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Gaps in Bioinvasion Phenomenon Studies: The First Occurrence of *Serejohyale spinidactyloides* (Schellenberg, 1939) (Crustacea: Amphipoda) in the Mediterranean Sea Raises Some Issues on the Taxonomic Identifications Within the Genus

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ABSTRACT

Reliable identification of non-indigenous species (NIS) is essential for preventing and managing biological invasions. In marine environments, this process is often hampered by limited research on small-sized taxa and a decline in taxonomic expertise. Misidentifications have been reported for decades and continue to occur in certain invertebrate groups. This study highlights this issue within an amphipod genus currently invading the Mediterranean Sea. The Atlantic benthic amphipod *Serejohyale spinidactyloides* (Schellenberg, 1939) was sampled between 2016 and 2017 at two Sicilian intertidal sites: Stagnone di Marsala Lagoon and Altavilla Milicia (southern Italy, central Mediterranean). Both sites were characterised by mytilid beds of the Lessepsian mussel *Brachidontes pharaonis* (P. Fischer, 1870). The finding represents the first record of both the genus and the species in Italian waters, and the second record of the genus in the Mediterranean since 2019 (Bizerte Lagoon, Tunisia). We provided a redescription of *S. spinidactyloides* based on the Sicilian specimens and the holotype from the Museum für Naturkunde, Berlin. Diagnostic characters of congeneric *Serejohyale* species were reassessed to improve future monitoring of NIS. Based on growth-related morphological changes, we suggest a synonymy between *Serejohyale ramalhoi* (Reid, 1939) and *Serejohyale spinidactylus* (Chevreux, 1926), and propose an updated Atlanto-Mediterranean distribution for the genus.

1 | Introduction

Two primary objectives of assessing marine biodiversity are evaluating species richness and identifying new species entering geographical areas where they had been absent before. Biodiversity is globally declining, mainly due to anthropogenic pressures such as habitat destruction, pollution, climate change and biological

invasions. Concurrently, our comprehension of the abundance and distribution of numerous marine species remains constrained to specific cases (e.g., [1, 2]). This is due in part to persistent taxonomic impediments [3–5], a lack of trained specialists, and the limited scope or resolution of many monitoring programmes, particularly in ecologically strategic areas and less accessible habitats.

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The paucity of knowledge is well documented in the extant Mediterranean literature, which continues to report new records of species even within well-studied taxa (e.g., Polychaeta; [6]) and in habitats subject to intense scrutiny, such as harbour fouling communities [1, 7, 8]. These findings suggest that taxa and habitats which have been traditionally considered to be well-known are, in fact, still underexplored or mischaracterised [9]. Consequently, even subtle shifts in fauna may go unnoticed, impeding the timely detection of biodiversity change.

Under such an assumption, detecting bioinvasion patterns remains particularly challenging [9, 10]. Carlton and Schwindt [11] emphasised the necessity of expanding both taxonomic and habitat scopes in marine biodiversity assessments. The authors advocate for the reinforcement of a biogeographical framework as a core principle in regional and global bioinvasion studies, especially in transitional or hotspot areas such as the Mediterranean Sea. The order Amphipoda serves to illustrate these complexities. Though it is a dominant component of benthic communities and widely distributed across marine ecosystems, its ecology, distributional range and functional traits remain poorly understood in many regions [12–14]. The group is under constant taxonomic revision, and its classification is regularly updated via the World Amphipoda Database [15]. Despite this, misidentification of amphipods is common due to the intra-genus morphological similarity, the paucity of molecular diagnostic characters and specific overlapping distributions, which can distort biodiversity assessments and invasion record detection.

A notable example is *Ptilohyale explorator* (Arresti, 1989) [16], which was initially listed as a non-indigenous species (NIS) in the Mediterranean Sea, causing a domino effect on successive papers and reports. Later, it was revealed to be *Parhyale plumicornis* (Heller, 1886) [17], a native and likely endemic Mediterranean species, thanks to a taxonomic clarification [18, 19]. These studies refined the species diagnosis and paved the way for the accurate recognition of a further *Ptilohyale* species as a truly non-indigenous genus in the basin, marked by a verified first record [20].

This paper presents a case study illustrating how biased taxonomic assessments can generate significant gaps in understanding bioinvasion dynamics, a key limitation also noted by Ojaveer et al. [3] and Carlton and Schwindt [11]. In this study, we undertake a thorough re-examination of the diagnosis of species within the genus *Serejohyale*. We propose a taxonomic revision involving synonymy and provide an update on the known distribution of the congeneric members.

