Journal of the Marine Biological Association of the United Kingdom

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Marine Record

Cite this article: Goatley C, Seaby R, Somes R, Kamanli SA, Clark B and Clark P (2026) First record of the swimming crab *Charybdis* (*Archias*) *hoplites* (Wood-Mason, 1877) (Portunidae) in the Atlantic. *Journal of the Marine Biological Association of the United Kingdom* **106**, **e19**, 1–9. https://doi.org/10.1017/S0025315426101131

Received: 18 November 2025
Revised: 8 January 2026
Accepted: 19 January 2026

Keywords:
ballast water, invasive species, Southampton Water, swimming crab, United Kingdom

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First record of the swimming crab *Charybdis* (*Archias*) *hoplites* (Wood-Mason, 1877) (Portunidae) in the Atlantic

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Abstract

Portunid crabs of the genus *Charybdis* De Haan, 1833 are among the most frequently reported marine invaders worldwide. Here, we report the first record of *Charybdis* (*Archias*) *hoplites* (Wood-Mason, 1877) outside its native Indo-West Pacific range, collected from the Test Estuary, Southampton Water, United Kingdom. Morphological and molecular analyses confirm the specimen's identity and clarify diagnostic features useful for distinguishing *C.* (*A.*) *hoplites* from closely related taxa. This represents the northernmost record of any *Charybdis* species and suggests a long-distance dispersal event, associated with shipping activities in the Port of Southampton. Environmental data indicate that salinity and turbidity at the collection site are within known tolerances for *Charybdis* spp., although low winter temperatures may limit survival and establishment. The detection of this warm-water species in a major international port highlights the ongoing need to monitor non-native marine fauna.

Introduction

Decapod crustaceans are some of the most successful invasive species across freshwater, brackish, and marine ecosystems worldwide (Karatayev *et al.*, 2009; Brockerhoff and McLay, 2011; Hänfling *et al.*, 2011; Rato *et al.*, 2021). Of these invasive decapods, the brachyuran crabs are highly successful (Howard *et al.*, 2017). Often with broad diets and environmental tolerances (Hänfling *et al.*, 2011), crabs can establish high population densities (Lord and Williams, 2017; Hilliam and Tuck, 2022; Castriota *et al.*, 2024) and cause considerable impacts in their new environments through predation (Kotta *et al.*, 2018), competition (Baillie and Grabowski, 2018), introduced parasites (Frizzera *et al.*, 2021), and physical manipulation of their habitats (Rudnick *et al.*, 2005; Gonzalez *et al.*, 2024).

Within the Brachyura, portunid swimming crabs are the most frequently reported alien species (*sensu* Colautti and MacIsaac, 2004), particularly those in the genus *Charybdis* De Haan, 1883 (Brockerhoff and McLay, 2011; Swart *et al.*, 2018). At least six species from two *Charybdis* subgenera (*C.* (*Charybdis*) and *C.* (*Archias*)) have been reported globally as alien species, and at least five of these have established invasive populations (Table 1). While several of these species are Suez invaders, spreading from the Red Sea into the Mediterranean and becoming established, the most common vector for translocations appears to be via shipping (Table 1).

The Port of Southampton is one of the busiest ports in the UK, handling a large number of container ships, car transporters, and cruise ships (Asgari *et al.*, 2015; Roberts *et al.*, 2020). Large vessel movements connect Southampton to more than 200 other ports worldwide, and the region is a hotspot for recreational boating, increasing localised connections (Tidbury *et al.*, 2016). With hull fouling, ballast, and bilge water serving as vectors for the transport of alien species, this region has been identified as being at high risk from invasive marine species (Tidbury *et al.*, 2016). Indeed, Southampton Water – the tidal estuary of the Rivers Itchen and Test – has the highest number of alien marine species on the UK south coast (Arenas *et al.*, 2006; Minchin *et al.*, 2013; Taylor *et al.*, 2022). However, barring a single record of the Chinese mitten crab, *Eriocheir sinensis*, no non-native crabs have been reported in this region (GBIF, 2025).

Here, we report an observation of a single specimen of the alien portunid, *Charybdis* (*Archias*) *hoplites* in Southampton Water. This represents the first record of this species outside its native range and the most northerly record of any species within the genus. As this species is rarely discussed in the literature, this observation of *C.* (*A.*) *hoplites* also provides opportunities to clarify its diagnostic characters, aiding future studies and monitoring efforts.

