

A new protictithere from the late Miocene hominoid locality Ravin de la Pluie of Axios Valley (Macedonia, Greece)

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Abstract This article concerns the study of a protictithere from the late Miocene of Axios Valley (Macedonia, Greece). The material was found in the hominoid-bearing mammal locality Ravin de la Pluie (RPI), which is correlated with the late Vallesian, MN 10. The available material, including maxillary and mandibular elements, is described and compared morphologically and metrically with the known Eurasian protictitheres. The small size, the low cusps(-ids) of the teeth, the protocone of the P4, which is in line with the mesial border of the parastyle, the large molars (especially the M2), the small buccal projection of the M1 paracone, the strongly molarized p4, the strong metaconid and large talonid with high entoconid of the m1 separate the RPI protictithere from the known Eurasian protictitheres and allow the erection of a new species, named *P. thessalonikensis* n. sp.

Keywords Mammalia · Hyainidae · Systematic · New species · Miocene

Kurzfassung Der vorliegende Artikel bezieht sich auf die Studie eines Protictitheres aus dem oberen Miozän Axios-Tal (Mazedonien, Griechenland). Das Material wurde in der Gegend Ravin de la Pluie (RPL) gefunden, in der hominoide Säugetiere vorkamen, und die mit dem oberen Vallesium, MN 10, entspricht. Das zur Verfügung stehende Material, einschließlich Überbleibseln von Ober- und Unterkiefern, wird morphologisch und metrisch mit dem bekannten eurasischen Protictitheres beschrieben und

verglichen. Die geringe Größe, die niedrigen Höcker in den Zähnen, das auf der gleichen Linie mit dem Vorderrand der Parastyle befindliche Protocon des P4, die großen Backenzähne (vor allem die M2), die kleine bukkale Projektion der Paracone in der M1, die stark molarisierten p4, das starke Metaconid und das große Talonid mit hohem Entoconid im M1, unterscheiden die RPL Protictithere von den beiden wichtigsten eurasischen Taxa *P. gaillardi* und *P. crassum* und erlauben die Errichtung einer neuen Spezies namens *Protictitherium thessalonikensis* n. sp.

Schlüsselwörter Säugetiere · Hyainidae · Systematisch · Neue Spezies · Miozän

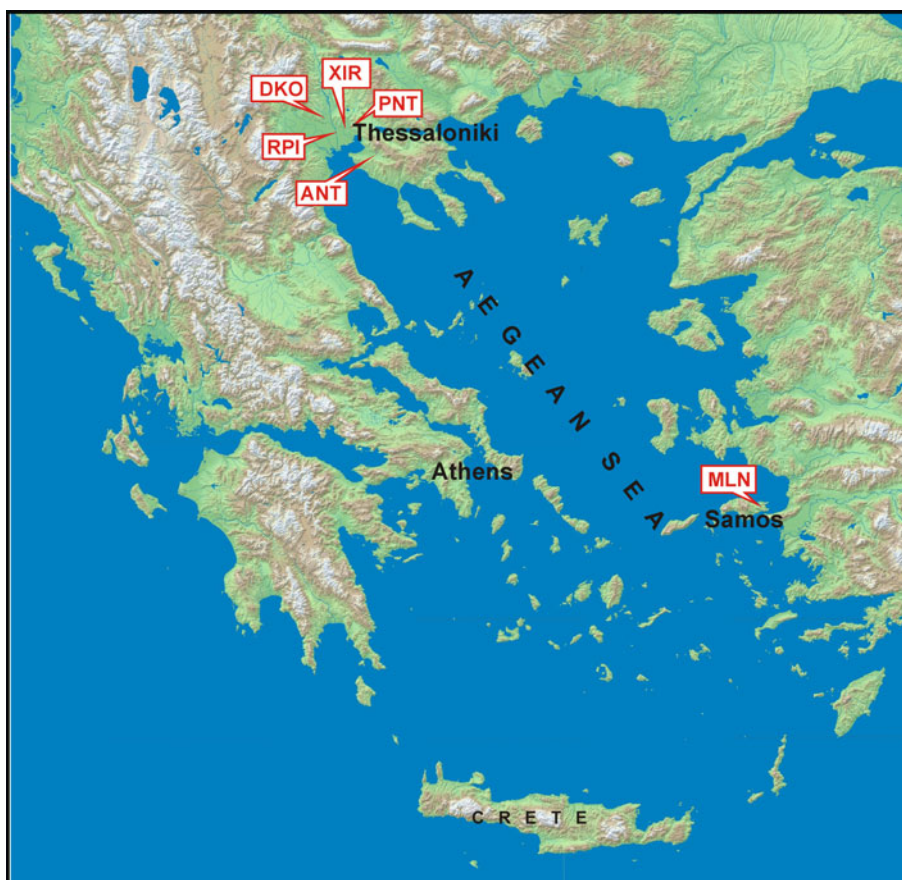
Introduction

The late Miocene mammal fossiliferous sites of the Axios Valley have been known since the beginning of the last century (Arambourg and Piveteau 1929). A new field campaign in the Axios Valley, started in 1972, has led to the relocation of the previously known localities, the discovery of new ones and the collection of numerous fossils (Koufos 2006a, in press and ref. cited). Among the new localities is Ravin de la Pluie (RPI), situated near the village of Nea Messimvria about 25 km west of Thessaloniki (Fig. 1). The RPI fauna is rich, and its study indicated that it is more primitive than that of Pikermi and the other Greek Turolian faunas, correlated to the late Vallesian, MN 10; the magnetostratigraphic data of the associated deposits suggest an estimated age of ~9.3 Ma (Koufos 2006a; Sen et al. 2000). Although the RPI carnivoran remains are rare in comparison to the other mammal groups of the fauna, their composition is interesting and is comprised of the following taxa: *Eomellivora wimani*, *Adcrocuta eximia*

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Fig. 1 Map of Greece with the *Protictitherium* bearing mammal localities.