The first Italian record of *Serejohyale spinidactyloides* (Schellenberg, 1939) [21], collected on *Brachidontes pharaonis* (P. Fischer, 1870) [22] mussel beds in Sicily, is herein reported. Sicily is the Mediterranean's largest island, bordered by the Tyrrhenian Sea to the north, the Ionian Sea to the east and the Strait of Sicily to the south. It serves as a strategic natural observatory for monitoring marine biodiversity [6, 23, 24]. A plethora of studies have emphasised its importance in detecting both neglected native taxa and invasive NIS within the Mediterranean Sea [8, 9, 25].

The genus *Serejohyale*, which was first described by Bousfield and Hendrycks [26], encompasses four species that inhabit shallow coastal environments. The following species are recognised: *Serejohyale ramalhoi* (Reid, 1939) [27], *S. spinidactyloides* [21], *S. spinidactylus* (Chevreux, 1926) [28], and *S. youngi* (Serejo,

2001) [29]. With a known pan-Atlantic distribution [29], the genus appears to be expanding into the Mediterranean Sea [30, 31], making it a relevant model for investigating the challenges of marine bioinvasion monitoring, taxonomic resolution and the ecological significance of overlooked or cryptogenic species.

2 | Materials and Methods

A study of the littoral benthos marine communities was conducted, aiming to detect rare or overlooked amphipod species. The amphipod individuals here investigated were found associated with the mytilid *Brachidontes pharaonis* (P. Fischer, 1870), a non-indigenous mussel originating from the Red Sea that has successfully colonised the Mediterranean Sea passing through the Suez Canal [2]. The mytilid aggregations were collected by hand from two different intertidal stations: in Stagnone di Marsala Lagoon (Western Sicily, Southern Tyrrhenian; 37°52' N–12°28' E), November 2016, and in Altavilla Milicia locality, close to Palermo city (Western Sicily, Southern Tyrrhenian; 38°3' N–13°33' E), January 2017.

The material examined was identified under a stereomicroscope by following the taxonomic keys [26, 29] and the comparison with the holotype. Photos were produced (Figures 1 and S1) highlighting the diagnostic characters. The body lengths, from tip of rostrum to apex of telson, were measured using ImageJ software. Selected specimens were dissected under a microscope. All appendages were drawn using a camera lucida and iconography was produced (Figures 2 and S2). The absence of sufficient quantitative data did not lead to performing statistical analyses.

The holotype of *Serejohyale* (formerly *Hyale*) *spinidactyloides* [21] was requested from the Crustacean Collection of the Museum für Naturkunde, Berlin, Germany. The type material code ZMB-25065 was loaned to the authors of the present paper and used to draw the iconography. Regrettably, following a move, the holotype was lost. The present paper reports the drawings of appendages observed from the entire specimen and the related photo (Figures S1 and S2). A further note to designate the neotype is planned.

The characters detected in the Sicilian specimens were compared with those shown in the other co-generic species, including their original descriptions and further redescrptions.

A1, first antenna (antennula); A2, second antenna (antenna); Cx 1–7, coxal plates of the first to the seventh pereopod; Ep1–Ep3, first to third epimeral plates; Gn1, first gnathopod; Gn2, second gnathopod; Lb, lower lip (labium); Lbr, upper lip (labrum); Md, mandible; Mx1, first maxilla (maxillula); Mx2, second maxilla (maxilla); Mxp, maxilliped; P3–P7, third to seventh pereopods; Pl1–Pl3, first to third pleopods; U1–U3, first to third uropods; T, telson.

3 | Results

One hundred and sixteen individuals were collected associated with the mussel *Brachidontes pharaonis* and identified as belonging to the *Serejohyale* genus thanks to the presence of two peduncular distal spines on the first uropod (Figure 1). The identification to species level was performed through the taxonomic

