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Review of *Macropodia* in the Black Sea supported by molecular barcoding data; with the redescription of the type material, observations on ecology and epibiosis of *Macropodia czernjawskii* (Brandt, 1880) and notes on other Atlanto-Mediterranean species of *Macropodia* Leach, 1814 (Crustacea, Decapoda, Inachidae)

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Abstract

Macropodia czernjawskii (Brandt, 1880), described from the Black Sea, was ignored in the regional faunal accounts for more than a century, although it was recognised in the Mediterranean. Instead, *M. longirostris* (Fabricius, 1775) and *M. rostrata* (Linnaeus, 1761) were frequently listed for the Black Sea. We selected a lectotype and redescribed the species on the basis of the type series from the Crimean Peninsula and the new material collected in the Black Sea. Historical and new collections, as well as the analysis of publications, indicate that *M. czernjawskii* is the only *Macropodia* species occurring in the Black Sea. Molecular barcode (COI gene marker) data show that *M. czernjawskii* is a species well-diverged from other studied species of the group. Furthermore, *M. parva* van Noort & Adema, 1985 has very low genetic distances from *M. rostrata* and *M. longipes* A. Milne-Edwards & Bouvier, 1899 is indistinguishable from *M. tenuirostris* (Leach, 1814), using COI sequences. The respective synonimisations, supported by morphological data, are proposed. *M. czernjawskii* is a Black Sea – Mediterranean endemic occurring also in the neighbouring Atlantic coastal zone of the Iberian Peninsula and occupying shallower depth, compared to other Mediterranean species of *Macropodia*. As an upper subtidal inshore species, it is particularly specialised in self-decoration and stimulates abundant epibiosis, providing masking and protection. The bulk of epibiosis consists of algae and cyanobacteria. Amongst the 25 autotrophic eukaryote taxa, identified to the lowest possible level, green chlorophytes *Cladophora* sp. and calcareous rhodophytes Corallinales gen. sp. were most commonly recorded. Non-indigenous red alga *Bonnemaisonia hamifera* Hariot, first officially recorded at the Caucasian coast of the Black Sea in 2015, was present in the epibiosis of *M. czernjawskii* in Crimea as early as 2011.

Key Words

Majoidea, historical collections, upper subtidal biotopes, endemism, Mediterranean, egg size, epibiosis, non-indigenous species

Introduction

The spider crab genus *Macropodia* Leach, 1814 currently includes 18 species, mostly from the Atlantic and Mediterranean. These are cryptic long-legged inhabitants of macrophytes or other live substrata. The Mediterranean fauna comprises of 5 species: *Macropodia czernjawskii* (Brandt, 1880), *Macropodia linaresi* Forest & Zariquiey

Álvarez, 1964, *Macropodia longirostris* (Fabricius, 1775), *Macropodia rostrata* (Linnaeus, 1761) and *Macropodia tenuirostris* (Leach, 1814) (d'Udekem d'Acoz 1999). The Black Sea is an outpost of the Mediterranean Basin and its marine fauna is largely of relatively recent Mediterranean origin (Sowinsky 1902; Zenkevich 1963). Since the mid-20th century, most of faunal accounts list two species of *Macropodia* as occurring in the Black Sea: *M. longirostris* and *M. rostrata* (Băcescu 1967; Kobjakova and Dolgopolskaya 1969; Makarov 2004). No inventories, except relatively recent ones by d'Udekem d'Acoz (1999) and Micu and Micu (2006), mention the presence of *M. czernjawskii* in the Black Sea. This is surprising because *M. czernjawskii* was described from the Black Sea (Brandt 1880). Furthermore, the type specimens have been deposited in the Zoological Institute of the Russian Academy Sciences and were seen by at least some researchers, i.e. Z.I. Kobjakova who published reviews of the Black Sea Decapoda (Spiridonov and Petryashov 2011). Important details of the past studies of *Macropodia* in the Black Sea are presented below in a separate section on the taxonomic history of *M. czernjawskii*.

We have examined the type specimens of *Stenorhynchus czernjawskii* Brandt, 1880 and all available collections of *Macropodia* spp. in the Russian museums and the Senckenberg Museum in Frankfurt on Main, as well as collected new material in the Black Sea and the North East Atlantic. This fresh material made it possible to perform standard molecular genetic barcoding, based on the mitochondrial cytochromoxidase gene (COI) and allowed us to not only characterise *M. czernjawskii*, but also to discuss the status of the problematic species, such as *Macropodia longipes* A. Milne-Edwards & Bouvier, 1899 and *Macropodia parva* van Noort et Adema, 1985 (d'Udekem d'Acoz 1999; Raupach et al. 2015). The new records also made it possible to obtain new data on the ecology and epibiosis of *M. czernjawskii*. In order to clarify the taxonomic status and synonymy of the species that is recognised in the Mediterranean and has been largely ignored in the area of the type locality, the present study aims at revision of the available material of *Macropodia* from the Black Sea, re-description of the type material of *M. czernjawskii* and providing update of its ecological characteristics.

Taxonomic history of *Macropodia* from the Black Sea

The first Black Sea specimens of *Macropodia* were collected by Vladimir Ivanovich Czerniavsky, then a student of the Imperial Kharkov University (see Rusanov 2016) in Yalta, Crimean Peninsula in 1867. He described the locality as following: "At St. Ioann Cape, in dense algae covering large stones located near shoreline at depth 3 – 5 feet; there I caught several specimens by hand and using Müller's net at several occasions in July and the first half of August; once two specimens were collected at the same time. All were females with significant number of eggs." (Czerniavsky 1868: 77). Brandt (1880: 398) indicated that Czerniavsky collected females of *Macropodia* in Yalta both in 1867 and 1869, when he spent two months collecting there (Rusanov 2016). Czerniavsky (1868) identified these specimens as *Stenorhynchus longirostris* (Fabricius, 1798).

In the late 1870s, Alexander Fedorovich (Alexander Julius) Brandt, the conservator of the Zoological Museum of the Russian Imperial Academy of Sciences in St. Petersburg (now Zoological Institute of Russian Academy of Sciences, ZIN-RAS) was working with the collection of Mediterranean decapods and with the associated manuscript donated to the museum by the prominent German zoologist Rudolph Amandus Philippi (Brandt 1880) right before Philippi's immigration to Chile in 1851 (see Kabat and Coan 2017). Brandt (1880: 399) explained his intention as following: "Erst vor ein Paar Jahren machten sich mein Freund Wold. Czernjawsky und ich an das Phillip'sche Manuscript, in der Absicht es unter Benutzung der Originalexemplare in extenso gemeinsam zu ediren. Gegenwärtig sehen wir uns jedoch, leider genötight dieses Vorhaben aufzugeben und uns auf eine gelegenliche Veröffentlichung einzelner Fragmente aus dem Manuskript zu beschänken. Als solches ist der gegenwärtige kleine Aufsatz anzusehen, welcher ursprünglich dazu bestimmt war den Anfang der zusammenhängen Bearbeitung des Ganzes zu bilden. Ein weiter Fragment wird demnaechst Czernjawsky in seinem "Miscellanea carcinologica" im Bulletin de la Soc. Imp. d. Natur. de Moscou, zum Abdruck bringen". ("In the last two years, my friend Woldemar (Vladimir) Czerniavsky and I have been dealing with Philippi's original manuscript with the purpose to prepare it for publication as it is. At the present time, however, we see ourselves, unfortunately, forced to abandon this project and to confine ourselves to ad hoc publication of individual parts of the manuscript. As such, the present small essay, which was originally intended to form the beginning of the coherent processing of the whole, is presented. The next fragment will be published by Czerniavsky in his "Miscellanea carcinologica" in the Bulletin de la Société des Naturalistes de Moscou").

The article on Mediterranean majoid crabs, finally published by Brandt (1880), was largely based on Philippi's collection, but included Brandt's own observations and illustrations. He also recognised the differences between the specimens identified as *Stenorhynchus longirostris* from the Mediterranean and the Black Sea. By that time, two more males from Sevastopol, Crimea became available for study. On the basis of these and Czerniavsky's specimens, Brandt (1880) described a new species, naming it in honour of his friend and colleague *Stenorhynchus czernjawskii*. The title of Brandt's (1880) paper clearly focused on the Mediterranean species and seemed to have no impact on the subsequent studies of the Black Sea decapod fauna. First of all and most surprisingly, Czerniavsky himself ignored the species dedicated to him. In the later published monograph of the Black Sea Decapoda, he listed the ovigerous females from

Yalta as *Stenorhynchus egyptius* H. Milne Edwards, 1834 (“*aegyptius*“in his spelling, p. 127) and one of the males used by Brandt for the description of his species along with another male as *S. longirostris* (Czerniavsky 1884: 129). The difference between these two species in Czerniavsky’s concept can be deduced from his key as follows.

“Rostrum pedunculo anten. exter. longius. Antennarum exter. articulus peduncularis 1-mus infra (2–5) spinosus; …. – *St. longirostris*”.

“Rostrum pedunculo anten. ext. brevius, dimidium articuli non superans. Anten extrum articulus pedunc. 1-mus infra (2–4) spinosus … *St. egyptius*” (Czerniavsky 1884: 124).

Czerniavsky (1884) also mentioned the presence of *Stenorhynchus phalangium* (Pennant, 1777), which he distinguished from *S. egyptius* by the unarmed basal antennal segment. However, his listing of this species in the Black Sea fauna was based not on the original material, but on the literature record by Grebnitzky (1873). Grebnitzky’s study was dedicated to the zoogeographical analysis of the Black Sea fauna. He presented a list (in the form of a table) of the Black Sea species and discussed their commonality in this basin and the occurrence in the Mediterranean, North Sea, the Atlantic and the Arctic Oceans. In this table, Grebnitzky (1873: 215) included *Stenorhynchus longirostris* and *S. phalangium*, however, providing no information on the sources of the listings. Since only *S. longirostris* was recorded earlier (Czernjavsky 1868), we could suppose that the listing of *S. phalangium* was based on Grebnitzky’s own record and identification. Traces of his material were, however, never found.

In his comprehensive account of the Black Sea fauna, Sowinsky (1902) listed three species of *Stenorhynchus* on the basis of Czerniavsky’s (1884) monograph. Subsequent general development of taxonomy and clarification of nomenclature included such important steps as transferring of some species, including the Atlanto-Mediterranean ones from *Stenorhynchus* Lamarck, 1818 to *Macropodia* Leach, 1814 (Rathbun 1897) and recognising *Cancer phalangium* Pennant, 1777 (= *Stenorhynchus phalangium*) as a junior synonym of *Cancer rostratus* Linnaeus, 1761 (= *Macropodia rostrata*) (Forest, 1964). Furthermore, the type series of *Macropodia egyptia* (Milne Edwards, 1834) was shown to be heterogenous, but at least three of four extant specimens have been re-identified as *M. longirostris* and this name was accepted as a senior synonym (Forest 1964). Forest (1964) and Forest and Zariquiey Álvarez (1964) considered then *M. czernjawskii* as a valid name and suggested several characters to distinguish this species from *M. longirostris* in the Mediterranean. The length of the rostrum in relation to the antennal peduncle was shown to be a variable character, not optimal to distinguish between these species when taken alone; the armature of the dactylus of the 5th pereopod was shown to be the most reliable diagnostic character for both males and females (Zariquiey Álvarez 1968). However, Forest (1964: p. 353) was apparently not aware of the fate of the *M. czernjawskii* type material and thought it desirable to designate a neotype.

Like Brandt’s publication eighty five years earlier, the studies by Forest and Zariquieyi Álvarez in the 1960s seemed to have little effect on the taxonomic treatment of *Macropodia* in the Black Sea. Băcescu (1967) listed three species, *M. egyptia*, *M. longirostris* and *M. rostrata* in his monograph of Romania’s Decapoda. He, however, clearly stated that only *M. egyptia* was found on the Romanian coast and referred to Czerniavsky and other Russian, Bulgarian and Soviet authors who had recorded other species. Kobjakova and Dolgopolskaya (1969) considered *M. egyptia* and *M. longirostris* synonyms (although not referring to Forest 1964). They thus listed only *M. longirostris* and *M. rostrata* in the Black Sea list, having referred to previous authors, beginning from Czerniavsky. Only at the turn of the 20th century, d’Udekem d’Acoz (1999) re-identified the *M. egyptia* of Băcescu (1967) (on the basis of his figures) as *M. czernjawskii*.

Material and methods

The new material was collected by authors during the field trips along the coast of Crimean Peninsula, Kerch Strait, Taman Bay and the mainland north-eastern (Cis-Caucasian) coast of the Black Sea (Krasnodarskiy Krai of Russia) between 2008 and 2018 (Fig. 1). From 2012, we specifically surveyed algal biotopes where species with cryptic habits, including *Macropodia* spp., could hide. SCUBA diving and snorkelling were used to collect the specimens. In one case, *Macropodia czernjawskii* was caught in a dredge during the annual monitoring survey of Inal village (Cis-Caucasian Coast). Collected specimens were photographed to document life colouration and fixed in 96% ethanol.

Historical collections of *Macropodia* spp., including the type series of *Stenorhynchus czernjawskii* were examined in the Zoological Institute of Russian Academy of Sciences, St. Petersburg (ZIN-RAS), Zoological Museum of the Moscow University (ZMMU) and the Senckenberg Research Institute, Frankfurt on Main (SMF). Measurements of crabs were done using a caliper with an accuracy of 0.1 mm. The following measurements were made: total length (TL) from the tip of rostrum to posterior margin of carapace; postrostral carapace length (PCL), from the basis of rostrum at the level of anterior end of orbital eave to posterior carapace margin; maximum carapace width (CW); right chela length (ChL), along the lower margin of chela; maximum right chela height (ChL); maximum right chela thickness (ChT).

Terminology of morphological descriptions generally follows Ingle (1980). Synonymy is given comprehensively for *Macropodia czernjawskii* and restricted to the main synonyms and combinations for other species. Parts of the Black Sea coastal zone, where our material was collected,

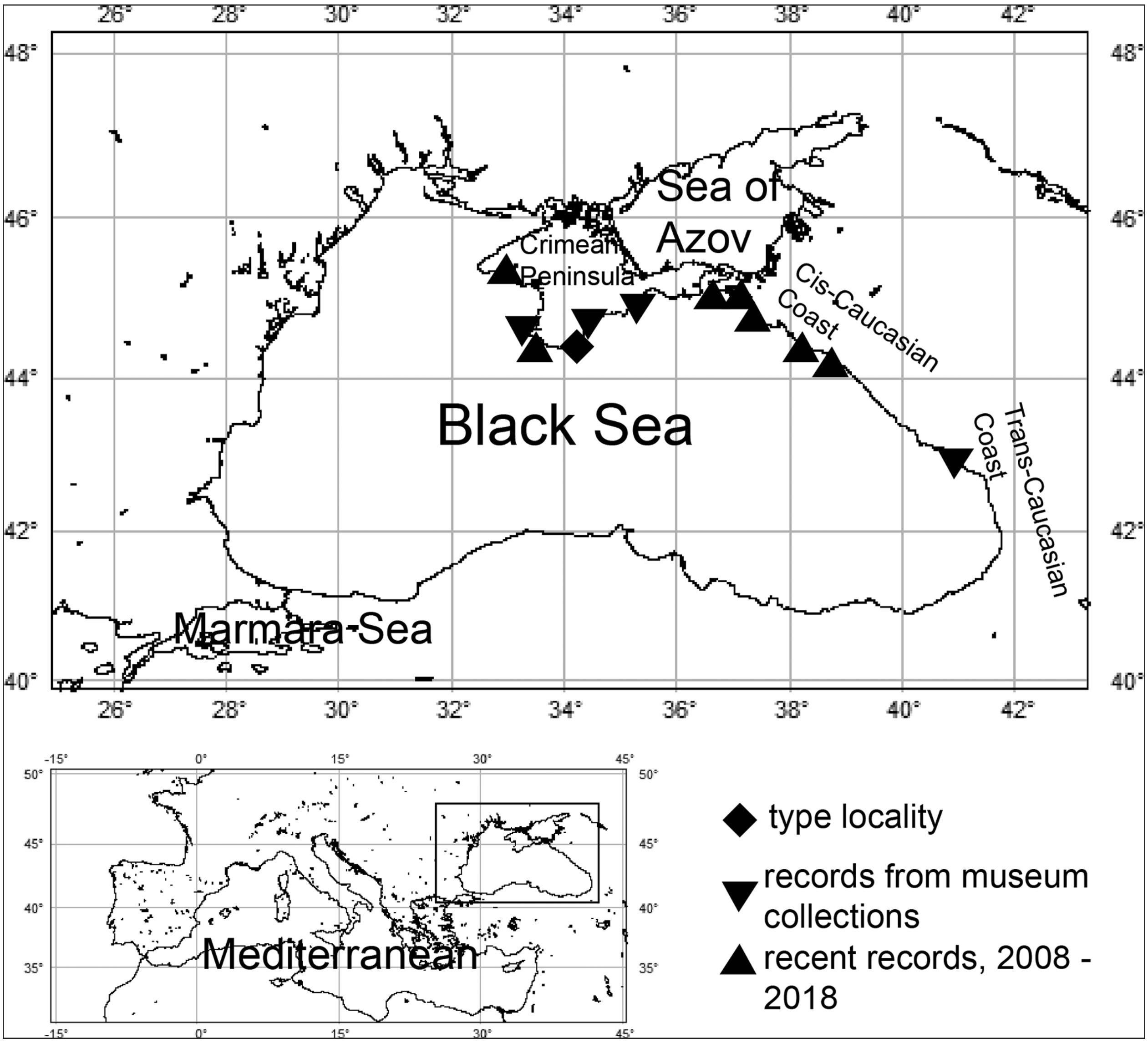

Figure 1. Study area and the original records of *Macropodia czernjawskii* in the Black Sea presented in this study.

are conventionally referred to as the Crimean Peninsula, the Cis-Caucasian Coast (mainland to the west and northwest of the Major Caucasian Ridge, MCR) and the Trans-Caucasian Coast (to the south and southwest of the MCR, up to the coast of Asia Minor in Turkey) (Fig. 1). Abbreviations used in the descriptions: leg – collector; P – pereopod.

