



The age and diversification of metacrangonyctid subterranean amphipod crustaceans revisited

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ABSTRACT

The Metacrangonyctidae are a small family of amphipod crustaceans of marine origin found only in subterranean continental waters. They display a broad but punctuated distribution between the Caribbean and the Arabian Peninsula, with major disjunctions either due to vicariance by plate tectonics or to occurrence of recent episodes of long-distance transoceanic dispersal. We re-examine the phylogeny of the family and the time frame for its diversification using mitochondrial genomes in the light of two key taxa recently discovered, from Oman (Arabian Peninsula) and the Rif area of Morocco, respectively. We also use a novel fossil calibration scheme of the mitogenome phylogeny. Results of previous analyses based on palaeogeographic calibrations are not contradicted by the new approach, with vicariance by plate tectonics remaining as the main explanatory factor for the *amphi*-Atlantic distribution displayed by this ancient group of subterranean amphipods.

1. Introduction

The Metacrangonyctidae (Crustacea: Amphipoda) show a puzzling distribution for a taxon limited to occur in continental subterranean waters (Bauzà-Ribot et al., 2012, and references therein). Their known distribution covers both sides of the Atlantic (Hispaniola in the Caribbean; Fuerteventura in the Canary Islands), several western Mediterranean islands (Majorca, Minorca, Elba), plus Morocco and Algeria in North Africa, and the Dead Sea Depression and the Sinai Peninsula in the Middle East. Metacrangonyctids live in caves, wells and other subterranean habitats from the seashore up to 1800 m altitude in areas that were covered by the sea in the geological past. The family presumably derives from marine ancestors that become isolated in inland subterranean waters after episodes of marine regression (Boutin, 1994).

The molecular systematics and historical biogeography of the Metacrangonyctidae were recently examined through a phylogenetic analysis of their mitogenome sequences (Bauzà-Ribot et al., 2012). There, we suggested the group experienced an ancient diversification compatible with a scenario of vicariance by plate tectonics. Our conclusions were objected by Phillips et al. (2013), who criticised our tree calibration approach (based on palaeogeographic events instead of on fossil records) and our analytical implementation of the nucleotide

substitution rates (but see Bauzà-Ribot et al. (2013) for a rebuttal).

Recently, two new species of *Metacrangonyx* discovered in broadly separated areas might prove relevant elucidating the early evolutionary history of the family. *Metacrangonyx dhofarensis* Jaume and Vonk, 2012 was described from the coastal plains of southwestern Oman, extending the distribution of the family to the shores of the Indian Ocean (Jaume and Vonk, 2012). Furthermore, a second species still pending formal description was collected in wells at the ancient Roman city of Volubilis in northern Morocco (near Meknès). This finding, made in a transition area between the Mediterranean and the Atlantic Ocean, represents the northernmost record of metacrangonyctids in North Africa.

Here we take advantage of the discovery of these two new taxa to sequence their complete mitogenomes and revisit the phylogeny of the family. We estimate the temporal framework for the divergence of the different metacrangonyctid clades using two crustacean fossils and test its congruence with our previous estimations based on palaeogeographic events. Our aim is to explore whether the time frames are compatible with a scenario of vicariance by plate tectonics or, alternatively, they point to the involvement of recent episodes of long-distance transoceanic dispersal in causing the current distribution pattern of the family. Under the hypothesis of an ancient age (> 110 Myr) of the Metacrangonyctidae and assuming an East-to-West progradation of

