



Taxonomic assessment of deep-sea decapod crustaceans collected from polymetallic nodule fields of the East Pacific Ocean using an integrative approach

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Abstract

Deep-sea decapod crustaceans (Crustacea: Decapoda) collected during nine research cruises to the Clarion-Clipperton Zone (CCZ) in the NE Pacific Ocean and the Peru Basin in the SE Pacific Ocean were studied comprehensively using an integrative taxonomic approach. The abyssal seafloors of both areas are rich in economically interesting polymetallic nodules. All specimens were morphologically identified and genetically analysed using a fragment of the mitochondrial cytochrome c oxidase subunit I (COI). Eight species were collected, comprising three anomurans, three carideans, one dendrobranchiate, and one brachyuran, from water depths ranging between 4089 and 4511 m. COI sequences for representatives of the genera *Parapagurus* Smith, 1879, *Ethusina* SI Smith, 1884, and *Bathystylodactylus* Hanamura & Takeda, 1996 are provided for the first time. The molecular barcodes of the species provided herein will be valuable for the full taxonomic assignment of sequences produced in future metabarcoding and eDNA monitoring work. The new records extend the geographical distributional ranges or fill geographical gaps of the species reported, although none of the species is endemic to polymetallic nodule areas. This study is part of a taxonomic series aiming to describe the biodiversity of areas targeted for future deep-sea mining.

Keywords Deep-sea mining · Anomura · Brachyura · Caridea · Dendrobranchiata · Peru Basin · Clarion-Clipperton Zone

Introduction

In large parts of the world's oceans, nodules rich in valuable metals such as Ni, Cu, Co and Mn (Hein et al. 2013; Miller et al. 2018) are present at abyssal depths. These areas have been identified as being of economic interest and are being targeted for potential mining, despite the hitherto limited information on their

intrinsic biodiversity (Amon et al. 2016). The largest known deposits of polymetallic nodules occur in the Clarion-Clipperton Zone (CCZ), spanning an area of about 6 million km² in size between Hawaii and Mexico. Additional important occurrences have been found in the Peru Basin (e.g. Hein et al. 2013; Miller et al. 2018), around the Cook Islands (Hein et al. 2015), and in the Central Indian Ocean (Mukhopadhyay et al. 2008). Nodule mining comes with significant environmental concerns, such as habitat loss, fragmentation or modification after the removal of nodules and associated organisms, and the generation of sediment plumes that may bury organisms or clog their feeding apparatuses (Ramirez-Llodra et al. 2011; Vanreusel et al. 2016; Van Dover et al. 2017; Niner et al. 2018; Stratmann et al. 2018). Studies have suggested that abyssal fields appear to support higher densities of both sessile and mobile epifauna in locations with high nodule coverage compared to those lacking nodules (Amon et al. 2016; Vanreusel et al. 2016; Simon-Lledó et al. 2019a, 2019b, 2019c, 2020). The deposits of the CCZ as well as those of the Peru Basin and the Indian Ocean lie in waters beyond National Jurisdictions, and thus fall under the legal mandate of the International Seabed Authority, ISA (Wedding et al. 2013). The ISA has issued, so far,

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16 contract areas for the exploration for polymetallic nodules in the CCZ. Prior to exploitation, a benthic biological baseline study must be undertaken by the contractor for each exploration area, and effective environmental impact assessments and management, monitoring and contingency plans responding to possible environmental impacts arising from mining should be developed (Wedding et al. 2015). Furthermore, the ISA assigned a series of Areas of Particular Environmental Interest (APEIs) outside these contract areas, where exploitation is prohibited. The thirteen APEIs areas were installed to preserve and protect source populations, which may then recolonize future impacted areas (Lodge et al. 2014). Accurate documentation of species diversity and geographic distribution are essential for marine ecosystems' management, which, despite recent scientific studies (i.e. Kersken et al. 2018, 2019; Jakiel et al. 2019; Christodoulou et al. 2020; Malyutina et al. 2020; Gooday et al. 2020), still remains poorly documented across the CCZ.

Decapods are one of the most diverse group of crustaceans numbering over 15,000 living species (De Grave et al. 2009), and are a significant faunal component in an impressive variety of habitats, although the majority of decapods are marine species with ranges spanning intertidal to hadal depths (Jamieson et al. 2009). Because of their ecological and morphological diversity, and coupled with their economic importance and size, they are the most thoroughly studied of all crustaceans. Nevertheless, studies describing the abyssal decapod fauna and specifically that of polymetallic areas of the East Pacific are limited, including a few historical studies resulting from the great expeditions of the late nineteenth and early twentieth centuries such as “HMS Challenger” (Spence Bate 1888) and “Albatross” (Faxon 1893, 1895). Only a handful of recent studies exist, all reporting a number of image-based putative species (Amon et al. 2017; Simon-Lledó et al. 2019a). As such, the diversity of the deep-sea decapod fauna in the CCZ and Peru Basin remain only fragmentarily known. Thus, the aim of this study was to provide morphology-based species identifications of decapods together with molecular species assignments using COI sequences in an integrative approach, thereby compiling a reference library for future genetic work.

Material and methods

Study areas

The study areas (Fig. 1) are located within the Clarion and Clipperton Zone (CCZ) in the northeast equatorial Pacific Ocean and at the DISCOL Experimental Area (DEA) in the Peru Basin, an area in which the German project DISCOL (DISturbance and reCOLonisation experiment) was performed in the late 1980s (Thiel and Schriever 1990; Thiel et al. 2001). Water depths vary from 4050 m to 4933 m (Hein et al. 2013). In the CCZ, Decapod samples were collected from the UKSRL and

OMS contract areas (UK Seabed Resources Ltd, UK; Ocean Mineral Singapore Ltd), the BGR contract area (German Federal Institute for Geoscience and Natural Resources, Germany) and the GSR contract area (Global Sea Mineral Resources NV, Belgium), as well as from one APEI (APEI#6) during nine scientific cruises between 2013 and 2019: ABYSSLINE I (R/V *Melville*), ABYSSLINE II (R/V *Thompson*), MANGAN 2013 (R/V *Kilo Moana*), JPIO-EcoResponse/SO239 (R/V *Sonne*), MIDAS JC120 (R/V James Cook), MANGAN 2016 (R/V *Kilo Moana*), MANGAN 2018 (R/V *Sonne*), and JPIO-Mining Impact/SO268-1, SO268-2 (R/V *Sonne*). Furthermore, the DEA area in the Peru Basin was revisited in 2015 in the framework of the JPIO Pilot Action “Ecological Aspects of Deep-Sea Mining”. Decapod samples were collected from the DEA during cruise SO241-2 using the R/V *Sonne*.

