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REPORT

“Hidden” biodiversity: a new amphipod genus dominates epifauna in association with a mesophotic black coral forest

Sandra Navarro-Mayoral¹ · Benoit Gouillieux² · Victoria Fernandez-Gonzalez³ · Fernando Tuya¹ · Ninon Lecoquierre⁴ · Lorenzo Bramanti^{5,8} · Lucas Terrana^{6,7} · Fernando Espino¹ · Jean-François Flot^{4,10} · Ricardo Haroun¹ · Francisco Otero-Ferrer^{1,9}

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Abstract Black corals are important components of mesophotic and deep-water marine habitats. Their presence at great depths (e.g., 50 to 200 m) makes accessibility difficult, limiting our understanding of the associated biodiversity. Amphipods dominate vagile epifauna in marine habitats around the world, fulfilling important ecosystem functions. However, there are no studies on amphipods exclusively associated with black corals, including relationships between their ecological patterns (e.g., abundances) and the size of coral colonies. We investigated the epifaunal composition

and abundance associated with black coral colonies of *Antipathella wollastoni* in the subtropical eastern Atlantic Ocean. In total, 1,736 epifaunal individuals were identified, of which 1,706 (98.27%) were amphipods, belonging to 6 taxa. We identified and described a new amphipod genus and species within the Stenothoidae family, *Wollastenothoe minuta* gen. nov., sp. nov., which outnumbered the amphipod assemblage (86.15%) and provided a complete taxonomic key of Stenothoidae family including this new finding. For the first time, the association between an amphipod species and a black coral was described, including a strong correlation between coral colony size and amphipod abundances. This study demonstrates that epifauna associated with mesophotic black corals remains largely undescribed.

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Introduction

Corals are key components of sublittoral ecosystems not only in tropical (Spalding et al. 2001), but also subtropical (Czechowska et al. 2020), temperate, and cold ecosystems (Orejas et al. 2009; Bo et al. 2014; Buhl-Mortensen et al. 2018). While there are an increasing number in the studies on the classes of Scleractinia and Octocorallia, inhabiting various depth zones, Antipatharia (Cnidaria: Anthozoa: Hexacorallia) has received relatively less attention (Bo et al. 2012). Antipatharians, commonly known as black corals, encompasses over 300 accepted species (Molodtsova and Opresko 2023) and, under favorable environmental conditions, can form dense aggregations, creating “coral forests” (a type of animal forests, sensu Rossi et al. 2017) or “coral gardens” (sensu Hall-Spencer and Tasker 2006). These communities have some structural and functional similarities with terrestrial forests, with the main difference that they are dominated by animals instead of plants (Rossi et al. 2017). Their colony morphology varies from branched, bush-like, and feather-like to whip types (Wagner et al. 2012). The dense canopies they form can change local physical conditions and generate a three-dimensional habitat, which provide shelter to associated species and, ultimately, increase biodiversity (Freiwald et al. 2004; Buhl-Mortensen et al. 2010; De Clippele et al. 2019). One of the main components of the visible black coral forests-associated biodiversity is accounted by epifauna (i.e., crustaceans, polychaetes and molluscs, Lavelle 2012; Wagner et al. 2012), which can find habitat (Herler 2007), food (Angel 1990; Bo et al. 2012), and protection against predators (Lavelle 2012).

Amphipods are one of the most abundant and diverse taxa of marine macro-invertebrates (Arfianti et al. 2018), as well as a diverse and important component of deep-sea habitats worldwide (Arfianti and Costello 2020a, b). Amphipods include species with different trophic strategies (e.g., detritivores, omnivores, carnivores, and herbivores), and they are predated by other crustaceans, polychaetes, and fishes (Guerra-García et al. 2014; Jiménez Prada et al. 2015). Moreover, they play an important role in marine food webs, by directly or indirectly recycling nutrients and linking

different trophic levels (Karlson et al. 2007; Havermans and Smetacek 2018).

The amphipod family Stenothoidae includes marine benthic species ranging from the shallow subtidal to depths over 3,000 m (Krapp-Schickel 2015; Krapp-Schickel and Vader 2015). Several species of Stenothoidae have received attention from the scientific community due to their biological association (i.e., commensalism) with marine sessile cnidaria, such as anemones (Vader and Krapp-Schickel 1996; Auster et al. 2011) and hydrozoans (Lewis 1992), on which they find food, nesting grounds, and shelter (Marin and Sinelnikov 2017). However, to date, there are no studies on amphipods and their ecological interactions with black corals.

In the present study, we investigated the epifaunal composition and abundance in mesophotic forests created by the black coral *Antipathella wollastoni* (Gray 1857) from Lanzarote Island over time (Canary Islands, eastern Atlantic Ocean). Identification of sampled specimens has been performed in a robust taxonomic framework and resulted in the description of a new amphipod genus and species within the Stenothoidae family, for which a complete key to genera is provided. Then, we described the first biological association between an amphipod species (i.e., *Wollastenothoe minuta* gen. nov., sp. nov.) and a black coral species. Specifically, the relationship between coral colony size and amphipod abundances was tested for both the entire amphipod assemblage and the new described species, suggesting an exclusive association.

Material and methods

Study region

The study was conducted in the Southeastern coast of Lanzarote Island (Canary Islands, eastern Atlantic Ocean) at Puerto del Carmen (28°55'26.81" N, 13° 39' 12.61" W) (Fig. 1a, b). The site was selected based on previous records of *A. wollastoni* in the shallower limits of its depth distribution range (ca. 60 m depth, Fig. 1c, d) (Bianchi et al. 2000; Czechowska et al. 2020). In this area, local topography is characterized by narrow rocky shelves and steep slopes, typical of oceanic volcanic islands (Acosta et al. 2005; Tuya et al. 2021). Local hydrography is complex, with NE trade winds affecting shallow subtidal habitats by generating wind waves and near-bottom turbulence (Mann and Lazier 2013). The high nutrient load transported by currents may affect the upper limit of black coral distribution, by either providing food or physically smothering the corals (Wagner et al. 2012; Czechowska et al. 2020).

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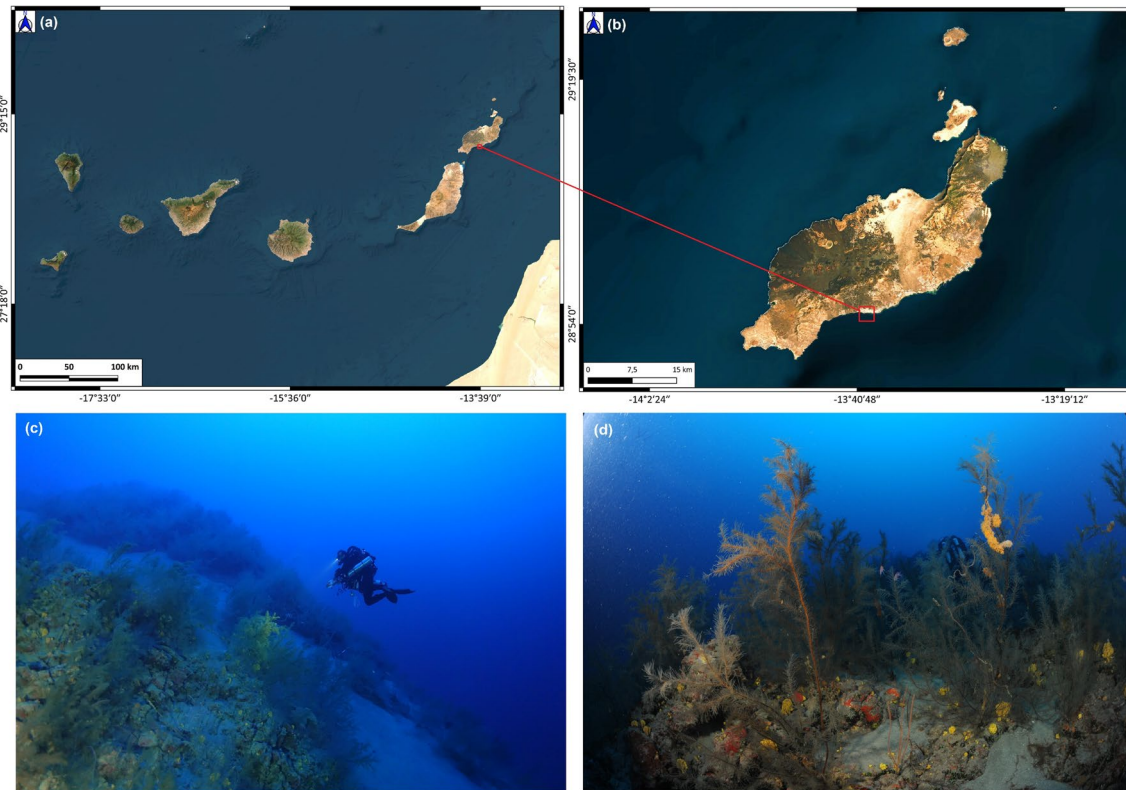


