

The first record of *Anancus* (Mammalia, Proboscidea) in the late Miocene of Greece
and reappraisal of the primitive anancines from Europe

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RH: KONIDARIS AND ROUSSIAKIS—LATE MIOCENE *ANANCUS* FROM
GREECE

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3 ABSTRACT—In this article we present the tetralophodont proboscideans from the
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5 late Miocene (Turolian) locality Chomateri (Greece), near the classical locality
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7 Pikermi. The material consists of juvenile teeth, whose morphological features, such
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9 as the dislocation of the half-loph(id)s and the resultant alternate arrangement of the
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11 successive loph(id)s (anancoidy), permit the allocation to *Anancus*. However, the
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13 anancoidy is rather weak and the occlusal morphology simple, both regarded as
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15 primitive features within anancines. The re-examination of the late Miocene
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17 anancines from Europe reveals that they all share primitive molar features (weak
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19 anancoidy, simple morphology, thick enamel) with the material from Hohenwarth
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21 (Austria) showing further primitive skull features, such as the longer mandibular
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23 symphysis compared to other anancines. The proper name to refer to the late Miocene
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25 anancines from Europe is *Anancus lehmanni* (Gaziry, 1997) with type locality Dorn-
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27 Dürkheim 1 (Turolian; Germany). The presence of *Anancus* in Chomateri consists the
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29 first late Miocene record of the genus in Greece and the first faunal element that
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31 clearly indicates that Chomateri post-dates Pikermi. We discuss the biogeography and
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33 the biostratigraphy of the late Miocene anancines of the Old World. *Anancus*
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35 originated possibly at ~9.0–8.5 Ma in Asia and entered Europe during the second half
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37 of the Turolian, at ~7.2 Ma (Tortonian/Messinian boundary). The arrival of *Anancus*
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39 in Europe coincides with a faunal turnover in both the eastern and western sector of
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41 the European Mediterranean region, and in the Southern Balkans in particular, with
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43 the decline of the ‘Pikermian’ large mammal fauna.
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50 INTRODUCTION

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3 The fossiliferous locality Chomateri or Kisdari (Attica, Greece) is located in a
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5 clay pit about 2 km east of the classical site Pikermi (Fig. 1). Stratigraphically, both
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7 Chomateri and Pikermi localities are situated in the Pikermi Formation (dated to
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9 7.37–7.11 Ma), which is divided into the lower Red Conglomeratic Member
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11 (including the classical Pikermian bone accumulations [e.g., Gaudry, 1862;
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13 Woodward, 1901], the new ‘Pikermi Valley’ localities PV1–4 [Theodorou et al.,
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15 2010, Roussiakis et al., 2014], the lower fossiliferous Chomateri levels partly
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17 excavated by Symeonidis and Bachmayer during 1972–1980 and Pyrgos Vassilissis
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19 [Freyberg, 1949]), and the upper Chomateri Member (including the upper
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21 fossiliferous Chomateri levels where Symeonidis and Bachmayer excavated during
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23 1979–1980) (Böhme et al., 2017). Bio-, magneto- and cyclo-stratigraphy indicate that
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25 the Red Conglomeratic Member is dated to 7.37–7.17 Ma (the classical Pikermi
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27 mammal fauna at ~7.3 Ma) and the Chomateri Member to 7.17–7.11 Ma (Böhme et
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29 al., 2017). Details on the geology, age and palaeoenvironment of the Pikermi region
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31 can be found in Böhme et al. (2017).
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35 The locality of Chomateri was discovered in 1971 and was excavated from
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37 1972 until 1980 by a joint team of the National and Kapodistrian University of Athens
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39 and the Natural History Museum of Vienna (Marinos and Symeonidis, 1972, 1974;
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41 Bachmayer et al., 1982). Two large-mammal-bearing horizons were spotted in the
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43 Chomateri area, but the majority of the fossils originate from the one that was first
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45 identified in 1971 and is dated to ~7.2 Ma (Böhme et al., 2017). The second and
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47 slightly younger fossiliferous level, was discovered in 1979. We note herein that, in
48
49 Chomateri, a fossil accumulation was originally planned as an in situ fossil exhibition
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51 and thus some of the fossils remained still there (Bachmayer et al., 1982). Apart from
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53 the first publications (Symeonidis, 1973a, 1973b, 1978; Symeonidis et al., 1973), later
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on other researchers studied further specimens from the Chomateri collection (Zapfe, 1991; Roussiakis, 2009). However, the large mammal assemblage from Chomateri is not studied in detail as a whole, so its faunal context and correlation with Pikermi, as well as with other Turolian localities of Greece and the wider region, is not yet clear. Roussiakis (2009) studied the bovids *Prostrepsiceros* and *Protragelaphus* from Chomateri and noticed the similarities of the specimens with those of Pikermi; however, Roussiakis pointed their different percentages of representation in the respective assemblages, concluding to possible different palaeoecological conditions and/or slight differences in age. Concerning the proboscideans, in the rich vertebrate collections of Pikermi (AMPG, MNHN, NHMUK, SNSB-BSPG) four proboscideans are present, the deinothere *Deinotherium proavum* (Eichwald, 1831), the zygodont *Mammut* sp., the trilophodont gomphothere *Choerolophodon pentelici* (Gaudry and Lartet, 1856) and the tetralophodont amebelodontine *Konobelodon atticus* (Wagner, 1857). In the far smaller Chomateri collections the two only known proboscidean specimens, one at AMPG and the other at NHMW, belong to *Anancus*, indicating chronological difference with Pikermi (Konidaris, 2013; Konidaris et al., 2014, 2017). Preliminary results of this study were presented by Konidaris and Koufos (2013) and Konidaris and Roussiakis (2017).

The large mammal fauna of Chomateri includes the following taxa (Koufos 2006; Roussiakis, 2009, personal observations; Athanassiou et al., 2014; this study): *Mesopithecus pentelicus*, “*Metailurus parvulus*”, *Anancus lehmanni*, *Hipparion mediterraneum*, *Chalicotherium goldfussi*, *Acerorhinus neleus*, *Microstonyx major*, *Pliocervus pentelici*, *Palaeotragus rouenii*, *Miotragocerus valenciennesi*, *Prostrepsiceros rotundicornis*, *Protragelaphus skouzesi*, *Palaeoreas lindermayeri* and *Gazella* sp. Micromammals were also collected from the wider Chomateri area, but

from about 12 meters above the layers with the large vertebrates from the marshy clays with lacustrine molluscs of the lower part of the Rafina Formation, recently dated to ~ 7.1 Ma (de Bruijn, 1976; López Martínez, 1976; Rümke, 1976; de Bruijn et al., 1999; Böhme et al., 2017). Note that in several publications the correlation of the Chomateri fauna is based on this micromammal assemblage.

MATERIAL AND METHODS

The material from Chomateri studied in this article is stored at AMPG and NHMW. Both specimens are labeled with a date indication “1972”; therefore, most possibly they derive from the 1972 excavation season and thus from the first explored and older fossiliferous level of Chomateri. The dental terminology is after Tassy (1996). Measurements were taken with a digital caliper and are given in mm (Table 1). Comparative material has been studied in AMPG, FSL, HGI, HLMD, ML, MNHN, SMF and SNSB-BSPG. The studied juvenile material of *Anancus arvernensis* originates from the French localities Montpellier (MN 14; FSL), Perrier-les-Étouaires (MN 16, FSL, MNHN) and St. Vallier (MN 17; ML).

Institutional Abbreviations—**AMPG**, Athens Museum of Palaeontology and Geology (Greece); **FSL**, Faculté des Sciences de Lyon (France); **HGI**, Hungarian Geological Institute (Budapest); **HLMD**, Hessisches Landesmuseum Darmstadt (Germany); **ML**, Musée des Confluences, Lyon (France); **NHMW**, Naturhistorisches Museum Wien (Austria); **MNHN**, Muséum National d’Histoire Naturelle (Paris, France); **SMF**, Senckenberg Museum Frankfurt am Main (Germany); **SNSB-BSPG**, Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie (Munich, Germany).

Anatomical Abbreviations—**apocc**, anterior posttrite central conule; **aprcc**, anterior pretrite central conule; **dp/DP**, lower/upper deciduous premolars; **m/M**, lower/upper molars; **ppocc**, posterior posttrite central conule; **pprcc**, posterior pretrite central conule (e.g., pprcc1, posterior pretrite central conule of the first loph[id]).

SYSTEMATIC PALEONTOLOGY

Order PROBOSCIDEA Illiger, 1811

Superfamily ELEPHANTOIDEA Gray, 1821

Family GOMPHOTHERIIDAE Hay, 1922

Subfamily ANANCINAE Hay, 1922

Genus *ANANCUS* Aymard in Dorlhac, 1855

Diagnosis—(according to Tassy, 1986; Hautier et al., 2009). Gomphothere with a high and short skull. Elevated dome. Enlarged tympanic bulla. Short mandible without tusks. Straight upper tusks without enamel. Loss of premolars (retained in *A. kenyensis*). Tetralophodont (to pentalophodont in some species) intermediate molars. Reduced posterior pretrite central conules on upper molars and anterior pretrite central conules on lower molars. Dislocation of the pretrite and posttrite half-loph(id)s and alternate arrangement of the successive loph(id)s.

Type Species—*Anancus arvernensis* (Croizet and Jobert, 1828), Pliocene–early Pleistocene of Europe.

Type Locality—Perrier-les-Étouaires, France (late Pliocene, MN 16).

Lectotype—Right maxilla fragment with DP2–DP3, MNHN-A.C. 1830 coll. Croizet.

ANANCUS LEHMANNI (Gaziry, 1997)

(Fig. 2)

Mastodon cf. *longirostris* Kaup, 1832: Schlosser, 1907:2, pl. 1, figs. 28, 29.

Mastodon longirostris Kaup, 1832: Schlosser, 1921:12.

Mastodon (Bunolophodon) longirostris Kaup, 1832 - *Mastodon (Anancus)*

arvernensis (Croizet and Jobert, 1828): Zapfe, 1957:392, pl. 24, figs. 1, 2, pl.

25, figs. 1–3, pl. 26, pl. 27.

Trilophodon (Choerolophodon) pentelicus var. *minor* Bergounioux and Crouzel,

1958:318, pl. 59, fig. a.

Mastodon pentelicus Gaudry and Lartet, 1856: Marinos and Symeonidis 1972:164, pl.

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Mastodon pentelicus Gaudry and Lartet, 1856: Marinos and Symeonidis 1974:7, pl. 7.

Tetralophodon longirostris Kaup, 1832: Franzen and Storch 1975:255, pl. 8, fig. 71.

Tetralophodon longirostris Kaup, 1832: Mazo, 1981:173: pl. 1, figs. 1, 2.

cf. *Anancus arvernensis* (Croizet and Jobert, 1828): Mazo, 1981:179: pl. 1, figs. 5, 6.

Anancus arvernensis tuoliensis Gaziry, 1997:83, pl. 2, figs. 1, 2.

Stegotetrabelodon lehmanni Gaziry, 1997:85, pl. 3, figs. 1–3, pl. 4, fig. 4.

Tetralophodon longirostris Kaup, 1832: Gaziry, 1997:77, pl. 1, figs. 2, 3.

Anancus arvernensis (Croizet and Jobert, 1828): Montoya et al., 2002:19, pl. 2, fig. 6.

Anancus sp. Spassov and Geraads, 2008:3, fig. 3.

Anancus sp. Spassov et al., 2012:140.

Holotype—Right M3, SMF-DD 3151 (Gaziry, 1997:pl. 3, fig. 3).

Type Locality—Dorn-Dürkheim 1, Germany.

Age and Occurrence—Middle-late Turolian (late Miocene) of western Eurasia.

Diagnosis—Anancine with trilophodont third deciduous premolars and tetralophodont intermediate molars. Third molars with 5 (to 6) loph(id)s. Brachyodont intermediate molars and third molars. Thick and unfolded to coarsely folded enamel on the molars. Weak anancoidy and simple occlusal morphology. Upper tusks sub-parallel, straight, downturned and lacking enamel. Premaxillae parallel and straight. Orbit above the dentition. Tuskless mandibular symphysis, longer than other anancines.

Locality—Chomateri (Kisdari), Attica, Greece; Pikermi Formation (Böhme et al., 2017).

Age—Middle Turolian, MN 12 (late Miocene), ~7.2 Ma (Böhme et al., 2017).

Material—Right maxilla fragment with DP2–DP4, AMPG-13II/1972; left dp4, NHMW-1972/1567.

Description

The DP2 is strongly worn and damaged, so that its exact morphology cannot be observed (Fig. 2A–C). It is formed of two lophs; the protoloph is higher. Loph 2 is separated from the first one and it seems to be broader. It had probably a distal cingulum, which however, is not clearly visible.

