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First description of a fossil chamaeleonid from Greece and its relevance for the European biogeographic history of the group

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Abstract

The fossil record of Chamaeleonidae is very scarce and any new specimen is therefore considered important for our understanding of the evolutionary and biogeographic history of the group. New specimens from the early Miocene of Aliveri (Evia Island), Greece constitute the only fossils of these lizards from southeastern Europe. Skull roofing material is tentatively attributed to the Czech species *Chamaeleo* cf. *andrusovi*, revealing a range extension for this taxon, whereas tooth bearing elements are described as indeterminate chamaeleonids. The Aliveri fossils rank well among the oldest known reptiles from Greece, provide evidence for

the dispersal routes of chameleons out of Africa towards the European continent and, additionally, imply strong affinities with coeval chamaeleonids from Central Europe.

Keywords Chamaeleonidae, Squamata, Miocene, Biogeography, Aliveri

Introduction

Chameleons (Squamata, Chamaeleonidae) constitute a rather diverse group with more than 200 species that are now distributed in Africa, Madagascar and several other Indian Ocean islands, southern Asia, Cyprus and southern parts of Mediterranean Europe (Glaw 2015). Cryptic diversity appears to be prominent within the group, with several new species having been described only during the current decade, mostly on the basis of molecular data (Gehring et al. 2011; Crottini et al. 2012; Greenbaum et al. 2012; Stipala et al. 2011, 2012; Tilbury and Tolley 2015). The size range of chamaeleonids is also broad and astonishing, with the larger members of the family surpassing 600 mm in total length (Glaw and Vences 1994), whereas the smallest species rank well among the tiniest known reptiles, both extant (*Brookesia micra*, attaining only 29 mm [Glaw et al. 2012]) and extinct (e.g. *Jucaraseps grandipes* [Bolet and Evans 2012]). The ability of some species to ‘change’ colour, along with their peculiar external morphology, have gained the attention of the public for centuries and render them readily distinguishable even for non-specialists (Teyssier et al. 2015). Moreover, their bizarre external appearance, acrodont dentition, unique skeletal anatomy, as even their specialized feeding and locomotor habits, have long lead herpetologists to consider chameleons as a monophyletic group (Camp 1923; Estes 1983). Their relationships to other squamates, however, are yet not fully resolved, mostly because of the uncertainty of the position of Iguania, but it is widely accepted that Chamaeleonidae constitute a group within the iguanian clade Acrodonta (Estes et al. 1988; Townsend et al. 2004; Kumazawa 2007; Conrad 2008;

Vidal and Hedges 2009; Gauthier et al. 2012; Wiens et al. 2012; Pyron et al. 2013; Reeder et al. 2015), even if their affinities with Agamidae are a matter of debate, with different topologies arising on the basis of morphological and molecular data (Bolet and Evans 2013; Tolley and Menegon 2013).

Despite the broad geographic distribution among extant taxa, the fossil record of Chamaeleonidae is rather patchy (Bolet and Evans 2013). A Cretaceous origin of the group, is commonly accepted based on molecular data (Tolley et al. 2013), but with their first fossil record dating back to the early Miocene (Moody and Roček 1980; Pickford 1986), such molecular divergence date cannot be thoroughly tested. The dispersal of chamaeleonids to Europe and Asia seems to have occurred later (Bolet and Evans 2013; Tolley et al. 2013); indeed, their Neogene record on the European continent is rather scanty with few, scattered occurrences only across the early to middle Miocene of Central Europe (Moody and Roček 1980; Böhme and Ilg 2003; Čerňanský 2010; Bolet and Evans 2013).

Europe currently harbours two extant taxa of chamaeleonids: *Chamaeleo chamaeleon* (Linnaeus, 1758) and *Chamaeleo africanus* Laurenti, 1768 (Dimaki et al. 2000, 2008, 2015). The Greek distribution of the former species now solely comprises Samos island, as populations inhabiting Crete and Chios seem to have gone extinct recently. It is worth noting, however, that Sillero et al. (2014) reported this species as still present in Crete, considering it allochthonous. The distribution of *C. africanus* in Greece (restricted only to a small region near the town of Pylos, Peloponnese) is the sole European population for this African species and most probably is a product of human introduction during early antiquity (Fig. 2) (Böhme et al. 1998; Kosuch et al. 1999; Dimaki et al. 2000, 2008).

Despite their occurrence in the extant herpetofauna of the country, chamaeleonids have never been previously described from Greek fossil localities. Here we report on three new chamaeleonid fossils found in the early Miocene (MN 4) locality of Aliveri, Evia Island,

which indicate the Neogene existence of these lizards in Greece. One of these specimens is tentatively attributed to the species *Chamaeleo cf. andrusovi* Čerňanský, 2010, which was previously known only from the early Miocene of the Czech Republic, whereas the other two specimens represent indeterminate chamaeleonids.

Geological setting

Aliveri is a fossiliferous locality, located within the Neogene sedimentary basin of Aliveri / Kymi, in Evia (also spelled Euboea) Island in Central Greece. Along with the Gavathas site, Lesvos Island, it has yielded the oldest known Greek Neogene land mammal fauna (Koufos 2006a, b; van den Hoek Ostende et al. 2015). Aliveri was discovered in 1977 and was initially dated to the MN 3 zone (de Bruijn et al. 1980). Nevertheless, there is a general consensus now that it is referable to MN 4 (Doukas 2003; Koufos 2006b; van den Hoek Ostende et al. 2015). More specifically, as was recently stated by van den Hoek Ostende et al. (2015:276), ‘although undeniably an MN 4 assemblage, Aliveri is one of the oldest localities from that MN unit, and presumably co-eval with many of the MN 3 assemblages from western and central Europe’. The age of Aliveri is tentatively estimated between 18 and 17.5 Ma, and corresponds to the Burdigalian stage (Orleanian Continental Stage) (Koufos 2006b; van den Hoek Ostende et al. 2015). A detailed description of the geology of Aliveri is provided by de Bruijn et al. (1980).

