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MOLECULAR PHYLOGENETIC REASSESSMENT OF EASTERN  
ATLANTIC *CALLINECTES* (BRACHYURA, PORTUNIDAE)

BY

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ABSTRACT

Several species from the genus *Callinectes* are economically important, yet the number of species and their geographic distributions remain unclear. Recently, one of the American species, *Callinectes larvatus*, was synonymized with one of the African species, *C. marginatus*, making *C. marginatus* the only species of the genus regarded to be ampho-Atlantic in distribution. However, there was no formal taxonomic study to support this taxonomic change, which was in contradiction to earlier studies that had provided morphological characters to support the taxonomic separation of the eastern Atlantic species from those of western Atlantic distribution. *Callinectes maracaiboensis* has also been questionably resurrected. Here we present a molecular based analysis for all species of *Callinectes*, using the two common mitochondrial genes 16S and 12S. Our molecular data support the presence of three eastern Atlantic, three eastern Pacific, and nine western Atlantic species. Historically, it appears that the separation of Africa and South America with the opening of the Atlantic basin gave rise to sister species distributed on opposite sides of the Atlantic Ocean. In a second isolation event, the emergence of the Panamanian isthmus resulted in pairs of geminate species distributed in eastern Pacific and western Atlantic waters.

Key words. — Swimming crabs, ampho-Atlantic distribution, mitochondrial genes, taxonomy

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## RESUMEN

Varias especies del género *Callinectes* son económicamente importantes, pero el número de especies y su distribución geográfica aún no están claros. Recientemente, una de las especies americanas, *Callinectes larvatus*, fue sinonimizada con una de las especies africanas *C. marginatus*, lo que convierte a *C. marginatus* en la única especie de *Callinectes* con distribución anfiatlántica. Sin embargo, no hubo un estudio taxonómico formal respaldando este cambio taxonómico lo que estaba en contradicción con estudios anteriores que habían proporcionado caracteres morfológicos que apoyaban la validez de las especies distribuidas en el Atlántico oriental como diferentes a las del Atlántico occidental. *Callinectes maracaiboensis* también ha sido cuestionablemente resucitado. Aquí presentamos un análisis molecular de todas las especies de *Callinectes*, utilizando los dos genes mitocondriales comunes 16S y 12S. Nuestros datos moleculares respaldan la presencia de tres especies en el Atlántico oriental, tres en el Pacífico oriental y nueve especies en el Atlántico occidental. Históricamente, parece que fue la separación de África y América del Sur, con la apertura de la cuenca atlántica, la que dio lugar a especies hermanas distribuidas en lados opuestos del Océano Atlántico. En un segundo evento de aislamiento, el surgimiento del istmo panameño indujo la formación de pares de especies geminadas distribuidas en el Pacífico oriental y el Atlántico occidental.

Palabras clave. — Jaibas, distribución anfi-atlántica, genes mitocondriales, taxonomía

## INTRODUCTION

Species of the genus *Callinectes* Stimpson, 1860 are commonly distributed along coastal waters of the Neotropics and subtropics both in the Atlantic and Pacific coasts of America and western Africa (Williams, 1974). Some of these species constitute key resources in local fisheries along their distribution. For instance, in the United States *C. sapidus* Rathbun, 1896, is the most captured species of *Callinectes* along the Gulf of Mexico and eastern U.S. coasts (Sharov et al., 2003). On the Mexican Pacific coast, both *C. bellicosus* Stimpson, 1859 and *C. arcuatus* Ordway, 1863 support local fisheries in the states of Sonora and Sinaloa (Rodríguez-Domínguez et al., 2014). On Mexican coasts of the Gulf of Mexico, *C. sapidus* and *C. rathbunae* Contreras, 1930 are fished in the states of Veracruz, Tabasco, and Yucatan (Morales-Azpeitia et al., 2021). In South America, both *C. sapidus* and *C. bocourti* A. Milne-Edwards, 1879 have been reported as economically important in the region of Falcón, Venezuela, although their fisheries are mostly artisanal (Carmona-Suárez & Conde, 2002). Given the economic importance of this group, readily available information about its taxonomy remains confusing. A simple search of *Callinectes* on the World Wide Web indicates 15 species worldwide in the World Register of Marine Species (DecaNet, 2024) and the same number of species, with some under different species names, in the Integrated Taxonomic Information System ITIS (2024).

