial wall of the trigonid, constricting slightly the paralophid posteriorly. The median labial groove (ectoflexid) is deep and acute. A prominent continuous labial cingulum is developed on the base of the labial wall. There is no lingual cingulum. In lingual view, the trigonid valley is open and steep anterolingually. The talonid valley is also open and V-shaped. In occlusal view, the metalophid is vertical and the metaconid is not constricted. The hypolophid is curved, not angular. The entoconid bends little lingually and is merely constricted at its top.

The third lower premolar is also well preserved. The paralophid is long and bends lingually reaching the level of metaconid and entoconid. There is no anterior groove on the labial wall of the trigonid and the ectoflexid is less marked. A continuous labial cingulum is developed on the base of the labial wall. In occlusal view, the metalophid is angular and the metaconid is not constricted. The hypolophid is curved and the entoconid is slightly constricted at its top. In lingual view, the trigonid and talonid valleys are V-shaped. There is no lingual cingulum. The fourth lower premolar is larger than the third one, but has similar morphology. Its talonid is poorly preserved.

All three lower molars are morphologically quite uniform despite the different stages of wear. The second molar is larger than the other two. The last molar is very little worn and its lowest part not fully erupted. The paralophid is long and bends lingually reaching the level of metaconid and entoconid. The ectoflexid is deep but somewhat wider than in the premolars. The labial cingulum is practically absent in the molars and only little developed on the labial wall of the talonid of m2. In lingual view, the trigonid and talonid valleys are markedly V-shaped. There is no lingual cingulum. As in the premolars, the metalophid is more angular and the hypolophid oblique. The metaconid and the entoconid are not constricted.

Description of juvenile mandible: AMPG:AVL-4 is the left side of a fragmentary juvenile mandible (Pl. 2: fig. 1-3). The symphysis and the ascending ramus are broken. The mandibular corpus is merely preserved below the toothrow. There is no sign of a marked longitudinal depression (linea mylohyoidea) on the lingual side of the horizontal ramus. The traces of broken roots in the alveolus of the first lower milk molar verify the presence of a double-rooted d1. Only the second and the third lower milk molars are preserved intact. They are little affected by wear indicating a very young individual. The missing last fourth milk molar must have been only slightly erupted from its alveolus.

The second lower milk molar is narrower than the third one. The anterior tip of the paralophid is slightly broken, so it is not clear if it was doubled. A quite prominent

anterior cingulum lowers down labially and fades into cingular rugosities at the base of the ectolophid. There is a well-marked anterior labial groove on the labial wall of the trigonid constricting paralophid and paraconid. It faints down above the labial cingular rugosities. The ectoflexid is hardly deeper but better marked and continuous down to the base of the crown interrupting the labial cingular traces. Lingually, the anterior cingulum projects only slightly at the base of the paralophid. The trigonid and talonid valleys are still filled with hard sediment matrix. The trigonid valley is steep and open anterolingually. The metaconid appears to be slightly constricted at its top. The talonid valley is open and V-shaped, the entoconid bends very little lingually and is slightly constricted at its top. There is no lingual groove developed on its base.

The third lower milk molar is more similar to its permanent counterpart. The paralophid is longer than in the second milk molar and curves lingually, reaching the level of metaconid and entoconid. The trigonid valley is filled with matrix, but some dentine traces indicate that the paralophid could have been doubled, the two branches merging lingually, thus forming a shallow closed paralophid groove. The marked anterior cingulum projects slightly on the labial wall. There is no anterior labial groove on the ectolophid. The ectoflexid is marked but not deep. A tiny cingular button is developed on its base just above a small depression between the roots. The posterior cingulum was slightly worn by the erupting missing last milk molar. There is no trace of lingual cingula or rugosities. The trigonid and talonid valleys are V-shaped in lingual view. The lingual base of the paralophid is broken. The metalophid is more worn than in the d2 and the metaconid is not constricted. The hypolophid is oblique. The hypocoid is the lowest cusp of the talonid at this early stage of wear. The almost unworn entoconid is higher and bends little lingually. It is slightly constricted at its top.