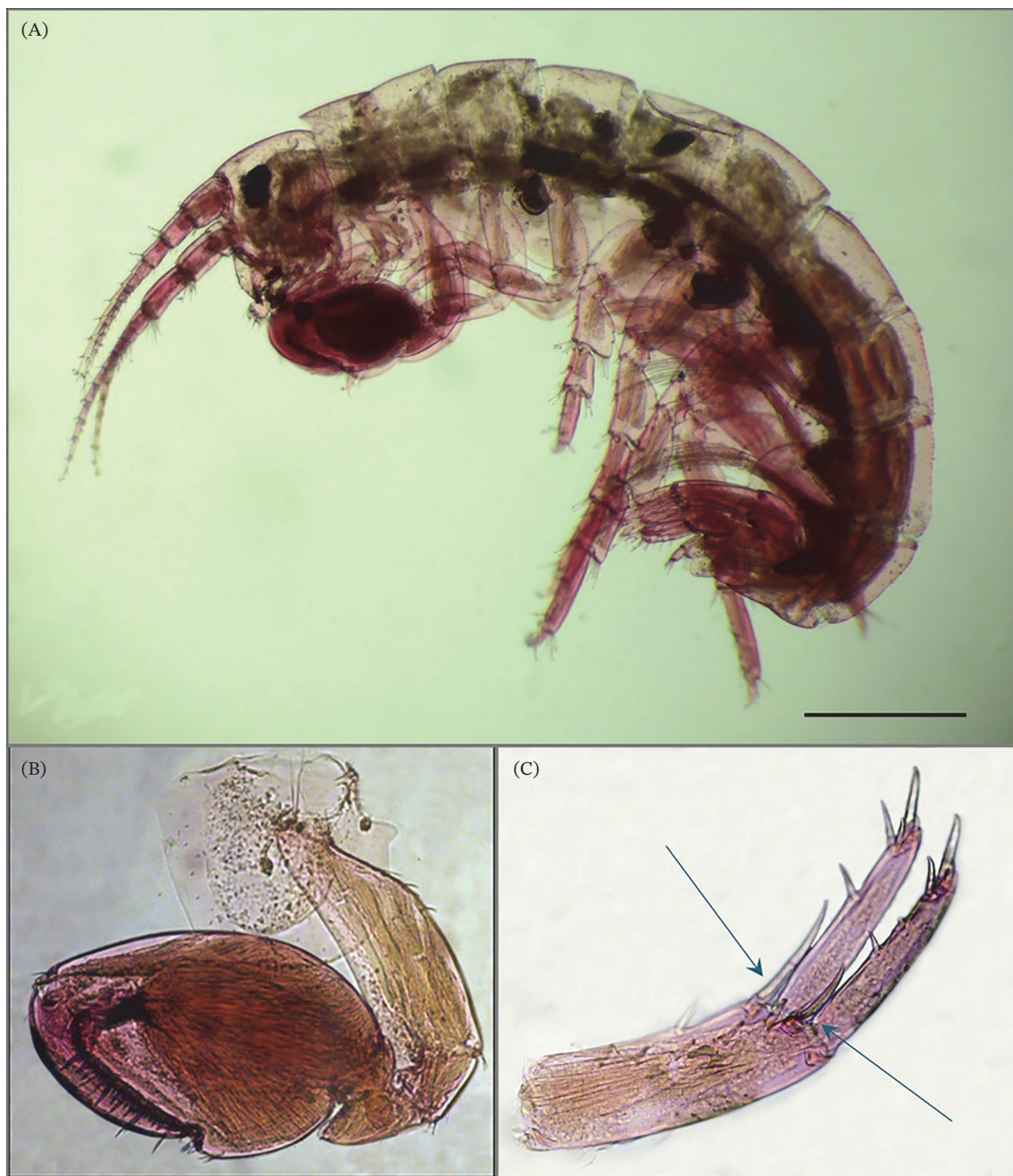


FIGURE 1 | *Serejohyale spinidactyloides*, Italian specimen. (A) Habitus, male 6.84 mm; scale bar 1 mm. (B) Focus on the second gnathopod. (C) First uropod with focus (arrows) on the distomedial and the distolateral peduncular spines, diagnostic character for the *Serejohyale* genus.

key by Bousfield and Hendrycks [26] and the descriptions in Serejo [29] and Schellenberg [21]. It corresponded to *Serejohyale spinidactyloides* [21], which was confirmed by the comparison with the museum holotype (Figures S1 and S2). The number of specimens collected in the different stations of the two localities is shown in Table S1; 73 individuals were collected at the Stagnone di Marsala Lagoon locality and 43 at the Altavilla Milicia locality. Both populations included males, females and juveniles. The length ranged between 4.73 and 6.84 mm in males, 3.73 and 6.56 mm in females and 3.34 and 4.93 mm in juveniles, with a mean value equal to 5.3 mm overall (Table S2).

3.1 | Morphological Re-Description of *Serejohyale spinidactyloides*

The following characters were observed in the Italian samples and the holotype specimen (Figures 2 and S2). Male, 7.3 mm. Head with large and oval eyes. Antenna 1 reaching about 1/5 of body length; flagellum with 6–8 articles. Antenna 2 reaching about 1/4 of body length; flagellum with 7–10 articles. Upper lip large with many short apical spines. Mandible without palp; molar process powerful; *lacinia mobilis* with a single row of six teeth. Maxilla 1 inner lobe with two feathered apical spines, outer lobe as long as the inner lobe and defined by seven spines