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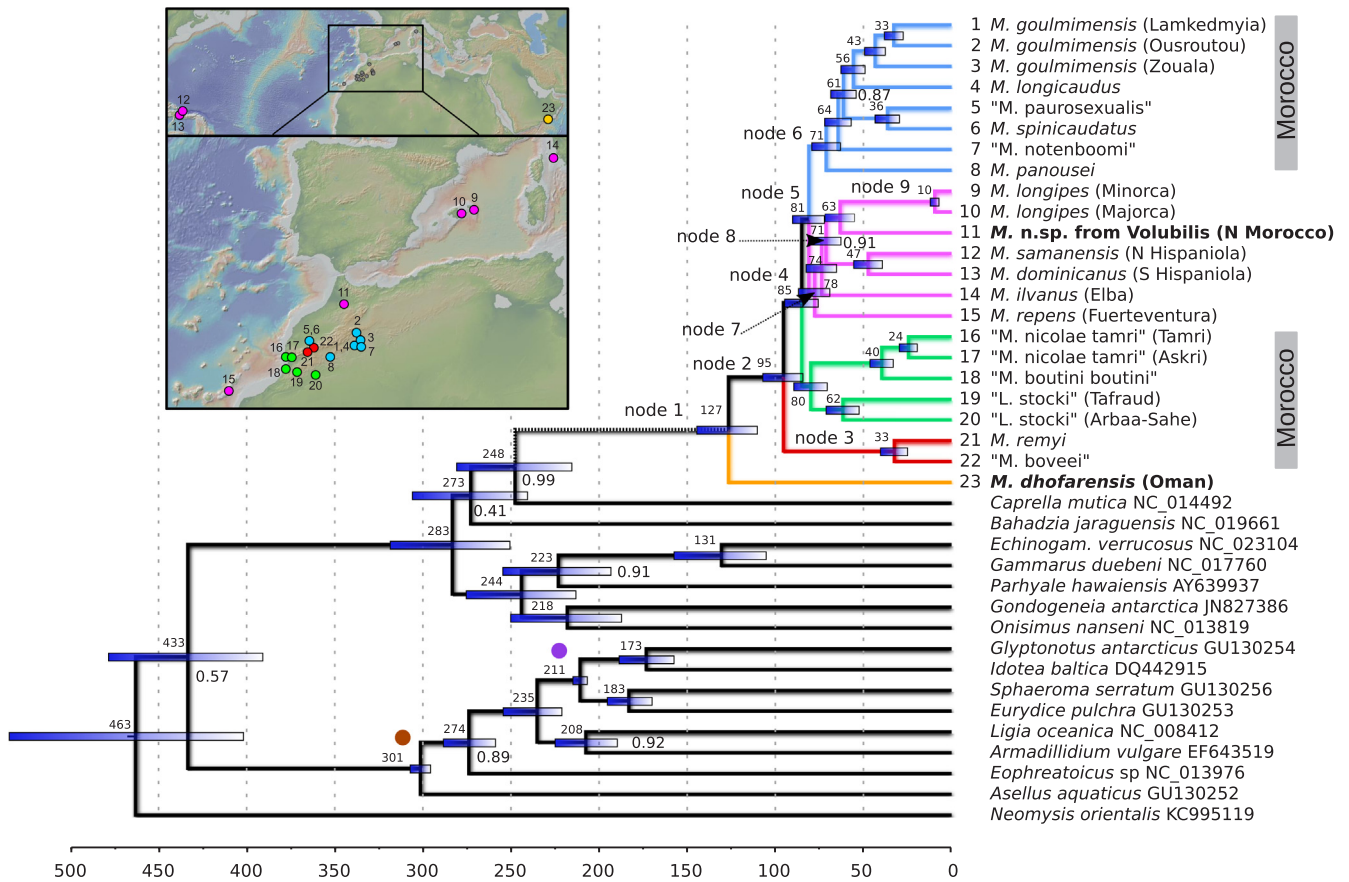


Fig. 1. Clock-like tree of the Metacrangonyctidae using 13 concatenated mitochondrial protein-coding genes as three independent codon partitions with uncorrelated log-normal relaxed clocks and a Yule branching model (right panel). Node constraints indicated with dots, the placement of *Hesslerella shermani* and *Eliosorerolis alpina* marked in brown and purple, respectively. Bars on nodes indicate 95% confidence intervals of node age estimates. Bayesian credibility support indicated for nodes with values < 1. Map on the left shows sampling locations of the metacrangonyctid species included in this study, with numbers matching those shown in the phylogenetic tree. Map was built using GeoMapApp v. 3.6.8 available at <http://www.geomapp.org/>. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the opening of the Tethys Sea (see Smith et al., 1994), the new species from the coastal plains of Arabia facing the Indian Ocean should represent an early offshoot lineage of Metacrangonyctidae. Furthermore, the newly discovered taxon from northern Morocco should display a differentiated phylogenetic position from the remainder of the North African lineages due to its particular geographic emplacement between the Riffian block and the rest of Morocco (see Capella et al., 2018; Krijgsman et al., 2018).

2. Material and methods

2.1. Sampling

The sample included the mitogenomes from the 21 metacrangonyctid taxa previously analysed by our research group (Bauzà-Ribot et al., 2012; Pons et al., 2014) plus the two newly sequenced ones, *Metacrangonyx dhofarensis* from Oman (acc. Number MH592124) and the new *Metacrangonyx* from Volubilis, Morocco (acc. Number MN124287) (see map in Fig. 1). The dataset was completed with the mitogenomes of 16 outgroup crustaceans retrieved from GenBank (see Fig. 1).