Ng et al. (2008) presented an annotated checklist of the extant brachyuran crabs of the world. They included almost 6800 brachyuran valid names from

around the world. That list was the result of a great effort but presented some inconsistencies, at least among the portunid crabs. For example, the list included sixteen species of *Callinectes* Stimpson, 1860. However, among these 16 species was *C. maracaiboensis* Taissoun, 1962, which had been shown to be a synonym of *C. bocourti* A. Milne-Edwards, 1879 by Robles et al. (2007) based on a molecular phylogenetic analysis of all the American species of *Callinectes*. Along with *C. maracaiboensis*, Ng et al. (2008) listed eight more species of western Atlantic distribution (*C. affinis* Fausto, 1980, *C. bocourti*, *C. danae* Smith, 1869, *C. exasperatus* (Gerstaecker, 1856), *C. ornatus* Ordway, 1863, *C. rathbunae*, *C. sapidus*, and *C. similis* Williams, 1966); three species of eastern Atlantic distribution (*C. amnicola* (De Rochebrune, 1883), *C. gladiator* Benedict, 1893, *C. pallidus* (De Rochebrune, 1883); and one additional species of ampho-Atlantic distribution, namely *C. marginatus* (A. Milne-Edwards, 1861). The other three species listed by Ng et al. (2008) are of eastern Pacific distribution (*C. arcuatus*, *C. bellicosus*, and *C. toxotes* Ordway, 1863).

Other studies have followed in part the list of valid species proposed by Ng et al. (2008), even if the authors did not present new or original data to support resurrection of *C. maracaiboensis* and *C. gladiator* or synonymizing *C. larvatus* and *C. marginatus*. For example, *C. marginatus* was listed as one of the seven species reported from northern Brazil (Coelho et al., 2008). The same species was cited as a Floridian species in a molecular phylogenetic analysis of swimming crabs by Evans (2018) and was listed as a swimming crab distributed at the Sistema Arrecifal Lobos-Tuxpam and Arrecifal-Veracruzano (Hermoso-Salazar et al., 2019).

More recently, Koch et al. (2023) listed *C. larvatus* and *C. marginatus* as valid species in their review of the genera of Portuninae Rafinesque, 1815 and also included *C. gladiator* in their account, although the latter species had been synonymized long before, being considered a juvenile of *C. pallidus* by Manning & Holthuis (1981). In another recent study, Muñoz et al. (2024) provided an extensive list of crabs from the African coasts of Guinea-Bissau along with DNA barcodes for most specimens. Therein, they compared their barcode sequences of African *Callinectes* to some COI sequences already in GenBank or BOLD and their 16S sequences to those already in GenBank. In their analysis, Muñoz et al. (2024) compared their sequences to those of animals from Florida, Venezuela, and Brazil, but they did not reach a decision about whether *C. marginatus* and *C. larvatus* are different species, deferring that decision for additional study.

Our previous molecular-based study showed that all American *Callinectes* were part of a single clade (Robles et al., 2007). Also in that study, *C. maracaiboensis* was concluded to be a synonym of *C. bocourti*. The results supported the hypothesis that *Callinectes* evolved as two lineages, as previously suggested

by Norse & Fox-Norse (1979) who termed them the “*bocourti*” group and the “*danae*” group. However, our earlier study did not include all known species of *Callinectes*, with the African species *C. amnicola*, *C. marginatus* and *C. pallidus* not represented (Robles et al., 2007). Nonetheless, on the basis of morphological and physiological characters we proposed that *C. amnicola* would probably cluster with other members of the “*bocourti*” group and that both *C. pallidus* and *C. marginatus* were likely to be included within the “*danae*” group (Robles et al., 2007).

Herein, we present a molecular-based phylogenetic analysis, based on two mitochondrial genes, including all the American and African species of *Callinectes* in order to clarify the evolutionary history of all currently known species within this group. At the same time, we examine genetic distances among selected species pairs of relationships to either confirm or refute the presence of amphi-Atlantic species within the genus *Callinectes*.