ANT = Antonios, MN 4/5;
DKO = Dytiko 3, MN 13;
MLN = Mytilinii-4, MN 11;
PNT = Pentalophos 1, ?MN 9;
RPI = Ravin de la Pluie, MN 10;
XIR = Xirochori 1, MN 10.
The map is taken from www.shaded-relief.com



leptoryncha, *Protictitherium* cf. *intermedium*, *Protictitherium* aff. *gaillardi*, *?Hyaenictis* sp. and *Metailurus parvulus* (Koufos 2000, 2011a). Among them is a small-sized hyaenid, described as *Protictitherium* aff. *gaillardi* (de Bonis and Koufos 1991; Koufos 2000). The known material of *P.* aff. *gaillardi* has been augmented with some new remains, found during the last field expeditions (2004–2009). The present study provides new descriptions of the material and comparisons with the known Eurasian protictitheres to define it more precisely.

Materials and methods

The studied material is housed in LGPUT. The material has been measured using a digital caliper, and the measurements are given in mm. The bivariate plots were produced using Excell 2007. The software PAST (Hammer et al. 2001) was used for the Principal Component Analysis (PCA). The lacking measurements of the compared specimens are replaced by column average substitution. In the given analysis specimens lacking more than four measurements are excluded. The morphological comparison is based on direct comparisons of the studied material with original material or casts of the various Eurasian protictitheres.

Abbreviations

a.a.c.	anterior accessory cusp(-id)
BSPM	Bayerische Staatssammlung für Paläontologie und Historische Geologie, München
ANT	Antonios, Chalkidiki, Greece
DKO	Dytiko 3, Axios Valley, Greece
LGPUT	Laboratory of Geology and Palaeontology, University of Thessaloniki
MLN	Mytilinii-4, Samos, Greece
MNHN	Museum national d'Histoire naturelle, Paris
p.a.c.	posterior accessory cusp(-id)
PNT	Pentalophos 1, Axios Valley, Greece
RPI	Ravin de la Pluie, Axios Valley, Greece
XIR	Xirochori-1, Axios Valley, Greece

Systematic palaeontology

Carnivora Bowdich 1821
Hyaenidae Gray 1869
Ictitheriinae Trouessart 1897
Protictitherium Kretzoi 1938
Protictitherium thessalonikensis n. sp.

Synonyms 1980 *Plioviverrops orbignyi* Koufos, p. 67; pl. IX, Fig. 1

1991 *Protictitherium* aff. *gaillardi* Bonis and Koufos, p. 368; pl. III, Fig. 2

2000 *Protictitherium* aff. *gaillardi* Koufos, p. 59

Locality Ravin de la Pluie (RPI), Axios Valley, Macedonia, Greece.

Age Late Vallesian, MN 10, (Late Miocene); GPTS = ~9.3 Ma.

Holotype Right maxillary fragment with C-M2, RPI-69 (Fig. 2c).

Paratypes Maxilla with C-M2 dex and P3-P4 sin, RPI-60; right maxillary fragment with C-P4, RPI-16 (the distal border of the P4 is slightly broken); left P1, RPI-69a; left P2, RPI-69b (these specimens were found together with RPI-69 and possibly belong to the same individual); left P3, RPI-51; right mandibular fragment with c-m2 dex, RPI-68.

Measurements See Table 1.

Etymology From the name of the city Thessaloniki, situated near the delta of the Axios River. Thessaloniki was

the sister of Alexander the Great, and the city was founded in her honor in 316/15 BC.

Diagnosis Small size; low cusps(-ids) in the teeth; protocone of the P4 in line with the mesial border of the parastyle; large molars, especially M2; slight buccal projection of the paracone in the M1; strongly molarized p4; strong metaconid and large talonid with high entoconid in the m1.

Differential diagnosis *P. thessalonikensis* differs from *P. gaillardi* in the smaller size, lower main cusps(-ids), presence of the p.a.c. and absence of the mesial cingular projection in the P2,3, stronger parastyle and protocone of the P4, position of the upper carnassial's protocone, smaller buccal projection of the M1's paracone, markedly larger M2, absence of the a.a.c. in the p3, more molarized p4, stronger metaconid of the m1, and larger talonid with stronger entoconid of the m1. It differs from *P. crassum* in the remarkably smaller size, position of the P4's protocone, weaker p.a.c. of the lower premolars, weaker a.a.c. of the p3,4, relatively larger talonid of the m1, and relatively lower entoconid of the m1.