To count the eggs carried by females, the entire clutch was separated from the pleopods and weighed, from which a subsample was weighed, distributed in a Petri dish so that all eggs were distributed evenly and flat on the bottom and photographed. On the photograph, the eggs were counted and their diameter was measured (average of 10 measurements). The total number of eggs in the clutch was estimated, based on number of eggs and their weight in the subsample

Developmental stages of eggs, carried by females on pleopods, were identified using a system developed by Burukovsky (1992) and adopted for the brachyurans by Zalota (2017).

Eight recently collected and fixed in 96% ethanol specimens of *M. czernjawskii* and nine specimens of *Macropodia tenuirostris* (Leach, 1814) were used for the molecular genetic barcode study of the sequence of subunit I of the mitochondrial cytochrome oxidase gene (COI). Additional material was obtained from the GenBank (Table 1). DNA extraction followed the modified silica-based method (Ivanova et al. 2008). The Magnetic Beads, coated with SiO_2, were used. To amplify the COI, specific fragments of the Folmer primers (Folmer et al. 1994) were used. If the amplification with the Folmer primer pair failed, then one of the CrustF1 or CrustF2 was used instead of LCO1490 as a forward primer (Costa et al. 2007). The amplifications were carried out in a T100 Thermal Cycler (Bio-Rad) thermal cycler, using a pre-made Polymerase Chain Reaction (PCR) mix (ScreenMix) from Evrogene. The Master mix consisted of 1× ScreenMixc plus 0.6 µM of each primer and 1 µl of DNA template and complet-

Table 1. Original and other available material of COI sequences of *Macropodia* spp. and outgroup taxa (*Inachus aguiarii* de Brito Capello, 1876 and *Hyas araneus* (Linnaeus, 1758)) used in the molecular-genetic analysis in the present study. BoLD – Barcoding of Life Data – http://www.boldsystems.org; GenBank – https://www.ncbi.nlm.nih.gov.

Species	BoLD accession numbers	GenBank accession number	Area	Voucher specimen museum catalogue number	Reference
M. czernjawskii	BLS565	MT311174	Black Sea, Cis-Caucasian coast	ZMMU Ma 3545	This study
M. czernjawskii	BLS566	MT311175	Same	ZMMU Ma 3547a	This study
M. czernjawskii	BLS567	MT311176	Same	ZMMU Ma 3547b	This study
M. czernjawskii	BLS568	MT311177	Same	ZMMU Ma 3547c	This study
M. czernjawskii	BLS569	MT31117	Same	ZMMU Ma 3547d	This study
M. czernjawskii	BLS571	MT311179	Black Sea, Sevastopol,	ZMMU Ma 3551	This study
M. czernjawskii	BLS465	MT311173	Same	ZMMU Ma 3550	This study
M. tenuirostris	BLS1010	MT311180	NE Atlantic, Cadíz Bay,	ZMMU Ma 3576a	This study
M. tenuirostris	BLS1011	MT311181	Same	ZMMU Ma 3576b	This study
M. tenuirostris	BLS1012	MT311182	Same	ZMMU Ma 3576c	This study
M. tenuirostris	BLS1013	MT311183	Same	ZMMU Ma 3576d	This study
M. tenuirostris	BLS1014	MT311184	Same	ZMMU Ma 3576e	This study
M. tenuirostris	BLS1015	MT311185	Same	ZMMU Ma 3576f	This study
M. tenuirostris	BLS1016	MT311186	Same	ZMMU Ma 3577a	This study
M. tenuirostris	BLS1017	MT311187	Same	ZMMU Ma 3577b	This study
M. rostrata	NA	KT208_ - 209_	North Sea	NA	Raupach et al. 2015
M. parva	NA	KT208_ - 209_	North Sea	NA	Raupach et al. 2015
M. rostrata	NA	JQ306015-16	NE Atlantic	NA	Matzen da Silva et al. 2011
M. rostrata	NA	KC866334	Western Mediterranean	NA	Marco-Herrero et al. 2013
M. longipes	NA	JN107573	NE Atlantic	NA	Matzen da Silva et al. 2011
M. longipes	NA	KC866333	Western Mediterranean	NA	Marco-Herrero et al. 2013
M. tenuirostris	NA	KT208_ - 209_	North Sea	NA	Raupach et al. 2015
M. tenuirostris	NA	JQ305_-JQ306_	NE Atlantic	NA	Matzen da Silva et al. 2011
Macropodia sp.	NA	KP369147	West coast of Portugal	NA	Lobo et al. 2013
Inachus aguiarii	NA	KU163294	NE Atlantic	NA	Colavite et al. 2019
Hyas araneus	NA	KT208434	North Sea	NA	Raupach et al. 2015

ed with milliQ-grade water to make up a total volume of 20 µl. PCR tubes with the mix were preheated (95 °C, 5 min). Annealing temperature was 48 °C (30 sec) during the first 5 cycles and 52 °C (30 sec) during the next 32 cycles. The resulting PCR product was visualised in a 2% agarose gel, purified and sequenced using ABI PRISM BigDye Terminator v. 3.1 on Applied Biosystems DNA Analyzer 3500 ABI. Chromatograms were processed using the Codone Code Aligner. Fasta files were aligned using MAFFT v7.308 (Kazutaka 2013). Alignment included 71 sequences (15 were obtained in the current work). The overall length of the aligment was 700 bp. The trees were constructed using MrBayes 3.2.6 (posterior probability, chain length 2 100 000, G=4, 4 heated chains, hcTemp 0.2, subsampling freq. 200, burn-in length 100 000) and RaxML (with rapid bootstrapping and search for best scouring ML tree, 1000 bootstrap replicates). The topologies of the trees obtained by both methods were identical. Distances of evolutionary divergence K2P were calculated using the Kimura 2 parameters model (Kimura 1980).

Statistical calculations were performed using PaST package (Hammer 2013).

The dataset with records of *Macropodia czernjawskii* in the Black Sea, data on their morphometry, clutch size and epibiosis are provided as Suppl. material 1, Table S1 and uploaded to GBIF (Spiridonov et al. 2020).

Results

Taxonomy

Class Malacostraca Latreille, 1802

Order Decapoda Latreille, 1802

Suborder Pleocyemata Burkenroad, 1963

Infraorder Brachyura Linnaeus, 1758

Section Heterotremata Guinot, 1977

Superfamily Majoidea Samouelle, 1819

Family Inachidae MacLeay, 1838

Macropodia czernjawskii **(Brandt, 1880)**

Figs 2–8

Stenorhynchus Czernjawskii Brandt, 1880: 399–400.

Stenorhynchus czernjawskii – Spiridonov and Petryashov 2011: 282, fig. 5 (location and status of the type material).

Macropodia czerniavskii (misspelling) – Forest 1964: 348, 351–354; Forest and Zariquiey Álvarez 1964: 230, figs 4, 9, 10, 15; Zariquiey Álvarez 1968: 478 (key), 479, figs 161a, 162d; Noël 1992: 136 (key).

Macropodia czernjawskii – d'Udekem d'Acoz 1992: 129, figs 1–5; d'Udekem d'Acoz 1994: 14; d'Udekem d'Acoz 1999: 199; Ďuriš, Ateş, Özalp and Katağan 2013: 53, fig. 4E, F.

Stenorhynchus longirostris – Czerniavsky 1868: 77 (nec *Cancer longirostris* Fabricius, 1775).

Macropodia longirostris – Kobjakova and Dolgopolskaya 1969: 289; Makarov 2004: 328, figs 158–160; Marin 2013: 101, pl. 43 fig. 2 (nec *Cancer longirostris* Fabricius, 1775).

Stenorhynchus aegyptius – Czerniavsky 1884: 127 (nec *Stenorhynchus egyptius* H. Milne Edwards, 1834).

Macropodia aegyptia – Băcescu 1967: 271, figs 117–119 (nec *Stenorhynchus egyptius* H. Milne Edwards, 1834).

? *Macropodia rostrata* – Makarov 2004: 332, figs 161–163 (nec *Cancer rostratus* Linnaeus, 1766).

Type material. The type series from the Crimean Peninsula, Black Sea included, as reported by Brandt (1880), six syntypes: four ovigerous females collected by Czerniavsky in Yalta, one male from Sevastopol, collected by Ussov in 1876 and another male collected by Herzenstein and Tatarykov in Sevastopol in 1875. These four females were also listed by Czerniavsky (1884: 129)

The lot of ZIN-RAS 1609 was identified as containing type specimens of the species (Spiridonov and Petryashov 2011): one male (all pereopods detached, right cheliped present), one separated pereopod of male, one female ovigerous (both chelipeds undetached) in a separate jar; and three female ov (all pereopods detached, one pleon detached) in another jar. The label affixed on the first jar is probably an original label given at registration in the Museum's collection: "*Stenorhynchus czernjawskyi* A. Brandt. Sinus Yaltensis. Czernyavskyi, 1869". Inside the jar, there were two additional labels: "*Macropodia aegyptia* (Milne-Edw.) det. V. Makarov" and "*Macropodia longirostris* (Fabricius) (=*M. aegyptia*), det. Z. Kobjakova". Similar labels (but not the old one) are present in the second jar of the same lot (with three females). The first label is the result of the work with the collection of Vladimir Vladimirovich Makarov, the curator of Decapoda in the ZIN-RAS in the late 1930s and the second one may be clearly attributed to the studies of Zinaida Ivanovna Kobjakova at the time of preparation of the Black Sea Fauna Guide (Kobjakova and Dolgopolskaja 1969).

The year given on the label is not precise, because as mentioned above, at least part of the ovigerous females were collected in 1867. In the later monograph, Czerniavsky (1884: 127) indicated that the females identified as *Stenorhynchus longirostris* were collected in 1867–1869, although there is no possibility of identifying which of the female syntypes were collected in 1867 and 1869.

The size of the single extant male (TL 17.9 mm, CW 9.0 mm), stored together with the female syntype, does not correspond to the CW of the male syntype collected by Herzenstein and Tatarykov and reported by Brandt (1880: 398) as "junges, nur 8 mm grosses Mänchen". Brandt did not mention the size of another male syntype collected in Sevastopol by Ussov, but Czerniavsky (1884: 129) indicated that this specimen's CW was 7.2 mm. He also reported another, presumably male specimen collected together with four ovigerous females, which were described by Brandt (1880) as syntypes. Its CW is 9 mm, thus corresponding to the male from ZIN-RAS 1609. Most probably the male specimen, stored together with one of the female syntypes, was collected by Czerniavsky together with females, but was either not examined or not mentioned by Brandt (1880) in his species description. Thus its status would be better regarded as unclear, although it cannot be excluded that Brandt had seen it when describing *Stenorhynchus czernjawskii* (a possible syntype). The male syntypes collected by Ussov and Herzenstein and Tatarykov originated from the collection of St. Petersburg University (Brandt 1880), which was also used for teaching purposes. They were probably returned to the University (Spiridonov and Petryashov 2011), but to date, we have failed to locate them there.

Taking into account numerous confusions with the identification of *Macropodia* in the Black Sea and aiming at nomenclature clarity, it is necessary to select a lectotype for *Stenorhynchus czernjawskii*. Owing to the undoubted syntype status of the females from lot ZIN-RAS 1609 collected in Yalta, we have selected one of them, (the female stored together with the male) as a lectotype for *Stenorhynchus czernjawskii*; its new catalogue number is ZIN-RAS 88751. The remaining three females, collected in Yalta, thus become paralectotypes retaining the catalogue number ZIN-RAS 1609. The male from this lot with a status of possible paralectotype, or at least a specimen collected in a topotypic locality synchronously with the type series, has received a new catalogue number ZIN-RAS 88750. The present interpretation of this specimen's status is different from that given by Spiridonov and Petryashov (2011) who regarded it as an undoubted syntype.

