



Species diversification in the Mediterranean genus *Chiliadenus* (Inuleae-Asteraceae)

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Abstract

Chiliadenus is a small genus in the Inuleae (Asteraceae), consisting of ten species with allopatric distributions along the southern edge of the Mediterranean Sea. The different species have restricted areas of distribution, with only one being more widely distributed. The first molecular phylogenetic study of the genus with complete sampling, as well as a biogeographic analysis of the origin and biogeographic patterns leading to the current diversity of *Chiliadenus* is presented. Results confirm *Chiliadenus* as monophyletic and placed as sister to *Dittrichia*. The ancestor of *Chiliadenus* is dated to have diverged from that of *Dittrichia* around 5.45 Ma ago, coinciding with the Messinian salinity crisis, whereas the *Chiliadenus* crown group is dated to 2.29 Ma, around 3 million years later. Ancestral area reconstructions show the crown group to likely have originated in the area around Morocco and northwestern Algeria, which is also the area where the early divergences have occurred. *Chiliadenus* has then later diverged and dispersed over the Mediterranean to its current distribution. The evolution of the *Chiliadenus* crown group coincides with the onset of the Mediterranean climate, and its evolution may be connected to the subsequent climatic changes.

Keywords Asteraceae · Biogeography · *Chiliadenus* · Inuleae · Mediterranean

Introduction

The Mediterranean basin is well known for its high plant diversity and its high level of endemism. The flora comprises around 24–25.000 plant species, up to around 60% of which are endemic to the area (Greuter 1991). The high diversity has often been explained by a combination of the heterogeneous landscape and the results of important geological events, climatic oscillations, the complex geography, and topography of the area (Thompson 2005; Bonanno and Veneziano 2016). However, much remains unknown, and studies of the taxa that together make up the Mediterranean flora are therefore of great interest.

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One representative of the Mediterranean flora is *Chiliadenus* Cass., a small genus of ten species of the Inuleae-Inuleineae of the daisy family (Asteraceae), consisting of woody perennial herbs or shrublets with (mostly) discoid heads and yellow flowers (Fig. 1) (Englund et al. 2009; Anderberg 2012; Nylander and Anderberg 2015). The species of the genus have often been treated as members of *Jasonia* Cass. and/or *Varthemia* DC. in floras, but were moved into the genus *Chiliadenus* by Brullo (1979) based on morphology. Phylogenetic analyses (Englund et al. 2009; Nylander and Anderberg 2015) have shown that *Chiliadenus* is not related to *Varthemia*, and that its sister group is the widely distributed and often weedy genus *Dittrichia* Greuter.

The *Chiliadenus* species are predominantly distributed along the southern edge of the Mediterranean Sea, with one species extending into continental southwestern Europe. All species grow in rocky environments, and only *Chiliadenus saxatilis* has a wider distribution (Fig. 2) (Brullo 1979; Gómiz 2000). All ten *Chiliadenus* species have allopatric distributions around the Mediterranean basin; *Chiliadenus antiatlanticus* (Emb. & Maire) Gómiz (northern Morocco), *C. bocconeii* Brullo (Malta), *C. candicans* (Delile) Brullo (northeastern Libya, northwestern Egypt), *C. hesperius*

