

Original Article

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Author for correspondence:

Andrés Arias, E-mail: ariasandres@uniovi.es

First record of the rare deep-sea polychaete *Rhamphobrachium* (*Rhamphobrachium*) *agassizii* (Annelida: Onuphidae) in European waters

Andrés Arias¹  and Hannelore Paxton^{2,3}

¹Departamento de Biología de Organismos y Sistemas (Zoología), Universidad de Oviedo, Oviedo, 33071, Spain;

²Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia and ³Australian Museum Research Institute, Australian Museum, 1 William Street, Sydney, NSW 2010, Australia

Abstract

Rhamphobrachium (*Rhamphobrachium*) *agassizii* is reported from the Cantabrian Sea, Spain, from depths of 925–1207 m. This is its first record off the Iberian Peninsula and in European waters, representing its northernmost distribution in the North Atlantic Ocean to date. Previous reports of *R. (R.) agassizii* from the eastern and western North Atlantic demonstrate its apparent ampho-Atlantic distribution, which appears consistent with the distribution of the main Atlantic currents. It is a typical deep-water species with its deepest record at 2165 m from the Azores archipelago. The specimens were collected singly at two stations, attesting to the rarity of the species in contrast to its congener *R. (Spinigerium) brevibrachiatum* which was the most dominant polychaete species in a previous study.

Introduction

Onuphidae is one of the dominant benthic polychaete families in soft-sediment communities of the Atlantic Ocean (Gillet & Dauvin, 2000; Paxton & Gillet, 2004; Louzao *et al.*, 2010). However, current knowledge of deep-sea Atlantic onuphids and their distribution is still far from comprehensive and has been the scope of several recent publications, involving the description of new species, formal re-descriptions of conflicting taxa and new species records (Arias & Paxton, 2014; 2015, 2016; Paxton & Arias, 2014, 2016; Arias *et al.*, 2017). As part of an extensive project off the Iberian Peninsula and its vicinity, aimed to catalogue the Iberian marine biodiversity, a total of 36 species of Onuphidae in 10 genera were identified. Among them, two different species belonging to the genus *Rhamphobrachium* Ehlers, 1887 were found in the deep-sea samples from the Avilés submarine Canyon Systems and El Cachucho seamount (=Le Danois Bank), Cantabrian Sea, Bay of Biscay. One of them was *R. (Spinigerium) brevibrachiatum* (Ehlers, 1875), a species that has been repeatedly reported from the Iberian continental slope and NE Atlantic deep waters (Fauvel, 1923; Amoureux, 1972; Louzao *et al.*, 2010; Paxton & Arias, 2014), whilst the other belonged to a different sub-genus, *R. (Rhamphobrachium)*, and was consistent with the diagnosis of *R. (R.) agassizii* Ehlers, 1887. This species constitutes the first record of the taxon from the Iberian Peninsula and the European Atlantic waters. Here, we present a detailed description and illustration of the species, including brief notes on its ecology and distribution at the new locality.

Materials and methods

We have re-examined the polychaete material collected during the COCACE (Oceanographic Cruise of the Central Cantabrian Sea), Fauna Ibérica and BIOCANT oceanographic campaigns. The COCACE cruise took place from April 1987 to February 1988; the benthic fauna was collected with an anchor dredge and/or a Hessler and Sanders epibenthic dredge at 42 sampling stations located in the continental shelf and the upper slope (between 31 and 1400 m depth) of the central Cantabrian Sea, Bay of Biscay (Louzao *et al.*, 2010; Fernández-Rodríguez *et al.*, 2019). The campaign Fauna Ibérica II was conducted in June 1991 on the Atlantic coast off Galicia and the Cantabrian Sea continental shelf and slope (from 0 to 1025 m depth); benthic samples were taken at 92 sampling stations by an anchor dredge and/or an epibenthic sledge, depending on substrate characteristics and meteorological conditions. The BIOCANT cruise was carried out from March 2012 to May 2013, at 11 sampling stations from a variety of substrates of the slope and abyssal areas (between 1500 and 4700 m depth) of the Avilés Canyons System (ACS), Cantabrian Sea (Romero-Romero *et al.*, 2016). In the 'Material examined' section of the species description, all stations (localities) with detailed collection data and additional information are fully listed.