Table 1. Examples of non-native populations or records of *Charybdis* spp

Charybdis species	Native range	Introduced range	References	Method of introduction	Status
C. (*Archias*) *longicollis*	Type locality: Red Sea, Egypt	Eastern Mediterranean	Galil and Kevrekidis, 2002, Innocenti and Galil, 2007, Yokes *et al.*, 2007	Suez invasion	Established
	Range: Red Sea & Western India Ocean				
C. (*Charybdis*) *hellerii*	Type locality: New Caledonia	Eastern Mediterranean	Galil *et al.*, 2002, Özcan *et al.*, 2010, Yokes *et al.*, 2007	Suez invasion	Established
	Range: Indo-West Pacific	West Atlantic: South Carolina, USA–Santa Catarina, Brazil	Cintra *et al.*, 2023, Negri *et al.*, 2018, Tavares and de Mendonça Jr, 1996	Shipping-mediated	Established
		East Atlantic: Spain-Benin	Cuesta *et al.*, 2016, Dessouassi *et al.*, 2019, Muñoz *et al.*, 2024	Shipping-mediated	Established (Benin only)
		East Pacific: Mexico	Salas-Maldonado *et al.*, 2025	Shipping-mediated	Not established
		Central Pacific: Hawai'i	Evans *et al.*, 2018	Shipping-mediated	Not established
C. (*C.*) *japonica*	Type locality: Japan*	New Zealand, South and Western Australia	Hilliam and Tuck, 2022, Hourston *et al.*, 2015, Smith *et al.*, 2003	Shipping-mediated	Established (NZ)
	Range: Malaysia-Japan	North Coast of Central Mediterranean,	Froglia, 2012, Froglia *et al.*, 2022	Shipping-mediated	Not established
C. (*C.*) *feriata*	Type locality: New Caledonia	North Coast of Western & Central Mediterranean	Abelló and Hispano, 2006, Colmenero *et al.*, 2019, Froglia *et al.*, 2024, Pinto *et al.*, 2023, Rojas *et al.*, 2023	Shipping-mediated and possible escapes	Not established
	Range: Indo-West Pacific				
C. (*C.*) *lucifer*	Type locality: Indian Ocean*	North Coast of Central Mediterranean	Mizzan and Vianello, 2008	Shipping-mediated	Not established
	Range: Indo-West Pacific				
C. (*C.*) *natator*	Type locality: Indian Ocean*	Eastern and South Coast of Central Mediterranean	Nour *et al.*, 2022, Orfanidis *et al.*, 2021	Shipping-mediated and Suez invasion	Not established
	Range: Indo-West Pacific				

*Not explicitly stated in description.

Materials and methods

Specimen collection

The recently deceased specimen of *Charybdis* (*Archias*) *hoplites* was collected from the Test Estuary, Southampton, United Kingdom, at the cooling water intake of Marchwood Power Station (50.9014°, −1.4407°; Figure 1), on the 24th of July 2025. The water temperature at the collection site was 21°C, and the salinity was 33 psu; both within the expected range for this time of year (Environment Agency, 2025). The specimen was collected during a monthly 24 h impingement survey assessing the fish and invertebrates screened prior to entrainment into the power station's cooling water system. The specimen was immediately identified as unusual due to its elongate sixth anterolateral teeth and was photographed in the field and preserved in 70% isopropanol, with the second and third left pereiopods removed and preserved separately in 80% ethanol for molecular analysis.

DNA amplification and phylogenetics

DNA was extracted from muscle tissue of the left second pereiopod of the specimen using a PureLink™ Genomic DNA kit (Invitrogen) following the manufacturer's protocol with two replicate 40 µl elutions.

We sequenced a segment of the mitochondrial gene *cytochrome c oxidase subunit I* (COI) using the primers dgLCO-1490 and dgHCO-2198 (Meyer, 2003). A PCR reaction (50 µl) was made using 25 µl of One*Taq*® 2X Master Mix (New England Biolabs), 1 µl of each primer (10 µM), 10 µl of template DNA, and 13 µl of Milli-Q water. PCR thermocycling conditions were 2.5 min at 94°C for initial denaturation, followed by 40 cycles of 30 s at 90°C (denaturation), 1 min at 48°C (annealing), 1 min at 72°C (extension), and a final extension step at 72°C for 10 min. PCR success was confirmed by gel electrophoresis, and the amplified product was purified using a peqGOLD Cycle-Pure KIT (VWR International) before Sanger sequencing at Eurofins Genomics, Ebersberg, Germany.

Sequence data were manually trimmed by removing low-quality bases at the ends of raw reads, and bidirectional reads were aligned in ChromasPro 2.2. The sequence data were then compared against the NCBI GenBank database (Sayers *et al.*, 2025) using BLASTn (Johnson *et al.*, 2008).

To further investigate relationships among closely related taxa and to help identify our specimen, we created a Bayesian phylogeny. Sequence data were downloaded for the 50 closest hits