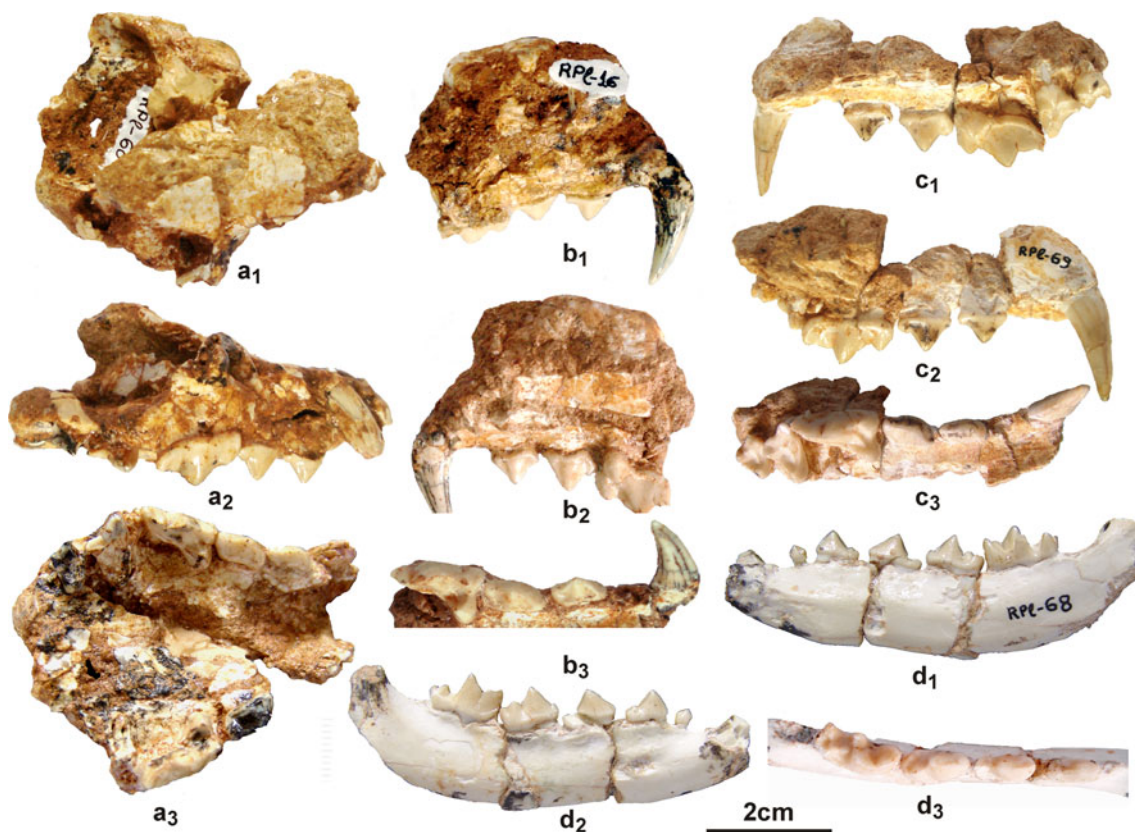


Fig. 2 *Protictitherium thessalonikensis*. Ravin de la Pluie (RPI), Axios Valley, Greece, late Vallesian, MN 10. **a.** Maxilla with C-M2 dex and P3-P4 sin, RPI-60; **a**₁. dorsal, **a**₂. lateral, and **a**₃. occlusal view. **b.** Right maxillary fragment with C-P4, RPI-16; **b**₁. buccal, **b**₂.

lingual, and **b**₃. occlusal view. **c.** Right maxillary fragment with C-M2, RPI-69, HOLOTYPE; **c**₁. buccal, **c**₂. lingual, and **c**₃. occlusal view. **d.** Right mandibular fragment with c-m2, RPI-68; **d**₁. buccal, **d**₂. lingual, and **d**₃. occlusal view

Table 1 Dental dimensions of *P. thessalonikensis* from RPI, Axios Valley, Macedonia, Greece

	<i>Proticttherium thessalonikensis</i>									
	RPI-60		RPI-16	RPI-51	RPI-69	RPI-69a	RPI-69b	RPI-68		
	Ravin de la Pluie, Axios Valley									
	dex	sin	dex	sin	dex	sin	sin		dex	
LC	–	–	5.8	–	5.9	–	–	Lc	–	
BC	–	–	4.0	–	4.0	–	–	Bc	–	
LP1	–	–	–	–	–	3.1	–	Lp1	2.5	
BP1	–	–	–	–	–	2.4	–	Bp1	1.8	
LP2	7.0	–	7.2	–	7.3	–	7.3	Lp2	6.5	
BP2	3.3	–	3.2	–	3.5	–	3.4	Bp2	3.1	
LP3	8.0	8.2	8.2	8.3	8.1	–	–	Lp3	8.2	
BP3	4.1	4.1	4.0	4.0	4.5	–	–	Bp3	3.6	
LP4	12.0	12.5	12.0	–	12.7	–	–	Lp4	9.0	
BP4	7.1	7.2	7.6	–	7.8	–	–	Bp4	4.2	
LM1	6.3	–	–	–	6.2	–	–	Lm1	11.4	
BM1	10.0	–	–	–	10.8	–	–	Bm1	5.0	
LM2	5.1	–	–	–	5.0	–	–	Ltrig	8.0	
BM2	7.2	–	–	–	7.1	–	–	–	–	

Description Except RPI-69, which is a new find, all the other specimens are mentioned in the previous publications for the RPI carnivores (Koufos 1980, 2000; de Bonis and Koufos 1991). The available maxillary fragments preserve only small parts of the skull (Fig. 2), providing little information on its morphology. The most complete specimen is RPI-60, which exhibits crushing and compressing deformation; its morphology is thus difficult to assess (Fig. 2a). The palate of RPI-60 is narrow at the level of the canines and P2, yet widens to a breadth of 37 mm at the distal border of the carnassials (Fig. 2a₃). The anterior border of the choanae cannot be detected in the preserved part of the palate; it should be well behind the distal border of the M2. The preserved part of the orbits is strongly deformed; their anterior border is above the middle of the carnassial (Fig. 2a_{1,2}). The infraorbital foramen is large. The upper dentition is better preserved in RPI-69; in RPI-60 the teeth are more worn than in the other two specimens (Fig. 2a). The canine is completely preserved in RPI-16, 69; in RPI-60 only its root is present (Fig. 2). It is high and pointed with an elliptical cross section, a strong mesio-labial crest and a weaker distal one running from the base to its apex, convex buccal and flattened lingual surface, and strong root slightly curved backwards. The P1 is small, single-rooted, monocuspid and with an elliptical crown; its alveole is clearly distinguished in RPI-16, 60 (Fig. 2b₃, c₃). The P2 has very small p.a.c., strong lingual and weaker buccal cingulum and lacks a.a.c.; in its mesio-lingual corner there is a very small cingular projection, formed from the joining of the basal cingulum with a crest running from the apex to the base of the main cusp. The

P3 is similar to P2 but larger and more robust with stronger p.a.c. and cingulum; the lingual cingulum is slightly projected in the distal part of the tooth. The upper carnassial is short and wide with a large and well-separated protocone that does not exceed the mesial border of the parastyle, short and curved buccally metastyle blade, as well as very strong lingual and weaker buccal cingulum. The observed small size difference among the upper premolars of the studied specimens (Table 1) could indicate sexual dimorphism. The M1 is characterized by triangular shape, dominance of the protocone, slight buccal projection of the paracone and the development of a deep fovea between the cusps. In the unworn or slightly worn teeth, the fovea is divided in two parts by a crest from the protocone's apex to that of the paracone; the anterior fovea is very small. This feature gradually disappears with attrition and the occlusal surface flattens (RPI-60). The M2 is similar to M1, but is smaller and exhibits an elliptical occlusal contour, as its paracone is not buccally projected.