Other material. Black Sea. 1 female; Crimean Peninsula; Feodosia; 3–4 fathoms (about 6 m); OF Retovsky leg; ZIN-RAS 35099. 2 males; of Crimean Peninsula; RV "Meotida", Stat 41; 1909; SA Zernov leg; ZIN-RAS 35102. 1 male; Crimean Peninsula, of Laspi; 44°29.30'N, 33°28.14'E; 3–5 m depth, in algae; SCUBA; 17.07.2009; SE Anosov leg; ZMMU Ma3543. 1 female ovigerous; Crimean Peninsula, of Laspi; 44°29.30'N, 33°28.10'E; 1–2 m depth, in macrophytes; snorkelling; 18.08.2009; SE Anosov leg; ZMMU Ma3546. 1 female ovigerous; Crimean Peninsula, Sevastopol, Kruglaya (Omega) Cove; 44°36.07'N, 33°26.50'E; 2011; SE Anosov leg; ZMMU Ma3542. 1 male; Crimean Peninsula, Sevastopol, Cape Vinogradnyi; 44°31.01'N, 33°28.14'E; 5–6 m depth, sand, detached algae; SCUBA; September 2014; SE Anosov leg; ZMMU Ma3544. 1 female ovigerous; Crimean Peninsula, Sevastopol; 2016; VA Timofeev leg; ZMMU Ma3550. 1 female; Crimean Peninsula, Sevastopol, Kruglaya (Omega) Cove; 44°36.10'N, 33°26.50'E; 08.10'; 2017; VA Timofeev leg; ZMMU Ma3551. 1 female ovigerous; Crimean Peninsula, Sevastopol, Kazachia Cove; 44°34.50'N, 33°24.80'E; 0.5 m depth, in algal meadow; hand collecting; 23.05.2018; VA Timofeev leg; ZMMU Ma3611. 1 male; Crimean Peninsula, Liman Donuzlav; 45°20.70'N, 32°58.30'E; 1 m depth, snorkelling; 15.06.2018; VA Timofeev leg; ZMMU Ma3610. 1 female ovigerous; Cis-Caucasian Coast, east of Zheleznyi Rog Cape; 45°06.18'N, 36°45.39'E; 2–3 m depth, mergel reefs with sparse macrophyte growth; SCUBA, 08.08.2012, VA Spiridonov leg; ZMMU Ma3538. 2 males, 3 females ovigerous; Cis-Caucasian Coast, near Blagoveschenskaya, in vicinity of Anapa; 45°02.16'N, 37°05.18'E; sand, 2–3 m depth, from fouling on sunken ropes and on sand (male); snorkelling; June 2013; SE Anosov and AK Zalota leg; ZMMU Ma3547. 1 male; Cis-Caucasian Coast, off Inal; RV "Ashamba" Stat 7, 44°19.729'N, 38°36.887'E; 9–12.8 m depth, sand, shell, macrobenthos dominated by *Chamellea gallina*, *Diogenes pugilator* and *Rapana venosa*; dredge; 02.07.2015, 15:02–15:20; GA Kolyuchkina, AA Vedenin, V Kokarev and AB Basin leg; ZMMU Ma 3545.1 male Cis-Caucasian coast, nature reserve Utrish; 44°44.645'N, 37°24.491'E; transect 1; 6–8 m depth, gravel and pebble, SCUBA, 28.07.2018; UV Simakova leg; ZMMU Ma3615. 1 male; Cis-Caucasian coast, Golubaya Cove, near Gelendzhik; 44°34.5'N, 37°58.7'E; 2–3 m depth, walking on sand, patches of *Zostera noltei*, algae, snorkelling, August 2008, GA Kolyuchkina and UV Simakova leg, ZMMU Ma3548. 1 male; Cis-Caucasian coast, Tuaphat, near Gelndzhik; 44°34.5'N, 37°56.6'E; 2.5 m depth, rock, shell, *Cystoseira* patch; snorkelling; September 2010; SE Anosov leg; ZMMU Ma3549. 1 male; Trans-Caucasian coast, Abkhazia, Sukhum, in front of boulevard; 4–8 m depth, in *Cystoseira*; Sigsbee trawl; 31.07.1908; K Yagodovsky leg; ZIN-RAS 35101. 1 female; 1 male; Black Sea; RV "Ledokol # 1", Stat 38; SA Zernov's Expedition leg; ZIN-RAS 35096. 1 female; Black Sea; vessel not indicated; Stat 4, 1914; AN Derzhavin leg; ZIN-RAS 35097.1 female; Black Sea; RV "Gaidamak", Stat 19, August 1911; SA Zernov leg; ZI N-RAS 35100.

Mediterranean. 2 males; Aegean Sea, Crete; Cruiser "Bogatyr"; Bachinsky leg; ZIN-RAS 35098. 1 female; Aegean Sea, Greece, Gulf of Euvaia, 10.06.1971; A Koukouras leg; SMF 7442. 1 male; Aegean Sea, Greece, Kyra; 39°18.40'N, 24°03'E; 6–8 m depth, 01.07.1978; M Türkay leg; SMF 12700. 1 male; Adriatic Sea, Croatia, 6 km south of Rovinj, Dvije Sestice; 32 m depth; dredge; 10.09.1985; Frankfurt University Excursion leg; SMF 13979. 1 female; Adriatic Sea, Croatia, Istria, Bale Dudit, south of Cape Guobinja; 4 m depth; August 1982; Pettke leg; SMF 14055.

Diagnosis. Cephalothorax, pleon and thoracopods densely and unevenly setose. Rostral spines covered with large curled setae, moderately ascending, slightly convex to straight in lateral view, somewhat over-reaching (in males), reaching or nearly reaching end of antennal peduncle, usually about as long as 30% of total carapace length in females and about 35% in males. Epistome trapezoidal with two conspicuous lateral spinules on each side. All carapace protuberances, spines and tubercles setose. Gastric region with a pair of lateral protogastric protuberances or spines, a pair of mesogastric tubercles and robust median metagastric spine of moderate height, directed slightly anteriorly or straight dorsally. Two conspicuous hepatic protuberances on each side, lower being most robust. Pterygostomial process seen dorsally in males, but barely in females. Cardiac region elevated, with strong median obtuse spine directed slightly posteriorly. Intestinal region with median spiniform tubercle at border with cardiac region. Basal antennal segment with three (in some specimens two or four) spines. Merus of P 2–5 with a distal dorsal spine. Dactyli of P 4 and 5 little narrower than propodi, markedly curved (sickle-shaped), with a dense row of robust sharp spinules located on flexor margin, along with setae; adductor face with few setae and mostly naked.

Description. Females. Cephalothorax pyriform, elongated in anterior part. Postrostral carapace length to maximum width ratio from 1.2 to 1.4. Carapace surface, sternal area, pleon and chelipeds unevenly and densely covered with pile. Regions well defined. Rostral horns straight to slightly convex (lectotype), closely set together reaching or hardly reaching end of antennal peduncle, as long as 20–34% of total carapace length. Ten – fifteen conspicuous hooked, curled and coiled (ansiform) setae on each dorsolateral margin. Dorsal orbital eave well-expressed, markedly elevated over frontal region (Figs 2; 5d–c).

Region between eave and hepatic region broader than basis of rostrum, anterolateral angles of buccal cavity are not seen dorsally. Epistome trapezoidal with two conspicuous lateral spinules on each side. Pair of tubercles mesially of posterior spinules at buccal margin. Anterior margin of buccal cavity costate, broadly V-shaped medially, anterolateral corners as broad quasitriangular lobes directed ventrally, visible in dorsal view (Figs 2b; 7a, b).

Gastric region with large protogastric protuberance on each lateral side. Two closely set median gastric tubercles, located slightly anteriorly to lateral gastric protuberances. Metagastric median spine (directed slightly anteriorly or straight dorsally) robust, obtuse. Hepatic region with two closely-set robust lateral protuberances, lower one largest, ending in bunch of straight setae (obsolete in lectotype). Pterygostomial region with shorter ventrolateral spine located ventrally just anterior to cervical groove; usually barely seen dorsally. Branchyal region with obtuse posterior spine (protuberance), standing approximately at mid-distance from posterior margin to cervical groove and two obtuse upper protuberances located along urogastric region. One or two spinules at posterolateral face. Cardiac region elevated, with low, obtuse, robust median spine directed slightly posteriorly. A median spiniform tubercle may be present at border between cardiac and intestinal regions. Large spiniform tubercle or protuberance at each metabranchial region. Spinules may be present at posterior carapace margin an-

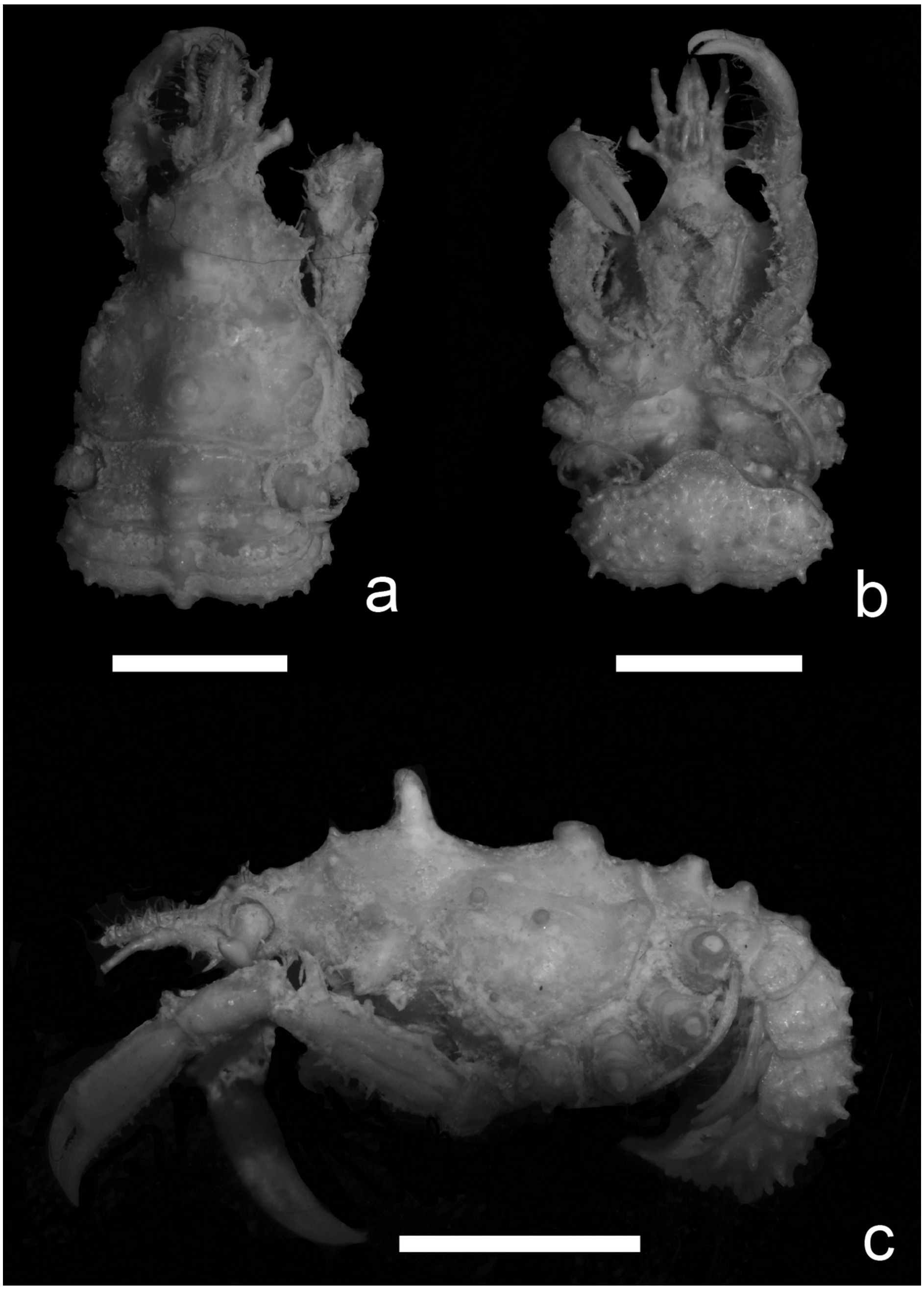

Figure 2. *Macropodia czernjawskii* (Brandt, 1880), female lectotype (ZIN-RAS 88751). **a.** Dorsal view. **b.** Ventral view. **c.** Lateral view. Scale bar: 5 mm.

terior to coxae of last pereopods (Fig. 2). All large spines, protuberances and tubercles end in sparse bunch of setae (obsolete in lectotype).

Thoracic sternum with indistinct sutures, with two lateral depressions in anterior part, separated by setose ridge-like elevation. Margins of 4th sternite and episternites 5–7 form a ridge bordering sterno-abdominal cavity (Fig. 2b).

Eyestalks relatively robust, directed perpendicular to orbital eave, with distal doubled setae dorsally. Cornea occupying about 1/5 of eyestalk.

Antennular fossae elongated, occupying most of the ventral part of frontal region of carapace; posterior margin of each fossa with a spinule. Interseptum between fossae bears a pronounced quasitriangular tooth (Fig. 3c). Antennules folded longitudinally, basal segment of antennule with sublongitudinal row of spinules (in lectotype, two on right antennules and three on left one), reaches to anterior tooth on lateral margin. Second segment reaches to about 7/8 of fossae extension.

Basal antennal segment extends along margin of antennular fossum, fixed in proximal half, distally free, reaching to anterior margin of antenullar fossae; with three spines on ventral face of fixed part, directed anterolaterally and visible not only in ventral but in lateral view, posterior spine usually smallest (Figs 2b, c; 3c; 6a,

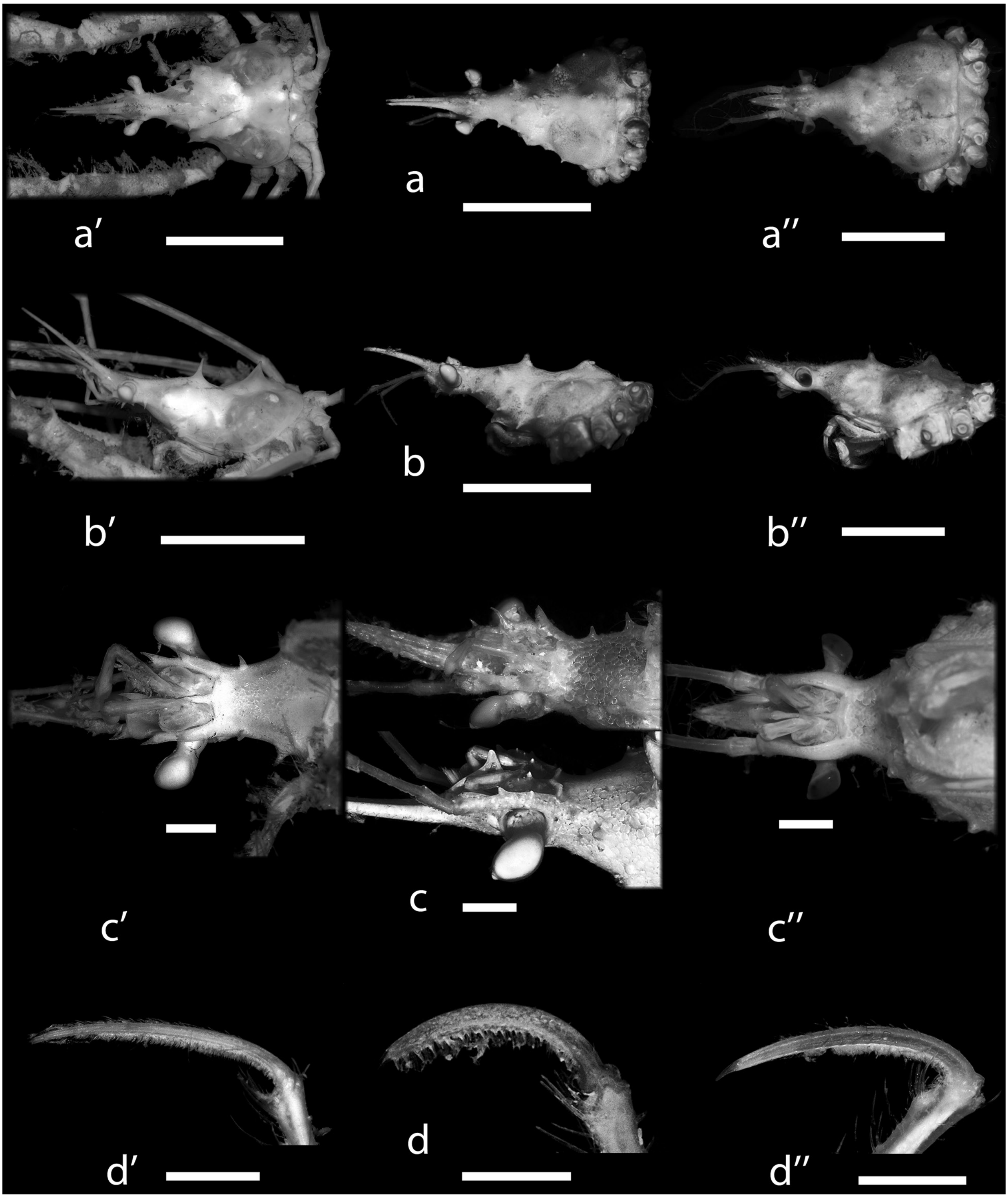

Figure 3. Comparison of *Macropodia czernjawskii* (**a–d.** possible paralectotype, male, ZIN-RAS 88750) to *Macropodia tenuirostris* (Leach, 1814) (**a'–d'.** male, SMF 3749) and *Macropodia rostrata* (Linnaeus, 1761) (**a"–d".** SMF 40660). **a.** Dorsal view. **b.** Lateral view. **c.** Anterior part of the body, with antennules, basal antennal segments, and epistome, ventral view. **d.** Dactylus of pereopod 5. Scale bars: 10 mm (**a–a"–b–b"**), 1 mm (**c–c"–d–d"**).

b). Spine on distoventral margin, near articulation with 2nd article, 2nd article about as long as free part of basal article; 3rd article long, hardly reaching the tip of rostral spine, with sparse setae along length and a fan of setae directed mesially and anteriorly. Antennal flagellum reaching to about tip of cheliped extended anteriorly; with sparse setae of different size.