The specimens were anaesthetized in 7% MgCl₂, fixed in 10% neutral buffered formalin, and later transferred to 70% ethanol. Specimens were examined under a dissecting stereomicroscope. Temporary glycerol slides of parapodia were prepared to examine parapodial structures, chaetal morphology and its distribution, and examined under a compound light



microscope. Photomicrographs were taken with a Spot Flex Digital Camera System mounted on a Leica MZ 16 stereo dissection microscope.

The width of the 10th chaetiger (without parapodia) was taken as a measure of the specimen size. Chaetal and prostomial appendages terminology follows Paxton (1986a, 1998 respectively).

The specimens examined in this study are deposited in the Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), the Museum of Comparative Zoology, Cambridge, MA, USA (MCZ) and the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM).

Results and discussion

Systematics

Family ONUPHIDAE Kinberg, 1865

Subfamily ONUPHINAE Kinberg, 1865

Genus *Rhamphobrachium* Ehlers, 1887

Rhamphobrachium Ehlers, 1887, p. 70. – Paxton, 1986a, p. 44. – Paxton & Budaeva, 2015, p. 622.

Paranorthia Moore, 1903, p. 448.

Type species: *Rhamphobrachium agassizii* Ehlers, 1887, p. 70, by subsequent designation of Hartman, 1944, p. 47. Gender: neuter.

Diagnosis

Prostomium with short palps and antennae, ceratophores with 2–5 rings; frontal lips and peristomial cirri usually present (except in subgenus *Minibrachium*); anterior two or three pairs of parapodia prolonged, with three distally recurved hooks each; hooks with two rows of moveable spines, chaetal sacs extending to chaetiger 20–60; branchiae present or absent.

Subgenus *Rhamphobrachium* Paxton, 1986

Diagnosis

Peristomial cirri inserted close together; all limbate chaetae simple; subacicular hooks reaching a maximum number of 3–6 per parapodium on chaetigers 15–30; maxilla VI present.

Rhamphobrachium (*Rhamphobrachium*) *agassizii* Ehlers, 1887 (Figures 1–3)

Rhamphobrachium agassizii Ehlers, 1887, p. 70, pl. 17 figs 1–5, pl. 18 figs 1–9 (in part) (Carysfort Reef, Florida, USA, 642 m). – Fauvel, 1914, p. 126 (Azores and Morocco); Treadwell, 1939, p. 258, fig. 76 (Puerto Rico); [?] Intes & Le Loeuff, 1975, p. 312 (Ivory Coast); Paxton, 1986a, p. 44, fig. 27 (definition of genus); Paxton, 1986b, pp. 85–86.

Material examined

1 specimen (MNCN 16.01/14705), Spain, Cantabrian Sea, COCACE station: Y7A (I4a) 43°55.07'N 5°54.30'W, 1207 m, mud substrate, 4 July 1987; 1 specimen (MNCN 16.01/18729), Spain, Cantabrian Sea, Fauna Ibérica station: F-II (159 A) 43°49.10'–43°49.33'N, 04°52.74'–04°53.47'W, 925–1025 m, 25 June 1991.

Comparative material examined

LECTOTYPE (MCZ 789), USA, Florida: Blake, off Carysfort Reef, 642 m, 23 March 1869; 3 specimens (USNM 20070), Puerto Rico, Johnson-Smithsonian Expedition station 67–354E, 18°32'18"N 65°46'12"W, 549–599 m, 23 February 1933.

Diagnosis

Early unmodified parapodia with well-developed triangular postchaetal lobes; branchiae from chaetiger 15–17. Recurved hooks weakly pseudocompound.

Description

Medium-sized species, up to 90 mm length (for about 90 chaetigers); maximal width of 6 mm through chaetiger 10. Alcohol-stored specimens overall iridescent pinkish coloured with brown pigment on base of dorsal cirri and branchial filaments (Figure 1A–D). Prostomium anteriorly rounded; paired ovoid frontal lips almost twice as long as wide; lower lips with distinct anterior median section. Palps reaching chaetiger 1, lateral antennae on median part of prostomium, reaching chaetiger 2–4, median antenna reaching chaetiger 1–3; ceratophores of palps and antennae with 2–3 proximal rings and longer distal ring (Figure 1A, B). No prostomial eyes visible. Nuchal grooves with small middorsal separation. Peristomium a third longer than first chaetiger (Figure 1B), peristomial cirri subulate, inserted distally on peristomium, very long, to near distal end of frontal palps; inserted close together, lying between median and lateral antennae (Figure 1B, D).