The micromammal assemblage of Aliveri is rather diverse and has been the subject of several studies (de Bruijn et al. 1980; Meulen and de Bruijn 1982; Schmidt-Kittler 1983; Klein Hofmeijer and de Bruijn 1985, 1988; Doukas 1986; López Martínez 1986; Álvarez Sierra et al. 1987). It includes erinaceids, dimylids, heterosoricids, talpids, soricids, ochotonids, eomyids, many sciurids, cricetids, anomalomyids, spalacids and glirids. Larger mammals are less known, but palaeogalids, equids, palaeomerycids, cervids and bovids are

present, as well as the viverrid *Euboictis* (van den Hoek Ostende et al. 2015). As for the herpetofauna of Aliveri, anurans, crocodylians, anguids, lacertids, as well as indeterminate lizards, snakes and turtles are present but have not been described. The study of these amphibians and reptiles will be the subject of a forthcoming publication.

Material and methods

All three chamaeleonid specimens described herein, belong to the collections of the Department of Earth Sciences in the University of Utrecht and are accessioned under the repository numbers UU AL 3501-3503. All specimens were found in the early Miocene locality of Aliveri in three different field seasons, in 1977 (UU AL 3502), 1978 (UU AL 3501) and 1980 (UU AL 3503), led by the University of Utrecht. As with the micromammal material that has also been collected from this locality, all chamaeleonid fossils have been recovered from the underclay of the lignite occurring North of Aliveri, along the eastern edge of the basin where the lignite wedges out against Mesozoic limestones (de Bruijn et al. 1980). For comparison purposes, skeletal material of extant chamaeleonids was studied in the herpetological collections of the University of Torino and the Muséum national d'Histoire naturelle, Paris. Photos of the fossil specimens were taken using the Leica M205 microscope and the Leica application suite V 3.3.0, in the University of Torino.

Results

Systematic Palaeontology

Reptilia Laurenti 1768

Squamata Opperl, 1811

Iguania Cope, 1864

Acrodonta Cope, 1864

Chamaeleonidae Gray, 1825

Chamaeleo Laurenti, 1768

Chamaeleo cf. *andrusovi* Čerňanský, 2010

(Fig. 1a, b, c, d)

Material: The specimen here referred to *Chamaeleo* cf. *andrusovi* is a skull roofing bone fragment (UU AL 3501).

Description: UU AL 3501 is a skull roofing bone fragment about 3 x 3 mm in diameter. A comparison with extant chamaeleonid material, stored in the collections of the University of Torino and the Muséum national d'Histoire naturelle, Paris, suggests that the fragment can be part of the circumorbital region (i.e. either a prefrontal or a postorbital), but its fragmentary status prevents a more precise determination. The fragment is flattened and its external surface is covered by an ornamentation made by various small tubercles grouped in four, well-separated and rounded clusters. Two of the four clusters are aligned along one of the margins of the fragment, which is a natural border and not the result of breakage (as the other margins). If our interpretation of the fragment as part of a circumorbital bone is correct, this would be the orbital margin. The inner surface of the specimen is smooth.

Chamaeleonidae indet.

(Fig. 1e, f, g, h)

Material: Two additional specimens from the same locality are assigned to Chamaeleonidae, but cannot be attributed to the species level. These two specimens are both tooth bearing bones (UU AL 3502 and UU AL 3503).

Description: UU AL 3502 and UU AL 3503 are very fragmentary tooth-bearing bones. However, they clearly bear acrodont, large and triangular teeth, which are well-spaced and located on the edge of the bones. Two of them are preserved in UU AL 3502 and three of

them are visible in UU AL 3503, even if in the latter specimen only one is well preserved. Small accessory cusps are recognizable anteriorly and posteriorly to the main one in one tooth of UU AL 3502 and in two teeth of UU AL 3503. Ventrally directed interdental grooves are present on the lateral surface. Due to the fragmentary nature of both specimens, it is currently impossible to determine whether these two tooth-bearing elements originate from the dentary or the maxilla.

Taxonomic Identification

The specimens described herein were preliminarily described in an unpublished report by Delfino (2004), who attributed them to Chamaeleonidae indet.. On the other hand, Böhme and Ilg (2003) cited for the same locality the presence of *Chamaeleo* cf. *C. caroliquarti* in their online database, without further details or describing any material.

Because of the complex ornamentation and the well-spaced and complex clusters of tubercles (= pustular protuberances of Čerňanský [2010]), the skull bone fragment (UU AL 3501) from Aliveri can be referred to *Chamaeleo* cf. *andrusovi*. In the original diagnosis provided for this species, Čerňanský (2010:609) stated that *C. andrusovi* was a small chamaeleonid, differing from all other taxa in several features, but most notably by ‘its typical strongly pustular ornamentation of the external surfaces of the skull roofing bones. Differs from adult *Chamaeleo calyptratus*, *Triceros* (sic) *hoehneli* or *Calumma globifer* in regard to the concentration, distribution and shape of the protuberances – mostly complicated pustular protuberances are moderately spaced and rather evenly distributed, covering the otherwise smooth external surface’. This diagnostic feature appears also in the Greek specimen; therefore the skull roofing bone is attributed to *Chamaeleo* cf. *andrusovi*.