2.2. DNA sequencing

The mitogenome of *Metacrangonyx* n.sp. from Volubilis (Morocco) was obtained using long PCR amplification and sequencing with the 454 technology, while the mitogenome of *M. dhofarensis* by sequencing

total genomic DNA at low coverage in an Illumina run using 2 × 150 bp paired-ends. Details on methods for sequencing, genome assembly, gene annotation, DNA sequence alignment and estimation of best partition scheme are described in Supplementary Methods.

2.3. Phylogenetic methods

Tree topologies, model parameter values and node ages were co-estimated and optimized in BEAST v1.8.4 (Suchard et al., 2018) from the concatenated mitochondrial DNA sequences of the 13 protein-coding genes. The best partition scheme resulted in independent substitution models for first codon (GTR + I + G), second (GTR + I + G) and third codon positions (HKY + I + G) as in our previous work (Bauzà-Ribot et al., 2012). Two independent Bayesian analyses were run for 300 million generations each to avoid local optima, and effective sample size convergence above 200 was confirmed in Tracer v1.6 (Rambaut et al., 2018). Runs were combined using LogCombiner specifying a burnin fraction of 10%, while confidence intervals of parameters and ages were estimated in TreeAnnotator. Default priors for all parameters were implemented except for the clock and tree models to ensure convergence during path-sampling (see Supplementary Methods). We co-estimated node ages and tree topologies under two types of relaxed clocks where rates on descendant branches are independent of the rate at the parent branch: uncorrelated log-normal clock (UCLN) and random local clocks (RLC). RLC analyses were run for 1 billion generations since it took about 500 million generations to reach convergence, that were discarded as burnin. Both clock models

were statistically compared based on Bayes Factors (BF), which were calculated from marginal likelihoods estimated using path-sampling. We performed 20 steps of 25 million generations each using a path scheme with a betaQuantile 0.33 (Baele et al., 2012), discarding 25% of each step as burnin. Finally, we also estimated topologies and node ages removing third codon positions since several studies suggest that saturation on these sites may prevent an accurate estimation of topologies, branch lengths and node ages, although the phylogenetic informativeness of 3rd codon sites is controversial (Simmons, 2017).

2.4. Estimation of divergence times

In our previous study (Bauzà-Ribot et al., 2012) we used two palaeogeographic events to calibrate the phylogeny of the family, namely the ages of emersion of the High Atlas in Morocco and of the Balearic Islands in the western Mediterranean, since both regions harbour a pair of sister taxa whose split we assumed to be related to the existence of emerged land. Here we use a different approach relying uniquely on fossil data to calibrate the tree and test the congruence between these two approaches. Since the fossil record of Amphipoda is limited and does not extend beyond the Eocene (45–50 Ma; Jazdzewski et al., 2014; Starr et al., 2016), we rely instead on relevant fossils of other peracarids to estimate divergence dates. We use two isopods – a group with a rich fossil record that extends back to the Palaeozoic – to assign a minimum age constraint on the divergence event at the base of their respective clades. Namely, the oldest fossil isopod known, the Carboniferous (Middle Pennsylvanian) Phreatoicidean *Hesslerella shermani* Schram, 1970 (see Wilson and Edgecombe 2003), and the oldest undisputed record of the Sphaeromatidea, *Elioserosolis alpina* Basso & Tintori, 1994, from the Late Triassic (Norian) of the southern Alps (Basso and Tintori, 1994). The fossils ages were considered as soft constraints with a parametric log-normal distribution that assigns non-zero probabilities to all possible age values. We defined a log-normal distribution as constraints for these two nodes with a log mean (M) = 5.71 and Standard deviation = 0.01 (CI: 296.0–307.8 Myr) for *Hesslerella* and M = 5.35 and S = 0.01 (CI: 206.5–214.8 Myr) for *Elioserosolis*. The age distribution of each fossil was arbitrarily fixed within an age range assigned in the geological time scale to the stage or series at which the fossil was originally attributed (Middle Pennsylvanian and Norian, respectively). Despite the fact that the membership of these two fossils to any modern family cannot be assigned with confidence, the robust ascription to the suborder Phreatoicidea of *Hesslerella* allows to assign a crown age for all the isopod species included in the analysis (Etter 2014). Seemingly, the assignment of *Elioserosolis* to the Sphaeromatidea (suborder to which the extant taxa *Sphaeroma serratum* and *Eurydice pulchra* belong) is clear-cut, providing a calibration point for the minimum stem age of the lineage (Etter 2014). Congruence among calibration points was explored performing a cross-validation analysis, i.e. comparing ages estimated using a single constraint. The kml file to project the phylogeny on Google Earth was obtained using the online version of Global Positioning Trees available at <http://ppuigbo.me/programs/GPT/>.