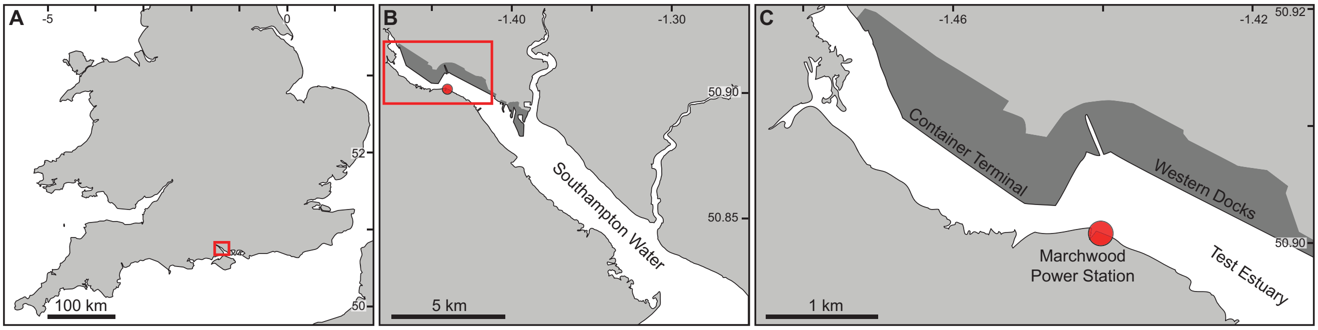

Figure 1. Collection location of *Charybdis* (*Archias*) *hoplites*, Marchwood Power Station, Test Estuary, Southampton Water, UK. Red rectangles in panels (A) and (B) show positions of subsequent, finer-scale panels. The red circles in panels (B) and (C) indicate the location of the Marchwood Power Station cooling water intake. Dark grey shaded areas in panels (B) and (C) indicate the location of the Port of Southampton. Latitude and longitude are presented in decimal degrees.

from our BLASTn search, along with three sequences from the closely related genus *Thalamita* (Evans, 2018; Negri *et al.*, 2018) for use as an outgroup. Sequences were aligned using ClustalW and trimmed in MEGA 12 (Thompson *et al.*, 1994; Kumar *et al.*, 2024). The Bayesian phylogeny was then computed using MrBayes (Ronquist *et al.*, 2012) through the NGPhylogeny.fr web service (Lemoine *et al.*, 2019) using a General Time Reversible (GTR) model and gamma distributed rates. The analysis consisted of two parallel Markov Chain Monte Carlo runs, each with four chains, run for 10×10^6 generations, sampled every 500 generations with a burn-in fraction of 0.25. The consensus tree, with Bayesian posterior probabilities, was visualised using Interactive Tree of Life (Letunic and Bork, 2024). The sequence data created for this project were deposited in GenBank (Accession number: PX830597).

Morphology and identification

Diagnostic characters were recorded using the terminology of Davie *et al.* (2015), Lai *et al.* (2010), Ng (1998), and Wee and Ng (1995). Identification was initially undertaken using FAO identification guides (Ng, 1998; Tavares, 2003), followed by further assessment using keys and detailed taxonomic works, as detailed in the results. As the first gonopods of males are important diagnostic characters in *Charybdis* (Stephenson *et al.*, 1957), these were dissected from the specimen for computerised tomography scanning.

Computerised tomography scanning

The male first gonopod was securely positioned in a 0.5 ml Eppendorf Safe-Lock tube using plastic foam, with a small amount of ethanol added to prevent desiccation following the method outlined in Goatley and Tornabene (2022). The specimen was scanned using a Zeiss Xradia 520 Versa at the Natural History Museum, London. The X-ray source was operated at 110 kV and 91 µA with an exposure time of 3 s. A 0.4X lens was used, and 2034 projection images were acquired. Image reconstruction was performed using the Zeiss Reconstructor software, yielding a voxel size range of 4.2 µm.

VGStudio Max (version 2.2) was applied to visualise the scans, converting the data into TIFF stack formats for further processing with the open-source 3D surface rendering software Drishti (Limaye, 2012; Ng *et al.*, 2021). For visualisation in this study, screen grabs were captured and edited in Adobe Photoshop CS6 to enhance image quality and resolution to 300 dpi. These were saved in .TIFF format. Scan data created for this project were deposited in MorphoSource (www.morphosource.org; ark:/87602/m4/805675).

Results

Phylogenetic analysis

Our BLASTn search revealed that our COI sequence data (658 base pairs) were identical to two records and 99.84% similar to a third record on GenBank. Two of these records are identified as *Charybdis* sp., while one of the identical matches is identified as *Charybdis* (*Archias*) *pusilla* in Cubelio *et al.* (2023). Pairwise distance calculations, with variance estimated from 1000 bootstrap replicates, indicate that these four samples are highly similar, with all standard error intervals overlapping zero (Table 2).

The molecular phylogeny (Figure 2, Fig. S1) resolves our specimen as inseparable from the three aforementioned records on GenBank. These are positioned within *C.* (*Archias*), which forms a well-supported monophyletic group. Following the phylogenies of Evans (2018) and Negri *et al.* (2018), the validity of *C.* (*Charybdis*) remains uncertain, as our phylogeny resolves this subgenus as a poorly supported and polyphyletic group with *C.* (*C.*) *feriata* sister to all other members of the ingroup. Notably, within the *C.* (*Charybdis*) *japonica* group, there were some unexpected taxa, including six records of *Gaetice depressus* (Varunidae), suggesting that some GenBank records for these taxa are misidentified (Fig. S1).

Morphology and identification

The hexagonal carapace, six anterolateral teeth and paddle-like last walking legs suggested the specimen was best placed within the Portunidae (Ng, 1998; Tavares, 2003). The presence of six anterolateral teeth indicated that this specimen was unlike any portunids from the Atlantic (Tavares, 2003). Using Indo-Pacific identification keys (Ng, 1998), six teeth on the anterolateral margin and a frontal carapace margin distinctly less than half the greatest width of the carapace (Figures 3–6) suggest that the Southampton specimen is placed in *Charybdis*, a conclusion supported by the molecular data.

