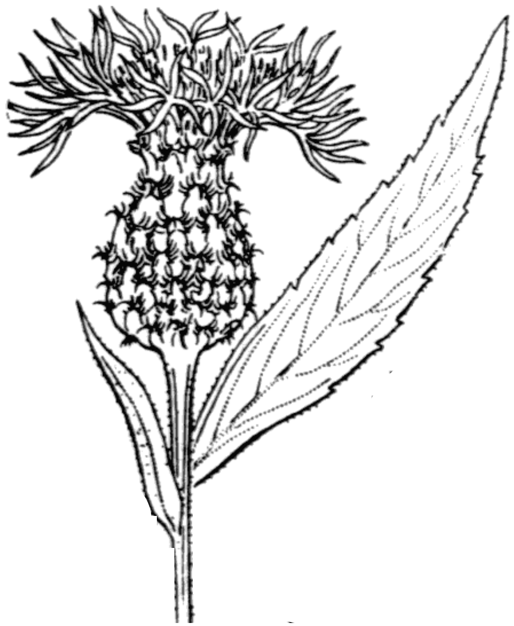
Cytogenetic insights into plant diversification: *Asteraceae* as a case study

J. Pellicer, O. Hidalgo, D. Vitales, J. Vallès, A. Santos-Guerra, A. García, S. Siljak-Yakovlev

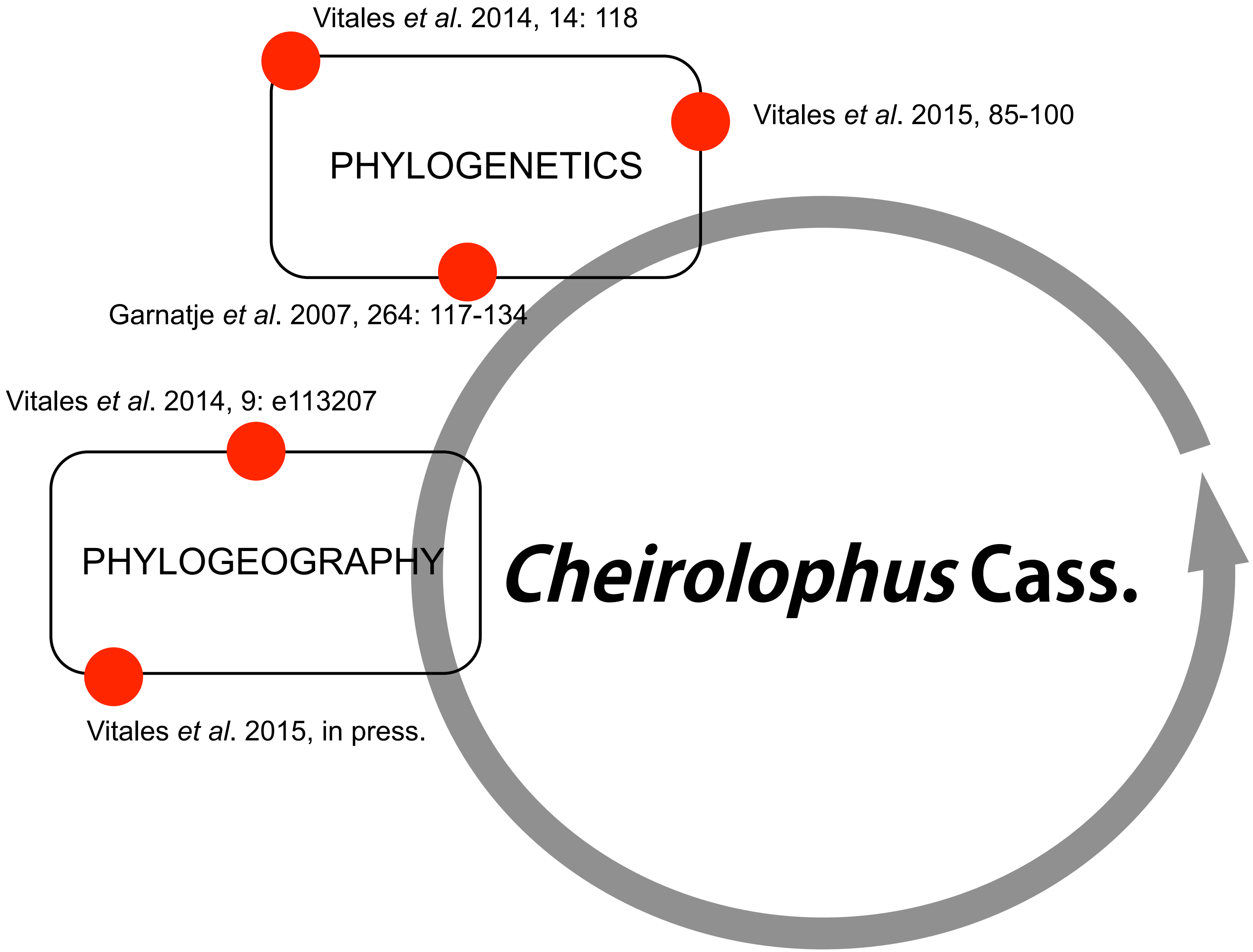
Royal Botanic Gardens Kew
CSIC Consejo Superior de Investigaciones Científicas
institut botànic de Barcelona
Universitat de Barcelona
Gobierno de Canarias Instituto Canario de Investigaciones Agrarias
Universidad Rey Juan Carlos
Université Paris Sud
université Paris-Saclay

Talk outline:

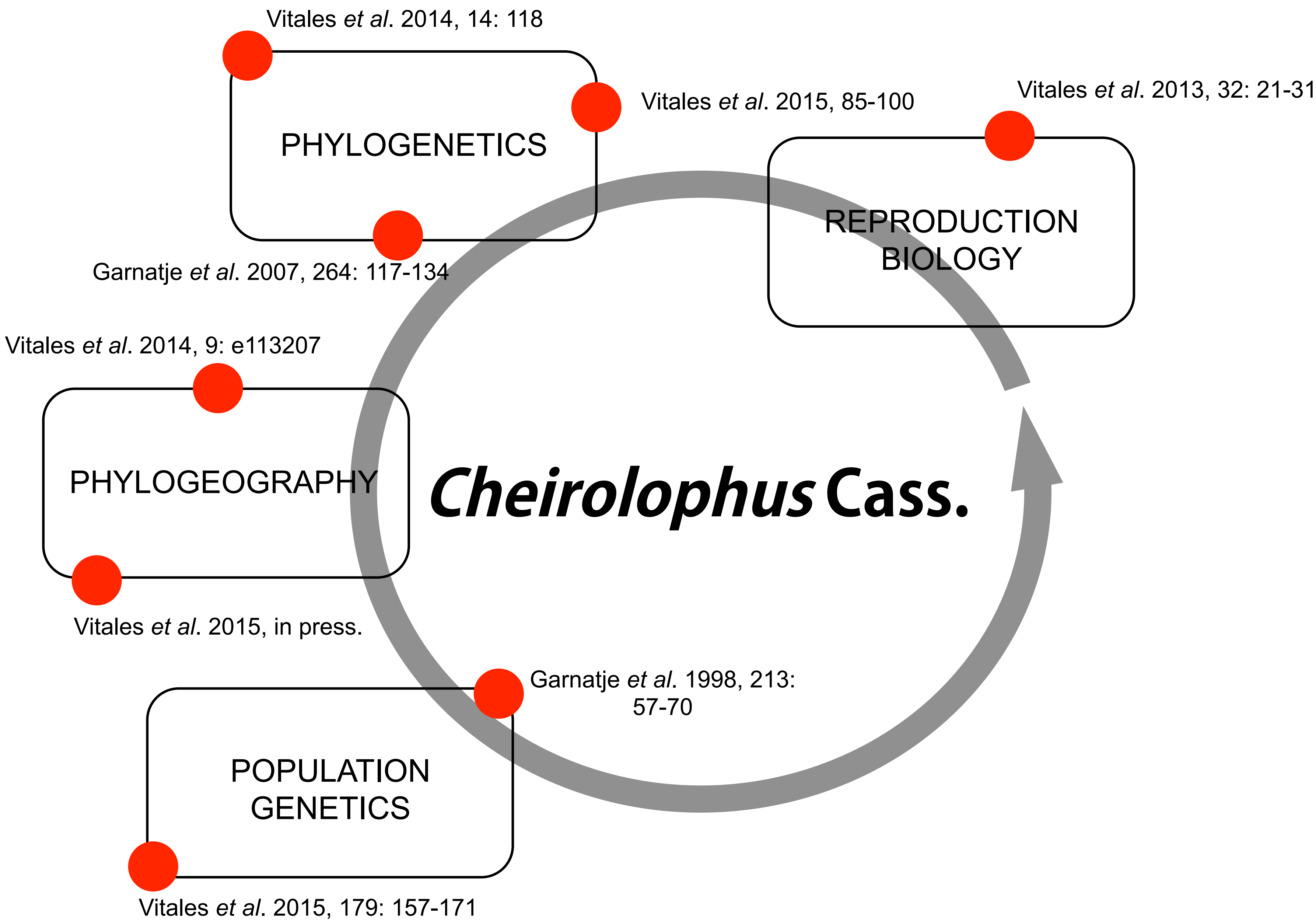
- The genus *Cheirolophus* Cass.
- Phylogenetics and diversification patterns across the Mediterranean basin and Macaronesia
- Evolution of cytogenetic traits in *Cheirolophus*:
    - Chromosome data
    - Genome size
    - Ribosomal DNA loci

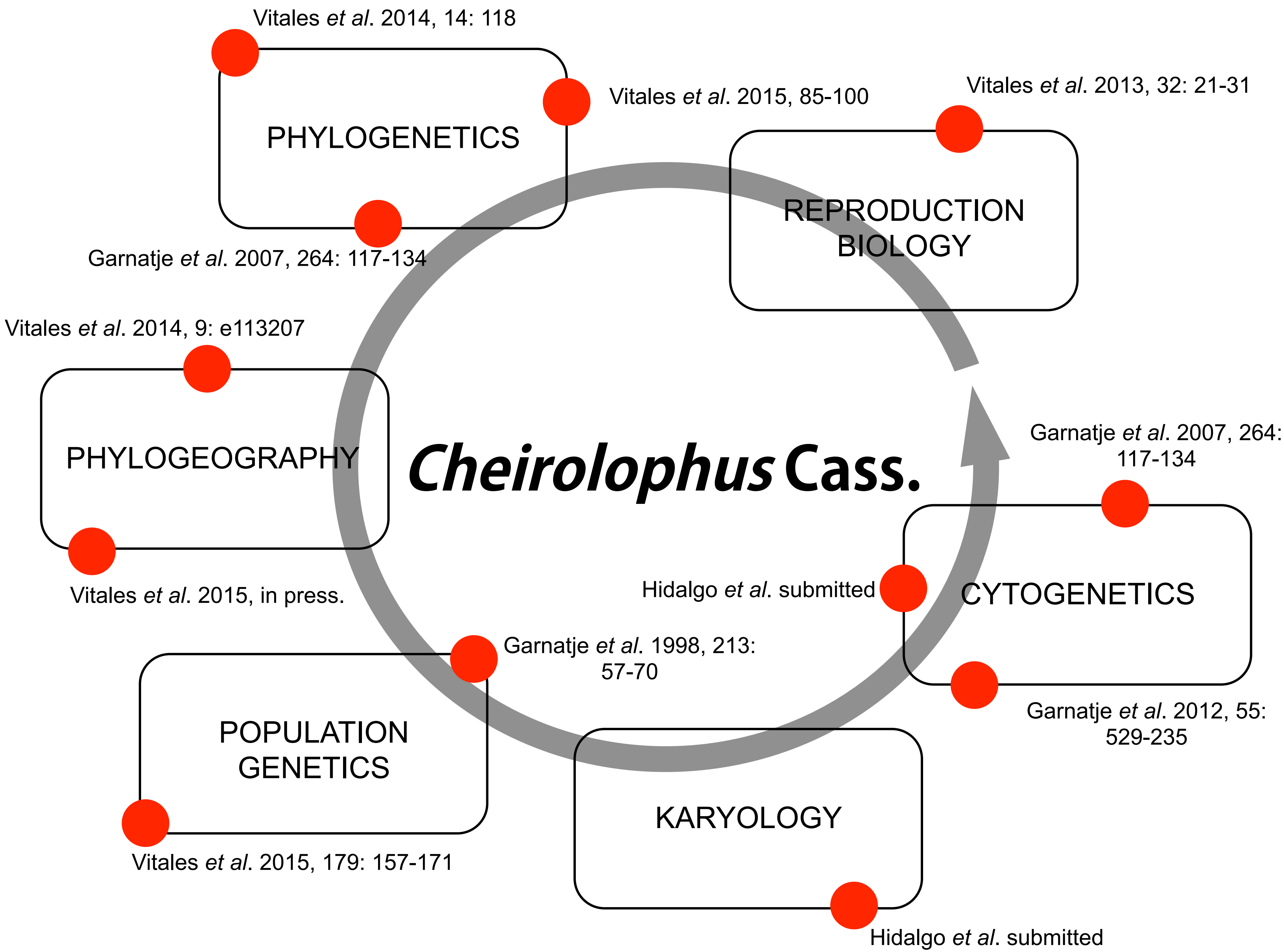


Why *Cheirolophus*?

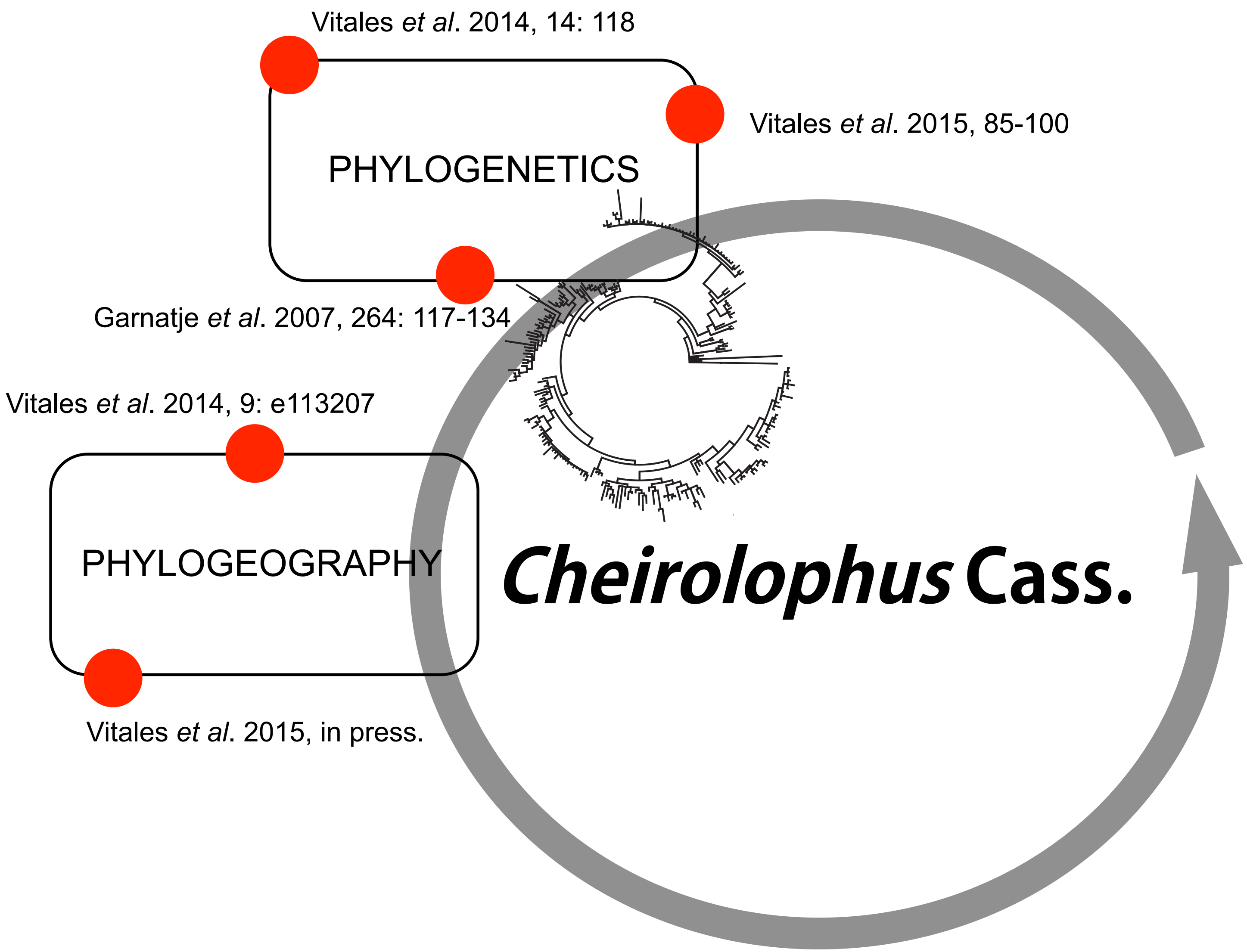


Vitales et al. 2014, 14: 118
Vitales et al. 2015, 85-100
PHYLOGENETICS
Garnatje et al. 2007, 264: 117-134
Vitales et al. 2014, 9: e113207
PHYLOGEOGRAPHY
Vitales et al. 2015, in press.
Cheirolophus Cass.

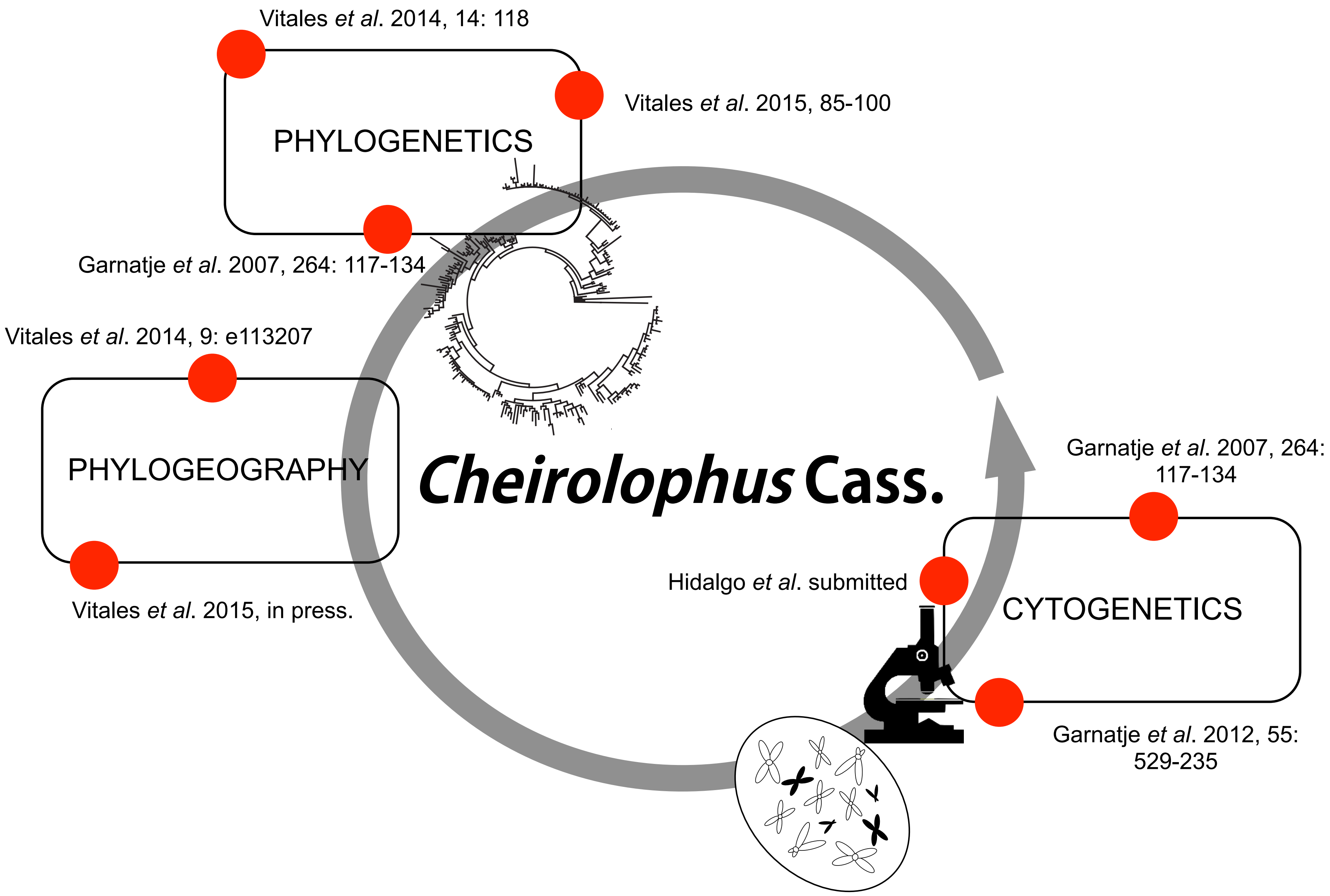

Vitales *et al*. 2014, 14: 118
Vitales *et al*. 2015, 85-100
Vitales *et al*. 2013, 32: 21-31
PHYLOGENETICS
REPRODUCTION BIOLOGY
Garnatje *et al*. 2007, 264: 117-134
Vitales *et al*. 2014, 9: e113207
PHYLOGEOGRAPHY
Cheirolophus Cass.
Vitales *et al*. 2015, in press.
Garnatje *et al*. 1998, 213: 57-70
POPULATION GENETICS
Vitales *et al*. 2015, 179: 157-171



Vitales *et al*. 2014, 14: 118
Vitales *et al*. 2015, 85-100
PHYLOGENETICS
Garnatje *et al*. 2007, 264: 117-134
Vitales *et al*. 2013, 32: 21-31
REPRODUCTION BIOLOGY
Vitales *et al*. 2014, 9: e113207
PHYLOGEOGRAPHY
Vitales *et al*. 2015, in press.
Cheirolophus Cass.
Garnatje *et al*. 2007, 264: 117-134
CYTOGENETICS
Hidalgo *et al*. submitted
Garnatje *et al*. 1998, 213: 57-70
Garnatje *et al*. 2012, 55: 529-235
POPULATION GENETICS
Vitales *et al*. 2015, 179: 157-171
KARYOLOGY
Hidalgo *et al*. submitted

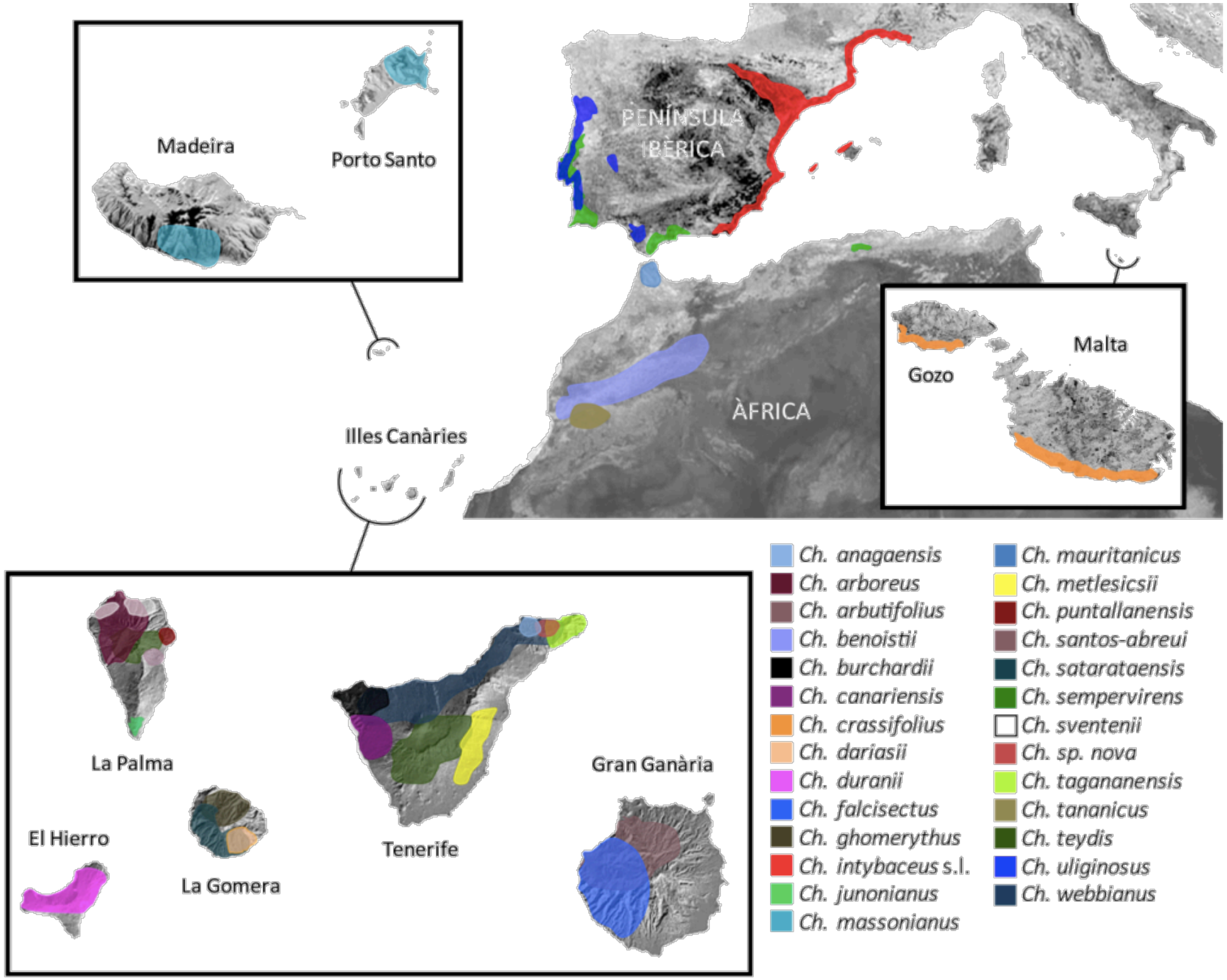


Vitales et al. 2014, 14: 118
Vitales et al. 2015, 85-100
PHYLOGENETICS
Garnatje et al. 2007, 264: 117-134
Vitales et al. 2014, 9: e113207
PHYLOGEOGRAPHY
Vitales et al. 2015, in press.
Cheirolophus Cass.