Maxiliped 3: ischium of endopod relatively narrow, medially convex, postero-mesial end deflected; with row of three spinules along lateral margin on external face, another row of three spinules and sparse setae close to mesial margin interspaced by scattered strong setae. These rows, consisting of two or three spinules each, continue in merus. Merus prismatic, narrower than ischium, nearly as broad in dorso-vental dimension as in mesio-lateral one, with rounded anterior margin and strong directed forward spinule at antero-lateral angle, smaller spinule subdistally on lateral margin may be present; strong sparse setae at mesial corner. Carpus little shorter than merus, markedly broadening mesially, with concave smooth extensor face and convex setose flexor face; a small spinule at antero-lateral corner. Propodus little shorter than carpus, with densely setose flexor face; dactylus narrow, nearly as long as carpus, setose on margins.

Cheliped homoiochelic, markedly setose. Coxa and basis short, massive; ischium prismatic, with rows of 4 sharp spines margin of flattened flexor face; a strong distal spine at extensor face. Merus prismatic, with rows of 5–7 spines along flattened margins, being continuations of respective rows of ischium. Another row of 6–7 spines along mesial face; strong distal dorsal spine; extensor margin with a row of 3–4 tubercles ending in seta and a long distal setose spine. Carpus with flat flexor face, bearing a stong setose proximal spine and irregular rows of 2–3 spines along its margins, few spines in mid-part may be present; extensor face convex, tuberculate, setose, with one proximal and two distal setose spines or large tubercles (Fig. 2b, c). Chela with 3–5 sharp small spinules along upper face and a row of minute spinules along lower face. No molariform tooth present at proximal part of dactylus cutting edge; cutting edges with numerous small sharp papiliform teeth.

Post-cheliped pereopods long, P 2 longest, about 1.25 times as long as cheliped and about 1.5 times as long as P 5, which is the shortest of pereopods. In P 2 and P 3, the merus comprises about third of leg length, with distal sharp spine at extensor face, followed by propodus; dactylus over half of propodus length, thin, mostly straight, slightly curved distally, with long setae (Fig. 5c, d). In P 4 and P 5, the merus comprises over third of leg length, about as long as postrostral carapace length, with distal spine at extensor face; dactylus not much narrower than propodus, curved (sickle-shaped), with a dense row of strong spinules, exceeding length of setae along flexor margin; adductor margin with sparse setae or naked.

Pleon as broad as carapace. Each tergum with a median protuberance. Terga relatively densely covered with rounded granules terminating in short curled setae and numerous spinules laterally (Figs 2b, c; 5d). Genital opening slit-shaped, with rounded cap (Fig. 6d).

Males (only characters different from females). Cephalothorax pyriform, seemingly more elongated than in females in anterior part. Carapace surface, sternal area, pleon and chelipeds less densely covered with pile and setae than in females. Postrostral length to maximum width ratio ranges from 1.3 to 1.5 (Figs 3a, b; 4d; 5a, b).

Rostral spines slightly convex to straight in lateral view, closely set together, with narrow slit, slightly diverging in distal part or touching one another over entire length (Figs 3a, b; 4c, d); somewhat over-reaching (as in largest-studied specimens; Fig. 3a) or reaching end of antennal peduncle, as long as 20–37% of total carapace length (Fig. 4c, d). Seven to nine large curled setae located on each side of their dorsolateral margins; 7–15 thin moderately-curved to straight setae irregularly placed on dorsal face. Short setae on ventral face. Dorsal orbital eave less pronounced than in females, setose (Figs 3a, b; 4c, d).

Gastric region with pair of mesogastric tubercles, which may bear few straight setae; and a pair of spiny protogastric protuberances (directed slightly anterolaterally) and acute and less robust than in females metagastric spine (directed dorsally or slightly posteriorly), with bunch of straight setae (Figs 3a, b; 4c, d). Cardiac region elevated, with relatively sharp (compared to females) median spine, smaller than posterior gastric spine (Fig. 3b).

Thoracic sternum with lateral concavities, separated by median ridge, pair of spiniform tubercle with bunches of setae mesially on 4th sternites. Suture of thoracic sternum with 5th sternite indistinct. Episternites fused with sternites. Sternites 5–7 each with scattered granules and a spinule holding lateral position compared to spiniform tubercles on 4th sternite. Sutures between sternites 5 and 6 interrupted, between other posterior sternites well developed.

Chela setose; dorsal face with row of 4–5 spines of varying spines, similar row along midline of inner face, a row of 6–8 spinules on lower face, continuing to lower face of dactylus (Figs 4a, b; 7a).

Chela fingers about 40% of chela length, curved inside, covered with setae mostly on mesial face. Pollex of morphometrically mature male with proximal quadrate tooth; similar tooth at occlusive edge of dactylus; in closed chela, its posterior margin touching anterior margin of first tooth; distally of them, finger edges form a broad gap, contacting each other in distal-most third; small serial papilliform teeth on both finger cutting edges in this contact zone (Fig. 7a).

Pleon with locking mechanism comprising of button at proximal part of sternite 5 and sockets at antero-lateral angles of pleomere 6. All pleomeres separated, each of terga 4–6 with large median tubercle and pair of small lateral tubercles on both sides; telson semi-oval.

Gonopod 1 relatively slender, mostly straight, with short r-shaped distal tip, aperture opens anteriorly (Fig. 8a, b). Gonopod 2 very short. Penis in canal formed by posterior lobe of sternite and groove.

Variation. Variable characters include relative length of rostral spines, which slightly exceeds antennal peduncle in the largest males (Fig. 3a), usually reaching the distal margin of the peduncle in other males (Fig. 5d) and usually only approaching it in females (Fig. 2c). Tubercles, located mesially of the posterior spinules bordering epistome, may be obsolete in females. In the Black Sea specimens, the two mesogastric median tubercles are, in most cases, separate, but may be reduced. On the basis of

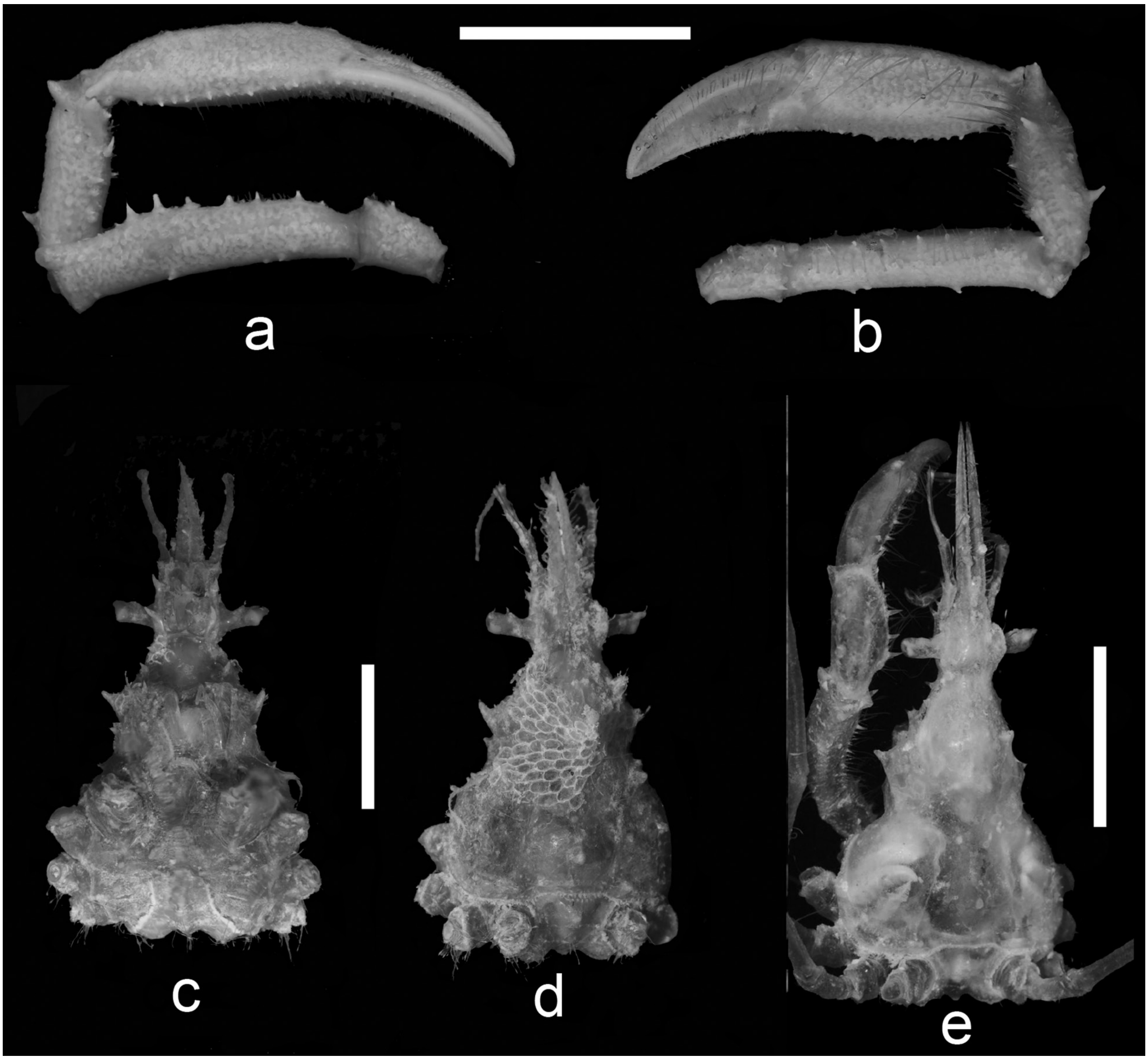

Figure 4. *Macropodia czernjawskii* (**a, b.** possible paralectotype ZIN-RAS 1609; **c, d.** ZIN-RAS 35102) and *Macropodia longirostris* (JC Fabricius, 1775) (**e.** SMF 3752). **a.** Right cheliped, ventral view. **b.** Right cheliped, dorsal view. **c.** Cphalothorax, dorsal view. **d.** Cephalothorax, ventral view. **e.** Cephalothorax, dorsal view. Scale bar: 10 mm.

examination of the specimens from the Western Mediterranean, Zariquiey Álvarez (1968: 478, fig. 161a) reported them to be fused; this condition was also confirmed by Ďuriš et al. (2013) for a specimen from the southern Dardanelles. D'Udekem d'Acoz (1992) reported specimens with separated tubercles from both southern Portugal and the Aegean Sea. The specimens from the Mediterranean, studied by us, have these tubercles closely set, reduced and, in one case, fused. The number of spines of the basal antennal segment is also variable. The Black Sea specimens usually have three spines, in small specimens (i.e. ZMMU Ma 3547) only two can be recognisable. The female from Sevastopol (CW 7.0 mm, ZMMU Ma 3611) has four strong spines on the left basal antennal segment and five spines (with a small posterior one) on the right segment. It also possesses a spine on the 2nd antennal segment. The Mediterranean specimens frequently possess four spines, two of them being large and the other two interspaced with them (Zariquiey Álvarez 1968; Ďuriš et al. 2013). Most geographical variation reported so far is related to less-developed spines and protuberances on the carapace, the basal antennal segment in the specimens from Portugal's coast (d'Udekem d'Acoz 1992: figs 1a; 2a; 3a-c) compared to the Mediterranean and the Black Sea specimens.

In the male (ZMMU Ma3543), chela fingers are not opposed, but strongly crossed (Fig. 7c) and this may be an apparent abnormality of development or a result of a traumatic event.

Size, chela morphometry and reproductive characteristics. The female lectotype measures 13.0 mm (TL) and 7.0 mm (CW). The ovigerous female paralectotypes measure 8.0 and 8.5 mm (CW); the 4th paralectotype is

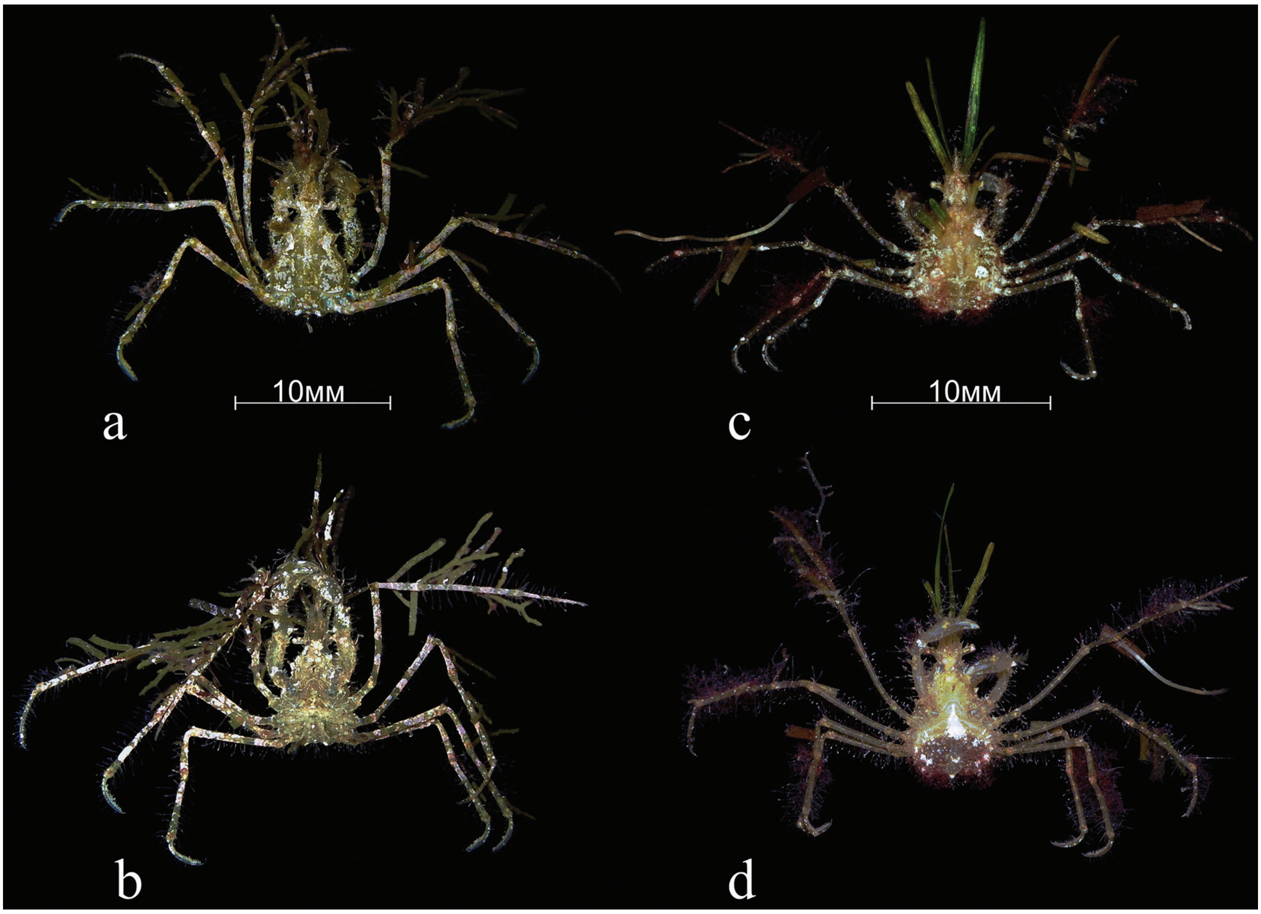

Figure 5. *Macropodia czernjawskii*, photographs in natural coloration. **a.** male (ZMMU Ma 3547), dorsal view. **b.** Same specimen as **a.** ventral view. **c.** female ov (ZMMU Ma 3542), dorsal view. **d.** Same specimen as **c.** ventral view. Scale bar: 10 mm. Photographs by SE Anosov.

damaged and not measured. Non-ovigerous female: CW 5.8 mm (Black Sea). Ovigerous females CW: 5.7–9.0 mm (Black Sea); 4.5–7.5 mm (Mediterranean). Males CW 4.0–8.5 mm (Black Sea), 6.3–6.5 mm (Mediterranean). The maximum TL of the Black Sea and the Mediterranean specimens does not exceed 15 mm which is distinctly less than the TL of the specimens from Portugal, 23.5 mm (d'Udekem d'Acoz 1992).

