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"Júlio de Mesquita Filho"

INSTITUTO DE BIOCIÊNCIAS DE BOTUCATU

Vinícius Vilela Carvalho

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Vinícius Vilela Carvalho

Orientador: Gilmar Perbiche Neves

Dissertação apresentada ao Instituto de Biociências, Universidade Estadual Paulista - Campus de Botucatu – como parte dos requisitos para obtenção do título de Mestre em Ciências Biológicas – Área de concentração: Zoologia

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RESUMO

Cladóceros são microcrustáceos encontrados em ambientes aquáticos continentais, constituindo um importante componente do zooplâncton em lagos e reservatórios. Existem aproximadamente 600 espécies descritas em todo o mundo, e sua taxonomia apresenta diversas lacunas. Muitos táxons são compostos por espécies crípticas descritas no século XIX com base em caracteres superficiais. Entre essas espécies, *Ceriodaphnia cornuta* é um complexo de espécies crípticas que apresentam alta plasticidade fenotípica. A literatura indica que essa espécie não pode ser diferenciada por métodos morfológicos convencionais, sendo necessárias abordagens mais recentes, como o estudo de machos e fêmeas efipiais e patas torácicas. O objetivo deste estudo foi realizar uma revisão taxonômica das populações brasileiras do complexo - *Ceriodaphnia cornuta* utilizando taxonomia integrativa. As populações analisadas foram coletadas em diferentes corpos d'água, dissecadas, e estruturas de alto valor taxonômico, como cabeça, apêndices torácicos e pós-abdômen, foram estudadas. Os resultados morfométricos revelaram diferenciação entre as populações. Os espinhos da carapaça apresentaram variação significativa e baixa correlação com os valores alométricos. A população JMED mostrou a maior diferenciação, principalmente devido a forma da carapaça, estrutura da pata II, e no número de dentículos anais. Sua morfologia efipial também se destacou por diferenças na forma e na ornamentação das colunas do efípio. Portanto, esse conjunto de caracteres é suficiente para definir uma nova espécie brasileira de *Ceriodaphnia*. As populações brasileiras também se diferenciaram quanto ao número de setas no IDL da pata I, e recomenda-se a realização de análises moleculares futuras com foco nessas populações para verificar sua diferenciação.

Palavras-Chave: biogeografia, efípios, espécies crípticas, polimorfismo, zooplâncton.

ABSTRACT

Cladocerans, are microcrustaceans found in continental aquatic environments, constituting an important component of the zooplankton in lakes and reservoirs. There are approximately 600 described species worldwide, and their taxonomy exhibits numerous gaps. Many taxa consist of cryptic species that were described in the 19th century based on superficial characters. Among these species, *Ceriodaphnia cornuta* is a complex of cryptic species exhibiting high phenotypic plasticity. The literature indicates that the species cannot be differentiated through conventional morphological methods, necessitating the use of novel approaches such as studying male, ephippial females and thoracic limbs. The objective of this study was to conduct a taxonomic revision of Brazilian *Ceriodaphnia cornuta* – complex populations using integrative taxonomy. The populations used in the study were collected from various water bodies, dissected, and structures with high taxonomical value such as head, thoracic limbs, and postabdomen were studied. The morphometric results revealed differentiation among the populations. Carapace spines exhibited significant variation and low correlation with allometric values. The JMED population showed the greatest divergence, primarily due to differences in carapace shape, limb II structure and anal teeth. Its ephippial morphology differed in both shape and the ornamentation of the ephippial columns. Thus, this set of characters is sufficient to define a new Brazilian *Ceriodaphnia* species. Brazilian populations also differed in the number of setae on the IDL of limb I, and future molecular analyses focusing on these populations are recommended to verify their distinctiveness.

Keywords: biogeography, cryptic species, ephippia, polymorphism, zooplankton.

SUMÁRIO

IDENTIFICAÇÃO

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TÍTULO: Revisão taxonômica do complexo – *Ceriodaphnia cornuta* no Brasil: uma abordagem integrativa.

APRESENTAÇÃO

A presente dissertação foi convertida em formato de artigo científico e traduzido para a língua inglesa. A formatação segue as normas da revista Hydrobiologia, Special issue: Cryptic Diversity.

INTRODUCTION

Among the microcrustaceans of continental aquatic environments, the superorder Cladocera is distinguished by its notable species richness and biomass. These organisms play a crucial role in the ecosystem of lakes and reservoirs, where they function as essential components of plankton. Beyond their presence in open waters, cladocerans have also been observed to inhabit association with vegetation, fine-grained sediments, and interstitial habitats (Smirnov, 1974; Elmoor-Loureiro, 1997; Kotov, 2006; Sousa et al., 2015). Preliminary estimates of global diversity suggest the presence of approximately 600 valid described species. However, it is important to note that this estimate may be two to four times higher than the actual number of species in existence. Of these, approximately 200 species (one third of the total) have been documented from the Neotropical region (Forró et al., 2008). According to the most recent findings and species redescriptions, the Brazilian cladoceran fauna comprises more than 84% of the described diversity in the Neotropics (Elmoor-Loureiro et al., 2023).

Taxonomic research on the group has advanced significantly in recent years; however, several Neotropical species already known in the literature require taxonomic revision. A significant number of these species were described in the 19th century based on a limited set of superficial and fragile morphological characteristics, which hinders accurate differentiation among them. Furthermore, the existence of cryptic species—defined as those that are morphologically indistinguishable—results in an underestimation of biodiversity within the group (Van Damme et al., 2011; Sousa et al., 2015).