The two tooth bearing elements from Aliveri (UU AL 3502 and UU AL 3503) can be attributed to the Chamaeleonidae on the basis of the well-spaced and apically located acrodont

teeth (Delfino et al. 2008 and references therein). The identification of chamaeleonid tooth bearing bones is severely hampered by the widespread, homoplastic features surrounding their anatomy. Generally, the dentaries of Acrodonta share several common features that should prompt us being rather cautious when dealing with taxonomic assignments to either agamids or chamaeleonids (Augé 1997; Delfino et al. 2008; Rage and Bailon 2011). Even if the two fragmentary tooth bearing bones cannot be identified as portions of maxillae or dentaries, it is worth noting that Čerňanský (2010) has shown that dentaries of chamaeleonids are not diagnostic to the species level. Assigning the tooth bearing bones to *Chamaeleo* cf. *andrusovi* on just the base of the taxonomic allocation of the skull roofing bone, seems premature for the moment, as fossil evidence has shown that distinct chameleon species could have co-existed in sympatry: different morphologies that have been observed among the dentaries of *C. caroliquarti* (Čerňanský 2010) could indicate the existence of more than one chameleon at Dolnice. The fact that *C. caroliquarti* was a very large species (around 500 mm in total length) (Bolet and Evans 2013), whereas *C. andrusovi* was originally described as ‘a small species of *Chamaeleo*’ (Čerňanský 2010:609), prompts us to leave open the possibility that Dolnice could harbor at least two different chamaeleonid taxa. The idea of two or more sympatric chamaeleonid species in the same locality is reminiscent of a similar situation in several extant species (Raselimanana and Rakotomalala 2003; Tolley and Menegon 2013). Such higher species diversity within a single region has been also recently inferred for fossil chamaeleonids (Dollion et al. 2015). On the other hand, many regions harbor only monospecific communities of extant chamaeleonids (Tolley and Menegon 2013). Taking all these into consideration, whether Aliveri hosted a monospecific chameleon assemblage, or whether multiple sympatric species coexisted, remains only to be revealed on the light of new and more complete specimens from the locality. As such, we refrain from attributing the two

tooth bearing elements to the same species as the skull roofing bone (*Chamaeleo* cf. *andrusovi*) and we thus tentatively consider them as ‘Chamaeleonidae indet.’.

Discussion

The Taxonomy of European Neogene chamaeleonids

Six Miocene species have already been named on the basis of rare European fossil remains, which mostly do not comprise overlapping material (Bolet and Evans 2013): *Chamaeleo caroliquarti* Moody and Roček, 1980, *Chamaeleo bavaricus* Schleich, 1983, *Chamaeleo pfeili* Schleich, 1984, *Chamaeleo simplex* Schleich, 1994, *Chamaeleo sulcodentatus* Schleich, 1994 and *Chamaeleo andrusovi* Čerňanský, 2010. Several anatomical characters appear to be ubiquitous within chamaeleonids, rendering the validity of most of these taxa as tentative or even dubious (Čerňanský 2011). This applies especially to characters in the dentaries of these squamates, which appear to be widespread and indistinguishable from extant representatives. Čerňanský (2010) revised the first named European fossil taxon *Chamaeleo caroliquarti* and regarded it as a nomen dubium, as he could not differentiate the holotype dentary from several extant taxa, whereas the paratype dentary appeared to belong to a distinct morphotype. We acknowledge here, however, that on several occasions, even fragmentary fossils can bear diagnostic characters. This is the situation, for example, when geometric morphometric approaches are used (Bastir et al. 2014; Cornette et al. 2015), a case study that has also been recently applied to fossil chamaeleonids (Dollion et al. 2015). The latter authors characteristically noted that even small fragments, such as parts of the maxilla and the parietal could be useful in taxonomic identification. It is, however, beyond the scope of this paper to evaluate the status of *Chamaeleo caroliquarti*, and acknowledge that a complete phylogenetic analysis which will, in fact, include enough dentary characters from multiple extant taxa, is needed in order to decipher the systematics of European Neogene chameleons.

The Aliveri chameleons

The identification of the Aliveri specimens described herein, as chamaeleonids, confirms the presence of this squamate group in the fossil record of Greece. Another purported acrodont taxon, *Uromastyx spinipes* (Daudin, 1802) [= *Uromastyx aegyptia* (Forskål, 1775)] was reported by Mangili (1980) from the Late Pleistocene of Grotta Simonelli in Crete, on the basis of an isolated, 43 mm long, tibia that was not figured and not described in detail, hindering any evaluation of its identity. The location of this fossil is currently unknown. However, since the comparative morphology of lizard tibiae is poorly known, this specimen should be considered an indeterminate squamate. As such, the specimens from Aliveri comprise the sole record of fossil chameleons from Greece.

The taxonomic assignment of the Aliveri skull roofing element as *Chamaeleo* cf. *andrusovi* provides a significant range extension for that species. *Chamaeleo andrusovi* was until now known only from the early Miocene (MN 4) of Dolnice, Czech Republic (Čerňanský 2010). This new record indicates that this species was widely distributed in the early Miocene of Central and Southern Europe. Such a broad distribution is congruent with that of several extant members of the genus *Chamaeleo* (e.g. *Chamaeleo chamaeleon* and *C. africanus* are widespread species with populations being adapted to different environments and ecological settings [Dimaki et al. 2000, 2008]). However, the high degree of cryptic speciation in modern chamaeleonids has led to the ‘split’ of several widespread extant taxa, mostly on the base of molecular data, but with few or no morphological characters that could distinguish them (e.g. Andreone et al. 2001; Nečas et al. 2003, 2005, 2009; Gehring et al. 2010, 2011; Crottini et al. 2012; Greenbaum et al. 2012; Stipala et al. 2011, 2012; Tilbury and Tolley 2015). This fact is further problematic for the fossil record of chamaeleonids, as for

their identification we have to rely only on morphological evidence, and no assumption about cryptic speciation within extinct species can be suggested.