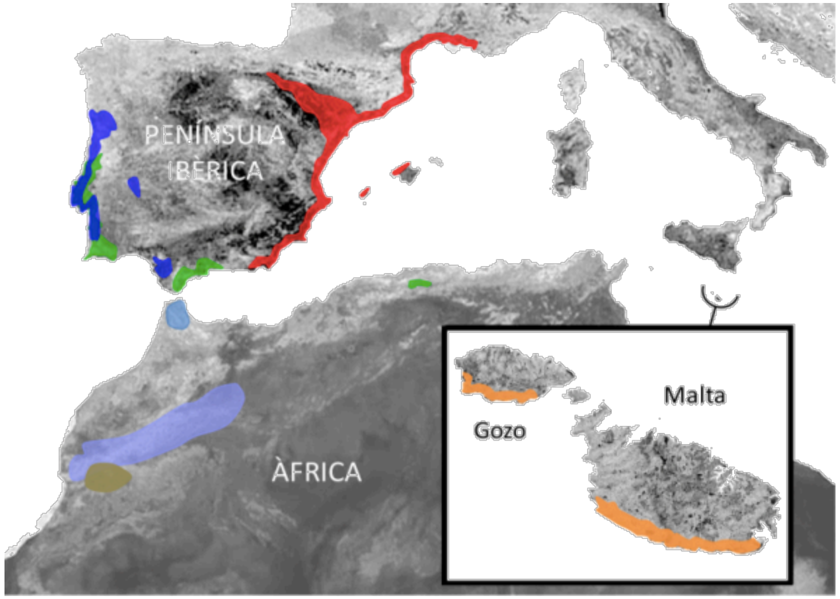


Vitales *et al*. 2014, 14: 118
Vitales *et al*. 2015, 85-100
PHYLOGENETICS
Garnatje *et al*. 2007, 264: 117-134
Vitales *et al*. 2014, 9: e113207
PHYLOGEOGRAPHY
Vitales *et al*. 2015, in press.
Cheirolophus Cass.
Garnatje *et al*. 2007, 264: 117-134
Hidalgo *et al*. submitted
CYTOGENETICS
Garnatje *et al*. 2012, 55: 529-235

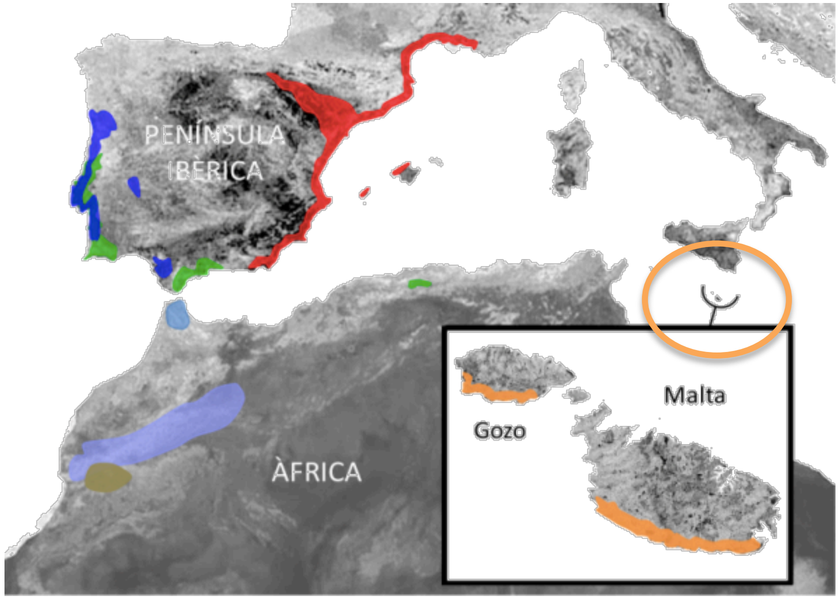
Cheirolophus Cass.: c. 28 spp



Cheirolophus Cass.: c. 28 spp

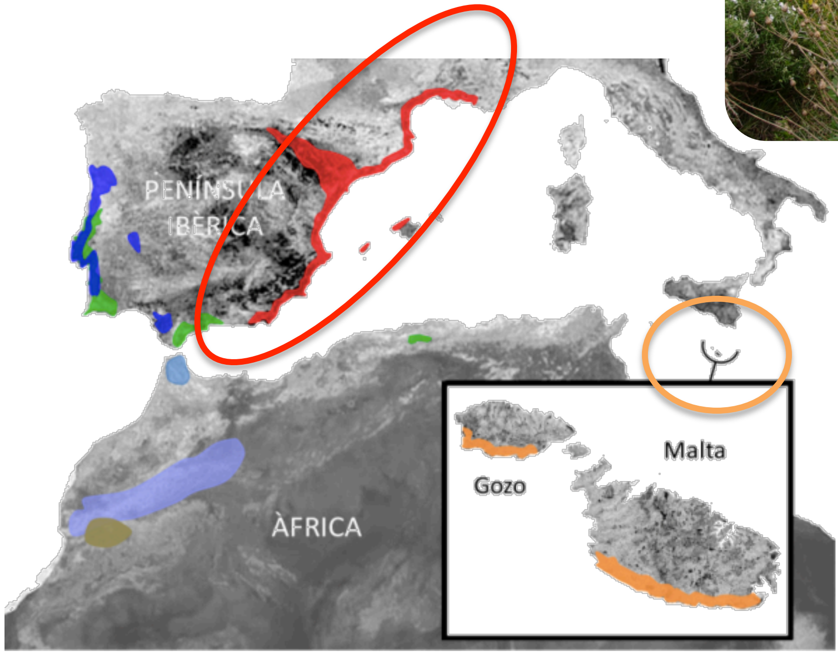


Cheirolophus Cass.: c. 28 spp



Cheirolophus crassifolius

Cheirolophus Cass.: c. 28 spp



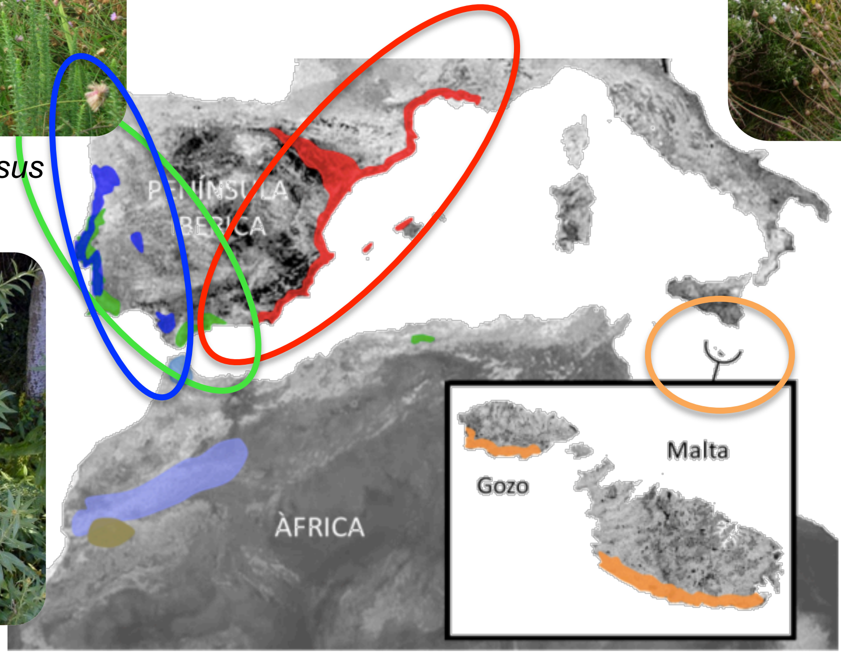
Cheirolophus intybaceus

Cheirolophus crassifolius

Cheirolophus Cass.: c. 28 spp

Cheirolophus uliginosus

Cheirolophus intybaceus



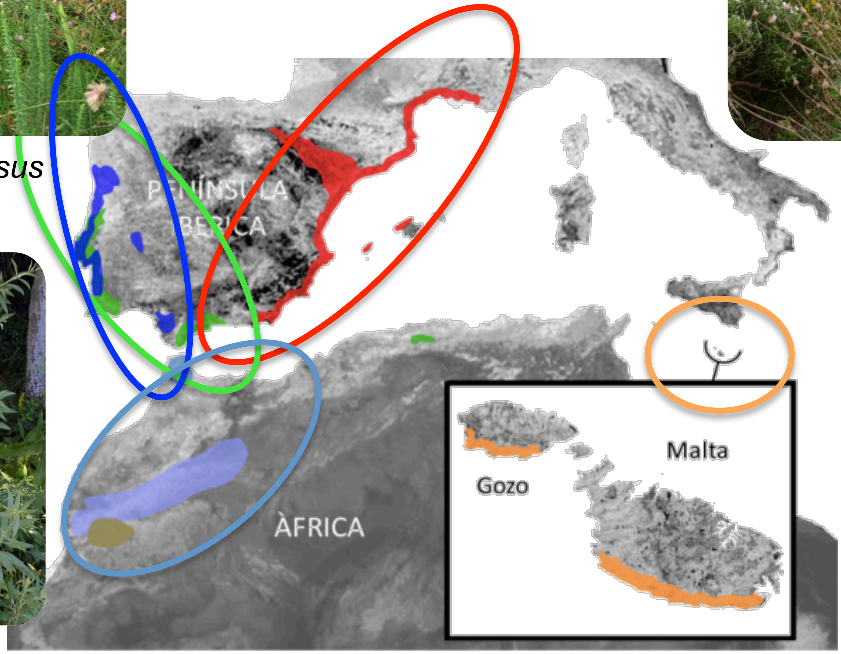
Cheirolophus sempervirens

Cheirolophus crassifolius

Cheirolophus Cass.: c. 28 spp

Cheirolophus uliginosus

Cheirolophus intybaceus

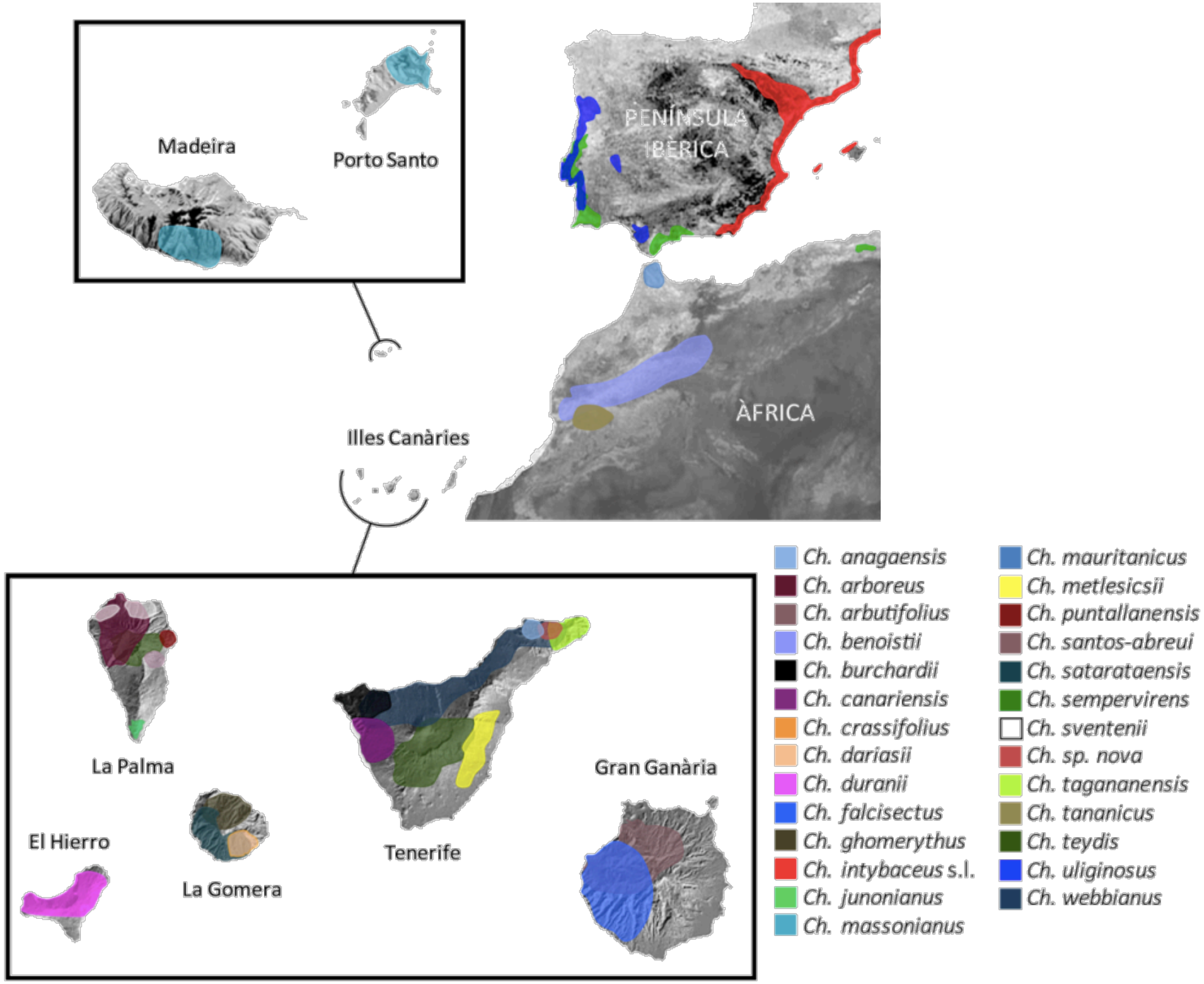


Cheirolophus sempervirens

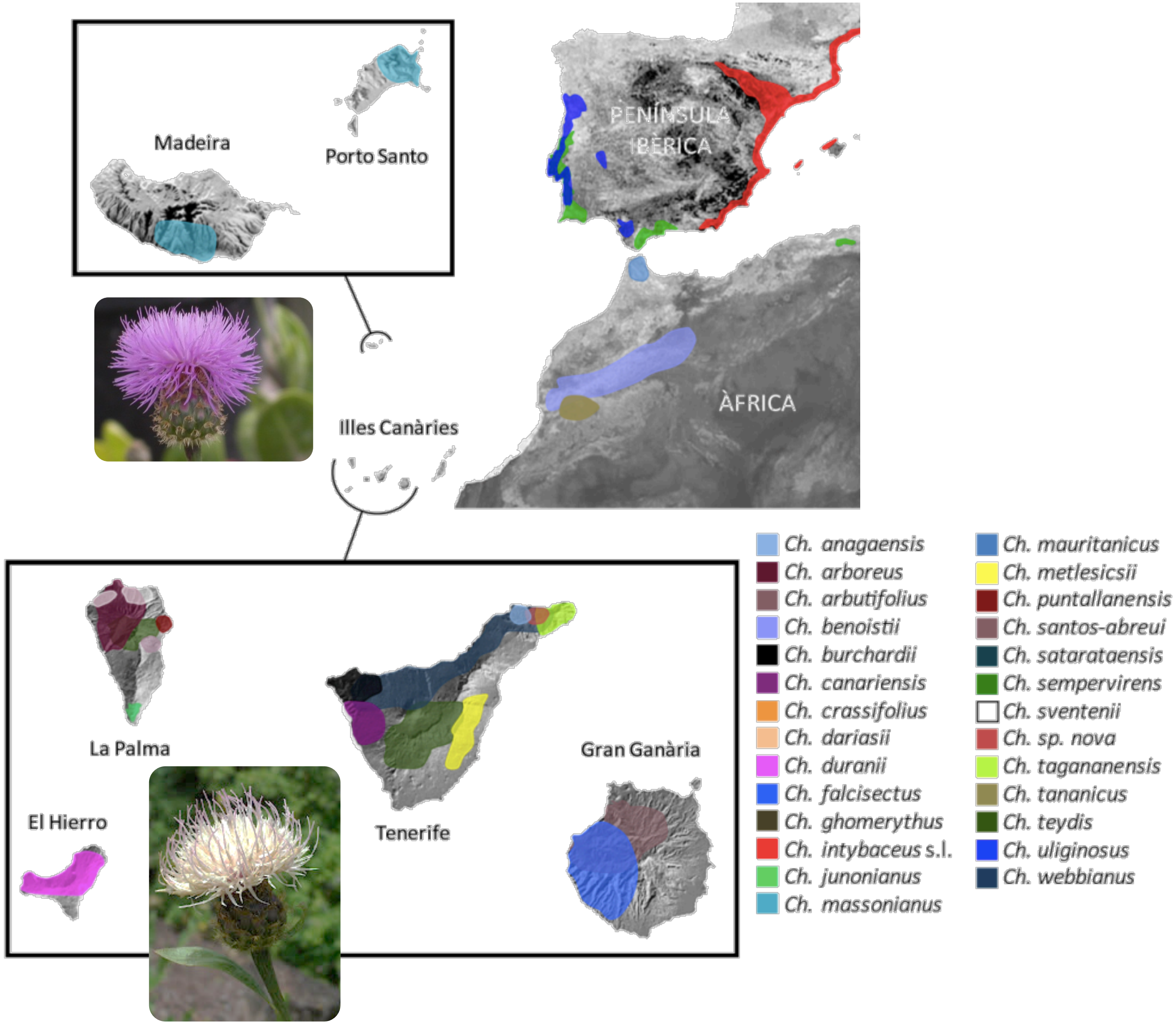
Cheirolophus tananicus, Ch. benoistii and Ch. mauritanicus

Cheirolophus crassifolius

Cheirolophus Cass.: c. 28 spp



Cheirolophus Cass.: c. 28 spp



Cheirolophus burchardii

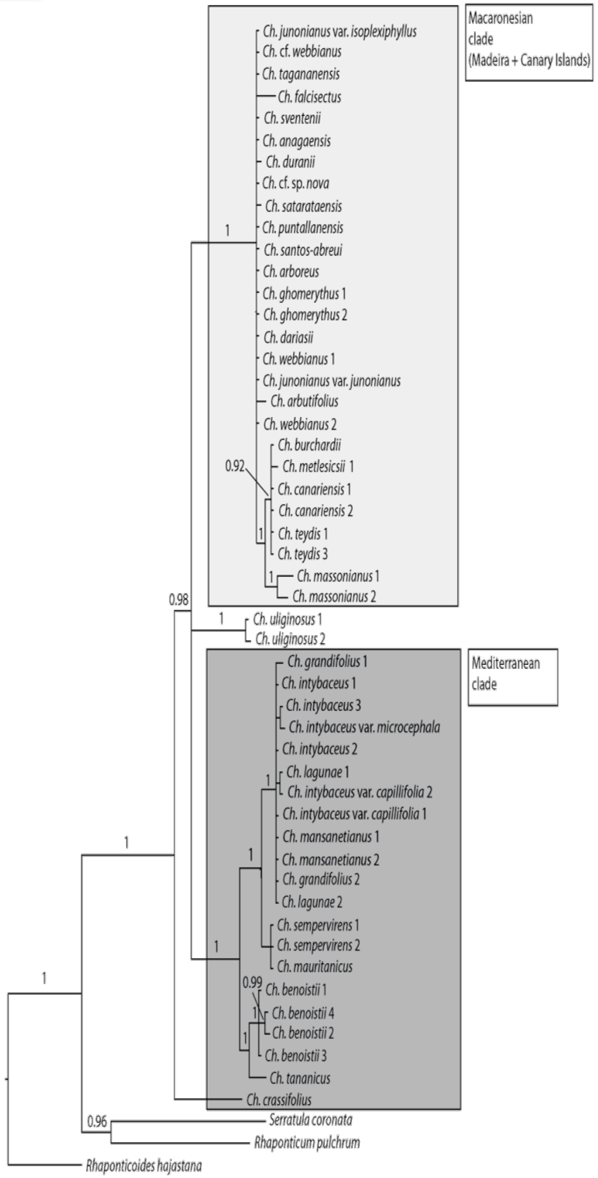
Cheirolophus satarataensis

Cheirolophus falcisectus

Cheirolophus Cass.:

Phylogenetics and diversification

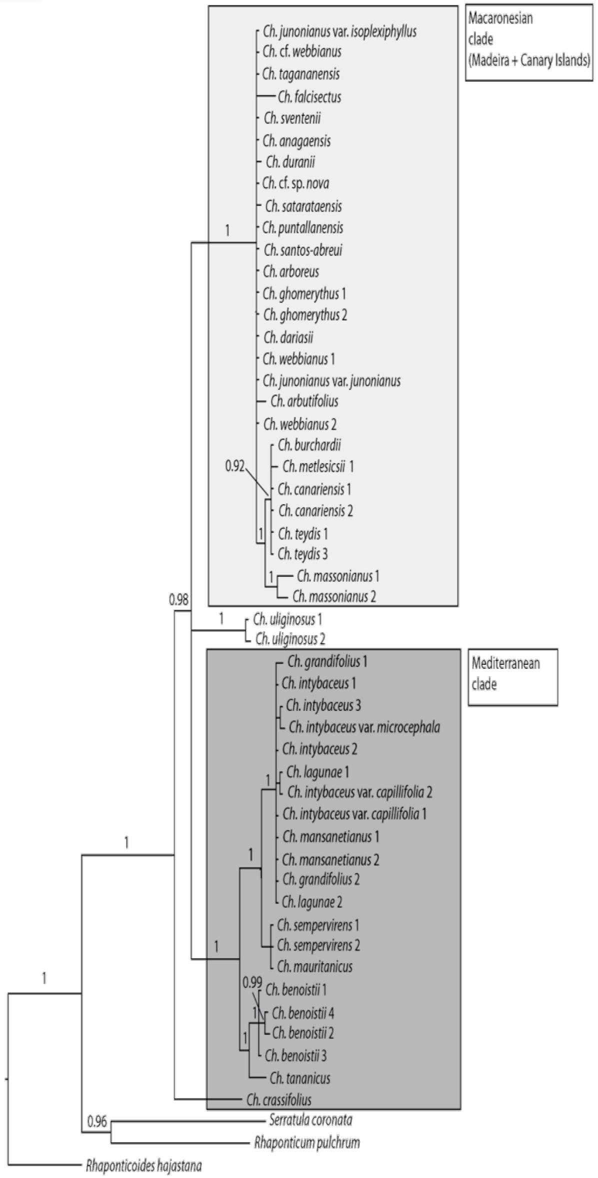
Phylogenetics and diversification of *Cheirolophus*



- ITS and ETS provides resolution at the backbone of the tree.
- Monophyly of the genus and early-diverged position of *Ch. crassifolius* from Malta.
- Early-branching of the Iberian hemicryptophyte *Ch. uliginosus*, but not entirely resolved.
- Well defined Mediterranean clade, reflecting morphologic and geographic affinities among the species.
- Macaronesian clade poorly resolved.