Males with CW equal to and greater than 5.0 mm (with the molariform tooth) have, respectively, larger chela than females (Fig. 9a). The chela morphometrics of the smallest male (CW = 4.0 mm) are closer (within 95% confidence limit) to the values predicted from the regression lines calculated for females rather than those for males (Fig. 9a; Table 2). Although regression coefficients between some chela measurements and CW in females were not particularly high, while in males, correlation coefficients between chela morphometrics and crab size were statistically non-significant (Table 2).

Five of the eight studied ovigerous females from the Black Sea, collected in the late spring to summer (from May to August in the years from 2009 to 2016) had eggs at the I stage of embryonic development; one female had eggs at stage II, one at stage IV and the largest female (CW 9.0 mm) had a clutch at the latest stage V in June 2013. The latter clutch was also the largest one of those observed and consisted of 1239 developing embryos while the other females carried from 351 to 986 eggs (see dataset in Spiridonov et al. 2020). There was a weak and statistically non-significant positive correlation between the female size (CW) and the number of eggs at embryonic development stages I–II (Fig. 9b). Egg diameter at embryonic development stages I and II ranged from 0.371 to 0.537 mm (mean 0.45 + 0.03 mm; n = 6) showed a weak negative correlation with the female size ($r = -0.385$, $t = -0.834$, $p = 0.451$). The volume of eggs at these stage averaged 0.051 + 0.0093 mm^3.

Colouration. Mimicking substrate and algae: carapace with whitish pattern on greenish background, legs greyish, with irregular whitish transverse bands (Fig. 5).

Ecology and epibiosis. In the Black Sea, the species was recorded between 0.5 and 9–12.8 m depth, but mostly within the upper 5–6 m on various substrates from rock and boulders to sand (Fig. 10e, f), in growing or detached aquatic vegetation, i.e. *Ulva* sp., filamentous green algae, *Cystoseira* sp., red algae (Fig. 10d). One male was also recorded in a community dominated by clams *Chamelea gallina*

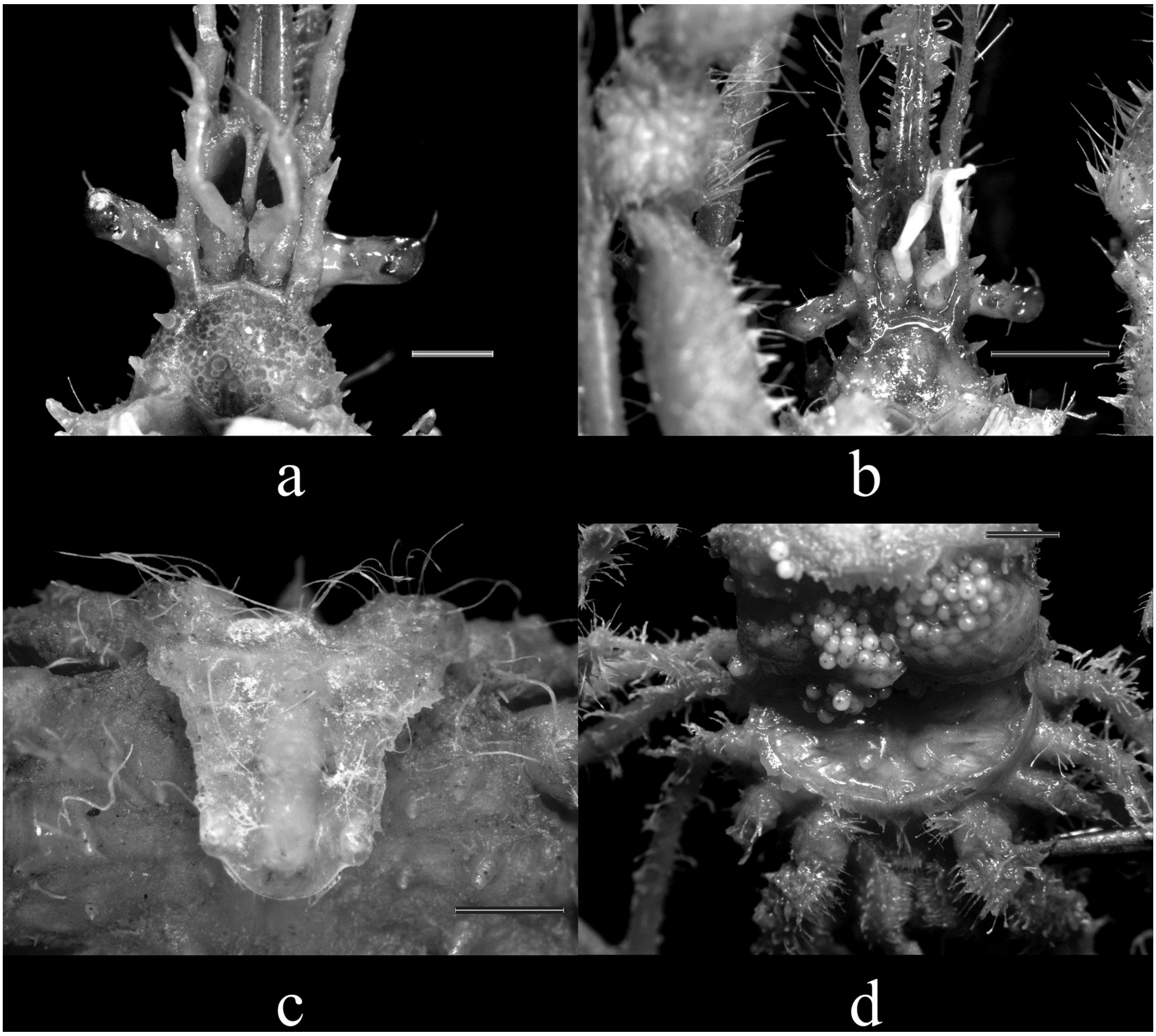

Figure 6. *Macropodia czernjawskii*. **a.** Anterior part of the body with basal antennal segment (ZMMU Ma 3543); **b.** Anterior part of the body with basal antennal segments, male (ZMMU Ma 3547). **c.** Male pleon (ZMMU Ma 3547); **d.** Female sterno-pleonal cavity with exposed genital segment (ZMMU Ma 3538). Scale bar: 1 mm.

Table 2. Linear regression of morphometric characteristics of right chela and carapace width (CW) in *Macropodia czernjawskii* from the Black Sea. ChL: chela length; ChH – chela height; ChGM – geometric mean of chela length, height and thickness; r – correlation coefficient; p – probablility level of statistical significance; NS – non significant.

Characteristics	Females		Males	
	Regression	r	Regression	r
ChL	0.3338CW + 2.6335	0.763 p < 0.05	1.0357CW + 0.0143	0.806 p = 0.05
ChH	0.2624CW – 0.3073	0.768 p < 0.05	0.380CW – 0.003	0.730 NS
ChGM	0.2632CW – 0.0025	0.895 p < 0.01	0.6003CW – 0.7835	0.744 NS

(Linnaeus, 1758), hermit crabs *Diogenes pugilator* (Roux, 1829) and predatory whelks *Rapana venosa* (Valenciennes, 1846) at about 10 m depth, where macrophyte vegetation is generally lacking, according to the underwater observations by the authors. It is very difficult to spot the crabs when they are hiding in algae (Fig. 10a). However, the males (but not females) were repeatedly observed walking on bare substrate, although a short distance from shelters and being decorated with pieces of algae (Fig. 10c).

Practically all crabs examined shortly after the collection and preservation in 2008–2018 had significant epibiosis. In some females, i.e. (ZMMU Ma 3538 and 3546), organisms of epibiosis covered 100% of the dorsal carapace surface and most of their legs. Males were seeming-

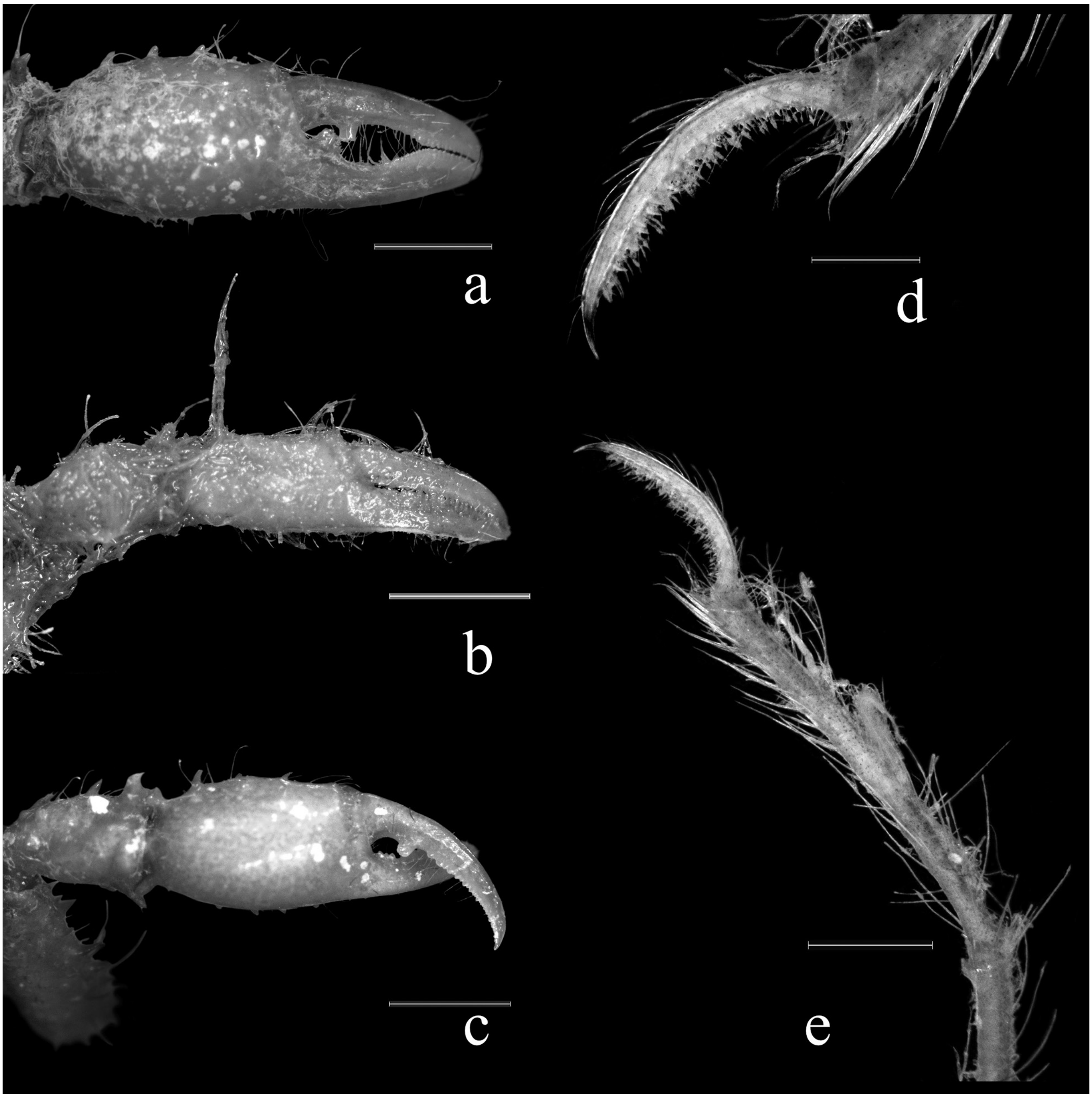

Figure 7. *Macropodia czernjawskii*. **a.** Right chela, male, CW 11.0 (ZMMU Ma 3547); **b.** Right chela, male. CW 6.0 mm (ZMMU Ma 3544) **c.** Malformed right chela, male, CW 8.0 mm (ZMMU Ma 3543); **d, e.** Same specimen as **c.** dactylus and propodus of P 5. Scale bars: 1 mm (**a–c, e**), 0.5 mm (**d**).

ly less decorated, with significant area of the carapace and pereopods without epibiosis.

The bulk of epibiosis consisted of algae and cyanobacteria. In twelve carefully examined specimens, 25 autotrophic eukaryote taxa were found, identified to the lowest possible level (see dataset in Spiridonov et al. 2020). Green algae *Cladophora* sp. and calcareous Corallinales gen. sp. were most commonly recorded (in 50% of specimens). They were followed by phaeophytes *Pilayella* cf. *littoralis*, *Sphacelaria cirrosa* (Roth) C. Agardh and rhodophytes *Ceramium siliquosum* (Kützing) Maggs and Hommersand and *Asterocytis* sp. Of particular interest is the finding of the non-indigenous red alga *Bonnemaisonia hamifera* Hariot, which was first officially recorded at the Caucasian coast of the Black Sea in 2015 (Simakova and Smirnov 2017). The present record, however, indicated that the male of *M. czernjawskii* (ZMMu Ma 3542) carried this introduced species in Crimea as far back as in 2011.

Sessile animals were not as diverse and abundant as the autotrophic taxa. They included unidentified (in poor condition) hydroids and sponges, sedentary polychaets *Janua pagenstecheri* (Quatrefages, 1865) (Spirorbidae; in two cases, on the ventral side) and, in one case, a colony of the bryozoan *Lepralia* sp. Remains of a similar bryozoan colony were also found in the material from

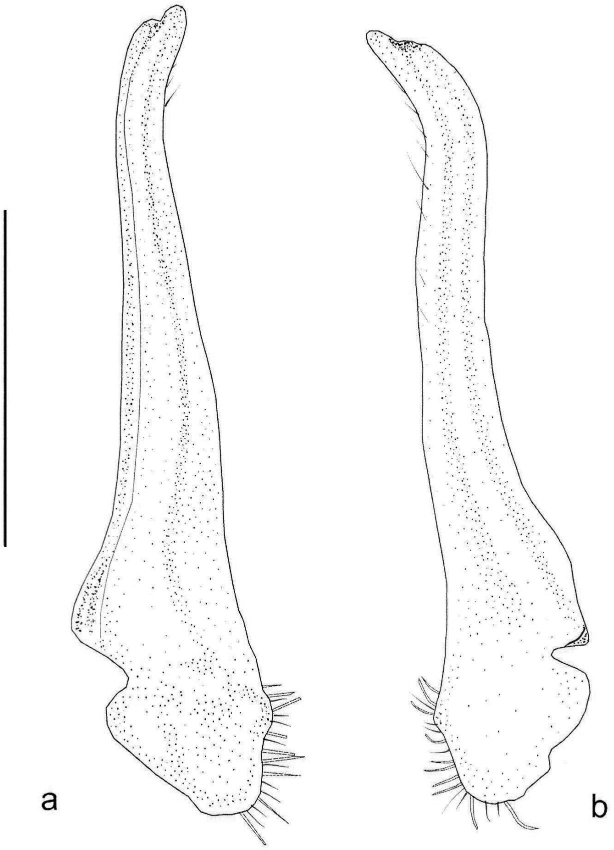

Figure 8. *Macropodia czernjawskii*. Male (ZMMU Ma 3543), right gonopod . **a.** Pleonal view. **b.** Sternal view. Scale bar: 1 mm.

t*he old* coll*ection (Z*IN-RAS 35099, Crimean Peninsula, about 6 m depth) (Fig. 4d).

