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Molecular analysis separates the Atlantic population of Montagu's stellate barnacle into two cryptic species

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Abstract

The distribution of the intertidal barnacle Chthamalus montagui spans the West Mediterranean Sea and the Northeast Atlantic shores of Europe and West Africa. Knowledge of the phylogeography of this species has been limited to the Mediterranean and the European shores of the Atlantic. The present study considers the populations of West Europe, but also focuses on the overlooked populations of West Africa. We performed a molecular analysis using two markers: the mitochondrial COI gene and the nuclear rRNA ITS gene. Whereas ITS proved to be non-informative, COI has demonstrated that the East Atlantic population of C. montagui comprises two genetically distinct clades: a northern clade that ranges from Mauritania to Scotland and a southern clade that comprises the populations from Senegal. These clades are separated by the Cape Verde Front, which stretches west of the upwelling area off Mauritania. We consider these clades as two cryptic species of the nominal species C. montagui.

KEYWORDS

Cape Verde Front, Chthamalus montagui, cryptic species, Mauritania, Senegal, upwelling

INTRODUCTION 1

Chthamalus (Crustacea: Cirripedia) is a species-rich genus of barnacles, comprising 28 nominal species (Chan et al., 2021), including C. montagui, whose presence in the Mediterranean and north east Atlantic was already reported by Southward (1976). Using gel electrophoresis, Dando et al. (1979) confirmed its existence in the Adriatic, and found difference between the Adriatic and North Atlantic (off Southwest England) populations. These results led Dando and Southward (1981) to suggest that these populations represent cryptic species.

Pannacciulli et al. (1997, 2017) studied the genetic structure of C. montagui in the Mediterranean Sea and the Northeastern Atlantic Ocean. They revealed that there are three geographically discrete populations: Northeastern Atlantic Ocean, Western-central Mediterranean Sea and the Aegean Sea-Black Sea. The oceanic barriers that block gene flow between these basins are the Almeria-Oran Front, marking the Atlantic-Mediterranean break, and Cyclades Islands, marking the break between the Western-central Mediterranean and the Aegean Sea.

While the population structure of C. montagui from the Mediterranean Sea and the Northeastern Atlantic

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has already been studied using genetics, the populations of West Africa have so far been relatively neglected. Stubbings (1967) summarised the cirriped fauna of West Africa and reported the presence of *Chthamalus stellatus* from this region. However, this was done before the recognition of *C. montagui* as a distinct species, and it is therefore highly likely that some of the populations reported as *C. stellatus* are in fact *C. montagui*. Hawkins et al. (2000), Pannacciulli et al. (2009) and Tikochinski et al. (2020) have studied the barnacle populations on the East Atlantic Macaronesian Islands—Madeira, the Canary Islands, Azores and Cape Verde Islands. Using the mitochondrial marker COI, Tikochinski et al. (2020) assigned the Cape Verde Islands population to a cryptic species of *C. stellatus*.

This study aims to fill the gap in current knowledge regarding the *C. montagui* population in the North-East Atlantic by adding new data gained from across this region. The range of samples used in the current analysis spans from Loch Sween in Scotland to the north of the Saloum Delta in Senegal. We used a combination of morphological diagnoses, phylogenetic inference and population genetic approaches in the current analysis. Applying two genetic markers, the mitochondrial COI gene and the nuclear ITS, we confirm that the populations from Senegal form an isolated cryptic species of *C. montagui*.

2 | MATERIALS AND METHODS

2.1 | Sampling and morphological diagnosis

Samples of *C. montagui* were collected from 13 different locations (Figure 1, Table 1). The samples were collected at the intertidal zone, mainly at low tide. Samples were fixed in the field and stored in 96% ethanol. All material was deposited in the National Natural History Collections, The Hebrew University of Jerusalem.

We randomly selected specimens from Agadir (Morocco) and Ngor (Senegal) for the morphological analyses (see Morphological Analysis S1). Comparison of allometric parameters between (1) *C. stellatus*, (2) *C. montagui* from different locations in the Mediterranean and Europe (Southward, 1976) and (3) *C. montagui* from Senegal, indicates that morphologically, the population from Senegal does not differ from the northeastern population.

2.2 | Molecular analysis

The soft tissue of the barnacles was separated from the shell and used for DNA extraction. Remnants left after the PCR are deposited at the National Natural History Collections, The Hebrew University of Jerusalem. Collection numbers are presented in Table S1.

Two genes were used in the molecular analysis: the mitochondrial COI gene and the nuclear ITS. Sequences were aligned using the Molecular Evolution Genetics Analysis (MEGA X; Kumar et al., 2018) software. All sequences used in the present study have been deposited in GenBank; accession numbers are given in Table S2.

2.3 | Statistical analyses

2.3.1 | COI

Altogether, we analysed 237 individuals from 13 locations. After a multiple alignment of all the sequences, we were left with 497 positions for each sequence. Pairwise distances between the COI haplotypes were calculated by the Kimura two-parameter model, using the MEGA X software.