#### MATERIAL AND METHODS

Sequences included in this study were taken primarily from Robles et al. (2007), augmented by new sequences for three eastern Atlantic specimens. The latter included sequences of *C. marginatus* from a preserved specimen originating from Senegal (small lagoon near mouth of Somone River, about 60 km southeast of Dakar), RMNH.CRUS.D.41170, Naturalis Biodiversity Center (ex Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands. Additionally, collections of fresh specimens by one of us (CDS) allowed the inclusion of sequences from *C. amnicola* and *C. pallidus* obtained from two specimens freshly collected in 2001 from Ghana and deposited at the University of Louisiana Lafayette Collection (ULLZ, now transferred to the Smithsonian Institution, Museum of Natural History, USNM, Washington, D.C.). These were *C. amnicola* from Ghana (Ada Foah, Voltu Estuary, 15 July 2001), ULLZ 4650 = USNM 1535070; and *C. pallidus* from Ghana (Cape Coast, from coastal fishermen, 4 July, 2001), ULLZ 4649 = USNM 1538108. Since the University of Louisiana at Lafayette (ULLZ) collections are now cross-listed within databases of the National Museum of Natural History (USNM), Smithsonian Institution (Washington, DC, U.S.A.), both catalogue numbers are sometimes shown.

Sequences of the two African specimens from Ghana were obtained at the University of Louisiana at Lafayette. Sequences of *C. marginatus* from Senegal were obtained at the Department of Zoology & Evolution, University of Regensburg. All DNA extractions, PCR amplifications, PCR purifications, and DNA sequencing protocols followed Robles et al. (2007); new sequences have been submitted to GenBank (table I).

TABLE I

List of species included in this study followed by the country code where the specimen was collected

Species with country code used in fig. 1	Collection location	Catalogue number	GenBank accession numbers 16S/12S
<i>Callinectes affinis</i> BRA	Brazil: Rio Grande do Norte	ULLZ 5170	DQ407677/DQ407701
<i>Callinectes amnicola</i> GHA	Ghana: Voltu Estuary	ULLZ 4650	<b>PP911384/PP911389</b>
<i>Callinectes arcuatus</i> NIC	Nicaragua: Estero de Padre Ramos	ULLZ 4370	DQ407668/DQ407687
<i>Callinectes bellicosus</i> MEX	México: Baja California	CNCR 5021	DQ407671/DQ407690
<i>Callinectes bocourti</i> VEN	Venezuela: Falcón	IVIC-LEGP-C-30 = ULLZ 4180	AJ298170/DQ407695
<i>Callinectes danae</i> BRA	Brazil: São Paulo	ULLZ 4179	DQ407680/DQ407706
<i>Callinectes exasperatus</i> VEN	Venezuela: Isla Margarita	ULLZ 4366	DQ407682/DQ407708
<i>Callinectes larvatus</i> VEN	Venezuela: Falcón: Adícora	ULLZ 5171	DQ407678/DQ407702
<i>Callinectes marginatus</i> SEN	Senegal: Somone River	RMNH 41170	<b>PP911386/PP911391</b>
<i>Callinectes ornatus</i> VEN	Venezuela: Falcón	ULLZ 5185	DQ407679/DQ407704
<i>Callinectes pallidus</i> GHA	Ghana: Cape Coast	ULLZ 4649	<b>PP911385/PP911390</b>
<i>Callinectes rathbunae</i> MEX	México: Tabasco	CNCR 17056	DQ407673/DQ407693
<i>Callinectes sapidus</i> U.S.A.	U.S.A.: Louisiana	ULLZ 3895	AJ130813/DQ407691
<i>Callinectes similis</i> U.S.A.	U.S.A.: Louisiana	ULLZ 4371	DQ407672/DQ407692
<i>Callinectes toxotes</i> HON	Honduras: Golfo de Fonseca	ULLZ 5172	DQ407681/DQ407707
<i>Arenaeus cribrarius</i> VEN	Venezuela: Falcón	ULLZ 5173	DQ407667/DQ407686
<i>Charybdis helleri</i> VEN	Venezuela: Falcón	ULLZ 4631	DQ407666/DQ407684

Accession numbers in bold indicate specimens for which 16S mtDNA and 12S mtDNA were sequenced for this study. ULLZ, University of Louisiana, Lafayette Zoological Collection; CNCR, Colección Nacional de Crustáceos, Instituto de Biología, UNAM; IVIC-LEGP, Instituto Venezolano de Investigaciones Científicas-Laboratorio de Ecología y Genética de Poblaciones; RMNH-L, Rijksmuseum van Natuurlijke Historie, Leiden.