Habitats recorded outside the Black Sea include the following: upper subtidal, rock with algae, seagrass in the Eastern Mediterranean (d'Udekem d'Acoz 1994); in Zostera and Cymodocea meadows (števćić 1990, 1993) and colonies of athecate hydroids *Eumendrium racemosum* (Gmelin, 1791) in the Adriatic (Martinelli et al. 2008a); rock, *Posidonia oceanica* (L.) meadows in Sicily's waters (Pipitone and Arcuelo 2003); between 10 and 30 m depth, (Zariquiey Álvarez 1968) or up to 80 m depth (Forest and Zariquiey Álvarez 1964); on muddy gravel and hard substrates (Grimes et al. 2016), between 2 and 9 m depth in *Posidonia oceanica* (L.) beds (García Raso 1990; Mateo-Ramírez et al. 2016) in the Western Mediterranean; in *Caulerpa* meadows on sand and clay at 1–3.3 m depth in Cadíz Bay (López de la Rosa et al. 2006); and intertidal, in sea grass in Portugal (d'Udekem d'Acoz 1992). Ďuriš et al. (2013) reported the species at 6 m depth from *Posidonia* leaf surrounded by the tentacles of the sea anemone *Anemonia viridis* (Forsskål, 1775). They considered this association accidental.

Distribution. Black Sea. Crimean coast: Donuzlav lagoon, Sevastopol, Yalta (type locality) (Czerniavsky 1868, 1884; Brandt 1880; this study); Cis-Caucasian coast (this study), Trans-Caucasian coast in Abkhazia (this study), North-western coast (Băcescu 1967; Micu and Micu 2006).

Mediterranean: Dardanelles (Ďuriš et al. 2013); Aegean Sea (Koukouras et al. 1992; d'Udekem d'Acoz 1994); Levantine Sea (Shiber 1981); Italian coast (Martinelli et al. 2008a) and Istria (Števćić 1990) in Adriatic Sea, Iberian coast, Alboran Sea (García Raso 1990; Mateo-Ramírez et al. 2016), Arzew and Bou Ismail Bays at Algerian coast (Grimes et al. 2016).

North-East Atlantic: inner Bay of Cádiz (López de la Rosa et al. 2006; Marco-Herrero et al. 2012); southern Portugal (d'Udekem d'Acoz 1992).

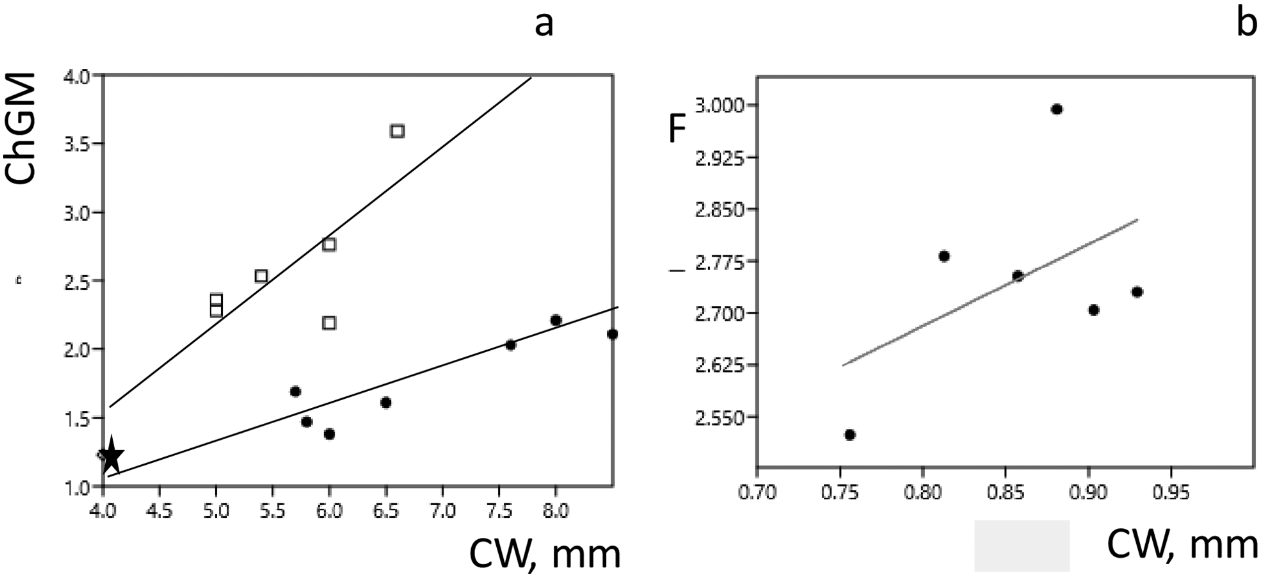

Figure 9. Morphometric relationships and fecundity characteristics of *Macropodia czernjawskii*. **a.** Relationships between carapace width (CW) and the geometric mean of chela length, height and thickness (ChGM). **b.** Relationships between CW and decimal logarithm of the number of developing eggs (I or II stage of development) on pleopods (F). For statistical data see Table 2.

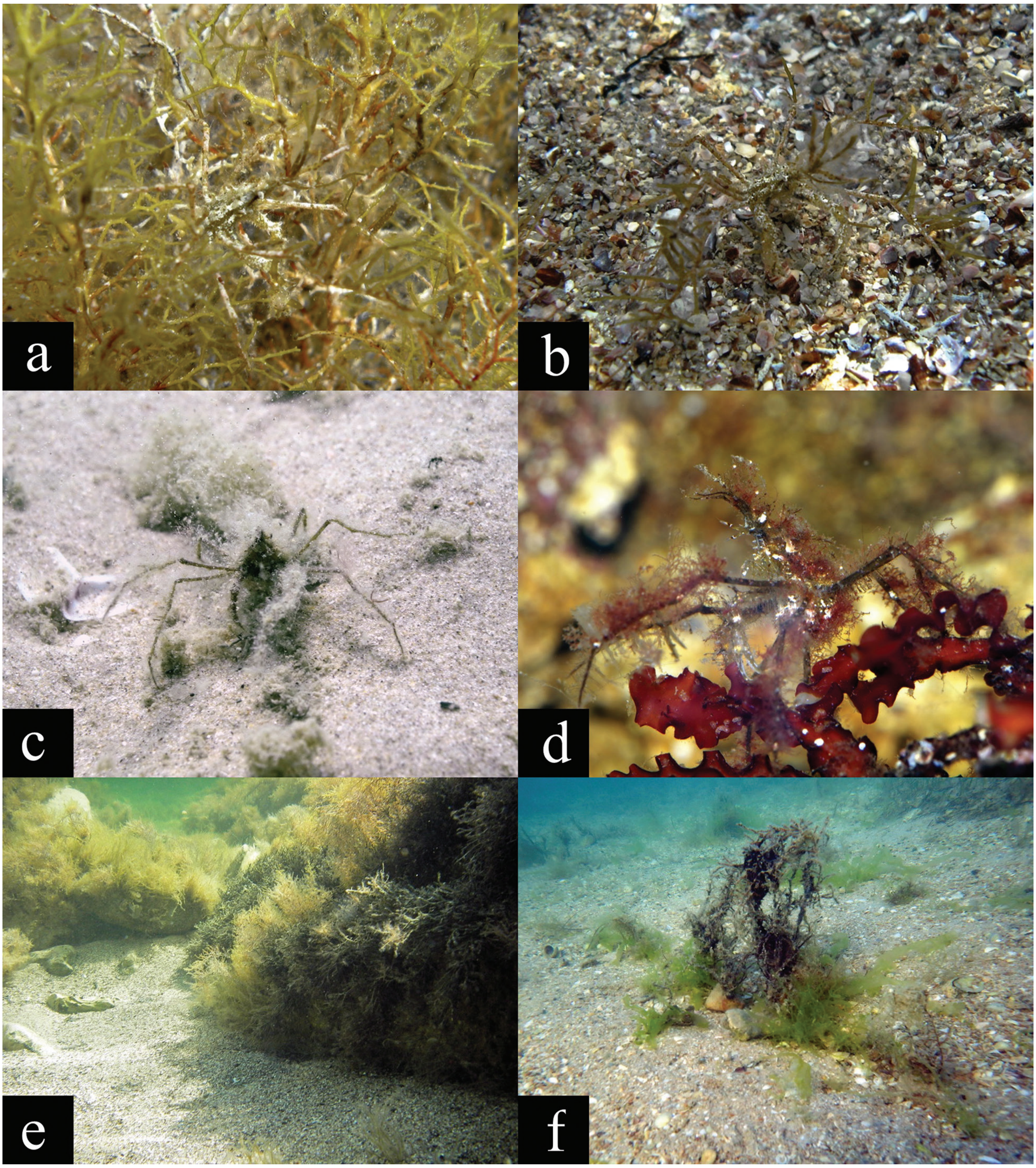

Figure 10. Natural habitats of *Macropodiz czernjawskii* in the Black Sea. **a, b.** Male (ZMMU Ma 3549) in *Cystoseira* sp., on rock, Tuaphat coastal rock masif, near Gelendzhik. **c.** Male (ZMMU Ma 3547), on sand, of Blagoveschenskaya village, near Anapa. **d.** Specimen collected of Blagoveschensakya in aquarium, decorated with red algae after few days of keeping. **e.** A characteristic biotope of *M. czernjawskii* in Tuaphat. **f.** Biotope in Kazachya Cove, Crimean Peninsula where *M. czernjawskii* has been repeatedly observed. Photographs by SE Anosov.

Remarks. In the time when the presence of *Macropodia czernjawskii* in the Black Sea was neglected by researchers from its coastal countries, the descriptions and illustrations of *Macropodia* species from this region were published in three regional monographs of Decapoda (Băcescu 1967; Kobjakova and Dolgopolskaya 1969; Makarov 2004). It was also treated under the incorrect name *Macropodia longirostris* by Marin (2013) in his atlas of Russian decapods. Two decades ago, Băcescu's (1967) record of *Macropodia aegyptia* was recognised to be *M. czernjawskii* by d'Udekem d'Acoz (1992, 1999) and the species was listed in the Romanian f*auna by Micu a*nd Micu (2006). As it follows from the labels of the type material in ZIN-RAS (*see above), Kob*jakova and Dolgopolskaya (1969) saw the types and probably other specimens of M. *czernjawskii in the ZIN-RAS collection (which in reality does not include any specimens of M. longirostris) when they were preparing their account. However, they treated this material as M. longirostris*. The illustration of adult *M. longirostris* by Makarov (2004: fig. 158) is of insufficient quality. However, some details (dactyli of P 4 and P 5, lateral view) on the figure allow us to recognise *M. czernjawskii* rather than *M. longirostris*.

The identity of *Macropodia rostrata* in Makarov's (2004) monograph remains problematic. The illustration of an adult specimen (Makarov 2004: fig. 161) is difficult to attribute to any species of the genus, although the dactylus of P 5 points to *M. czernjawskii* rather than to *M. rostrata*. The illustrations of larvae of the two presumed *Macropodia* species presented by Makarov (2004: figs 159–160, 162–163) do not show any principal differences between these "species"; however, the description does not allow any consistent comparison. Some characters (dorsal spine of carapace, antennal protopod tip) of zoea 1 and 2 of both "species" illustrated by Makarov (2004) are more similar to the respective stages of *M. czernjawskii*, described by Marco-Herrero et al. (2012). However, these larvae (Makarov 2004: figs 159, 162) have lateral spines on the telson, which were not observed in the zoea of *M. czernjawskii* from the Cadíz area (Marco-Herrero et al. 2012: fig. 7A, B).

Macropodia longirostris (Fabricius, 1775)

Fig. 4e

Cancer longirostris Fabricius, 1775: 408.
Stenorhynchus longirostris – Heller 1863: 23, pl. 1, figs 1, 2.
Macropodia longirostris – Pesta 1918: 314, fig. 98 (partim); Forest 1964: 350–354 (discussion of synonymy and historical misidentifications); Forest and Zariquiey Álvarez 1964: 228, figs 3, 7, 8, 14; Zariquiey Álvarez 1968: 478, figs 161d, 162c, 184a, b; d'Udekem d'Acoz 1999: 200.
Stenorhynchus egyptius H. Milne Edwards, 1834: 280.
Nec *Stenorhynchus longirostris* – Czerniavsky 1868: 77; Czerniavsky 1884: 129 (= *Macropodia czernjawskii*).
Nec *Macropodia longirostris* – Kobjakova and Dolgopolskaya 1969: 289 (= *Macropodia czernjawskii*).
Nec *Macropodia longirostris* – Makarov 2004: 328, figs 158–160 (= *Macropodia czernjawskii*).
Nec *Stenorhynchus aegyptius* – Czerniavsky 1884: 127 (= *Macropodia czernjawskii*)
Nec *Macropodia aegyptia* – Băcescu 1967: 271, figs 117 – 119 (= *Macropodia czernjawskii*)

Material. 1 male (SMF 3750), Mediterranean, Italy, Liguria, Portofino; 1 female (SMF 3752), Mediterranean, Italy, Liguria, Portofino; 1 male, 1 female ovigerous (SMF 3754), Mediterranean, Italy, Liguria, Portofino.

Diagnosis. Cephalothorax, pleon and chelipeds moderately and unevenly covered with short pile and setae. Rostral spines ascending, over-reaching end of antennal peduncle, but not antennal flagellae, about as long as 30% of total carapace length in females and 35% in males; with lateral rows of conspicuous curled setae (Fig. 4e). Epistome trapezoidal, with constricted anterior portion, with two sharp lateral spinules on each side. All carapace tubercles and spines setose. Gastric region with two median mesogastric tubercles, pair of sharp lateral protogastric spines and sharp and long median metagastric spine directed dorsally. Lower hepatic spine moderate, sharp; pterygostomial process spiny, visible dorsally. Cardiac region elevated, with sharp median spine. Tubercle on intestinal region present. Basal antennal segment with 4–5 spines. Merus of pereopods 2–5 with distal dorsal spine. Dactyli of pereopods 4 and 5, moderately curved, somewhat narrower than propodi, with a dense row of moderate spinules intermittent with setae along flexor margin and setal emargination of adductor margin.

Size (CW). Non-ovigerous female 9.5 mm; ovigerous female 10.0 mm; males 4.5–9.5 mm.

Ecology. Mostly upper subtidal; between 2 and 50 m depth (Zariquiey Álvarez 1968; Garcia Raso 1984; d'Udekem d'Acoz 1999; Ardizone et al. 2000; Pipitone and Aculeo 2003; López de la Rosa et al. 2006; Çelik et al. 2007). Forest and Zariquiey Álvarez (1964) communicated the lowest limit of bathymetric range at 130 m, while Števćić (1990) reported it to be at 230 m. D'Udekem d'Acoz (1999) doubted in particular the latter deepest record. The species is reported in muddy, sandy substrates and rock overgrown by algae (Števćić 1990; Pipitone and Aculeo 2003), *Posidonia oceanica* beds (García Raso 1990), *Caulerpa* meadows on sand and clay (López de la Rosa et al. 2006). In the artificial reef community, the species was reported to colonise this new biotope during the mussel (*Mytilus galloprovincialis* Lamarck, 1819) dominance phase (Ardizone et al. 2000). Porporato et al. (2011) reported association of *M. longirostris* with sea pen *Pteroeides spinosum* (Ellis, 1764).

Distribution. Mediterranean: Iberian Peninsula coast (Zariquiey Álvarez 1968; García Raso 1990); Alboran Sea (Garcia Raso 1984); Tyrrhenian Sea (Zariquiey Álvarez 1968; Ardizone et al. 2000; this study); Adriatic Sea (Števćić 1990); Ionian Sea (Pastore 1972; Porporato et al. 2011; Tsagarakis et al. 2013); Levantine Sea (Holthuis 1961); Dardanelles (Çelik et al. 2007).

Remarks. For a long time, this species was supposed to occur in the Black Sea. However, the first historical records by Czerniavsky (1868, 1884) were based on the type material of *Stenorhynchus czernjawskii*. The material, described and illustrated by Băcescu (1967), was re-identified by d'Udekem d'Acoz (1999). This and the i*llustration by Makarov* (2004: figs 158–160; see above) undoubtedly suggest Macropodi*a czernjawskii.* Kobj*akova and Dolgopolskaya (1969) apparently used the name M. longirostris for M. czernjawskii* occurring in the Black Sea and reproduced the illustration by Bouvier (1940), based on the Mediterranean material (their fig. 1). Other references of *Macropodia longirostris* for the Black Sea are either only records of a species of *Macropodia*, identified as *M. egyptia* or *M. longirostris* (i.e. Lyakhov 1940; Bilgin and Çelik 2004; Karaçuha et al. 2009), which are currently difficult to verify or just a mention of the name, secondary references included in the regional faunal lists (Sowinsky 1902; Öztürk 1998; Gönlügür-Demirci 2006; Balkis et al. 2012).