It is worth noting that the faunal assemblage of Aliveri is chronologically older than other MN 4 faunas in Europe (van den Hoek Ostende et al. 2015) and that the Greek skull roofing bone assigned to *Chamaeleo* cf. *andrusovi* is therefore older than the conspecific specimens from the type locality of Dolnice, Czech Republic. As such, the Aliveri specimen ranks among the oldest named chamaeleonids of Europe, being only slightly younger than *C. caroliquarti* which has been recorded from the early Miocene (MN 3) localities of Merkur Nord (Czech Republic) and Wintershof West (Germany).

The locality of Aliveri is well known for its rich micromammal fauna. The overall diverse and abundant fauna of flying squirrels suggest a forest biotope (de Bruijn et al. 1980). A relatively humid environment for the locality has also been suggested (van den Hoek Ostende et al. 2015). The new identification of *Chamaeleo* cf. *andrusovi* in Aliveri further confirms the already proposed ecological settings of the locality, as the presence of chamaeleonids is well known to be indicative of warm climates (Moody and Roček 1980) and further suggests relatively dense vegetation (Maul et al. 2011), although several extant genera are known to occur in both closed and open habitats (Tolley et al. 2008; Dollion et al. 2015).

Palaeobiogeography of the Chamaeleonidae

The biogeographic history of chamaeleonids is hampered by their extremely poor fossil record. Most of the material recovered is fragmentary, thus not permitting identification beyond the family level. Notable exceptions, however, are known to occur, with few exceptional Miocene specimens from Kenya documenting the morphological conservativeness and a relative evolutionary stasis within the group throughout time (Hillenius 1978a; Rieppel et al. 1992). Stem representatives of Chamaeleonidae are not

known or at least they have not yet been identified, rendering their early evolutionary history tantalizing and obscure (Bolet and Evans 2013; Simões et al. 2015). Molecular data support a Cretaceous dichotomy between chamaeleonids and other Acrodonta, although the exact dates vary among different researches (Raxworthy et al. 2002; Wiens et al. 2006; Townsend et al. 2011; Bolet and Evans 2013; Dollion et al. 2015). Africa and Madagascar have long been proposed as potential centres of origin for chamaeleonids (Hillenius 1959, 1978b; Blanc 1972; Klaver 1977; Tolley et al. 2013; Dollion et al. 2015). More specifically, Tolley et al. (2013) suggested, on the base of molecular data, that chamaeleonids originated in Africa around the Late Cretaceous, after the break-up of the supercontinent Gondwana, with two independent oceanic dispersals to Madagascar (their modern biodiversity hotspot) during the Palaeocene and the Oligocene. Frustratingly, however, no Cretaceous and Palaeogene fossils are known, and it is characteristic that the first definite known chamaeleonid fossils are documented only in the early Miocene of Africa and Europe (Bolet and Evans 2013; Dollion et al. 2015).

Several enigmatic Palaeogene taxa from Asia bear superficial resemblance with chamaeleonids, however, they are now thought to represent convergent stem acrodonts (Bolet and Evans 2013). It is worth noting here, that the taxonomic status of *Anqingosaurus brevicephalus* Hou, 1976 (variously cited also under the incorrect spelling *Anquingosaurus*), an enigmatic species from the Palaeocene of China, is pivotal to our understanding of chamaeleonid evolution. Bolet and Evans (2013:184) doubted the status of *A. brevicephalus* as a chamaeleonid, mentioning characteristically that ‘there is nothing to suggest that it is a chameleon’. That being said, there is currently no definite record of a chamaeleonid from the Palaeogene or even the Neogene of Asia. In fact, the only known Asian fossil chamaeleonids are recorded in the Middle Pleistocene of Israel and the Palaeolithic of Lebanon (Haas 1952;

Hooijer 1961; Maul et al. 2011; Bolet and Evans 2013), but palaeogeographically Middle East was part of Gondwana and not Asia.

Neogene chameleons in Europe appear to be restricted, both geographically and chronologically, with only few published occurrences from the early to middle Miocene of Czech Republic, Germany and Switzerland, and perhaps also Poland and Spain (Fig. 2) (Moody and Roček 1980; Roček 1984; Schleich 1984; Bolliger 1992; Fejfar and Schleich 1994; Mörs 2002; Böhme and Ilg 2003; Böhme 2010; Čerňanský 2010, 2011; Bolet and Evans 2013). The earliest occurrence of a chamaeleonid in Europe is documented in the early Miocene (MN 3) of Merkur Nord in Czech Republic and Wintershof West in Germany (Čerňanský 2010; Bolet and Evans 2013). A still undescribed chamaeleonid from the early Miocene (MN 3 / MN 4) of Agramon, Spain, cited in the online database of Böhme and Ilg (2003), needs further investigation about its exact taxonomic affinities; if it is indeed a chamaeleonid though, then it represents one of the earliest European records of the group. Interestingly, chameleons are neither recovered from the well-known MN 2 squamate fauna of Wiesbaden-Amöneburg (Germany), nor in any other MN 2 European locality, leading Čerňanský et al. (2015) to suggest that their absence in the earliest Miocene is genuine and they only dispersed into Europe shortly thereafter. The presence of chamaeleonids in Central Europe during the early Miocene coincides with the Miocene Climatic Optimum (Böhme 2003), which enabled several other squamate groups to achieve their northernmost distribution (e.g. varanids and cordylids; Bolet and Evans 2013; Delfino et al. 2013). One or more widespread and / or even distinct, sympatric species could be present in the early Miocene of Central Europe at the time of this climatic optimum, as high temperatures favor the diversification of squamates. In any case, the permanence of Miocene chamaeleonids in Europe did not last long as suggested by their last published occurrence in the MN 6 of Ornberg in the Molasse Basin, Switzerland (Bolliger 1992; Čerňanský 2011), whereas an