The DP3 is trilophodont with a mesial and distal cingulum (Fig. 2A–C). It is much worn, especially in loph 1, and the enamel of the lateral walls is damaged. The mesial cingulum is not clearly visible; it connects through a ‘dentine channel’ with the first pretrite half-loph. In loph 1, the half-lophs are placed the one opposite to the

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3 other, but the mesoconelts cannot be distinguished. In the first transverse valley the
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5 ppoccl is connected with the aprcc2. In the labial side of the valley, one more but
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7 weaker posterior central conule of the first loph is located. Lingually in the valley
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9 there is one low conelet, possibly a remnant of a lingual cingulum. In loph 2, the
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11 pretrite half-loph is more mesially located than the the posttrite one. Cusp
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13 morphology is not visible due the wear. In the second transverse valley there is
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15 posttrite-pretrite connection of the half-lophs. The posttrite half-loph of loph 3 is
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17 partly damaged. The distal cingulum consists of several conelets; it does not continue
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19 in the labial wall of loph 3. The enamel is strongly folded (a trait of deciduous teeth).
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22 The DP4 is almost unworn (Fig. 2A–C). The enamel is damaged and partly
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24 missing from lateral walls. The tooth is tetralophodont with a mesial and distal
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26 cingulum. The mesial cingulum is composed of conelets, which increase in height and
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28 strength from the labial towards the lingual side, until it connects to the first pretrite
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30 half-loph. In the mesiolingual part the cingulum continues with some weaker and
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32 lower conelets. In loph 1, the half-lophs are situated the one opposite to the other,
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34 whereas in the lophs 2 and 3 the pretrite half-lophs are slightly more mesially located.
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36 The posttrite half-lophs are comprised of the main cusp and two mesoconelets
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38 attached to each other. The pretrite half-lophs consist of the main cusp and from one
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40 to two mesoconelts, apart from the loph 1 where they are absent. Almost in the middle
41
42 of the transverse valleys an alternating connection of the successive lophs is
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44 established, between the posterior and weaker posttrite central conules and the
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46 anterior and stronger pretrite ones. In the lingual side of the transverse valleys there is
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48 one low conelet, stronger in the first and second valley. The distal cingulum consists
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50 of four rather strong and of equal height conelets arranged in a row.
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3 The dp4 is damaged in several parts; however, its overall morphology can be
4 well observed (Fig. 2D–F). It is tetralophodont with a mesial and distal cingulum. The
5 roots are also preserved, of which the distal one is clearly larger. The mesial cingulum
6 is broken, but a conelet is visible in the mesial part of the protoconid. In lophid 1, the
7 half-lophids are almost aligned. In lophids 2 and 3, the pretrite half-lophids are more
8 distally located compared to the posttrite ones, and in lophid 4 a weak ‘chevron’
9 structure is formed. In the transverse valleys there is alternating contact of the pprcc’s
10 with the apoccs. The distal cingulum consists of two conelets situated in the middle;
11 the posttrite one is stronger. The enamel is wrinkled.
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24 Comparison

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26 AMPG-13II/1972 was illustrated without further description by Marinos and
27 Symeonidis (1972, 1974), who attributed it to ‘*Mastodon pentelicus*’ (= *Choerolophodon pentelici*). However, the clearly formed third loph in the DP3 and
28 the four lophs in the DP4 exclude an allocation to the trilophodont *Choerolophodon*
29 and indicate an elephantoid of tetralophodont grade.
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37 The DP2 is not well preserved so that a comparison is not feasible. Although
38 the Chomateri DP3 is much worn, it reveals certain differences with those of the
39 tetralophodont amebelodontine *Konobelodon atticus* from Pikermi (AMPG-
40 PA3933/91, SNSB-BSPG-AS II 182, MNHN-PIK-1704a) (Fig. 3A–B, Konidaris et
41 al., 2014:figs. 2a, b, 3p). In *K. atticus*, although there is alternating contact (posttrite-
42 pretrite) between the successive lophs, the dislocation of the half-lophs in loph 2 is
43 very weak, the main cusps are placed almost the one opposite to the other, and the
44 interlophs (transverse valleys) are almost straight (Fig. 3A–B). In contrast, in the
45 Chomateri specimen there is a significant dislocation in loph 2 and the interlophs
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(especially the first one) have a rather sigmoid form (Fig. 3D). Metrically, the DP3 from Chomateri is smaller than the known *K. atticus* specimens (Fig. 3H). The DP3s of *Tetralophodon longirostris* from Eppelsheim (Germany; Kaup, 1835:pl. 17, fig. 12), Laaerberg (Austria; Schlesinger, 1917:pl. 12, fig. 1) and Azambujeira (Portugal; Antunes and Mazo, 1983:pl.1 fig. 6) present a slight dislocation in the second loph, however, less than the Chomateri one, and are of smaller size (Fig. 3C, H). Similar dislocation (second pretrite half-loph mesially offset and in contact with the first posttrite half-loph in loph 2) exhibit the specimens of *Anancus* from Concud (Spain; Mazo, 1981), Middle Awash-Kuseralee Mb. (Ethiopia; Saegusa and Haile-Selassie, 2009), Montpellier and Perrier-les-Étouaires (France; FSL-40462, FSL-211225, MNHN-A.C. 1830, nn; Metz-Muller, 1996) (Fig. 3F–G). Among these specimens, the Montpellier and Perrier-les-Étouaires ones are characterized by a more complicated occlusal morphology with multiplication of the accessory cusplets, whereas the Chomateri, Concud and Middle Awash ones are simpler. Metrically, the DP3 from Chomateri is slightly shorter than that from Concud, slightly longer than the Montpellier one and presents equal length with the specimen from Middle Awash (Fig. 3H); the precise width of the Chomateri specimen cannot be measured due to its damaged lateral walls.

In the DP4 of *Konobelodon atticus* (e.g., AMPG-PA3933/91 from Pikermi and MNHN-MAR-4009 from Maragheh), as well as of *Tetralophodon longirostris* from Eppelsheim (Kaup, 1835:pl. 16, fig. 1; pl. 17, figs., 13, 14) and Laaerberg (Schlesinger, 1917:pl. 12, fig. 1), the contact between the successive lophs is accomplished through the anterior and posterior central conules of the pretrite half-lophs (pretrite-pretrite contact). On the contrary, in the Chomateri DP4 there is alternating contact (posttrite-pretrite) between the ppoc's and aprcc's (Fig. 4A–B, E).

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3 In this aspect, it is similar with the DP4 of *Anancus* from Venta del Moro (Spain;
4 Montoya et al., 2002) and that of *A. arvernensis* MNHN-nn from Perrier-les-Étouaires
5 (Fig. 4C). The Perrier-les-Étouaires specimen shows also weak dislocation of the half-
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7 lophs as the Chomateri one, but it characterized by a more complicated occlusal
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9 morphology with multiplication of accessory cusplets. Moreover, pprcc's are absent
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11 in the Chomateri specimen, like the Perrier-les-Étouaires one. The DP4 from the Apak
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13 Mb. of Lothagam (5.0–4.2 Ma; Kenya) shows more complex morphology and
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15 outlined fifth loph accompanied by distal cingulum (Tassy, 2003). This tooth was
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17 originally attributed to *A. kenyensis*, but all the anancine material from this
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19 stratigraphic unit of Lukeino was transferred to *A. ultimus* (Sanders, 2011).
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24 In the Chomateri dp4 the more distal location of the pretrite half-lophids and
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26 the alternating contact (pretrite-posttrite) between the half-lophids are typical *Anancus*
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28 features, similar to the dp4s of *A. arvernensis* from Dorkovo (Metz-Muller, 2000:pl.
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30 11, fig. 5), St. Vallier (France; ML-164218; Guérin, 2004), Liventsovka (Russia;
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32 Titov, 2008), and of *A. osiris* Arambourg, 1945, from Ahl al Oughlam (Morocco;
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34 Geraads and Metz-Muller, 1999); however, the dislocation of the half-lophids is more
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36 expressed in the St. Vallier and Liventsovka dp4s, and the morphology is more
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38 complex in the Dorkovo, St. Vallier and Ahl al Oughlam ones. In contrast to the
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40 dislocation of all former specimens, in the dp4s of *K. atticus* from Pikermi (AMPG-
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42 PA3708/91) and Cimişlia (Moldavia; Simionescu and Barbu, 1939:fig. 3, pl. 1, fig. 3)
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44 the three mesial lophids are almost aligned and the contacts are pretrite-pretrite (Fig.
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46 5A–B). Moreover, although the robustness index in the Pikermi and Chomateri dp4s
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48 is the same (49.8), the hypsodonty index in the Pikermi dp4 (96.9; Konidaris et al.,
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50 2014:tab. 2) is much higher than in the Chomateri one (76.7) (Table 1). The dp4s of
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52 *Tetralophodon longirostris* from Rudabánya (Hungary) differ in the absence of
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3 anancoidy and in the oblique arrangement of the second and third lophids (Gasparik,
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5 2005). Metrically, the Chomateri specimen is larger than *T. longirostris* from
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7 Rudabánya and slightly larger than *K. atticus* from Pikermi (Fig. 5E). It is longer than
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9 *Anancus* from Ahl al Oughlam and is placed within the size range of *A. arvernensis*
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11 from Dorkovo, which presents a wide metrical variability.
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14 The clear similarities of the Chomateri DP3, DP4 and dp4 with *Anancus* allow
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16 the attribution to this genus. The differences with corresponding specimens of *A.*
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18 *arvernensis* from the Pliocene and Pleistocene of Europe could imply a possible
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20 attribution to a distinct species. In the subsequent chapter, we will examine the
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22 taxonomy of the Turolian anancines from Europe, aiming to clarify the taxonomical
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24 status of the Chomateri specimens.
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28 29 TAXONOMICAL REMARKS AND REAPPRAISAL OF THE LATE MIOCENE 30 31 ANANCINES FROM EUROPE 32 33 34

35 Anancine gomphotheres, represented by the single genus *Anancus*, have
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37 tetralophodont (to pentalophodont) intermediate molars, whose main morphological
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39 feature is the dislocation of the pretrite and posttrite half-loph(id)s and the resultant
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41 alternate arrangement of the successive loph(id)s (anancoidy). In particular, in upper
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43 molars the pretrite half-lophs are mesially offset, whereas in lower molars the pretrite
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45 half-lophids are distally dislocated, establishing thus an alternate contact of the
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47 successive loph(id)s (Tassy, 1986). Other anancine characters include the high and
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49 short cranium with domed and elevated vault, the enlarged tympanic bullae, the
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51 brevirostrine mandible without tusks, the straight upper tusks lacking enamel and the
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53 absence of premolars, except in *A. kenyensis* (Tassy, 1986; Hautier et al., 2009).
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3 Although *Anancus* flourished during the Pliocene until the early Pleistocene of the
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5 Old World, its earliest occurrences are traced during the Turolian (late Miocene),
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7 when it derived possibly from an Asian tetralophodont ancestor, and was
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9 subsequently dispersed and distributed across three continents (see below).
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11 Tassy (1986) included the species *A. perimensis* (Falconer and Cautley, 1847)
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13 from India and Pakistan, *A. cuneatus* (Teilhard de Chardin and Trassaert, 1937) /
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15 *paisuyensis* Hsieh, 1962, from China (both synonymized with the Pliocene *A. sinensis*
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17 [Hopwood, 1935] by Tobien et al., 1988 and Metz-Muller, 2000) and the late
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19 Miocene European *Anancus* sp. in a paraphyletic group, which does not exhibit the
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21 derived *Anancus* features. Metz-Muller (2000) studied the phylogenetic relationships
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23 among the anancine species and proposed two groups: (1) primitive group,
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25 comprising of *A. perimensis* from the late Miocene of south-central Asia, *A.*
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27 *kazakhstanensis* Aubekerova, 1974, from the Pliocene of Kazakhstan (considered
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29 possibly synonymous of either *A. arvernensis* or *A. sinensis* in Shoshani and Tassy,
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31 1996:app. C.1), and the specimens from Hohenwarth (Austria, Turolian; Zapfe, 1957)
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33 and Dorn-Dürkheim 1 (Germany, Turolian; Gaziry, 1997), and (2) advanced group,
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35 including all the other anancine species. The primitive group is characterized by an
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37 initial alternate arrangement of the half-loph(id)s in the molars and by an established
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39 contact between the successive pretrite and posttrite half-loph(id)s, although in some
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41 specimens a pretrite-pretrite contact is still retained; the advanced group shares all the
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43 diagnostic features of the genus (Metz-Muller, 2000).
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48 The late Miocene specimens of *Anancus* from Europe are limited and of
49
50 problematic taxonomical status at specific level. Tassy (1986) and Markov (2008)
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52 mentioned that it is possible among this sample to exist more than one species.
53
54 However, recent studies prove the high morphological variability within *Anancus*
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populations or even between the upper and lower molars of the same individual, which might display a mixture of primitive/derived dental characters (Metz-Muller, 2000; Saegusa and Hlusko, 2007; Saegusa and Haile-Selassie, 2009; Hautier et al., 2009). Thus, as was mentioned by Markov (2014) the inclusion of all Turolian anancines from Europe to a single species, although tentative, seems plausible. Nonetheless, even when indeed we consider a single species, there are several nomenclatural issues concerning the appropriate name to refer to the Turolian anancines from Europe. Crucial in this aspect is the rather rich material from Dorn-Dürkheim 1 (Germany), which, unfortunately consists only of isolated teeth. Apart from the deinotheres, which were attributed to *Deinotherium proavum* and further confirmed the Turolian age of the locality (Pickford and Pourabrishami, 2013), Gaziry (1997) studied the elephantoids and described four taxa: *Tetralophodon longirostris*, *Anancus arvernensis turoliensis*, *Stegotetrabelodon lehmanni* and *Stegolophodon caementifer*; the second one as new subspecies and the latter two as new species. The Dorn-Dürkheim 1 elephantoids need a complete revision, but several observations on the anancines are included in this article. In agreement with Gaziry (1997), the dental morphology of the Dorn-Dürkheim 1 anancine is more primitive than *A. arvernensis*, indicating a distinct taxon. However, apart from the material referred by this author to ‘*A. a. turoliensis*’, we include here also to *Anancus* the holotype of *S. lehmanni* and other specimens attributed to this species, as well as specimens of *T. longirostris* (synonymy list; cf. Metz-Muller, 2000 and Markov, 2008). The species name ‘*lehmanni*’ has nomenclatural priority over the subspecies name ‘*turoliensis*’ due to its original higher taxonomical ranking (Markov, 2008; article 24.1 of the code of the International Commission on Zoological Nomenclature (ICZN): Automatic determination of precedence of names: When homonyms or synonyms are established

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2
3 simultaneously, but proposed at different ranks, in the family group, genus group or
4 species group, the name proposed at higher rank takes precedence). Therefore, even if
5
6 not all Turolian anancines from Europe belong to this species, the anancine material
7
8 from Dorn-Dürkheim 1, at least, should be referred to *A. lehmanni*.
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10