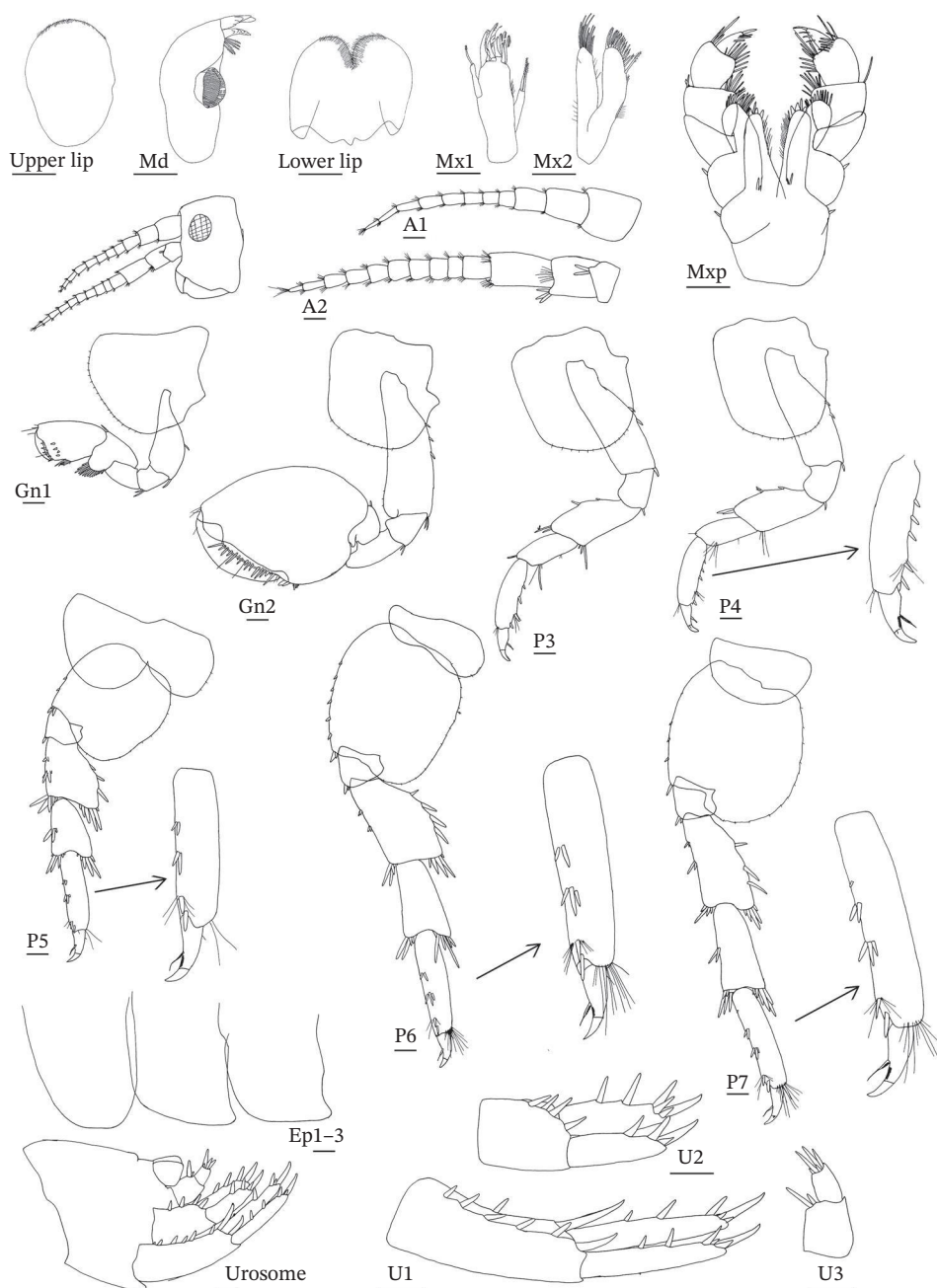


FIGURE 2 | Iconography of *Serejohyale spinidactyloides*, Sicilian specimen. See text for terminology. Scale bar 0.1 m.

strongly serrated; palp 1-articulated, constricted in the middle, with one short apical seta. Maxilla 2 inner lobe with 10 dentate spines, several simple setae and two plumose setae. Maxilliped palps robust, maxilliped inner lobe reaching the second article of the palp, defined by three apical teeth and a few setae.

Gnathopods 1–2 distinctly different in size. Gnathopod 1 basis robust; carpus large and lobate with 17 setae; propodus posterior margin with a medial group of setae, palm slightly oblique, defined by stout spine; dactylus fitting palm. Gnathopod 2 basis and ischium lobate; propodus palm straight with few spines and setae, proximally with concavity to fit dactylus, bordered by two spines; dactylus fitting palm. Coxae 1–4 with cusp, posterior processes acutely produced.

Pereopod 3 propodus posterior margin with four groups of spines sub-equal in length. Pereopod 4 propodus posterior margin with five groups of spines, sub-equal in length. In both pereopods the penultimate spine is surrounded by long setae. Pereopods 5–7 basis expanded; propodus anterior margin with two groups of spines followed by a spine surrounded by setae and one distal spine larger than the others, inserted near dactylus articulation. Pereopods 5–7 postero-medial margin lacking setae. Inner margin of dactylus of pereopods 3–7 striate, sub-terminal setae very stout and striate, resembling bifid dactylus.