Charybdis comprises ca. 60 species assigned to several subgenera (Ng *et al.*, 2008). The status of these subgenera has been in constant revision, but currently these are *C.* (*Charybdis*) De Haan, 1833; *C.* (*Archias*) Paulson, 1875; and *C.* (*Gonioneptunus*) Ortmann, 1893. According to Wee and Ng (1995) and Ng (1998), the angle between the posterolateral carapace margin and the posterior carapace margin is a reliable character to separate subgenera:

Table 2. The number of base differences per site between sequences of the *Charybdis* (*Archias*) *hoplites* specimen from Southampton Water and the three closest hits using BLASTn on NCBI GenBank. GenBank accession numbers are presented following names. Standard error estimates from 1000 bootstraps are shown above the diagonal (italic). Analyses were conducted in MEGA12 (Kumar *et al.,* 2024)

	Southampton Water *Charybdis*	*Charybdis pusilla* OK383015	*Charybdis* sp. MK816430	*Charybdis* sp. MZ438256
Southampton Water *Charybdis*		*0.000*	*0.000*	*0.002*
Charybdis pusilla OK383015	0.000		*0.000*	*0.002*
Charybdis sp. MK816430	0.000	0.000		*0.002*
Charybdis sp. MZ438256	0.002	0.002	0.002	

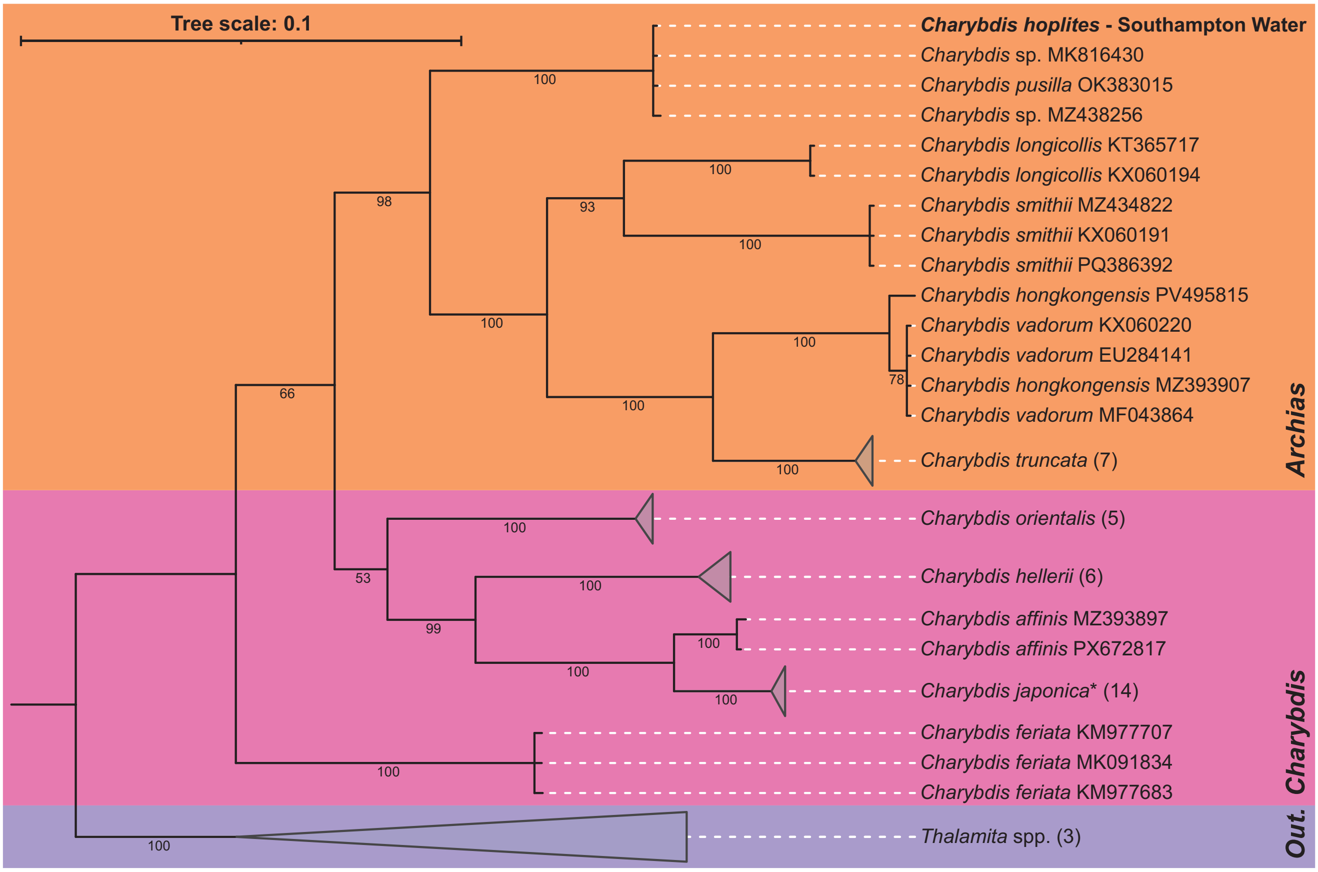

Figure 2. Bayesian phylogeny calculated from the 50 closest hits to the *Charybdis* (*Archias*) *hoplites* specimen collected from Southampton Water, and three *Thalamita* spp. as an outgroup. Numbers adjacent to branches indicate posterior probabilities. Tip labels include GenBank accession numbers. The number of sequences resolved within collapsed nodes is indicated in parentheses following the tip labels. * indicates a grouping of species identified as *Charybdis* (*Archias*) *japonica* (×8) and *Gaetice depressus*, Varunidae (×6) from GenBank. Coloured backgrounds delineate the subgenera: *C.* (*Archias*), Orange; *C.* (*Charybdis*), pink; outgroup, *Thalamita* spp., Purple. Complete phylogeny – without collapsed nodes – is provided in Figure S1.

angular versus round. The presence of an angular junction in the Southampton specimen suggests it should be assigned to *C.* (*Archias*).