3. Results and discussion

The phylogenetic analyses performed, irrespective of whether they included third codon sites or not, unambiguously and consistently showed *M. dhofarensis* as sister to the remaining metacranonyctids (Fig. 1 and Fig. S1). The new species from Volubilis in northern Morocco – the other species added in the new analysis – appeared clustered in the insular clade of Bauzà-Ribot et al. (2012) (node 7 in Fig. 1). The age estimated for the root of the Metacranonyctidae was considerably younger (mean value 90.75 Myr) when implementing Random Local Clocks compared to the age obtained using a UCLN clock (126.67 Myr; see Table 1), but as noted before (Bauzà-Ribot et al., 2013) the latter provided a better fit to the data based on Bayes factors (BF = 191).

Furthermore, the age of the two fossils used to calibrate the tree showed reciprocal age congruence (Table 1, Fig. 1, and Fig. S1). When third codon positions were excluded from the analysis, all nodes in the phylogeny were estimated to be considerably older (Table 1).

Phillips et al. (2013) found no support for the involvement of plate tectonics in the evolutionary history of the Metacranonyctidae. In their re-analysis of our original data (Bauzà-Ribot et al. 2012), they excluded third codon positions and used an RLC model, and fossil calibrations to claim that the divergence between taxa separated by the Atlantic was much younger than our estimated age (39.9 Myr; 47.5–34.3 Myr 95% highest posterior distribution). However, we objected that their results were in part determined by the modification they introduced in our original data set and their inaccurate placement of fossils to calibrate the tree (Bauzà-Ribot et al., 2013). Here, we show that the addition of the mitogenomes of two key species to the initial data set combined with the application of a carefully chosen fossil calibration scheme, do not alter our previous statement that UCLN clock models are better suited than RLC models to explain the data, irrespective of considering third codon positions in the analyses. The latter render age estimates compatible with the involvement of plate tectonics in the diversification and distribution pattern of the Metacranonyctidae (see Figs. S2 and S3).

The phylogeny and ages estimated in the light of the new mitogenomes and fossil calibrations show that the family Metacranonyctidae comprises five major clades with a crown node age estimated to fall in the Cretaceous (node 1 in Table 1 and Fig. 1), thus in accordance with our previous statement (Bauzà-Ribot et al. 2012; 2013), although rendering an even an older age for the family after adding the omani lineage. The UCLN clock model selected by BF estimates an age with a 95% highest posterior distribution between 144.6 and 110.2 Myr (mean 126.7 Myr) for the separation of the lineage located at the easternmost sector of the current distribution of the Metacranonyctidae (represented by *M. dhofarensis* from Oman; see Fig. 1) from the rest of lineages, which are currently distributed across the Mediterranean and the Atlantic. At that time, the Tethys Sea was a circum-Tropical ocean and the area currently comprising the Arabian Peninsula was almost submerged and integrated into Gondwana (Smith et al. 1994). Thus, the closure of the connection between sectors of Tethys currently corresponding to the Mediterranean and Indian Ocean (that took place 20–16 Myr ago; Rögl 1998) can be confidently discarded as the cause for the split between the Omani lineage and the rest of metacranonyctids. The next major cladogenetic event in the phylogeny of the Metacranonyctidae separated a lineage composed of two species from the western High Atlas of Morocco – *M. remyi* Ruffo, 1953 and “*M. boveei*” (see Messouli 1994) – from the rest. Our analysis estimates this divergence to occur at 107.1–84.3 Myr (Fig. 1, and node 2 in Table 1 and Fig. 1). This High Atlas Moroccan lineage presumably remained in the sea at least until the Atlas domain started to emerge (Late Eocene; 37.2–33.9 Myr ago), and most probably until the onset of the first significant period of folding in the area (Oligocene-Early Miocene; ca. 25 Myr ago) (Frizon de Lamotte et al., 2008). Remarkably, the separation of *M. remyi* - “*M. boveei*” at about 40.3–25.0 Myr ago (node 3 in Table 1 and Fig. 1) obtained using our fossil calibration would be compatible with the uplift of emerged land that we implemented as a biogeographic age constraint in our previous analysis (37.2–25 Myr; Bauzà-Ribot et al. 2012).