5. Discussion and comparisons

During the Pliocene and Pleistocene, rhinoceroses were a common element of the European fauna. The works of GUÉRIN (1980) and FORTÉLIUS et al. (1993) provide, beside the detailed revision of important collections, also an excellent review of the immense literature made available during the last two centuries. A comment on the nomenclature of the species is necessary, since several disagreements exist among the authors.

Apart from the woolly rhino *Coelodonta antiquitatis* (BLUMENBACH, 1799), the European Plio-Pleistocene tandem horned species have been often assigned to the extant genus *Dicerorhinus* GLOGER, 1841 (e.g. STAESCHE, 1941; AMBROSETTI, 1972; GUÉRIN et al., 1969; GUÉRIN, 1972; LOOSE, 1975; MAZZA, 1988), despite their notable differences compared to the small and highly plesiomorphic Sumatra rhino, *Dicerorhinus sumatrensis* (GROVES, 1983; HEISSIG, 1981; GUÉRIN, 1989; FORTÉLIUS et al., 1993). We follow here to some extent FORTÉLIUS et al. (1993), by placing in the genus *Stephanorhinus* KRETZOI, 1942 only

the species that have a partial ossified nasal septum and no permanent anterior dentition. These include the species *Stephanorhinus etruscus* (FALCONER, 1868), *S. hundsheimensis* (TOULA, 1902), *S. jeanvireti* (GUÉRIN, 1972), *S. hemitoechus* (FALCONER, 1868) and *S. kirchbergensis* (JÄGER, 1839). We exclude, however, the species *Rhinoceros megarhinus* DE CHRISTOL, 1834 from *Stephanorhinus* (contra FORTÉLIUS et al., 1993:66) and place it within the genus *Dihoplus* BRANDT, 1878. We regard the absence of a nasal septum and the presence of permanent anterior dentition (even vestigial incisors) in *Dihoplus* as sufficient diagnostic characters at generic level (GIAOURTSAKIS, 2003; GIAOURTSAKIS et al., 2006). These features are perfectly demonstrated by a well-preserved Early Pliocene skull of *D. megarhinus* with associated mandible (MNHN: AC 2683) from Montpellier (Hérault, France), figured also by GUÉRIN (1980: pl. 10). This systematic arrangement corresponds to the concept of GUÉRIN (1980, 1989), who did not include *D. megarhinus* together with the other Plio-Pleistocene species in his (sub)genus *Brandtorhinus*. The subgenus *Dicerorhinus* (*Brandtorhinus*) was erected by GUÉRIN (1980:443) with the type species “*Dicerorhinus etruscus etruscus*” [sic] and was later raised to genus level (GUÉRIN, 1989). However, KRETZOI (1942:312) has also created the genus *Stephanorhinus* with the type species *Rhinoceros etruscus* FALCONER, 1868 thus having priority over *Brandtorhinus*, which remains in effect an objective junior synonym despite the different concept (compare also FORTÉLIUS et al. 1993:65). Another source of confusion is the type skull of *Rhinoceros merckii* var. *brachycephala* SCHROEDER, 1903 from Daxlanden (illustrated in detail by LOOSE, 1975). After a close examination of the skull from Daxlanden (SMNK: Qp/650), we agree with STAESCHE (1941), LOOSE (1975), MAZZA (1988) and FORTÉLIUS et al. (1993) that it must be referred to *S. kirchbergensis*. Further, the species name *Rhinoceros kirchbergensis* JÄGER, 1839 has priority over *Rhinoceros merckii* KAUP, 1841 (KRETZOI, 1942; LOOSE, 1975, FORTÉLIUS et al., 1993). At a time where nomenclatural rules were not consistent, KAUP (1841) has deliberately replaced JÄGER’s name to honour MERCK who was the first to have described specimens of this species. The Late Pliocene species *Dicerorhinus miguelcrusafonti* GUÉRIN & SANTAFÉ, 1978 is excluded from the discussion, because the skull morphology is unknown (GUÉRIN & SANTAFÉ, 1978; GUÉRIN, 1980).