Epimeral plates 2–3 with postero-ventral margin slightly sinuous. Uropod 1 peduncle robust, slightly longer than rami, with five spines on outer margin, one spine on inner margin and two

well-developed distolateral spines (stout distolateral and distomedial spines sensu [26]); rami with two marginal spines and several distal spines. Uropod 2 shorter than uropod 1; peduncle robust with four spines on outer margin and one spine on inner margin; rami with one-two marginal spines and two-three apical spines. Uropod 3 peduncle with two distal spines, one spine less than 1/5 length of the other; ramus with five distal spines. Telson deeply cleft.

Female, 5.9 mm. Gnathopod 1 palm oblique with several long setae, defined by two large spines. Gnathopod 2 larger than gnathopod 1; carpus well-developed; palm oblique with several long setae, defined by two large spines. Second oostegite triangular, third and fourth oostegites rectangular and fifth oostegite sub-triangular and smaller than other ones.

3.2 | Morphological Comparison Among Congeneric Species

According to the taxonomic literature, three diagnostic features in males were selected to compare the original descriptions and iconographies in previous papers of the four *Serejohyale* species, aiming to clarify and validate the effective distribution of the congeneric species. The characters were (1) the shape of the propodus of the second gnathopod; (2) the length of the distal spine on the sixth and seventh pereopods adjoining the dactylus; (3) the presence of a group of setae on the medial posterior margin of the propodus of the sixth and seventh pereopods. The comparison is outlined in Figure 3 and shows which species share the same characters and which identifications from the literature should be revised.

Based on the selected characters, *Serejohyale cf. youngi* recorded by Krapp-Schichkel et al. [30] in Tarifa Island in the Strait of Gibraltar, a transition area across the Atlantic and Mediterranean Sea, should be identified as *Serejohyale spinidactyloides*. The *S. cf. youngi* specimens recorded by Krapp-Schichkel et al. [30] were different from the description by Serejo [29], where *S. youngi* shows the Gn2 propodus palm straight, parallel to the anterior margin and the distal spine on the propodus of pereopods 5–7 is smaller, about half the size of the proximal spines.

Serejohyale ramalhoi [27] should be placed in synonymy with *Serejohyale spinidactylus*. The original descriptions of the two species did not show differences. Further, *S. ramalhoi* was collected only once by Reid [27] and within the geographical range of *S. spinidactylus*. *Serejohyale ramalhoi* could be considered a morphotype of *S. spinidactylus*, as a result of the common polymorphism within the family Hyalidae, correlated to the growth of specimens.

Arresti [32] described a variation of the propodus palmar margin, from younger to older specimens, demonstrating a variation of the shape of the second gnathopod along the growth, as also observed by Serejo [29]. Based on such previous observations, the second gnathopod described in *S. ramalhoi* could be an old-aged stage with a proximal protuberance of the palmar margin, a concave palm and the dactylus very long, thin at the apex and broad at the base, fitting palm (Figure 3). Considering the adult *S. ramalhoi* as an older stage of *S. spinidactylus*, the former having 12 flagellum articles in antenna 1 and 20 in antenna 2 compared to the 12 and 16–17 of the latter, a meristic character

increasing with moults, it could be another example of morphological changes during growth of *S. spinidactylus*.

4 | Discussion

A rapidly changing global climate is causing a worrying decline in fragile marine ecosystems around the world. The impact on ecosystems is becoming increasingly extreme, particularly in coastal and littoral habitats, which are highly vulnerable to increasing stressors [33]. It is imperative to study the species inhabiting shallow waters and their association with stress and changing environmental conditions, as this knowledge is of the utmost importance for effective ecosystem monitoring [33, 34]. In these exposed habitats, intertidal amphipods play a pivotal role as herbivores, detritivores and macropredators, thereby constituting a crucial component of aquatic communities [15]. These organisms have adapted in accordance with their semi-terrestrial and amphibious lifestyle [34]. This particular taxonomic group has been identified as being highly susceptible to the spread of NIS [35]. It highlights the value of amphipod monitoring as a tool for assessing the ecological impacts of bioinvasion-related stressors [36, 37].

The *Serejohyale* genus was considered endemic to the rocky surf beaches of the north and south Atlantic Ocean [26]. Recently, it has entered the Mediterranean Sea, spreading along coastal habitats. The first record of the genus in the Mediterranean basin occurred in Tunisia (Bizerte lagoon) in 2017 [31]. The authors collected *Serejohyale spinidactylus* among algae and *Cymodocea nodosa* meadows. Subsequently, *Serejohyale spinidactyloides* was collected along the Sicilian coast, on the mytilid *Brachidontes pharaonis* beds (this paper).