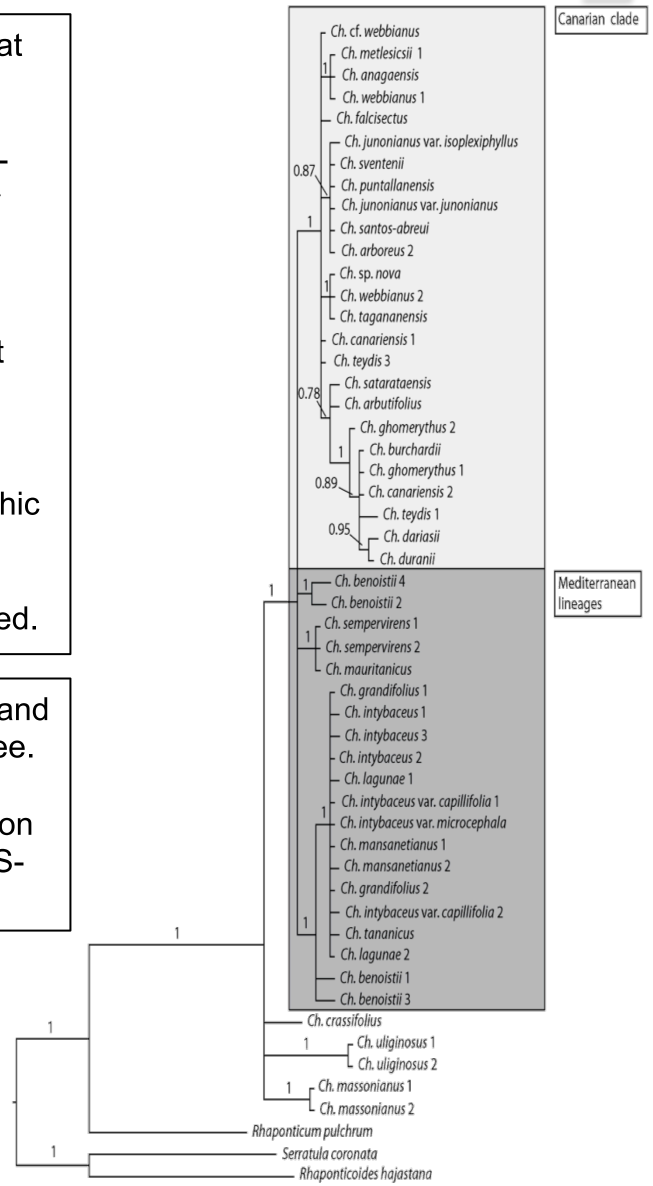
Vitales *et al*. 2014, 14: 118

Phylogenetics and diversification of *Cheirolophus*



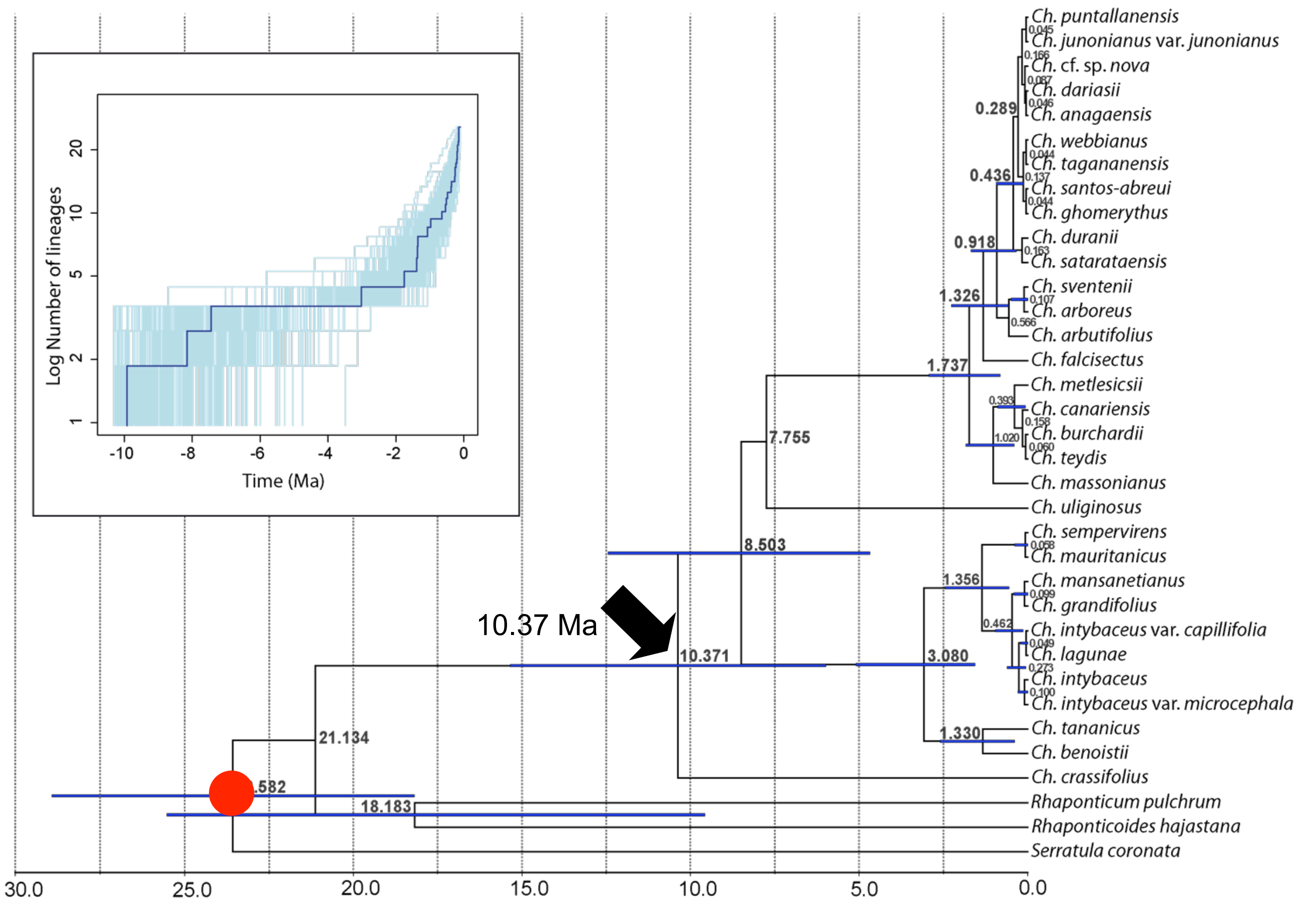
- ITS and ETS provides resolution at the backbone of the tree.
- Monophyly of the genus and early-diverged position of *Ch. crassifolius* from Malta.
- Early-branching of the Iberian hemicryptophyte *Ch. uliginosus*, but not entirely resolved.
- Well defined Mediterranean clade, reflecting morphologic and geographic affinities among the species.
- Macaronesian clade poorly resolved.

- Plastid DNA shows less variability and resolution at the backbone of the tree.
- More variability and better resolution within the Canarian lineage than ITS-ETS.



Vitales *et al*. 2014, 14: 118

Phylogenetics and diversification of *Cheirolophus*

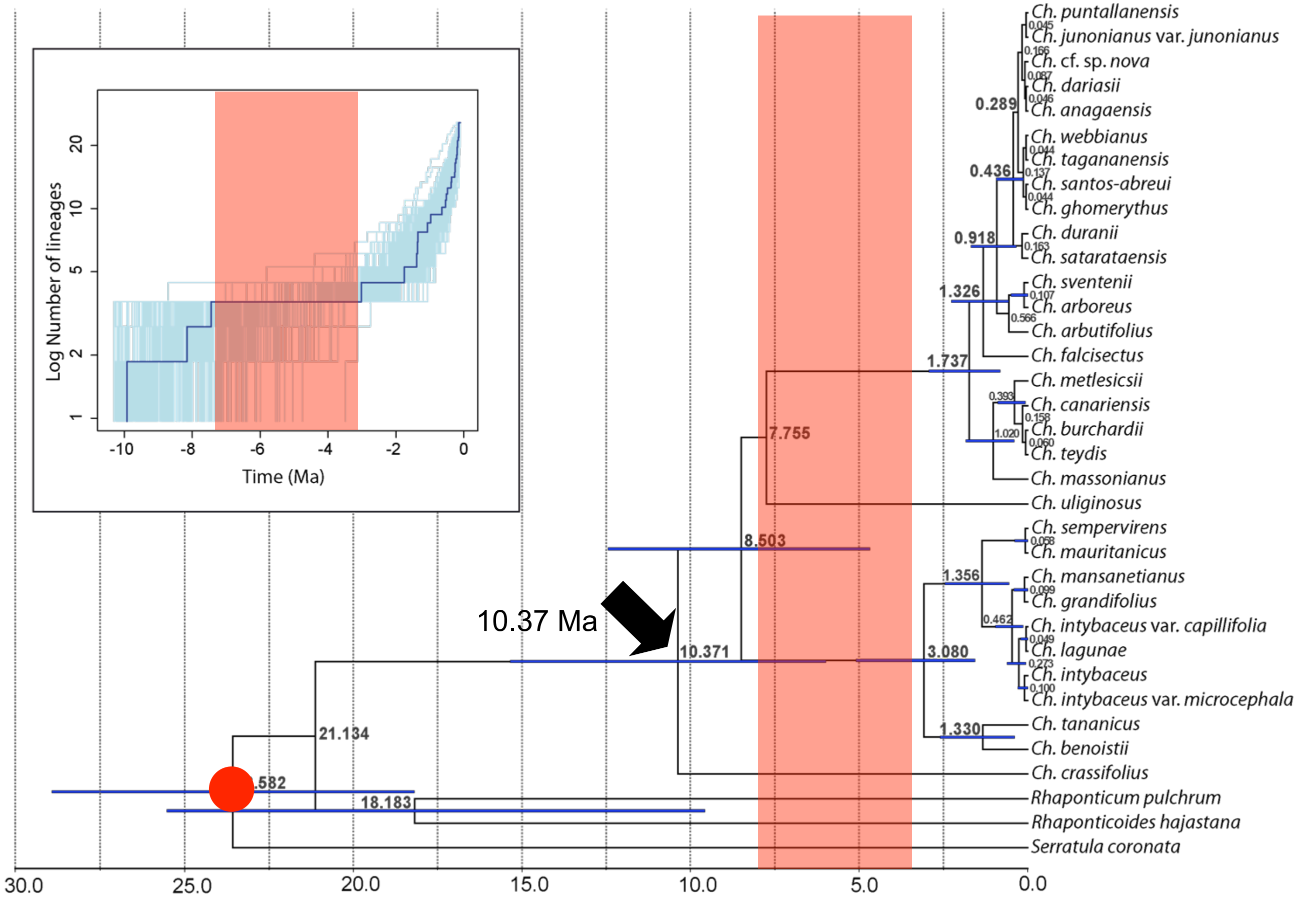


i) Origin of the genus: mid-late Miocene

● 24.51 Ma; Barres *et al*. 2013.

Vitales *et al*. 2014, 14: 118

Phylogenetics and diversification of *Cheirolophus*



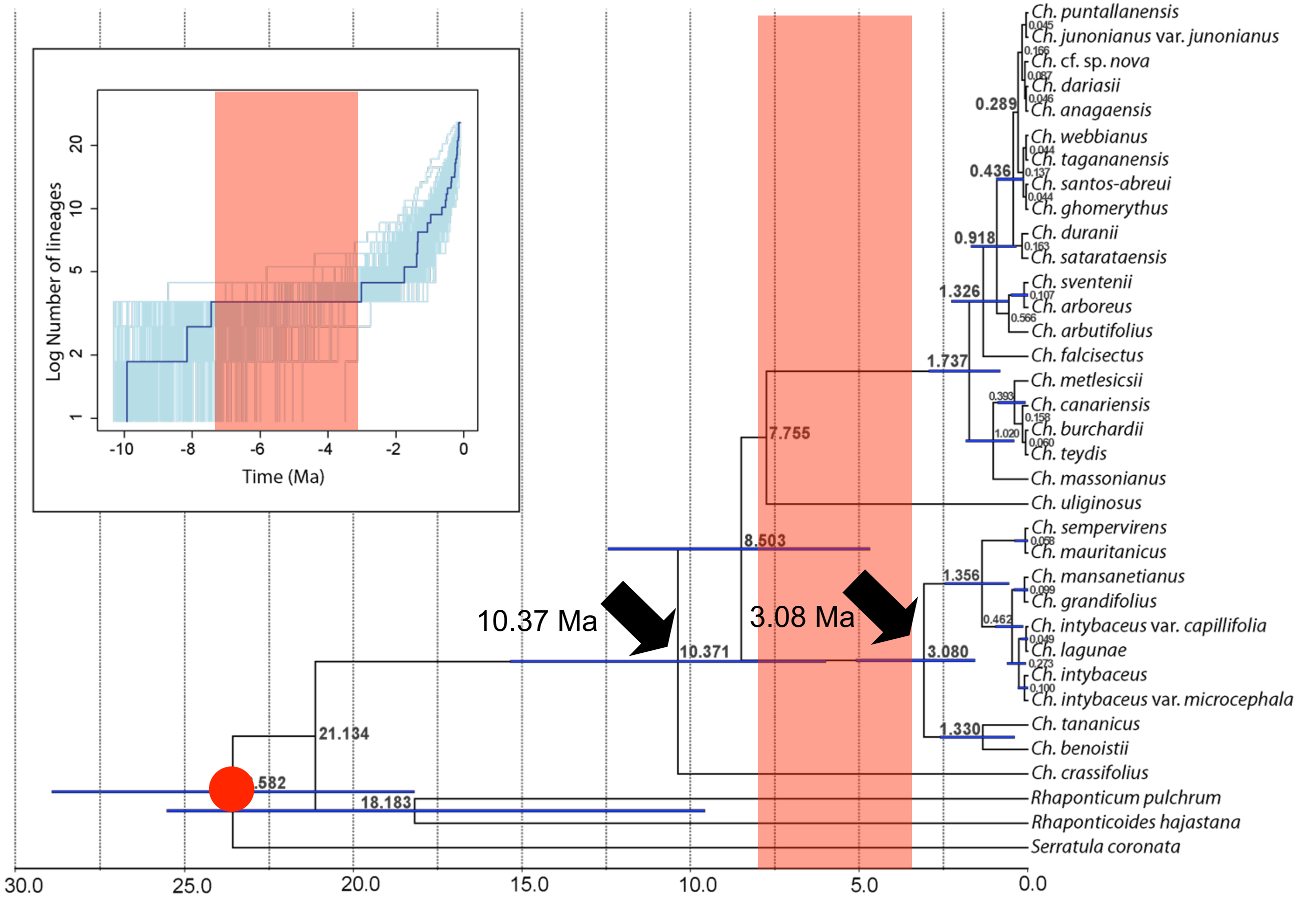
24.51 Ma; Barres *et al*. 2013.

i) Origin of the genus: mid-late Miocene

ii) Gap in diversification during 5 My.

Vitales *et al*. 2014, 14: 118

Phylogenetics and diversification of *Cheirolophus*



24.51 Ma; Barres *et al*. 2013.

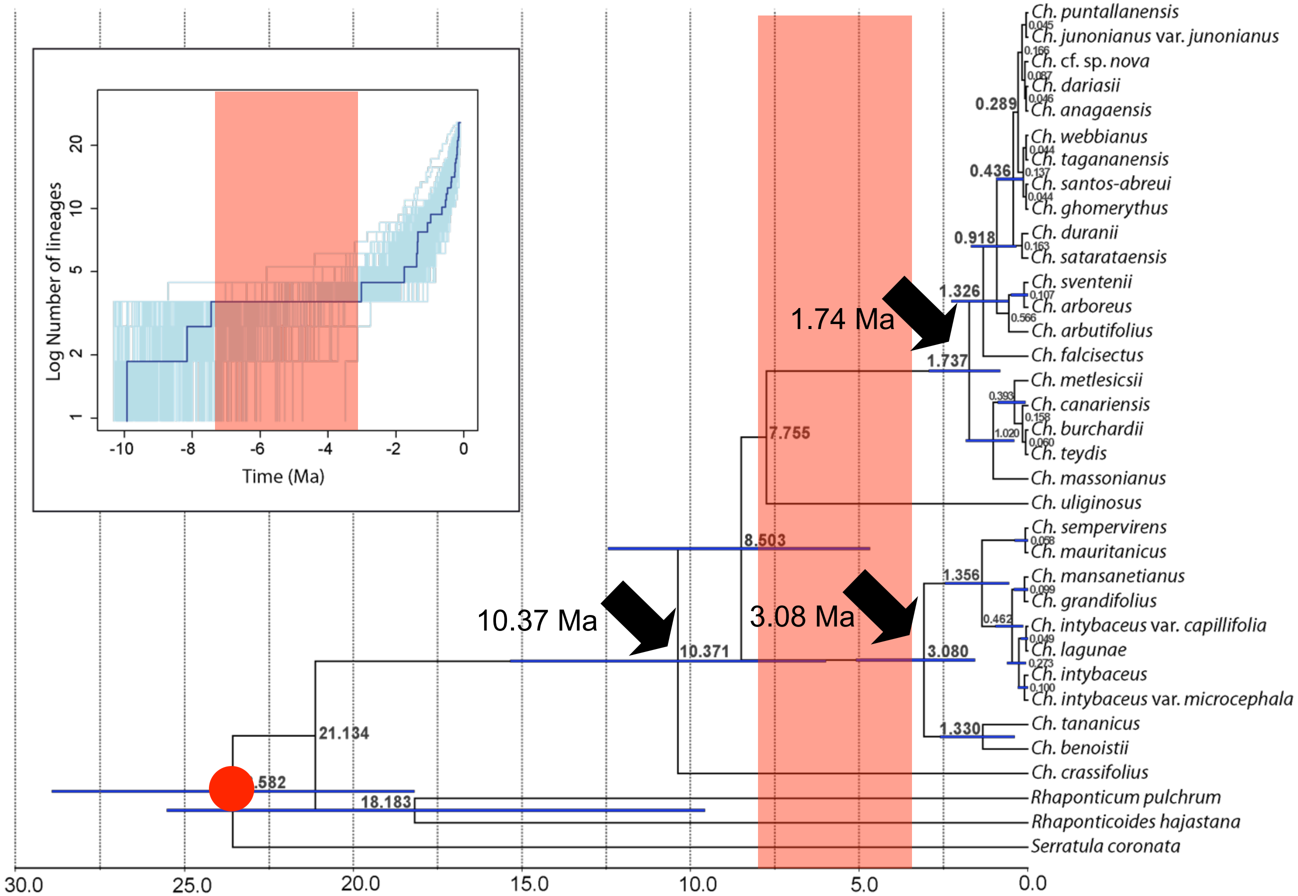
i) Origin of the genus: mid-late Miocene

ii) Gap in diversification during 5 My.

iii) New burst of diversification after 3 Ma. (Mediterranean)

Vitales *et al*. 2014, 14: 118

Phylogenetics and diversification of *Cheirolophus*



i) Origin of the genus: mid-late Miocene

ii) Gap in diversification during 5 My.

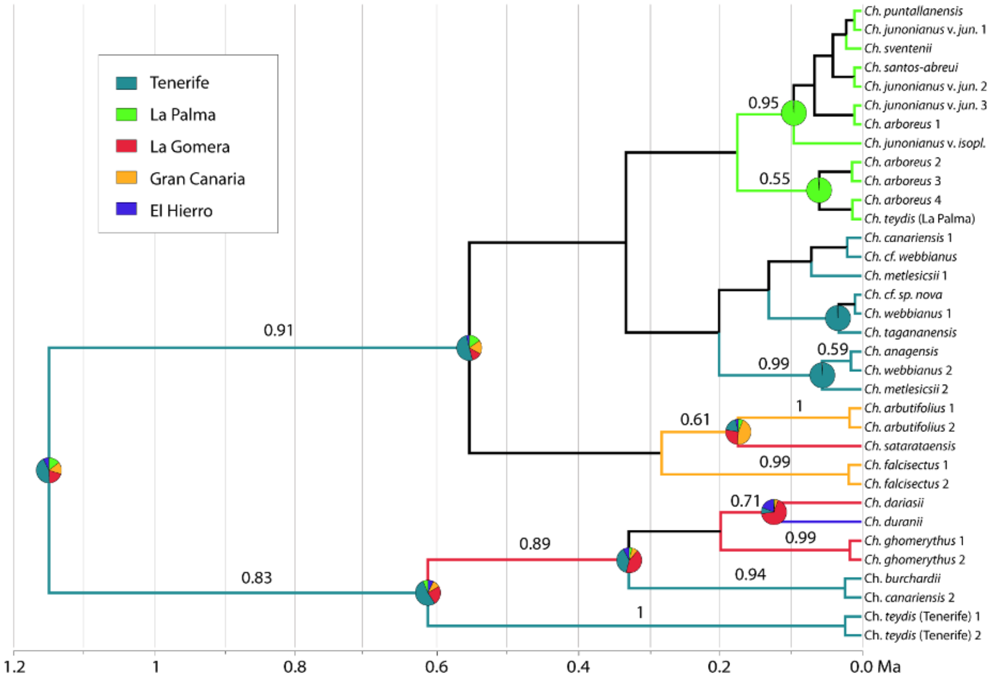
iii) New burst of diversification after 3 Ma. (Mediterranean)

iv) New burst of accelerated diversification after 1.7 Ma. (Macaronesia)

● 24.51 Ma; Barres *et al*. 2013.

