

On some anthracotheriid (Artiodactyla, Mammalia) remains from northern Greece: comments on the palaeozoogeography and phylogeny of *Elomeryx*

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Abstract A few isolated mammal teeth from some Greek coal samples of unknown origin represent a small bothriodontine anthracotheriid, ascribed to *Elomeryx*. Analysis of the coalification stage of the fossil-bearing coal samples indicates the Lower Miocene Moschopotamos coal pits (Katerini Basin) as the most probable site of origin. The studied teeth are metrically close to *E. crispus* from Western Europe but share dental apomorphies with *E. borbonicus*, and *E. japonicus* and along with *Elomeryx* material from some Greek and Turkish sites pose a number of systematic, biochronologic, zoogeographic and phylogenetic questions. In the light of new evidence it seems that a small but advanced *Elomeryx* spanned the Oligo-Miocene boundary of S. Balkans. Furthermore, a revision of the old southern Balkan record together with a parsimony analysis suggest that *Bakalovia* is a first stage within the evolutionary history of *Elomeryx*, which complicated phylogeography is further discussed.

Keywords Bothriodontinae · *Elomeryx* · Greece · Oligo-Miocene · Phylogeny · Palaeogeography

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Introduction

Anthracotheriidae, a primitive and extinct group of Palaeogene to Pliocene artiodactyls known from the Old World and North America, is central to the discussion about the origin of hippos (e.g., Boisserie et al. 2005; Pickford 2008). Varying greatly in size, anthracotheriids are characterized by a long and narrow amastoid skull, orbits behind the M2 in derived taxa, heavy zygomatic arches, open post-orbital bar, narrow palate, complete dental formula, brachyodont and bunoselenodont molars with diverse trends in molar selenodonty, sexually dimorphic incisors and canines, upper molars with four or five cusps without hypocone but with a well-developed metaconule, enlarged third molars and a well-developed hypoconulid on the m3 (Coombs and Coombs 1977; Lihoreau and Ducrocq 2007). Botriodontine anthracotheriids are widely distributed in the Old World and North America, known by several genera and species (Lihoreau and Ducrocq 2007). Among them, *Elomeryx* Marsh, 1894 is the most widespread taxon but its intra- and intergeneric phylogenetic relationships are not yet fully understood (Hellmund 1991; Ducrocq and Lihoreau 2006; Lihoreau and Ducrocq 2007; Lihoreau et al. 2009; Tsubamoto and Kohno 2011).

Lüttig and Thenius (1961) were probably the first to record the presence of *Elomeryx* in the Greek part of Thrace (Fig. 1b). Over the next few years Ozansoy (1962), and Nikolov (1967) described more material of the same genus from Eastern (Turkish) Thrace, and Bulgaria, respectively (Fig. 1b). Nikolov and Heissig (1985) proposed later ascribing the Bulgarian sample from Burgas to the new genus *Bakalovia*. Since the 1960s no more *Elomeryx* material has been reported from the area, but recently a mandible of *Elomeryx* from Tozakli, Eastern Thrace, was briefly discussed by Islamoğlu et al. (2010) (Fig. 1b).

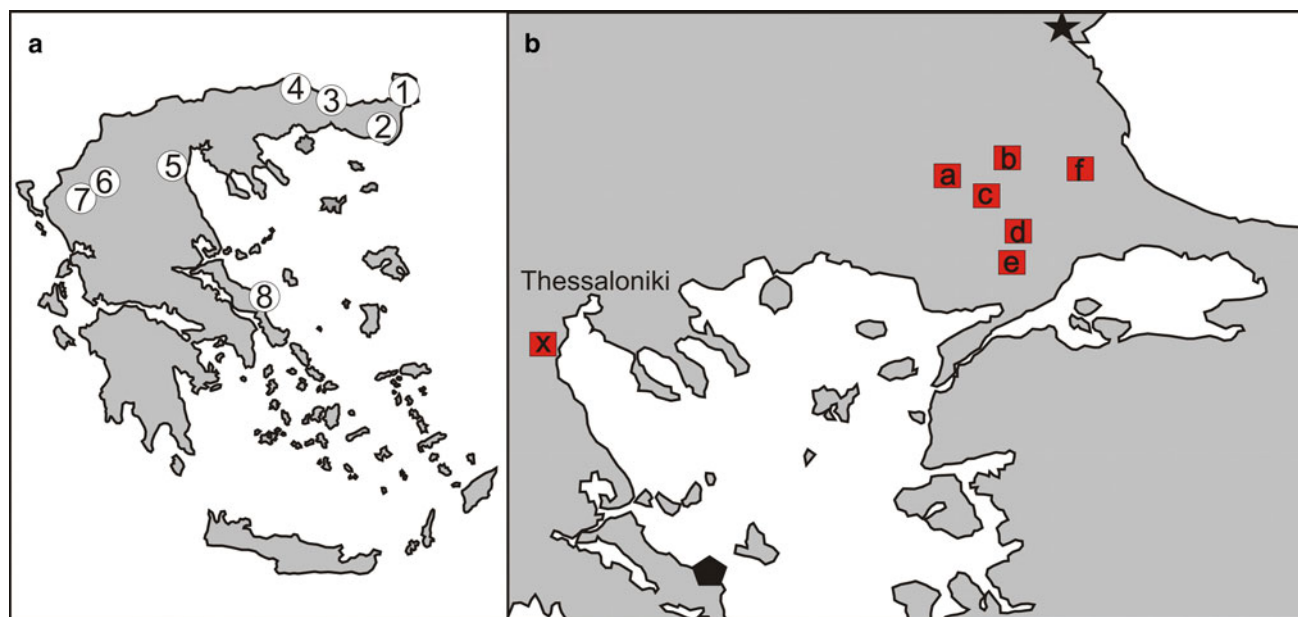


Fig. 1 Greek Palaeogene–early Miocene coal deposits (a) and local geographic distribution of bothriodontine anthracotheriids (b). 1 Orestias, 2 Alexandroupolis, 3 Kotili, 4 Paranesti, 5 Moschopotamos, 6 Middle Hellenic trough, 7 Ioanian flysh (Zagoria), 8 Aliveri-Kymi, black pentagon *Brachyodus*, Kalimeriani, Euboia; asterisk *Bakalovia*, Burgas, Bulgaria; squares *Elomeryx* from a Chandras,

Greece, b Haskoy, Turkey, c Sigircili, Turkey, d Tekirdağ, Turkey, e Tekirdağ-Malkara, Turkey, f Tozakli, Turkey, x possible provenance of studied sample: Moschopotamos coal pits (data from Christanis 2004; Islamoğlu et al. 2010; Lüttig and Thenius 1961; Melentis 1965; Nikolov 1967; Ozansoy 1962; Papanicolaou et al. 2004)

The 2009 reorganization and updated cataloging of the collections of the Museum of Geology and Palaeontology of the Geological Department of the Aristotle University of Thessaloniki (LGPUT) revealed a number of coal blocks containing isolated teeth of a bothriodontine anthracotheriid described and discussed here. Although small, this fossil sample is significant in view of the extreme rarity of pre-middle Miocene large mammals in Greece and the Southern Balkans and the inadequate knowledge of SE European anthracotheriids.

Unfortunately, the fossil-bearing coal blocks lack geographic and/or stratigraphic labels, requiring an indirect inquiry of their origin. Coal deposits are widely distributed in Greece. Most of them occur in latest Neogene–Quaternary stratigraphic sequences that undoubtedly postdate the known time-range of Eurasian anthracotheriids. Palaeogene–middle Miocene Greek coal deposits are rare, being known mainly in western Thrace–Eastern Macedonia (1–4 in Fig. 1a), Katerini District (5 in Fig. 1a), Central Euboia (8 in Fig. 1a), and Western Greece (6, 7 in Fig. 1a) (Christanis 2004; Papanicolaou et al. 2004). Apart from Western Greek coal locations that are related to syn- and post-orogenic processes and marine–brackish environments, all the other mentioned sites could be considered as possible provenance areas of the studied material.