The woolly rhino *Coelodonta antiquitatis* is a later immigrant in Europe with a separate evolutionary history. It is the most advanced and specialized species of the Dicerorhinini tribe bearing numerous autapomorphies such as the complete ossified nasal septum, the very hypsodont and plagiolophodont dentition and more posteriorly inclined occipital (GUÉRIN, 1980). The origin of *Coelodonta* is placed in Eastern Asia where it evolved independently from the European *Stephanorhinus* clade before invading Europe during the late Middle Pleistocene. Well-preserved material of the oldest representative *C. nihowanensis* CHOW, 1978 has been recently recovered from the ~2.5 Ma Pliocene deposits of Longdan in Linxia basin (Gansu Province, China) showing that this species

had already achieved the autapomorphic characters of the genus (DENG, 2002). *Coelodonta* has also a characteristic lower dental morphology, easily distinguished from the *Stephanorhinus* clade. The ventral profile of the mandibular corpus is very convex. The dentition is highly hypsodont with increased presence of cement. The ectolophid groove on the labial wall of the lower teeth is smooth and shallow. The metaconid and the entoconid are markedly constricted bending strongly lingually. Especially in the premolars, there is a tendency to close the posterior (talonid) valleys very early, forming closed fossettid. Additionally, compared with the material from Aivaliki, *C. antiquitatis* has longer molars and relatively shorter premolars; the p2 is particularly reduced, its paralophid is curved without constriction (anterior labial groove not marked). Furthermore, the p2 and d2 of *C. antiquitatis* are lacking the labial cingulum and very frequently have a closed talonid valley.

Among the species referred to *Stephanorhinus*, the Middle-Late Pleistocene *S. kirchbergensis* is the most distinctive, primarily because of its larger size (GUÉRIN, 1980; FORTELIUS et al., 1993). An assignment to this species can be easily excluded. Nearly all dental measurements of the lower dentition from Aivaliki are well below the minimum values reported for *S. kirchbergensis* (Table 1). Direct comparison with material (BSPG: 1887.V.2) from Taubach (Weimar, Germany) verifies the different size and morphology of the mandible and lower dentition. For the same reason, the large-sized Pliocene species *Dihoplos megarhinus* can also be excluded (GUÉRIN, 1980: tab. 89). Several authors have considered *S. kirchbergensis* as a descendant of *D. megarhinus* (WÜST, 1922; STAESCHE, 1941). This view was also favoured by FORTELIUS et al. (1993: fig. 28), who placed the clade “S.” *megarhinus* and *S. kirchbergensis* separated from the complex formed by the *etruscus*-group (*S. jeanvireti*, *S. etruscus*, *S. hundsheimensis*) plus *S. hemitoechus*.

Stephanorhinus hemitoechus has a characteristic dentition with reduced anterior premolars and hypsodont, enlarged molars, especially the last one (FORTELIUS et al., 1993). The lower dentition from Aivaliki is in comparison brachydont and the molars are much smaller, especially the last one (Tab. 1). This is well reflected in the different proportions between molars and premolars. The premolar length of the AVL-1 mandible lies near the maximum values observed in *S. hemitoechus*, but the molar length remains well below the lowest values of this species (Tab. 1). According to FORTELIUS et al. (1993), one of the most striking and consistent differences between *S. hemitoechus* on the one side and *S. etruscus* plus *S. hundsheimensis* on the other, is the high occurrence of a lingual cingulum in *S. hemitoechus* below the entrance of the distal valley of the lower teeth, usually forming a very broad V and U with the centre directly beneath the valley bottom. This feature, also documented by GUÉRIN (1980: p. 658-659), is absent in the AVL-1 mandible. Overall, lingual cingula are rarely observed in *S. etruscus* and *S. hundsheimensis* (GUÉRIN 1980, FORTELIUS et al. 1993: tab. 4, fig. 2)