11 12 13 **Comparison of the Mandible, Cranium and Tusks** 14

15
16 Except of the less expressed anancoidy on the intermediate and third molars of
17
18 the late Miocene anancines from Europe (examined below), cranial and mandibular
19
20 features distinguish them from the later and more derived representatives.
21

22 A feature that has to be considered is the length of the mandibular symphysis. Two
23
24 specimens are crucial in this aspect. The first one is a tuskless mandible from
25
26 Hohenwarth (Austria; Fig. 6A) preserving the heavily worn m1s, the m2s in function
27
28 and the m3s inside the bone (age class 9, according to the categories of Metz-Muller,
29
30 2000), associated with a cranial fragment bearing upper tusks (Fig. 7B), the strongly
31
32 worn M1, the left partial M2 and the partial M3s. This specimen was described by
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34 Zapfe (1957), who considered it as an intermediate form between *Tetralophodon*
35
36 *longirostris* and *Anancus arvernensis*. The mandibular symphysis is longer than *A.*
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38 *arvernensis*, but certainly not of the longirostrine condition of *T. longirostris*, e.g.,
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40 from Eppelsheim, Esselborn, Bermersheim (Germany), Laarberg, Kornberg (Austria)
41
42 and Polinyá (Spain) (Fig. 6; see also Mottl, 1969:pl. 13, 14, and Alberdi, 1971), which
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44 moreover either preserve the lower tusks or their alveoli. Although the European
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46 *Tetralophodon* sample is characterized by an evident variability in the morphology
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48 and size of the symphysis and the lower tusks (attributed to polymorphism of *T.*
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50 *longirostris* by Tassy, 1985), all of the known specimens have long symphysis
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52 equipped with tusks (Fig. 6). Therefore, the Hohenwarth mandible, with anancoidy on
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the m2 (see below), is clearly different from *Tetralophodon*; its shorter and tuskless mandibular symphysis, combined with anancoid molars, cannot be attributed to intraspecific variability/sexual dimorphism of *T. longirostris*. The Hohenwarth mandible is also different from those of other late Miocene tetralophodonts *Stegotetrabelodon* and *Konobelodon*, both having elongated symphyses bearing long lower tusks (Sanders et al., 2010; Konidaris et al., 2014). On the other hand, the anancoidy on the molars (even if initial), the straight upper tusks, the absence of lower tusks or alveolus and the relatively high position of the mandibular angle place the specimen to *Anancus* (Figs. 5, 6; Tassy, 1985, 1986). Nonetheless, the Hohenwarth specimen differs from *A. arvernensis* from Dorkovo (MN 14, Bulgaria; e.g., the close in ontogenetic age mandibles DKV246 [age class 8] and DKV159 [age class 9]) in Fig. 6; Metz-Muller, 2000) and Valdarno (Italy; Metz-Muller, 2000:pl. 28; Rook et al., 2013:figs. 3, 9), and *A. kenyensis* (MacInnes, 1942) from Toros-Menalla (Chad; Hautier et al., 2009), Tugen Hills-Lukeino Fm. (Kenya; Tassy, 1986), Lemudong'o (Kenya; Saegusa and Hlusko, 2007) and Middle Awash-Kuseralee Mb. (Ethiopia; Saegusa and Haille-Selassie, 2009), which show a shorter symphysis, higher ramus with high position of the condyle compared to the coronoid process, and more elevated position of the mandibular angle. All these features of the Hohenwarth mandible are well consistent with a more primitive anancine. Unfortunately, the morphology of the mandibular symphysis of *A. perimensis* is unknown, because the two isolated symphyses from Punjab, attributed to "*Mastodon perimensis*" by Lydekker (1880:pl. 43), one without tusks and the other one with cross-sectioned small tusks, are not directly associated with teeth.

The second mandibular specimen, recognized also as a transitional form between *T. longirostris* and *A. arvernensis* by Schlosser (1907), and subsequently by

Schlesinger (1917:131), Klähn (1922:109) and Lehmann (1950:216), concerns a mandible (the presence of tusks was questioned by Lehmann, 1950) bearing the second molars, the upper tusks and the second upper molars from Cueva Rubbia (Teruel, Spain), which according to Alcalá (1994) and Mazo and van der Made (2012) corresponds to Barranco de las Calaveras, Concud (MN 12). Originally stored at the Munich collection, this material was probably destroyed during World War II. Unfortunately, the complete specimen was never figured, but thanks to the descriptions and the illustrations of the teeth, we can get fairly adequate information. The molars showed an anancoid pattern and the upper tusks were rather straight (Figs. 4D, 5C; Schlosser, 1907; Lehmann, 1950). The anterior part of the mandibular symphysis was broken, but according to Schlosser (1907) the symphysis was shorter than that of the holotype of *T. longirostris* from Eppelsheim (Fig. 6J, K) and longer than *A. arvernensis* from Valdarno (Italy; apparently Schlosser refers to the specimens described by Nesti in 1808 and 1825, see Rook et al., 2013). Therefore, it seems plausible to assume that the Concud mandible was not the longirostrine type of *T. longirostris*, but also not the brevirostrine type of *A. arvernensis*.

Concerning the cranial morphology, the only specimen is the cranial fragment from Hohenwarth, associated with the above discussed mandible. In this specimen, the premaxillary tusk alveoli are parallel, the tusks sub-parallel and almost straight, and the orbit is located above the M2 (Fig. 7B). In *A. arvernensis* and *A. kenyensis*, both premaxillae and tusks are laterally divergent (although the degree of divergence is variable), and the orbit is more anteriorly located (Fig. 7C; Weithofer, 1890; Tassy, 1986; Boeuf, 1992; Hautier et al., 2009; Metz-Muller, 2000:pl. 27, 28). In these features, the Hohenwarth specimen is closer to *A. perimensis* (Fig. 7A), which additionally differs from other anancines in the redressment of the basicranium and

the less elevated cranial vault (Falconer and Cautley, 1846:pl. 38, 39, 43, 45; Tobien, 1978:figs. 1–3; Tassy, 1986:fig. 35).

Comparison of the Dentition

A comparison of the m2 from Concud and Hohenwarth (Fig. 5C–D; both belonging to the above discussed mandibles), as well as from Los Mansuetos (Spain; Mazo, 1981:fig. 2), reveals great similarities, indicating that they are most possibly conspecific. Similar are also the M2 from Concud (Fig. 4D) with the M2s SMF-DD 1 (Franzen and Storch, 1975), SMF-DD 3142 and SMF-DD 5362a (DD 1 and DD 5362a are regarded as M1 in Gaziry, 1997) of *A. lehmanni* from Dorn-Dürkheim 1, as well as the fragmentary M3 from Hohenwarth with the M3s of the holotypes of ‘*Stegotetrabelodon lehmanni*’ and ‘*Anancus arvernensis turoliensis*’ from Dorn-Dürkheim 1 (Gaziry, 1997). The holotype of ‘*Stegotetrabelodon lehmanni*’ shows a slightly more complicated morphology (as does the morphological similar SMF-DD 46) than the holotype of ‘*Anancus arvernensis turoliensis*’; however, not a complex one as was quantified by Metz-Muller (1995), and the arrangement of the mesoconelets and central conules is similar between them. Overall, the molar material from Concud, Los Mansuetos, Dorn-Dürkheim 1 and Hohenwarth is characterized by (1) weak anancoidy (involving the pprcc’s and the posttrite mesoconelets in the lower dentition; the ppoccc’s and the aprcc’s in the upper dentition, in Dorn-Dürkheim 1 variably also the posttrite mesoconelets and the aprcc’s or pretrite-pretrite contact in some lophs), (2) rather simple occlusal morphology, (3) absence of aprcc on the lower molars and reduction/absence of pprcc in the upper molars, (4) thick and unfolded (or coarse) enamel, and (5) 5 (to 6) loph(id)s in the third molars, with most of these features regarded as primitive within anancines (Table 2; Metz-Muller, 2000; Sanders,

2007, 2011). Based on the high morphological variability within *Anancus* populations, minor differences (e.g., presence of some accessory conelets) among the European sample, are regarded as intraspecific variability. Therefore, all this material can be attributed to the same species: *A. lehmanni*. The comparison of the anancine deciduous dentition was conducted in the previous section. The only deciduous teeth from the Turolian of Europe are those of Chomateri, the DP3 from Concud and the DP4 from Vental del Moro (SMF-DD 3145 from Dorn-Dürkheim 1 is regarded here as a M1). However, the comparison of the Chomateri dp4/DP4 with other intermediate molars from Concud, Los Mansuetos, Dorn-Dürkheim 1 and Hohenwarth (see also Figs. 4B–D, 5B, D) indicates that except of the thinner and folded enamel (juvenile characters), they are similar in features (1)–(3), and therefore can be regarded as conspecific, belonging therefore to *A. lehmanni*.

Taxonomic Conclusions

All the above comparisons indicate that the late Miocene anancines from Europe are well distinguished from the roughly contemporaneous, but more derived *A. kenyensis*, and the Plio–Pleistocene *A. arvernensis*, as well as from other anancines, in the morphology of the mandible (length of symphysis, position of the mandibular angle and of the condyles), the cranium (premaxillae, position of the orbit), the upper tusks (running almost parallel) and the cheek teeth (weak anancoidy, simple occlusal morphology). The combination of the above traits is unique among anancines and permits the distinction at the species level. Although we acknowledge the difficulty to discriminate isolated dental findings independent from accompanying fauna and biostratigraphy, and thus taxonomical/biochronological conclusions based on a small sample of isolated teeth should be taken with caution, we believe that late

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3 Miocene anancines from Europe should be recognized as a species in their own right,
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5 distinct from *A. arvernensis* and other anancines, which, following the proposal of
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7 Markov (2008) is *A. lehmanni*. This species and *A. perimensis* are characterized by
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9 their primitive stage in all of their examined dental features (Table 2) and they share
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11 also some cranial features. Taken also into consideration their late Miocene age (see
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13 following section), they represent the most basal species among anancines. The
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15 discovery of cranial and mandibular material from *A. lehmanni* and *A. perimensis*,
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17 respectively, as well as the complete revision of all their known material, will help to
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19 clarify their relationships.
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24 BIOGEOGRAPHY AND BIOSTRATIGRAPHY OF THE LATE MIOCENE 25 26 ANANCINES 27 28 29 30

31 The oldest records of anancine gomphotheres are documented in Asia from
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33 Perim Island, Haritalyangar (India) and the Potwar Plateau (Pakistan) (Figs. 8, 9).
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35 From the Potwar Plateau *A. perimensis* is known from the Dhok Pathan Fm. of
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37 Middle Siwaliks, which dates between 9.8 and ~3.5 Ma; however, most of the
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39 localities belong to its lower part and until 6.0 Ma (Tassy, 1983a, 1983b; Barry et al.,
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41 2013). In Haritalyangar section, the oldest reported site is dated to ~10.1 Ma, the
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43 majority of the fossils to the interval 9.3–8.1 Ma (correlated to the lower part of the
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45 Dhok Pathan Fm of the Potwar Plateau) and the mammal occurrences do not extend to
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47 sediments younger than 7.0 Ma; proboscideans including *Anancus* are recorded from
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49 8.6–8.1 Ma (Pillans et al., 2005; Flynn et al., 2013:357; Patnaik, 2013:430, 438). The
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51 dating of Perim Island (type locality of *A. perimensis*) is more problematic. Tobien
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53 (1978) and Tassy (1983a, 1983b) consider a correlation to the Dhok Pathan Fm.,
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Pickford and Pourabrishami (2013) to the European middle Turolian (MN 12), and Patnaik (2016) assumes an age between 10.0 and 9.0 Ma. A primitive anancine comparable to *A. perimensis* is also reported from the Irrawaddy sediments of Myanmar (Saegusa et al., 2014), so that a distribution towards Indochina is possible for the species.

Further to the east (Figs. 8, 9), the first appearance of *Anancus* in China is traced within and towards the end the Baodean Land Mammal Stage/Age (~7.1–5.3 Ma) (Qiu et al., 2013:65, fig. 1.7b). In this stage *Anancus* is known from Licent's Loc. 32 (Dongzhuang, Yushe Basin, Shanxi Province), located in the basal part of the Gaozhuang Fm, dated at ~5.8 Ma (Qiu et al., 2013:fig. 1.6). *Anancus paisuyensis* from Nan-ho Village, Pai-Sui-Hsian (Shanxi Province; Hsieh, 1962) could potentially originate also from this stage, because it is possibly correlated to the European Turolian (Tobien et al., 1988); however, no recent data are available. *Anancus cuneatus* was described by Teilhard de Chardin and Trassaert (1937) from Loc. 27 (Shencun) and 4 (Zhaozhuang) in the Yushe Basin of Shanxi Province. Both localities are correlated to the European Ruscinian (Pliocene) by Tobien et al. (1988). Loc. 4 is situated in the basal part of the Mazegou Fm, whose lower boundary is dated at ~3.7 Ma and thus is indeed of Pliocene age (Qiu et al., 2013:fig. 1.6). Pending revision of the Chinese material, we include all the anancines from China to *A. sinensis* as was proposed by Tobien et al. (1988) and Metz-Muller (2000).