The large number of individuals prevents us from displaying a legible phylogenetic tree that includes all individuals. Instead, we first proceeded with a population-based analysis of the 13 locations by considering the means of the 78 between-population distances. The overall 13×13 distance matrix served to construct a population phylogenetic tree by the UPGMA (unweighted pair group method with arithmetic mean) algorithm, using the MVSP software (Kovach Computing Services, 2013).

In addition to the phylogenetic tree, the Automatic Barcode Gap Discovery (ABGD) method (Puillandre et al., 2012) was also employed to detect possible clustering of individuals by considering the distribution of all 27,966 pairwise distances.

A median-joining haplotype network was constructed using the POPART software (Leigh & Bryant, 2015).

Following the insight gained by the population-based tree, we then focused on the genetic differentiation of the *C. montagui* populations on the Atlantic coast of West Africa, using an individual-based analysis. For this analysis, we considered only the populations of Agadir, Dakhla, St. Louis, Ngor, Joal Fadiout and Palmarin. From the pairwise distances between the individual haplotypes, we constructed a bootstrap-generated (1000 replications) neighbour-joining tree, using the MEGA X software.

2.3.2 | ITS

Altogether, we analysed 190 individuals from 12 locations. After a multiple alignment of all the sequences, we FIGURE 1 Map showing the 13 collection sites of Chthamalus montagui in the current study.



TABLE 1 Number of individuals (N) from each location
 (arranged from North to South).

		N	
Location	Coordinates	COI	ITS
Tayvallich, Scotland	56°01' N 05°38' W	21	12
Plymouth, England	50°22' N 04°08' W	19	15
Dinard, France	48°38' N 02°03' W	18	17
Biarritz, France	43°29' N 01°34' W	30	-
Vila do Conde, Portugal	41°21′ N 08°45′ W	22	22
Boca do Inferno, Portugal	38°41′ N 09°26′ W	17	15
Cadiz, Spain	36°32' N 06°17' W	19	16
Agadir, Morocco	30°25' N 09°37' W	17	19
Dakhla, Western Sahara	23°46' N 15°56' W	14	6
St. Louis, Senegal	16°00' N 16°30' W	8	6
Ngor, Senegal	14°45′ N 17°31′ W	32	21
Joal Fadiout, Senegal	14°09' N 16°50' W	11	21
Palmarin, Senegal	13°59' N 16°46' W	9	20
Total		237	190

Note: Coordinates are rounded to the nearest minute.

were left with 677 positions for each sequence. Pairwise distances between the ITS haplotypes were calculated by the Kimura two-parameter model, using the MEGA X software.

The ABGD method was employed to detect possible clustering of individuals by considering the distribution of all 17,955 pairwise distances.

RESULTS 3

COI 3.1

The between-population distance matrix is presented in Table S3, and is the basis for constructing the population dendrogram (Figure 2). The analysis displays a geographic structure, dividing the populations into two main clusters. All Senegal locations (St. Louis, Ngor, Joal Fadiout and Palmarin) are included in one cluster, which we refer to as the 'Southern' Clade, whereas all other locations (i.e. from Dakhla northwards) are included in the second cluster, the 'Northern' Clade. The mean pairwise distance within the Northern Clade is 0.0062 ± 0.0014 , and the mean pairwise distance within the Southern Clade is 0.0052 ± 0.0011 (mean \pm SE), whereas the mean pairwise distance between the two clades is 0.0313 ± 0.0075 , and is significantly larger than the means within clades (standard errors were estimated by 1000 bootstrap replications).

The ABGD method displays a bimodal distribution of the individual pairwise distances (Figure 3). The first mode largely represents the within-clade distances, and the second mode corresponds to the pairwise distances between the two clades.

The haplotype network is presented in Figure 4. It clearly displays the division of the COI haplotypes into the two distinct clades, which are consistent with the clades already demonstrated in Figure 2 (except for a single individual from Dakhla, which is included in the Southern Clade, here and in Figure 5 as well).



FIGURE 2 A unweighted pair group method with arithmetic mean tree, based on COI distances, depicting the relationship between the 13 *Chthamalus montagui* populations.



FIGURE 3 The bimodal distribution of all COI pairwise distances (with regard to the Automatic Barcode Gap Discovery method).

Figure 5 focuses on the transition region between the Northern and the Southern Clades and includes the populations of the Atlantic coast of West Africa. It demonstrates that the border between the Northern and the Southern Clades lies between Dakhla (in Western Sahara) and Senegal, presumably in the region of the boundary zone between two water masses, the North Atlantic Central Water and the South Atlantic Central Water.

3.2 | ITS

The mean pairwise distance in this marker is merely 0.0005 ± 0.0001 (mean \pm SE; standard error was estimated by 1000 bootstrap replications). The ABGD method

displays a unimodal distribution of the individual pairwise distances, with a maximum at the origin. The conclusion is that ITS is not informative as a distinguishing marker between the *C. montagui* populations of the East Atlantic (see, however, Shemesh et al., 2009).