The proportional differences and the morphological fea-

tures described above for the Aivaliki mandible are only in accordance with the size and morphology documented for the rhinoceroses of the *etruscus*-group. *Stephanorhinus etruscus* and *S. hundsheimensis* have relative brachydont teeth compared to the other species and a dentition of even proportions between the molars and premolars (GUÉRIN, 1980; MAZZA, 1988; FORTELIUS et al., 1993). The morphology of the older, Early Pliocene species *S. jeanvireti* is also similar, but not as well documented to allow detailed comparisons (GUÉRIN, 1980). It is very interesting that the size of the lower molars from Aivaliki lies close to the minimum values observed for the *etruscus*-group (Tab. 1), a character that can be interpreted as primitive. Another primitive feature is the second lower premolar, which is well developed, with a deep ectoflexid and a constricted prominent paralophid. The presence of a labial cingulum, especially on the premolars, has been documented for both species, but it is more frequent in *S. etruscus* (GUÉRIN, 1980: 467-469; FORTELIUS et al., 1993: tab. 4). As mentioned above, lingual cingula are rarely preserved in all species. Despite the evident assignment of the Aivaliki rhino to the *etruscus* - group, it is rather difficult to locate accurately its position within the lineage based on the available material. Most differences between both species are primarily related to skull and upper teeth morphology and, at a lesser degree, to general trends of some postcranial elements (GUÉRIN, 1980; FORTELIUS et al., 1993). Morphological distinction between lower dentition is in most cases rather difficult. Nevertheless, a direct comparison with the type material of *S. hundsheimensis* from Hundsheim, Austria (TOULA, 1902, 1906) at the collections of NHMW shows some significant size differences. The teeth of the AVL-1 mandible are more brachydont and notably smaller, especially the molars. Similar differences occur in comparison with well-preserved mandibles (SMNK: M.351, M.352) of *S. hundsheimensis* from the early Middle Pleistocene locality of Mauer, Germany (SCHREIBER, 1999, 2005). On the other hand, the lower dentition from Aivaliki shows no significant morphological difference to the material traditionally ascribed to *S. etruscus* (MAZZA, 1988:20-23, tab. 3a,b and pl. 3, fig. 2; AMBROSETTI, 1972: pl. 2, fig. 2-3; GUÉRIN, 1980:467-469 and pl. 13, fig. D1-D2; pl. 14, fig. D). Especially the well-preserved mandibles from Senéze figured by GUÉRIN (1980, *ibid.*) demonstrate the even proportions between molars and premolars, the small and brachydont molars (particularly clear from the less worn m3) and the unreduced p2 with a marked anterior labial groove and well-developed paralophid. According to FORTELIUS et al. (1993), *S. hundsheimensis* is a larger and heavier animal with a more robust mandible. The size incensement from Villafranchian *S. etruscus* to Middle-Late Pleistocene *S. hundsheimensis* has been also documented by GUÉRIN (1980:1008 and tab. 156).

The most striking feature of the AVL-1 mandible is the rather small size of the dentition with quite brachydont and unspecialized teeth, especially the molars. The significance of the occurrence of populations of small-sized rhinoceroses of the *etruscus*-group during the latest Early Pleistocene was underlined by MAZZA et al. (1993)