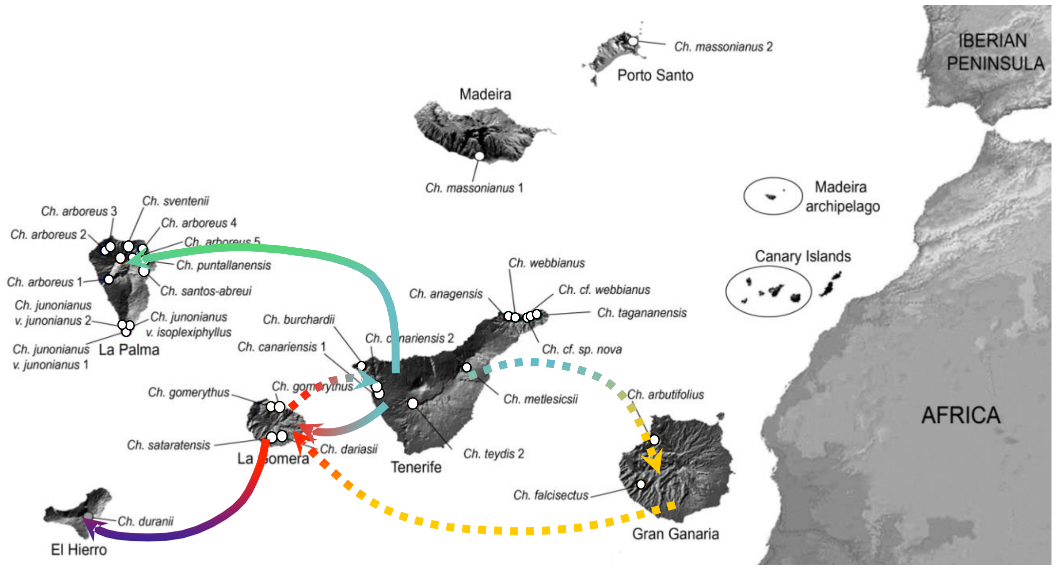
Vitales *et al*. 2014, 14: 118

Phylogenetics and diversification of *Cheirolophus*



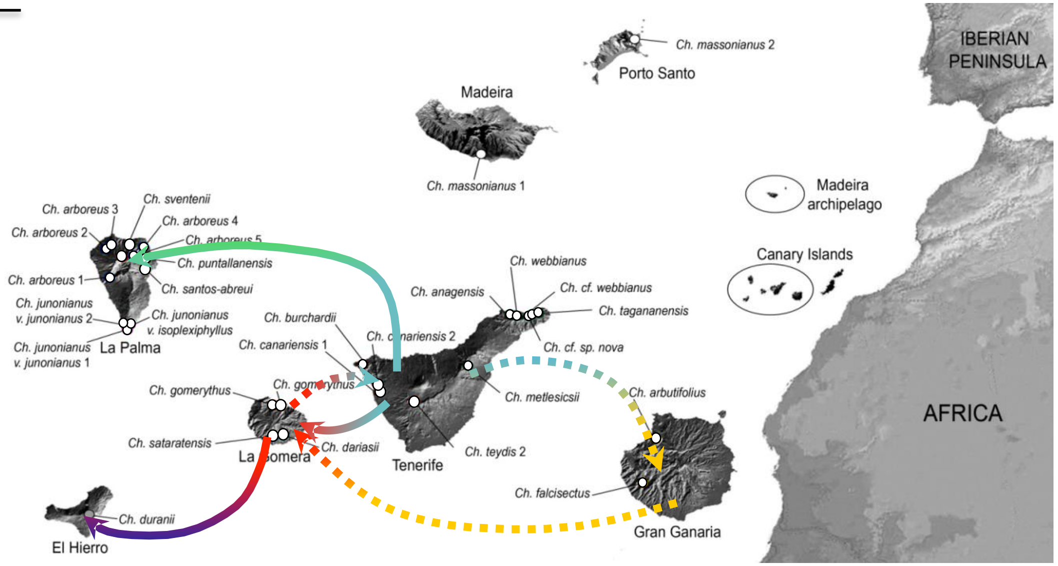
Multiple processes involved in radiation:

- Colonisation between islands
- Intra-island allopatric speciation
- Incipient ecological adaptation
- Hybridisation signals



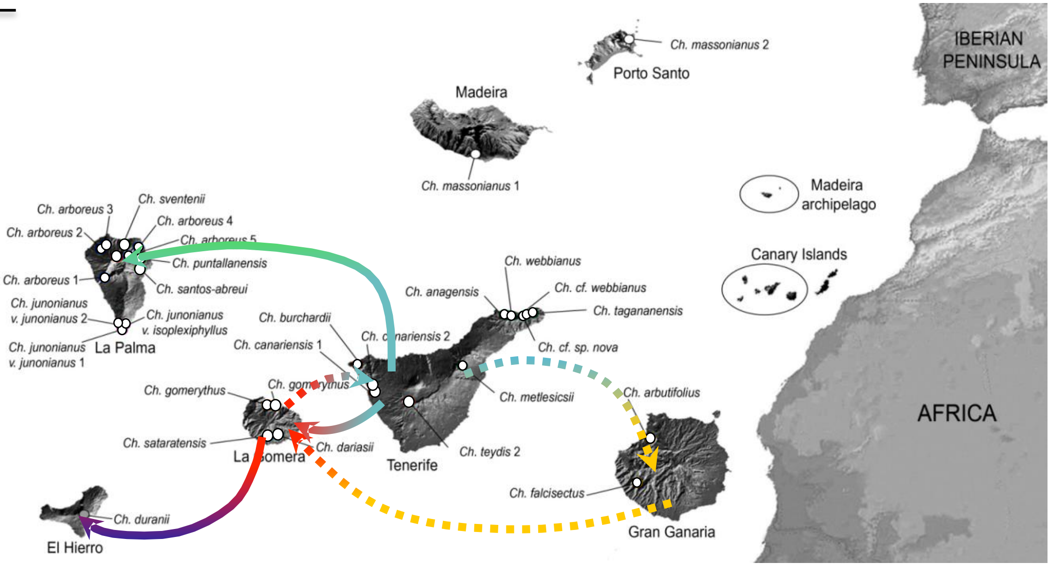
Vitales *et al*. 2014, 14: 118

Phylogenetics and diversification of *Cheirolophus*

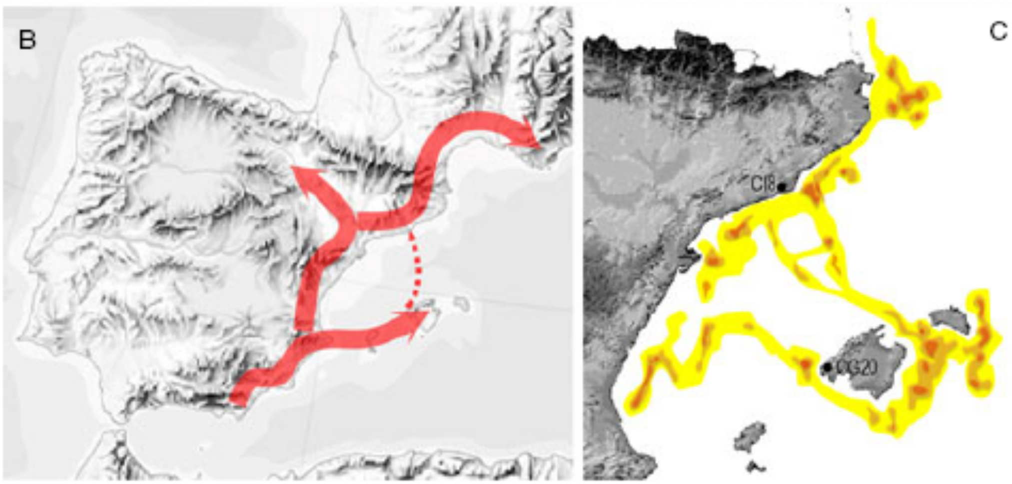


- Multiple colonizations intra- and inter-islands
- Sporadic long distance dispersal ability

Phylogenetics and diversification of *Cheirolophus*



- Multiple colonizations intra- and inter-islands
- Sporadic long distance dispersal ability



Ch. intybaceus; Garnatje et al. (2012)

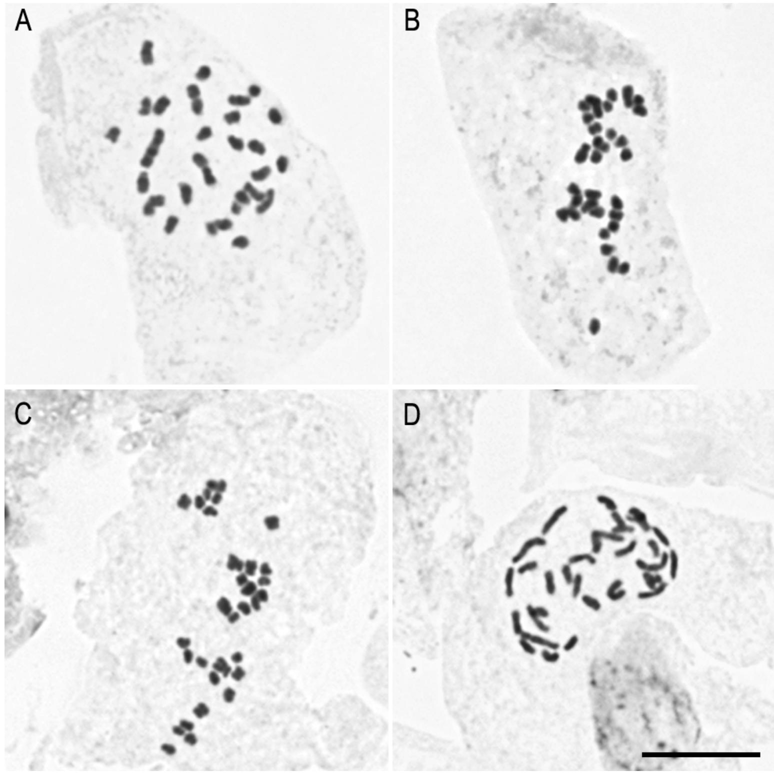
Calonectris diomedea

Cheirolophus Cass.:

Chromosome evolution

Chromosome evolution in *Cheirolophus*

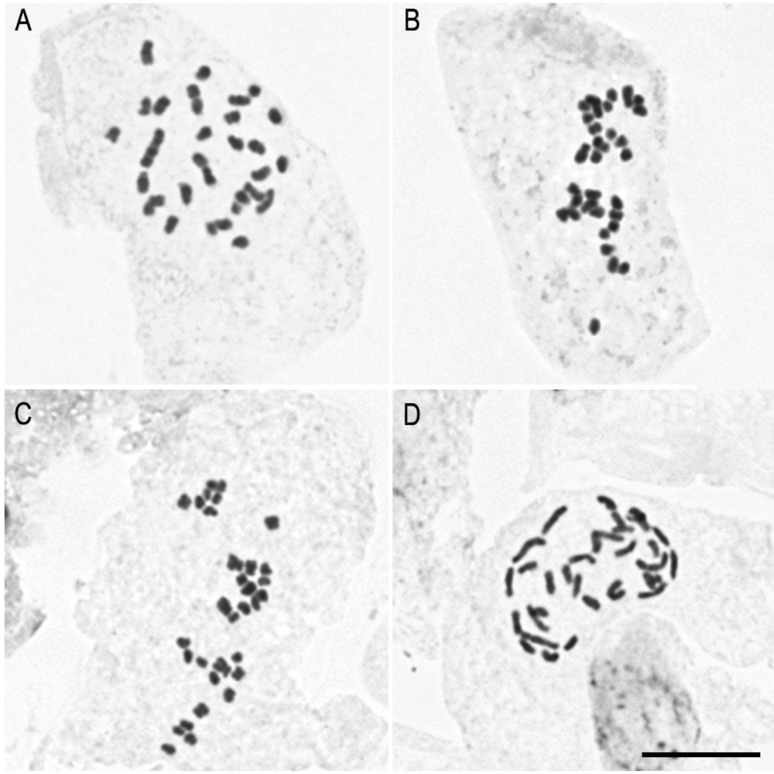
Chromosome numbers



- Chromosome counts for c. 25 spp. 2n = 30,32

Chromosome evolution in *Cheirolophus*

Chromosome numbers



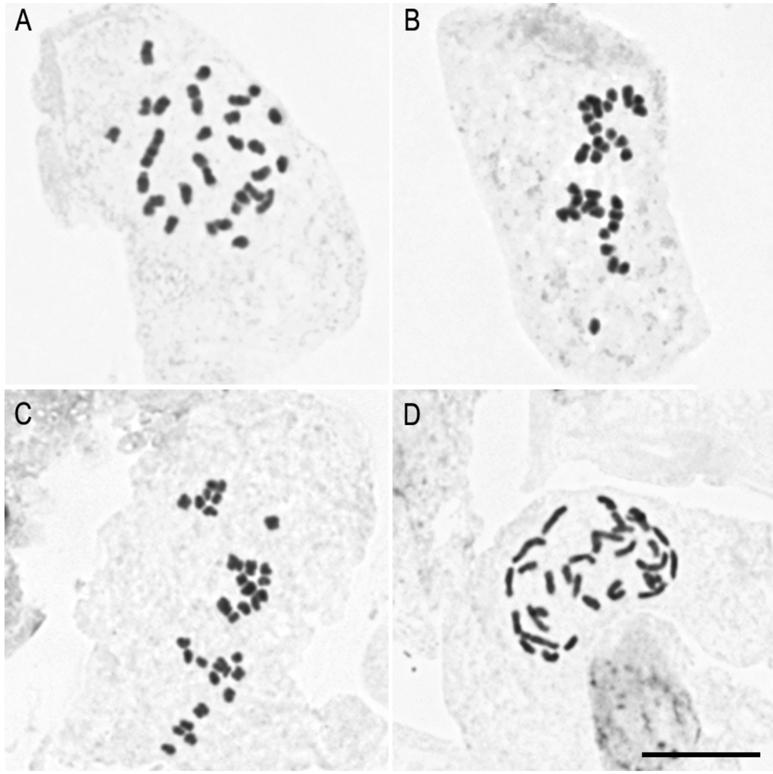
• Chromosome counts for c. 25 spp. 2n = 30,32

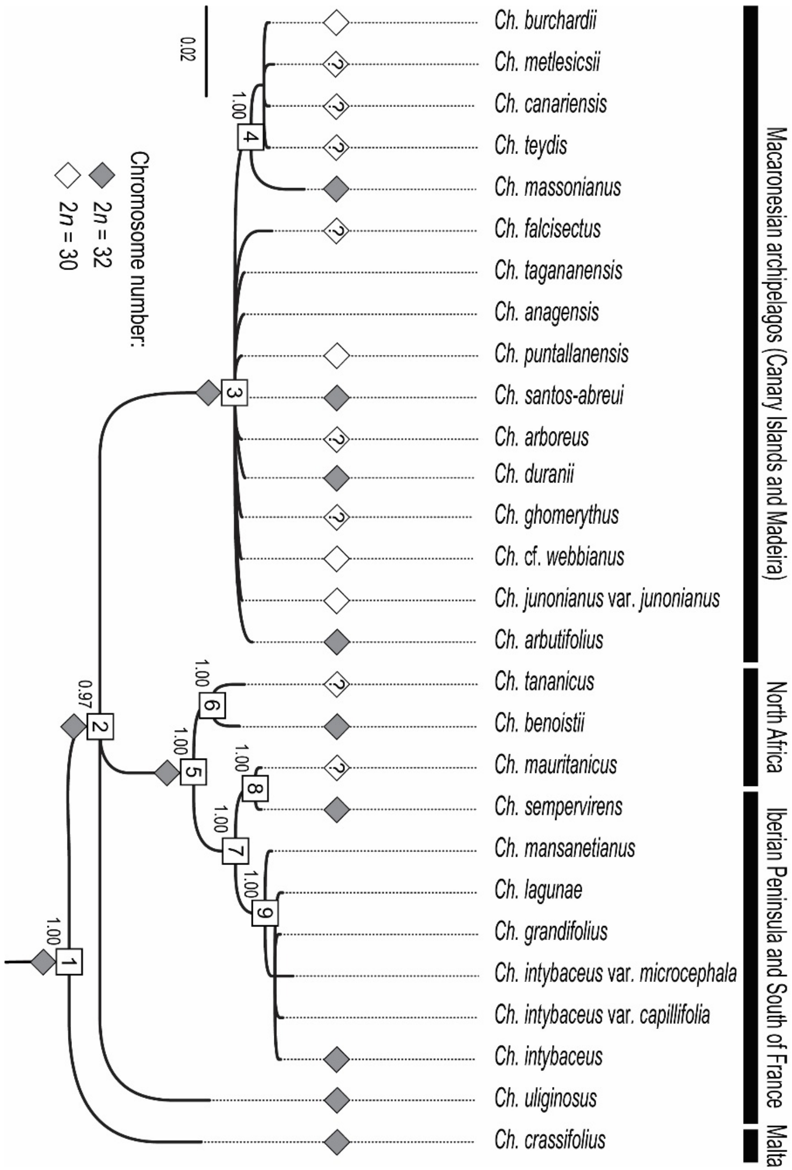
• The chromosome number 2n = 32 is more frequent than previously reported.

• The ancestral chromosome number in *Cheirolophus* is 2n = 32, appearing 2n = 30 several independent times in the evolutionary history of the genus.

Chromosome evolution in *Cheirolophus*

Chromosome numbers





- Chromosome counts for c. 25 spp. 2n = 30,32
- The chromosome number 2n = 32 is more frequent than previously reported.
- The ancestral chromosome number in *Cheirolophus* is 2n = 32, appearing 2n = 30 several independent times in the evolutionary history of the genus.

Chromosome evolution in islands

Chromosome evolution in islands

Oceanic islands → STASIS...

Chromosome evolution in islands

Oceanic islands → STASIS...

ENDEMICS

314 *Tod F. Stuessy and Daniel J. Crawford*

Table 12.4. *Known chromosome counts among species of endemic genera of the Canary Islands with two or more species*

Genus	Number of endemic species on islands	Number of species counted	Chromosome number
Allagopappus (Compositae)	2	2	$n = 10$
Gonospermum (Compositae)	4	4	$n = 9$
Greenovia (Crassulaceae)	4	3	$n = 18$
Parolinia (Cruciferae)	4	4	$n = 11$
Schizogyne (Compositae)	2	2	$n = 9$
Spartocytisus (Leguminosae)	2	2	$n = 24$

Data from Ardévol González, Borgen & Pérez de Pax (1993)

Stuessy & Crawford 1998, 307-321

Chromosome evolution in islands

Oceanic islands → STASIS...

ENDEMICS

Table 12.4. *Known chromosome counts among species of endemic genera of the Canary Islands with two or more species*

Genus	Number of endemic species on islands	Number of species counted	Chromosome number
Allagopappus (Compositae)	2	2	$n = 10$
Gonospermum (Compositae)	4	4	$n = 9$
Greenovia (Crassulaceae)	4	3	$n = 18$
Parolinia (Cruciferae)	4	4	$n = 11$
Schizogyne (Compositae)	2	2	$n = 9$
Spartocytisus (Leguminosae)	2	2	$n = 24$

Data from Ardévol González, Borgen & Pérez de Pax (1993)

NON-ENDEMICS

Table 12.5. *Selected genera of the Canary Islands that have considerable numbers of endemic species and for which cytological data are available*

Genus	Number of endemic species on islands	Number of species counted	Chromosome number(s)
Aeonium (Crassulaceae)	28	28	$n = 18, 36$
Argyranthemum (Compositae)	17[a]	17	$n = 9$
Centaurea (Compositae)	10	7	$n = 14, 15, 16$
Convolvulus (Convolvulaceae)	10	4	$n = 12, 15$
Echium (Boraginaceae)	22	14	$n = 8$
Euphorbia (Euphorbiaceae)	11	6	$n = 10, 30$
Limonium (Plumbaginaceae)	13	12	$n = 6, 7, 12, 16$
Lotus (Leguminosae)	12	12	$n = 7, 14$
Monanthes (Crassulaceae)	13	9	$n = 18, 36$
Senecio (Compositae)	12	8	$n = 20, 30$
Sonchus (Compositae)	28	28	$n = 9$
Taeckholmia (Compositae)	3	3	$n = 9$
Tolpis (Compositae)	6	6	$n = 9$

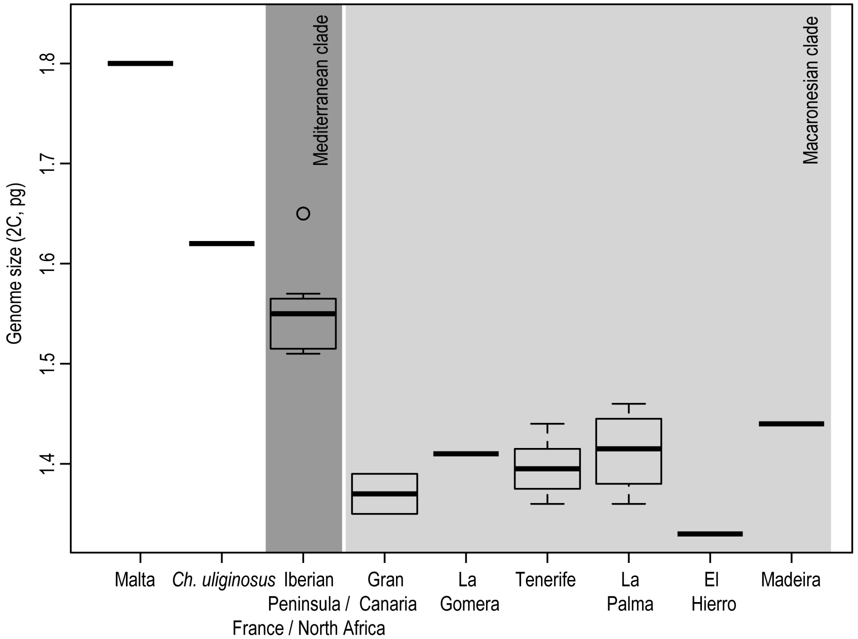
[a] A total of 22 species in Macaronesia (Humphries, 1976; Bremer & Humphries, 1993)
From Ardévol Gonzáles, Borgen & Pérez de Pax (1993)

Stuessy & Crawford 1998, 307-321

Cheirolophus Cass.:

Nuclear DNA contents

Genome size evolution in *Cheirolophus*

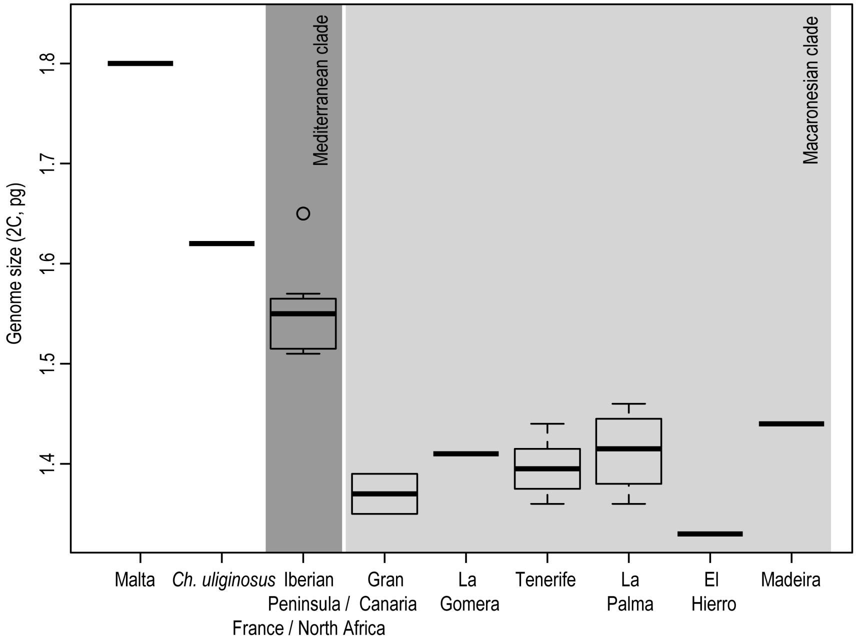


2C-values: 1.30-1.80 pg

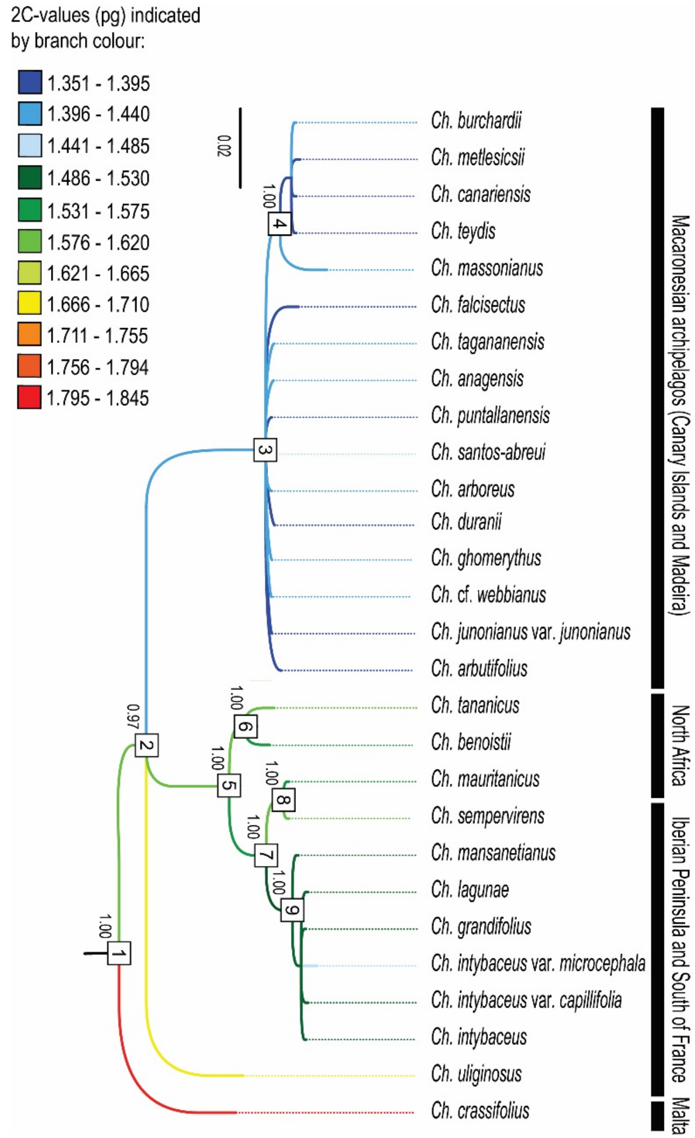
• New data confirm that of Garnatje et al. (2007), where significant differences in GS among Mediterranean and Macaronesian species were observed

• *Ch. crassifolius* shows the highest value of DNA amount, indicating a progressive decline of GS since the origin of the diversification of the genus.