even later occurrence for the group is listed in the online database of Böhme and Ilg (2003), where an indeterminate reptile, that was initially described by Młynarski et al. (1982) from the middle Miocene (MN 7) of Poland, is there re-identified as a chamaeleonid. Whatever their last appearance datum, they likely went extinct due to climatic deterioration in Europe and / or ecological competition with newly arrived squamates. Interestingly, a new land bridge has been suggested to exist between Afro-Arabia and Asia during MN 6, which, apparently, favoured a new wave of dispersal of immigrants to Europe (Koufos et al. 2005). Indeed, several African groups are known to have dispersed by this land bridge (e.g. aardvarks) (Koufos et al. 2005; Lehmann 2009), a situation that could have applied also to African squamates. No chamaeleonid fossils are found after the middle Miocene, but a latest immigration event seems to have taken place much more recently, involving the extant species *Chamaeleo chamaeleon*, which still inhabits several parts of the Mediterranean Europe: a sporadic fossil occurrence from the Holocene of Spain (Talavera and Sanchíz 1983) probably supports this recent wave of dispersal. This latest dispersal event seemingly concerns also the extant Greek populations of *Chamaeleo chamaeleon* in the islands of Samos and Chios, right adjacent to the coasts of Anatolia; the (recently extinct) population of *C. chamaeleon* in Crete, as also the other extant species occurring in Greece, *C. africanus*, is most probably a product of human introduction during antiquity (Böhme et al. 1998; Dimaki et al. 2015).

With such a scarce fossil record and a rather small temporal and regional European distribution, the dispersal routes of the earliest chamaeleonids remain unclear. Čerňanský et al. (2015) suggested that chamaeleonids (probably along with cordylids) entered Europe no earlier than the MN 3, but they did not suggest any possible route from Africa to Europe. Here we propose three different possible routes (Fig. 3): i) a marine dispersal from northwestern Africa to southwestern Europe; ii) a land dispersal from Afro-Arabia to Asia

and then via Anatolia to southeastern Europe, and iii) a land dispersal from Afro-Arabia to Asia and then northwards and eastwards, with an entrance in Europe through Central Asia.

The first scenario involves a marine dispersal from Africa to Europe across the Mediterranean. Such oceanic dispersals are well documented in chamaeleonid biogeographic history with molecular data suggesting multiple waves of colonization in Madagascar, Comoros, Seychelles and Socotra (Tolley et al. 2013; Tolley and Menegon 2013). Squamates in general are considered to be very efficient in trans-oceanic dispersal, with multiple lineages colonizing even the furthest and most remote of the Pacific Ocean islands (Beckon 1992; Fisher et al. 1997; Pregill et al. 2004; Zug et al. 2011). These data, along with the extant distribution of chamaeleonids overseas in the Indian Ocean, suggest that the Palaeogene and Early Neogene Mediterranean and Paratethys seas (especially in the western part that is estimated to be rather narrower [Rögl 1999]) should not appear as a severe obstacle for these capable marine navigators. However, their absence from Palaeogene and early Miocene localities from Western Europe could possibly indicate that chamaeleonids did not disperse from this direction. Indeed, the extensive sampling of Western European localities for over a century could probably attest that this absence of chamaeleonids from this region is genuine and not sample biased. The supposed record of an indeterminate chamaeleonid from the early Miocene (MN 3/ MN 4) of Agramon is tantalizing, since it could represent the only exception; however, the specimen has not been formally described and its whereabouts are currently unknown (Zbigniew Szyndlar, personal communication, November 2015). We further note here that short-time existing land connections between Africa and Western Europe have also been suggested (Gheerbrandt and Rage 2006; Zarccone et al. 2010), however, without unveiling any dispersal of chamaeleonids to Europe. A natural or ecological barrier could have prevented these squamates from immigrating to Western Europe either through water rafting or any hypothetical land bridge.

The second scenario involves a land dispersal from Afro-Arabia to Asia and then via Anatolia to Europe. This is supposed to take place in the early Miocene through the so called ‘*Gomphotherium* Landbridge’, a large landmass that arose after the collision of Afro-Arabia with Asia during the MN 3 stage (Rögl 1999; Koufos et al. 2005). This collision provided a connection between Africa and Asia, dividing the huge sea that previously prevented dispersal of terrestrial taxa from Africa to Eurasia. The Afro-Arabian plate acted therefore as a platform for these terrestrial groups that could afterwards use Anatolia and then the Balkans in order to disperse northwards to Central Europe. A similar route had already been mentioned for chameleons by Barbadillo et al. (1997). According to this scenario, Greece seems to have acted as the first ‘step’ of these African and / or Anatolian immigrants into Europe. Through the ‘*Gomphotherium* Landbridge’ numerous terrestrial tetrapod groups are documented to have dispersed out of Africa, most eminently proboscideans (Rögl 1999; Koufos et al. 2003, 2005). If chameleons used this dispersal scenario, then they were among the first immigrants out of Africa, accompanying proboscideans and other mammal groups; they then rapidly dispersed to Central Europe in a short time interval, as it is shown by the presence of chamaeleonids in Germany and the Czech Republic already by the MN 3 (Roček 1984; Fejfar and Schleich 1994). Interestingly, several other tetrapod groups (e.g. aardvarks, hominoids) dispersed out of Africa much later, using another land bridge that arose during the middle Miocene (MN 6) (Lehmann 2009), but this datum is younger than the majority of fossil occurrences of chamaeleonids in Europe. Different ecological barriers probably existed that prevented or favoured the dispersal of certain groups at different periods.