The biogenic habitats constructed by *B. pharaonis* are known to host alien species in high abundances [38]. The present paper highlights a further case of NIS, the Atlantic *Serejohyale spinidactyloides*, settled on such Lessepsian NIS, in two different localities, which could support an instance of ‘invasional meltdown’ (sensu [39]). Invasional meltdown is a hypothesised phenomenon in which the successful establishment of one invasive species in a new environment facilitates other NIS to invade [39]. The cases concerning amphipod species are not rare. Several marine NIS are modifying the habitat in a way that favours introduced amphipod species over the natives. The example of the invasive bryozoan *Amathia verticillata*, frequently found in association with highly abundant non-indigenous amphipods [40], underscores how specific traits of the basibiont, such as its arborescent structure and capacity for massive growth, can facilitate the establishment of non-indigenous amphipod species.

Such associations illustrate how habitat-forming invaders may act as ecological catalysts for amphipods, amplifying the success of subsequent colonisers. Understanding these dynamics is therefore crucial for predicting invasion trajectories and for developing targeted management strategies to mitigate cascading impacts on native biodiversity. Future records of *S. spinidactyloides* in the Mediterranean will be essential to clarify whether *B. pharaonis* exerts a positive influence on its establishment and persistence.

The observed association between a non-indigenous basibiont and a non-indigenous vagile amphipod species represents a

particularly relevant model for advancing our understanding of how habitat-forming species shape bioinvasion dynamics. Such interactions may significantly enhance the establishment success of secondary invaders, thereby amplifying invasion impacts. Consequently, habitat-forming NIS should be regarded as a critical risk factor in bioinvasion alerts and monitoring strategies.

The results obtained demonstrate the presence of two species of *Serejohyale* in the Mediterranean Sea: *S. spinidactylus* in the Tunisian coast [31] and *S. spinidactyloides* in the southern Italian coast. It is noteworthy that neither species is native to the Mediterranean basin, and, as such, they should be considered as early detection records.

In view of the occurrence of the two non-indigenous *Serejohyale* species in the Mediterranean Sea, a reassessment of the morphological diagnostic characters (Figure 3) was conducted, and an updated taxonomy and biogeographical distribution of the genus (Figure 4) was proposed. The establishment of the three valid species is reported as follows: *S. youngi*, *S. spinidactylus* and *S. spinidactyloides*.

Serejohyale ramalhoi [27] is here considered a synonym of *S. spinidactylus*. Both original descriptions reveal no diagnostic differences, and the former was reported only once within the latter's distributional range. Morphological variation in the second gnathopod and antennal segmentation, previously interpreted

as species-level distinctions, is more consistent with growth-related polymorphism common in Hyalidae. Thus, *S. ramalhoi* likely represents a morphotype of *S. spinidactylus*.

Serejohyale youngi should be considered endemic to the Brazilian coast in the western Atlantic area. It occurred in three localities: Rio de Janeiro (*locus typicus*), São Paulo and Bahia [29] (Figure 3). *Serejohyale spinidactylus* is distributed in the eastern Atlantic Ocean, from the Spanish coast of the Gulf of Biscay to the Gulf of Guinea, in the equatorial region [27, 32, 41–44]. It recently occurred in the Strait of Gibraltar [30], the Atlanto-Mediterranean transition zone and in the southern Mediterranean Sea (Tunisia; [31]) (Figure 4). *Serejohyale spinidactyloides* was described and detected in the east-central equatorial Atlantic region [21, 45]; successively, reported in the Strait of Gibraltar [30] and in the central Mediterranean Sea (this paper) (Figure 4).

Serejohyale spinidactylus and *S. spinidactyloides* are distributed in the eastern Atlantic Ocean with a partially overlapping native geographical range. Robust diagnostic characters were herein recognised to overcome the typical polymorphism along the growth, that is, from juveniles to adult males [29, 32], which often obscure the correct taxonomic identification and monitoring [5, 46].

As the NIS monitoring is of interest at an international scale [25], supporting efforts to prevent the introduction and spread of NIS