Genome size evolution in *Cheirolophus*



2C-values: 1.30-1.80 pg

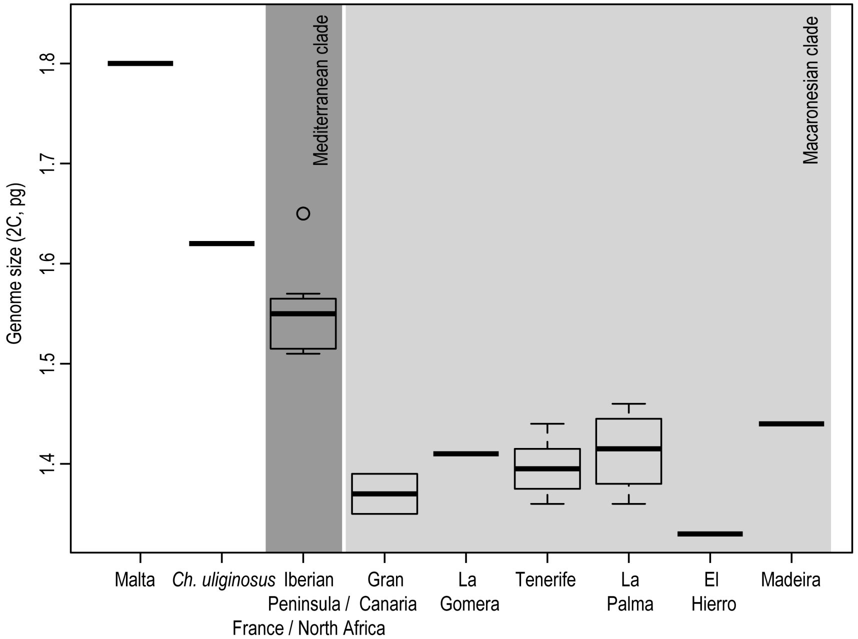


- New data confirm that of Garnatje et al. (2007), where significant differences in GS among Mediterranean and Macaronesian species were observed

- *Ch. crassifolius* shows the highest value of DNA amount, indicating a progressive decline of GS since the origin of the diversification of the genus.

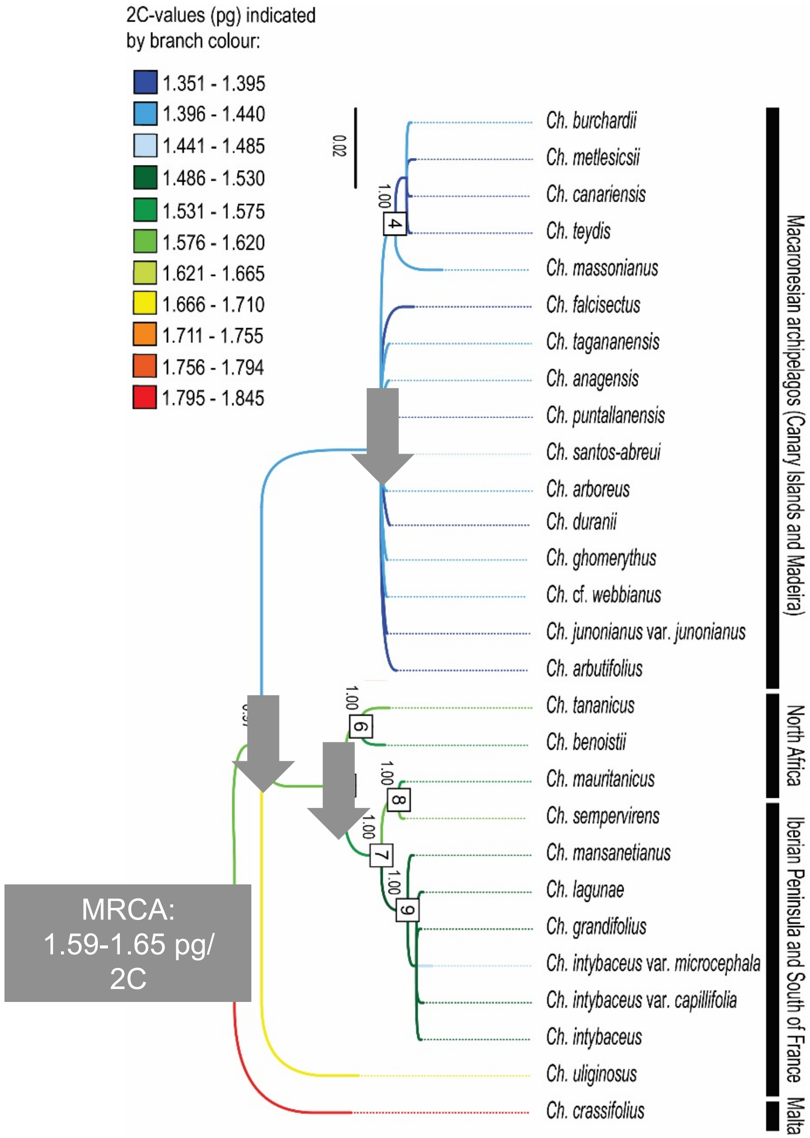
- The descending pattern would be particularly strong in the oceanic islands, consistent with the results found in other plant groups.

Genome size evolution in *Cheirolophus*



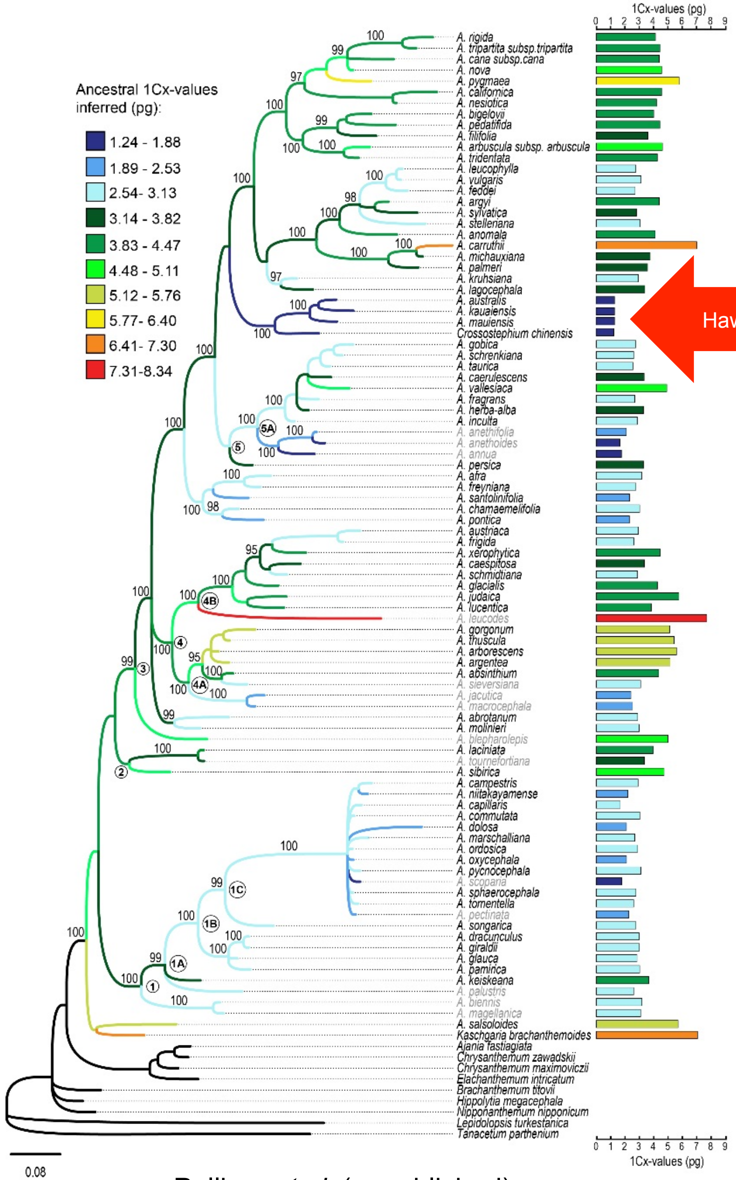
2C-values: 1.30-1.80 pg

- New data confirm that of Garnatje et al. (2007), where significant differences in GS among Mediterranean and Macaronesian species were observed
- *Ch. crassifolius* shows the highest value of DNA amount, indicating a progressive decline of GS since the origin of the diversification of the genus.
- The descending pattern would be particularly strong in the oceanic islands, consistent with the results found in other plant groups.

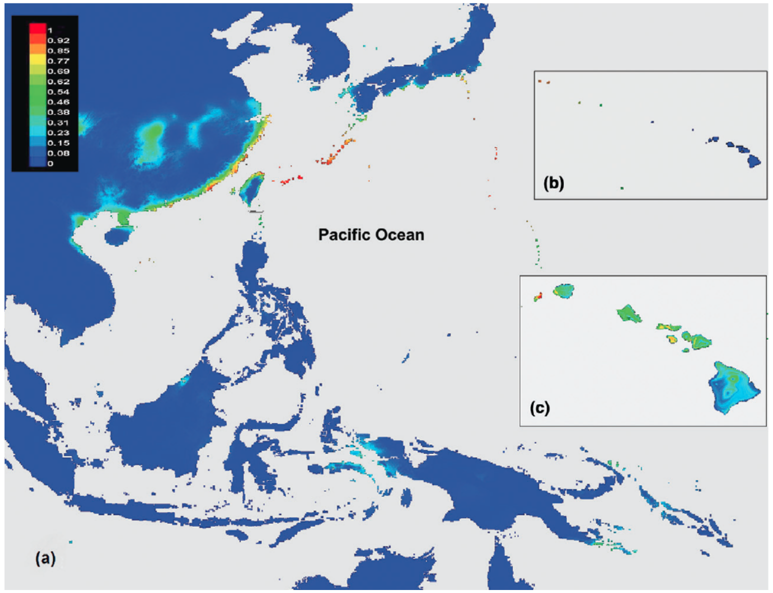


Genome size evolution: island colonisations

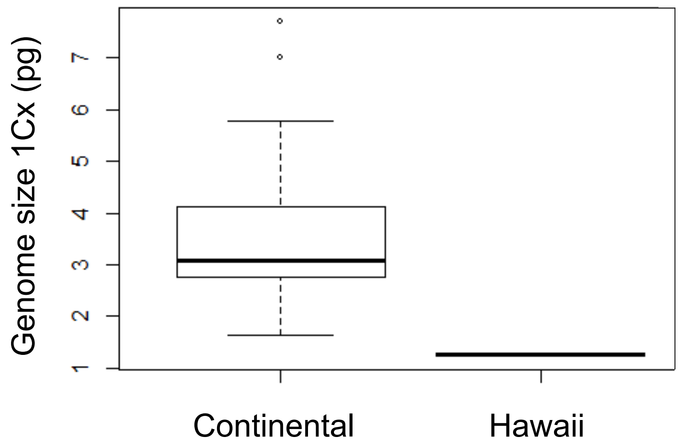
Artemisia



Pellicer *et al.* (unpublished)

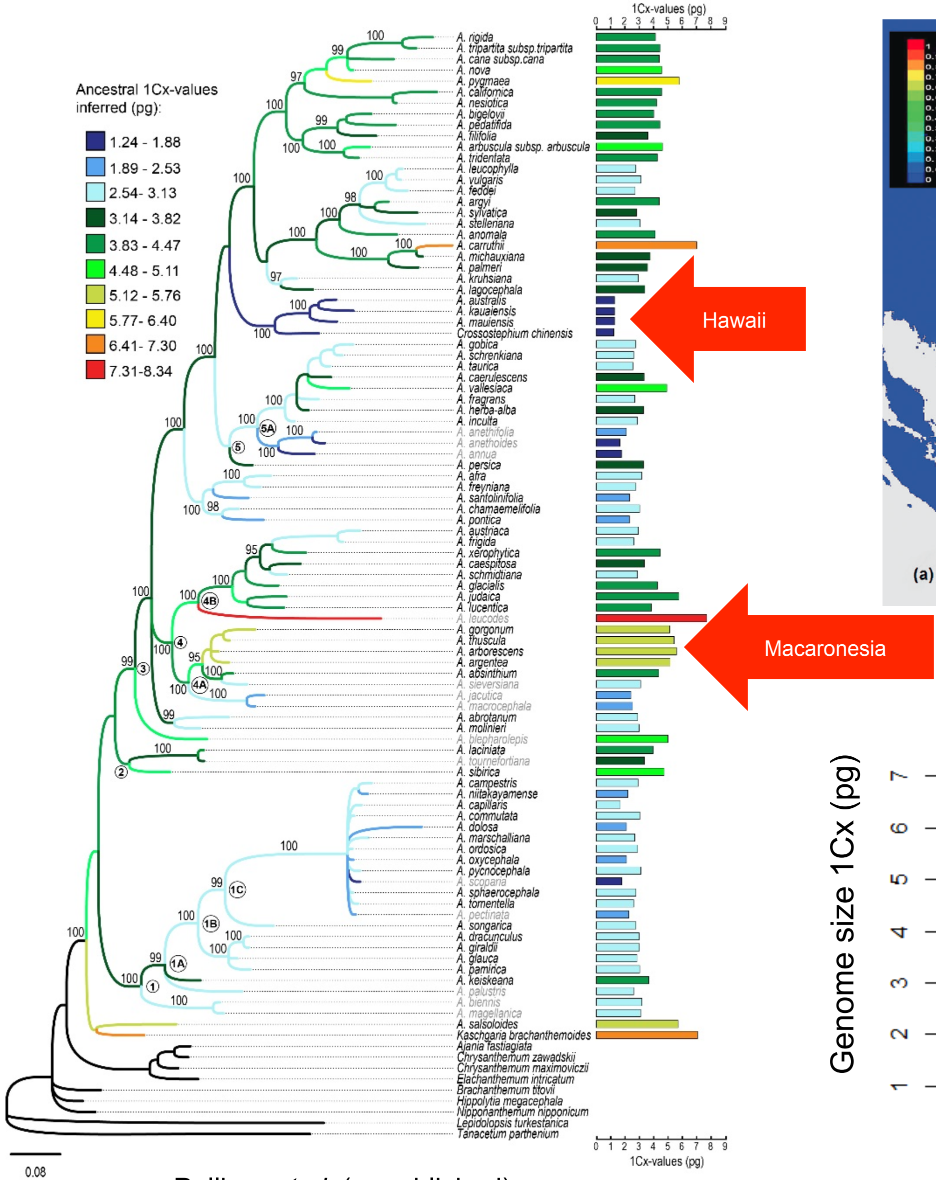


Hobbs & Baldwin 2013, 40: 442-454

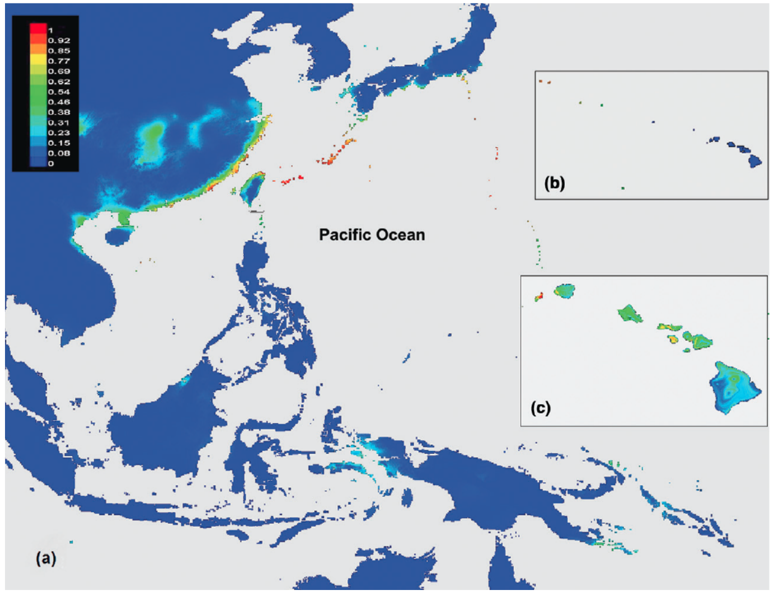


Genome size evolution: island colonisations

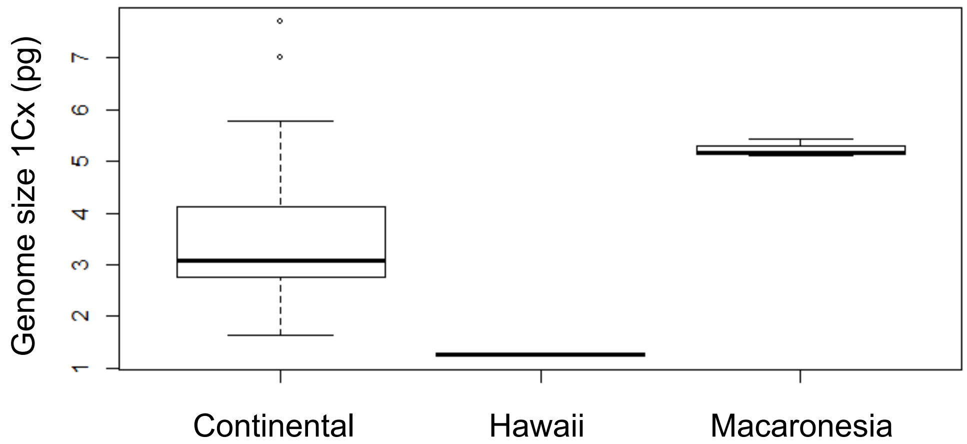
Artemisia



Pellicer *et al*. (unpublished)



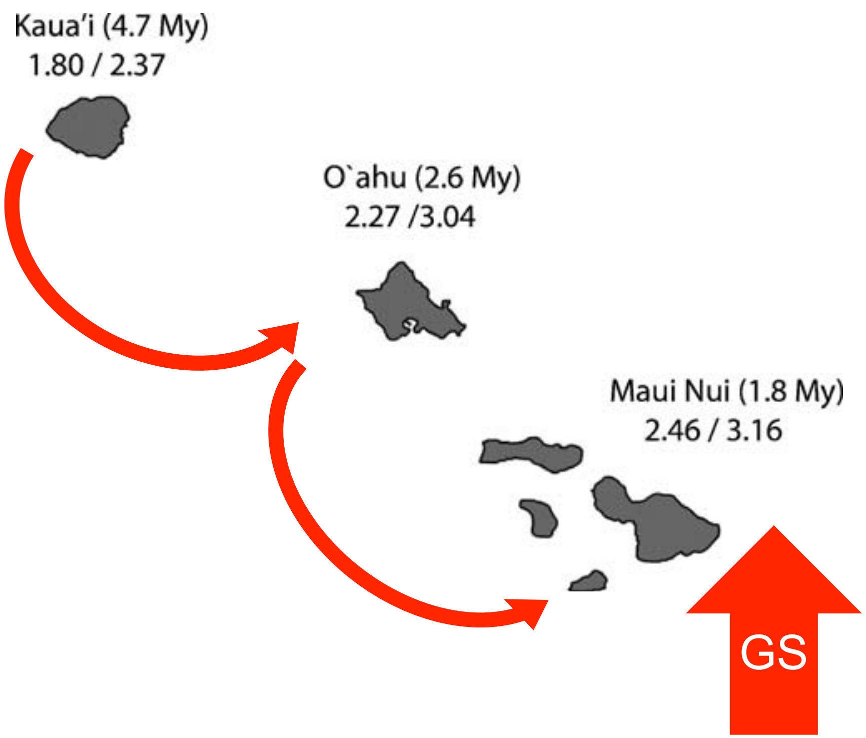
Hobbs & Baldwin 2013, 40: 442-454



Genome size evolution: island colonisations

Hawaiian *Schiedea*

..."Unexpectedly, genomes of *Schiedea* species appeared to be relatively compact (1.41 to 3.74 pg/cell), compared to *Honckenya* (8.57 to 10.66 pg/cell)"...



(Kapralov & Filatov, 2009, 2:77-83)

Genome size evolution: island colonisations

Hawaiian *Schiedea*

..."Unexpectedly, genomes of *Schiedea* species appeared to be relatively compact (1.41 to 3.74 pg/cell), compared to *Honckenya* (8.57 to 10.66 pg/cell)"...

Research Article

Does Large Genome Size Limit Speciation in Endemic Island Floras?