The third scenario involves a land dispersal of chamaeleonids from Afro-Arabia to Asia and then northwards and entrance in Europe through Central Asia. This should involve again the usage of the ‘*Gomphotherium* Landbridge’ but then after dispersal eastwards and not westwards to the Balkans. We note here that the collision of the Afro-Arabian plate with

Asia divided the Paratethys Sea and isolated the Kotsakhurian Sea in the eastern Paratethys region (fig. 6, in Rögl 1999). This would further put rather severe obstacles in the spread of the African immigrants to the North. Therefore, only a westwards and an eastwards direction for these immigrants would seem possible. If chamaeleonids took the eastward direction, that would mean that they had to disperse to southern Asia, spread to Central Asia, and then, after getting around the huge perimeter of the Kotsakhurian Sea, enter Central Europe. That way, their entrance into Europe should take place at the level of the northwestern edge of the Kotsakhurian Sea. However, the ubiquitous absence of chamaeleonid fossils in the several known early Miocene localities from this region does not seem to favour this hypothesis.

We acknowledge that the available fossil material is limited in order to fully support any of the proposed dispersal routes. However, the new Greek specimens provide evidence in favour of our second proposed scenario: a route from Greece towards Central Europe. Moreover, the slightly older age of the Aliveri fauna compared to all other MN 4 European localities, and more specifically from the also chamaeleonid-bearing Dolnice, could indicate a step-wise pathway of these squamates from south to northwards, and hints as Greece being the first European territory to which the group initially arrived from Africa via Anatolia. The presence of chamaeleonids in MN 3 Central European localities (Merkur Nord and Wintershof West), which are slightly older than Aliveri, could indicate that their dispersal and colonization of Europe took place quite fast. The purported record of the chamaeleonid from Agramon (MN 3 / MN 4) (Böhme and Ilg 2003), if verified, could hint for very similar dispersal routes of these squamates to proboscideans: the latter group of large mammals are known to have used the '*Gomphotherium* Landbridge' at the MN 3 stage and rapidly dispersed into the European continent, reaching the Iberian Peninsula at the beginning of MN 4 (Tassy 1990; Koufos et al. 2005). The idea, however, of a combination of both the first and the second biogeographic scenarios should not be ruled out: the presence of chamaeleonids

from Aliveri in the Balkan Peninsula, along with that from Agramon in the Iberian Peninsula, may indicate that these squamates could have used different pathways to Europe, from both northwestern and northeastern Africa. Such complex, double or even multiple dispersal events are far from unknown for southern European squamates. To the contrary, they have been well documented for extant gekkotan lizards (Rato et al. 2010, 2011) and Neogene elapid snakes (Szyndlar and Rage 1990). As far as it concerns the latter, the cobra *Naja iberica* from Spain has been described as ‘undoubtedly an African invader’, which, however, most likely never crossed the Pyrenees barrier and spread to the rest of Europe, which was inhabited by different congeners (Szyndlar and Rage 1990:398). Such barrier could have also prevented early Miocene Iberian chamaeleonids from dispersing northwards, if they indeed ever reached the Peninsula during the early Neogene.

The Aliveri fauna bears a close resemblance to several coeval early Miocene ones from Anatolia, indicating biogeographic correlation and possible dispersal routes (van den Hoek Ostende et al. 2015). Notably, the viverrid *Euboictis* from Aliveri, seems to share close affinities with a rather primitive congener form from Sabuncubeli in Anatolia (early MN 3), pointing towards an Asian origin for this mammal group (Koufos et al. 2005; van den Hoek Ostende et al. 2015). In contrast, Aliveri shares with coeval Central European faunas several micromammals, such as the eomyids and the flying squirrels. Curiously, eomyids are not present in the Turkish fossil record and, therefore may indicate the existence of an ecological barrier between southern Balkan Peninsula and Anatolia (van den Hoek Ostende et al. 2015). It is also characteristic that the Aliveri rodent *Anomalomys aliveriensis* shares congener species with the early Miocene of Dolnice, Czech Republic, which is also the type locality of *Chamaeleo andrusovi*. It is therefore obvious that the Aliveri fauna comprised a faunal mosaic of Anatolian and Central European taxa, acting as a biogeographic passage between Anatolia and Central Europe. Frustratingly, however, no chamaeleonid has ever been reported

from any of the Anatolian localities (van den Hoek Ostende et al. 2015). More specimens from the early Miocene of Greece and generally from the Balkans and Anatolia are needed in order to fully test our hypothesis about the dispersal routes of chamaeleonids. This is unfortunately hindered by the scarcity of such localities in Greece (Koufos 2006b), as also by the generally limited interest of palaeontologists in fossil reptile finds in the area (Georgalis and Kear 2013). The confirmed presence of chamaeleonids in the early Miocene of Greece, however, allows us to expect that other localities between the MN 3 and MN 4 time intervals in the southern Balkans and Anatolia, will also yield similar fossil forms that will only then allow a more accurate reconstruction of the dispersal routes of these charismatic lizards.

Chamaeleo cf. andrusovi from Aliveri represents only the third reptile species identified from the early Miocene of Greece. Mesozoic and Palaeogene reptiles are yet unknown from this country. *Chamaeleo cf. andrusovi*, the pleurodire turtle *Nostimochelone lampra* and the pythonid snake *Python euboicus* are therefore the oldest reptiles in the Greek fossil record (Römer 1870; Georgalis et al. 2013; Georgalis and Kear 2013). As the Aliveri specimens confirm the presence of Chamaeleonidae in the area, it is possible to speculate that several other reptile groups that have a fossil record in the early Neogene of Central Europe, such as cordylids, elapids, boines and choristoderans (Rage 1984; Szyndlar and Rage 1990, 2003; Szyndlar 1991; Evans and Klembara 2005; Rage and Szyndlar 2005; Čerňanský 2012) may be recovered from the Greek localities in the future. Especially for cordylids, it will be rather interesting to test whether this African lizard group (that has an almost identical, restricted fossil distribution in the early Miocene of Central Europe with chamaeleonids [Roček 1984; Čerňanský 2012]) used the same dispersal routes and if they can be identified in Greece and the rest of southeastern Europe as well. Unlike chameleons, however, cordylids are known to have also a Palaeogene fossil record from Europe; therefore, their presence in the same early Miocene localities with chamaeleonids during the climatic optimum, could

suggest either a continuous presence from the Palaeogene onwards to the Miocene, or indeed a Palaeogene extinction and a later dispersal event along with chameleons (Čerňanský 2012). More fossil specimens and a revision of the already named taxa under a modern phylogenetic context are definitely needed in order to shed more light on the European squamate palaeobiogeography.