Genus/ character	Genus <i>Serejohyale</i> Bousfield and Hendrycks [22]									
	Uropod 1, peduncle with stout one distolateral and one distomedial spine [22]					Pereopods 3–7, dactyls inner margin striate, with stout striated median seta [22]				
Proposed species	<i>Serejohyale spinidactyloides</i> [24]		<i>Serejohyale spinidactylus</i> [35]							<i>Serejohyale youngi</i> [25]
Revised species/ character	<i>Serejohyale spinidactyloides</i> [24]	<i>Serejohyale youngi</i> drawn according to Krapp-Schichkel et al. [26]	<i>Serejohyale spinidactylus</i> [35]	<i>Serejohyale spinidactylus</i> , young, according to Arresti [28]	<i>Serejohyale spinidactylus</i> , adult, according to Arresti [28]	<i>Serejohyale spinidactylus</i> according to Serejo [25]	<i>Serejohyale spinidactylus</i> drawn according to Krapp-Schichkel et al. [26]	<i>Serejohyale ramalhoi</i> [23] juvenile	<i>Serejohyale ramalhoi</i> [23] adult	<i>Serejohyale youngi</i> [25]
Shape of Gn2 propodus	Propodus palm straight with few spines and setae, proximally with concavity to fit dactylus, bordered by two spines; dactylus fitting palm		Propodus palm with a concavity and a distal process, with few spines (lost in older specimens) and setae; dactylus fitting palm, in some cases very long, thin at the apex and broad at the base, reaching well to the end of the palmar margin							Propodus palm straight, parallel to the anterior margin, with few spines and setae, proximally with concavity to fit dactylus, bordered by two spines
Distal spines on propodus of pereopods 5–7	Distal spine larger than the others		na	Distal spine a little longer than the proximal spine			na	na	na	Distal spine smaller, about half the size of the proximal spines
Medial posterior margin of propodus of pereopods 6–7	Lacking setae							na		Lacking setae

FIGURE 3 | Schematic representation of the diagnostic characters of the genus *Serejohyale* (above), regarding the uropod 1 and the pereopods 3–7. (Below) A scheme comparing the diagnostic characters among the original descriptions and the identifications of congeneric species retrieved from the literature. According to the comparison, *Serejohyale* cf. *youngi* recorded by Krapp-Schichkel et al. [30] should be ascribable to *Serejohyale spinidactyloides*; and *Serejohyale ramalhoi* should be placed in synonymy with *Serejohyale spinidactylus*.