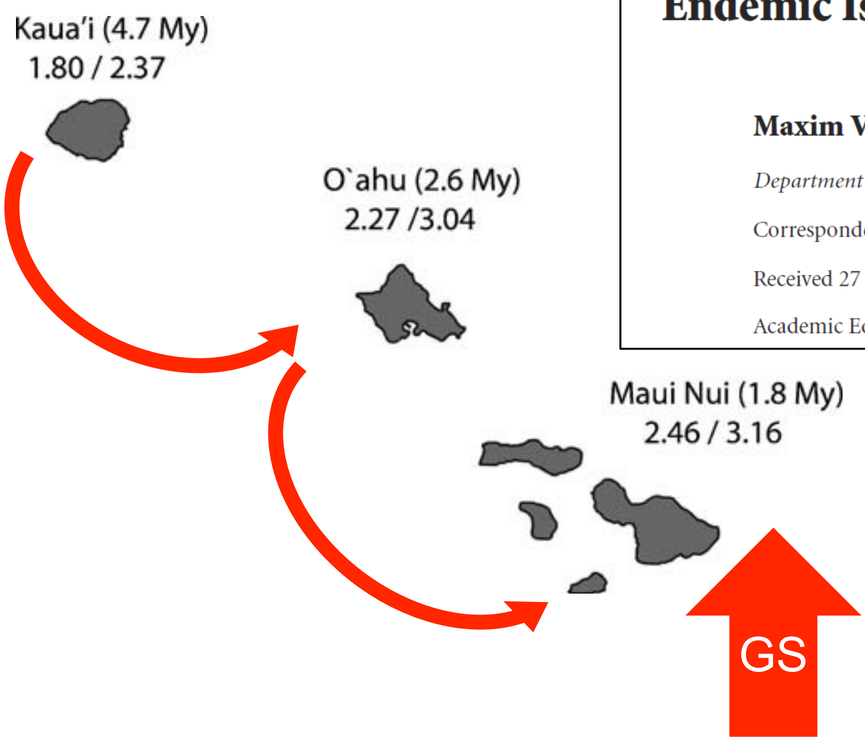
Maxim V. Kapralov and Dmitry A. Filatov

Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB, UK

Correspondence should be addressed to Maxim V. Kapralov, maxim.kapralov@plants.ox.ac.uk

Received 27 May 2011; Accepted 28 August 2011

Academic Editor: Andrea Polle



(Kapralov & Filatov, 2009, 2:77-83)

Genome size evolution: island colonisations

Hawaiian *Schiedea*

..."Unexpectedly, genomes of *Schiedea* species appeared to be relatively compact (1.41 to 3.74 pg/cell), compared to *Honckenya* (8.57 to 10.66 pg/cell)"...

Research Article

Does Large Genome Size Limit Speciation in Endemic Island Floras?

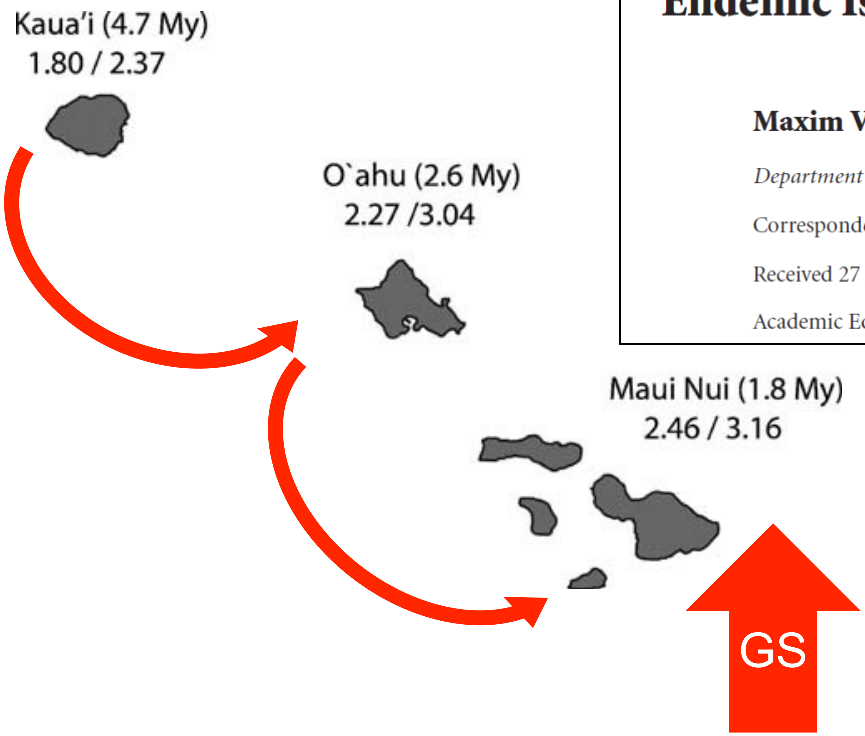
Maxim V. Kapralov and Dmitry A. Filatov

Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB, UK

Correspondence should be addressed to Maxim V. Kapralov, maxim.kapralov@plants.ox.ac.uk

Received 27 May 2011; Accepted 28 August 2011

Academic Editor: Andrea Polle



YES, but...

(Kapralov & Filatov, 2009, 2:77-83)

Genome size evolution: island colonisations

Research Article

Does Large Genome Size Limit Speciation in Endemic Island Floras?

Maxim V. Kapralov and Dmitry A. Filatov

Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB, UK

Correspondence should be addressed to Maxim V. Kapralov, maxim.kapralov@plants.ox.ac.uk

Received 27 May 2011; Accepted 28 August 2011

Academic Editor: Andrea Polle

- Radiation processes only takes place involving species with smaller genome sizes

Genome size evolution: island colonisations

Research Article

Does Large Genome Size Limit Speciation in Endemic Island Floras?

Maxim V. Kapralov and Dmitry A. Filatov

Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB, UK

Correspondence should be addressed to Maxim V. Kapralov, maxim.kapralov@plants.ox.ac.uk

Received 27 May 2011; Accepted 28 August 2011

Academic Editor: Andrea Polle

- Radiation processes only takes place involving species with smaller genome sizes
- Genome downsizing has a direct impact in facilitating/enhancing the radiation process

Genome size evolution: island colonisations

Research Article

Does Large Genome Size Limit Speciation in Endemic Island Floras?

Maxim V. Kapralov and Dmitry A. Filatov

Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB, UK

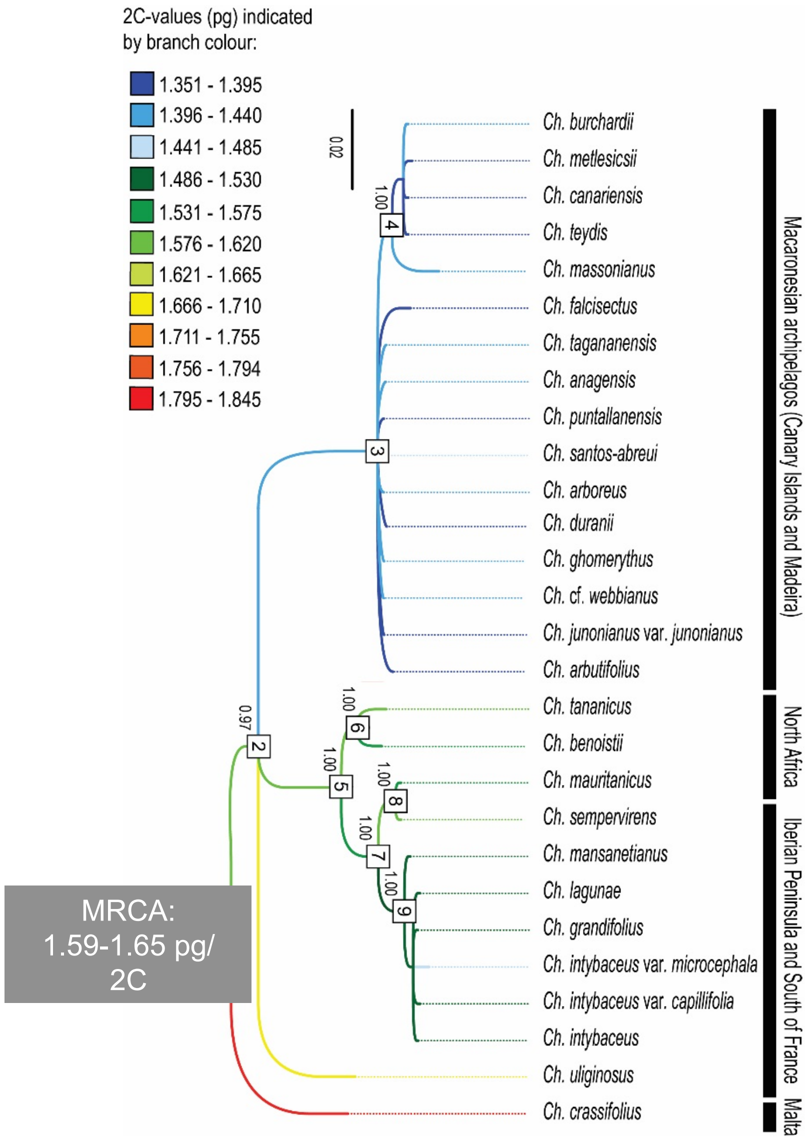
Correspondence should be addressed to Maxim V. Kapralov, maxim.kapralov@plants.ox.ac.uk

Received 27 May 2011; Accepted 28 August 2011

Academic Editor: Andrea Polle

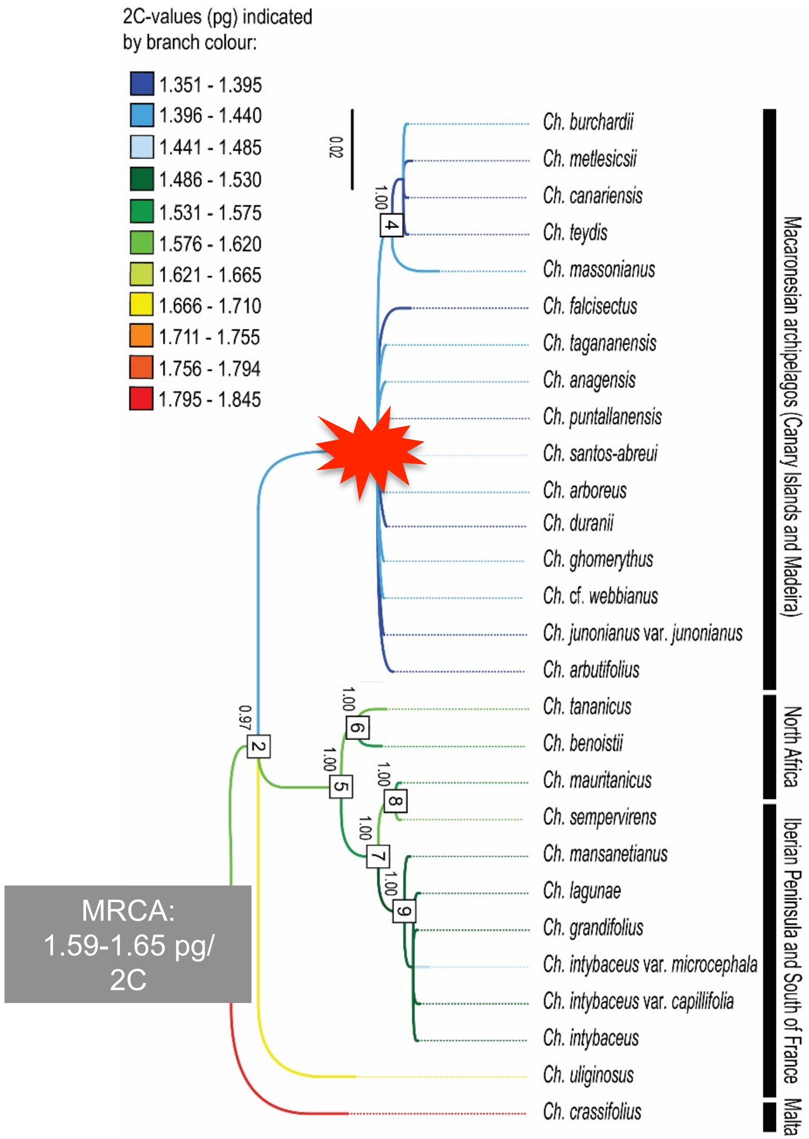
- Radiation processes only takes place involving species with smaller genome sizes
- Genome downsizing has a direct impact in facilitating/enhancing the radiation process
- Genome downsizing is just a consequence of the radiation, with no role in the evolutionary processes

Genome size evolution in *Cheirolophus*



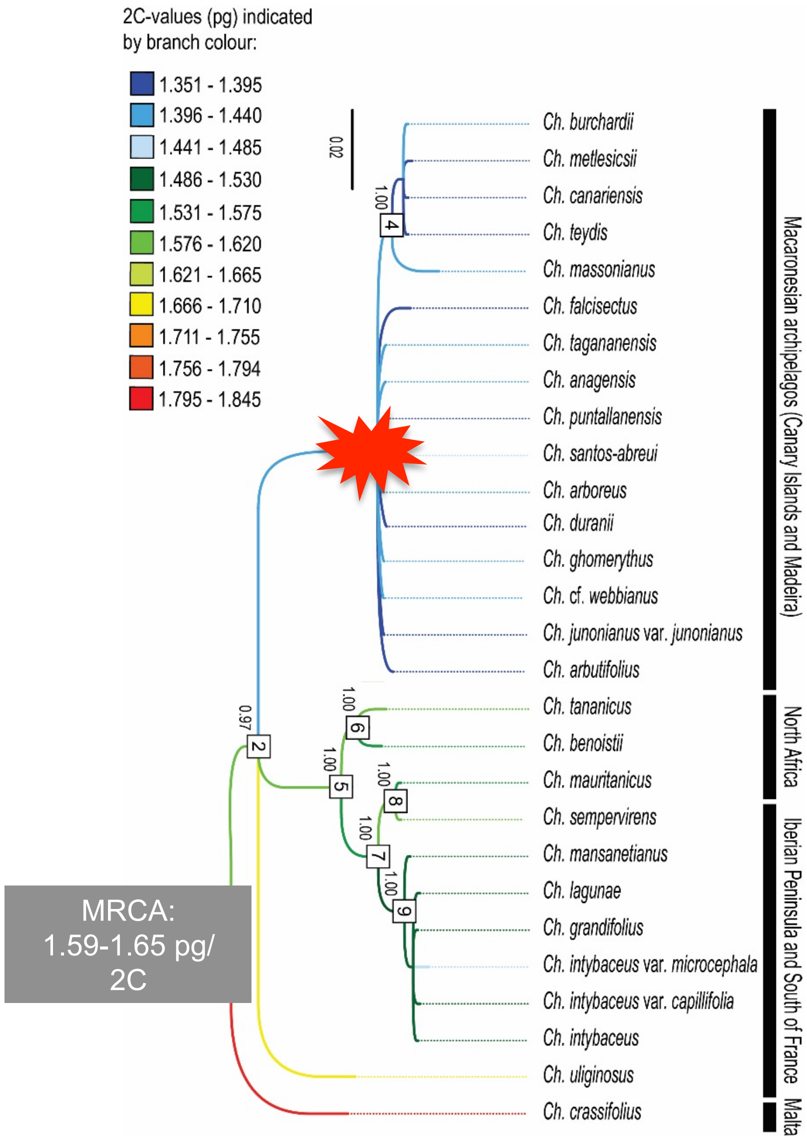
- Selective forces favour species with small genome: MRCA c.1.6pg/2C

Genome size evolution in *Cheirolophus*



- Selective forces favour species with small genome: MRCA c.1.6pg/2C
- Most substantial genome downsizing coincident with the Macaronesian radiation

Genome size evolution in *Cheirolophus*



- Selective forces favour species with small genome: MRCA c.1.6pg/2C
- Most substantial genome downsizing coincident with the Macaronesian radiation

GS as a trigger for radiation…

Cheirolophus Cass.:

rDNA evolution

rDNA evolution in *Cheirolophus*

Swarm of terminal 35S in *Cheirolophus* (Asteraceae, Centaureinae)

T. Garnatje, O. Hidalgo, D. Vitales, J. Pellicer, J. Vallès, O. Robin, S. Garcia, and S. Siljak-Yakovlev

Abstract: Island radiation constitutes a playground for species diversification, which has long fascinated researchers and still does today. Because only a small subset of taxa within the pool of island colonizers is concerned by this process, the question is raised on whether some factors could make a taxon prone to radiate. *Cheirolophus* is the only genus of Centaureinae subtribe to have experienced a radiation in the Canary Islands. Cytogenetic characterization through FISH of 5S and 35S ribosomal RNA genes in eight *Cheirolophus* species from continent and Canary Islands revealed an unusually high number of 35S predominantly at terminal position, together with a single interstitial 5S rDNA locus in all the studied taxa. Such an abundance of 35S rDNA signals is unique among Centaureinae and predates *Cheirolophus* arrival in Canary Islands. The possible link of the rDNA profile with radiation process is discussed through a comparison with two other case studies, the closely related *Rhaponticum* group and the genus *Centaurea*.

Garnatje *et al*. 2012, 55: 529-235

rDNA evolution in *Cheirolophus*

Swarm of terminal 35S in *Cheirolophus* (Asteraceae, Centaureinae)

T. Garnatje, O. Hidalgo, D. Vitales, J. Pellicer, J. Vallès, O. Robin, S. Garcia, and S. Siljak-Yakovlev

Abstract: Island radiation constitutes a playground for species diversification, which has long fascinated researchers and still does today. Because only a small subset of taxa within the pool of island colonizers is concerned by this process, the question is raised on whether some factors could make a taxon prone to radiate. *Cheirolophus* is the only genus of Centaureinae subtribe to have experienced a radiation in the Canary Islands. Cytogenetic characterization through FISH of 5S and 35S ribosomal RNA genes in eight *Cheirolophus* species from continent and Canary Islands revealed an unusually high number of 35S predominantly at terminal position, together with a single interstitial 5S rDNA locus in all the studied taxa. Such an abundance of 35S rDNA signals is unique among Centaureinae and predates *Cheirolophus* arrival in Canary Islands. The possible link of the rDNA profile with radiation process is discussed through a comparison with two other case studies, the closely related *Rhaponticum* group and the genus *Centaurea*.

Garnatje *et al*. 2012, 55: 529-235

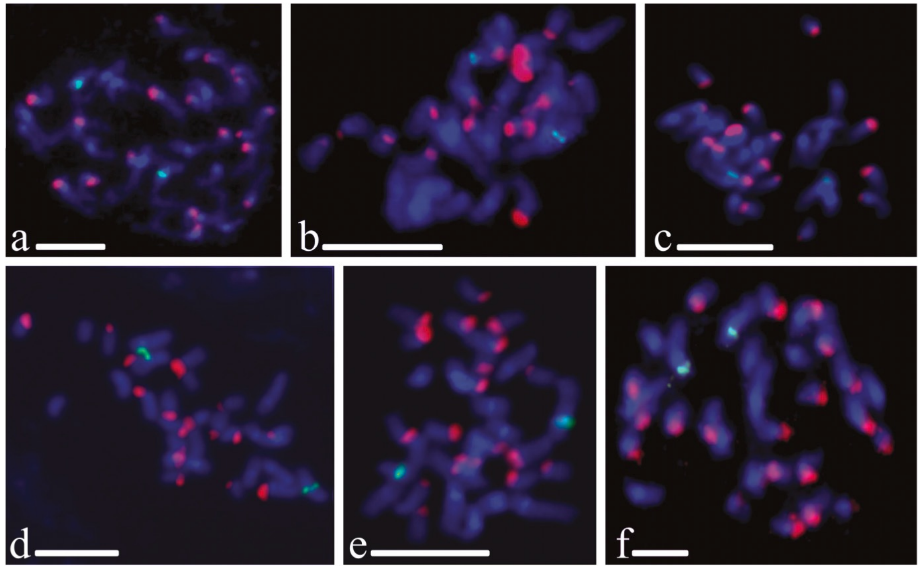
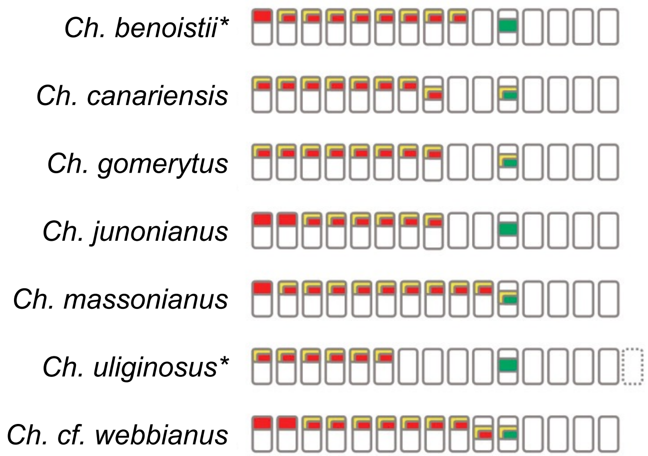


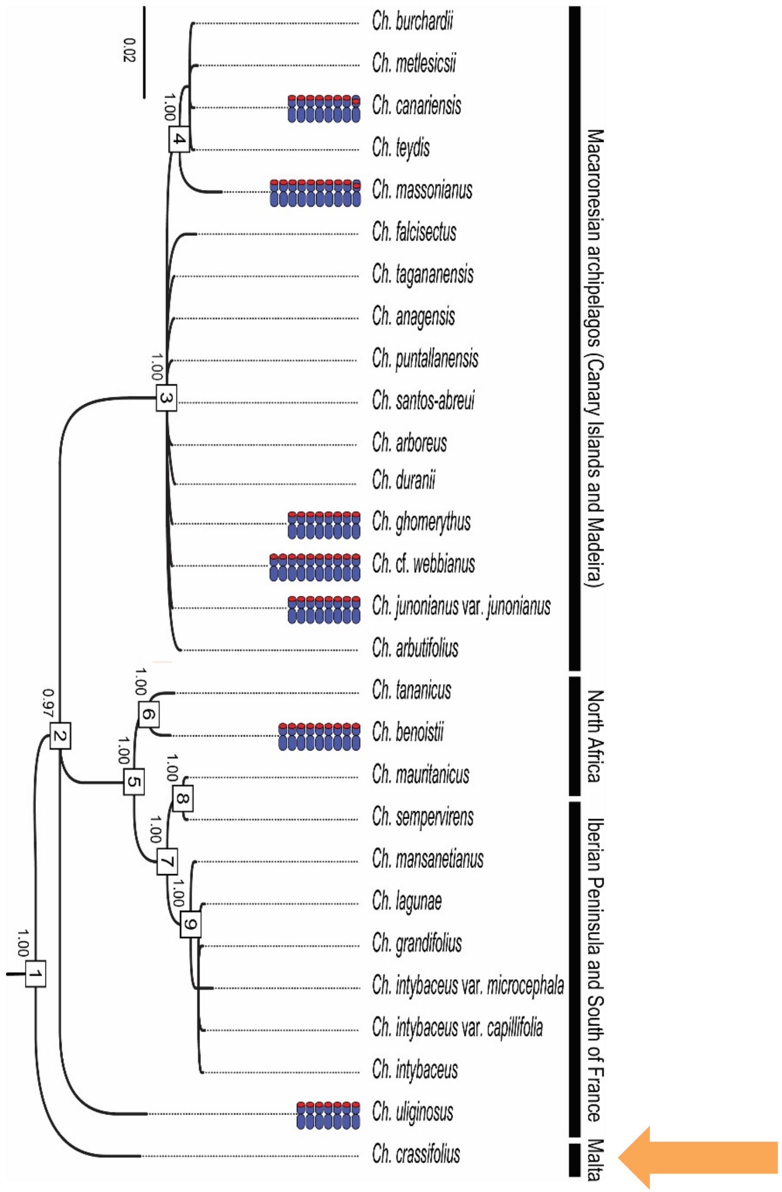
Table 2. Number of chromosomes (2*n*), genome size (2C value), number of chromomycin A3-positive bands (CMA), and 35S and 5S rDNA sites for the species studied.