		Aivaliki	<i>S. etruscus</i>		<i>S. hundsheimensis</i>		<i>S. hemitoechus</i>		<i>S. kirchbergensis</i>	<i>C. antiquitatis</i>
		AMPG AVL-1	FORTELIUS et al. (1992)	GUÉRIN (1980)	FORTELIUS et al. (1992)	GUÉRIN (1980)	FORTELIUS et al. (1992)	GUÉRIN (1980)	GUÉRIN (1980)	GUÉRIN (1980)
p2	L	28.5	27-32	25-33	27-35	27-39	23-31	26-30.5	31-34	19-34
	WA	17.2	15-20	—	15-21	—	13-20	—	—	—
	WP	20.4	17-21	16-21.5	19-26	16-33	15-21	14.5-20.5	20-21.5	14-20.5
p3	L	35.1	31-38	31.5-37	30-41	33-42.5	28-36	27-40	35-46	25-42
	WA	22.3	20-25	—	21-27	—	19-24	—	—	—
	WP	25.3	23-30	21.5-29	23-31	21-37	21-28	21-27	27-35.5	19-30.5
p4	L	38.8	34-43	35-39.5	33-44	33-45	34-43	35-42	38-51	33-46.5
	WA	25.9	24-30	—	23-32	—	21-28	—	—	—
	WP	—	25-31	24-31	23-34	24-35	24-32	26-30.5	28.5-38.5	24-35
m1	L	39.4	38-49	37-43	37-49	37-57	38-47	36.5-52	43-59	38-51.5
	WA	26.3	25-31	—	25-35	—	26-33	—	—	—
	WP	27.3	26-33	26.5-33	27-36	25-37	27-34	26-35	33-42	24-36
m2	L	42.7	40-49	40.5-47.5	39-51	42-57.5	40-52	41-55	53-63	42-55.5
	WA	27.6	27-34	—	26-36	—	27-34	—	—	—
	WP	28.8	25-32	27-33.5	26-34	23.5-35	28-34	28-36	32-40	28-36
m3	L	41.8	39-48	41-50	40-51	44-59	42-54	45-58	50-64	43-63
	WA	25.8	26-33	—	26-34	—	26-35	—	—	—
	WP	—	25-31	26-33	25-33	25-33	27-34	26.5-34	31-39	26-36
p2-p4		104.2	—	87-108	—	99-116	—	86.5-108	113.5-127	74.5-123
m1-m3		123.6	—	121-143	—	119-163.5	—	131-160	139-195	123.5-181
p2-m3		227.2	—	210-252	—	228-263.5	—	224-266	266-290	183-262

Table 1: Comparative dimensions (in mm) of the lower permanent dentition of Plio-Pleistocene rhinoceroses.

and FORTELIUS et al. (1993). According to these authors, they might represent a useful stratigraphic marker, as they appear to be widely dispersed throughout Europe and have a restricted temporal distribution. Remains of these small-sized populations with etruscoid affinities occur at Pietrafitta (Umbria, Central Italy), Westerhoven (Brabant, Netherlands) Colle Curti (Colfiorito Basin, Macerata, central Italy), Loreto (Venosa, southern Italy) and Wissel (Kalkar, Germany). The faunal association of these localities comprises characteristic species of the latest Late Villafranchian faunas that are chronologically referable to the latest Early Pleistocene (FORTELIUS et al., 1993). According to FORTELIUS et al. (1993), the small etruscoid rhinoceroses might be considered as transitional forms showing various intermediate stages between *S. etruscus* and *S. hundsheimensis*, or they might be seen as small-sized populations of the lineage unrelated to a speciation event. As a possible explanation for the size reduction, the authors suggest potential environmental stress associated with the changing climatic conditions that characterized the end of the Early Pleistocene. The material from Pietrafitta has been tentatively assigned to *S. cf. hundsheimensis* by MAZZA et al. (1993), based mainly on the postcranial morphology. According to the authors, the postcranial skeleton of the rhinos from Pietrafitta resemble that of *S. hundsheimensis* primarily in morphological characters and proportions but not in size, since they are smaller than TOULA'S (1902, 1906) species. On the contrary, the morphology of the numerous

dental remains from Pietrafitta is closer to the *S. etruscus*, especially the mandible (MAZZA et al., 1993:29 and pl. 1, fig. 4-6). An intermediate status between *S. etruscus* and *S. hundsheimensis* has been preliminary granted for the material from Pirro (Gargano Peninsula, Italy) and Westerhoven (Brabant, The Netherlands), as well (MAZZA et al., 1993:38).

The smaller size and unspecialized morphology of the material from Aivaliki might be correlated to these small-sized etruscoid populations and an Early Pleistocene age seems very plausible and in accordance with the sedimentological history of the locality (KRONBERG & SCHENCK, 1974). Since the dental and mandibular morphology of the Aivaliki specimens are closer to the more conservative *S. etruscus* and clearly different from the younger populations of *S. hundsheimensis* (especially the type specimen), they are provisionally referred here to as *Stephanorhinus cf. etruscus*. If this material is related to the small sized Early Pleistocene populations, this could imply that at least some of them are probably unrelated to a speciation event and most likely influenced by local palaeogeographical and palaeoenvironmental factors, a possibility also underlined by MAZZA et al. (1993). Nevertheless, additional material and an associated fauna are required for a more accurate specific and stratigraphic determination.