Anterior three pairs of parapodia modified, greatly enlarged, extending beyond anterior margin of prostomium (Figure 1B–D). Each of parapodia with three short papilliform lobes and one longer subulate postchaetal lobe. On chaetiger 4 low prechaetal and triangular postchaetal lobes, latter decreasing in size and absent from chaetiger 10. Dorsal cirri digitiform, long on anterior 3 chaetigers, shorter on chaetiger 4 and 5, remaining constant from chaetiger 6 onwards (Figure 1C, D). Ventral cirri subulate on first 3 chaetigers, fourth transitional, replaced by ventral glandular pads from chaetiger 5 (Figure 1D). Single or bifid branchiae from chaetiger 15–17 (Figures 1E & 2C), reaching maximum of 5 filaments by chaetiger 30 (Figure 2C).

Modified parapodia with weakly pseudocompound, long, recurved hooks; chaetal sacs to chaetiger 55. Pectinate chaetae comb-shaped with 12–25 teeth and limbate chaetae from chaetiger 4; latter longest in upper position, shorter in median, and short spine-like in lower position. Three to four protruding distal ends of aciculae, brown-coloured with blunted tips (Figure 2A, B). One to three subacicular hooks per parapodium from chaetiger 14–16 (Figure 2A), maximum of three to five from chaetiger 15–16 to about chaetiger 20 (Figure 2B), two from there to end of body.

Jaws (Paxton, 1986a: fig. 27k, l) with strongly calcified mandibular shafts and slender, cutting plates distally serrated; maxillae weakly sclerotized, light brown; maxillary formula: Mx I = 1 + 1; Mx II = 8 + 8 (8–9); Mx III = 7 (6–7) + 0; Mx IV = 6 + 8 (7–9); Mx V = 1 + 1; Mx VI toothless plate. Tubes round in transverse section, with parchment-like inner layer and outer layer of mud and sand (Figure 1F); no eggs or developing embryos were found inside or attached to tubes.

Remarks

The Spanish specimens are almost complete and were both collected within their tubes (Figure 1F). The larger of the two specimens measures 89 mm in length for about 90 chaetigers and has a width of 6 mm through 10th chaetiger. The other consists of two fragments, measuring together 51 mm for about 60 chaetigers with a width of 3.5 mm. In general, the studied specimens agree well with the definition of the species given by Paxton (1986a, 1986b) except for some details, i.e. the early branchiae were reported as single filaments starting on chaetiger 16–17, while in our specimens the branchiae appear on chaetiger 15 as bifid (i.e. with two filaments). Also, the subacicular hooks were reported to start as one to two per parapodium, whilst in our specimens they appear from two to three in number.

Rhamphobrachium (*R.*) *agassizii* can be easily distinguished from the other European member of the genus, *R.* (*S.*) *brevibrachiatum*, by the absence of pseudocompound to compound lower limbate chaetae (=spinigers), that are present from chaetiger