The mandibular fragment RPI-68 preserves part of the horizontal ramus with the toothrow; the canine and p1 are broken, while the alveole of the m2 is clearly distinguished (Fig. 2d₃). The mandibular corpus is relatively high, preserving a large mental foramen, situated below the p2. The root of the canine indicates that it has an elliptical transverse section. The p1 is small, single-rooted, and has an elliptical occlusal outline. The p2 lacks a.a.c., but has a well-developed p.a.c., situated in a strong distal projection of the distal cingulum; the latter is strong and elevated distally. The

disto-buccal part of the p3 is slightly broken; the tooth is similar to the p2, but it is larger and has a vestigial a.a.c. The p4 has a small but clear a.a.c., while its distal part is talonid-like. The p.a.c. is situated in the buccal border of a strong distal cingular projection, whose lingual part is elevated, giving the appearance of an “entoconid.” The carnassial has a relatively strong and high metaconid, which is slightly lower than the protoconid. The talonid is relatively large and wide with three cusps; the entoconid dominates. A small cuspid is developed in the middle of the valley between trigonid and talonid, joining their junction with the hypoconid.

Metrical comparison

The available material of the various protictitheres is scarce, and the metrical comparisons are limited. Despite these limitations, using the available dental material and measurements, the RPI sample is compared with the two better known and common Eurasian protictitheres (*P. gaillardii* and *P. crassum*) through Principal Component Analysis (PCA) (Fig. 3). The distinction of *P. gaillardii*-*P. aff. gaillardii* from *P. crassum* is clear by Component 1 (PC1) in the PCA for the upper dentition (Fig. 3a). The RPI sample is clearly separated from the above two taxa, situated in the first quadrant of the diagram and in the left limit of PC1 (Fig. 3a). This position of the RPI sample is due to its smaller size and having molars larger than *P. gaillardii*-*P. aff. gaillardii*. In the second character the RPI protictithere resembles *P. aegaeum*, which also has larger molars than those of *P. crassum* from Spain. In the PCA diagram for the lower dentition (Fig. 3b) PC1 clearly separates the small *P. gaillardii*-*P. aff. gaillardii* from *P. crassum*-*P. cf. crassum*. The sole RPI specimen is separated from the others by being smaller than *P. gaillardii* and *P. crassum*. The metrical comparison of the RPI *Protictitherium* with the other two taxa indicates that it is smaller than them, representing something different. Further investigation of its size and morphology may lead to its specific determination.

The upper premolars of the RPI sample are clearly smaller than those of *P. gaillardii* from the European localities, as well as from *P. aff. gaillardii* from Çandır, Turkey (Fig. 4a, b). The RPI P4, although it is metrically closer to *P. gaillardii* from the Spanish localities of Hostalets and Can Llobateres, is still smaller than all known material of *P. gaillardii* (Fig. 4b). On the other hand, the upper molars of the RPI sample are larger than those of *P. gaillardii* (Fig. 4c, d). The M1 is clearly separated from *P. gaillardii* by its larger length. The M2 is markedly larger, clearly distinguishing the RPI protictithere from *P. gaillardii*. The p3 and the lower carnassial are clearly smaller than those of *P. gaillardii*, while the p4 has similar size to the latter taxon (Fig. 4e, f, g).

Morphological comparison

The metrical comparison of the RPI protictithere with the known material indicates that it is closer to *P. gaillardii*, as has been previously mentioned (de Bonis and Koufos 1991; Koufos 2000). A precise morphological comparison first with the material of this taxon and then with the other taxa of *Protictitherium* will provide useful information for its taxonomic determination.

Comparison with the French protictitheres. The type material (maxilla and mandible) of *P. gaillardii* originates from the locality La Grive and was originally described as *Herpestes crassus* (Gaillard 1899, p. 60; pl. II, Figs. 1, 3), although it was later transferred to *Progenetta gaillardii* (Forsyth-Mayor 1903). The materials from La Grive and the taxon *Herpestes crassus* were considered as the genotype of the new genus *Protictitherium* (Kretzoi 1938). However, the taxon has long been referred to as *Progenetta gaillardii* (Viret 1951; Mein 1958; Crusafont-Pairó and Petter 1969) until its transfer to *Protictitherium* by Schmidt-Kittler (1976). The RPI protictithere differs from the type material of *P. gaillardii* in the following (Fig. 5a–d): (1) its main cusps(-ids) are lower; (2) the P2,3 lack mesial cingular projection, which is strongly developed in the type material of *P. gaillardii*, and they bear a clear p.a.c. instead of a distal cingular projection in the type; (3) the carnassial has a stronger parastyle, lower paracone, shorter and more curved buccally metastyle blade and stronger protocone, situated in line with the mesial border of the parastyle; in the type material the protocone clearly exceeds the mesial border of the parastyle; (4) the M1 has a less buccally projected paracone and stronger protocone; (5) the M2 is remarkably larger; (6) the p3 lacks a.a.c., while in the type there is a vestigial one; (7) the p4 has stronger p.a.c., as well as stronger and more elevated lingual projection of the disto-lingual cingulum, suggesting higher molarization than the type; (8) the lower carnassial has a stronger metaconid and larger talonid with stronger entoconid; the talonid's dimensions are 4.92×4.91 mm in RPI-68 and $2.53\text{--}3.68 \times 3.50\text{--}4.22$ in *P. gaillardii*.

In addition to La Grive, *P. gaillardii* is also known from the French localities of Simorre and En Pejouan. Two mandibular fragments are known from En Pejouan, housed in MNHN (Fig. 6b). The RPI-68 mandible, besides being smaller, differs from this material in its lower main cusps, weaker a.a.c. of the p4, larger talonid and weaker entoconid of the m1 (Fig. 6a, b). A mandibular fragment of *P. gaillardii* from Simorre is also housed in MNHN (Fig. 6c); it has similar differences from the RPI-68 as those referred to above (Fig. 6a, c).