4 | DISCUSSION

The genetic analysis of *C. montagui* from the East Atlantic exhibits genetic structuring. The level of divergence between the clade that includes the northern populations, ranging from Tayvallich all the way to Dakhla, and the clade that includes the four populations from Senegal justifies their splitting into two distinct species. This conclusion is based on the differences between the COI sequences; the ITS gene turned out to be uninformative as a distinguishing marker for the populations of our study. However, there are currently no diagnostic morphological features that enable taxonomic identification and separation of these two clades. We, therefore, consider them as cryptic species of *C. montagui*.

Moreover, Pannacciulli et al. (2017) studied the genetic structure of *C.montagui* in the Mediterranean Sea and the Northeastern Atlantic Ocean. They distinguished three geographically discrete populations: Northeastern Atlantic Ocean, Western-central Mediterranean Sea and the Aegean Sea-Black Sea. Looking into the COI sequences of their study, we can measure the mean genetic distances between these populations and compare them with the two populations of our study. It turns out that the incorporated analysis reveals that *C.montagui*



FIGURE 4 A Chthamalus montagui median-joining haplotype network, comprising 237 COI sequences from the 13 studied locations.

is divided into three distinct clades—the Mediterranean, the Northeastern Atlantic and the Senegal—with similar mean distances, ranging from 3.3% to 3.5%, between them. Thus, we can extrapolate and suggest that the nominal species of *C.montagui* really comprises three cryptic species.

The concept that nominal barnacle species present assemblies of cryptic species is well established (Wares, 2020). Within the genus Chthamalus, it has been demonstrated that some populations that cannot be separated using morphological characters are a cluster of cryptic species. Tsang et al. (2008) and Tsang, Wu, et al. (2012) identified within Chthamalus malayensis four genetically differentiated allopatric clades they regarded as cryptic species. The nominal species Chthamalus moro from east Asia comprises three distinct genetic lineages, representing three cryptic species (Wu et al., 2015). Hawkins et al. (2000) and Pannacciulli et al. (2009) reported the presence of C. stellatus in the Atlantic Macaronesian islands. Tikochinski et al. (2020) demonstrated that the Cape Verde Islands population of C. stellatus is a cryptic species, genetically different from the European and Mediterranean population of this species. It is most probable that other Macaronesian barnacles belong to cryptic species of C. stellatus. Based on molecular analysis, Motro et al. (2023) recently suggested that the nominal species Chthamalus dentatus is a cluster of three cryptic species. These cryptic species are separated by a series of upwelling systems that are likely to act as barriers to the distribution of the propagules. In an additional chthamalid,

Hexechamaesipho pilsbryi, two mitochondrial lineages, one from Japan and Okinawa and another from Taiwan and Southeast Asia, represent two cryptic species (Tsang et al., 2013).

Cryptic species are also found in other cirripedes. In *Tetraclita*, Chan et al. (2007a, 2007b) demonstrated that in the Indo-West Pacific, the nominal species *T. squamosa* is a complex of cryptic species. Similarly, *Tetraclita serrata* consists of two evolutionarily significant units along the east to the west coast of South Africa. These units could not be distinguished by morphological analysis, but mito-chondrial DNA confirms that they are two cryptic species (Tsang, Achituv, et al., 2012).

The genetic structure of C. montagui presented in the current study has a plausible biogeographical explanation. Whereas ocean currents act against forming marine biogeographical barriers, wind-driven upwelling systems are one of the most important causes shaping the distribution of shallow water organisms. The oceanographic setup in the central Eastern Atlantic presents such conditions. The western coast of Africa is characterised by a series of upwelling systems—surface winds that blow parallel to the coastline and the Coriolis effect push the surface water away from the coast to the ocean. Such upwellings bring cold and nutrient-rich water up from the deep to the surface, thus preventing the transport of thermophilic larvae along the coast. A permanent (year-round) upwelling system is located off Cape Blanc on the Mauritanian coast (approximately 21° N 17° W), in the southern part of the North-West African upwelling system. The Cape



FIGURE 5 A COI-based neighbour-joining tree of *Chthamalus montagui* individuals from the Atlantic coast of West Africa. Individuals are from Morocco (Agadir), Western Sahara (Dakhla) and Senegal (St. Louis, Ngor, Joal Fadiout and Palmarin). The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) is shown only if larger than 80%.



FIGURE 6 The Cape Verde Front, west of the Mauritanian coast.

Blanc area is also situated within the boundary zone between the relatively salty North Atlantic Central Water and the South Atlantic Central Water. The convergence of these two water masses forms the Cape Verde Front (Meunier et al., 2012; Tiedemann et al., 2018), which runs from Cape Blanc to Cape Verde Islands (Figure 6). Olivar et al. (2016) recorded substantial differences in fish assembles between both sides of this front. We suggest that Cape Verde Front can serve as the barrier between the two clades of *C. montagui*.

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CONFLICT OF INTEREST STATEMENT

No potential conflict of interest was reported by the authors.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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