Materials and methods

In order to assess the possible origin of the fossil material ('unknown' coal sample #1), a random coal sample was collected from four coal deposits suspected to have yielded the fossils, namely Avantas (Eastern Greek Thrace; sample #2), Xanthi (Western Greek Thrace; sample #3), Siderokastro (Eastern Macedonia; sample #4) and Moschopotamos (Katerini Basin; sample #5). As the petrological, chemical and mineralogical compositions of coal vary strongly from place to place within one deposit, the comparison among various coal samples cannot depend on the maceral, geochemical and mineralogical analyses, respectively. In contrast, the huminite/vitrinite reflectance provides a tool for measuring the coal rank, i.e., the coalification (sensu maturity) stage a coal has reached. The rank within a coal deposit varies slightly or usually not at all. As the measurement is carried out on a single maceral group (huminite), particularly on one specific maceral only, namely eu-ulminite B, petrographic, chemical or mineralogical variability is avoided (Taylor et al. 1998).

All the samples were dried at 105 °C in order to remove residual moisture and then crushed to –1 mm and homogenized. Polished blocks were prepared according to International Standards (ISO 7404-2 2004a): the crushed samples were firstly embedded with epoxic resin (Epofix of

STRUERS[®]) in cylindrical mounts and the prepared blocks were ground using a series of grinding papers (no. 320, 500, 800, 1200, and 2400), then polished using diamond pastes ($\varnothing < 3 \mu\text{m}$ and $\varnothing < 1 \mu\text{m}$) and finally, alumina suspension ($\varnothing < 0.06 \mu\text{m}$). The blocks were examined under a LEICA DMRX coal-petrography microscope equipped with an MPV photometer in oil immersion and 500 \times total magnification. Random huminite reflectance (R_r) was measured on eu-ulminite B according to ISO 7404-5 (2004b).

Dental terminology follows Coombs and Coombs (1977) and Lihoreau and Ducrocq (2007: fig. 7.1). The taxonomy follows Hellmund (1991) with the exception of *Brachyodus cluai* Deperet, 1906 that is considered to be a distinct species of *Elomeryx* (in agreement with Ducrocq and Lihoreau 2006). All measurements are in mm.

The studied material is compared with *E. crispus* samples from: Möhren 13, Möhren 9 and Grafenmühle 10 stored in the Bayerische Staatssammlung für Paläontologie und Historische Geologie, München (BSPM); *E. borbonicus* samples stored in the Centre de Conservation du Musée des Confluences, Lyon (CCMCL) and in the Laboratoire de Géology, Université Claude-Bernard Lyon I (GUL); the cast of PIUW 16397 (here referred to as the Chandras palate) described by Lüttig and Thenius (1961) and stored in the Department of Paleontology, University of Vienna (PIUW); *Elomeryx* sample from Sigircili, Eastern Thrace stored in BSPM; *Elomeryx* material from Tekirdağ-Malkara, and Tozakli Eastern Thrace stored in the Paleontological Department of Natural History Museum of the Mineral Research and Exploration Institute of Turkey, Ankara (MTA).

The phylogenetic relationships among *Elomeryx* species and related taxa discussed in this paper were obtained through a parsimony analysis based on 23 binary and 7 multistate dental, and mandible, characters, 19 of them adopted from Lihoreau and Ducrocq (2007) (Electronic Supplementary Material, Appendices I and II). The branch and bound algorithm and Fitch optimization criteria have been followed using PAST ver. 2.12 free software (Hammer et al. 2001). The cladogram was rooted to *Siamotherium* Suteethorn et al., 1998, regarded as the most primitive

member of the family Anthracotheriidae (Lihoreau and Ducrocq 2007).

Origin and age of the material

The results of the reflectance measurements are presented in Table 1. The Oligocene Xanthi (sample #3) coal deposits display higher mean random reflectance values (0.7 %) than the unknown one (sample #1; 0.39 %). High mean reflectance values are also reported for Upper Paleogene coals from Turkey and the Balkans (Belkin et al. 2010; Karayigit et al. 2002), whereas mean reflectance values of the rich Upper Miocene to Pliocene Greek coals are usually below 0.35 % (Christanis 2004). Both samples picked up from the Oligocene Avantas (sample #2) and the Oligo-Miocene Siderokastro (sample #4) coal deposits show minimum reflectance values close to the maximum value of the unknown sample (sample #1), but they exhibit a significantly higher coalification stage on the average (Table 1). The reflectance of the unknown (#1) sample is absolutely similar to the ranges reported for Lower Miocene coals from Serbia, and Turkey (Demirel and Karayigit 1999; Gürdal and Bozcu 2011; Karayigit 2005; Žitović et al. 2005, 2010), and identical to that from Moschopotamos sample (sample #5 in Table 1) that proved to have reflectance values ranging from 0.35 to 0.45 %, in agreement with the data provided by other researchers (Kalkreuth et al. 1991; Kotis 1997; Papanicolaou 1994; Papanicolaou et al. 2000). Thus, Moschopotamos seems to be the most probable site of origin of the unknown coal sample and consequently of the fossils in question.

The Moschopotamos coal deposit is located 15 km west of the city of Katerini, N. Greece (5 in Fig. 1a; 40°19'20"N, 22°18'51"E). The lignite derived from helophytic reed-sedge and tree vegetation and it belongs to the Moschopotamos lithostratigraphic formation (Fm) of Katerini Basin that is exposed around the homonymous village and represents a low deltaic depositional environment (Kotis 1997; Sylvestrou 2002 and literature therein). Moschopotamos Fm consists of clays, sands, silts, and marly silts with lignite intercalations few cm to 1 m thick.

Table 1 Results of the random mean reflectance measurements ($R_{r,oil}$ in %)

Sample	Provenance	Mean $R_{r,oil}$	Maximum $R_{r,oil}$	Minimum $R_{r,oil}$	SD	<i>N</i>
#1	Unknown	0.388	0.445	0.347	0.037	20
#2	Avantas	0.498	0.524	0.428	0.047	4
#3	Xanthi	0.666	0.790	0.515	0.068	13
#4	Siderokastro	0.506	0.589	0.441	0.037	20
#5	Moschopotamos ^a		0.45	0.35		

^a Values from Kotis (1997)

Biochronological data based on pollen and micromammals indicate that the Moschopotamos Fm is most likely to be of late Lower Miocene age (Benda and Meulenkamp 1979; Ioakim and 1986; Kotis 1997; Sylvestrou 2002).

Systematic palaeontology

Class: Mammalia Linnaeus, 1758
 Order: Artiodactyla Owen, 1848
 Family: Anthracotheriidae Leidy, 1869
 Subfamily: Bothriodontinae Scott, 1940
 Genus: *Elomeryx* Marsh, 1894
 Type species: *Elomeryx armatus* Marsh, 1894
 Diagnosis: in Lihoreau and Ducrocq (2007: 95)

Elomeryx sp.

Studied material

Upper right canine, LGPUT MP35; right P3, LGPUT MP36; right P4, LGPUT MP37; right m1 or m2, LGPUT MP38; right m3, LGPUT MP39.