Approximately 35 years ago, Frey (1987) proposed the concept of non-cosmopolitanism in cladocerans, establishing the foundation for taxonomists to conduct detailed analyses of species with restricted distributions on each continent. This shift facilitated the development of new methodologies in cladoceran research, including biogeographic studies. In the Neotropical region, several species were no longer considered cosmopolitan and underwent redescriptions (Sinev, 1998; Sinev & Elmoor-Loureiro, 2010; Van Damme et al., 2011). Despite these efforts, many taxa in Brazil are still regarded as cosmopolitan, which contradicts the concept advocated by Frey (e.g., *Moina macrocopa* Strauss, 1820; *Moina micrura* Kurz, 1874).

Among these groups, the one known as the *Ceriodaphnia cornuta* - complex stands out. The taxonomic history of *Ceriodaphnia cornuta* Sars, 1885 is complex, following the pattern seen in other cladoceran species. The species from Australia was originally described by Georg

Sars in 1885, based solely on the presence of carapace spines. These spines were located on the rostrum, head, fornice, and as bifurcated projections on the posterior region of the carapace. Almost a decade later, Richard described a second species of *Ceriodaphnia*, which he designated *Ceriodaphnia rigaudi* Richard, 1894. This species exhibited minimal differences from *C. cornuta*, primarily by the absence of a head spine and having a simple, non-bifurcated posterior spine.

Four years later, Daday (1898) published a study based on populations from Sri Lanka, where he identified both species of *Ceriodaphnia* occurring at the same locality. Additionally, he observed the presence of intermediate forms—some with a bifurcated posterior spine but lacking the head spine, and others with a simple posterior spine but possessing the head spine. Consequently, he concluded that the two species were not truly distinct, but rather local varieties of the same species, *C. cornuta*.

The controversy surrounding the classification of the group persisted throughout the first half of the 20th century. While some authors supported Daday's view that the two "species" were simply local forms (e.g., Gurney, 1916; Bär, 1924), others proposed that four forms should be recognized based on the presence of spines: *C. cornuta rigaudi*, *C. cornuta intermedia*, *C. cornuta cornuta*, and *C. cornuta paradoxa* (Jenkin, 1934).

Starting in the 1950s, studies on *Ceriodaphnia* began incorporating statistical and ecological approaches. The study of Rzoska (1956), based on populations from the Nile River (Africa), was particularly important, as he demonstrated that carapace spines are variable characters subject to phenotypic plasticity. Consequently, it was proposed that *C. rigaudi* be considered a junior synonym of *C. cornuta*. The phenotypic plasticity of the *C. cornuta* carapace has since been the focus of several studies, which indicate that spine formation is induced by kairomones released by predators into the water (Zaret, 1969; Rietzler, 2008; Gu et al., 2021). This type of plasticity has also been proposed and investigated in other daphniids (e.g., Dodson, 1974; Pijanowska, 1990), highlighting the role of morphological changes as a response to predation. The compound eye is another structure known to exhibit polymorphism. Zaret (1969) and Mort & Kerfoot (1988) reported forms with high coefficients of variation (75-89%) in the pigmented area of the compound eye in their studies on *C. cornuta* in Lake Gatún, Panama.

In the 1980s, Dorothy Berner utilized Scanning Electron Microscopy to investigate the comparative morphology of ephippia from *C. cornuta* and *C. rigaudi*, although without testing

any formal taxonomic hypotheses. She observed some differences in the ornamentation of these ephippia and, based on this, revived the controversy suggesting that the two species might indeed be distinct (Berner, 1985). However, this hypothesis proved inconsistent, given that the geographic distribution of *Ceriodaphnia cornuta* (Australasia) and *Ceriodaphnia rigaudi* (Afrotropical region) differs. Furthermore, other morphological characters and molecular data should be taken into account to verify this differentiation.

Currently, taxonomists have paid little attention to the issues involving *Ceriodaphnia* species, including those related to *Ceriodaphnia cornuta*. Sharma and Kotov (2013) verified Australian populations of the *cornuta*-complex using molecular methods. Mitochondrial markers COI and 16S, as well as the nuclear marker 28S, were employed in the study. Based on these analyses, they identified three distinct local populations with low levels of differentiation among them. However, other populations of *C. cornuta* have been identified outside its native range, such as in the Iberian Peninsula (Alonso, 1996), South Korea (Kotov et al., 2022a), Central and North America (Elías-Gutiérrez et al., 2008), and South America (Elmoor-Loureiro et al., 2023; Fuentes-Reinés et al., 2022). Thus, molecular data suggest that *C. cornuta* represents a complex of cryptic species that cannot be differentiated using traditional techniques, such as the morphology of parthenogenetic females. Therefore, alternative methods are required as proxies for species delineation.

A widely accepted method among taxonomists is the use of thoracic limbs. This approach was introduced in taxonomic studies only in the 1960s—nearly 100 years after the first monographs describing cladocerans were published (Smirnov, 1966). The morphology of these structures holds high taxonomic value for distinguishing species within various families, particularly the Chydoridae family (Smirnov, 1996; Kotov, 2013). Regarding the genus *Ceriodaphnia*, recent studies have demonstrated the taxonomic utility of thoracic limbs for species differentiation (Sharma, 2014; Alonso et al., 2021; Garibian et al., 2023). However, this approach has been underutilized for identifying species complexes such as *C. cornuta*, representing a gap that needs further investigation.

Three aspects of the *Ceriodaphnia cornuta* - complex taxonomy remain incomplete: the study of the limbs of parthenogenetic females, the study of males, and the knowledge of ephippial females, which is based on Berner's work. For many cladoceran groups, the presence of males is crucial for distinguishing species when females lack consistent morphological differences (Kotov, 2015). Male morphology has been successfully used to support the

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