A third major cladogenetic event separated a lineage comprising a cluster of taxa from SW Morocco from the remaining species (Fig. 1, node 4). These taxa correspond to three not yet formally described species (informally called “*M. nicoleae tamri*”, “*Longipodacranonyx stocki*” and “*M. boutini boutini*” in Messouli 1994) which are distributed across a region covering roughly from Agadir to Sidi-Ifni on the Atlantic coast and as far inland as Tafraout in the Anti-Atlas (Fig. 1). Our analysis dates their initial diversification split at 94.8–75.7 Myr ago. Finally, a last major split –almost coetaneous to the previous one– can be dated at about 90.3–72.2 Myr ago (Fig. 1, node 5), separating a

Table 1

Node age (Myr) for key nodes in Fig. 1, and marginal likelihood value for different clock models. Last column shows values of analysis discarding third codon sites.

node	UCLN 2 fossils	RLC 2 fossils	UCLN oldest Phreatoicoidean	UCLN oldest Sphaeromatidea	UCLN codon 1 + 2 only
node1	126.67 (110.24–144.61)	90.75 (75.90–104.29)	128.09 (110.83–146.62)	124.40 (105.66–143.65)	152.93 (130.51–174.87)
node2	95.51 (84.35–107.12)	64.51 (54.03–73.98)	96.54 (84.58–108.7)	93.79 (80.92–106.92)	114.05 (99.12–128.98)
node3	32.54 (25.01–40.32)	24.35 (19.77–28.67)	32.86 (25.23–40.72)	31.93 (24.33–40.06)	40.74 (29.84–52.04)
node8	71.30 (62.78–79.77)	47.26 (39.44–54.16)	72.08 (63.21–81.50)	69.99 (60.74–80.08)	79.06 (68.02–90.06)
node9	9.60 (7.19–12.08)	6.85 (5.49–8.15)	9.70 (7.27–21.21)	9.43 (7.06–12.03)	11.87 (8.49–15.73)
root	463.12 (401.87–534.79)	403.25 (370.34–435.38)	467.77 (405.76–542.47)	454.65 (385.02–531.27)	523.84 (442.57–621.64)
Ln	–263331.22	–263426.72	n/a	n/a	n/a

lineage comprising eight taxa from eastern Morocco (node 6) from a species group formed mostly by insular taxa (node 7; see below). The Moroccan species are distributed at both sides of the High Atlas (in the Errachidia-Boudnib-Erfoud and Ouarzazate basins on the south –*M. goulmimensis* Messouli, Boutin & Coineau, 1991, *M. longicaudus* Ruffo, 1954, “*M. notenboomi*” (see Messouli 1994), *M. panousei* Ruffo, 1953–, but also in the Haouz Plain on the north –“*M. paurosexualis*” (see Messouli, 1994), *M. spinicaudatus* Karaman & Pesce, 1980, see map Fig. 1). As in the two preceding major splits involving Moroccan taxa, all the species occur in areas that were covered by the great Cenomanian-early Turonian marine transgression (96–88 Myr ago), and it is conceivable that subsequent diversifications within each of these lineages were driven by episodes of marine regression (see Boutin et al., 2001; Boutin and Messouli, 1992; Boutin, 1994; Ait Boudrous et al., 2007, and references therein).