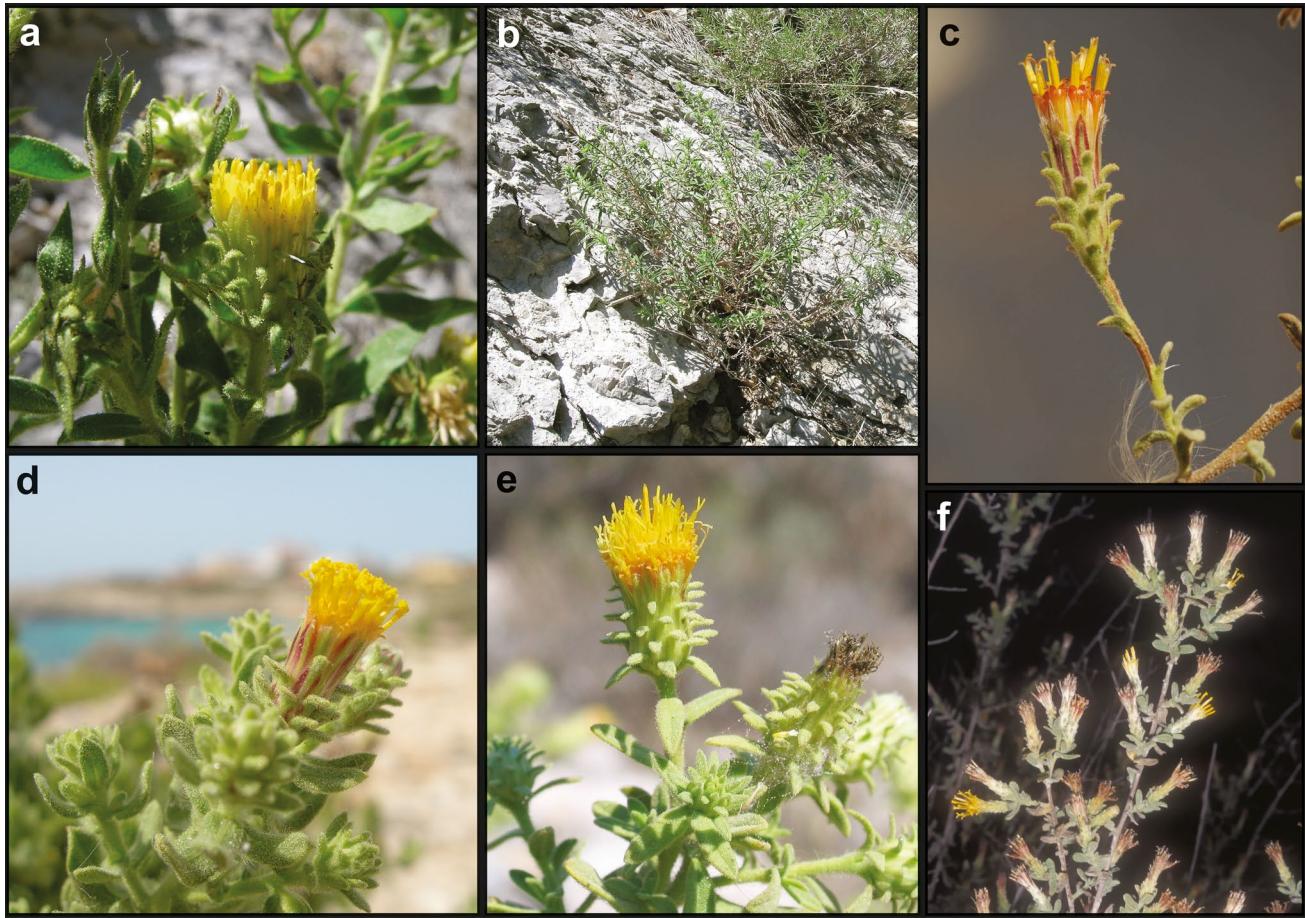


Fig. 1 **a, b** *Chiliadenus saxatilis*, photos by M. Englund; **c** *C. montanus*, photo by O. Fragman-Sapir; **d** *C. lopadusanus*, photo by R. Anderberg; **e** *C. bocconei*, photo by S. Mifsud; **f** *C. iphionoides*, photo by O. Fragman-Sapir

(Maire & Wilczek) Brullo (southern Morocco), *C. lopadusanus* Brullo (Italy; Lampedusa island), *C. iphionoides* (Boiss & C.I.Blanche) Brullo (Israel, Egypt; Sinai, Lebanon), *C. montanus* (Vahl) Brullo (Egypt; Sinai, Jordan), *C. rupestris* (Pomel) Brullo (northeastern Morocco, northwestern Algeria), *C. saxatilis* (Lam.) Brullo (Spain, France, northern Morocco) and *C. sericeus* (Batt. & Trab.) Brullo (Algeria; central Sahara) (Fig. 2). The different *Chiliadenus* species all have restricted areas of distribution, with some being limited to very small areas, something that made Brullo (1979) hypothesize a pre-Quaternary origin for the group. The current distribution pattern of *Chiliadenus*, mainly consisting of local endemics, with only a few more widespread species, and all with distributions around the Mediterranean basin could be the result of fragmentation and geographic isolation of a once widespread ancestor. An alternative explanation would be dispersal across the sea and to the relatively isolated habitats now inhabited by the present day species.

The age and biogeographical origin of the genus *Chiliadenus* has never been studied, and whether its current diversity and distribution is the result of fragmentation from a

once widespread ancestor or from dispersal is therefore unknown. The aim of the study is to produce a dated species phylogeny and to analyze the biogeographic patterns resulting in the current diversity and distribution of *Chiliadenus*.