Fig. 1 Map of the Canary Islands in the eastern Atlantic Ocean (a), including the study site located in the Southeastern coast of Lanzarote Island (b). Mesophotic black coral forest of *Antipathella wollastoni* (c and d)

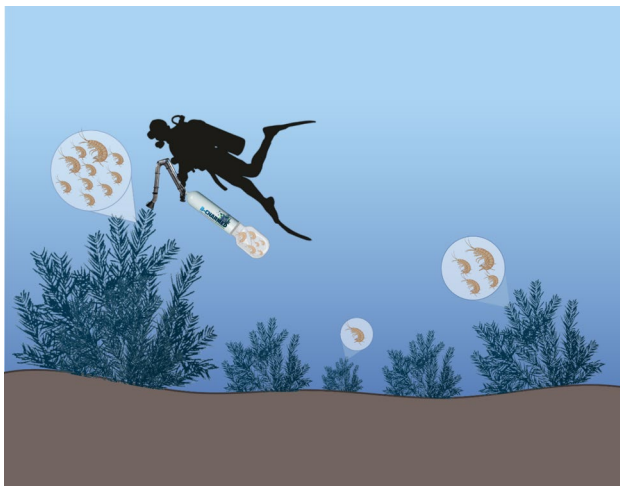


Fig. 2 Epifauna was collected in mesophotic forests of *A. wollastoni* by sucking up coral branches through a small vacuum cleaner for 20 s

Sampling design and collection of samples

Epifauna was collected in mesophotic monospecific forests of *A. wollastoni* at three times during 2021: T1 (February),

T2 (April), and T3 (October). At each time, 10 colonies spanning between 40 and 180 cm (total height from the seafloor to the upper tip of the colony) were selected randomly, for a total of 30 colonies. All sampling was carried out at the same depth (*ca.* 60 m), taking care to not sample twice the same area. Sampling was carried out by two divers using mixed-gas rebreather diving. On each colony, samples of associated epifauna were collected by sucking up on their top branches through a vacuum cleaner for 20 s (Fig. 2). The temperature was monitored between February and October 2021 by a temperature data logger (Hobo data-logger Pedant Temp-Light, Onset Computer Corporation, USA; sampling frequency 15 min) positioned next to the black corals.

Specimen processing

Collected epifauna was directly brought to the laboratory after surfacing in sealed containers filled with seawater. Then, each sample was carefully inspected, rinsed, and sorted to separate epifauna from marine debris and coral mucus. Each organism was then stored in 96% ethanol and identified to the lowest taxonomical level. Identifications were implemented by using a stereoscopic microscope (Leica, EZ4W, Wetzlar,

Germany). The taxonomic guide provided by Barnard and Karaman (1991), Ruffo (1998), and specific references from the Stenothoidae family (i.e., Krapp-Schickel 2000, 2011, 2015) was used for amphipod identification. Specifically, 68 specimens of the new amphipod genus/species were dissected in alcohol and mounted on microscope slides using dimethylhydantoin–formaldehyde resin for morphological description. Appendages were observed under a Nikon SMZ800N stereomicroscope and a Nikon Eclipse Ci microscope and photographed with a Nikon DS-Fi2 camera. Body length (BL) was measured with NIS-Elements Analysis software from the anterior margin of the head to the posterior end of the telson. Drawings were carried out from pictures using Inkscape software (v.0.48). For scanning electron microscope (SEM) observations, 12 specimens were dehydrated in a graded ethanol series, critical point dried, using carbon dioxide as a medium, mounted on stubs, coated with gold for 60 s sputter coated with gold, and photographed with a Hitachi tabletop microscope TM3030Plus.

DNA sequencing

DNA extraction was performed on a pool of 23 ethanol-preserved specimens using the MagAttract DNA Extraction Kit (Qiagen) following the manufacturer's protocol. Folmer's 658-bp fragment of the first subunit of cytochrome *c* oxidase mitochondrial gene (COI) was amplified using primers LCO1490 and HCO2198 (Folmer et al. 1994). In addition, a fragment of the 28S rRNA gene (28S) was amplified using primers from Verovnik et al. (2005). All amplifications were performed using DreamTaq Green PCR Master Mix (ThermoScientific). For COI, the PCR protocol involved an initial denaturation period at 94 °C for 3 min, followed by 50 cycles of denaturation at 94 °C for 30 s, annealing at 45 °C for 1 min, and elongation at 72 °C for 1 min. For 28S, the PCR protocol comprised an initial denaturation period at 94 °C for 3 min, then 40 cycles of denaturation at 94 °C for 20 s, annealing at 50 °C for 50 s, and elongation at 72 °C for 1 min. PCR products were checked on 1% agarose gel, and subsequently, 1–2 µL of each PCR product (depending on band intensity) was pooled (together with other PCR products from unrelated research projects). The pool was then cleaned up using the InnuPREP PCRpure Kit (Innuscreen) and used to prepare a SKQ-LSK114 library that was sequenced on a FLO-FLG114 Nanopore Flongle flow cell featuring R10.4.1 pore proteins. The resulting reads (1264 for COI and 1932 for 28S) were assembled using amplicon_sorter (Vierstraete and Braeckman 2022).

Phylogenetic analyses

For the COI marker, all Stenothoidae sequences available in GenBank on 19 November 2023 were collected and

complemented with sequences of *Iphimedia obesa* and *Gitana sarsi* as outgroups. Alignment was performed by hand in MEGA11 (Tamura et al. 2021) taking into account the amino acid translation of the sequences, followed by maximum likelihood phylogenetic analysis using IQtree2 (Minh et al. 2020) with automatic model selection (Kalyanamoorthy et al. 2017) and 100,000 ultrafast bootstraps (Hoang et al. 2018). The resulting Newick tree was displayed, re-rooted, and turned into PDF in MEGA11.

Statistical analyses

All modeling and testing were conducted using R (Rstudio Team 2022). Mixed effects generalized linear models (GLMs) were fitted to univariate responses, including the total abundance of amphipods and the abundance of the new genus and species, *Wollastenothoe minuta* gen. nov., sp. nov. GLMs were fitted by means of the 'lme4' (Bates et al. 2014) and 'lmerTest' packages (Kuznetsova et al. 2017) considering time (three levels) as a random factor and the size of colonies of *A. wollastoni* as a covariate. Models were fitted using a 'negative binomial', as the family distribution of residuals, with a 'log' link function. For all fitted GLMs, diagnosis plots of residuals and Q-Q plots were visually inspected to check the appropriateness of the fitted models (Harrison et al. 2018). We realized simple linear regressions tested whether the total abundance of amphipod and the abundance of *W. minuta* gen. nov., sp. nov., were predicted by the colony size.

Results

Taxonomy

Class Malacostraca Latreille 1806

Order Amphipoda Latreille 1816

Suborder Senticaudata Lowry & Myers 2013

Family Stenothoidae Boeck 1871

Genus *Wollastenothoe* Gouillieux & Navarro-Mayoral gen. nov.

urn:lsid:zoobank.org:act:5FFE2706-D2F1-4EB9-B6A8-B341FF6D10D5.

Type species. *Wollastenothoe minuta* Gouillieux & Navarro-Mayoral gen. nov., sp. nov., here designated.

Diagnosis of the new genus

Body dorsally smooth. Head without rostrum. Antenna 1 article 1 not nasiform; accessory flagellum with 1 article. Mandible palp with 1 article, molar process conical. Maxilla 1 palp with 2 articles. Gnathopod 1 and 2 subchelate,

subequal. P5 basis rectilinear without posterodistal lobe. P6-7 basis widened.

Etymology

The genus name, *Wollastenothoe*, refers the combination of host name corresponding to the species of black coral (i.e., *Antipathella wollastoni*) with the genus name *Stenothoe* belonging to the Stenothoidae family.