The Pliocene and Pleistocene record of the family Rhinocerotidae in Greece is rather poor compared to the diverse and abundant Late Miocene record, particularly from the

classic localities of Pikermi, Samos and Axios Valley (GIAOURTSAKIS, 2003). The following review is indented only as a brief up-to-date summary of the known localities, pending further revision and discoveries in the future.

Early Pliocene (Ruscinian), localities with large mammals are extremely rare in Greece and the occurrence of Rhinocerotidae indet. has been cited only at the faunal lists of Apollakia (VAN DE WEERD et al., 1982) and Alatini (MARINOS, 1965). Late Pliocene - Early Pleistocene (Villafranchian) localities are more frequent in Greece (KOUFOS & KOSTOPOULOS, 1997). Despite the numerous localities, knowledge of rhinos remains also limited during this time of period, because of the scanty material. It is notable that the published material exceeds the number of five specimens in very few sites. The presence of *Stephanorhinus* cf. *etruscus* has been reported with more or less certainty from several localities: Libakos (STEENSMA, 1988), Krimni (SAKELLARIOU-MANE et al., 1979), Sesklo (SYMEONIDES, 1992; ATHANASSIOU, 1998), Marathousa (SICKENBERG, 1975), Tourkovounia (SYMEONIDIS & DE VOS 1976), Molykrio (SYMEONIDIS et al., 1986), Psychiko (PARASKEVAIDIS, 1953) and Serres (MARINOS, 1965). The referred material comprises usually a few isolated dental and/or postcranial remains, so it is not directly comparable with the mandibles from Aivaliki. A small mandibular fragment from Psychiko was described as *Stephanorhinus* cf. *etruscus* (PARASKEVAIDIS, 1953). MARINOS (1965) reported a rhino mandible from an indefinite locality in Early Pleistocene deposits of Serres Basin. This is the closest locality to Aivaliki, but neither figure or description were provided to allow comparison. Another mandibular fragment from an unspecified locality near Aliakmonas river (PSARIANOS, 1958) is referred here as Rhinocerotidae indet. Unidentifiable rhino specimens have been further reported at Alykes (ATHANASSIOU, 1998), Apollonia (KOUFOS et al., 1992), Kythira (BARTSIOKAS, 1998), Neapolis (BRUNN, 1956), Volakas (SICKENBERG, 1968) and Alatini (MARINOS, 1965).

Middle and Late Pleistocene rhinoceros are quite rare in Greece as well. Only the presence of *Stephanorhinus hemitoechus* has been documented with numerous dental and postcranial specimens at Petralona Cave (TSOUKALA, 1989). The occurrence of the species in Larisa based on an isolated left M2 (BOESSNECK, 1965) is, however, questionable. The woolly rhino *Coelodonta antiquitatis* has been reported in the localities of Gephyra (TSOUKALA, 1991), Aggitis (KOUFOS, 1981) and Perdikas (PAVLIDES, 1985), but the material is very scarce. A skull of *C. antiquitatis* described by MELENTIS (1965) from Megalopolis might belong to an old mislabelled exchanged specimen from Russia and is excluded from the review. The rest of the material from Megalopolis at AMPG is quite limited and provisionally referred to as *Stephanorhinus* sp.. A summary of the Pliocene and Pleistocene occurrence of the family Rhinocerotidae in Greece is presented in the map of Fig. 2. Unfortunately, the available material is currently insufficient for discussing potential evolutionary trends of the family during this time of period in Greece.

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PLATE 1

Stephanorhinus cf. etruscus from Aivaliki

- Fig. 1 Adult mandible dex. (AMPG:AVL-2) in dorsal view.
- Fig. 2 Adult mandible sin.. (AMPG:AVL-1) in dorsal view.
- Fig. 3 Adult mandible sin. (AMPG:AVL-1) in lateral view.
- Fig. 4 Adult mandible sin. (AMPG:AVL-1) in medial view.