Materials and methods

Taxon sampling

All ten *Chiliadenus* species were included in the study, with several representatives of all taxa except from *C. sericeus* where only few herbarium specimens were found, selected to cover the geographic range of the species. Outgroup taxa were selected based on earlier studies of Inuleae (Englund et al. 2009; Nylander and Anderberg 2015). Four plastid (*ndhF*, *rpl32-trnL*, *trnH-psbA*, and *trnL-trnF*) and two nuclear (ITS and ETS) regions were sequenced for the study. 124 new sequences were generated; the remaining sequences were obtained from GenBank. Geographical information on species distributions was taken from Brullo (1979) as well as

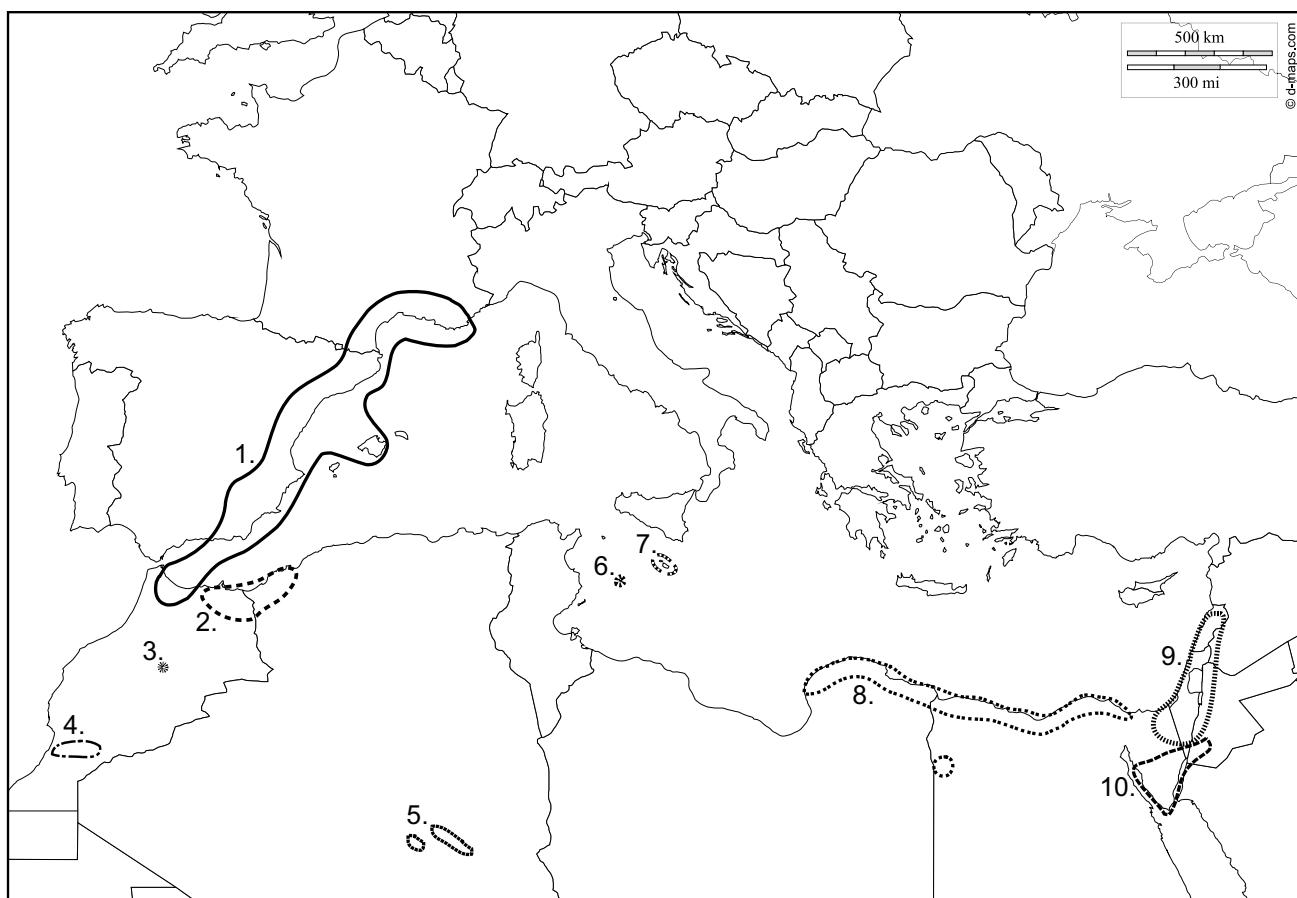


Fig. 2 Current distribution of *Chiliadenus*; 1 *C. saxatilis*, 2 *C. rupestris*, 3 *C. antiatlanticus*, 4 *C. hesperius*, 5 *C. sericeus*, 6 *C. lopadusanus*, 7 *C. bocconei*, 8 *C. candicans*, 9 *C. iphionoides*, 10 *C. montanus*. Map from <http://www.d-maps.com>

from herbarium specimens (from herbaria: BC, HUJ, MPU, S, and W). Voucher information and GenBank accession numbers for the taxa included in the molecular study are provided in Supplementary Material (Online Resource 1).