Given the unknown native range of the Southampton specimen, its lack of chelae, and the limited number of global keys for *Charybdis* (*Archias*) spp., several keys were used to identify the Southampton Water specimen.

Using the Wee and Ng (1995) guide to Malaysian and Singaporean *Charybdis* and *Thalamita* species, the Southampton specimen keyed out as *C.* (*Archias*) *hongkongensis*. Using Ng (1998), the specimen keyed out as *C.* (*Archias*) *truncata* – the only member of *C.* (*Archias*) in this guide. The pattern of granulation on the carapace of the Southampton specimen differs from both of these species, with a medial triangular patch of granules (Figure 4) not reported in either. Furthermore, the margin of the penultimate segment of the male abdomen is convex in *C.* (*A.*) *hongkongensis* and *C.* (*A.*) *truncata* versus straight in the Southampton specimen (cf. Leene, 1938; Figure 4).

Using the global portunid key of Leene (1938) and the keys of Alcock (1899b), Apel and Spiridonov (1998), and Türkay and Spiridonov (2006) for India, the Arabian Gulf, and Western Indian Ocean, respectively, the Southampton specimen was identified as *Charybdis* (*Archias*) *hoplites* (Wood-Mason, 1877). All characters of the Southampton Water specimen agree with the descriptions in Alcock (1899b), Leene (1938), and Wood-Mason (1877), supporting this identification.

While the molecular evidence suggested that the Southampton Water specimen was *C.* (*A.*) *pusilla*, this actually strengthens the

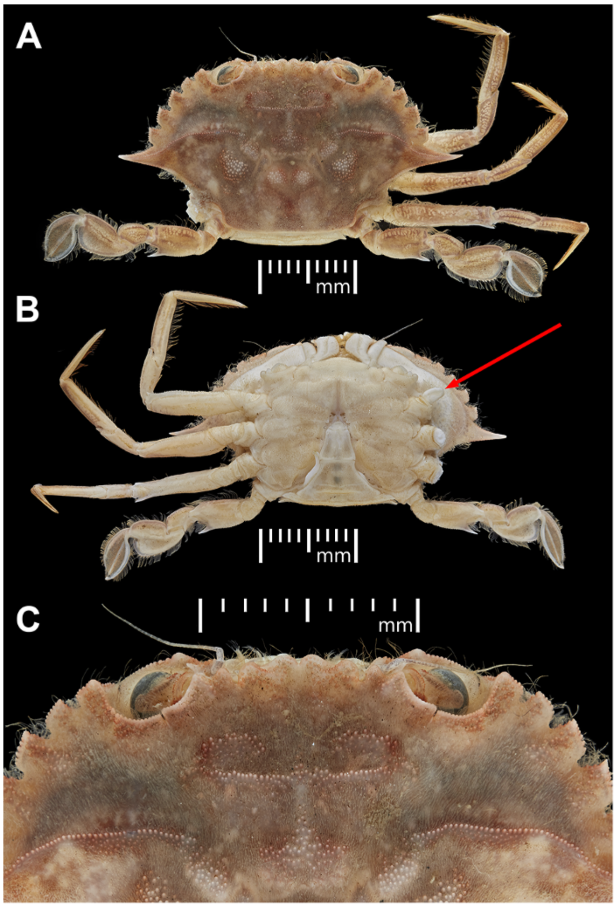

Figure 3. Preserved specimen of *Charybdis* (*Archias*) *hoplites* (Wood-Mason, 1877), male, Southampton Water, NHMUK reg. 2025.2075. (A) Dorsal view; (B) Ventral view with arrow indicating regeneration bud of left first pereiopod; (C) Dorsal view of frontal margin. Images taken by Peter Grugeon, NHM Publishing and Image Resources.

argument for its placement within *C.* (*A.*) *hoplites*. *Charybdis* (*A.*) *pusilla* has long been recognised as being similar to *C.* (*A.*) *hoplites*, with Alcock (1899b) describing *C.* (*A.*) *pusilla* as *C.* (*Goniohellenus*) *hoplites* var. *pusilla*, and Apel and Spiridonov (1998) and Türkay and Spiridonov (2006) recognising it as a subspecies of *C.* (*A.*) *hoplites*. Cubelio *et al.* (2023), however, recognised *C.* (*A.*) *pusilla* as a species, and it is their specimens that are accessioned in GenBank, matching our Southampton Water specimen.