Remarks on genus assignation and Stenothoidae diagnosis

Characters of the present new genus agree with the diagnosis of the Stenothoidae family except for the molar process of the mandible. In the present new genus, molar process is slightly developed, conical, whereas the diagnosis for the family Stenothoidae includes a molar process evanescent. This conical shape of the molar process is already present in other genera of Stenothoidae, such as *Antatelson*, *Pseudothamatelson*, *Ptychotelson*, *Raukumara* or *Thamatelsonella*. According to Horton et al. (2022), 46 genera belong to the family Stenothoidae, and only 12 present a mandibular palp uniaarticulate: *Ausatelson* J.L. Barnard 1972; *Metopelloides* Gurjanova 1938; *Paraprobolisca* Ren in Ren & Huang 1991; *Prostenothoe* Gurjanova 1938; *Prothamatelson* Schellenberg 1931; *Pseudothamatelson* Schellenberg 1931; *Ptychotelson* Krapp-Schickel 2000; *Stenothoides* Chevreux 1900; *Stenula* J.L. Barnard 1962; *Victometopa* Krapp-Schickel 2011; *Vonimetopa* Barnard & Karaman 1987 and *Zaikometopa* Barnard & Karaman 1987. *Wollastenothoe* gen. nov. can be distinguished from *Ausatelson*, *Metopelloides*, *Prostenothoe*, *Prothamatelson*, *Ptychotelson*, *Stenula*, *Vonimetopa* and *Zaikometopa* by the presence of an uniaarticulate accessory flagellum (vs absence), with *Paraprobolisca* and *Pseudothamatelson* by pereopod 7 basis expanded (vs rectilinear), with *Victometopa* by pereopod 5 without posterodistal lobe (vs with) and with *Stenothoides* by 2-articulate maxilla 1 palp (vs 1-articulate). In the case of *Paraprobolisca*, the only species of this genus, *Paraprobolisca leptopoda* Ren in Ren & Huang 1991 was synonymized with *Probolisca ovata* (Stebbing 1888) by Krapp-Schickel and Koenemann (2006). They based their diagnosis on the morphological similarities of the gnathopods and the mouthparts and considered that the uropod 3 described as being one-articulated in *Paraprobolisca leptopoda*, a character of the genus, has simply been overlooked and should be two-articulated as for *Probolisca ovata*. Even if most of species have uropod 3 ramus two-articulated, some have an one-articulated uropod 3 ramus as some *Raukumara* J.L. Barnard 1972 species. Furthermore, *Probolisca*

ovata presents uropods 1 and 2 peduncles marginally bares, whereas *Paraprobolisca leptopoda* has uropods 1 and 2 peduncles with many robust setae along outer margin. Thus, based on the original descriptions, we consider *Paraprobolisca leptopoda* as a valid species that should not be synonymized with *Probolisca ovata*.

Wollastenothoe minuta Gouillieux & Navarro-Mayoral **sp. nov.**

urn:lsid:zoobank.org:act:7A70A805-5499-4FC6-93AD-1A8CE17C53DE **Description of *Wollastenothoe minuta*.**

Type material.

Holotype: brooding female, BL = 1.38 mm, 1 egg (MNHN-IU-2016-3389). Paratypes: brooding female, BL = 1.21 mm, 1 egg, dissected specimen, 11 slides (MNHN-IU-2016-3388); brooding female, BL = 1.45 mm, 2 eggs, dissected specimen, 11 slides (MNHN-IU-2016-3387); female with oostegites, BL = 1.37 mm, dissected specimen, 12 slides (MNHN-IU-2021-8807). Atlantic Ocean, European waters, Canary Islands, Puerto del Carmen in Lanzarote Island. 28°55'26"81" N, 13°39'12"61" W, October 2021, 60 m depth, collected by technical diving and rebreathers with the air-vacuum method on black coral branches. Collectors: Francisco Otero-Ferrer, Lorenzo Bramanti and Lucas Terrana.

Additional material: 5 juveniles, 53 females and 10 specimens sex not determined (MNHN-IU-2016-3359), 12 specimens used for SEM pictures (MNHN-IU-2021-8808). Same data as holotype and paratypes.

Diagnosis

Body length less than 1.5 mm. Antenna subequal, shorter than half length of body. Antenna 1 accessory flagellum with 1 small article. Gnathopod 1 and 2 subchelate, subequal. Pereonite 4 slightly longer than pereonite 3. Coxa 4 ventral margin concave. Coxae 5–7 posterior margin with a notch. P5 basis rectilinear without posterodistal lobe. P6-7 basis widened with posterodistal lobe reaching along half of ischium, merus posterodistal lobe reaching more than half length of carpus. Telson with dorsal spines.

Description based on holotype and paratypes (Figs. 3, 4, 5, 6, 7).

Body (Fig. 6a) dorsally smooth, very compressed laterally. Pereonite 4 slightly longer than pereonite 3. Urosomites free.

Head. Antennae subequal in length, setose. **Antenna 1** (Fig. 3aA) peduncle article 1 slightly tapering distally, about 2 times longer than wide; article 2 cylindrical, about half length of article 1; article 3 cylindrical, subequal to article 2; flagellum consists of 4 articles increasing in length, accessory flagellum 1 articulate, very small, with 1 to 3 distal setae. **Antenna 2** (Fig. 3bB) peduncular article 3 cylindrical, as long as wide;

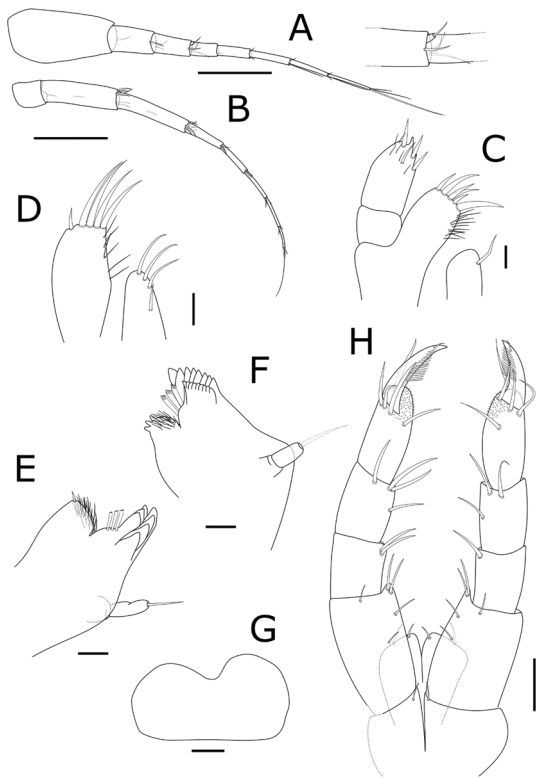


Fig. 3 *Wollastenotheoe minuta* gen. nov., sp. nov. **a, b, e, f, h**: Paratype MNHN-IU-2016-3387, BL: 1.37 mm. **c, d**: Paratype MNHN-IU-2016-3388, BL: 1.21 mm. **g**: Based on SEM picture, MNHN-IU-2021-8808. **a** Right antenna 1 with a focus on accessory flagellum; **b** Right antenna 2; **c** Left maxilla 1; **d** Left maxilla 2, **e** Mandible left; **f** Mandible right; **g** Upper lip; **h** Maxilliped. Scale bars: **a, b**: 0.1 mm; **c-g**: 0.01 mm; **h**: 0.025 mm

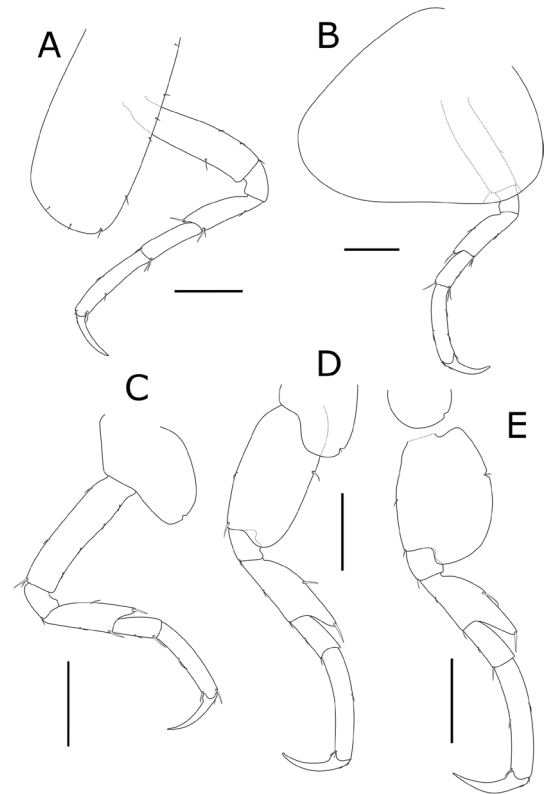


Fig. 5 *Wollastenotheoe minuta* gen. nov., sp. nov. **a, b**: Paratype MNHN-IU-2016-3387, BL: 1.37 mm. **c, e**: Paratype MNHN-IU-2016-3388, BL=1.21 mm. **a-e**: Left pereopods 3-7. Scale bars: **a-e**: 0.1 mm