Specimen sampling and processing

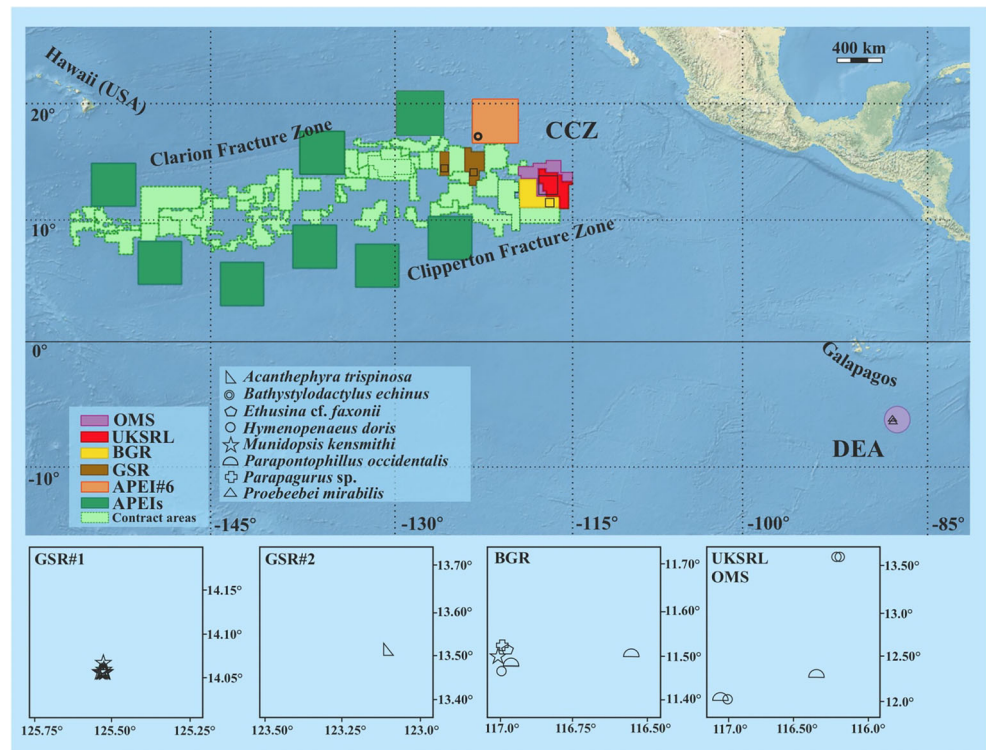
Anomura and Brachyura were collected with a remotely operated vehicle (ROV 6000, Kiel, GEOMAR) using either the ROV's suction sampler or the manipulator arm by direct picking. Following their collection, specimens were preserved in pre-cooled 96% EtOH. For all specimens the ethanol was decanted after 24 hours and replaced with new 96% EtOH to guarantee sufficient ethanol concentration for preservation of high-quality DNA, and subsequently stored at -20°C . Caridea and Dendrobranchiata were collected using baited traps, trawling and a Brenke-type epibenthic sledge (EBS), following standard deployment procedures (Brenke 2005). The cod ends of the suprabenthic- and epibenthic-net were sieved through a 500 μm - and 300 μm -mesh with cold ($+10^{\circ}\text{C}$) sea water and immediately transferred to pre-cooled (-20°C) 96% EtOH. In the laboratory at Senckenberg am Meer, Germany, an integrative molecular-morphological approach was implemented for the identification of the decapod specimens. Voucher specimens are stored at Senckenberg am Meer, DZMB, Wilhelmshaven, Germany and in the Oxford University Museum of Natural History, Oxford, UK. Carapace length (cl) was measured from the posterior margin of the orbit to the posterior margin of the carapace for the Caridea and Dendrobranchiata, and from the tip of the frontal teeth to the posterior margin of the carapace for the Brachyura. Postorbital carapace length (pcl) and shield length (sl) was measured from the tip of the rostrum to the midpoint of the posterior margin of the carapace or shield in Munidopsidae and Parapaguridae, respectively.

Barcoding data collection

DNA extraction, amplification, and sequencing

For the mtDNA COI analyses, genomic DNA was extracted from abdominal or pereopod tissue. DNA extractions were

Fig. 1 Compilation of study areas in the Clarion-Clipperton Zone (CCZ) and in the DISCOL Experimental Area (DEA, Peru Basin). Insets represent detailed maps of sampling locations in the GSR#1, GSR#2, OMS, BGR and UKSRL exploration contract areas for polymetallic nodules. Copyright for shapefiles (for CCZ area): © International Seabed Authority 2009–2019; copyright for raster file (bathymetry): © Natural Earth 2009–2020



carried out using 30 μL Chelex (InstaGene Matrix, Bio-Rad) according to the protocol of Estoup et al. (1996) and directly used as DNA template for PCR. All DNA samples were stored at -20°C . A fragment of 658bp of the mitochondrial cytochrome c oxidase subunit (COI) was amplified by polymerase chain reaction (PCR). Amplifications were performed using AccuStart PCR SuperMix (ThermoFisher Scientific) in a 25- μL volume containing 12.5 μL AccuStart PCR SuperMix, 9.5 μL ddH₂O, 0.5 μL of each primer (10 pmol μL^{-1}) and 2 μL of DNA template. For the COI amplification the forward primer jgLCO1490 and the reverse primer jgHCO2198 (Geller et al. 2013), tailed with M13F and M13R-pUC, respectively were used. The amplification conditions consisted of an initial denaturation step of 3 min at 94°C , 35 cycles of 30 s at 94°C , 60 s at 47°C and 1 min at 72°C , followed by a final extension step of 5 min at 72°C . All PCR products were purified using ExoSap-IT (ThermoFisher Scientific). Amplified fragments were sequenced in both directions at MacroGen Europe Laboratory (Amsterdam, The Netherlands).

Alignment, genetic divergence

The obtained COI sequences were compared with the GenBank nucleotide database using BLASTN (Altschul et al. 1990). Forward and reverse sequences for each individual were assembled and edited using Geneious v.9.1.7 (www.geneious.com; Kearse et al. 2012). The edited COI

sequences and over 500 bp in length were aligned using MAFFT v7.308 under G-INS-I algorithm (Katoh et al. 2002), while alignments were further manually edited. The sequence of *B. echinus* was omitted from the alignment because of its short length (315 bp). Sequence data are available in GenBank (Table 1). The sequences, trace files, collection data and photos for each specimen are listed in the datasets CCZ-DEA_Decapoda (<https://doi.org/10.5883/DS-CCZ2>) in BOLD (Ratnasingham and Hebert 2007).

Results

Taxonomic and systematic remarks

Order Decapoda Latreille, 1802

Suborder Dendrobranchiata Spence Bate, 1888

Family Solenoceridae Wood-Mason in Wood-Mason & Alcock, 1891

Hymenopenaeus doris (Faxon, 1893)

(Fig. 2)

Haliporus doris Faxon 1893: 214 [type locality: off Cabo Velas, Costa Rica, $10^{\circ}14'N$ $96^{\circ}28'W$, 4082 m, *Albatross* stn. 3414; S of Punta Maldonado, Guerrero, Mexico, $14^{\circ}46'N$ $98^{\circ}40'W$, 3436 m, *Albatross* stn. 3415]. — Faxon 1895: 191; Plate 49, Figs. 1a–c.

Hymenopenaeus doris. — Burkenroad 1938: 60. — Crosnier and Forest 1973: Fig. 83d. — Perez-Farfante 1977: 283; Figs.

Table 1 Specimen codes, collection area, BIN, and GenBank accession numbers for COI sequences of the specimens collected in the present study

Species	Specimen code	Area collected	BIN	GenBank accession number
<i>Hymenopenaeus doris</i>	AB01_TR01_1	CCZ-UKSRL	ADJ1207	OM892127
	AB01_TR01_2	CCZ-UKSRL	ADJ1207	OM892117
	AB02_EB04_1	CCZ-OMS	ADJ1207	OM892125
	MA13_18_35	CCZ-BGR	ADJ1207	OM892118
<i>Munidopsis kensmithi</i>	SO268-1_75	CCZ-GSR	AEE8202	OM892130
	SO268-1_101	CCZ-GSR	AEE8202	OM892126
	SO268-2_32	CCZ-GSR	AEE8202	OM892124
	SO268-2_43	CCZ-GSR	AEE8202	OM892114
	SO268-2_44	CCZ-GSR	AEE8202	OM892123
	SO268-2_45	CCZ-GSR	AEE8202	OM892120
	SO268-2_46	CCZ-GSR	AEE8202	OM892119
	SO242-2_216_1	DEA	AEF2798	OM892131
SO242-2_222_1	DEA	AEF2798	OM892112	
<i>Parapagurus microps</i>	SO268-2_95	CCZ-BGR	AEE1943	OM892128
<i>Ethusina cf. faxonii</i>	SO268-2_137	CCZ-BGR	AEF1483	OM892122
<i>Acanthephyra trispinosa</i>	SO239_133_1252	CCZ-GSR	AEE1684	OM892121
<i>Parapontophilus occidentalis</i>	AB02_EB04_2	CCZ-OMS	ADP7198	OM892113
	AB02_EB07_1	CCZ-UKSRL	ADP7198	OM892115
	MA16_28_1	CCZ-BGR	ADP7198	OM892116
	MA18_59_1	CCZ-BGR	ADP7198	OM892129
<i>Bathystylodactylus echinus</i>	OUMNH-ZC.2018.01.041	CCZ-APEI-6	-----	OM951239

9, 17, 18a, 19-20. — Hanamura 1983: 55; Fig. 2. — Hendrickx 2001: 97. — Hendrickx 2008: 999; Fig. 1. — Hendrickx 2013: 442.

Aliporis doris. — del Solar 1972: 7.

Material examined. Clarion Clipperton Zone: ABYSSLINE1 cruise, R/V *Melville*, stn. TR01 (baited trap),

13°52.933N 116°26.931W (UKSRL contract area), 4203 m, 08.10.2013, 2 females, cl 30.2 mm (AB01_TR01_1) and 24.9 mm (AB01_TR01_2); ABYSSLINE2 cruise, R/V *Thompson*, stn. EB04 (epibenthic sled), 12°07.83N 117°18.67W (OMS contract area), 4111 m, 25.02.2015, 1 female, cl 6.1 mm (AB02_EB04_1); MANGAN13 cruise, R/V *Kilo Moana*, stn. 18EBS (epibenthic sled), 11°49.754N

Fig. 2 *Hymenopenaeus doris* (Faxon, 1893): female (cl 24.9 mm), AB01_TR01_2, lateral view. Scale 1.0 cm (photo by Inga Mohrbeck)



117°0.371W (BGR contract area), 4133 m, 14.03.2013, 1 male, cl 20.0 mm (MA13_18_35).