The type material of *P. crassum* also originates from the locality La Grive. It was originally described as *Herpestes*

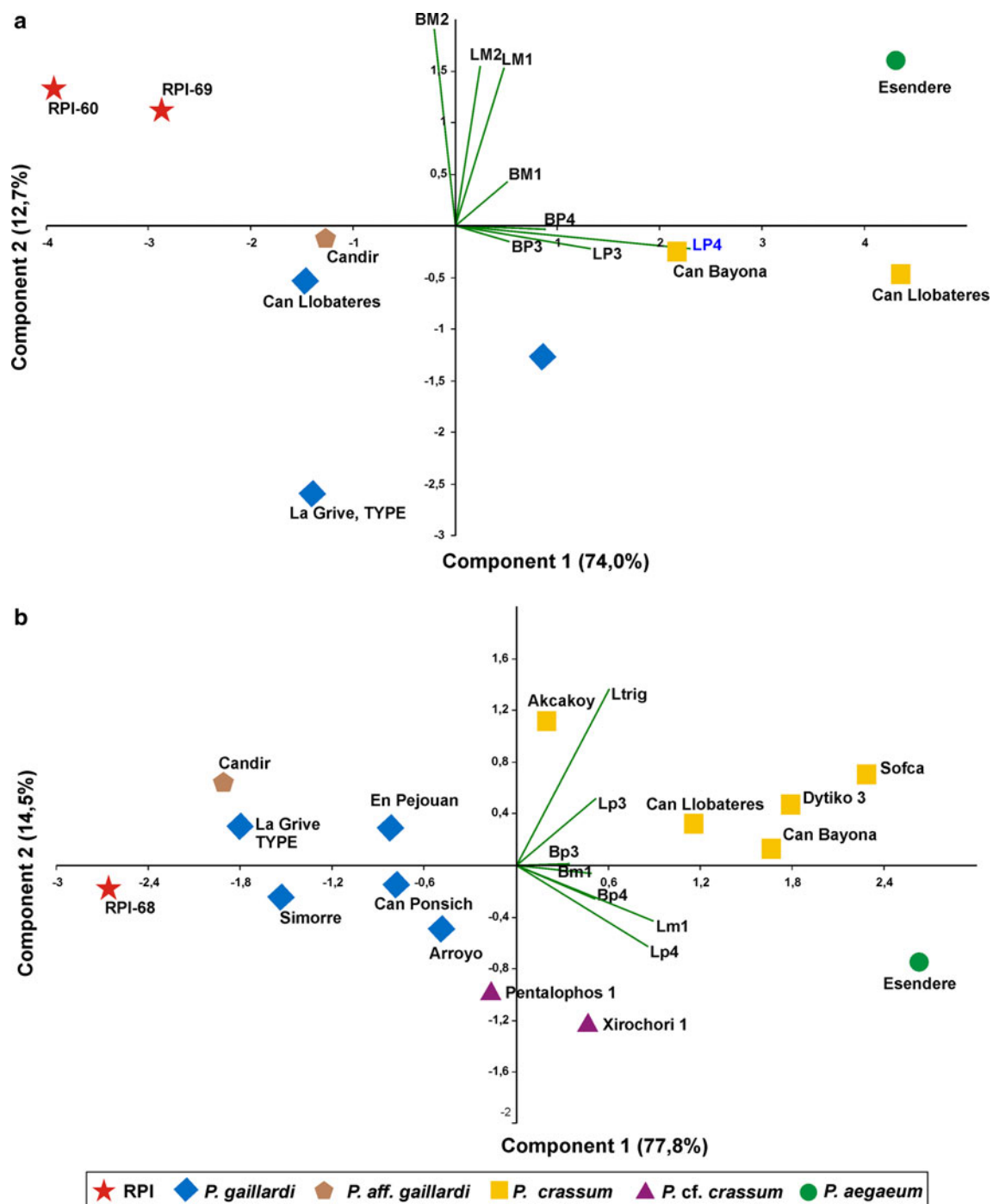


Fig. 3 Principal component analysis of the upper (a) and lower (b) dentition of *Protictitherium* from various localities

crassum based on some mandibular remains (Depéret 1892 p. 31; pl. I, Figs.14–17); for its history and synonyms, see Werdelin and Solounias (1991). Based on the description and illustrations of the type material (Depéret 1892; Viret 1951; Mein 1958), *P. crassum* differs from the RPI protictithere in the larger size (Figs. 3, 4), the position of the carnassial's protocone (it is situated in front of the mesial border of the parastyle), the stronger p.a.c. of the lower

premolars, the stronger a.a.c. of the p3,4, and the relatively smaller talonid and lower entoconid of the m1.

Comparison with the Greek protictitheres. The Greek protictitheres are referred to two main taxa *P. gaillardii* and *P. crassum*, while an isolated m1 from RPI is referred to *P. aff. intermedium* (Koufos 2006a, 2011b). A maxillary fragment with P4-M1 dex and a mandibular fragment with p4 sin of *P. gaillardii* have been described from the early/