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Figures

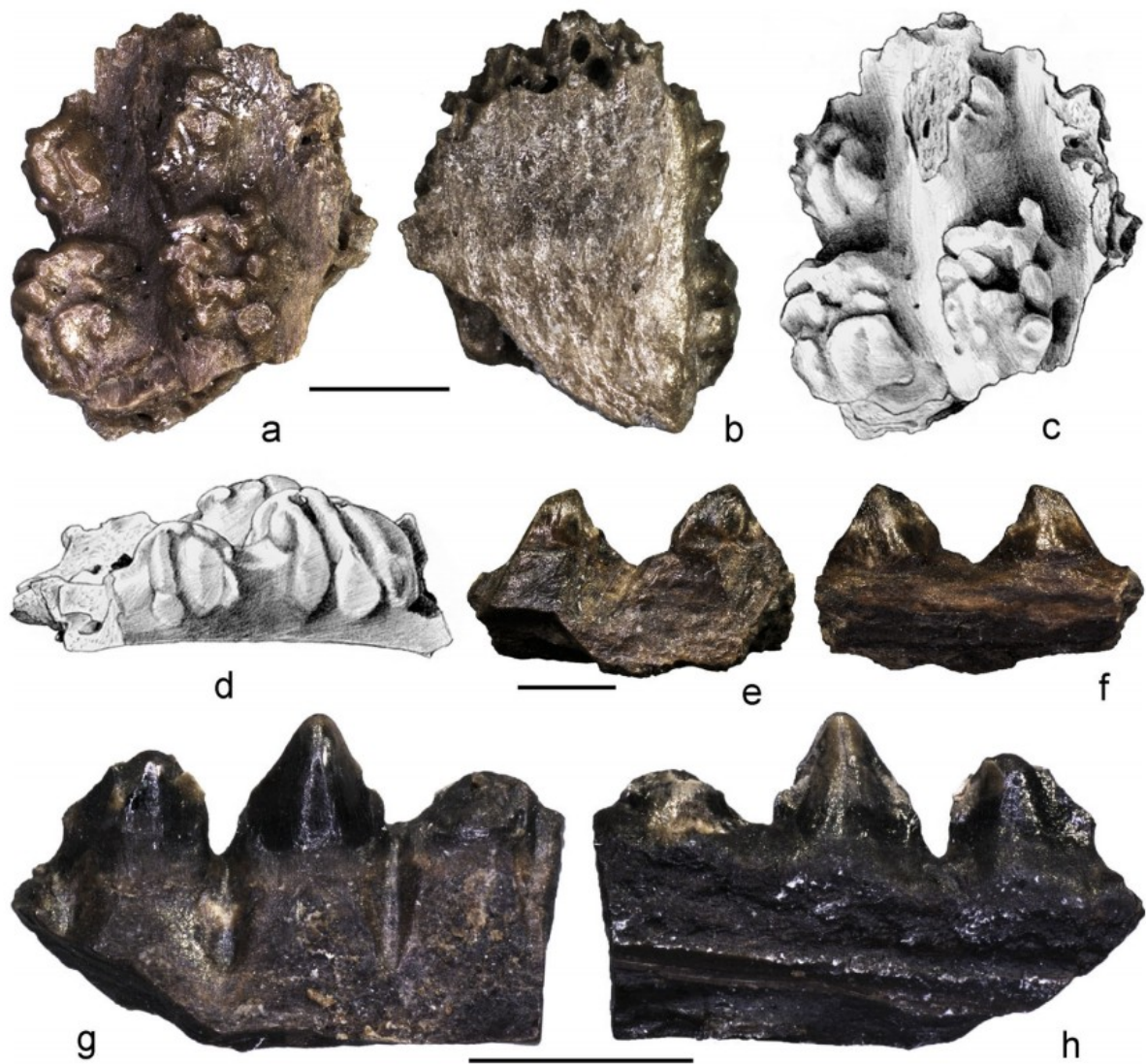


Fig. 1 Fossil chamaeleonids from Aliveri. **a, b, c, d** *Chamaeleo* cf. *andrusovi*: skull roofing bone, UU AL 3501, in external (a) and internal (b) views, and its interpretative drawing in external (c) and lateral (d) views. **e, f, g, h** Chamaeleonidae indet.: tooth bearing bones, UU AL 3502 (e–f) and UU AL 3503 (g–h), in lateral (e, g) and medial (f, h) views. Scale bars represent 1 mm