DNA extraction, amplification, and sequencing

DNA was extracted from herbarium material using a DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) according to the manufacturer's instructions. The DNA regions of interest were amplified using Hot Start Mix RTG beads (GE Healthcare, Little Chalfront, UK) according to the standard protocol of the manufacturer. The internal transcribed spacer (ITS; including ITS1, ITS2 and the 5.8S gene) was amplified using primers 18SF, 26SR (Rydin et al. 2004), 5.8F-chrys (Howis et al. 2009) and 5.8SRPEny (Nylander et al. 2013), and the external transcribed spacer (ETS) using primers Ast-1 (Markos and Baldwin 2001) and 18S-ETS (Baldwin and Markos 1998). The plastid *trnL-trnF* region (including the *trnL* intron and *trnL-trnF* intergenic spacer) was amplified using the “c”, “d” “e” and “f” primers of

Taberlet et al. (1991), and the plastid *trnH-psbA* spacer using the *trnH*(GUG) and *psbA*-Lec primers of Hamilton (1999). The plastid *ndhF* region was amplified using primers RJ1, RJ14 (Kim and Jansen 1995), *ndhF16* (Källersjö et al. 2000), *ndhF5* (Olmstead and Sweere 1994), 1750R-Ast2, 1650F-Ast (Nylander et al. 2013), *ndhF520R*-Ast (Anderberg and Swenson 2003) and *ndhF431F* (Eldenäs et al. 1999), and the plastid *rpl32-trnL* region using the primers of Shaw et al. (2007). A thermal profile of 95 °C 5 min, (95 °C 30 s, 54 °C 30 s, 72 °C 1 min 15 s) × 4, (95 °C 30 s, 53 °C 30 s, 72 °C 1 min 15 s) × 4, (95 °C 30 s, 50 °C 30 s, 72 °C 1 min 15 s) × 35, 72 °C 8 min was used for amplification of all regions. Amplified products were purified using one portion of Exonuclease I (20 u/μl) and four portions FastAP™ Thermosensitive Alkaline Phosphatase (1 u/μl; Thermo Scientific, Lithuania). Sequencing reactions were performed using an ABI BigDye Terminator Kit v. 3.1 (Applied Biosystems, Warrington, UK) according to the manufacturer's instructions. The products were cleaned using a DyeEx® 96 Kit (Qiagen, Hilden, Germany), and analyzed on an ABI3130xl automated sequencer. Sequences were assembled and edited

using the Staden package (Staden 1996), aligned using MUSCLE (Edgar 2004) as implemented in Aliview v. 1.17.1 (Larsson 2014) and manually edited using BioEdit v. 7.2.5 (Hall 1999). Individual loci were model tested for the best fitting substitution model using jModeltest v. 2.1.5 (Darriba et al. 2012) under the Akaike information criterion (AIC; Akaike 1973).

Molecular age estimation and ancestral area reconstructions

Prior to combining the individual loci of the dataset, separate Bayesian inference analyses were conducted (using MrBayes, v. 3.2.2; Huelsenbeck and Ronquist 2001) of each marker to check for incongruence. Divergence times and ancestral areas were estimated using BEAST v. 1.8.0 (Drummond et al. 2012), using the online XSEDE platform on the CIPRES Science Gateway (<https://www.phylo.org/porta12/>). The dataset was partitioned according to the six separate markers, substitution models and molecular clock rates were unlinked for all partitions except for the plastid regions (*ndhF*, *rpl32-trnL*, *trnH-psbA* and *trnL-trnF*) which were treated as a united supergene. Substitution models were set to TIM3ef+Γ for ITS, HKY+Γ for ETS, and TPM3uf+Γ for the plastid markers, suggested as best fit for the data by the model tests. Speciation was modeled by a birth/death prior (Gernhard 2008). Substitution rates were assigned exponential decays with the mean 0.1 (substitutions/site/time unit) to suggest vague but reasonable assumptions on the limits of rate distributions and avoid using uninformative priors. All other priors were left unconstrained. Due to a lack of fossil evidence relating to Inuleae, we have used ITS substitution rates from previously published studies (Schmidt and Schilling 2000; Kay et al. 2006; Lancaster 2010) for calibration purposes. ITS substitution rate estimates derived from three different Asteraceae representatives (*Artemisia* L., 1.69×10^{-9} , *Ericameria* Nutt., 2.17×10^{-9} , *Eupatorium* L. 2.51×10^{-9}) with a life span similar to that of *Chiliadenus* were utilized. The calibration was modeled by a normal distribution using the published rates as mean with a 95% credibility interval corresponding to the full uncertainty of the three rates, following Nylander et al. (2014).