Macropodia rostrata (Linnaeus, 1761)

Fig. 3 a''–d''

Cancer rostratus Linneus, 1761: 493.

Macropodia (*Stenorhynchus*) *rostrata* – Pesta, 1918: 318, fig. 9.

Macropodia rostrata – Bouvier 1940: 362, fig. 219; Forest and Zariquiey Álvarez 1964: 225, figs 1, 12; Zariquiey Álvarez 1968: 479, figs 161c, b, 163; Forest 1978: 327, figs 2, 6, 13, 14, 18; Manning and Holthuis 1981: 301–302 (comparison with *Macropodia spinulosa*); Ingle and Manning 1982: 272, fig. 1; van Noort and Adema 1985: 364, figs 1–4.; d'Udekem d'Acoz 1999: 201.

Cancer phalangium Pennant, 1777: 8, pl. 9, fig. 17.

Macropodia phalangium – Leach 1815, pl. 23, fig. 6.

Stenorhynchus phalangium – H. Milne Edwards 1834: 279.

Macropodia parva van Noort & Adema, 1985: 371, fig. 12.

? *Stenorhynchus inermis* Heller, 1856: 3.

Nec *Macropodia rostrata* – Makarov 2004: 332, figs 161–163 (? = *M. czernjawskii*)

Material. North Sea. 6 males, 3 females; North Sea, German Bight; 53°45'N, 37°13'E; SMF 40660.

Mediterranean. 1 female; RV *Akademik Kowalevsky*, 87th Cruise, Stat 1303; 37°08.00'N, 12°00.70'E; 78 m depth; Sigsbee trawl; 13.09.1978; VV Murina leg; ZMMU Ma4338. 1 male, 1 female, 1 female ov; RV *Akademik Kowalevsky*, 87th Cruise, Stat 1308; 37°08.9'N, 12°05.2'E, 65 m depth; September 1978; VV Murina leg; ZMMU Ma4336. 1 male; RV *Akademik Kowalevsky*, 87th Cruise, Stat1316; near Lampeduza, 18.10.1979; VV Murina leg; ZMMU Ma4334. 1 female ov; RV *Akademik Kowalevsky*, 87th Cruise, Stat 1317(3); 35°28.50'N, 11.0°37.90'E; 72 m depth; 18.09.1979; expedition staff leg; ZMMU Ma3122. 3 males, 2 damaged; RV *Akademik Kowalevsky*, 90th Cruise, Stat 1396 (2); 37°15'N, 12°08.5'E; 76 m depth, tight sand; 07.09.1980; expedition staff leg; ZMMU Ma4337. 2 males; RV *Akademik Kowalevsky*, 90th Cruise, Stat 1398 (2); 39°23.60'N, 12°16.50'E, 70 m depth, September 1980; expedition staff leg; ZMMU Ma4335.

Diagnosis. Cephalothorax, pleon and chelipeds sparsely setose, with significant area smooth. Rostral spines horizontal or slightly ascending in lateral view, usually not reaching the end of 4th article of antennal peduncle, about as long as 8–16% of total carapace length in males and females, with lateral rows of conspicuous curled setae (Fig. 3a''). Epistome with two obtuse lateral protuberances near buccal frame corners (Fig. 3c''). All carapace protuberances, spines and tubercles setose. Gastric region with pair of short lateral protogastric protuberances, without median mesogastric tubercles and obtuse and relatively low median metagastric spine, directed dorsally. Two low hepatic protuberances on each side, lower being more robust. Pterygostomial process visible dorsally in males, but barely in females. Cardiac region elevated, with robust median conical protuberance, directed dorsally or inclined posteriorly. Intestinal region with conspicuous median tubercle (Fig. 3a'', b''). Basal antennal segment without spines (Fig. 3c''). Merus in pereopods 2–4 with single distal dorsal spine. Dactyli of pereopods 4 and 5 somewhat narrower than propodi, thin, moderately curved, with a dense row of minute to moderate spinules hidden in dense setal band along flexor margin and moderate coverage of longer setae on adductor margin (Fig. 3d'').

Variation. The specimens from the Mediterranean are all characterised by thin and relatively high gastric and cardiac spines in contrast to relatively low protuberances in the specimens from the North Sea.

Size. (CW). North Sea: females 11.5 mm, female ov 9.5 mm. Males 8.5–11.6 mm. Mediterranean: females 3.7–4.7 mm, females ov 5.0–6.5 mm, males 3.0–6.0 mm.

Ecology. In the Mediterranean, the species occurs from the upper subtidal zone to about 80 m depth, but usually deeper than 10 m, on a variety of substrates, both soft and hard, including algal and *Posidonia oceanica* (L.) biotopes (Zariquiey Álvarez 1968; Pastore 1972; Ingle and Manning 1982; Števčić 1990; d'Udekem d'Acoz 1999; Pipitone and Aculeo 2003; Çelik et al. 2007; Mateo-Ramírez et al. 2016; present study). In the Atlantic, *M. rostrata* is common and abundant from the intertidal zone to low subtidal zone, primarily on soft bottom, known in seagrass beds (review in d'Udekem d'Acoz 1999) and, in *Caulerpa* meadows, on sand and clay at 1–3.3 m depth (López de la Rosa et al. 2006, as *Macropodia parva*).

Distribution. Mediterranean: Western Mediterranean (Zariquiey Álvarez 1968); Alboran Sea (García Raso 1984; Mateo-Ramírez et al. 2016); waters around Sicily (Pipitone and Aculeo 2003); Ionian Sea (Pastore 1972; Tsagarakis et al. 2013); Adriatic Sea (Števčić 1990); south-central Mediterranean (Pipitone and Tumbiolo 1993); Levant Sea (Holthuis and Gotltieb 1958); Dardanelles (Çelik et al. 2007). North-East Atlantic: from the coast of Iberian Peninsula to North Sea, Shetland Islands and south-eastern Norway (reviewed by d'Udekem d'Acoz 1999).

Remarks. *Macropodia parva*, occurring in the North Sea (and reported from some other areas in the Atlantic, i.e. López de la Rosa et al. 2006), is a smaller species than *Macropodia rostrata*. It may be distinguished by the relative length of antennal segments 3–4 and 5 and the morphology of the dactyli of P 4 and 5. However, these diagnostic characters are subtle and may refer to juveniles of *M. rostrata* (d'Udekem d'Acoz 1999). The Mediterranean specimens of *M. rostrata*, examined by us, show little differences from the North Sea specimens, but have spinules at the inner (flexor) margin of P 5 dactylus nearly over the entire dactylus length, which is the character of *M. parva* (van Noort and Adema 1985: 378). On the contrary, Manning and Holthuis (1981: 302) found that the dactylus of P 5 in the Mediterranean specimens "has low denticles only on the proximal third". Raupach et al. (2015) found no differences in the sequences of the COI gene in samples of specimens identified as *M. rostrata* and *M. parva* from the North Sea. Taking into account morphological variability and molecular genetic data, we regard *M. parva* as a junior synonym of *M. rostrata*.

Manning and Holthuis (1981) also suggested that, if the differences between the Atlantic and the Mediterranea specimens of *M. rostrata* prove to be constant, the Mediterrannean form might deserve a separate status under the name *Macropodia inermis* (Heller, 1856). However, we have not yet found a substantial support for this view on the basis of morphology. In addition, the genetic markers data for the Mediterranean populations of *M. rostrata* are lacking. Thus, for the time being, we consider *Macropodia inermis* (= *Stenorhynchus imermis* Heller, 1856) as a junior subjective synonym of *M. rostrata*.

Macropodia rostrata was repeatedly listed for the Black Sea, although, as shown in the introduction, most of these listings could be dated back to Grebnitzky's (1873) record included in Czerniavsky's (1884) monograph. This species name continues to "travel" from one regional faunal list to another, up to relatively recent ones (i.e. Gönlügür-Demirci 2006). Kobjakova and Dolgopolskaya (1969) wrote that *M. rostrata* "occurs in the same places as the other species (*M. longirostris* in their concept = *M. czernjawskii*) but is, probably a more rarely found species". Although they published an original illustration of *M. rostrata* (Kobjakova and Dolgopolskaya 1969: pl. VI, fig. 2), it is not clear from the text if these authors ever had any material from the Black Sea. It was a common practice in the Soviet Union to order professional artists to do illustrations for regional faunistic monographs and manuals. They could use various types of material for drawing, not necessarily originating from the region. If Kobjakova and Dolgopolskaya (1969) had the material of *M. rostrata* from the Black Sea, it would likely reside in the ZIN-RAS collections, which were apparently used in the process for preparation of their publication. However, it is not the case. We have shown above that it is likely that the "*M. rostrata*" in Makarov's (2004) monograph represents *M. czernjawskii*. Besides this, there are two original records of the species: an old one from Crimea, within a comparative study of decapod fecundity (Vinogradova 1951); and a recent one from the Turkish coast in the southern Black Sea, within a faunistic-ecological study of *Zostera* meadows (Bilgin et al. 2007). In both cases, no details were provided, thus, assuring that these records had not been based on misidentification.

Macropodia tenuirostris (Leach, 1814)

Fig. 3a'–d'

Leptopodia tenuirostris Leach 1814: 383–437.

Macrodia tenuirostris – Leach 1815: pl. 23, figs 1–5 (misspelling).

Macropodia tenuirostris – Forest and Zariquiey Álvarez 1964: 223; Zariquiey Álvarez 1968: 482; van Noort and Adema 1985: 367, fig. 5; d'Udekem d'Acoz 1999: 201.

Macropodia tenuirostris ssp. *tenuirostris* – Forest 1978: 333, figs 4, 8, 15, 21.

Macropodia tenuirostris ssp. *longipes* – Forest 1978: 337, figs 9, 16.

Stenorhynchus tenuirostris – Bell 1844: 6.

Stenorhynchus longipes A. Milne-Edwards & Bouvier, 1899: 48; A. Milne-Edwards and Bouvier 1900: 157, pl. 21, fig. 18, pl. 22, figs 7–11.

Macropodia longipes – Forest and Zariquiey Álvarez 1964: 226, figs 2, 6, 13. Zariquiey Álvarez 1968: 482, figs 161c, 164c–d; Manning and Holthuis 1981: 295 (key), 300.

Macropodia longirostris – Bouvier 1940 (partim): 365, fig. 21 (nec *Cancer longirostris* Fabricius, 1775).

Material. Mediterranean. 1 male; Mediterranean, no other data; SMF 3749 (identified as *Macropodia longirostris*). 1 female; RV *Akademik Kowalevsky*, Stat 1192/129; 40°03.0'N, 0°56.1'E; 105 m depth; 1980; expedition staff leg; ZMMU Ma4341. 1 male, RV *Akademik Kowalevsky*, Stat 1314/60; 35°31.40'N, 12°02.60'E; 75 m depth, beam-trawl; 18.09.1979; VV Murina leg; ZMMU Ma4339. 1 female, RV *Akademik Alexander Kowalevsky*; Stat 1111 (30), 43°21.70'N, 14°46.90'E, 110 m depth, Sigsbee trawl, 01.05.1979; VV Murina leg; ZMMU Ma4340.

Atlantic Ocean. 4 males, 3 females ov; Cadíz Bay; RV *Miguel Oliver*, ARSA Cruise; ca. 36°45.00'N, 06°45.00'E, 90 m depth; commercial trawl; 09.11.2017; Lischenko leg; ZMMU Ma3576. 1 male, 1 female; Cadíz Bay; RV *Miguel Oliver*, ARSA Cruise; ca. 36°45.00'N, 06°45.00'E; 90 m depth; commercial trawl; 09.11.2017; Lischenko leg; ZMMU Ma3577.

Diagnosis. Cephalothorax, pleon and chelipeds sparsely covered with curled and hooked setae. Pereopods covered with sparse small coiled and longer straight setae, with large surface area smooth. Rostral spines ascending, over-reaching end of antennal peduncle and, in larger specimens, over-reaching antennal flagellae (Fig. 3a'), about as long as 33–41% of total carapace length in females and 39–45% in males; with lateral rows of small coiled setae. Epistome trapezoidal with constricted anterior portion, with two pairs of sharp lateral spinules, irregular spiniform tubercles may be present in anterior part (Fig. 3c’). Gastric region without median mesogastric tubercles, with pair of sharp lateral protogastric spines and sharp and long median metagastric spine, directed dorsally. Lower hepatic spine thin and sharp. Pterygostomial and branchial protuberances spiny. Cardiac region elevated, with sharp median spine directed dorsally (Fig. 3a’, b’). Basal antennal segment with three spines directed anteriorly, median largest (Fig. 3c’). Merus of pereopods 2–5 with distal double dorsal spine. Dactyli of pereopods 4 and 5 distinctly narrower than propodi, thin, moderately curved, with dense row of minute spinules intermmitent with longer setae along flexor margin and setal emargination of adductor margin (Fig. 3d’).

Size (CW). Atlantic: non-ovigerous females 8.2 mm, ovigerous females 9.0–11.5 mm, males 8.1–13.6 mm. Mediterranean: females 5.5–8.4 mm, male 9.0 mm.

Ecology. The species occurs between 9 (García Raso 1984) and 748 m depth (Abelló et al. 1988), mostly between 40 and 270 m depth (García Raso 1984; this study), on a variety of substrates, both soft and hard (Števćić 1990; Pipitone and Aculeo 2003).

Distribution. Mediterranean: Western Mediterranean (Zariquiey Álvarez 1968); Alboran Sea (García Raso 1984); waters around Sicily (Pipitone and Aculeo 2003); Ionian Sea (d’Udekem d’Acoz 1999); Adriatic Sea (Števćić 1990); south-central Mediterranean (Pipitone and Tumbiolo 1993); Aegean Sea (d’Udekem d’Acoz 1994); Levant Sea (Holthuis and Gotltieb 1958). In North-East Atlantic from Islands of Cabo Verde to Faroe Islands (reviewed by d’Udekem d’Acoz 1999).

Remarks. *Macropodia longipes* was described on the basis of a single specimen from the Atlantic waters. Forest (1978) found significant overlapping of its diagnostic characters with *M. tenuirostris* and treated *M. longipes* as a subspecies of the latter. It is generally characteristic for the southern part of its distribution range, in particular the Mediterranean. D’Udekem d’Acoz (1999) has considered *M. longipes* as a gracile intraspecific form of *M. tenuirostris*, while, in general, currently this is an accepted name (Ng et al. 2008; WoRMS 2020). A single unequivocall character used for distinguishing between *M. tenuirostris* and *M. longipes* is the relative length of rostrum which exceeds the antennal flagellum in *M. longipes* and does not reach to its tip in *M. tenuirostris* (Zariquiey Álvarez 1968). Our specimens correspond to the “gracile” habitus of *M. longipes*. While larger specimens from the Cadíz Bay (CW > 11 mm, ZMMU Ma 3576) have rostrums exceeding antennal flagellae, they are nearly equal in a male with CW 10.4 mm. Rostrums of a smaller male and female from the same locality (CW < 8.3 mm, ZMMU Ma 3577) are shorter than antennal flagellae. Rostrums of all Mediterranean specimens either do not reach or nearly reach antennal flagellae.