Comparative description

Nearly all fossil specimens extracted from or still in the coal samples belong to an extremely deformed and crashed mandible and maxillae of a single old male individual, judging from the size and shape of the canine and the wear stage of the m3. The low-crowned cheek teeth are of bunoselenodont type with finely wrinkled enamel and rather weak cingula. P4 have well-developed cingula and the distal crest of the lingual cusp does not reach the distal cingulum; the buccal cuspids of the m1 or m2, and the m3 are highly crescentic and wider than the lingual ones; the hypoconulid of the m3 forms a transversely compressed loop that is rather narrow and buccally displaced; the prehypocristid (cristid obliquid) of the m3 is strong, descending on the distal trigonid wall but without reaching the lingual wall of the tooth; four cristids issue from the m3 metaconid. This set of features suggests *Elomeryx* as the most likely generic affiliation (Hellmund 1991; Lihoreau and Ducrocq 2007; Lihoreau et al. 2009; Tsubamoto and Kohno 2011). European species of *Elomeryx* include *E. crispus* known from the latest middle Eocene to early late Oligocene, *E. borbonicus* known from the late Oligocene–early Miocene, and *E. cluai* (considered by Hellmund 1991 to be subspecies of *E. crispus*) known exclusively from the late early Oligocene of Spain (Hellmund 1991; Ducrocq and Lihoreau 2006; Lihoreau et al. 2009).

The thin enameled, pointed and caniniform upper canine is compressed transversally, and has an elongated tear-

shaped cross section with a rather sharp and finely serrated distal edge (Fig. 2). This condition differs from the one usually seen in *E. crispus* and *E. cluai* and is more similar to the upper canine morphology reported for *E. borbonicus* (Hellmund 1991). Original comparison of LGPUT MP35 with the male canine of GUL FSL8514 of *E. borbonicus* from St. Henri, France (Geais 1934), shows close morphological resemblance with similar flattening ($TDb/APDb \times 100 = 57.7$ and 53.6% , respectively) and backward curvature; nevertheless, the Greek specimen is about 30% smaller in linear measurements (Table 2). Two upper male canines of *E. crispus* from Möhren 13 (namely, BSPM1529, and BSPM1480) are similar in size with LGPUT MP35 (Table 2) but less compressed transversally ($TDb/APDb \times 100 = 74.5$ and 64.0% , respectively), and not serrated distally. Hellmund (1991) indicated male upper canine serration as a diagnostic feature of *E. borbonicus*, whereas Lihoreau and Ducrocq (2007) designate this character as diagnostic at the generic level. Although the total number of canine specimens per species is rather inadequate for definite conclusions, we are inclined to recognize this feature as characteristic of advanced *Elomeryx* species.

The P3 (Table 3) is small for *E. borbonicus* (P3 length > 15.7 ; Lihoreau et al. 2009) and slightly narrower than that of *E. crispus* (P3 width > 10.6 ; Lihoreau et al. 2009), metrically approaching the Spanish *E. cluai* (Lihoreau et al. 2009: tab. 1). The tooth is heavily worn but it shows a typical disto-lingual talon. In occlusal view the tooth outlines a right triangle with the right angle at disto-lingual position. The tooth looks more symmetrical than

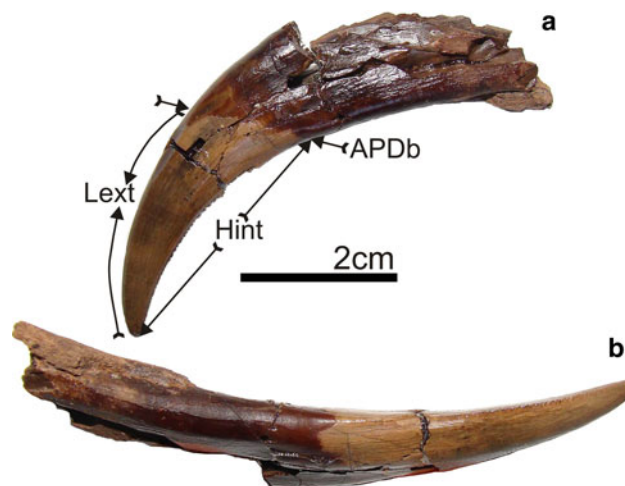


Fig. 2 Upper canine LGPUT MP35 in **a** mesial and **b** lingual view. *APDb* anteroposterior diameter at the base of the crown, *TDb* (not shown) buccolingual diameter at the base of the crown (obtained perpendicularly to *APDb*), *Lext* length of the canine crown along its anterior surface, *Hint* distal height of the canine from the tip to the base of the crown

Table 2 Metrical comparison of the upper canine of *E. crispus*, *E. borbonicus* and *Elomeryx* from Moschopotamos

	LGPU T MP34	<i>E. borbonicus</i>	<i>Elomeryx crispus</i>	
		St. Henri	Möhren 13	
		FSL8514	BSPM1529	BSPM1480
APDb	12.3	16.8	11.3	12.0
TDb	7.1	9.0	8.4	7.7
Hint	31.0	46.5	27.2 ^a	37.0 ^a
Lext	37.0	50.0	31.5 ^a	43.0 ^a

Abbreviations as in Fig. 2

^a Maximum estimated values

Table 3 Teeth measurements of *Elomeryx* from Moschopotamos, Greece

	Length	Width	
		Anterior lobe	Posterior lobe
P3, LGPUT MP36	12.6	9.9	
P4, LGPUT MP37	9.2	13.8	
m1 or m2, LGPUT MP38	16.7	13.2	12.6
m3, LGPUT MP39	25.6	14.5	13.9

those of *E. crispus* figured by Hellmund (1991) and Lihoreau et al. (2009) and seems to be rather closer to the symmetrical P3 morphology seen in *E. armatus* (Hellmund 1991: Pl. 1, fig. 1) but intraspecific variation may be great. The buccal cingulum is weak and the distal and palatal roots are fused together, a condition also seen on some specimens of *E. crispus* (Hellmund 1991).

The P4 is metrically similar to that from the Chandras palate (Lüttig and Thenius 1961), i.e., slightly shorter and significantly narrower than the P4 of *E. borbonicus*, and within the size ranges of both *E. crispus* and *E. cluai* (Fig. 3; Table 3). The cingulum of the P4 is strong and the distal crest of the lingual cusp does not reach the distal border of the tooth as in all *Elomeryx* species (Lihoreau et al. 2009) (Fig. 4). 82 % of the P4 of *E. crispus* lack lingual crests on the lingual cusp, whereas 16 % of the specimens bear a disto-lingual crest (Hellmund 1991). In the studied sample the lingual cusp of P4 bears a rather strong crest trending mesio-lingually to lingually (as in some specimens of *E. cluai* and *E. borbonicus* according to Hellmund 1991; Schaub 1948), whereas another weak disto-lingual crest is present, though weakly developed (Fig. 4). The mesial border of the P4 is rather straight instead of concave and therefore more similar to *E. borbonicus* than to *E. crispus*.