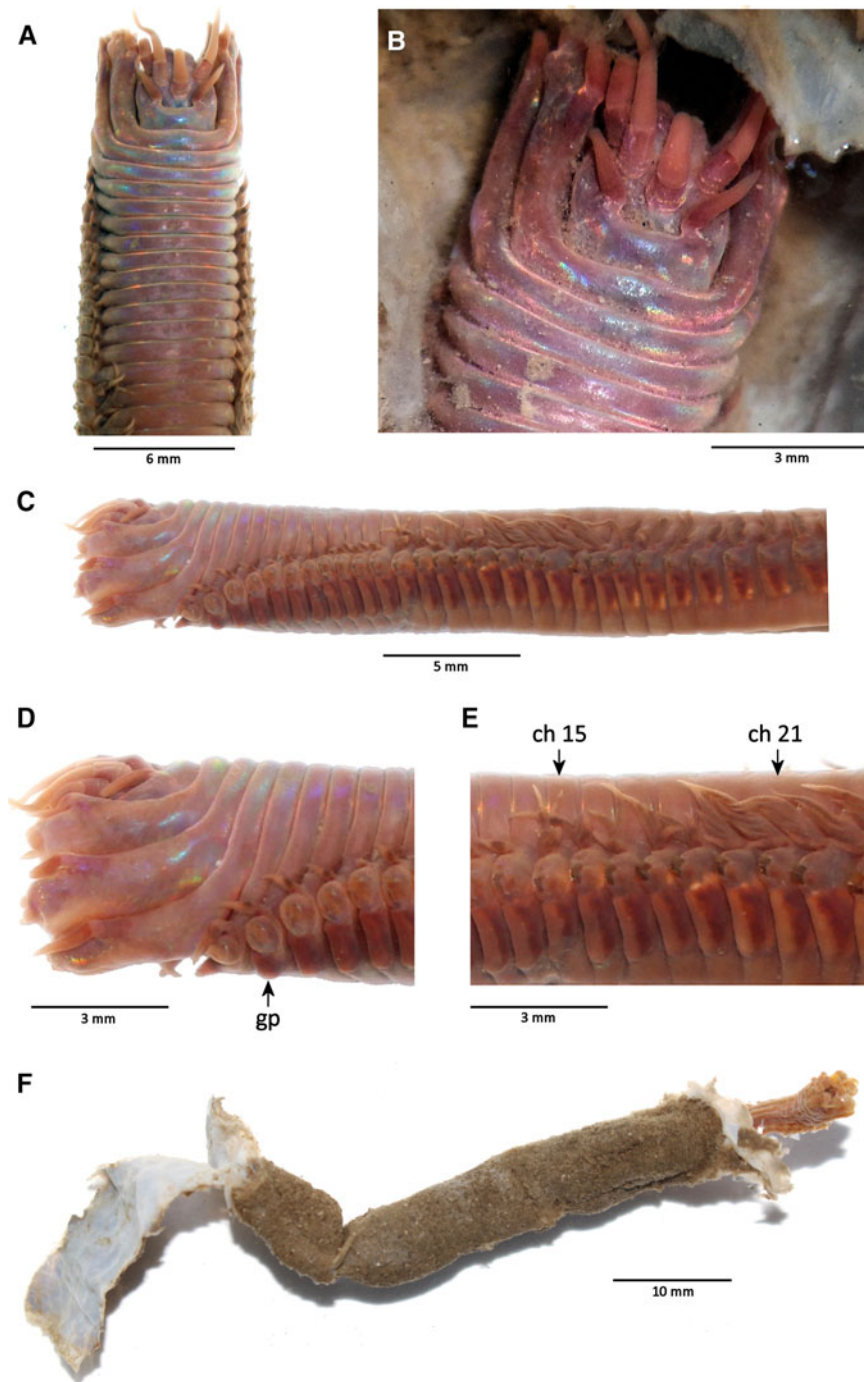


Fig. 1. Photographs of *Rhamphobrachium* (*Rhamphobrachium*) *agassizii*: (A) anterior end, dorsal view; (B) detailed view of prostomium, peristomium and modified parapodia, dorsal view; (C) anterior end, lateral view; (D) detailed view of prostomium, peristomium and modified parapodia, lateral view; (E) median parapodia, lateral view; (F) tube. ch: chaetiger; gp: glandular pad.

4 in the latter; by the more posterior origin of branchiae, from chaetiger 15–17 in *R. (R.) agassizii* while in *R. (S.) brevibrachiatum* they first appear from chaetiger 11–13. Furthermore, their tubes are strikingly different; *R. (R.) agassizii* builds its tubes with scarcely any ornamentation, consisting mostly of silt and fine sand (Figure 1F), while *R. (S.) brevibrachiatum* tubes are highly ornamented with foreign material, mainly shells, shell fragments and Foraminifera, for most of their length. Two other East Atlantic species of the *Rhamphobrachium* ‘sensu lato’ complex belong to the genus *Longibrachium* Paxton, 1986a for having the first four anterior pairs of parapodia prolonged, with more than three distally recurved hooks (with two rows of immoveable spines) each and having chaetal sacs that are extending to at least chaetiger 25. One of these is *L. falcigerum* Paxton & Gillet, 2004 from the Azores seamounts and the second has been reported as *L. atlanticum* (Day, 1973) by Cantone *et al.* (1997) from shallow

waters of the Tyrrhenian Sea (central Mediterranean Sea). We agree with Langeneck *et al.* (2020) that the latter record differs in various salient features from *L. atlanticum* and, rather than being a non-indigenous species, probably represents an undescribed native species.