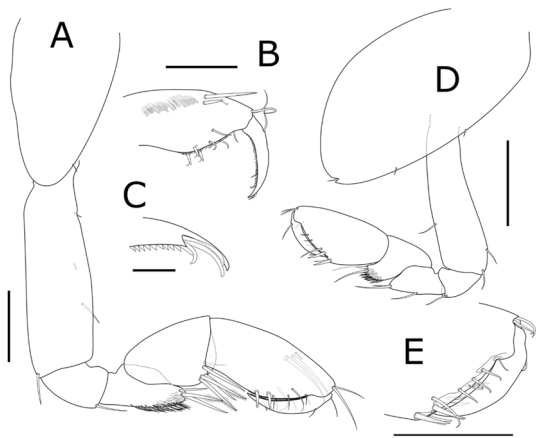


Fig. 4 *Wollastenotheoe minuta* gen. nov., sp. nov. **a, d**: Paratype MNHN-IU-2016-3387, BL: 1.37. **b, c, e**: Based on SEM picture. **a** Gnathopod 1 right, outer view; **b** Gnathopod 1 left, propodus and dactylus, inner view; **c** Gnathopod 2, distal part of dactylus, outer view; **d** Gnathopod 1 left outer view; **e** Gnathopod 2 right, propodus and dactylus, outer view. Scale bars: **a, b, e**: 0.05 mm; **c**: 0.01 mm; **d**: 0.1 mm

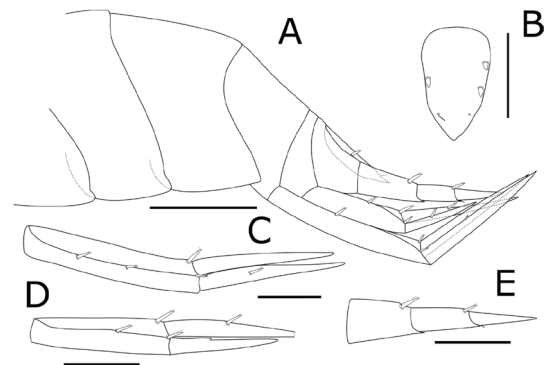


Fig. 6 *Wollastenotheoe minuta* gen. nov., sp. nov. **a**: Paratype MNHN-IU-2016-3388. **b**: Based on SEM picture, MNHN-IU-2021-8808. **c, d, e**: Paratype MNHN-IU-2016-3388, BL: 1.21 mm. **a** Posterior part, lateral view; **b** Telson, dorsal view; **c** Right uropod 1; **d** Left uropod 2, distal part of outer ramus broken; **e** right uropod 3. Scale bars: **a**: 0.1 mm; **b-e**: 0.05 mm

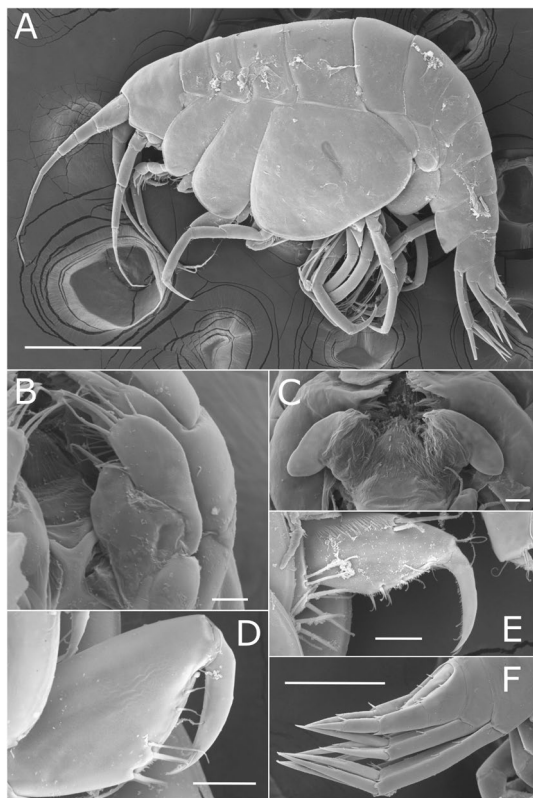


Fig. 7 *Wollastenothoe minuta* gen. nov., sp. nov. SEM pictures, MNHN-IU-2021-8808. **a** Lateral view; **b** Maxilla 2, left; **c** Lower lip; **d** Gnathopod 2, outer face, dactylus and propodus; **e** Gnathopod 1, inner face, dactylus and propodus; **f** Urosome, lateral view. Scale bars: **a**: 0.25 mm; **b**: 0.01 mm; **c**: 0.01 mm, **d**, **e**: 0.02; **f**: 0.1 mm

article 4 and 5 subequal, about 2.8 times longer than article 3; flagellum consists of 5 articles of decreasing length.

Mouthparts. **Upper lip** (Fig. 3g) cleft at the apex, asymmetric lobes. **Mandible** (Fig. 3e–f) Palp uni-articulate with 1 or 2 distal setae, about 1.4 to 2.6 longer than wide, partial suture line sometimes visible at the base of the palp; incisor and lacinia mobilis multi-dentate; accessory setarow consists of 3 blades with comb-shaped distal part; molar process slightly developed, conical, finely setose. **Lower Lip** (Fig. 7c) Lower lip with many setae, inner lobes coalesced, mandibular lobes well developed. **Maxilla 1** (Fig. 3c) inner plate inner margin with a single simple setae, outer plate distal part with 6 large stiff robust setae; palp two-articulate, article 1 smooth, about 2 times shorter than article 2; article 2, with three distolateral robust setae, a subdistal simple seta and some little simple setae on distal part and inner plate. **Maxilla 2** (Fig. 3d, 7b) inner plate with 4 long robust setae; apical margin rounded and armed with 3 setae;

outer plate inner margin with row of 6 simple setae, distal part with 4 long and 1 short robust setae. **Maxilliped** (Fig. 3h) with reduced outer plate, inner plate with 2 distal simple setae; palp 4-articulate: article 3 the longest, with many very small setae distally; article 4 with lateral row of setae.

Gnathopods. **Gnathopod 1** (Figs. 4a, b, 7e) subchelate, slightly smaller to gnathopod 2; coxa tapering distally, about 1.5 times longer than wide; basis and ischium with few setae; merus posterior and distal margins with dense small simple setae, posterodistal margin with long simple and plumose setae; carpus widening distally, posterodistal corner with long simple and plumose setae; propodus about twice as long as wide, dorsal margin bare except 2 dorsodistal setae, inner face with row of fine and small plumose setae and 2 or 3 long subdorsal setae; propodus palmar edge serrate, 3 stout robust setae at the base of propodus; dactylus with serrate cutting margin and 2 or 3 simple setae, subdistal notch with 4 setae. **Gnathopod 2** (Figs. 4c–e, 7d) subchelate; coxa anteroventral margin regularly rounded, 1.8 times longer than wide, posteroventral corner notched; basis to carpus similar to gnathopod 1; propodus about twice as long as wide, dorsal margin bare except 2 dorsodistal setae; propodus palmar edge not serrated except a small part between 4 stout robust setae at the base of propodus; dactylus with 1 or 2 simple setae along cutting margin, not serrate, subdistal setae present without subdistal notch.