Distribution. Eastern Pacific Ocean. Previously known from Mexico (Gulf of California, south of Punta Maldonado), Costa Rica (off Cabo Velas, Cocos Island), Peru (Guanape) and Dowd Tablemount in the Northeast Pacific; at depths of 549–4082 m (Faxon 1893; Burkenroad 1938; del Solar 1972; Perez-Farfante 1977; Hanamura 1983; Hendrickx 2001, 2008, 2013). The present specimens reported from the UKSRL, OMS and BGR contract areas at depths of 4078–4203 m represent new records for the CCZ, slightly extending the known geographical range of the species to the west and its bathymetric distribution by more than 120 m.

Remarks. The genus *Hymenopenaeus* Smith, 1882 is currently composed of 17 species, with the vast majority occurring in the Indian and Pacific Oceans (Perez-Farfante 1977; Crosnier 1995; Crosnier and Dall 2004). In the East Pacific where the CCZ is located, only *H. doris* and *H. nereus* (Faxon, 1893) are known to occur (Hendrickx 2008). *Hymenopenaeus nereus* has been reported from the CCZ and specifically from the UKSRL and BGR contract areas (as *H. cf. nereus*: Amon et al. 2017, as *H. nereus*: Hendrickx and Wicksten 2016; Harbour et al. 2020), while this is the first time *H. doris* is reported from this area. The females of *Hymenopenaeus doris* can be distinguished from those of *H. nereus* by having a strong setose triangular protrusion (cusp) between the bases of the fifth pereopods rather than a low non-dentate ridge and two triangular lamellae (projections) flanking the transverse diaphragm between the fourth pereopods (Faxon 1893, 1895; Burkenroad 1938; Crosnier and Forest 1973; Perez-Farfante 1977). The males of both species can be distinguished by the shape of their petasma and the form of their appendices masculina and interna (Hanamura 1983; Hendrickx 2008). The morphology of the largest female collected agrees well with the descriptions and illustrations provided by Faxon (1895), Crosnier and Forest (1973) and Perez-Farfante (1977). Although the cusp on the 14th sternite (between P5 bases) is not as dentate as illustrated by Crosnier and Forest (1973), a clear and strong cusp is present. The two smaller females differ from the typical form of *H. doris* by having a much smaller triangular cusp and less distinct triangular lamellae. The characteristics of the male specimen collected agree well with the description and illustrations provided by Hanamura (1983) picturing a younger individual than the one described by Hendrickx (2008).

This is the first time COI sequences (OM892117, OM892118, OM892125, OM892127) have been made available for this species. All collected specimens shared the same haplotype and differ significantly from other *Hymenopenaeus* species (p-distance: < 10.91%–17.14%) present in Genbank (Fig. 3).

Suborder Pleocyemata Burkenroad, 1963

Infraorder Anomura MacLeay, 1838

Superfamily Galattheoidea Samouelle, 1819

Family Munidopsidae Ortmann, 1898

***Munidopsis kensmithi* Jones & Macpherson, 2007**

(Fig. 4)

Munidopsis kensmithi Jones and Macpherson 2007: 485; Figs 5–6 [type locality: off California, 34°50'N 123°00'W, 4100 m]. — Dong et al. 2017: 394; Figs. 3b–c, 4c.

Material examined. Clarion Clipperton Zone: SO268-1 cruise, R/V *Sonne*, stn. 64 (dive ROV09), 14°06.76746'N 125°52.25934'W (GSR contract area), 4507 m, 17.03.2019, 1 male, pcl 34.93 mm (SO268-1_75); SO268-1 cruise, R/V *Sonne*, stn. 64 (dive ROV09), 14°06.7677'N 125°52.26018'W (GSR contract area), 4507 m, 17.03.2019, 1 female, pcl 35.31 mm (SO268-1_76). SO268-1 cruise, R/V *Sonne*, stn. 77 (dive ROV12), 14°07.10280'N 125°52.0356'W (GSR contract area), 4511 m, 20.03.2019, 1 female, pcl 33.47 mm (SO268-1_101). SO268-2 cruise, R/V *Sonne*, stn. 134 (dive ROV19), 14°06.78372'N 125°52.2565'W (GSR contract area), 4508 m, 17.04.2019, 1 female pcl 39.45 mm (SO268-2_32). SO268-2 cruise, R/V *Sonne*, stn. 137 (dive ROV20), 14°06.68514'N 125°52.30224'W (GSR contract area), 4496 m, 18.04.2019, 1 male, pcl 34.78 mm (SO268-2_43); SO268-2 cruise, R/V *Sonne*, stn. 137 (dive ROV20), 14°06.67074'N 125°52.2912'W (GSR contract area), 4497 m, 18.04.2019, 1 male, pcl 30.11 mm (SO268-2_44); SO268-2 cruise, R/V *Sonne*, stn. 137 (dive ROV20), 14°06.65148'N 125°52.27782'W (GSR contract area), 4496 m, 18.04.2019, 1 male, pcl 26.16 mm (SO268-2_45); SO268-2 cruise, R/V *Sonne*, stn. 137 (dive ROV20), 14°06.63096'N 125°52.26186'W (GSR contract area), 4496 m, 18.04.2019, 1 male, pcl 30.96 mm (SO268-2_46). SO268-2 cruise, R/V *Sonne*, stn. 174 (dive ROV28), 11°50.61690'N 117°03.49254'W (BGR contract area), 4137 m, 09.05.2019, 1 female, pcl 39.33 mm (SO268-2_131).

Distribution. Tropical Pacific Ocean. Previously known from off California (eastern Pacific Ocean) at 4100 m (Jones and Macpherson 2007) and Lamont Guyot, east Mariana Trench (tropical west Pacific Ocean) (Dong et al. 2017); at depths of 4100 and 4833 m respectively. The present study records the species in the CCZ, eastern Pacific Ocean for the first time, at 4137–4511 m.

Coloration in life. Whole body is pale-white. Cornea pale pink. However, *in-situ* photographs show a white-brown appearance because of sedimental mud on the body surface and pereopods (Fig. 2).

Remarks. The genus *Munidopsis* is the second most species-rich genus of squat lobsters, numbering 272 species (WoRMS Editorial Board, 2022; accessed at: 2022-05-11). In the Eastern Pacific the genus is represented by at least 48 species (Hendrickx and Ayón-Parente 2013; Poore 2014). *Munidopsis kensmithi* can be morphologically distinguished from all other *Munidopsis* species by the presence of