Ancestral areas were reconstructed using the discrete phylogeographical trait implementation in BEAST, integrating over the uncertainty of the tree topology as well as the trait model. The distribution of *Chiliadenus* was divided into five areas, and the different species coded according to distribution (Figs. 2, 3). Species with a wide distribution were coded as multistate. A reversible rate matrix assigned equal prior probabilities for transitions between any two areas (continental southwestern Europe, Morocco and northwestern Algeria, Algeria (central Sahara), south Mediterranean islands

(Malta and Lampedusa), and the eastern Mediterranean region; see Fig. 3).

Analyses were performed using a Markov chain Monte Carlo (MCMC) and were run three times for 80 million generations each, logging parameters every 8000 generations. All runs were initiated on random starting trees. Convergence and mixing of Markov chains and effective sample size (ESS) values for all parameters were checked using Tracer v. 1.5 (Rambaut and Drummond 2009). The posterior distributions of trees were summarized using TreeAnnotator v. 1.8.0 (Drummond et al. 2012), removing a proportion of each run as burn-in, and visualized using FigTree v. 1.3.1 (Rambaut 2009).

Results

The dataset consisted of 5897 aligned nucleotide characters, 174 of which were informative. A description of the dataset is given in Table 1. No signs of incongruences were detected when analyzing the separate markers independently.

The dated BEAST MCC tree, including ancestral area reconstructions, is shown in Fig. 3. Our analyses confirm the genus *Chiliadenus* as monophyletic (PP = 1.0; Fig. 3) and placed as sister to *Dittrichia* (PP = 1.0; Fig. 3). *Chiliadenus* is estimated to have diverged from *Dittrichia* around 5.45 Ma (95% HPD 3.25–8.55 Ma; Fig. 3, node 1), with continental southwestern Europe (area A, see Fig. 3), Morocco and northwestern Algeria (B) estimated as the most probable ancestral area [with a posterior probability (pp) of 0.43 for A, 0.26 for B]. The crown age of *Chiliadenus* is in our analyses estimated to 2.29 Ma (1.37–3.58 Ma), and ancestral area reconstructions show Morocco and northwestern Algeria (B) as most probable ancestral area (pp = 0.67; Fig. 3, node 2). The phylogenetic relationships of the different species within *Chiliadenus* are resolved (Fig. 3). A clade consisting of *Chiliadenus saxatilis*, *C. sericeus*, and *C. antiatlanticus* (PP = 1.0; Fig. 3, node 3), with current distributions in continental southwestern Europe, Morocco and Algeria, respectively, is estimated to 1.03 Ma (0.42–1.91 Ma). Morocco and northwestern Algeria (B) is estimated as the most probable ancestral area (pp = 0.7; Fig. 3, node 3). The crown age of the rest of *Chiliadenus* is estimated to 1.96 Ma (1.15–3.04 Ma), with Morocco and northwestern Algeria (B) as most probable ancestral area (pp = 0.69; Fig. 3, node 4). *Chiliadenus bocconeii* and *C. lopadusanus*, with distributions of Malta and Lampedusa, respectively, are shown to be sisters (PP = 1.0; Fig. 3, node 7), with the south Mediterranean islands (D) as most probable ancestral area (pp = 0.89; Fig. 3, node 7). Their stem node is estimated to have diverged from the eastern Mediterranean clade (consisting of *Chiliadenus candicans*, *C. montanus* and *C. iphionoides*) around 1.58 Ma (0.9–2.49 Ma; Fig. 3, node 5), and ancestral