Pereopods. **Pereopods 3–7** subequal in length, with few setae; ischium posterodistal seta absent for pereopods 3–4, present for pereopods 5–7; merus with distal lobe increasing in length, dactylus with dorsal seta. **Pereopod 3** (Fig. 5a) coxa elongate, somewhat rectangular, posteroventral corner notched; length ratio of articles from basis to dactylus about 3.3:1:1.9:1.8:2.7:1.5; basis rectilinear, about 3.8 times longer than wide; merus about twice as long as wide, with small distodorsal lobe reaching 0.2 length of carpus; carpus 3.5 as long as wide; propodus elongated, about 5.5 times longer than wide. **Pereopod 4** (Fig. 5b) similar in shape to pereopod 3 except for coxa very large, subtriangular, about the same length as the first four segments of the thorax, reaching half-length of ischium, smooth, unarmed, ventral margin slightly concave; length ratio of articles from basis to dactylus about 4.5:1:2.7:1.8:3.3:1.7. **Pereopods 5–7** ischium to dactylus similar in shape, merus increasingly expanded. **Pereopod 5** (Fig. 5c) coxa mostly developed posteriorly, posterior margin notched with a simple seta inside; length ratio of articles from basis to dactylus about 4.3:1:2.1:1.4:2.8:1.8; basis rectilinear, without posterodistal lobe. **Pereopod 6** (Fig. 5d) coxa posterior margin notched with a simple seta inside; length ratio of articles from basis

to dactylus about 5:1:2.6:1.6:4:2; basis slightly expanded, about 2 times longer than wide, posterior margin notched with a simple seta inside, posterodistal lobe reaching half-length of ischium. **Pereopod 7** (Fig. 5e) coxa rounded, posterior margin notched with a simple seta inside; length ratio of articles from basis to dactylus about 6.3:1:2:1.6:3.8:2.1; basis expanded, slightly longer than wide, posterior margin notched with a simple seta inside, posterodistal lobe reaching two-thirds of ischium length; merus about 1.4 longer than wide, posterodistal lobe reaching 0.7 length of carpus.

Epimeral plates (Fig. 6a) 1–3 smooth, posteroventral corner weakly produced in a blunt lobe, more or less pronounced; posterior margin weakly convex.

Uropods (Figs. 6a, 7f). **Uropod 1** (Fig. 6c) biramous; peduncle about 1.2 times longer than rami, with 2 robust setae on outer margin and a distal one, and 1 distal robust seta on inner margin; rami subequal, outer ramus with 1 dorsal robust seta, inner ramus with or without 1 dorsal robust seta. **Uropod 2** (Fig. 6d) biramous; peduncle with 2 robust setae on outer margin and 1 distal robust seta on inner margin; rami unequal, inner ramus slightly longer than peduncle, 1.3 times longer than outer ramus, with 1 dorsal robust seta, inner ramus slightly smaller

than peduncle, with or without 1 dorsal robust seta. **Uropod 3** (Fig. 6e) uniramous, ramus 2-articulate, length ratio of peduncle and articles variable between 1:1:1.1 and 1.4:1:1.2; peduncle with 1 dorsodistal robust seta, ventrodistal corner produced into a small tooth; article 1 with 1 dorsodistal robust seta, ventrodistal corner produced into a small tooth with 1 simple seta, article 2 unarmed, smooth.

Telson (Fig. 6b) entire, tapering distally, with 1 or 2 lateral robust setae and a small subdistal seta on each side.

Male: unknown.

Color in vivo: Whitish brown.

Type locality. Puerto del Carmen (28°55'26.81" N, 13° 39' 12.61" W), Lanzarote, Canary Islands, Spain.

Etymology. The epithet specific of the species, *minuta*, refers to its small size.

Key to Genera of Stenothoidae (based on Barnard & Karaman 1991 key with inclusion of recent subsequent new genera descriptions)

1. Article 2 of pereopod 7 rectilinear.....	2
Article 2 of pereopod 7 expanded	26
2. Telson thickened and fleshy	3
Telson flat and laminar.....	13
3. Gnathopod 2 chelate.....	4
Gnathopod 2 subchelate or simple.....	6
4. Gnathopod 1 chelate.....	<i>Raumahara</i> J.L. Barnard 1972
Gnathopod 1 subchelate or simple.....	5
5. Article 1 of antenna 1 nasiform	<i>Prothaumatelson</i> Schellenberg 1931
Antenna 1 not nasiform	<i>Ptychotelson</i> Krapp-Schickel 2000
6. Mandibular palp 2 to 3-articulate	7
Mandibular palp 0 to 1-articulate	9
7. Article 1 of antenna 1 nasiform	8
Article 1 of antenna 1 not nasiform.....	<i>Thaumatelson</i> Walker 1906
8. Pleonite 3 with erect dorsal process	<i>Antatelson</i> J.L. Barnard 1972
Pleonite 3 without erect dorsal process	<i>Thaumatelsonella</i> Rauschert & Andres 1991
9. Uropod 3 reduced, inner ramus of uropods 1-2 shortened, article 1 of antenna 1 nasiform or not.....	<i>Chuculba</i> J.L. Barnard 1974
Uropods 1-3 ordinary, article 1 of antenna 1 nasiform.....	10
10. Gnathopods 1-2 alike.....	<i>Parathaumatelson</i> Gurjanova 1938
Gnathopods 1-2 dissimilar.....	11
11. Gnathopod 2 dactylus minute.....	<i>Verticotelson</i> Krapp-Schickel 2006
Gnathopod 2 dactylus normal.....	12
12. Urosomite 1 weakly extended posterodorsally, urosomites 2-3 fused	<i>Ausatelson</i> J.L. Barnard 1972
Urosomite 1 strongly extended posterodorsally, urosomites 1-3 free.....	<i>Pseudothaumatelson</i> Schellenberg 1931
13. Pleonite 4 with dorsal process	14
Pleonite 4 lacking dorsal process	19
14. Gnathopods chelate	<i>Raumahara</i> J.L. Barnard 1972
Gnathopods subchelate or simple.....	15
15. Palp of mandible 2 to 3-articulate	<i>Hardametopa</i> Barnard & Karaman 1991
Palp of mandible 0 – 1-articulate	16
16. Palp of mandible absent	<i>Yarra</i> Krapp-Schickel 2000
Palp of mandible 1 articulate.....	17
17. Article 1 of antenna 1 not nasiform.....	<i>Paraprobolisca</i> Ren in Ren & Huang 1991
Article 1 of palp 1 nasiform	18
18. Inner plates of maxillipeds mostly fused together, pereonite 4 highly elongate, palp of maxilla 1 1-articulate.....	<i>Zaikometopa</i> Barnard & Karaman, 1987
Inner plates of maxillipeds well separated, pereonite 4 slightly elongate and tumid, palp of maxilla 1 2-articulate.....	<i>Pseudothaumatelson</i> Schellenberg 1931
19. Palp of maxilla 1 2-articulate	20
Palp of maxilla 1 1-articulate	22
20. Palp of mandible 2-3 articulate	<i>Probolisca</i> Gurjanova 1938
Palp of mandible 0-1 articulate	21
21. Gnathopod 2 subchelate	<i>Sandrothoe</i> Krapp-Schickel 2006
Gnathopod 2 chelate.....	<i>Raukumara</i> Krapp-Schickel 2000
22. Mandibular palp absent	23
Mandibular palp present.....	24
23. Gnathopod 2 subchelate	<i>Parametopella</i> Guryanova 1938
Gnathopod 2 chelate.....	<i>Pycnopyge</i> Krapp-Schickel 2000
24. Mandibular palp 2 to 3-articulate, antenna 1 accessory flagellum present	<i>Metopella</i> Sars 1892
Mandibular palp 1-articulate, antenna 1 accessory flagellum absent.....	25
25. Inner plates of maxillipeds partly fused, gnathopod 1 subchelate.....	<i>Metopelloides</i> Gurjanova 1938
Inner plates of maxillipeds fully separated, gnathopod 1 simple, propodus elongate	<i>Vonimetopa</i> Barnard & Karaman 1987