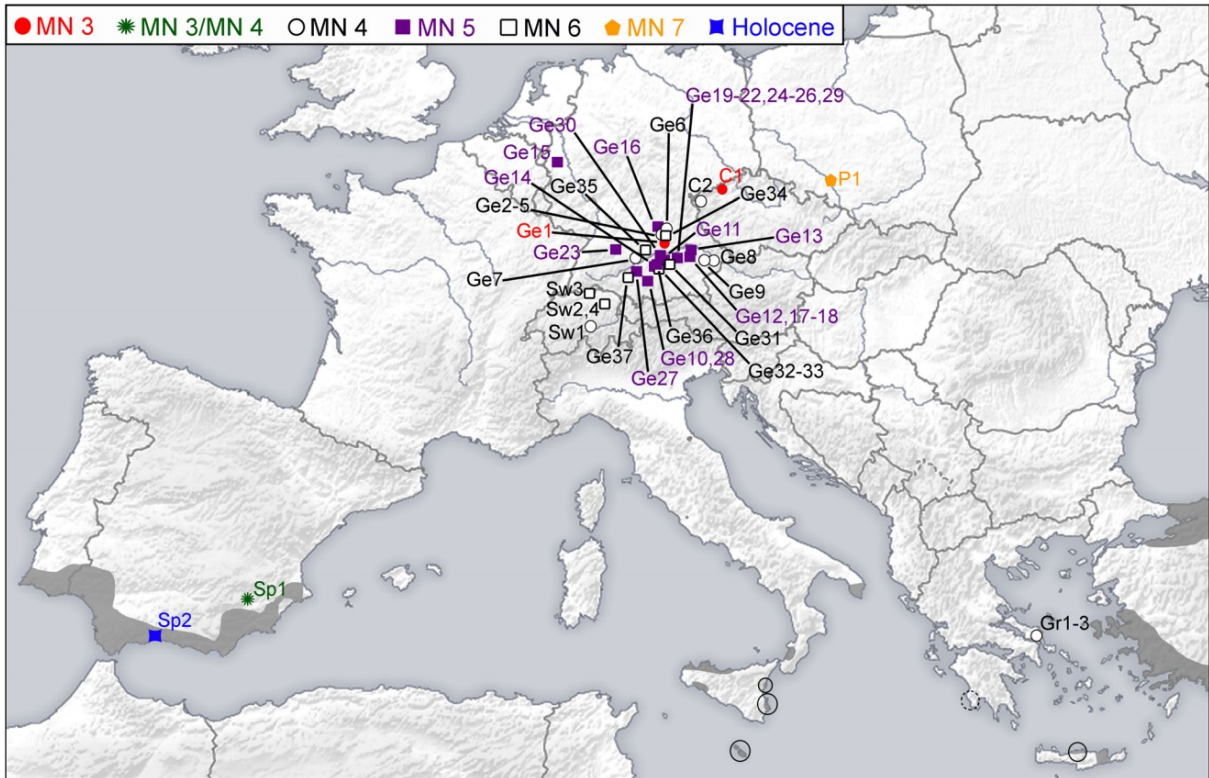


Fig. 2 Fossil chamaeleonids from Europe. See Online Resource for a list of localities and taxa identified. Grey and encircled areas represent the range of extant chameleons in Europe and Western Anatolia, including autochthonous, introduced and recently extinct populations; the dashed circle indicates the probably introduced in antiquity population of *C. africanus* near Pylos, whereas the remaining areas refer to *C. chamaeleon*. Distributional data come from Gasc et al. (1997), Sindaco and Jeremčenko (2008), Sperone et al. (2010) and Sillero et al. (2014)

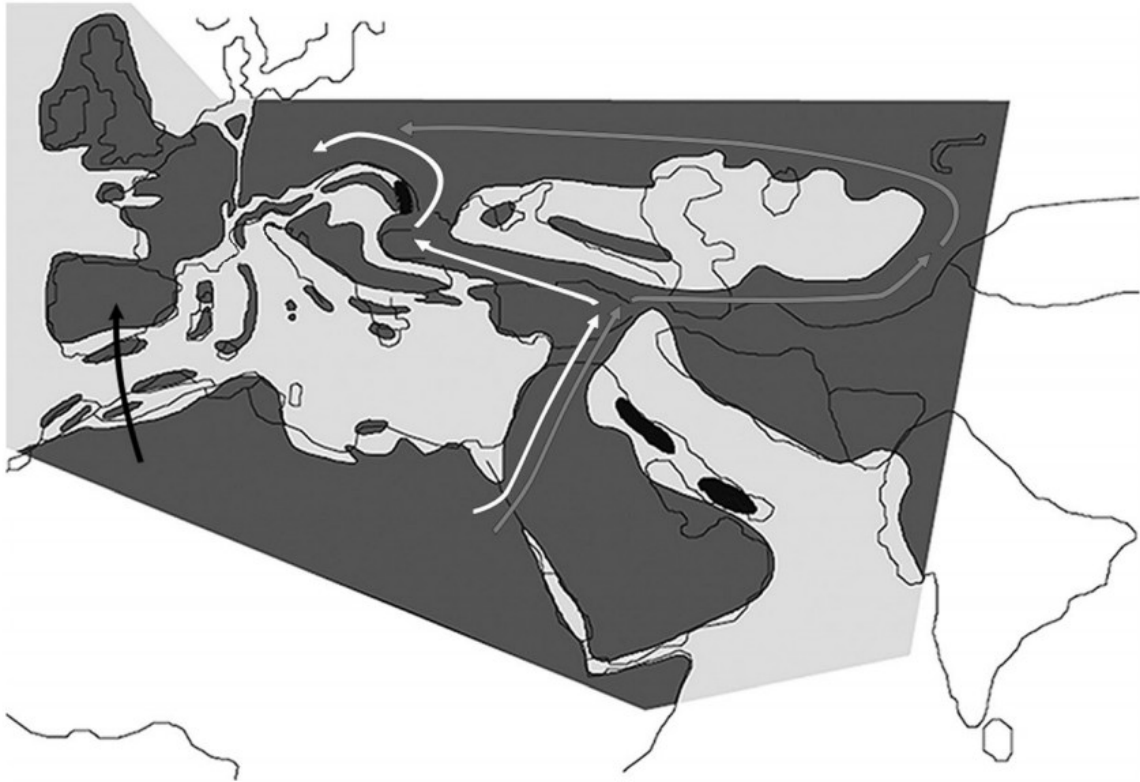


Fig. 3 Map showing the three biogeographic scenarios described in the text: the first one is represented by a black arrow, the second one by white arrows and the third one by grey arrows. Palaeogeographic map modified from Rögl 1999