In western Eurasia (Fig. 8), Dorn-Dürkheim 1 is correlated to the early Turolian, MN 11 (Franzen et al., 2013). Based on the presence of *Anancus*, Gaziry (1997), Metz-Muller (2000), Markov (2008) and Pickford and Pourabrishami (2013) proposed a middle–late Turolian age (MN 12–MN 13) for the proboscideans. Spassov et al. (2006, 2012) considered possible reworking of the Dorn-Dürkheim 1 material, a

case that should be considered in light of recent studies in the Eppelsheim Fm. (Dinotheriensande) of the Mainz Basin (Böhme et al., 2012; Pickford and Pourabrisham, 2013) and the biostratigraphic record from other European *Anancus*-bearing localities, which all imply a later than early Turolian appearance of this genus (Fig. 8). The current data indicate that late Miocene anancines were well distributed during the second half of the Turolian (e.g., Concud, Los Mansuetos, Azmaka, Chomateri) and during MN 13 (e.g., Venta del Moro) (Gasparik, 2001; Markov, 2008; Mazo and van der Made, 2012; Spassov et al., 2012). Concerning Hohenwarth, the presence of a very large deinother (Zapfe, 1957; Huttunen, 2002), i.e., *D. proavum*, clearly indicates a Turolian age. Hohenwarth belongs to the upper part of the Hollabrunn-Mistelbach Fm. (late Miocene) of the North Alpine Foreland Basin and is correlated with the upper Pannonian of the Central Paratethys regional stratigraphy (Roetzel et al. 1999; Harzhauser et al. 2004; Nehyba & Roetzel 2004). Although the top of the Pannonian is controversial (Piller et al., 2007), a correlation of the locality close to the Tortonian/Messinian boundary or to the Messinian, and therefore MN 12 or MN 13 (Bernor et al., 2017) is possible for the Hohenwarth anancine.

In the Southern Balkans *Anancus* is absent in the fossil-rich middle Turolian (MN 12) locality Pikermi (Konidaris, 2013), dated to ~7.3 Ma (Böhme et al., 2017), as well as in pre-Pikermian sites such as Hadjidimovo (Bulgaria), correlated to the beginning of MN 12 (Spassov, 2002; Markov, 2008). The earliest occurrences of *Anancus* with the species *A. lehmanni* are traced at Azmaka and Chomateri at ~7.2 Ma, followed by the records Concud and Los Mansuetos at ~7.1 Ma (van Dam et al., 2006:sup.; Böhme et al., 2017) (Fig. 8). The so far known latest occurrence of *A. lehmanni* is traced in Venta del Moro at ~6.2 Ma (Gibert et al., 2013). The replacement of *A. lehmanni* by *A. arvernensis* is vague (Markov et al., 2014). The

latter species is present at Dorkovo (Bulgaria), correlated to the early Ruscinian (MN 14, early Pliocene; Thomas et al., 1986; Spassov, 2005). Therefore, the replacement might have occurred at the end of the late Miocene or the beginning of the early Pliocene. *Anancus* is referred from several Bulgarian localities (e.g., Hrabarsko, Staniantzi, Lozents) correlated to the Turolian/Ruscinian (Miocene/Pliocene) boundary (Spassov, 2002, 2005), which could provide data on this issue. From Staniantzi in particular, dated to 5.8–5.35 Ma, a mandible bearing the m3s is attributed to *Anancus* sp.; this occurrence could represent the last record of *A. lehmanni* or the first one of *A. arvernensis*, considering the transitional character of the fauna and the presence of Ruscinian immigrants (Böhme et al., 2013; Markov et al. 2014).

The presence of *Anancus* in Chomateri indicates that the locality post-dates Pikermi, because in the rich vertebrate collections of Pikermi with several proboscidean specimens *Anancus* is absent, whereas in the far smaller Chomateri collections the two only known proboscidean specimens belong to this genus. The age difference between Pikermi (MN 12) and Chomateri should be rather narrow taking into account their overall faunal similarity, and their differences with the late Turolian (MN 13) fauna from the Dytiko localities (Axios valley; Greece), which are regarded pre-Messinian-Salinity-Crisis in age (Koufos, 2013; Koufos and Vassileiadou, 2015). Thus, a correlation to the end of MN 12/beginning of MN 13 (the top of MN 12 is controversial) is possible for Chomateri, in agreement with the dating of the locality (Böhme et al., 2017). This period corresponds in the Eastern Mediterranean region (Southern Balkans and Turkey) to the collapse of the ‘Pikermian’ (middle Turolian) large mammal fauna, at the Tortonian/Messinian boundary (~7.2 Ma), when an important faunal renewal took place in the mammal record coinciding with the

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3 aridification and cooling of the Mediterranean (Kostopoulos, 2009; Böhme et al.,
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5 2017). A faunal turnover based on the micromammal record is also reported at ~7.2–
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7 7.0 Ma in the western Mediterranean region (van Dam and Weltje, 1999; Agustí et al.,
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9 2006, van Dam et al., 2006). As part of this event and the reorganizations of the
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11 faunas in Europe, *Anancus* of Asian origin, is a newcomer in the European mammal
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13 communities.
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15 At around that time or slightly later, *Anancus* migrated to Africa (Figs. 8, 9)
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17 leading to *A. kenyensis* in Eastern and Central Africa (Toros-Menalla, Chad and
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19 Tugen Hills, Kenya dated to ~7.0–6.0 Ma, and Lothagam-Lower Mb. of the Nawata
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21 Fm., Kenya, dated 7.4–6.5 Ma [Sanders et al., 2010 and references cited therein]).
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23 This southern migration of *Anancus* was possibly facilitated by the draught of the
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25 Mediterranean Sea during the late Miocene, when new land bridges were formed
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27 between Northern Africa and Eurasia (e.g., Gibraltar Strait, Gulf of Aden) enabling
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29 faunal exchanges (Kalb et al., 1996; Rögl, 1999; Metz-Muller, 2000; Sanders et al.,
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31 2010). The age calibration for the onset of this ecological crisis (Messinian salinity
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33 crisis) is recently refined at 5.97 Ma (Manzi et al., 2013); however, a first restriction
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35 of the Mediterranean-Atlantic water exchange is likely at ~8.5 Ma, followed by
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37 significant restrictions at 7.16 and 6.7 Ma (Seidenkrantz et al., 2000; Roveri et al.,
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39 2014).
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46 CONCLUSIONS

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50 Previously known only from the Pliocene and the Pleistocene of Greece (e.g.,
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52 Tsoukala and Mol, 2016; Athanassiou, 2016) this is the first report of *Anancus* from
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54 the late Miocene, marking its earliest occurrence in the Greek fossil record. Moreover,
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3 it is the first clear faunal evidence that Chomateri post-dates Pikermi. The material of
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5 *Anancus* from the late Miocene of western Eurasia is limited; however, all of them
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7 share the same primitive dental features, and are distinguished from *A. arvernensis*
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9 and other anancines of the Old World. The cranium and mandible of *Anancus* from
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11 the Austrian locality Hohenwarth indicate also a more primitive stage compared to
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13 more derived anancines. We believe that all these differences support the specific
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15 separation of the late Miocene anancines from western Eurasia, which are here all
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17 attributed to *A. lehmanni*. Further investigations and new discoveries (ideally a
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19 cranium of *A. lehmanni* and a mandible with symphysis of *A. perimensis*) are needed
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21 in order to enrich our knowledge on these species, and to clarify the relationships
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23 between them as well as with other anancines. To our current knowledge, the origin of
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25 *Anancus* is traced at ~9.0–8.5 Ma in Asia, from where the genus dispersed
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27 subsequently to the East, being present in three continents towards the end of the late
28
29 Miocene. *Anancus* entered Europe at ~7.2 Ma and around the same time or slightly
30
31 later also Africa. During this period new land bridges were formed between Northern
32
33 Africa and Eurasia as a result of changes in the environmental conditions in the
34
35 Mediterranean Sea, enabling faunal exchanges. The arrival of *Anancus* in Europe
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37 coincides with a faunal turnover in both the eastern and western sector of the
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39 European Mediterranean region, and in the Southern Balkans in particular, with the
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41 decline of the ‘Pikermian’ large mammal fauna.
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FIGURE CAPTIONS

FIGURE 1. Geographic position of Pikermi and Chomateri within Greece (**A**), Attica (**B**) and the Pikermi region (**C**). Map of Greece taken from www.shadedrelief.com and the rest from Google Earth. [planned for page width]

FIGURE 2. *Anancus lehmanni* from Chomateri, Greece. **A–C**, right maxilla fragment with DP2–DP4 (AMPG-13II/1972), in **A**, occlusal, **B**, labial, and **C**, lingual views; **D–F**, left dp4 (NHMW-1972/1567), in **D**, occlusal, **E**, labial, and **F**, lingual views. [planned for page width]

FIGURE 3. Morphological (**A–G**, all in occlusal views) and metrical (**H**) comparison of the DP3. **A**, *Konobelodon atticus*, Pikermi, Greece, left DP3 (reversed), SNSB-BSPG-AS II 182; **B**, *Konobelodon atticus*, Pikermi, Greece, right DP3, MNHN-PIK-1704a; **C**, *Tetralophodon longirostris*, Eppelsheim, Germany, cast of left DP3 (reversed), MNHN-268; **D**, *Anancus lehmanni*, Chomateri, Greece, right DP3, AMPG-13II/1972; **E**, *Anancus lehmanni*, Concud, Spain, left DP3 (reversed), taken from Mazo (1981); **F**, *Anancus arvernensis*, Montpellier, France, left DP3 (reversed), FSL-40462; **G**, *Anancus arvernensis* (from the lectotype), Perrier-les-Étouaires, France, right DP3, MNHN-A.C. 1830 coll. Croizet; **H**, scatter diagrams (length vs. width) of the DP3 of tetralophodonts from various localities. Data from Schlesinger (1917), Mazo (1981), Antunes and Mazo (1983), Metz-Muller (1996), Saegusa and Haile-Selassie (2009), Konidaris et al. (2014 and references cited therein for *Konobelodon atticus*) and own measurements at FSL, HLMD, MNHN and SNSB-BSPG. [planned for page width]

FIGURE 4. Morphological (**A–D**, all in occlusal views) and metrical (**E**) comparison of the DP4 and M2. **A**, *Konobelodon atticus*, Pikermi, Greece, right DP4, AMPG-PA3933/91; **B**, *Anancus lehmanni*, Chomateri, Greece, right DP4, AMPG-13II/1972; **C**, *Anancus arvernensis*, Perrier-les-Étouaires, France, right DP4, MNHN-nn coll.

Bravard; **D**, *Anancus lehmanni*, Cueva Rubbia (Concud), Spain, left M2 (reversed) with dental terminology, taken from Schlosser (1907); **E**, scatter diagrams (length vs. width) of the DP4 of tetralophodonts from various localities. Data from Schlesinger (1917), Metz-Muller (2000), Konidaris et al. (2014 and references cited therein for *Konobelodon atticus*), and own measurements at HGI, HLMD, and MNHN. [planned for page width]

FIGURE 5. Morphological (**A–D**, all in occlusal views) and metrical (**E**) comparison of the dp4 and m2. **A**, *Konobelodon atticus*, Pikermi, Greece, left dp4, AMPG-PA3708/91; **B**, *Anancus lehmanni*, Chomateri, Greece, left dp4, NHMW-1972/1567; **C**, *Anancus lehmanni*, Hohenwarth, Austria, left m2, taken from Zapfe (1957); **D**, *Anancus lehmanni*, Cueva Rubbia (Concud), Spain, left m2, taken from Schlosser (1907); **E**, scatter diagrams (length vs. width) of the dp4 of tetralophodonts from various localities. Data from Geraads and Metz-Muller (1999), Metz-Muller (2000), Gasparik (2005), Konidaris et al. (2014 and references cited therein for *Konobelodon atticus*), and own measurements at FSL and NHMW. [planned for page width]

FIGURE 6. Schematic representation comparing the mandibles of *Tetralophodon* and *Anancus* from various European localities. The mandibles are of different ontogenetic age, but all bear the m2. All specimens are drawn in the same size based on the m2. In (a) mandibles are placed according to the distal margin of the symphysis in dorsal view, and in (b) according to the mesial margin of the anterior molar or its alveolus in lateral view. **A**, Dorkovo, Bulgaria, DKV246 (reversed) (Metz-Muller, 2000); **B–C**, Dorkovo, Bulgaria, DKV159 (Metz-Muller, 2000); **D–E**, Hohenwarth, Austria (Zapfe, 1957); **F–G**, Laarberg, Austria (reversed) (Schlesinger, 1917); **H–I**, Esselborn, Germany, HLMD-Din 1087; **J–K**, Eppelsheim, Germany, HLMD-Din

111; **L–M**, Bermersheim, Germany (Tobien, 1980; the rostrum is partially restored).
[planned for page width]

FIGURE 7. Schematic representation comparing the rostral part of the cranium and the upper tusks. **A**, *Anancus perimensis*, Perim Island, India (Falconer and Cautley, 1846); **B**, *A. lehmanni*, Hohenwarth, Austria (Zapfe, 1957); **C**, *A. arvernensis*, Percussina (Valdarno), Italy (Weithofer, 1890). Specimens are in the same size based on the distance anterior border of zygomatic arch – anterior border of premaxillae.