Distribution, habitat and ecology

Apparently, *R. (R.) agassizii* displays an amphi-Atlantic distribution pattern (i.e. species occurring on both eastern and western basins of the Atlantic Ocean) (Figure 3A). The species has been recorded from Florida (off Carysfort Reef: type locality) and Puerto Rico (USA) in the western North Atlantic and from the Azores and Cape Verde archipelagos, Morocco and Ivory Coast in the eastern North Atlantic (Paxton, 1986a, 1986b). This is the first report of *R. (R.) agassizii* off the Iberian Peninsula and also in European waters, constituting its northernmost

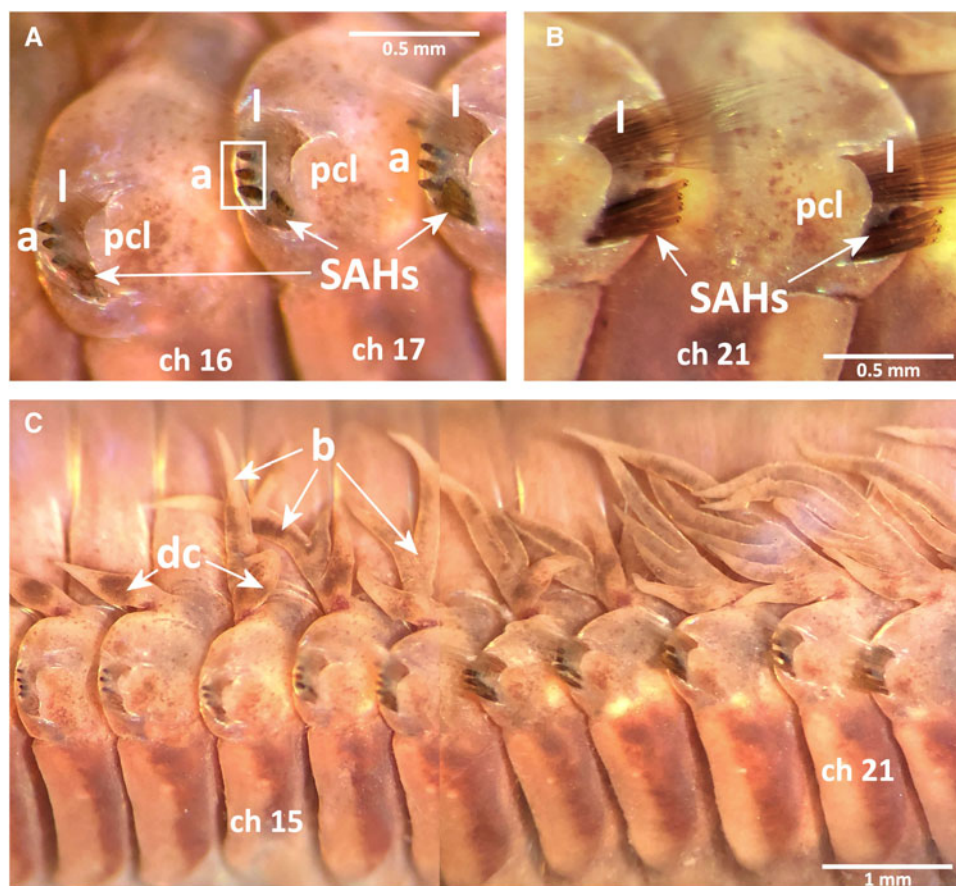


Fig. 2. Micrographs of *Rhamphobranchium (Rhamphobranchium) agassizii*: (A) parapodia from chaetiger 16 and 17, posterolateral view; (B) parapodia from chaetiger 20 and 21, posterolateral view; (C) median parapodia, lateral view. a: aciculae; b: branchiae; ch: chaetiger; dc: dorsal cirrus; l: limbate chaetae; pcl: postchaetal lobe; SAHs: subacicular hooks.

distribution in the eastern North Atlantic to date (Figure 3A). However, Ariño (1987) confusingly included this species in his bibliographic checklist of Iberian polychaetes, because he also included the Azores fauna in his paper, presumably due to the allegiance of this archipelago to Portugal. He based this record on the work of Fauvel (1914), in which *R. (R.) agassizii* is reported from the Azores archipelago (as primary record), Cape Verde and Morocco, neither from the Iberian Peninsula nor Madeira Island (locality also treated by Fauvel in his study).