The main morphological characters distinguishing *C.* (*A.*) *pusilla* and *C.* (*A.*) *hoplites* are size (Alcock, 1899b; Leene, 1938) and the relative length of the merus of the last ambulatory leg (Apel and Spiridonov, 1998). Type material of *C.* (*A.*) *pusilla* has a maximum carapace width of 16 mm (Alcock, 1899b). By contrast, *C.* (*A.*) *hoplites* has an adult size range of 28.5–57.5 mm (Apel and Spiridonov, 1998). The merus of the swimming leg of *C.* (*A.*) *pusilla* is described as being 'twice as long as broad' versus 1.6 times in *C.* (*A.*) *hoplites* (Apel and Spiridonov, 1998). The Southampton specimen has a carapace width of 35 mm, and a swimming leg merus 1.6 times longer than wide. Placement in *C.* (*A.*) *hoplites*, therefore, seems parsimonious.

Taxonomy

Superfamily Portunoidea Rafinesque, 1815
Family Portunidae Rafinesque, 1815
Subfamily Thalamitinae Paulson, 1875
Genus *Charybdis* De Haan, 1833
Subgenus *Charybdis* (*Archias*) Paulson, 1875
Charybdis (*Archias*) *hoplites* (Wood-Mason, 1877)
Figures 3–6
Synonyms:

Goniosoma hoplites Wood-Mason 1877: 422; Alcock & Anderson 1894: 184, 1896: pl. 23, Figure 6; Alcock 1899: 67–68; Gordon 1931: 534–536.

Charybdis (*Goniohellenus*) *hoplites* – Alcock 1899b: 64–65; Leene 1938: 99, figs 53–54; Chhapgar 1957: 423, fig. 7h; Gordon 1931: text fig. 12a, b, b′; Naderloo 2017: 182, figs 20.13a, 20.15; Apel & Spiridonov 1998: 211–213, figs 31, 33.

Charybdis hoplites forma typica – Leene 1938: 99–102, figs 53–54

Charybdis hoplites – Tirmizi & Kazmi 1996: 28 (key), 29–32, figs 13–14.

Charybdis (*Archias*) *hoplites* – Ng et al. 2008: 153–154 (list)

Abbreviations used: coll. = collected by, cw = carapace width taken as the maximum width between the tips of the lateral carapace spines in mm, reg. = registration number, stn = station.

Distribution: Madras, Bay of Bengal (Wood-Mason, 1877); RIMS Investigator, Bay of Bengal, stn 159, 14.0986°, 80.4222°, 205 m; stn 170, 13.0183°, 80.6155°, 196 m; stn 172, NE of Ceylon (Sri Lanka), 13.0183°, 81.2958°, 365–640 m (Alcock and Anderson, 1894); Coromandel Coast, the Eastern Ghats, Indian state of Tamil Nadu, 146–201 m (Alcock, 1899a, 1899b); off the Indus Delta, 29–80 m (Alcock, 1899b); Iran (Nobili, 1906; Naderloo, 2017); Bahrain (Stephensen, 1946); Saudi Arabia (Basson *et al.*, 1977); Off Pakistan (Tirmizi and Kazmi, 1996); Arabian Gulf (Apel and Spiridonov, 1998).

Charybdis (*Archias*) *hoplites*: 1♂, cw 34.97 mm, damaged, without chelae and left pereiopod 1, cooling water intake of Marchwood Power Station during fish/crustacean impingement monitoring, 50.9014°, −1.4407°, River Test, Southampton Water, Hampshire, England, coll. Robin Somes & Richard Seaby, Pisces Conservation Ltd, and Christopher Goatley, University of Southampton, 24/07/2025, NHMUK reg. 2025.2075.

Material examined: *Charybdis* (*Goniohellenus*) *hoplites* stn 70, 25.5700°, 57.3917° to 25.5500°, 57.4200°; 25.xi 1933, 196 m, coll. HEMS Mabahiss, John Murray Expedition, det. Michael Türkay, July 1982, NHM reg. 1991.153.9, 6♂, 1 damaged, cw 39.51–48.83 mm, 3♀, cw 33.22–38.61 mm; stn 75, 25.1800°, 56.7917° to 25.1633°, 56.7917°; 28.xi 1933, 201 m, coll. HEMS Mabahiss, John Murray Expedition, det. Michael Türkay, July 1982, NHM reg. 1991.162.1, 1♂, cw 31.50 mm.

Description: Carapace transversely hexagonal, width 1.97 times length (Figure 3); frontal margin 0.25 times carapace width with eight rounded teeth (including inner orbital teeth), notch between teeth two and three (from orbit) twice as deep as others (Figure 4); six anterolateral teeth, first five pointed anteriorly, posterior tooth pointing laterally and more than double length of others (Figures 3 and 4); junction between posterolateral carapace margin and posterior margin of carapace angular; carapace with lines and patches of granules, scroll shaped line anteromedially followed by medial triangular patch, epibranchial ridge sinuous expanding medially into teardrop shaped patch, four patches posterior to cervical groove medial patches circular, lateral patches larger and pyriform, lines and patches of granules scattered around carapace margins (Figure 4). Second male pleomere with straight lateral margins; proximal width 1.8 times distal width (Figure 4).