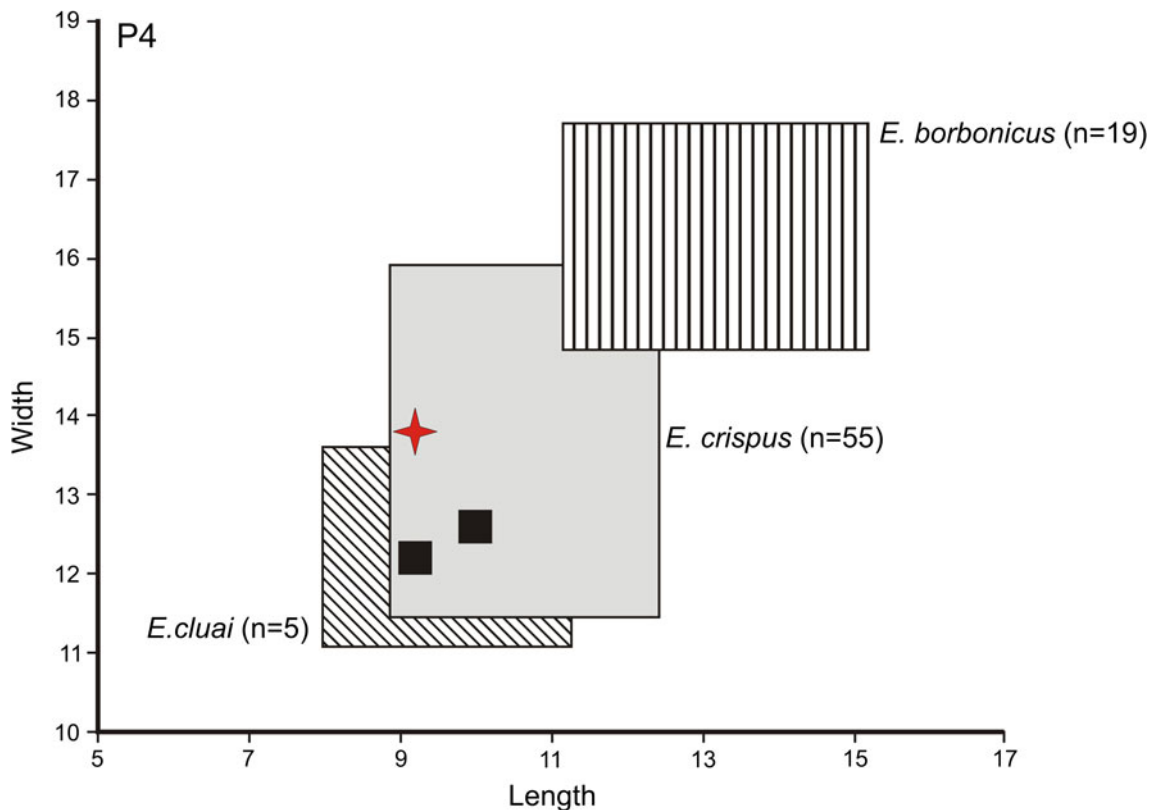


Fig. 3 Metrical comparison of P4 of the European species of *Elomeryx*. Cross LGPUT MP37, squares *Elomeryx* palate from Chandras, Greek Thrace (data from Hellmund 1991; Lihoreau et al. 2009; Lüttig and Thenius 1961)

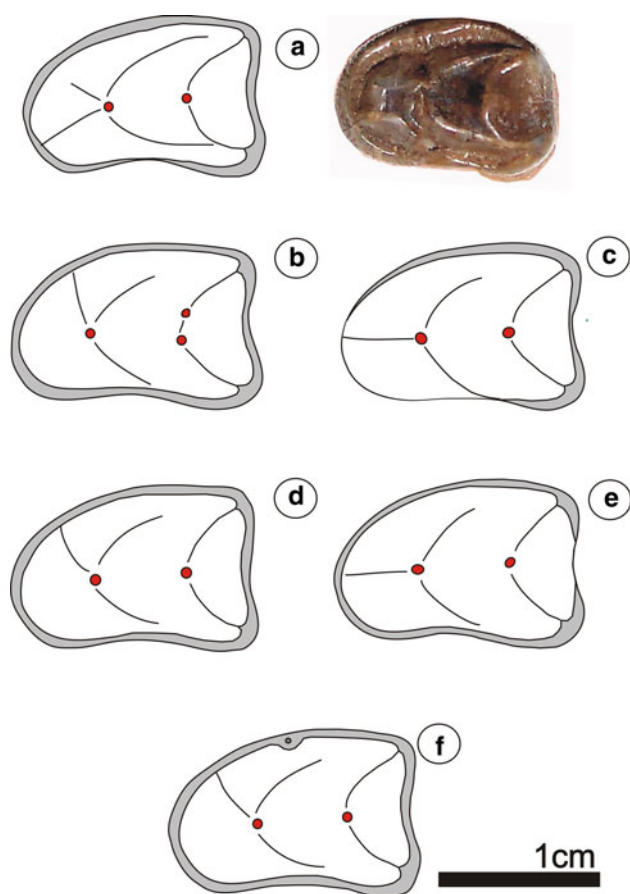


Fig. 4 Morphological comparison of P4, LGPUT MP37. **a** Occlusal morphology of LGPUT MP37; **b**, **c**, **f** P4 morphotypes of *E. borbonicus*; **d** P4 morphotype of *E. borbonicus* and advanced *E. crispus*; **e** P4 morphotype of *E. cluai* (data from Hellmund 1991)

The m1 or m2 is slightly larger than that of *E. cluai*, and within the size range of both *E. borbonicus* and *E. crispus* (Table 3; metrical comparison with data provided by Hellmund 1991). The tooth is strongly worn prohibiting detailed morphological observations. A weak mesial and a less developed distal cingulum are still present. The posthypocristid is rather short and thus the posterior lobe appears open disto-lingually but this may be only due to the advanced wear stage.

The m3 is larger than that of *E. cluai* and shorter than that of *E. borbonicus*, being well within the reported size range of *E. crispus* (Fig. 5; Table 3). The hypoconulid of LGPUT MP39 is bicuspid like that of *E. crispus* from Detan Dvorce (Czech Republic) illustrated by Hellmund (1991: Pl. 4, fig. 6), and much less compressed bucco-lingually than that of *E. borbonicus*. Similar to *E. borbonicus* and advanced (sensu Hellmund 1991: fig. 7) *E. crispus* the posterior lobe shows a characteristic “Y” pattern resulting from the crossing of the prehypocristid with the preentocristid, whereas a direct mesial entoconid–hypoconid connection is absent (Fig. 5). The postectometacristid of

LGPUT MP39 is less prominent than in *E. crispus* (e.g., Hellmund 1991, Pl. 4, figs 5–8) and comparable to that of *E. borbonicus*. LGPUT MP39 also shows a weak and short posthypocristid, linked with the prehypocristid (or pre-hypoconulid cristid) but also with the entoconid through a weak accessory transverse crest (Fig. 5). This character is unlike *E. crispus* and *E. borbonicus*, both of which exhibit a strong crest directly connecting the hypoconid with the entoconid distally, and intermediate between *Elomeryx* and *Bakalovia* (Nikolov 1967; Nikolov and Heissig 1985; Hellmund 1991), the latter lacking the junction between the posthypocristid and postentocristid in the lower molars. The specimen LGPUT MP39 is close dimensionally to *Bakalovia palaeopontica* and smaller than *Bakalovia astica* which, however, might show an incipient transverse crest on the entoconid of some m3 (Nikolov 1967: pl. 18, fig. 3).