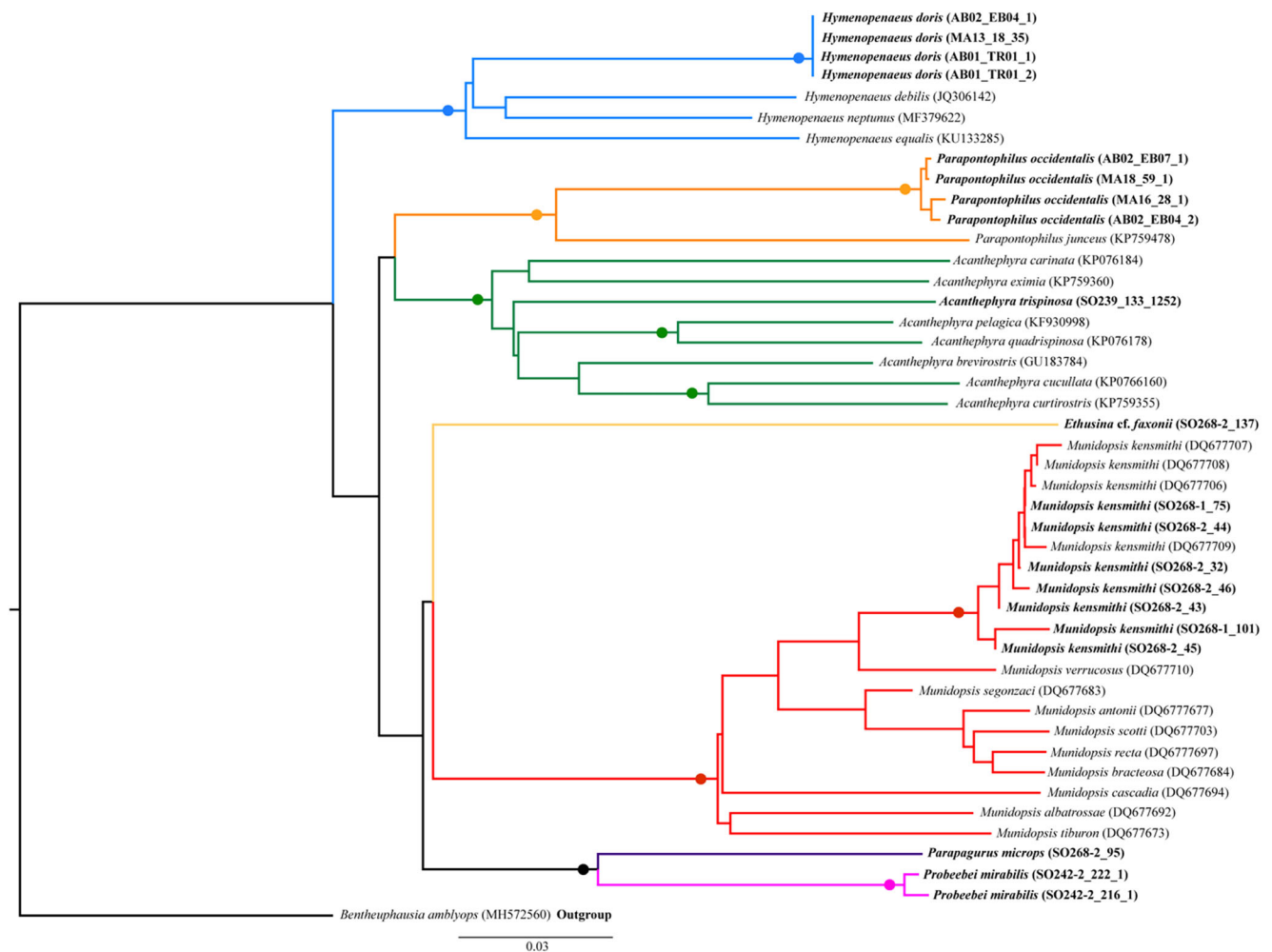


Fig. 3 Neighbour-joining tree (p-distance) based on COI DNA barcodes. Black circles on branches represent bootstrap supports over 90 %. Species studied in the current study are shown in bold

numerous granules on the dorsal surface of the carapace, pleon and pereopods; the presence of a spiniform median process on the second, third and fourth pleon segments; the narrower and slightly directed upwards rostrum; the longer distal spines of the antennular basal segment and the equal spacing between the penultimate and ultimate teeth and dactylus, respectively (Jones and Macpherson 2007). The present specimens agree well with the original description of *M. kensmithi* (Jones and Macpherson 2007) and represent the second record since its original description.

The COI sequences (OM892114, OM892119, OM892120, OM892123, OM892124, OM892126, OM892130) are identical or very similar (p-distance: < 0.0%–3.0%) to COI sequences from the type series of *M. kensmithi* (DQ677706–DQ677709). The mean intraspecific genetic divergence (p-distance) ranged from 0% to 3.0%, including the sequences provided in Jones and Macpherson (2007), while when compared with other *Munidopsis* species from the East Pacific Ocean (Fig. 3), the interspecific genetic divergence (p-distance) ranged from 5.3% to 13.98%.

Superfamily Paguroidea Latreille, 1802

Family Parapaguridae Smith, 1882

Probebeii mirabilis Boone, 1926

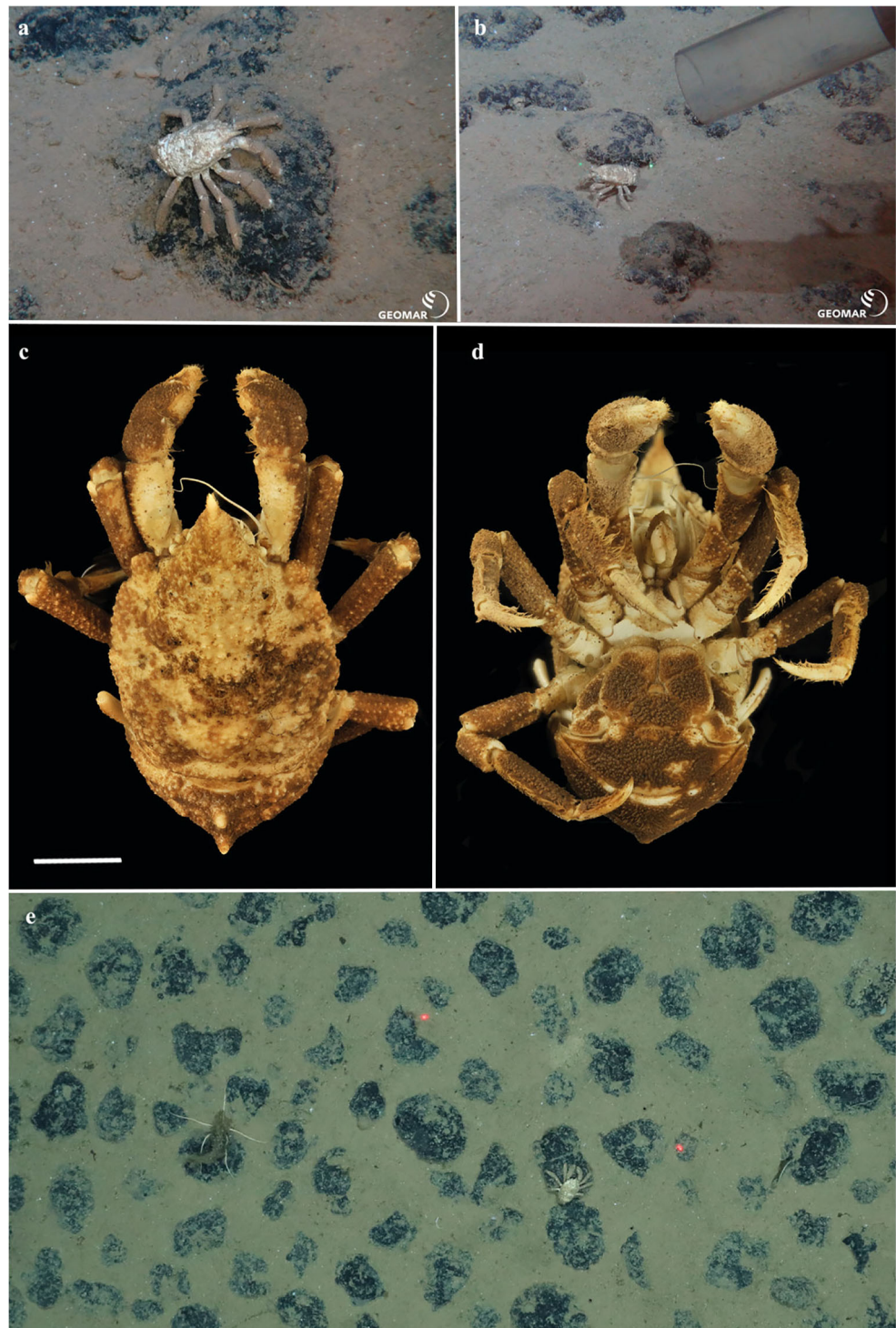
(Fig. 5)

Probebeii mirabilis Boone 1926: 73; unnumbered figure [type locality: eastern Pacific, off Peru, *Albatross* stn. 4647, 04°33'S 87°42'30"W, 3667 m]. — Wolff 1961: 12; Figs. 1–10. — Garth and Haig: 6.5. — Lemaitre 1998: 300; Figs. 2b–d, 3b. — Bluhm 2001: 3847. — Drazen et al. 2019: 3139; Fig. 6n.

Material examined. DISCOL Experimental Area (DEA), Peru Basin: SO242-2 cruise, R/V *Sonne*, stn. 216 (dive ROV19), 07°07.52781'S 88°27.05246'W, 4197 m, 22.09.2015, 1 male, sl 20.65 mm (SO242-2_216_1). SO242-2 cruise, R/V *Sonne*, stn. 222 (dive ROV21), 07°04.68467'S 88°27.46078'W, 4193 m, 24.09.2015, 1 male, sl 29.84 mm (SO242-2_222_1).