26. Article 2 of pereopod 5-7 evenly but weakly expanded.....	<i>Goratelson</i> J.L. Barnard 1972	
Article 2 of pereopods 5-7 diversely expanded.....		27
27. Article 2 of pereopod 6 linear.....		28
Article 2 of pereopod 6 expanded.....		31
28. Pleonite 3 smooth.....		29
Pleonite 3 with dorsal process.....	<i>Mesoproboloides</i> Gurjanova 1938	
29. Mandibular palp 0 to 1-articulate.....	<i>Stenothoides</i> Chevreux 1900	
Mandibular palp 2 to 3-articulate.....		30
30. Article 2 of pereopod 7 tapering, basally expanded, antenna 1 accessory flagellum present.....	<i>Mesometopa</i> Guryanova 1938	
Article 2 of pereopod 7 evenly expanded, antenna 1 accessory flagellum absent.....		
	<i>Metopella</i> Sars 1892	
31. Mandibular palp 0-1 articulate.....		32
Mandibular palp 2-3 articulate.....		41
32. Pereopod 5 basis with posterodistal lobe.....		33
Pereopod 5 basis without posterodistal lobe.....		34
33. Article 1 of antenna 1 not nasiform.....	<i>Victometopa</i> Krapp-Schickel 2011	
Article 1 of antenna 1 nasiform.....	<i>Parametopa</i> Chevreux 1901	
34. Gnathopod 1 > gnathopod 2.....	<i>Sudanea</i> Krapp-Schickel 2015	
Gnathopod 1 = or < gnathopod 2.....		35
35. Palp of maxilla 1 1-articulate.....		36
Palp of maxilla 1 2-articulate.....		37
36. Antenna 1 accessory flagellum, present, minute.....	<i>Wallametopa</i> J.L. Barnard 1974	
Antenna 1 accessory flagellum absent.....	<i>Stenula</i> J.L. Barnard 1962	
37. Head with conspicuous rostrum.....	<i>Synkope</i> Krapp-Schickel 1999	
Head without rostrum.....		38
38. Mandibular palp present.....		39
Mandibular palp absent.....		40
39. Antenna 1 accessory flagellum absent.....	<i>Prostenothoe</i> Gurjanova 1938	
Antenna 1 accessory flagellum, present, minute.....	<i>Wollastenotheo</i> gen. nov	
40. Antenna 2 as long as antenna 1, coxa 2 bevelled anteroventrally.....	<i>Stenothoe</i> Dana 1852	
Antenna 2 half as long as antenna 1, coxa 2 subquadrate and protrusive anteroventrally.....		
	<i>Knysmetopa</i> Barnard & Karaman 1987	
41. Pereopod 5 basis without posterodistal lobe.....		42
Pereopod 5 basis with posterodistal lobe.....		46
42. Palp of maxilla 1 1-articulate.....		43
Palp of maxilla 1 2-articulate.....		44
43. Article 1 of antenna 1 not nasiform.....	<i>Metopa</i> Boeck 1871	
Article 1 of antenna 1 nasiform.....	<i>Prometopa</i> Schellenberg 1926	
44. Gnathopod 1 simple, barely subchelate.....	<i>Probolooides</i> Della Valle 1893	
Gnathopod 1 distinctly subchelate.....		45
45. Antenna 1 accessory flagellum absent or 1 articulate.....	<i>Metopoides</i> Della Valle 1893	
Antenna 1 accessory flagellum 2 articulate.....	<i>Aurometopa</i> Barnard & Karaman 1987	
46. Gnathopod 1 simple, barely subchelate.....	<i>Torometopa</i> Barnard & Karaman 1987	
Gnathopod 1 distinctly subchelate.....		47
47. Antenna 1 accessory flagellum absent or 1 articulate.....		48
Antenna 1 accessory flagellum 2 articulate.....		49
48. P6, 7 basis posteriorly narrowing.....	<i>Malvinometopa</i> Krapp-Schickel 2011	
P6, 7 basis regularly rounded.....	<i>Kyphometopa</i> Krapp-Schickel 2013	
49. Gnathopods different in size and shape, gnathopod 1 very weak and elongate, carpus propodus, both long and thin, palm oblique.....	<i>Scaphodactylus</i> Rauschert & Andres 1993	
Gnathopods with relatively small difference in size and shape, gnathopod 1 carpus longer than or equal to propodus, palm rounded.....	<i>Ligulodactylus</i> Krapp-Schickel 2013	

Table 1 Epifauna living on colonies of the black coral *Antipathella wollastoni*. For each taxon, the total abundances recorded during the study, and their proportion with respect to the total epifaunal abundance, are shown

Phylum	Class	Order	Family/genus/species	Abundance	Relative abundance (%)
Arthropoda	Malacostraca	Amphipoda	<i>Wollastenothoe minuta</i> gen. nov., sp. nov	1496	86.17
Arthropoda	Malacostraca	Amphipoda	<i>Phtisica marina</i>	145	8.35
Arthropoda	Malacostraca	Amphipoda	Pleustidae sp.	62	3.57
Arthropoda	Malacostraca	Amphipoda	<i>Jassa</i> sp.	1	0.06
Arthropoda	Malacostraca	Amphipoda	Oedicerotidae sp.	1	0.06
Arthropoda	Malacostraca	Amphipoda	Lyssianasidae sp.	1	0.06
Arthropoda	Malacostraca	Decapoda	<i>Dardanus arrosor</i>	1	0.06
Arthropoda	Malacostraca	Decapoda	Hippolytidae sp.	17	0.98
Arthropoda	Polychaeta	–	–	4	0.23
Mollusca	Gastropoda	–	–	8	0.46

Fig. 8 Temporal variation in the total abundance of amphipods (a) and *Wollastenothoe minuta* gen. nov., sp. nov. (b), at T1 (February), T2 (April) and T3 (October). Relationship between colony size of *Antipathella wollastoni* and the total abundance of amphipods (c) and *W. minuta* gen. nov., sp. nov., at different times (d)

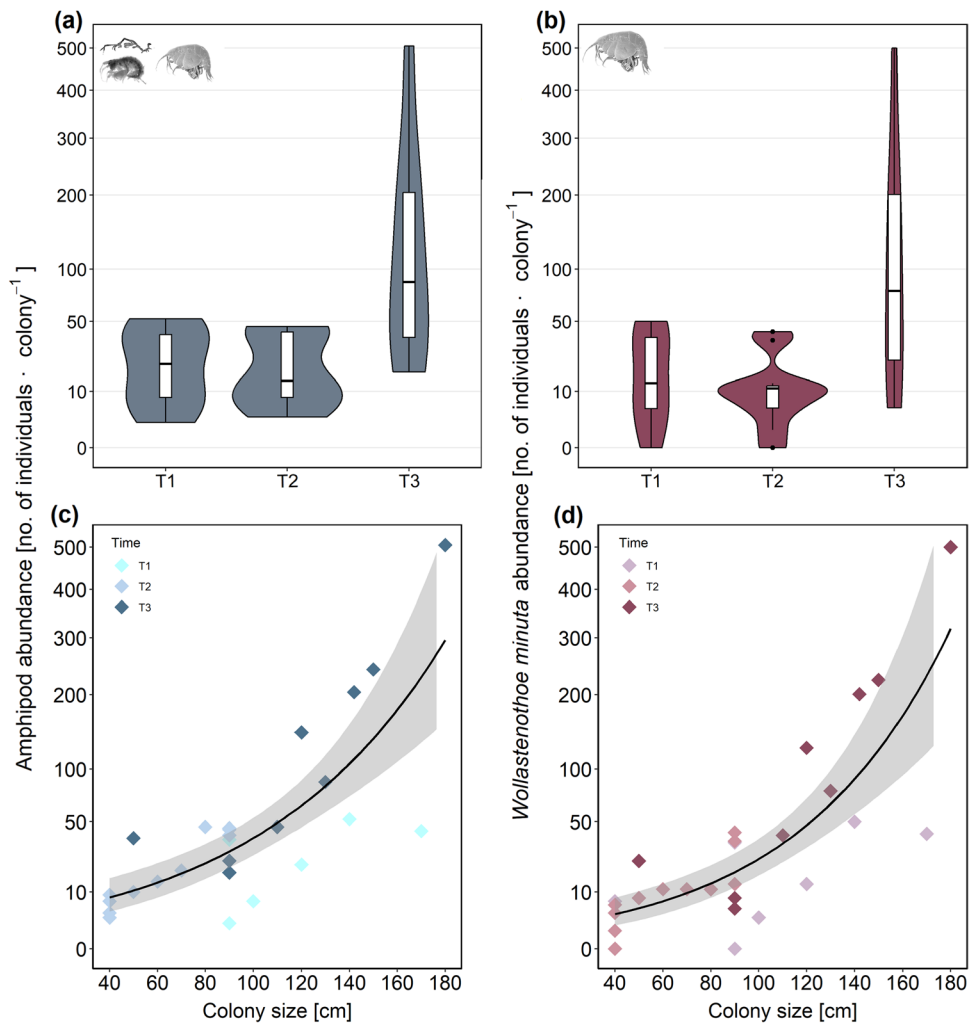
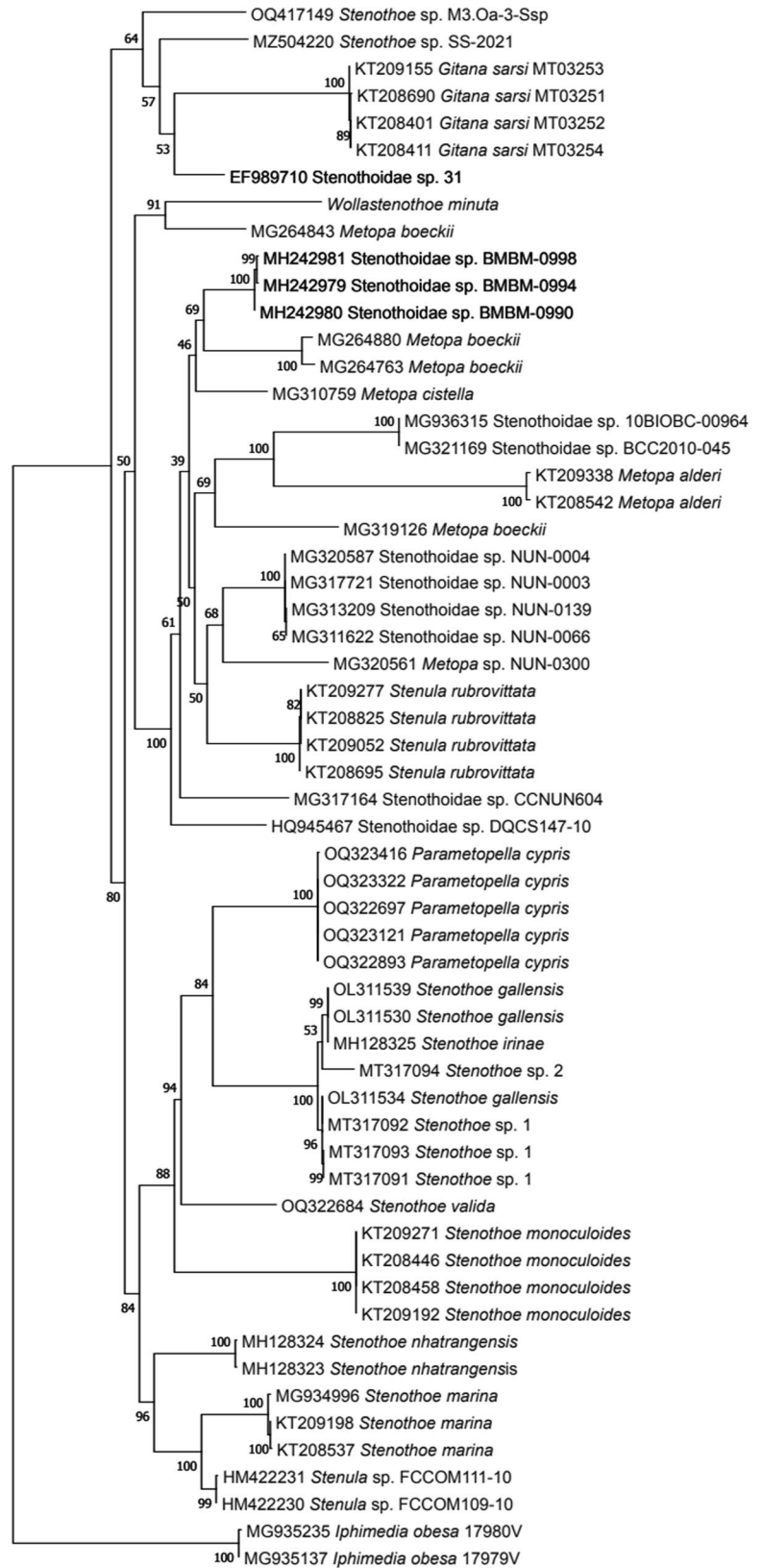