PLATE 1

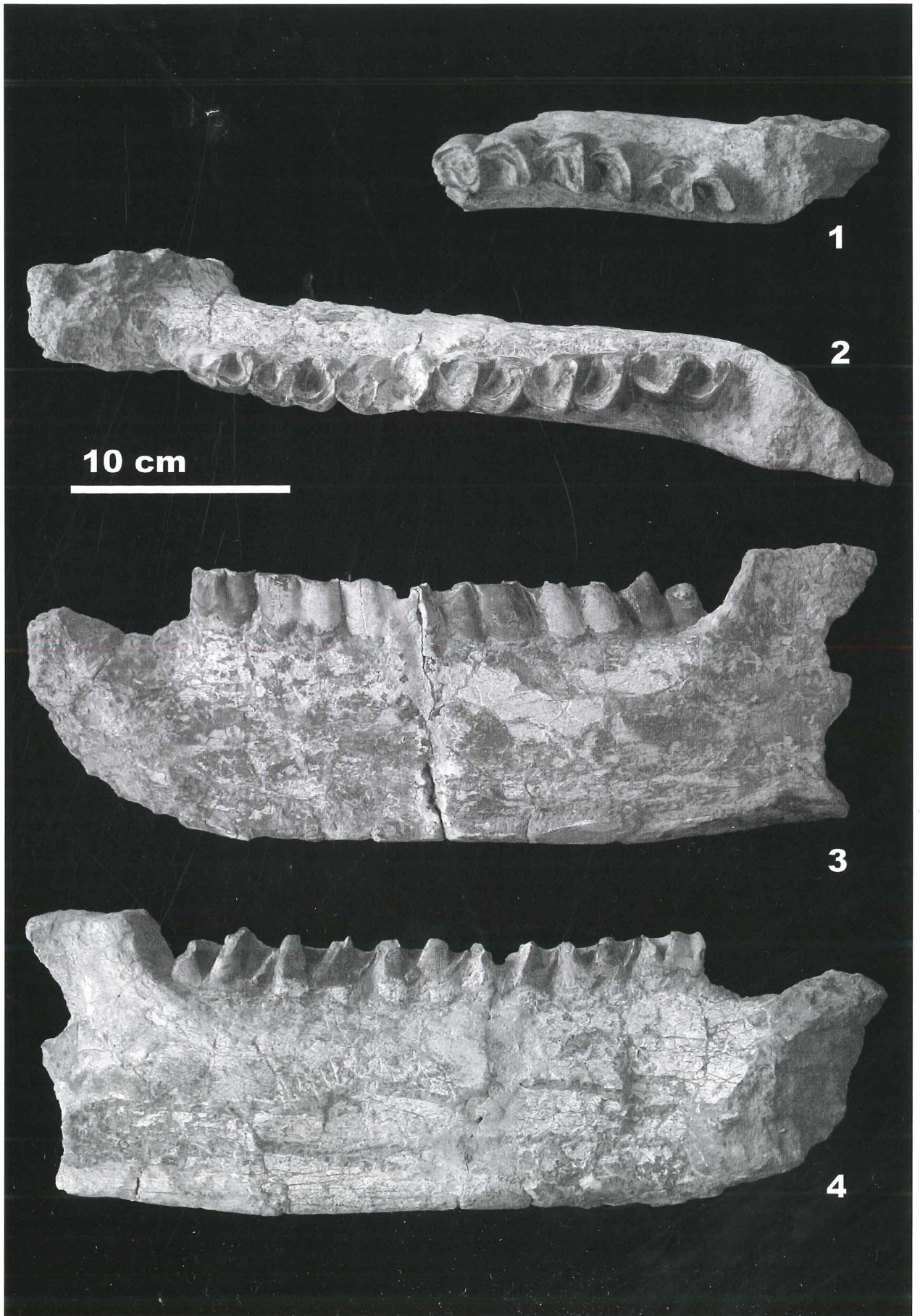
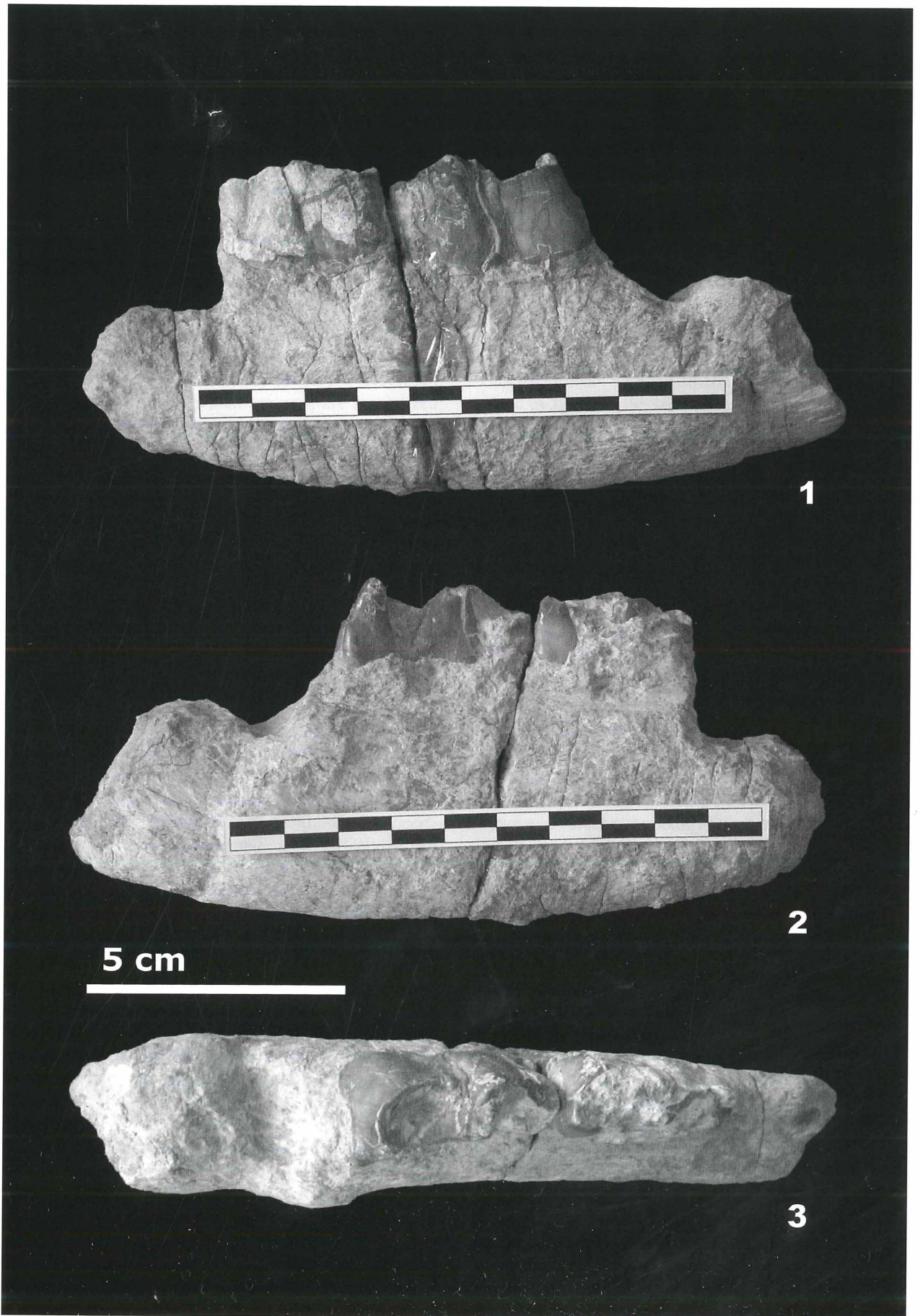


PLATE 2

Stephanorhinus cf. etruscus from Aivaliki

- Fig. 1 Juvenile mandible sin. (AMPG:AVL-4) in lateral view.
- Fig. 2 Juvenile mandible sin. (AMPG:AVL-4) in medial view.
- Fig. 3 Juvenile mandible sin. (AMPG:AVL-4) in dorsal view.

PLATE 2



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Autor(en)/Author(s): Symeonidis Nikolaos K., Seemann Robert,
Giaourtsakis Ioannis X., Giannopoulos Vassileios I.

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