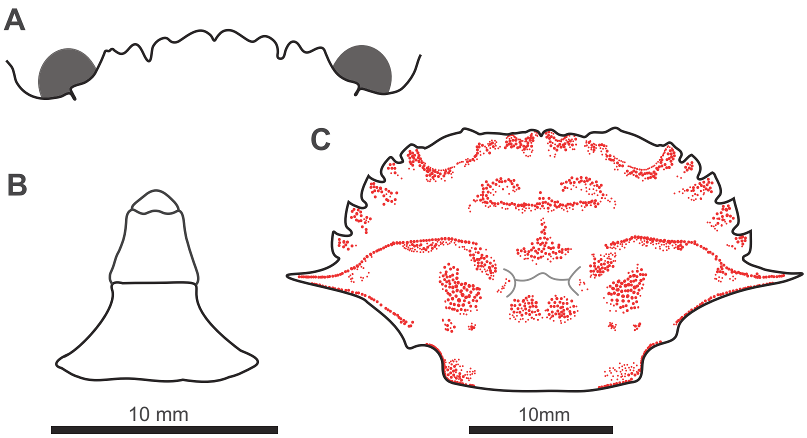

Figure 4. Diagnostic characters of *Charybdis* (*Archias*) *hoplites* (Wood-Mason, 1877). (A) The frontal margin. (B) The abdomen of the single male specimen. (C) The pattern of granulation on the carapace (red stippling). Grey lines indicate the cervical groove (sinuous epibranchial line running from sixth anterolateral tooth). Scale bar for (A) and (B) beneath panel (B).

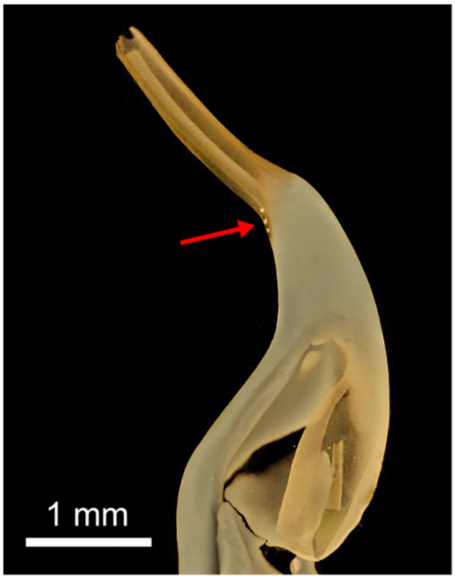

Figure 5. A computerised tomography scan of the distal tip of first gonopod of *Charybdis* (*Archias*) *hoplites* (Wood-Mason, 1877). Red arrow indicates a row of three small, distinct tubercles.

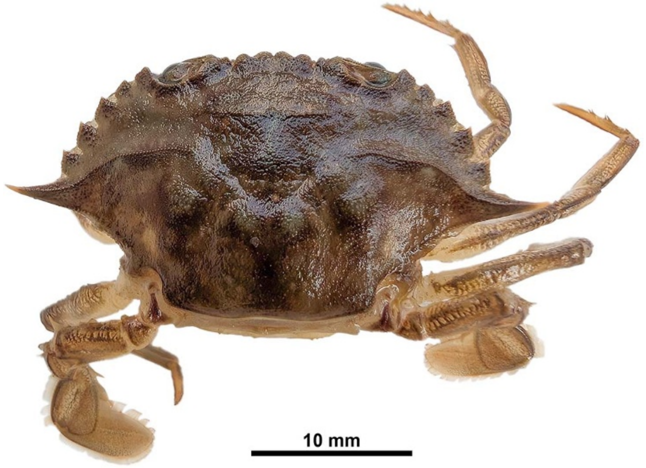

Figure 6. Fresh specimen of *Charybdis* (*Archias*) *hoplites* (Wood-Mason, 1877) from Southampton Water, displaying live colouration.

Merus of all ambulatory legs with spine on posterior distal margin; merus of swimming leg 1.6 times longer than wide (Figure 3). Distal tip of first gonopod with a row of three small, distinct tubercles (Figure 5).

Colour in life: Carapace green-brown; walking legs pale brown with covering of short, darker pubescence (Figure 6); anterior surfaces pale cream-brown.

Colour in preservation: Carapace orange-brown with granulations appearing paler; walking legs pale brown with covering of short, pubescence darker brown; anterior surfaces pale cream (Figure 3).

Remarks: Ng *et al.* (2008) commented that the name *Archias* Paulson, 1875 (type species *A. sexdentatus* Paulson, 1875), has precedence over *Charybdis* (*Goniohellenus*) Alcock, 1899 (type species *Goniosoma hoplites* Wood-Mason, 1877). Noting, however, that the type species of *Archias* (*A. sexdentatus* Paulson, 1875) is poorly known, they deferred from a revision. It was treated as a possible junior subjective synonym of *C.* (*Goniohellenus*) *hoplites* (Wood-Mason, 1877) or *C.* (*G.*) *longicollis* Leene, 1938 (see discussion in Apel and Spiridonov, 1998), but its precise classification was unclear until fresh specimens became available. A neotype will probably be necessary to stabilise the taxonomy of these names. The figures of *A. sexdentatus* provided by Paulson (1875: pl. 8 Figure 3–3b), however, agreed well with what is now known as *C.* (*G.*) *hoplites*, and there appears to be little doubt that they belong to the same subgenus. Prema *et al.* (2021) recognised this and used *Archias* Paulson, 1875, in place of *Goniohellenus* Alcock, 1899.