[planned for page width]

FIGURE 8. Biochronological distribution of the Old World anancines and chronology of selected localities mentioned in the text. Data from references cited in the text plus Leakey and Harris (2003) and Haile-Selassie and WoldeGabriel (2009). [planned for page width]

FIGURE 9. Geographical distribution of *Anancus* in the Old World during the late Miocene with selected localities. **1**, Germany (Dorn-Dürkheim 1; Gaziry, 1997); **2**, Austria (Hohenwarth; Zapfe, 1957); **3**, Slovakia (Tóth, 2010); **4**, Hungary (Gasparik, 2001); **5**, Spain (e.g., Concud, Los Mansuetos, Vental del Moro; Mazo and van der Made, 2012); **6**, Romania (Derşida; Codrea et al., 2002); **7**, FYROM (Dolni Disan; Markov, 2008); **8**, Bulgaria (e.g., Ahmatovo, Azmaka, Ezerovo, Maritza-Iztok; Markov, 2008; Spassov et al., 2012); **9**, Greece (Chomateri); **10**, Northern Caucasus (Tesakov et al., 2017); **11**, Turkey (Develi; Mayda et al., 2014); **12**, Dhok Pathan Fm. (Pakistan; Tassy, 1983b); **13**, Haritalyangar (India; Patnaik, 2013); **14**, Perim Island (India; Tobien, 1978; Tassy, 1983b); **15**, Shanxi Province (China; Qiu et al., 2013); **16**, Torros Menalla (Chad); **17**, Kossom Bougoudi (Chad); **18**, Manonga Valley (Tanzania); **19**, Lemudong'o (Kenya); **20**, Kanam East (Kenya); **21**, Tugen Hills

(Kenya); **22**, Lothagam (Kenya); **23**, Middle Awash (Ethiopia); **16–23**, from Sanders
et al. (2010) and references cited therein. [planned for page width]



Figure 1 (color)

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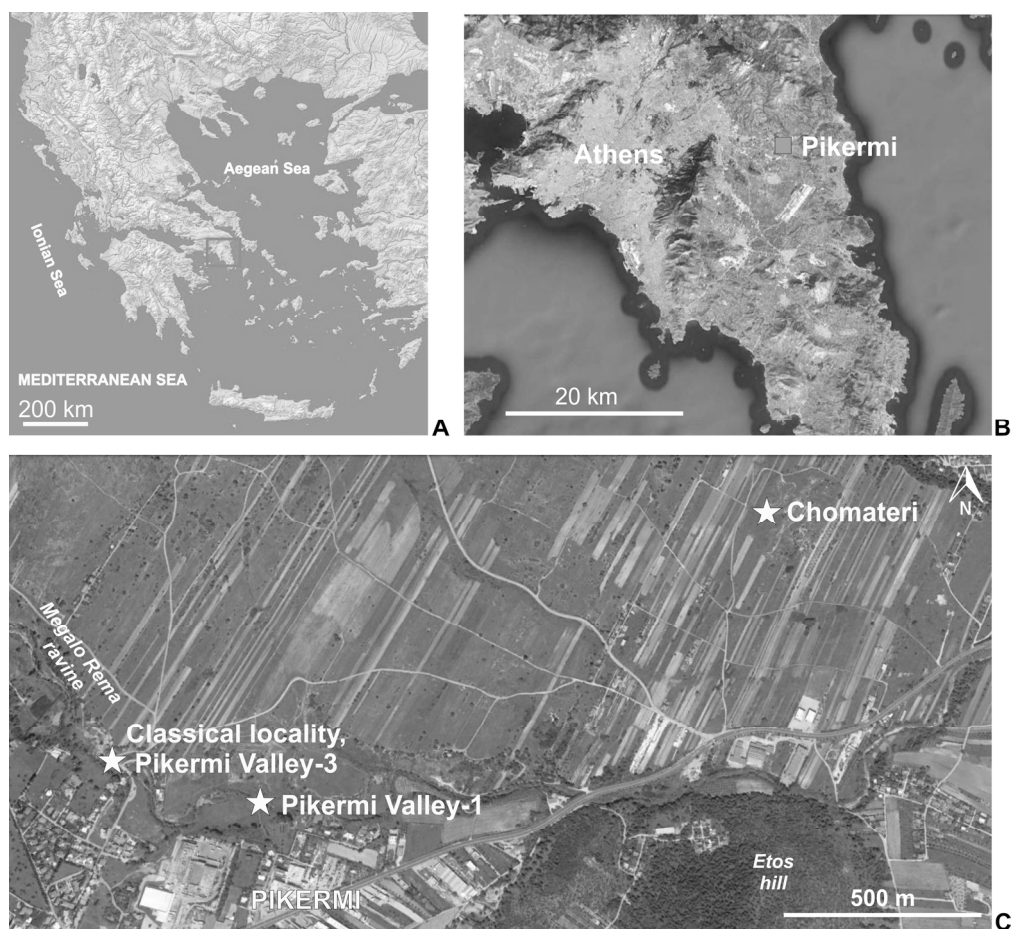


Figure 1 (grayscale)

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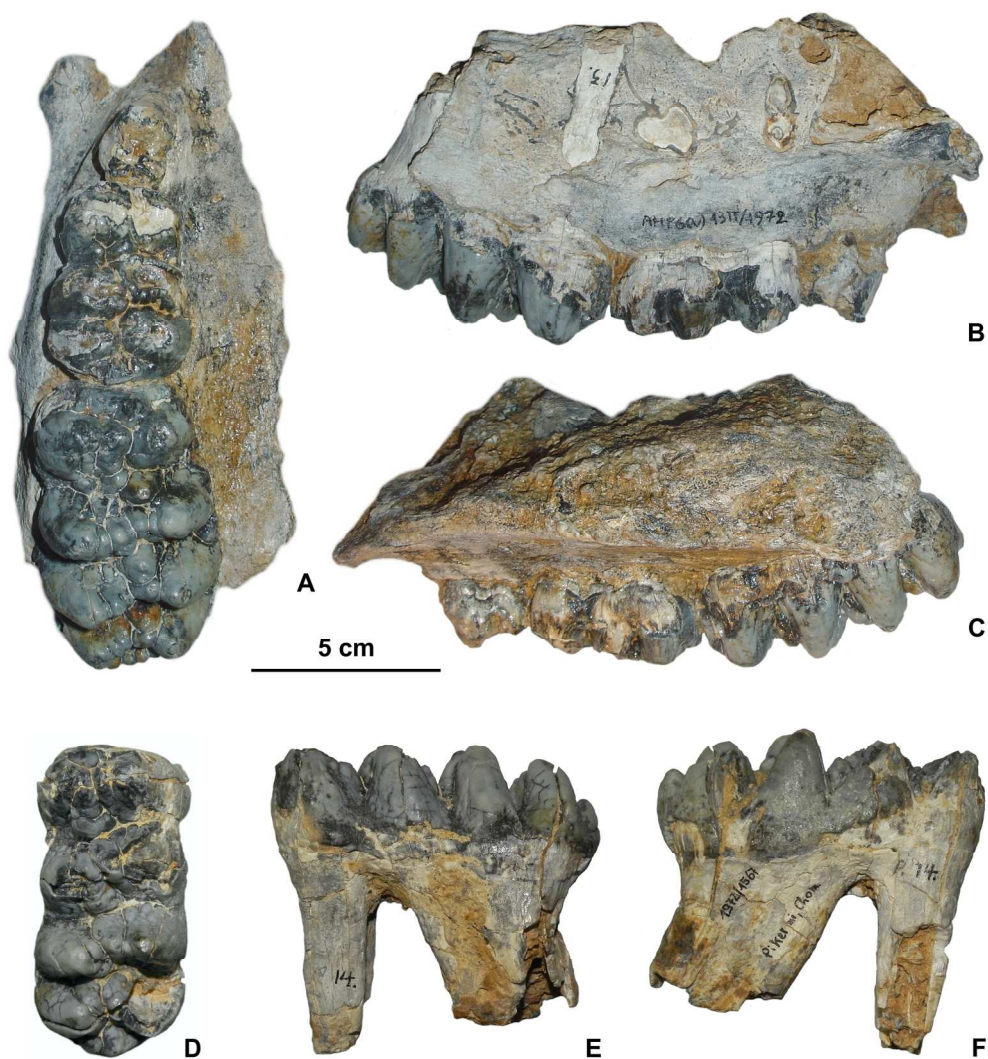


Figure 2 (color)

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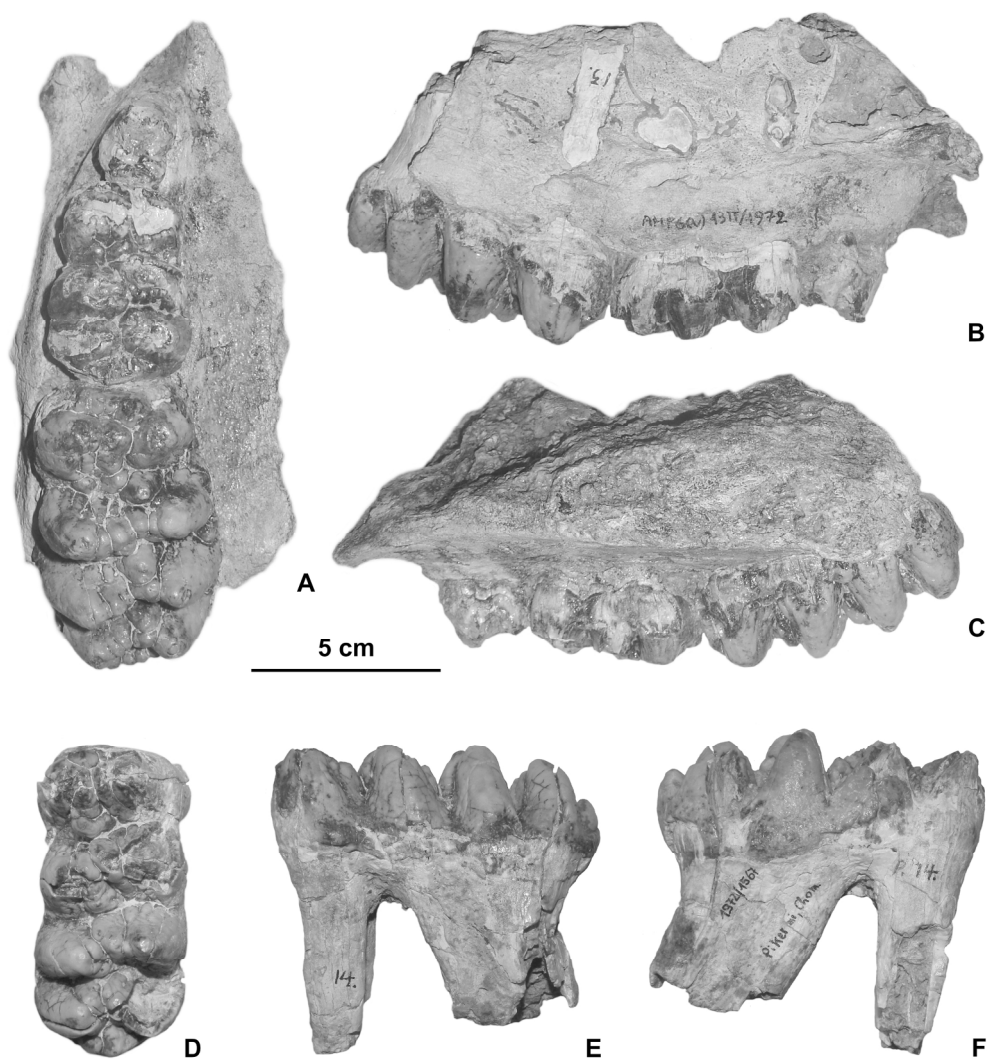


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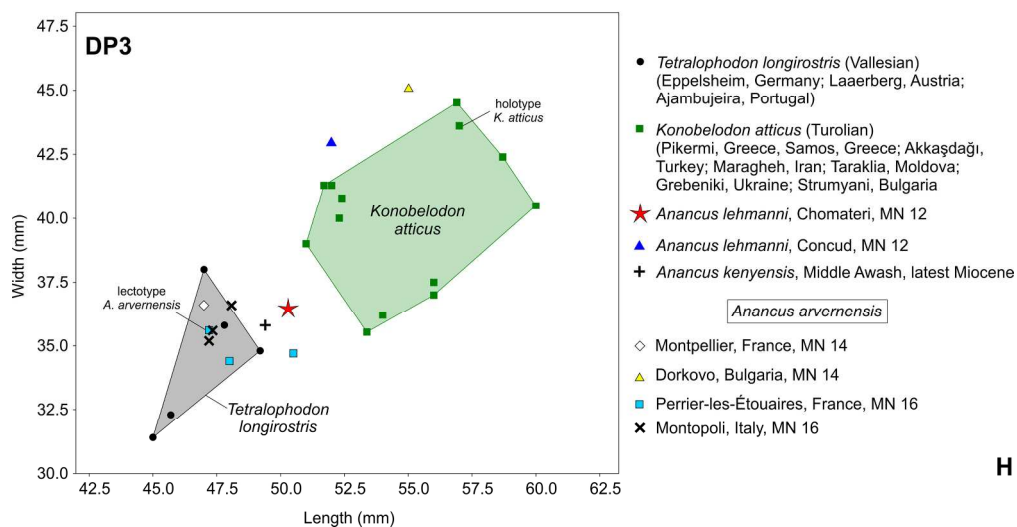
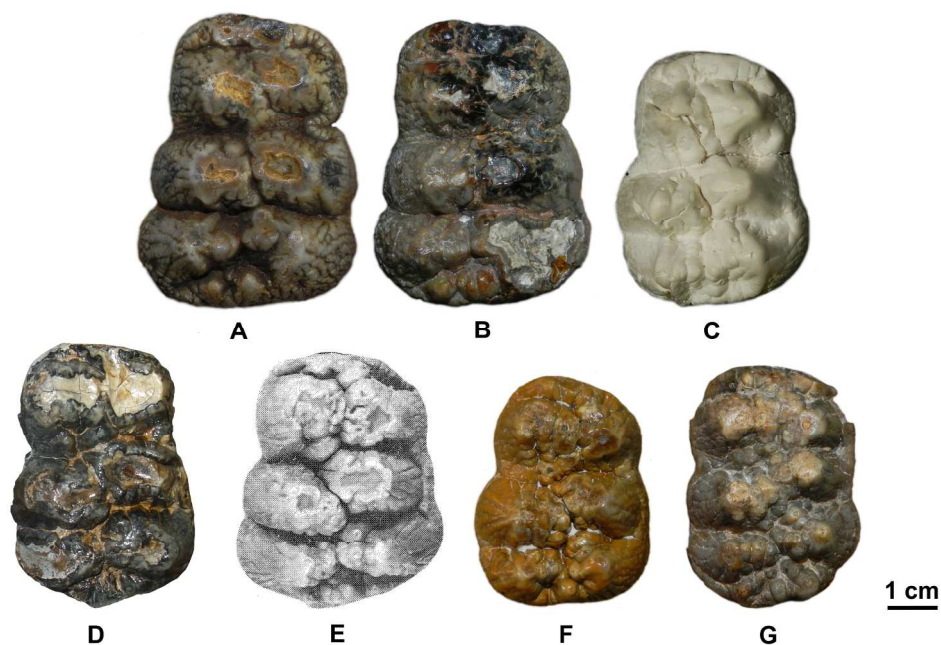