Fig. 9 Maximum-likelihood tree obtained using IQtree2 with 100,000 ultrafast bootstraps showing the relationships between *Wollastenothoe minuta* gen. nov., sp. nov., and other Stenothoidae COI sequences available in GenBank. *Iphimedia obesa* (Iphimediidae) and *Gitana sarsi* (Amphilochiidae) were used as outgroups. These sequences attributed to Stenothoidae grouped with *Gitana sarsi* suggesting that these sequences may come from misidentified specimens, but as the corresponding nodes have low ultrafast bootstrap support values (<65%), this grouping is not strongly supported



Abundance patterns

In total, 1,736 epifaunal individuals were sampled, with amphipods representing a 98.3% of the total epifauna (Table 1); there were 1,721 amphipods belonging to 6 species (Table 1). Significant variation in the total abundance of amphipod was mainly explained by colony size ($Pseudo-R^2=0.85$; Table S1), while the random factor time hardly explained variability ($Pseudo-R^2=0.13$). The highest abundances of amphipods (mean \pm SE) were recorded in T3 (163.3 ± 36.2 ind. colony⁻¹), relative to T1 and T2 (27.6 ± 8.7 and 35.1 ± 9.4 ind. colony⁻¹, respectively; Fig. 8a; Table S2). *Wollastenothoe minuta* gen. nov., sp. nov., was the most abundant species (Table 1) over time, accounting for 86.6% of amphipods in T1, 59.3% in T2 and 92% in T3 (Fig. 8b). These differences were mostly explained by colony size ($Pseudo-R^2=0.97$; Table S1) and, to a lesser extent, by different sampling times ($Pseudo-R^2=0.10$). A significant positive correlation between the total abundance of amphipods and the size of the coral colonies was found, i.e., the bigger the colonies, the larger the abundances of amphipods (Fig. 8c). A similar pattern was found for *W. minuta* gen. nov., sp. nov. (Fig. 8d). The highest abundances found in T3 (October) coincided with the higher average monthly temperature recorded in our study (Fig. S1).

The new genus and species were found with other amphipod species belonging to five different families: Caprellidae (i.e., *Phthisica marina* Slabber 1769), Pleustidae (Buchholz, 1874), Ischyroceridae Stebbing, 1899 (i.e., *Jassa* Leach, 1814), Lysianassidae (Dana, 1849) and Oedicerotidae (Lilljeborg, 1965).

Phylogeny

Molecular data were successfully obtained at the two independent loci investigated. The COI sequence (GenBank accession number PP595991) was 658 bp length, and molecular phylogenetic analyses were consistent with the position of the new genus and species within the Stenothoidae family (Fig. 9), confirming its distinctiveness from other genera for which COI sequence data are currently available. The closest sequence (p-distance = 0.25) was from a specimen identified as *Metopa boeckii* G.O. Sars, 1892, but sequences attributed to this species were found at three different places in our Stenothoidae COI tree (with p-distances among them of about 0.25), suggesting that some of these sequences come from misidentified specimens. The 28S sequence fragment (GenBank accession number PP594429) was 1025 bp long—due to the dearth of Stenothoidae 28S sequences currently available in GenBank; no phylogenetic analysis was conducted for this marker.

Discussion

This is the first study to date describing the temporal patterns of a new genus and species of amphipod associated with a black coral (i.e., *Antipathella wollastoni*). *Wollastenothoe minuta* gen. nov., sp. nov., was the most abundant and recurrent over time amphipod associated with this habitat, and we found that the abundances of this new genus and species were directly related to colony size.

The 46 valid genera of Stenothoidae include around 280 species (Horton et al. 2022), among which the genera *Metopa* Boeck 1871 and *Stenothoe* Dana 1852 are represented by more than 40% of the total species. Among these, 17 genera include only one species, and 10 genera are represented by only 2 species (Horton et al. 2022). *W. minuta* gen. nov., sp. nov., represents the eleventh monotypic genus and the tenth Stenothoid genus in European waters. Its small size (i.e., 1.21—1.45 mm), combined with the difficult accessibility of the mesophotic black coral habitat where the species lives, may explain why this genus had not been yet discovered. Our results suggest a high specificity of *W. minuta* gen. nov., sp. nov., for *A. wollastoni* as a host. To date, studies conducted in other habitats from the Canary Islands such as rhodoliths (Otero-Ferrer et al. 2019; Navarro-Mayoral et al. 2020), seagrasses (i.e., *Cymodocea nodosa*; Navarro-Mayoral et al. 2023), seaweeds (i.e., *Caulerpa prolifera*; Tuya et al. 2014), or sediments (Riera et al. 2012) have not revealed the presence of this genus and species.