Distribution. East Pacific Ocean. Previously known from off Peru at 3869–3995 m (Garth and Haig 1971); south of Cocos

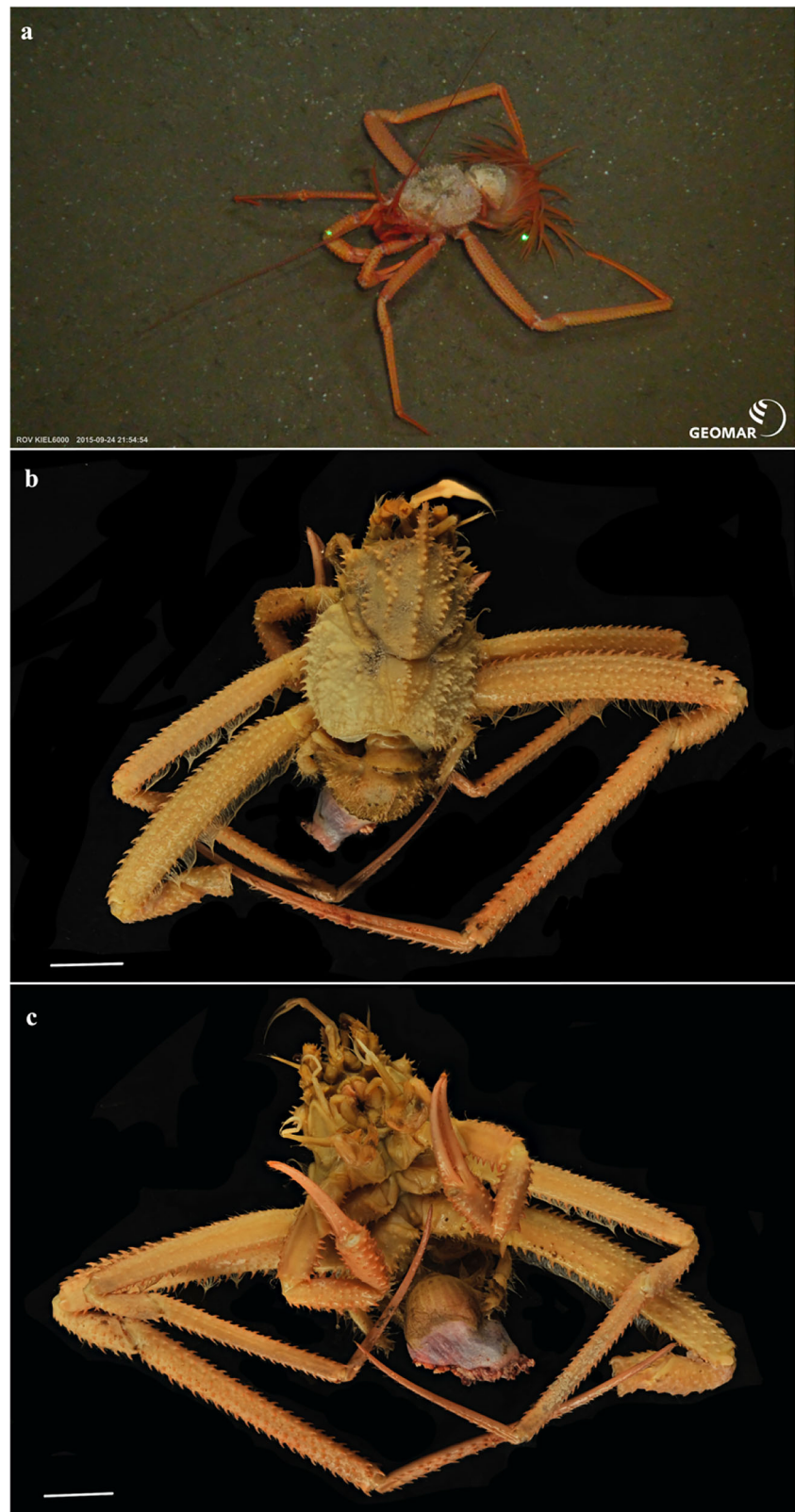
Fig. 4 *Munidopsis kensmithi* Jones & Macpherson, 2007: **a** male, pcl 30.96 mm (SO268-2_46) in situ; 1 female, pcl 33.47 mm (SO268-1_101); **b** in situ (up); **c** dorsal and ventral view (down). Scale 1.0 cm (photo by Nicol Mahnken) **d** example of *Munidopsis* cf. *kensmithi* image taken using OFOS



Island to southwest of Galapagos at 1145–4775 m depth (Lemaitre 1998); DISCOL Experimental Area (DEA) in the Peru Basin at 4057–4220 m (Bluhm 2001; Drazen et al. 2019). **Coloration in life.** Carapace and abdomen generally pale white; chelipeds and ambulatory legs pale orange. Cornea black (Fig. 5).

Remarks. *Probeebei mirabilis* is the sole species of the genus *Probeebei*, an exclusively abyssal inhabitant (Lemaitre 1998) found usually with an attached anemone on its pleon (Drazen et al. 2019; present study). *Probeebei mirabilis* resembles *Tylaspis anomala* Henderson, 1885, another parapagurid, in having a partially fused and calcified cephalothorax, unprotected by a gastropod, a unique character within parapagurids

Fig. 5 *Probeebei mirabilis*
Boone, 1926, male, sl 29.83 mm
(SO242-2_222_1): **a** *in situ*; **b**
dorsal view; **c** ventral view. Scale
1.0 cm (photos by Nicol
Mahnken)



but can easily be distinguished from *T. anomala* and other parapagurids by the long rostrum often exceeding the ocular peduncles (Lemaitre 1998). Additionally, the abdomen of

T. anomala is slightly twisted to the right and mostly membranous, while that of *P. mirabilis* is well-calcified (and asymmetrical in females) up to the fifth tergite and armed with

spines. The present male specimens, both bearing anemones on their pleons and having symmetrical abdomens, agree well with the description provided by Wolff (1961) and Lemaitre (1998).

This is the first time COI sequences (OM892112, OM892131) are available for this species. The COI sequences are very similar with an intraspecific variability (p-distance) of 0.76%.

***Parapagurus microps* de Saint Laurent, 1972**
(Fig. 6)

Parapagurus microps de Saint Laurent 1972: 104; Figs. 1, 13, Plate 1, Fig. 8 [type locality: Galapagos (0°04'S 117°07'W), 4250 m, *Albatross* stn. 4742]. — Lemaitre 1999: 322; Figs. 10 and 11.

Material examined. Clarion Clipperton Zone: SO268-2 cruise, R/V *Sonne*, stn. 163 (dive ROV25), 11°55.76172'N 117°01.43946'W (BGR contract area), 4089 m, 28.04.2019, 1 male, sl 9.85 mm (SO268-2_95).

Distribution. Eastern Pacific Ocean. *Parapagurus microps* was previously known from off the Galapagos Islands at 3812–4721 (de Saint Laurent 1972); the DISCOL