Phylogenetic relationships

The cladistic analysis carried out by Lihoreau and Ducrocq (2007: fig. 7.2) failed to adequately resolve the phylogenetic relationships among *Elomeryx* species and its allies, due to the morphological stability at the genus level, as well as to the high degree of homoplasies among anthracotheriids. The parsimony analysis conducted here is principally based on a subset of the data matrix used by the above authors (Lihoreau and Ducrocq 2007: table 7.1) with minor modifications and addition of 11 dental characters (ESM Appendices I and II), as well as with the introduction of three more taxa: *Bakalovia* Nikolov and Heissig, 1985 from Bulgaria (Nikolov 1967), *Elomeryx japonicus* (Matsumoto in Tokunaga, 1925) from Japan (Tsubamoto and Kohno 2011) and *Elomeryx* from Moschopotamos, Greece (ESM Appendix I). The analysis provided three maximally parsimonious trees 56 steps long (Fig. 6). As in Lihoreau and Ducrocq (2007: fig. 7.2), the monophyly of *Elomeryx* is demolished. All trees support *Bakalovia* as the sister group of *Elomeryx* plus advanced bothriodontines (node 2 in Fig. 6). The Miocene Indo-Pakistani *Sivameryx* appears as the sister group of a clade incorporating *Elomeryx* species and *Arretotherium* (node 3 in Fig. 6). Nevertheless, some character changes interpreted as homoplasies in the current analysis [i.e., 27(1), d(1), f(1) and j(2)] might indicate closer relationships between *Sivameryx* and advanced *Elomeryx* species (e.g., Lihoreau 2003). Based on a single reversal [12(0)] *Arretotherium* appears as the sister group of *Elomeryx armatus*; this North American clade is branching next to *E. crispus* and appears as the sister group of an unresolved clade incorporating advanced Eurasian *Elomeryx* species (*E. borbonicus*, *E. japonicus*, and *Elomeryx* from Moschopotamos) (node 6 in Fig. 6).

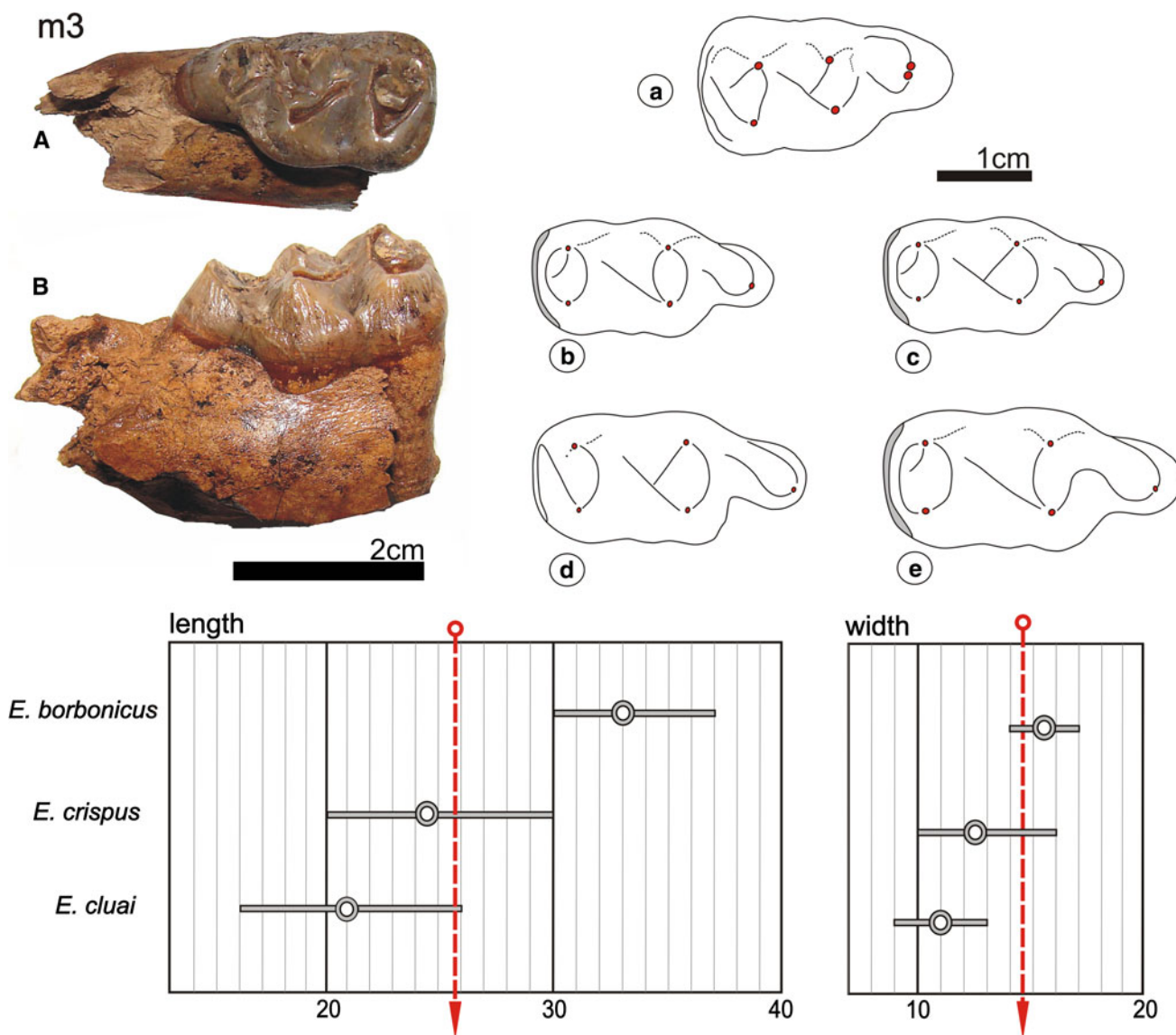


Fig. 5 Metrical and morphological comparison of m3, LGPUT MP39. Circles represent mode values, dashed lines represent measurements of LGPUT MP39, A occlusal and B buccal views of LGPUTh MP39. a Occlusal basic morphological pattern of LGPUT

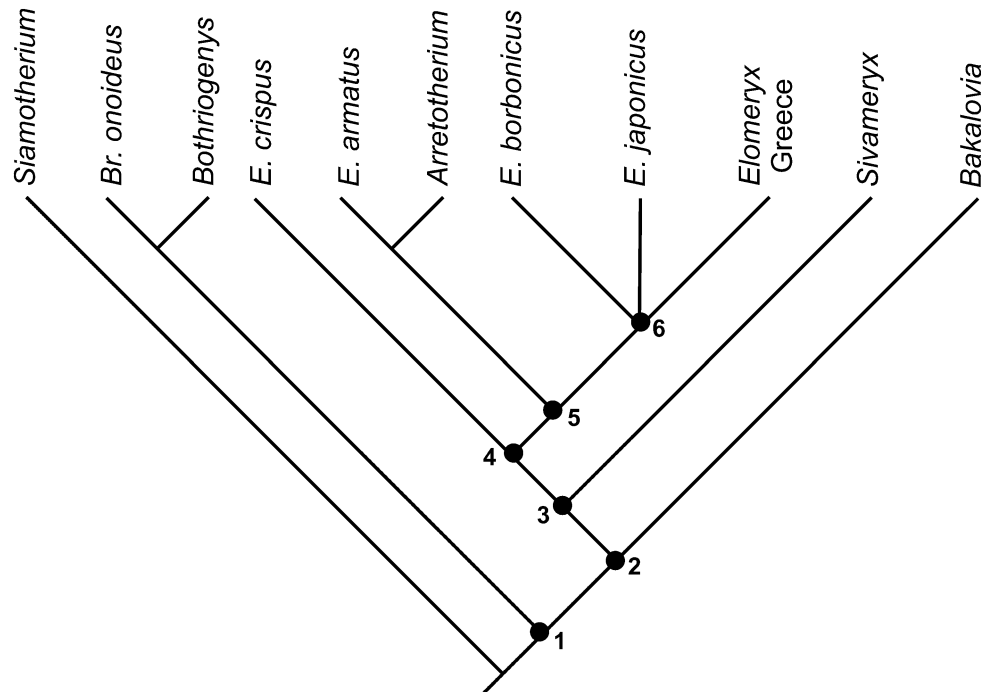
MP39 (reversed), b m3 morphotype of *E. crispus*, c m3 morphotype of advanced *E. crispus*, d m3 morphotype of *E. borbonicus*, e m3 morphotype of *Bakalovia* (data from Hellmund 1991)