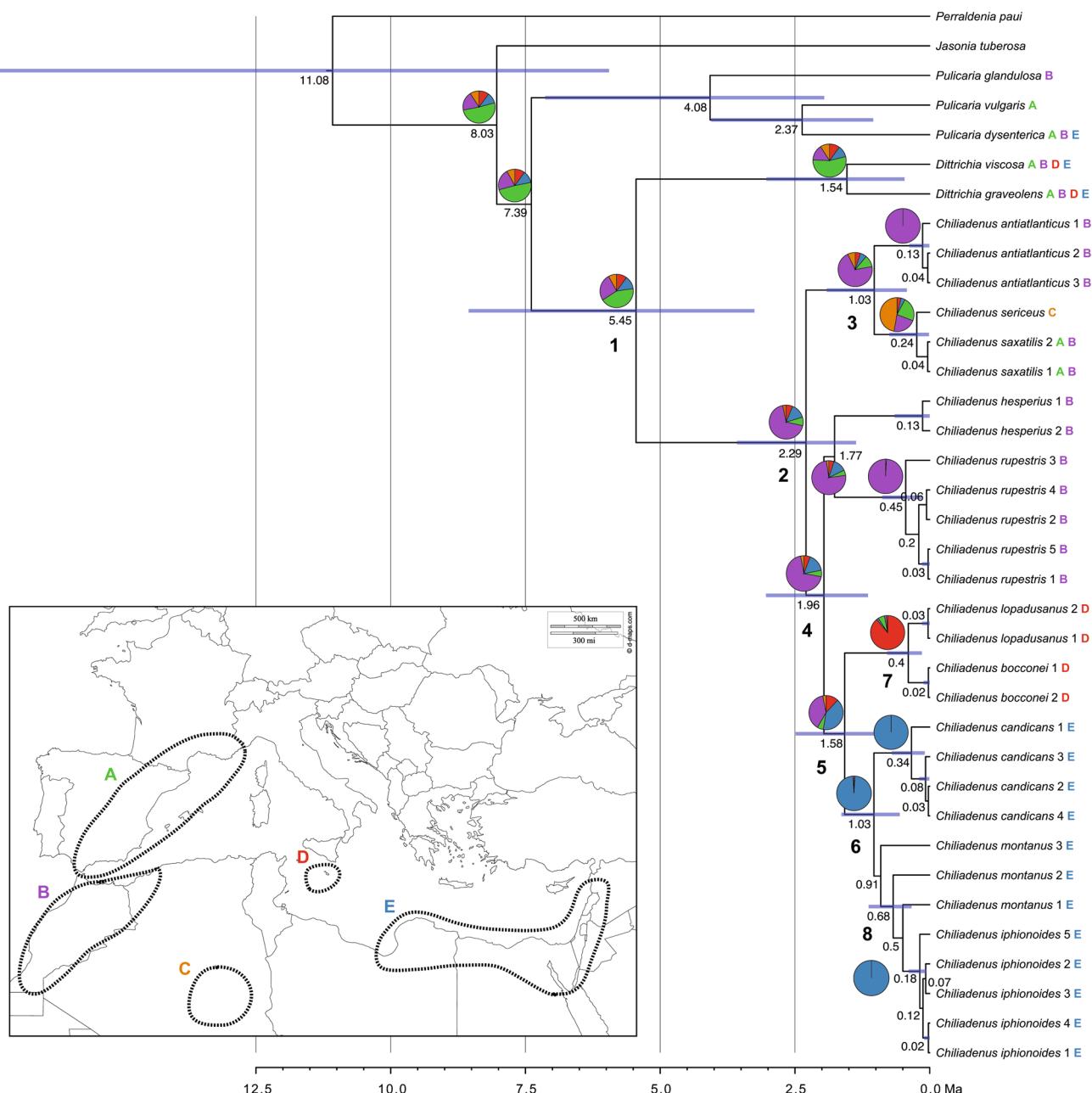


Fig. 3 Maximum clade credibility (MCC) tree with median node ages for *Chiliadenus*. Strongly supported nodes (posterior values ≥ 0.95) are presented with node bars, representing the 95% highest posterior density (HPD) intervals. Relative probabilities of ancestral areas for selected nodes are shown as pie charts. Extant distributions are indicated after the taxon names. Map showing areas used in ancestral area

reconstructions (A continental southwestern Europe, B Morocco and northwestern Algeria, C Algeria; central Sahara, D south Mediterranean islands, E eastern Mediterranean region). Numbers after taxon names are linked to voucher specimens (see Online Resource 1). Map from <http://www.d-maps.com>

Table 1 Taxa and character information for the different regions of the dataset

	ETS	ITS	ndhF	rpl32-trnL	trnH-psbA	trnL-trnF	All
No. of taxa	29	35	30	17	36	30	36
No. of characters/aligned length	553	805	2280	940	437	882	5897
Variable characters	77	120	76	14	34	28	349
Informative characters	50	61	34	8	10	11	174

area reconstructions show the eastern Mediterranean region (E; $pp = 0.4$) and Morocco and northwestern Algeria (B; $pp = 0.38$) as most probable ancestral area (Fig. 3, node 5). The crown age of *Chiliadenus candicans*, *C. montanus*, and *C. iphionoides* ($PP = 1.0$; Fig. 3, node 6) is dated to 1.03 Ma (0.56–1.64 Ma), with the eastern Mediterranean region (E) as most probable ancestral area ($pp = 0.98$; Fig. 3, node 6).