Discussion

Recorded here is an observation of a non-native species of portunid crab in Southampton Water, United Kingdom. This specimen of *Charybdis* (*Archias*) *hoplites* (Wood-Mason, 1877) represents the first record of this species in the Atlantic and the highest latitude record of any member of this genus (GBIF, 2025). Members of this genus are well known for their capacity to exploit novel habitats, with at least six species being reported as alien species worldwide (Table 1). The most likely method of introduction of our specimen is in ballast water or hull fouling from one of the many ships visiting the Port of Southampton.

The native range of C. (*A.*) *hoplites* includes the Persian/Arabian Gulf, Gulf of Oman, Arabian Sea, and Bay of Bengal, with a single record from the Southern Red Sea (Türkay and Spiridonov, 2006; GBIF, 2025). Direct transport to the Port of Southampton in ballast water could be possible, as regular cargo services run direct from the home range of *C.* (*A.*) *hoplites*, with a journey time of approximately 30 days (CMA CGM, 2025; DP World, 2025; ONE, 2025). This falls within the range of larval durations of other members of the genus (Dineen *et al.,* 2001), and survival of adults in ballast water is likely. Alternatively, transport could have been from another port outside the home range of *C.* (*A.*) *hoplites* with an undetected population of these crabs. Transport of adults on hull fouling is also possible, particularly if shorter distances from such undetected populations are considered (Cuesta *et al.,* 2016).

As only a single male specimen was recorded and the environmental conditions in Southampton Water differ considerably from those in the native habitats of *C.* (*A.*) *hoplites*, this species record will hopefully represent a transient occurrence. The collection location has shallow (<15 m) water depth and moderate turbidity. Between November 2024 and October 2025, salinity at the collection site in the Test Estuary ranged from 27.8 to 33 psu, and water temperature varied from 7.5°C in February to 21°C in August (Environment Agency, 2025).

The depth, turbidity, and salinity of the collection location are within the known tolerances of *Charybdis* spp. (Türkay and Spiridonov, 2006; Narita *et al.,* 2008; Fowler *et al.,* 2010). Winter temperatures would seem likely to pose challenges to the persistence of warm-water *C.* (*A.*) *hoplites* in Southampton. Specific information on temperature tolerance for this species is limited, but the congeneric *C.* (*C.*) *feriata* (Linnaeus, 1758) exhibits markedly reduced survival at 20°C (Baylon and Suzuki, 2007). By contrast, larval *C.* (*C.*) *japonica* show high tolerance to low temperature conditions (10°C) (Fowler *et al.,* 2010). Given that *C.* (*A.*) *hoplites* occupies depths exceeding 360 m in the Indian Ocean (Türkay and Spiridonov, 2006), where temperatures drop below 11°C (Ray *et al.,* 2024), the species' survival under cooler conditions cannot be ruled out.

Reliable identification of invasive species requires appropriate taxonomic resources. In the case of *Charybdis*, identification of the Southampton Water specimen required the use of multiple regional and global keys (Leene, 1938; Wee and Ng, 1995; Apel and Spiridonov, 1998; Ng, 1998; Türkay and Spiridonov, 2006). Conflicting outcomes, a complex taxonomic history (see Remarks), and probable misidentifications in GenBank indicate that taxonomic resources for *Charybdis* remain incomplete. Given the prevalence of crabs as invasive species worldwide (Brockerhoff and McLay, 2011), there is a clear need for new genus-level keys, together with curated DNA voucher material and reliable barcodes. These resources would facilitate early detection and support eDNA-based monitoring of alien species.

Once reported, almost two-thirds of alien crabs become established (Brockerhoff and McLay, 2011) – a pattern common among alien marine organisms (Minchin *et al.,* 2013) – and the Port of Southampton is at high risk from invasive species (Arenas *et al.,* 2006; Minchin *et al.,* 2013; Tidbury *et al.,* 2016). The occurrence of *C. (A.) hoplites* in Southampton Water illustrates how global shipping continues to link distant marine ecosystems. Whether this individual represents an isolated vagrant or the first sign of an emerging population remains uncertain, underscoring the importance of continued monitoring to detect alien species and, if necessary, implement control measures prior to their establishment.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315426101131.

Author contributions. Designing the study: R.M.H.S. and R.S.; Carrying out the study: C.H.R.G., R.M.H.S., and R.S.; Analysing the data: C.H.R.G., R.S., S.A.K., B.C., and P.F.C.; Writing – original draft: C.H.R.G.; Writing – review and editing: all authors.

Funding. Field sampling for this study was funded by Marchwood Power Station, as part of their impingement monitoring project. DNA sequencing was funded by the School of Ocean and Earth Science, University of Southampton.

Competing interests. The authors declare no conflict of interest. The findings and views expressed are those of the authors and do not necessarily represent the views of Marchwood Power Station or its staff.

Ethical standards. N/A.

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