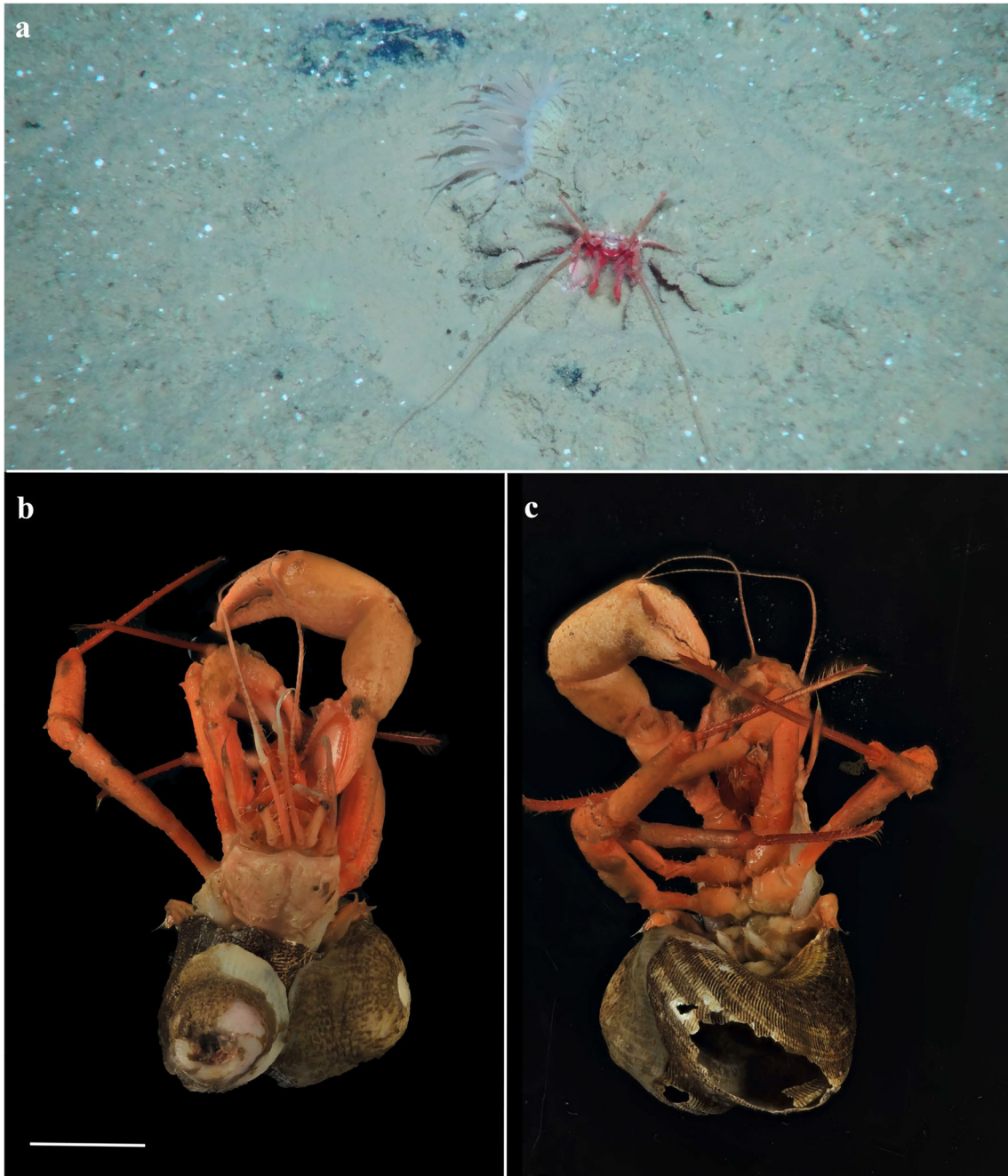


Fig. 6 *Parapagurus microps*., male, sl 9.85 mm (SO268-2_95): **a** *in situ*; **b**, **c** dorsal and ventral view. Scale 1.0 cm (photos by Nicol Mahnken)

Experimental Area at 4154–4261 m and off Peru at 2710–3080 m (Lemaitre 1999). The present specimens reported from the BGR contract area represent a new record of this species in the CCZ.

Coloration in life. Carapace and abdomen generally pale orange; chelipeds and ambulatory legs orange. Cornea black (Fig. 6).

Remarks. The genus *Parapagurus* Smith, 1879 is represented by 17 species worldwide (Lemaitre 1999). In the eastern Pacific, the following six species have been reported: *Parapagurus benedicti* de Saint Laurent, 1972; *P. foraminosus* Lemaitre, 1999; *P. holthuisi* Lemaitre, 1989; *P. janetae* Lemaitre, 1999; *P. microps* de Saint Laurent, 1972; *P. wolffi* Lemaitre, 1999. *Parapagurus microps* can be distinguished from its congeneric species in having the merus, carpus, and propodus of ambulatory legs armed on the mesial and lateral faces with numerous tubercles and spines, the anterodistal margin of the branchiostegite unarmed and the propodal rasp of the fourth pereopod with one irregular row of lanceolate scales. The collected specimen, bearing two anemones on its pleon, agrees well with these diagnostic characters.

This is the first time a COI sequence (OM892128) is available for this genus and species.

Infraorder Brachyura Latreille, 1802

Family Ethusidae Guinot, 1977

Ethusina cf. *faxonii* Rathbun, 1933

(Fig. 7)

Ethusina faxonii Rathbun 1933: 185, [type locality: S. of Gulf of Tehuantepec, 10°14'00"N 96°28'00"W, 4082 m, *Albatross* stn. 3414]. — Rathbun 1937: 93; Plate 26, Fig. 3; Plate 27, Fig. 3.—Garth 1960: 120. — Garth and Haig 1971: 6.9.—Hendrickx 1995: 128.

Material examined. Clarion Clipperton Zone: SO268-2 cruise, R/V *Sonne*, stn. 193 (dive ROV30), 11°51.79002'N 117°00.77862'W (BGR contract area), 4128 m, 13.05.2019, 1 male, 8.69 mm (SO268-2_137).

Distribution. Eastern Pacific Ocean. *Ethusina faxonii* was previously known from off Mexico, south of the Gulf of Tehuantepec at 4081 m (Rathbun 1933); northwest of Tres Marias Islands at 2999 m (Garth 1960); and off Peru at 3086 to 3995 m (Garth and Haig 1971). The present specimen from the BGR contract area represent the first record of this genus and probably of the species from the CCZ.

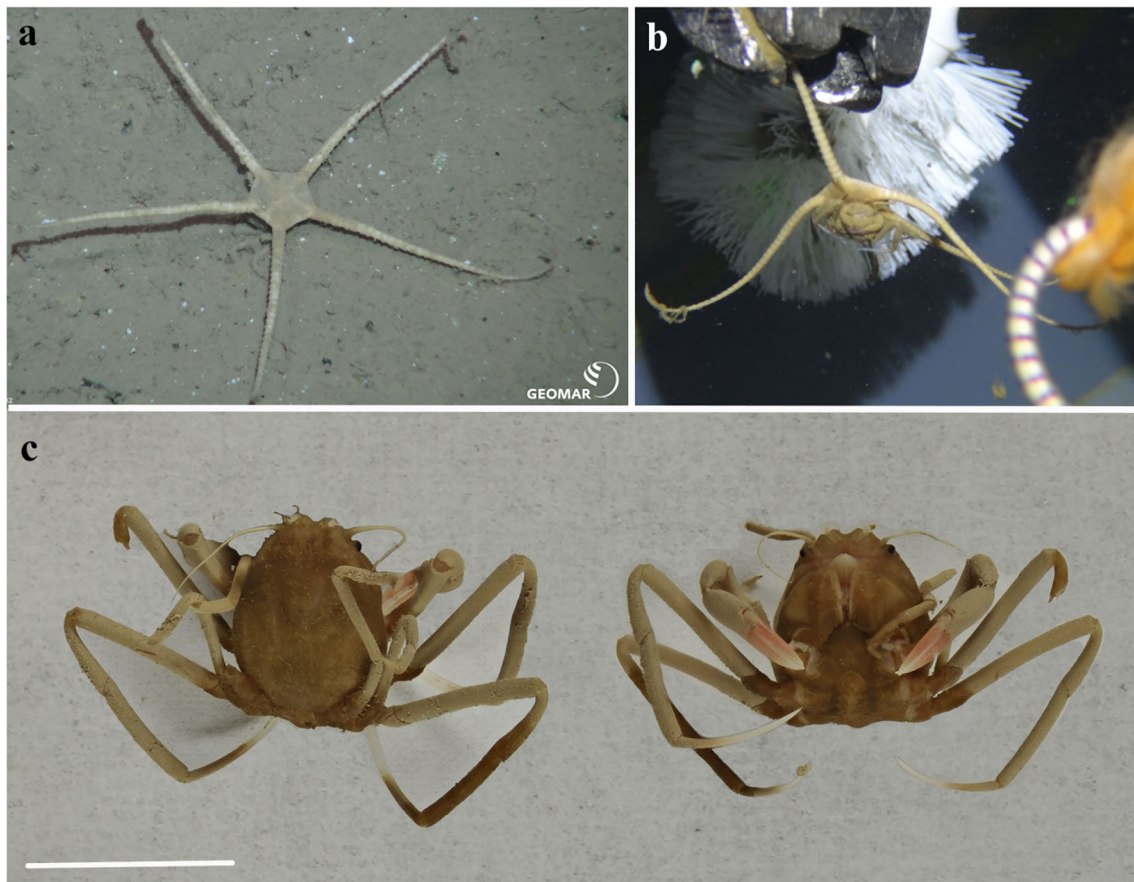


Fig. 7 *Ethusina* cf. *faxonii* Rathbun, 1933, 1 male, cl 8.69 mm (SO268-2_137): **a** specimen under an ophiuroid, *in situ*; **b** *in situ* collection of a crab together with an ophiuroid using the ROV arm; **c** dorsal and ventral view. Scale 1.0 cm (photos by Nicol Mahnken)

Coloration in life. Carapace and abdomen generally light brown; chelipeds and ambulatory legs pale white with orange chelae. Cornea black (Fig. 5).