Discussion

Chiliadenus is here confirmed to be monophyletic ($PP = 1.0$), in agreement with earlier studies (Englund et al. 2009; Nylander and Anderberg 2015), and the interrelationships of the different species resolved (Fig. 3). The position of *Chiliadenus* as sister to *Dittrichia* is recovered with high support ($PP = 1.0$; Fig. 3). The estimated ages found in the present study fit well within the age of the Inuleae recovered by earlier studies (Nylander et al. 2016). The ancestors of *Chiliadenus* and *Dittrichia* are estimated to have diverged around 5.45 Ma (3.25–8.55 Ma) somewhere in the area around continental southwestern Europe, Morocco, and northwestern Algeria (Fig. 3, node 1). The ancestral *Chiliadenus* then continued to evolve in northern Africa, whereas *Dittrichia* continued to evolve in Europe (Fig. 3). The Mediterranean basin was desiccated in the Miocene during what is referred to as the “Messinian salinity crisis” between 5.96 and 5.33 Ma ago, after the Strait of Gibraltar closed (Hsü et al. 1973; Krijgsman et al. 1999). Toward the end of this period, the Mediterranean basin would have been almost desiccated giving opportunities for plants and animals to colonize the land areas between Europe and North Africa, until it was once again submerged by the “Zanclean flood” ca. 5.33 Ma ago when the Atlantic waters found a way through the Strait of Gibraltar and refilled the Mediterranean basin (Garcia-Castellanos et al. 2009). It is possible that the desiccated Mediterranean may have provided opportunities for dispersal and range expansion for a widespread ancestor of *Chiliadenus* and *Dittrichia* until a vicariant event, possibly the Zanclean flood, led to the divergence of the ancestors of *Dittrichia* in continental Europe and *Chiliadenus* in northern Africa.

The *Chiliadenus* crown group is here determined to 2.29 Ma (1.37–3.58 Ma; Fig. 3, node 2). Ancestral area reconstructions show Morocco and northwestern Algeria as the most probable ancestral area for the *Chiliadenus* crown group and the area where most of the early divergences have occurred (Fig. 3). *Chiliadenus* has then later diverged and dispersed eastwards to the eastern Mediterranean region and to the south Mediterranean islands, as well as northward to continental southwestern Europe, and south to the central Sahara to its current distribution (Fig. 3).

A clade consisting of *Chiliadenus antiatlanticus*, *C. saxatilis* and *C. sericeus* ($PP = 1.0$; Fig. 3, node 3), with a main

distribution in Morocco, Algeria, and Spain started diversifying ca. 1.03 Ma (0.42–1.91 Ma) and is sister to the rest of *Chiliadenus*. *Chiliadenus sericeus*, a species that has an isolated distribution in the central Sahara, far from the other species, is here placed as sister to *C. saxatilis* (Fig. 1a, b) with a wide distribution ranging from southern France to northern Morocco (Figs. 2, 3). There were, however, difficulties in sequencing DNA regions from the few available old specimens of *Chiliadenus sericeus*, only two out of six marker sequences could be generated, and its position must therefore be seen as somewhat uncertain. *Chiliadenus antiatlanticus* is found in the Anti-Atlas mountain range of Morocco. The ancestor of the group likely evolved in the area around Morocco and northwestern Algeria, with the current distributions of *Chiliadenus saxatilis* and *C. sericeus* the result of later dispersal and diversification (Fig. 3, node 3). The crown age of the rest of *Chiliadenus* is estimated to around 1.96 Ma (1.15–3.04 Ma; Fig. 3, node 4). *Chiliadenus rupestris* and *C. hesperius*, found in northern and southwestern Morocco (Fig. 2), are placed together although the node lacks support and are placed as sisters to the rest of the clade (Fig. 3). *Chiliadenus bocconeii* and *C. lopadusanus* (Fig. 1d, e), endemic to the Maltese islands and Lampedusa island, respectively, are shown to be sisters ($PP = 1.0$; Fig. 3, node 7) and estimated to have started diversifying ca. 0.4 Ma (0.14–0.79 Ma). Their ancestor is estimated to have diverged from the ancestor of an eastern Mediterranean clade consisting of *Chiliadenus candicans*, *C. montanus*, and *C. iphionoides* around 1.58 Ma (0.9–2.49 Ma; Fig. 3, node 5), and to have spread to the south Mediterranean islands after that. Ancestral area reconstructions detect an eastward change in distribution from Morocco and northwestern Algeria to the eastern Mediterranean region sometime between 1.96 and 1.58 Ma (Fig. 3). The ancestor of the two clades appears to have dispersed eastward, expanding its range and for some time being present in both areas, and later gone extinct in the west (Fig. 3, node 5). The ancestor of the eastern clade has then continued to expand its range eastwards and *Chiliadenus candicans*, *C. montanus*, and *C. iphionoides* all appear to have evolved in the eastern Mediterranean region (Fig. 3, node 6). *Chiliadenus candicans*, found in Libya, and *C. montanus* and *C. iphionoides* (Fig. 1c, f), with distributions in the Sinai Peninsula and in Israel, respectively, form a clade with an estimated crown age of 1.03 Ma (0.56–1.64 Ma; Fig. 3, node 6) where *C. candicans* is placed as sister to the others.