Figure 3 (color)

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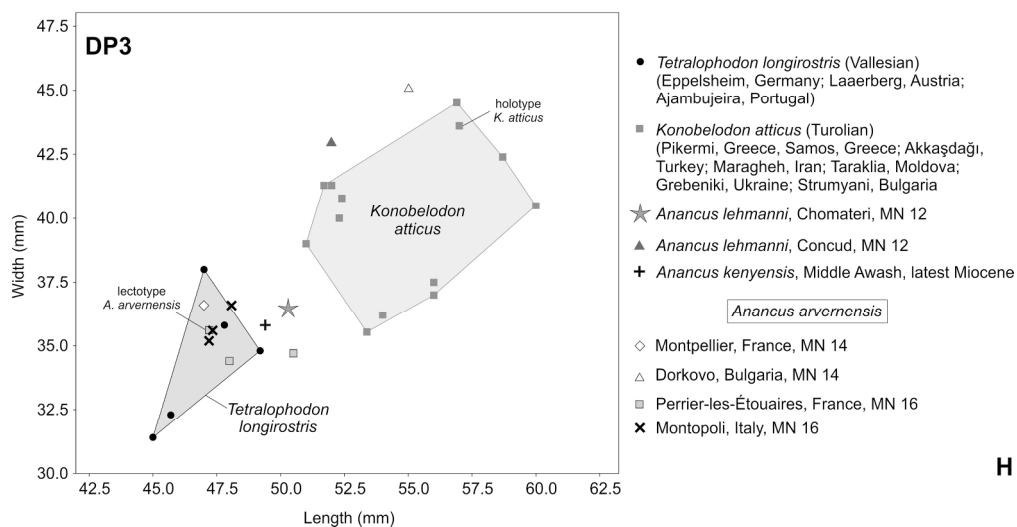
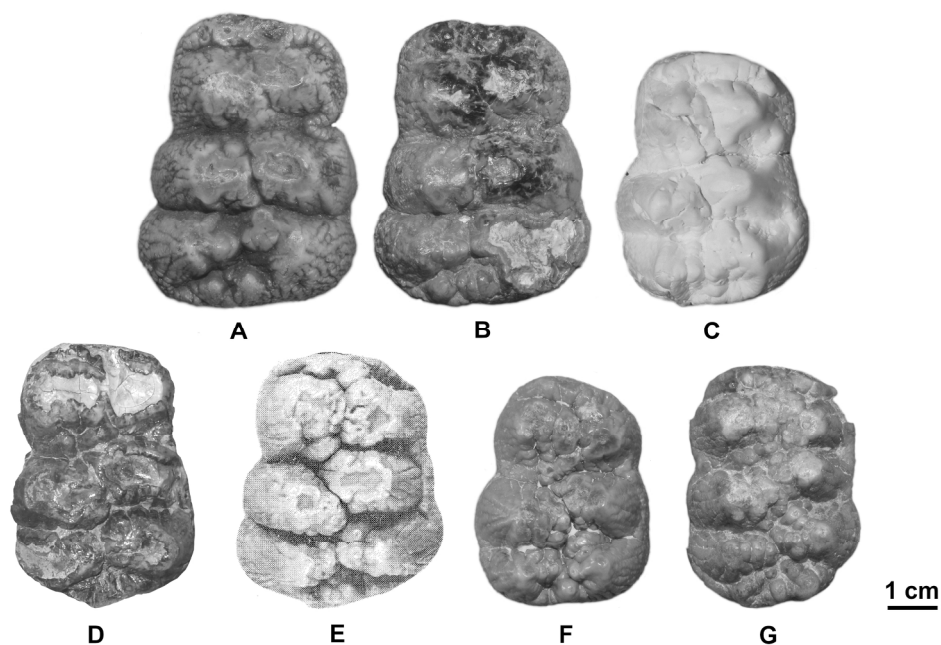


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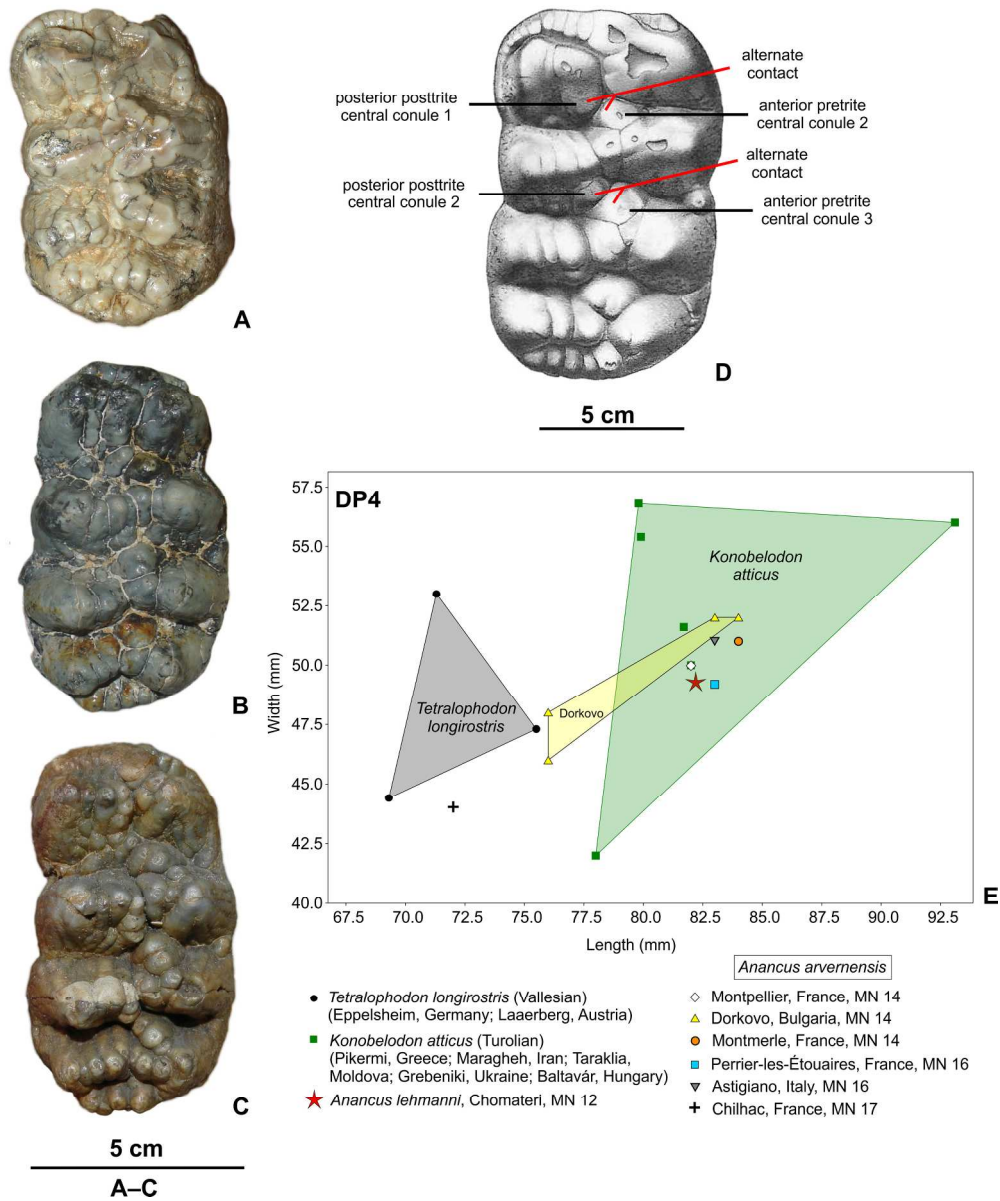


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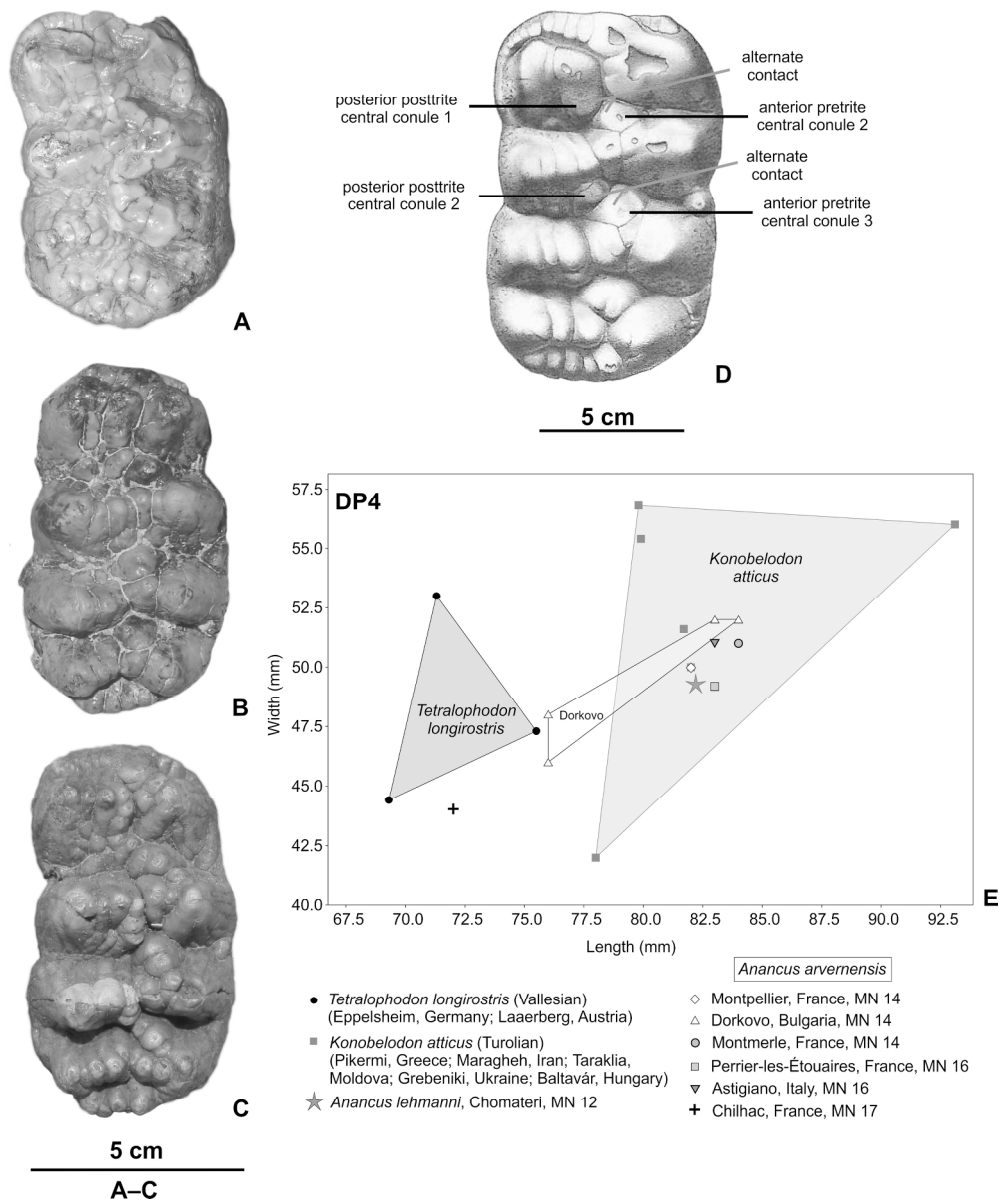


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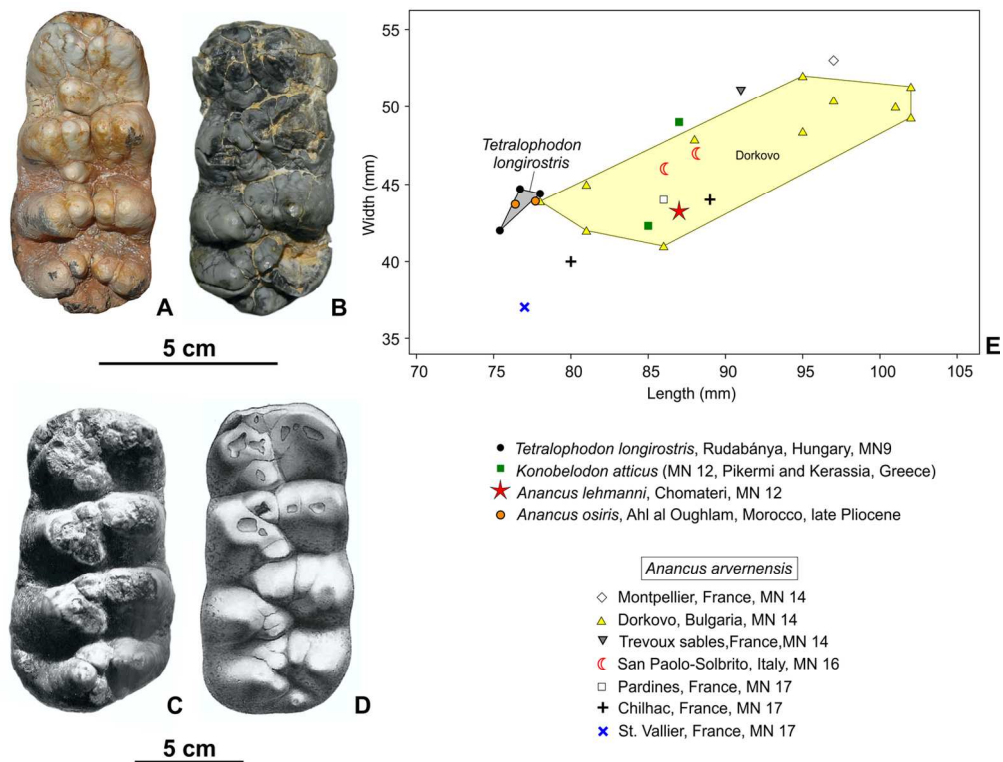