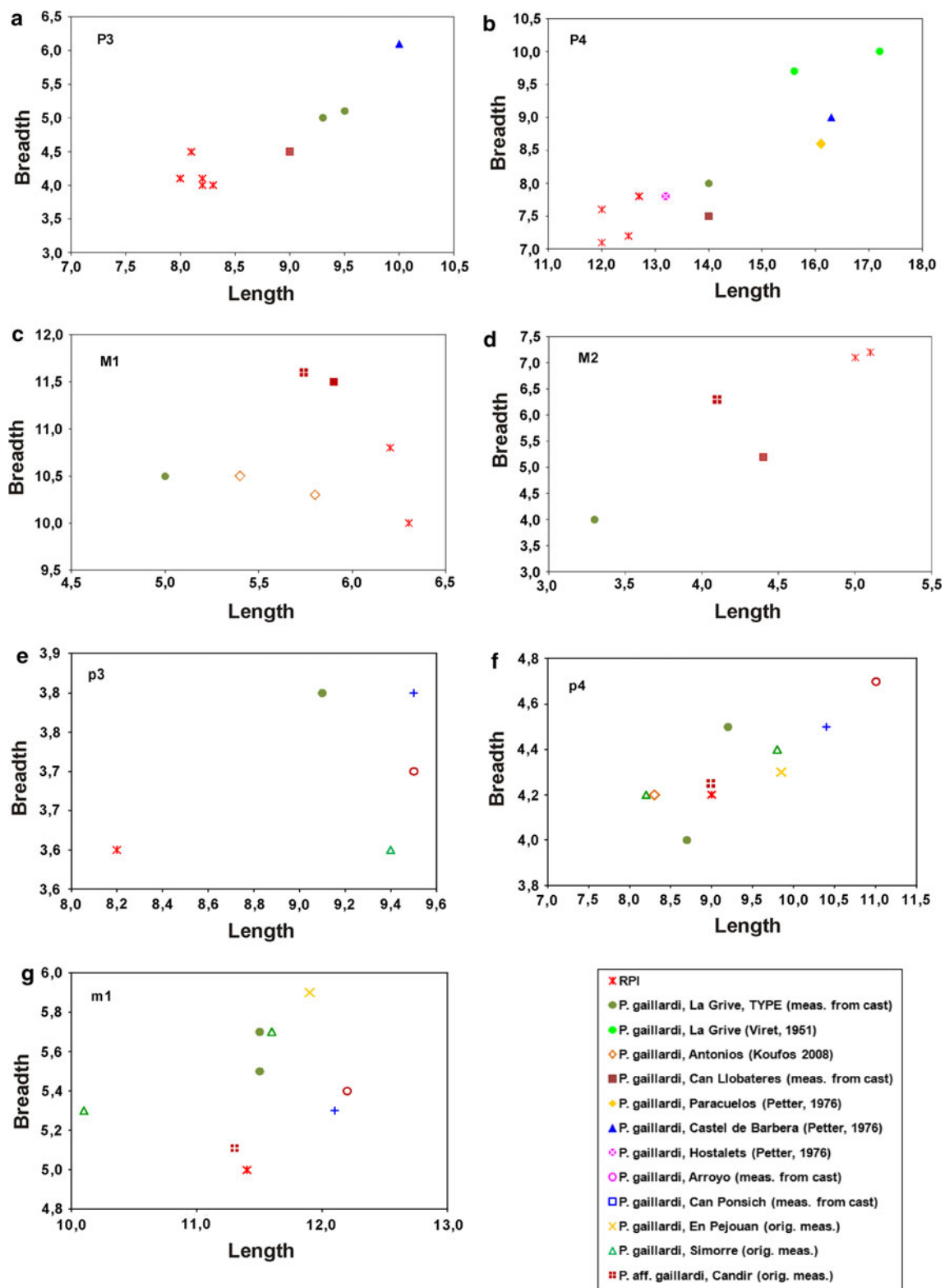


Fig. 4 Bivariate plot comparing the upper and lower teeth of *P. thessalonikensis* with *P. gaillardi* from various Eurasian localities

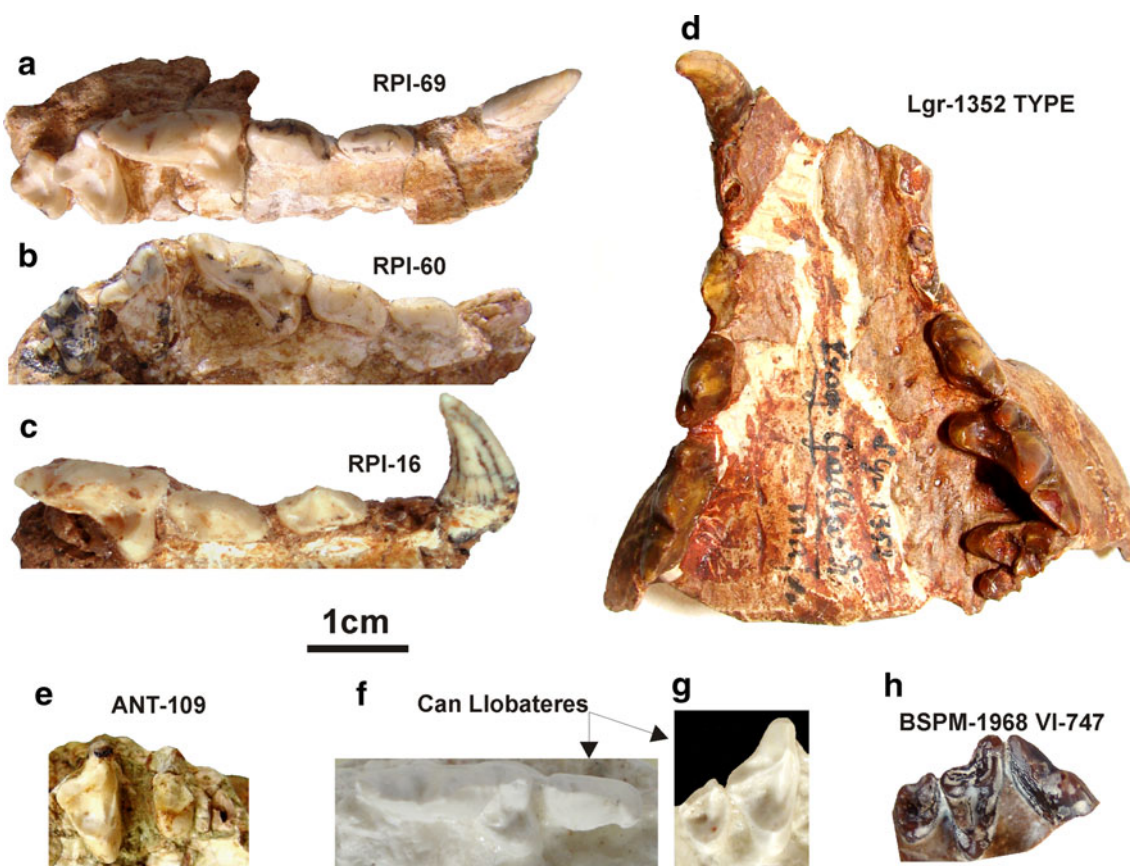


Fig. 5 Comparison of the upper dentition of *P. thessalonikensis* with *P. gaillardii* from various Eurasian localities. **a–c.** *P. gaillardii*, Ravin de la Pluie, Greece; **d.** *P. gaillardii*, La Grive, France; **e.** *P. gaillardii*,

Antonios, Greece; **f, g.** *P. gaillardii*, Can Llobateres, Spain (casts); **h.** *P. aff. gaillardii*, Çandır, Turkey

middle Miocene locality of Antonios (Koufos 2008). The RPI M1 is larger than that of Antonios, with a less buccally projected paracone and a larger protocone (Fig. 5a, b, e). *P. crassum* is known from two localities of the Axios Valley; a mandible has been reported from XIR and a hemimandible from DKO (Koufos 2000). The weaker p.a.c. of the premolars, the weaker a.a.c. of the p4 and the relatively stronger metaconid of the m1 distinguish the RPI material from the XIR and DKO *P. crassum*. Two mandibular fragments from the locality PNT of the Axios Valley are referred to *P. cf. crassum* (Koufos 2000). Their larger size, more molarized p4, relatively higher and more pointed cuspids, and stronger a.a.c. of the p4 separate them from RPI-68. Recently, *P. crassum* was recognized in the locality MLN of Samos from a mandible with almost complete dentition (Koufos 2009). The larger size and more molarized premolars of the Samos specimen distinguish it from the RPI-68.