Many species of amphipods live in close association with a wide variety of cnidarians (e.g., sea anemones, gorgonians and corals), through different types of specializations with their hosts (Vader 1983), which vary depending on the family and genus. Amphipods on black corals have been described as opportunistic (Wagner et al. 2012), based on the observations of caprellid amphipods feeding on living tissue of *Antipathes* sp., which led to the death of the entire colony (Tazioli et al. 2007). However, these observations are limited to caprellids and cannot be extended to all amphipods. Furthermore, it is not clear if the cause of death of *Antipathes* sp. is directly linked to the presence of amphipods, or to any previous disturbance. In our study with *A. wollastoni*, we reported a different pattern relative to Tazioli et al. (2007), with large abundances of amphipods that varied over time, while we did not observe any tissue necrosis of colonies throughout the study (almost 1 year). In fact, the most abundant species, *W. minuta* gen. nov., sp. nov., belongs to Stenothoidae, a family that include some species which tends to establish a biological association and display a strongly specificity with their hosts, as it has been observed with hydroids, for example (Vader and Krapp-Schickel 1996). This fact implies that amphipods spend their entire

life cycle on their hosts, where they find shelter and food, such as *Stenothoe brevicornis* with the sea anemone *Actinostola callosa* (Vader 1983). Regarding the relationships between corals and amphipods, multiple ecological roles between them have been reported. *Stenula nordmanni*, for example, was observed in mutualistic relationship with some octocorals (e.g., *Gersemia rubiformis*, Caulier et al. 2021) and *Stenothoe valida* in commensalism with some hydrocorals (e.g., *Millepora complanata*, Lewis 1992). Understanding the interspecific relationships between black corals and amphipods is of great importance, especially in the case of *W. minuta* gen. nov., sp. nov., which was the dominant species over time in all *A. wollastoni* colonies. Regarding their population structure, we did not find any males among the dissected individuals. This result was expected, considering that we dissected 68 specimens out of 1496, and other studies have observed a skewed sex ratio toward females in species of the family Stenothoidae, such as *Stenothoe valida* that exhibited a sex ratio of up to 0.79 for females (Lee and Park 2021).

We found that amphipods were the dominant epifauna on *A. wollastoni* colonies over time, accounting for 98.3% of the total abundances, with *W. minuta* gen. nov., sp. nov., as the most abundant species by far (87.6% of the amphipods). Contrary to our results, the few previous studies on epifauna associated with black corals did not report a dominance of amphipods (Bo et al. 2012; Wagner et al. 2012; Deidun et al. 2015; Matamoros-Calderón et al. 2021), except Love et al. (2007), who reported a dominance of the amphipod *Erichthonius rubricornis* Stimpson 1853 on *Antipathes dendrochristos* Opresko 2005. However, this result was obtained from a single dead coral colony, and it is not easily comparable with our results, as in this case it is not sure if amphipods may be found in living colonies. Moreover, in our study, the abundances of amphipods were consistently large throughout the study, despite some variation among times. We observed the colonization of the near sea bottom by epibionts, such as sponges (e.g., *Axinella* spp.), and the presence of ascidians (e.g., *Stolonica* sp. and *Pycnoclavella* sp.) on the branches of *A. wollastoni*, but in the latter case the presence in the colonies was relatively infrequent or rare. Temporal variation in the abundances of amphipods can be attributed to changes in habitat structure throughout varying time scales, which alter habitat complexity via increased occurrence of epiphytes and associated algae (Jacobucci et al. 2009; Navarro-Mayoral et al. 2020). However, unlike other ecosystem engineers, such as seagrasses (e.g., *Zostera noltii*; Vermaat and Verhagen 1996), the primary habitat generated by *A. wollastoni* is stable over time and does not experience seasonal changes.

Our results showed that variation in amphipod abundances was correlated by the size of the colonies of *A. wollastoni*, with a significant (positive) relationship between

coral colony size and amphipod abundances, both for the entire amphipod assemblage and for *W. minuta* gen. nov., sp. nov. Moreover, there is a colony size influence on the high variability of abundances within the times, especially in T3, where a greater difference in heights between the randomly selected colonies led to larger variations in abundances between replicates. Therefore, this suggests that the presence of amphipods is determined by habitat availability (i.e., colony size). Colonies of *A. wollastoni* dwell on rocky platforms, where they provide three-dimensional complexity to the substratum, offering a variety of microhabitats for several species (Czechowska et al. 2020). When *A. wollastoni* colonies are dense enough, they form a canopy (marine animal forest, sensu Rossi et al. 2017) that gives shelter and protection against strong currents and predators (Buhl-Mortensen et al. 2018). Thus, amphipods can benefit from different habitats provided by black corals, including (1) branches surface, (2) cavities within tissues or skeletons, and (3) free space between branches (Buhl-Mortensen and Mortensen 2004). This is consistent with the relatively large body of research that relates differences in abundances of marine invertebrates, in general, and amphipods in particular, with changes in the availability of habitat (Osman 1977; Aikins and Kikuchi 2001), so a higher abundance is observed in habitats with greater complexity and more available surface. Moreover, at these depths, there is a more limited availability of biogenic habitats compared to shallow waters, e.g., coral reefs, kelp forests, or seagrass meadows (Arfianti and Costello 2020a, b). Thus, the presence of *A. wollastoni* provides a 3-dimensional habitat for many species.

We found that the highest amphipod abundances were recorded in October (T3), which coincided with the highest temperature recorded. Some amphipods in shallow water environments show a turnover (i.e., growth and reproduction), which it is commonly adjusted to seasonal variation in terms of environmental conditions (e.g., temperature, photoperiod) and food resources (e.g., epiphytic biomass for herbivorous amphipods) (Neuparth et al. 2002; Martins et al. 2002; Navarro-Mayoral et al. 2020; Fernandez-Gonzalez et al. 2021). It is known that the temperature-induced changes in amphipod metabolic rates can lead to important physiological constraints to reproduction and determine of life history patterns of amphipods (Sainte-Marie 1991). For example, under laboratory conditions, *Gammarus locusta* showed faster individual growth, anticipated age at maturity, and higher population growth rate at a temperature of 20°C compared to 15°C (Neuparth et al. 2002). In our case, the difference between the minimum and maximum temperatures was 3.9°C and controlled studies would be necessary to know exactly the direct relationship between temperature and the abundances of *W. minuta* gen. nov., sp. nov. Of course, temperature is typically correlated with a range of environmental and

ecological processes. For example, an interesting observation was that the highest abundances of *W. minuta* gen. nov., sp. nov., coincided with a high amount of mucus generated by the colonies (personal observations). Mucus production is a strategy adopted by corals to obtain protection against sedimentation, which also plays a role in the food chain of habitats generated by corals (Galil 1987; Vytöpil and Willis 2001; Wee et al. 2019; Fraser et al. 2020). Thus, mucus can catch detritus and phytoplankton that facilitate the feeding of amphipods, as observed in decapod taxa that feed on particles trapped by coral mucus (Galil 1987). Most of the species of the Stenothoid family are detritivorous and/or carnivorous species (Krapp-Schickel 1993; Moore et al. 1994; Sano et al. 2003; Tandberg et al. 2010; Auster et al. 2011; Vázquez-Luis et al. 2013; Guerra-García et al. 2014; Sedano et al. 2020), and *W. minuta* gen. nov., sp. nov., could take advantage of *A. wollastoni* secretions for feeding. Therefore, the amount of food available in the form of mucus could also be playing a role in the abundance pattern of amphipods, and specially of *W. minuta* gen. nov., sp. nov. However, more studies are needed to clarify the biological associations between deep-sea corals and epifauna, particularly focusing on the relationship between this black coral and this new genus and species of amphipod that dominated the associated epifauna community over time. Overall, this study supports that black coral forests in mesophotic depths have enormous potential for overlooked biodiversity and that much of the associated diversity remains undescribed.

Conclusions

We here reported patterns in composition and abundances of epifauna associated with *Antipathella wollastoni* over time, showing that amphipods were the dominant group. Our results confirmed that marine animal forests host an important, but somehow unknown, associated biodiversity. The new genus and species of the Stenothoidae family seem to be coral specific, displaying a direct relationship with the availability of habitat generated by the coral host. Our study reinforces the necessity to increase research effort in animal forest to improve management and conservation of these key habitats.

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Author's contribution Conceptualization was performed by FOF, LB, SNM; method design by FOF, LB, SNM; investigation by FOF, LB, SNM, LT, FE, RH; analysis by SNM, FT; interpretation of data by SNM, FT, FOF, LB; taxonomy work by BG, SNM, VFG; drawings and taxonomic preparation by BG; DNA extraction, PCR amplification, and

nanopore sequencing by NL; assembly and analysis of DNA sequences by JFF; funding acquisition by FOF, LT, JFF; supervision by FOF, FT; writing—original draft preparation by SNM; writing—review and editing by all authors.

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Declarations

Conflict of interest All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript. The contents of this document are the sole responsibility of the authors and can, under no circumstances, be regarded as reflecting the position of the EU, nor of the OFB and AFD.

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