Consensus of complementary new sequences from every specimen were obtained with the Sequencher software program (ver. 4.7; Genecodes, Ann Arbor, MI, U.S.A.). These consensus sequences were combined into the original alignments of Robles et al. (2007), retrieved from GenBank as a Pop Set, using BioEdit v.7.08.0 (Hall, 1999). There was no need of removing saturated parts of the alignments.

It should be noted that our objective was to evaluate the validity of the African species that were missing in our 2007 analysis, and that we thus here included only one specimen of every species of *Callinectes* included in our previous analysis (see table I). We did not include *C. maracaiboensis* because previous results have already unambiguously shown that *C. maracaiboensis* is a synonym of *C. bocourti*

(Schubart et al., 2001; Robles et al., 2007). Since we have no additional data to suggest *C. affinis* being a synonym of *C. bocourti*, as already discussed by Robles et al. (2007), we herein included sequences of both species, *C. bocourti* and *C. affinis*. We also included the same specimens of the portunid crabs as in our previous study, *Arenaeus cribrarius* (Lamarck, 1818) and *Charybdis helleri* (A. Milne-Edwards, 1867), to serve as outgroups for rooting of the phylogenetic analyses.

We performed a single Maximum likelihood phylogenetic analysis (ML) with the combined data on the concatenated alignment of the two databases (16S and 12S) using RAxML-HPC BlackBox (8.2.12) as implemented on CIPRES Science Gateway (Miller et al., 2010). All model parameters were estimated by RAxML (Stamatakis, 2014) using the GTR (General Time Reversible) model of nucleotide substitution. Confidence values for the obtained ML trees were obtained by selecting the option to automatically determine the number of bootstraps to be run in RAxML. Thus, 150 bootstrap pseudoreplicates were run, and values >50% are shown on the resulting tree.

We also constructed a genetic distance matrix based on the concatenated alignment of the 16S and 12S genes. The matrix was calculated under the Kimura two parameter (K2P) model (Kimura, 1980) as implemented in MEGA v.11 (Tamura et al., 2021). The matrix is used as reference, but it is not shown.

## RESULTS

### Phylogenetic results

Our analysis incorporated 15 individuals representing 15 species of *Callinectes*; this number included the newly obtained sequences of the African species *C. amnicola* from Ghana, *C. marginatus* from Senegal, and *C. pallidus* from Ghana. Although our analysis is based in part on results previously published by Robles et al. (2007), we herein used only one individual per species for construction of a molecular phylogenetic tree (fig. 1) to avoid redundant representation. Our alignment contained a total of 996 bp, 434 from the 12S and 562 from the 16S genes, excluding primer regions. By using the same concatenated database, we assumed that both genes followed the same evolutionary history, and all phylogenetic analyses were performed with the combined dataset.

Our phylogenetic analysis supports the hypothesis that the genus *Callinectes* is monophyletic, placing all species within a single clade. The 15 species were divided into two major lineages named the *bocourti*-group and the *danae*-groups (after Norse & Fox-Norse, 1979). Within the *bocourti*-group, the African species *C. amnicola* was found to be sister to the clade composed of *C. bocourti*/*C. affinis*,