Remarks. The genus *Ethusina* SI Smith, 1884 comprises of 33 species, with most of them occurring in the Indo-west Pacific region (WoRMS Editorial Board, 2022; accessed at: 2022-05-11), and only two species recorded with certainty from the Eastern Pacific (*E. faxonii* and *E. smithiana*; Hendrickx 1995; Castro 2005), with Castro (2005) considering the records of *E. robusta* and *E. gracilipes* to belong to an undescribed species. *Ethusina faxonii* can easily be distinguished from most other species of *Ethusina* by the sinuous shape of the frontal portion of its carapace with the concave median lobes lacking terminal teeth (Rathbun 1933). *Ethusina faxonii* is very similar to *E. challengerii* but differs in having more slender chelae, fourth and fifth pereopods and minute orbital teeth instead of rounded tubercle-like outer orbital teeth (Rathbun 1933). Since the original description of *E. faxonii*, less than a handful records have come to light, most females and only one male (Garth and Haig 1971). The current male specimen agrees well with the above characters, but differs in having a narrower and less inflated carapace than the female one illustrated by Rathbun (1933; Plate 26-27). This difference can perhaps be attributed to sexual dimorphism within the species but until a detailed morphological comparison is undertaken of all available specimens, the current specimen is conservatively identified as *E. cf. faxonii*. This is the

first time a COI sequence (OM892122) is available for the genus *Ethusina*.

Infraorder Caridea Dana, 1852

Family Acanthephyridae Spence Bate, 1888

Acanthephyra trispinosa Kemp, 1939

(Fig. 8)

Acanthephyra trispinosa Kemp 1939: 577 [type locality: west coast of Central America from 7°N to 4°S, extending westwards to 116°W].— Chace 1986: 9; Figs. 3m, 4y, 5y, 7l, 10h. — Vereshchaka 1990: 139. — Guzman 2003: 3.

Material examined. Clarion Clipperton Zone: SO239 cruise, R/V *Sonne*, stn. 133EBS, 13°51.31002'N 123°13.72998'W (GSR contract area), 4507 m, 10.04.2015, 1 female, cl 20.01 mm (SO239_133_1252).

Distribution. Eastern Pacific Ocean. Reported from west coast of Central America between 7°N and 4°S (off Peru), westward to 116°W (Chace 1986); off Chile, from Sala y Gomez and Nazca seamounts (21°41'–25°40'S 81°19'–86°34'W) at 160–2280 m (Vereshchaka 1990) and 18°25'–21°04'S 70°40'–71°3'W at 374–540 m (Guzman 2003). The present specimens reported from the GSR contract area represent a new record for the CCZ, and significantly extend the geographical range of the species to the north (13°N) and west (123°W) as well as its bathymetric distribution to abyssal (4507 m) depths.



Fig. 8 *Acanthephyra trispinosa* Kemp, 1939: female, cl 20.01 mm (SO239_133_1252), lateral view. Scale 1.0 cm (photo by Nicol Mahnken)

Remarks. The genus *Acantheephyra* A. Milne-Edwards, 1881, contains 27 species (De Grave and Fransen 2011) of which 12 have been recorded in the eastern Pacific. *Acantheephyra trispinosa* can be distinguished from all species in the genus by the presence of a dorsal posteromedian tooth on the third to sixth somites, with that of the third being the largest; telson with three pairs of dorsolateral cuspidate setae; small branchiostegal tooth supported by a short-rounded ridge; sixth somite length about twice its posterior width; and the rostrum being shorter than the carapace, extending to or slightly beyond the scaphocerite (Kemp 1939; Chace 1986). The present specimen agrees well with these diagnostic characters, despite having a broken rostrum tip. The rostrum bears 7 dorsal and five ventral teeth, as also mentioned by Guzman (2003).

This is the first time a COI sequence (OM892121) is available for this species. The haplotype of the collected specimen different significantly from other *Acantheephyra* species present in Genbank (p-distance: < 12.35%–17.61%).

Family Crangonidae Haworth, 1825

Parapontophilus occidentalis (Faxon, 1893)

(Fig. 9)

Pontophilus occidentalis Faxon 1893: 200 [type locality: off Ecuador, 01°07.0'N 80°21.0'W, 2831 m; Gulf of Panama, 02°34.0'N 92°06.0'W, 2448 m; 04°56.0'N 80°52.30'W, 3243 m; 05°43.0'N 85°50.0'W, 1760 m; 06°10.0'N 83°06.0'W, 2648 m; 06°21.0'N 80°41.0'W,

3281 m; 07°05.30'N 79°40.0'W 2286 m; off Costa Rica, 10°14.0'N 96°28.0'W, 4018 m; off Guatemala, 14°46.0'N 98°40.0'W, 3190 m].— Zarenkov 1976: 14; Fig. 6.

Pontophilus gracilis occidentalis.— Wicksten and Hendrickx 2003: 69.

Parapontophilus occidentalis. — Wicksten 1977: 963. — Komai 2008: 287; Figs. 8, 20d. — Hendrickx 2012: 329; Fig. 5a. — Moscoso 2012: 60. — Hendrickx 2015: 373; Figs. 2, 3, 4.

Material examined. Clarion Clipperton Zone: ABYSSLINE II cruise, R/V *Thompson*, stn. EB04 (EBS), 12°07.83'N 117°18.67'W (OMS contract area), 4111 m, 25.02.2015, 1 female, cl 10.13 mm (AB02_EB04_2); ABYSSLINE II cruise, R/V *Thompson*, stn. EB07 (EBS), 12°27.08'N 116°38.80'W (UKSRL contract area), 4145 m, 02.03.2015, 1 female, cl 15.14 mm (AB02_EB07_1); MANGAN16 cruise, R/V *Kilo Moana*, stn. 28EBS, 11°49.654'N 117°00.299'W (BGR contract area), 4143 m, 01.05.2016, 1 ovigerous female, cl 18.35 mm (MA16_28_1); MANGAN18 cruise, R/V *Sonne*, stn. 59EBS, 11°50.055'N 116°59.530'W (BGR contract area), 4128 m, 23.04.2018, 1 ovigerous female, cl 18.27 mm (MA18_59_1).

Distribution. Eastern Pacific Ocean. Previously known from off Ecuador to Costa Rica, between 01°–14°N and 79°–92°W at depths between 1760 and 4018 m (Faxon 1893; Komai 2008); off Chile at 1910–2120 m and off Peru at 1850–2100 m (Zarenkov 1976); off San Clemente Island, California at 1810 m (Wicksten 1977); Gulf of California at 837–840 m (Hendrickx



Fig. 9 *Parapontophilus occidentalis* (Faxon, 1893): female, cl 18.35 mm (MA16_28_1), lateral view. Scale 1.0 cm

2012); off Peru at 3475 m (Moscoso 2012). These records extend the known geographical range of the species to the northwest (116°–117°W) and its bathymetric distribution to 4145 m.

Remarks. The genus *Parapontophilus* Christoffersen, 1988, currently includes 19 species (De Grave and Fransen 2011; Kim and Chan 2020). *Parapontophilus occidentalis* is the only member of the genus recorded for the eastern Pacific. Diagnostic characters of *P. occidentalis* include the presence of cardiac and epibranchial teeth on the carapace; rostrum failing to reach distal margins of coxae; coxae bearing two pairs of small lateral teeth; postorbital ridge on carapace conspicuous; non-pigmented partly faceted corneal surface; subequal anterior and posterior epigastric teeth on carapace; and the dactyli of fourth and fifth pereopod being more than half the propodi length (Faxon 1893; Komai 2008; Hendrickx 2015). The present specimens have faceted coxae as observed by Hendrickx (2015), which are not present in the syntypes (Faxon 1893; Komai 2008). Otherwise, the specimens agree well with the description of *P. occidentalis* provided by Faxon (1893) and Komai (2008).

This is the first time COI sequences (OM892113, OM892115, OM892116, OM892129) are available for this species.

Family Stylodactylidae Spence Bate, 1888

Bathystylodactylus echinus Wicksten & Martin, 2004

(Fig. 10)

Bathystylodactylus echinus Wicksten and Martin 2004: 377; Figs. 1, 2, 3, 4, 5 [type locality: Basin of Magdalena

Bay, Baja California, Mexico (24°35'N 113°25'W), 3563–3621 m].

Material examined. Clarion Clipperton Zone: MIDAS JC120 cruise, R/V *James Cook*, 17°15.08'N 123°03.73'W (APEI-6), 4160 m, 28.04.2015, 1 female, poel 42.0 mm (OUMNH-ZC.2018.01.041).