Palaeontological, oceanographic and developmental data are commonly proposed to explain amphi-Atlantic distributions in marine invertebrates (Briggs, 2003; Carmona *et al.*, 2011). Trans-Atlantic passive dispersal by ocean currents plays an important role in the distribution of different species with indirect development (Briggs, 2003; Carmona *et al.*, 2011). Regarding *R. (R.) agassizii*, to date no evidence of direct development was found (i.e. lack of developing eggs or embryos inside or attached to its tube), suggesting that the species undergoes indirect development with planktonic larvae. Thereby, their presumed planktonic larvae may be capable of dispersal or rafting, serving as a vector of gene flow between distant populations and explaining the current amphi-Atlantic distribution of the species (Figure 3A). This distribution seems consistent with the distribution of the main Atlantic currents (Figure 3B).

With regards to the habitat, this is a typical deep-water species, with its deepest record of 2165 m from the Azores archipelago (Fauvel, 1914). In the Cantabrian Sea, the species was found between 925 and 1207 m depth from the muddy substrates of the boundaries of the Avilés Canyons System (ACS) and the marginal basin of ‘El Cachucho’ seamount. Both locations are highly

productive areas that harbour a great biodiversity. The ACS is a Site of Community Importance (SCI) within the Natura 2000 Network (ESZZ12003, Commission Implementing Decision (EU) 2016/2335) and host of vulnerable habitats for such organisms as deep-sea corals, sponges and deep-sea sharks (Cristobo *et al.*, 2009; Sánchez *et al.*, 2014). On the other hand, ‘El Cachucho’ seamount is the largest offshore Marine Protected Area (MPA) in Spain. It is well-known that this seamount influences the general circulation pattern of the water masses in the Cantabrian Sea and that it hosts higher values of biodiversity (including vulnerable taxa), and species richness compared with the surrounding open ocean (Sánchez *et al.*, 2008; Rodríguez-Cabello *et al.*, 2009).

To date, *R. (R.) agassizii* was only collected singly at two stations of a total of 145 analysed stations (from three different oceanographic campaigns, a great variety of substrates and a wide bathymetric range, from shallow water to 4700 m depth) in the European Atlantic, indicating a very low population density and suggesting that it is apparently a very rare species within this region. The other species records have a similar history, as they are also only based on one or very few specimens (Paxton, 1986b), confirming the rarity of this species throughout its known distribution range. This contrasts with the great abundance of its congener, *R. (S.) brevibrachiatum*, on Irving and Meteor north-eastern Atlantic seamounts, where 63 and 114 specimens were collected respectively, by the ‘Seamount 2’ expedition (Gillet & Dauvin, 2003). Furthermore, in the Meteor seamount samples, *R. (S.) brevibrachiatum* was the most dominant polychaete species found, accounting for 61% (Gillet & Dauvin, 2003).