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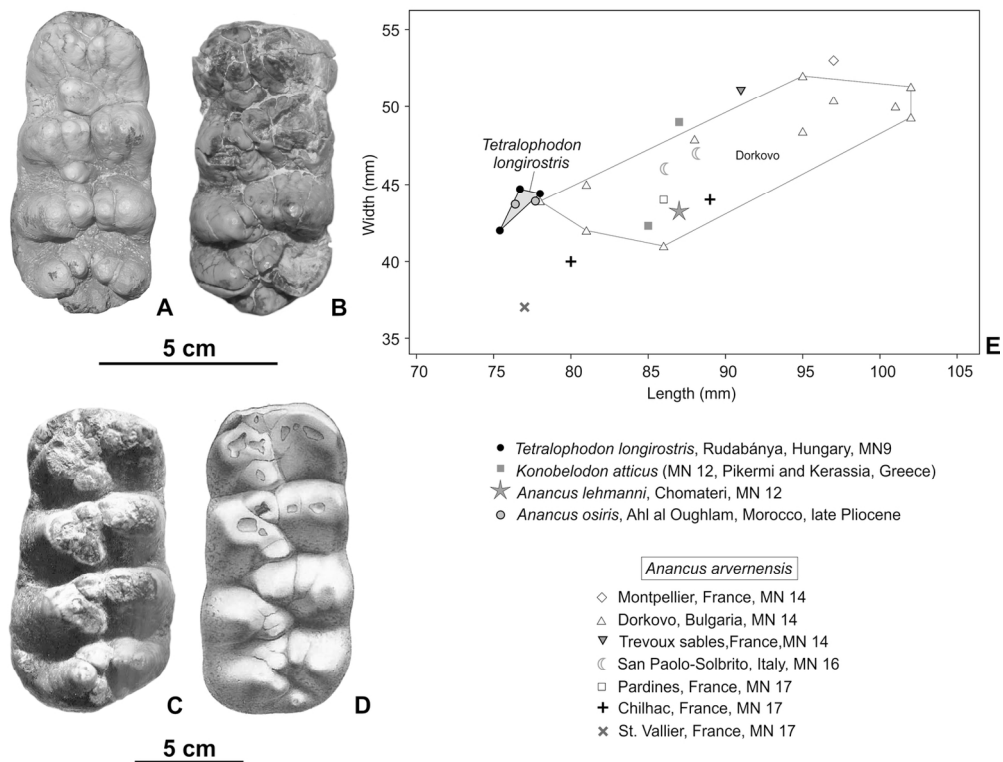


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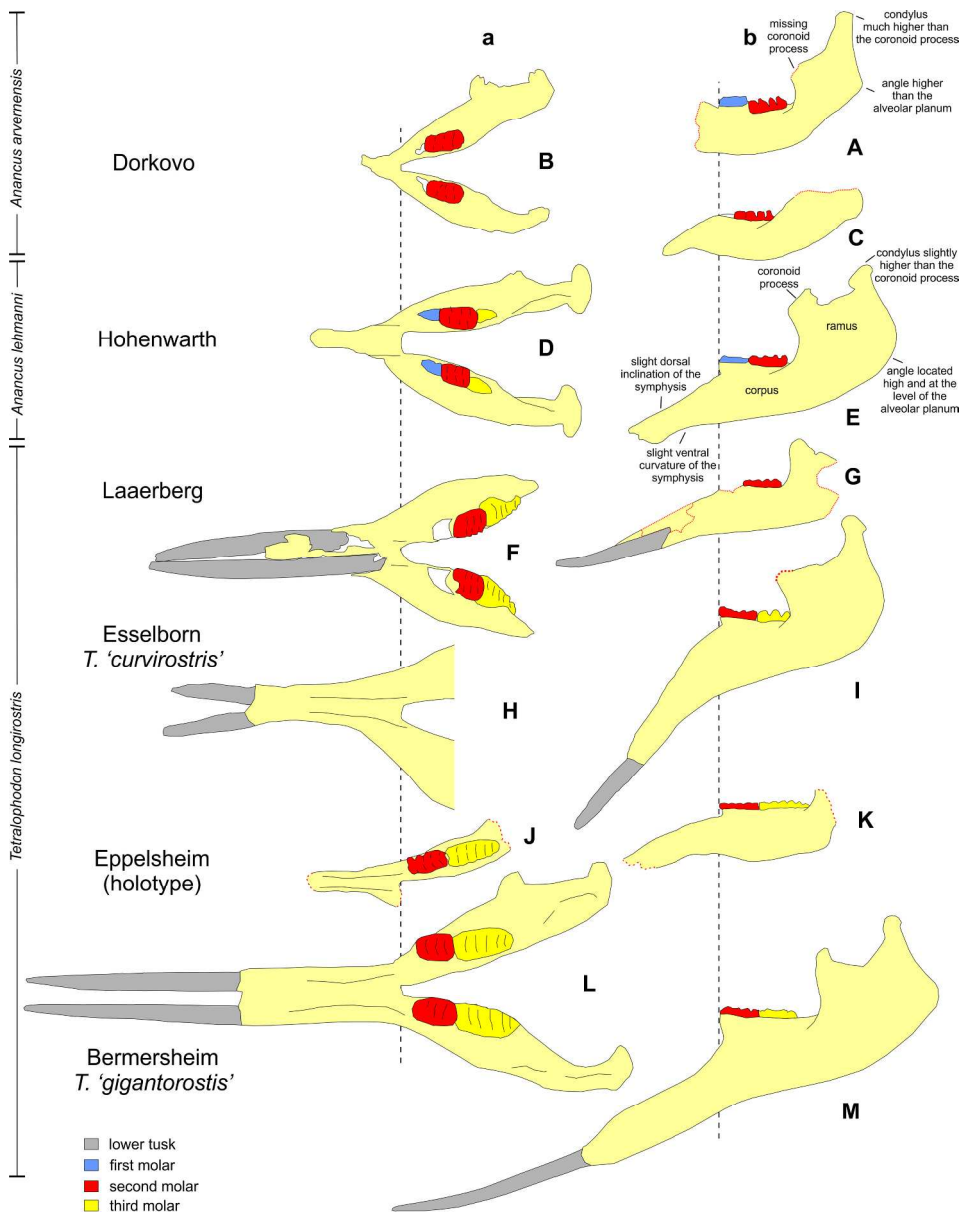


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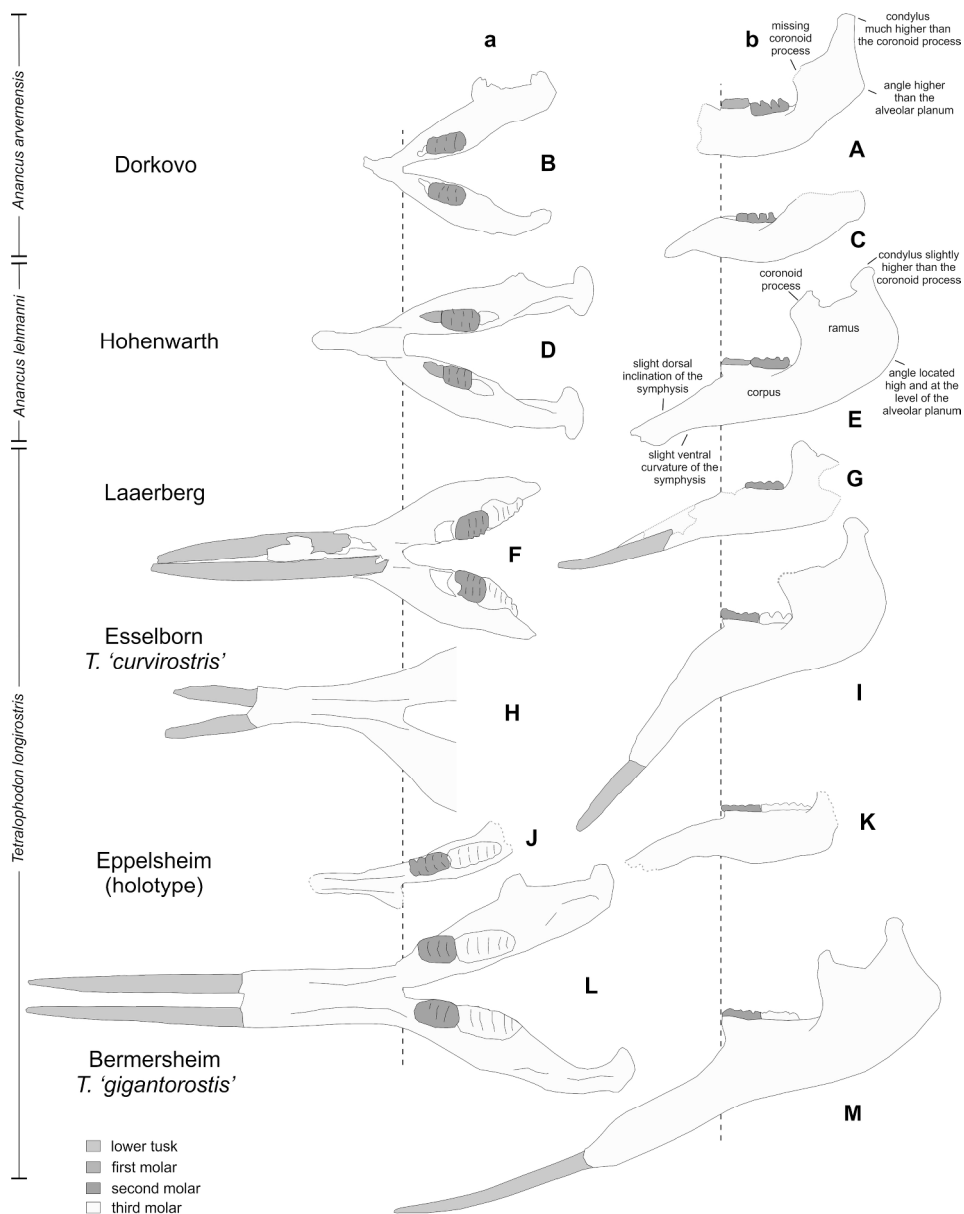


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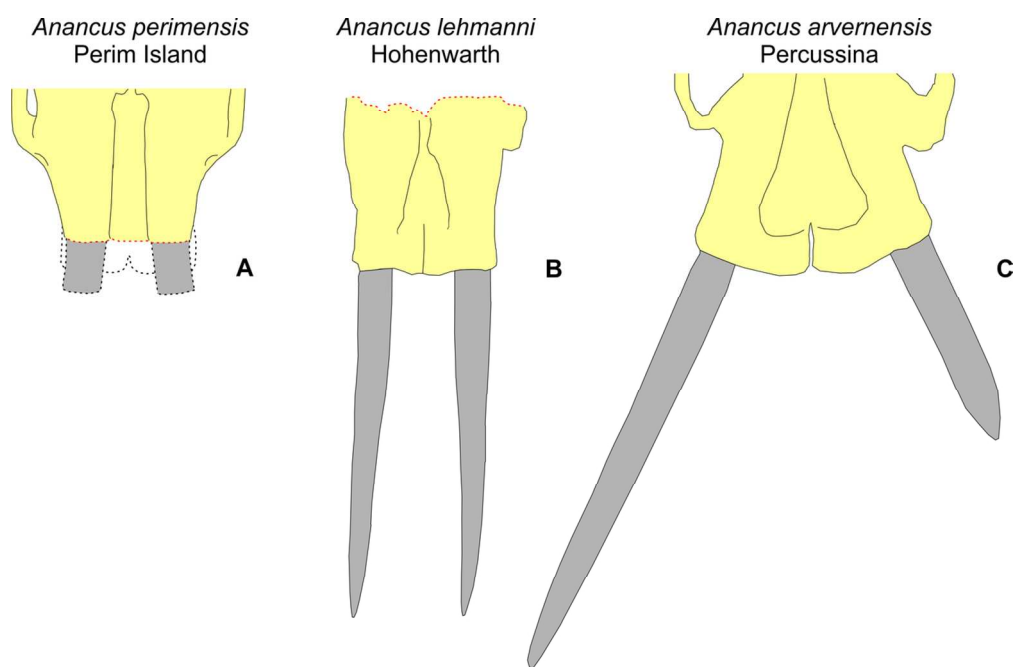


Figure 7 (color)