Discussion and concluding remarks

The Paleogene–early Miocene Thrace and adjacent areas of the Southern Balkans represented a suitable environment for anthracotheriids, especially bothriodontines: *Brachyodus*, *Bakalovia* and *Elomeryx* have a sporadic but certain fossil record here (Fig. 1b), whereas *Elomeryx* appears diachronously. Hellmund (1991) attributed most of the old Greek and Turkish *Elomeryx* material to *Elomeryx crispus*. Reexamination of the Chandras palate (PIUW 16397), originally described by Lüttig and Thenius (1961: fig. 1), leaves no doubts about its generic attribution (typically

pentacuspitate molars with small paraconule almost equal in size to the protocone; protocone with a single preprotocrista and double postprotocrista; preprotocrista in contact with the paraconule; postparacristule in contact with the buccal postprotocrista). Nevertheless, some particular features, as well as the tooth proportions, make the species affiliations more delicate. The metaconule displays three crests, the strong mesio-lingual one present in *E. cluai* and *E. crispus* but not in *E. borbonicus*. The less worn M2 and M3 show a weak lingual postprotocrista that does not reach the mesio-buccal crest of the metaconule (or premetacristule) but such a join is clear on the M1 (Lüttig and Thenius

Fig. 6 Strict consensus of three most parsimonious trees (Length: 56; ECI: 0.64; ERI: 0.84) from analysis of the data matrix in ESM Appendix I. Character changes supporting nodes: node 1 16(1), 17(1), 34(1; reversed in *Bakalovia*), 38(1); node 2 7(1), 8(1), 12(1), 24(1), 29(1), 38(2); node 3 26(1), b(1); character changes 17(2), 18(1; reversed in *Arretotherium*), and 39(1) may further support node 2 or node 3; node 4 23(1), 35(1), g(1; reversed in *Elomeryx* from Moschopotamos); node 5 27(1), a(1), i(1), k(1), j(2); node 6 6(1), 9(1), b(2)



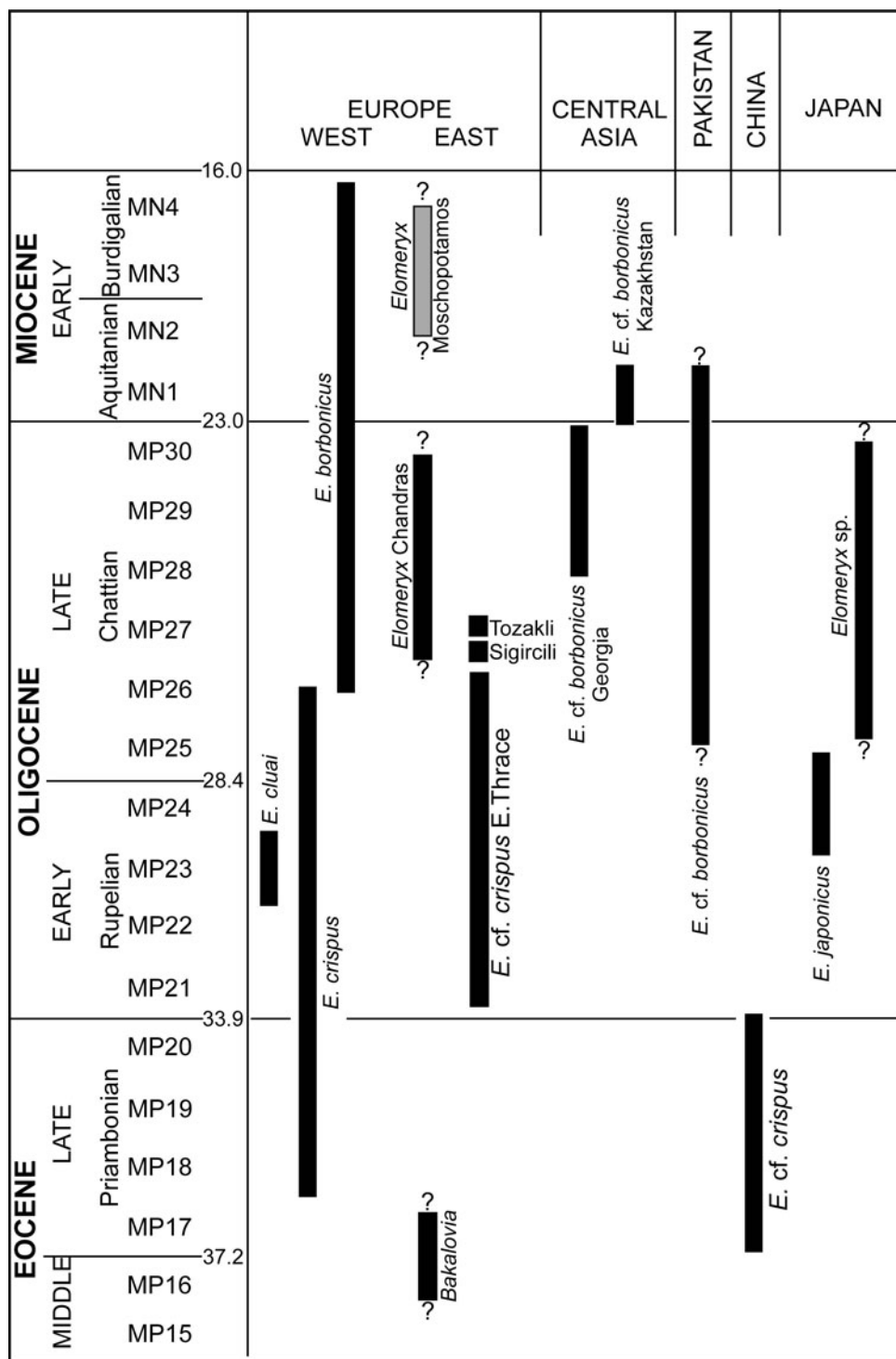
1961: fig. 1). Thus, the transverse valley is continuous on the M2 and M3, as in *E. borbonicus*, but blocked lingually in the M1, as in *E. crispus*. The postprotocrista is buccally directed and connected with the postparacristule. The P4 is similar to that from Moschopotamos, but with an additional tubercle emerging from the mesial cingulum (like in types “B”, “J”, “L” and “M” of Hellmund 1991: text-fig. 3). The M2 and M3 are comparable in size to those of *E. crispus* from Detan Dvrce, Czech Republic, which is considered to be one of the earliest known and smaller specimens of this species (comparison based on data provided by Lihoreau et al. 2009: table 1). Lüttig and Thenius (1961) supposed the Chandras *Elomeryx* palate is of early Oligocene age, based on its similarities with west European samples of this genus. However, Kopp (1965) summarized local lithostratigraphic and mollusk biochronological evidence and showed that the coal deposits in which the specimen was found are most likely of upper Oligocene age (Fig. 7).

The *Elomeryx* record from Turkish Thrace (Ozansoy 1962) seems to cover almost the entire Oligocene (Fig. 7). The lower coal levels (levels III–V in Lebküchner 1974), where *E. cf. crispus* is associated with *Anthracotherium praealsaticum* Ozansoy, 1963 and *Anthracotherium cf. monspialense* de Zigno, 1882, have been correlated with the early–middle Oligocene with the use of micromammals (Ünay-Bayraktar 1989). The upper coal levels (levels VI–X in Lebküchner 1974), where *E. cf. crispus* is associated with *Anthracotherium magnum*, are certainly younger and most likely correspond to an early late Oligocene age (MP25–MP27) (Ünay-Bayraktar 1989; Ruckert-Ulkumen

1992). Direct comparison with *Elomeryx* material described by Ozansoy (1962; see also Lebküchner 1974) was unfortunately limited. A right toothrow with M1–M3 from Tekirdağ–Malkara in the MTA, illustrated by Ozansoy (1962: pl. II, figs 1, 2; photos kindly provided by E. Albayrak), shows a typical *E. crispus* morphology with a third marked crest on the lingual side of the metaconule and, different from the Chandras palate, a clear join between the lingual postprotocrista and the premetacristule.