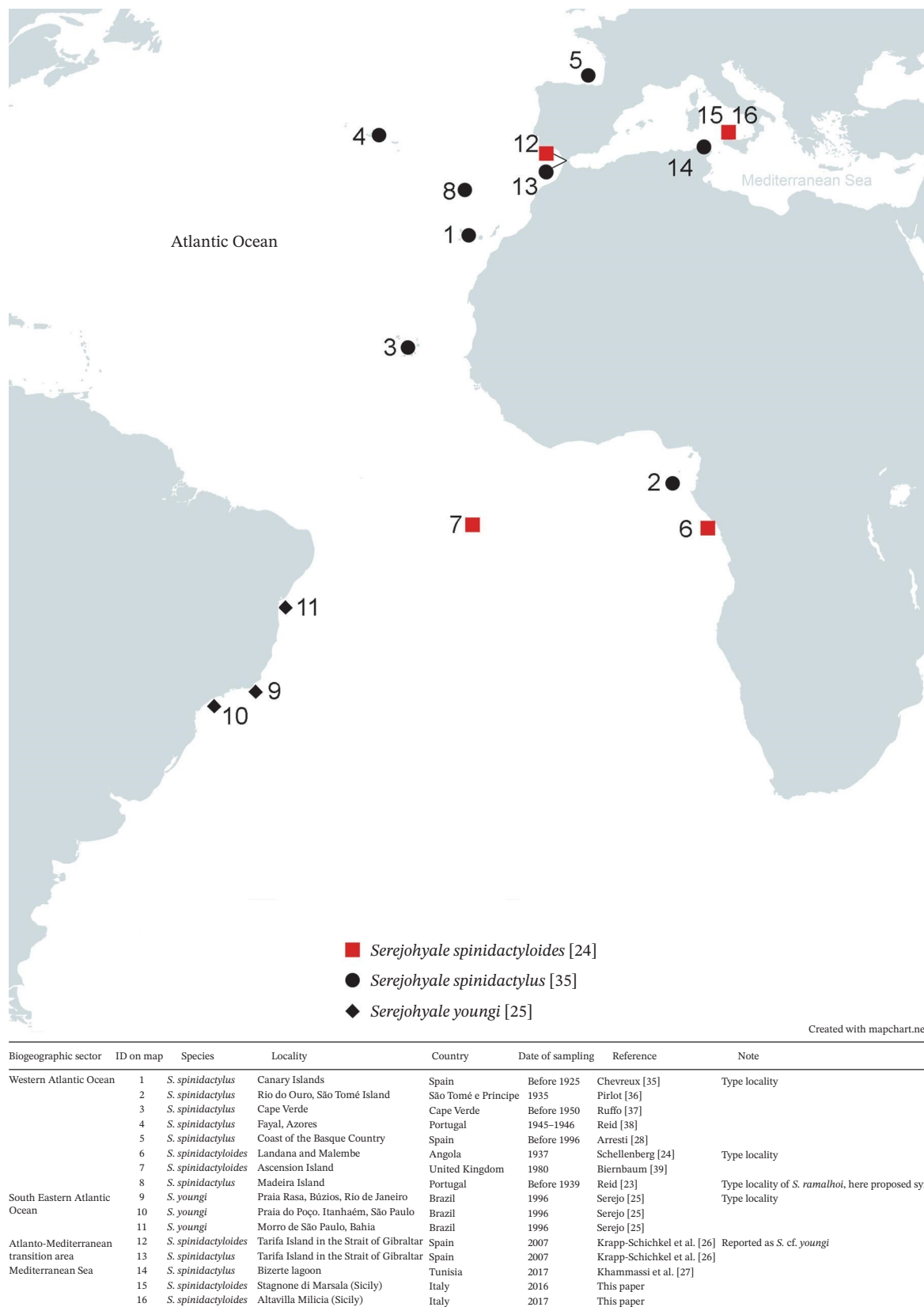


FIGURE 4 | Occurrence of the three *Serejohyale* species, including the sampling sites of this paper (ID 15 and 16). The details of the records pointed out on the map are summarised in the table.

should be based on the assumption that we can correctly identify NIS. Yet, in the marine realm, there persists a paucity of information and a considerable degree of uncertainty regarding many of the small-sized phyla due to limited research efforts and the ongoing loss of taxonomic expertise [11]. The misidentification of taxa mistaken for indigenous species, and vice versa, cannot be

considered rare in the last decades [3, 47], and there is evidence to suggest that this bias is continuing for certain taxa [5, 11, 19]. This is especially true for small, morphologically variable taxa like the amphipods. In the absence of a rigorous identification, the distinction between native and non-native faunas can become indistinct.

In order to address this issue, it is necessary to integrate a number of approaches, including morphological analysis, DNA barcoding, validated species inventories and expert taxonomic networks [48, 49]. Nevertheless, despite the existence of these tools, persistent challenges persist, including the limitation of regional baselines. Taxonomic expertise is reducing globally, and the Mediterranean region is facing a critical shortfall in capacity to document faunal change at a local scale [11, 50].

4.1 | Status of Non-Native Established Species for the Mediterranean Sea

Serejohyale spinidactyloides is here recommended as a non-native established species (*sensu* Soto et al. [51]) currently invading the Mediterranean Sea. It is a non-native species that has established self-sustaining populations in the new area, as demonstrated by the Mediterranean samples of different maturity stages (adults and juveniles).

This statement follows the 'Biogeographic Barrier Criterion' *sensu* Essl et al. [52], which assigns the status of non-native (or alien) to a taxon crossing biogeographic barriers between the range edge and the new occurrence area.

The genus *Serejohyale* has its historic biogeographic boundaries in the Atlantic region, where *S. spinidactyloides* native range was demonstrated to be located (Figure 4). The species was first recorded in the eastern tropical Atlantic region and subsequently detected in the temperate Mediterranean Sea. Its present distribution appears to be disjunct (Figure 4), a pattern that is more consistent with human-mediated spread than with a natural range expansion.

A natural dispersal beyond its native biogeographic range would be expected to occur through a progressive and stepwise expansion, accompanied by sequential records along the Atlanto-Mediterranean trajectory. However, such a pattern has not been observed.

The Atlanto-Mediterranean axis is among the most intensively investigated marine areas for amphipods. Data retrieved from the Global Biodiversity Information Facility (GBIF) [53, 54], indicate more than 2000 occurrence records of Amphipoda within this area. Hence, given this extensive sampling effort, it is reasonable to assume that *Serejohyale spinidactyloides* inhabiting shallow, accessible habitats would have been detected, if present, along the hypothesised natural expansion pathway. Conversely, the discontinuous distribution pattern suggests the involvement of introduction vectors capable of facilitating a long-distance transport and subsequent establishment in the Mediterranean area.

The earlier findings also fit with the 'Prior Absence Criterion' for recognising non-native species *sensu* Carlton and Schwindt [11]. According to the authors, the evidence of prior absence is one of the strongest criteria for recognising a non-native species,

especially for species unlikely to have been overlooked for decades in well-studied areas.

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Conflicts of Interest

The authors declare no conflicts of Interest.

Data Availability Statement

The data that support the findings of this study are available in the Supporting Information section of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Supporting Information.** Figure S1. *Serejohyale spinidactyloides* [21], holotype. Type specimen from the Museum für Naturkunde, Berlin, Germany, male 4.5 mm. Scale bar 1 mm. Figure S2. Iconography of *Serejohyale spinidactyloides*, holotype, from the Museum für Naturkunde, Berlin, Germany, male 4.5 mm. See text for terminology. Scale bar 0.1 mm. Table S1. Number of male, female and juvenile specimens collected in different points of the two localities and date of sampling. The collection points were stations so close to each other within each locality that it was not possible to provide different geographical coordinates. Table S2. Length measurements of all specimens.