Comparison with the Spanish protictitheres. The protictitheres are quite common in Spain, referred from several localities with *P. gaillardii* and *P. crassum* (Crusafont-Pairó and Petter 1969; Petter 1976). *P. gaillardii* is known from

the locality of Can Llobateres by a maxillary fragment with P3-P4 dex and another with M1-M2 dex (Petter 1976). A direct comparison of the studied RPI sample with these specimens indicates that the former has weaker p.a.c. in the P3, a protocone in line with the mesial border of the parastyle in the P4, a less buccally projected paracone and a stronger protocone in the M1, as well as a significantly larger M2 (Fig. 5a–c, f, g). A mandibular fragment with p3-m1 from the locality Arroyo del Val IV was described as *P. gaillardii* form A (Crusafont-Pairó and Petter 1969). Besides its smaller size, the RPI protictithere differs from Arroyo *P. gaillardii* in the absence of a.a.c. in the p3 (the Arroyo p3 has a vestigial a.a.c.), the significantly weaker a.a.c. and p.a.c. of the p4 (in RPI-68 the a.a.c. is rudimentary), the stronger and elevated lingual projection of the disto-lingual cingulum of the p4 (more molarized) and the relatively lower parastylid and paraconid, stronger metaconid, stronger and wider talonid and stronger entoconid of the m1 (Fig. 6a, e). Another mandibular fragment of *P. gaillardii* from the locality Can Ponsich was described as *P. gaillardii* form B (Crusafont-Pairó and Petter 1969). The comparison of the RPI-68 dentition with a cast of this

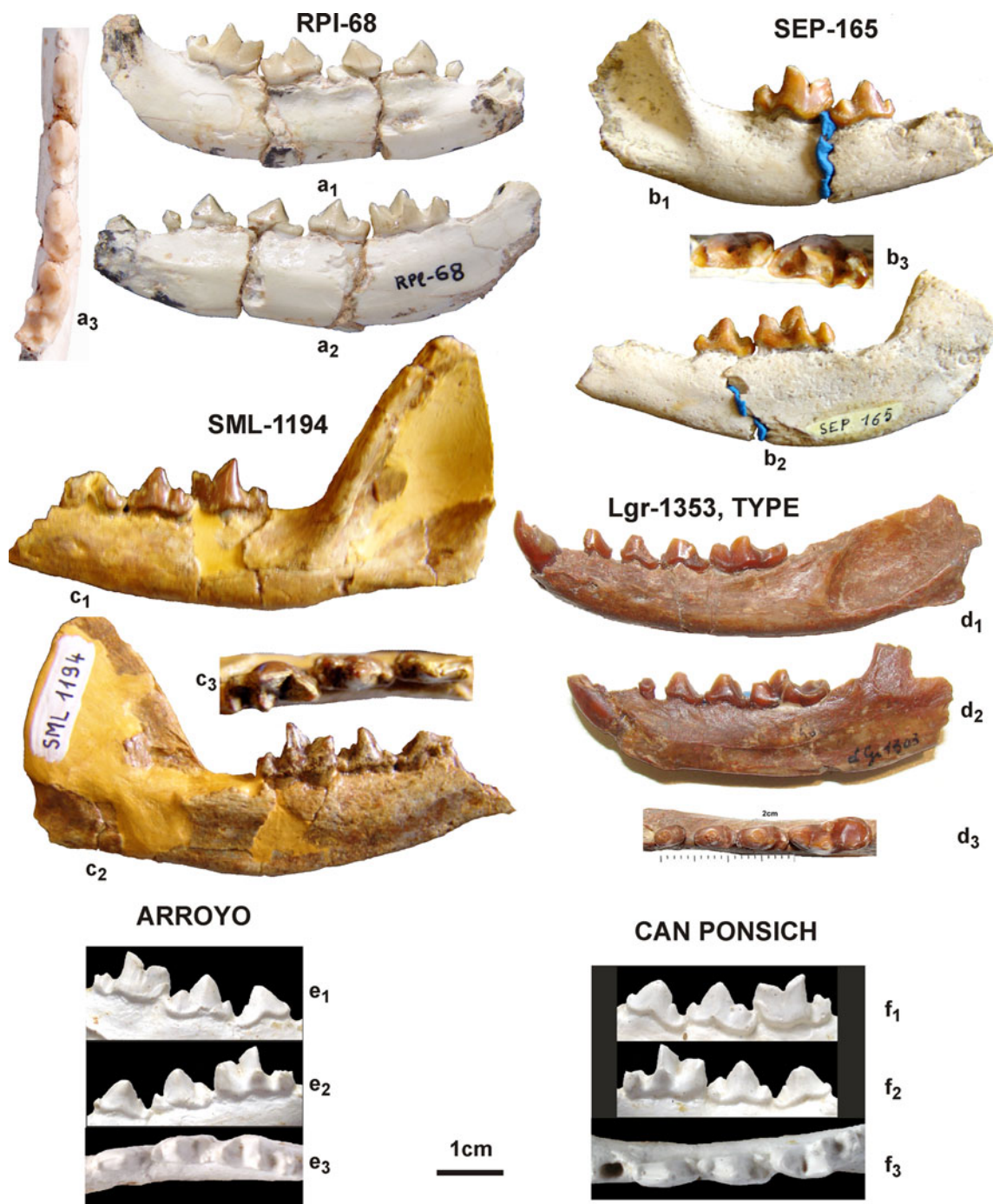


Fig. 6 Comparison of the lower dentition of *P. thessalonikensis* with *P. gaillardia* from various Eurasian localities. **a.** *P. gaillardia*, Ravin de la Pluie, Greece; **b.** *P. gaillardia*, En Pejouan, France; **c.** *P. gaillardia*,

Simorre, France; **d.** *P. gaillardia*, La Grive, France; **e.** *P. gaillardia* form-A, Arroyo, Spain (cast); **f.** *P. gaillardia* form B, Can Ponsich, Spain (cast). **1.** buccal, **2.** labial and **3.** occlusal view

specimen indicates the same differences as those seen in Arroyo material (Fig. 6a, f). *P. crassum* is also well known in Spain from several localities (NOW 2011). Some maxillary and mandibular remains from Can Bayona are described as *P. crassum llopsi* (Crusafont-Pairó and Petter 1969). The slenderer P3 (Table 1), the weaker p.a.c. and cingulum of the P3, the protocone in line with the mesial

border of the parastyle in the P4, the weaker p.a.c. of the lower premolars, the weaker a.a.c. of the p3,4 and the relatively stronger metaconid in the m1 of the RPI protictither, as well as its smaller size, distinguish it from Can Bayona *P. crassum*.