The Sigircili-Edirne *Elomeryx* material discussed by Hellmund (1991) and the Tozakli mandible described by Islamoğlu et al. (2010) come most probably from coal seams of the Danişman Formation, Eastern Thrace of upper Oligocene age, probably younger than 26–27 Ma (Fig. 7) (Siyako and Huvaz 2007: figs 1, 5; Islamoğlu et al. 2010; Islamoğlu pers. comm. 2011). Some Sigircili-Edirne specimens in BSPM allocated by Hellmund (1991) to *E. crispus*, exhibit an advanced lower molar morphology with “Y crest pattern”, strong hypoconid–entoconid distal connection and strong premetacristid in contact with the preprotocristid (type “b” of Hellmund 1991: text-fig. 6). The Sigircili P4 lacks the weak disto-lingual crest seen in Moschopotamos and Chandras, the transverse valley of the M3 is blocked lingually (Hellmund 1991: Pl. 7, fig. 6) and its lingual postprotocrista is strong, differing from the Chandras palate. Reexamination of the Tozakli mandible (stored in MTA; photos and measurements kindly provided by E. Albayrak) ascribed to *E. borbonicus* by Islamoğlu et al. (2010) shows that the teeth fall dimensionally within the lower limits of the *E. borbonicus* size range. Although the “Y” pattern between prehypocristid–preentocristid is

Fig. 7 Chrono-spatial distribution of Eurasian *Elomeryx* species (based on data by Ducrocq and Lihoreau 2006; Hellmund 1991; Lihoreau et al. 2009; Made 1996; Tsubamoto and Kohno 2011; Sach and Heizmann 2001; Scherler et al. 2011; this study)



hardly observable due to the state of preservation, the molars lack a direct hypoconid–entoconid mesial connection, but they do show a clear premetacristid and a rather strong protoconid–metaconid mesial connection.

In the light of new evidence on the origin and expansion of *Elomeryx* (see discussions in Ducrocq and Lihoreau 2006; Tsubamoto and Kohno 2011), SE Europe seems to represent a key area for the understanding of the

zoogeography and evolution of the genus. Previous fossil evidence indicates that *Elomeryx* originated in East Asia during the late middle Eocene, with the most primitive known representative “*Bothriodon tientongensis* Xu, 1977” coming from the Bose Basin of southern China (Ducrocq and Lihoreau 2006). Until the end of the Eocene, *Elomeryx* spread into western Europe, leading to *E. crispus*, and slightly later entered North America, leading to

E. armatus (Ducrocq and Lihoreau 2006; Lihoreau and Ducrocq 2007). Unfortunately, the great chrono-spatial gap between the East Asian and the West European Eo-Oligocene *Elomeryx* record (Fig. 7; Ducrocq and Lihoreau 2006: fig. 4) prohibit more comprehensive phylogeographic interpretation (e.g., Lihoreau and Ducrocq 2007), whereas the position of the closely related but poorly known Balkan genus *Bakalovia* in the evolutionary history of *Elomeryx* remained uncertain.

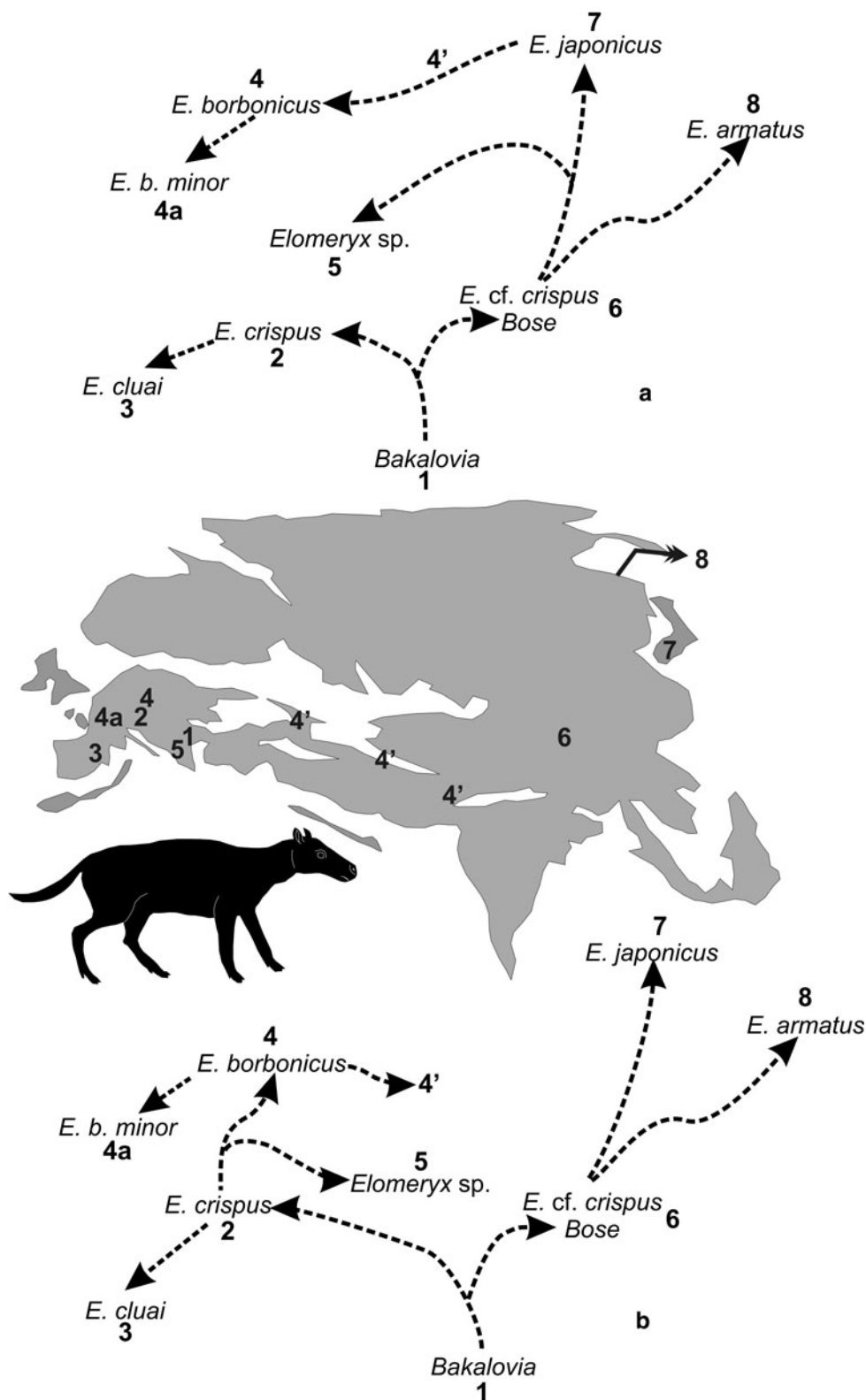
Through comparisons of the lithological sequence of the *Bakalovia* type locality provided by Nikolov (1967) with the updated stratigraphy of the Burgas Palaeogene deposits (Juránov 1992; Kostova and Markova 2005), it appears that the fossils come from the lower coal level of the Ravneč Formation of most likely late middle Eocene age (Bartonian, MP16). This may imply that *Bakalovia* slightly predates the oldest records of *E. crispus* at La Débruge, France (MP18), and Detan Dvërce, Czech Republic (MP21) (de Bonis 1964; Fejfar and Kaiser 2005; Lihoreau et al. 2009) (Fig. 7). The absence of a distal entoconid–hypoconid connection (character 23 in ESM Appendix I), the three cristids issued from the hypoconid (character 26), the preentocristid position (character 27), the absence of diastemata between c-p1 and p1–p2 (characters 34 and 35, respectively) and the simple lower premolar morphology (character “b” in ESM Appendix I; see also Hellmund 1991: text-fig-2; but note that the author mistakenly illustrated the buccal instead of the lingual side of *Bakalovia* lower premolars) of *Bakalovia* should be regarded as primitive features within the *Elomeryx* lineage, a scheme additionally supported by the present parsimony analysis (Fig. 6) and the revised chronological data. Interestingly, “*Bothriodon tientongensis* Xu” from southern China seems more advanced than *Bakalovia* in the stronger distal entoconid–hypoconid connection on the m3 (compare Nikolov 1967: pl. 17, fig. 1 and pl. 18, figs 2, 3 with Ducrocq and Lihoreau 2006: fig. 1H), the better developed talonid of the p3 and p4 and the stronger p4 paraconid (compare Hellmund 1991: pl. 12 with Tsubamoto and Kohno 2011: fig. 5). Such evidence would therefore place the origin of *Elomeryx* more westward than previously thought, around the current Black Sea region, from where *E. crispus* spread into Europe and *E. cf. crispus* reached the Far East at early late Eocene times (Fig. 8). A branch of the Asian *E. cf. crispus* might have dispersed to N. America at the basal Oligocene, leading to *E. armatus* and its relatives, while another branch might have led to *E. japonicus* (Fig. 8).