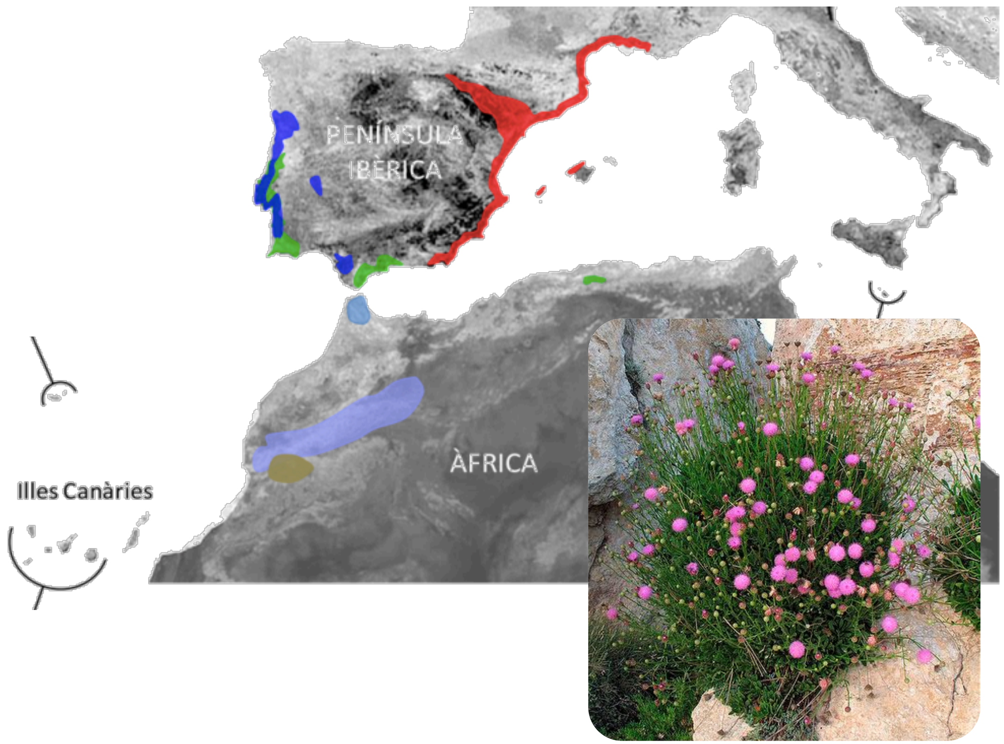
Species	2*n*	2C (pg)*	CMA	35S sites	5S sites
Ch. benoistii	30	1.55	16	18	2 (2i)
Ch. burchardii	30	1.42	16	—	—
Ch. canariensis	30	1.38	18 (4i)	16 (2i)	2 (2i)
Ch. gomerythus	30	1.41	18 (2i)	16	2 (2i)
Ch. junonianus	—	1.37	12	16	2 (2i)
Ch. massonianus	30	1.44	20 (2i)	20	2 (2i)
Ch. uliginosus	~32	1.69	12	12	2 (2i)
Ch. cf. *webbianus*	30	1.38	18 (4i)	20 (2i)	2 (2i)

Note: Indication of positive signals with interstitial position (i) is provided.
*Garnatje et al. (2007).

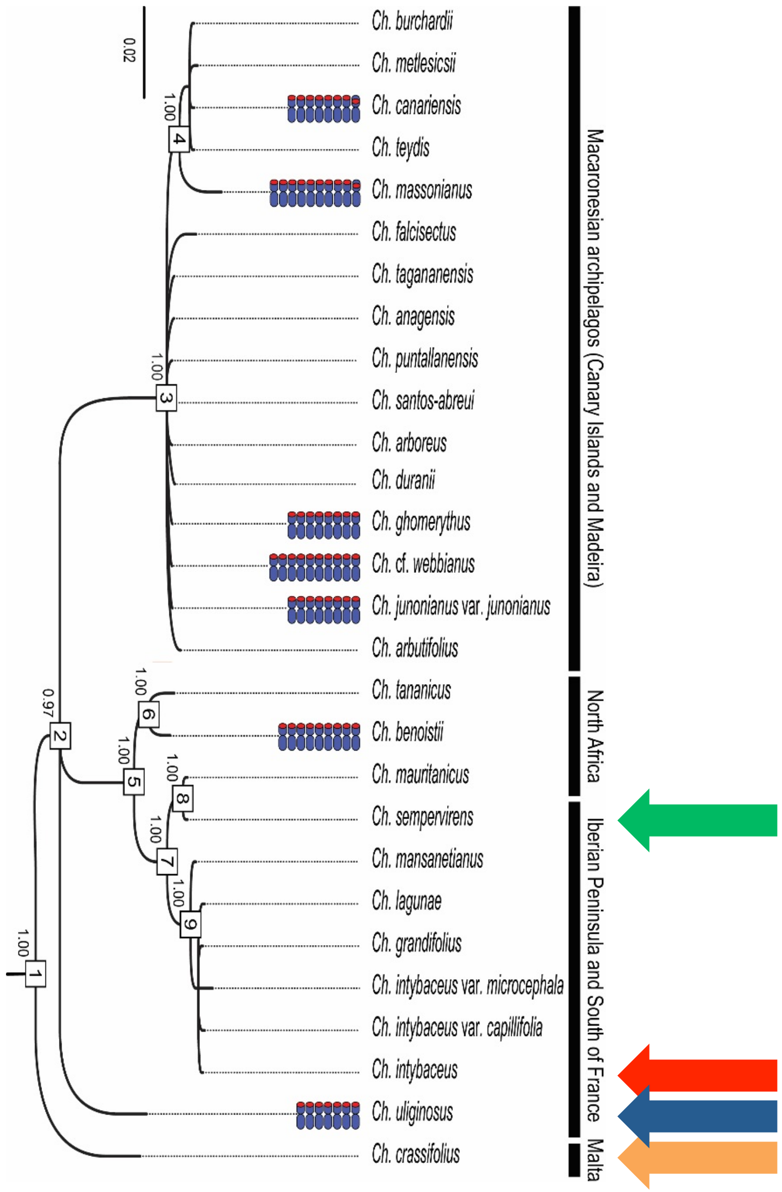


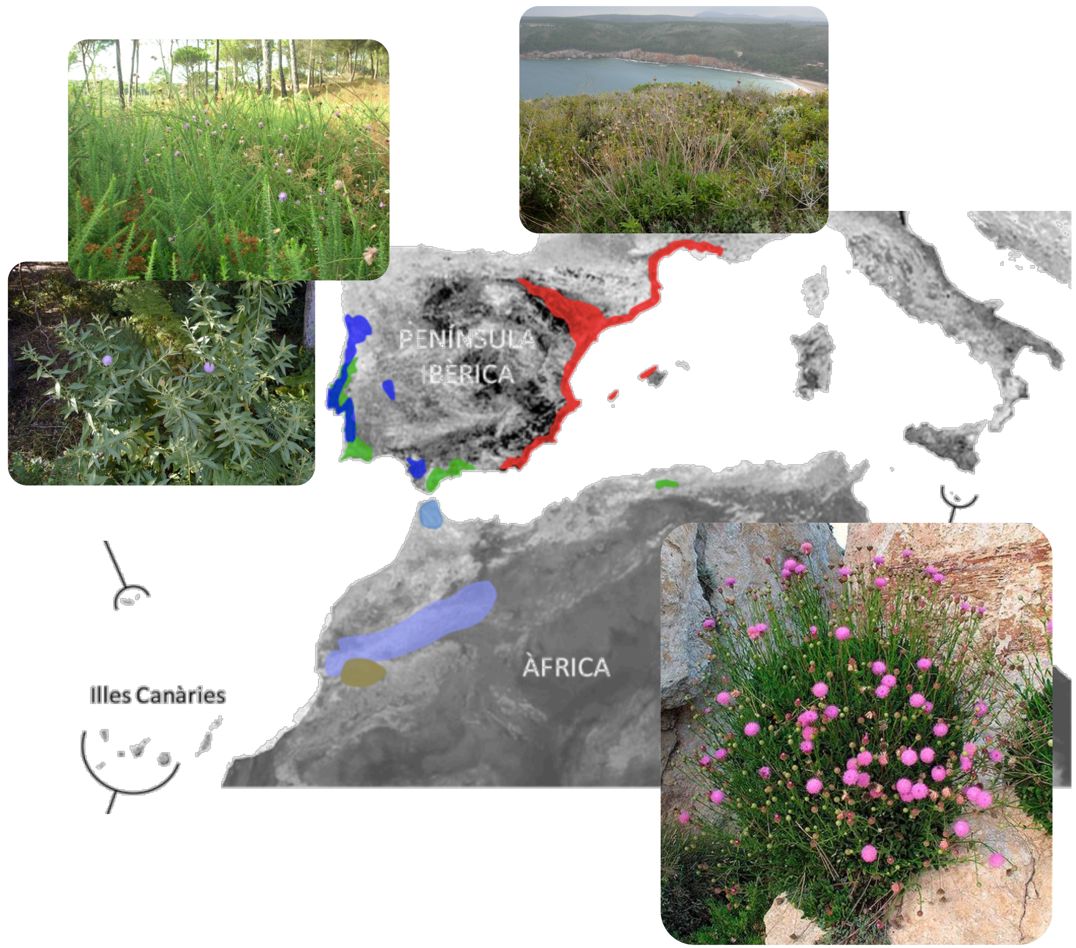
rDNA evolution in *Cheirolophus*



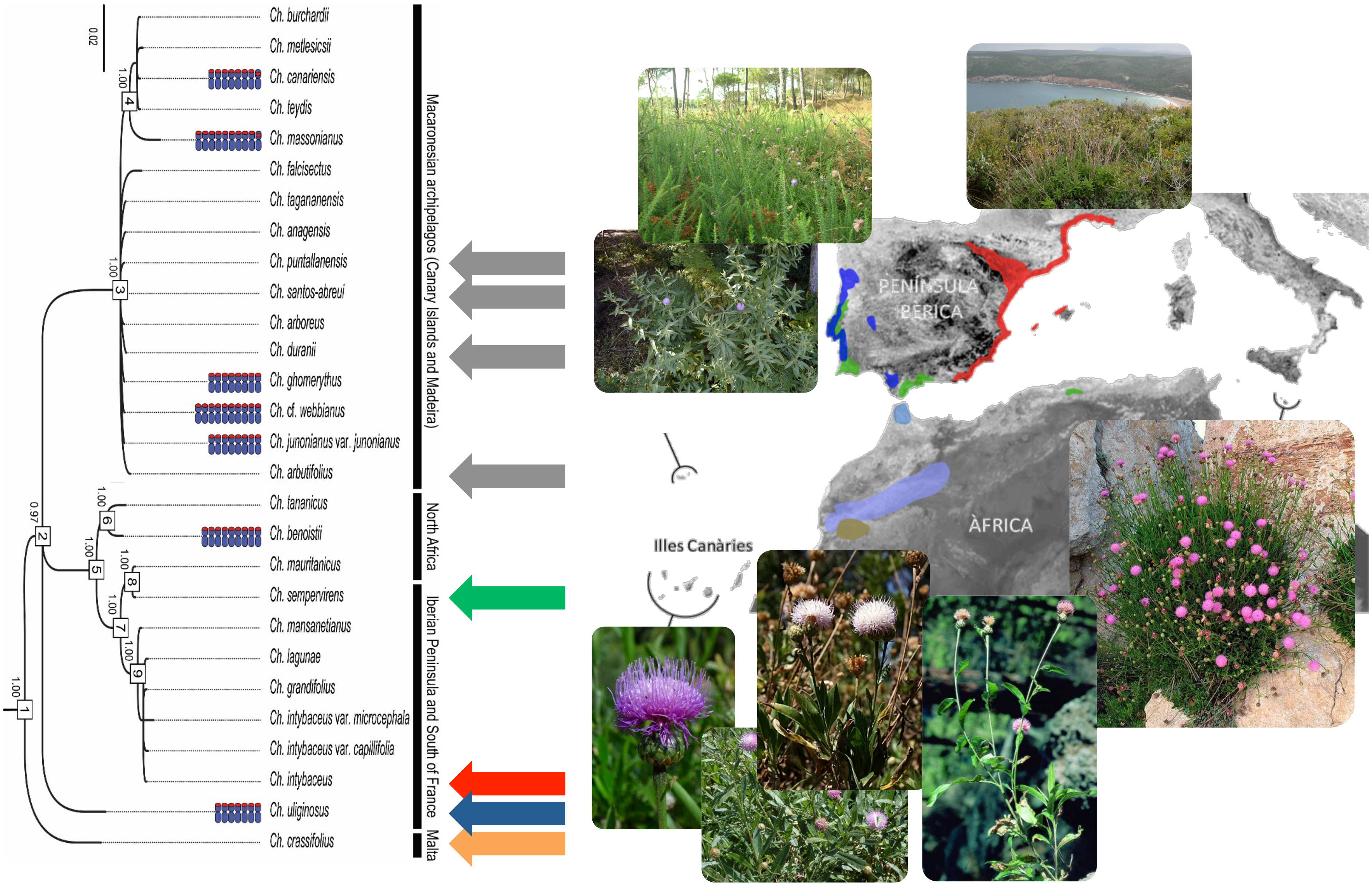


rDNA evolution in *Cheirolophus*

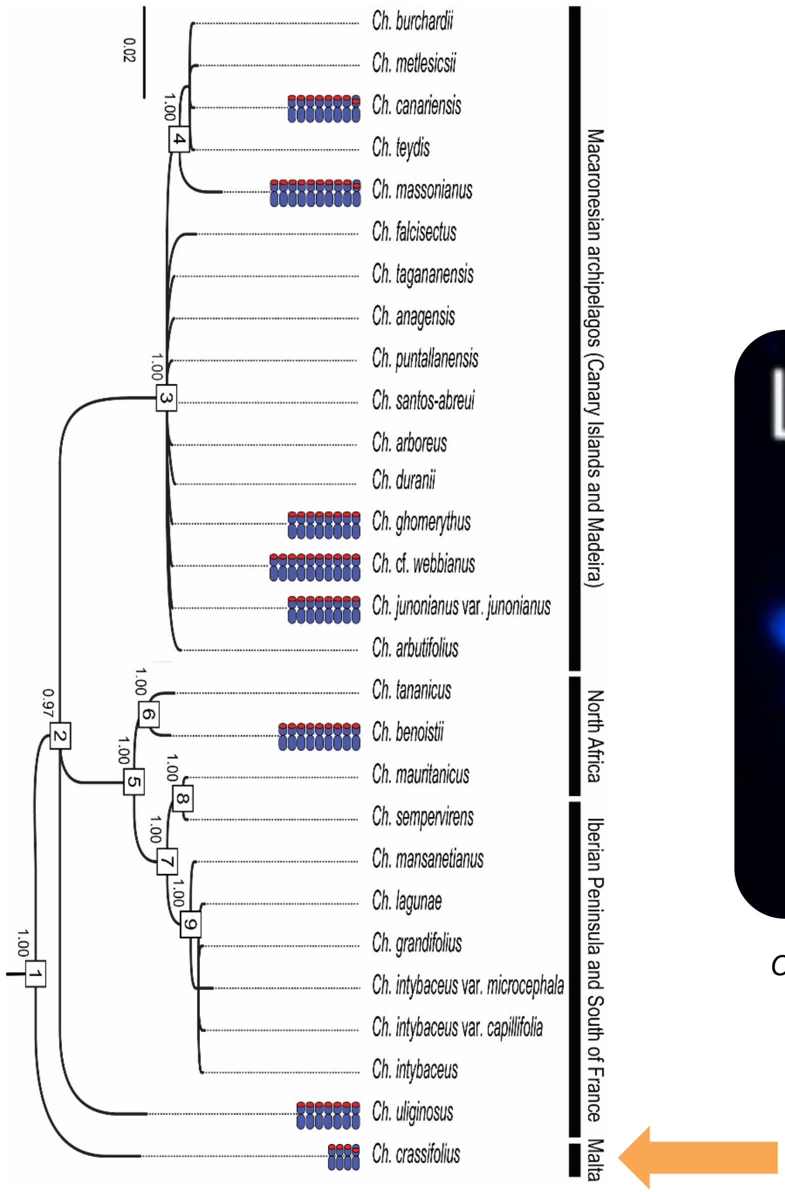


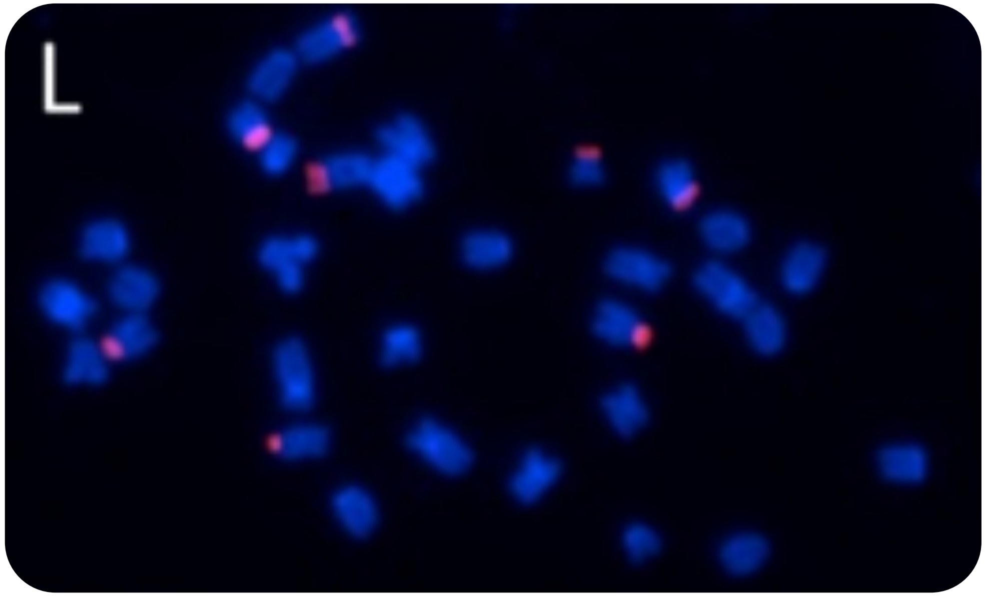


rDNA evolution in *Cheirolophus*



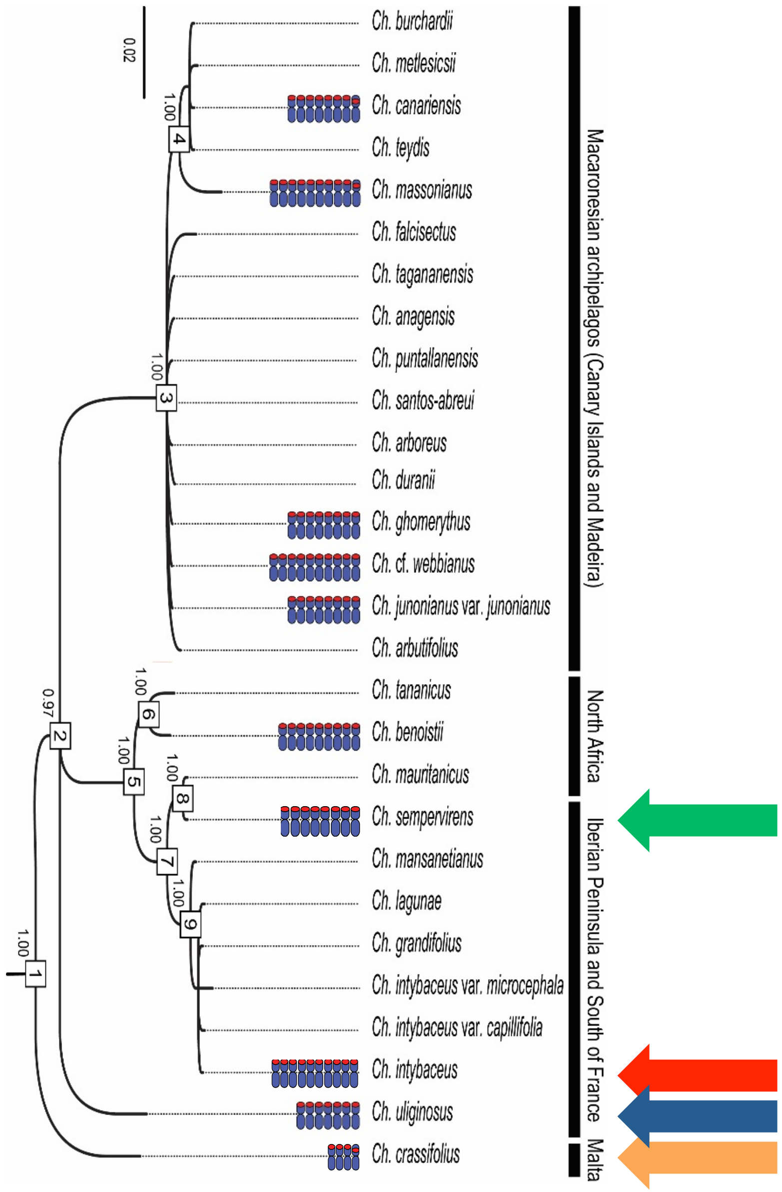
rDNA evolution in *Cheirolophus*

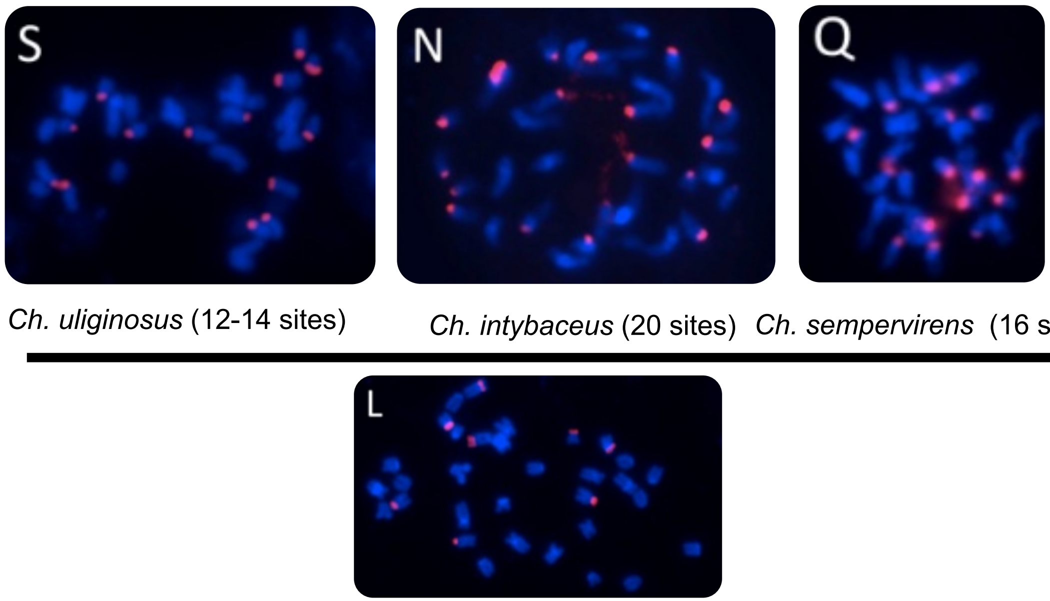




Ch. crassifolius (8 sites)

rDNA evolution in *Cheirolophus*

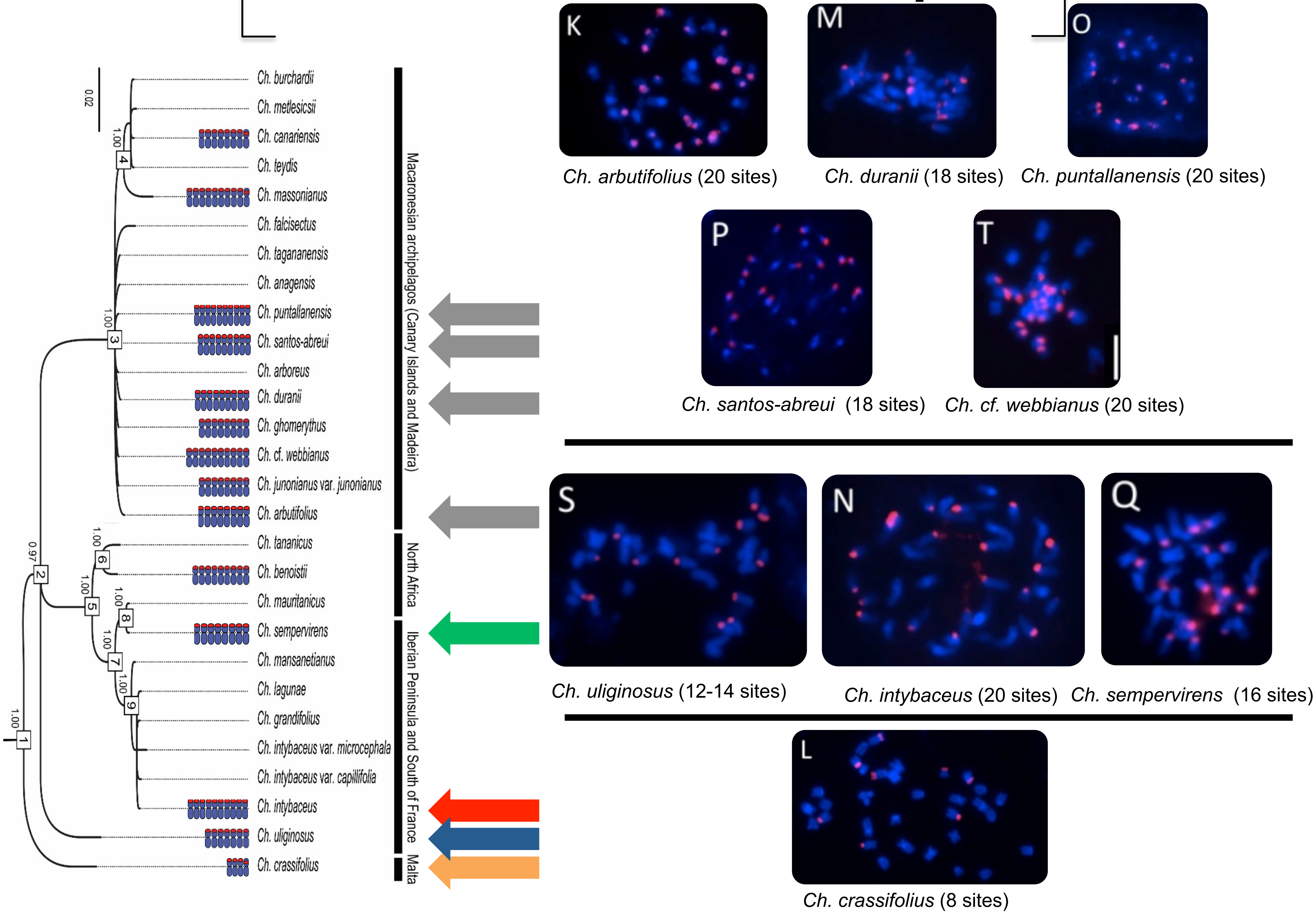




Ch. uliginosus (12-14 sites) *Ch. intybaceus* (20 sites) *Ch. sempervirens* (16 sites)