The ancestor of *Chiliadenus* and *Dittrichia* is here estimated to have diverged around 5.45 Ma (3.25–8.55 Ma), whereas the *Chiliadenus* crown group is only dated to 2.29 Ma (1.37–3.58 Ma), showing a temporal gap of 3 million years (Fig. 3). The temporal gap (5.45–2.29 Ma) approximately spans from the beginning of the Messinian salinity crisis (5.96–5.33 Ma; Krijgsman et al. 1999) to the

onset of the Mediterranean climate, a pattern detected in several other Mediterranean lineages as well (Fiz-Palacios and Valcárcel 2011, 2013). The Mediterranean climate, characterized by dry summers, with rainfall concentrated during the other seasons and with low temperatures during the winter, is thought to have originated around 3.2 Ma, with the summer draughts becoming stable around 2.8 Ma. Prior to that, moist climatic conditions (with rainy summers) would have prevailed (Suc 1984). The establishment of the Mediterranean climate at 3.2–2.8 Ma meant a significant environmental change, and the transition from moist climatic conditions to a climate with seasonal warm drought periods had a great impact on the flora. Another climatic change occurred around 2.3 Ma with the oldest xeric phase and the start of the Quaternary-type Mediterranean climatic fluctuations (Suc 1984). Fossil pollen shows a reduction in forest cover and an enlargement of steppe communities, indicating drier and milder climatic conditions at this time (Suc 1984). The diversification of *Chiliadenus* is dated to have occurred around the time of the climatic changes, and the evolution of the group may be connected to the climatic changes. At 2.29 Ma, around the time of the beginning of the Quaternary-type climatic fluctuations, the ancestral *Chiliadenus* had started to evolve into two genetically distinct groups, where one continued to evolve and spread in Morocco and Algeria, and later in southern continental Europe, eventually resulting in *C. saxatilis*, *C. sericeus* and *C. antatlanticus* (Fig. 3). The other group that started to diversify around 1.96 Ma spread and diversified with time into a western and an eastern group at 1.77 and 1.58 Ma, respectively, where the western group eventually evolved into *Chiliadenus rupestrис* and *C. hesperius* (Fig. 3). The eastern group spread and diversified further into an island clade representing *Chiliadenus lopadusanus* and *C. bocconeи* and an eastern Mediterranean mainland clade, which eventually evolved into *C. candicans*, *C. montanus* and *C. iphionoides* (Fig. 3).

Conclusions

Ancestral *Chiliadenus* diverged from its sister *Dittrichia* around 5.45 Ma, possibly as an effect of the Messinian salinity crisis and subsequent Zanclean flooding of the Mediterranean basin. The *Chiliadenus* crown group likely evolved and started to diversify in the area around Morocco and northwestern Algeria. The different taxa have since spread and continued to diversify around the Mediterranean region eventually resulting in the current diversity and distribution of the genus. The diversification of *Chiliadenus* seems to coincide with the onset of the Mediterranean climate becoming increasingly dryer, and the diversification of the different species groups may be connected to the climatic changes.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Information on Electronic Supplementary Material

Online Resource 1. Voucher information and GenBank accession numbers.

Online Resource 2. DNA sequence alignments in nexus format.

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