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A test of color-based taxonomy in nudibranchs: Molecular phylogeny and species delimitation of the *Felimida clenchi* (Mollusca: Chromodorididae) species complex

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ABSTRACT

Traditionally, species identification in nudibranch gastropods relies heavily on body color pattern. The *Felimida clenchi* species complex, a group of brightly colored Atlantic and Mediterranean species in the family Chromodorididae, has a history of exceptional controversy and discussion among taxonomists. The most widely accepted hypothesis is that the complex includes four species (*Felimida clenchi*, *F. neona*, *F. binza* and *F. britoi*), each with a characteristic body color pattern. In this study, we investigated the taxonomic value of coloration in the *Felimida clenchi* complex, using molecular phylogenetics, species-delimitation analyses (ABGD, GMYC, PTP), haplotype-network methods, and the anatomy of the reproductive system. None of our analyses recovered the traditional separation into four species. Our results indicated the existence of three species, a result inconsistent with previous taxonomic hypotheses. We distinguished an undescribed species of *Felimida* and redefined the concepts of *F. clenchi* and *F. binza*, both highly polychromatic species. For the first time, molecular data support the existence of extreme color polymorphism in chromatic nudibranch species, with direct implications for the taxonomy of the group and its diversity. The polychromatism observed in the *F. clenchi* complex apparently correlates with the regional occurrence of similar color patterns in congeneric species, suggesting different mimicry circles. This may represent a parallel in the marine environment to the mechanisms that play a major role in the diversification of color in terrestrial and fresh-water chromatic groups, such as heliconian butterflies.

1. Introduction

Nudibranchs are one of the most colorful and diverse groups of marine invertebrates; and similarly to most chromatic animal groups, such as butterflies, frogs and reef fish, color is an important character used to diagnose species or groups of species. In fact, the external morphology and color patterns are the most common features used to identify species, as can be seen in many guidebooks (Valdés et al., 2006; Debelius and Kuiter, 2007; Gosliner et al., 2008) and specialized nudibranch websites (Sea Slug Forum; NudiPixel).

The Chromodorididae is the largest family among dorid nudibranchs, with over 300 described species occurring primarily in tropical and subtropical seas (Turner and Wilson, 2007; Johnson and Gosliner, 2012). As the name suggests, most chromodorids are brightly colored, and are a favorite target of underwater macrophotographers. They are among the most colorful nudibranchs, ranging from millimeters to a few centimeters in length, living mostly on hard substrates in the intertidal and shallow subtidal zones. Chromodorids feed on sponges, and many species can obtain, accumulate, and also transform toxic compounds for use in their own defense (Cimino and Ghiselin, 2009; Cheney et al., 2016). Species richness is high in the Indo-West Pacific region, where

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many species groups with similar color patterns and morphology were proposed and described (Rudman, 1982, 1983, 1985, 1986a, b, 1987, 1990, 1991). The number of species in the Atlantic Ocean and Mediterranean Sea is considerably smaller. However, some highly charismatic species color groups are present in these regions, such as the group of blue *Felimare* species distributed mostly in the eastern Atlantic and the Mediterranean Sea (Ros, 1976; Ortea et al., 1996).

In recent years, the first molecular studies focused on chromodorid species were published. Turner and Wilson (2007) recovered evidence of paraphyly or polyphyly in different, widespread genera, a view that was later confirmed and examined further, with the addition of more species (Johnson and Gosliner, 2012). These latter authors resurrected old available names for new clades identified in their phylogenetic hypotheses, and, for example, have found that the type genus of the family, *Chromodoris*, which was previously thought to be circumglobal across temperate and tropical latitudes, represents a radiation endemic to the Indo-West Pacific. The species of *Chromodoris* from the eastern Pacific, Atlantic and Mediterranean Sea were thus ascribed to the genus '*Felimida*', but the monophyly of this group still needs to be tested by including a larger number of species (Johnson and Gosliner, 2012; Ortigosa et al., 2014). Nevertheless, this generic name is now commonly used by the scientific community (Ortigosa et al., 2014; Padula et al., 2014a).

1.1. The Felimida clenchi species complex

Among '*Felimida*' taxa, the *Felimida clenchi* species complex has a history of exceptional controversy and discussion among taxonomists (Meyer, 1977; Thompson, 1980; Edmunds and Just, 1985; Ortea and Pérez, 1983; Gosliner, 1990; Ortea et al., 1994). The original scanty descriptions with black-and white-illustrations may have contributed to this situation (Fig. 1A and B). Four nominal species are presently included in the complex: *Felimida clenchi* (Russell, 1935), *Felimida neona* (Marcus, 1955), *Felimida binza* (Marcus and Marcus, 1963) and *Felimida britoi* (Ortea and Pérez, 1983).