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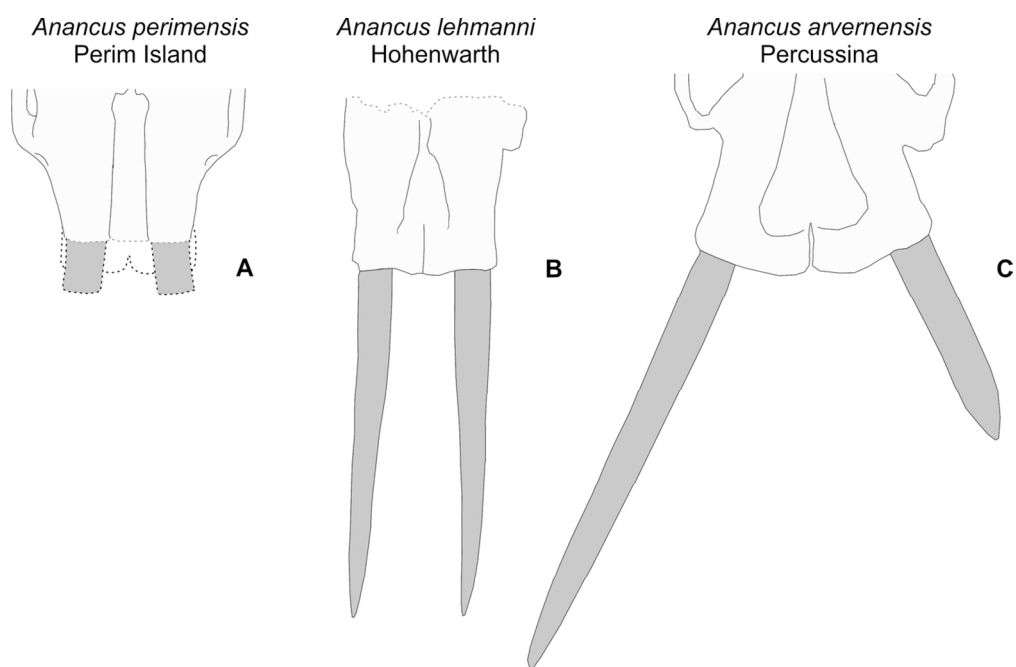


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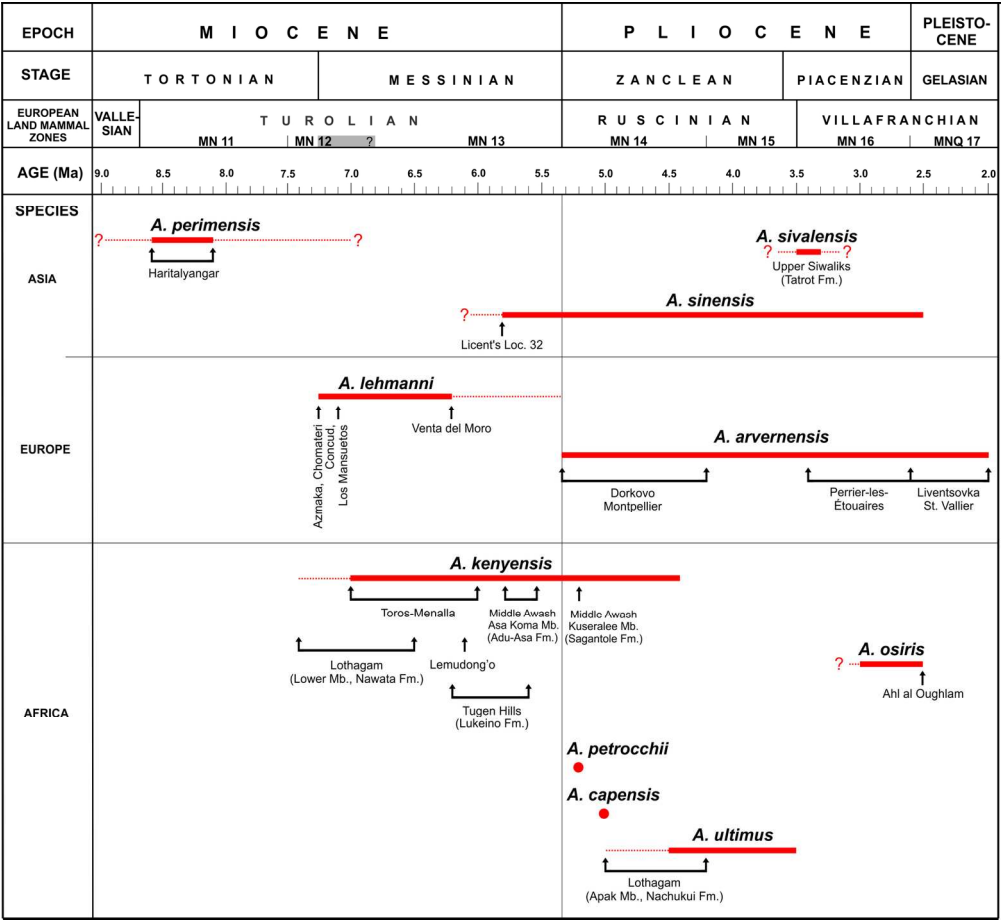


Figure 8 (color)

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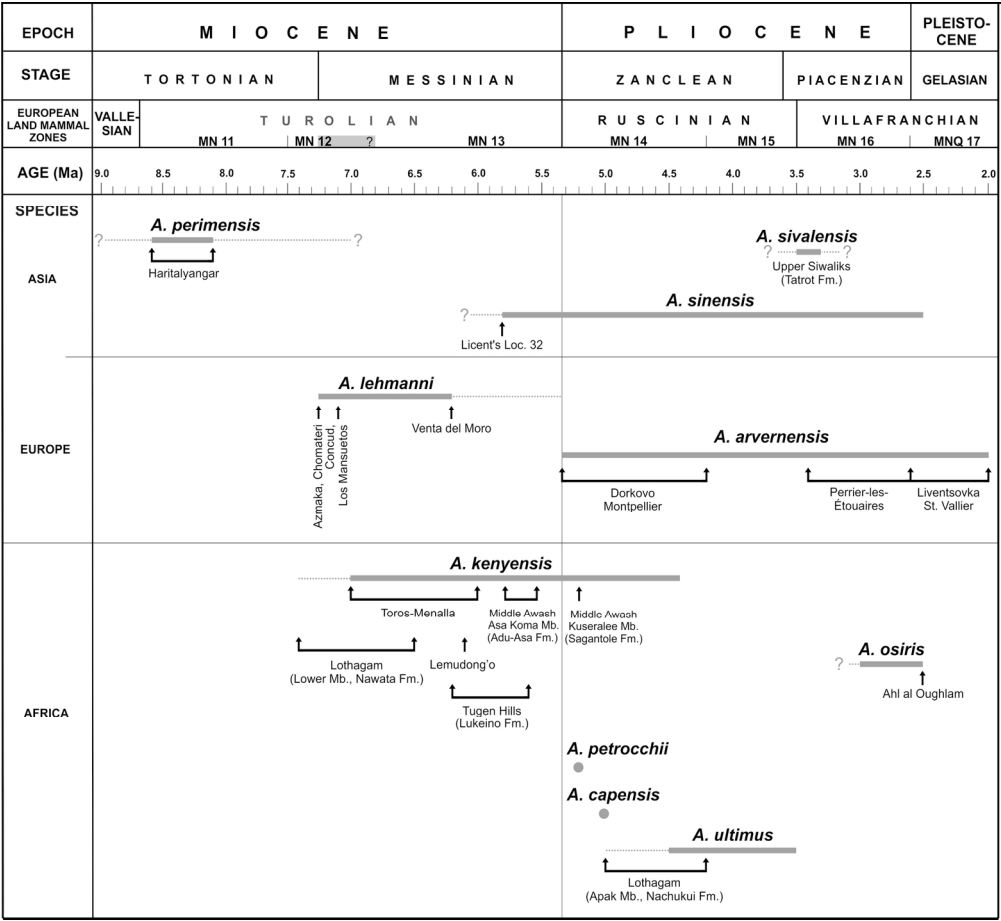


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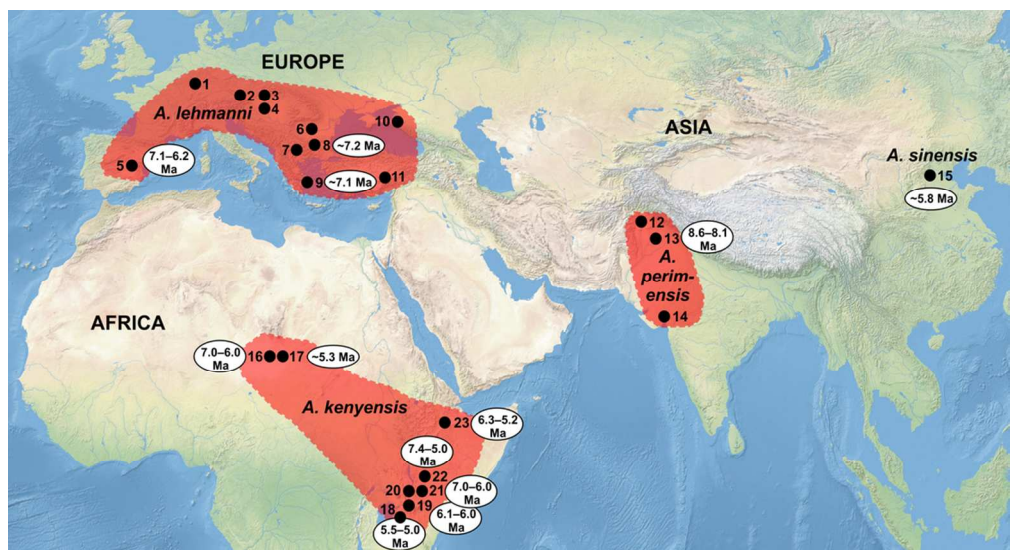


Figure 9 (color)

98x53mm (300 x 300 DPI)

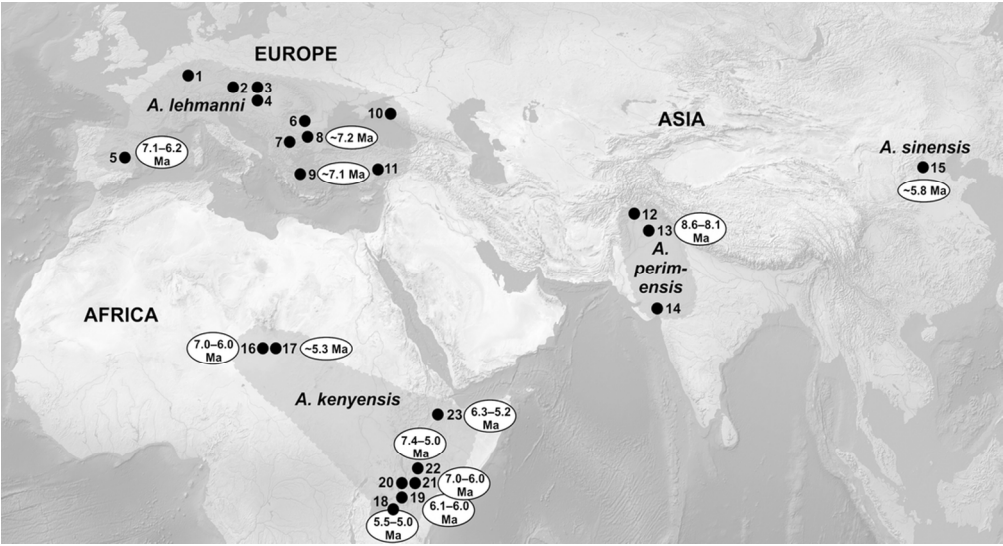


Figure 9 (grayscale)

98x53mm (300 x 300 DPI)

TABLE 1. Dental measurements (in mm) of *Anancus lehmanni* from Chomateri, Greece. **Abbreviations:** **L**, length; **W**, width; **RI**, robustness index ($100 \times W/L$); **H**, height; **HI**, hypsodonty index ($100 \times H/W$). Measurements in parentheses represent the greatest measureable value of the parameter. Numbers in superscripts indicate the loph(id), where the maximal height was measured.

Tooth	Inventory number	Side	L	W1	W2	W3	W4	H	RI	HI
NHMW-										
dp4	1972/1567	left	87.0	(38)	40.0	43.1	43.3	33.2 ⁽³⁾	49.8	76.7
		right	(23.5						~74.	
DP2	AMPG-13Π/1972	t)	15.8	17.6			worn	9	-
		right		(31.5	(35.5	(36.5			~72.	
DP3	AMPG-13Π/1972	t	50.3)))		worn	6	-
		right		(42.3	(46.6	(49.3	(46.0		~60.	~66.9
DP4	AMPG-13Π/1972	t	82.2))))	33.0 ⁽²⁾	0	

TABLE 2. Comparison of dental features in the Eurasian and African species of *Anancus*. Data from Metz-Muller (2000), Sanders (2011) and own observations. Asterisks indicate primitive stage.

Species	Age	Geographic distribution	Intermediate molars	Third molars	Anancoidy	Crown complexity	Enamel folding (molars)
Europe- Western							
<i>A. lehmanni</i>	late Miocene	Asia	4*	5*–6	weak*	simple*	absent*–coarse*
<i>A. arvernensis</i>			4* (or 5 in			simple*–	
(Dorkovo)	early Pliocene	Bulgaria (Europe)	m2)	5*–6	pronounced	complex	absent*–coarse*
Central-Southern							
<i>A. perimensis</i>	late Miocene	Asia	4*	5*–6	weak*	simple*	absent*
Central-Southern							
<i>A. sivalensis</i>	Pliocene	Asia	4* (or 5 in M2)	6	pronounced	simple*	coarse*–moderate
'A.							
<i>paisuyensis</i>	?late Miocene	China (Asia)	?	6	weak*	simple*	unknown

TABLE 2

(Continued)

<i>A. sinensis</i>	Pliocene	China (Asia)	4*	6	pronounced	simple*	absent*—moderate
	late Miocene-early	Central-Eastern					
<i>A. kenyensis</i>	Pliocene	Africa	4*	5*–6	weak*	simple*	absent*—coarse*
		Central-Eastern			moderate—		
<i>A. ultimus</i>	early-middle Pliocene	Africa	5	6–7	pronounced	complex	moderate-fine
<i>A. capensis</i>	early Pliocene	South Africa	4*	6–7	pronounced	complex	moderate-fine
	late Miocene-early						
<i>A. petrocchii</i>	Pliocene	Libya (Africa)	5	6	weak*	simple*	unknown
<i>A. osiris</i>	late Pliocene	North Africa	4*	5*–6	pronounced	simple*	absent*—coarse*