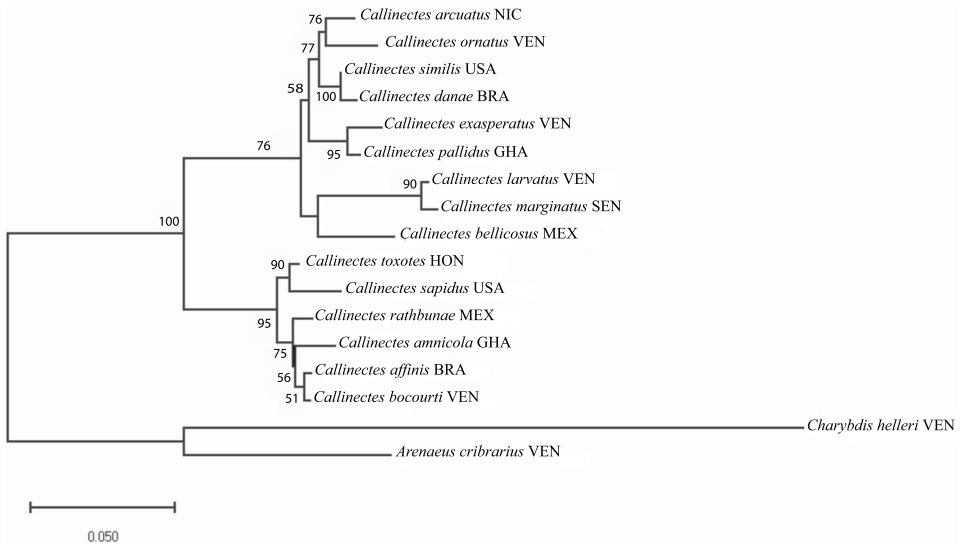


Fig. 1. Phylogeny for 15 species of *Callinectes* inferred from Maximum likelihood analysis of 964 bp (551 bp of 16S and 413 bp of 12S rRNA) of mitochondrial DNA. Bootstrap values shown only if value equal to or higher than 50%. Country codes follow table I.

while within the *danae*-group *C. pallidus* was found to be the sister species of the American *C. exasperatus*, and *C. marginatus* was found to be the sister species of *C. larvatus*.

## DISCUSSION

A previous molecular-based analysis including only the American species of *Callinectes* showed the existence of two major evolutionary groups (Robles et al., 2007). Adopting terms from an earlier study by Norse & Fox-Norse (1979), these are called the “bocourti” and the “danae” groups. By including the African species of *Callinectes*, *C. amnicola*, *C. marginatus* and *C. pallidus* in the present study, we were able to test our previous hypothesis suggesting that *C. amnicola* would belong to the “bocourti” group while both *C. marginatus* and *C. pallidus* would belong to the “danae” group (see Robles et al., 2007: table 3) based on morphology and physiology provided by previous studies (Williams, 1974; see Manning & Holthuis, 1981). Indeed, the “bocourti” group is composed of the six valid species *C. affinis*, *C. amnicola*, *C. bocourti*, *C. rathbunae*, *C. sapidus*, and *C. toxotes* (fig. 1), while the “danae” group comprises nine valid species *C. arcuatus*, *C. bellicosus*, *C. danae*, *C. exasperatus*, *C. larvatus*, *C. marginatus*, *C. ornatus*, *C. pallidus* and *C. similis*.

Species-level separations among decapods are not necessarily proportional to the degree of DNA sequence divergence. However, within the genus *Callinectes*,

it is clear that other sister species like *C. similis* and *C. danae*, which exhibit only 0.00527 genetic distance, or another couple of sister species like *C. bocourti* and *C. affinis*, which exhibit only 0.00438 genetic distance, are considered different species without any doubt. Thus, a genetic distance of only 0.00742 between the sister species *C. larvatus* and *C. marginatus* is well within the range recognized to separate sister species within the genus *Callinectes*.

We find no need to further discuss the validity of the morphological characters proposed by Manning & Holthuis (1981: 93-94), which in our opinion support separations for almost all mature specimens. Instead, our phylogenetic analysis is undertaken to show that *C. marginatus* and *C. larvatus* are sister species and that comparison of genetic distances to others species pairs within the genus supports our conclusion that they are valid separate species.

As previously discussed in Robles et al. (2007), separation of the eastern Pacific and Atlantic by repeated elevation events of the Panamanian Isthmus isolated certain populations of species of *Callinectes* and was followed by speciation of the so-called geminated species, *C. arcuatus* and *C. ornatus*. Separation of the eastern from western Atlantic species of the genus has been more difficult to prove since there is no clear barrier, as is the case with the Panamanian Isthmus. Instead, separation was likely driven by a steadily widening ocean that could potentially be crossed only by dispersal of larval stages, by rafting individuals or by using islands as generational stepping stones to maintain genetic flow among different populations across the Atlantic (Williams, 1974). The detailed morphological analysis of Manning & Holthuis (1981) provided the first indication that African and American sister species are the result of isolated populations produced by separation of the South American and African landmasses. Our genetic results now support this pattern unambiguously.

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