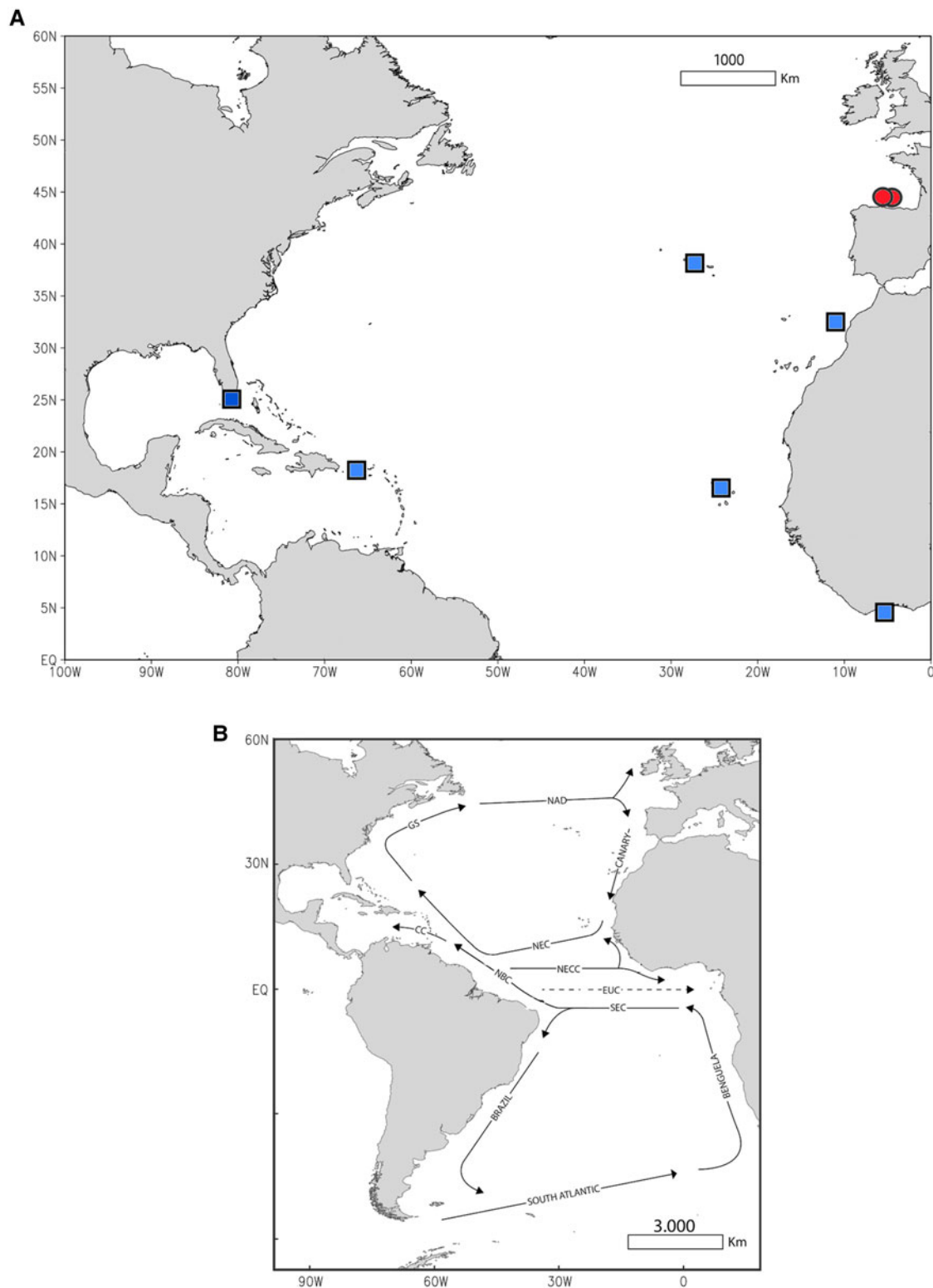


Fig. 3. Maps of the Atlantic realm: (A) global distribution of *Rhamphobranchium agassizii*, circles: localities from the present study, squares: localities from bibliography data; (B) main Atlantic oceanic currents after Sissini *et al.* (2017). CC, Caribbean Current; EUC, Equatorial Undercurrent; GS, Gulf Stream; NAD, North Atlantic Drift; NBC, North Brazil Current; NEC, North Equatorial Current; NECC, North Equatorial Countercurrent; SEC, South Equatorial Current.

Our results together with previous studies (Paxton, 1986a, 1986b) strongly suggest that *R. (R.) agassizii* has a restricted bathymetric range with narrow habitat and small population size, making it vulnerable to local extinctions. The provided revision of the biogeography of the species demonstrates its apparent amphiatlantic distribution, which appears consistent with the distribution of the main Atlantic currents.

However, our work underlines the need for molecular studies to test the conspecificity of the eastern and western populations in order to support our hypothesis of an amphiatlantic distribution or to accept the existence of a cryptic species complex.

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