The analysis of molecular barcode, COI indicates that all our specimens from the Cadíz Bay are conspecific and are broadly placed within a large sample of specimens

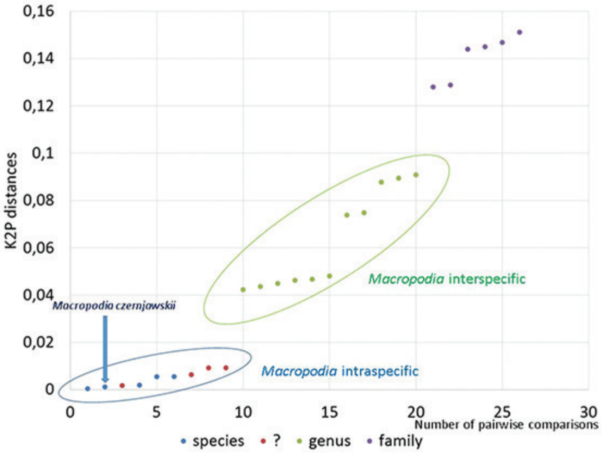

Figure 11. Estimates of evolutionary divergence over sequence pairs within and between species of *Macropodia* (*M. czernjawskii*; *M. rostrata – M. parva; M. tenuirostris – M. longipes*; the latter two pairs and *M. parva*, *M. rostrata – Macropodia* sp. are indicated as “?”, meaning their possible conspecificity); and between genera of Majoidea. The number of base substitutions per site from averaging over all sequence pairs between groups are shown. Analyses were conducted using the Kimura 2-parameter mode. For values of K2P see also Table 3.

Table 3. Estimates of evolutionary divergence over sequence pairs between particular species of *Macropodia* and outgroups (*Inachus aguiarii*, *Hyas araneus*). K2P – the number of base substitutions per site averaged per all sequence pairs between groups are shown; SE – standard error estimates. The analyses were conducted using the Kimura 2-parameter model (Kimura 1980). NA – not available.

Species	*Macropodia tenuirostris (M. t.)*		*Macropodia parva (M.p.)*		*Macropodia longipes (M.l.)*		*Macropodia rostrata (M.r.)*		*Macropodia* sp. *(M. sp.)*		*Macropodia czerhjawskii (M.c.)*		*Inachus*
	K2P	SE	K2P	SE	K2P	SE	K2P	SE	K2P	SE	K2P	SE	K2P
M. t.	0.002	0.001											
M. p.	0.044	0.008	0.014	0.003									
M. l.	0.002	0.001	0.042	0.008	0.000	0.000							
M. r.	0.048	0.009	0.009	0.002	0.047	0.009	0.006	0.002					
M. sp	0.046	0.009	0.009	0.002	0.045	0.009	0.006	0.002	NA	NA			
M. c.	0.075	0.013	0.088	0.013	0.074	0.013	0.089	0.014	0.091	0.014	0.001	0.001	
Inachus	0.129	0.015	0.144	0.017	0.128	0.015	0.145	0.017	0.147	0.017	0.151	0.019	
Hyas	0.205	0..021	0..205	0..021	0..202	0..021	0..204	0..021	0..206	0..021	0.218	0.023	0.217 (SE 0.022)

from various localities, originally identified either as M. tenuirostris or *M. longipes* (Fig. 10). In our opinion, *M. longipes* represents an intraspecific form within *M. tenuirostrus*, being a result of both size-related and geographical phenotypic variation. We, thus regard *M. longipes* as a junior subjective synonym of *M. tenuirostris*.

Phylogenetic relationships based on COI gene marker

Estimates of evolutionary divergence of the studied *Macropodia* species show a clear gradation corresponding to the levels of taxonomic hierarchy in Majoidea (Table 3; Fig. 11). *Macropodia czernjawskii* specimens from the Black Sea are represented by two haplotypes, differing by one nucleotide substitution. They are characterised by the lowest, out of all species, divergence coefficient (K2P) of 0.001. *M. rostrata* and *M. tenuirostris* show somewhat higher values of interspecific divergence (0.002–0.005; Table 3). The distances within the pairs of presumably the same species: (see Systematic account) *M. rostrata* – *M. parva* and *M. tenuirostris* – *M. longipes*, fall entirely within the intraspecific divergence range. This supports the conclusion that *M. parva* should be considered as a junior synonym of *M. rostrata* and *M. longipes* is synonymous to *M. tenuirostris*. *M. czernjawskii* shows sister relationships to *M. tenuirostris* / *longipes* and both of them

Figure 12. Phylogenetic relationships of *Macropodia* spp. based on partial sequence of the COI gene, obtained using Bayesian inference. Tips of the tree colored according to their morphological identification. Numbers above the branches are the posterior probabilities.

are a sister group to M. rostrata / parva (Fig. 12). Intergeneric divergence between *Macropodia* species and *Inachus aguiarii* de Brito Capello, 1876 range from 0.129 to 0.157 and K2P between inachid genera and *Hyas araneus* (Linnaeus, 1761) (Oregonidae) falls within 0.202–0.218 (Table 3; Fig. 11).

Discussion

How many species of *Macropodia* live in the Black Sea?

The present study indicates the occurrence of only one species of *Macropodia* in the Black Sea, *M. czernjawskii*. No other species was found in the historical collections, nor collected along the Crimean and the continental coasts of the Black Sea in our targeted survey. We know only of a few primary records or *Macropodia rostrata* in literature, which remain unconfirmed. However, the name "*rostrata*" travels from one faunal list to another, thus providing a basis for further misidentifications. Frequent inclusion of *Macropodia longirostris* in the regional fauna lists is based on the misidentification of the type specimens of *M. czernjawskii* by Czerniavsky himself and the long-lasting impact of his work.

It is difficult to explain why Czerniavsky did not recognise the new species, nor commented on it, particularly taking into account that, before publishing the monograph in 1884, he was working in the Zoological Museum of the Russian Imperial Academy of Sciences in St. Petersburg in close contact and even collaboration with Brandt in late 1870s and early 1880s (Brandt 1880; Spiridonov and Petryashov 2011; Shadrin 2016). We speculate that the manuscript of the monograph on Decapoda (Czerniavsky 1884) was finished some time before Brandt established *Stenorhynchus czernjawskii*, i.e. by 1878–1879. Later, Czerniavsky was mostly concerned with the preparation of monographs on mysids, polychaets and sponges and studies of the archaeology and ethnography of Abkhazia (Spiridonov and Petryashov 2011; Shadrin 2016). Furthermore, he had some health problems, forcing him to leave St. Petersburg and return to Sukhum, Abkhazia, where he had a villa. There were also indications that, from the late 1870s, Czerniavsky was losing interest in his previously favourite research topics in the Black Sea zoology (Spiridonov and Petryashov 2011; Rusanov 2016; Shadrin 2016). Busy with other things, he probably simply did not attend to making changes in the manuscript that had already been prepared for publication.

The recognition of a single *Macropodia* species in the Black Sea fauna (vs. five species in the Mediterranean) makes the number of Majoidea species in this region similar to the impoverished composition of most of the other anomuran and brachyuran families and superfamilies. Disregarding non-indigenous species, Porcellanidae and Paguridae are represented by one species each; Diogenidae by two species; Xanthoidea, Eriphoidea, Pilumnoidea by one species; Grapsoidea by two species; and only Portunoidea have seven species in the Black Sea fauna, with four species belonging to *Liocarcinu*s Stimpson, 1871 (Anosov 2016). This agrees with the historically-recognised pattern of a relatively-recent colonisation of the Black Sea by the Mediterranean species and the presence of environmental barriers (such as low salinity and low winter temperatures) for many truly marine taxa (Sowinsky 1902; Zenkevich 1963).

Molecular-genetic barcoding data

The present data on the COI genetic marker provide solid support for a clearly separate status of the Black Sea – Mediterranean endemic species *Macropodia czernjawskii*. Its divergence from other examined species of the genus, expressed by the K2P coefficient (0.075–0.091), falls close to the average value for Majidae (0.096), the most closely-related taxon to *Macropodia* in the species sample studied by Matzen da Silva et al. (2011). The genetic distance between the Atlantic – Mediterranean species *M. rostrata* and *M. tenuirostris* (0.042–0.048) is smaller than their distances to *M. czernjawskii*, corresponding to the lower range of intrageneric divergence (Matzen da Silva et al. 2011). *M. czernjawskii* may have a closer phylogenetic relationship to *Macropodia deflexa* Forest, 1978. This North-East Atlantic species is, in many respects, similar to *M. czernjawskii*, but does not overlap with it in the distribution (Forest 1978; Heard 2005). However, the genetic markers' data for *M. deflexa* remain unavailable.

Our analysis supports the opinion of d'Udekem d'Acoz (1999), based on the morphological observations and the results of the first molecular barcoding study of *Macropodia* by Raupach et al. (2015) that *Macropodia parva* is conspecific to *Macropodia rostrata* and *Macropodia longipes* represents an interspecific variation of *Macropodia tenuirostris*. While age-related (or size-related) phenotypic variation is likely the cause of the first pair of "species" (d'Udekem d'Acoz 1999), in the second pair, it is complicated by geographical variation, since no *M. longipes* was ever reported from the northern part of the *M. tenuirostris* range (van Noort and Adema 1985; Forest 1978). However, early stages of evolutionary divergence, i.e. in the process of ecological speciation (Nosil 2012), cannot be excluded.

Life history traits and ecology of *Macropodia czernjawskii*

Although the sample of *Macropodia czernjawskii*, studied for morphometry and reproductive characteristics, is small, a complete absence of respective data on *Macropodia* spp. in literature calls for their preliminary discussion. Males are not larger than females and show a clear sexual dimorphism in chela size, with much larger chelae in males upon reaching a certain size (Fig. 9) that is generally typical for Majoidea. In the best studied case of commerc*ially important sp*ecies Chionoecetes opilio (O. Fabricius, 1798) (Majoidea: Oregonidae), male chelae become distinctly broad when crabs attain morphometric maturity and do not grow further after the terminal moult. The size of crabs entering the terminal moult varies in space and time, so do relationships between the body and chela sizes (Sainte-Marie et al. 1995). Terminal moult is probably characteristic for all majoid crabs, in particula*r it can be inferre*d for Macropodia rostrata on the basis of data by Perez (1928) and is known for other Inachidae (Wirtz and Diesel 1983; Diesel 1986). Poor correlation between male chela sizes and CW (Table 2) in our small and spatially heterogenous sample may be interpreted as the presence of terminal moult and attaining morphometric maturation at CW of about or larger than 5 mm, but with considerable variation in different local populations of *M. czernjawskii*.

Females of *M. czernjawskii* also become mature, lay eggs and do not grow after the terminal moult. On average, they have larger egg volume than Portunoidea, Xanthoidea and Grapsoidea (mean values in the range 0.02–0.03 mm^3) but smaller than the average Majoidea, about 0.13 mm^3 (Brockerhoff and McLay 2011). However, most of studied majoids are themselves larger as adults. In addition, the larval period of *M. czernjawskii* includes only two zoea stages and a relatively short larval period, of only about a week (Marco-Herrero et al. 2012). This suggests a tendency towards K-strategy in comparison to many other brachyuran groups. As an upper subtidal species with certain habitat preferences, *M. czernjawskii* possesses a trait of carrying a smaller number of larger eggs for longer time and shortening of the planktonic larval period. We suppose this to be an adaptation to decrease larval dispersion offshore, to the areas that are unfavourable for settlement.

Macropodia czernjawskii is indeed the shallowest-living (largely within the upper 10 m) species of the genus in the gross Mediterranean realm. For *M. longirostris*, a deeper lower limit of occurrence is reported (50 or 130 m vs 30 m; see above). *Macropodia linaresi* and *M. rostrata* occupy intermediate depth and *M. tenuirostris* is the most deep-living, lower subtidal species.

Schäfer (1954) proposed a classification of eco-morphological types of crabs with such basic categories as runners/walkers, burrowers, swimmers and climbers; and considered most of majoid crabs as climbers. Indeed, females of *M. czernjawskii* were always found on particular kinds of living substrata as climbers, while males were often recorded walking on bottom sediments. In another inachid spider crab *Inachus phalangium* (Fabricius, 1775), females are relatively stationary, living in association with sea anemones, while males are patrolling the area where several females are present (Diesel 1986). It is likely that *M. czernjawskii* has a somewhat similar habit, with settling females and more active males, moving from one algal or sessile epifauna patch to another. It is thus not a genuine climber, which usually have relatively short pereopods (Schäfer 1954). At least, the males of this species may be characterised as "walking climbers".

As an inhabitant of the photic zone where hiding and mimicking are extremely important for protection, *M. czernjawskii* is capable of decorating itself with pieces of macrophytes, attaching them with the help of setae (Martinelli et al. 2008a, b), and cultivating a broad array of cyanobacteria, algae and sedentary invertebrates on its carapace and legs. Such epibiosis is generally considered effective as protection from predators (Wicksten 1983; Wahl 2009) and is also characteristic for several other shallow-living majoid crabs (Thanh et al. 2004; Ibrahim and Amin 2013). Masking material can be also used as food storage (Rorandelli et al. 2007). Abundant and diverse setae (Martinelli et al. 2008b; present study) and the occurrence in algal biotopes with numerous sources of epibiosis make *M. czernjawskii* particularly specialised in decorating and using epibiosis for protection in comparison to other, deeper living congeners.

General implications of the *Macropodia* case for the Black Sea biodiversity assessment

The case of *Macropodia czernjawskii*, as the species described in the Black Sea, but neglected for a long time in the region of its description although recognised outside, is not unique. Some decapod species, living in the Black Sea for a long time, were mistakenly supposed to be identical to particular Mediterranean congeners (Spiridonov and Petryashov 2011; Anosov 2016). In particular, a single species of *Pilumnus*, living in the Black Sea and the adjacent part of the Sea of Azov was, for nearly two centuries, identified as *P. hirtellus* (Linnaeus, 1761). Only recently, it became evident that this species is identical to *Pilumnus spinulosus* Kessler, 1861, described from the Black Sea, which in turn is a senior synonym of *Pilumnus aestuarii* Nardo, 1869, described from the Adriatic (Marin 2018; Marin and d'Udekem d'Acoz 2019).

The story of the polychaet *Spio decorata* Bobretzky, 1870 (Spionidae) is identical to the one of *M. czernjawskii* in every detail. Although described from Sevastopol, the Crimean Peninsula, this species was practically not listed for the Black Sea, but recorded elsewhere in the North-East Atlantic realm. Again, only recently, it came into view that many records of *Spio fillicornis* (Müller, 1776) in fact refer to *S. decorata*; and that *S. filliformis* does not occur in the Black Sea (Boltacheva and Lisitskaya 2019; Syomin and Simakova 2019). This calls for a more cautious attitude towards historical records and it is important to emphasise the need for a careful revision of taxa described from the Black Sea and then synonymised or disregarded.

Conclusions

Macropodia czernjawskii has been re-described here on the basis of the type and the topotypic material and provided with molecular barcode (COI gene) data from the topotypic specimens. It is a distinct species, described *from the B*lack Sea, although it was *missing in the* regional faunal accounts for more than a century due to the interplay of historical circumstances and personal research attitudes. The present analysis is based on historical and new collections and *the review of published regional records of Macropodia spp. These indicate that M. czernjawskii is very likely the only species of the genus that occurs in the Black Sea. The extended dataset of the molecular barcodes has provided a better understanding of the status and the relationships of M. czernjawskii* and some of its congeners. However, it is far from being complete and it is important to emphasise the need for further research of phylogenetic relationships of *Macropodia*, covering other species of the genus and Mediterranean populations of *M. czernjawskii*, *M. rostrata* and *M. tenuirostris* that still require genetic studies.

Although all *Macropodia* species have epibiosis, *M. czernjawskii* (as a shallow-water species living in the photic zone) is particularly specialised for self-decoration and stimulates abundant epibiosis of autotrophic taxa that provides masking of the crabs on the substrate. Finding of the non-indigenous species of red alga *Bonnemaisonia hamifera* Hariot in the epibiosis of *M. czernjawskii* four years prior to its first record on the seabed substrata of the Black Sea in 2015 is of a particular interest for further explorations. It suggests that museum and monitoring collections of species with abundant epibiosis (in particular inachid crabs) may be used as an additional tool to record and monitor introduction and establishments of sessile non-indigenous species.

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Supplementary material 1

Table S1

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Data type: Species data

Explanation note: This dataset contains the collection, morphometric and epibiosis data of *Macropodia czernjawskii* specimens recently collected within this study in the Black Sea.

Link: https://doi.org/10.3897/zse.96.48342.suppl1