Distribution. Eastern Pacific Ocean. Previously known with certainty only from its type locality, off Magdalena Bay, Baja California, Mexico at depths of 3563–3621 m (Wicksten and Martin 2004). Simon-Lledó et al. (2019a) reported *Bathystylodactylus* cf. *echinus* from the Area of Particular Environmental Interest 6 (APEI-6), in the CCZ during an AUV survey. A specimen was collected and was identified in the current study, confirming the presence of this species in the proposed conservation zone APEI-6, in the CCZ. Amon et al. (2017) reported the presence of *Bathystylodactylus* sp. from the UKSRL contract area and although highly likable to be *B. echinus* since no specimen was collected its presence cannot be confirmed yet.

Remarks. Three species of *Bathystylodactylus* Hanamura & Takeda, 1996 are currently known: *B. bathyalis* (Cleva, 1994) from the West Pacific (Coral Sea), *B. inflatus* Hanamura & Takeda, 1996 from off Taiwan, West Pacific and *B. echinus* from off Magdalena Bay (Baja California), East Pacific (Cleva 1994; Hanamura and Takeda 1996; Wicksten and Martin 2004). *Bathystylodactylus echinus* can be distinguished from the other two species by its curved rostrum; presence of a



Fig. 10 *Bathystylodactylus echinus* Wicksten & Martin, 2004: female, poel 42.0 mm (OUMNH-ZC.2018.01.041), lateral view. Scale 1.0 cm (photo by National Oceanography Centre Southampton)

sharp tooth on the ventral margin of the third abdominal pleuron; lack of a wide elevation near the posterodorsal margin of the carapace; less sinuous shape of the suprabranchial carina; and fewer spinules on the carapace posterior to the rostrum (Wicksten and Martin 2004). The specimen collected agrees well with the diagnosis of *B. echinus* provided by Wicksten and Martin (2004).

This is the first time a COI sequence (OM951239) is available for this species, and indeed the genus.

Discussion

The present study is part of a series of studies (i.e. Kersken et al. 2018, 2019; Christodoulou et al. 2019, 2020) that aim to document the megafaunal biodiversity in the CCZ and DEA based on a combination of morphological and genetic evidence. As a result, the presence of eight species is revealed, of which six were reported for the first time from the CCZ and DEA using integrative taxonomy. The finding of these previously unreported decapod species is the direct result of a longer-term sampling effort, in which a greater number of specimens (23 specimens, 8 species) from a larger sampling area were collected than during any previous studies in the DEA or in the CCZ, spanning over three exploration contract areas and one APEL. Furthermore, the use of different sampling equipment, such as Epibenthic Sledge (EBS), Remotely Operated Vehicle (ROV) and baited traps permitted the collection of species with different life modes. Nevertheless, decapods, due to their high mobility, remain a challenging group to sample in the abyss. The collection of specimens allowed the compilation of a DNA barcode reference library with COI sequences given for the first time for the genera *Parapagurus*, *Ethusina*, and *Bathystylodactylus*. The sequences acquired will allow the future assignment of unknown or damaged specimens to a taxon name, thus producing more accurate and reproducible data in monitoring studies. Furthermore, taxonomically validated and curated reference libraries based on voucher specimens such as the one herein will be a great support for biodiversity studies based on environmental DNA or metabarcoding (Vieira et al. 2021).

The accurate documentation of species diversity through integrative taxonomy together with their geographic distribution and life history is essential for the prediction and management of possible environmental impacts of mining in the CCZ (Lodge et al. 2014; Wedding et al. 2015; Glover et al. 2018). Integrative taxonomy is even more imperative in the deep sea, where most known species have only recently been identified, while the vast majority remain undiscovered (Glover et al. 2018). Modelling the ecosystem-wide impacts of deep-sea exploitation is not possible without any knowledge of the animals that live there (Glover et al. 2018).

Environmental impacts caused by mining can include removal of abyssal nodules and severe habitat disruption, generation of large sediment plumes, and immediate loss of local biodiversity in the mined sites (Vanreusel et al. 2016; Miller et al. 2018). The removal of nodule-associated and habitat-forming benthic species such as corals and sponges will affect species, among which decapods, that utilise these habitats for food or shelter (Christiansen et al. 2020). A survey carried out in the DISCOL area showed that the scavenging deep-sea fish density was lower in the first years following disturbance, but increased over time reaching to zero net difference after 26 years (Drazen et al. 2019). The scavenging community besides fish included shrimps (*H. nereus*, *Cerataspis monstrosus*, *Benthiscymus* sp.), and the hermit crab *Probeebei mirabilis*. Although no firm conclusions were drawn for the decapod scavengers, it was speculated that extensive disturbance in their habitat would have a negative effect (Drazen et al. 2019). However, decapods most likely can avoid direct mining activities and since not one of the species found herein is endemic to the CCZ or DEA area, no regional species extinctions are expected. Nevertheless, long-term habitat loss at larger spatial scales and the dispersion of sediment plumes impairing feeding well beyond the mined sites could result in local population declines. Deep-sea decapods obtain food as carnivores by preying on small benthic and benthopelagic invertebrates or by scavenging on carcasses of dead animals (i.e. whales), or as detritivores or omnivores by feeding on any nutritional source available (Wicksten 2020). Observations on *Bathystylodactylus* species from the Marianas Trench and the CCZ show that shrimps probably filter-feed on small particles carried by currents using their fringed first and second pereopods (Wicksten et al. 2017). The generation of plumes could impair the ability of these shrimps to feed. The shrimps *H. nereus* (Drazen et al. 2019) and *H. doris* (personal observations), the hermit crab *Probeebei mirabilis* (Drazen et al. 2019) and the squat lobster *M. kensmithi* (personal observations) scavenge on any available dead prey. It has been argued that olfactory sensing is likely the main mechanism for deep-sea scavengers to detect bait (Sainte-Marie 1992). Although any mining-generated sediment plumes are expected to influence mainly filter- and suspension-feeders they could potentially interfere in a smaller scale with odour plumes released from food falls, resulting in lower detection rates and generally lower food availability for scavengers (Christiansen et al. 2020).

Despite the fact that the CCZ is perhaps the most persistently-studied abyssal ecosystem (Glover et al. 2018), the high proportion of new species recorded and discovered (i.e. Bonifacio et al. 2020; Christodoulou et al. 2019, 2020; Brix et al. 2020) underlines the limited information presently available on its biodiversity. Megafauna biodiversity assessments in the CCZ and DEA areas are largely dependent on

seafloor image surveys (i.e. Tilot et al. 2018; Simon-Lledó et al. 2019a, 2019b, 2020; Shoening et al. 2020; Drazen et al. 2019, 2021), which, due to their minimal disturbance and cost efficiency (Beisiegel et al. 2017), are considered to be a good and environmentally-friendly exploratory tool. However, although the collection of biological samples is not a full prerequisite for biodiversity studies, a comprehensive image-based assessment essentially requires prior knowledge of the area's species, effectively through specimen collection (Hanafi-Portier et al. 2021; Horton et al. 2021). Recent surveys in the CCZ and DEA resulted in the development of a baseline image catalogue, documenting the fauna recorded on images or videos (Simon-Lledó et al. 2020 and references within). Although this is a significant step in the right direction, most of the images are not linked to voucher specimens, leading to potential misidentifications or biodiversity underestimates. This is especially the case with the cryptic and pseudo-cryptic taxa that are prevalent in Decapoda, and likely cannot be distinguished in the often-crude imagery routinely available (Fig. 4 and compare Figs. 4 and 5 vs Fig. 2e in Simon-Lledó et al. 2019b, Fig. 4i in Drazen et al. 2021) (Hanafi-Portier et al. 2021). ROVs can produce much higher-resolution imagery, as well as collect voucher specimens, but their use is costlier than more routinely used towed cameras (i.e., OFOS, Ocean Floor Observation System) and AUVs (Autonomous Underwater Vehicles). A fully integrative taxonomic approach, linking DNA sequences to the morphological identification of voucher specimens and matched with *in-situ* photos (supplemented by *in vitro*, ship-board photos as needed) as applied to the Decapoda in this study allows for a more complete documentation of biodiversity, which in turn informs larger scale, cost-effective monitoring work by means of OFOS and/or AUVs.

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Declarations

Conflict of interest The authors declare no competing interests.

Ethics approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Sampling and field studies Permits for sampling and observational field studies are not applicable.

Data availability DNA sequences, trace files, collection data and taxonomic remarks are available in the datasets CCZ-DEA_Decapoda in BOLD. Furthermore, the DNA sequences and their accompany collection data are also available in GenBank.

Author contribution PMA and AV designed the sampling. PMA, AV and MC carried out the sampling and processed the specimens on board. MC performed the genetic lab work. MC and SDG conducted the morphological identifications. MC took the lead in writing the manuscript in collaboration with all authors.

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