The insular cluster mentioned above includes the *Metacrangonyx* species from Fuerteventura (Canaries), Hispaniola (Caribbean; two species), the Balearics and Elba Island (Mediterranean), but also the aforementioned species not yet formally described from the ancient Roman city of Volubilis in northern Morocco (Fig. 1). The diversification within this clade seems to have proceeded by a rapid divergence ultimately leading to speciation in the isolated populations (hard polytomy; Bauzà-Ribot et al., 2012), with the sister-relationship among the composing taxa remaining mostly unresolved. Nevertheless, the origin of each insular lineage seems to be much older than the age of the respective islands where they dwell in. Thus, the age of Fuerteventura (Canaries) (22 Myr; Coello et al. 1992) is by far much younger than the 86.9–69.1 Myr attributed in our analysis to the lineage established there, currently represented by *M. repens* (Stock & Rondé-Broekhuizen, 1986). The same holds for Elba Island (Tuscan Archipelago; Italy): Elba is a portion of the Corso-Sardinian microplate detached 20 Myr ago from the Pyrenees (Alvarez, 1972), and consequently its existence as emerged land prone to be colonized by *Metacrangonyx* is much more recent than the age attributed in our analysis to the endemic lineage it harbours (currently represented by *M. ilvanus* Stoch, 1997; 82.6–65.3 Myr). Seemingly, the lineage from Hispaniola (Caribbean) differentiated ca. 79.8–62.8 Myr ago, therefore long before the conformation of any current Antillean island as a geographical entity –which are all post-Middle Eocene in age (< 40 Myr; Iturralde-Vinent 2006). Furthermore, the isolation of the major islands of the Greater Antilles as independent geographic entities was not completed until the Middle Miocene (16–14 Myr ago; Iturralde-Vinent 2006); therefore, the split between the two Hispaniolan species *M. dominicanus* Jaume & Christenson, 2001 and *M. samanensis* Jaume & Christenson, 2001, dated back at 55.5–39.3 Myr in our tree, cannot be related to the emersion of the Hispaniola island either. In any case, the occupation of the portion of Tethys that currently corresponds to the Antillean Region by the Metacrangonyctidae precedes the full disconnection between the east and west shores of the opening of the Atlantic (see below). This pattern of “species lineages older than the age of the islands in which the presently occur” has been linked to the presence of a shallow-water marine ancestor of the present insular *Metacrangonyx* lineage in banks and ephemeral islands in the Paleomacaronesia and the Proto-Caribbean. This lineage would have

subsequently colonized the islands when they emerged (Bauzà-Ribot et al. 2012).

The case of the lineage present on the Balearics (western Mediterranean; *M. longipes* Chevreux, 1909) is similar to the preceding ones: it differentiated from its sister lineage from northern Morocco at 71.8–55.1 Myr ago, but the islands only started to emerge at the end of the Miocene (Langhian; 16–13.6 Myr ago; Mein & Adrover 1982). The estimated age for the split of the populations of *M. longipes* from Majorca and Minorca islands (node 8; 12.1–7.2 Myr) is compatible with the palaeogeographic constraint we used in our previous study (Bauzà-Ribot et al., 2012) to calibrate the tree (emergence of the islands between 16.0 and 5.5 Myr ago). Seemingly, the new, not yet formally described species from Volubilis (northern Morocco), may derive from a marine ancestor since the area where it occurs –the former South Rifian Corridor), one of the narrow sea gates that connected the Mediterranean with the open ocean during the Tortonian (Krijgsman et al., 2018)– emerged from the sea only 7.0 Myr ago (Capella et al., 2018; Krijgsman et al., 2018).

Our updated molecular phylogeny confirms previous analyses in that *Metacrangonyx* is a remarkably ancient group, with an evolutionary history that extends back until at least the early Cretaceous. A remarkably similar pattern in terms of age, vicariance by continental drift and lineages far older than the territories they inhabit has been recently put forward by Copilaş-Ciocianu et al. (2019) for the Holarctic amphipod subterranean superfamily Crangonyctoidea, a group of presumed Early Cretaceous origin that shows a relict biogeography.

Our revised estimated age for the sister metacrangonyctid lineages placed at opposite sides of the Atlantic Ocean (79.8–62.8 Myr), although younger, fall within our previous estimations (101–57 Myr; Bauzà-Ribot et al., 2012) and is roughly coetaneous with the disconnection that took place in Santonian times (86.3–83.6 Myr ago) between the east and west Atlantic shores by plate tectonic movements (Jones et al., 1995). During the Upper Cretaceous, the rifting Atlantic attained already ca. 1200 km of width and water depths exceeding 5,000 m close to its continental margins; furthermore, the full transfer of surface water between the North and South Atlantic was totally established (Jones et al., 1995). These features would have hindered the dispersal of Metacrangonyctids across the Atlantic Ocean.

4. Conclusions

The recently discovered species of *Metacrangonyx* from Oman appears as the single known representative of the earliest lineage that diverged within the Metacrangonyctidae, in accordance with the East-to-West opening of the Tethys Sea. On the other hand, the new taxon from Volubilis in northern Morocco seems to be more closely related to a group of insular taxa rather than to the rest of North African species. Considering the uncertainties associated with both the reconstruction of Tethys palaeogeography and molecular clock estimations, our fossil-calibrated phylogeny shows a temporal framework for the evolutionary history of the group consistent with a scenario of vicariance by plate tectonics in accordance with our previous estimations based on palaeogeographic calibrations.

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Declaration of Competing Interest

The authors declare no competing interests that could inappropriately influence (bias) their work.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ympev.2019.106599>. These data include Google maps of the most important areas described in this article.

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