The Japanese species, originally attributed to *Brachyodus*, has been discussed by Ducrocq and Lihoreau (2006) and was more recently revised by Tsubamoto and Kohno (2011). *E. japonicus* is the oldest record marking the shift from the small to the large and more advanced dentally

Eurasian *Elomeryx*. The single known mandibular fragment is indirectly aged by the fission track method at about 29 Ma (that is equivalent to Rupelian, MP25), that is just before the emergence of the European *E. borbonicus*, first occurred at St. Henri, France (late Oligocene, MP26) (Fig. 7). According to its revised diagnosis, *E. japonicus* differs from other *Elomeryx* species in having a wider p4 talonid with better developed distobuccal cingulum (Tsubamoto and Kohno 2011: 119). Apart from the latter character, *E. japonicus* is rather similar in size (Tsubamoto and Kohno 2011: table 1) and morphology to *E. borbonicus* (Tsubamoto and Kohno 2011: fig. 4; note the “Y” crest pattern on molars and strong p4 paraconid and talonid) and as the present phylogenetic analysis implies (Fig. 6), they could be closely related. The large late Oligocene *Elomeryx* sp. from Nabeshima Island, Japan (Ducrocq and Lihoreau 2006; Tsubamoto and Kohno 2011) may also provide evidence for such a relationship, but morphological data are limited. Ducrocq and Lihoreau (2006) further recognized *E. borbonicus* in several central Asian sites of Oligo-Miocene age, widening the geographic distribution of this species from CW Europe to Pakistan via Georgia and Kazakhstan (Fig. 7). Although *E. borbonicus* is usually regarded to be a direct descendant of the European *E. crispus* (e.g., Hellmund 1991: 77; Lihoreau et al. 2009), a scenario that cannot be easily excluded by the available data (Fig. 8b), the parsimony analysis provided here (Fig. 6) and that of Lihoreau and Ducrocq (2007: fig. 7.2) may well allow alternative interpretations (see also Tsubamoto and Kohno 2011: fig. 7). Thus, an Asiatic origin and westward dispersal of *E. borbonicus* related to the late Oligocene warming (Zachos et al. 2001) cannot, in our opinion, be excluded (Fig. 8a).

In western Europe, *E. borbonicus* replaced *E. crispus* around 27 Ma ago (Lihoreau et al. 2009; Scherler et al. 2011) and probably survived until the late early Miocene (Fig. 7), as it has been reported from the MN3–MN4 site of Becken in the Swiss Molasse Basin and from the MN4 site of Eggingen-Mittelhart 3 in S. Germany (Hellmund 1991; Lihoreau et al. 2009; Made 1996; Sach and Heizmann 2001; Scherler et al. 2011). There is also evidence that west European *E. borbonicus* decreased in overall size and reduced its premolar length during the early Miocene, leading to *E. b. minor* (Depéret, 1906) (e.g., Schaub 1948; Made 1996). At the same time, the Greek record and at least some Eastern Thrace samples indicate that another advanced *Elomeryx* species, dimensionally close to *E. crispus* or even to the smaller Iberian *E. cluiai*, spanned the southern Balkan Oligo-Miocene boundary. The early Miocene *Elomeryx* sample under study shares with advanced *Elomeryx* species the compressed and distally serrated upper canines [character states 6(1) and a(1) in Fig. 6] and the “Y” crest pattern on the posterior lobe of

Fig. 8 Two evolutionary scenarios (a and b) of *Elomeryx* species, correlated with their geographical distribution, here extrapolated on a simplified Oligocene palaeogeographic map. Scenario a in accordance with present parsimony analysis; scenario b in accordance with the traditional European *E. crispus*-to-*E. borbonicus* concept. 1 *Bakalovia*, Bulgaria; 2 *E. crispus*, CW Europe; 3 *E. cluiai*, Spain; 4 *E. borbonicus*, CW Europe; 4a *E. borbonicus minor* CW Europe; 4' *E. cf. borbonicus* from Pakistan, Kazakhstan, and Georgia (Ducrocq and Lihoreau 2006); 5 *Elomeryx* sp. from Moschopotamos Greece; 6 *E. cf. crispus* from Bose Basin, China; 7 *E. japonicus*, Japan; 8 *E. armatus*, N. America



the m3 [character state 27(1) in Fig. 6], but it still retains some primitive features, such as the bucco-lingually uncompressed m3 hypoconulid, the weak posthypocristid and the strong mesio-lingual entocristid [character states

f(0), g(0) and h(0), respectively], the latter character seen also in *E. japonicus* but not in *E. borbonicus*.

Because of missing data, any hypothesis about the origin of the Balkan species and its taxonomy is rather fragile,

and depends largely on the preferred scenario of origin of *E. borbonicus*. Following the traditional concept of *E. crispus*-to-*E. borbonicus* evolutionary scheme (Hellmund 1991; Lihoreau et al. 2009), the advanced *Elomeryx* from the southern Balkans, should represent a grade or subspecies within this lineage (Fig. 8b); Hellmund (1991) already recognized an “advanced *E. crispus*” in Europe that shares with *E. borbonicus*, *E. japonicus* and the Balkan species the derived “Y crest pattern” on the lower molars. Assuming, however, that *E. borbonicus* descended from an Asian *E. japonicus*-like stock, in accordance with the present cladistic analysis, the advanced *Elomeryx* from the southern Balkans would have a similar biogeographic history; it could have split off from this lineage possibly before the emergence of *E. japonicus* and dispersed westwards at late Oligocene times (Fig. 8a). Within the current systematic status of European *E. crispus* (sensu Hellmund 1991), both evolutionary schemes imply the parallel phylogenetic development of similar dental features in the Asian and European *Elomeryx* lineages.

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