Comparison with the Asia Minor protictitheres. In Turkey *P. gaillardia* is known from Paşalar by a p4 and m1

described as *P. aff. gaillardi* (Schmidt-Kittler 1976). The dental comparison with RPI-68 indicates that the RPI p4 has smaller p.a.c., as well as more lingually projected and elevated disto-lingual cingulum, while the RPI m1 has smaller talonid with relatively smaller metaconid and entoconid; the dimensions of the talonid are 3.2×4.1 mm in Paşalar m1 versus 4.92×4.91 in RPI-68. A maxillary fragment with M1-M2 dex from Çandır is described as *P. aff. gaillardi* (Schmidt-Kittler 1976). The RPI molars are larger (especially the M2), and the paracone of the M1 is less buccally projected than that of the Çandır specimen (Fig. 5a–c, h). Two mandibular fragments of *P. aff. gaillardi* are also known from Çandır (Nagel 2003). Based on the illustrations of Nagel (2003: pl. 2, Fig. 2), their larger size, stronger a.a.c. of the p2,3 and higher main cuspids of the m1 distinguish it from RPI-68. *P. crassum* is reported from the localities Sofça, Akçakoy and Mahmutgazi (Schmidt-Kittler 1976). It has similar differences from the RPI sample as those referred to above. A new protictitherid was described from the locality Esendere (Karaburum Peninsula) under the name *P. aegaemum* (Kaya et al. 2005). It is larger (size of *P. crassum*) and clearly distinguished from the RPI sample; according to the authors it is closely related to *P. crassum* from which it differs in the high p4 and the high trigonid of the m1.

Some mandibular remains of a small-sized protictitherid, named *P. intermedium*, are known from the localities of Çandır and Paşalar (Schmidt-Kittler 1976). Comparison of the RPI-68 with its holotype (BSPM-1968II-736), in addition to the larger size of the former, shows some morphological differences. The RPI p2 has a lower main cuspid and a large distal cingular projection with a clear p.a.c. In *P. intermedium* the p2 lacks p.a.c. or cingular projection, but it bears two vestigial prominences in the distal border of the main cuspid and a rudimentary distal projection of the distal cingulum; moreover, in its mesiolingual base there is a vestigial cingular projection, which is absent in RPI-68. There are no substantial morphological differences in their carnassials. However, the cuspids of RPI-68 are higher, and the valley distinguishing the trigonid from talonid is deeper in the m1 of *P. intermedium*. A mandibular fragment from Paşalar (BSPM-1968VI-735) is also referred to *P. intermedium* (Schmidt-Kittler 1976). It has similar size to the holotype of the taxon, and it is smaller than RPI-68.

Another small-sized protictitherid from Turkey is *P. cingulatum*, described from the locality of Eskihisar on some mandibular remains (Schmidt-Kittler 1976). In comparison to RPI-68, besides its smaller size, it has a relatively stronger p.a.c. in the p2, an a.a.c. in the p3 (absent in RPI-68), relatively stronger a.a.c. in the p4, relatively smaller talonid in the m1 and stronger cingulum in all teeth. The upper dentition of *P. cingulatum* is only known by an isolated P3 and a single M1. The P3 has

similar size and morphology to the RPI one, but it has a much stronger lingual cingulum. The M1 of *P. cingulatum* is smaller with stronger buccal projection of the paracone and a less developed metacone than those of the RPI one. The smaller size and especially the strong cingulum distinguish *P. cingulatum* from the RPI material.

Conclusion

The locality RPI of the Axios Valley is well known because of the presence of the hominoid primate *Ouranopithecus macedoniensis* (Koufos 2006, in press and ref. cited). The RPI mammal fauna is rich, dominated by bovids and giraffids with several equids, a few carnivores and rare rhinos. The Vallesian palaeoenvironment of the Axios Valley and the wider area of the Eastern Mediterranean was open (savannah-like) with some small trees, shrubs, bushes and thick grass (de Bonis et al. 1992, 1999; Koufos 2006b; Merceron et al. 2005, 2007; Koufos and Konidaris 2011).

The protictitheres were unknown in Greece until the beginning of the 1980s when they were recognized in the DKO fauna of the Axios Valley by a hemimandible of *P. crassum* (Koufos 1980). During the following decades, more material has been unearthed from the various Axios Valley localities, enriching our knowledge about their diversity in Greece (de Bonis and Koufos 1991; Koufos 2000); recently, they were traced in the locality MLN of Samos Island (Koufos 2009). Except for the DKO and MLN protictitheres, which are dated to the Turolian, all the others originate from the Vallesian localities of PNT, XIR and RPI (Koufos 2000). The first RPI protictitherid was the specimen RPI-16, which was described as *Plioviverrops orbigny* (Koufos, 1980), the only known small hyaenid taxon from Greece at that time. This specimen, as well as the RPI-51, 60 and 68 have been referred to *P. aff. gaillardi* because of their smaller size (de Bonis and Koufos 1991; Koufos 2000). Despite some differences with that species a new species was not originally proposed for the RPI material, since the known material of the Eurasian protictitheres at that time was scanty and fragmentary with several synonymies and high taxonomic inflation (de Bonis and Koufos 1991; Koufos 2000). Three possibilities have been considered for the RPI protictitherid. Either it is a new species or subspecies, or a *P. gaillardi* with great geographic and stratigraphic distribution (Koufos 2000). The discovery of the maxillary fragment RPI-69 offered the opportunity for a re-examination of this material and for comparisons with several protictitherid remains, housed in MNHN and BSPM, as well as with some Spanish material. This comparison showed clear morphological differences from *P. gaillardi* and allows the recognition of a new species, named *Protictitherium thessalonikensis* n. sp.

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