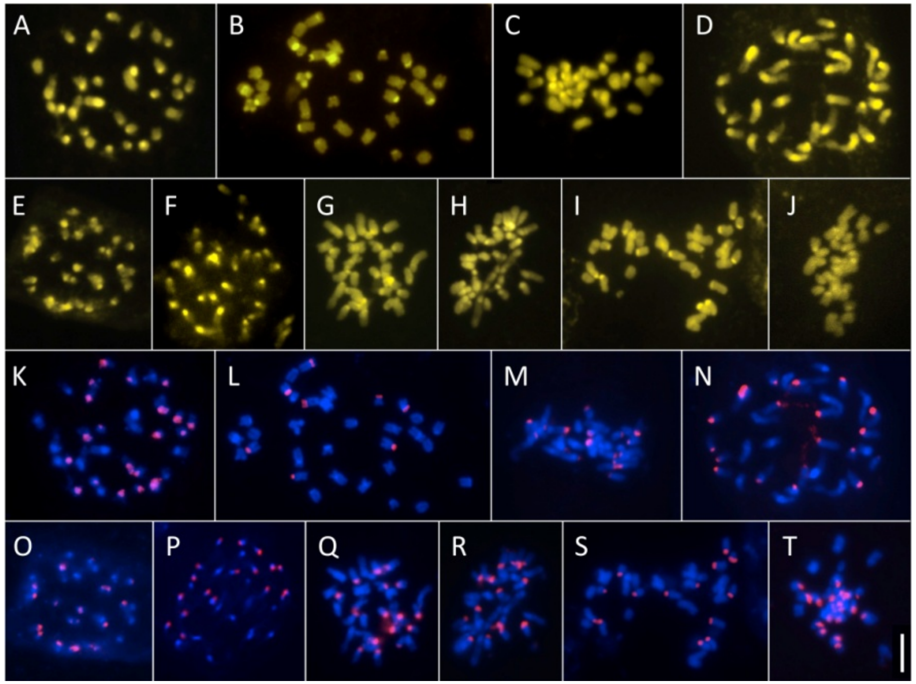
Ch. crassifolius (8 sites)

rDNA evolution in *Cheirolophus*



rDNA evolution in *Cheirolophus*

rDNA loci and GC-rich DNA sequences



- Surprisingly high number of CMA+ and 35S signals, particularly compared to closely related genera.
- 35S loci mainly located on terminal positions.
- *Ch. crassifolius* shows the lowest number of loci, highly similar to other closely related genera.

Taxon	Distribution	CMA	35S
1. ***Ch. anagaensis*** A.Santos	Ca(T)	-	-
2. *Ch. arboreus* (Sch. Bip.) Holub	Ca(P)	-	-
3. *Ch. arbutifolius* (Svent.) G.Kunkel	Ca(C)	-	20
4. *Ch. benoistii* (Humbert) Holub	Ma	16	18
5. *Ch. burchardii* A.Susanna	Ca(T)	16	-
6. *Ch. canariensis* (Willd.) Holub	Ca(T)	18(4i)	16(2i)
7. *Ch. crassifolius* (Bertol.) Susanna	Si(M)	-	8
8. *Ch. dariasii* (Svent.) Bramwell	Ca(G)	-	
9. *Ch. duranii* (Burchard) Holub	Ca(H)	-	18
10. *Ch. falcisectus* Montelongo & Moraleda	Ca(C)	-	-
11. *Ch. ghomerythus* (Svent.) Holub	Ca(G)	18(2i)	16
● *Ch. ghomerythus* var. *integrifolius* (Svent.) Holub		-	-
12. *Ch. grandifolius* (Font Quer) Stübing & al.	Bl(I, M)		
13. *Ch. intybaceus* (Lam.) Dostál	Ga(F), Hs(S)		20
● *Ch. intybaceus* var. *capillifolius* (Sandwith) J.R. Nebot & al.	Hs(S)		-
● *Ch. intybaceus* var. *microcephala* Rouy	Ga(F)		-
14. *Ch. junonianus* (Svent.) Holub	Ca(P)	12	16
● *Ch. junonianus* subsp. *junonianus*[1]	Ca(P)	12	16
● *Ch. junonianus* subsp. *isoplexiphyllus*[1]		-	-
15. *Ch. lagunae* A.Olivares & al.	Hs(S)	-	-
16. *Ch. massonianus* (Lowe) A.Hansen & Sunding	Md(M, P)	20(2i)	20
17. *Ch mauritanicus* (Font Quer) Susanna	Ag, Ma	-	-
18. *Ch. metlesicsii* Montelongo	Ca(T)	-	-
19. *Ch. puntallanensis* A.Santos	Ca(P)	-	20
20. *Ch. santos-abreui* A.Santos	Ca(P)	-	18
21. *Ch. satarataensis* (Svent.) Holub	Ca(G)	-	-
22. *Ch. sempervirens* (L.) Pomel	Hs(S), Lu	-	16
23. *Ch. sventenii* (A.Santos) G.Kunkel	Ca(P)	-	-
● *Ch. sventenii* subsp. *gracilis* A.Santos	Ca(P)	-	-
24. *Ch. tagananensis* (Svent.) Holub	Ca(T)	-	-
25. *Ch. tananicus* (Maire) Holub	Ma	-	-
26. *Ch. teydis* (Buch) G.López [= *Ch. argutus* (Nees) Holub]	Ca(P,T)	-	-
27. *Ch. uliginosus* (Brot.) Dostál	Hs(S), Lu	12	12-14
28. *Ch. webbianus* (Sch. Bip.) Holub	Ca(T)	-	-
Putative new species of *Ch. webbianus* complex			
***Ch.* cf. *webbianus* [**	Ca(T)	18(4i)	20(2i)
***Ch.* cf. sp. nova**	Ca(T)	-	-

rDNA evolution in *Cheirolophus*

Mechanisms involved:

rDNA evolution in *Cheirolophus*

Mechanisms involved:

- Polyploidy

rDNA evolution in *Cheirolophus*

Mechanisms involved:

- Polyploidy
- Locus duplication via illegitimate recombination

rDNA evolution in *Cheirolophus*

Mechanisms involved:

- Polyploidy
- Locus duplication via illegitimate recombination
- Amplification of orphaned rDNA loci (transposon-mediated insertions)

rDNA evolution in *Cheirolophus*

Mechanisms involved:

- Polyploidy
- Locus duplication via illegitimate recombination
- Amplification of orphaned rDNA loci (transposon-mediated insertions)
- Chromosome translocations

rDNA evolution in *Cheirolophus*

Mechanisms involved:

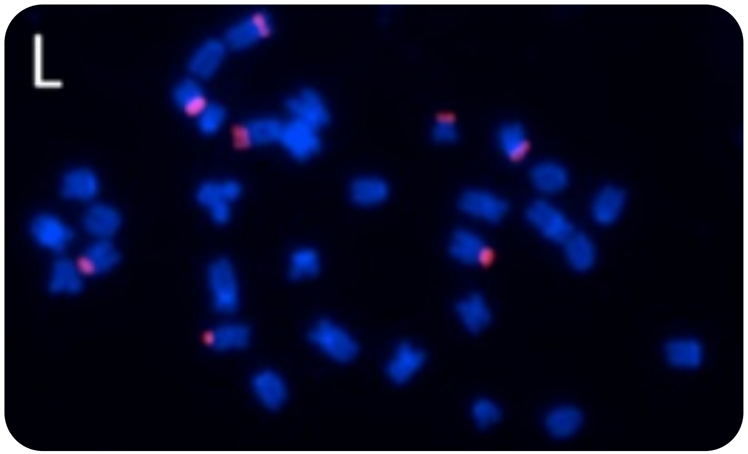
- Locus duplication via illegitimate recombination

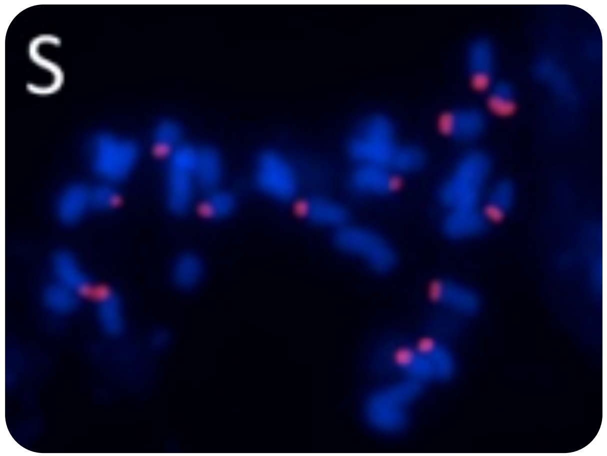
rDNA evolution in *Cheirolophus*

Mechanisms involved:

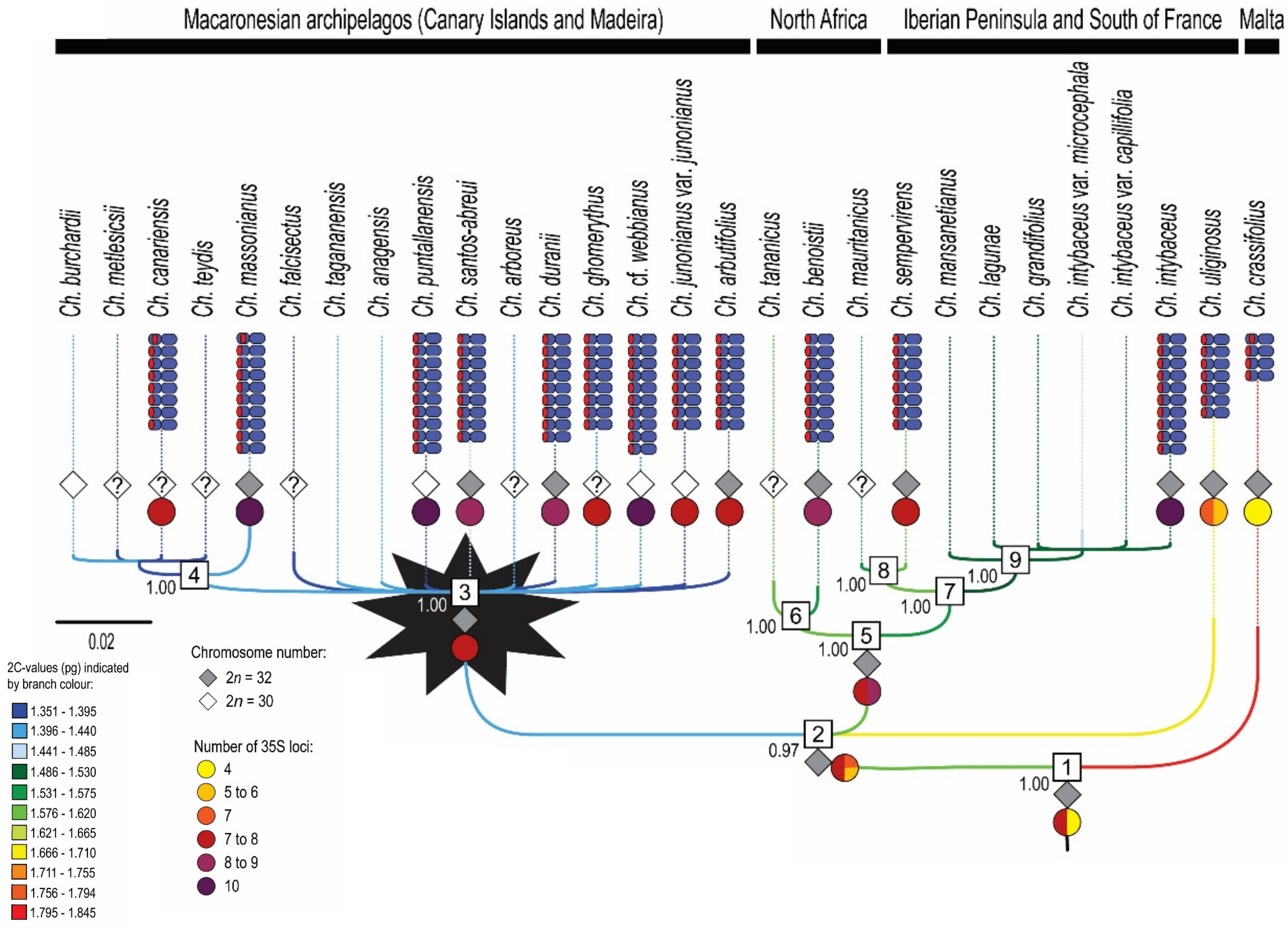
- Locus duplication via illegitimate recombination

  - Preserved loci position at T/St-position
  - Genome downsizing
  - rDNA is highly conserved: heterologous recombination

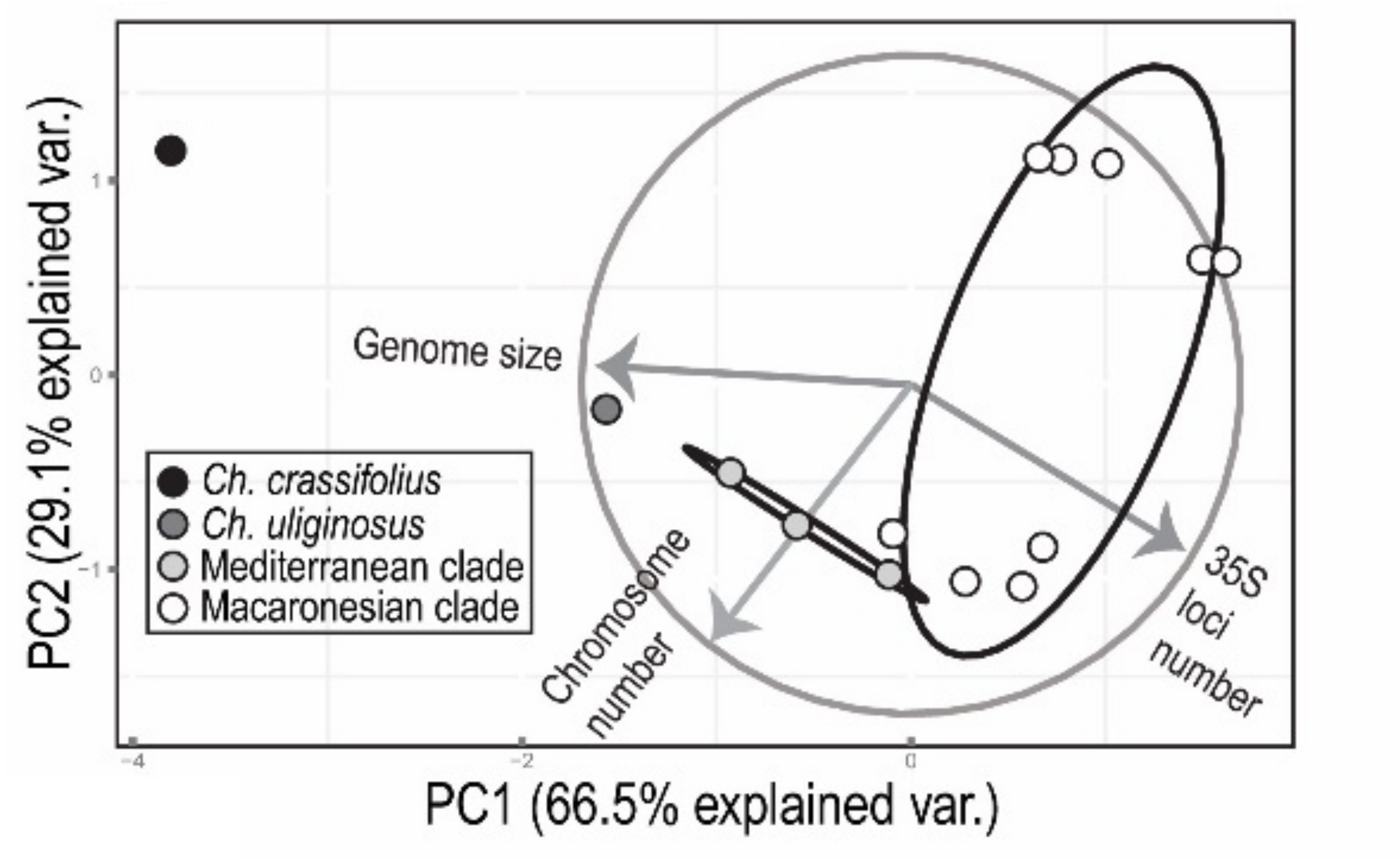




rDNA evolution in *Cheirolophus*

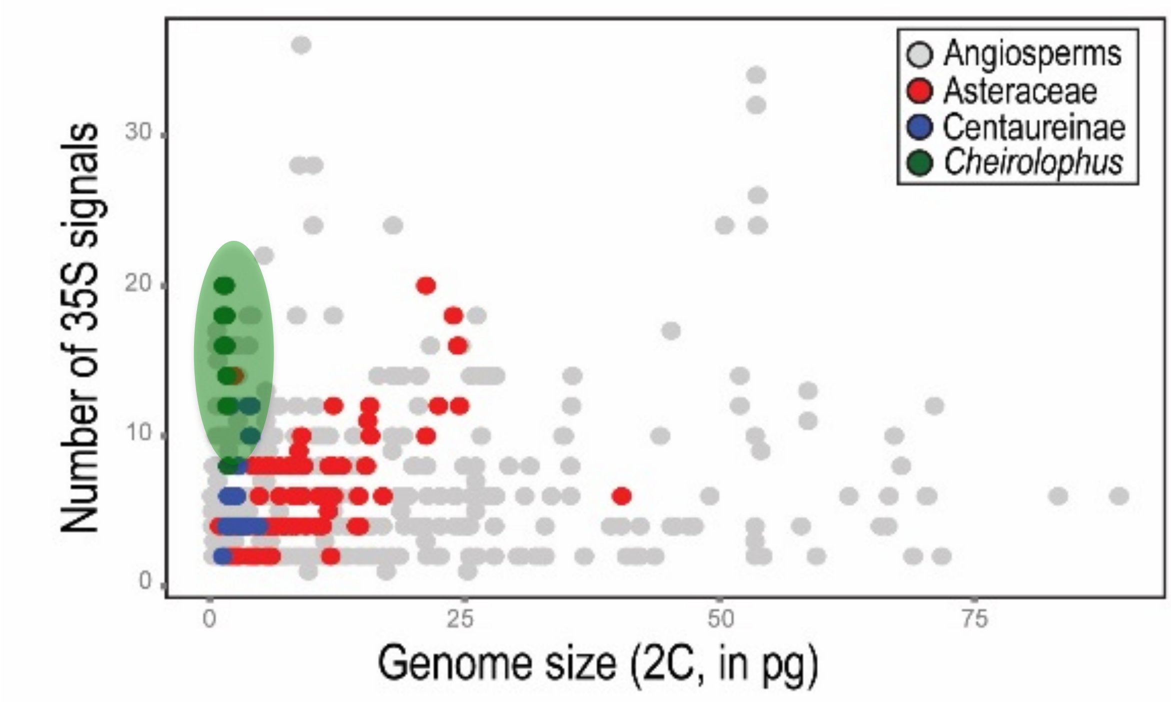


rDNA evolution in *Cheirolophus*



rDNA evolution in *Cheirolophus*

Marginal genomic landscape for *Cheirolophus*: distinctive cytogenetic traits



In summary...

In summary...

- Originated in Malta, diversified westwards along the Mediterranean basin and Macaronesia.

In summary...

- Originated in Malta, diversified westwards along the Mediterranean basin and Macaronesia.
- The Macaronesian diversification started around 1.74 Ma, followed by an explosive event of radiation during the late Pleistocene and particularly at the Holocene (0.5 Ma).

In summary...

- Originated in Malta, diversified westwards along the Mediterranean basin and Macaronesia.

- The Macaronesian diversification started around 1.74 Ma, followed by an explosive event of radiation during the late Pleistocene and particularly at the Holocene (0.5 Ma).

- The distinctiveness of *Cheirolophus* relies on a relative chromosomal stasis, which contrasts with the dynamics of GS and rDNA evolution seen.

In summary…

- Originated in Malta, diversified westwards along the Mediterranean basin and Macaronesia.
- The Macaronesian diversification started around 1.74 Ma, followed by an explosive event of radiation during the late Pleistocene and particularly at the Holocene (0.5 Ma).
- The distinctiveness of *Cheirolophus* relies on a relative chromosomal stasis, which contrasts with the dynamics of GS and rDNA evolution seen.
- The Macaronesian radiation is characterised by an enhancement of pre-existing traits since early in the diversification of the genus…

Acknowledgements...

- Dr. Ilia J. Leitch (Royal Botanic Gardens, Kew)
- Miquel Veny (Botanical Institute of Barcelona)
- Dr. Francesco M. Raimondo (Palermo Botanical Garden)

Thank you!

QUESTIONS?