Felimida clenchi was described based on a single specimen, 9 mm in length, found in Bermuda. The description includes simple drawings of the specimen in ventral and dorsal positions, where it is possible to see the dorsal elliptical and elongated opaque areas encircling the rhinophores, and the white submarginal mantle band characteristic of the species (Fig. 1A). No internal structures were described. *Felimida neona* was described based on two specimens from São Paulo in southeastern Brazil, and is easily distinguishable from *F. clenchi* by the absence of dorsal oval or circular opaque-white spots and the presence of fluorescent red lines on the mantle (Marcus, 1955). The original description of *Felimida binza*, based on two specimens from Curaçao, shows a species similar to *F. clenchi*, but with many dorsal circular spots and narrow transverse dark dashes on the margin of the mantle, as can be seen in the original figure (Fig. 1B). Marcus and Marcus (1963) neither mentioned nor discussed the potential similarities between *F. binza* and *F. clenchi.* Marcus and Marcus, 1967 studied three different specimens from Florida. Two of them clearly correspond to the original descriptions and illustrations of *F. clenchi* and *F. binza*, respectively, but, surprisingly, the authors grouped all of them under the name *F. neona*, without further discussion (Marcus and Marcus, 1967, Figs. 58, 58A). Meyer (1977), based on specimens collected on the coast of Panama, synonymized *F. neona* with *F. clenchi* and commented that *F. clenchi* is highly variable in color and internal morphology, an opinion followed by Thompson (1980) and Edmunds and Just (1985) in their studies based on specimens from Jamaica and Barbados, respectively.

An additional species was described later from the Canary Islands by Ortea and Pérez (1983), namely *Felimida britoi*, a species with a purple mantle with dorsal yellow or white lines and spots.

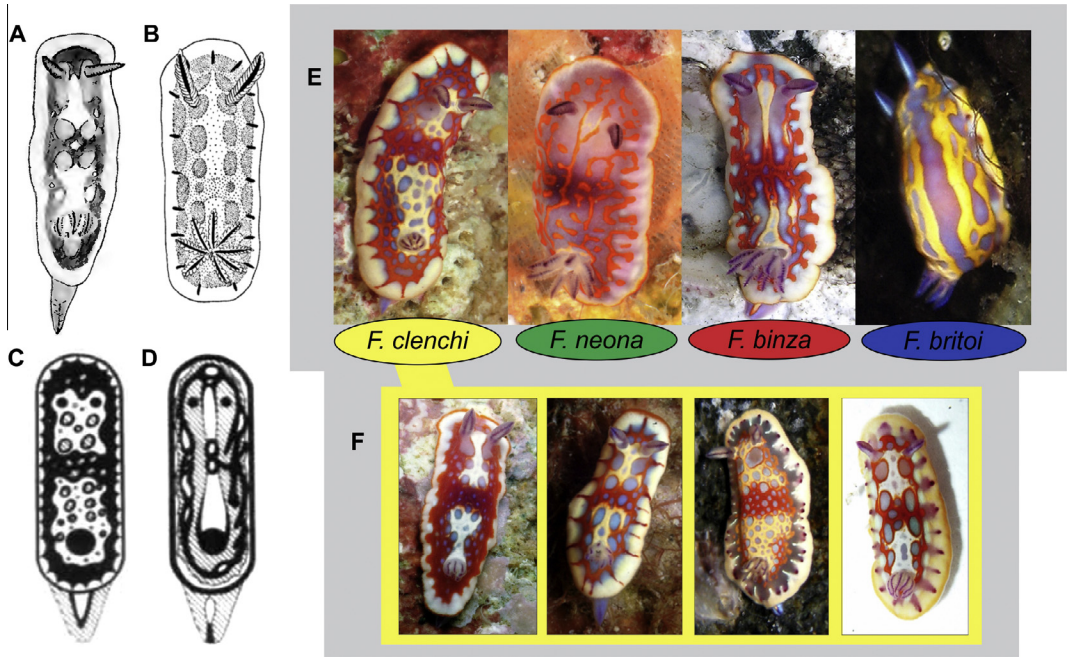

Fig. 1. Colors and patterns in the *Felimida clenchi* complex. (A) Original illustration of *Felimida clenchi* from Russell (1935). (B) Original illustration of *Felimida binza* from Marcus and Marcus (1963). (C) Illustration of *F. clenchi* from Ortea et al. (1994). (D) Illustration of *F. binza* from Ortea et al. (1994). (E) Current concepts in the color patterns of the *F. clenchi* species group, after Ortea et al. (1994). Color codes for each pattern are used in subsequent figures. (F) Variation in the spot patterns of specimens currently under the name *F. clenchi*, which may represent different species. (A. Figure A, plate 4, from Russell (1935) used with permission of *The Nautilus*. B. Figure 30 from Marcus and Marcus (1963) in *Studies on the fauna of Curaçao and other Caribbean Islands*, No. 79. C and D. Figures from Ortea et al. *North Atlantic nudibranchs of the* Chromodoris clenchi *color group (Opisthobranchia: Chromododoridae)*. Journal of Molluscan Studies, 1994, 60: 237–248 by permission of Oxford University Press. E–F photos by the authors, with the exception of *F. britoi*, taken by Peter Wirtz). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)